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A revision of *Smallanthus* (Asteraceae, Millerieae), the “yacón” genus

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Abstract

Smallanthus (Asteraceae, Millerieae), the “yacón” genus, comprises 23 species ranging from southeastern United States to central Argentina, with the greatest diversity in Peru and Mexico. Species of *Smallanthus* are herbs, shrubs or small trees with tuberous roots, opposite, trinerved or triplinerved leaves, paleate receptacle, ray corollas externally hairy at the base, pappus lacking, and marginal cypselae partially embraced by the inner phyllaries of the involucre. As a result of this revision: *Smallanthus araucariophilus* and *S. riograndensis* are considered synonyms of *S. macroscyphus*; lectotypes are designated for nine names; and the geographical distribution of *S. latisquamus*, *S. lundelli*, *S. riparius*, and *S. siegesbeckia* is extended. A comprehensive key to the species and detailed descriptions, geographical distribution, phenology, illustrations and distribution maps are provided for all taxa.

Resumen

Smallanthus (Asteraceae, Millerieae), el género del “yacón”, comprende 23 especies que se distribuyen desde los Estados Unidos hasta el centro de Argentina, con la mayor diversidad en Perú y México. El género se define por su hábito herbáceo, arbustivo o arbóreo, raíces tuberosas, hojas opuestas trinervadas o triplinervadas, receptáculo paleáceo, corolas del radio externamente pilosas en la base, papus ausente, y cipselas marginales parcialmente cubiertas por las filarias internas del involucre. Como resultado de esta revisión: *Smallanthus araucariophilus* y *S. riograndensis* se consideran sinónimos de *S. macroscyphus*; se designan los lectotipos de nueve nombres; y se amplía la distribución geográfica de *S. latisquamus*, *S. lundelli*, *S. riparius*, y *S. siegesbeckia*. Se provee una clave de especies y descripciones detalladas, distribución geográfica, fenología, ilustraciones y mapas de distribución para cada especie.

Introduction

The Andean region has been the cradle of some economically important crops, such as the potato, tomato, and maize races. Also many edible tubers and roots have been used as food for centuries by the Andean inhabitants. One of these, the “yacón”, a species of the genus *Smallanthus* Mackenzie (1933: 1406), is attracting global attention. *Smallanthus* (Asteraceae, Millerieae), with 23 species, ranges from southeastern United States to central Argentina, and has its greatest diversity in Peru and Mexico. Species of *Smallanthus* are herbs, shrubs or small trees with tuberous roots, opposite, trinerved or triplinerved leaves, paleaceous receptacle, ray corollas externally hairy at the base, pappus lacking, and marginal cypselae partially embraced by the inner phyllaries of the involucre. Because its high content of non-digestible oligosaccharides, roots of *Smallanthus sonchifolius* (Poeppig) H. Robinson (1978: 51), “yacón”, have been used as natural sweeteners and syrups. The traditional Andean populations attribute anti-diabetic properties to dry yacon leaves (Choque Delgado *et al.* 2013). There are other species of *Smallanthus* with edible and/or medicinal attributes, such as *Smallanthus connatus* (Sprengel) H. Robinson (1978: 49) (Bach *et al.* 2007) and *Smallanthus macroscyphus* (Baker ex Martius) A. Grau in Grau & Rea (1997: 205) (Coll Aráoz *et al.* 2008).

The genus *Smallanthus* was originally described by Mackenzie on the basis of just one North American species, *Smallanthus uvedalius* (Linné) Mackenzie (1933: 1406) based on *Osteospermum uvedalia* Linné (1753: 923). This species was transferred to *Polymnia* L. (1753: 926) (Wells 1965) and later re-incorporated to *Smallanthus* by Robinson (1978). Other 18 species of *Polymnia* were transferred to *Smallanthus* by Robinson (1978), who also described a new species. The number of species of the genus further increased to 24 with new combinations and the description of new species (Turner 1988, 2010, Zuloaga & Morrone 1999, Mondin 2004).

Smallanthus was morphologically related to *Rumfordia* Candolle (1836: 549) and *Polymnia* (Sanders 1977) and, in general, phylogenetic analyses on the tribe Heliantheae sensu lato (Karis 1993, Panero *et al.* 1999, Rauscher 2002) coincide in a sister or a close relationship of *Smallanthus* to *Rumfordia*.

The phylogenetic relationships among species of *Smallanthus* were first established by Rauscher (2002) with the use of molecular data and a sampling of 13 species. More recently, a phylogenetic analysis based on morphological data was carried out by Vitali and Viera Barreto (2014) sampling all species of *Smallanthus* on the basis of the information of Vitali (2014). In the analyses, this genus resulted monophyletic.

Despite the extensive literature on the yacón, *Smallanthus sonchifolius*, it is quite surprising that such an economically important genus still lacks a systematic study that includes its entire species. The objective of this contribution is to perform such study.

Materials and methods

This study is based on the specimens or photographs of the following herbaria (Holmgren *et al.* 1990): AS, B, BAB, BM, BR, C, CAS, COL, F, G, GH, HASU, ICN, K, LIL, LL, LP, M, MA, MICH, MO, NY, P, PACA, PR, QCNE, S, SI, TEX, US, W, and on field studies. The information of locality, date, phenology, height of the plants and corolla color is taken from the herbarium specimens and protologues for most species.

For microscopic examination, vegetative and reproductive parts were rehydrated, treated with a clearing process, stained with 2 % safranin, and mounted on microscopic slides. Plant organs were isolated and free hand cut transversely. Drawings were made using a stereomicroscope Wild M5 and a Nikon Eclipse E 200 microscope with camera-lucida attachment. Light microscope photographs were taken with a Nikon Coolpix S10.

Pollen was acetolyzed, chlorinated, and mounted in glycerol jelly in the standard way (Erdtman 1960). Measurements of the polar (P) and equatorial (E) diameters are based on averages from 25 grains and measurements of exine thickness and spine length are based on 15 pollen grains. For SEM, acetolyzed pollen grains were suspended in 90 % ethanol, mounted on stubs, and examined in a JEOL JSM T-100 SEM. The size classification was taken from Erdtman (1969).

General terminology follows Ramayya (1962), Metcalfe & Chalk (1979), Harris & Wolf Harris (1994), and Punt *et al.* (2007). Leaf laminae were measured in their maximum width.

Habit

Two species of *Smallanthus* (*S. jelskii*, *S. pyramidalis*) are trees up to 10 m high (Fig. 1A). Most species of *Smallanthus*, however, are erect, tall, perennial herbs that reach 5 m high (e.g., *S. connatus*, *S. mcvaughii*, *S. quichensis*; Fig. 1B, C). Shrubs up to 7 m high (e.g., *S. cocuyensis*, *S. parviceps*) may also be found in *Smallanthus*.

Roots

The root system in *Smallanthus* is composed by several fleshy tuberous storage roots and an extensive development of thin fibrous roots. In some species like the yacón, *S. sonchifolius*, the tubers may reach 25 × 10 cm (Grau & Rea 1997) (Fig. 1D). An external bark reflects the secondary growth of the roots. The internal fleshiness of the root is caused by several layers of parenchyma tissue that accumulates sugars and contains schizogenous secretory ducts (Fig. 2A). The several carbohydrates stored in the roots of *S. sonchifolius* (fructose, glucose, sucrose, low polymerization degree oligosaccharides, and traces of starch and inulin; Asami *et al.* 1989, Ohyama *et al.* 1990) are responsible for the extensive use of this species.

Stem

All species of *Smallanthus* have ramified, hollow stems, even in the arboreal species such as *S. pyramidalis* (Guzmán Avendaño & Barrera Adame 2010). The stems are usually pubescent, and occasionally they are glabrescent or more densely pubescent at the apex. The stem cortex is constituted by several layers of collenchyma below the epidermis (Fig. 2B), and parenchyma tissue with secretory ducts. The stem in primary growth has an epidermal layer with simple conical and glandular biseriate hairs (Fig. 2C). The vascular bundles are surrounded by a sclerenchyma sheath, and enclose a parenchymatous pith with thickened cell walls that becomes hollow at the center of the stem (Fig. 2B).

Leaves

The leaves are simple, opposite superposed (the opposite leaves arise in the same plane at successive nodes) or decussate (each opposite pair of leaves are at right angles to each other) or occasionally verticillate, apically with ca. four leaves per node (*S. fruticosus*, *S. microcephalus*, *S. pyramidalis*). They are sessile (e.g., *Smallanthus apus*, *S. siegesbeckia*; Fig. 3A) or more commonly petiolate (Fig. 3 B–E), with a winged petiole. Occasionally, the lower leaves are petiolate and the upper ones sessile (e.g., *S. macroscyphus*). The petiole wings may be uniform in width (e.g., *S. jelskii*; Fig. 3B) or may gradually decrease in width from the blade towards the leaf insertion to the stem (e.g., *S. latisquamus*, *S. uvedalius*; Fig. 3C). The petiole wing margins may be entire or lobulate (e.g., *S. obscurus*; Fig. 3D), and the wing bases auriculate, with the auricle discontinuous (*S. putlanus*) (Fig. 3F), or continuous with the opposite leaf (*S. connatus*; Fig. 3G). The size of the auricle commonly varies in the same plant, i.e. larger in the lower nodes and smaller in the upper ones, or the auricle may be completely absent (e.g., *S. maculatus*).

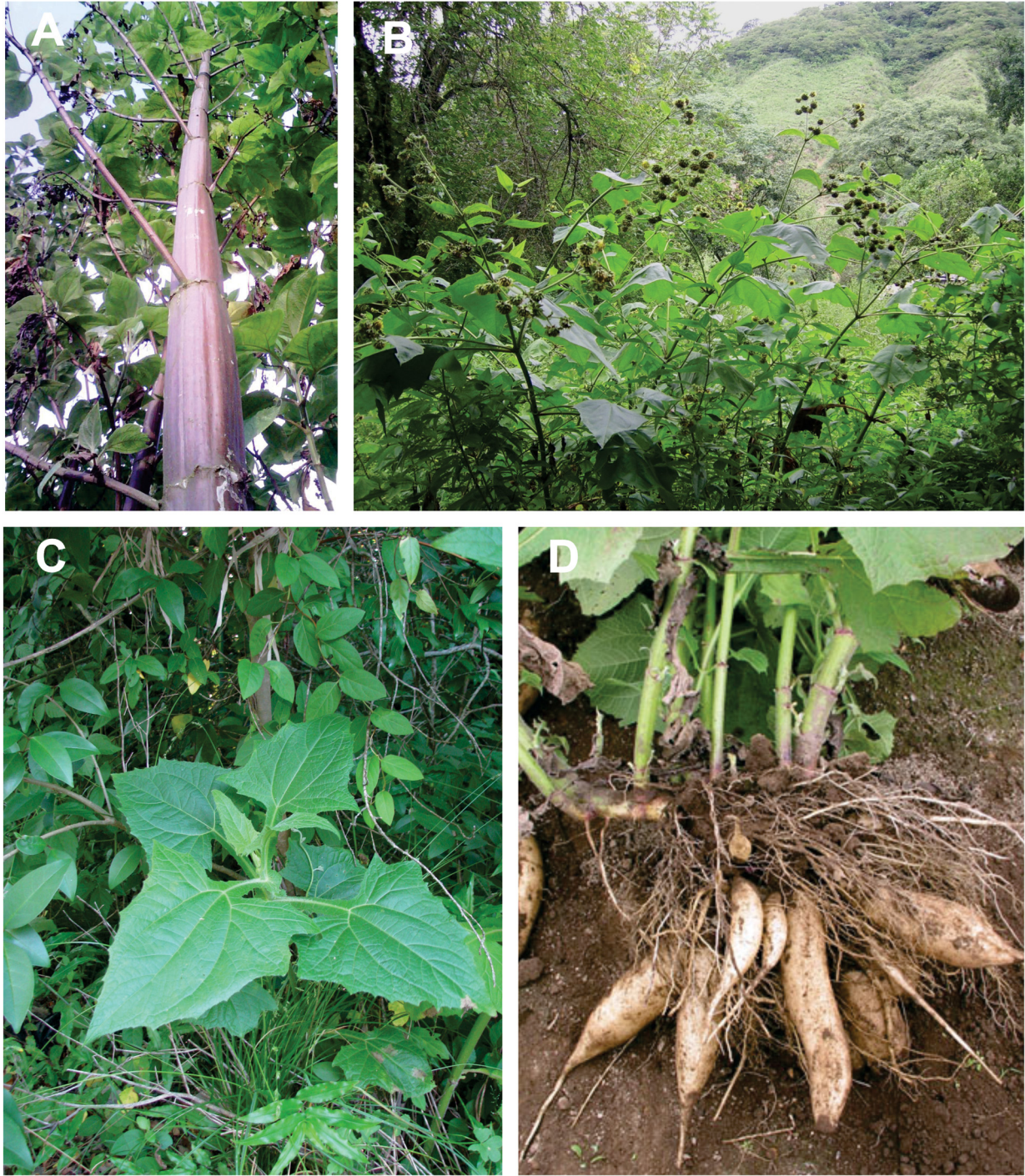


FIGURE 1. A–C. Habit of *Smalanthus*. **A.** Tree, *Smalanthus pyramidalis*. **B.** Herb, *S. parviceps*. **C.** Herb, *S. connatus*. **D.** Roots, *S. sonchifolius*. Photographs: A, <http://mariasimonaeneljardin.blogspot.com.ar/2008/03/arboloco-bogotano.html>; B, C, D. Gutiérrez; D, http://es.wikipedia.org/wiki/Smalanthus_sonchifolius.

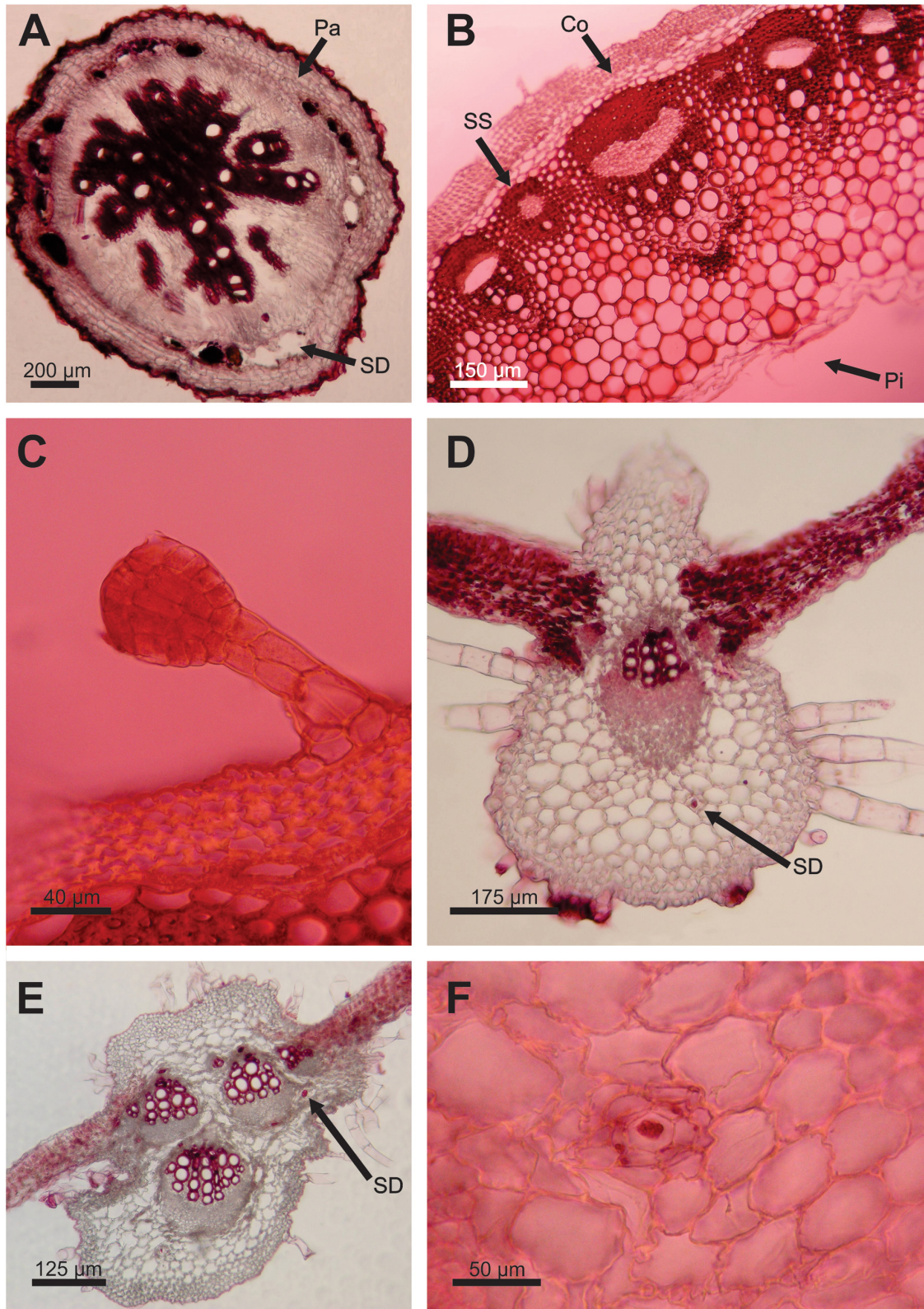


FIGURE 2. Root, stem, and leaf anatomy. Co = collenchyma, Pa = parenchyma, Pi = pith, SD = secretory duct, SS = schlerenchyma sheath. **A.** Root cross section of *Smallanthus connatus* (Pedersen 9551, LP). **B.** Stem cross section of *S. siegesbeckia*, Dusén 9503 (LP). **C.** Glandular hair of stem of *S. siegesbeckia* (Dusén 9503, LP). **D.** Leaf cross section showing a midrib with one vascular bundle, *S. maculatus* (Hidalgo y s.n., LP). **E.** Leaf cross section showing a midrib with three vascular bundles, *S. siegesbeckia* (Isern 2272, F). **F.** Leaf secretory duct of *S. fruticosus* (Ruiz & Pavón s.n., F).

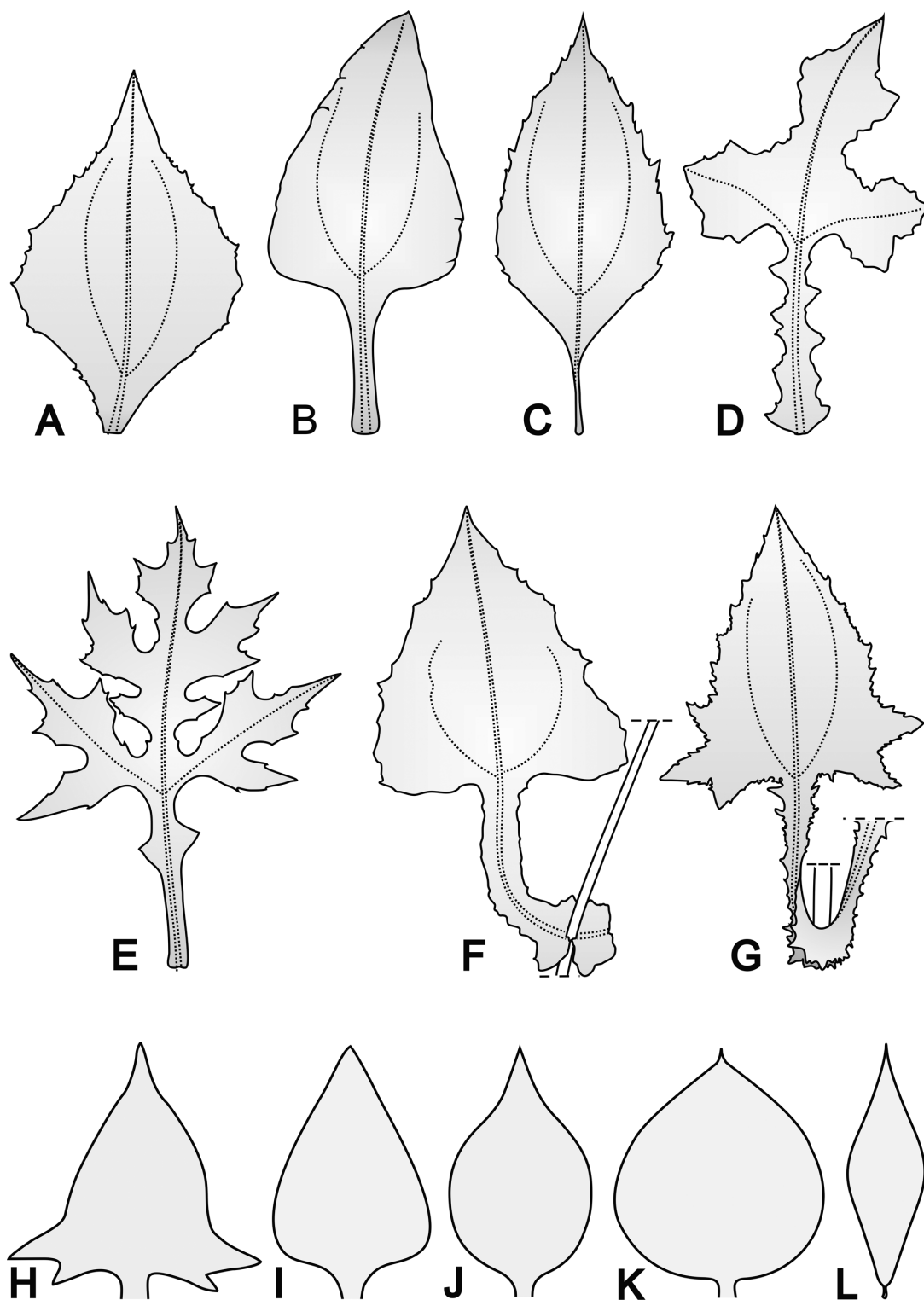


FIGURE 3. Leaves of *Smalanthus*. **A–G.** Examples of margins, petiole features, and venation types. **A.** Sessile, triplinerved, and acrodromous in *S. siegesbeckia* (drawn from Buchtien 748, G). **B.** Petiole wings uniform in width from the base of the lamina to the node in *S. latisquamus* (drawn from Stork 2071, GH). **C.** Margin denticulate, petiole wings decreasing in width from the base of the lamina to the node in *S. jelskii* (drawn from Wurdack 618, LP). **D.** 3-partite, petiole wings lobulate, trinerved, and actinodromous in *S. obscurus* (drawn from Breedlove 41387, TEX). **E.** Pinnatisect in *S. macvaughii* (drawn from Panero *et al.* 2875, TEX). **F.** Base of the petiole wing auriculate and discontinuous with the auricle of opposite leaf in *S. putlanus* (drawn from Gutiérrez 3099, TEX). **G.** Base of the petiole wing auriculate and continuous (connate) with the auricle of opposite leaf in *S. connatus* (drawn from Lafranchi 429, LP). **H–L.** Examples of leaf lamina shapes and bases. **H.** Subtriangular, base hastate. **I.** Subtriangular, base truncate. **J.** Ovate, base obtuse. **K.** Orbicular, base rounded. **L.** Elliptic, base attenuate.

Leaf lamina is very variable in size, ranging from 6–55 cm long and 2–30 cm wide. Shape is usually subtriangular, ovate, orbicular and elliptic, with base hastate, truncate, obtuse, rounded or attenuate (Fig. 3H–L), although intermediates may also be found. Lamina shape may vary in the same plant and the plants are either heterophyllous, or homophyllous and retain more or less the same shape throughout. The margins are mucronate and entire (e.g., *S. fruticosus*, *S. jelskii*; Fig. 3B), denticulate, dentate (*S. latisquamus*, *S. quichensis*; Fig. 3C), lobulate (*S. connatus*; Fig. 3G), 3-partite (*S. putlanus*, *S. uvedalius*; Fig. 3D) or pinnatisect (*S. mcvaughii*; Fig. 3E). In general the leaf margin is uniform in the whole plant, but in some species (e.g., *S. oaxacanus*) may vary, with pinnatisect lower leaves and entire upper leaves.

Leaves in *Smallanthus* are trinerved (the two lateral main veins arise at the base of the blade) or triplinerved (the two lateral main veins arise slightly above the base of the blade), and acrodromous (the two main lateral veins run in convergent arches toward the blade apex; Fig. 3A–C) or actinodromous (the three main veins diverge from one point; Fig. 3D, E).

The leaf has a dorsiventral mesophyll, one or more vascular bundles at the midrib level (Fig. 2D, E) and many secretory ducts (Fig. 2D–F) that are continuous with those of petiole. The stomata are mostly distributed in the abaxial epidermis. Stomata also may be found in the phyllaries of the involucre, paleae, and in some species (*S. cocuyensis*, *S. jelskii*, *S. latisquamus*, *S. parviceps*, *S. siegesbeckia*) in the upper part of the corollas.

Leaves are in general conspicuously pubescent, with the exception of *S. glabratus* with glabrous leaves, and *S. latisquamus*, *S. mcvaughii*, and *S. parviceps* that are glabrescent. The hairs are tector and glandular. Tector hairs are usually found in vegetative organs and in disc florets (e.g., *S. parviceps*). On leaves they may be found in bunches on ribs (e.g., *S. macroscyphus*, *S. maculatus*, *S. pyramidalis*, *S. sonchifolius*; Fig. 2D). They are usually dense at the base of the true ray corollas, which is a distinguishing feature of *Smallanthus* respect to closely related genera. Glandular hairs are commonly found on leaves and stems of most species.

Capitula

Capitula in *Smallanthus* are radiate, heterogamous, and pedunculate. They are rarely solitary (*S. latisquamus*) or in cymes of up to three capitula (e.g., *S. obscurus*); most commonly the capitula are grouped into open or dense, terminal, often leafy corymbiform, racemiform or occasionally paniculiform cymes of small and numerous (up to ca. 100) capitula or large and up to 20 capitula (Fig. 4A).

The involucre is campanulate or hemispherical, with one, two (*S. connatus*, *S. cocuyensis*, *S. macroscyphus*) or usually three series of dimorphic, herbaceous, rarely scarious phyllaries. The phyllaries may be pubescent and/or glandular, rarely glabrescent. The outer phyllaries are foliaceous, 1-seriate, in number of four or five, planate, spreading or reflexed (in live specimens), generally ovate, ovate-lanceolate or obovate with an acute to obtuse apex and ca. seven main veins (Fig. 4B). The inner phyllaries are 8 to 30, arranged in 1 or 2 series, ovate, incurvate and embracing the cypselae; they are acute, obtuse, attenuate or occasionally caudate (*S. riparius*, *S. siegesbeckia*) at the apex, with ca. six conspicuous veins.

The receptacle is flat, alveolate (rarely scrobiculate; e.g., *S. jelskii*), glabrous, and paleate. The paleae are variable in size and shape, namely elliptic, ovate, obovate, oblong, oblanceolate, linear-ovate or rhombic, acute, entire, denticulate or trifid at the apex, with 3–7 conspicuous veins, usually glabrescent, with glandular and/or tector hairs.

The capitula of the species of *Smallanthus* have marginal, female, true ray florets and internal, functionally male disc florets. The number of ray florets vary between 8 and 30 per capitulum and are usually 1-seriate, rarely 2-seriate (Fig. 4B) coinciding with the number of series of the inner phyllaries (*Smallanthus cocuyensis*, *S. connatus*, *S. macroscyphus*). The corollas are yellow or orange true rays (Fig. 4C). Only *S. jelskii* has bilabiate marginal corollas (Fig. 4C), with an oblong, obovate, elliptic, or orbicular limb with ca. seven main veins and 3-dentate or rarely 3-lobate apex. As already mentioned, the ray florets of *Smallanthus* have a bunch of tector hairs, externally, on the corolla base (Fig. 4C). The style shaft ends into two linear to oblong, long branches that are acute to obtuse at the apex. The outer and inner branches' surface is papillose, with the internal papillae confined to two marginal bands extending throughout the length of each branch.

The number of disc florets range from 20 to 100 per capitulum. The corollas are yellow, hairy, tubular or campanulate (*S. fruticosus*, *S. glabratus*, *S. jelskii*, *S. microcephalus*, *S. parviceps*), and 5-lobate at the apex. Disc florets are functionally male and have abortive ovaries and a partial or complete fusion of the style branches which are dorsally hairy (Fig. 4D). The anthers are linear to oblong, calcarate, and shortly caudate, yellow, sometimes

purplish or black. The apical anther appendage is ovate to subtriangular, acute or obtuse at the apex (Fig. 4E). Each anther has an anther collar with thickened cell walls at their base.

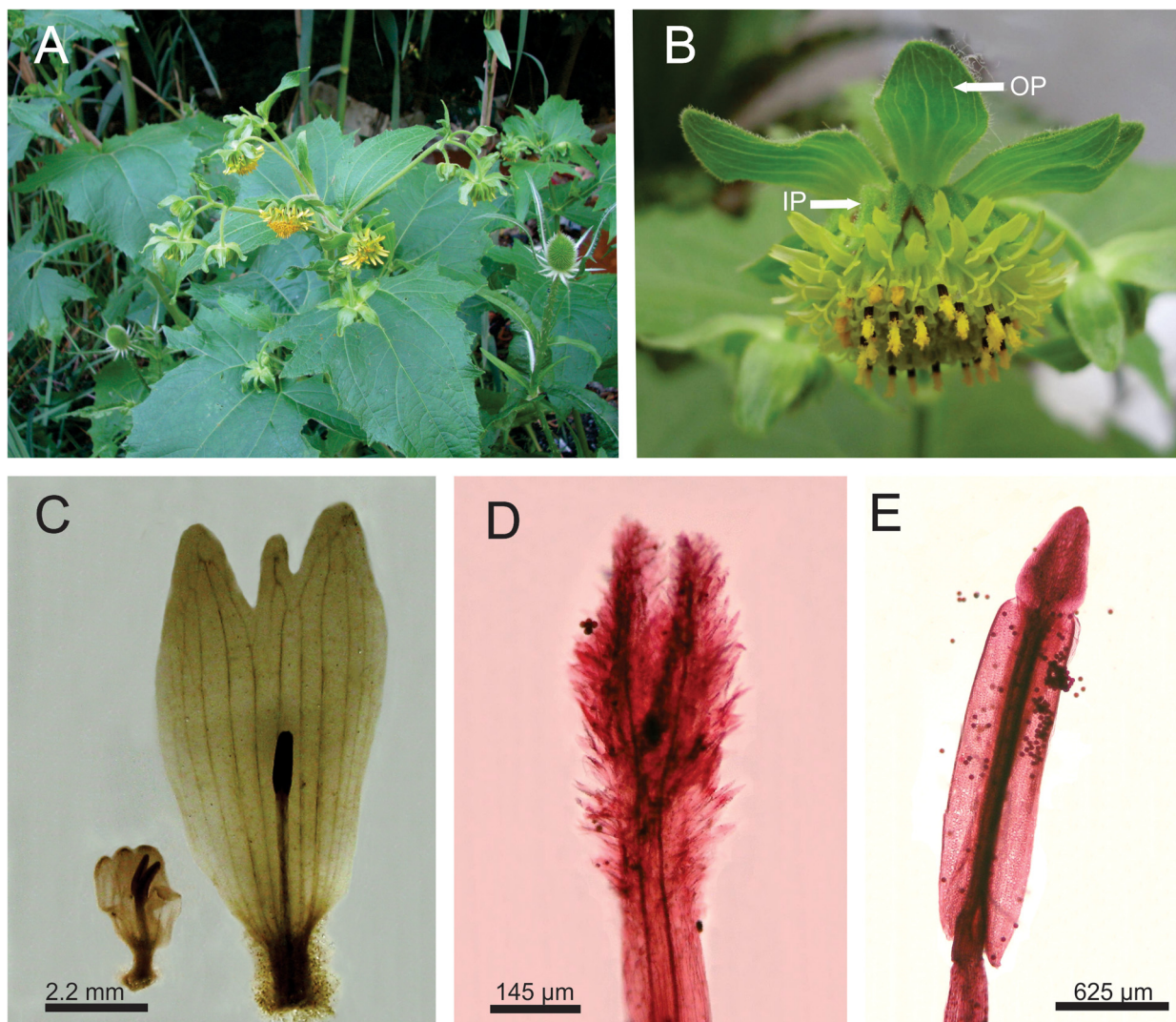


FIGURE 4. Reproductive characters in *Smalanthus*. OP = outer phyllary, IP = inner phyllary. **A, B.** *Smalanthus connatus*. **A.** Capitulescence of ca. 15 capitula. **B.** Capitulum. **C.** Marginal florets (without cypselae), on the left bilabiate corolla of *S. jelskii* (López & Sagástegui 5471, LP); on the right ray corolla of *S. sonchifolius* (Fiebrig 2852, K). **D.** Style of disc floret of *S. riparius* (Weberbauer 6016, GH). **E.** Stamen of disc floret of *S. connatus* (Torres Robles & Voglino 1178, LP). Photographs: A, Gutiérrez, D.; B, Vitali, M.

Cypselae

The cypselae of *Smalanthus* are commonly obovate or rounded-obovate, globose, brown or black, glabrous, and faintly costate. The cypselae surface is smooth although in some species (*S. macroscyphus*, *S. oaxacanus*) is irregularly verrucate. Cypselae are surrounded by the incurvate inner phyllaries. The pappus is lacking in the genus.

Pollen

The general description of pollen of *Smalanthus* is based on the analysis of pollen of eleven species (Table 1):

Pollen radially symmetrical, tricolporate, spheroidal-sub-spheroidal. Circular in polar view. Size medium ($P \times E = 23\text{--}34 \mu\text{m} \times 24\text{--}35 \mu\text{m}$). Colpi long with acute ends, ora lalongate. Exine tectate, caveate, echinate, exine thickness among spines 2–5 μm . Spines 4–9.5 μm length, acute at the apex, with apical channel.

TABLE 1. Pollen of the species examined of *Smallanthus*, showing measurements of polar (P) and equatorial (E) diameters, exine thickness among spines, and spines length.

Species	P (µm)	E (µm)	Exine (µm)	Spines length (µm)
<i>S. connatus</i>	27.5–33	28.5–32	3–4	7–8
<i>S. fruticosus</i>	25–29	27–30	3–4	5–6
<i>S. macroscyphus</i>	23–28.5	25–29	3–4	6–7
<i>S. maculatus</i>	24–28.5	26–28.5	3–4	5–7
<i>S. meridensis</i>	25–28	24–28	3–4	5–6
<i>S. pyramidalis</i>	25–28.5	26–28.5	3–4	5–7
<i>S. quichensis</i>	27–34	28–35	3–5	4–8.5
<i>S. riparius</i>	26–28	27–29	3	6–7
<i>S. siegesbeckia</i>	24–28.5	24–27	2–4	6–9.5
<i>S. sonchifolius</i>	23–27.5	25–27.5	3–4	4–5
<i>S. uvedalius</i>	27–29	27.5–29	3–4	6–9.5
Total range	23–34	24–35	2–5	4–9.5

The pollen of *Smallanthus connatus*, *S. maculatus*, *S. oaxacanus* (Fig. 5), *S. quichensis*, *S. sonchifolius*, and *S. uvedalius* shows some variation in the grain size and shape and spine length. This variation was already noted by Wells (1971) in some species of *Smallanthus* (under the name *Polymnia*) when he compared the pollen of potential hybrids of *S. maculatus* with their parental forms and with *S. uvedalius*.

Palynologic features of species of *Smallanthus* fit in general with the pollen description developed by Blackmore *et al.* (2009) for the whole tribe Millerieae (34 genera, ca. 400 species). Pollen studies performed in genera of Milleriinae (11 genera, ca 85 species), on the other hand, are apparently lacking with the exception of that by Wells (1971) mentioned above. The analyses involve selected species for palynologic atlases or in the context of palynologic studies of Heliantheae sensu lato, for example *Milleria quinqueflora* Linné (1753: 919) (Skvarla & Turner 1966), *Rumfordia floribunda* Candolle (1836: 550) (Stix 1960), *Sigesbeckia orientalis* Linné (1753: 900) (APSA Members 2007).

Regarding possible pollination agents, Seminario *et al.* (2003) found insects belonging to Coleoptera, Himenoptera, Diptera, Hemiptera and Lepidoptera visiting flowers of *Smallanthus sonchifolius* (yacón). Some herbarium labels of *S. connatus* and *S. macroscyphus* specimens cite *Apis mellifera* (common bees) as visitors.

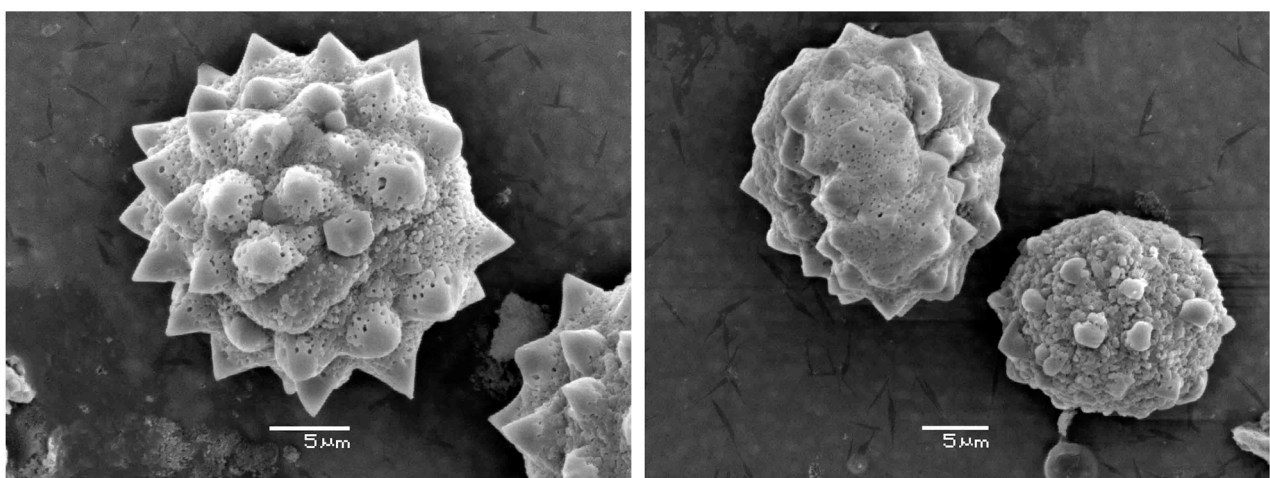


FIGURE 5. Pollen variants in equatorial view of *Smallanthus oaxacanus* (L. Williams *et al.* 14665, GH).

Distribution

Smallanthus distributes throughout the Americas, from southeastern United States to central-east Argentina (Fig. 6). It occurs in a wide range of usually humid habitats such as rain forests, and shady and swampy areas, from sea level to 4000 m. Some species grow in drier areas such as ravines, mountain slopes, and on disturbed soils like roadsides and cultivated fields (e.g., *S. connatus*, *S. maculatus*).

Even when some species are widespread (e.g., *Smallanthus maculatus*, *S. uvedalius*) most of them are restricted to specific areas. For example, there are endemics to the high forests of Guatemala and Mexico (*S. lundelli*), and in the Andes of Venezuela (*S. meridensis*), Colombia (*S. cocuyensis*), and Peru (*S. jelskii*). Most of endemics occur in Mexico (e.g., *S. apus*, *S. mcvaughii*, *S. obscurus*, *S. putlanus*).

There is an interesting case of possible island naturalization in one species of *Smallanthus*. Blake (1917a) established three varieties in the island of Bermuda for the North American *S. uvedalius*, and explained this distribution by mutation or segregation of populations in the island. This is the only case of a species of *Smallanthus* inhabiting the Caribbean. Turner (1988), on the other hand, suggested that these populations are all apparently derived from a single human introduction from mainland probably between 1883 and 1905. In addition, the yacón (*S. sonchifolius*) is widely distributed in South America and in the last decades its cultivation has extended to other continents (Grau & Rea 1997).

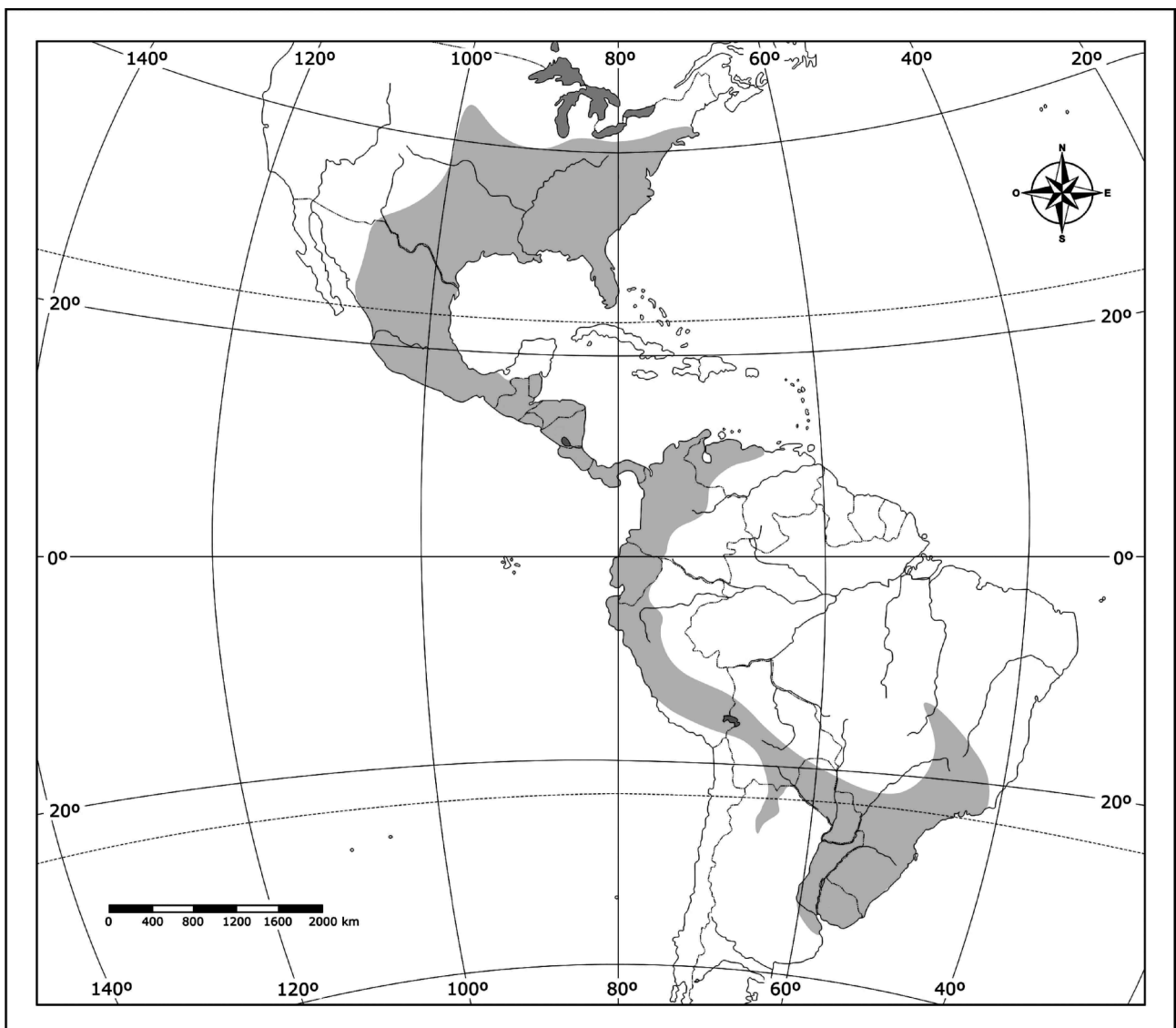


FIGURE 6. Geographical distribution of the genus *Smallanthus*.

Taxonomic treatment

Smallanthus Mackenzie (1933: 1406). Type species:—*Smallanthus uvedalius* (Linné) Mackenzie.

Polymniastrum Small (1913: 302) *nom. illeg.* (non Lamarck ex Cassini 1829)

Perennial herbs, shrubs or small trees, homophyllous or heterophyllous, with fleshy, tuberous, storage roots and thin, fibrous roots. Stems erect, branched, hollow, striate, generally pubescent, rarely glabrous. Leaves opposite, occasionally verticillate, sessile or petiolate; lamina ovate, subtriangular, elliptic or orbicular, acute, attenuate or obtuse at the apex, obtuse, truncate, hastate, rounded or attenuate at the base; margins entire, mucronate, denticulate, dentate, lobulate, 3-partite or pinnatisect, trinerved or triplinerved, actinodromous or acrodromous, pubescent, glabrescent, rarely glabrous; petiole winged, wings uniformly wide or gradually decreasing in width towards the node, wing margins entire or lobulate, auriculate or not auriculate at the base, sometimes the auricles of opposite leaf continuous. Capitula radiate, heterogamous, 1 to ca. 100, rarely solitary or grouped into open or dense, terminal, often leafy, corymbiform, racemiform or paniculiform cymes of usually 3–20, pedunculate. Involucre campanulate, hemispherical; phyllaries dimorphic, 1–3-seriate, 3–10-veined, pubescent and/or glandular, outer phyllaries 4 or 5, herbaceous, ovate, ovate-lanceolate or obovate, foliaceous, planate, acute or obtuse at the apex, inner phyllaries 8–30, herbaceous or scarious, ovate, incurvate partially embracing the cypselae of the ray florets, acute, obtuse, attenuate, or caudate at the apex. Receptacle flat, alveolate, rarely scrobiculate, glabrous, paleate; paleae elliptic, ovate, obovate, oblong, oblanceolate or rhombic, acute, entire, denticulate, or trifid at the apex, 3–7-veined, usually glabrescent. True ray florets present, female, 8–30, 1- or 2-seriate, corollas yellow or orange, rarely bilabiate, limb oblong, obovate, elliptic, or orbicular, 3–10-veined, apex 2- or 3-dentate, occasionally entire, the teeth equal in size or the central one larger; tube with a bunch of hairs at the base; style branches linear or oblong, acute to obtuse at the apex. Disc florets functionally male, 20–100; corollas yellow, hairy, tubular or campanulate, apex 5-lobate; anthers linear to oblong, yellow, purplish or black, calcarate, shortly caudate, apical appendage ovate to subtriangular, acute or obtuse at the apex, anther collar with thickened cell walls; ovaries abortive, style branches linear, acute to obtuse at the apex, sometimes fused, dorsally hairy. Cypselae obovate, rounded-obovate, brown to black, glabrous, surface striate, smooth or irregularly verrucate. Pappus absent.

Etymology:—For the American botanist John Kunkel Small (1869–1938), explorer and expert in the flora of southeastern United States; and from the Greek, *anthos*, flower.

Distribution:—Twenty-three species distributed in southeastern United States, México, Guatemala, Belice, El Salvador, Honduras, Nicaragua, Costa Rica, Panamá, Colombia, Venezuela, Ecuador, Perú, Bolivia, Paraguay, Uruguay, Brazil, and Argentina.

Notes:—The name *Polymniastrum* was published by Lamarck (1823: t. 712), in *Tableau Encyclopédique et Methodique ... Botanique*, heading an iconography of a plant with capitulum details, but without providing a generic description for the name. In the same year and journal, but in another volume, Poiret performed the combination: *Polymniastrum variabile* (Poiret) Poiret (1823: 287) on the basis of *Polymnia variabilis* Poiret (1804: 505), with a brief species re-description. The type of *Polymnia variabilis* is a specimen collected by Poiret in the French Guiana (deposited in P) and is currently a synonym of *Polymnia canadensis* Linné (1753: 926) (Wells 1965). The first generic description of *Polymniastrum* was performed by Cassini (1829: 246), thus validating the name. Cassini mentioned the iconography of Lamarck but did not cite the type species *P. variabile*, instead he described the new species *Polymniastrum urticifolium* Cassini (1829: 246).

Independently, in 1913 Small described the new genus *Polymniastrum* with its type species *Polymniastrum uvedalia* (Linné) Small (1913: 302), based on *Osteospermum uvedalia* Linné (1753: 923) whose type specimen was collected in Virginia, USA (deposited in LINN). Since the name *Polymniastrum* had been already validly published (Cassini 1829), the first legitimate generic name for this taxon was provided by Mackenzie in 1933 as *Smallanthus* Mackenzie, with its type species *Smallanthus uvedalius* (Linné) Mackenzie.

KEY TO THE SPECIES OF *SMALLANTHUS*

1. Lower leaves sessile 2
- Lower leaves petiolate 3

2.	Lower leaves blade elliptic-suborbicular	<i>S. apus</i>
-	Lower leaves blade ovate	<i>S. siegesbeckia</i>
3.	Margin of the lower leaves entire, dentate or lobulate	4
-	Margin of the lower leaves partite or pinnatisect	19
4.	Many (more than 20) capitula per inflorescence	5
-	Few (3–20) capitula per inflorescence	9
5.	True ray corollas bilabiate	<i>S. jelskii</i>
-	True ray corollas not bilabiate	6
6.	Inner phyllaries of the involucre scarious	<i>S. pyramidalis</i>
-	Inner phyllaries of the involucre herbaceous	7
7.	Paleae of the receptacle trifid at the apex	8
-	Paleae of the receptacle entire, not trifid at the apex	<i>S. parviceps</i>
8.	Stems and leaves glabrous	<i>S. glabratus</i>
-	Stems and leaves pubescent	<i>S. microcephalus</i>
9.	Disc corollas campanulate	<i>S. fruticosus</i>
-	Disc corollas tubular	10
10.	Leaf venation actinodromous (main veins diverging from one point)	11
-	Leaf venation acrodromous (main veins converging at the apex)	13
11.	Ray florets in two series	<i>S. cocuyensis</i>
-	Ray florets in one series	12
12.	Capitula arranged in paniculiform cymes	<i>S. maculatus</i>
-	Capitula arranged in corymbiform cymes	<i>S. meridensis</i>
13.	Inflorescences with 1–3 capitula	14
-	Inflorescences with more than 3 capitula	16
14.	Base of the lower leaves blade hastate or obtuse	15
-	Base of the lower leaves attenuate	<i>S. quichensis</i>
15.	Margin of the lower leaves irregularly dentate. Disc florets ca. 50	<i>S. latisquamus</i>
-	Margin of the lower leaves entire to lobulate. Disc florets ca. 100	<i>S. lundelli</i>
16.	Opposite lower leaves connate by their auricles	<i>S. connatus</i>
-	Opposite lower leaves not connate	17
17.	Ray florets in two series	<i>S. macroscyphus</i>
-	Ray florets in one series	18
18.	Inner phyllaries of the involucre longly caudate at the apex. Limb of ray corollas elliptic	<i>S. riparius</i>
-	Inner phyllaries of the involucre acute at the apex. Limb of ray corollas oblong	<i>S. sonchifolius</i>
19.	Lower leaves 3-partite	20
-	Lower leaves pinnatisect, with more than 3 lobes	21
20.	Capitula 10–17 mm long. Limb of ray corollas elliptic	<i>S. obscurus</i>
-	Capitula 8–10 mm long. Limb of ray corollas oblong	<i>S. uvedalius</i>
21.	Petiole wings of lower leaves lobulate. Outer phyllaries attenuate at the apex	<i>S. mcvaughii</i>
-	Petiole wings of lower leaves entire. Outer phyllaries acute at the apex	22
22.	Inner phyllaries of the involucre attenuate at the apex. Limb of ray corollas obovate or elliptic	<i>S. oaxacanus</i>
-	Inner phyllaries of the involucre acute at the apex. Limb of ray corollas oblong	<i>S. putlanus</i>

SPECIES DESCRIPTION

Smallanthus apus (Blake) Robinson (1978: 49).

Polymnia apus Blake (1924: 604). Type:—MEXICO. Zacatecas: Between Santa Gertrudis and Santa Teresa, 8 August 1897, J. N. Rose 2079 (holotype US 300979, digital image!).

Herbs 1.5–3 m tall, homophyllous, stems pubescent at the apex. Leaves opposite, 13.5–25.5 × 8.7–25 cm, elliptic, elliptic-suborbicular, acute or obtuse at the apex, truncate at the base, margins irregularly dentate, mucronate, triplinerved, acrodromous, pubescent, sessile. Capitula ca. 14 × 21 mm, ca. 15 arranged in corymbiform cymes; peduncles 60–80 mm long, pubescent on both faces. Involucre campanulate to hemispherical; phyllaries arranged in 2 series, herbaceous, ovate-lanceolate, acute at the apex, outer phyllaries 17–25 × 5–9 mm, inner phyllaries ca. 11 × 4 mm. Receptacle with paleae ca. 7 × 3 mm, ovate-lanceolate, apex entire. True ray florets 10, 1-seriate, corollas yellow, ray-limb oblong, ca. 17 × 5 mm, apex 3-dentate, central tooth larger. Disc florets ca. 30, corollas yellow, tubular, 6.5–8 mm long, lobes 1.5 mm long. Cypsela rounded-obovate, ca. 5 × 3 mm, smooth. n=16 (Wells 1965). (Fig. 7).

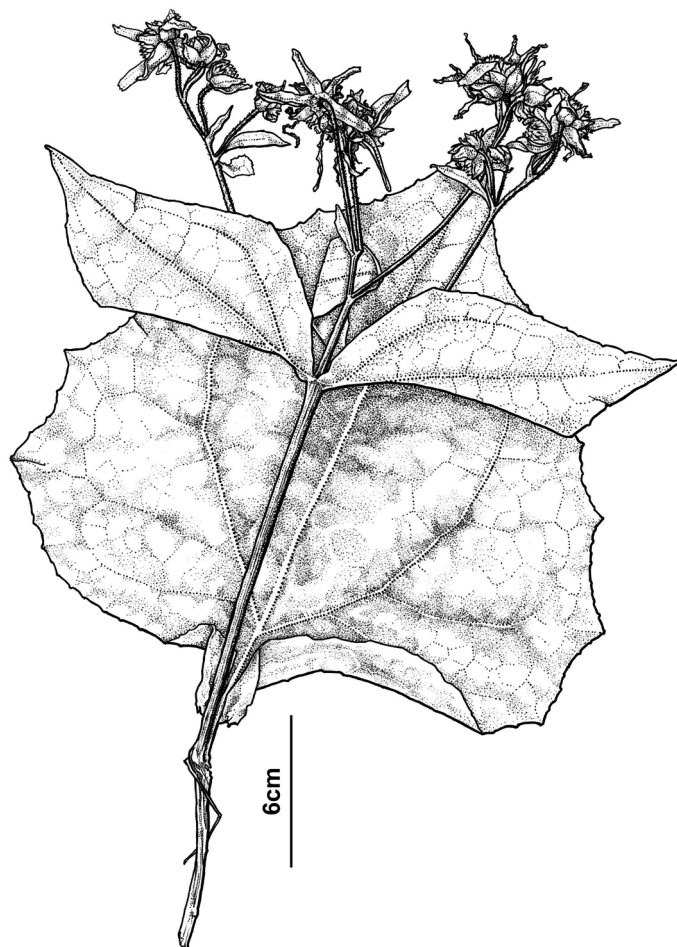


FIGURE 7. *Smallanthus apus* (S.F. Blake) H. Robinson. Habit (drawn from the digital image Rose 2077, NY).

Etymology:—From the Greek *ἄπους* (*apus*), stalkless, probably due to the sessile leaves.

Distribution and ecology:—Central Mexico (Fig. 8). This species is endemic to the Mesoamerican Mountain biogeographical province, which encompasses the Sierra Madre Occidental, Sierra Madre Oriental, Serranías Meridionales, and Serranías Transísmicas. Specimens with flowers were collected in August.

Notes:—Because we based the species description on observation of photographs, some plant features such as ray floret tube, styles, and style branch length, and shape of apical anther appendage could not be measured.

Additional specimens examined:—MEXICO. State Nayarit: Entre Santa Gertrudis y Santa Teresa, 8 August 1897, *J. Rose 2077* (digital image NY).

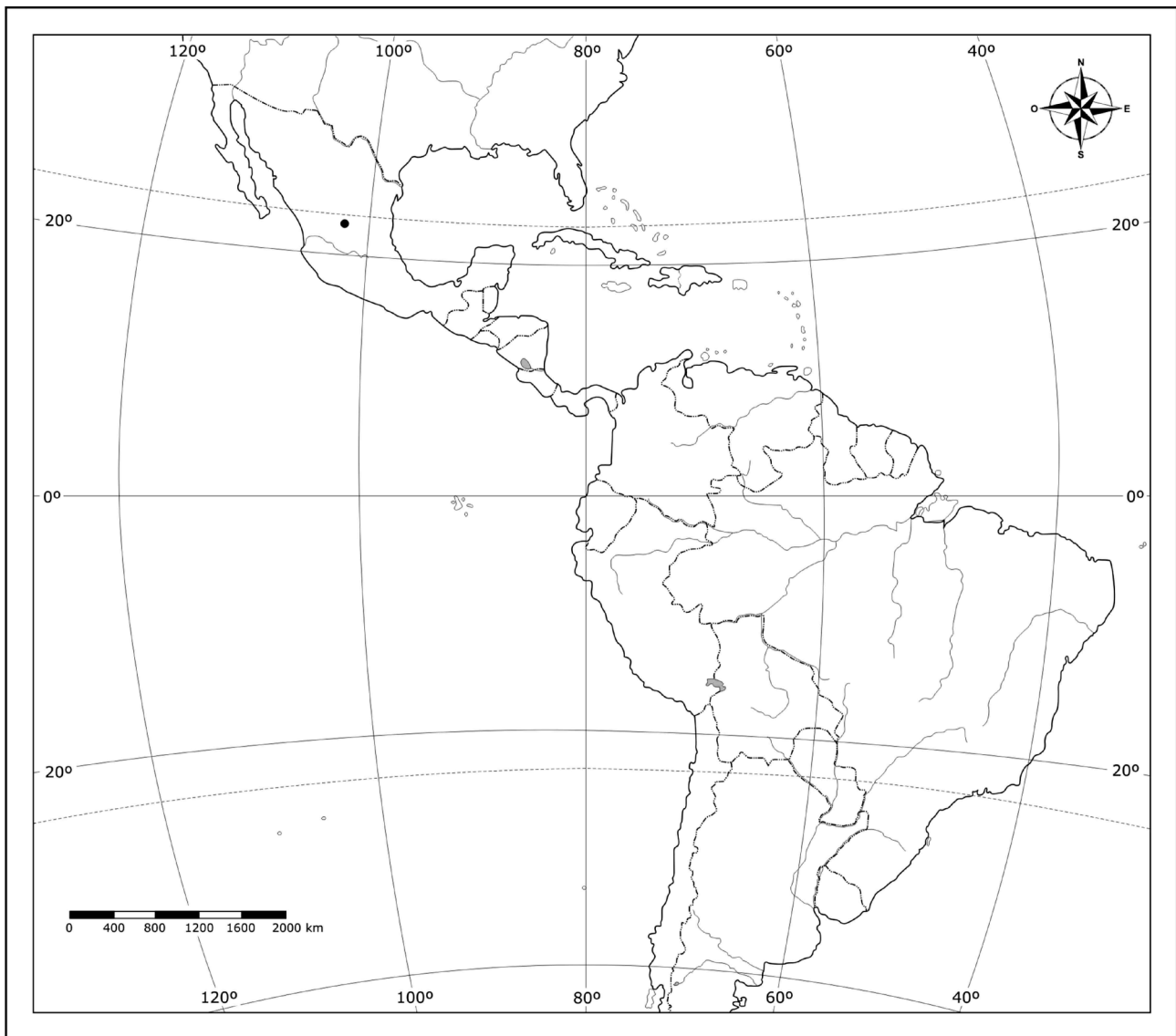


FIGURE 8. Geographical distribution of *Smalanthus apus*.

Smalanthus cocuyensis (Cuatrecasas) Vitali & Viera Barreto (2014: 83).

Polymnia cocuyensis Cuatrecasas (1954: 247). Type:—COLOMBIA. Boyacá: Cocuy, alrededores, 2750 m. alt., 14 September 1938, J. Cuatrecasas & H. García Barriga 1700 (holotype F!, isotypes COL 5360, digital image!).

Shrubs ca. 3 m tall, homophyllous, stems pubescent. Leaves opposite, petiolate, 24–40 cm long, lamina 20–28 cm wide, ovate-subtriangular, acute at the apex, truncate at the base, margins irregularly denticulate-mucronate, mucronate, lobulate, trinerved, actinodromous, pubescent on both faces, petiolate; petioles 7–13 cm long, winged, wings uniform in width, slightly lobulate, auriculate at the base, the auricles discontinuous with the opposite leaf. Capitula ca. 10 × 20 mm, up to three arranged in cymes; peduncles 70–100 mm long, densely pubescent. Involucre hemispherical; phyllaries arranged in 3 series, herbaceous, ovate, outer phyllaries 11–15 × 8–13 mm, obtuse at the apex, inner phyllaries 9–11 × 4 mm, attenuate at the apex. Receptacle with paleae 7 × 2 mm, oblong to lanceolate, apex entire. True ray florets ca. 20, 2-seriate, corollas yellow, ray-limb oblong, 8–10 × 4–5 mm, apex 2- or 3-dentate, teeth equal in length, tube 1.5–2 mm long. Style 3.5–5 mm long, branches 1.5–2 mm long. Disc florets ca. 50, corollas yellow, tubular, 5–7 mm long, lobes 1–1.2 mm long. Anthers with apical appendage ovate. Style 6 mm long, branches 0.5 mm long. Cypselae obovate, 4–5 × 2–3 mm, smooth. (Fig. 9).

Etymology:—From the locality of Cocuy, in Colombia, where the type specimen was collected.

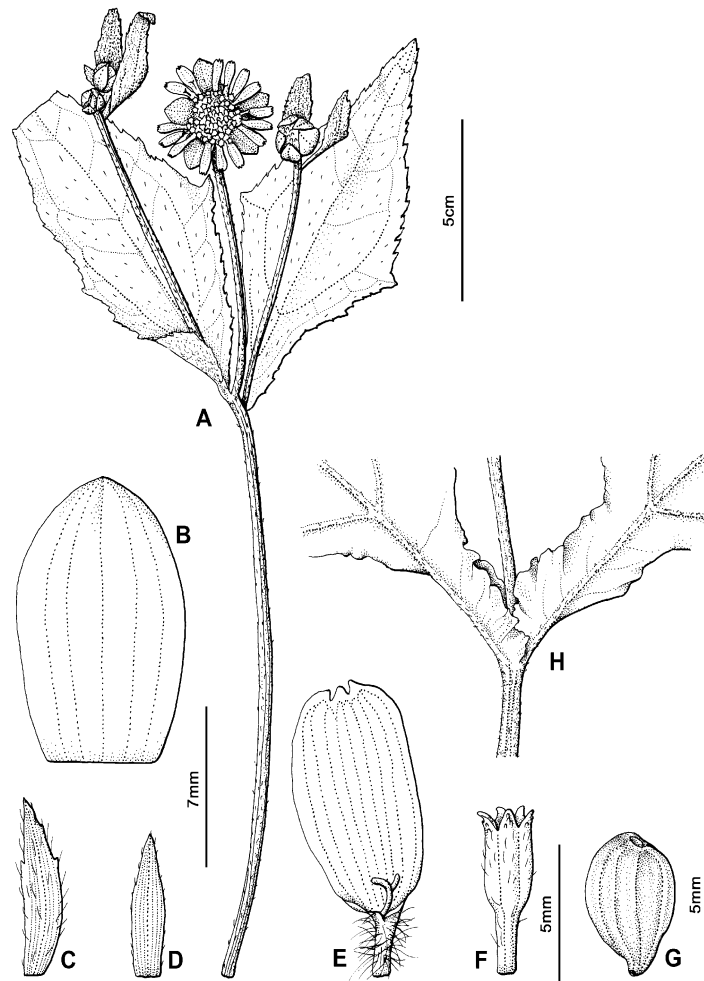


FIGURE 9. *Smallanthus cocuyensis* (Cuatrecasas) Vitali & Viera Barreto. **A.** Habit. **B.** Outer phyllary. **C.** Inner phyllary. **D.** Palea. **E.** Ray floret without cypselae. **F.** Disc corolla. **G.** Cypselae. **H.** Detail of leaf base (*Grant & Fosberg 9375*, F).

Distribution and ecology:—Colombia. This species grows in the northern yungas of the Oriental Andes (Fig. 10), at ca. 2000 m. Flowering from May to September.

Notes:—Wells (1965), in his revision of *Polymnia*, considered *P. cocuyensis* a synonym of *P. meridensis*. Robinson (1978), on the other hand, when reestablishing the genus *Smallanthus*, transferred to this genus *P. meridensis* but he did not transfer *P. cocuyensis*, apparently considering them not only different species but also belonging to different genera. *Polymnia cocuyensis* was finally transferred to *Smallanthus* (Vitali & Viera Barreto 2014) because its incurvate inner phyllaries embracing the cypselae of the true ray florets, and the bunch of trichomes at the base of the ray corollas, both typical characters of *Smallanthus* (*vs.* inner phyllaries not embracing the cypselae of ray florets and glabrous ray corolla base). This species is also distinguished from *P. meridensis* by differences in habit, number of series of phyllaries, palea pubescence, and the shape of ray corolla limb.

The label of the holotype of *Polymnia cocuyensis* reads *J. Cuatrecasas 1700* as the only collector of the specimens, whereas the labels of isotypes read *J. Cuatrecasas and H. García Barriga 1700*. Despite this difference, the remaining label information is similar and they are all considered types.

Additional specimens examined:—COLOMBIA. Dept. Cundinamarca: Valle del río Guavio, 4 km N de Ubalá, 29 May 1944, *M. Grant & F. Fosberg 9375* (F).

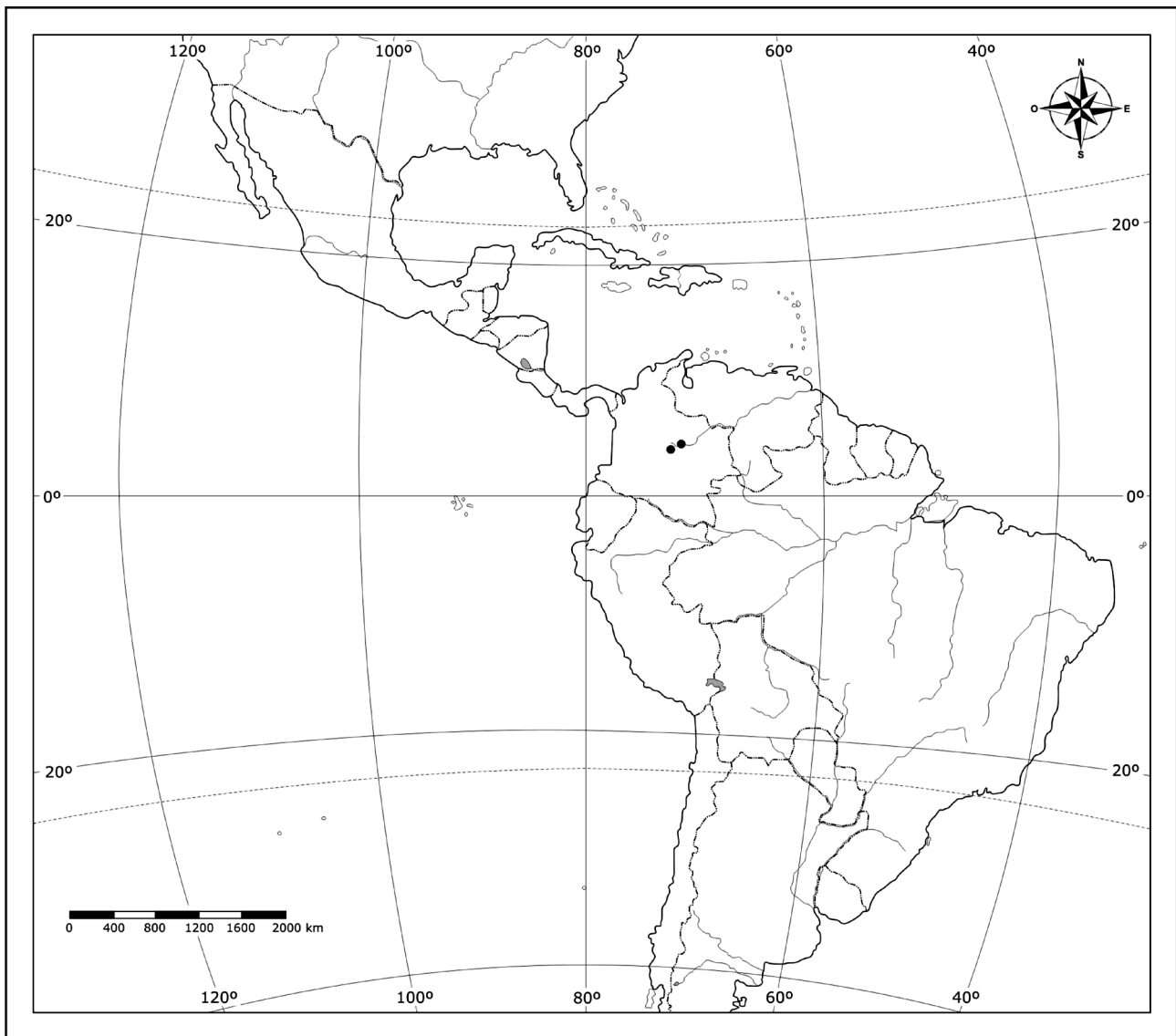


FIGURE 10. Geographical distribution of *Smalanthus cocuyensis*.

Smalanthus connatus (Sprengel) Robinson (1978: 49).

Gymnolomia connata [as *connatum*] Sprengel (1826: 610). *Polymnia connata* (Sprengel) Blake (1930: 238). Type:—BRAZIL.

“Monte Video”, without date, *F. Sellow* s.n. (holotype P 2716980, digital image!; isotype K 486959, digital image!).

Polymnia silphioides Candolle (1836: 516). Type:—BRAZIL. Rio Grande, 1833, Herb. Mus. Imp. Bras. 885, *T. Gaudichaud* s.n. (holotype G-DC 209806, digital image!; isotype P 2716984, digital image!).

Polymnia silphioides var. *perennis* Spegazzini ex Bettfreund in Bettfreund *et al.* (1899: 116). Type:—ARGENTINA. Buenos Aires: Palermo, San Isidro, *C. Bettfreund* s.n. (type not found).

Polymnia andrei Arechavaleta (1925: 35). Type:—URUGUAY. Without locality: Parajes húmedos, sombríos, primavera, *J. Arechavaleta* s.n. (holotype probably at MVM, isotype W 33155, digital image!).

Herbs 1.5–3 m tall, heterohyllous, stems pubescent. Leaves opposite, petiolate, acute at the apex, trinerved, acrodromous, pubescent on both faces, petiole winged, wings uniform in width, lobulate, auriculate at the base, auricles connate with those of the opposite leaf; lower leaves 11–24 cm long, lamina 5–16 cm wide, ovate to subtriangular, attenuate, sagittate or truncate at the base, margins 2–4-lobulate, irregularly dentate, mucronate, petiole 3.8–8.5 cm long; upper leaves 8–14.5 cm long, lamina 2.5–9 cm wide, ovate-elliptic, elliptic, attenuate or obtuse at the base, margins denticulate, mucronate, petiole 1.3–4.1 cm long. Capitula 5–15 × 4–17 mm, ca. 10 arranged in racemiform cymes; peduncles 30–90 mm long, densely pubescent. Involucre campanulate to

hemispherical; phyllaries arranged in 3 series, herbaceous, ovate, acute at the apex, outer phyllaries 11–16 × 4–10 mm, inner phyllaries 5–9 × 2–4 mm. Receptacle with paleae 4–7 × 1–2 mm, subovate or oblong, apex entire. True ray florets ca. 20, 2-seriate, corollas yellow, ray-limb ovate to oblong, 4–6 × 1–2 mm, apex 2- or 3-dentate, teeth equal in size, tube 2 mm long. Style 4–5 mm long, branches 0.8–1 mm long. Disc florets ca. 40, corollas yellow, tubular, 5–7 mm long, lobes 1 mm long. Anthers with apical appendage subovate. Style 4 mm long, branches 0.5 mm long. Cypselae obovate, 3–5 × 2.5–3.5 mm, smooth. (Fig. 11).

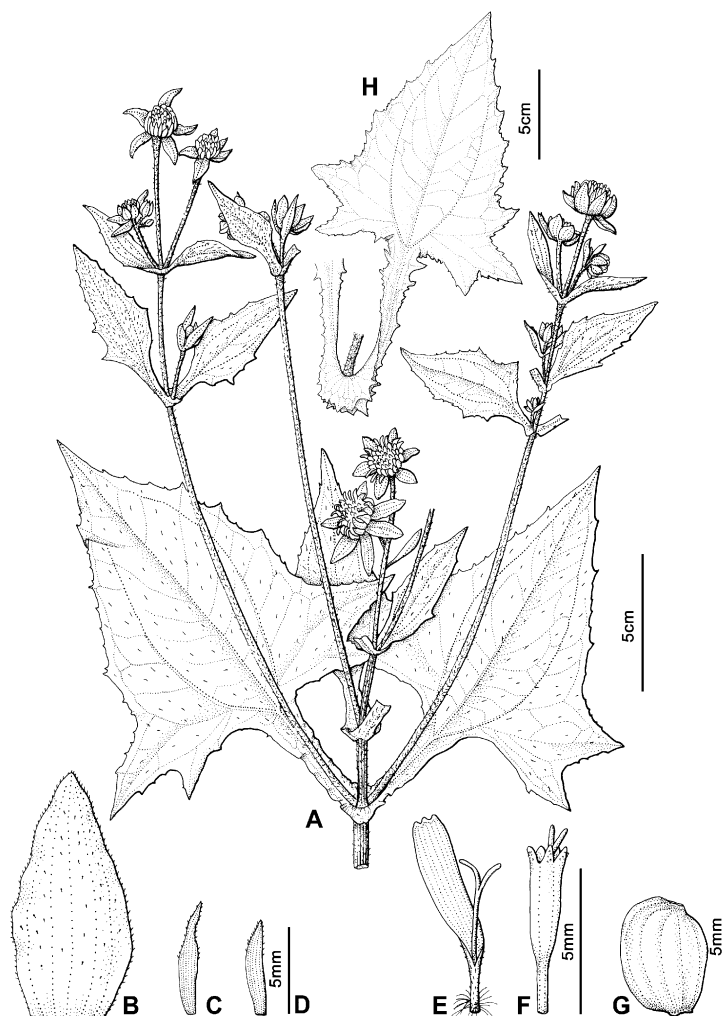


FIGURE 11. *Smallanthus connatus* (Sprengel) H. Robinson. **A.** Habit. **B.** Outer phyllary. **C.** Inner phyllary. **D.** Palea. **E.** Ray floret (without cypselae). **F.** Disc floret (without ovary). **G.** Cypselae. **H.** Detail of leaf and petiole (*Lanfranchi 429*, LP).

Etymology:—From the Latin *connatus*, connate or fused, in reference to the connate auricles of the opposite leaves.

Distribution and ecology:—Eastern Argentina, southern Brazil, Paraguay, and Uruguay (Fig. 12). It grows along margins of forests, wet places such as marshes and river banks, and in roadsides, at 0–1200 m. Flowering from September to April.

Vernacular names and uses:—Girasolcito, jaguarete, ka'a, yacón-gaúcho, yacón-nativo. The seeds of this species have been cited with potential use as fuel (*Kinupp 3204*, ICN).

Notes:—See Notes under *S. macroscyphus*.

Additional specimens examined:—ARGENTINA. Prov. Buenos Aires: Partido La Plata, alrededores de La Plata, Dock central, 7 December 1927, *A. Cabrera 127* (LP); id., Los Talas, 26 March 1933, *A. Cabrera 2784* (LP); La Plata, about 10 km NW of La Plata, on NW bank of Río de la Plata, 8 December 1938, *W. Eyerdam et al. 23363* (G, GH); Delta Paraná Secc. 1a, Arroyo Gálvez, February 1942, *J. Hunziker 3384* (LP); id., 6 January 1946, *J. Hunziker 1545* (GH); Punta Lara, 5 December 1950, *A. Ruiz Leal & F. Roig15931* (LP); id., 15 December 1960, *H.*

Fabris 2458 (LP), 14 December 1939, *R. Santesson 43* (S), 30 November 1944, *V. Rodríguez 560* (GH, S), 21 March 1981, *E. Zardini 1334* (LP), March 1939, *A. Rodrigo 2214* (LP), 11 January 1939, *A. Cabrera 4906* (LP); Punta Lara-Villa Elisa, 21 December 1980, *E. Zardini 1295* (LP); Isla Santiago, cerca de La Plata, 12 April 1931, *A. Cabrera 1711* (LP); Delta, Tuyuparí, January 1914, *A. Scala 435* (LP); Tigre, 23 November 1945, *A. Lanfranchi 429* (LP); Capital Federal, Golf, 12 December 1925, *A. Clos 1842* (LP); Palermo, February 1883, *C. Spegazzini s.n.* (LPS 10203 in LP); Buenos Aires, 1852, *Andersson s.n.* (S); Palo Blanco, 30 November 1945, *A. Krapovickas 2700* (GH); Partido Punta Indio, Reserva de la Biosfera Parque Costero del Sur, estancia Juan Gerónimo, 19 March 2003, *S. Torres Robles 1342* (LP); Magdalena, Punta de Indio, 28 December 1945, *A. Rodrigo 3479* (LP); id., estancia Luis Chico, 15 January 2007, *J. Hurrell & D. Buzzano 6336* (LP); Partido Magdalena, Rincón de Noario, 5 December 1941, *A. Cabrera 7423* (LP); Partido Baradero, estancia Los Alamos, 7 December 2002, *S. Torres Robles & D. Voglino 1178* (LP); Isla Martín García, 12 November 1961, *J. Gamerro 1001* (LP); id., cerca de la cantera, 14 October 1995, *J. Hurrell et al. 2520* (LP), muelle, 22 January 1996, *J. Hurrell et al. 2816* (LP), cantera, 22 January 1996, *J. Hurrell et al. 2817* (LP). Prov. Corrientes: Dept. Santo Tomé, Establecimiento Las Martas, RN 14, 7 km S de Gobernador Virasoro, 30 November 1970, *A. Krapovickas et al. 16652* (LP); Dept. San Martín, Yapeyú, 18 December 1946, *A. Huidobro 3726* (F, S); Tapebicua, 18 December 1946, *A. Huidobro 3788* (F); Dept. Santo Tomé, ruta 40 y arroyo Chimiray, 12 November 1974, *A. Schinini & R. Carnevali 10670* (G); arroyo Chimiray y ruta 40, 13 February 1991, *S. Tressens et al. 3862* (F, GH). Prov. Misiones: 20 km E de Wanda a J. J. Lanusse, 24 January 1973, *A. Schinini & A. Fernández 6020* (LP); Dept. Apóstoles, Apóstoles (pueblo), 3 September 1944, *C. Ibarrola 975* (S); ruta 203, entre ruta 14 y ruta 1, 13 February 1978, *A. Cabrera & A. Sáenz 29177* (LP); Dept. Cainguás, Puerto Leoni, 27 November 1945, *G. Schwarz 1572* (F); Dept. Candelaria, Santa Ana, 14 November 1945, *J. Montes 1447* (GH); Garupá, 13 October 1945, *Bertoni 2184* (F, K); Loreto, 3 December 1930, *Gruner 591* (LP); Dept. Capital, Posadas, 26 December 1907, *E. Ekman 1027* (LP, S); Dept. Concepción, arroyo Persiguero, 14 December 1946, *G. Schwarz 3632* (LP); Dept. Guaraní, Paraje Puerto Argentino, aldea aborígen Taruma Poty, arroyo Soberbio, 18 January 2006, *H. Keller 3396* (K); Dept. Iguazú, Puerto Delicia, 19 December 1950, *J. Montes 10758* (LP); Las Delicias, April 1926, *Raffaelli s.n.* (LPS 10204 in LP); Parque Nacional del Iguazú, camino a Cabureí, ruta 101, km 22, 13 December 1986, *C. Xifreda & S. Maldonado 455* (LP); Parque Nacional Iguazú, 8 km E de Pto. de las Canoas, 18 December 1991, *R. Vanni et al. 2964* (F, GH); Dept. Leandro N Alem, ruta 4, a 4 km al E de L. N. Alem, arroyo Saracura, 18 December 1986, *C. Xifreda & S. Maldonado 538* (LP); Dept. San Pedro, San Pedro a Thomas, ruta 14, 21 April 1950, *E. Schwindt 2998* (LP). Without province: Argentina, without date, *Tweedie s.n.* (GH).

BRAZIL. State Paraná: Estrada Curitiba-S. Paulo (BR 2), km 78, September 1964, *L. Dombrowski 239* (GH); Mun. Laranjeiras do Sul, Río das Cobras, 6 December 1968, *G. Hatschbach & O. Guimarães 20520* (LP); Mun. Medianeira, Rio Ocui, 9 February 1969, *G. Hatschbach 21091* (LP); Ponta Grossa, 9 December 1903, *P. Dusén 2494* (S); id., 1 December 1910, *P. Dusén 10932* (S). State Rio de Janeiro: Itatiaia, December 1892, *O. Kuntze s.n.* (G). State Rio grande do Sul: Ijuhy, 30 March 1893, *A. Malme 738* (S); Carazinho, Quinta San José, Instituto La Salle, 27 December 1943, *I. Augusto s.n.* (ICN 31718); Caçapava do Sul, 9 December 2005, *V. Kinupp & H. Lorenzi 3132* (ICN); Bom Jesús, 6 January 1988, *M. Ritter 204* (F, K); Bom Jesús, Aparados da Serra, Fazenda Bernardo Vehlo, 29 December 1946, *B. Rambo 35097* (S); Bom Jesús, Faz. Cavaúna, 1 February 1937, *Dutra 1470* (ICN); Gramado dos Loureiros, 7 December 1974, *L. Batista et al. s.n.* (ICN 26834); Caracol, 8 km N de Canela, 3 January 1973, *A. Girardi s.n.* (ICN 21953); Mun. de Nova Prata, Nova Pratinha, 7 January 1978, *M. Fleig 940* (ICN); Porto Alegre, Bairro Agronomia, cultivado na Faculdade de Agronomia (UFRGS), 22 December 2004, *V. Kinupp 2968* (ICN); id., 16 September 2005, *V. Kinupp 2994* (ICN); Porto Alegre, Bairro Bom Jesús, 16 October 2006, *V. Kinupp 3204* (ICN); Canôas, prope Porto Alegre, 14 December 1901, *G. Malme 861* (S); Encruzilhada do Sul, Projeto de Assentamento Padre Réus, 16 December 2007, *M. Grings 441* (ICN); Santa María, 4 December 1936, *W. Rau 19* (LP); São Francisco de Paula, Villa Oliva, 6 January 1946, *L. Rambo 30992* (LP); São Francisco de Paula, FLONA, 9 December 2002, *C. Mondin 2858* (HASU); Triunfo, Barretos, AES Florestal, 6 April 2002, *C. Mondin 2643* (HASU); without locality, *B. Rambo 11475* (LP). State Santa Catarina: Mun. Campos Novos, 33 km SE of Campos Novos, on the road to São José do Cerrito (Carú), 10 February 1957, *L. Smith & R. Klein 11204* (LP); Mun. Guraciaba, Rio Liso, 13 km NW of São Miguel d'Oeste, ca. 26° 32' S, 53° 34' W, 19 December 1964, *L. Smith & R. Klein 14157* (GH, LP); Lages, 10 January 1951, *B. Rambo 49620* (S).

PARAGUAY. Dept. Alto Paraná: Alto Paraná, October 1909, *K. Fiebrig 5728* (GH); Estancia Rio Bonito, 25° 37' 54" S, 54° 48' 19" W, 27 December 1994, *E. Zardini & L. Guerrero 41908* (K). Dept. Canindeyú: Ipé-hu,

Sierra de Maracayú, November (without year), *E. Hassler 5341* (F, GH, S). Dept. Misiones: Santiago, Estancia La Soledad, 13 December 1969, *T. Pedersen 9551* (GH, LP, S). Dept. Paraguari: Route conduisant de Paraguari à Yaguraon, 20 November 1876, *B. Balansa 916* (S).

URUGUAY. Dept. Colonia: Arroyo San Juan, near mouth, 20 December 1943, *H. Bartlett 21260* (GH). Dept. Maldonado: La Barra, San José, February 1936, *J. Chebataroff 969* (LP). Dept. Río Negro: Fray Bentos, 28 January 1877, *Fruchart s.n.* (LP). Dept. Rocha: Palmares de Castillos, 25 km N of Castillos, 22 January 1944, *H. Bartlett 21385* (GH, LP). Dept. Tacuarembó: Valle Edén, December 1942, *J. Chebataroff 8964* (LP); quebrada Gruta de los Cuervos, 18 January 1944, *C. Legrand 3372* (LP). Dept. Treinta y Tres: Vergara, December 1947, *W. Herter 379* (F).

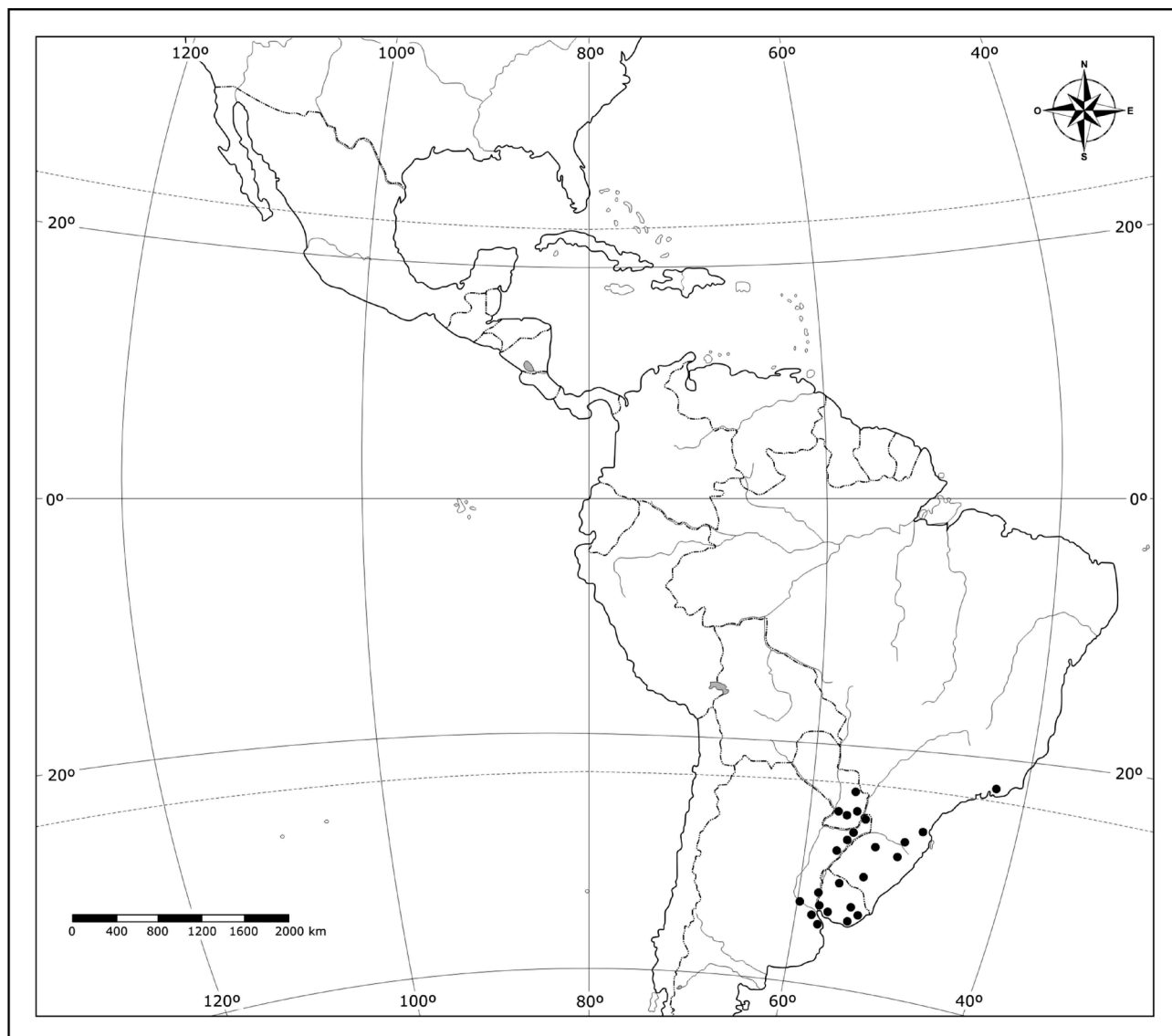


FIGURE 12. Geographical distribution of *Smallanthus connatus*.

Smallanthus fruticosus (Bentham) Robinson (1978: 49).

Polymnia fruticosa Bentham (1845: 209). Type:—PERU. Cajamarca: In montibus Quimia, prope Rumibamba, *C. Hartweg 1158* (lectotype here designated K 486957!, isotypes BM 1009548, E 385954, F 51061, K 486955, LD 1075844, NY 232587, US 128389, digital images!).

Polymnia arborea Hieronymus (1900: 33). Type:—ECUADOR. Without locality: Crescit in silvis subandinis et in altiplanitiebus, nomine vernaculo Polaco, *A. Sodiro 24/4* (lectotype here designated US 128387 digital image!, epitype here designated photograph F n. 15157)

Shrubs 3–5 m tall, homophyllous, stems pubescent. Leaves opposite, occasionally verticillate, more numerous at the apex, petiolate, 8–28.5 cm long, lamina 1.7–12.4 cm wide, ovate-lanceolate, acute at the apex, attenuate or obtuse at the base, margins entire, triplinerved, acrodromous, pubescent above, densely pubescent below; petioles 2.8–8 cm long, winged, wings uniform in width, entire, not auriculate at the base. Capitula 4–10 × 6–13 mm, ca. 50 arranged in corymbiform cymes; peduncles 8–30 mm long, pubescent. Involucre hemispherical; phyllaries arranged in 2 series, herbaceous, ovate, outer phyllaries 5–13 × 3–7 mm, obtuse at the apex, inner phyllaries 4–7 × 2–6 mm, attenuate or acute at the apex. Receptacle with paleae 3–5 × 1–2 mm, ovate, apex denticulate. True ray florets ca. 15, 1-seriate, corollas yellow, ray-, limb oblong, 4–15 × 3–5 mm, apex 3-dentate, teeth equal in size, tube 1–1.5 mm long. Style 3–5 mm long, branches 0.5–2 mm long. Disc florets ca. 40, corollas yellow, campanulate, 3–5 mm long, lobes 0.5–1 mm long. Anthers with apical appendage ovate. Style 2 mm long, branches 0.3 mm long. Cypselsae obovate, 2–3.5 × 1–3 mm, smooth. $n > 25$ (Wells 1965). (Fig. 13).



FIGURE 13. *Smallanthus fruticosus* (Bentham) H. Robinson. **A.** Habit. **B.** Outer phyllary. **C.** Inner phyllary. **D.** Palea. **E.** Ray floret (without cypselae). **F.** Disc corolla. **G.** Cypselae (Holmgren 921, S).

Etymology:—From the Latin *frutex*, shrub, by the habit of this species.

Distribution and ecology:—Bolivia, Colombia, Ecuador, and Peru (Fig. 14). It grows in grasslands, rocky slopes, and shrublands, at 1000–3300 m. Flowering from November to June.

Vernacular names and uses:—Colla, colla culapa, polaco, shita, shitadeloso. The infusion of leaves, stems and flowers has been cited as anti-inflammatory of urinary tract (Cerón 17656, QCNE).

Notes:—The original holotype at B was destroyed during The World War II (Hiepko 1987). According to Art. 9.2 of the ICN (McNeill *et al.* 2012) we designate here the specimen at US as the lectotype of *Polymnia arborea* Hieronymus. The specimen at US is a fragment, thus according to Art. 9.8 we also designate as epitype the photograph of the destroyed holotype at B preserved in the Field Museum (number 15157).

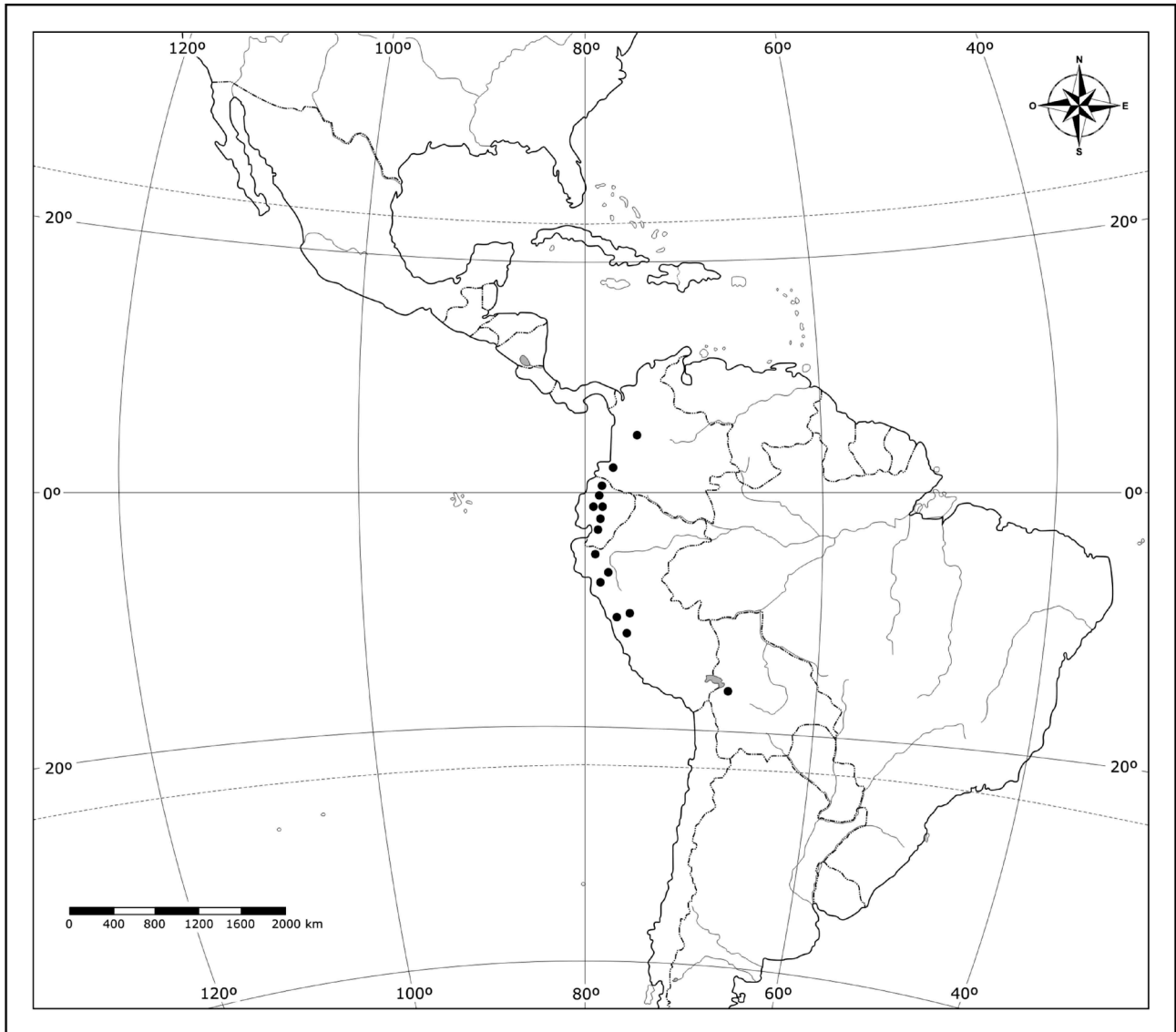


FIGURE 14. Geographical distribution of *Smalanthus fruticosus*.

Additional specimens examined:—BOLIVIA. Prov. Larecaja: Viciniis Sorata, 18 September 1818, *G. Mandon* 30 (F, G, GH, S).

COLOMBIA. Dept. Caldas: Salento to Laguneta, old Quindio trail, 1 August 1922, *P. Ellsworth et al.* 9099 (GH). Dept. Cundinamarca: Cercanías de San Bernardo hacia Sasaima, 23 June 1940, *J. Cuatrecasas* 9602 (F); Cordillera Oriental, ca. 10 km NE de Bogotá, 22 June 1965, *R. King & A. Guevara* 5701 (F); id., 16 km NE Bogotá, 22 June 1965, *R. King & A. Guevara* 5702 (F); id., ca. 2 km SE of Bogotá, *R. King & A. Guevara* 5771 (F); eastern Cordillera, ca. 18 km ENE of La Mesa, *R. King et al.* 5825 (F). Dept. Nariño: Samaniego road, 5 km from Tuquerres, headwaters of rio Pasqual, 7 February 1945, *A. Ewan* 16893 (F).

ECUADOR Prov. Azuay: Near Tarqui, along the rio Tarqui, 4–18 km S of Cuenca, 7 March 1945, *W. Camp* 2036 (K); id., 27 June 1945, *W. Camp* 3902 (S). Prov. Bolívar: Pucará de Telimbela, 18 November 1943, *M. Acosta Solís* 6814 (F); Casichagua, 29 September 1943, *M. Acosta Solís* 5995 (F); entre El Salto e Illubin, 25 October 1943, *M. Acosta Solís* 6557 (F); western cordillera, valley of river Chimbo, near town of Guaranda, without date, *A. Rimbach* 629 (F, S). Prov. Cañar: Along the Pan-American highway, route 1, ca. 1 km SE of Cañar, 30 January 1974, *R. King* 6621 (F); about 25 km N of Cañar, 21 January 1979, *R. King & F. Almeida* 7738 (F, G, K); Parroquia Suscal, 2° 29' 30" S, 79° 07' 20" W, 30 November 1991, *C. Cerón* 17656 (QCNE). Prov. Chimborazo: Östlich Riobamba, rio Chamba, 16 March 1934, *H. Schimpff* 827 (G); along the road to Riobamba, ca. 25 km SE of Riobamba, 31 January 1976, *R. King & R. Garvey* 6971 (F). Prov. Imbabura: Carretera Ibarra-Zuleta-Otavalo,

volcán Imbabura, 0° 15' N, 78° 05' W, 18 April 1988, *V. Zak & J. Jaramillo 3647* (GH); in monte Cotocachi, 30 August 1920, *I. Holmgren 921* (S). Prov. Pichincha: Camino de La Magdalena al Cinto, 25 October 1921, *C. Firmin 676* (F); carretera Chillogallo-Raya, San Juan-Chiriboga-Empalme, volcán Atacazo, 24 November 1985, *B. Larsen 302* (F); cráter de Pululahua, 1 Jun 1951, sin leg. *1106* (GH); W of Nono, 12 June 1968, *G. Harling et al. 10243* (F); Lloa valley, below Lloa, just W of Quito, 2 February 1981, *H. Balslev 1911* (F); Cotocollao, August 1897, *L. Mille 490* (GH); Quito, 20 August 1949, *M. Acosta Solis 13585* (F); Quitensian Andes, 1 November 1855, *J. Couthouy s.n.* (GH); carretera Quito-Nono-Tandayapa-Pto. Quito, en alrededores de Nono, 0° 3' S, 78° 30' W, 28 November 1987, *V. Zak & J. Jaramillo 3024* (K). Prov. Tungurahua: Vicinity of Patate, hacienda Leito, 1 August 1939, *E. Asplund 7981* (S); Östlich Baños, 15 January 1934, *H. Schimpff 633* (G). Without province and locality: *A. Sodiro s.n.* (G 189269).

PERU. Dept. Ancash: Prov. Recuay, km 102, on road from Pativilca to Recuay, 27 January 1983, *M. Dillon et al. 3088* (F, S); Prov. Huaylas, Huascarán National Park, trail between Auquispuquio and cerro Cunka, 8° 50' S, 77° 59' W, 10 April 1986, *D. Smith et al. 12137* (F). Dept. Cajamarca: Prov. Contumazá, cerro Chungarrán, Guzmango, 24 May 1978, *A. Sagástegui A. & J. Mostacero 9206* (F); La Herilla, Guzmango, 2 April 1981, *A. Sagástegui A. et al. 9702* (F); ca. 2 km from Contumazá, on route to Cascas, 7° 22' S, 78° 49' W, *M. Dillon et al. 4545* (F); alrededores de Contumazá, ruta a Cascas, 17 April 1992, *A. Sagástegui A. et al. 14560* (F); río Lledén, ruta Lledén-San Martín, 29 March 1997, *S. Leiva et al. 1953* (F); Prov. San Marcos, bajada de la Totorilla, siguiendo el curso del río Shitamalca, 31 October 1992, *I. Sánchez Vega & J. Torres 6414* (F); Prov. Celendín, Balsas-Celendín road, 40–45 km from Balsas, 6° 50' S, 78° 06' W, 24 February 1984, *D. Smith 6210* (F); Choctapampa, cerca a Celendín, 3 July 1975, *I. Sánchez Vega et al. 1658* (F, SI); Prov. San Miguel, Vista Alegre, Niepos, 15 February 1992, *S. Llatas Quiróz 3063* (F); Prov. Cajamarca, al W de Cajamarca, bajando a Chetilla, 16 October 1993, *I. Sánchez Vega 6640* (F); near Lucto, 1856, *Jameston 856* (G). Dept. Huánuco: Huánuco, 1824, Herb. Ruiz et Pavon (F 842785). Dept. La Libertad: Prov. Otuzco, arriba de Piedra Gorda, ruta Salpo-Samne, 14 June 1994, *S. Leiva et al. 1196* (F); arriba de La Chivada, camino Salpo-Pagash, 12 June 1992, *S. Leiva & P. Leiva 596* (F); debajo de Shitahuara, camino a San Andrés de Otuzco, 16 May 1991, *S. Leiva & P. Leiva 314* (F); arriba de Piedra Gorda, ruta a Samne, 27 May 1993, *S. Leiva et al. 756* (F). Dept. Lima: Tamboraque, Oroya railway, near the railway station, May 1938, *C. Sandeman s.n.* (K); San Buenaventura, 17 June 1925, *F. Pennell 14542* (F, GH, S); Chosica, 28 April–2 May 1922, *Macbride & Featherstone 532* (F, GH); San Mateo, E Lima, 20 May 1959, *L. Diers 1021* (LP). Dept. Piura: Prov. Huancabamba, Salala, al N de Huancabamba, km 27, 1 May 1990, *I. Sánchez Vega et al. 5187* (F). Without department: Vice-regno Peruviano et Chilensi, 1778–1788, Herb. Ruiz et Pavón 30/36 (F).

Smallanthus glabratus (Candolle) Robinson (1978: 49).

Polymnia glabrata Candolle (1836: 515). Type:—CHILE?. Without locality and date: Chilenses, *T. Haenke s.n.* (holotype PR 612155, digital image!).

Polymnia glabrata var. *angustifolia* Candolle (1836: 515). Type:—CHILE?. Without locality and date: Cordillera du Chile, *T. Haenke s.n.* (holotype PR 612154, digital image!).

Shrubs 1–6 m tall, homophyllous, stems glabrous. Leaves opposite, petiolate, 19–23 cm long, blade 6–8 cm wide, ovate-lanceolate, acute at the apex, obtuse at the base, margin entire, triplinerved, acrodromous, glabrous; petioles 5.5–9 cm long, winged, wings uniform in width, entire, not auriculate at the base. Capitula ca. 5 × 7 mm, ca. 50 arranged in paniculiform cymes; peduncles 9–25 mm long, glabrescent. Involucre hemispherical; phyllaries arranged in 2 series, herbaceous, ovate, ovate-lanceolate, outer phyllaries 5–6 × 3–4 mm, acute or obtuse at the apex, inner phyllaries 4–5 × 2–3 mm, acute at the apex. Receptacle with paleae obovate, 3 × 2 mm, trifid at the apex with the central tooth longer. True ray florets ca. 10, 1-seriate, corollas yellow, ray-limb oblong, 4.5–5 × 3–3.5 mm, apex with the 3 teeth, tube 0.5–0.8 mm long. Style 2 mm long, branches 1 mm long. Disc florets ca. 30, corollas yellow, campanulate, 2–3 mm long, lobes 0.5 mm long. Anthers with apical appendage ovate or subtriangular. Style 2.5 mm long, branches 0.3–0.5 mm long. Cypselae obovate, 2–3 × 1–1.5 mm, smooth. $2n=30$ (Carr *et al.* 1999). (Fig. 15).

Etymology:—From the Latin adjective *glabratus*, made nearly glabrous, by the lack of pubescence in stems and leaves.

Distribution and ecology:—Bolivia and Peru (Fig. 16). This is a common species that grows in open slopes, river banks, and in margins of shrublands and roadsides, at 2400–3900 m. Flowers from January to September.

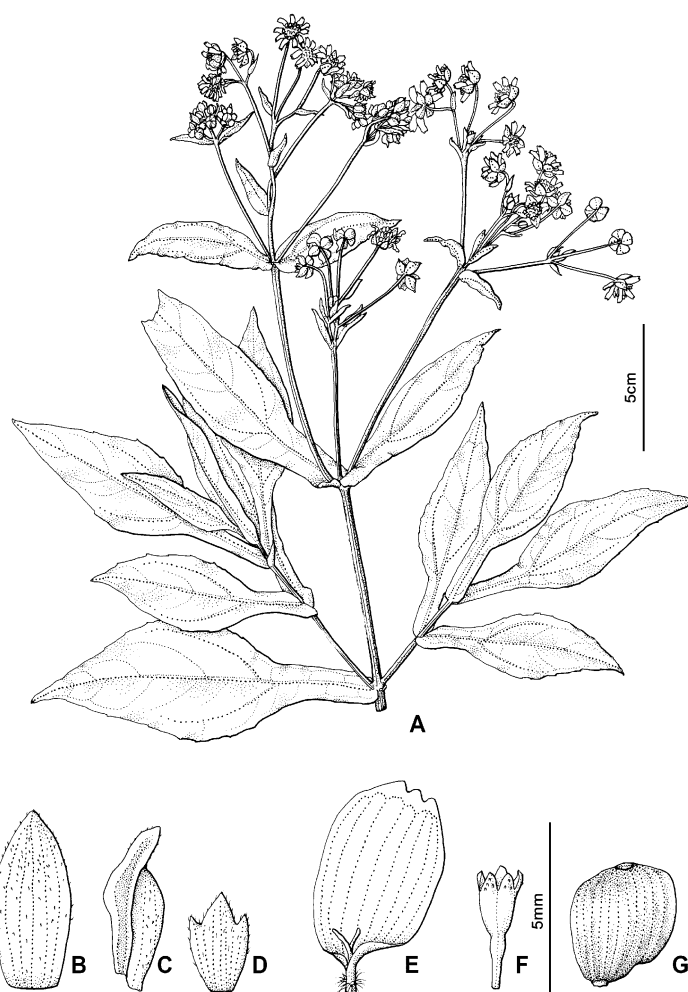


FIGURE 15. *Smallanthus glabratus* (de Candolle) H. Robinson. **A.** Habit. **B.** Outer phyllary. **C.** Inner phyllary. **D.** Palea. **E.** Ray floret (without cypselum). **F.** Disc corolla. **G.** Cypselum (*Asplund 11375*, S).

Vernacular names and uses:—Garita, poque, putaca, shita, taraca. It has been mentioned the use of the leaves and the flowers of this species against rheumatism (*Carter s/n*, F), and for colds (*Macbride & Featherstone 1554*, F).

Notes:—Wells (1965) established that the type of *Polymnia glabrata* is the specimen *Haenke 8192* deposited in G, without mentioning if he indeed saw this specimen. We could not find that specimen in G but we found a specimen in PR, the herbarium where Haenke deposited his collections, that fits with the protologue of the species. Stafleu & Cowan (1976) indicate that types of de Candolle based on Haenke collections are at PR. Therefore, we consider the specimen at PR as the holotype of *P. glabrata*.

Besides the locality mentioned on the label of the type specimen of *Polymnia glabrata*, we did not find other records in Chile of this species, which typically grows in Peru with a few collections originated in western Bolivia. Reiche (1905: 77), in his flora of Chile, mentioned that *Polymnia glabrata* has not been seen in Chile in more than a century and that Haenke probably collected the species in Peru.

Additional specimens examined:—BOLIVIA. Dept. La Paz, Unduavi, October 1885, *H. Rusby 1670* (F); Prov. Saavedra, Curva, above village of Charazani, 15° 07' S, 69° 03' W, April 1978, *W. Carter s.n.* (F); Sorata, September 1888, *H. Rusby 1669* (GH, K). Without department: *M. Bang 1813* (G, GH, S).

PERU. Dept. Amazonas: 17 km along road ascending mountain SE of Chachapoyas, 20 January 1983, *R. King & L. Bishop 9269* (G). Dept. Ancash: Prov. Huaraz, 10 km by road from Cachabamba, 9° 27' S, 77° 51' W, 6–8 June 1985, *D. Smith & M. Buddensiek 10933* (F). Dept. Cajamarca: Prov. Celendín, carretera Celendín-Balsas, cerca a Jelig, 14 April 1982, *I. Sánchez Vega 2781* (F); 9 km N along road from Cajamarca to Bambamarca, 8 January 1983, *R. King & L. Bishop 9111* (G, K); 41 km NE of Cajamarca, along the road to Celendín, 9 January

1983, *R. King & L. Bishop* 9138 (G, K). Dept. Cusco: Prov. Abancay, Apurimac, January 1938, *C. Vargas* 781 (F); Prov. Pataz, Pataz, along trail from Yalen to los Alisos, 77° 30' W, 21 February 1986, *K. Young* 2940 (F); Pillahuata, Paucartambo-Pilcopata road, km 126, 29 June 1978, *A. Gentry et al.* 23509 (F); Prov. Urubamba, Lucmayoc, 30 March 1942, *C. Vargas* 2802 (F); Dist. Machu Picchu, Pampacahua, km 94, 13° 06' S, 72° 16' W, 21 January 2005, *L. Valenzuela et al.* 4585 (K). Dept. Huancavelica: Prov. Castrovirreina, near Córdova, 27–28 March 1942, *R. Metcalf* 30279 (G, GH). Dept. Huánuco: Prov. Huánuco, Huánuco-La Unión road, km 29–35, Heda. Mitoambo, 2 March 1978, *J. Luteyn* 5496 (F). Dept. Junín: Tarma, carretera central, passim 11–4 km W of Tarma, 5 July 1966, *G. Edwin & J. Schunke* V. 3904 (F); Mito, 8–22 July 1922, *Macbride & Featherstone* 1554 (F, GH); id., 23 July–14 August 1922, *Macbride & Featherstone* 1741 (F). Dept. La Libertad: Prov. Otuzco, El Granero, Had. Llaguén, 1 June 1951, *A. López* 603 (LP). Dept. Lambayeque: Prov. Lambayeque, entre Huaratara y Colaya, 5 July 1986, *S. Llatas Quiroz* 1977 (F). Dept. Lima: Chiuchín, without date, *Pavón* s.n. (G 189273); Prov. Huarochiri, río Blanco, at an irrigation ditch, 4 June 1940, *E. Asplund* 11375 (S); río Blanco, 17 April 1929, *E. Killip & A. Smith* 21647 (F); San Mateo, 28 May 1940, *E. Asplund* 11186 (S). Dept. Puno: Prov. Sandía, near Limbani, 14–16 May 1942, *R. Metcalf* 30488 (G, GH). Dept. Piura: At Tres Asequias, 10 km N of Huancabamba, 15 September 1964, *P. Hutchinson & J. Wright* 6602 (F).

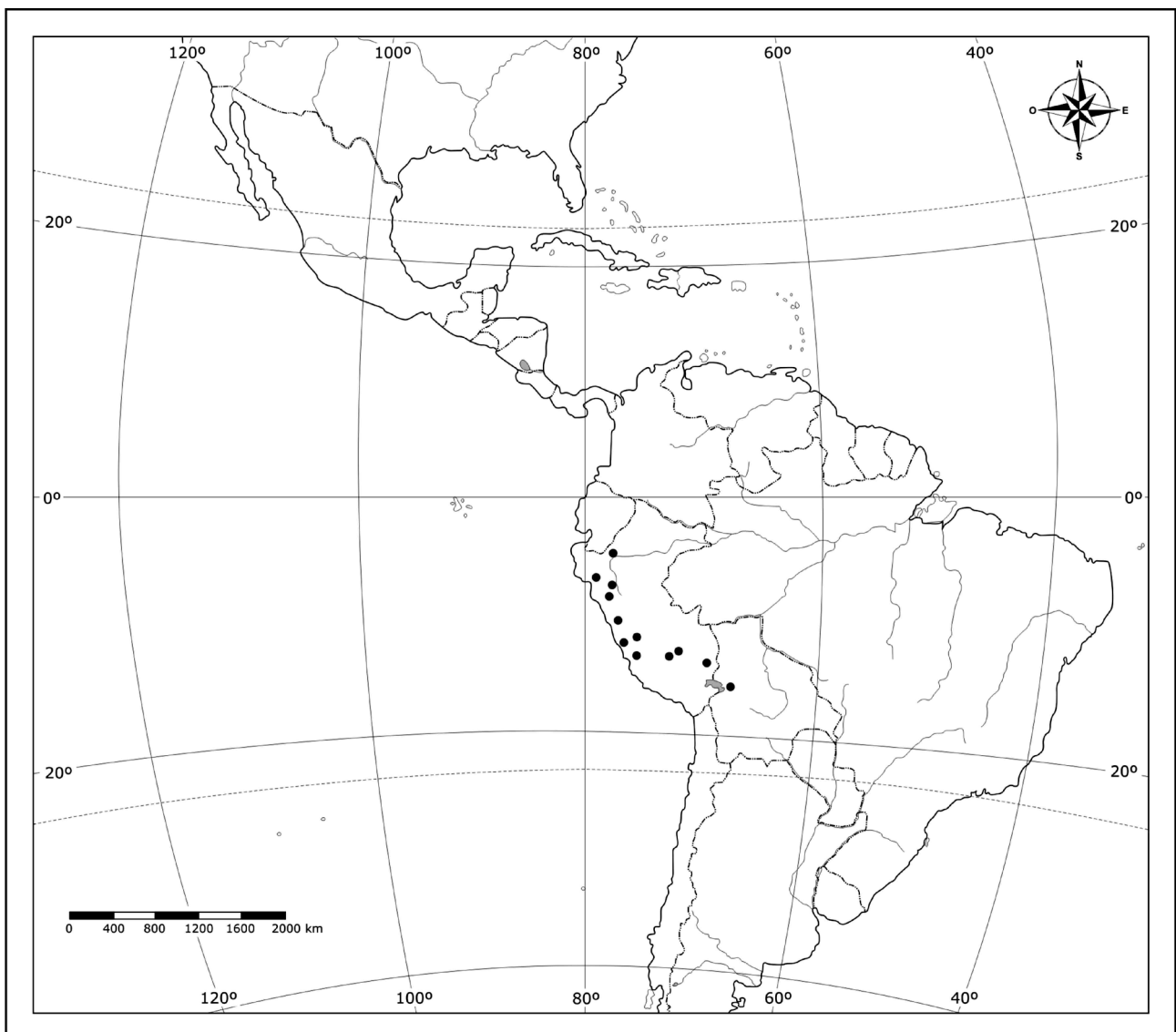


FIGURE 16. Geographical distribution of *Smalanthus glabratus*.

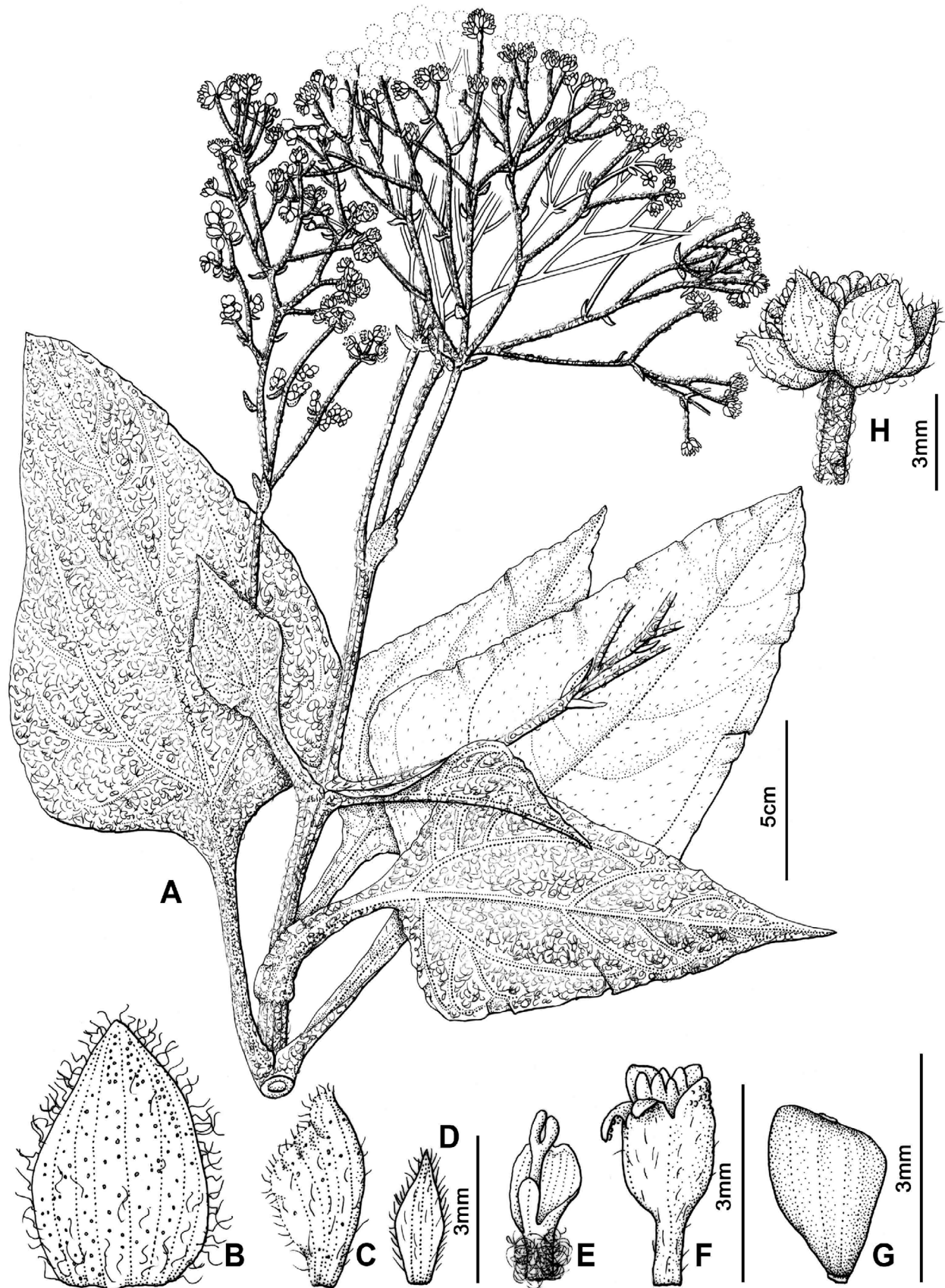


FIGURE 17. *Smalanthus jelskii* (Hieronymus) H. Robinson. **A.** Habit. **B.** Outer phyllary. **C.** Inner phyllary. **D.** Palea. **E.** Bilabiate marginal floret (without cypselar). **F.** Disc floret (without ovary). **G.** Cypselar. **H.** Capitulum (*Wurdack 618*, LP).

Smallanthus jelskii (Hieronymus) Robinson (1978: 49).

Polymnia jelskii Hieronymus (1905: 484). Type:—PERU. Cajamarca: Near Callacate, 1879, *C. von Jelski 687* (lectotype here designated US 128390, digital image!, epitype here designated photograph F n. 15158!).

Trees 3–7 m tall, homophyllous, stems densely pubescent at the apex. Leaves opposite, petiolate, 26–47 cm long, lamina 11–20 cm wide, ovate-subtriangular, acute at the apex, obtuse or truncate at the base, margins entire or dentate, triplinerved, acrodromous, pubescent above, densely pubescent below; petioles 8–9 cm long, winged, wings uniform in width, entire, not auriculate at the base. Capitula 4–7 × 2–8 mm, ca. 100 arranged in compact corymbiform cymes; peduncles 5–30 mm long, densely pubescent. Involucre hemispherical; phyllaries arranged in 2 series, outer phyllaries 5–8 × 4–5 mm, ovate, acute or obtuse at the apex, herbaceous, inner phyllaries 2–4 × 1–1.5 mm, obovate, obtuse at the apex, scarious. Receptacle with paleae rhombic, 2–3 × 1 mm, apex entire. Marginal florets ca. 10, 1-seriate, corollas yellow, bilabiate, external lip orbicular, 1.5–6 × 1.2–5 mm, apex with 2- or 3-dentate, internal lip ovate or oblong, 1.5–2.6 × 0.5–1.5 mm, tube 1–6 mm long. Style 2–3 mm long, branches 0.7–1 mm long. Disc florets ca. 50, corollas yellow, campanulate, 2–3 mm long, lobes 0.6 mm long. Anthers with apical appendage widely ovate, subtriangular. Style 1–2 mm long, branches 0.1 mm long. Cypselae obovate, 1–2.5 × 1–1.5 mm, smooth. (Fig. 17).

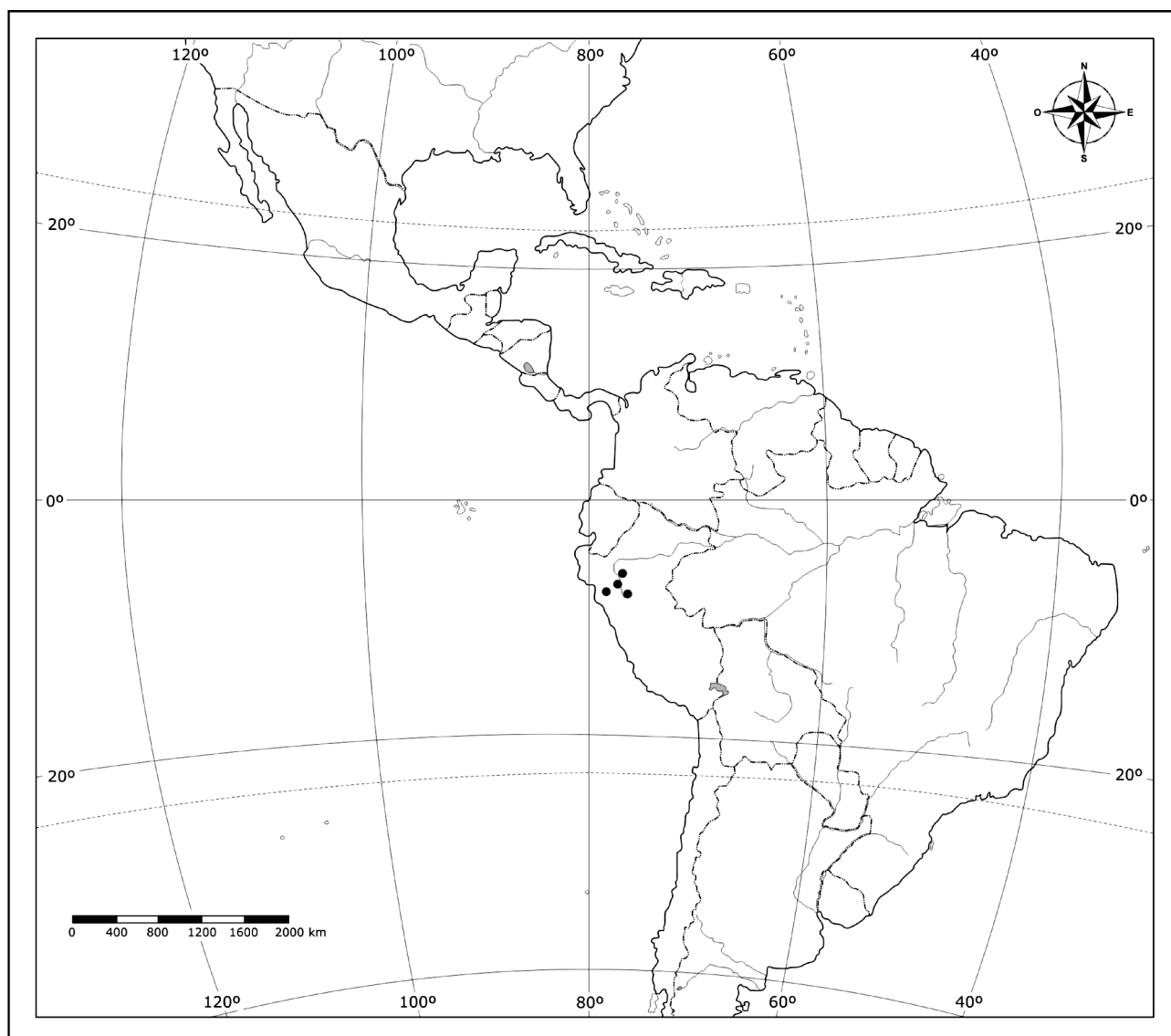


FIGURE 18. Geographical distribution of *Smallanthus jelskii*.

Etymology:—In honor of the Polish naturalist Constantin von Jelski (1837–1896), collector of the type specimen, who made significant collections, mainly zoological but also was interested in the botany of Peru and French Guiana.

Distribution and ecology:—Northwestern Peru (Fig. 18). It grows in rocky slopes, ravines, mountain fragmented forests, evergreen cloud forests, at 2200–3350 m. Flowering from November to April.

Vernacular names:—Shita.

Notes:—The original holotype at B was destroyed during the World War II (Hiepko 1987). According to Art. 9.2 of the ICN (McNeill *et al.* 2012) here we designate the specimen at US as the lectotype of *Polymnia jelskii* Hieronymus. The specimen at US is a fragment, thus according to Art. 9.8 we also designate as epitype the photograph of the destroyed holotype at B kept in the Field Museum (number 15158).

This species is very distinctive because is the only one with bilabiate corollas in the genus *Smallanthus*.

Additional specimens examined:—PERU. Dept. Amazonas: Prov. Chachapoyas, Quebrada Molino, 5 km below Chachapoyas, 30 May 1962, *J. Wurdack 618* (F, GH, LP). Dept. Cajamarca: Prov. Cajamarca, La Encañada-Jalca de Kumulca, 17 June 1975, *A. Sagástegui A. et al. 8090* (F, SI); Cajamarca, km 61 carretera Celendín hacia Cajamarca, a 21 km de La Pampa del Toro hacia Cajamarca, 10 February 1984, *C. Cowan 4422* (F); entre La Encañada y Kumullca, 17 June 1975, *I. Sánchez Vega & J. Sánchez Vega 1589* (F, SI); Prov. Chota, near village El Campamento, ca. 21 km WNW of Huambos, 6° 24' 23" S, 79° 01' 19" W, 20 April 1993, *M. Dillon et al. 6422* (F); Chota-Bambamarca, 27 May 1965, *A. López & A. Sagástegui 5471* (LP); Prov. Cutervo, Madre Mía, entre el Suro y la Flor, al NW del Parque, 25 June 1992, *I. Sánchez Vega & A. Miranda 6331* (F); Prov. Celendín, Guañambra-Sendamal, 19 August 1984, *A. Sagástegui A. et al. 12197* (F).

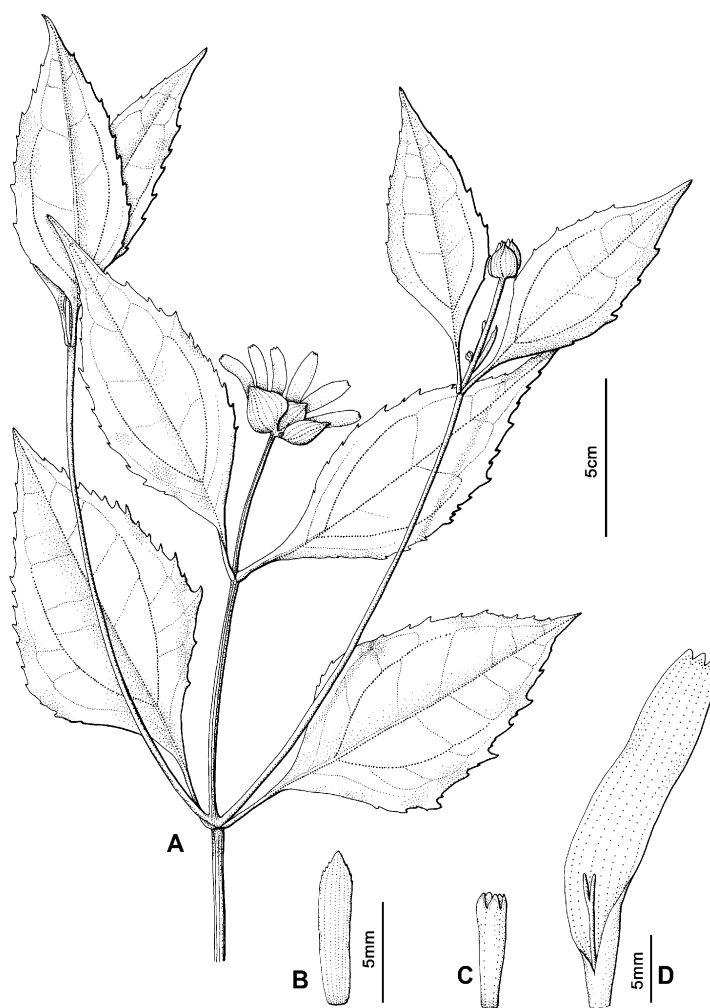


FIGURE 19. *Smallanthus latisquamus* (S.F. Blake) H. Robinson **A.** Habit. **B.** Palea. **C.** Disc corolla. **D.** Ray floret (without cypsela) (Stork 2071, GH).

Smallanthus latisquamus (Blake) Robinson (1978: 49).

Polymnia latisquama Blake (1926: 421). Type:—COSTA RICA. Cartago: Along stream, southern slope of Volcán de Turrialba, near the Finca del Volcán de Turrialba, alt. 2000–2400 meters, 22 February 1924, *P. C. Standley 35340* (holotype US 128391 [1227055], digital image!, isotype GH 11388, digital image!).

Herbs 1–3 m tall, homophyllous, stems glabrescent. Leaves opposite, petiolate, 9–23 cm long, blade 4.5–15 cm wide, ovate-lanceolate, acute to slightly attenuate at the apex, obtuse, slightly attenuate at the base, margins irregularly dentate, triplinerved, acrodromous, pubescent on both faces; petioles 0.5–3 cm long, winged, wings decreasing in width from the blade to the leaf node, entire, not auriculate at the base. Capitula 10–20 × 15–30 mm, solitary or up to three arranged in cymes; peduncles 30–90 mm long, glabrescent. Involucre hemispherical; phyllaries arranged in 2 series, herbaceous, outer phyllaries 20–23 × 15–20 mm, orbicular, acute or obtuse at the apex, inner phyllaries 10–13 × 8 mm, ovate, acute at the apex. Receptacle with paleae 7–9 × 2–3 mm, oblong, apex entire. True ray florets ca. 8, 1-seriate, corollas yellow, ray-limb oblong, ca. 25 × 13 mm, apex with 3-dentate, teeth equal in size, tube 1.5 mm long. Style 7 mm long, branches 3 mm long. Disc florets ca. 50, corollas yellow, tubular, 8 mm long, lobes 1–2 mm long. Anthers with apical appendage ovate. Style 8 mm long, branches 1 mm long. Cypselae rounded-obovate, 6–8 × 5–6 mm, smooth. $2n=16$ (Carr *et al.* 1999). (Fig. 19).

Etymology:—From the Latin *latus*, broad, wide, and *squama*, scale, by the orbicular shape of the outer phyllaries.

Distribution and ecology:—Costa Rica, Guatemala, and Mexico (Fig. 20). This species grows in cloud forests, humid shrublands, and stream banks, from sea level to 3000 m. Flowering from October to July.

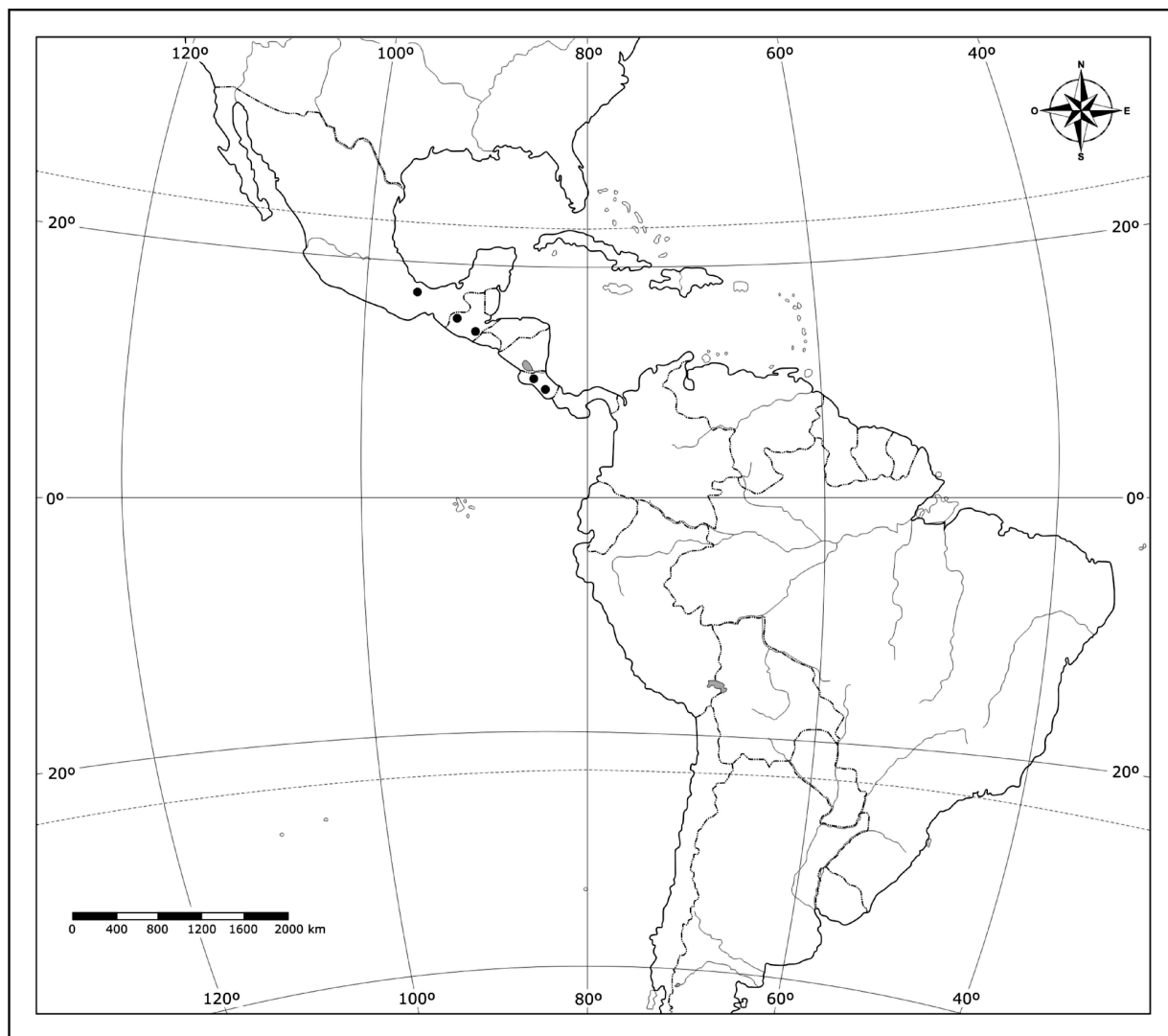


FIGURE 20. Geographical distribution of *S. latisquamus*.

Notes:—Wells (1965) considered this species a synonym of *Smallanthus quichensis*. In this work both species are regarded as separate entities by differences in the size of the capitula (10–20 × 15–30 mm vs. 7–15 × 12–14 mm in *S. quichensis*), and the shape of the outer phyllaries of the involucre (orbicular vs. ovate). This species was traditionally considered endemic to Costa Rica and Guatemala. However, it has been found here one specimen of Mexico thus extending the species distribution.

Additional specimens examined:—COSTA RICA. Dept. Cartago: Along río Birris, volcán Irazú, 9° 57' 5" N, 83° 51' W, 30 July 1977, *G. Webster 22131* (F); E of Irazú, 17 May 1928, *H. Stork 2071* (GH); río Birris, volcán Irazú, 23 February 1924, *P. Standley 34412* (GH); road to volcano Irazú, 23 August 1940, *M. Chrysler 5544* (F); Prov. San José, along the trail from Canaán to cerro Chirripó, above the Rio Talari in the Rio Chirripó del Pacífico, 9° 27' N, 83° 31' W, 20–25 August 1971, *W. Burger & L. Gomez P. 8362* (F, TEX).

GUATEMALA. Dept. Baja Verapaz: Sierra de las Minas, 3 km SE of Purulhá, 2 January 1974, *L. Williams 43124* (F). Dept. Huehuetenango: Municipio San Mateo Ixtatan, 4 miles E of San Mateo Ixtatan, on road to Barillas, 7 February 1965, *D. Breedlove 8724* (F); around Cruz de Limón, 3 1/2 miles E of San Mateo Ixtatán, sierra de los Cuchumatanes, 10 July 1942, *J. Steyermark 48502* (F). Dept. Jalapa: Vicinity of Soledad, montaña Miramundo, between Jalapa and Mataquesuintla, 4 December 1939, *J. Steyermark 32621* (F).

MEXICO. State Oaxaca: District of Tuxtepec, Chiltepec and vicinity, 24 October 1941, *G. Martínez Calderón 741* (GH).

Smallanthus lundelli Robinson (1978: 49). Type:—GUATEMALA. Baja Verapaz: Unión Barrios, on the Salama-Coban Road, south of km 147, in high forest on hill, 5 February 1975, *C. L. Lundell & E. Contreras 18916* (holotype US 128408, digital image!, isotypes F 51411, LL 734000, S 12–25780, TEX, digital images!).

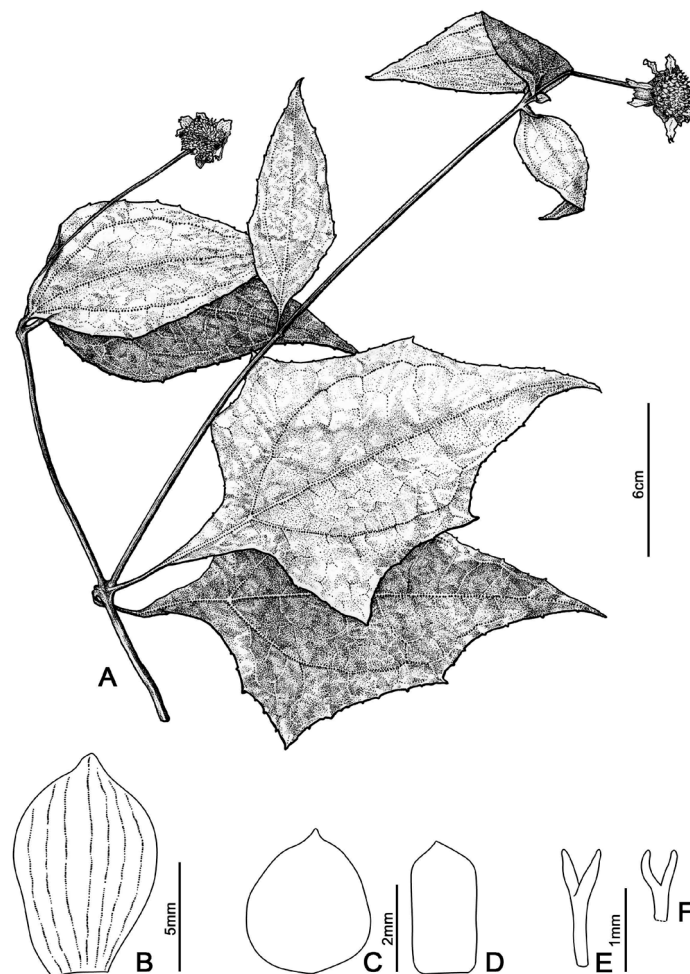


FIGURE 21. *Smallanthus lundelli* H. Robinson. **A.** Habit. **B.** Outer phyllary. **C.** Inner phyllary. **D.** Palea. **E.** Style of disc florets. **F.** Style of ray florets (*Contreras 11065*, S).

Herbs 1 m tall, heterophyllous, stems pubescent. Leaves opposite, petiolate, attenuate at the apex, margin mucronate, triplinerved or trinerved, acrodromous, pubescent on both faces, petioles winged, wings decreasing in width from the blade to the leaf node, entire, not auriculate at the base; lower leaves 15–25 cm long, lamina 8–13 cm wide, ovate, attenuate to acute at the apex, hastate at the base, margins entire or conspicuously to slightly irregularly lobulate, petioles 4–6.5 cm long; upper leaves 5–15 cm long, blade 5–7 cm wide, ovate to lanceolate, obtuse, attenuate at the base, petioles 2–5 cm long. Capitula 10–12 × 10–15 mm, up to three arranged in cymes; peduncles 30–120 mm long, pubescent. Involucre hemispherical; phyllaries arranged in 2 series, herbaceous, outer phyllaries 6–20 × 6–12 mm, ovate or orbicular, acute at the apex, inner phyllaries 2.5–10 × 1–4 mm, orbicular, obtuse or acute at the apex. Receptacle with paleae 2.5–4 × 0.5–1 mm, oblong, apex entire. True ray florets ca. 10, 1-seriate, corollas yellow, ray-limb oblong, 12–20 × 5–8 mm, apex 3-dentate, teeth equal in size, tube 2 mm long. Style 1–3 mm long, branches 0.5–1 mm long. Disc florets ca. 100, corollas yellow, tubular, 6–6.5 mm long, lobes 1 mm long. Anthers with apical appendage ovate. Style 1–2 mm long, branches 0.5–1 mm long. Cypselae rounded-obovate, 4–5 × 3 mm long, smooth. (Fig. 21).

Etymology:—In honor of the American botanist Cyrus L. Lundell (1907–1994), one of the collectors of the type specimen and discoverer of the Maya city of Calakmul which had been hidden in jungles for 1000 years.

Distribution and ecology:—Guatemala and Mexico (Fig. 22). Populations were found in forests and on hills, at 2000–3000 m. Specimens with flowers were collected in February and August.

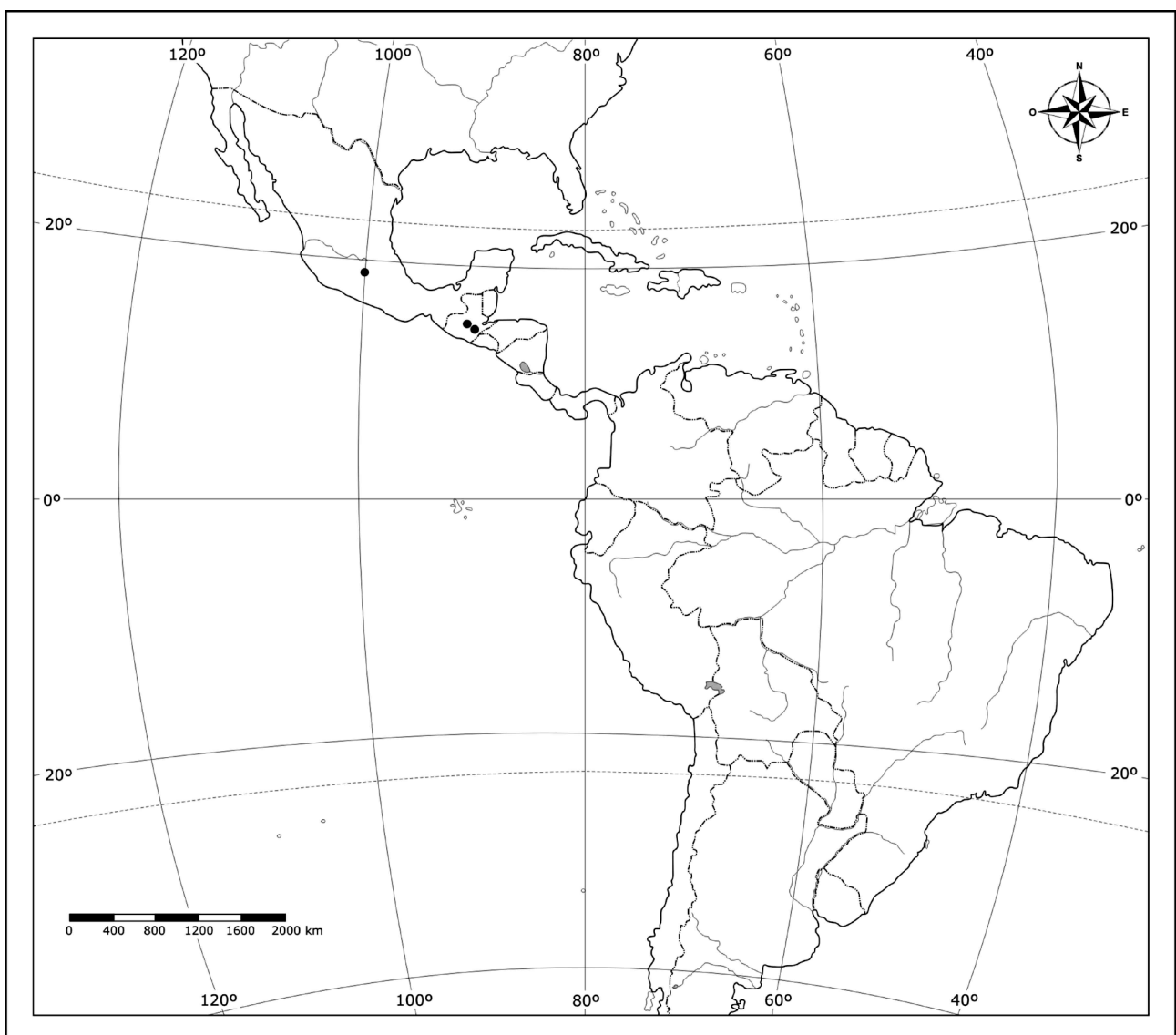


FIGURE 22. Geographical distribution of *Smallanthus lundelli*.

Notes:—This species was traditionally considered endemic to Guatemala, however, during this work we have found specimens from Mexico, thus extending the species distribution.

Also see Notes under *S. maculatus*.

Additional specimens examined:—GUATEMALA. Dept. Baja Verapaz: Unión Barrios, 27 February 1972, *E. Contreras 11065* (S). Dept. El Progreso: N of Finca Piamonte, between Finca Piamonte and summit of volcán Santa Luisa, 5 February 1942, *J. Steyermark 43592* (F, GH).

MEXICO. State Mexico: District Temascaltepec, Tequesquipan, 20 August 1932, *G. Hinton 1347* (GH). Without state: Nueva España, without date, *H. Pavón s.n.* (G 189326).

Smallanthus macroscyphus (Baker) A. Grau ex Sáenz in Zuloaga & Morrone (1999: 1245).

Polymnia macroscypha Baker (1884: 158). Type:—BRAZIL. Minas Gerais: Caldas, in Villa Regnelli, Junio 1854, *G. A. Lindberg 5* (lectotype here designated BR 5522972, digital image!).

Smallanthus riograndensis Mondin (2004: 2). Type:—BRAZIL. Rio Grande do Sul: Serra do Pinto, Mun. São Francisco de Paula, Tainhas, Aratinga, 27 April 2002, *C. Mondin & A. Iob 2653* (holotype ICN 137590, digital image!, isotypes HASU, PACA).

Smallanthus araucariophilus Mondin (2004: 3). Type:—BRAZIL. Rio Grande do Sul: Cambará do Sul, na estrada para Sao José dos Ausentes, 13 February 2002, *C. Mondin & A. Iob 2553* (holotype ICN 137593, digital image!, isotypes HASU, PACA).

Herbs 1–3 m tall, sometimes robust, heterophyllous, stems pubescent. Leaves opposite, acute at the apex, margin irregularly dentate, mucronate, triplinerved, acrodromous or actinodromous, pubescent on both faces; lower leaves 10–35 cm long, lamina 6–26.5 cm wide, orbicular, ovate, ovate-subtriangular, sometimes lobate, truncate, rounded or slightly hastate at the base, petiolate, petioles 2–5 cm long, winged, petiole wings uniform in width, entire, auriculate or not auriculate at the base; upper leaves 7–18.3 cm long, lamina 3–10.5 cm wide, ovate, lanceolate, ovate-lanceolate, attenuate or obtuse at the base, subsessile to petiolate, petioles 1.5–3 cm long, similar to those of lower leaves. Capitula 5–17 × 7–13 mm, ca. 15 arranged in corymbiform or paniculiform cymes; peduncles 3–39 mm long, pubescent. Involucre campanulate to hemispherical; phyllaries arranged in 2–3 series, herbaceous, ovate, obovate, ovate-lanceolate, outer phyllaries 5.5–12 × 3–7.5 mm, obtuse or acute at the apex, inner phyllaries 5–11 × 2.5–4 mm, acute at the apex. Receptacle with paleae 2.5–6 × 1.3–3 mm, ovate, lanceolate or elliptical, apex entire. True ray florets 20–25, 1- or 2-seriate, corollas yellow, ray-limb oblong, 3.5–6 × 1–2 mm, apex entire or 3-dentate, teeth equal in size, tube 1.5–2.5 mm long. Style 4–6 mm long, branches 0.7–1.5 mm long. Disc florets 30–60, corollas yellow, tubular, 5–8 mm long, lobes 0.8–1 mm long. Anthers with apical appendage ovate, subtriangular. Style 4–7 mm long, branches 0.5–1 mm long. Cypselae obovate, 3–5 × 3–4 mm, smooth or irregularly verrucate. (Fig. 23).

Etymology:—From the Greek *μακρος* (macros), large, and *σκιφος* (scyphos), cup, probably by the large capitula.

Distribution and ecology:—Northwestern and eastern Argentina, Bolivia, southeastern Brazil, and Paraguay (Fig. 24). It grows in humid ravines with gallery forests, river margins, temperate humid mountain forests, *Araucaria angustifolia* (Araucariaceae) forests, and capoeiras, at 0–2200 m. Commonly invasive of abandoned cultivated fields and shrubby vegetation patches among cultivated fields (Grau & Rea 1997). Flowering from December to June.

Vernacular names and uses:—Yacón de campo. The leaves of this species have an hypoglycemic effect (Cabrera *et al.* 2007).

Notes:—Wells (1965) indicated as isotype of *Polymnia macroscypha* a specimen at F without indication of either its collector or collection number. However, Baker (1884) indicated four syntypes in the protologue of this species. Here we designate the syntype *G. A. Lindberg 5* as lectotype because it allows the identification of the species, belongs to Martius's herbarium, and has the handwritten name of this species by Baker.

Grau (Grau & Rea 1997) published the new combination *Smallanthus macroscyphus* (Baker) Grau without indication of the basionym. Sáenz (1999) stated the basionym and provided a full and direct reference to the protologue of *Polymnia macroscypha* Baker, thus, according to Art. 41.1 of the ICN (McNeill *et al.* 2012), the new combination is here attributed to Sáenz.

The syntypes of *Polymnia macroscypha* Baker (1884: 158) are indicated as follows: BRAZIL. Minas Gerais: Caldas, 20 February 1866, *A. F. Regnell I-195* (syntypes S 10–31442!, S 10–31443!, S 10–31444!); 1854/6, *J. Weir 505* (syntype F 51063, digital image!).

Wells (1965) regarded this species a synonym of *Polymnia connata* (= *Smallanthus connatus*). However, *Smallanthus macroscyphus* differs from *S. connatus* by its leaf shape (orbicular or ovate vs. subtriangular in *S. connatus*), and petiole base (auricles discontinuous with the opposite leaf vs. auricles continuous).

Mondin (2004) distinguished his two new species, *S. araucariophilus* and *S. riograndensis*, from *S. connatus* by their leaf auricles discontinuous with the opposite leaf. However, this author did not compare the new species with *S. macroscyphus*, which also occurs in Brazil. From our point of view, *S. araucariophilus*, *S. riograndensis*, and *S. macroscyphus* are morphologically similar and thus, Mondin's species are regarded as synonyms of *S. macroscyphus*.

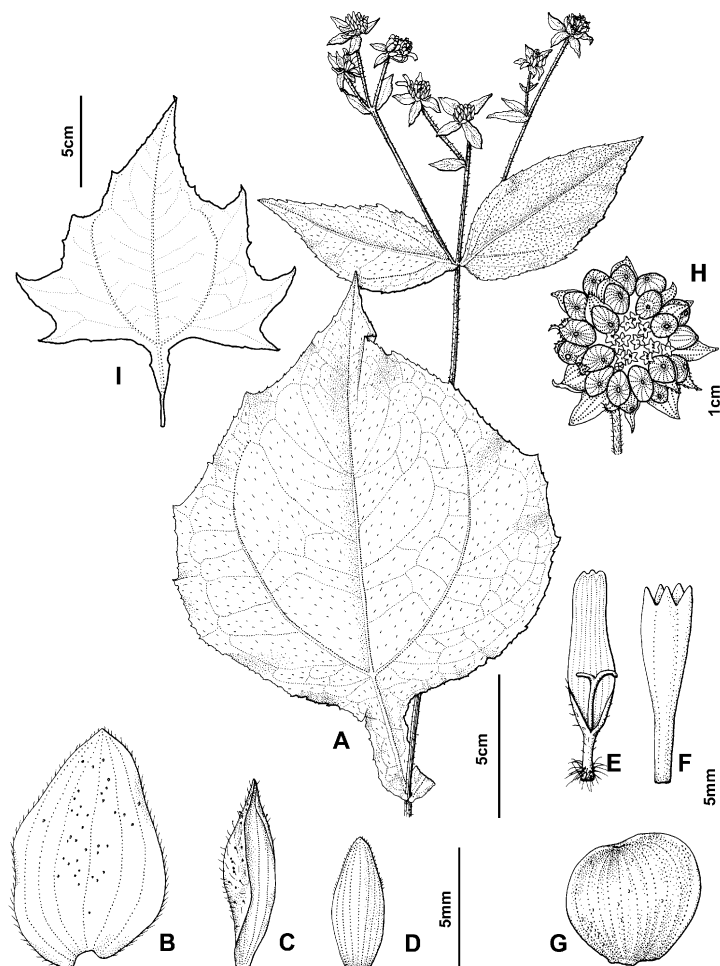


FIGURE 23. *Smallanthus macroscyphus* (Baker) A. Grau. **A.** Habit. **B.** Outer phyllary. **C.** Inner phyllary. **D.** Palea. **E.** Ray floret (without cypselum). **F.** Disc corolla. **G.** Cypselum. **H.** Capitulum showing mature cypselae. **I.** Basal leaf (*Novara 6484*, S).

Additional specimens examined:—ARGENTINA. Prov. Jujuy: Dept. Capital, El Cucho, cerro Labrado, 9 March 1966, *E. de la Sota 4309* (LP); La Almona, 14 March 1967, *A. Cabrera & D. Añón Suarez 18514* (LP); Termas de Reyes, 28 February 1945, *D. Abbiatti & L. Claps 785* (LP); id., 23 February 1959, *A. Cabrera et al. 13266* (LP); de Yala a Laguna de Yala, 8 April 1945, *C. O'Donnell 2991* (S); camino de Termas a Reyes, 27 April 1981, *E. Zardini 1346* (F); Puente de Sala, 30 April 1981, *E. Zardini 1373* (F); camino a El Cucho, Los Blancos, 28 April 1981, *E. Zardini 1347* (F, S); Dept. Manuel Belgrano, La Almona, 28 April 1981, *E. Zardini 1353* (F); Dep. Santa Bárbara, Abra de los Morteros a El Fuerte, 20 April 1975, *A. Cabrera et al. 26188* (LP); Dept. Tumbaya, La Volcan village, just S of Tumbaya, 20 August 1987, *D. Soejarto et al. 6082* (F); Dept. Valle Grande, serranía de Calilegua, senda a Alto Calilegua, 18 February 1964, *H. Fabris et al. 5351* (LP); senda de San Francisco a Alto Calilegua, Pino Hachado, 23° 37' 35''S, 64° 56' 07'' W, 21 February 2009, *F. Zuloaga et al. 11123* (SI). Prov. Misiones: Dept. San Pedro, Parque Provincial Moconá, 16 December 1992, *G. Seijo et al. 223* (G). Prov. Salta: Dept. Capital, Quebrada de San Lorenzo, 5 March 1958, *A. Cabrera & J. Marchionni 12815* (LP); Dept. Chicoana,

La Viña, 5–7 km S de Rosario de Lerma, 20 March 1988, *L. Novara* 7846 (G, S); Los Laureles, entrando a la Quebrada de Escoipe, frente a la planta de AGAS, 9 February 1987, *L. Novara* 5932 (G, S); Los Laureles, 5 Feb 1944, *A. Cabrera* 8413 (LP); camino cornisa Salta-Jujuy, 29 January 1947, *A. Schulz* 6604 (F, G); Dept. La Caldera, Alto de la Sierra, ruta 68 km 1637–1638, pasando Vialidad Nacional, 12 February 1989, *L. Novara* 8575 (G, S); Dept. Orán, Sierra de Zenta, Trancas, 23° 07' 73" S, 64° 54' 59,7 " W, 21 April 1998, *A. Schinini et al.* 34710 (F, GH); Cuesta del Arca-Trancas, January 1897, *C. Spegazzini s.n.* (LP 45264); Dept. Rosario de Lerma, Quebrada del Toro, frente a Río Blanco, 7 April 1987, *L. Novara* 6484 (G, S); El Pacará, ruta 23, 4 km al NE de Rosario de Lerma, 15 March 1987, *L. Novara* 6288 (G, S); Quebrada del Toro, ruta 51, km 28–29, 15 May 1988, *L. Novara* 7993 (G, S); Quebrada del Río Blanco, 5 km al SE (aguas arriba) del río Toro, 4,5–6,5 km al W de Campo Quijano, 28 January 1988, *L. Novara* 7613 (G, S). Prov. Tucumán: Dept. Burruyacú, Cerro del Campo, January 1918, *E. Bailetti* 59 (GH); cerro del Duraznillo, 21 February 1986, *L. Monetti s. n.* (GH); Dept. Monteros, Negro Potrero, 16 February 1907, *M. Lillo* 5832 (GH); Dept. Tafí, 15 February 1924, *S. Venturi* 152 (BAB, GH); Dept. Trancas, Arroyo Ceibalito, merendero, 8 May 1981, *E. Zardini* 1381 (F); Pie de la Cuesta, 20 April 1926, *S. Venturi* 4121 (LP); La Criolla, 6 March 1912, *Rodríguez* 374 (GH); Dept. Yerba Buena, Naranjal, 13 February 1921, *Schreiter* 4120 (GH).

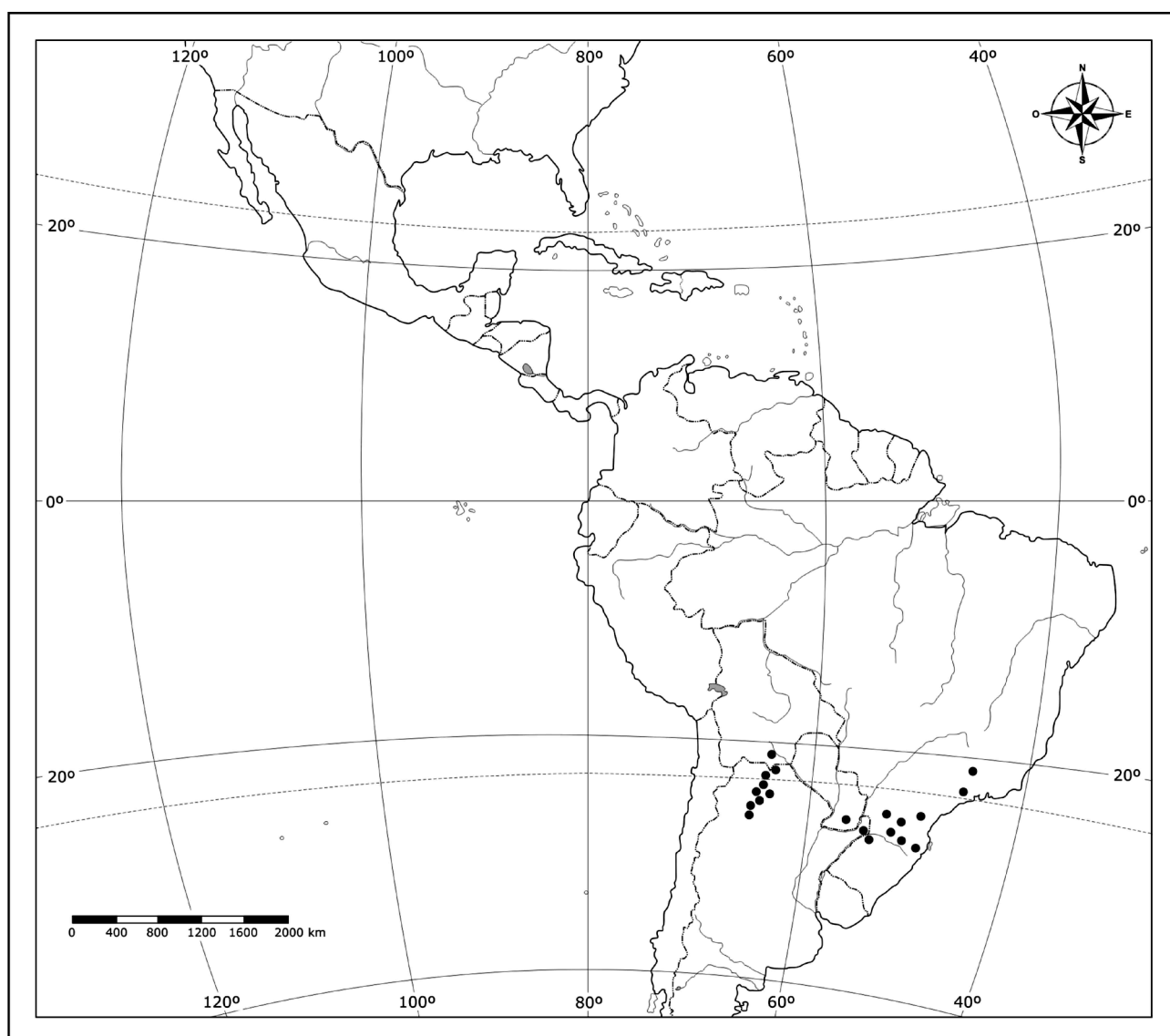


FIGURE 24. Geographical distribution of *Smalanthus macroscyphus*.

BOLIVIA. Dept. Tarija: Prov. O'Connor, 20 km antes de Entre Ríos, 21 February 1988, *R. Ehrich* 426 (S).

BRAZIL. State Paraná: Quebrada Funde, Mun. Rio Branco do Sul, 7 December 1967, *G. Hatschbach* 17808

(LP); Mun. Curitiba, Parque Rio Iguaçu, 27 December 1979, *R. Kummrow 1298* (LP); Mun. Laranjeiras do Sul, Foz de Chopim, 9 June 1968, *G. Hatschbach 19314* & *O. Guimarães 307* (LP); Ponta Grossa, 1 March 1919, *P. Dusén s.n.* (S 870027); id., 15 February 1911, *P. Dusén 11362* (S); Nord-Paraná, Gebiet des mittleren Ivahy, 24 March 1937, *G. Tessmann 6124* (G), *6127* (GH); Mun. São José dos Pinhais, Castelhanos, 19 February 1998, *J. Silva et al. 2280* (K); Fazenda Reserva, ca. 85 km SE of Guarapuava, towards Rio Iguaçu, 8 March 1967, *J. Lindeman & de Haas 4713* (F, K). State Rio Grande do Sul: Parque Est. Turvo, Tenente, Portela, 21 December 1982, *N. Matzenbacher s.n.* (ICN 53449); Ouro Verde, January 2002, *M. Sobral et al. 9514* (ICN). State Santa Catarina: Mun. São Joaquim, Ruderal, near Mantiqueira, 27 km E of São Joaquim, 16 January 1957, *L. Smith & R. Reitz 10222* (LP); São José do Cerrito, 1 February 1963, *R. Reitz 6472* (LP); Herval Velho, 27 December 1963, *R. Reitz & R. Klein 16356* (LP); Urubici, Serra do Corvo Branco, February 1996, *M. Sobral & J. Jarenkow 8055* (ICN); Lacerdópolis, Capinzal, 12 April 1963, *R. Reitz & R. Klein 14704* (LP); Rio do Meio, Lauro Müller, 20 February 1959, *R. Reitz & R. Klein 8472* (LP). State Santa Catarina: Mun. Caçador-Curitibaños, 14 km SE of Caçador, on the road to Lebon Regis (47 km), 8 February 1957, *L. Smith & R. Klein 11023* (LP). State São Paulo: Lema de Caracol, 25 February 1874, *Hillosín 1418* (LP). Without state and locality: *Burchell AA95* (GH).

PARAGUAY. Dept. Caazapá: National Park Caaguazú, 26° 05' 52"S, 55° 26' 35" W, 24 November 1997, *M. Zardini & A. Benítez 47372* (K).

Smallanthus maculatus (Cavanilles) Robinson (1978: 50).

Polymnia maculata Cavanilles (1794 [1795]: 14, t. 227). Type:—Icon. 3: t. 227. 1794 [1795] (lectotype selected by Vitali, in press; epitype: MEXICO. "Plantae Novae Hispaniae, 1787–1795–1804, *Sessé, Mocino & Maldonado s.n.*, MA 606169, selected by Vitali, in press).

Polymnia maculata var. *adenotricha* Blake (1917b: 34). Type:—GUATEMALA. Baja Verapaz: Dept. Santa Rosa, Chupadero, August 1892, *E. Heyde & E. Lux 3807* (holotype GH 11390, digital image!, isotypes G!, K!, F, M, US, digital images!).

Polymnia maculata var. *glabricaulis* Blake (1935: 313). Type:—MEXICO. Tamaulipas: Cerro Carrizo, near San José, 19 July 1930, *H. Bartlett 10508* (holotype US!, isotype MICH, digital image!).

Polymnia maculata var. *hypomalaca* Blake (1917b: 33). Type:—MEXICO. Mexico: Barranca above Santa Fe, 2590 m, 1 September 1905, *C. G. Pringle 13564* (holotype GH 11391, digital image!, isotypes G!, S!, SI!, US!).

Polymnia maculata var. *vulgaris* Blake (1917b: 33). Type:—MEXICO. Michoacán: Fields near Patzcuaro, 23 October 1890, *C. G. Pringle 3326* (lectotype here designated GH!; isolectotypes F!, G!, K!, S!).

Herbs 1–3 m tall, homophyllous, stems pubescent. Leaves opposite, petiolate, 10–34.5 cm long, lamina 7.5–23 cm wide, ovate, acute at the apex, truncate or obtuse at the base, margins irregularly lobate, mucronate, trinerved, actinodromous, pubescent on both faces; petioles 3–13.5 cm long, winged, wings uniform in width, entire or lobulate, auriculate or not auriculate at the base, the auricles discontinuous when present. Capitula 6–13 × 8–14 mm, ca. 20, arranged in corymbiform, racemiform or paniculiform cymes; peduncles 9–50 mm long, densely pubescent. Involucre campanulate to hemispherical; phyllaries arranged in 2 series, herbaceous, pubescent, outer phyllaries 8–13 × 3.5–12 mm, obovate, obtuse at the apex, inner phyllaries 5–12 × 2–10 mm, ovate or elliptic, acute at the apex. Receptacle with paleae 3–7 × 1.5–3 mm, elliptical, apex entire. True ray florets ca. 15, 1-seriate, corollas yellow, ray-limb oblong, 6–14 × 4–5 mm, apex 3-dentate, teeth equal in size, tube 1–3 mm long. Style 4–7 mm long, branches 1–2 mm long. Disc florets ca. 50, corollas yellow, tubular to campanulate, 4.5–7 mm long, lobes 0.5–1 mm long. Anthers with apical appendage ovate, subtriangular. Style 5–8 mm long, branches 1 mm long. Cypselae obovate to rounded-obovate, 3–6 × 1.5–4 mm, smooth. $n=16$ (Wells 1965). (Fig. 25).

Etymology:—From the Latin adjective *maculatus*, spotted, by the purple spots in the stems of some specimens of this species.

Distribution and ecology:—From Mexico to Panama (Fig. 26). It grows abundantly in deciduous, mixed, cloud, humid, and premontane forests, and in humid ravines, shrublands, and disturbed places such as roadsides, along railroad tracks, and cultivated fields, from sea level to 3000 m. Flowering throughout the year.

Vernacular names and uses:—Ax, árnicá, balim k'in, batzil, chocotorro, gigantón, gua-gua, ik'al, k'ail, k'ayil, margarita, mirasol, mirasol de monte, purca, tora, shti-pú (female in Maya language), tz'ibal. It has been cited as detergent (*Vovides 26*, F), the leaves in a bath as sedative for children, and against "mal de ojo" (evil eye) (*Balick et al. 2216*, GH). Some South American cultures believe that the evil eye is a look of a given person, sometimes without intention, which is able to cause headache, injury or misfortune for the person at whom it is directed for reasons of envy, dislike, or covetousness.

Notes:—The syntypes of *Polymnia maculata* var. *vulgaris* Blake are indicated as follows: MEXICO. Veracruz: Orizaba, 20 August 1891, *H. E. Seaton* 420 (syntype GH!); id., without date, *Botteri* 237 (syntype GH!); Patzcuaro, 10 October 1899, *E. Holway* 3598 (syntype GH!). GUATEMALA. Retalhuleu: San Felipe, April 1892, *J. D. Smith* 2863 (syntype G!); Alta Verapaz: Coban, January 1887, *H. von Türckheim* 1105 (syntype GH!); Coban, November 1902, *H. von Türckheim* 8427 (syntypes F!, GH!, S!); Coban, August 1906, *H. von Türckheim II* 1334 (syntypes F!, G!, GH!); Escuintla: Escuintla, March 1890, *J. Smith* 2384 (syntypes GH!, K!); Quetzaltenango: Volcán de Agua, above village of Santa María, 4 March 1916, *E. Holway* 553 (syntype GH!); Zacapa: Gualan, 20 January 1905, *C. Deam* 236 (syntype GH!); Santa Rosa: Las Cruces, October 1894, *E. Heyde & E. Lux* 6161 (syntypes G!, GH!). COSTA RICA. Puntarenas: Rio Ceibo, February 1842, *Pittier* 4923 (syntypes G!, GH!).

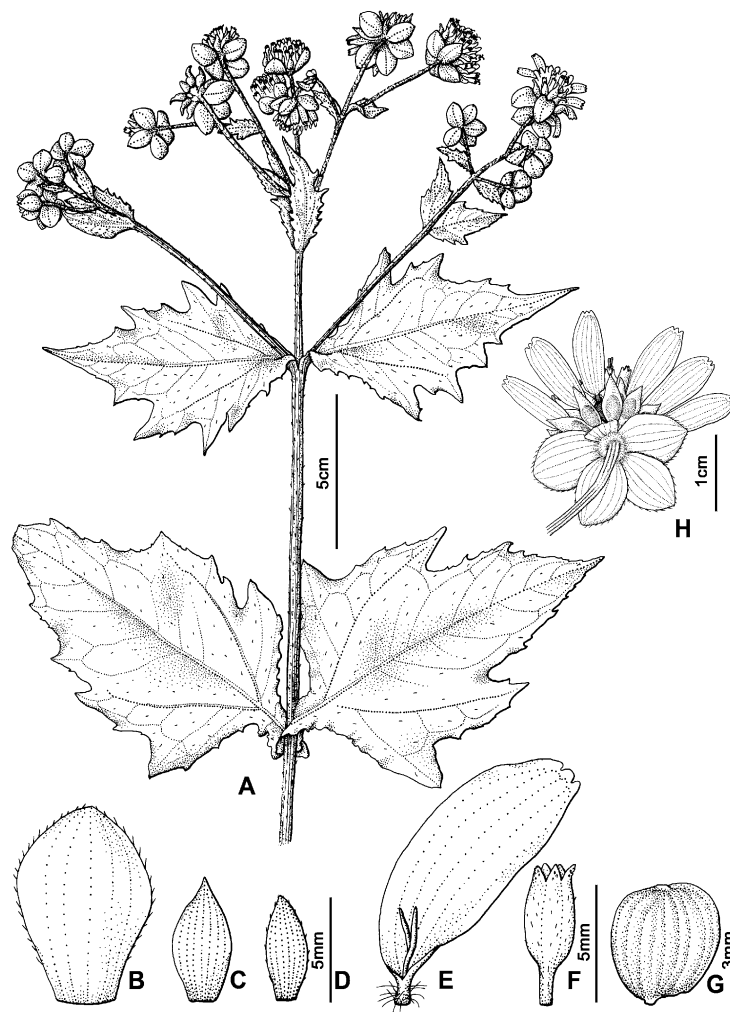


FIGURE 25. *Smallanthus maculatus* (Cavanilles) H. Robinson. **A.** Habit. **B.** Outer phyllary. **C.** Inner phyllary. **D.** Palea. **E.** Ray floret (without cypselas). **F.** Disc corolla. **G.** Cypselas. **H.** Capitulum abaxial view (*Molina* 30729, F).

Pruski (2013) considered that *Smallanthus lundelli* and *S. obscurus* are synonyms of *Smallanthus maculatus*. The three taxa are here regarded as separate entities. *Smallanthus lundelli* differs from *S. maculatus* by the petiole wings decreasing in width from the blade to the node (*vs.* wings uniform in width throughout the petiole in *S. maculatus*), inner phyllaries orbicular (*vs.* ovate or elliptical), ca. 100 disc florets per capitula (*vs.* 50). On the other hand, *Smallanthus obscurus* differs from *S. maculatus* by its lower leaves with the blade 3-partite (*vs.* irregularly lobate in *S. maculatus*), outer phyllaries ovate (*vs.* obovate), and paleae obovate with the apex irregularly dentate (*vs.* elliptical with the apex entire).

Additional specimens examined:—BELICE. Cayo District: Smokey Branch Camp, 13 May 1995, *C. Whitefoord* 9306 (F); Maccal river, bridge between Augustine and Cuevas, 7 October 1972, *J. Dwyer & R. Pippin* 10194 (F); San Antonio, 17° 05' N, 89° 01' W, 22 November 1989, *M. Balick et al.* 2216 (GH); Succotz, bordering

río Mopan, 29 September 1967, *E. Contreras* 7148 (F); Vaca, 22 February 1938, *P. Gentle* 2215 (F, GH, K); El Cayo, 30 March 1931, *H. Bartlett* 12096 (GH). Stann Creek District: Kendal, 28 June 1931, *W. Schipp* 804 (F, G, GH, K, S).

COSTA RICA. Prov. Alajuela: Entre Naranjo y San Juanilla de Naranjo, camino a San Carlos, 30 March 1963, *A. Jiménez* 555 (F, G); Zarcero, 1 October 1937, *A. Smith* 462 (F). Prov. Cartago: Río Turrialba, 19 July 1932, *H. Stork* 3233 (GH); 1–4 km W of Troya, on the road to Muñeco, bordering the río Navarro, 28 February 1981, *F. Almeda & K. Nakai* 4642 (F); volcán Irazú, along route 8, ca. 5 km N of Cartago, 18 June 1974, *R. King* 6810 (F); Cartago, December 1887, *J. Cooper* 5827 (F, GH); San Rafael de Cartago, 28 August 1892, *H. Pittier* 6993 (GH). Prov. Puntarenas: Monteverde, 17 October 1963, *A. Jiménez* 1209 (F); Pensión Quetzal, 2 km W of Monte Verde, 5 August 1981, *B. Turner & G. Turner* 15019 (F). Prov. San José: S of San Pedro, E of San José, 27 July 1961, *G. Rossbach* 3428 (GH); San José, July 1935, *M. Valerio* 1344 (F); id., 19 June 1925, *F. Solís* 246 (F); vicinity of San José, February 1924, *P. Standley* 33300 (GH); Hatillo, 4 January 1935, *F. Solís* 68 (F); San Rafael de Coronado, 20 August 1938, *J. Orozco* 266 (F); bords de chemins á La Verbena, prés Alajuelita, July 1894, *A. Tonduz* 8891 (G); bords du rio Tiliri a S. José, June 1891, *H. Pittier* 4251 (G); orillas del río Damas, en San Antonio de Desamparados, 7 November 1940, *J. León* 242 (F); Pérez Zeledón, Barú, Tinamaste, Finca de los Suizos, 9° 17' 54" N, 83° 46' 20" W, 3 December 1999, *A. Estrada & H. Binder* 2286 (K).

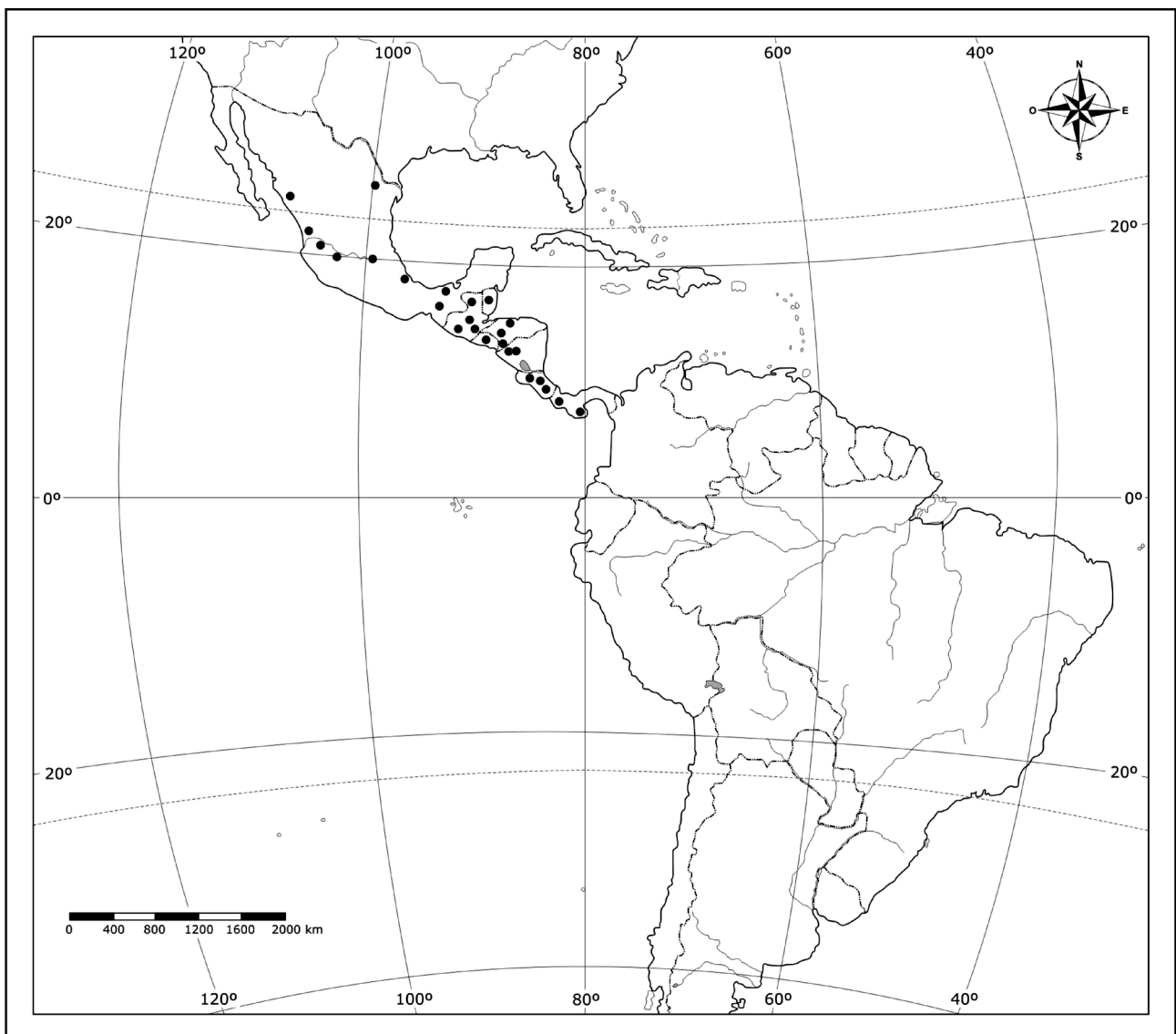


FIGURE 26. Geographical distribution of *Smalanthus maculatus*.

EL SALVADOR. Dept. Santa Ana: San José Ingenio, P. N. Montecristo, 14° 25' N, 89° 21' W, 8 September

2001, *V. Martínez s.n.* (K); Parque Nacional Montecristo, camino a Miramundo, 14° 24' N, 89° 27' W, 5 November 2002, *R. Carballo & J. Aldana 570* (K); slope of Ayeco, volcán Santa Ana, 13° 52' N, 89° 39' W, 23 April 1942, *J. Tucker 1281* (F). Dept. San Salvador: El Picacho, NE of El Boquerón, volcán San Salvador, 1 March 1968, *A. Molina R. & E. Montalvo 21838* (F). Dept. San Vicente: Volcán de San Vicente, 7–8 March 1922, *P. Standley 21498* (GH).

GUATEMALA. Dept. Alta Verapaz: Cobán, December 1912, *H. von Türckheim 4015* (F); near Cobán, 26 March–15 April 1939, *P. Standley 69260, 69485* (F); entre Cobán y Santa Cruz, 10 May 1963, *A. Molina R. 11962* (F); about 10 km S of Cobán, approx. 15° 25' N, 90° 20' W, 25 January 1969, *L. Williams et al. 40062* (F); about 10 km N of Cobán, 4 January 1973, *L. Williams et al. 42055* (F); near San Cristóbal Verapaz, 6 January 1973, *L. Williams et al. 42220* (F). Dept. Baja Verapaz: 17 miles from Salamá, on road to Cobán, Patal, 7 December 1958, *J. Hawkes et al. 1936* (F, K, S). Dept. Chimaltenango: Calderas, 25 October 1937, *J. Johnston 1103* (F); Cuilapa, 31 October 1937, *J. Johnston 1088* (F); near Finca La Alameda, near Chimaltenango, 7 December 1938, *P. Standley 59065* (F). Dept. Chiquimula: La Cumbre, old road to Quezaltepeque, 28 September 1971, *A. Molina R. & A. R. Molina 26820* (F); volcán Ipala, near Amatillo, 25 October 1939, *J. Steyermark 30499* (F); cerro Tixixí, 3–5 miles N of Jocotán, 10 November 1939, *J. Steyermark 31553* (F). Dept. Escuintla: Along railroad track, 5 km N of Escuintla, 7 August 1970, *W. Harmon & J. Dwyer 2977* (F, GH). Dept. Guatemala: San Rafael, 10 January 1915, *W. Holway 62* (GH); 10 km S of San Raimundo, 18 January 1939, *P. Standley 62889* (F); along the road to San Jose Pinula, ca. 12 km generally ENE of San Jose Pinula, 28 June 1976, *R. King & R. Renner 7141* (K); without locality, 1939 *I. Aguilar 366* (F); lake Amatitlan, 16 February 1947, *J. Brenckle 47–239* (S). Dept. Huehuetenango: Between San Martín and Todos Santos, 25 December 1895, *E. Nelson 3616* (F); Huehuetenango, 15° 19' N, 91° 28' W, 17 February 2000, *J. Castillo & A. Castillo 2315* (F); Todos los Santos, 11 September 1896, *E. Seler 2727* (GH). Dept. Izábal: Quebradas, 19–22 May 1919, *H. Pittier 8617* (GH). Dept. Jalapa: Volcán Jumay, 8 January 1908, *W. Kellerman 7701* (F); vicinity of Jalapa, 7–18 November 1940, *P. Standley 77151* (F). Dept. Jutiapa: Near San José Acatepa, 19 November 1940, *P. Standley 77567* (F). Dept. Petén: Chincila, W of Sebol road, ca. 5 km from San Luis, 11 October 1966, *E. Contreras 6378* (F); La Cumbre, Ixobobo, km 128 of Cadenas road, 14 August 1969, *E. Contreras 8938* (F); Santa Elena, en orillando el camino de Melchor de Mencor, km 75, 27 April 1970, *R. Tún Ortiz 1048* (F); camino para Poctún, km 84, lado poniente, 23 September 1970, *R. Tún Ortiz 1326* (F). Dept. Quetzaltenango: Below Fuentes Georginas, just above Zunil, 20 January 1940, *J. Steyermark 34483* (F); montaña Chicharro, volcán Santa María, 2–4 miles S of Santa María de Jesús, 17 January 1940, *J. Steyermark 34270* (F); coffee plantation of Coatepeque, 16 November 1971, *A. Molina R. 27123* (F); along old road between Finca Pirineos and Patzulín, 9 February 1941, *P. Standley 86756* (F). Dept. Quiché: Nebaj, 21 November 1934, *A. Skutch s.n.* (GH); SE of Nebaj, along road to Boquerón, 25 June–17 August 1964, *G. Proctor 25374* (F). Dept. Retalhuleu: San Felipe, 4 February 1906, *W. Kellerman 5447* (F); vicinity of Las Delicias, S of Retalhuleu, 22 February 1941, *P. Standley 88113* (F). Dept. Sacatepéquez: Volcán de Agua, S of Santa María de Jesús, 10 December 1938, *P. Standley 59505* (F); above Pastores, 23 December 1938, *P. Standley 60771* (F); volcán de Agua, camino Sta María de Jesús-Palín, 7 November 1965, *A. Molina R. 15385* (F); Volcán de Agua, 22 July? 1937, *J. Johnston 811* (F). Dept. Santa Rosa: Near Cuilapa, 20–27 November 1940, *P. Standley 77993* (F); near Cuilapilla, 23 November 1940, *P. Standley 78023* (F). Dept. Sololá: N of Lago de Atitlán, 1.4 mi. NW of Panajachel, at Puente San Buena Ventura, 24 October 1984, *M. Spooner & O. Dorado 2678* (F). Dept. Suchitepéquez: Mazatenango, 2 March 1905, *W. Kellerman 5305* (F); id., 13 February 1906, *W. Kellerman 5384* (F); near Patulul, 5 January 1939, *P. Standley 62171* (F); Mazatenango, May 1870, *G. Bernoulli 576* (G, K). Dept. Totonicapán: Near Momostenango, 21 November 1967, *A. Molina R. 21436* (F). Dept. Zacapa: Sierra de las Minas, along trail between Río Hondo and summit of mountain at Finca Alejandria, 11 October 1939, *J. Steyermark 29748* (F).

HONDURAS. Dept. Copán: Quebrada Titoror, 2 miles SW of Sta. Rita, 27 August 1975, *A. Molina R. & A. Molina 30729* (F). Dept. Atlántida: Vicinity of La Ceiba, 12 July 1938, *T. Yuncker et al. 8422* (F, GH, S); valley near San Francisco, 2 May 1970, *J. Hernández R. & M. Hernández M. 5170* (GH). Dept. Comayagua: Along trail about 6 km N of Siguatepeque, 8 April 1936, *T. Yuncker et al. 6311* (F, G, K, S); Quebrada Montañuelas, entre Trincheras y Montañuelas, 18 July 1962, *A. Molina R. 10872* (F). Dept. Cortés: Along río Lindo, Peña Blanca near Lake Yojoa, 8 August 1948, *L. Williams & A. Molina R. 14593* (GH). Dept. Choluteca: Highway 5 km between El Espino and San Marcos de Colón, 7 November 1968, *A. Molina R. 23231* (F). Dept. Intibucá: Cordillera Opalaca, between Calaveras and Pela Nariz, road to La Esperanza, 3 September 1968, *A. Molina R. 22606* (F). Dept. El Paraíso: El volcán de Monserrat, 12 August 1971, *A. Molina R. 26140* (F). Dept. Morazán: Zamorano, 1 November

1943, *J. Rodríguez* 1435 (F); Hoya Grande, 25 August 1946, *L. Williams & A. Molina R.* 10442 (F); Mt. Uyuca, in Guamil, 8 July 1948, *S. Glassman* 2173 (F); cerro de Uyuca, along trail from Las Flores toward Tatumbla, 17 August 1949, *P. Standley* 22733 (F); drainage of the río Yeguaré, at about 14° N, 87° W, 4 September 1948, *A. Molina R.* 1096 (F); La Cumbre, on mountain Lepaterique, 4 October 1970, *A. Molina R. & A. R. Molina* 25871 (F); Las Flores, Cerro de Uyuca, 20 October 1948, *P. Standley* 13319 (F); río Caparrosa, region of El Jicarito, above el Zamorano, 1 December 1949, *P. Standley* 24857 (F); Montaña Grande, entre Santa Lucía y Valle de Los Ángeles, 26 September 1950, *A. Molina R.* 3317 (F, GH). Dept. Olancho: Vicinity of Catacamas, 18–26 March 1949, *P. Standley* 18416 (F). Dept. Santa Bárbara: Along Sesecapa river, vicinity of Sta. Bárbara town, 22 August 1968, *A. Molina R.* 21993 (F). Dept. Sololá: Along quebrada Patanatic, 6 km of Panajachel, without date, *A. Molina R. & A. R. Molina* 26667 (F).

MEXICO. State Chiapas: Chiapas, etc., 1864–70, *Ghiesbreght* 577 (GH); near km post 18, ca. 12 mi. NW of Ocozocoautla, ca. 16° 55' N, 93° 30' W, 16 August 1972, *B. Webster et al.* 17910 (GH); S base of volcán Tacana, 2 km S of Cacahuatan, to the NW of Tapachula, 4 November 1970, *A. Cronquist & J. Fay* 10874 (F, GH, S); Volcán Tacana, Talquián, 3 km al N de Unión Juárez, a lo largo del camino a Chiquihuite, 18 October 1985, *J. Villaseñor et al.* 865 (F); about Ocuilapa, 21 August 1895, *E. Nelson* 3040 (GH); Acacoyagua, 29 February 1948, *E. Matuda* 17527 (F); Siltepec, 31 December 1936, *E. Matuda* 764 (GH); Municipio of Tenejapa, trail above the Sumidero of Yochib from Pokolum, in the Barrio of Sisim, the paraje of Koltol Te', 11 July 1964, *D. Breedlove* 6168 (F); Municipio of Tenejapa, W of Tenejapa center, along the trail to Paraíso, 4 August 1964, *D. Breedlove* 6839 (F); Municipio Tenejapa, paraje of Yehts 'Uk'um, 23 November 1964, *D. Breedlove* 7483 (F); Municipio Ocosingo, en Ixcán, sobre el río Lacantun, 7 September 1992, *E. Martínez et al.* 25213 (K). State Coahuila, La Casita, 22 August 1948, *Kenoyer & Crum* 3010 (GH). Federal District: El Rosario, 1 September 1936, *L. MacDaniels* 704 (F). State Hidalgo: District Zimapán, by road between highway and Encarnación, 6 August 1948, *H. Moore & C. Wood Jr.* 4363 (GH); Chapulhuacán, 27 November 1937, *L. Kenoyer* 756 (F); Municipio Huehuetla, El Mirador, 3 km en Terracería a Santa Úrsula, 2 June 1976, *A. Vovides* 26 (F); Jacala, Hidalgo-San Luis Potosí border, km 343–344, on highway below Chapulhuacán, 22 September 1949, *H. Moore* 5041 (G, GH); Dept. Huancavelica, Vallée de Cordova, 24 Dec 1865, *E. Bourgeau* 1635 (G, K). State Jalisco: Sierra del Tigre, 3 miles S of Mazamitla, 22 September 1952, *R. MacVaugh* 13169 (K). State México: 4 km al E de Chimalpa, carretera México-Toluca, vía Naucalpán, 3 September 1967, *M. Hidalgo & Anda s.n.* (F 1664060, LP); Jicaltepec, April 1941, *Liebmann* 8991/305 (F); District Temascaltepec, Nanchititla, 18 November 1933, *G. Hinton* 5227 (F, GH). State Michoacán: Loma Sta. María, prés Morelia, 4 September 1910, *G. Arsène s.n.* (F, G, GH, K); id., *G. Arsène* 5882 (GH, K, S); vicinity of Morelia, Rincón Carrieres, 17 October 1912, *G. Arsène* 8284 (F, GH); 6 km al SE de Pátzcuaro, 10 August 1986, *H. Díaz-Barriga* 2888 (F). State Michoacán: 12–14.5 miles E of Morelia, on México hwy. 15, 12 miles E of Morelia, 9 October 1966, *W. Anderson & C. Liskowski* 3912 (F). State Nayarit: Between Tuxpan and Tepic, 1 October 1955, *B. Templeton* 7538 (F); ca. 8 km NW of Tepic, 12 September 1974, *A. Cronquist & K. Becker* 11187 (GH). State Nuevo León: El Diente canyon, S of Monterrey, 19 June 1934, *F. Pennell* 16861 (GH); id., near Monterrey, July 1933, *C. Mueller & M. Mueller* 250 (F, GH). State Querétaro: Municipio de Pinal de Montes, +- 1 km al SE del Llano de San Francisco, 15 August 1990, *E. Carranza* 2647 (F). State San Luis Potosí: 20 mi. E of San Luis Potosí, on road to Rio Verde, 20 August 1957, *O. Solbrig & R. Ornduff* 4560 (G, GH); near Tancanhuitz, 2 May 1898, *E. Nelson* 4401 (F, GH); 15 km al ENE de Ciudad del Maíz, 30 June 1959, *Rzedowski* 11146 (LP); road to Jalpan, ca. 7 miles NE of Xilitla, 1 April 1961, *R. King* 4427 (F). State Sinaloa: Road from Rosario to Plomosas, about 3.5 miles W of La Rastra and 0.7 mile up the grade from the river crossing, about 33 miles W of Mexico Highway 15 at Chilillos, 8 October 1975, *J. Reveal & R. Harley* 4057 (GH, K). State Tabasco: Municipio Tacotalpa, Rancho Villa Luz, 10 May 1985, *F. Ventura* 21475 (F). State Veracruz: Santa Fe, Vallée de Mexico, 22 Jul 1865, *E. Bourgeau* 596 (G); id., 1865, *E. Bourgeau* 514 (G); near Jalapa, 30 August 1935, *L. Bailey* 356 (F); Boca del Monte, September 1908, *L. Purpus* 3024 (F, S); ca. 10 km E of Cordoba, Rte 150, 24 March 1970, *R. Long & D. Burch* 3139 (F); carretera rumbo Actopán Vista Hermosa, km 4, Jilotepec, 25 June 1976, *R. Ortega* 286 (F); Municipio Yeguatla, a 3 km adelante de Santa Rita, sierra de Chiconquiaco, 19° 48' N, 20 August 1978, *J. Calzada* 4712 (F); above San José de Gracia, 1 mile S of highway between Córdoba and Veracruz, 28 June 1977, *T. Croat* 39629 (F); Municipio de Jalapa, Palo Blanco, 14 September 1970, *F. Ventura* 2373 (F); en el Porvenir, carretera a Plan de Las Hayas, Juchique de Ferrer, 7 July 1977, *J. Calzada* 3228 (F); Sierra de los Tuxtles, 5 km by rd. S of Santecomapan (Zontecomapan), 13 km by rd. and 7 km by air NE of Catemaco, 18° 29' N, 95° 05' W, 26 July 1978, *T. Cochran et al.* 8629 (F); Mun. Poza Rica, 1 km N of Poza Rica, 20° 33' N, 97° 28' W, 23 June 1980, *B. Hansen*

& *M. Nee* 7411 (F); Córdoba, 21 July 1882, *E. Kerber* 8 (G); id., 27 July 1932, *O. Plunkett* 191 (F); id., 27 July 1935, *L. Fisher* 35356 (F, S); Municipio Huatusco, Puente Jamapa, carretera Huatusco-Córdoba, 12 September 1975, *W. Márquez & M. Yong* 372 (F); La Concepción, Puente Moisés, 25 June 1976, *M. Zola* 458 (F); Orizaba, 12 August 1938, *L. Kenoyer* 166 (F); San Andrés Tenejapa, entre San Andrés Tenejapa y El Naranjo, 15 July 1976, *V. Vázquez* 438 (F); Santiago Tuxtla, cerro Blanco al NW de Santiago Tuxtla, 9 August 1972, *J. Beaman* 6425 (F); Municipio de Teocelo, Teocelo, 7 April 1970, *F. Ventura* 840 (F). Without state: Mirador, without date, *Sartorius s.n.* (GH); without locality and date, *Schimtz* 250 (GH); Novae Hispaniae, 1787–1795–1804, *Sessé et al.* 3972 (F).

NICARAGUA. Dept. Zelaya. Área del Ocotol, río Grande, 23 April 1949, *A. Molina R.* 2338 (F, GH). Dept. Esteli: Salto de Estanzuela, río Estanzuela, ca. 6 km S of Estelí, ca. 13° 01' N, 86° 20' W, 1 October 1979, *W. Stevens et al.* 14458 (F). Dept. Jinotega: Camino entre Wiwili y El Carmen, río Coco, 13° 37' N, 85° 50' W, 2 March 1980, *M. Araquistain & P. Moreno* 1582 (F). Dept. Matagalpa: Carretera al Tuma, 10 km NE de la ciudad de Matagalpa, 8 September 1980, *M. Gasmán et al.* 731 (F).

PANAMA. Prov. Chiriquí: 6.7 miles W of Boquete, turn left 0.6 miles N of Hotel Fundadores in Boquete and follow the road through El Sato to its end, 23 July 1970, *J. Luteyn* 1498 (F); above Cerro Punta, on slope of Cerro Respinga, 8 August 1972, *J. D'Arcy & W. D'Arcy* 6529 (F); vicinity of Boquete, from Boquete to 3 miles N, 12–13 December 1966, *W. Lewis et al.* 633 (GH). Prov. Los Santos: Los Toretos, 8 October 1962, *J. Dwyer* 2419 (GH). Without country: Barba, 20 December 1940, *J. León* 458 (F).

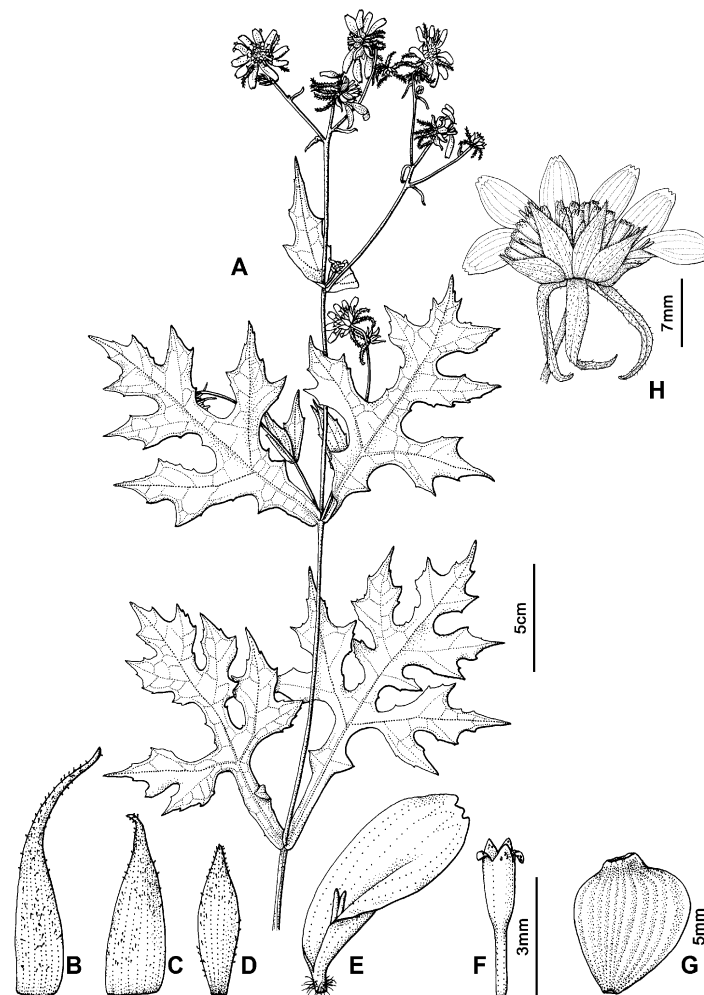


FIGURE 27. *Smallanthus mcvaughii* (J.R. Wells) H. Robinson. **A.** Habit. **B.** Outer phyllary. **C.** Inner phyllary. **D.** Palea. **E.** Ray floret (without cypsela). **F.** Disc corolla. **G.** Cypsela. **H.** Capitulum (*Panero et al.* 2875, TEX).

Smallanthus mcvaughii (Wells) Robinson (1978: 50).

Polymnia mcvaughii Wells (1967: 392). Type:—MEXICO. Jalisco: Sierra de Manantlán (30–35 km SE of Autlán), precipitous

seaward-facing slopes 1–4 km below the summit called La Cumbre, near lumber road between El Chante and Cuzalapa, and above the abandoned site of Durazno, lat. 19° 32' N, long. 104° 14' W, deciduous forest, 1500–1900 m, 22–23 March 1959, *R. McVaugh* 23189 (holotype MICH 1107632, digital image!, isotypes CAS, LL, MO, digital images!).

Herbs up to 5 m tall, homophyllous, stems glabrescent. Leaves opposite, petiolate, 20–55 cm long, lamina 5–20 cm wide, widely ovate, acute or attenuate at the apex, truncate or hastate at the base, margins pinnatisect or irregularly lobate, triplinerved, actinodromous, glabrescent; petioles 3–13 cm long, winged, wings uniform in width, lobulate, not auriculate at the base. Capitula 9–10 × 10–15 mm, ca. 10, arranged in corymbiform or racemiform cymes; peduncles 2–120 mm long, glabrescent. Involucre campanulate to hemispherical; phyllaries arranged in 2 series, herbaceous, ovate, outer phyllaries 7–17 × 2–4 mm, attenuate at the apex, inner phyllaries 5–9 × 2.5–4 mm, acute or attenuate at the apex. Receptacle with paleae 4–9 × 2–3 mm, elliptical, apex entire. True ray florets ca. 10, 1-seriate, corollas yellow, ray-limb obovate, 7–12.5 × 3.5–5 mm, apex 3-dentate, teeth equal in size, tube 2–2.5 mm long. Style 5 mm long, branches 1.5–1.8 mm long. Disc florets ca. 70, corollas yellow, tubular to campanulate, 4–9 mm long, lobes 1 mm long. Anthers with apical appendage ovate-subtriangular. Style 5 mm long, branches 0.5 mm long. Cypselae asymmetrically obovate, 4–5 × 2.5–4 mm, smooth. (Fig. 27).

Etymology:—In honor of the American botanist Roger McVaugh (1909–2009), internationally renowned for his expertise in the flora of Mexico, as well as in botanical history and nomenclature.

Distribution and ecology:—Mexico (Fig. 28). It grows inside humid forests, in shaded areas of mountain forests, in the margin of forests, and in ravines, at 150–1950 m. Flowering from November to March.

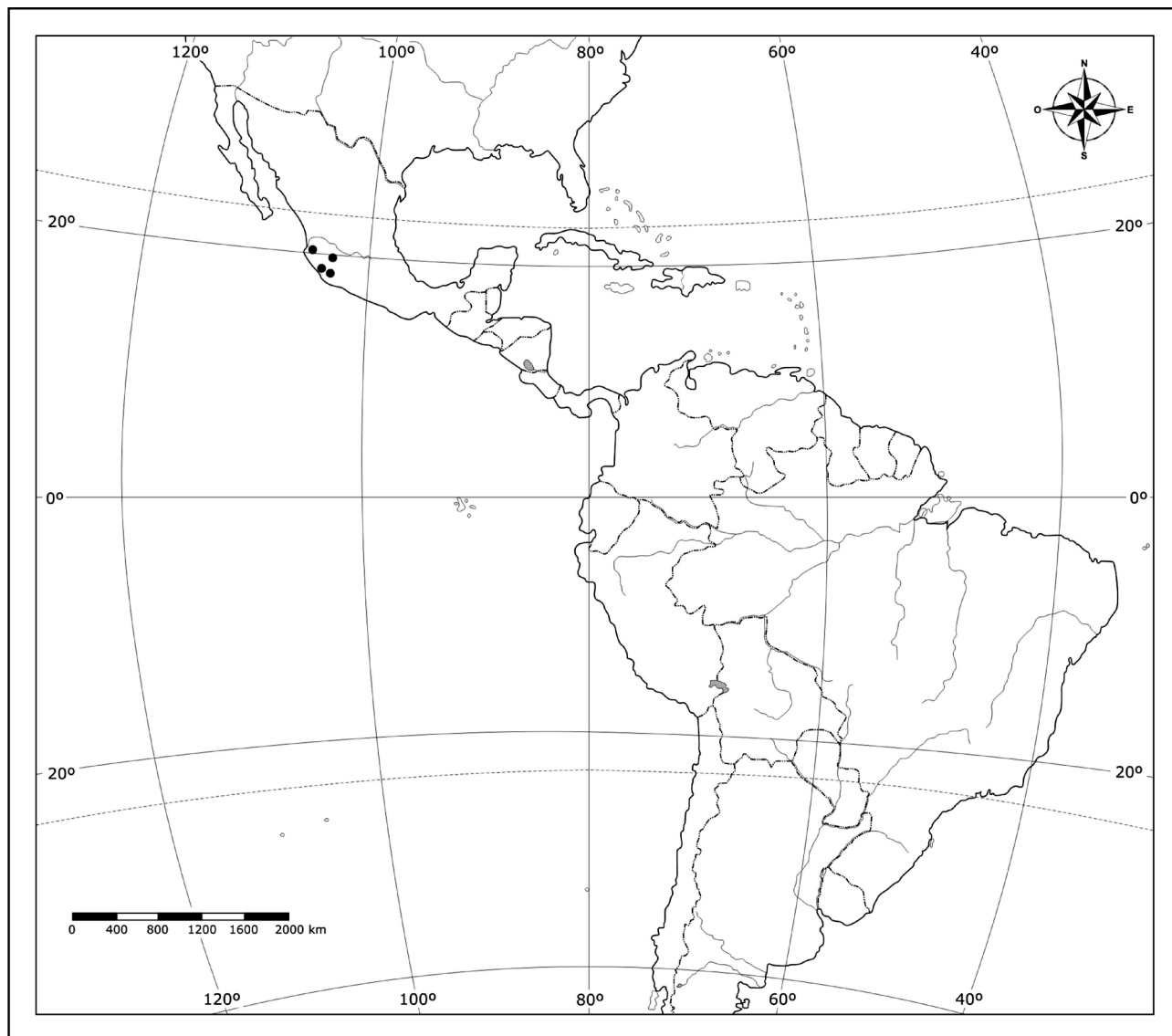


FIGURE 28. Geographical distribution of *Smalanthus mcvaughii*.

Additional specimens examined:—MEXICO. State Jalisco: Estación de Biología Las Joyas, en la Sierra de Manantlán, entrando por El Chante, carr. Autlan-El Grullo, 19° 34' N, 104° 14' W, 9 March 1992, *A. Campos et al.* 4563 (GH); at Las Joyas Field Station, 19° 35' N, 104° 15' W, 10 March 1987, *H. Iltis et al.* 29436 (F); ca. 2.5 km (air) SE of Estacion Biológica Las Joyas, 13 km (air) SSE of Ahuacapán, arroyo San Campus, NE slope of Sierra de Manantlán (occidental), 19° 34' 31" N, 104° 15' 12" W, 19 March 1989, *M. Wetter et al.* 2034 (TEX); Sierra de Manantlán, Cerro Las Capillas, a aproximadamente 2–3 hs de camino de Rincón de Manantlán, 9 March 1992, *J. Panero et al.* 2875 (TEX); headwaters of rio Mascota, 20–25 km airline, SE of Talpa de Allende, 12–13 km above (S of) El Rincón, on road to Aserradero La Cumbre, 3 April 1965, *R. McVaugh* 23456 (TEX).

Smallanthus meridensis (Steyermark) Robinson (1978: 51).

Polymnia meridensis Steyermark (1953: 667). Type:—VENEZUELA. Mérida: Rocky thickets on slopes below Chachopo, altitude 2045 m, 22 July 1944, *J. A. Steyermark* 57519 (holotype F!).

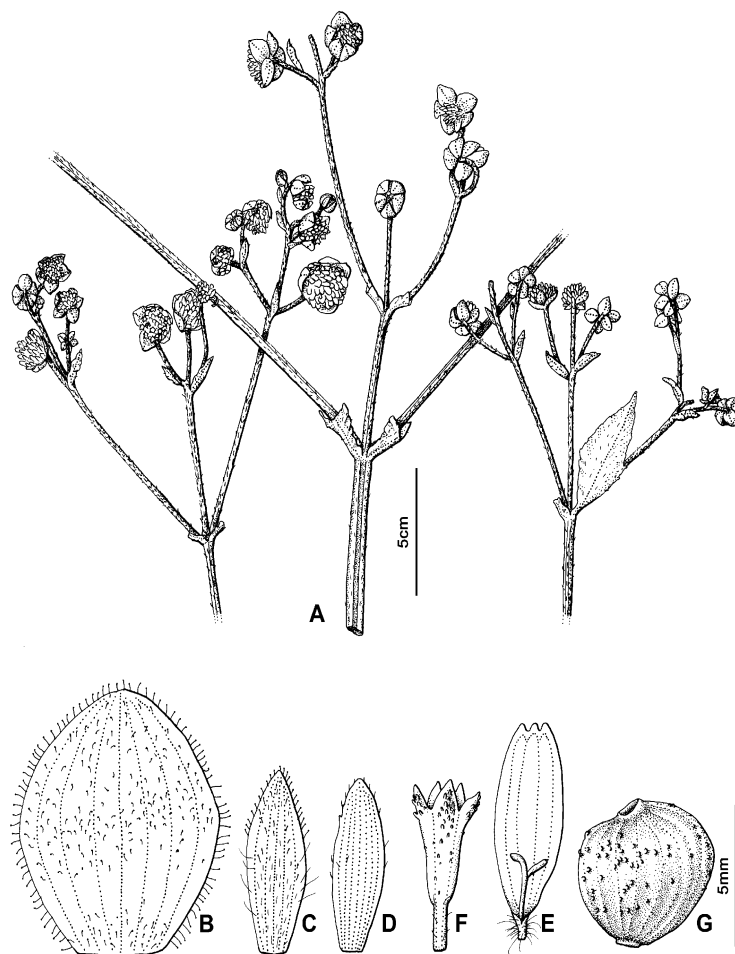


FIGURE 29. *Smallanthus meridensis* (Steyermark) H. Robinson. **A.** Capitulescence. **B.** Outer phyllary. **C.** Inner phyllary. **D.** Palea. **E.** Ray floret (without cypsela). **F.** Disc corolla. **G.** Cypsela (*Steyermark* 57519, F).

Herbs 1–1.7 m tall, homophyllous, stems pubescent. Leaves opposite, petiolate, 15–25 cm long, lamina 15–20 cm wide, ovate-subtriangular, acute at the apex, truncate or hastate at the base, margins irregularly denticulate-mucronate or mucronate, triplinerved, actinodromous, pubescent on both faces; petioles 3.5–8 cm long, winged, wings uniform in width, entire, not auriculate at the base. Capitula ca. 10 × 12 mm, ca. 15 arranged in corymbiform cymes; peduncles 6–20 mm long, densely pubescent. Involucre hemispherical; phyllaries arranged in 2 series, herbaceous, outer phyllaries 7–13 × 5–12 mm, ovate, acute or obtuse at the apex, inner phyllaries 6.5–7 × 2.5–3.5 mm, ovate to elliptic, acute at the apex. Receptacle with paleae oblong-lanceolate, 5–7 × 1.5–2 mm, apex entire.

True ray florets ca. 10, 1-seriate, corollas yellow, ray-limb ovate to elliptic, 6–12 × 2.5–3 mm, apex 3-dentate, teeth equal in size, tube 1 mm long. Style 3–5 mm long, branches 1–2 mm long. Disc florets ca. 50, corollas pale yellow, tubular to campanulate, 5–8 mm long, lobes 1 mm long. Anthers with apical appendage ovate. Style 5–6 mm long, branches 1.5 mm long. Cypselae obovate, 2–5 × 2–3 mm, smooth or irregularly verrucate. (Fig. 29).

Etymology:—For the state of Mérida, Venezuela, the area where the type specimen was collected.

Distribution and ecology:—Venezuela (Fig. 30). It grows in rocky slopes, at 2500–3100 m. Flowering from July to September.

Vernacular names and uses:—Escorzonera. Medicinal (*Aristeguieta 2484*, F).

Notes:—See Notes under *S. cocuyensis*.

Additional specimens examined:—VENEZUELA. State Mérida: La Carbonera, September 1956, *L. Aristeguieta 2484* (F).

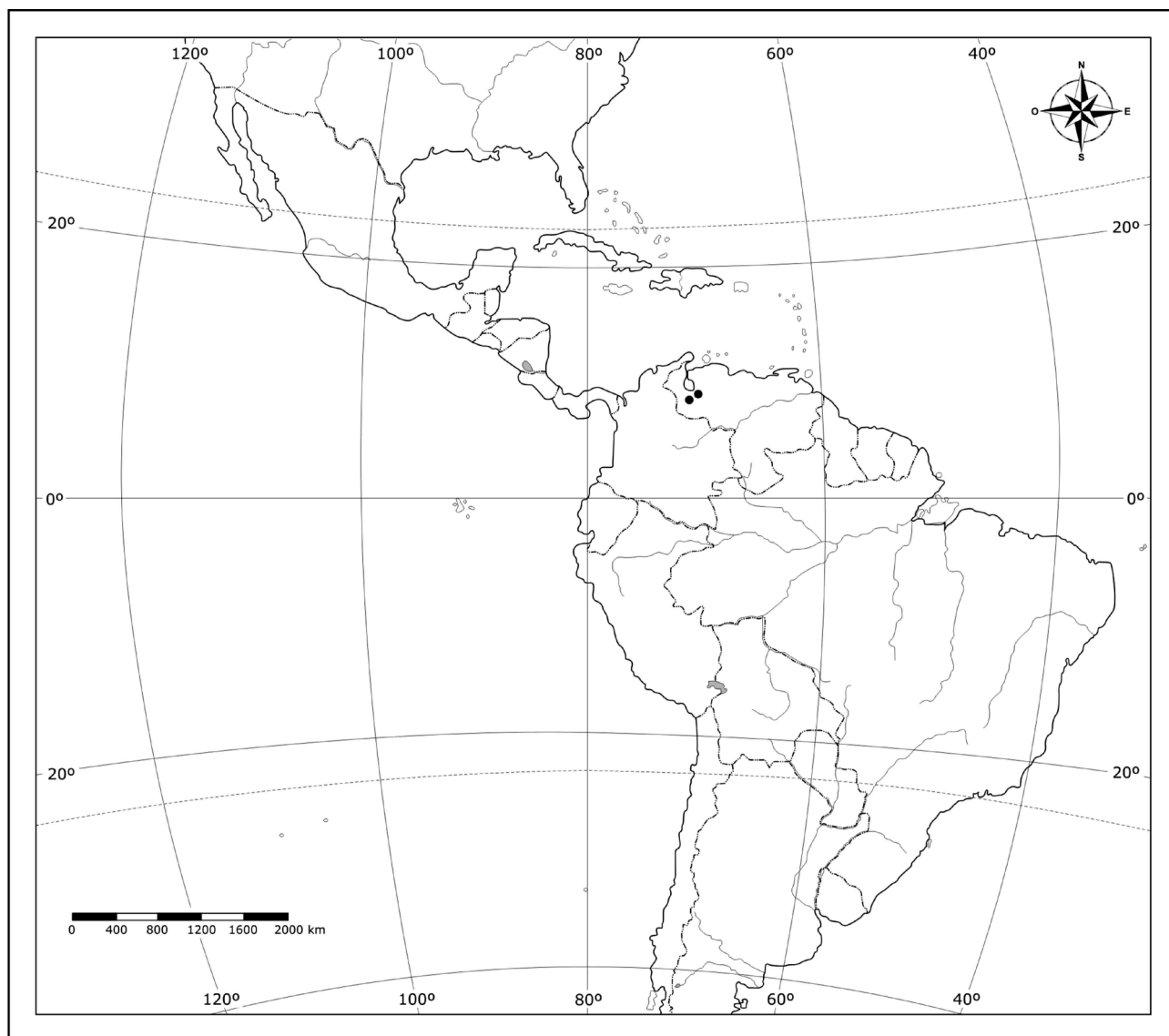


FIGURE 30. Geographical distribution of *Smallanthus meridensis*.

Smallanthus microcephalus (Hieronymus) Robinson (1978: 51).

Polymnia microcephala Hieronymus (1900: 33). Type:—ECUADOR. Chimborazo: Crescit in valle Pallatanga, alt. s. m. 2000 m., *A. Sodiro 24/2* (lectotype here designated US 128397, digital image!, epitype here designated photograph F n. 15160!).

Polymnia lehmannii Hieronymus (1901: 599). Type:—ECUADOR. Without locality, 1901, *F. C. Lehmann 4895* (lectotype here designated US 128392 digital image!).

Shrubs 3–7 m tall, homophyllous, stems pubescent. Leaves opposite, occasionally verticillate, 13–30 cm long, lamina 6–20 cm wide, petiolate, ovate, acute at the apex, truncate or obtuse at the base, margins denticulate-mucronate, triplinerved, acrodromous, pubescent on both faces; petioles 3–9 cm long, winged, wings uniform in width, entire, not auriculate at the base. Capitula 4–6 × 4–5 mm, ca. 50 arranged in corymbiform or paniculiform cymes; peduncles 10–40 mm long, glabrescent. Involucre campanulate to hemispherical; phyllaries arranged in 2 series, herbaceous, ovate, acute at the apex, outer phyllaries 3–6 × 2 mm, inner phyllaries 3–5 × 2 mm. Receptacle with paleae obovate, 2–3 × 0.5–1 mm, trifid at the apex with the central tooth longer. True ray florets 10–15, 1-seriate, corollas yellow, ray-limb oblong or elliptic, 7–8 × 3–4.3 mm, apex 3-dentate, teeth equal in size, tube 1 mm long. Style 2 mm long, branches 1.3 mm long. Disc florets ca. 50, corollas yellow, campanulate, 2.5–3 mm long, lobes 0.5 mm long. Anthers with apical appendage ovate. Style 2 mm long, branches 0.5 mm long. Cypselae obovate, 1.5–3 × 1 mm, smooth. $n=27-30$ (Robinson *et al.* 1981). (Fig. 31).

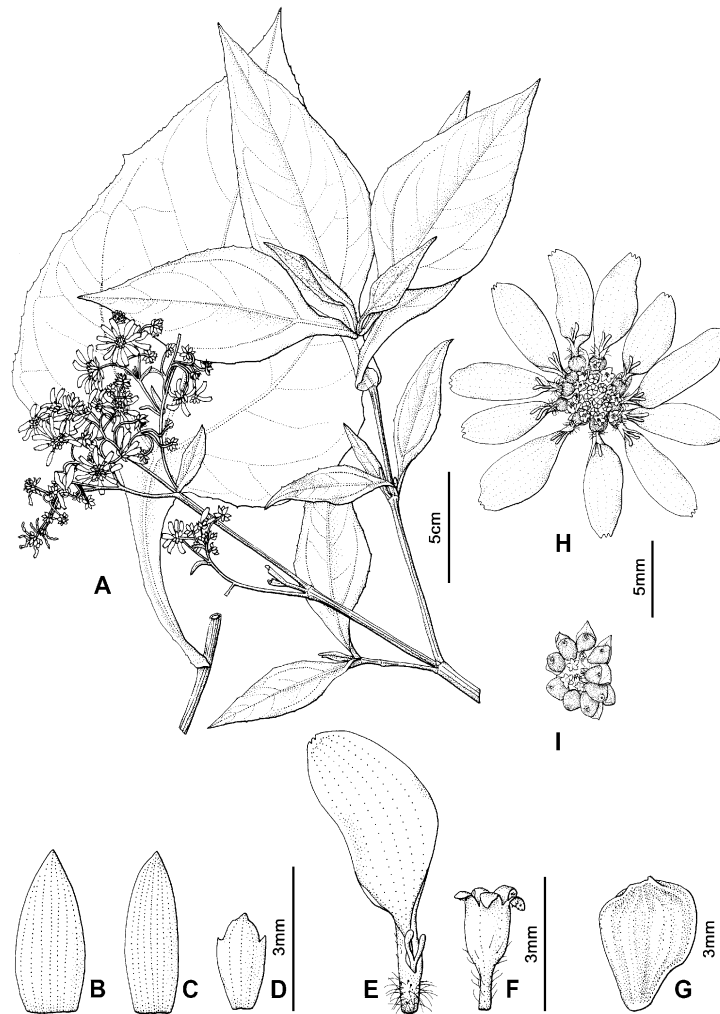


FIGURE 31. *Smallanthus microcephalus* (Hieronymus) H. Robinson. **A.** Habit. **B.** Outer phyllary. **C.** Inner phyllary. **D.** Palea. **E.** Ray floret (without cypselae). **F.** Disc corolla. **G.** Cypselae. **H.** Capitulum. **I.** Detail of the capitulum without the ray corollas (Panero & Clark 2906, TEX).

Etymology:—From the Latin *micro*, small, and *cephalus*, headed, by the small size of the capitula of the plants of this species.

Distribution and ecology:—Ecuador and northern Peru (Fig. 32). It grows in disturbed places and in the subpáramo, a transitional zone between the Páramo and the Andean forest, between 2000–3000 m. Flowering from January to July.

Vernacular names:—Tucte.

Notes:—The original holotype at B was destroyed during The World War II (Hiepko 1987). According to Art. 9.2 of the ICN (McNeill *et al.* 2012) we designate here the specimen at US as the lectotype of *Polymnia*

microcephala. The specimen at US is a fragment, thus according to Art. 9.8 we also designate as epitype the photograph of the destroyed holotype at B preserved in the Field Museum (number 15160).

Additional specimens examined:—ECUADOR. Prov. Cañar: 2–6 km NE of Pindilíg toward Rivera, ca. 2° 36' S, 78° 49' W, 19 January 1985, *J. Luteyn & E. Cotton 11133* (F); Cañar border, between Santa Rosa and Joyagshi, 6 July 1945, *W. Camp 4033* (S). Prov. Chimborazo: 13.8 km N of southernmost entrance of Huigra, along the Pan American Highway on road to Riobamba, 3 July 1992, *J. Panero & B. Clark 2906* (TEX).

PERU. Dept. Ancash: Prov. Recuay, carretera Pativilca-Conococha, 27 May 1970, *A. López M. et al. 7608* (LP). Dept. Cajamarca: Prov. Contumazá, El Molino (Cascas-Contumazá), 31 May 1990, *A. Sagástegui et al. 14271* (TEX); Molino de Singarrán (Cascas), 11 June 1981, *A. Sagástegui et al. 9973* (F); without locality: 1909–1014, *A. Weberbauer 5557* (F). Dept. Lima: Huamantanga, without date, *H. Pavon s.n.* (G 189322).

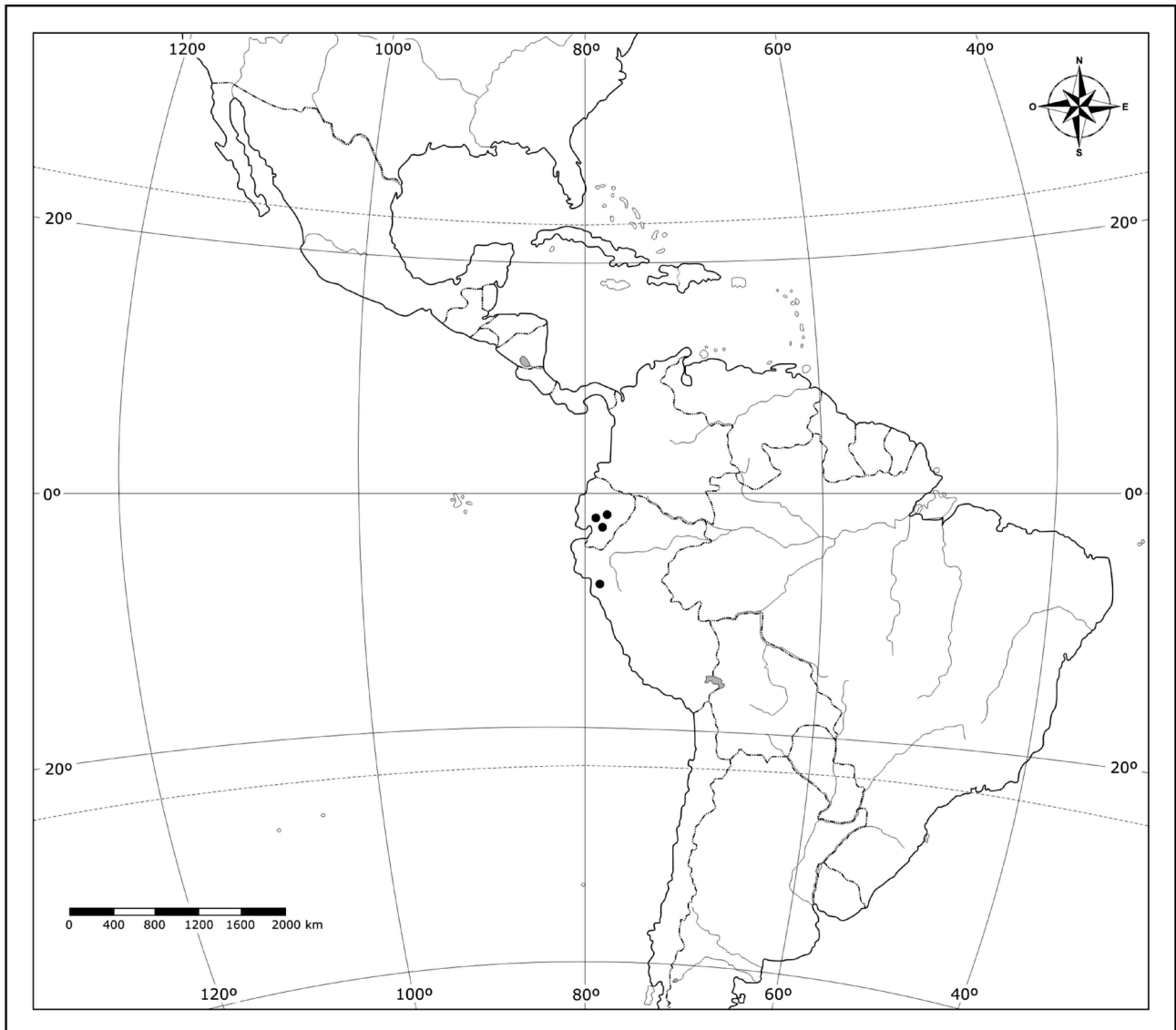


FIGURE 32. Geographical distribution of *Smallanthus microcephalus*.

Smallanthus oaxacanus (Schultz Bipontinus ex Klatt) Robinson (1978: 51).

Polymnia oaxacana Schultz Bipontinus ex Klatt (1887: 89). Type:—MEXICO. Oaxaca:Trapiche de la Concepción, without date, *F. M. Liebmann 387, Pl. Mex. 8994* (lectotype here designated C 10007790, digital image!, isolectotypes C 10007789, C 10007788, F, GH, US, digital images!).

Polymnia nelsonii Greenman (1903: 99). Type:—MEXICO. Chiapas: Near San Cristóbal de Las Casas, alt. 2150–2450 m, 18 September 1895, *E. W. Nelson 3221a* (lectotype designated here US 128398 [233061] digital image!; isolectotype GH 11392 digital image!).

Herbs 0.5–2 m tall, homophyllous or heterophyllous, stems pubescent. Leaves opposite, petiolate, acute or attenuate at the apex, margins mucronate, pubescent on both faces, petioles winged, wings uniform in width, entire, auriculate or not auriculate at the base, the auricles, when present, discontinuous with the opposite leaf; lower leaves 9.5–26 cm long, lamina 5–19 cm wide, widely ovate, truncate or hastate at the base, margins pinnatisect, trinerved, actinodromous, petioles 3.5–11 cm long; upper leaves 5.5–13 cm long, lamina 2–7 cm wide, ovate to narrowly ovate, obtuse at the base, margins entire, triplinerved, acrodromous, petiole 1.3–4 cm long. Capitula 5–10 × 7–10 mm, 3–10 arranged in racemiform cymes; peduncles 8–100 mm long, pubescent. Involucre campanulate to hemispherical; phyllaries arranged in 2 series, herbaceous, ovate, outer phyllaries 5–12 × 2.5–6 mm long, acute at the apex, inner phyllaries 5–10 × 1.5–3 mm, attenuate at the apex. Receptacle with paleae 4–6 × 1 mm, oblong, apex entire. True ray florets ca. 12, 1-seriate, corollas orange, ray-limb obovate to elliptic, 8–12 × 2–4 mm, apex 3-dentate, teeth equal in size, tube 1 mm long. Style 4–5 mm long, branches 1–2 mm. Disc florets ca. 30, corollas orange, tubular, 5–8 mm long, lobes 1–1.5 mm long. Anthers with apical appendage ovate. Style 5.5–8 mm long, branches ca. 0.7 mm long. Cypselae obovate, 2–3.5 × 1.2–2 mm, smooth or irregularly verrucate. $n \approx 20$ (Wells 1965). (Fig. 33).

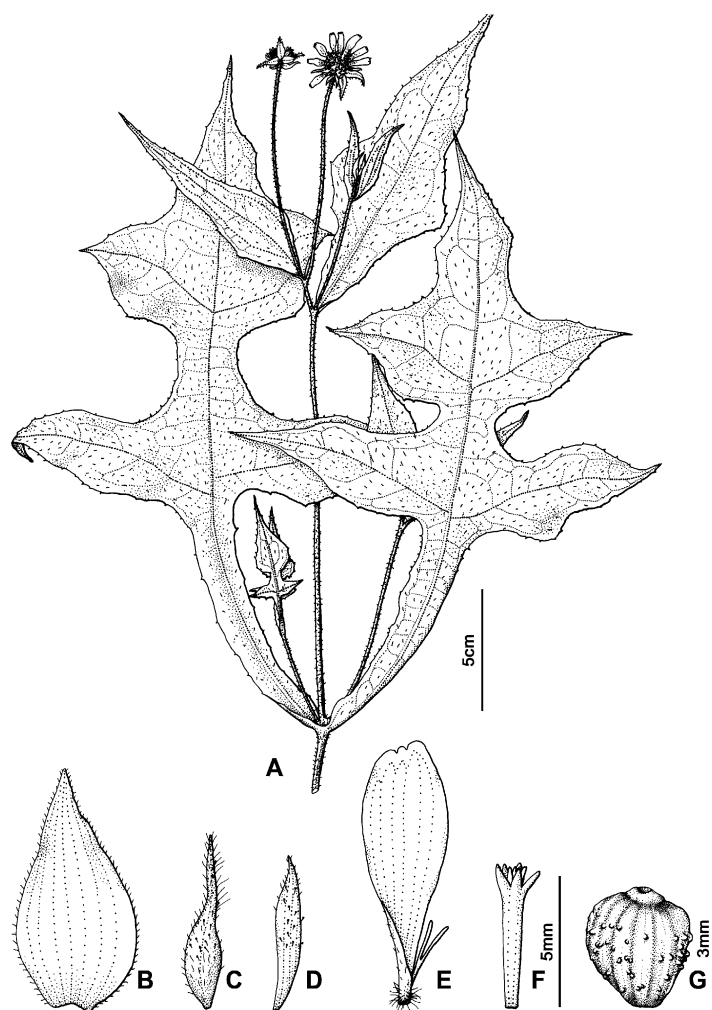


FIGURE 33. *Smallanthus oxacanus* (Schultz Bipontinus ex Klatt) H. Robinson. **A.** Habit. **B.** Outer phyllary. **C.** Inner phyllary. **D.** Palea. **E.** Ray floret (without cypselae). **F.** Disc floret (without ovary). **G.** Cypselae (*Molina 10854*, F).

Etymology:—For the Mexican state of Oaxaca, where the type specimen was found, in the hacienda Trapiche de la Concepción.

Distribution and ecology:—Guatemala, Honduras, and Southern Mexico (Fig. 34). It grows abundantly in humid subtropical forests and shrublands, hill slopes, stream margins and disturbed places such as roadsides, between 800–2000 m. Flowering from July to September.

Vernacular names:—Cambray.

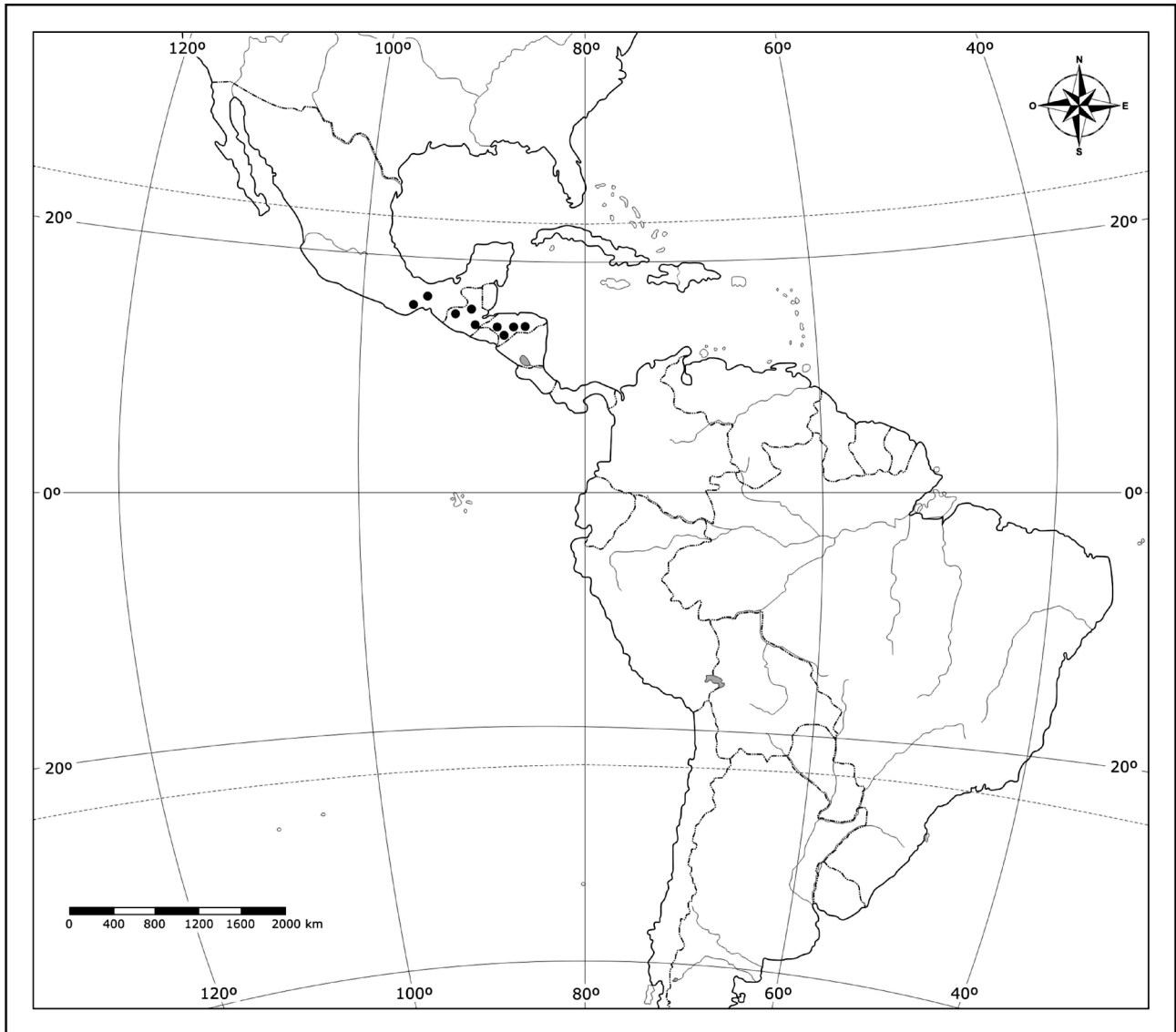


FIGURE 34. Geographical distribution of *Smalanthus oxacanus*.

Notes:—Stafleu & Cowan (1979) indicate that Klatt’s herbarium was sold to about 120 botanists. Solbrig (1965) assigned to GH the Klatt’s types of Asteraceae. The specimen *Liebmann* 387 at GH is a small leaf fragment accompanied by a drawing of a complete plant with a stamp saying “Klatt Herbarium”. From our point of view, it is unlikely that the small fragment at GH is the holotype on which Klatt based his description. On the other hand, there is a specimen at US that fits exactly with the drawing at GH. Pruski (2013) indicated that the holotype of *Polymnia oxacana* is at C, although there are three sheets in that herbarium. We designate here a lectotype to clarify the confused typification of this name, by selecting the specimen at C (number 10007790). This specimen allows the correct identification of the species and also has the label saying “Herb. Hort. Bot. Hafn.” as indicated in the protologue.

The labels of most specimens analyzed describe an orange color for the disc and ray florets of *Smalanthus oxacanus*. Pruski (2013) mentioned that this color, unusual for the genus, could be related to a different pollination syndrome regarding the other species of *Smalanthus*. In addition, Wells (1965) suggested that the corolla color in this species would turn into violet or purple in herbarium specimens.

See also Notes under *S. obscurus*.

Additional specimens examined:—GUATEMALA. Dept. Alta Verapaz: Cobán, May 1886, *H. von Türckheim* 187 (F, GH); id., August 1907, *H. von Türckheim II* 1494 (F, G, GH, S), 1919, *H. Johnson* 20 (GH); NW de Tactic, 6 km a Estor, 15 May 1963, *A. Molina R.* & *A. R. Molina* 12330 (F); near La Presa, about 6–8 km SE of

Cobán +- 15° 28' N, 90° 17' W, 29 January 1969, *L. Williams et al.* 40308 (F); near San Juan Chamelco, 13 April 1941, *P. Standley* 92502 (F); id., 15 May 1963, *P. Standley* 12330 (F); near San Cristóbal Verapaz, 6 January 1973, *L. Williams et al.* 42223 (F); city limits of San Cristóbal Verapaz, 24 June 1976, *R. King & R. Renner* 7109 (K). Dept. Baja Verapaz: 16 miles from Salamá, on road to Cobán, Patal, 11 November 1958, *J. Hawkes et al.* 1932 (F, S). Dept. Chiquimula: Quebrada Resimiento, 4 km N of Esquipulas, 27 September 1971, *A. Molina R. & A. R. Molina* 26794 (F). Dept. Huehuetenango: Trail between Democracia and Santa Ana Hista, Sierra de los Cuchumatanes, 5 August 1942, *J. Steyermark* 51306 (F, G, GH); id., 26 August 1942, *J. Steyermark* 51309 (F). Dept. Quiché: Without locality, 1942, *J. Aguilar* 1193 (F).

HONDURAS. Dept. Choluteca: Mountain above Suyapa, 26 September 1969, *F. Barkley* 39547 (GH). Dept. Comayagua: Near El Achote, above the plains of Siguatepeque, 21 July 1936, *T. Yuncker et al.* 6000 (G, GH, S); Barranco de Trincheras, 29 August 1955, *A. Molina* 5815 (F); id., 8 August 1948, *L. Williams & A. Molina* 14665 (F, GH); Barranco Trincheras, 20 km N de Siguatepeque, 8 July 1962, *A. Molina* 10854 (F). Dept. El Paraíso: Near Piedra Herrada, 11 September 1949, *L. Williams* 15973 (F). Dept. Intibuca: Sierra Opalaca, 13 miles from Esperanza on road to Siguatepeque, Pela Nariz, 26 November 1958, *J. Hawkes et al.* 2083 (F, G, K, S); Cordillera Opalaca, between Calaveras and Pela Nariz, road to La Esperanza, 3 September 1968, *A. Molina* 22605 (F). Dept. Morazán: Uyuca, 9 September 1943, *J. Rodríguez* 804 (F); about 3 miles W of Zamorano, 26 July 1946, *L. Williams & A. Molina* 10151 (F, GH); cerro de Uyuca, 22 February 1947, *P. Standley* 4217 (F); Piedra Herrada, 26 July 1947, *A. Molina* 423 (F, GH); Piedra Herrada, cerro de Uyuca, 7 August 1947, *P. Standley* 12001 (F); Mt. Uyuca, 5 July 1948, *S. Glassman* 1857 (F, GH); along and near Río Agua Amarilla, above El Zamorano, October–November 1948, *P. Standley* 12753 (F); La Montañita, 18 November 1948, *P. Standley* 14781 (F); id., 28 July 1946, *L. Williams & A. Molina* 10160 (F); Cerro de Uyuca, trail between Las Flores and La Labranza, 30 June 1949, *P. Standley* 20568 (F); cerro de Uyuca, La Labranza and vicinity, 2 July 1949, *P. Standley* 20707 (F); Mt. Uyuca, entre Quebrada Granadillo y Las Flores, 27 July 1950, *A. Molina* 2749 (GH, F); caserío de Agua Amarilla, along and near Río Agua Amarilla, above El Zamorano, 8 September 1950, *P. Standley* 26586 (F, GH); Montaña Grande, entre Santa Lucía y Valle de Ángeles, 26 September 1950, *A. Molina* 3325 (F, GH); montaña Uyuca, drainage of Río Yeguaré, at ca. 14° N, 87° W, 28 August 1951, *A. Molina* 4093 (F, GH); Montaña Uyuca, 3 August 1960, *A. Molina* 10011 (F, GH); faldas de montaña Uyuca, 19 July 1963, *A. Molina* 12793 (F); entre Monte Oscuro y Cuesta de Los Muertos, 14 July 1964, *A. Molina* 14515 (F); along Agua Amarilla creek, 5 km N of El Zamorano, 24 August 1971, *A. Molina* 26266 (F). Dept. Ocotepeque: Cordillera Merendón, 10 km from Nueva Ocotepeque, road to El Portillo, 26 August 1968, *A. Molina* 22225 (F); San Rafael Las Matarras creek, 6 miles NE of Ocotepeque, 1 September 1975, *A. Molina & A. Molina* 30971 (F).

MEXICO. State Chiapas: Hacienda Monserrate, September 1923, *C. Purpus* 9102 (GH); Chiapas, without date, *Ghiesbrecht* 106 (GH).

Smallanthus obscurus Turner (1988: 406). Type:—MEXICO. Oaxaca: Mpio. San Cristobal, Las Casas, along road to Chanal, 16–20 Km E of Chilil, 2380 m, 10 November 1976, *D. F. Breedlove* 41387 (*sphalm.* 42387) (holotype TEX!, isotypes CAS, MEXU, MO, digital images!).

Herbs 1–2 m tall, heterophyllous, stems pubescent. Leaves opposite, petiolate, acute at the apex, truncate or hastate at the base, margins irregularly dentate, mucronate, trinerved, actinodromous, pubescent on both faces, petioles winged, wings uniform in width, not auriculate at the base; lower leaves 12–25 cm long, lamina 8–20 cm wide, widely ovate, 3-partite, petioles 4–10 cm, wing margins lobulate; upper leaves 6–8 cm long, lamina 3–5 cm wide, ovate-subtriangular, irregularly lobulate, petiole 1–3 cm long, wings irregularly dentate. Capitula 10–17 × 12–14 mm, up to three arranged in cymes; peduncles 40–70 mm long, pubescent. Involucre campanulate to hemispherical; phyllaries arranged in 2 series, herbaceous, ovate, outer phyllaries 8–10 × 5–7 mm, acute at the apex, inner phyllaries 7–10 × 3–4 mm, attenuate at the apex. Receptacle with paleae 5–6 × 1.5–3 mm, obovate, apex irregularly dentate. True ray florets ca. 14, 1-seriate, corollas yellow, ray-limb elliptic, 8–13 × 3.3–4 mm, apex 3-dentate, teeth equal in length, tube ca. 2.5 mm long. Style 6 mm long, branches 2.3 mm long. Disc florets ca. 50, corollas yellow, tubular to campanulate, 6–7 mm long, lobes 1 mm long. Anthers with apical appendage ovate. Style ca. 3.5 mm long, branches 0.6 mm long. Cypselae obovate or rounded-obovate, 3.5–4.5 × 3–4 mm, smooth. n=16 (Wells 1965). (Fig. 35).

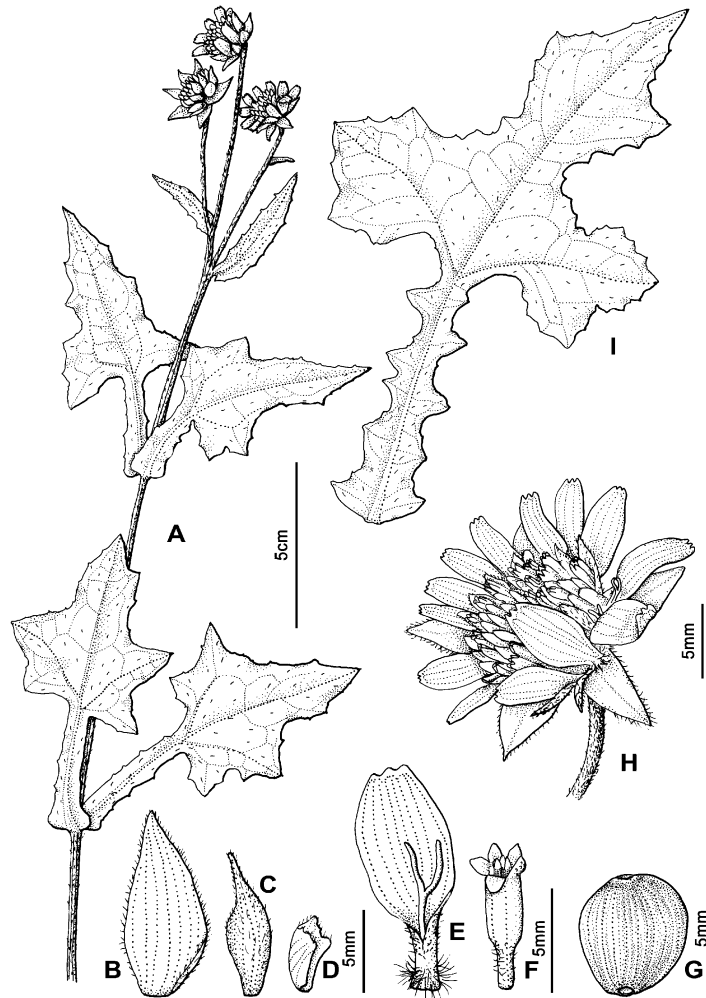


FIGURE 35. *Smalanthus obscurus* B.L. Turner. **A.** Habit. **B.** Outer phyllary. **C.** Inner phyllary. **D.** Palea. **E.** Ray floret (without cypselum). **F.** Disc floret (without ovary). **G.** Cypselum. **H.** Capitulum. **I.** Leaf (*Breedlove 41387*, TEX).

Etymology:—From the Latin *obscurus*, dark, indistinct, probably due to the brownish and reddish stems observed by the author of the species name.

Distribution and ecology:—Mexico (Fig. 36). This species grows in rocky slopes, at ca. 2300 m. Flowering from July to November.

Notes:—*Smalanthus obscurus*, *S. oaxacanus*, *S. putlanus*, and *S. uvedalius* apparently constitute a species complex with similar morphology and overlapping distribution (southern Mexico) that would allow potential mutual hybridization. Turner (1988) considered that *S. obscurus* shares features with *S. oaxacanus* and *S. uvedalius*, and is perhaps an ancestral hybrid derivative of these two species. We also observed several morphological similarities between *S. obscurus* and *S. putlanus*. Further genetic studies are required to assess hybridization processes which apparently occurred in *Smalanthus* (Grau & Rea 1997).

The protologue indicates by mistake “*Breedlove 42387*” as the type specimen of *S. obscurus* (Turner 1988). However, the labels of the type specimens indicate “*Breedlove 41387*”.

See also Notes under *S. maculatus*.

Additional specimens examined:—MEXICO. State Chiapas: Municipio of Teopisca, near ranch house on the S edge of Teopisca, 13 October 1965, *D. Breedlove & P. Raven 13091* (F). State Jalisco: Chapala, 1893, without leg. (F 354699). State Guanajuato: Xichú road, 20 August 1947, *L. Kenoyer 2226* (GH).

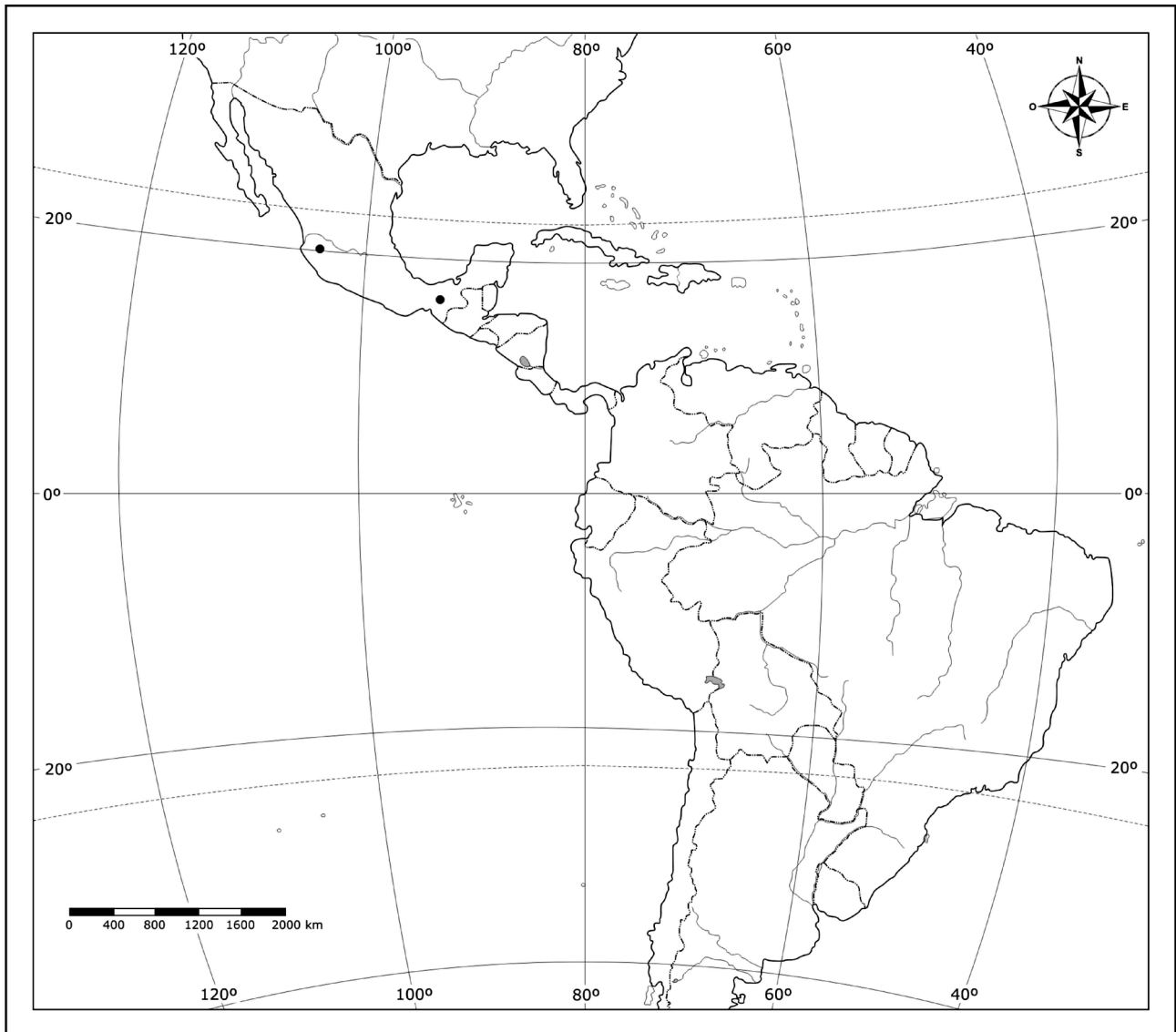


FIGURE 36. Geographical distribution of *Smalanthus obscurus*.

Smalanthus parviceps (Blake) Robinson (1978: 51).

Polymnia parviceps Blake (1924: 604). Type:—PERU. Cusco: Torontoy, Urubamba Valley, altitude about 2400 meters, 20 May 1915, *O. F. Cook & G. B. Gilbert 818* (holotype US 128401, digital image!).

Herbs 2–7 m tall, homophyllous, stems glabrescent. Leaves opposite, petiolate, 10–40 cm long, lamina 4–19.5 cm wide, ovate, acute at the apex, obtuse at the base, margins irregularly dentate, triplinerved, acrodromous, glabrescent; petioles 2.5–14.5 cm long, winged, wings uniform in width, entire, auriculate at the base, the auricles discontinuous with the opposite leaf. Capitula 5–7 × 6–8 mm, ca. 100 arranged in corymbiform cymes; peduncles 3–20 mm long, pubescent. Involucre campanulate to hemispherical; phyllaries arranged in 2 series, herbaceous, ovate, acute at the apex, outer phyllaries 4–5 × 1.8–2.5 mm, inner phyllaries 2–4 × 2–4 mm. Receptacle with paleae 2.8–4 × 2 mm, obovate, apex entire. True ray florets ca. 10, 1-seriate, corollas yellow, ray-limb oblong, 2–7 × 2–3 mm, apex 3-dentate, teeth equal in size, tube 1–3 mm long. Style 4 mm long, branches 0.7 mm long. Disc florets ca. 30, corollas yellow, campanulate, 3–10 mm long, lobes 0.6–0.7 mm long. Anthers with apical appendage ovate to subtriangular. Style ca. 2.3 mm long, branches 0.5 mm long. Cypselae obovate, 1.5–3 × 1–2 mm, smooth. (Fig. 37).



FIGURE 37. *Smallanthus parviceps* (S.F. Blake) H. Robinson. **A.** Habit. **B.** Outer phyllary. **C.** Inner phyllary. **D.** Palea. **E.** Ray floret (without cypsela). **F.** Disc floret (without ovary). **G.** Cypsela (*Herrera 1480*, GH).

Etymology:—From the Latin *parvus*, little, and *ceps*, from *caput*, head, by the small size of the capitula of this species.

Distribution and ecology:—Northern Bolivia and Peru (Fig. 38). This species grows in open, shrubby hills, ravines and river banks, between 1000–3600 m. Flowering from January to July.

Vernacular names and uses:—Jareta, shita, wila-wila, yareta, yarita. Medicinal (*Herrera 1480*, GH), and used to make ‘llipta’ to chew with coca (*Johns 81–54*, F).

Additional specimens examined:—BOLIVIA. Dept. La Paz: Prov. Larecaja, Sorata, 21 April 1920, *E. Holway & M. Holway 558* (GH); Prov. Murillo, valle de Zongo, del lago de Zongo bajando 30 km, 3 March 1990, *S. Beck 17529* (SI).

PERU. Dept. Ancash: Prov. Bologna, cerca a Chiquián, 15 May 1950, *R. Ferreyra 7456* (LP). Dept. Apurimac: Prov. Abancay, Ampuy, 12 February 1939, *H. Stork et al. 10600* (F, GH). Dept. Ayacucho: Pampalca, between Huanta and río Apurimac, 4, 5, 18 May 1929, *E. Killip & A. Smith 22268* (F). Dept. Cuzco: Prov. Quispicanchis, Hda. Tio, Mascapata, 1 January 1943, *C. Vargas C. 3065* (LP); Prov. Calca, Vilcabamba, 7 January 1944, *C. Vargas C. 3972* (LP); Cusco, 15 March 1927, *F. Herrera 1480* (GH); Cillapuyu, El Chaccan, 7 March 1973, *G. Brunel 556* (F). Dept. Cajamarca: Prov. Contumazá, El Túnel (Cascas-Contumazá), 6 April 1985, *A. Sagástegui A. et al. 12634* (F). Dept. Huancavelica: Prov. Tayacaja, Ampurco, 19 April 1962, *O. Tovar 3789* (LP). Dept. Piura: Yacupampacuyas, Ayabaca, 26 May 1971, *A. López et al. 7764* (LP). Dept. Puno: Prov. Sandía, Cuyo-Cuyo, 69° 35' S, 14° 25' W, 18 July 1981, *T. Johns 81–54* (F); Ollachea to San Gabon, 17–24 July 1978, *M. Dillon et al. 1110* (F). Without department: Pérou, 1839–1840, *C. Gay s.n.* (LP); Tabina?, without date, *Lechler 2129* (K).

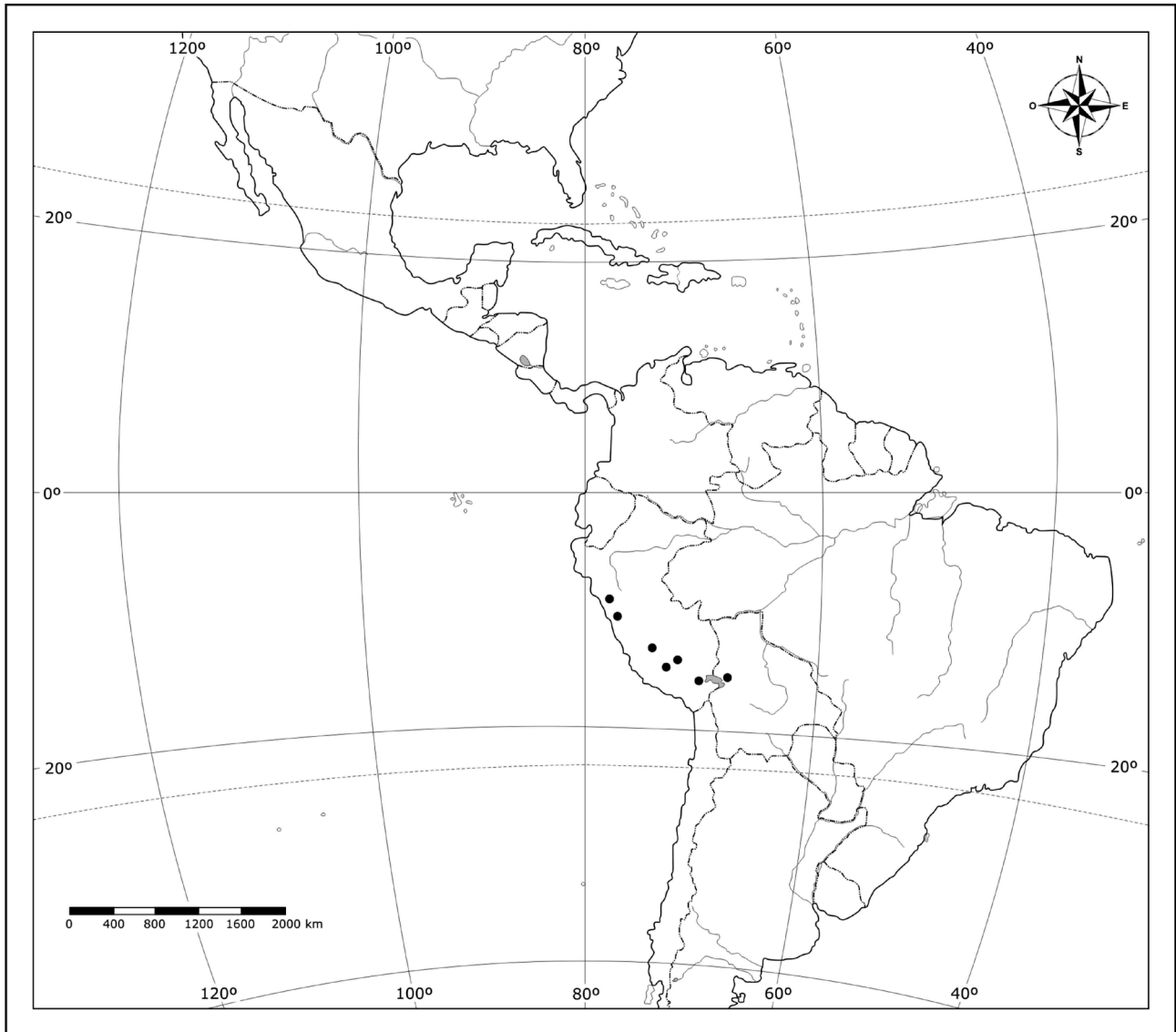


FIGURE 38. Geographical distribution of *Smalanthus parviceps*.

Smalanthus putlanus Turner (2010: 358). Type:—MEXICO. Oaxaca: Distrito de Putla, Mpio. Santa Cruz Itundujia, a 0.5 km en LR (W) de la Agencia de la Victoria, bosque de pino-encino secundario, ca.1091 m, 16° 44' 7'' N, 97° 45' 36'' W, 2 August 2008, *K. V. Gutiérrez et al.* 3099 (holotype TEX!).

Herbs 0.5–1.5 m tall, heterophyllous, stems pubescent. Leaves variable in shape throughout the stem, opposite, petiolate, 20–30 cm long, lamina 10–14 cm wide, widely ovate, acute or attenuate at the apex, truncate or hastate at the base, margins mucronate, 3-partite or pinnatisect, trinerved, actinodromous, pubescent on both faces; petioles 5–9 cm long, winged, wings uniform in width, entire, not auriculate at the base or sometimes auriculate, the auricles, if present, discontinuous with the opposite leaf. Capitula 7–15 × 8–10 mm, up to three arranged in cymes; peduncles 20–40 mm long, pubescent. Involucre campanulate to hemispherical; phyllaries arranged in 2 series, herbaceous, outer phyllaries 5–8 × 2–4 mm, obovate, obtuse at the apex, inner phyllaries 2.5–4 × 1.6–2 mm, acute at the apex. Receptacle with paleae 3–5 × 0.5–1.7 mm, linear-ovate, apex irregularly denticulate. True ray florets ca. 10, 1-seriate, corolla yellow, ray-limb oblong, 10–12 × 3.3–4.3 mm, apex 3-dentate, teeth equal in size, tube 0.8 mm long. Style 5–6 mm long, branches 3 mm long. Disc florets ca. 40, corollas yellow, tubular, 5–6 mm long, lobes ca. 1 mm long. Anthers with apical appendage ovate. Style 5 mm long, branches 0.8 mm long. Cypselae rounded-obovate, 1–2 × 1–1.5 mm, smooth. (Fig. 39).

Etymology:—For the Putla district in the state of Oaxaca, Mexico, where the type specimen was found.

Distribution and ecology:—Southern Mexico (Fig. 40). This species grows in forests of *Pinus* sp. and *Quercus* sp., between 1000–2000 m. It was found with flowers in August.

Notes:—See Notes under *S. obscurus*.

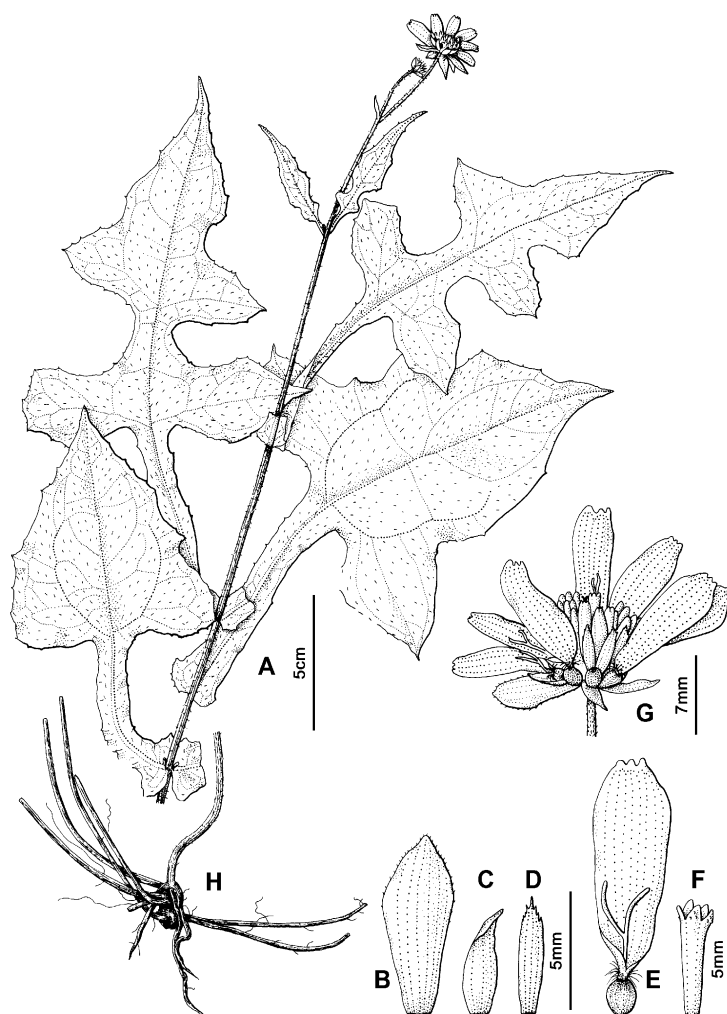


FIGURE 39. *Smallanthus putlanus* B.L. Turner. **A.** Habit. **B.** Outer phyllary. **C.** Inner phyllary. **D.** Palea. **E.** Ray floret. **F.** Disc corolla. **G.** Capitulum. **H.** Root (Gutiérrez *et al.* 3099, TEX).

Smallanthus pyramidalis (Triana) Robinson (1978: 51).

Polymnia pyramidalis Triana (1858: 40). Type:—COLOMBIA. Without locality and date: New Granada, *J. Triana 1323* (holotype probably at COL; isotypes F, K, US, digital images!).

Polymnia eurylepis Blake (1922: 415). Type:—ECUADOR. Azuay: Cuenca, 10 September 1920, *E. W. D. Holway & M. M. Holway 974* (holotype US 128388 [1058639], digital image!).

Tree up to 10 m tall, homophyllous, stems generally glabrescent, sometimes pubescent at the apex. Leaves opposite, occasionally verticillate, petiolate, 15–30 cm long, lamina 8–15 cm wide, ovate, acute at the apex, rounded or truncate at the base, margins mucronate, triplinerved, acrodromous, glabrescent above, lanuginose below; petioles 5–8 cm long, winged, wings decreasing in width from the blade to the node, entire, not auriculate at the base. Capitula 6–10 × 9–12 mm, ca. 50 arranged in paniculiform or corymbiform cymes; peduncles 18–20 mm long, densely pubescent. Involucre campanulate to hemispherical; phyllaries arranged in 2 series, ovate, outer phyllaries 7–11 × 5–7 mm, obtuse at the apex, herbaceous, inner phyllaries 4–6 × 2–5 mm, acute at the apex, scarious. Receptacle with paleae 3–5 × 2–5 mm, obovate, apex entire. True ray florets ca. 16, 1-seriate, corollas yellow, ray-limb oblong, 4–8 × 2–3 mm, apex 3-dentate, teeth equal in size, tube 1–1.5 mm long. Style 2–3 mm long, branches 1 mm long. Disc florets ca. 50, corollas yellow, campanulate, 3–4 mm long, lobes 0.7–1 mm long.

Anthers with apical appendage ovate to subtriangular. Style 2–3.5 mm long, branches 1 mm long. Cypselae obovate, 2–4.5 × 1–3 mm, smooth. $2n=29$ (Carr *et al.* 1999). (Fig. 41).

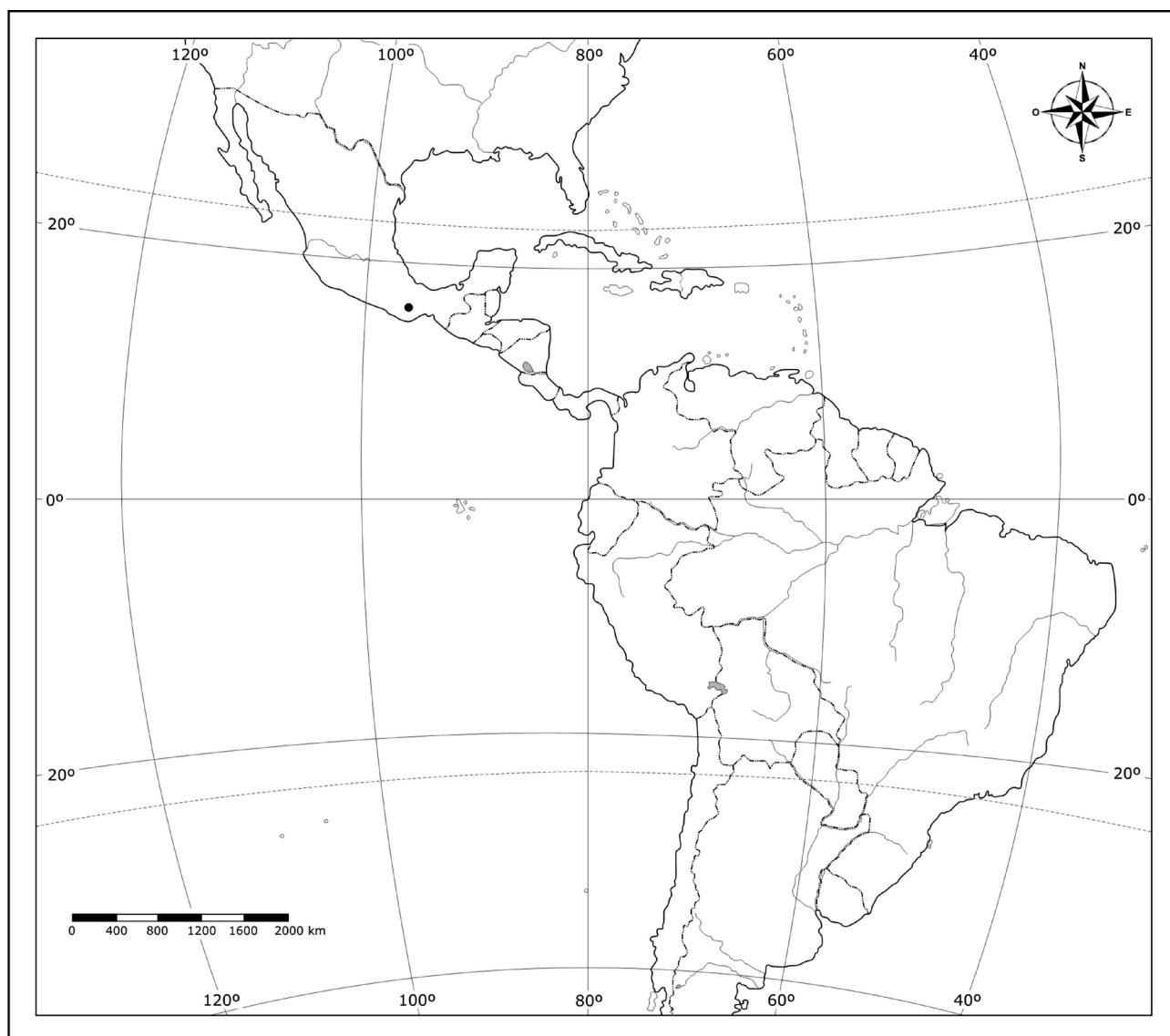


FIGURE 40. Geographical distribution of *Smallanthus putlanus*.

Etymology:—From the Greek *πλάμις*, angular structure with a pointed apex, by the general shape of the inflorescence.

Distribution and ecology:—Colombia, Ecuador, and western Venezuela (Fig. 42). It grows in montane forests, rocky slopes, ravines, Andean valleys, shrublands, river banks, wastelands, and on boulders along stream beds, between 1500–3500 m. Flowering from January to October.

Vernacular names and uses:—Anime, anime manso, anime negro, arbolaco, arboloco, colla, (f)tajuash, polaco. Used to mitigate the headache by heating the leaves and putting them over forehead (*Steyermark 57280*, F), in other parts of the body for rheumatism (*Cerón 15672*, K, QCNE), and against colds and bruises (*Cerón 15811*, QCNE). Also used as ornamental (*Cerón 16048*, QCNE). It has been postulated the importance of members of this species for the sustainable development of wetlands and its possible application in the use and conservation of these ecosystems (Guzmán Avendaño & Barrera Adame 2010).



FIGURE 41. *Smallanthus pyramidalis* (Triana) H. Robinson. **A.** Habit. **B.** Outer phyllary. **C.** Inner phyllary. **D.** Palea. **E.** Ray floret (without cypsela). **F.** Disc corolla. **G.** Cypsela (*Cuatrecasas* 20886, F).

Additional specimens examined:—COLOMBIA. Dept. Boyacá: S of río Gomeza (Río Arzobispo), 6 km E of Socha, 6° N, 72° 55–57' W, 11 November 1944, *F. Fosberg* 22308 (F). Dept. Cundinamarca: Guasca, 28 May 1947, *O. Haught* 5773 (LP); cordillera Oriental, sabana de Bogotá, 8 January 1942, *J. Cuatrecasas* 13548 (F, LP); Páramo de Chisacá, ca. 1 km S of Usme, 18 June 1965, *R. King et al.* 5660 (F); NE edge of Bogotá (E of calle 72), 19 March 1945, *E. Little & R. Little* 9792 (F, LP); Boquerón de Bogotá, without date, *E. André* 1244 (K); macizo de Bogotá, término de Choachí, hoja del río Blanco, quebrada de Aquadulce, frente a El Rejadero, 8 February 1969, *J. Cuatrecasas & M. del Llano* 27325 (F, G); Bogotá, February 1948, *C. Sandeman* 5765 (K); Suba hill, near Bogotá, 7 September 1945, *H. Schiefer* 899 (GH); entre Cachipay y La Florida, 22 March 1942, *J. Cuatrecasas* 13614 (F); SE of Bogotá, on trail towards Ubaqué, 7 February 1945, *E. Little & R. Little* 9238 (F). Dept. Del Valle: Hoya del río Bugalgrande, Las Alegrías, 27 March 1946, *J. Cuatrecasas* 20455 (F); Cordillera central, hoyo del río Bugalgrande, Barragán, La Laguna, Barragán, La Laguna, 17 April 1946, *J. Cuatrecasas* 20886 (F). Dept. El Cauca: Cordillera Central, Coconuco, 17–18 June 1922, *E. Killip* 6859 (GH). Dept. Nariño: Entre El Encano y Pasto, entre Páramo del Tábano y Laguna, 11 January 1941, *J. Cuatrecasas* 11964 (F). Dept. Putumayo: Valle de Sibundoy, 5 km S Sibundoy, 10 February 1963, *P. Chindoy* 78 (GH). Dept. Santander: Vicinity of La Baja, 31 January 1927, *E. Killip & A. Smith* 18043 (GH). Dept. Norte de Santander: Between Mutiscua and Pamplona, 23 February 1927, *E. Killip & A. Smith* 19693 (GH); Culagá valley, near Tapatá, N of Toledo, 3–8 March 1927, *E. Killip & A. Smith* 20484 (GH).

ECUADOR. Prov. Azuay: Parroquia Cochapata, 3° 23' S, 79° 05' W, 8 August 1991, *C. Cerón* 16048 (QCNE). Prov. Cañar: Ingapirca, 78° 52' W, 2° 32' S, 27 December 1979, *L. Holm-Nielsen* 20880 (GH); near El Tambo, ca.

69 km by RR S of Sibambe, 22 April 1945, *W. Camp E-2791* (S); Parroquia Chorocote, 2° 34' S, 78° 56' W, 1 August 1991, *C. Cerón 15811* (QCNE). Prov. Carchi: Entre Paja Blanca y El Cucho, 17 July 1945, *M. Acosta Solís 10475* (F). Prov. Chimborazo: Ad Riobamba, 1920, *L. Mille 566* (GH); Riobamba, río Guano, 8 April 1934, *Schimpff 937* (G); Alausi, Parroquia Pumallacta, 2° 15' 24" S, 78° 48' 30" W, 15 July 1991, *C. Cerón 15672* (K, QCNE); between Chunchi and Sbambe, 28 October 1952, *F. Fagerling & G. Wibom 766* (S). Prov. Imbabura: Sector La Joya-Huagshia-San Vicente, al SW de Otavalo, aprox. 0° 15' N, 78° 16' W, 11 September 1983, *J. Jaramillo & V. Wimmerskjold 5945* (F). Prov. Pichincha: Quito, 20 August 1949, *M. Acosta Solís 13455* (F). Without province: Outer slope of western Cordillera, November, *A. Rimbach 85* (GH); without locality: *A. Sodiro 114* (S). VENEZUELA. State Mérida: Mpio. Rangel, alrededores de Mucuruba, 23 October 1972, *V. Badillo 5320* (F); about 12 km E of Tabay off of the Carretera Transandina, 17 January 1993, *R. King et al. 10411* (F, GH, K, S); San Rafael, 4 April 1930, *M. Gehriger 10* (F, G, GH); San Rafael, 22 February 1922, *A. Jahn 787* (GH); Mpio. Miranda, Timotes, 9 February 1928, *H. Pittier 12942* (GH); de Mérida ad Mucuchies, 1976, *A. Charpin & F. Jacquemoud 13599* (F, G, S); Sto. Domingo-Apartaderos, September 1956, *L. Aristeguieta 2421* (F); La Honda, alrededores Quebrada El Medio, Santo Domingo, 2 May 1969, *C. Rojas 664* (F). State Táchira: Above Betania, at base of Páramo de Tamá, 14 July 1944, *J. Steyermark 57280* (F); W of Timotes, 22 March 1944, *J. Steyermark 55684* (F).

Without country: 1870, herb. I. Anderson (K).

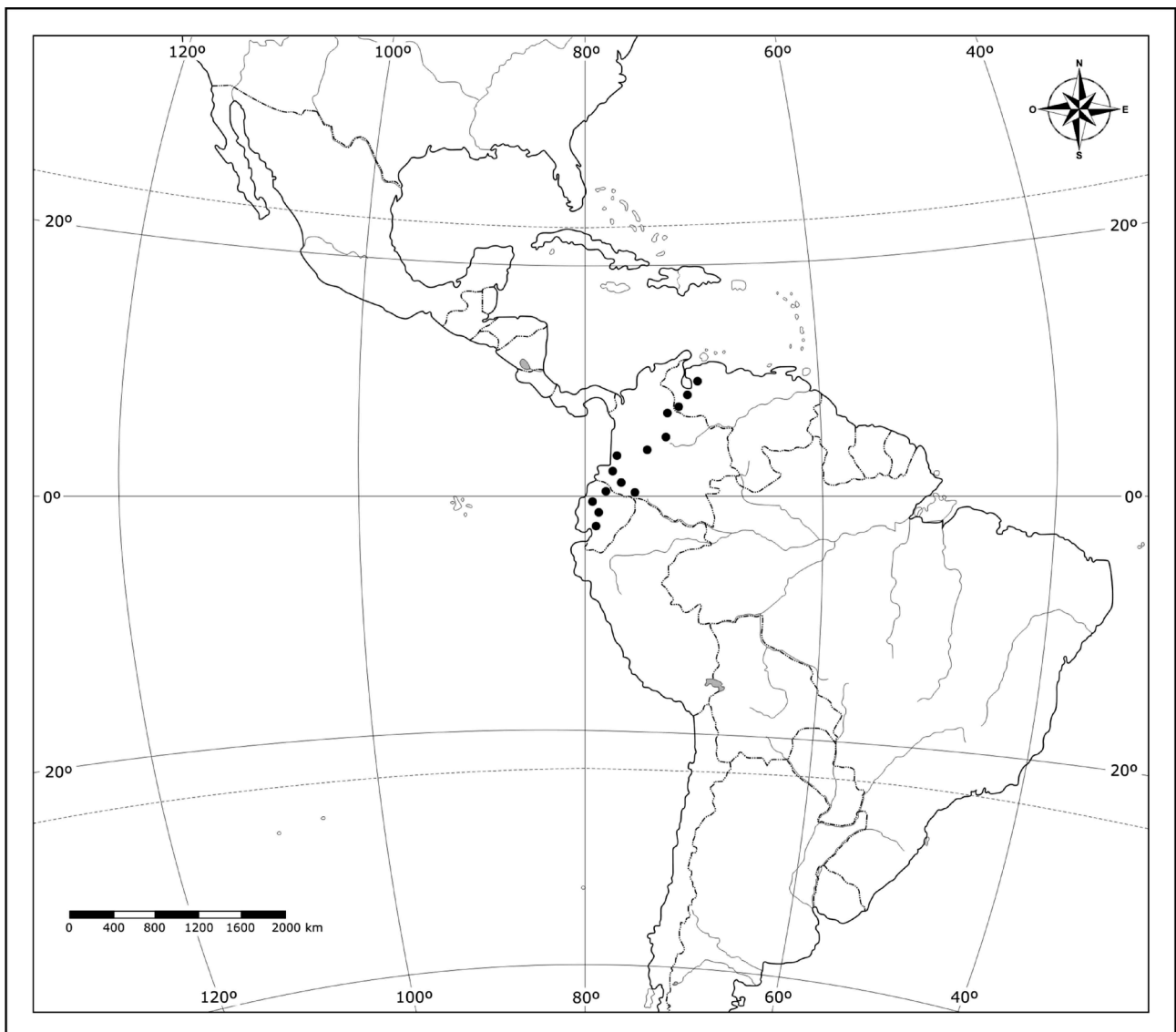


FIGURE 42. Geographical distribution of *Smalanthus pyramidalis*.

Smallanthus quichensis (Coulter) Robinson (1978: 51).

Polymnia quichensis Coulter (1895: 48). Type:—GUATEMALA. Quiché: Chiul, alt. 8000 ft, April 1892, E. Heyde & E. Lux 3375 (holotype F!, isotypes GH, K, M, MO, NY, US digital images!).

Herbs 1–3 m tall, homophyllous, stems glabrescent. Leaves opposite, petiolate, 12–25 cm long, lamina 3–8 cm wide, ovate-lanceolate, acute or attenuate at the apex, attenuate at the base, margins irregularly dentate, trinerved or triplinerved, acrodromous, pubescent on both faces; petioles 0.9–3.5 cm long, winged or sometimes not winged, wings decreasing in width from the blade to the node, entire, not auriculate at the base. Capitula 7–15 × 12–14 mm, solitary or up to three arranged in cymes; peduncles 20–80 mm long, pubescent. Involucre campanulate to hemispherical; phyllaries arranged in 2 series, herbaceous, ovate, acute at the apex, outer phyllaries 7–16 × 8–11 mm, inner phyllaries 6–11 × 5–7 mm. Receptacle with paleae 4–7.5 × 2 mm, oblong, apex entire. True ray florets ca. 10, 1-seriate, corollas yellow, ray-limb elliptic, 10–27 × 3.2–3.8 mm, apex 3-dentate, teeth equal in size, tube 2 mm long. Style 7 mm long, branches 1.5–3 mm long. Disc florets ca. 50, corollas yellow, slightly campanulate, 6–9 mm long, lobes 1–1.5 mm long. Anthers with apical appendage ovate. Style 8 mm long, branches 1.5 mm long. Cypselsae rounded-obovate, 4–7 × 3–6 mm, smooth. (Fig. 43).



FIGURE 43. *Smallanthus quichensis* (J.M. Coulter) H. Robinson. **A.** Habit. **B.** Outer phyllary. **C.** Inner phyllary. **D.** Palea. **E.** Ray floret (without cypsela). **F.** Disc floret (without ovary). **G.** Cypsela (Heyde & Lux 3375, G).

Etymology:—For the Quiché Department, Guatemala, where the type specimen was found.

Distribution and ecology:—Costa Rica and Guatemala (Fig. 44). This species grows in forests, ravines, and humid shrublands, at 1800–3000 m. Flowering from August to November.

Vernacular names:—Árnica, carricillo.

Notes:—See Notes under *Smallanthus latisquamus*.

Additional specimens examined:—COSTA RICA. Prov. San José: Perez Zeledón, R. F. Los Santos, Cuenca del Savegre, San Gerardo de Dota, trail to waterfall along Río Savegre, 9° 32' 20" N, 83° 49' 07" W, 10 March 2005, *Boyle 7579* (S). Without locality: 30 March 1888, *H. Pittier 42* (K).

GUATEMALA. Dept. Huehuetenango: At Cruz de Limón, between San Mateo Ixtatán and Nucá, Sierra de los Cuchumatanes, 31 July 1942, *J. Steyermark 49833* (F, G); Municipio of San Mateo Ixtatán, near Kurus Lemun, 4 miles E of San Mateo Ixtatán, along road to Barillas, 7 August 1965, *D. Breedlove 11598* (F). Dept. Quiché: Nebaj, 17 November 1934, *A. Skutch 1704* (GH). Dept. San Marcos: Along road above Barranco Eminencia, 14 March 1939, *P. Standley 68555, 68575* (F); Barranco Eminencia, above San Rafael, Pie de la Cuesta, 15–16 March 1939, *P. Standley 68472* (F); between San Sebastián and Todos Santos, volcán Tajumulco, 1 March 1940, *J. Steyermark 36952* (F); Barranco Eminencia, road between San Marcos and San Rafael Pie de la Cuesta, between Finca La Lucha and Buena Vista, 6 February 1941, *P. Standley 86225* (F), *86278* (F, G), *86364* (F), *86418* (F); near Aldea Fraternidad, between San Rafael Pie de la Cuesta and Palo Gordo, Sierra Madre mountains, 10–18 December 1963, *L. Williams et al. 25600* (F), *25809* (F, G), *26262* (F); outer slopes of Tajumulco Volcano, Sierra Madre mountains, about 8–10 km W of San Marcos, 31 December 1964/ 1 January 1965, *L. Williams et al. 26804* (F); outer slopes of Tajumulco volcano, Sierra Madre mountains, about 10 km W of San Marcos, 3 January 1965, *L. Williams et al. 27187* (F).

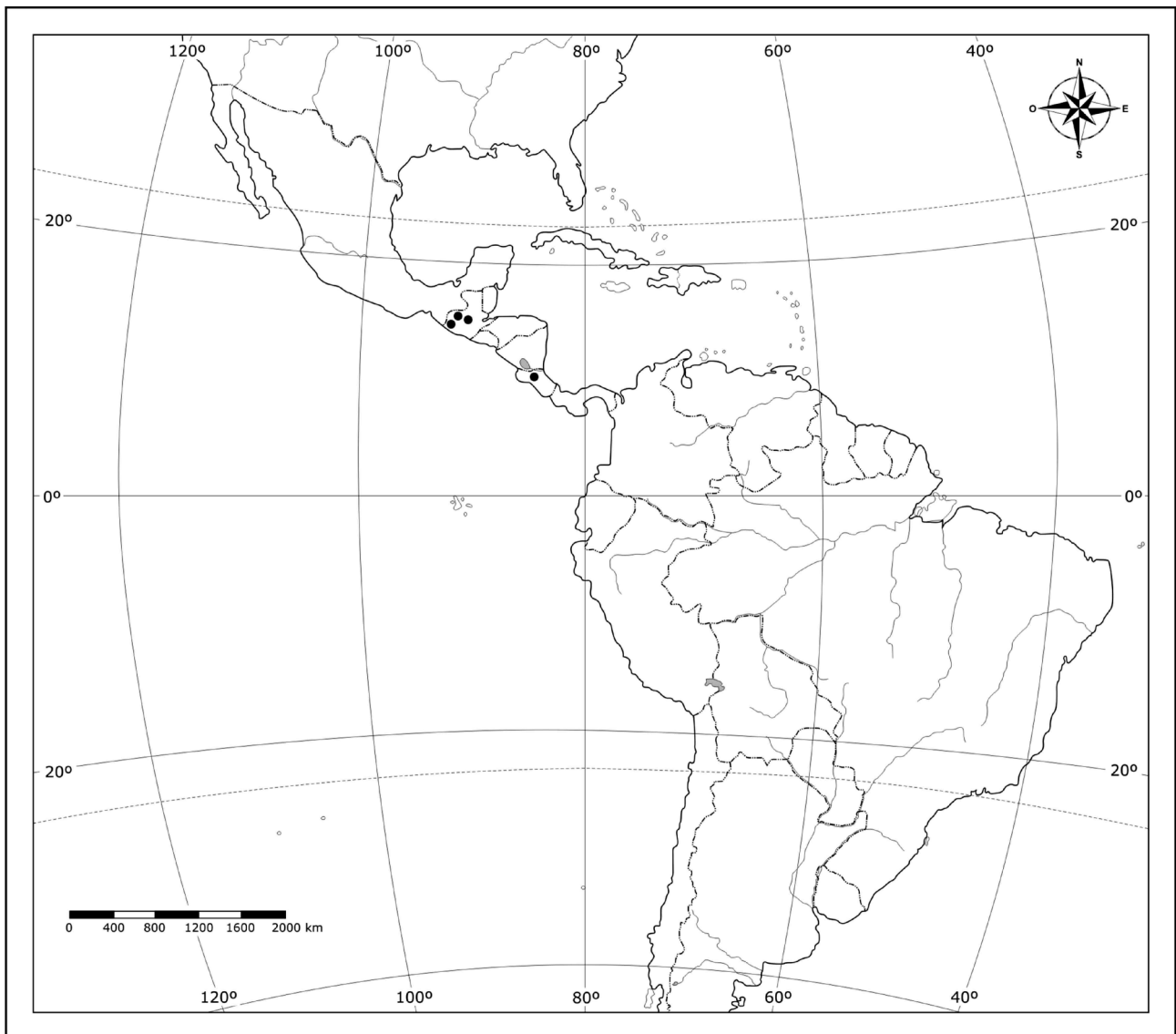


FIGURE 44. Geographical distribution of *Smallanthus quichensis*.

Smallanthus riparius (Kunth) Robinson (1978: 51).

Polymnia riparia Kunth in Humboldt, Bonpland & Kunth (1818: 222). Type:—COLOMBIA. Cesar: Prope Cascajo, Río Magdalena, May 1801, *A. Humboldt & A. Bonpland 1640* (holotype P 320278, digital image!, isotype B probably destroyed, photograph F n. 15161!).

Shrubs 1–5 m tall, homophyllous, stems pubescent. Leaves opposite, petiolate, 14–34 cm long, lamina 12–22.4 cm wide, ovate-subtriangular to widely ovate, acute, attenuate at the apex, truncate or hastate at the base, margins denticulate-mucronate, irregularly lobate, triplinerved, acrodromous, pubescent on both faces; petioles 4.5–11.7 cm long, winged, wings uniform in width or decreasing in width from the blade to the node, entire, not auriculate at the base. Capitula 6–10 × 8–16 mm, ca. 10 arranged in racemiform or corymbiform cymes; peduncles 13–70 mm long, pubescent. Involucre hemispherical; phyllaries arranged in 2 series, herbaceous, outer phyllaries 3–13 × 4–9 mm, ovate to oblong, obtuse at the apex, inner phyllaries 7–11 × 2–6 mm, ovate, caudate at the apex. Receptacle with paleae 5–6 × 1.5–2 mm, oblanceolate, apex entire. True ray florets ca. 10, 1-seriate, corollas yellow, ray-limb elliptic, 6–13 × 4–7 mm, apex 3-dentate, teeth equal in size, tube ca. 2 mm. Style ca. 5 mm long, branches 1.5 mm long. Disc florets ca. 40, corollas yellow, tubular to slightly campanulate, 5–7 mm long, lobes 1 mm long. Anthers with apical appendage ovate-subtriangular. Style ca. 7 mm long, branches 0.2 mm long. Cypselae obovate, 2.5–5 × 2–4 mm, smooth. $n=16$ (Robinson *et al.* 1981). (Fig. 45).



FIGURE 45. *Smallanthus riparius*. A. Habit. B. Outer phyllary. C. Palea. D. Ray floret (without cypselae). E. Disc corolla. F. Cypselae. G. Capitulum (Killip 16437, GH).

Etymology:—From the Latin *riparius*, of stream banks, by the Magdalena river shore, Colombia, where the type specimen was found.

Distribution and ecology:—Colombia, Costa Rica, Ecuador, Perú, and Venezuela (Fig. 46). It grows in flat grasslands, shrublands, and river and roadsides, 700–2000 m. Flowering from January to October.

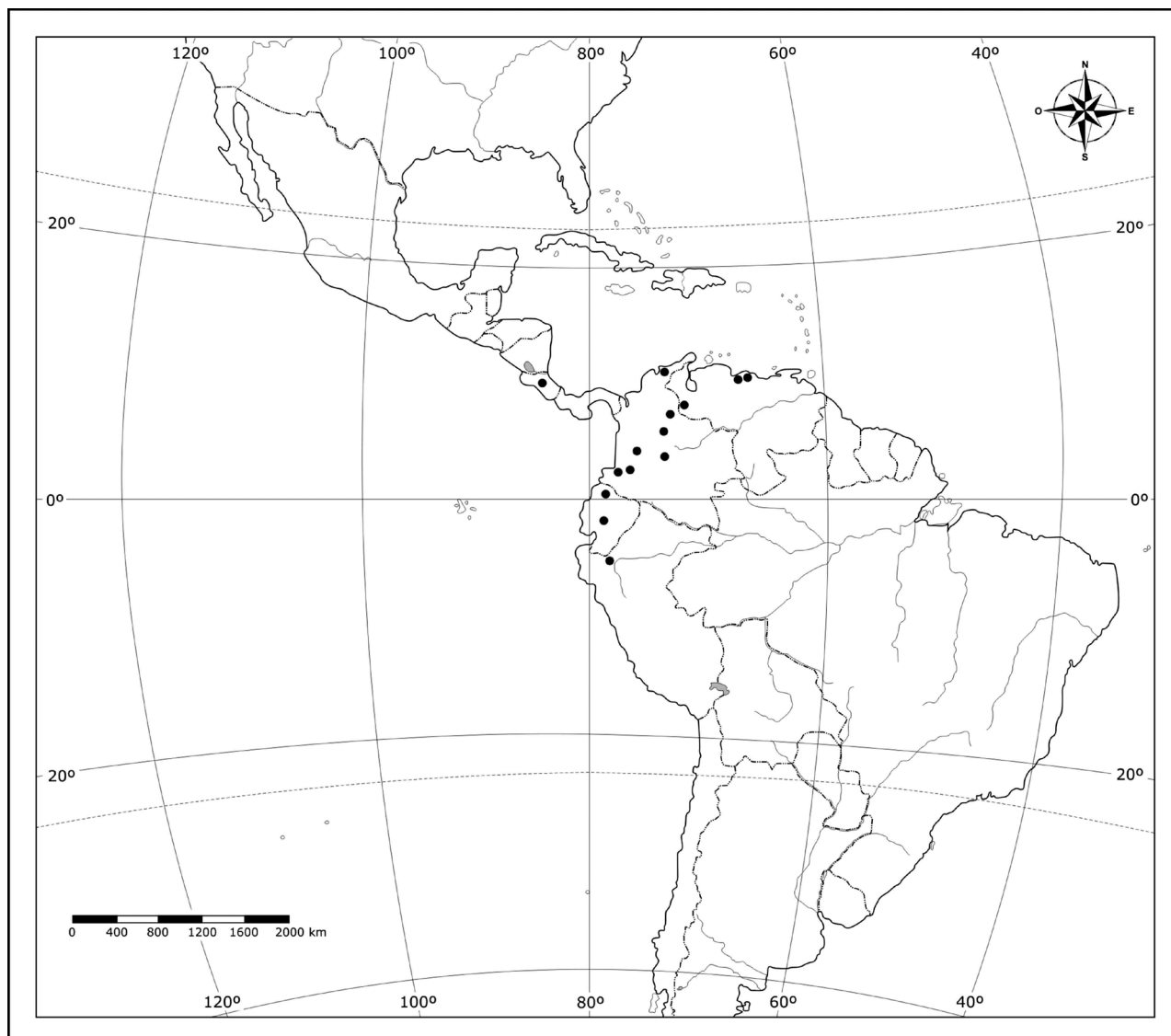


FIGURE 46. Geographical distribution of *Smallanthus riparius*.

Vernacular names:—Colla, pailon.

Notes:—According to Hind & Jeffrey (2001), the citation collecting number and locality given by Bonpland on the label of the specimen at Humboldt & Bonpland herbarium (P) is: “*Bonpl. mss. 1640*. Prope Cascajo, Río Magdalena Maj. 1801”.

The finding of one specimen of *S. riparius* in Costa Rica, distant from other collection localities in South America, may be due to a lack of sampling of this species in Panama.

Additional specimens examined:—COLOMBIA. Dept. Boyacá: Region of Mt. Chapon, extreme western part of Dept. Boyacá, 1932, *A. Lawrence 225* (F, GH, K). Dept. Caldas: Salento, 25–31 July 1922, *F. Pennell 8931* (GH); Rio Quindio, above Armenia, 25 July 1922, *F. Pennell et al. 8702, 8731* (GH). Dept. Cauca: La Gallera, Micay valley, near Rio San Joaquín, 29–30 June 1922, *E. Killip 7842* (GH); Hoya del río Palo, entre Tacueyó y La Tolda, 19 December 1944, *J. Cuatrecasas 19511* (F); Quebrada del Bermejil, 10 March 1947, *J. Cuatrecasas 23762* (F); Quebrada de Samanga, Popayán, March 1948, *S. Yepes A. 170* (F); Mun. Popayán, March 1948, *S. Yepes A. 250* (F); Popayán, without date, *H. March 4549* (F); id., without date, *F. Lehmann 5528* (F). Dept. Cundinamarca: Sasaima, July 1931, *Bro. Apolinar-María s.n.* (F 990120); ca. 6 km S of Sasaima, 14 July 1965, *R. King et al. 5947* (F); Guaduas, July 1923, *Bro. Ariste-Joseph 1015* (GH); Monte Redondo to Quetame, 7

September 1917, *F. Pennell 1844* (GH); La Vega, 4 June 1939, *J. Cuatrecasas et al. 5342* (F). Dept. Del Valle: Hoya del río Sanquinini, La Laguna, 10–20 December 1943, *J. Cuatrecasas 15539* (F). Dept. Magdalena: Santa Marta, Jan 1898–99, *H. Smith 913* (F, GH, S). Dept. Meta: Villavicencio, January 1927, *Bro. Apolinar-María 451* (F); id., 1898–99, *T. Sprague 144* (K). Dept. Norte de Santander: Región de Sarare, hoya del río Margua, Quebrada del Sararito, entre Miranda y el Alto de la Aurora, 23 November 1941, *J. Cuatrecasas 13412* (F). Dept. Santander: Río Suratá valley, between El Jaboncillo and Suratá, 3 January 1927, *E. Killip 16437* (GH). Dept. Tolima: Toche, 27 April 1942, *K. von Sneidern 3300* (S).

COSTA RICA. Prov. San José: Pérez Zeledón, R. F. Los Santos, Cuenca del Savegre, Río Nuevo, El Brujo, 6 km N y 500 m W del Brujo, 9° 28' 47" N, 83° 56' 36" W, 6 February 2001, *A. Rodríguez et al. 6992* (G).

ECUADOR. Prov. Cotopaxi: Tenefuerste, Río Pilalo, km 52–53, Quevedo-Latacunga, 19 July 1982, *C. Dodson & A. Embree 13362* (F); Tenefuerste, río Pilalo, km 52–53, Quevedo-Latacunga, 12 June 1983, *C. Dodson et al. 13936* (QCNE); road Quevedo-Latacunga, below Macuchi, 5 May 1968, *G. Harling et al. 9148* (F). Prov. Pichincha: Chiriboga, 26 April 1955, *E. Asplund 16066* (S); ad marg viae inter Cansacoto et Tandapi, 17 July 1920, *I. Holmgren 804* (S); Cantón Quito, Parroquia Nanegal, along río Saguanal between Marianitas and Est. Piscícola, 0° 08' N, 78° 39.5' W, 0.3 km W of Marianitas, 6–7 July 1991, *G. Webster & K. Bullock 28802* (QCNE); Parroquia Nanegal, road between Marianitas and Nanegal, 0° 08' N, 78° 39' W, 15 July 1990, *G. Webster & M. Ríos 28297* (QCNE). Prov. Tungurahua: Río Verde, along the road Baños-Puyo, 17 July 1967, *B. Sparre 17685* (S).

PERU. Dept. Junín: Vitoc, 1794 without leg. 60, Herb. Boissier (G 189323).

VENEZUELA. State Aragua: Colonia Tovar, 1854–5, *A. Fendler 775* (GH). State Miranda: Ocumare del Tuy, 15 October 1939, *L. Williams 12443* (F, S); vicinity of Petare, 11 September 1921, *H. Pittier 9787* (GH); Los Teques, Parque de los Bárbaros, 19 October 1917, *H. Pittier 7510* (GH). State Sucre: Los Venados, Parque Nacional El Avila, 6 September 1968, *G. de Wolf Jr. 1953* (GH); Los Venados, Caracas, August 1939, *Bro. Elias 52* (F); id., 1 Oct 1940, *C. Vogl 470* (F). State Táchira: Inter Betania, Villa Paez et Delicias, 14 November 1976, *A. Charpin & F. Jacquemoud 13361* (F, G).

Smallanthus siegesbeckia (Candolle) Robinson (1978: 51), “*siegesbeckius*”.

Polymnia siegesbeckia Candolle (1836: 516), “*Siegesbeckia*”. Type:—BRAZIL. Rio de Janeiro: In Brasilia, circa Rio-Janeiro, 1834, *Gaudichaud 692* (holotype G-DC 209807, digital image!; isotype F!, G 226652 digital image!).

Herbs 1–5 m tall, homophyllous, stems pubescent. Leaves opposite, sessile, 7–16 × 3–12 cm, ovate, acute at the apex, obtuse at the base, margins mucronate, trinerved, acrodromous, pubescent on both faces. Capitula 4–9 × 5–12 mm, ca. 15 arranged in racemiform or paniculiform cymes; peduncles 5–60 mm long, pubescent. Involucre campanulate to hemispherical; phyllaries arranged in 2 series, herbaceous, ovate, outer phyllaries 4–9 × 2–5.5 mm, acute at the apex, inner phyllaries 4–10 × 1–3 mm, caudate at the apex. Receptacle with paleae 4–6 × 1–2 mm, obovate, apex entire. True ray florets ca. 12, 1-seriate, corollas yellow, ray-limb oblong, 2–6 × 1–1.2 mm, apex 3-dentate, teeth equal in size, tube 1–2 mm long. Style 4 mm long, branches 0.5–1 mm long. Disc florets ca. 20, corollas yellow, campanulate, 1.5–6 mm long, lobes 0.5 mm long. Anthers with apical appendage ovate. Style 4 mm long, branches 0.5 mm long. Cypselae obovate, 3–3.5 × 1–3 mm, smooth. (Fig. 47).

Etymology:—After the generic name *Siegesbeckia*, which had been given in honor of the German physician and botanist Johann Georg Siegesbeck (1686–1755), professor of Botany at the Russian Academy of Sciences.

Distribution and ecology:—Bolivia, Brazil, Ecuador, Paraguay, and Peru (Fig. 48). It grows in montane forests, rocky slopes, and roadsides, between 600–1600 m. This species is a common invader of abandoned fields and a weed in plantations (Grau & Rea 1997). Flowering from October to March.

Notes:—The type specimen at G indicates “1833” as collection date.

The species epithet was spelled “*Siegesbeckia*” in the protologue, thus indicating the use of a noun in apposition. When transferring the name *Polymnia siegesbeckia* to *Smallanthus*, Robinson (1978) mistook the species epithet for an adjective to be agreed in gender with the generic epithet, thus publishing the new combination “*Smallanthus siegesbeckius*”. This spelling is to be corrected to *S. siegesbeckia* under Art. 23.5 of the ICN.

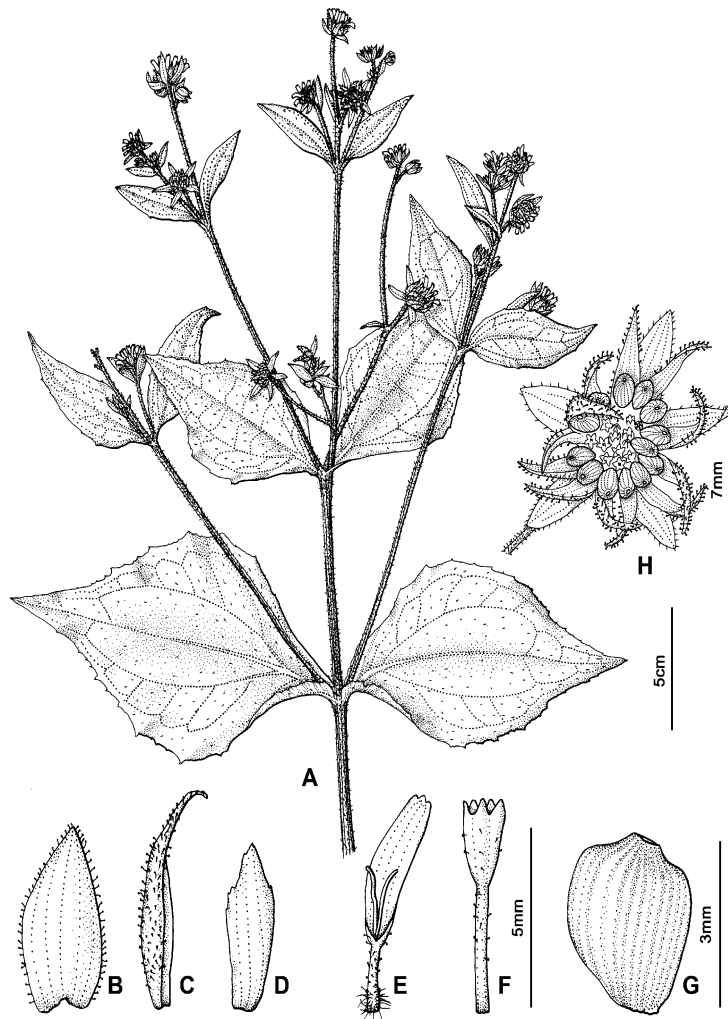


FIGURE 47. *Smallanthus siegesbeckia* (Candolle) H. Robinson. **A.** Habit. **B.** Outer phyllary. **C.** Inner phyllary. **D.** Palea. **E.** Ray floret (without cypselas). **F.** Disc corolla. **G.** Cypselas **H.** Capitulum (Buchtien 748, G).

Additional specimens examined:—BOLIVIA. Dept. La Paz: Yungas, 1890, *M. Bang* 466 (G); Nord Yungas, Milliguaya, December 1917, *O. Buchtien* 748 (G, S); along the road to Irupana, ca. 1 km from Chulumani, 26 January 1978, *R. King & L. Bishop* 7424 (K); Prov. Nor Yungas, subida a Coroico, 3 km desde Yolosa, 30 December 1983, *S. Beck* 8709 (SI); Coroico-Yolosa, subiendo el río San Juan, a 10 km, 1 April 1982, *S. Beck* 7500 (SI); Straßenrand 4 km unterhalb des Ortes, 15 February 1980, *J. Krach* 8533 (SI).

BRASIL. Distrito Federal: Brasília, without date, *Riedel s.n.* (G, GH). State Minas Gerais: Viçosa, E.S.A., 18 January 1935, *J. Kuhlmann* 2778 (LP); Lagoa Santa, without date, *Warming s.n.* (S 870027); without locality, 1845, *Widgren s.n.* (GH, S). State Paraná: Ponta Grossa, 6 March 1910, *P. Dusén* 9503 (GH, LP); on the Parana, 26°–27° S lat., April 1883, *D. Parodi* 23 (K). State Rio de Janeiro: Rio de Janeiro, 1896, *Gardner* 253 (G); environs de Rio Janeiro et d'Ouro Preto, May 1885, *A. Glaziou* 15071 (K).

ECUADOR. Prov. Santiago-Zamora: Macas, 13 March 1956, *E. Asplund* 19733 (S).

PARAGUAY. Dept. Guairá: Villarica, January 1930, *P. Jorgensen* 4444 (F, GH, LP, S); Colonia Independencia, región del Guairá, March 1924, *T. Rojas* 4833 (LP).

PERU. Dept. Cajamarca: 6 km N of San Ignacio, 23 January 1983, *R. King & L. Bishop* 9299 (G); Prov. Jaén, ruta Huahuaya Tabaconas, 2 August 1994, *S. Leiva et al.* 1267 (F). Dept. Cuzco: Cocalpampa, Chaullay, Maranura, Quillabamba La Convención, Quintalpata, +- 150 km NW from Cuzco on the road from Cuzco to Kiteni, 29–30 December 1986, *W. Percy Nuñez & M. Cruz* 6807 (F); Urubamba, alrededores de Santa Rita, 28 March 1942, *C. Vargas C.* 2680 (F). Dept. Junín: Chanchamayo, October 1863, *J. Isern* 625 (F); id., 15 October 1863, *J. Isern* 2272 (F); Hacienda Huacara, Chanchamayo, zentral Peru, 7 June 1959, *L. Diers* 1241 (LP); Prov. Chanchamayo, La

Merced, 10–24 August 1923, *F. Macbride* 5388 (F, GH). Dept. San Martín: Zepelacio, near Moyabamba, December 1933, *G. Klug* 3399 (F, G, GH).

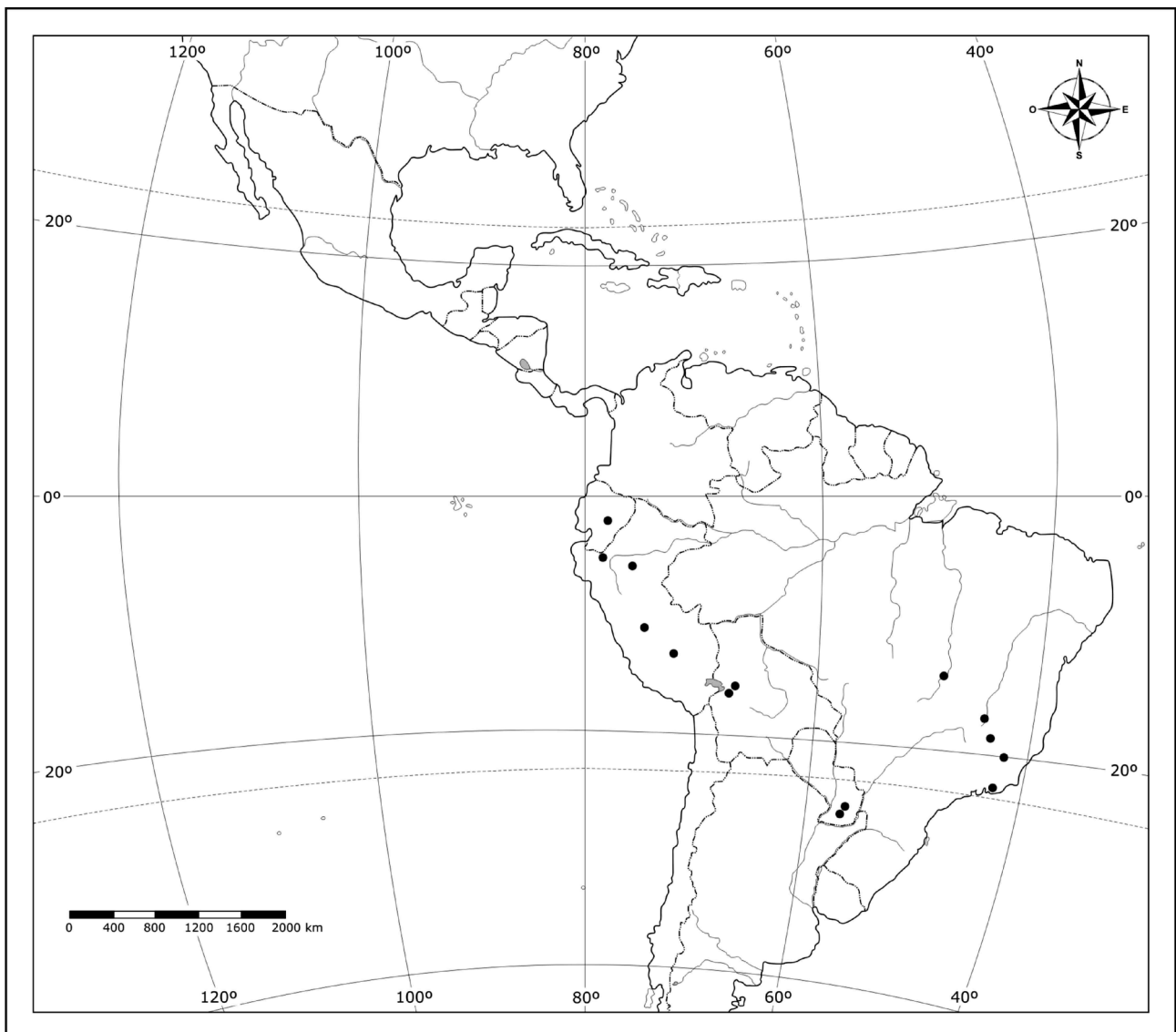


FIGURE 48. Geographical distribution of *Smalanthus siegesbeckia*.

Smalanthus sonchifolius (Poeppig) Robinson (1978: 51).

Polymnia sonchifolia Poeppig. (1843: 47, tab. 254). Type:—PERU. Huanuco: Peruvia subandinis, in montibus siccis ad Cassapi, January 1830, *E. F. Poeppig* 1653 (holotype W 48647, digital image!, isotype F!, NY, W 48648, digital images!).

Polymnia edulis Weddell (1857: 114). Type:—COLOMBIA. ‘Sponte crescit prope Quetame, in declivitate orientali Andium Bogotensium, ad altitudinem 2000 metr. (*Triana*)’ (holotype probably at P).

Shrubs 1.5–3 m tall, heterophyllous, stems pubescent. Leaves opposite, petiolate, acute at the apex, margins irregularly dentate, mucronate, trinerved, triplinerved, acrodromous, petioles winged, wings uniform in width, entire, auriculate at the base, auricles discontinuous with the opposite leaf, pubescent on both faces; lower leaves 17–30 cm long, lamina 10–23 cm wide, subtriangular, truncate at the base, petioles 6–13 cm long; upper leaves 9–25 cm long, lamina 4.5–11 cm wide, ovate or elliptic, obtuse at the base, petioles 1.5–4 cm long. Capitula 5–12 × 8–19 mm, ca. 20 arranged in racemiform or paniculiform cymes; peduncles 12–60 mm long, pubescent. Involucre campanulate to hemispherical; phyllaries arranged in 2 series, herbaceous, ovate, acute at the apex, outer phyllaries 7–20 × 3–10 mm, inner phyllaries 5–7 × 2–4 mm. Receptacle with paleae 3–6 × 1–2 mm, oblanceolate, apex entire.

True ray florets ca. 15, 1-seriate, corollas yellow, ray-limb obovate to oblong, $4\text{--}7 \times 1.8\text{--}2$ mm, apex 3-dentate or 3-lobate, lobes slightly different in size, tube 2 mm long. Style 4–6 mm long, branches 1–2.5 mm long. Disc florets ca. 60, corollas yellow, tubular to campanulate, 3–9 mm long, lobes 0.5 mm long. Style 6 mm long, branches 0.5 mm long. Anthers with apical appendage ovate. Cypselae obovoid, $2\text{--}6 \times 1.5\text{--}2.5$ mm, smooth. $n=30$ (Wells 1965). (Fig. 49).

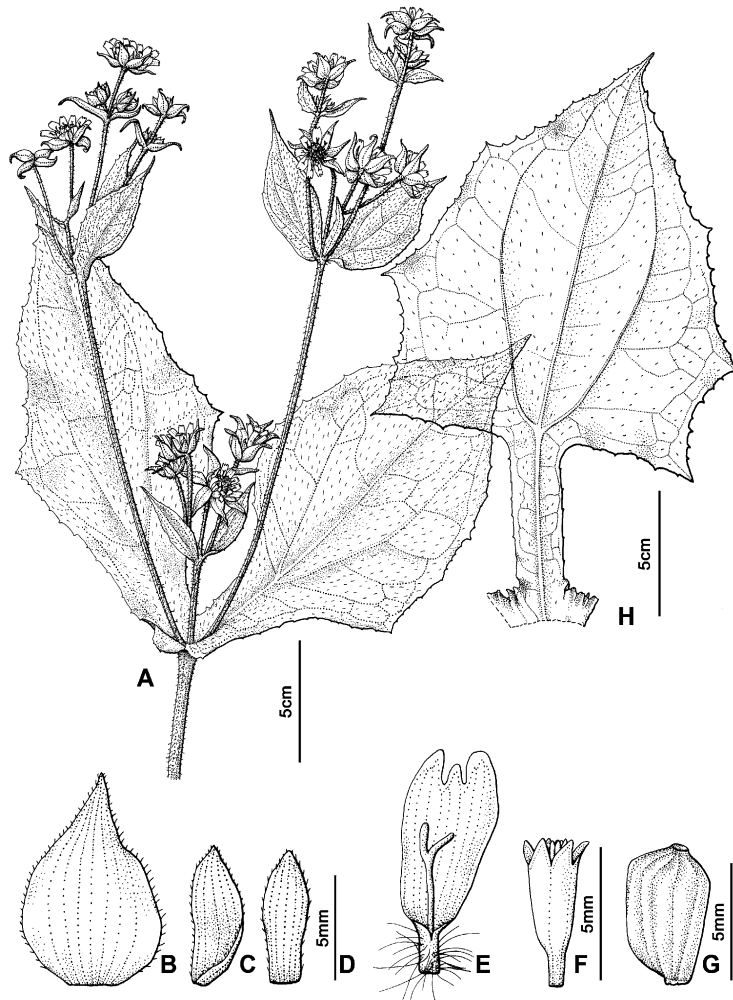


FIGURE 49. *Smallanthus sonchifolius* (Poeppig) H. Robinson. **A.** Habit. **B.** Outer phyllary. **C.** Inner phyllary. **D.** Palea. **E.** Ray floret (without cypselae). **F.** Disc floret (without ovary). **G.** Cypselae. **H.** Leaf (Sánchez Vega 5550, F).

Etymology:—From *Sonchus*, a genus of Cichorieae (Asteraceae), and from the Latin *folium*, leaf, by the general shape of the leaves in members of this species that resembles those of some species of *Sonchus* L.

Distribution and ecology:—Northern Bolivia to central Peru is the postulated area of origin of yacón, which expanded its range to the north (Ecuador) and to the south (northwestern Argentina) through the humid slopes of the Andes to the dry inter-Andean valleys (Fig. 50). Currently, yacón is a rare crop in northwestern Argentina, present only in a few localities in Salta and Jujuy provinces and close to extinction in this country (Grau & Rea 1997).

Because of its multiple uses, the yacón has been cultivated and is part of the Andean diet since pre-Columbian times (Choque Delgado *et al.* 2013). Cultivation of yacón in South American countries (e.g., Venezuela, Colombia) has been reported in the literature (e.g., Wells 1965, Zardini 1991) and herbarium labels, and extended to other continents. In its natural range, this species is commonly found in the mountain forests, inter-Andean valleys, coastal areas, and disturbed habitats such as river banks, roadsides, and close to cultivation fields generally taking advantage of vegetation gaps, from sea level to above 2000 m. Flowering from April to July.

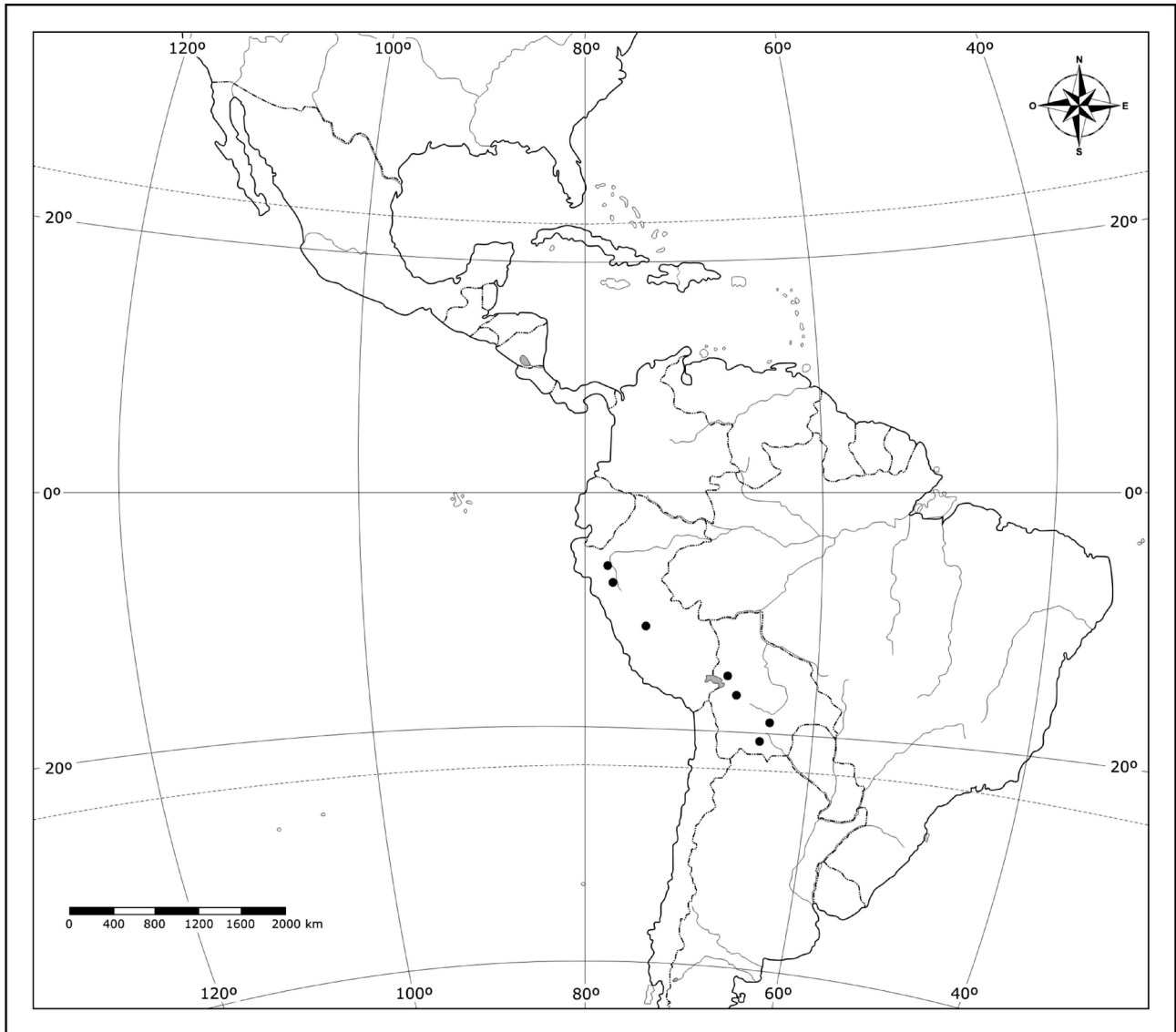


FIGURE 50. Natural range of distribution of *Smilax sonchifolia*.

Vernacular names and uses:—The most widely known vernacular name for plants of this species is yacón, but other names are: aricama, aricama, chicama, jicama, jíquima, jiquimilla, llaqon, llacum, llacuma, shicama, yacumpi. There are two intimately linked factors that make the yacón a widely known crop: its edible value and its medicinal properties. In contrast to other tuberous crops with high starch content, yacón contains fructooligosaccharides, inulin and phenolic compounds which improves the growth of bifidobacteria in the colon, enhances mineral absorption and gastrointestinal metabolism, and plays a role in the regulation of serum cholesterol. For these reasons yacón is regarded as “functional food” (Choque Delgado *et al.* 2013). The hypoglycemic effect of the water extract of yacón leaves in diabetic rats (Aybar *et al.* 2001, Castro *et al.* 2006) and of fresh roots consumed by people (Mayta *et al.* 2004) was demonstrated. Yacón also has properties to treat kidney ailments, skin-rejuvenating activity, and as a prebiotic (Lachman *et al.* 2003). Yacón tuberous roots have a sweet flavour and crunchiness and is commonly eaten raw. In producer countries of this crop, there is a wide variety of products derived from yacón roots, such as flour, slices, juices, purees and sweeteners in the form of syrup. Dried leaves are consumed as tea (Choque Delgado *et al.* 2013) being Japan and Brazil the main producers of yacón tea (Seminario *et al.* 2003). Grau & Rea (1997) developed a very complete report about the vernacular names and the uses of the yacón.

Note:—There are two specimens of *Polymnia sonchifolia* at W with the same collector and number: *E. Poeppig* 1653. However, one of them (W 48647) indicates: “Peruvia subandina. In montibus siccis ad Cassapi,

Januario 1836”, which agrees exactly with the locality indicated in the protologue, and therefore is regarded here as the holotype of *Polymnia sonchifolia*. The other specimen (W 48648) indicates “Cuchero. Peruvia”.

We failed to find the holotype of *Polymnia edulis*, which is probably in P. In the Herbarium COL we found one Triana’s specimen with the following data: Colombia, Andes Granadinos, “jiquimilla”, alt. 2700–2800 m, February 1854, *J. J. Triana 2475*. Because the label information of this specimen does not match exactly with the protologue of the species, we can not establish with certainty whether the COL specimen corresponds to type material of *P. edulis* or not.

Additional specimens examined:—BOLIVIA. Dept. Cochabamba: Cochabamba, 1891, *M. Bang 1229* (G, GH, K). Dept. La Paz: Sorata, April 1859, *G. Mandon 28* (G, S); cerca de Sorata, April 1947, *Cárdenas 3820* (SI). Dept. Santa Cruz: Prov. Vallegrande, Huasacañada, 5 km al S de Vallegrande 18° 31’ 05” S, 64° 05’ 08” W, 15 June 1991, *I. Vargas C. 1012* (F). Dept. Tarija: Tarija, 24 April 1904, *K. Fiebrig 2852* (G, GH, K, S).

PERU. Dept. Cajamarca: Prov. Celendín, Choctapampa, cerca a Celendín, 3 July 1975, *I. Sánchez Vega 1648* (F); Prov. Cajabamba, Distrito Cajabamba, caserío Campana, carretera a Lluchubamba, 11 April 1991, *I. Sánchez Vega & F. Flores 5550* (F). Dept. Junín: Prov. La Merced, km 73.5 on Tarma-San Rafael road (Rt 20B), 6 July 1987, *M. Warnock & S. Warnock 6211* (TEX); Mito, 8–18 April 1923, *J. Macbride 3421* (F). Dept. Piura Prov. Huancabamba, San Antonio, March 1912, *A. Weberbauer 6016* (F, GH).

Cultivated: ARGENTINA. Prov. Jujuy: Dept. Capital, quebrada del Jaire, camino a Tiracsi, cultivado, 20 May 1962, *A. Cabrera et al. 14710* (LP). Prov. Buenos Aires: La Plata, Jardín Botánico de la Facultad de Agronomía de La Plata, April 1938, *A. Cabrera s.n.* (LP 69181).

COLOMBIA. Dept. Cauca: Mun. Silvia Guambia, April 1948, *S. Agredo 216* (F).

COSTA RICA: Prov. Cartago: Paraíso, March 1893, *J. Smith 6609* (K). Prov. San José: Chemin de la Poudrière a San José, July 1892, *A. Tonduz 699* (G).

ECUADOR. Prov. Pichincha: Quito, in hortulo, 29 December 1919, *I. Holmgren 130* (S); Cantón Quito, Parroquia Calacali, Reserva Geobotánica Pululahua, 0° 05’ N, 78° 30’ W, 17 September 1987, *C. Cerón 2215* (QCNE). Prov. Loja: Jardín Botánico Reinaldo Espinosa, Universidad Nacional de Loja, 4 April 1994, *H. Pedersen 104043* (QCNE). Prov. Chimborazo: Riobamba, interandines Hochland, April 1836, *A. Rimbach 727* (F, S). Prov. Loja: Between Loja and San Lucas, cultivated, 3 August 1980, *M. Mathias & D. Taylor 5288* (F). Prov. El Oro: Entre río Ambocas y Chiguango, SE Zaruma, May 1948, *R. Espinosa 2396* (F).

Smallanthus uvedalius (Linné) Mackenzie (1933: 1406).

Osteospermum uvedalia Linné (1753: 923). *Polymnia uvedalia* (Linné) Linné (1763: 1303). *Polymniastrum uvedalium* (Linné) Small (1913: 302), *nom. illeg.* Type:—UNITED STATES OF AMERICA. Virginia: Habitat in Virginia, without date and collector [lectotype LINN n. 1033.3, designated by Wells (1965), digital image!]. Virginia: Virginia, without date, *Clayton 221* (syntype BM, digital image!)

Polymnia macrophylla Rafinesque (1817: 70). Type:—UNITED STATES OF AMERICA. Louisiana (type not found).

Polymnia uvedalia var. *densipilis* Blake (1917a: 48). Type:—UNITED STATES OF AMERICA. Texas: New Braunfels, August 1850, *F. Lindheimer 381* (holotype GH 11386, digital image!).

Polymnia uvedalia var. *floridana* Blake (1917a: 48). Type:—UNITED STATES OF AMERICA Florida: Brevard Co., Indian River region, 2 December 1902, *A. Fredholm 5626* (holotype GH 11387, digital image!, isotype US 128405, digital image!).

Polymnia uvedalia var. *genuina* [*uvedalia*] Blake (1917a: 47), *nom. inval.* (art. 24.3 of the ICN, McNeill *et al.* 2012).

Herbs 1–5 m tall, homophyllous, stems glabrescent. Leaves opposite, petiolate, 17–30 cm long, lamina 11.5–20 cm wide, widely ovate or subtriangular, acute at the apex, truncate or obtuse at the base, margins 3-partite, mucronate, trinerved, triplinerved, actinodromous, pubescent; petioles 4.5–10 cm long, winged, wings decreasing in width from the blade to the node, entire or lobulate, not auriculate at the base. Capitula 8–10 × 10–14 mm, ca. 15 arranged in corymbiform cymes; peduncles 17–70 mm long, pubescent. Involucre campanulate to hemispherical; phyllaries arranged in 2 series, herbaceous, ovate, outer phyllaries 10–15 × 7–10 mm, acute at the apex, inner phyllaries 6–12 × 4–10 mm, attenuate at the apex. Receptacle with paleae obovate, 4–7 × 1–3 mm, elliptic, apex entire. True ray florets ca. 10, 1-seriate, corollas yellow, ray-limb oblong, 8–17 × 5–7 mm, apex 3-dentate, teeth equal in size, tube 1 mm long. Style 5 mm long, branches 1–2.5 mm long. Disc florets ca. 40, corollas yellow, tubular to campanulate, 5–8 mm long, lobes 1 mm long. Anthers with apical appendage ovate. Style 7–9 mm long, branches 2 mm long. Cypselae rounded-obovate, 3–7 × 2–5 mm, smooth. n=16 (Wells 1965). (Fig. 51).

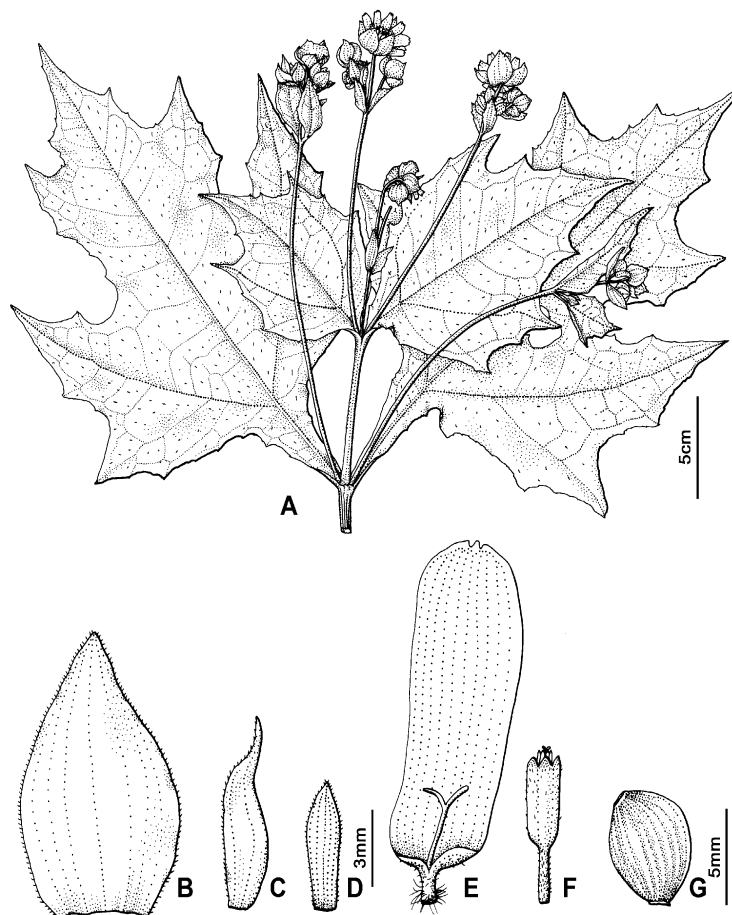


FIGURE 51. *Smallanthus uvedalius* (Linné) Mackenzie. **A.** Habit. **B.** Outer phyllary. **C.** Inner phyllary. **D.** Palea. **E.** Ray floret (without cypsela). **F.** Disc floret (without ovary). **G.** Cypsela (*Tanger s.n.*, GH).

Etymology:—From the Latin *uvidus*, wet, damp, by the humid habitats where members of this species are generally found.

Vernacular names:—Mirasol, paira, purca, xilil.

Distribution and ecology:—United States to Panama. This species is considered naturalized in Bermudas (see Distribution) (Fig. 52). It grows in open, deciduous forests, humid mountain forests and shrublands, margin of forests, margins of streams, roadsides, and marshes, at 0–700 m. Flowering from July to September.

Notes:—When Linné described *Osteospermum uvedalium* (1753: 923), he cited previous works with descriptions of the genus *Osteospermum*: *Hortus Cliffortianus* (Linné 1737), *Florae Leydensis Prodrromus* (Royen 1740), *Flora Virginica* (Gronovius 1743), and *Hortus Upsaliensis* (Linné 1748). Because these works were published before Linné’ *Species Plantarum* (1753), in none of them there is a binomial for *Osteospermum*. However, the *Flora Virginica* is the only one where specimens are cited: *Clayton 138* and *Clayton 221*. Many specimens collected by John Clayton would constitute the syntypes of Linné’s names (Blake 1918), suggesting that the specimens 138 and 221 are possibly the types of *O. uvedalium*. A search of these two specimens resulted in the finding of *Clayton 221* at BM. Apparently, the specimen *Clayton 138* was never found (Mark Spencer, Natural History Museum of London, pers. comm.). For this reason, despite the fact that a lectotype of LINN has been assigned to *Osteospermum uvedalium* by Wells (1965), we establish the specimen *Clayton 221* at BM as a syntype of this species.

See Notes in *S. obscurus*.

Additional specimens examined:—BELIZE. District Belize: Clearing sittee R., 24 April 1907, *M. Peck 875* (GH).

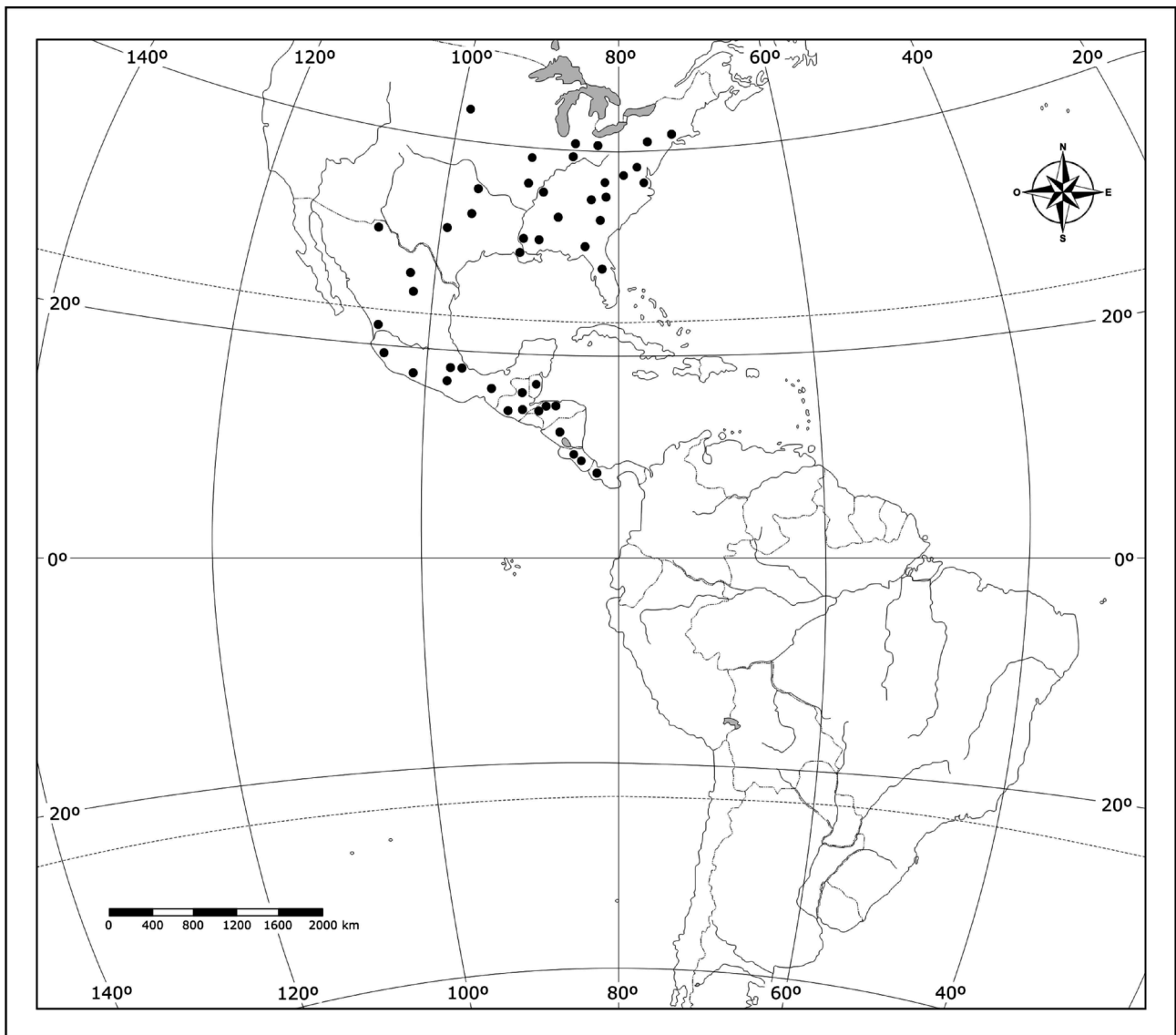


FIGURE 52. Natural range of distribution of *Smallanthus uvedalius*.

BERMUDA. Hamilton Parish: Near Bailey's Bay, February-March 1908, *S. Brown 494* (GH). Paget Parish: Paget, 16 January 1912, *B. Robinson 50* (GH); id., 21 August 1913, *F. Collins 348* (GH); Bob. Garden Paget, June 1905, *W. Harchberger s.n.* (GH). Smith's Parish: Without locality, 21 July 1905, *A. Moore 3061* (GH); Sir Howard Trott's Farm, 28 August 1963, *EAM 359* (GH); S road between Harris Bay and St. Marks, 2 May 1949, *R. Taylor 49-1216* (GH). St. George's Parish: Near Tuckers Town, September 1905, *S. Brown & N. Britton 321* (GH); Tucker's town, February-March 1908, *S. Brown 470* (GH).

COSTA RICA. Prov. San José: Aserri, cuenca del Tárcoles, carretera a Tarbaca, después de la entrada a Barrio Lourdes, 9° 50' 25" N, 84° 06' 28" W, 9 August 2001, *L. Acosta & V. Ramírez 3136* (S); San José, 5 January 1935, *F. Solís 75* (F); Puriscal, cuenca del Pirris-Damas, El Estero, 9° 51' 45" N, 84° 17' 30" W, 12 September 2001, *L. Acosta 3153* (S). Prov. Cartago: Poco antes de llegar a Orosi, esta localidad parece el comienzo de un camino viejo para llegar al valle de Orosi, 7 October 1964, *A. Jiménez M. 2413* (F).

GUATEMALA. Dept. Chimaltenango: Near Tecpam, 12 September 1933, *A. Skutch 608* (GH); at La Soledad, ca. 10 miles W of San Miguel Dueñas, on the road to Yepocapa, 7 August 1960, *J. Beaman 4022a* (GH). Dept. Guatemala: Alameda, 20 November 1936, *J. Johnston 369* (F, GH); vicinity of San Andrecillo, 26 September 1972, *A. Molina R. & A. R. Molina 27547* (F). Dept. Jalapa: Cerro Alcoba, just E of Jalapa, 2 December 1939, *J. Steyermark 32544* (F). Dept. Quezaltenango: Finca Pirineos, volcán Santa María, between Santa María de Jesús and Calahuaché, 31 December 1939, *J. Steyermark 33194* (F); along Quebrada San Gerónimo, Finca Pirineos,

volcán Santa María, between Santa María de Jesús and Calahuaché, 1–2 January 1940, *J. Steyermark* 33486 (F); Finca La Providencia Peláez, near Colomba, 29 May 1944, *S. White* 5222 (F). Dept. Retalhuleu: Vicinity of Retalhuleu, 17 February–1 March 1941, *P. Standley* 88673 (F); id., 27 March 1939, *P. Standley* 66676 (F). Dept. San Marcos: Near Aldea Fraternidad, between San Rafael Pie de la Cuesta and Palo Gordo, Sierra Madre mountains, 10–18 December 1963, *L. Williams et al.* 25711 (F); between Finca El Porvenir and Loma Corona, 9 miles NW of El Porvenir, SW of volcán Tajumulco, 14 March 1940, *J. Steyermark* 37758 (F, GH); Tajumulco volcano, Sierra Madre mountains, about 8–10 km W of San Marcos, 31 December–1 January 1965, *L. Williams et al.* 26927 (F); río Cabús, near Malacatán, 15 March 1939, *P. Standley* 68880 (F). Dept. San Miguel: Finca Santa Emilia, near Pacayal, 19 February 1931, *J. Bequaert* 23 (F, GH). Dept. Sololá: Vol. Atitlán, February 1907, *W. Kellerman* 6310 (F); above Lake Atitlán, about 3–5 km W of Panajachel, 6–7 December 1963, *L. Williams et al.* 25268 (F).

HONDURAS. Dept. Cortes: Río Lindo, 1 km de Cañaverales, 25–26 August 1955, *A. Molina R.* 5511 (F). Dept. Atlántida: Cordillera Nombre de Dios, road from Olanchite to La Ceiba, 22 May 1987, *S. Blackmore & M. Chorley* 4084 (F).

MEXICO. State Coahuila: District Arteaga, Sierra Arteaga, 24 July 1949, *G. Hinton et al.* 16816 (GH); 15 mi. South Arteaga, 16 August 1948, *Kenoyer & Crum* 2884 (GH). State Nayarit: 11 mi. W of Jalisco, 21° 20' N, 104° 55' W, 19 October 1970, *G. Webster & G. Breckon* 15745 (GH). State Nuevo León: Municipality Zaragoza, cerro El Viejo, 15 mi. W Dulces Nombres, 19 August 1948, *F. Meyer & D. Rogers* 3031 (GH). State Veracruz: 4 miles NW of Cordoba, San Nicolás, 16 October 1965, *A. Cronquist & M. Sousa* 10353 (GH); Mun. Ixtaczoquiátlán, 2 km (by air) SE of Fortín, 18° 53' 30" N, 97° 01' W, 7 December 1981, *M. Nee* 23860 (F, GH); Prov. Huasteca, Wartenberg, near Tantoyuca, 1858, *L. Ervendberg* 286 (GH); Orizaba, 9 August 1924, *G. Fisher s.n.* (F 554862); region of San Andres Tuxtla, near Tapalapan, NW of Santiago Tuxtla, 11 August 1953, *R. Dressler & Q. Jones* 48 (GH); Amatitlán, Villa Nueva, November 1889, *E. Heyde & E. Lux* 4509 (F); Zacuapán, December 1907, *C. Purpus* 2853 (GH).

NICARAGUA. Dept. Jinotega: Santa Lastenia, between Matagalpa and Jinotega, 13° 02' N, 85° 57' W, 22 August 1984, *W. Stevens* 23003 (F).

PANAMA. Prov. Chiriquí: At about one mile SW of Boquete, 20 July 1947, *P. Allen* 4726 (GH); Boquete Plentiful about town, 7 August 1972, *W. D'Arcy & J. D'Arcy* 6505 (F); District Boqueli, volcán de Chiriquí, 15 July 1938, *M. Davidson* 978 (F, GH); Boquete, Fred Collins Finca, 3 August 1960, *J. Ebinger* 718 (F).

UNITED STATES OF AMERICA. State Alabama: Clay Co., July 1902, *W. Sherwood s.n.* (GH); Marshall Co., Bucks Pocket State Park, 10 August 1973, *R. Kral* 51114 (GH); Clay Co., without locality, July 1902, *T. Harbison s.n.* (GH). State Arkansas: Hempstead Co., Fulton, 8 September 1917, *E. Palmer* 12681 (GH); Hot Springs Co., Malvern, 19 September 1937, *D. Demaree* 16292 (GH); Johnson Co., Mount Levi, 22 August 1939, *D. Demaree* 20281 (GH); Garland Co., Blakely Mountain Dam Reservoir, Cedar Glades, 28 August 1939, *D. Demaree* 20497 (GH); Montgomery Co., Bluffs in Blakely Dam Reservoir, Silver, 19 September 1953, *D. Demaree* 34313 (GH); Sevier Co., Ben Lomond, 20 September 1959, *D. Demaree* 41622 (GH). State Delaware: New Castle Co., Alapokas, on Brandywine Creek, just N of Wilmington, 31 August 1937, *R. Tanttall* 3504 (GH); Wilmington, August 1842, *E. Iatrall s.n.* (GH); coast of Delaware, Rehoboth, 13 September 1908, *J. Churchill s.n.* (GH). State Florida: Without locality and date, *A. Chapman s.n.* (GH), *J. Lowell s.n.* (GH); Apalachicola, July–August 1897, *A. Chapman* 788c (GH); Hammock, S of Daytona, 8 May 1918, *J. Small* 8690 (GH); Rock Bluff Landing, Apalachicola River, 6 August 1927, *K. Wiegand & W. Manning* 3314 (GH); Volusia Co., Canal Rd. in Daytona, 6 September 1943, *E. Butts s.n.* (GH); Liberty Co., Apalachicola river bluffs at Aspalaga, 25 July 1956, *R. Kral* 3090 (GH); Escambia Co., near Bayou San Marcus Creek, W of Pensacola, 28 September 1957, *R. Kral & R. Godfrey* 6035 (GH); Alachua Co., 1.5 mi. S of Gainesville, 9 August 1965, *D. Burch* 691 (GH); Leon Co., Tallahassee, 7/9 August 1896, *G. Nash* 2327 (G, GH). State Georgia: Whitfield Co., roadside in W part of the county, 27 July 1900, *R. Harper* 316 (K); Upson Co., along Double Branch, above Flint R., SE of Woodbury, 17 July 1948, *A. Cronquist* 5504 (GH); Bartow Co., Allatoona Creek, 3 mi. S of Allatoona Dam., 19 July 1948, *W. Duncan* 8416 (GH); Douglas Co., 2 mi. E of Villa Rica, 27 July 1948, *A. Cronquist* 5565 (GH); Wilkes Co., Kettle Creek, 6 1/2 mi SE of Washington, 18 July 1950, *W. Duncan* 11409 (GH, LP); McIntosh Co., near S end of Sapelo Island, 19 July 1956, *W. Duncan* 20324 (S); Rabun Co., N flank of Bit Mt., south of Rock Gorge, 21 July 1968, *D. DuMond* 1306 (G); Murray Co., along Muskrat Creek road, near US Forest Service work center, 2.9 mi. E of Eton, 5.3 mi. NE of Chatsworth, 28 August 1979, *S. Jones* 23438 (GH); Early Co., near Chattahoochee river, 14 August 1901, *R.*

Harper 1225 (GH). State Indiana: Orange Co., along Lick Creek, about 3 mi. W of Paoli, 14 July 1915, *C. Deam 17347* (GH). State Kentucky: Harlan Co., Big Black Mountain, August 1893, *T. Kearney 251* (G, GH, S); Fayette Co., Broome Creek, 28 August 1926, *W. Anderson 357* (GH); Wayne Co., NW of Monticello, 17 July 1937, *L. Smith & A. Hodgdon 4018* (GH); Clark Co., Grimes Mill road, 16 July 1955, *M. Beckett 689* (GH); Fayette Co., Ranan Run, 4 August 1955, *M. Wharton 9285* (GH); Clark Co., Jonett Creek, 29 August 1955, *M. Beckett 954* (GH); banks of the Kentucky, July 1933, *H. Griswold 2273* (GH); Lexington, Kentucky river, Comb's ferry, July 1833, *R. Peter s.n.* (K); rocky borders of water conser., *C. Short s.n.* (K). State Louisiana: Without locality, *C. Duvand s.n.* (GH). State Maryland: Prince Georges Co., Accokeek, just E of Charles Co. line marker, 26 August 1984, *S. Hill & M. Klein 15367* (GH); near Plummer Island, above Cabin John, 28 September 1902, *P. Dowell 1748* (GH). State Mississippi: Oktibbeha Co., 6 mil N of Starkville, 9 July 1956, *J. Ray 6730* (GH); Jefferson Co., 5 mi. NNW of Church Hill, 5 September 1966, *S. Jones & B. Noble 10226* (GH); Bilexi, 7 April 1900, *S. Tracy 6972* (G). State Missouri: Jackson Co., Ocean Springs, 22 August 1951, *D. Demaree 31224* (GH); Jasper Co., Oronogo, 22 August 1920, *E. Palmer 13458* (GH); Barry Co., 11 September 1935, *B. Bush 15193* (G); Bapter, 11 September 1935, *B. Bush 15183* (G); State New York: Weehawken, near New York, 8 August 1864, *T. Allen s.n.* (GH); Cayuga Co., Big Guly Ravine, Springport, 14 September 1919, *A. Eames et al. 13156* (GH); State North Carolina: Martin Co., near Conoho Creek, 4.2 miles NW of Williamston, 9 August 1958, *A. Radford 39502* (S); Caldwell Co., Blowing Rock Mountain, 31 July 1891, *J. Small & A. Heller s.n.* (GH, S); McDowell Co., 1 mile E of Little Switzerland, 23 August 1927, *K. Wiegand & W. Manning 3315* (GH); Wake Co., near Raleigh, 18 August 1937, *R. Godfrey s.n.* (GH); Wake Co., Raleigh, 8 August 1938, *R. Godfrey 5927* (GH); Halifax Co., near Winton, 18 August 1938, *R. Godfrey 5185* (GH); Pender Co., Northeast river, near Rocky Point, 25 August 1950, *R. Godfrey & S. Boyce 50485* (GH); Transylvania Co., Windy Falls at trail end, Horsepasture river, ca. 1.7 mi. SE of rte. 281, 16 August 1988, *S. Hill & J. Hains 19845* (GH); near Biltmore, 9 August 1897, *Biltmore 788a* (GH). State Ohio: W of Hamilton, 22 July 1932, *L. Ferguson s.n.* (G); Fernbank, ad ripas fluminis Ohio, prope North Bend, without date, *X. Short s.n.* (K). State Oklahoma: Sapulpa, 19 September 1895, *B. Bush 1329* (K); Johnston Co., near Fishormingo, October 1915, *H. Houghton 3518* (GH); Oklahoma Co., basin of N Canadian River, 1 mi. S of Harrah, 26 July 1941, *U. Waterfall 3098* (GH); Cherokee Nation, 20 August 1895, *J. Blankinship s.n.* (GH). State Pennsylvania: Lafayette, College, Easton, 30 August 1869, *T. Porter s.n.* (GH); Greene Co., Perry Jwp., 20 August 1922, *S. Dickey 129* (GH); Lancaster Co., 1/2 mile SE of Millersville, 1 August 1938, *L. Tanger s.n.* (GH); Alleheny Co., Natrona, 21 July 1901, *J. Shafer 1473* (GH). State South Carolina: McCormick Co., near Ivoy, 18 August 1921, *J. Davis 2055* (G); Santee Canal, 1 mile N of Moncks Corners, 13 July 1927, *K. Wiegand & W. Manning 3311* (GH); Jasper Co., 4 miles E of Coosawhatchie, 20 July 1927, *K. Wiegand & W. Manning 3312* (GH); Williamsburg Co., 8 miles SE of Gourdin, 10 July 1939, *R. Godfrey & R. Tryon 454* (GH); Pickens Co., Eastatoe Creek Gorge at the end of County road 92, 35° 2' 22" N, 82° 49' 03" W, 18 July 1975, *D. Boufford & E. Wood 17426* (GH); Pickens Co., 12 Mile Creek, W of Pickens, 22 August 1956, *A. Radford 16587* (GH); Oconee Co., rte. 76, 5.8 mi. N of Chauga river bridge, 4.1 mi. S of Long Creek, 13 September 1987, *S. Hill 18812* (GH); Sumter Co., boat landing at Wateree river on US 378, 2 September 1994, *J. Nelson 16141* (K); Santee Canal, June (without year), *H. Ravenel s.n.* (GH). State South Dakota: 1 1/2 miles N of Huron, 11 August 1935, *R. Kriebel 3592* (GH). State Tennessee: Davidson Co., Joelton, 16 July 1922, *H. Svenson 120* (GH); Cheatham Co., Craggie Hope, 22 August 1930, *H. Svenson 4216* (GH); Knoxville, August 1931, *Ruth s.n.* (S); Clinton, 6 August 1931, *W. Rhoades 350/C* (S); Davidson Co., Bordeaux, 23 July 1935, *H. Svenson 7331* (GH); Jackson Co., along Big Bottom Road, about 2 miles N of Gainsboro, 18 August 1992, *V. McNeilus 92-788* (GH); Cowan, 21 August 1997, *T. Harbison s.n.* (GH); Marshall Co., about 1 mile S of Rt. 99, 3 September 1998, *V. McNeilus 98-850* (GH); Chilhowee Mts., August (without year), *A. Curtiss 1380* (G). State Texas: Guadalupe, 1847-48, *F. Lindheimer 437* (GH); Guadalupe, September 1847, *F. Lindheimer 637* (GH, K); Knoxville, 15 August 1894, *A. Ruth 52* (GH); Comanche Spring, new Braunfels, etc., August 1850, *F. Lindheimer 954* (G, GH); Terrant Co., 24 September 1923, *A. Ruth 331* (GH); Comal Co., near New Braunfels, at KL Ranch campgrounds, 21 July 1996, *M. Enquist 3099* (GH); Gregg Co., 1 September 1941, *C. York s.n.* (GH); Huckley, 1884, *F. Huroc. s.n.* (GH); without locality and date, *C. Wright s.n.* (GH). State Virginia: Smyth Co., Fork Holston River, at St. Clair's bottom, 30 July 1892, *J. Small s.n.* (GH, K); Cheaspeake Bay region, Fom Rule Run, 16 August 1902, *G. Shull 225* (GH); Beford Co., 30 August 1872, *A. Curtiss s.n.* (S); Fairfax Co., Great Falls, 25 August 1918, *S. Blake 7110* (S); Williamsburg, edge of town, 11 August 1921, *E. Grimes 4219* (GH); Rockbridge Co., about Lexington, 21 August 1924, *J. Churchill s.n.* (GH); Surrey Co., Scotland Wharf, James River, 1 September 1930, *E. Walker 1314* (LP); Virginia Co.,

Alexandria, 18 July 1918, *W. Hunnewell 5490* (GH); Princess Ann Co., N of Blackwater river, 7 August 1934, *M. Fernald & B. Long 4253* (GH); Princess Ann Co., Great Neck, 5 September 1935, *M. Fernald & B. Long 5116, 5118* (GH); Henrico Co., Westhampton, August 1936, *M. Fernald et al. 6722* (GH); Gloucester Co., south of White Marsh, 22 July 1938, *M. Fernald & B. Long 8892* (GH); Surry Co., James River, 23 August 1938, *M. Fernald & B. Long 9197* (GH); Sussex Co., along Nottoway River, Double Bridge, about 6 miles NW of Jarratt, 18 August 1939, *M. Fernald & B. Long 11193* (GH); Surry Co., Cobham Bay, James River, 25 August 1940, *M. Fernald & B. Long 12877* (GH); Isle of Wight Co., back of sand beach of Burwell's Bay, James River, below Fort Boykin, 30 August 1940, *M. Fernald & B. Long 12876* (GH); Brunswick Co., Seward forest, near Triplett, 12 September 1944, *M. Fernald & J. Lewis 14754* (GH); Shenandoah Co., near Strasburg, 31 July 1946, *F. Hunnewell 18709* (GH); Shenandoah Co., Strasburg, 24 August 1939, *H. Allard 7305* (GH); Giles Co., along Sinking Creek, near Newport, 9 July 1962, *J. Hardin 2503* (G); Amhers Co., James River Gorge, between Snowden and Balcony Falls, 16 August 1954, *R. Freer 2257* (GH); Mingo Co., near Varney School, 7 July 1930, *W.V.U. Botanical Expedition s.n.* (GH); Marion Co., 4 miles N of Fairview, 15 August 1922, *S. Dickey 101* (GH); Pendleton Co., Hermit Island, 7 August 1930, *E. Berkeley s.n.* (GH); Cabell Co., Pleasant Valley, 1 August 1938, *F. Gilbert 743* (GH); Arlington, without date, *D. Lidestrom 8131* (GH); Botetourt Co., along rt 622, down James river from Arcadia, 28 July 1954, *R. Freer 2189* (GH). Washington DC.: Washington DC. and vicinity, 1 September 1896 / August 1897, *E. Steele s.n.* (G); in vicinis Washington DC., 21 September 1879, *L. Ward s.n.* (GH); Without or dubious state: Saint Louis?, without date, *Drummonds? s.n.* (K); Hort. Cantab., 1884, without leg., Herb. A. Gray (GH); Hort. Cantab., Monts Cavi, 1845, Herb. Asa Gray (GH); Anna. Ill., 16 August 1880, *A. Seymour 1209* (GH); Lausar's heard, Lo. Cec., 13 August 1881, *J. Smith s.n.* (GH); La., without date, *Hacler s.n.* (GH).

Without country and locality: *F. Blatt 323* (GH); Herb S 09-46531 (S); Herb S 09-46524 (S); Herb. J. Gay (K H2010/00307 64); Herb. B. Goodenough (K H2010/00307 74).

EXCLUDED SPECIES

Smallanthus suffruticosus (Baker) Robinson (1978: 51), based on *Melampodium suffruticosum* Baker (1884: 162) = *Polymnia suffruticosa* (Baker) Badillo (1946: 310). It is currently a synonym of *Unxia suffruticosa* (Baker) Stuessy (1969: 319). Type:—VENEZUELA. Prope Esmeralda, ad flumen Orinoco, December 1853, *Spruce 3225* (holotype K, digital image!).

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APENDIX I

Collector Index

Species acronyms: SA = *Smallanthus apus*; SC = *S. cocuyensis*; SCO = *S. connatus*; SF = *S. fruticosus*; SG = *S. glabratus*; SJ = *S. jelskii*; SL = *S. latisquamus*; SLU = *S. lundellii*; SM = *S. macroscyphus*; SMA = *S. maculatus*; SMC = *S. mcvaughii*; SME = *S. meridensis*; SMI = *S. microcephalus*; SO = *S. oaxacanus*; SOB = *S. obscurus*; SP = *S. parviceps*; SPU = *S. putlanus*; SPY = *S. pyramidalis*; SQ = *S. quichensis*; SRI = *S. riparius*; SS = *S. siegesbeckia*; SSO = *S. sonchifolius*; SU = *S. uvedalius*.

Abbiatti & Claps 785 (SM)
Acosta 3153 (SU)
Acosta & Ramírez 3136 (SU)
Acosta Solís 5995, 6557, 6814 (SF), 10475, 13455 (SPY), 13585 (SF)
Agredo 216 (SSO)
Aguilar 366 (SMA), 1193 (SO)
Allard 7305 (SU)
Allen 4726 (SU)
Almeda & Nakai 4642 (SMA)
Anderson 357 (SU)
Anderson & Liskowski 3912 (SMA)
André 1244 (SPY)
Apolinar-María 451 (SRI)
Araquistain & Moreno 1582 (SMA)
Aristeguieta 2421 (SPY), 2484 (SME)
Ariste-Joseph 1015 (SRI)
Arsène 5882, 8284 (SMA)
Asplund 7981 (SF), 11186, 11375 (SG), 16066 (SRI), 19733 (SS)
Badillo 5320 (SPY)
Bailetti 59 (SM)
Bailey 356 (SMA)
Balansa. 916 (SCO)
Balick et al. 2216 (SMA)
Balslev 1911 (SF)
Bang 466 (SS), 1229 (SSO), 1813 (SG)
Barkley 39547 (SO)
Bartlett 10508 (SMA, type), 12096 (SMA), 21260, 21385 (SCO)
Beaman 4022a (SU), 6425 (SMA)
Beck 7500, 8709 (SS), 17529 (SP)
Beckett 954 (SU)
Bequaert 23 (SU)
Bernoulli 576 (SMA)
Bertoni 2184 (SCO)
Biltmore 788a (SU)
Blackmore & Chorley 4084 (SU)
Blake 7110 (SU)
Blatt 323 (SU)
Bonpland 1640 (SRI, type)
Botteri 237 (SMA, type)
Boufford & Wood 17426 (SU)
Bourgeau 514, 596, 1635 (SMA)
Boyle 7579 (SQ)
Breedlove 41387 (SOB, type), 6168, 6839, 7483 (SMA), 8724 (SL), 11598 (SQ)
Breedlove & Raven 13091 (SOB)
Brenckle 47–239 (SMA)
Brown 470, 494 (SU)
Brown & Britton 321 (SU)
Brunel 556 (SP)
Buchtien 748 (SS)
Burch 691 (SU)
Burchell AA95 (SM)

Burger & Gomez P. 8362 (SL)
Bush 1329 (SU)
Bush 15183, 15193 (SU)
Cabrera 127, 1711, 2784, 4906, 7423 (SCO), 8413 (SM)
Cabrera & Añón Suarez 18514 (SM)
Cabrera & Marchionni 12815 (SM)
Cabrera & Sáenz 29177 (SCO)
Cabrera et al. 13266 (SM), 14710 (SSO), 26188 (SM)
Calzada 3228, 4712 (SMA)
Camp 2036, 3902 (SF), 4033 (SMI), E-2791 (SPY)
Campos et al. 4563 (SMC)
Carballo & Aldana 570 (SMA)
Cárdenas 3820 (SSO)
Carranza 2647 (SMA)
Castillo & Castillo 2315 (SMA)
Cerón 2215 (SSO), 15672, 15811 (SPY), 17656 (SF)
Chapman 788c (SU)
Charpin & Jacquemoud 13361 (SRI), 13599 (SPY)
Chebataroff 969, 8964 (SCO)
Chindoy 78 (SPY)
Chrysler 5544 (SL)
Clayton 221 (SU, type)
Clos 1842 (SCO)
Cochrane et al. 8629 (SMA)
Collins 348 (SU)
Contreras 6378, 7148, 8938 (SMA), 11065 (SLU)
Cook & Gilbert 818 (SP, type)
Cooper 5827 (SMA)
Cowan 4422 (SJ)
Croat 39629 (SMA)
Cronquist 5504, 5565 (SU)
Cronquist & Becker 11187 (SMA)
Cronquist & Fay 10874 (SMA)
Cronquist & Sousa 10353 (SU)
Cuatrecasas 9602 (SF), 11964 (SPY), 13412 (SRI), 13548, 13614 (SPY), 15539, 19511 (SRI), 20455, 20886 (SPY), 23762 (SRI)
Cuatrecasas & del Llano 27325 (SPY)
Cuatrecasas & García Barriga 1700 (SC, type)
Cuatrecasas et al. 5342 (SRI)
Curtiss 1380 (SU)
D'Arcy & D'Arcy 6505 (SU), 6529 (SMA)
Davidson 978 (SU)
Davis 2055 (SU)
de la Sota 4309 (SM)
de Wolf Jr. 1953 (SRI)
Deam 236 (SMA, type), 17347 (SU)
Demaree 16292, 20281, 20497, 31224, 34313, 41622 (SU)
Díaz-Barriga 2888 (SMA)
Dickey 101, 129 (SU)
Diers 1021 (SF), 1241 (SS)
Dillon et al. 1110 (SP), 3088, 4545 (SF), 6422 (SJ)
Dodson & Embree 13362 (SRI)
Dodson et al. 13936 (SRI)
Dombrowski 23 (SCO)
Dowell 1748 (SU)
Dressler & Jones 48 (SU)
DuMond 1306 (SU)
Duncan 8416, 11409, 20324 (SU)
Dusén 2494 (SCO), 9503 (SS), 10932 (SCO), 11362 (SM)

Dutra 1470 (SCO)
Dwyer 2419 (SMA)
Dwyer & Pippin 10194 (SMA)
EAM 359 (SU)
Eames et al. 13156 (SU)
Ebinger 718 (SU)
Edwin & Schunke V. 3904 (SG)
Ehrich 426 (SM)
Ekman 1027 (SCO)
Elias 52 (SRI)
Ellsworth et al. 9099 (SF)
Enquist 3099 (SU)
Ervendberg 286 (SU)
Espinosa 2396 (SSO)
Estrada & Binder 2286 (SMA)
Ewan 16893 (SF)
Eyerdam et al. 23363 (SCO)
Fabris 2458 (SCO)
Fabris et al. 5351 (SM)
Fagerling & Wibom 766 (SPY)
Fendler 775 (SRI)
Fernald & Lewis 14754 (SU)
Fernald & Long 4253, 5116, 5118, 8892, 9197, 11193, 12876, 12877 (SU)
Fernald et al. 6722 (SU)
Ferreyra 7456 (SP)
Fiebrig 2852 (SSO), 5728 (SCO)
Firmin 676 (SF)
Fleig 940 (SCO)
Fosberg 22308 (SPY)
Fredholm 5626 (SU)
Freer 2189, 2257 (SU)
Gamerro 1001 (SCO)
Gardner 253 (SS)
Gaudichaud 692 (SS, type), 885 (SCO, type)
Gehriger 10 (SPY)
Gentle 2215 (SMA)
Gentry et al. 23509 (SG)
Ghiesbrecht 106 (SO), 577 (SMA)
Gilbert 743 (SU)
Glassman 1857 (SO), 2173 (SMA)
Glaziou 15071 (SS)
Godfrey 5185, 5927 (SU)
Godfrey & Boyce 50485 (SU)
Godfrey & Tryon 454 (SU)
Grant & Fosberg 9375 (SC)
Grimes 4219 (SU)
Grings 441 (SCO)
Griswold 2273 (SU)
Gruner 591 (SCO)
Gusmán et al. 731 (SMA)
Gutiérrez et al. 3099 (SPU, type)
Hansen & Nee 7411 (SMA)
Hardin 2503 (SU)
Harling et al. 9148 (SRI), 10243 (SF)
Harmon & Dwyer 2977 (SMA)
Harper 316, 1225 (SU)
Hartweg 1158 (SF, type)
Hassler 5341 (SCO)
Hatschbach 17808 (SM), 21091 (SCO)

Hatschbach 19314 & Guimarães 307 (SM)
Hatschbach & Guimarães 20520 (SCO)
Haught 5773 (SPY)
Hawkes et al. 1932 (SO), *1936* (SMA), *2083* (SO)
Hernández & Hernández 5170 (SMA)
Herrera 1480 (SP)
Herter 379 (SCO)
Heyde & Lux 3375 (SQ, type), *3807* (SMA, type), *4509* (SU), *6161* (type, SMA)
Hill 18812 (SU)
Hill & Hains 15367,19845 (SU)
Hillosín 1418 (SM)
Hinton 1347 (SLU), *5227* (SMA)
Hinton et al. 16816 (SU)
Holmgren 130 (SSO), *804* (SRI), *921* (SF)
Holm-Nielsen 20880 (SPY)
Holway 62 (SMA), *553* (SMA, type), *3598* (SMA, type)
Holway & Holway 558 (SP), *974* (SPY, type)
Hougleton 3518 (SU)
Huidobro 3726, 3788 (SCO)
Hunnewell 5490, 18709 (SU)
Hunziker 3384, 1545 (SCO)
Hurrell & Buzzano 6336 (SCO)
Hurrell et al. 2520, 2816, 2817 (SCO)
Hutchinson & Wright 6602 (SG)
Ibarrola 975 (SCO)
Iltis et al. 29436 (SMC)
Isern 625, 2272 (SS)
Jahn 787 (SPY)
Jameston 856 (SF)
Jarmillo & Winnerskjold 5945 (SPY)
Jiménez 555, 1209 (SMA), *2413* (SU)
Johns 81–54 (SP)
Johnson 20 (SO)
Johnston 369 (SU), *811, 1088, 1103* (SMA)
Jones 23438 (SU)
Jones & Noble 10226 (SU)
Jorgensen 4444 (SS)
Kearney 251 (SU)
Keller 3396 (SCO)
Kellerman 5305, 5384, 5447 (SMA), *6310* (SU), *7701* (SMA)
Kenoyer 166, 756 (SMA), *2226* (SOB)
Kenoyer & Crum 2884 (SU), *3010* (SMA)
Killip 6859 (SPY), *7842, 16437* (SRI)
Killip & Smith 18043, 19693, 20484 (SPY), *21647* (SG), *22268* (SP)
King 4427 (SMA), *6621* (SF), *6810* (SMA)
King & Almeida 7738 (SF)
King & Bishop 7424 (SS), *9111, 9138, 9269* (SG), *9299* (SS)
King & Garvey 6971 (SF)
King & Guevara 5701, 5702, 5771 (SF)
King & Renner 7109 (SO), *7141* (SMA)
King et al. 5660 (SPY), *5825* (SF), *5947* (SRI), *10411* (SPY)
Kimupp 2968, 2994, 3204 (SCO)
Kimupp & Lorenzi 3132 (SCO)
Klug 3399 (SS)
Krach 8533 (SS)
Kral 3090, 51114 (SU)
Kral & Godfrey 6035 (SU)
Krapovickas 2700 (SCO)
Krapovickas et al. 16652 (SCO)

Kriebel 3592 (SU)
Kuhlmann 2778 (SS)
Kummrow 1298 (SM)
Lanfranchi 429 (SCO)
Larsen 302 (SF)
Lawrence 225 (SRI)
Lechler 2129 (SP)
Legrand 3372 (SCO)
Lehmann 4895 (SMI), 5528 (SRI)
Leiva & Leiva 314, 596 (SF)
Leiva et al. 756, 1196 (SF), 1267 (SS), 1953 (SF)
León 242, 458 (SMA)
Lewis et al. 633 (SMA)
Lidestrom 8131 (SU)
Liebmann 387 (SO, type), 8991/305 (SMA)
Lillo 5832 (SM)
Lindberg 5 (SM, type)
Lindeman & de Haas 4713 (SM)
Lindheimer 381 (SU, type), 437, 637, 954 (SU)
Little & Little 9238, 9792 (SPY)
Llatas Quiroz 1977 (SG), 3063 (SF)
Long & Burch 3139 (SMA)
López 603 (SG)
López & Sagástegui 5471 (SJ)
López et al. 7608 (SMI), 7764 (SP)
Lundell & Contreras 18916 (SLU, type)
Luteyn 1498 (SMA), 5496 (SG)
Luteyn & Cotton 11133 (SMI)
Macbride 5388 (SS)
Macbride & Featherstone 1554, 1741 (SG), 532 (SF)
MacDaniels 704 (SMA)
MacVaugh 13169 (SMA)
Malme 738, 861 (SCO)
Mandon 28 (SSO), 30 (SF)
March 4549 (SRI)
Márquez & Yong 372 (SMA)
Martínez Calderón 741 (SL)
Martínez et al. 25213 (SMA)
Mathias & Taylor 5288 (SSO)
Matuda 764, 17527 (SMA)
McNeilus 92–788, 98–850 (SU)
McVaugh 23189 (SMC, type), 23456 (SMC)
Metcalf 30279, 30488 (SG)
Meyer & Rogers 3031 (SU)
Mille 490 (SF), 566 (SPY)
Molina 423, 2749, 3325, 4093, 5815, 10011, 10854, 12793, 14515, 22225, 22605, 26266 (SO)
Molina R. 1096, 2338, 3317 (SMA), 5511 (SU), 10872, 11962, 15385, 21436, 21993, 22606, 23231, 26140, 27123 (SMA)
Molina R. & A. Molina 30971, 12330 (SO), 25871, 26667 (SMA), 26794 (SO), 26820 (SMA), 27547, 30729 (SU)
Molina R. & Montalvo 21838 (SMA)
Mondin 2643, 2858 (SCO)
Mondin & Iob 2553 (SM), 2653 (SM, type)
Montes 1447, 10758 (SCO)
Moore & Wood Jr. 4363 (SMA)
Moore 3061 (SU), 5041 (SMA)
Mueller & Mueller 250 (SMA)
Nash 2327 (SU)
Nee 23860 (SU)
Nelson 3221a (SO, type), 3616, 4401 (SMA), 16141 (SU),

Novara 5932, 6288, 6484, 7613, 7846, 7993, 8575 (SM)
O'Donell 2991 (SM)
Orozco 266 (SMA)
Ortega 286 (SMA)
Palmer 12681, 13458 (SU)
Panero & Clark 2906 (SMI)
Panero et al. 2875 (SMC)
Parodi 23 (SS)
Peck 875 (SU)
Pedersen 9551 (SCO), 104043 (SSO)
Pennell 1844, 8931 (SRI), 14542 (SF), 16861 (SMA)
Pennell et al. 8702, 8731 (SRI)
Percy Nuñez & Cruz 6807 (SS)
Pittier 12942 (SPY)
Pittier 42 (SQ), 4251 (SMA), 4923 (SMA, type), 6993 (SMA), 7510 (SRI), 8617 (SMA), 9787 (SRI)
Plunkett 191 (SMA)
Poepfig 1653 (SSO, type)
Pringle 3326 (SMA, type), 13564 (SMA, type)
Proctor 25374 (SMA)
Purpus 2853 (SU), 3024 (SMA), 9102 (SO)
Radford 16587, 39502 (SU)
Rambo 11475, 30992, 35097, 49620 (SCO)
Rau 19 (SCO)
Ray 6730 (SU)
Regnell 195 (SM, type)
Reitz 6472 (SM)
Reitz & Klein 8472, 14704, 16356 (SM)
Reveal & Harley 4057 (SMA)
Rhoades 350/C (SU)
Rimbach 85 (SPY), 629 (SF), 727 (SSO)
Ritter 204 (SCO)
Robinson 50 (SU)
Rodrigo 2214, 3479 (SCO)
Rodríguez 374 (SM)
Rodríguez A. et al. 6992 (SRI)
Rodríguez J. 1435 (SMA), 804 (SO)
Rodríguez V. 560 (SCO)
Rojas 664 (SPY), 4833 (SS)
Rose 2077 (SA), 2079 (SA, type)
Rosbach 3428 (SMA)
Ruiz Leal & Roig 15931 (SCO)
Rusby 1669, 1670 (SG)
Ruth 52, 331 (SU)
Rzedowski 11146 (SMA)
Sagástegui & Mostacero 9206 (SF)
Sagástegui et al. 8090 (SJ), 9702 (SF), 9973 (SMI), 12197 (SJ), 12634 (SP), 14271 (SMI), 14560 (SF)
Sánchez Vega 1648 (SSO), 2781 (SG), 6640 (SF)
Sánchez Vega & Flores 5550 (SSO)
Sánchez Vega & Miranda 6331 (SJ)
Sánchez Vega & Sánchez Vega 1589 (SJ)
Sánchez Vega & Torres 6414 (SF)
Sánchez Vega et al. 1658, 5187 (SF)
Sandeman 5765 (SPY)
Santesson 43 (SCO)
Scala 435 (SCO)
Schiefer 899 (SPY)
Schimpff 633, 827 (SF), 937 (SPY)
Schimtz 250 (SMA)
Schinini & Carnevali 10670 (SCO)

Schinini & Fernández 6020 (SCO)
Schinini et al. 34710 (SM)
Schipp 804 (SMA)
Schreiter 4120 (SM)
Schulz 6604 (SM)
Schwarz 1572, 3632 (SCO)
Schwindt 2998 (SCO)
Seaton 420 (SMA, type)
Seijo et al. 223 (SM)
Seler 2727 (SMA)
Sello 2485 (SCO, type)
Sessé et al. 3972 (SMA)
Seymour 1209 (SU)
Shafer 1473 (SU)
Shull 225 (SU)
Silva et al. 2280
Skutch 608 (SU), 1704 (SQ)
Small 8690 (SU)
Smith 6609 (SSO), 913 (SRI)
Smith A. 462 (SMA)
Smith D. 6210 (SF)
Smith D. & Buddensiek 10933 (SG)
Smith D. et al. 12137 (SF)
Smith J. 2384 (SMA, type), 2863 (SMA, type)
Smith L. & Klein 11023 (SM), 11204, 14157 (SCO)
Smith L. & Hodgdon 4018 (SU)
Smith L. & Reitz 10222 (SM)
Sobral & Jarenkow 8055 (SM)
Sobral et al. 9514 (SM)
Sodiro 114 (SPY), 24/2 (SML, type), 24/4 (SF, type)
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Solbrig & Ornduff 4560 (SMA)
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