

Taxonomic Revision of the Neotropical Genus *Psiguria* (Cucurbitaceae)

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Abstract—*Psiguria* is a genus of lianas found throughout the Neotropics from sea level to 2,100 m, in dry or wet forests, in both light gaps and shade. *Psiguria* and its sister genera, *Gurania* and *Helmontia*, are unique among Cucurbitaceae having brightly colored flowers and butterfly and hummingbird pollinators. Historically, taxonomic revisions have described as many as 29 species, but this number has been inflated by misleading characteristics such as variable leaf and flower morphology. A thorough morphological investigation of 758 herbarium specimens and individuals from both greenhouse and natural settings, combined with a recent molecular phylogeny, supports the delineation of six species. In this revision, a review of over 35 yr of publications addressing ecological and natural history studies focusing on *Psiguria* is presented. A description and a distribution map of each species is provided along with two taxonomic keys: one that utilizes male flowers, and another that incorporates leaf characteristics and geographic distribution but uniquely identifies species according to DNA barcodes. With a list of characters that distinguish all pairs of geographically overlapping species, botanists and ecologists finally have the tools to confidently identify species of *Psiguria*.

Keywords—DNA barcoding, *Guraniinae*, *Heliconius*, *Helmontia*, tropical vines.

Psiguria Arn. is a genus of perennial, Neotropical vines occurring in dry and wet forests at elevations up to 2,100 m. The genus is most closely related to *Gurania* Cogn. and *Helmontia* Cogn. (Kocyan et al. 2007). The three were once classified as the tribe Guraniinae (Jeffrey 1963), but are now embedded in Coniandreae (Jeffrey 2005). Historically, taxonomic works have described as many as 29 species of *Psiguria*, but misleading characteristics such as leaf and flower morphology that varies over the life of an individual and a monoecious reproductive system consisting of temporally and spatially separated flowers have led to an inflated number. Six species are recognized here based on morphological studies, and a recent molecular phylogeny of *Psiguria* supported this number (Steele et al. 2010).

Psiguria is rare throughout its geographical range with distances between individuals of one km or more at the level of the forest floor (pers. obs.). The vines can grow up into the canopy, but it is unknown how extensive *Psiguria* growth is at that level. The plants are typically seen growing over the tops of shrubs, climbing with tendrils that wrap around the stems and leaves of other plants. Young *Psiguria* vines are herbaceous with membranous leaves, while older plants of some species become woody, and some mature leaves can be leathery. The leaves are arranged alternately along the stem, and can reach lengths of 75 mm and widths of 53 mm. Leaves are typically glabrous, but minute, soft trichomes may be seen along the veins and margins of some species. A number of different leaf shapes occur on the various species, and even on the same individual. It is not uncommon to see a simple, shallowly trilobed leaf adjacent to one that is trifoliate, and this variation is inconsistent among individuals of the same species. This is one reason why leaf characters alone cannot be used to distinguish species confidently, although historically they were used in taxonomic keys to *Psiguria* (e.g. Cogniaux 1916; Hampshire 1992). The vines have simple tendrils, which emerge from the stem at a 90 degree angle from the leaf node. Vegetative structures are bright green, and stems and tendrils on some species have small, darker green speckles or longitudinal blotches.

From some leaf nodes, male flowers emerge on long pedunculate racemes or spikes. Male flowers are seen in nature much more often than female flowers; therefore, their char-

acteristics are best used to identify species of *Psiguria*. Two characteristics that have been overlooked in previous keys are the number of flowers per millimeter along the peduncle and the length of pedicels. In some species, flowers occur so close together that more than one flower scar may be observed per millimeter. Additionally, some species are apedicellate while others have pedicels up to 19 mm long.

Both male and female flowers are salverform, with a tubular green calyx tube and outspreading petals. Petals may be various shades of pink, red, or orange. The calices of some species have darker green speckles, and sepal shapes and lengths may vary. These two characteristics were used by Wunderlin (1978) and, because they were found to be consistent, are included in the present keys. Another characteristic used by Wunderlin (1978) was the shape of the calyx tube, cylindrical or flask-shaped; however, widespread sampling revealed that this characteristic is inconsistent and may vary between flowers on the same inflorescence.

Inside the male flowers are only two anthers attached to the inner floral tube. The shape of the anthers (straight or folded) and the pubescence of small anther appendages near the tube throat were originally used by Cogniaux (1916) to distinguish species. While folded anther shape definitively separates *Psiguria pedata* (L.) R. A. Howard from all other species of *Psiguria*, in which the anthers are straight, the examination of many specimens revealed that the pubescence of the anther appendage is inconsistent.

Female flowers typically emerge at nodes on the apex of the vine that may be leafless or continue to produce mature leaves. At a given time, many female flowers may be open on a plant and at a node. Flowers are epigynous with a stigma that is divided into two, and these sections are further divided into two. The stigmatic surfaces are rugose, and their ends may just be seen emerging from the tube of a mature flower. Upon fertilization, the inferior ovary develops into a small, indehiscent, cucumber-like fruit that may be dark green or green and white striped. Because female flowers are rarely seen in nature, their morphological characteristics have not typically been used for identifying species of *Psiguria*.

Nomenclatural History—Linnaeus (1759) described three species, currently placed in *Psiguria*, under *Cucumis trilobatus* L., *C. trifoliata* L., and *C. pedatus* L. Von Jacquin (1760)

moved these to *Anguria* Jacq., a later homonym of *Anguria* Mill. (Miller 1754). Linnaeus (1762) published these three species under the name *Anguria*. De Necker (1790) realized that this generic name was incorrectly applied to these taxa, and he first published the name *Psiguria* in *Elementa Botanica*; however, the International Code of Botanical Nomenclature (ICBN) has suppressed all names in that publication (McNeill et al. 2006). Arnott (1841) published *Psiguria* Arn., but he did not list any binomials. Despite this, and because Linnaeus (1762) had used the name *Anguria*, in the mid to late-1800s, several additional species were described under *Anguria* (Roemer 1846; von Schlechtendal 1851; Cogniaux 1876, 1881). In 1916, the most recent and complete taxonomic revision of *Anguria* was published by Cogniaux in which the group was divided into two genera, *Anguria* (29 species) and *Gurania* (73 species), based on morphological differences.

Rickett and Stafleu (1960) first noted that *Anguria* was illegitimate, but Jeffrey (1962), in his discussion of the history of the name *Anguria*, proposed conserving the name *Psiguria*, but only if Cogniaux's (1916) split into two genera stood up to taxonomic scrutiny. Additionally, Jeffrey (1962) explained that, because von Jacquin's (1763) description of the fruit in his original generic diagnosis was derived from *A. pedata*, the lectotype for *Anguria* should be *A. pedata*. Along with other publications that indicated the equivalence of *Psiguria* with *Anguria* (Willis and Shaw 1966; Dandy 1967), Howard (1973) corroborated Jeffrey's (1962) assertion that many *Anguria* species needed to be transferred to *Psiguria*, and he made three new combinations in *Psiguria*; *P. pedata*, *P. trilobata* (L.) R. A. Howard, and *P. jacquiniana* (Schltdl.) R. A. Howard with the first name de facto becoming the type. In 1978, Wunderlin made three more combinations; *P. bignoniacea* (Poepp. & Endl.) Wunderlin, *P. longipedunculata* (Cogn.) Wunderlin, and *P. warscewiczii* (Hook. f.) Wunderlin. In the same year, Jeffrey (1978) circumscribed *Psiguria* (applied to those species previously described under *Anguria*) and *Gurania* based on floral syndromes. Jeffrey (1978) also argued that Cogniaux, in his 1916 treatment, recognized far too many species, and included numerous misidentifications. Nonetheless, Jeffrey (1978) made six new combinations; *P. ottomaniana* (Schltdl.) C. Jeffrey, *P. umbrosa* (Kunth) C. Jeffrey, *P. ovata* (Donn. Sm.) C. Jeffrey, *P. triphylla* (Miq.) C. Jeffrey, *P. warmingiana* (Cogn.) C. Jeffrey, and *P. ternata* (M. Roem.) C. Jeffrey, and described one new species, *P. racemosa* C. Jeffrey. Subsequently, four additional combinations were made in *Psiguria* as follows: *P. trifoliata* (L.) Alain (Liogier 1980), *P. dunlapii* (Standley) R. J. Hampshire (Hampshire 1992), *P. aurantiaca* (S. F. Blake) C. Nelson & Fern. Casas, and *P. diversifolia* (Cogn.) C. Nelson & Fern. Casas (Nelson Sutherland and Fernandez Casas 1998).

Phylogeny—The most recent phylogeny of Cucurbitaceae placed *Psiguria* in tribe Coniandreae, and supported the monophyly of a clade including *Psiguria*, *Helmontia*, and *Gurania*, but questioned the monophyly of *Psiguria* (Kocyan et al. 2007). The speciation event separating *Psiguria* and *Gurania* is estimated to be six \pm three million years ago (Schaefer et al. 2009). Steele et al. (2010) found strong support for the monophyly of the genus, as well as weak to strong support for only six species of *Psiguria* (Fig. 1, reproduced from Steele et al. 2010). These six, *P. pedata*, *P. ternata*, *P. umbrosa*, *P. warscewiczii*, *P. triphylla*, and *P. racemosa*, are also recognized here.

Comparative Morphology and Geographic Distribution—The relationships between the three genera in the clade

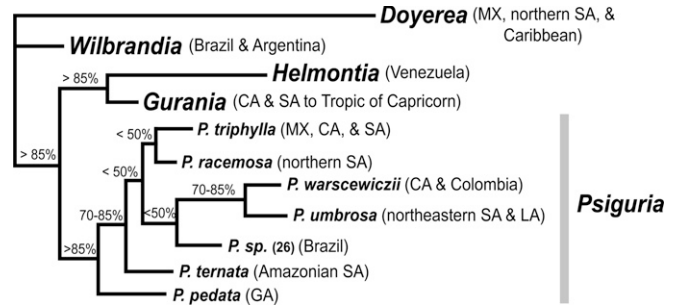


FIG. 1. Phylogeny of *Psiguria* (Cucurbitaceae) (reproduced from Steele et al. 2010, Fig. 5) inferred from a combination of eight chloroplast intergenic spacers, ITS, and the nuclear *serine/threonine phosphatase* gene intron. Bootstrap values are indicated above branches.

(*Psiguria*, *Gurania*, and *Helmontia*) are still unclear. In the molecular phylogeny of *Psiguria* based on plastid genes, *Gurania* and *Helmontia* form a clade sister to *Psiguria* (Fig. 1). The nuclear datasets present conflicting and poorly supported evolutionary histories. However, the molecular separation of *Psiguria* and *Gurania* supports Cogniaux's (1916) split of *Anguria* based on striking differences in flower morphology, but it does not explain the similarities between *Helmontia* and *Psiguria* flowers that differ mainly in petal color (*Psiguria*: red, pink, or orange, *Helmontia*: white). Additionally, pollen morphology would suggest that *Psiguria* and *Gurania* are sister because, although most cucurbits including *Helmontia* have single-grain pollen, *Psiguria* and *Gurania* shed pollen in tetrads (Jeffrey 1964; Roubik and Moreno 1991). All three genera consist of Neotropical vines with large leaves, and brightly colored flowers in *Psiguria* and *Gurania* distinguish them from most other cucurbits (Condon and Steck 1997). *Psiguria* is distinguished from *Gurania* by predominantly glabrous leaves and salverform flowers in which the green calyx forms a tube (see Fig. 2 for shape variations) ending in five short, green sepals, and red, pink, or orange petals spreading out beyond the throat of the tube. In contrast, *Gurania* flowers have predominantly pubescent leaves and bright orange, long, divided sepals with short, inconspicuous, yellow petals that are often mistaken for anthers. *Psiguria* and *Gurania* have geographic distributions stretching from southern Mexico to Paraguay, but only *Psiguria* extends into the Greater Antilles. *Helmontia* flowers are similar to those of *Psiguria* (other than petal color), but *Helmontia* is known only from northeastern South America.

Ecology and Natural History—Aspects of the pollination system, ecological interactions, phenology, and natural history of *Psiguria* have been studied at several field and greenhouse locations since the early 1970s (Gilbert 1972, 1975, 1977;

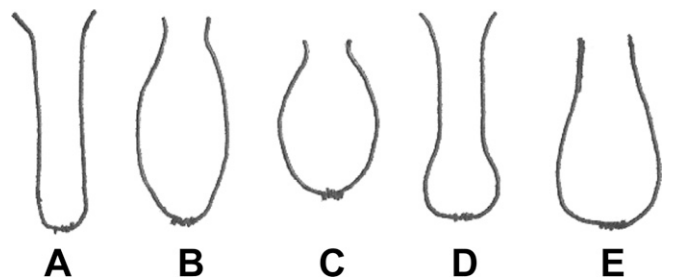


FIG. 2. Floral tube shapes. A. cylindrical, B. elliptical, C. oval, D. cylindrical with thickened base, E. flask-shaped.

Boggs et al. 1981; Gilbert 1983; Condon 1984; Murawski and Gilbert 1986; Murawski 1987; Condon and Gilbert 1988, 1990; Gilbert 1993; Condon and Norrbom 1994; Condon and Steck 1997; Condon et al. 2008). From the time of Cogniaux until these investigations, most species of *Psiguria* were thought to be dioecious. Despite the fact that several botanists before him described *Anguria* taxa under the category of monoecious (Linnaeus 1759, 1762; von Jacquin 1760; de Necker 1790), Cogniaux (1916) described the genus as having dioecious, rarely monoecious, members. This misdirected idea persisted until several long-term, detailed observations revealed that these plants were indeed monoecious with temporally and spatially separated male and female flowers (Gilbert 1983; Condon 1984; Condon and Gilbert 1988). Indeterminate, erect male inflorescences are first to emerge from leaf nodes of climbing vines, and produce flowers for three months to over a year (Gilbert 1975, 1983; Condon 1984; Condon and Gilbert 1988). Once stems reach adequate size, and after an intermediate flowerless period lasting a few days to several months, plants switch sex to produce female flowers at nodes on terminal branches, sometimes with reduced leaves and tendrils (Murawski 1987; Condon and Gilbert 1988, 1990). Some plants continue to produce male flowers when female flowers are produced, but this is rare (Murawski 1987). The time from seed germination to fruit set can be several years (Gilbert 1983). The temporal separation of male and female flowers may be an adaptation for outcrossing since artificially self-pollinated species have produced viable offspring (Condon and Gilbert 1990).

Female branches hang on other vegetation away from the main vine, and typically turn downward, dropping as much as two meters before producing the first flower (Condon and Gilbert 1990). A plant may have from one to as many as six female flowers per node, with fruits maturing about two to three weeks after pollination (Condon and Gilbert 1990). Female branches produce receptive flowers for about a week to ten days unless no fruit is set, in which case flowering may continue for an undetermined amount of time (Condon 1984; Condon and Gilbert 1988). Gilbert (1983) observed a *Psiguria triphylla* (called *Anguria pachyphylla* Donn. Sm.) individual at La Selva Biological Research Station in Costa Rica that, over an eight-year period, alternated between female flowering and fruiting until it reached 15 m in length. Additionally, large vines can alternate between flowering and vegetative states (Condon and Gilbert 1990).

Zero to three male flowers are typically open per inflorescence each day, while one to several female flowers at a node may be open at a time; however both types of flowers open only once for few to several hours before falling off or maturing into fruit (Condon 1984; Murawski 1987; Condon and Gilbert 1988). Both male and female flowers may emerge high in the canopy or in light gaps or shade at lower canopy levels, and neither has been described as having scent (Murawski 1987; Condon and Gilbert 1990).

Most *Psiguria* species can produce male flowers year-round, but the average daily number of inflorescences produced per plant varies over time, from zero to 46 (Gilbert 1977; Murawski and Gilbert 1986; Murawski 1987; Gilbert 1993). Additionally, seasonal fluctuations have been observed, with peaks often at the start of the rainy season (Condon 1984). For all species, a strongly male-biased flowering ratio (e.g. 32:1) has been observed (Gilbert 1975; Murawski and Gilbert 1986; Murawski 1987; Condon and Gilbert 1988). Extensive

flowering time, providing nearly constant pollen and nectar sources, may have influenced speciation in *Psiguria's* major pollinators, *Heliconius* Kluk butterflies (Gilbert 1972, 1975, 1977; Boggs et al. 1981; Murawski and Gilbert 1986; Condon and Gilbert 1990; Gilbert 1993).

Psiguria plays a role in a suite of plant-animal interactions, the most-studied of which is the relationship with its pollinators. Although *Psiguria* flowers are visited by several organisms such as hummingbirds, bees, moths, and butterflies, *Heliconius* butterflies have been observed making the most visits and transferring the greatest amount of pollen to the stigmas of female flowers (Gilbert 1972, 1975, 1977; Boggs et al. 1981; Gilbert 1983; Condon 1984; Murawski and Gilbert 1986; Murawski 1987; Condon and Gilbert 1990; Gilbert 1993). Because of the morphological similarity between male and female flowers, and the similar textures of anthers and stigmatic surfaces, it is hypothesized that the butterflies may visit female flowers "accidentally" while foraging for pollen (Condon and Gilbert 1990). This interaction makes *Psiguria* (along with sister genus *Gurania*) among the few cucurbit genera that are butterfly or bird-pollinated (Gilbert 1983). However, because *Psiguria* flowers are visited by many organisms that rob pollen rather than transferring it to female flowers, gene flow in the plant population will vary with visitor composition (Murawski and Gilbert 1986; Murawski 1987).

Heliconius butterflies provide a vital service for *Psiguria*, but the benefit to the pollinator cannot be understated. In fact, most species of *Heliconius* butterflies rely heavily on nutrients obtained from the pollen of *Psiguria* flowers. Unlike other lepidopterans that, during larval feeding, obtain nitrogenous compounds necessary for egg production, *Heliconius* butterflies as adults (both male and female) assimilate amino acids and proteins obtained from pollen of *Psiguria* and a few *Gurania* species (Gilbert 1972, 1975, 1977; Boggs et al. 1981). *Psiguria* and *Gurania* are preferred over other sources due to the large size of the pollen tetrads (Gilbert 1975; Boggs et al. 1981). Although most of the *Heliconius*-collected pollen produced by *Psiguria* is actually destroyed by the butterflies, a sufficient portion is transferred to female flowers fulfilling the butterfly's role as the primary pollen vector (Condon 1984; Murawski and Gilbert 1986). *Psiguria* flowers also provide nectar to *Heliconius* feeders. Butterflies scrape pollen from the anthers, combine it with nectar, and then massage the mixture with their proboscis. The butterflies then absorb amino acids from the pollen into their system. Female butterflies feed early in the morning, gathering pollen for its nutritional value, while males feed later in the morning on nectar, keeping both sexes nearby for times of breeding (Gilbert 1975; Condon 1984; Murawski and Gilbert 1986; Murawski 1987; Gilbert 1993). Not only does this system provide a pollination vector for the widely-spaced plants, but the steady food source contributes to the nearly constant egg-laying success of the long-lived (up to six months) butterflies (Gilbert 1977; Murawski 1987).

Several other plant-animal interactions involving *Psiguria* have been observed or studied. Bats are believed to be the primary fruit dispersal agents (Gilbert 1983; Condon 1984; Condon and Gilbert 1990). Parrots, squirrels, mice, and monkeys destroy the seeds or prey on immature fruits (Gilbert 1975, 1983; Condon and Gilbert 1990). Several insect parasites are associated with *Psiguria*, including pickleworm, *Diaphania nitidalis* Stoll (Pyralidae), and fruit flies, *Blepharoneura* Loew (Tephritidae) (Condon 1984; Condon and Gilbert 1990;

Condon and Norrbom 1994; Condon and Steck 1997; Condon et al. 2008). The latter of these two infest both male and female flowers, repelling butterfly pollinators, and feeding on seeds causing predispersal seed mortality (Gilbert 1983; Condon 1984; Murawski 1987; Condon and Gilbert 1990). Most recently it has been discovered that several morphologically similar, sympatric species of *Blepharoneura* feed on separate parts of *Psiguria* and *Gurania* plants that can host as many as 13 different *Blepharoneura* species (Condon and Norrbom 1994; Condon and Steck 1997; Condon et al. 2008).

MATERIALS AND METHODS

The present treatment is based on both herbarium and personal collections covering the geographic and morphological ranges of *Psiguria*. Personal collections are deposited in TEX and countries of collection, and specimens were borrowed from five additional herbaria; MO, NY, F, GH, and US. The examined collections totaled 758, and included representatives from each of the six species of *Psiguria* as follows (number in parentheses is number of collections): *P. pedata* (77), *P. racemosa* (18), *P. ternata* (73), *P. triphylla* (297), *P. umbrosa* (43), and *P. warscewiczii* (250). Type specimens were examined where possible, some of which included photographs or copies of type drawings. Preserved flowers were rehydrated by soaking them in diluted Aerosol OT surfactant for a maximum of 24 hr. Several flowers from plants growing in greenhouses at The University of Texas at Austin were collected and fixed in FAA before measuring. On 178 individuals from herbaria or living material, 43 quantitative characters were measured using either a metric ruler with millimeter divisions (for measurements greater than 10 mm), or the reticule of an Olympus SZ61 light microscope (for measurements less than 10 mm). Figure 3 shows a diagram of two measurements (leaf base depth and lobe depth), which may not be obvious. The number of specimens measured was determined by the geographic and morphological variability of each species. This included 25-*P. pedata*, 11-*P. racemosa*, 19-*P. ternata*, 65-*P. triphylla*, 23-*P. umbrosa*, and 35-*P. warscewiczii*. These data served as the basis for the species descriptions and keys.

Species Concept—Species are distinguished by their evolutionary history. Toward that end, components of both morphological and phylogenetic species concepts are incorporated by aligning the molecular phylogenetic results of Steele et al. (2010) with the current morphological observations and measurements from field, greenhouse, and herbarium specimens. A species is defined as the smallest monophyletic group

having weak to strong bootstrap support and consistently sharing one or more morphological character traits. These criteria exclude forms or races which have not been distinguished genetically, and the natural history, reproductive biology, and phenology are considered such that semaphorants are not confused as different species. Species are described such that, whenever possible, researchers can identify organisms using keys based on characters observed in the field and/or by comparing them with type specimens. When this is not possible, DNA barcodes are provided for species delineation.

TAXONOMIC TREATMENT

PSIGURIA Arn., Hook. Jour. Bot. 3: 247. 1841.—LECTOTYPE: *Psiguria pedata* (L.) R. A. Howard.

Monoecious, perennial, vines with simple tendrils, herbaceous but some becoming woody with greater stem size and age; stems, minutely sulcate, glabrous or puberulent, solid or light green with darker, linear splotches, 0.9–7.0 mm in diameter; tendrils glabrous or puberulent, solid or light green with darker speckles, 0.2–3.1 mm in diameter. Leaves petiolate, the blades membranous or coriaceous, upper surface darker green, lighter green below, and both surfaces glabrous with veins and margins sometimes puberulent, venation reticulate, main veins flush or prominent, margins entire or irregular, sometimes with irregularly-spaced veins extending beyond blade, simple, trifoliolate, pedate, or a combination of these; petioles glabrous or pubescent, 0.5–5.3 mm in diameter, 3–96 mm long; simple leaves lanceolate, elliptic, or trilobed, base auriculate, truncate, rounded, and/or acute, bases 5–33(–40) mm deep, apices acuminate, 39–219 mm long, 22–122(–178) mm wide, lobe depth average 62.5% of total length; petiolules glabrous or puberulent, sometimes winged, 0.6–3.6 mm in diameter, 0–48 mm long; compound leaves with center leaflet elliptic to oblanceolate, side leaflets lanceolate to oblanceolate, apices acuminate or cuspidate; bases of center leaflets acute or attenuate, 40–305 mm long, 17–132(–150) mm wide; bases of side leaflets acute, attenuate, truncate, sometimes oblique, 25–225 mm long, 13–124 mm wide; bases of outer leaflets on pedate leaves oblique, adaxial bases acute-attenuate and abaxial bases acute-truncate, 18–115(–145) mm long. Inflorescences pedunculate racemes or corymbs; peduncles glabrous or puberulent, solid green or light green with darker splotches, 0.5–4.6(–8.0) mm in diameter, (8–)21–395 mm long; pedicels absent or, if present, then pubescent, 0–19 mm long, with 0.24–1.2 flowers per mm. Staminate flowers axillary, first 2–3 flowers sometimes much larger than subsequent flowers, receptacle with trichomes; calyx salverform, glabrous or puberulent, solid green or light green with darker speckles, 4–17.0(–21.0) mm long, 1.0–7.0 mm wide, adaxial surface glabrous or puberulent with or without trichomes at throat; sepals 5, thin or thick, triangular or linear, color same as or darker than calyx, 0.5–8.5 mm long; corolla rotate, adnate to calyx tube, lobes 5, free, orange, pink, or red, ovate to obovate, venation reticulate, pubescent internally and externally, apex rounded to acuminate, 2.0–62.0 mm long, 2.0–40.0 mm wide, length-to-width ratio 1.2–2.1; anthers 2, free, filamentous and dorsifixed inside floral tube, bilocular, straight or folded backwards, (1.0–)3.4–11.0 mm long, anther appendage round or triangular, glabrous or papillose, 0.1–1.2 mm long, folded portion (if applicable) (0.7–)1.0–1.5 mm long. Pistillate flowers 2–5 per node, axillary or terminal; calyx salverform, cylindrical or various flask shapes, glabrous or puberulent, striped or solid, (4.9–)11.0–41.0 mm long, 0.9–10.0 mm wide, adaxial surface glabrous or puberulent, with or without trichomes at

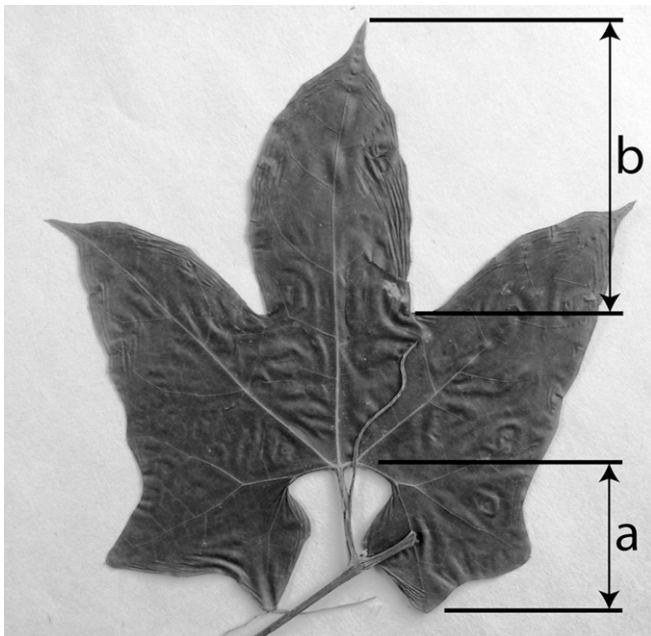


FIG. 3. Diagram of two leaf measurements. a. base depth, b. lobe depth.

throat; sepals 5, thin or thick, triangular or linear, color same as or darker than calyx, 0.5–3.7 mm long; corolla rotate, adnate to calyx tube, lobes 5, free, orange, pink, or red, elliptic to obovate, venation reticulate, both sides pubescent, apex rounded to acuminate, 4.5–16.0 mm long, 2.4–9.5 mm wide, length-to-width ratio 1.3–3.5; gynoecium 1, bilocular, ovary elliptic-oblong, 6.5–22.0 mm long, 1.9–7.0 mm wide, ovules numerous,

horizontal, style 1, 2.3–9.0 mm long, stigmas twice branched, stigmatic surfaces papillose, stigma 3.5–10.2(–12.0) mm long. Fruit a pepo, oblong, indehiscent, solid green or with lighter green or white stripes, 18–80 mm long, 10–24 mm wide, wall 0.7–3.0 mm thick. Seeds 30–88, ovate-oblong, flattened, without a distinct margin, whitish-gray, 5.0–10.0 mm long, 2.8–5.9 mm wide, 1.5–3.8 mm thick.

KEY TO SPECIES OF *PSIGURIA*

Two keys are provided: Key 1 for specimens with staminate flowers, and Key 2 for sterile or carpellate specimens. Because vines in tropical forests are often seen without flowers, it may be necessary to identify sterile specimens. However, because the leaf morphology of a *Psiguria* individual can change over its lifetime, morphological characters may not be enough for accurate identification. In this case, it will be necessary to narrow the identification down to two or three species with a few consistent stem and leaf characters plus geographic location, and then utilize DNA barcodes for exact identification as described in Steele et al. (2010), which contains a list of chloroplast DNA markers for distinguishing the six species of *Psiguria*. The second key below refers to markers and reference sequences from Table 4 in that publication.

KEY 1 TO SPECIES OF *PSIGURIA*

(specimens with staminate flowers)

1. Anther folded backwards 1. *P. pedata*
1. Anther straight 2
 2. Flowers > 0.75 per mm; pedicels absent or < 0.3 mm long 4. *P. triphylla*
 2. Flowers < or = to 0.75 per mm; pedicels present and > 0.5 mm long 3
 3. Pedicels > or = 2.0 mm long; petal apex acuminate 4
 4. Calyx and peduncle color solid; sepals same color as calyx; petals pink 2. *P. racemosa*
 4. Calyx and peduncle color speckled/splotched; sepal color darker than calyx; petals orange 5. *P. umbrosa*
 3. Pedicels < 2.0 mm long; petal apex rounded or rounded-acute 5
 5. Petals orange-red; sepal thick, triangular; sepal 0.5–1.5 mm long; sepal color darker than calyx, first 2–3 flowers not much larger than later flowers; geographic distribution N of equator 6. *P. warscewiczii*
 5. Petals pink; sepal thin, linear; sepal > 1.5 mm long; sepal color same as calyx, first 2–3 flowers much larger than later flowers; geographic distribution S of equator 3. *P. ternata*

KEY 2 TO SPECIES OF *PSIGURIA*

(sterile or carpellate specimens)

1. Leaves simple, trilobed or 5-lobed, sometimes deeply, but never trifoliolate 2
 2. Chloroplast DNA region *rpoB-trnC* matches *P. racemosa* reference sequence and geographic distribution in Colombia or Venezuela 2. *P. racemosa*
 2. Chloroplast DNA regions *rpoB-trnC* and/or *psbZ-trnM* match *P. umbrosa* reference sequences and geographic distribution in Venezuela, Brazil, or Lesser Antilles 5. *P. umbrosa*
1. Leaves bifid, trifoliolate, or pedate, with immature leaves often simple and lobed, or sometimes a combination of shapes 3
 3. Stem surface light green with darker green splotches, leaves trifoliolate, pedate, or seldom simple and trilobed, large lobes on outside of side leaflets, and chloroplast DNA region *ndhF-rpl32* matches *P. umbrosa* reference sequence, but not matching regions *rpoB-trnC* and/or *psbZ-trnM* with *P. umbrosa* reference sequences 6. *P. warscewiczii*
 3. Stem surface solid green, leaves bifid, trifoliolate, pedate, with immature leaves often simple and lobed, or sometimes a combination of complexities 4
 4. Leaf margins with veins extending beyond the margins of the leaves, chloroplast DNA region *ndhC-trnV* matches *P. pedata* reference sequence, and geographic distribution in Greater Antilles or rarely Costa Rica. 1. *P. pedata*
 4. Leaf margins seldom with veins extending beyond the margins of the leaves 5
 5. Leaves trifoliolate, or rarely pedate, and main vein in side leaflets strongly off-center, typically with small lobes on outside base of side leaflets, chloroplast DNA region *3rps16-trnQ* matches *P. ternata* reference sequence, and geographic distribution in Peru, Brazil, Bolivia, or Paraguay 3. *P. ternata*
 5. Leaves simple and elliptic, 2-lobed, trilobed, trifoliolate, or mixed complexities; main vein in side leaflets not strongly off-center, typically without lobes on outside base of side leaflets, chloroplast DNA regions *ndhC-trnV*, *ndhF-rpl32*, and/or *3rps16-trnQ* match *P. triphylla* reference sequences, and geographic distribution in Mexico, Central America, or South America 4. *P. triphylla*

1. *PSIGURIA PEDATA* (L.) R. A. Howard, J. Arnold Arbor. 54: 441. 1973. *Cucumis pedatus* L., Syst. Nat. ed. 10 p. 1279. 1759. *Anguria pedata* Jacq. Enum. Pl. Carib. p. 31. 1760. *Anguria polyphyllus* Schldt., Linnaea 24: 712. 1851. *Anguria pedata* var. *polyphyllus* (Schldt.) Cogn., Diagn. Cucurb. I: 22 p. 10. 1876.—TYPE: *Anguria polyphyllus*, *parvo fructu* C. Plumier, Plant. Amer. fasc. I. 13 *tabula* 23. 1755. (holotype!).

Cucumis trilobatus L., Syst. Nat. ed. 10 p. 1279. 1759. *Anguria trilobata* L., Enum. Syst. Pl. pp. 9 & 31. 1760. *Anguria plumieriana* Schldt., Linnaea 24: 709. 1851. *Psiguria trilobata* (L.) R. A. Howard, J. Arnold Arbor. 54(4): 442. 1973.—TYPE: C. Plumier, Plant. Amer. fasc. I. 13 *tabula* 22. 1755. (holotype!).

Anguria trifoliata L. Sp. Pl. 2 p. 1376. 1763. *Psiguria trifoliata* (L.) Alain, Phytologia 47(3): 192. 1980.—TYPE: *Cucumis*

triphyllus, fructo variegato, C. Plumier, Description des Plantes de L'Amérique 85 plate 99. 1693. (holotype!).

Anguria dentata Schltldl., Linnaea 24: 713. 1851. *Anguria pedata* var. *dentata* (Schltldl.) Cogn., Diagn. Cucurb. I: 22 p. 10. 1876.—TYPE: N. J. Jacquin, Sel. Stirp. Amer. Hist. pp. 242–246 tabula 155. 1763. (holotype!).

Anguria ottoniana Schltldl., Linnaea 24: 758. 1851. *Anguria pedata* var. *ottoniana* Sauv., Fl. Cubana p. 904. 1873. *Psiguria ottoniana* (Schltldl.) C. Jeffrey, Kew Bull. 33(2): 352. 1978.—TYPE: CUBA. Taburete: 16 May 1839, *Otto* 257 (holotype: B destroyed fide Jeffrey (1978)).

Anguria keithii Northr., Mem. Torr. Bot. Club. 12: 69–70 t. 18. 1902.—TYPE: BAHAMAS. Andros: Conch Sound, 8 May 1890, *Northrop* 556 (holotype: NY! fide Jeffrey (1978), photograph: F!).

Anguria cookiana Britton Britt & Wils., Sci. Surv. Puerto Rico & Virgin Islands 6: 267. 1925.—TYPE: PUERTO RICO. 20 Nov 1899, *Goll* 627 (holotype: NY!).

Stems glabrous or puberulent, solid green, 0.9–2.0 mm in diameter; tendrils glabrous, solid green, 0.3–1.0 mm in diameter. Leaves immature membranous, mature coriaceous, both surfaces glabrous with veins and margins sometimes puberulent, 3–5 main veins, flush, margins entire-irregular-crested, often with irregularly-spaced veins extending beyond blade, simple, trifoliolate, pedate (sometimes with outer leaflets further divided into 2 parts), or a combination of these; petioles puberulent, 0.5–2.2 mm in diameter, 9–45 mm long; simple leaves trilobed, base auriculate, base 12–20 mm deep, apex acuminate, 39–98 mm long, 40–79 mm wide, average lobe depth 44.6% of total length; petiolules winged and glabrous or puberulent, 0.6–1.3 mm in diameter, 0–12 mm long; complex leaves with center leaflet elliptic-rhombic-oblancoate and side leaflets lanceolate-elliptic-oblancoate, apices acuminate-cuspidate; center leaflet base acute-attenuate, 40–91(–128) mm long, (12–)21–43 mm wide; side leaflets base acute-attenuate, 45–93 mm long, (13–)20–40 mm wide; outer leaflets on pedate leaves base oblique, adaxial base acute-attenuate and abaxial base acute-truncate, (18–)24–78 mm long. Inflorescence a raceme; peduncles glabrous, solid green or rarely light green with darker splotches, 0.6–1.9 mm in diameter, (8–)21–105 mm long; pedicels puberulent, 1–16 mm long, with 0.27–0.56 flowers per mm. Staminate flowers, first 2–3 flowers not much larger than subsequent flowers; calyx salverform, oval, puberulent, solid green, 4–9.3 mm long, 1.0–6.0 mm wide, adaxial surface glabrous with trichomes at throat; sepals thin, triangular-linear, color same as calyx, 0.8–2.5 mm long; petals orange, ovate-rhombic, apex cuspidate, 4.0–15.0 mm long, 3.2–7.0 mm wide, length-to-width ratio 1.9; anthers folded backwards, 3.4–6.0 mm long, anther appendage round-triangular, glabrous-papillose, 0.1–0.7 mm long, folded portion (0.7–)1.0–1.5 mm long. Pistillate flowers 2–3 per node, axillary; calyx salverform, cylindrical-elliptical-elongated, glabrous, striped color, 17.0–30.0 mm long, 0.9–10.0 mm wide, adaxial surface glabrous or puberulent with trichomes at throat; sepals thin, linear, color same as calyx, 1.6–1.8 mm long; petals orange, elliptic, apex acute, length unknown, width unknown; ovary elliptic-oblong, 10–10.5 mm long, 3.0–3.5 mm wide, style 7.0–7.5 mm long, stigma 4.5–4.8 mm long. Fruits, green with lighter green stripes, 18–36 mm long, 10–18 mm wide, wall 0.7–1.3 mm thick. Seeds 44–46, 6.3–6.5 mm long, 3.9–4.1 mm wide, 2.0–2.4 mm thick.

Phenology—Flowering throughout the year. Of the 77 specimens examined, 70.1% had male flowers, 10.4% had female flowers or fruits, and the remainder were sterile.

Distribution and Habitat—Throughout the Greater Antilles and the Bahamas (Fig. 4), with one collection from Costa Rica with label stating “cloud forest exposed to Atlantic trade winds, Continental Divide.” Found at elevations from sea level to 1,200 m, in secondary, evergreen or deciduous, moist or dry forests, on rocky, limestone, or clay soils, in dense forest shade or on slopes, riverbanks, or ravines.

Discussion—The leaves of an individual *Psiguria pedata* change greatly over its life, and can take on various forms in adjacent positions along the stem (Fig. 5A–C). Because of this variability, the species has historically been split into several taxa.

The folded anther (Fig. 6A) most easily distinguishes *Psiguria pedata* from all other *Psiguria* species, which have straight anthers (Fig. 6B). Additionally, *P. pedata* is found predominantly in the Greater Antilles, with one exception, one herbarium specimen from Costa Rica, which grouped with other *P. pedata* samples in the molecular phylogeny (Steele et al. 2010). The collection did not contain male flowers, so the folded anther characteristic could not be confirmed in this sample. However, because of the special notation on the herbarium sheet label (quoted in the “Distribution and Habitat” section above), it is not unreasonable to think that seeds of the Greater Antilles *P. pedata* were carried to the continent in a hurricane or by means of the Atlantic trade winds.

Representative Specimens Examined—(collections marked with an asterisk were measured for species descriptions)

BAHAMAS. Andros Island: Mangrove Cay, Coppice, Lisbon Creek, 16 Jan 1910, *Small & Carter* 8454 (F, NY, US); Eleuthera Island: Governor’s Harbor, 15 Nov 1890, *Hitchcock* s. n. (F).

COSTA RICA. Guanacaste: La Chirripa ridge, 4 km NE El Dos de Tilarán, cloud forest exposed to Atlantic trade winds, continental divide, 1,000 m, 08 May 1986, *Haber et al.* 4860 (MO*).

CUBA. Camaguey: La Gloria, 30 Jan 1909, *Schaefer* 131 (NY); Havana: Marianao, Dec 1909, *Camilo* 1382 (NY); Isle of Pines: Nueva Gerona, 04 Jul 1900, *Palmer & Riley* 997 (NY); Matanzas: mouth of Buey Vaca, 28 Aug 1903, *Britton & Wilson* 70 (NY); Cardenas, 01 Sep 1903, *Britton & Wilson* 187 (NY*); Oriente: Antilla, 06 Mar 1912, *Britton et al.* 12499 (NY); Trail Navas to Camp Buena Vista, 650 m, 23 Mar 1910, *Shaefer* 4418 (NY); Pinar del Río: Baños San Vicente, 12 Sep 1910, *Britton et al.* 7394 (NY); Sierra de Anafe, 15 Dec 1911, *Wilson* 11328 (NY); base of Sierra Guane, 26 Nov

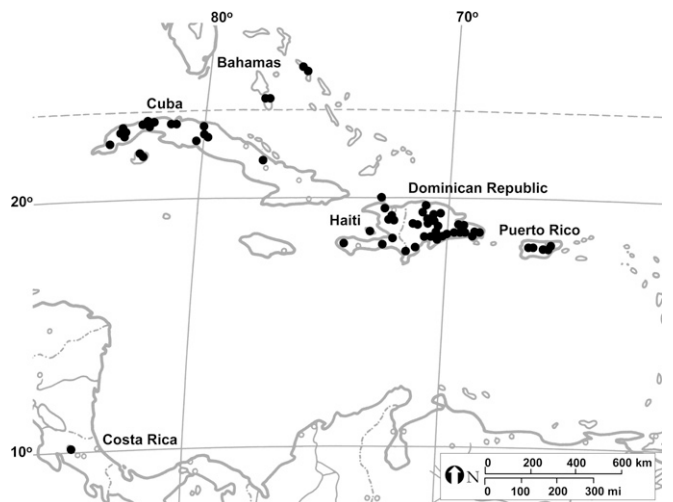


FIG. 4. Geographic distribution of *Psiguria pedata*. Open circles are part of the base map image.

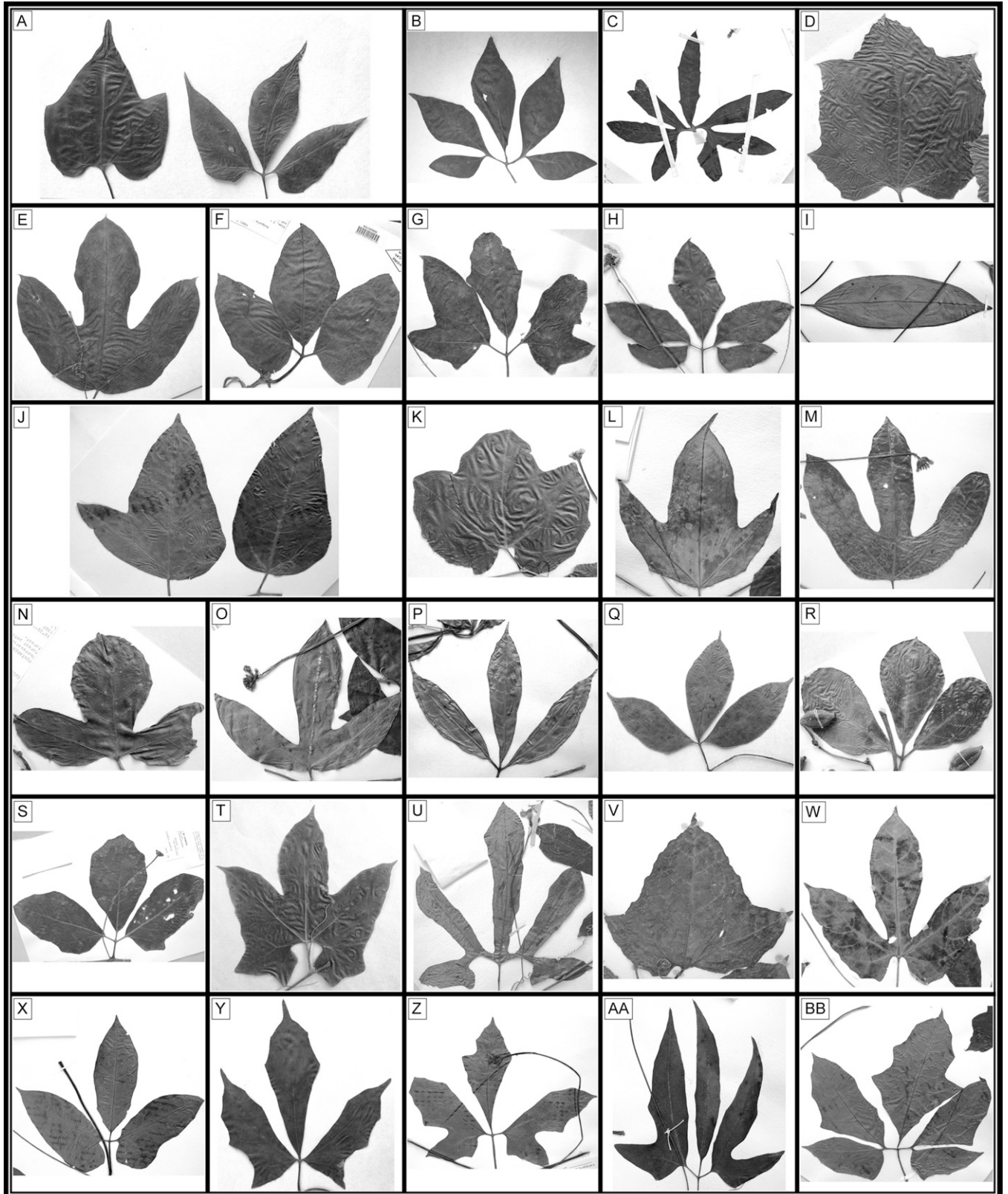


FIG. 5. Leaf morphology variation in the six species of *Psiguria*. A–C: *P. pedata*, D–E: *P. racemosa*, F–H: *P. ternata*, I–S: *P. triphylla*, T–U: *P. umbrosa*, V–BB: *P. warszewiczii*. A. adjacent leaves on an immature branch, B. mature pedate leaf, C. pedate with side leaflets further divided, D. shallowly trilobed, E. deeply trilobed, F. typical trifoliolate leaf with side leaflet midveins off-center, G. trifoliolate with lateral lobes on side leaflets, H. rare pedate leaf, I. simple, elliptic, J. adjacent leaves, one simple, lanceolate, and one beginning to divide, K. wide trilobed leaf, L. trilobed, M. deeply trilobed, variation #1, N. deeply trilobed, variation #2, O. deeply trilobed, variation #3, P. trifoliolate, variation #1, Q. trifoliolate, variation #2, R. trifoliolate, variation #3, S. trifoliolate with side leaflet midveins off-center, T. trilobed, U. deeply trilobed, V. shallowly trilobed, W. deeply trilobed, variation #1, Y) trifoliolate, variation #2, Z. trifoliolate, variation #3, nearly pedate, AA. trifoliolate, variation #4, nearly pedate, BB. pedate.

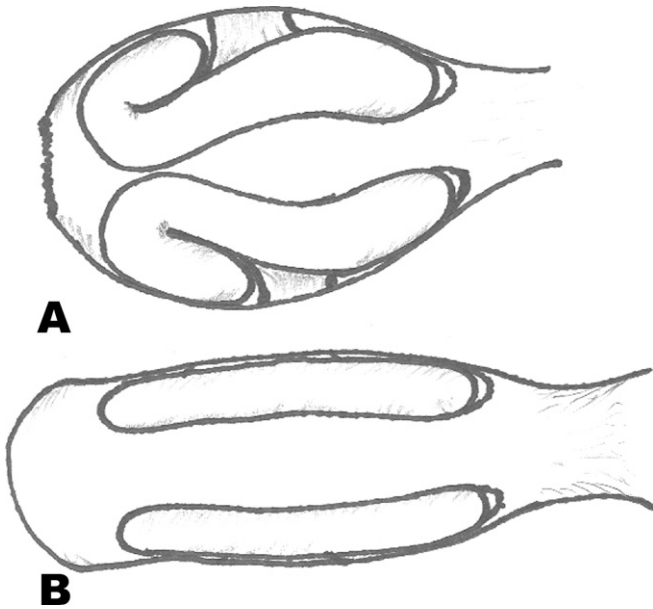


FIG. 6. Two types of anthers inside the male floral tube. To the left is the base of the flower, and on the right ends of the anthers are the anther appendages. A, folded anthers: *Psiguria pedata*, B, straight anthers: all other species of *Psiguria*. Drawn by PRS.

1911, *Shafer 10523* (NY, A*); Limestone Hills, Sumidero, 28 Jul 1912, *Shafer 13383* (NY); San Diego de los Baños: 05 Nov 1911, *Earle s. n.* (NY*); Santa Clara: Cienfuegos, 23 May 1893, *Combs 83* (GH, NY); Sagua, 05 Sep 1903, *Britton & Wilson 355* (NY); Soledad, Jun 1941, *Howard 4792* (NY); Sagua La Grande, 12 Aug 1920, *Loustalot 9459* (NY); Santiago: Aug 1940, *Clemente 2431* (NY); Southern Baracoa Region: 30 Jul 1924, *Leon 11916* (NY).

DOMINICAN REPUBLIC. Azua: Los Manantiales, Sección Galindo, 400 m, 14 Mar 1980, *Mejía 194* (NY); Barahona: Sierra Martín García, 4 km E of Las Salinas, 100–150 m, 30 Oct 1985, *García et al. 578* (NY*); Duarte: Cordillera Septentrional, 300–800 m, 06 May 1993, *Bastardo et al. 3* (MO); El Seibo: Los Haitises, Muelle Viejo, 21 Jan 1980, *Smith 10437* (NY); Parque Nacional Los Haitises, 2 km SW of la caseta de Monte Bonito, 200–300 m, 18 Sep 1985, *Mejía et al. 1597* (NY); La Altigracia: 2 km SW of Boca de Yuma, 10–20 m, 04 Feb 1981, *Zanoni et al. 10622* (NY); parallel to coast above La Playita, 40–60 m, 06 Feb 1981, *Zanoni et al. 10839* (NY); Boca de Yuma next to cave, 20–30 m, 11 Jan 2007, *Steele et al. 1034, 1035* (TEX*); La Romana: Río Cumayasa river valley, N of Boca de Cumayasa, 0–20 m, 11 Jun 1981, *Mejía & Rimirez 14796* (NY); La Vega: Jarabacoa, 1200 m, 18 Apr 1964, *Augusto 1469* (NY*); La Ciénega, 1100–1200 m, 13 Jul 1967, *Gastony et al. 161* (NY*, US); 7 km S of La Vega, 16 Sep 1973, *Jiménez 6207* (NY*); Macoris: Consuelo, 15 Nov 1909, *Taylor 166* (NY*); Mata Grande: Banks of Río Bao, 750 m, 03 Jun 1968, *Liogier 11514* (NY*); Pederenales: Las Mercedes, 400 m, 22 Feb 1969, *Liogier 14123* (NY*); Peravia: 9.8 km SW from Juan Aldian, 10 Jun 1980, *Mejía & Zanoni 6832* (NY); Piedra: Firme de Banilejo, 800 m, 01 Jun 1974, *Liogier 21687* (NY); Puerto Plata: Loma Isabel de Torres, 750 m, 30 Nov 1983, *Zanoni et al. 28069* (NY*); San Cristóbal: Cabirma de la Loma, 700 m, 28 Nov 1970, *Liogier 17756* (NY*); Santiago: Pico Diego de Ocampo, 1100 m, 17 Sep 1968, *Liogier 12694* (NY); Santo Domingo: Santo Domingo City, near Agua Cave, 24 Mar 1913, *Rose et al. 4129* (NY); Ciudad Trujillo, 0–25 m, 07 Jan 1946, *Allard 14416* (NY); Jardín Botánico, 0–20 m, 13 Jan 2007, *Steele et al. 1036* (TEX*).

HAITI. Gonave Island: Étroite, 15 Mar 1920, *Leonard 3399* (NY*); Nord: Marmelade, 800 m, 20 Dec 1925, *Leonard 8360* (NY); Tortue Island: La Vallée, Jan 1929, *Leonard & Leonard 11349*; Dept. unknown: Borgne, 0 m, 14 Aug 1903, *Nash 420* (F*, NY); Jacmel, 0 m, Jul 1935, *Thomas 23* (NY); Pétienville, 350 m, 15 Jun 1920, *Abbott 4915* (NY); Mornes a Cabrites, 300 m, 14 Dec 1941, *Holdridge 889* (NY).

PUERTO RICO. Arecibo: Caguana, Río Abajo Forest Preserve, 200–250 m, 05 Jan 2007, *Steele et al. 1030* (TEX*); Río Abajo Forest Preserve, 340 m, 18 Jan 1996, *Acevedo-Rdgz. & Axelrod 7781* (US*); W Sabana Hoyos, 26 Jun 2001, *Acevedo-Rdgz. & Chinae 11659* (US*); Dept. unknown: Aibonito, Cañón de San Cristóbal, 400 m, 18 Dec 1980, *Liogier et al. 31422* (NY); Cayey, barrio Pasto Viejo, 350 m, 14 Oct 1981, *Liogier et al. 32529* (NY*); Piñon, Coamo Road, 20 Nov 1899, *Goll et al. 627* (US*); Tijera, J. Diaz, 23 Nov 1899, *Goll et al. 762* (US).

2. *PSIGURIA RACEMOSA* C. Jeffrey, *Kew Bulletin* 33(2): 347. 1978.—TYPE: VENEZUELA. Aragua: Guamitas, *Williams 10130* (holotype: VEN fide Jeffrey (1978)).

Stems glabrous or puberulent, solid green, 1.3–4.7 mm in diameter; tendrils glabrous, solid green, 0.5–1.6 mm in diameter. Leaves membranous, both surfaces glabrous with veins sometimes puberulent, 3–5 main veins, flush, margins entire-irregular-wavy, with irregularly-spaced veins extending beyond blade, simple; petioles glabrous or pubescent, 1.2–3.0 mm in diameter, (3–)22–58 mm long; simple leaves trilobed, base auriculate-truncate-rounded-acute, base 7–30 mm deep, apex acuminate, 115–219 mm long, 32–70 mm wide, lobe depth average 67.3% of total length. Inflorescence an indeterminate corymb; peduncles glabrous or puberulent, solid green, 1.1–2.0 mm in diameter, 90–225 mm long; pedicels pubescent, 2.0–13.5 mm long, with 0.5–0.74(–0.83) flowers per mm. Staminate flowers, first 2–3 flowers not much larger than subsequent flowers; calyx salverform flask-shaped, glabrous or puberulent, solid green, 5.0–9.5 mm long, 1.4–5.5(–7.0) mm wide, adaxial surface glabrous with sparse to dense trichomes at throat; sepals thin, linear, color same as calyx, 1.5–4.0 mm long; petals pink with orange or yellow center, elliptic-rhombic, apex acuminate, 4.5–13.0 mm long, 2.2–7.0 mm wide, length-to-width ratio 2.1; anthers straight, 4.4–7.0 mm long, anther appendage triangular, papillose, 0.4–1.0 mm long. Pistillate flowers 3 per node, axillary; calyx salverform elongated ellipse, glabrous, solid green, 11.0 mm long, 3.3 mm wide, adaxial surface unknown; sepals thin, triangular, color same as calyx, 2.5 mm long; petals unknown, elliptic, apex acuminate, 8.8 mm long, 2.5 mm wide, length-to-width ratio 3.5; ovary elliptic-oblong, 6.5 mm long, 3.3 mm wide, style length unknown, stigma length unknown. Fruits, exocarp color unknown, 19.0 mm long, 12.0 mm wide, wall thickness unknown. Seeds not seen.

Phenology—Flowering April through July, and perhaps other times of the year. A few flowering individuals have also been collected in November and January. Of the 18 specimens examined, 66.7% had male flowers, 16.7% had female flowers or fruits, and the remainder were sterile.

Distribution and Habitat—Continental Colombia and Venezuela (Fig. 7). Found at elevations from 15 m to 1,750 m in tropical moist or dry broadleaf forests, and on slopes, in ravines, or climbing over rocks and shrubs.

Discussion—Compared to other species of *Psiguria*, the leaf morphology of *P. racemosa* is fairly consistent, trilobed and

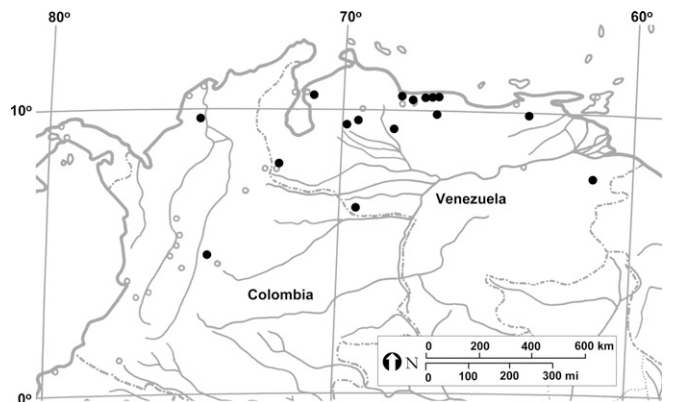


FIG. 7. Geographic distribution of *Psiguria racemosa*. Open circles are part of the base map image.

membranous, but with variable depth of lobes (Fig. 5 D, E). The geographic range of *P. racemosa* overlaps with *P. umbrosa* and *P. warscewiczii* in Venezuela, and all three have, or may have, simple, trilobed leaves. The characters that separate *P. racemosa* from the other two are its distinctive pink flower petals, and peduncles and calyx tubes that are solid green, as opposed to the orange or orange-red flower petals, and peduncles and calyx tubes that are light green with darker speckles in *P. umbrosa* and *P. warscewiczii*.

The geographic range of *Psiguria racemosa* also overlaps with *P. triphylla*; however, in this area, the simple, trilobed leaf morphs of *P. triphylla* have not been seen. Additional characteristics that distinguish these two species include male petal color (*P. racemosa* = pink; *P. triphylla* = deep red, typically with a yellow base), male flower pedicel average length (*P. racemosa* = 5.6 mm; *P. triphylla* = absent), and density of flowers along the peduncle (*P. racemosa* = < 0.75 flowers per mm; *P. triphylla* = > 0.75 flowers per mm). Despite these fairly obvious morphological differences, the molecular phylogeny did not strongly support the distinction of *P. racemosa* from *P. triphylla* (Steele et al. 2010). There have been few individuals of *P. racemosa* collected (only 18 examined in this study, and only five included in the molecular phylogeny). With more collections and molecular study, the lines between these two species may become better defined.

Representative Specimens Examined—(collections marked with an asterisk were measured for species descriptions)

COLOMBIA. Bolívar: near Sincé, 20 Apr 1963, Romero 9685 (MO*); Cundinamarca: Sasaima, Quebrada La María, 1,750 m, 07 Jan 1950, García-Barriga 13400 (NY*).

VENEZUELA. Antioquia: 22 Jun 1946, *Haught 4898* (US); Aragua: Selvas de Rancho Grande, Parque Nacional, 1,100 m, 17 May 1942, *Pittier 14999* (US*); Bolívar: Piar, La Camilera, 40 km W of El Manteco, 250–260 m, Jul 1978, *Delascio & Liesner 7096* (US*); E of Miamo, 400–550 m, 25 Jan 1961, *Steyermark 88837* (NY*); Carabobo: El Palito, near Puerto Cabello, 0–30 m, 02 Jul 1913, *Pittier 6426* (US*); Caracas: Lower Catuche wood, 1,000–1,200 m, 17 May 1918, *Pittier 7854* (US); Federal: bosque de Catuche, N of Caracas, 1,200–1,800 m, 01 Jun 1913, *Pittier 6294* (NY*); Lara: Palavecino, between Sarare & El Altar, 350 m, 02 Jun 1974, *Steyermark et al. 109898* (NY); Portuguesa: Araure, 5 km NE of Agua Blanca, 250 m, 05 May 1984, *Aymard & Ortega 2527* (NY); Guanare, terrenos de la UNELLEZ, 06 May 1983, *Stegios 5572* (NY); Tachira: between Aguas Calientes and La Rinconada, 550 m, 13 Nov 1979, *Steyermark et al. 120279* (MO*); Zulia: Bolívar, 6 km E of El Pensado, 150–200 m, 27 Apr 1982, *Bunting 11422* (NY*); Dept. unknown: 5 km W of Jusepin, Monagas on the Río Huarapiche, 30 Apr 1979, *Seigler 11153* (MO); Faldas sur del Avila, Aug 1937, *Tamayo 432* (US).

3. *PSIGURIA TERNATA* (M. Roem.) C. Jeffrey, *Kew Bulletin* 33(2): 354. 1978. *Anguria ternata* M. Roem., *Syn. Mon.* 2: 26. 1846.—TYPE: t. 2 in Vell., *Fl. Flumin.* p. 10. 1835. (holotype fide Jeffrey (1978)).

Anguria kunthiana Schldl., *Linnaea* 24: 762. 1851.—TYPE: BRAZIL. Dec, 1836, *Humbolt 8978* (holotype: B destroyed; photograph: F!).

Anguria grandiflora Cogn. *Diagn. Cucurb. fasc. I* p. 11. 1876.—TYPE: BRAZIL. Maynas: Yurimaguas, 1831, *Poeppig 2416* (holotype: W; photograph: F!).

Anguria gloriosa S. Moore, *Trans. Linn. Soc. Lond. ser. 2. Bot.* IV p. 366 t. 25. 1895.—TYPE: Locality unknown. 1891–1892, *Moore 659* (holotype: NY!).

Stems glabrous, solid green or light green with darker, linear splotches, 2.0–5.6 mm long; tendrils glabrous, solid green, 0.8–1.7 mm in diameter. Leaves coriaceous, both surfaces glabrous, veins flush or seldom abaxial main veins prominent, margins entire-irregular-wavy, with infrequent irregularly-

spaced veins extending beyond blade; trifoliolate (or rarely bifid or pedate); petioles glabrous, 1.3–3.3 mm in diameter, 14–80 mm long; petiolules glabrous or puberulent, 1.2–2.0 mm in diameter, 2–35 mm long; complex leaves with center leaflet rhombic-oblong-ovate-spatulate and side leaflets ovate-elliptic, oblique, and sometimes with small, lateral lobe, apices acuminate; center leaflet base acute-attenuate, 95–200 mm long, 45–115 mm wide; side leaflets base oblique, adaxial base acute-attenuate and abaxial base acute-truncate, 80–172 mm long, 29–97 mm wide. Inflorescence a compact raceme; peduncles glabrous or puberulent, solid green or light green with darker splotches, 1.5–3.0 mm in diameter, (78–)155–293 mm long; pedicels pubescent, (0.1–)0.5–1.6(–4.0) mm long, with 0.25–1.00 flowers per mm. Staminate flowers, first 2–3 flowers much larger than subsequent flowers; calyx salverform, cylindrical-elliptical, glabrous or puberulent, solid green or light green with darker speckles, 5.0–13.0 mm long, 2.0–6.4 mm wide, adaxial surface glabrous with trichomes at throat; sepals thin, linear, color same as calyx, 1.0–8.5 mm long; petals pink, rose, salmon-rose, or deep-rose, orbicular-obovate, apex rounded, 3.0–10.5 mm long (average first 3 flowers 62.0, 48.0, and 22.0 mm long), 2.4–7.2 mm wide (average first 3 flowers 40.0, 25.0, and 11.0 mm wide), length-to-width ratio 1.2; anthers straight, 4.4–8.0 mm long, anther appendage round-triangular, glabrous-papillose, 0.2–1.0 mm long. Pistillate flowers 2–4 per node, axillary, but at the ends of branches with reduced leaves; calyx salverform, cylindrical-elliptical, glabrous, solid green, 19.0–32.0 mm long, 2.5–5.2 mm wide, adaxial surface glabrous or puberulent with trichomes at throat; sepals thin, linear, color same as calyx, 2.3–3.7 mm long; petals pink, obovate, apex rounded or rarely cuspidate, 8.0–16.0 mm long, 3.5–9.0 mm wide, length-to-width ratio 2.1; ovary elliptic-oblong, 12.0–20.0 mm long, 4.2–7.0 mm wide, style 3.3–5.0 mm long, stigma 5.0–7.0(–12.0) mm long. Fruits, green, sometimes speckled with lighter green, 22–44 mm long, 10–18 mm wide, wall 0.7–2.0 mm thick. Seeds 44–54, 6.5–7.9 mm long, 4.5–4.9 mm wide, 1.9–3.0 mm thick.

Phenology—Flowering throughout the year with flowering peak from October through February. Of the 73 specimens examined, 71.2% had male flowers, 19.2% had female flowers or fruits, and the remainder were sterile.

Distribution and Habitat—Bolivia, Brazil, Perú, and Paraguay (Fig. 8). Found at elevations from 170 m to 1,800 m

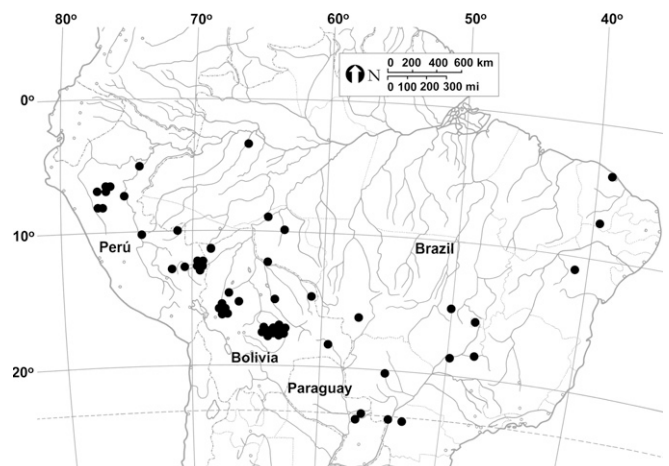


FIG. 8. Geographic distribution of *Psiguria ternata*. Open circles are part of the base map image.



FIG. 9. Comparison of the first two flowers of *Psiguria ternata* (large) with three subsequent flowers on the same inflorescence (small).

in tropical evergreen, deciduous, or semideciduous, moist or dry broadleaf forests, flooded grasslands, and xeric shrublands. May be found in disturbed or secondary forests, in dense shade or light gaps, on roadsides, riverbanks, or slopes, climbing over other vegetation, and on sandy or clay soils.

Discussion—The most distinctive characteristic of *Psiguria ternata* is the large size of the first two or three male flowers on the inflorescence, which can be six to seven times larger than subsequent flowers (Fig. 9). This characteristic is hypothesized to be an adaptation for attracting and training the pollinating butterflies to the locations of these widely separated plants (L. E. Gilbert, pers. comm.). Once the pollinator knows where to find the flowers, the plant no longer needs to allocate great resources to making a giant display.

The geographic distribution of *Psiguria ternata* overlaps with *P. triphylla* and a few *P. umbrosa*. Consistent trifoliolate (rarely pedate), coriaceous leaves and pink flowers easily distinguish *P. ternata* from *P. umbrosa*, which has simple 3- to 5-lobed, membranous leaves and orange flowers. Distinguishing *P. ternata* from *P. triphylla* is not quite as straightforward. Both have predominantly trifoliolate, coriaceous leaves, although more often in *P. ternata*, the midveins of the side leaflets are off-center (Fig. 5F–H), whereas midveins in *P. triphylla* side leaflets are typically centered, though not always (Fig. 5P–S). Also, male inflorescences of *P. ternata* are racemose, and the flower cluster has a triangular shape (Fig. 10A) with loosely spaced flowers and pink petals. Male inflorescences of

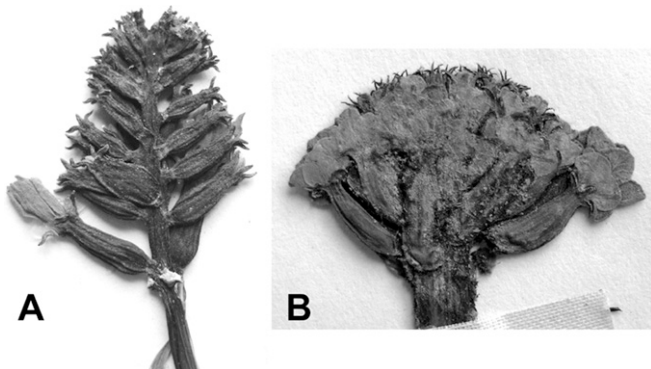


FIG. 10. Comparison of the flower clusters on *Psiguria ternata* (A. triangular) and *P. triphylla* (B. horizontal ellipse).

P. triphylla are spicate, and the flower cluster is shaped like a horizontal ellipse (Fig. 10B) with tightly clustered flowers and petals that are deep red, typically with a yellow base.

The molecular phylogeny strongly supported the clade of *Psiguria ternata* samples (Steele et al. 2010). Within this clade, two subclades were strongly supported. One clade included three samples from the tropical, moist forests of Perú, Brazil, and northern Bolivia, and the other included samples from the tropical, dry forests of south-central Bolivia. However, no morphological characteristics were identified to support a split into two taxa. Perhaps additional collections and molecular study will support a split of these clades into two species or subspecies in the future.

Representative Specimens Examined—(collections marked with an asterisk were measured for species descriptions)

BOLIVIA. El Beni: Ballivián, S of Misión Fatima, 300–500 m, 24 May 1988, *Beck et al.* 16469 (F); Cercado, Casarabe, 51 km E of Trinidad, 200 m, 14 Dec 1988, *Nee* 37179 (NY*); Rurrenabaque, 1,000 ft, 28 Nov 1921, *Cardenas* 1884 (NY); La Paz: Nor Yungas, 21 km NW of Chuspipata, 1,800 m, 05 Oct 1984, *Solomon & Escobar* 12460 (MO, NY); Nor Yungas, 9 km N of Yolosa, 1,150 m, 30 Oct 1984, *Nee & Solomon* 30243 (MO, NY); Nor Yungas, de Villa Barrientos 19 km hacia Arapata, 1125 m, 04 Jan 1990, *Beck* 17361A (NY); Nor Yungas, km 12 Coroico to Caranavi, 1,015 m, 23 Jan 1983, *Besse et al.* 1762 (F, MO); Nor Yungas, on road from Coroico to Caranavi, 1,150 m, 30 Oct 1984, *Nee & Solomon* 30243 (F, TEX, US); Sud Yungas, 450 m, 01 Jan 1988, *Seidel & Schulte* 2303 (NY); Pando: Nicolás Suárez, cerca de Cobija, 07 Jan 1983, *Fernández* 8054 (NY); Reyes: San Pedro, 25 Oct 1921, *White* 1541 (NY); Santa Cruz: Andrés Ibáñez, 2.8 km SE of turnoff from Santa Cruz to Puerto Pailas Hwy, 320 m, 07 Jan 1998, *Nee* 47832 (NY*); Andrés Ibáñez, 7 km SE of Naranjillos, 480 m, 30 Sep 1990, *Nee* 38959 (TEX*); Florida, 1 km NE of junction with Río Bermejo, 800 m, 16 Feb 1988, *Nee & Saldias* 36321 (NY); Florida, Bermejo, 700 m, 08 Dec 1988, *Nee* 37059 (NY); Ichilo, Parque Nacional Amorós, 500 m, 21 Jan 1988, *Saldias* 134 (NY); Santiesteban, 1.5 km SW of Montero, 295 m, 12 Jan 1987, *Nee* 33434 (NY); Sara, 260 m, 20 Dec 1995, *Nee* 46377 (NY); Velasco, Campamento Refugio, 180 m, 11 Feb 1995, *Guillen et al.* 3178 (NY); 300 m, 16 May 1991, *Gentry et al.* 73937 (F); derecho lado del sendero que está sur de puente a la Mistad, 317 m, 09 Jan 2008, *Steele et al.* 1040 (TEX*); Río Pirai, puente Taruma; 1 km sur de la carretera en oeste de sendero, 618 m, 10 Jan 2008, *Steele et al.* 1043 (TEX*).

BRAZIL. Amazonas: Camatian, 24 Jan 1949, *Fróes* 23975 (NY); Bahia: Jussari, Serra do Teimoso, 300 m, 31 Jan 1999, *Thomas et al.* 11882 (NY); Ceará: Crato, Chapada do Araripe, Parque Nacional do Araripe, 820 m, 19 Jan 1983, *Plowman* 12738 (F*, NY); Curitiba: Antonio João, Campestre, Mato Grosso do Sul, 16 Mar 1985, *Hatschbach & Zelma* 49096 (US); Mato Grosso, Ribeirão da Onçinha, Poconé, Cuiabá, 12 Feb 1980, *Macedo et al.* 1488 (NY); DF: Fazenda Maria Pereira, Região do Mesquita, GO, 05 Feb 1986, *Mendonça & Alvarenga* 608 (US); Goiás: Contraforte Central, 20 km NE of Catalão, 875 m, 23 Jan 1970, *Irwin et al.* 25200 (US*); Serra Dourada, 30 km SE of Goiás Velho, 700 m, 21 Jan 1966, *Irwin et al.* 11903 (NY); Minas Gerais: Capinópolis, Chácara, 15 Dec 1995, *Macedo* 4071 (MO*, US); Pará: Serra do Cachimbo, 425 m, 12 Dec 1956, *Pires et al.* 6158 (NY); Paraná: Curitiba, Sete Quedas, Guaira, 12 Dec 1977, *Hatschbach* 40595 (NY*); Parque Sete Quedas, 10 Jan 1979, *Bernardi* 19433 (NY); Rondônia: Porto Velho, reservatório da Usina Hidroelétrica de Samuel, 08 Jun 1986, *Ferreira et al.* 7405 (NY); Forte Príncipe de beira, local Baia, 05 Jan 1962, *Rodrigues & Wilson* 4245 (NY*); Mineração Taboca at massangana, 35 km WSW of Ariquemes, 11 Oct 1979, *Zarucchi et al.* 2678 (NY).

PARAGUAY. San Pedro: 27 Apr 1958, *Woolston* 960 (NY*, US); *Hassler* 7808 (NY*).

PERÚ. Cusco: Calca, Quebrada, 1,031 m, 26 Jan 2003, *Valenzuela et al.* 1387 (MO); Río Tambopata, 2 km of Colpa de Guacamayos, 280 m, 10 Nov 1986, *Núñez* 6511 (MO); Huáncayo: Pachitea, N of Puerto Inca, 250–300 m, 15 Sep 1982, *Foster* 8808 (MO); Loreto: Contamana, Quebrada de Maquia, 220 m, 16 Dec 1964, *Schunke* 6675 (MO); Río Ucayali, 1 hora surcando de Requena, 170 m, 04 Dec 1980, *Vásquez & Jaramillo* 872 (MO); Madre de Dios: Manu, Parque Nacional Manu, 400 m, 26 Oct 1986, *Foster & d'Achille* 12050 (F*); 39 km SW of Puerto Maldonado, 28 Jan 1989, *Smith et al.* 1644 (NY*); Parque Nacional Manu, Cocha Cashu Station, 350 m, 13 Jul 1984, *Foster* 9629 (F*); San Martín: Mariscal Cáceres, Tananta, margen izquierda del Río Huallaga, 06 Oct 1970, *Schunke* 4482 (NY); San Martín, hills to NW of Chazuta, 300–400 m, 18 May 1986, *Knapp & Alcorn* 7315 (MO); San Martín, Tarapoto, banks of Chumbaza river, 830 m, 25 Feb 1947, *Woytkowski* 35180 (F, MO); San Roque, Feb 1930, *Williams* 6946 (US); Alto Río Huallaga, 360–900 m, Dec 1929, *Williams* 6514 (F); Ucayali: Purús, Río Curanja, cerca la

comunidad nativa de Columbiana, 250 m, 22 Feb 2000, *Graham & Schunke 1061* (NY).

4. *PSIGURIA TRIPHYLLA* (Miq.) C. Jeffrey, *Kew Bulletin* 33(2): 347. 1978. *Anguria triphylla* Miq. *Linnaea* 19: 136. 1845.—TYPE: SURINAME. *Kappler 1728* (holotype: U fide Jeffrey (1978); photograph: F!).

Anguria schomburgkiana Schldtl., *Linnaea* 24: 765. 1851.—TYPE: GUYANA. *Schomburgk 1254* (holotype: B destroyed fide Jeffrey (1978); photographs: F!, MO!).

Anguria pallida Cogn., *Diagn. Cucurb. I*: 22. 1876. *Psiguria triphylla* var. *pallida* Cogn., *DC. Mon. Phan. III*. 670. 1881.—TYPE: ECUADOR. Chimborazo. Jun 1860, *Spruce 6205* (holotype: K fide Jeffrey (1978); photograph: F!).

Anguria longipedunculata Cogn. *Diagn. Cucurb. fasc. I p.* 21. 1876. *Psiguria longipedunculata* (Cogn.) Wunderlin, *Phytologia* 38(3): 219. 1978.—TYPE: MEXICO. Veracruz: Catemaco, Apr 1845, *Galeotti s. n.* (lectotype: BR fide Wunderlin (1978)).

Anguria boissieriana Cogn. *DC. Mon. Phan. III p.* 673. 1881.—TYPE: PERU. *Ruiz 34096* (holotype: G-BOIS; photographs: F!, MO!).

Anguria triphylla var. *acuminata* Cogn., *DC. Mon. Phan. III p.* 670. 1881.—TYPE: ECUADOR, Chimborazo *Spruce 6149* (holotype: K).

Anguria diversifolia Cogn., *Donn. Sm. Bot. Gaz. (Crawfordsville)* 16(1): 10. 1891. *Psiguria diversifolia* (Cogn.) C. Nelson, *Fern. & Casas, Fontqueria* 52: 4. 1998.—TYPE: GUATEMALA. Alta Verapaz, Nov 1888, *Turckheim 1414* (holotype: US! fide Jeffrey (1978)).

Anguria oblongifolia Cogn., *Bot. Gaz.* 16: 9. 1891.—TYPE: GUATEMALA. Livingston: Río Dulce, Mar 1889, *Smith 1510* (holotype: online photograph US!).

Anguria treslingiana Pulle, *Rec. Trav. Bot. Néerl.* 6: 289. 1909.—TYPE: SURINAME. Jul 1908. *Tresling 252* (holotype: online photograph U!).

Anguria pachyphylla Donn. Sm., *Bot. Gaz. (Crawfordsville)* 54: 236. 1912.—TYPE: COSTA RICA. *Tonduz 11535* (holotype: US fide Wunderlin (1978); online photograph!).

Anguria tabascensis Donn. Sm., *Bot. Gaz.* 54: 236–237. 1912.—TYPE: MEXICO. Tabasco, 4 Jul 1889, *Rovirosa 519* (holotype: US!; isotype: NY!).

Anguria elliptica Britton, *Bull. Torr. Bot. Cl.* 50: 54. 1923.—TYPE: TRINIDAD. Arima, 4 Mar 1921, *Britton 2084* (holotype: NY!; isotype: K fide Jeffrey (1978)).

Anguria dunlapii Standl., *Field Mus. Publ. Bot. Ser.* 4: 298. 1929. *Psiguria dunlapii* (Standl.) R. J. Hampshire, *Novon* 2: 339. 1992.—TYPE: PANAMA. Bocas del Toro: Farm Six, Changuinola Valley, 3 Mar 1924, *Dunlap 490* (holotype: US!; photographs: F!, MO!).

Anguria longeracemosa Pittier, *J. Wash. Acad. Sci.* 19: 185. 1929.—TYPE: PANAMA. Yaviza, southern Darien, on margin of forest, Apr 1914, *Pittier 6582* (holotype: US fide Wunderlin (1978); isotype: online photograph US!).

Anguria vogliana Suess., *Fedde Rep.* 30: 278. 1932.—TYPE: VENEZUELA. Maracay, 1928, *Vogl 302*, (holotype: M fide Jeffrey (1978); photographs: F!, MO!).

Stems puberulent at nodes, otherwise glabrous, flaking on older, woody stems, solid green or brown, 1.1–7.0(–32.0) mm in diameter; tendrils glabrous, solid green, 0.3–3.1 mm in diameter. Leaves coriaceous, both surfaces glabrous, veins flush or seldom abaxial and adaxial main veins prominent, margins entire-irregular-crisped-revolute, seldom with irregularly-spaced veins extending beyond blade, simple, trifoliolate, or a combination of these; petioles glabrous, 1.0–5.3 mm in diameter, 8–75 mm long; simple leaves lanceolate, elliptic, or trilobed, base auriculate-rounded-acute, base 5–30 mm deep, apex acuminate, 75–184 mm long, (22–)40–76(–178) mm wide, lobe depth average 53.2% of total length; petiolules glabrous, 0.9–3.6 mm in diameter, 2–48 mm long; complex leaves with center leaflet elliptic-obovate-oblancheolate and side leaflets ovate-elliptic-obovate, apices acuminate-cuspidate; center leaflet base acute-attenuate, 71–305 mm long, 22–132(–177) mm wide; side leaflets base cuneate-acute, rarely oblique, 55–225 mm long, 18–124 mm wide. Inflorescence an apedicellate, indeterminate corymb; peduncles glabrous, solid green, (0.6–)1.1–4.6(–8.0) mm in diameter, 63–395 mm long; pedicels absent or length less than 0.3 mm, with greater than 0.75 flowers per mm. Staminate flowers, first 2–3 flowers not much larger than subsequent flowers; calyx salverform cylindrical, often with a thickened base, rarely cylindrical, glabrous or puberulent, solid green, 5.5–15.0 mm long, 1.0–4.8 mm wide, adaxial surface glabrous with sparse to dense trichomes at throat; sepals thin, triangular-linear, color typically same as calyx, but sometimes darker, 0.6–2.7(–4.8) mm long; petals red with yellow center, orange-red, strong red, or scarlet, orbicular-rhombic-flask-shaped, apex cuspidate, 2.0–12.0 mm long, 2.0–10.0 mm wide, length-to-width ratio 1.6; anthers straight, 3.4–8.5 mm long, anther appendage round-triangular, glabrous-papillose, 0.1–1.2 mm long. Pistillate flowers 2–5 per node, terminal; calyx salverform, cylindrical, glabrous, solid green, 11.0–41.0 mm long, 1.4–6.5 mm wide, adaxial surface glabrous with trichomes at throat; sepals thin, triangular-linear, color typically same as calyx, but sometimes darker, 1.0–2.3 mm long; petals red, orange-red, or scarlet, orbicular-rhombic-oblancheolate, apex cuspidate, 4.5–9.5 mm long, 2.5–9.5 mm wide, length-to-width ratio 1.6; ovary elliptic-oblong, 14.0–22.0 mm long, 3.0–5.8 mm wide, style 4.6–9.0 mm long, stigma 6.1–10.2 mm long. Fruits, green with lighter green stripes, some turning yellow with age, 30–45 mm long, 15–24 mm wide, wall 0.7–3.0 mm thick. Seeds 32–46, 7.7–10.0 mm long, 4.2–5.9 mm wide, 1.8–3.8 mm thick.

Phenology—Flowering throughout the year. Of the 297 specimens examined, 75.0% had male flowers, 9.1% had female flowers or fruits, and the remainder were sterile.

Distribution and Habitat—Throughout the Continental range of *Psiguria*, from southern Mexico to northern Bolivia (Fig. 11). Found at elevations from sea level to 2,100 m in tropical and subtropical evergreen, deciduous, or semideciduous, moist or dry forests, cloud forests, and flooded grasslands, in the upper canopies or clearings of both primary and secondary forests. May be found in dense shade or light gaps, on roadsides, riverbanks, or slopes, climbing over other vegetation, and on limestone, sandy, or clay soils.

Discussion—Of the *Psiguria* species, *P. triphylla* has the most variable leaf morphology (Fig. 5I–S). Mature leaves range from simple and elliptic to various trilobed shapes and sizes to an assortment of trifoliolate profiles. It is also the most widely distributed geographically (Fig. 11). For characters used to distinguish *P. triphylla* from the other species, see the

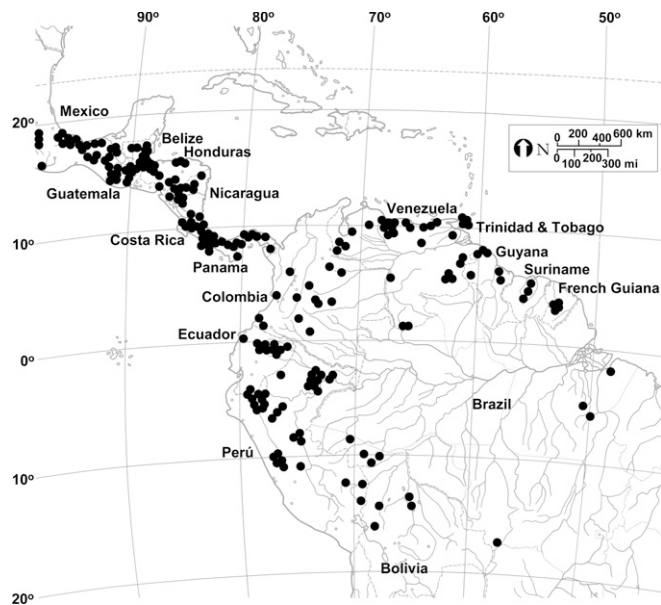


FIG. 11. Geographic distribution of *Psiguria triphylla*. Open circles are part of the base map image.

discussions under those taxonomic descriptions or the keys. *Psiguria triphylla* is most easily identified by flowers that lack pedicels, and a high density of flowers on an inflorescence (as many as three per millimeter). Figure 12 shows a typical *P. triphylla* inflorescence with flower scars covering the peduncle. Typically only one or two flowers open per day implying that this inflorescence (with approximately 383 flower scars) had been flowering for 7–13 mo at the time it was collected.

In the molecular phylogeny (Steele et al. 2010), all but one of the 28 *Psiguria triphylla* samples formed a moderately well-supported clade. Within this clade were several groupings of samples and some long branches. The lack of morphological variation in male flowers, and the great variation in leaf morphology do not help to explain these molecular groups. One exception may be the specimens from Los Tuxtlas and Catemaco, Veracruz, Mexico. Although four of the six samples included in the molecular phylogeny are clones of one another, artificially increasing the bootstrap support for the clade, it does not explain the rather long branch leading to it. The leaves of these specimens are simple, trilobed, and wide, but the lobing is much more shallow, and lobe tips are more rounded (Fig. 5K) than seen in the other trilobed *P. triphylla* leaf morphs. Additionally, although rarely seen in the field, the female corollas are typically reflexed downward rather than rotate (L. E. Gilbert pers. comm.). Additional collections undergoing molecular and morphological study may lead to



FIG. 12. Inflorescence of *Psiguria triphylla*, nearly 14 cm long, and containing approximately 383 flower scars.

the designation of a variety or subspecies containing these samples.

Psiguria triphylla also includes individuals that are different in stem size and overall robustness. Some mature, flowering individuals have small stems (1.0 mm) and almost delicate leaves, whereas others have robust, sturdy stems (up to 32 mm). Collections of widely varying sizes have been made throughout the geographic range. However, a notable exception is in northeastern Venezuela and in Trinidad where only the small-stemmed form is found.

Representative Specimens Examined—(collections marked with an asterisk were measured for species descriptions)

BELIZE. Cayo: Millionario, 1,800 ft, 30 May 1973, *Gentry 7692* (MO); Toledo: Cohune Ridge, 15 Mar 1945, *Gentle 5272*, (LL*); San Antonio, 03 Jan 1946, *Gentle 5469* (LL*); Manga Camp, 30 Apr 1948, *Gentle 6520*, (LL).

BOLIVIA. Beni: Ballivián, 1025 m, 25 Sep 1984, *Schmitt & Schmitt 141* (MO); La Paz: Larecaja, 1,200 m, 23 Jan 1988, *Solomon 17679* (MO*); Nor Yungas, 31 Oct 1984, *Solomon & Nee 12650* (NY).

BRAZIL. Acre: Brasília, 07 Nov 1991, *Ferreira & Ming 145* (NY*); Feijó, 01 Dec 1995, *Oliveira et al. 705* (NY); Pará: Belém, 17 Jun 1944, *Baldwin 4529A* (US*); Serra dos Carajás, 450 m, 17 Jun 1982, *Sperling et al. 6217* (NY*).

COLOMBIA. Boyaca: I30 M-N of Bogotá, 3,000 ft, 23 Mar 1933, *Lawrance 707* (A); Caqueta: 10 km S of San Jose de Fragua, 320 m, 11 Jan 1974, *Gentry et al. 9134* (MO); Choco: Pizarro, 16 Nov 1985, *Espina 1833* (MO); Cundinamarca: W of Guaduas, 1,040–1,320 m, 03 Nov 1945, *García-Barriga 11729* (US); El Meta: Villavicencio, Jun 1930, *Herb. Nac. Colombia 207* (US); El Valle: Río Digua Valley, 825 m, 02 Apr 1939, *Killip 34737* (F); Meta: Mesetas, 517–600 m, 29 Feb 1988, *Callejas & Marulanda 6033* (MO); Nariño: Espisella, Fumaco, 20 Jun 1951, *Romero 2794* (F); Ríosucio: Urabá, 20–300 m, 12 Feb 1988, *Cárdenas 1247* (MO); Santander: Caquetá, 100–700 m, 11 Aug 1935, *Haught 1874* (F*); Valle del Cauca: Bajo Calima, 100 m, 22 Mar 1985, *Monsalve 812* (MO).

COSTA RICA. Alajuela: N of San Ramón, 550–1,150 m, 08 Aug 1975, *Uttley & Uttley 2804* (F*); Hotel Villa Blanca, 1,100–1,200 m, 25 Jul 2005, *Steele & Fernández 1008* (TEX*); Cartago: Turrialba, 1,140 m, 16 Jul 1993, *Campos 144* (MO); Guanacaste: La Cruz de Abangares, 1,400 m, 15 Jul 1985, *Haber & Bello 2039* (MO); Heredia: La Selva, OTS Field Station on Río Puerto Viejo, 100 m, 27 Mar 1983, *Chacon 601* (F); Limón: Talamancá, 500 m, 18 Feb 1997, *Gonzales et al. 1756* (MO); Cerro Coronel, 10–100 m, 24 Jan 1986, *Stevens 23940* (MO); Parque Nacional Tortuguero, 40 m, 14 Mar 1988, *Robles 1728* (MO); Puntarenas: Burica Peninsula, 50–200 m, 22 Feb 1973, *Croat 22130* (MO*); Monteverde, 1,500 m, 24 Dec 1985, *Haber 3887* (MO*); Estación Biológica Las Cruces, 1,000–1,100 m, 08 Mar 1996, *Krings 246* (F); Cordillera de Tilarán, 1,500 m, 01 Aug 1996, *Krings 59* (F*).

ECUADOR. Esmeraldas: Bilsa Biological Reserve, 400–600 m, 15 Nov 1994, *Pitman & Clark 937* (MO); Guayas: Santiago-Zamora, 22 Jul 1960, *Mathias & Taylor 5232* (F); Napo: road Papallacta-Baeza, 2050 m, 06 Jun 1973, *Holm-Nielsen et al. 6964* (NY*); Cantón Archidona, 800–1,000 m, 23 Aug 1989, *Cerón & Factos 7619* (MO*); Jatún Sacha Biological Station, 450 m, 12 Jun 1995, *Acevedo-Rdgz. & Cedeño 7289* (US*); Tiputini Biodiversity Station, 200–300 m, 24 Oct 1998, *Burnham 1761* (F); Río Aguarico, 235 m, 15 Nov 1998, *Aguinda et al. 250* (F); Pichincha: Borja, 5,600 ft, 12 Aug 1960, *Grubb et al. 1276* (NY).

FRENCH GUIANA. Saül: Monts La Fumée, 200–300 m, 26 Jul 1987, *Hahn 3652* (NY); trail to Mt. Galbao, 250–300 m, 18 Aug 1988, *Mori et al. 19041* (NY*); Bélizon, 200–400 m, 03 Aug 1993, *Mori et al. 23084* (NY).

GUATEMALA. Alta Verapaz: Cubilquitz, 350 m, Apr 1901, *von Türckheim 775* (US); Chirriacté, 900 m, 09 Apr 1941, *Standley 91695* (F); Huehuetenango: Sierra de los Cuchumatanes, 1,500–1,600 m, 17 Jul 1942, *Steyermark 48982* (F); Izabal: Río Juyamá, 50–150 m, 08 Apr 1940, *Steyermark 39121* (F); NW of Lake Izabal, 500–600 m, 11 May 1966, *Jones & Facey 3361*, 3363 (NY*); Petén: Dos Lagunas in Zapotal, 26 Oct 1960, *Contreras 1561* (LL); Tikal National Park, 04 Mar 1961, *Lundell 16872* (LL*); Retalhuleu: Region of Ajaxá, 330 m, 23 Feb 1941, *Standley 88231* (F); San Marcos: Finca El Porvenir, 1,300 m, 06 Mar 1949, *Steyermark 37069* (F).

GUYANA. Morawhanna: Barima River, 14 Jan 1920, *Hitchcock 17499* (NY*); Northwest: Waini River, 06 Feb 1922, *de la Cruz 1297* (NY*); Upper Demerara-Berbice: 83 mi Bartica-Potaro Road, 400 ft, 24 Jun 1933, *Tutin 255* (US); Dept. unknown: Upper Mazaruni River region, 500 m, 15 Apr 1987, *Boom & Gopaul 7305* (NY*).

HONDURAS. Atlantida: Peru, 01 May 1970, *Barkley & Hernández 40227* (GH); Colón: 3 km E of Trujillo, 09 Jun 1980, *Saunders 309* (TEX); Cortés: Montaña La Cumbre, 600 m, 21 Mar 1962, *Molina 10545a* (F); El Paraíso: 25 km NE of Danlí, 16 May 1982, *Sánchez 184* (MO); Olancho: Montaña

Los Zapatos, 1,200–1,500 m, 25 Apr 1982, *Izaquirre 167* (MO); La Muralla National Park, 1,400 m, 06 Jun 1992, *Hawkins & Mejía 504* (MO); Santa Bárbara: San Pedro Sula, Jul 1887, *Thieme 186* (US).

MEXICO. Chiapas: Berriozábal, 900 m, 21 Apr 1972, *Breedlove 24811* (MO); Ocosingo, 170 m, 14 Jun 1985, *Martínez 12472* (MO*); Ocozocoautla, 550 m, 02 Apr 1983, *Calzada 9801* (F); Palenque, 170 m, 11 May 1982, *Davidse et al. 20329* (MO*); Trinitaria, 20 Sep 1984, *Méndez 7939* (MO); Oaxaca: Comaltepec, Tuxtpec, 1,100 m, 25 Jun 1966, *Martínez 906* (TEX); Tabasco: Balcan, La Palma, 01 Jun 1939, *Matuda 3313* (NY); 50–100 m, 12 Aug 1974, *Conrad & Conrad 2870* (MO); Veracruz: Atoyac, 13 May 1937, *Matuda 1404* (MO); Catemaco, 0 m, 13 Jul 1983, *Torres & Hernández 3281* (MO*); Catemaco, University of Texas greenhouse, 25 May 2005, *Steele 1004, 1038, 1058* (TEX*); Las Choapas, 160 m, 06 Mar 1978, *García 554* (F); Soteapan, 29 Jun 1982, *Nee et al. 24704* (NY); Tuxtla, 17 Jun 1971, *Ward 7904* (NY); Estación Biología Los Tuxtlas, 28 Dec 1969, *Gómez-Pompa & Rosas 3966* (F*); Hidalgotitlán, 140 m, 07 Sep 1974, *Dorantes 3510* (MO); Estación Biología Los Tuxtlas, 29 Mar 1979, *Dillon et al. 1780* (TEX*); Zacualpan, Dec 1915, *Purpus 7563* (MO).

NICARAGUA. Boaco: NE de Mombachito, 11 May 1982, *Sandino 2823* (MO); Esteli: Reserva Natural Miraflores, 1,200 m, 10 Jul 1999, *Rueda et al. 11651* (MO); Jinotega: Wiwili, Reserva Natural Kilambé, 900–1,200 m, 24 May 2001, *Rueda et al. 16360* (MO); Macizos de Peñas Blancas, 1,200–1,330 m, 16 Jan 1979, *Stevens 11548* (MO); Matagalpa: Santa María de Ostuma, 1,200–1,500 m, 01 Jan 1961, *Heller 7* (F); Fuente Pura, 1,400 m, 05 Jun 1982, *Stevens 21532* (MO); NW slope of Cerro El Picacho, 1,420–1,520 m, 25 May 1983, *Stevens & Moreno 22139* (MO*); San Juan: 0 m, 27 Mar 1971, *Nelson 5282* (MO); Zelaya: Siuna, 300–400 m, 15 Mar 1984, *Ortiz 1889* (MO).

PANAMA. Bocas del Toro: W of Campamento Corriente Grande, 23 Feb 1980, *Correa et al. 3725* (MO); Chiriquí: Río Colorado, 1,200–1,400 m, 17 Mar 1983, *Hamilton & Stockwell 3454* (MO); Coclé: Cerro Pilon, El Valle, 3,000 ft, 04 Jan 1968, *Duke & Lallathin 15007* (MO); Continental Divide, 1,500 ft, 20 Jun 1978, *Hammel 3516* (MO*); Colon: Santa Rita Ridge, 06 Apr 1969, *Lewis et al. 5283* (MO); Darién: S of El Real, 50 m, 31 Mar 1985, *McPherson 7085* (MO); Gamboa: Cerrado Pelado, 30–200 m, 18 Mar 1983, *Judziwicz 4520* (MO); Los Santos: Loma Prieta, 2,400–2,800 ft, 08 Jun 1967, *Lewis et al. 2217* (US); Panamá: Cerro Azul, 24 Mar 1969, *Porter et al. 4088* (NY); 1–2 mi beyond Goofy Lake, 01 Jan 1972, *Gentry & Dwyer 3412* (MO); El Llano-Carti Road, 350 m, 15 Feb 1975, *Mori et al. 4680* (MO*); Altos de Campana, 120 m del Motel Sulín, 3,065 ft, 26 Dec 1977, *Méndez 186* (MO); NW of Cerro Jefe, 650–750 m, 08 Nov 1979, *Antonio 2493* (MO); Barro Colorado Island, Canal Zone, Wheeler Trail, 17 Sep 1970, *Croat 12218* (MO*); Veraguas: beyond Tres Brazos River, 650 m, 24 Jul 1974, *Croat 25652* (MO).

PERÚ. Amazonas: Bagua, Yamayakat, 320 m, 16 Jul 1994, *Vásquez et al. 18738* (MO*); Huambisa, 180 m, 23 Nov 1979, *Tunqui 147* (MO); Río Cenepa, Huampami, 200–250 m, 1978, *Kujikat 219* (MO); Huáncó: Colpa, Río Monzón, 672 m, 06 Mar 1962, *Schunke 5804* (MO*); Leoncio Prado, 1,500–1,600 m, 23 Jun 1976, *Schunke 9364* (MO*); Bosque Nacional de Iparia, 300–400 m, 13 Feb 1967, *Schunke 1597* (F*); Junin: 51 km NE of Tarma, 1,550 m, 19 Dec 1978, *Dillon & Turner 1416* (F); Loreto: Alto Amazonas, 210 m, 05 Jun 1981, *Vásquez & Jaramillo 1912* (MO); Maynas, Iquitos, Río Momón, 09 Mar 1976, *Revilla 313* (MO*); Maynas, 140 m, 21 Nov 1991, *Vásquez 17577* (MO*); Previsto, Yurac Canyon, 420 m, 09 Oct 1962, *Woytkowski 7590* (F*); Río Amazonas S of Iquitos, 18 Aug 1972, *Croat 19325* (MO); Río Ampiyacu, Pucuraquillo, 08 Mar 1981, *Davis et al. 770* (F*); Carretera Iquitos, 133 m, 18 Jan 2008, *Steele & Meza 1052* (TEX*); Río Momon, Nanay, 125 m, 21 Jan 2008, *Steele et al. 1054* (TEX*); Madre de Dios: Manú, 24 Nov 1965, *Vargas 16951* (US); Tambopata Reserve, 250 m, 09 Mar 1981, *Young 42* (MO); Pasco: Oxapampa, 1,850 m, 09 Dec 1982, *Smith 2916* (MO*); San Martín: Huinguillo, 500 m, 05 Mar 1962, *Woytkowski 7150* (F); San Martín, Río Ponacillo, 570 m, 26 Jun 1984, *Knapp & Mallet 6542* (MO*); Ucayali: Purús, Río La Novia, 189 m, 19 Feb 2002, *Schunke & Graham S14849* (NY).

SURINAME. Brokopondo: Sectie, 19 Oct 1944, *Maguire & Stahl 25003* (NY); Rheno-Trai.: Lely Mts., 550–710 m, 26 Sep 1975, *Lindeman et al. 402* (F); Sipaliwini: Frederik Top, 500 m, 20 Aug 1963, *Irwin et al. 54907* (NY).

TRINIDAD & TOBAGO. Andrew Trace: Arima Pass, University of Texas greenhouse, 15 Feb 2008, *Steele 1056* (TEX*); Santa Isabella trail, 250–350 m, 10 Mar 1956, *Smith 10077* (US*); Arima: 04 Mar 1921, *Britton & Britton 2084* (US*); Tapaná Trace: Valencia-Matura Road, 30 Mar 1959, *Cowan & Forster 1395* (US); Dept. unknown: Balandra Bay, 08 Mar 1920, *Britton et al. 418* (NY*); Guanapo Road, 29 May 1975, *Philcox 7822* (NY).

VENEZUELA. Anzoátegui: NE of Bergantín, 500 m, 20 Feb 1945, *Steyermark 61005* (F); Aragua: Rancho Grande, 02 Apr 1926, *Pittier 12145* (US); Atures: Territorio Federal Amazonas, 80–100 m, 04 Mar 1982, *Guanchez 1585* (MO); Bolívar: N of Las Nieves, 600–650 m, 05 Feb 1961, *Steyermark 89251* (NY); La Gran Sabana, 900–1,000 m, 25 Apr 1988, *Liesner 23801* (MO); Lara: Guárico, San Isidro, Mar 1939, *Tamayo 685* (US);

Morán, 05 Mar 1983, *Aymard et al. 1889* (NY); Mérida: Tovar, 600–800 m, 29 Aug 1973, *Tillett & Hönig 738–544* (NY); Miranda: El Portachuelo, 29 Jan 1922, *Pittier 10142* (US); Guatopo National Park, 20 Feb 1981, *Condon 107* (TEX); Portuguesa: Sucre, 1,550 m, 16 Mar 1985, *Ortega & Smith 2575* (MO); Río Negro: Territorio Federal Amazonas, 1,250 m, 23 Mar 1984, *Stannard & Liesner 339* (F); Río Baria, 140 m, 17 Feb 1985, *Nee 30916* (NY); Tachira: Montaña de Guafitas, 250–300 m, 07 Nov 1979, *Steyermark et al. 119531* (MO); Trujillo: 900 m, *Pittier 13522* (F*); Tucupita: 200 m, 04 Apr 1979, *Davidse & González 16553* (MO); Yaracuy: El Amparo, 08 Mar 1973, *Diederichs 72* (NY*); Zulia: Miranda, Cerro Los Manantiales, 600 m, 03 Jun 1980, *Steyermark et al. 123263* (MO*).

5. *PSIGURIA UMBROSA* (Kunth) C. Jeffrey, *Kew Bulletin* 33(2): 347. 1978. *Anguria umbrosa* Kunth, *Nov. Gen. Spec.* 2:121. 1817.—TYPE: VENEZUELA. Sucre: Camanacoa, Bordonos, *Bonpland 165*, (holotype: P fide Jeffrey (1978); photograph: F!).

Anguria jacquiniana Schltdl., *Linnaea* 24: 708. 1851. *Psiguria jacquiniana* (Schltdl.) R. A. Howard, *J. Arnold Arbor.* 54(4): 442. 1973.—TYPE: N. J. Jacquin, *Sel. Stirp. Amer. Hist.* 242–246 *tabula 156*. 1763. (holotype!).

Anguria integrifolia Nees et Mart. *Nov. Acta Acad. nat. cur.* XII. 1. 9. 1825.—TYPE: BRAZIL. S. Pedro d'Alcantara, Dec 1816, *Wied s. n.* (holotype: online photograph BR!).

Anguria warmingiana Cogn. *Diagn. Cucurb.* I: 21. 1876. *Psiguria warmingiana* (Cogn.) C. Jeffrey, *Kew Bull.* 33(2): 354. 1978.—TYPE: BRAZIL. 1860, *Peckolt 512* (holotype: online photograph BR!).

Stems glabrous or puberulent, solid green, 1.2–3.9 mm in diameter; tendrils glabrous or puberulent, solid green or light green with darker speckles, 0.2–1.5 mm in diameter. Leaves membranous, both surfaces glabrous with veins seldom puberulent, 3–5 main veins, flush, margins entire, with irregularly-spaced veins extending beyond blade, simple; petioles puberulent or rarely glabrous, 0.7–2.0 mm in diameter, 12–75 mm long; simple leaves 3- to 5-lobed, base auriculate, base (5–)10–33(–40) mm deep, apex acuminate, 55–180 mm long, (23–)31–70 mm wide, lobe depth average 73.8% of total length. Inflorescence an indeterminate corymb; peduncles glabrous or rarely puberulent, light green with darker splotches, 0.5–1.6 mm in diameter, 70–205 mm long; pedicels puberulent, (0.5–)1.0–19 mm long, with 0.24–0.7 flowers per mm. Staminate flowers, first 2–3 flowers not much larger than subsequent flowers; calyx salverform flask, puberulent, light green with darker speckles, 5.5–12.0(–21.0) mm long, 1.5–6.5 mm wide, adaxial surface glabrous with trichomes at throat; sepals thin, linear, color darker than calyx, 1.0–3.5 mm long; petals orange, ovate-elliptic-rhombic, apex acuminate, 5.5–16.0 mm long, 2.5–7.3 mm wide, length-to-width ratio 2.0; anthers straight, 4.8–11 mm long, anther appendage round, minutely papillose, 0.3–0.8 mm long. Pistillate flowers 2–3 per node, axillary; calyx salverform, cylindrical, puberulent, solid green, 20.0–27.5 mm long, 1.3–6.5 mm wide, adaxial surface glabrous; sepals thin, linear, color same as or darker than calyx, 1.0–2.0 mm long; petals orange, oblong-elliptic-rhombic, apex acuminate, 4.5–6.5 mm long, 2.4–2.9 mm wide, length-to-width ratio 2.1; ovary elliptic-oblong, 10.0–15.0 mm long, 2.3–6.5 mm wide, style 4.5–5.5 mm long, stigma 3.5–5.0 mm long. Fruits, green, sometimes with lighter green stripes, 21–39 mm long, 12.5–18.0 mm wide, wall thickness unknown. Seeds 30–78, 5.0–6.0 mm long, 2.8–3.0 mm wide, 1.5–1.7 mm thick.

Phenology—Flowering throughout the year with flowering peak January through June. Of the 43 specimens examined, 74.4% had male flowers, 23.3% had female flowers or fruits, and the remainder were sterile.

Distribution and Habitat—Predominantly in northern South America and the Lesser Antilles, with a few individuals in eastern Brazil (Fig. 13). Found at elevations from 15–850 m, almost exclusively in tropical dry forests (with few individuals in moist tropical forests), along roadsides, riverbanks, slopes, or ravines, in shade or along forest edges, climbing over rocks, shrubs, or fallen trees.

Discussion—The distribution of *Psiguria umbrosa* overlaps with *P. racemosa*, *P. ternata*, and *P. triphylla*, and possibly comes into contact with *P. warscewiczii* in the southeastern-most edge of the *P. warscewiczii* range. Characteristics used to distinguish *P. umbrosa* from *P. racemosa* and *P. ternata* can be found under descriptions of those taxa or the keys. Typically, the trifoliolate leaf morphology of *P. triphylla* differentiates it from the simple, 3- to 5-lobed leaves of *P. umbrosa* (Fig. 5T, U), but there are simple, trilobed leaf morphs of *P. triphylla* (Fig. 5K–O) that can confuse identification. In those individuals, flowers are needed to distinguish the species. Male inflorescences of *P. umbrosa* are racemose (pedicel average length = 4.3 mm), peduncles and calices are light green with darker speckles, and petals are light orange. In *P. triphylla*, male inflorescences are spicate (pedicels absent), peduncles and calices are solid green, and petals are deep red, typically with a yellow base.

The molecular phylogeny of *Psiguria* resulted in a strongly supported clade of *P. umbrosa* samples that was sister to *P. warscewiczii* with moderate bootstrap support (Steele et al. 2010). However, if found in the small region of overlap, *P. umbrosa* can be difficult to distinguish from the trilobed morph of *P. warscewiczii*. Differences may exist such as male petal color and apex (*P. umbrosa* = light orange, acuminate; *P. warscewiczii* = dark orange, rounded-acute), and the outer margins of trilobed leaves (*P. umbrosa* = small indentation and lateral lobe; *P. warscewiczii* = larger indentation and lateral lobe), but variation in these characteristics can confound identification. The most consistent characters include the average lengths of pedicels on male flowers (*P. umbrosa* = 4.3 mm;

P. warscewiczii = 1.0 mm) and sepal characters (*P. umbrosa* = thin and linear; *P. warscewiczii* = thick and triangular).

Representative Specimens Examined—(collections marked with an asterisk were measured for species descriptions)

BRAZIL. Barra do Corda: 08 Mar 1983, *Schatz et al.* 890 (US*); Ceará: Crato, 700 m, 19 Jan 1983, *Plowman & Caçula* 12742 (F*); Goiás: Posse, 800 m, 10 Apr 1966, *Irwin et al.* 14593 (NY); Corumbá de Goiás, 700 m, 21 Jan 1968, *Irwin et al.* 18941 (F*); Maranhão: Fortuna, 21 Feb 1983, *Santos et al.* 646 (NY*); Pará: Conceição do Araguaia, 350–620 m, 08 Feb 1980, *Plowman et al.* 8512 (F*, MO*); Paraíba: 24 Jun 1959, 2201 (US).

FRENCH GUIANA. Mt. Rorota, ancient volcano, 24 Apr 1992, *Grimes & Acevedo* 3302 (NY).

MARTINIQUE. 1880, *Duss* 750–117 (NY*).

ST. LUCIA. Barre de l'Isle trail, 24 Jan 1985, *Howard et al.* 19874 (A*).

ST. VINCENT. 500–1,000 ft, 15 Oct 1890, *Smith & Britton* 234 (NY).

TRINIDAD & TOBAGO. Tobago: Great Dog River Valley, 12 Oct 1937, *Sandwith* 1748 (NY); Plymouth, 16 Jan 1953, *F. W. H.* 19999 (GH*); Old Province Road, 20 Jun 1981, *Baksh & Adams* 481 (NY*); Trinidad: San Juan, 13 Jun 1903, *Johnston* 14 (GH); Heights of St. Ann, 17 Mar 1920, *Coker & Rowland* 658 (US*); Matchepoorie, 11 Mar 1921, *Britton & Britton* 2207 (NY); Arima Valley, 1325 ft, 12 Jun 1973, *Philcox & Wood* 7079 (NY); Maracas Falls, 650 ft, 30 May 1975, *Philcox* 7825 (NY*); Ruiz Trace, 21 Jan 1982, *Harriman* 17631 (NY); *Broadway* 2009 (F*).

VENEZUELA. Aragua: La Trinidad de Maracay, 440 m, Feb 1913, *Pittier* 6048 (US); Villa de Cura, 03 Dec 1962, *Trujillo* 5493 (US); Carabobo: Hacienda de Cura, 480–1,200 m, 05 Jul 1918, *Pittier* 7931 (GH); Caraquita: 10 Mar 1911, *Bond et al.* 243 (US); Cristóbal Colón: near river, Jan 1923, *Broadway* 226 (NY*); Aricagua, Feb 1923, *Broadway* 493 (GH); Federal: Mamo Electric Plant, 23 Jun 1923, *Pittier* 11076 (US*); La Sabana, 100 m, 01 Nov 1962, *Steyermark* 90976 (US*); Island of Margarita: 450 m, 12 Aug 1903, *Johnston* 287 (GH); Miranda: Brión, 0–30 m, 27 May 1981, *Berry et al.* 3789 (MO*); Cúpira, 0–150 m, 16 May 1981, *Liesner & González* 11901 (MO); Monagas: Caripe, 850 m, 17 Apr 1945, *Steyermark* 62159 (F); Sucre: Puerto Hierro, 21 Aug 1961, *Aristequieta* 4748 (NY); Valdez, Güüria, 27 May 1983, *Fernández* 4014 (NY); Río Guagua, 230–300 m, 18 May 1945, *Steyermark* 62797 (F); Río el medio, 200 m, 15 Jul 1972, *Dumont et al.* VE-7685 (NY*).

6. *PSIGURIA WARSCEWICZII* (Hook. f.) Wunderlin, *Phytologia* 38(3): 219. 1978. *Anguria warscewiczii* Hook. f., *Bot. Mag.* 88 t. 5304. 1862.—TYPE: PANAMA. May 1861, *Hayes s. n.* (holotype: online photograph K!).

Anguria ovata Donn. Sm. *Bot. Gaz.* 31: 112. 1901. *Psiguria ovata* (Donn. Sm.) C. Jeffrey, *Kew Bull.* 33(2): 353. 1978.—TYPE: COSTA RICA. Las Vueltas: Tucurrique, Feb 1899, *Tonduz* 13006 (holotype: US!).

Anguria limonensis Pittier, *Contrib. U.S. Nat. Herb.* 13: 119 Fig. 25. 1910.—TYPE: COSTA RICA. between Port Limon and Moin, Sep 1899, *Pittier s. n.* (holotype: US!; isotype: NY!).

Anguria magdalena Pittier, *Contrib. U.S. Nat. Herb.* 13: 118 Fig. 24. 1910.—TYPE: COLOMBIA. Magdalena: around Río Frío between the Ciénega de Santa Marta and the foothills, 4 Jul 1906, *Pittier* 1630 (holotype: US!).

Anguria tonduzii Cogn. *Pflanzenreich* 66 (IV. 275. I): 191. 1916.—TYPE: COSTA RICA. Santo Domingo de Golfo Dulce, Apr 1896, *Tonduz* 9999 (holotype: K fide Jeffrey (1978); online photograph!; isotype: US!).

Anguria aurantiaca S. F. Blake, *Contrib. U.S. Natl. Herb.* 24(1): 26–27. 1922. *Psiguria aurantiaca* (S. F. Blake) C. Nelson, *Fern. & Casas, Fontqueria* 52: 4. 1998.—TYPE: HONDURAS. Copán: trail from Hacienda El Limón to El Paraíso, 12 May 1919, *Blake* 7355 (holotype: US!).

Stems glabrous or puberulent, light green with darker, linear splotches, 1.5–5.0 mm in diameter; tendrils glabrous or puberulent, light green with darker, speckles, 0.4–1.8 mm in diameter. Leaves immature membranous, mature coriaceous, both surfaces glabrous with veins and margins seldom puberulent, veins flush or seldom abaxial and adaxial main veins

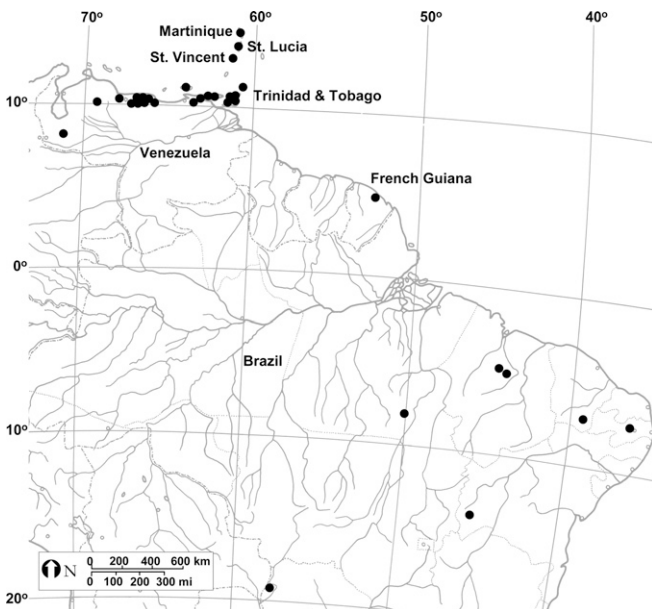


FIG. 13. Geographic distribution of *Psiguria umbrosa*. Open circles are part of the base map image.

prominent, margins entire-irregular-lobed, with irregularly-spaced veins extending beyond blade, simple, trifoliolate, or seldom pedate; petioles puberulent or rarely glabrous, 0.8–2.7 mm in diameter, 12–96 mm long; simple leaves trilobed, base auriculate, base 10–25 mm deep, apex acuminate, 86–183 mm long, 30–90(–122) mm wide, lobe depth average 73.5% of total length; petiolules winged and puberulent, 0.6–1.5(–2.1) mm in diameter, 0–20 mm long; complex leaves with center leaflet elliptic-rhombic-oblongate and side leaflets ovate-elliptic with lateral lobe, sometimes large, apices acuminate; center leaflet base acute-attenuate, 52–206 mm long, 17–75(–150) mm wide; side leaflets base oblique, adaxial base acute-attenuate and abaxial base acute-truncate, 25–169 mm long, 14–69 mm wide; outer leaflets on pedate leaves base oblique, adaxial base acute-attenuate and abaxial base acute-truncate, 40–115(–145) mm long. Inflorescence a compact raceme; peduncles glabrous, light green with darker splotches, 1.0–1.9 mm in diameter, (36–)130–285 mm long; pedicels puberulent, (0.1–)0.5–1.9 mm long, with 0.25–0.75(–1.2) flowers per mm. Staminate flowers, first 2–3 flowers not much larger than subsequent flowers; calyx salverform, cylindrical, rarely flask-shaped, glabrous, light green with darker speckles, 7.0–17.0 mm long, 1.0–4.6 mm wide, adaxial surface glabrous or puberulent with sparse trichomes at throat; sepals thick, triangular, color darker than calyx, 0.5–2.1 mm long; petals intense orange or orange-red, ovate-elliptic-orbicular, apex rounded-acute, 4.0–10.0 mm long, 3.0–7.0 mm wide, length-to-width ratio 1.6; anthers straight, (1.0–)6.0–10.9 mm long, anther appendage round or rarely triangular, glabrous or rarely papillose, 0.1–0.5(–0.7) mm long. Pistillate flowers 2 per node, axillary, but at the ends of branches with reduced leaves; calyx salverform, cylindrical, glabrous or puberulent, striped green, (4.9–)18.0–25.0 mm long, 1.0–3.6 mm wide, adaxial surface puberulent with sparse trichomes at throat; sepals thick, triangular-linear, color darker than calyx, 0.5–1.6 mm long; petals bright orange or orange-red, elliptic-orbicular, apex cuspidate, 4.5–9.2 mm long, 3.3–6.9 mm wide, length-to-width ratio 1.3; ovary elliptic-oblong, 10.0–15.0 mm long, 1.9–3.5 mm wide, style 2.3–4.5 mm long, stigma 5.5–7.2 mm long. Fruits, green with lighter green or white stripes, 34–80 mm long, 14–22 mm wide, wall 0.7–2.2 mm thick. Seeds 56–88, 6.4–8.7 mm long, 3.8–4.8 mm wide, 1.9–2.7 mm thick.

Phenology—Flowering throughout the year. Of the 250 specimens examined, 76.8% had male flowers, 9.6% had female flowers or fruits, and the remainder were sterile.

Distribution and Habitat—Continental from southern Mexico to northwestern Colombia and Venezuela (Fig. 14). Found at elevations from sea level to 1,600 m in tropical and subtropical evergreen or semideciduous, moist (but can extend into dry areas along riverbanks), primary or secondary forests, cloud forests, and flooded grasslands. May be found in dense shade or light gaps, on roadsides, riverbanks, or slopes, climbing over other vegetation, and on limestone, sandy, or clay soils.

Discussion—The geographic range of *Psiguria warscewiczii* overlaps with those of *P. racemosa*, *P. triphylla*, and one collection of *P. pedata* (in Costa Rica), and possibly comes into contact with *P. umbrosa* in the southeastern-most edge of the *P. warscewiczii* range. For characteristics used to distinguish *P. warscewiczii* from *P. racemosa* and *P. umbrosa*, see the discussion under each of their taxonomic descriptions or the keys. Leaf morphology in *P. warscewiczii* (Fig. 5V–BB) can take as many forms as that in *P. pedata*; therefore, the best way to distin-

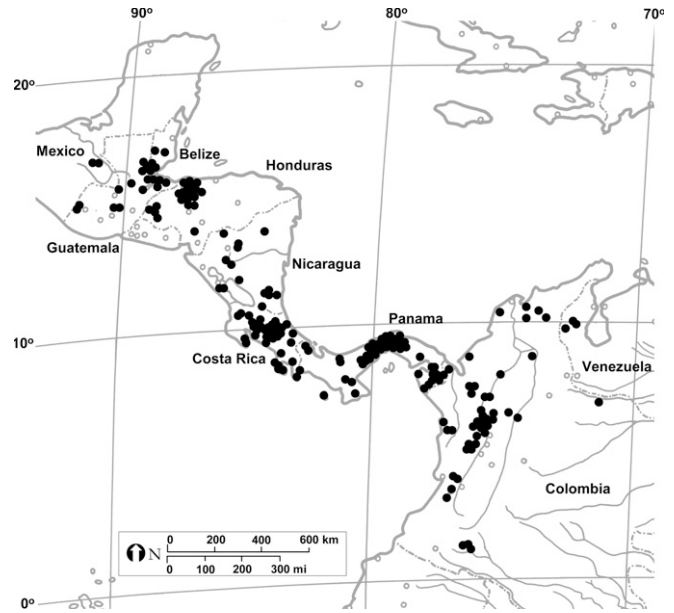


FIG. 14. Geographic distribution of *Psiguria warscewiczii*. Open circles are part of the base map image.

guish the two is with male flowers. They differ in anther shape (*P. warscewiczii* = straight; *P. pedata* = folded backwards), average pedicel length (*P. warscewiczii* = 1.0 mm; *P. pedata* = 5.2 mm), and calyx color and shape (*P. warscewiczii* = light green with darker speckles, cylinder or elongated flask; *P. pedata* = solid green, oval). The best characters to distinguish *P. warscewiczii* from *P. triphylla* include stem, peduncle, and calyx color (*P. warscewiczii* = light green with darker speckles; *P. triphylla* = solid green) and the density of flowers along the peduncle (*P. warscewiczii* = < 0.75 flowers per mm; *P. triphylla* = > 0.75 flowers per mm).

Morphological variation in *Psiguria warscewiczii* includes simple, trilobed leaves of varying depths (found in the southern end of the range), pedate leaves (found at the northern end of the range), and trifoliolate leaves with variable margins and lateral lobe sizes (found throughout the range) (Fig. 5V–BB). The molecular phylogeny revealed a weakly supported, monophyletic clade of *P. warscewiczii* samples, and this clade was split into two weakly supported clades (Steele et al. 2010). Although the trifoliolate morph is found in both clades, since the inner clades split predominantly along geographic lines (a northern clade and a southern clade), additional molecular and/or morphological characters may support a split of these clades into two species in the future.

Representative Specimens Examined—(collections marked with an asterisk were measured for species descriptions)

BELIZE. Stann Creek: Middlesex, 24 Jul 1939, *Gentle* 2937 (F); Toledo: Machaca, 50 ft, 07 Aug 1933, *Schipp* 5-298 (GH); Blue Creek, 100–200 m, 07 Jan 1994, *Lowman* & *Foster* 74 (F).

COLOMBIA. Antioquia: Arboletes, 30 m, 23 Mar 1987, *Zarucchi et al.* 4954 (MO); Sabanalarga, 1,100 m, 08 Apr 1986, *Callejas et al.* 2271 (NY*); Salgar, 1,410 m, 11 Nov 1989, *Girón & Ortíz* 263 (NY*); Segovia, 750 m, 21 Jul 1979, *Rentería* 1731 (MO); Bolívar: Quimari, Cordillera Occidental, 500 m, Mar 1949, *von Sneider* s. n. (NY*); Torrecilla, 150–300 m, 07 Nov 1926, *Killip & Smith* 14260 (NY*); Caldas: La Dorada, 200–400 m, 30 Dec 1936, *Haught* 2139 (US); Chocó: Bahía Solano, 0–75 m, 22 Feb 1939, *Killip & García* 33467 (NY); Riosucio, 16 Jun 1957, *Romero-Castañeda* 6263 (GH); San José del Palmar, 450 m, 30 Aug 1976, *Forero et al.* 2364 (MO); Uguía, 100–300 m, 19 Jul 1975, *Gentry & Enrique* 15301 (MO); Magdalena: Codazzi, 100 m, 17 Nov 1943, *Haught* 3851 (NY*); Mutatá: 150–200 m, 05 May 1987, *Fonnegra et al.* 2170 (MO); Río San Juan: 5 m, 31 May 1946, *Cuatrecasas* 21527 (F); Santa Marta: 300 ft, 30 Sep 1898, *Smith* 1601 (F, NY); Santander: Cimitarra, 200 m,

27 Jul 1975, *Gentry & Forero 15477A* (MO); Valle del Cauca: NW of Darien, 4,800 ft, 24 Jul 1962, *Robinson 97* (US).

COSTA RICA. Alajuela: Muelle San Carlos, 975 m, 01 Mar 1939, *Smith HI1691* (F); San Ramón, 1,100 m, 25 Apr 1981, *Liesner & Judziewicz 14894* (MO); Rancho Grande, 500 m, 14 Jul 1993, *Rivera 1449* (MO); Cartago: Turrialba, 500–600 m, 21 Jul 1949, *Holm & Illits 438* (A); Guanacaste: Serena, 700 m, 27 Jan 1926, *Standley & Valerio 46213* (US); La Cruz, 200 m, 01 Jan 1964, *Williams et al. 26451* (F); Tilarán, 03 Jan 1964, *Williams et al. 26563* (F); Cantón de Liberia, 750 m, 13 Aug 1996, *Morales 5639* (NY); Heredia: Puerto Viejo, 45 m, 12 Aug 1972, *Opler 1608* (MO); La Selva OTS Biological Research Station, 100 m, 02 Apr 1980, *Hammel 8408* (MO); Limón: Guápiles, 300–500 m, 12 Mar 1924, *Standley 37300* (US); Airport Limón, 26 Jul 1965, *Croat 522* (MO); Cerro Coronel, 20–170 m, 15 Sep 1986, *Stevens 24587* (MO); Cordillera de Talamanca, 400 m, 03 Sep 1988, *Grayum et al. 8730* (MO); Puntarenas: Osa Peninsula, 100 ft, 12 Aug 1967, *Raven 21722a* (NY); Corcovado National Park, 0–5 m, 06 Jul 1977, *Liesner 2893, 3001* (MO); Quebrada Bonita, 35–40 m, 11 Jun 1986, *Grayum et al. 7601* (MO); Cantón de Golfito, 50 m, 14 Sep 1992, *Aguilar 1305* (MO); Nicoya Peninsula, 200 m, 11 Sep 1995, *Sanders et al. 17856* (TEX); Cantón de Garabito, 20–30 m, 17 Aug 1996, *Hammel et al. 20374* (MO*); San José: Cantón de Mora, 900–1,000 m, 12 Jun 1996, *Cascante 1018* (F); Ciudad Colón, 900–1,000 m, 20 Jul 2005, *Steele & Fernández 1006* (TEX*).

GUATEMALA. Alta Verapaz: Panzós, 280 m, 04 Sep 1988, *Martínez 23488* (TEX); Tucuru, 280 m, 04 Sep 1988, *Martínez 23490* (MO); Izabal: Escoba, 0 m, 03 May 1939, *Standley 72877* (F); Puerto Barrios, 25 Feb 1905, *Deam 5* (GH); Quirigua, 75–225 m, May 1922, *Standley 24208* (GH); Quirigua, 72–150 m, 26 Apr 1939, *Standley 72209* (F); Montaña del Mico, 35–150 m, 07 Apr 1940, *Steyermark 39024* (F); El Estor, 03 Mar 1972, *Contreras 11117* (LL); Peten: Dolores, 21 Jun 1961, *Contreras 2497* (LL*); San Luis, 09 Oct 1966, *Contreras 6339* (LL*); Dept. unknown: La Cumbre, 31 Jul 1969, *Contreras 8809* (F, LL*).

HONDURAS. Atlántida: Tela, 25 ft, 21 Mar 1926, *Mitchell 37* (US); Progreso, 12 Aug 1929, *Bangham 365* (A); Jardín Botánico de Lancetilla, 100–150 m, 08 Jun 1985, *Téllez 8760* (TEX); Comayagua: Quebrada Montañuelas, 1,400 m, 18 Jul 1962, *Molina 10864* (NY); San José, 300 m, 27 Jan 1976, *Molina et al. 31471* (F); Copán: Santa Rita, 700 m, 21 Aug 1971, *Molina 26214* (F); Copán, 16 Jun 1977, *Poole & Watson 1167* (LL*); Cortés: San Juan Lindo, 200 m, 01 Dec 1950, *Molina 3479* (GH); Montaña Santa Ana, 210 m, 06 Dec 1950, *Molina 3611* (F); Puerto Cortés, 10 Aug 1975, *Nelson et al. 2841* (MO); El Cacao, 600 m, 25 Dec 1982, *Albertina et al. 32001* (MO*); Lempira: Cuábanos, 1,600 m, 25 Sep 1963, *Molina 12904* (US); Santa Bárbara: Nueva Arcadia, 13 Aug 1970, *Harmon & Dwyer 3809* (MO); Dept. unknown: Las Vegas, 3,500 ft, 21 Jun 1970, *Barkley & Smith 40860* (GH*); Tela River, 03 Apr 1903, *Wilson 658* (NY); Yoro: San José, 200–600 m, 06 Nov 1988, *MacDougal et al. 3293* (MO).

MEXICO. Chiapas: Ocosingo, 570 m, 04 Oct 1976, *Calzada et al. 2675* (MO*).

NICARAGUA. Atlántico Norte: Cerro Livico, 400–600 m, 12 Dec 1980, *Stevens 18708* (MO); Atlántico Sur: Caño Montecristo, 100 m, 06 Feb 1982, *Moreno & Sandino 14957* (MO); Zelaya, 70–80 m, 31 Jul 1982, *Sandino 3433* (MO); Nueva Guinea, 300 m, 13 Aug 1982, *Araquistain 3095* (MO); Boaco: El Portón, 370 m, 16 Jul 1978, *Stevens 9265* (MO); Granada: Volcán Mombacho, 600 m, 02 Jul 1983, *Grijalva & Ayesta 2722* (MO); Jinotega: El Cedro, 700 m, 19 Jun 1980, *Moreno 872* (MO); Matagalpa: Ranchería, 280 m, 21 Aug 1984, *Moreno 24467* (MO); Nueva Segovia: El Jicaro, 550–600 m, 02 Aug 1980, *Moreno 1662* (MO); Río San Juan: La Palma, 50 m, 21 Mar 1985, *Moreno 25513* (MO); Castillo, 100–200 m, 17 Mar 1999, *Rueda et al. 10434* (MO*); Rivas: Volcán Maderas, 600–800 m, 15 Sep 1983, *Nee & Téllez 28122* (MO).

PANAMA. Bocas del Toro: Changuinola Valley, 22 Feb 1924, *Dunlap 446* (F); Chiriqui Lagoon, 09 May 1941, *von Wedel 2429* (GH); Chiriqui: Burica Peninsula, 40 m, 06 Mar 1973, *Croat 22583* (MO); San Bartolo, 125 m, 10 Aug 1974, *Croat 26708* (MO); Cooclé: El Copé, 1,200–1,300 m, 13 May 1931, *Sytsma & Andersson 4566* (MO); El Valle de Anton, 1,000 m, 05 Jun 1939, *Alston 8788* (US); Penonomé, 1,200 ft, 24 May 1967, *Lewis et al. 1521* (MO); Llano Grande, 450 m, 07 May 1981, *Sytsma et al. 4426* (MO); Colón: Canal Zone, 08 Oct 1939, *Allen 2011* (MO); Portobelo, 30 Jan 1973, *Kennedy & Gra 2237* (US); Cerro Bruja, 20 May 1978, *Hammel 3218* (MO); Salamanca, 300–400 m, 12 Dec 1981, *Knapp & Sytsma 2404* (MO); Darién: Yaviza, 06 Jun 1959, *Stern et al. 134A* (MO); Paya, 12 Jun 1959, *Stern et al. 414* (MO); El Real, 06 Jul 1962, *Duke 5146* (MO); Pucro, 22 Jun 1967, *Duke 13072* (MO); Río Pirre, 14 Jul 1971, *Croat & Porter 15539* (MO); Garachiné, 500 ft, 09 May 1979, *Hammel 7313* (MO); Manene, 22 Dec 1980, *Hartman 12122* (MO*); Punta Guayabo Grande, 0–200 m, 25 Jan 1982, *Knapp & Mallet 3153* (MO); Santa Fé, 30–50 m, 26 Apr 1982, *Huft et al. 1969* (MO); Los Santos: Loma Prieta, 800–900 m, 08 Jun 1967, *Duke 11851* (MO); Panamá: Chepo, 60–80 m, Oct 1911, *Pittier 4541* (US); Matías Hernández, 25 Aug 1914, *Pittier 6765*

(US); Barro Colorado Island, 12 Jul 1927, *Kenoyer 567* (US*); Barro Colorado Island, east of laboratory, 23 Dec 1931, *Wetmore & Abbe 32* (F*); Canal Zone, Pedro Miguel, 17 Jun 1938, *White 133* (MO); Lefevre Park, 28 Jun 1940, *Bartlett & Lasser 16336* (LL); Río Chagres, 1 mi N of Madden Lake, 07 Oct 1961, *Duke 4485* (GH); Tocumen airport, 08 Sep 1963, *Dwyer 4369A* (MO); Fort Clayton, 25 May 1966, *Blum & Tyson 2328* (MO); Goofy Lake, 2,000 ft, 26 Nov 1966, *Dwyer 7112* (MO); Cerro Brewster, 1,000 ft, 14 Dec 1967, *Burch 3389* (MO); Barro Colorado Island, Lathrop Trail, 09 Mar 1969, *Croat 8499* (MO*); Carti-Tupile, 200 m, 18 Oct 1972, *Kennedy 1789B* (MO); Alcalde Diaz, 190 m, 23 Nov 1973, *Nee 8304* (US); Bayano Guipo, 07 Jun 1977, *Folsom 3517* (MO); Cerro Cabra, 30 May 1978, *Hammel 3265* (MO); Gigante Peninsula, 27 Jul 1982, *Schmalzel 726* (MO); Piriati, 200–400 m, 08 Aug 1982, *Hamilton 519* (MO); Cerro Campana, 03 Aug 1983, *Miller & Miller 1001* (MO); San Blas: Cangandi, 10 m, 05 Apr 1986, *Nevers et al. 7699* (MO); Veraguas: Santa Fé, 500–1,000 m, 12 Dec 1971, *Gentry 3010* (MO); Santiago, 150 m, 17 Jul 1976, *Sullivan 421* (MO); Santa Fé, 1,300 m, 08 Sep 1982, *Hamilton et al. 1238* (MO); Isla Coiba, 03 Sep 1995, *Aranda et al. 2340* (US).

VENEZUELA. Zulia: Perijá, 17 Oct 1966, *de Bruijn 1226* (US); Sierra de Perija, 300–700 m, 25 Aug 1967, *Steyermark & Fernández 99719* (NY).

EXCLUDED TAXA

Anguria affinis Schltdl., *Linnaea* 24: 760. 1851. *Anguria pedata* var. *affinis* (Schltdl.) Cogn., *Diagn. Cucurb.* I: 22, 27: 10. 1876.—TYPE: ANTILLES. *Kunth s. n.* (holotype: B, destroyed).

Anguria parviflora Cogn., *Pflanzenreich* 66 (IV, 275, I): 190. 1916.—TYPE: ECUADOR. Jan 1897, *Eggers 15496*, (holotype: B, destroyed).

Anguria plurilobata Cogn., *Pflanzenreich* 66. (IV. 275. I): 191, 1916.—TYPE: Costa Rica. *Tonduz 8175* (holotype: B, destroyed).

Anguria rosea Kunth, *Nov. Gen. Spec.* 2: 122. 1817.—TYPE: BRAZIL. Type unknown.

A. triphylla Klotzsch, *Schomb. Reisen Brit. Guiana* III p. 88. 1848. non Miq. Type unknown.

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