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Identification of the Mexican species of *Lycianthes* series *Piliferae* (Capsiceae, Solanaceae) and the rediscovery of *Lycianthes caeciliae*

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Abstract

Solanum piliferum was first described by Bentham in 1840, based on material collected in the state of Oaxaca, Mexico. In 1919, the species was transferred to the genus *Lycianthes* by Friedrich August Georg Bitter and became the type species of his series *Piliferae*. This article provides a key to separate the Mexican species included by Bitter in series *Piliferae*, with updated species descriptions, synonymy, typification, distribution, and images of characteristics (trichomes, flowers, fruits, seeds). We address the misplacement of *L. stephanocalyx* and *L. coffeifolia* in this series and suggest limiting the series to just the species *L. caeciliae*, *L. pilifera* and *L. quichensis* based on habitat preferences, floral morphology, and seed characters. However, the series is not recircumscribed at this time.

Keywords: Central America, *Lycianthes*, Mexico, taxonomy

Introduction

Lycianthes (Dunal 1852: 29) Hassler (1917: 180) (Solanaceae) has approximately 150 to 200 species (D'Arcy 1991; Hunziker 2001) and occurs in both the Old and New World. Its center of distribution and the majority of taxa are found in the New World (from Mexico to Argentina). The genus shares a distinctive calyx morphology with its closest relative *Capsicum* L. (1753: 188) (Bitter 1919; Särkinen *et al.* 2013) in which the five calyx lobes are truncated into a sleeve-like rim, below which may protrude five or ten appendages (sometimes called calyx teeth) (see D'Arcy 1986).

Lycianthes as a whole was last monographed by Friedrich August Georg Bitter (1919), who included 189 terminal taxa (species, subspecies, and varieties) divided into subgenera, sections, and series; he provided no identification keys to assist in distinguishing the species. Although the genus has been included in a number of floristic works (for example: Gentry & Standley 1974; Nee 1986), only four sections or series have been recently revised. These are series *Meizonodontae* Bitter (1919: 408) (Dean 2004), series *Microlobae* Bitter (1919: 421) (Dean *et al.* 2007), section *Synantheroides* Bitter (1919: 494) (Reyes Cornejo 2015), and series *Tricolores* Bitter (1919:385) (Dean *et al.* 2017).

Within *Lycianthes* section *Simplicipila* Bitter (1919: 426), Bitter created series *Piliferae* Bitter (1919: 426) for five species distinguished by their shrubby habit, simple trichomes, stamens of equal length, few-flowered inflorescences, and seeds that are larger than those of most species of *Lycianthes*. The taxa included by Bitter in the series are: *L. pilifera* (Bentham (1840: 68)) Bitter (1919: 427) and *L. pilifera* var. *pilosiuscula* (M. Martens & Galeotti (1845: 136)) Bitter (1919: 428), both from the state of Oaxaca, Mexico; *L. caeciliae* Bitter (1919: 429) and *L. symphyandra* Bitter (1919: 430) (both from the state of Veracruz, Mexico); *L. quichensis* (J. M. Coulter & Donnell Smith (1904: 422)) Bitter (1919: 428) (from Guatemala); and *L. coffeifolia* Bitter (1919: 432) (from Brazil). In a subsequent publication,

Bitter added a sixth species, *L. stephanocalyx* (Brandege (1917: 374)) Bitter (1922: 315) to the series (also from the state of Veracruz, Mexico). Due to the similar appearance of several of these species, and their partially overlapping distributions in southern Mexico and Guatemala, researchers have had problems identifying these species both in the field and herbaria. This article provides updated species descriptions, synonymy, and an identification key for the Mexican species, as well as maps of geographic distributions and images of specimens, trichomes, flowers, fruits, and seeds. We also discuss that the series lacks cohesiveness and unites species that may not be closely related. This continues our ongoing effort to update and revise *Lycianthes*.

Materials and methods

The circumscriptions of the species treated here in *Lycianthes* series *Piliferae* are based on examination of herbarium specimens (using an Olympus SZ61 microscope), cultivated plants, and field observations and are supported by morphological evidence; the only species not seen in the field or greenhouse is *Lycianthes coffeifolia*, which was examined in the herbarium NY. We measured 271 non-type specimens and examined and/or measured 38 type specimens from the following herbaria: A, ARIZ, BIGU, BRIT, BR, BREM, C, CAS, DAV, DUKE, F, G, GH, IBUG, IEB, K, LD, LE, LL, M, MEXU, MICH, MO, NY, TEX, UC, US, W, WIS, and XAL (herbarium codes follow Thiers (2019)). Throughout this work, herbarium specimens with an accession number are cited with the herbarium code followed by the number. In cases where the specimen has a barcode number (often type specimens), the barcode number is provided (preceded by the word “barcode”). If no number is cited, none was provided on the specimen (this is the case for some specimens from BRIT, LL, NY, TEX, WIS, and XAL). If only an image of a specimen was examined (either online or as a scanned image provided to us), the words “digital photo” are written after the barcode or accession number. Because we saw all specimens listed in the “Representative Specimens Examined” sections and confirmed the identifications, we did not use exclamation points to distinguish the specimens that we examined. In the typification and synonymy sections, however, we did use exclamation marks to distinguish the specimens that we examined from duplicates that are known to be at other herbaria but that we did not examine.

In order to create maps of the Mexican species, specimens were georeferenced by using either Geolocate, an online software-mapping package (Rios & Bart 2010), or manually, using Google Earth Pro (Sullivan 2009); for Mexican specimens, the latter was often used in conjunction with location data found in the Mexican Archivo Histórico de Localidades [The Archive of Mexican Historical Locations] (INEGI 2010).

The seed epidermis of two of the species, *L. pilifera* and *L. stephanocalyx* was examined using scanning electron microscopy. Seeds collected in the field were sonicated with water to remove residual pulp, then treated with cellulase for 24 hours as described in Lester and Durrands (1984). This treatment removed the anticlinal walls of the epidermal cells, exposing the structure of the periclinal walls. Treated seeds were dried in a vacuum chamber for 48 hours, mounted on stubs with silver paste, sputter-coated with gold (30–50 nm), and then examined with an ISI-130 scanning electron microscope set to 10 Kv. Although seeds of the other three species were not examined with scanning electron microscopy, photographs of the seeds were taken using stacked images and high magnification lenses with a Nikon DSLR.

The species concept used in this taxonomic treatment is a morphological species concept (Cronquist 1978), based on measurement of herbarium specimens from the previously cited herbaria. In separating the species, we emphasized discontinuities in pubescence, leaf, floral, fruit, and seed characters that are well preserved on herbarium specimens. The species recognized in this paper are well-defined entities. As discussed below, we are recognizing four species from Mexico and Guatemala (*Lycianthes caeciliae*, *L. pilifera*, *L. quichensis*, and *L. stephanocalyx*) and one from Brazil, *L. coffeifolia* (Figs. 1–6).

Results

Morphology

Habit:—The species that Bitter included within *Lycianthes* series *Piliferae* are variable in growth form. *Lycianthes caeciliae*, *L. pilifera*, and *L. quichensis* are well-developed shrubs between 1 and 5 m tall, whereas *L. stephanocalyx*

is an herb or subshrub with herbaceous stems arising from (and sometimes dying back to) rhizomes, often forming clonal thickets. The terminology used here to describe the sympodial branching pattern of the species follows that of Child and Lester (1991) and Bohs (1994) and has been used previously in *Lycianthes* (Dean 2004; Dean *et al.* 2017). The upper growth is sympodial in nature with difoliate units that terminate in inflorescences. These sympodial units emerge either singly (monochasial branching) or in pairs (dichasial branching) beneath the inflorescence of the prior sympodial unit.

Indument:—The trichomes of the taxa included by Bitter in series *Piliferae* are simple, uniseriate, multicellular, and eglandular (trichome terms in this paper are mostly taken from Roe (1971); individual trichomes may be appressed to the surfaces of the stems, leaves, pedicels, and calyces or patent (i.e., erect, at nearly a 90° angle from surface) (Fig. 7). The trichomes in the group range from whitish (*L. stephanocalyx*, *L. caeciliae*) to yellowish (*L. quichensis*) to brownish (*L. caeciliae*, *L. pilifera*), with some populations of *L. quichensis* and *L. pilifera* also having purplish trichomes. The cells of the trichomes of *L. caeciliae* and *L. pilifera* do not collapse upon drying and, thus, remain cylindrical throughout and acute at the apex upon drying, while those of most other species collapse and become flattened upon drying. The density of pubescence is variable in *L. pilifera*, and specimens with dense pubescence can look strikingly different than those with sparse pubescence.

Leaves:—The leaves of all the species are simple and petiolate (Figs. 1–5). The blade is ovate, elliptic, lanceolate, or obovate with a slightly undulate margin. When the branching of the upper sympodia is monochasial, the leaf arrangement is usually geminate, with one leaf usually smaller than the other, sometimes much more so. Geminate leaf pairs can be similar in shape, but often the smaller leaf is ovate or rounded, while the larger leaf is more variable in shape.

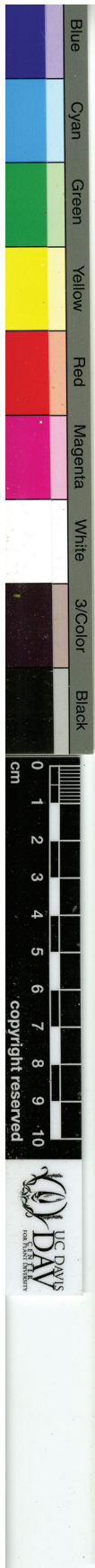
Inflorescence and pedicels:—In all species included in Bitter’s series *Piliferae*, the inflorescence of some individuals may consist of a solitary flower, but in only one species, *L. stephanocalyx*, is it consistently one-flowered. *Lycianthes quichensis* has one to two flowers per inflorescence and *L. caeciliae* has two to three flowers per inflorescence, while *L. pilifera* can have up to six and *L. coffeifolia* up to seven. As described for other *Lycianthes* (Dean 2004; Dean *et al.* 2017), the pedicels usually elongate over the days that a flower is open and as the fruit matures; the pedicels also thicken in diameter as the fruit matures.

Calyx:—All the species have five or ten calyx appendages that emerge below the truncated calyx rim. The appendages of *L. coffeifolia* are relatively small (Fig. 2), while those of the other four species are well-developed (Figs. 1, 3–5, 7). There is a difference in the color of the calyces among the species, with those of *L. pilifera* and *L. quichensis* sometimes having a striking purple color, while the other species usually have green calyces.

Corollas:—The corollas are sympetalous with the limb divided into five lobes connected to various degrees by thinner “interpetalar” tissue. While *L. pilifera* (Fig. 8) and *L. quichensis* (Fig. 9) have nearly entire corollas, those of *L. caeciliae* (Fig. 10), *L. stephanocalyx* (Fig. 11) and *L. coffeifolia* (Fig. 2; living flowers of *L. coffeifolia* were not photographed) are stellate, i.e., divided 1/3 to 2/3 of the way to the base. As described elsewhere (Dean 2001, 2004), the corollas of most *Lycianthes* species open and close on each of several successive days and grow in size during that period.

In many *Lycianthes* species, the corolla lobes bear stripes on the adaxial side that are darker in color than the corolla itself (often referred to as “nectar guides” in the literature, e.g., Endress 1994). In *L. quichensis*, the corolla is light purple with darker violet stripes and a basal green spot on the adaxial side of the lobes (Fig. 9B). In *L. pilifera*, corollas range from white to light purple with a dark purple ring on the adaxial side at the corolla base; often there is also a green ring or five green spots below the purple ring (Fig. 8C, D). In *L. caeciliae*, corollas range from light to dark purple with green markings on the adaxial side at the corolla base (Fig. 10B). The exact function of the green spots and rings are yet to be determined; although the glistening appearance suggests that they are nectaries (Lüttge 2013). They could be pseudonectaries, which mimic nectar droplets to guide pollinators into the flower (Endress 1994). *Lycianthes stephanocalyx* (Fig. 11C, D) and *L. coffeifolia* (Fig. 2) have white to light purple corollas without any other markings.

Stamens:—In all the flowers of the species of Bitter’s series *Piliferae*, the five stamens are equal in length, with filaments of equal length and anthers of equal length. In *L. caeciliae*, *L. pilifera*, and *L. quichensis*, the anthers are free of one another, while in *L. stephanocalyx*, the anthers are connivant to connate into a cone around the style, and in *L. coffeifolia*, the anthers are connivant and easily separated from one another. In *L. caeciliae*, *L. pilifera* and *L. quichensis*, the anthers are often purple, and less often yellow, while in *L. stephanocalyx* and *L. coffeifolia*, the anthers are always yellow.



1 of 3

Plants of Veracruz
Coatepec

Solanaceae

Lycianthes caeciliae Bitter

Mpio. Coatepec. La Cortadura, falda este del Cofre de Perote. Cloud forest with *Quercus*. Steep slope on sides of ridge. Primary forest remnant. Spindly shrub to 2 m tall. Flowers and fruits pendant under leaves. Corolla light to dark purple with green ring at base on adaxial side. Anthers dark purple, held together in a cone around the style. Style exserted from anther cone, stigma and style white. Some flowers still open at 1 pm when collected; other flowers already closed. Fruit dark purple. Seeds dark brown. Two shrubs growing together and others spread out along slopes; some sterile. This plant was also present along trail down below in secondary forest of Ainus, but sterile and small. Also present down below near farm in secondary forest of Liquidambar, but plants small and in bud only.
Latitude: 19° 29' 24" N; Longitude: 97° 2' 34" W; Elevation: 1800 m.

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8 May 2019

FIGURE 1. Specimen of *Lycianthes caeciliae* (Dean 10030, DAV).



FIGURE 2. Specimen of *Lycianthes coffeifolia* (Balslev 4843, NY).

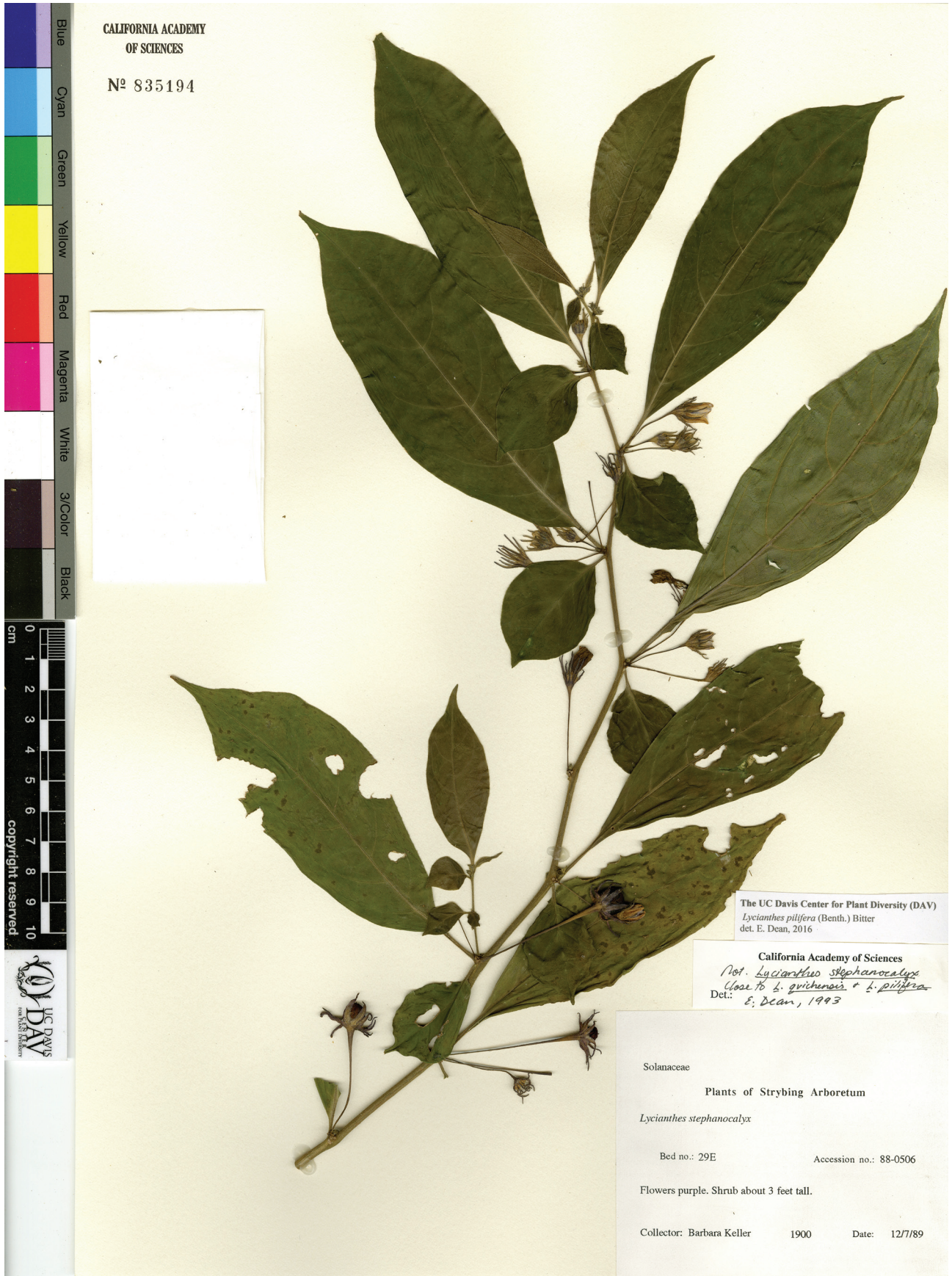


FIGURE 3. Specimen of *Lycianthes pilifera* (Keller 1900, CAS).



FIGURE 4. Specimen of *Lycianthes quichensis* (Breedlove 50023, CAS).

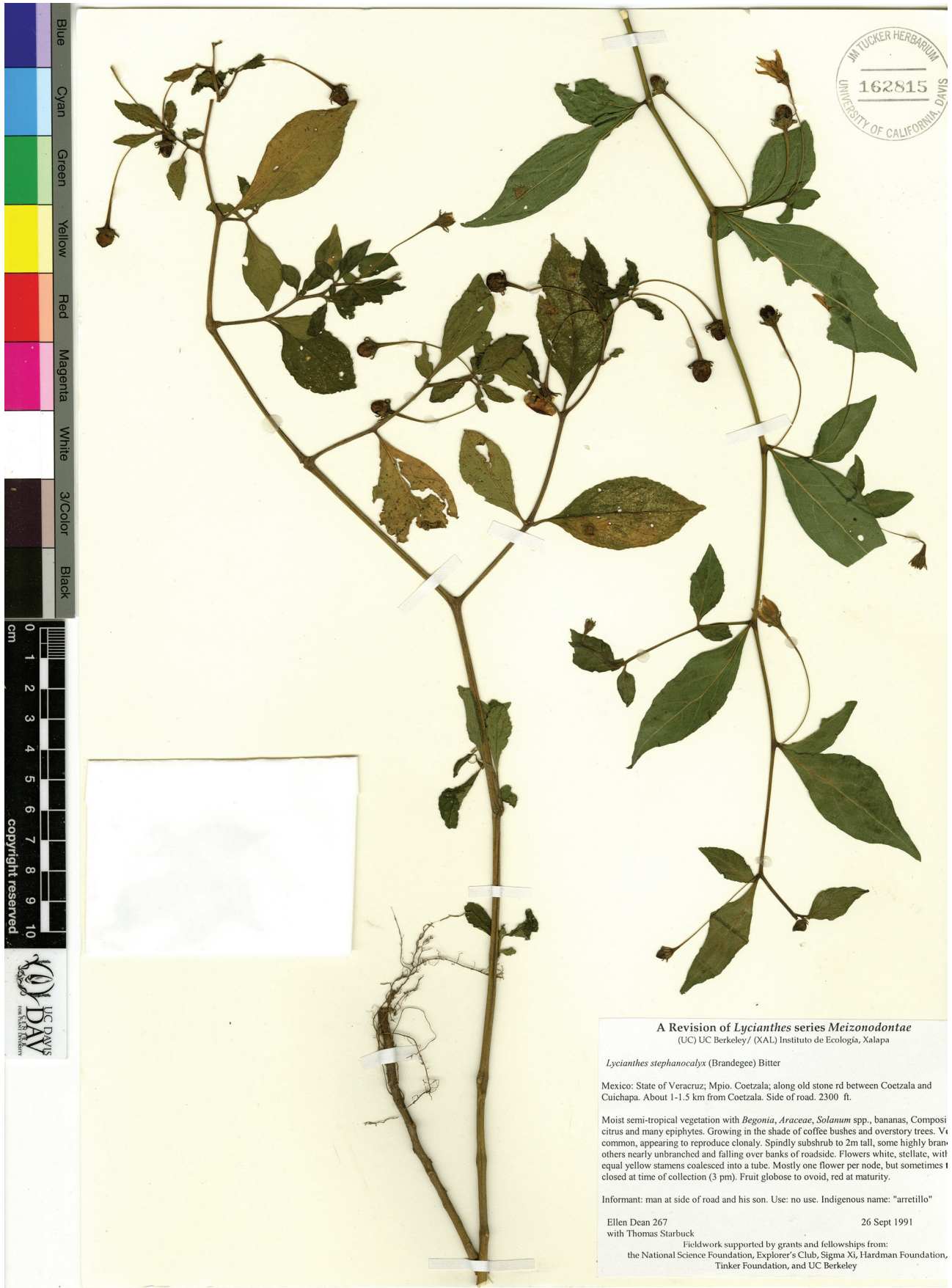


FIGURE 5. Specimen of *Lycianthes stephanocalyx* (Dean 267, DAV)

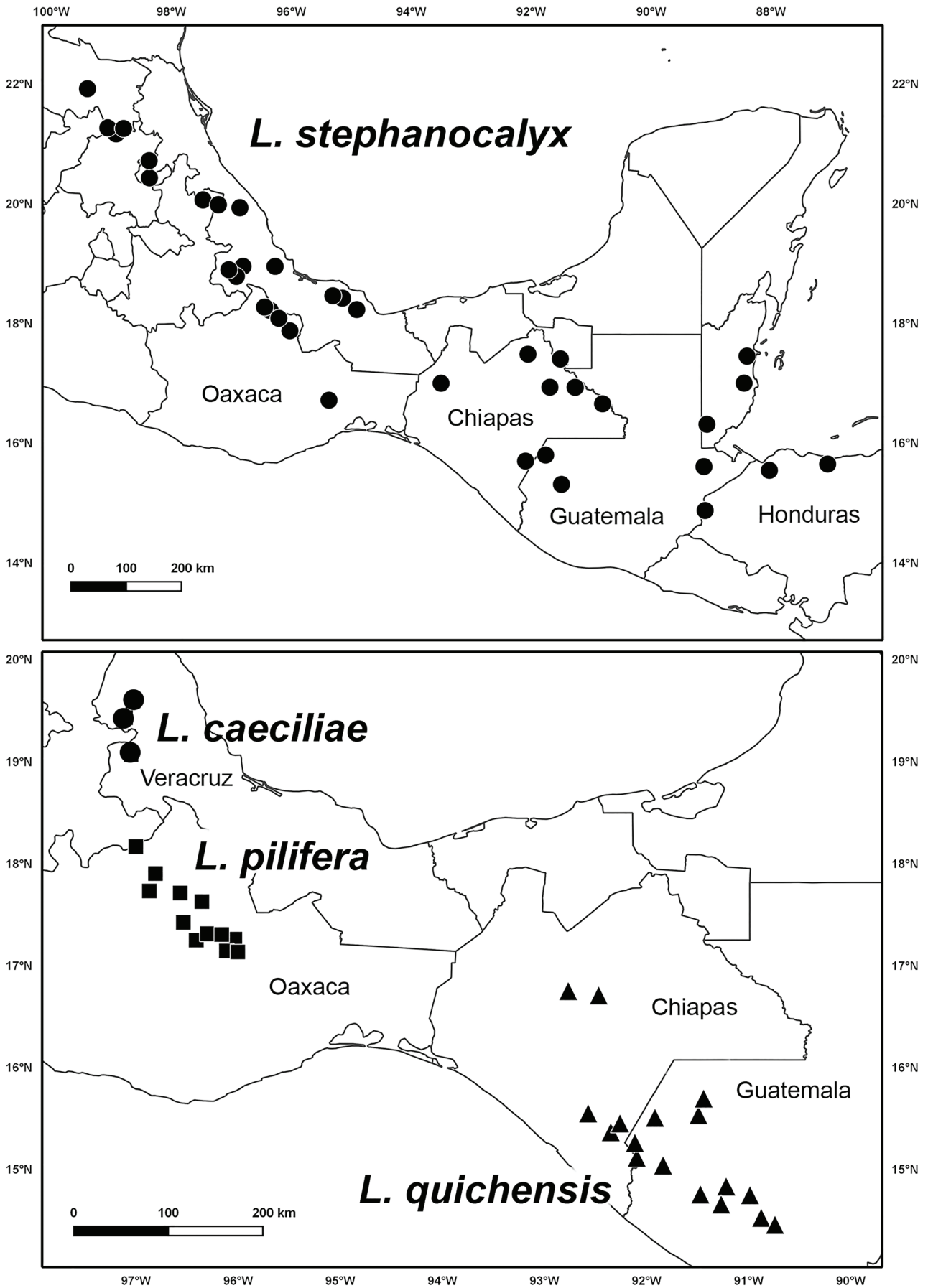


FIGURE 6. Distribution of *Lycianthes stephanocalyx* (top) and *L. caeciliae*, *L. pilifera* and *L. quichensis* (bottom).

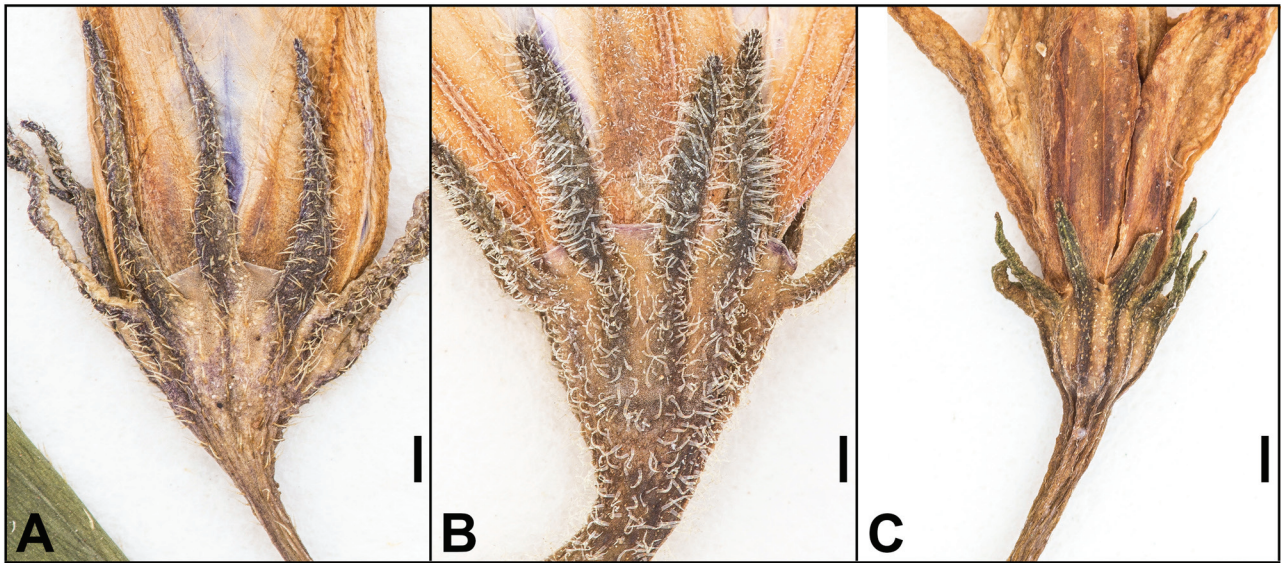


FIGURE 7. Calyces (with typical trichomes after drying) on herbarium specimens of the Mexican species of Bitter's series *Piliferae*. A. *Lycianthes pilifera* (Keller 1900, CAS); B. *L. quichensis* (Breedlove 50023, CAS); and C. *L. stephanocalyx* (Dean 267, DAV). Scale bar equals 1 mm.

Fruits:—The mature fruits of the species of Bitter's series *Piliferae* are berries, which are usually obovoid but may be globose in some plants, especially in *L. caeciliae*. In *L. quichensis* (Fig. 9D), *L. stephanocalyx* (Fig. 11F), and *L. coffeifolia* (Fig. 2), mature fruits are orange to red, while in *L. caeciliae* (Fig. 10C, D) and *L. pilifera* (Fig. 8E, F) they are glossy dark purple. The authors have not had sufficient experience with fresh fruits of *L. quichensis* and *L. coffeifolia* to comment on the internal tissues of the fruits of those species; however, the fruits of *L. caeciliae*, *L. pilifera*, and *L. stephanocalyx* have been observed fresh in the field and greenhouse. Those of *L. caeciliae* and *L. stephanocalyx* are typical berries in which the mesocarp and placental areas are soft, and juicy (Figs. 10D, 11F). Those of *L. pilifera* are unusual in the genus in that the mesocarp and placental areas are light purple and densely spongy, though they bleed purple juice (Fig. 8F). The fruits of the species of series *Piliferae* lack sclerotic granules, the aggregations of stone cells found in some *Lycianthes* fruits (well-illustrated in Barboza & Hunziker 1992).

Seeds:—Bitter placed species into series *Piliferae* partially based on their relatively large seeds. The seeds of the five species recognized here are not uniform in size and shape (seed shape terminology used in this paper is taken from Radford *et al.* (1974); seed surface terminology is taken from Gunn and Gaffney (1974). *Lycianthes pilifera* (Fig. 12A, B), *L. caeciliae* (Fig. 13A), and *L. quichensis* (Fig. 13B) have brown to black seeds that are variable in shape when viewed laterally (often depressed-ovate in outline, sometimes reniform with a notch on one side), compressed but not flat, and a reticulum with serpentine periclinal walls surrounding deep lumina. The seeds of *L. stephanocalyx* (Figs. 12C, D) and *L. coffeifolia* (Fig. 13C) are tan to orange, depressed ovate in outline (notched in *L. coffeifolia*), flattened, and have a reticulum with serpentine periclinal walls; in *L. stephanocalyx* the lumina are shallow, while in *L. coffeifolia*, the lumina are deep.

The seeds of *L. pilifera* (Fig. 12A, B), *L. caeciliae* (13A), and *L. quichensis* (Fig. 13B) bear an unusual ornamentation, described previously in other series of *Lycianthes* (Dean, 2004; Dean *et al.*, 2007), in which a serpentine reticulum is formed by elevated periclinal cell walls, which are further emphasized by protruding fibrils. In contrast, in *L. stephanocalyx* (Fig. 12C, D) and *L. coffeifolia* (Fig. 13C), the periclinal cell walls lack fibrils.

Habitat and Geographic Distribution

Lycianthes caeciliae is endemic to the state of Veracruz, Mexico (Fig. 6); *L. pilifera* is endemic to the state of Oaxaca, Mexico (Fig. 6); *L. quichensis* occurs in Chiapas, Mexico, and in Guatemala (Fig. 6); and *L. stephanocalyx* ranges from central Mexico south to Honduras (Fig. 6). The fifth species, *L. coffeifolia*, has been collected in Bolivia, Brazil, Colombia, Ecuador, and Peru. Both *L. pilifera* and *L. quichensis* grow in cold, wet cloud forest habitat at high to very high elevations. *Lycianthes pilifera* is found between 1,800 and 3,000 m in the Sierra Norte of Oaxaca (part of the

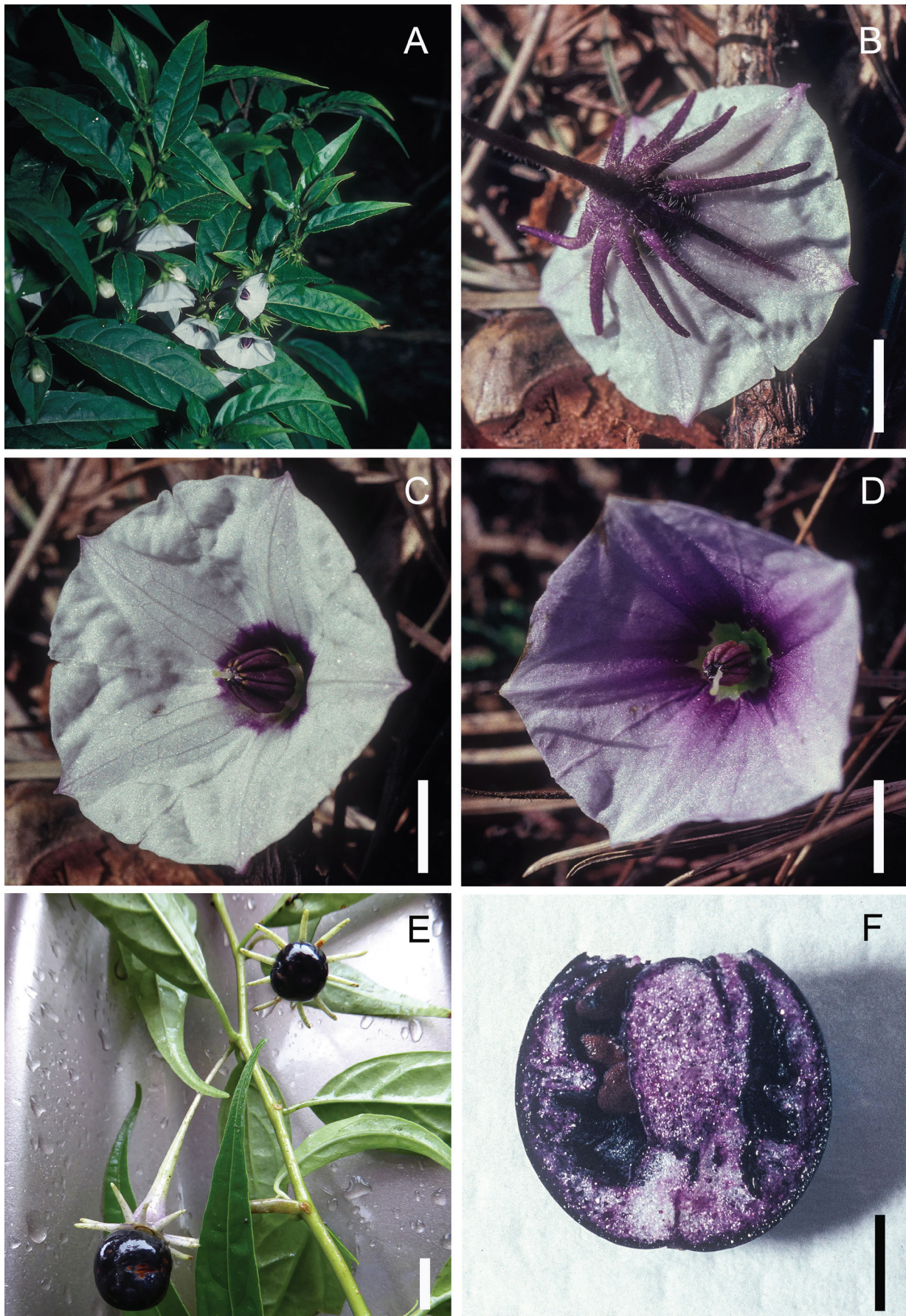


FIGURE 8. *Lycianthes pilifera*. A. Shrub habit with branch, leaves, and flowers (San Francisco Botanical Garden). B. Calyx (San Francisco Botanical Garden). C. White corolla (San Francisco Botanical Garden). D. Light purple corolla (San Francisco Botanical Garden). E. Fruit (taken in the field, *Dean 9522*). F. Long section of fruit (San Francisco Botanical Garden). All scale bars equal 5 mm.

Oaxacan Sierra Madre del Sur) and *L. quichensis* between 2,200 and 3,900 m in the Highlands of Chiapas, which continue into Guatemala. *Lycianthes caeciliae* is found in high, but somewhat warmer, wet, cloud forest habitat of the Sierra Madre Oriental between 1750 and 2250 m on the eastern side of two volcanoes in central Veracruz. In contrast, *L. stephanocalyx* is generally found at much lower elevations, from 30 to 1000 m, in warm, tropical forest habitat as well as cooler forest (and coffee plantations). The South American species, *L. coffeifolia*, occurs between 100 and 700 m, usually in warm forest habitat.

To help distinguish the often-confounded Mexican members of Bitter's series *Piliferae*, we provide a key to those four species, as well as synonymy, descriptions, and distribution maps; we also provide a summary of the rediscovery of *L. caeciliae*, a species described in 1919 but not included in previous Mexican floristic works (Nee 1986; Villaseñor 2016). As the distribution of *Lycianthes coffeifolia* in South America does not overlap with those of the other three species, and we have not studied that species in the field or greenhouse, we are not treating that species in this paper. Other authors have recently designated a lectotype for *Lycianthes coffeifolia* (Costa-Silva & de-Fátima-Agra 2018).

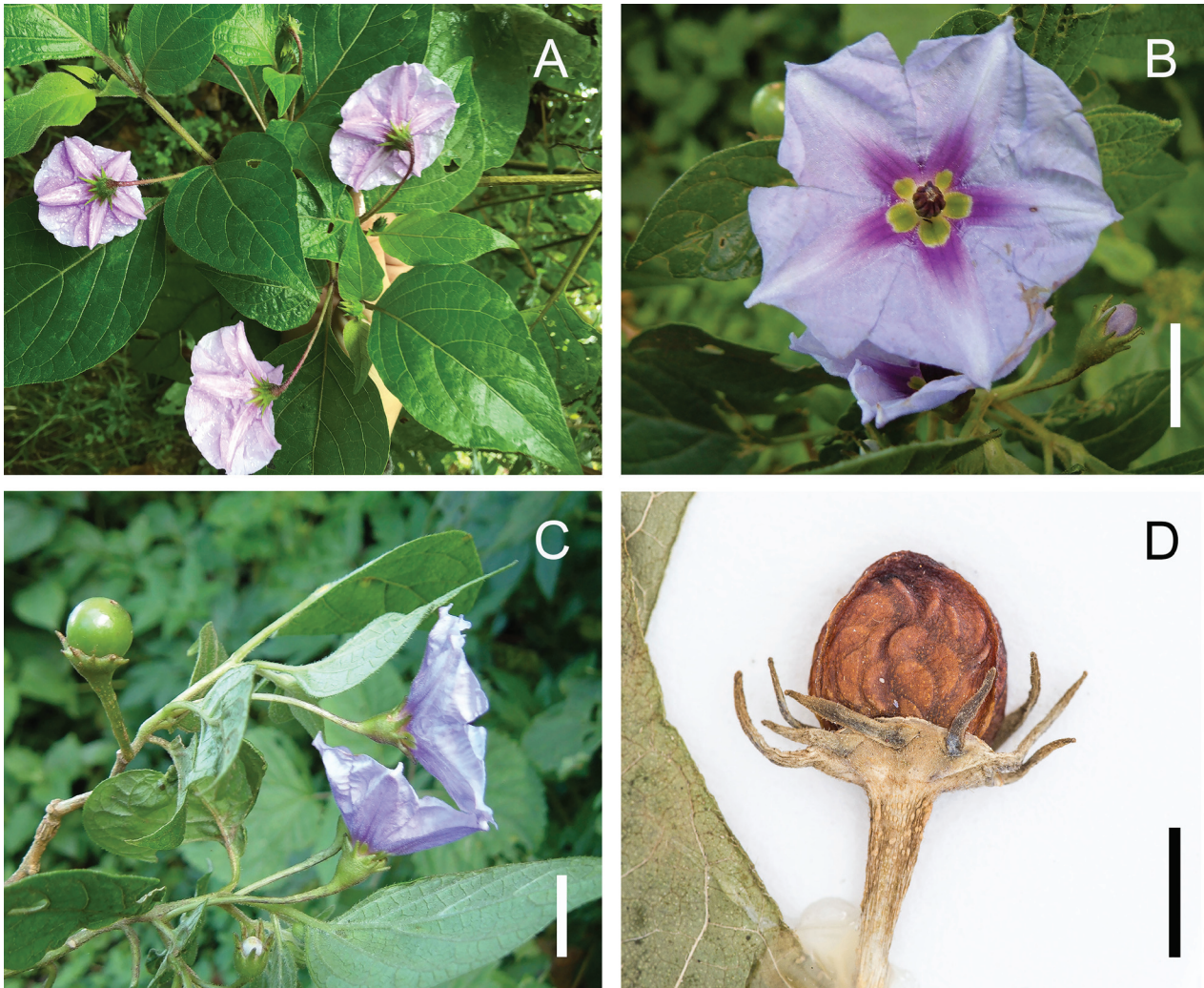


FIGURE 9. *Lycianthes quichensis*. A. Shrub habit showing branch with flowers (taken in the field by F. Archila). B. Corolla and stamens (taken in the field by M. Véliz). C. Immature fruit and flowers (taken in the field by M. Véliz). D. Fruit (*Breedlove 40387*, CAS). All scale bars equal 5 mm.

Taxonomic treatment

Key to the Mexican species of Bitter's *Lycianthes* series *Piliferae*

1. Perennial herb to subshrub from rhizomes; stem trichomes white to tan, to 0.6 mm long, generally curved and antrorsely appressed to stem; calyx green; corolla stellate, divided 1/3 to 2/3 of the way to the base, white to light purple, adaxially without dark purple or green markings; anthers connivant to connate to one another; fruit red at maturity; seeds flattened, tan to orange, the seed surface with fine shallow lumina *L. stephanocalyx*

- Woody shrubs; stem trichomes off-white, yellowish, or brown, to 1 mm long, usually not curved, patent to appressed to stem; calyx sometimes purple tinged; corolla nearly entire or stellate, white to purple, adaxially with darker purple stripes and/or green markings near the base; anthers free from one another; fruit red or dark purple at maturity; seeds compressed but not flattened, brown to black, the seed surface with deep lumina.....2
- 2. Stem trichomes white to yellow, becoming flattened and compressed upon drying; fruit red at maturity; Mexico, state of Chiapas, and Guatemala.....*L. quichensis*
- Stem trichomes off-white to brown, remaining cylindrical and acute at the apex upon drying; fruit dark purple at maturity; Mexico, states of Oaxaca and Veracruz.....3
- 3. Corolla pale to dark purple with green markings at base, stellate, divided 1/3 to 2/3 of the way to the base; Veracruz ..*L. caeciliae*
- Corolla white to light purple with dark purple ring and green markings at base, mostly entire; Oaxaca.....*L. pilifera*

1. *Lycianthes caeciliae* Bitter (1919: 429) (Figs. 1, 10). Type:—MEXICO. Veracruz: District Cordoba, Cerro de Chocomán, 12 May 1907, C. Seler & E. Seler 5168 (holotype: B, not found; isotype: GH barcode 00936203!).

Shrub, 1.5–3 m tall. Indument of off-white to light brown, multicellular, simple (very rarely furcate), eglandular, acute, appressed to patent trichomes, these usually remaining cylindrical throughout and acute at apex upon drying. Stems green to purple-green, terete, becoming brown and woody with age, somewhat to fully compressed upon drying; upper branching mostly monochasial with a few dichasial branching points, the upper sympodial units 1–8 cm long, 1–2.5 mm in diameter, difoliate, glabrous to moderately pubescent with appressed to patent trichomes to 1 mm long. Leaves of upper sympodia usually geminate, unequal in size, the larger ones with blades 4–16 × 1–5 cm, elliptic to obovate, the smaller ones with blades 1–6 × 0.5–3 cm, ovate, lanceolate, or obovate, chartaceous to thick chartaceous, glabrous to moderately pubescent with appressed to patent trichomes to 1 mm long, these more numerous on the veins, the primary veins of the large leaves 4–6 on each side of the midvein, the base cuneate, sometimes oblique, the margin entire to wavy, the apex acute to acuminate, the petioles absent or up to 0.8 cm. Flowers in groups of 2–3, axillary, the axes glabrous to moderately pubescent with appressed to patent trichomes 0.25–0.5 mm long; peduncles absent; pedicels 15–30 mm long and arching to deflexed in flower, to 42 mm long and arching to deflexed in fruit; calyx 3–3.5 mm long, 4–4.5 mm in diameter, campanulate, glabrous to sparsely pubescent with trichomes similar to those of the stem 0.25–0.5 mm long, the margin truncate, the 10 spreading, linear-subulate appendages 2–5 mm long, emerging 0.5–1 mm below the prominent, undulating rim, green, sometimes with purple hue; fruiting calyx accrescent, widely bowl-shaped, 2–2.5 mm long, 6–8 mm in diameter, the appendages widening but not significantly elongating to 7 mm long; corolla oriented horizontally to nodding, 0.7–1.6 cm long, campanulate to reflexed, stellate, lobed 1/3 to 2/3 of the way to the base, interpetalar tissue present at edges of lobes and connecting lobes at base, light to dark purple adaxially with green markings near the base, purple abaxially, sometimes with a single white line down the center of each lobe, glabrous; stamens equal, the filaments 1–2 mm long, glabrous; anthers 4–4.5 mm long, ovate to lanceolate, free, purple, the pores ovate, all opening toward the style; pistil with glabrous ovary, the style 5–7.5 mm, linear, glabrous, the stigma capitate. Fruit a berry, 7–13 mm long, 6–13 mm diameter, globose to ovoid, dark purple at maturity, glabrous. Seeds 10–50 per fruit, 3–4 × 2.5–3 mm, compressed but not flat, depressed ovate or reniform (with small notch), brown, the surface reticulum with a tight, serpentine pattern with deep lumina, with fibrils protruding from the cell walls.

Vernacular name:—none known.

Distribution:—*Lycianthes caeciliae* is endemic to Mexico (state of Veracruz) (Fig. 6). It grows on the eastern slopes of two volcanos, Cofre de Perote and Citlaltépetl, in oak cloud forest at 1750–2250 m elevation. On the Cofre de Perote at a site called the Reserva Ecológica de la Cortadura, the species is most abundant in well-preserved, original oak cloud forest (Bosque Mesófilo de Montaña according to the classification of Rzedowski [1978]), where it was observed in flower and fruit; although present in secondary forest of *Alnus* or *Liquidambar* at lower elevations, the plants are small and often sterile.

Phenology:—Specimens of *L. caeciliae* have been collected with both flowers and mature fruits from April through September. In the field, the first author observed that most of the corollas of this species were closed by 1 pm, but some of the corollas still remained open at that time. Corollas opening for the first time (the smallest on the plant) are a deep purple, while older, larger flowers are a pale purple. The green ring at the base of the corolla is more prominent in older flowers.

Notes:—*Lycianthes caeciliae* is a species that was poorly collected until the 21st century. Other than the type collection, it was just collected one other time in the 20th century by Eizi Matuda. The collectors of the type specimen, the German anthropologist Eduard Seler and his wife Caecilie, for whom this species was named, made six expeditions to the region of Mexico and Guatemala (1897 and 1909), collecting ca. 6000 specimens (Hiepko 2003). Seler's

collections were given to the Berlin Herbarium for identification, and from there, they were distributed to a number of U.S. herbaria, as well as K and MEXU (Hiepko 2003). The holotype cited by Bitter was at Berlin, and most Berlin type material, including that of Solanaceae, was destroyed when the Berlin herbarium was bombed in 1943 (Hiepko 1978, 1987).

Photos of some Berlin types are available at the Field Museum of Natural History (F) website (http://emuweb.fieldmuseum.org/botany/search_berlin.php); however, the site was searched, and a photo of the holotype of *L. caeciliae* was not found. Bitter took specimens with him to Bremen [BREM], where he published his treatment of *Lycianthes* (1919), and also to Göttingen [GOET], and some of Bitter's type material has been re-discovered at GOET (Vorontsova & Knapp 2010); however, the holotype of *L. caeciliae* has not yet been located. After researching herbaria where an isotype might be located, the first author contacted the Harvard University Herbaria, and after a short search, an isotype of *L. caeciliae* was located in their general collection.

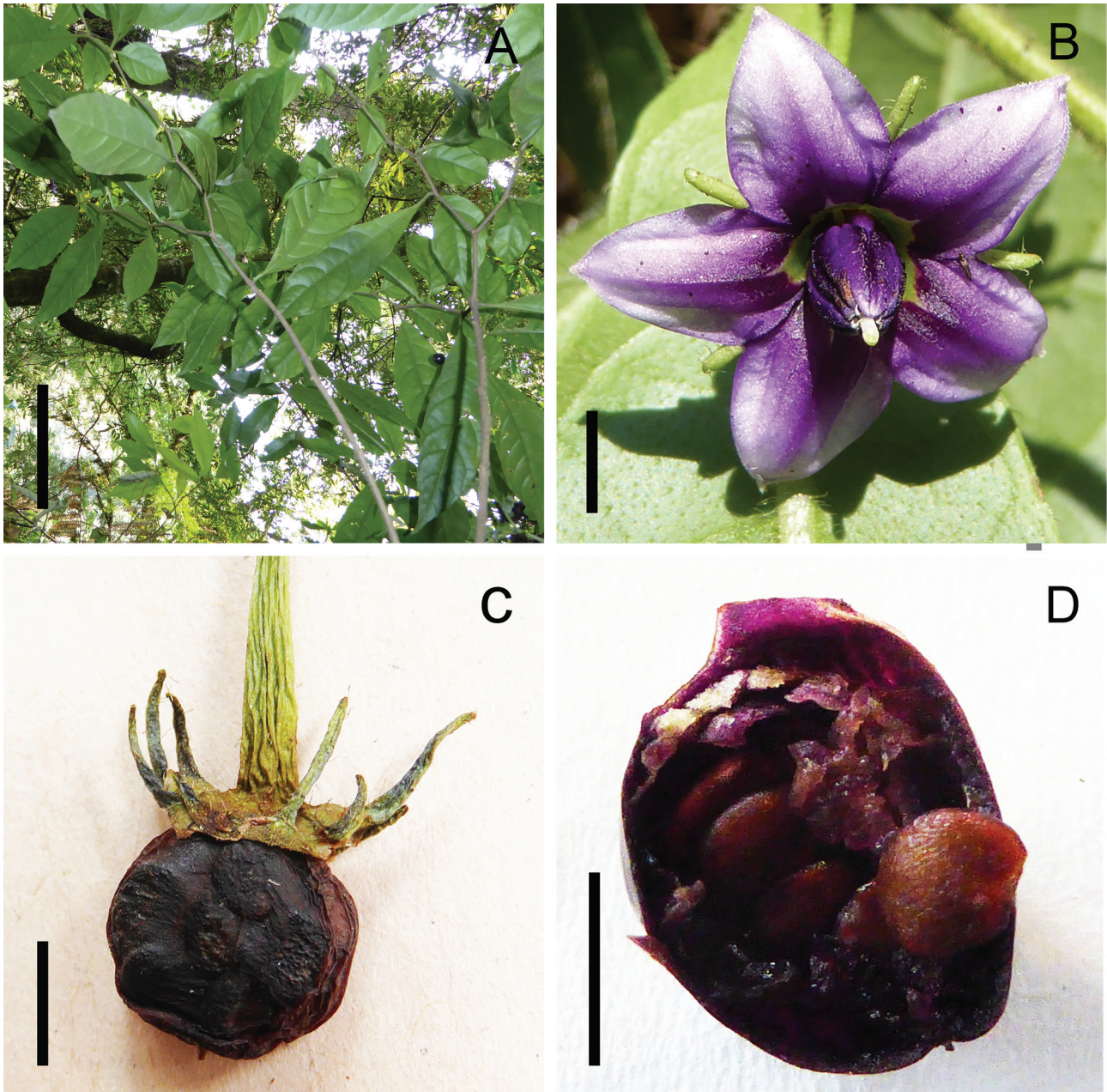


FIGURE 10. *Lycianthes caeciliae*. A. Shrub habit with branch, leaves, and fruit (Dean 10030 in field; scale bar equals 1 dm). B. Flower (Dean 10030 in field). C. Fruit (herbarium specimen of Dean 10030). D. Long section of fresh fruit (Dean 10030). All scale bars equal 5 mm except in A.

Due to the many excellent collections made at La Cortadura on the slopes of Cofre de Perote by the third author, Gonzalo Castillo-Campos, between 2005 and 2007, this species was rediscovered in the field, allowing the first author

to obtain photographs of the flowers and fruits. The tree species that grow with *L. caeciliae* in the original cloud forest include: *Alchornea latifolia*, *Clethra mexicana*, *Cyathea fulva*, *Hedyosmum mexicanum*, *Miconia chrysoneura*, *Miconia glaberrima*, *Miconia oligotricha*, *Cinnamomum psychotrioides*, *Prunus samyroides*, *Psychotria galeottiana*, *Quercus laurina*, *Turpinia occidentalis*, and *Vaccinium leucanthum*. The shrub layer includes *Cestrum elegans*, *Deppea grandiflora*, *Dicksonia sellowiana*, *Fuchsia microphylla*, *Hoffmannia excelsa*, *Moussonia deppeana*, *Roldana lanicaulis*, and *Solanum nudum*. The most common species in the herbaceous layer are *Anthurium scandens*, *Arachniodes denticulata*, *Blechnum stoloniferum*, *Elaphoglossum peltatum*, *Nopalxochia phyllanthoides*, *Peperomia tetraphylla*, *Polypodium* spp., and *Smilax* spp.

Lycianthes caeciliae is closely related to *L. pilifera*, with which it shares simple, straight, spreading trichomes that do not collapse upon drying, corollas with purple and green coloration, purple anthers, and dark purple fruit with large brown seeds (Fig. 10). *Lycianthes caeciliae* could be confused with *L. stephanocalyx*, a rhizomatous herb to subshrub which also occurs in Veracruz, but at lower elevations. *Lycianthes stephanocalyx* differs from *L. caeciliae* in having small incurved trichomes, yellow connate anthers, red fruits, and tan seeds.

Representative Specimens Examined—MEXICO. Veracruz: Mpio. Coatepec, La Cortadura, falda este del Cofre de Perote, 2100 m, 2 May 2005, G. Castillo-Campos 21514 (IEB215178, XAL); same location, 6 May 2005, G. Castillo-Campos 21543 (XAL); same location, 6 May 2005, G. Castillo-Campos 21552 (XAL); same location, 10 Aug 2005, G. Castillo-Campos 21766 (MEXU1394624, XAL); same location, 27 Feb 2005, G. Castillo-Campos 22271 (XAL); same location, 18 Apr 2007, G. Castillo-Campos 22711 (XAL); same location, 25 Apr 2007, G. Castillo-Campos 22754 (XAL); same location, 25 Apr 2007, G. Castillo-Campos 22773 (XAL); same location, 23 May 2007, G. Castillo-Campos 22828 (IEB214680, XAL); Mpio. Coatepec, La Cortadura, falda este del Cofre de Perote, 1800 m, 8 May 2019, E. Dean 10030 (DAV215178, MEXU, XAL); Mpio. Coscomatepec, 10 May 1987, E. Matuda 1309 (MEXU89925); Mpio. Xico, terracería, 1 km al NE de Oxtlapa, rumbo a Tonalco, faldas del Cofre de Perote, 2250 m, 27 Sep 2001, A. Rincón G. 2604 (MEXU1358400, XAL78678); Acajete, Plan de Cedeño, 1750 m, 23 Jun 1976, F. Ventura A. 12881 (IEB114958).

2. *Lycianthes pilifera* (Bentham (1840: 68)) Bitter (1919: 427) (Figs. 3, 7, 8). *Solanum piliferum* Benth.—Type: MEXICO. Oaxaca: Llano Verde, 1839, C. T. Hartweg 499 (Lectotype [designated by Dean and Reyes (2018)]: K barcode K000585745 [digital photo!]); isolectotype: LD barcode 1212266 [digital photo!]).

Lycianthes pilifera (Benth.) Bitter var. *pilosiuscula* (M. Martens & Galeotti (1845: 136)) Bitter (1919: 428). *Solanum pilosiusculum* M. Martens & Galeotti (1845: 136). Type: MEXICO. Oaxaca: Cerro del Malacate (Pelado Capulálpam [Capulálpam] and Llano Verde), near Villa Alta, 7500 ft, Nov–Apr 1840, H. Galeotti 1171 (lectotype [designated by Dean and Reyes (2018)]: BR barcode 000000552882 [digital photo!] [photo WIS!]; isolectotypes: BR barcode 000000552849 [digital photo!], BR barcode 000000552911 [digital photo!], G barcode G00343182 [digital photo!], K barcode K000585746 [digital photo!], LE barcode LE-00017009 [digital photo!], NY barcode 00139019 [digital photo!], US barcode 00027745 [digital photo!], W156335 [digital photo!], W0004160 [digital photo!]).

Shrub, 1–4 m tall. Indument of brown, multicellular, simple, eglandular, acute, appressed to patent trichomes, these usually remaining cylindrical throughout and acute at apex upon drying. Stems green to purple-green, terete, becoming brown and woody with age, not much compressed upon drying; upper branching mostly monochasial with a few dichasial branching points, the upper sympodial units 2.3–4 cm long, 1–2.5 mm in diameter, difoliate, glabrous to densely pubescent with appressed to patent trichomes to 1 mm long. Leaves of upper sympodia usually geminate, unequal in size, the larger ones with blades (3) 6–15 × (1) 2–6.5 cm, elliptic to obovate (sometimes narrowly so), the smaller ones with blades 1–6 × 0.6–3 cm, suborbicular, ovate, elliptic or obovate, thick chartaceous to subcoriaceous, glabrous to moderately pubescent with appressed to patent trichomes to 1.25 mm long, these more numerous on the veins, the primary veins of the large leaves 4–7 on each side of the midvein, the base cuneate, sometimes oblique (sometimes rounded in smaller leaves), the margin entire to wavy, the apex acute to acuminate, the petioles absent or up to 1 (3) cm. Flowers in groups of 1–6, axillary, the axes glabrous to densely pubescent with appressed to patent trichomes 0.25–1 mm long; peduncles absent; pedicels 15–60 mm long and arching in flower, 30–55 mm long (probably longer) and arching in fruit; calyx 2–3 mm long, 3–4.5 mm in diameter, campanulate, glabrous to densely pubescent with trichomes similar to those of the stem, the margin truncate, the 10 spreading, linear-subulate appendages 2–9 mm long, emerging 0.5–1 mm below rim, often purplish in color; fruiting calyx accrescent, widely bowl-shaped, 1.5–4 mm long, 7–9 mm in diameter, in some populations the appendages to 15 mm long; corolla oriented horizontally to nodding, 0.8–2.1 cm long, campanulate, entire to shallowly stellate, with abundant interpetalar tissue, white to light purple adaxially with darker purple ring near the base (sometimes with a green ring or spots at

base below the purple ring), white to purple abaxially, sometimes green near the veins of the lobes, nearly glabrous; stamens equal, the filaments 1–2 mm long, glabrous; anthers 5–6 mm long, ovate to lanceolate, free, yellow-purple to purple, the pores ovate, all opening toward the style; pistil with glabrous ovary, the style 10–11 mm, linear, glabrous, the stigma capitate. Fruit a berry, (6) 12–18 mm long, 9–15 mm diameter, ovoid, dark purple at maturity, glabrous. Seeds 10–30 per fruit, 2.5–4 × 2–2.5 mm, compressed but often slightly ridged near the edge or center and not flat, the outline variable in shape, shallowly crescent-shaped, semi-circular, depressed ovate, rhombic, or reniform (with small notch), medium-brown to nearly black, the surface reticulum with a serpentine to honeycomb pattern with deep lumina, appearing pitted, with fibrils protruding from the cell walls.

Vernacular Names:—Monte agua zapote, rojo monte papel (from herbarium specimens *Rivera Reyes JR-2609, JR-3141*)

Distribution:—*Lycianthes pilifera* is endemic to Mexico (state of Oaxaca) (Fig. 6). It grows in shady canyons, slopes, and drainages in cloud forest, semi-deciduous or deciduous forest, including oak forest, pine-oak forest, and mixed forests with *Ilex*, *Podocarpus*, *Weinmannia*, *Persea*, *Ocotea*, *Oreomunnea*, *Taxus* and/or *Cupressus* at elevations of 1800–3050 m.

Phenology:—Specimens with flowers and fruits have been collected most months of the year. The corollas on flowering specimens are often at least partially open, indicating that the corollas of this species probably stay open for a substantial amount of the day.

Notes:—*Lycianthes pilifera* is an attractive shrub with white to purple flowers and equal stamens (Fig. 8). It is extremely variable in width of leaves, size and coloration of flowers and calyx appendages, as well as density of trichomes. The type specimen has nearly glabrous, narrow leaves and relatively short calyx appendages. Forms with longer calyx appendages have been found in Oaxaca below 2000 m, and forms with shorter appendages have been found above that elevation. Very small-leaved, small-flowered, and small-fruited forms have been collected from near Concepción Pápalo, Oaxaca, at 2700 m.

Representative Specimens Examined—**MEXICO. Oaxaca:** Distrito de Ixtlán, Florística en Santa María Yavesia, 2910 m, 13 Apr 2002, *E. Benítez 10* (MEXU1210647); Distrito Ixtlán, Sierra Norte, Mpio. San Miguel Yotao, Yotao, hacia Calpulalpan, 2150 m, 12 May 1999, *A. Blanco M. 593* (MEXU1019824); Mpio. San Juan Comaltepec, just off Highway 175 (road from Ixtlán de Juárez to Valle Nacional), on Caribbean slope, 2250 m, 17 Oct 1990, *B. Boyle 550* (MEXU737926); 20 km northeast of Teotitlán del Camino on road to Huautla de Jiménez, 2130 m, 7 Nov 1983, *D. Breedlove 59916* (CAS694941); Northeast of Teotitlán del Camino on road to Huautla de Jiménez, 2260 m, 7 Nov 1983, *D. Breedlove 59916a* (MO3695516); northwest slope of Cerro Humo Chico, 43 km north of Ixtlán de Juárez junction on road to Valle Nacional, 2870 m, 9 Nov 1983, *D. Breedlove 59965* (MEXU643531); northeast slope of Cerro Humo, 9 Nov 1983, *D. Breedlove 59987* (CAS694672, MEXU482422, MO3695515); 35 km N of Ayutla along road from Mitla to Choapam, N slope of Cerro Zempoaltepetl, 2470 m, 26 Sep 1986, *D. Breedlove 64691* (NY, TEX barcode 00227040); same location 17 Apr 1988, *D. Breedlove 66854* (MEXU625959, MO4625615, NY); Distrito Ixtlán, Mpio. Capulalpam de Méndez, noreste de Río Natividad, 26 Sep 2002, *F. Brito S. 282* (MEXU1166540); Distrito Villa Alta, a 7 km de la desviación a San Andres Yaa, al sur de Villa Alta, camino a Oaxaca, 2030 m, 15 Mar 1982, *R. Cedillo T. 1199* (IBUG171062); a 5 km al N del Cerro Humo Chico, carr. Ixtlán a Valle Nacional, 2606 m, 26 Sep 1982, *R. Cedillo T. 1871* (MEXU1189542); Distrito Ixtlán, Sierra de Juárez, ruta 175 Tuxtepec a Oaxaca, 24 km por el camino norte de la desviación Yólox, 2000 m, 6 Apr 1981, *R. Cedillo T. 654* (MEXU338537, MO3032777); Distrito Ixtlán, camino de Tepananacualco, 28 Mar 1912, *C. Conzatti 190* (MEXU1402975, MEXU535391); along Hwy 175 between Valle Nacional and Oaxaca, 2.3 mi below summit of Cerro Pelón, 32.1 mi NNE of Ixtlán de Juárez, 2580 m, 22 Feb 1987, *T. Croat 65628* (MEXU633863, NY); Mpio. San Pedro Yólox, Sierra de Juárez, along Hwy 175 to the northeast of the turnoff to Comaltepec and northeast of the cabins and restaurant of Mirador, along old undeveloped road, 2022 m, 10 Sep 2017, *E. Dean 9522* (DAV225278); 30 Km by road ENE of Ayutla along road between Mitla and Zacatepec, just E of intersection with road to Totontepec, 2500 m, 22 Jun 1986, *G. Diggs 3928* (NY); Cerro del Malacate (Pelado Calpulalpan and Llano Verde), near Villa Alta, 7500 ft., Nov–Apr 1840, *H. Galeotti 1171* (G7842/17, MO1690668, WIS); Mpio. San Felipe Usila, cuenca del Río Perfume (ladera oeste), 8.1 km en línea recta al sur de Santa Cruz Tepetotutla, 2400 m, 31 Mar 1994, *C. Gallardo H. 1012* (CAS1164198, IEB199701, MEXU1198123, XAL); Mpio. San Felipe Usila, cuenca del Río Perfume (ladera oeste), 6.9 km en línea recta al sur de Santa Cruz Tepetotutla, 2000 m, 18 May 1994, *C. Gallardo H. 1078* (IEB214256, MEXU1198126, XAL); Mpio. San Felipe Usila, cuenca del Río Perfume (ladera oeste), 8 km en línea recta al sur de Santa Cruz Tepetotutla, 2500 m, 14 Sep 1994, *C. Gallardo H. 1186* (IEB202742, MEXU1198127, XAL); same location and date *C. Gallardo H. 1192* (IEB202741, MEXU1198129, XAL); Mpio. San Felipe Usila, camino a Cerro Carrizo, 3.1 km en línea recta al sur de Santa Cruz Tepetotutla, 2000 m, 22 Nov 1993, *C. Gallardo H. 846* (IEB199755, MEXU1192514, MEXU1198120, XAL); Distrito

Ixtlán, 13 km al norte de La Esperanza, 1900 m, 9 Apr 1987, *A. Garcia M. 3041* (IBUG159136, MEXU1091716); Distrito Cuicatlán, Mpio. Concepción Pápalo, 15 km al NE de Concepción Pápalo, cañada húmeda, 2700 m, 16 Nov 1993, *R. Garcia S. 155* (MEXU1228734); Distrito de Ixtlán, Sierra de Juárez; Ruta 175 Tuxtepec a Oaxaca, a 15 km al NE de la desviación a Yólox, 2200 m, 16 Apr 1982, *D. Lorence 4035* (CAS733845, MEXU389787); Distrito de Villa Alta, camino de Natividad a Talea de Castro, a 5 km al sur de la desviación a Yalina (comedor Maravillas), 2580 m, 3 Aug 1985, *D. Lorence 4713* (IBUG160154, MEXU1141151); Distrito Ixtlán, Mpio. Comaltepec, Sierra de Juárez, camino de Ruta 175 a la cascada (brecha 60 Comaltepec) al norte de Cerro Pelón, 2350 m, 5 Aug 1985, *D. Lorence 4738* (MEXU1423431, MEXU1427997); desviación a San Pedro Yólox, sobre la carretera Ixtlán-Valle Nacional, 2800 m, 15 Jan 1983, *C. Lorenzo 16* (MEXU604828); desviación a San Juan Acatepec sobre la carretera Ixtlán, 2200 m, 15 Jan 1983, *C. Lorenzo 9* (MEXU number not recorded); Carretera Oaxaca-Tuxtepec, km. 110 more or less, 24 May 63, *T. MacDougall s.n.* (MEXU118243, MEXU118246, MEXU244867); Distrito Ixtlán, Mpio. San Pedro Yólox, 8 km E of Yólox on road between Yólox and Hwy 175, 13 Apr 1981, *G. Martin 532* (MEXU504749, MO3661166, US3079600); Mpio. San Felipe Usila, cuenca del Río Perfume (ladera oeste), 9.1 km en línea recta al sur de Santa Cruz Tepetotutla, 2430 m, 30 May 1995, *J. Meave 1692* (IEB219723, MEXU1192521); Mpio. San Felipe Usila, poza con cascada, a orilla de terracería, 12.5 km en línea recta al sur de Santa Cruz Tepetotutla, 2720 m, 3 Jun 1995, *J. Meave 1720* (IEB219746, MEXU1192517, XAL); Mpio. San Felipe Usila, cuenca del Río Perfume (ladera oeste), terrenos de Santa Cruz Tepetotutla, 1930 m, 23 Nov 1996, *J. Meave 2051* (XAL); Mpio. Mazatlán Villa de Flores, Sierra Mazateca, San Pedro de los Encinos, 2325 m, 23 Apr 2002, *X. Munn-Estrada 2254* (NY); same location and date, *X. Munn-Estrada 2270* (NY); Sierra Mazateca, aprox. 30 km de Teotitlan de Flores Magón, por la carretera a Huautla de Jiménez (MEX 182), antes de llegar al Puerto de la Soledad, 2300 m, 3 Oct 2002, *X. Munn-Estrada 1483* (NY); Sierra Mazateca, aprox. 400 [m?] del Puerto de la Soledad, por la carretera de Huautla a Teotitlán de Flores Magón (MEX 182), 2320 m, 13 Feb 2002, *X. Munn-Estrada 1946* (NY); Distrito Ixtlán, Mpio. Santiago Comaltepec, Cerro La Esperanza, 1749 m, 30 Aug 2011, *J. Aragon Parada 96* (MEXU1366380); Distrito Ixtlán, Mpio. Comaltepec, Sierra Norte, brecha área de las cascadas, 2606 m, 21 Jun 2001, *G. Pérez P. 36* (IBUG159150, MEXU1030070); Mpio. San Felipe Usila, cuenca del Río Perfume (ladera oeste), 7.3 km en línea recta al sur de Santa Cruz Tepetotutla, 2220 m, 15 May 1994, *A. Rincón G. 416* (IEB199687, XAL); Mpio. San Felipe Usila, cuenca del Río Perfume (ladera oeste), 7.6 km en línea recta al S de Santa Cruz Tepetotutla, 2240 m, 16 May 1994, *A. Rincón G. 446* (IEB199685, MEXU1198111, XAL); same location and date, *A. Rincón G. 452* (IEB199684); same location but 2430 m, 9 Jul 1994, *A. Rincón G. 468* (IEB199683, MEXU1198112); Mpio. San Felipe Usila, cuenca del Río Perfume (ladera O), 8 km en línea recta al S de Santa Cruz Tepetotutla, 2000 m, 2 Nov 1994, *A. Rincón G. 514* (IEB199682, MEXU1198113); Mpio. San Felipe Usila, parteagua, sur de la cuenca del Río Perfume, 10.5 km en línea recta al sur de Santa Cruz Tepetotutla, 2560 m, 15 Sep 2004, *A. Rincón G. 3068*, (IEB199758, MEXU1198117, XAL); Distrito Mixe, Totontepec Villa de Morelos, Kets tekum, tonun kux, 17 Jul 1994, *J. Rivera R. 3141* (IBUG186073); same location, 2 Apr 1991, *J. Rivera R. 2609* (MEXU1140522); 39 km al sur de Valle Nacional sobre la carretera a Oaxaca, 1800 m, 26 Dec 1975, *J. Rzedowski 33768* (MEXU227370, NY); 39 km al sur de Valle Nacional sobre la carretera a Oaxaca, 10 Apr 1976, *J. Rzedowski 34028* (MEXU271451); San Juan Tepeuxila, Cuicatlán, 1990 m, 1 May 1993, *S. Salas M. 510* (MEXU1085157); N of Oaxaca about 40 miles, along hwy 175 to Tuxtepec, about 10–30 miles N of Ixtlán de Juárez, 2575 m, 24 Jul 1983, *C. Taylor 2452* (DUKE296155); Mpio. Teotitlán de Flores Magón, Puerto de la Soledad, 30 km al noreste de Teotitlán, 2360 m, 18 May 1986, *P. Tenorio L. 11284* (MEXU1132679); Distrito Teotitlán de Flores Magón, Mpio. Teotitlán de Flores Magón, Raya San Jerónimo, 4 km al SE de Plan de Guadalupe, brecha a Mazatlán de Flores, 2800 m, 15 Feb 1993, *P. Tenorio L. 18,547* (MEXU932212); Distrito Teotitlán de Flores Magón, Mpio. Teotitlán de Flores Magón, Puerto de la Soledad, 2105 m, 10 Apr 2001, *P. Tenorio L. 20020* (MEXU1408859); Distrito Ixtlán, Llano Verde, 16 km al sureste de Calpulalpan [Calpulálpam], 2230 m, 15 Apr 1982, *R. Torres C. 305* (IBUG159140, MEXU1133071); Distrito de Mixe, a 11 km al norte de Mixtepec ó 3 km al norte de la desviación a Metepec, sobre la brecha a Totontepec, 16 May 1982, *R. Torres C. 455* (IBUG159139, MEXU932228, NY); Distrito de Mixe, 5.2 km al noreste de la desviación a Zacatepec, 2380 m, 23 Apr 1983, *R. Torres C. 2681* (IBUG159138, MEXU1132625); Distrito de Villa Alta, 8.1 km al norte de Maravillas, camino a Talea de Castro por Yalina, 2370 m, 15 May 1983, *R. Torres C. 2939* (IBUG160005, MEXU1132775); Distrito de Mixe, entrada a Mixistlán, 30.8 Km al noreste de Tamazulapan [Tamazulapam], 2430 m, 7 Apr 1984, *R. Torres C. 4942* (IBUG159137, MEXU1132678); Distrito Mixe, 2 Km al suroeste de Totontepec, carretera a Oaxaca, 17 Jun 1986, *R. Torres C. 8650* (MEXU1132689); Distrito Ixtlán, Mpio. Comaltepec, 22 km al oeste de La Esperanza, carretera Tuxtepec-Oaxaca, 2900 m, 9 Apr 1987, *R. Torres C. 9518* (IBUG160007, MEXU1091714); same location and date, *R. Torres C. 9521*, (IBUG159135, MEXU1091715); Distrito Ixtlán, Mpio. San Juan Comaltepec, entrada a San Isidro Yólox, 10.9 km al suroeste de La Esperanza, carretera Tuxtepec-Oaxaca, 2070 m, 24 Feb 1988, *R. Torres C. 11712* (MEXU1163833); Distrito Mixe, Mpio. Totontepec Villa de Morelos, 1 km al norte de la desviación a Villa Alta,

la cual se encuentra 7.5 km al sur de Totontepec, 2460 m, 25 Feb 1988, *R. Torres C. 11789* (IBUG171066, MEXU1194584); Distrito Ixtlán, Mpio. San Juan Quiotepec, Cerro Zacate recorrido de la Cruz a la capilla, Santa María Nieves, 25 May 2002, *R. Torres C. 16414* (MEXU1067435); Distrito Ixtlán, Mpio. Comaltepec, 11.1 km suroeste de La Esperanza carretera Oaxaca-Tuxtepec, entrada al camino de San Isidro Yólox, 1950 m, 17 Dec 1987, *A. D. Campos Villanueva 910* (IBUG160006); Distrito Teotitlán, mountain ridges between Teotitlán del Camino and Huautla de Juárez, 7500–7800 ft, 8 Jul 1972, *G. Webster 17270* (DAV81437, DAV82751); Sierra Madre Oriental, ca. 3.5 mi NE of Cerro Pelón, 2250 m, 19 Jul 1972, *G. Webster 17455* (DAV81424, MEXU268061).

3. *Lycianthes quichensis* (J. M. Coulter & Donnell Smith (1904: 422)) Bitter (1919: 428) (Figs. 4, 7, 9). *Solanum quichense* J. M. Coulter & Donnell Smith (1904: 422). Type: GUATEMALA. Quiché: Chiul, Apr 1892, *E. T. Heyde & E. Lux, 3450* (holotype: F barcode 0073142F (F2647270) [digital photo!]; isotypes: GH barcode 00077532 [digital photo!], K barcode K000585747 [digital photo!], M barcode M0171931 [digital photo!], NY barcode 00139026, US barcode 00624010 [digital photo!], US barcode 00027769 [digital photo!]).

Lycianthes obliquifolia Standley (1940: 101). Type: MEXICO. Chiapas: Volcán de Tacana, 30 Mar 1939, *Matuda 2938* (holotype: F barcode 0072919F (F980247) [digital photo!]; isotypes: A barcode 00077523 [digital photo!], MEXU barcode MEXU-00082111 [digital photo!], MICH barcode 1109852 [digital photo!], NY barcode 00138706 [digital photo!]).

Shrub, 1–5 m tall. Indument of white to pale yellow, multicellular, simple, eglandular, acute, appressed to patent trichomes, the larger ones becoming flattened upon drying. Stems green, terete, not much compressed upon drying, becoming brown and woody with age; upper sympodial branching points mostly monochasial with a few dichasial branching points, the upper sympodial units to 2–5 cm long, 1–3 mm in diameter, usually difoliate, sparsely to densely pubescent with appressed to patent trichomes 0.1–1 mm long. Leaves of upper sympodia usually geminate, unequal in size, the larger ones with blades 4–15 (25) × 2.5–9 (14) cm, ovate to elliptic (sometimes very widely so), rarely lanceolate, the smaller ones with blades 1.5–9 × 1–5 cm, ovate, chartaceous, sparsely to moderately pubescent with appressed to patent trichomes to 1 mm long, these more numerous on the veins and sometimes quite dense in the abaxial leaf axils, the primary veins on the large leaves 4–7 on each side of the midvein, the base cuneate to truncate or rounded, sometimes oblique, the margin entire to wavy, the apex acute to acuminate, the petioles absent or up to 4 (6) cm. Flowers in groups of 2, axillary, the axes sparsely to densely pubescent with appressed to patent trichomes 0.25–1 mm long; peduncles absent; pedicels 20–60 mm long, erect and arching in flower, to 70 mm long (probably longer), arching to deflexed in fruit; calyx 3–4 mm long, 3.5–6 mm in diameter, campanulate, sparsely to densely pubescent with trichomes similar to those of the stem, the margin truncate, the 10 spreading, linear-subulate appendages 3–6 mm long, emerging 0.5 mm below rim, often purplish in color; fruiting calyx accrescent, widely bowl-shaped, 2–5 mm long, 7–13 mm in diameter, the appendages not greatly enlarging; corolla oriented horizontally, 1.2–3 cm long, rotate to campanulate, entire to shallowly stellate, with abundant interpetalar tissue, light purple adaxially with darker purple ring near the base and green markings at very base, light purple abaxially, sparsely to densely pubescent with small trichomes abaxially near the veins; stamens equal, the filaments 1.5–2 mm long, glabrous, the anthers 5–6 mm long, lanceolate, free, purple, the pores ovate, all opening toward the style; pistil with glabrous ovary, the style 10–12 mm, linear, glabrous, the stigma capitate. Fruit a berry, 9–17 mm long, 7–15 mm diameter, usually ovoid (round), red (drying dark purple on herbarium sheets), glabrous. Seeds 20–40 per fruit, 2.5–3 × 2–2.5 mm, compressed but not flat, variable in shape, shallowly crescent-shaped, triangular, or semi-circular, ridged on one side or near the center, orange-brown to nearly black, the surface reticulum with a serpentine to honeycomb pattern with deep lumina, appearing pitted, with fibrils protruding from the cell walls.

Vernacular names:—Chilete, choshel, coxel, flor de rosa, quilete, tomatillo blanco (Gentry & Standley 1974).

Distribution:—*Lycianthes quichensis* is known from Guatemala and southern Mexico (state of Chiapas) (Fig. 6). It grows in moist or wet thickets in cloud forest and oak/conifer forest with *Chiranthodendron*, *Symplocos*, *Drimys*, and *Clethra* at elevations of 2200–3900 m. In Guatemala it may occur in *Cupressus* or *Abies* forests.

Phenology:—Specimens with flowers and fruits have been collected most months of the year. The corollas on flowering specimens are often at least partially open, indicating that the corollas of this species probably stay open for a substantial amount of the day.

Notes:—*Lycianthes quichensis* is an attractive shrub that horticulturalists are trying to bring into cultivation and is sometimes available in seed catalogues. It has relatively large purple flowers with distinctive dark purple and green markings and widely ovate leaves (Fig. 9). As discussed above, it differs from *L. pilifera* in having widely ovate leaves and red, rather than dark purple, fruits.

Representative Specimens Examined—**GUATEMALA. Chimaltenango:** Volcán de Acatenango, 11 Sep 1993, *I. Arias 3291* (MEXU867916); Santa Helena, 5 Dec 1936, *J. Johnston 406* (NY); Volcán de Acatenango, 2800 m, 22 Apr 1999, *M. Véliz 7020* (BIGU11798, MEXU908243, MEXU992801, MEXU999504); slopes of Cerro Chichoy, above Tecpán, 2670 m, 6 Jul 1949, *L.O. Williams 16817* (MO1597647); Cerro de Tecpám, region of Santa Elena, 2400–2700 m, 26 Dec 1938, *P. Standley 61108* (NY). **Huehuetenango:** Mpio. San Mateo Ixtatán, along road to San Pedro Soloma, 3 mi. southwest of San Mateo Ixtatán, 9600 ft, 6 Feb 1965, *D. Breedlove 8630* (CAS-DS517521); along road to Huehuetenango, 5 miles south of San Juan Ixcoy, 9200 ft, 5 Aug 1965, *D. Breedlove 11485* (CAS-DS584753); ridge NE of Cerro Boquerón on road from El Rosario to Niquivil, 2255 m, 29 Nov 1986, *D. Breedlove 66145* (CAS757698); 5 m N of San Juan Ixcoy, 8950 ft, 12 Nov 1970, *W. Harmon 4832* (MO3673776); Mpio. La Libertad, Peña Blanca, 3193 m, 14 Dec 2000, *M. Véliz 10846* (BIGU45669, CAS1128035). **Quetzaltenango:** Mpio. Zunil, northwest slopes of Volcán Zunil, 2900 m, 14 May 2004, *T. Quedensley 654* (BIGU38791, TEX); Volcán Zunil, 3000–3200 m, 27 Dec 1976, *W. Schwabe s.n.* (MEXU236592); Cumbre de Alaska, 3100 m, 10 Sep 1999, *M. Véliz 7285* (BIGU12645, MEXU991669, MEXU1154901). **Sacatepequez:** Volcán de Agua, 5 Mar 1994, *G. Bill 3621* (MEXU367914, MEXU1154915); Volcán de Agua, road between Santa María de Jesús and crater, 2800–3300 m, 7 Jul 1986, *G. Diggs 4049* (NY); Volcán Agua, 3000 m, 13 Nov 1967, *A. Molina R. 21023* (NY); Santa María de Jesús, Volcán de Agua, 2852 m, 6 Feb 2006, *M. Véliz 16671* (BIGU32768, TEX). **San Marcos:** Mpio. San José Ojetenam, San José Ojetenam, 3100 m, 26 Nov 2009, *F. Pérez 18* (BIGU53456, BIGU58382); Cerro El Bonete, south of Volcán Tajumulco, 11 Mar 1971, *T. Plowman 3052* (TEX-DC14964); two miles S of San Sebastian, Sierra Madre Mountains, 10,000 ft, 13 Dec 1963, *L. Williams 25930* (NY, WIS). **Sololá:** Volcán Santa Clara, 2100–3000 m, 5 Jun 1942, *J. Steyermark 47001* (NY); San Pedro La Laguna, Volcán San Pedro, ladera noreste del volcán, 3006 m, 28 Jan 2005, *P. Pardo 27* (CAS1127678). **Totonicapán:** Lake Atitlán, ca 15 km N of Sololá, old road to Chichicastenango, 3000 m, 6 May 1972, *D. Burch 5949* (MO3480769); María Tecún, 3000–3600 m, 12–23 Jan 1966, *A. Molina R. 16399* (CAS-DS627148, NY); 5–10 km west of Los Encuentros, Cerro María Tecún, Sierra Madre Mountains, 2900–3100 m, 24 Dec 1972, *L.O. Williams 41742* (NY);

MEXICO. Chiapas: Mpio. Chamula, Civilhobeletic, Jul 1975, *T. Anderson s.n.* (CAS-DS648806); Mpio. San Cristobal de Las Casas, southwest of Mexican Highway 190 near Rancho Nuevo, about 14 km southeast of San Cristóbal de las Casas, steep slope near crest of ridge, 9000 ft, 20 Aug 1966, *D. Breedlove 15098* (CAS-DS590404); same location, 28 Jul 1981, *D. Breedlove 51805* (CAS665202, MEXU399126); Mpio. El Porvenir, 3–4 km west of El Porvenir along road from Huixtla to Siltepec, 2800 m, 17 Jan 1973, *D. Breedlove 31746* (CAS-DS652867, MEXU255860, MO2610584); Mpio. El Porvenir, northwest slope of Cerro Male, 3–4 km west of El Porvenir along road from Huixtla to Siltepec, 2800 m, 19 Sep 1976, *D. Breedlove 40387* (CAS-DS720602, MEXU254817, MO2611096, NY); Mpio. Motozintla de Mendoza, on the north and west slope of Cerro Mozotal, below the microwave tower along road from Huixtla to El Porvenir and Siltepec, 3000 m, 22 Nov 1976, *D. Breedlove 41749* (CAS-DS702823); Mpio. Zinacantan, at paraje Pij, 2460 m, 9 Mar 1981, *D. Breedlove 50023* (CAS663077, MEXU859643, MO3496320, NY); Mpio. Motozintla de Mendoza, Cerro Mozotal, near summit, 2750 m, 24 Nov 1981, *D. Breedlove 55915* (CAS671627); Cerro Mozotal, near summit, 2740 m, 27 Nov 1991, *D. Breedlove 72675* (CAS888240); Cerro Sontehuits, 10 miles by road from Las Casas [San Cristóbal de las Casas] to Tenejapa, then up trail to top, 3000 m, 28 Jan 1952, *M. Carlson 2399* (MEXU68438); Mpio. Chamula, Tzontehuitz, 2740 m, 20 Apr 1999, *L. Domínguez T. 70* (MEXU1454051); Mpio. Cristóbal de Las Casas, Estación Biológica Huitepec-PRONATURA, 2500 m, 22 Jan 1991, *M. González E. 1244* (MEXU606587, XAL); same location, 23 Oct 1991, *M. González E. 1616* (MEXU557028); Mpio. Chamula, Paraje Vo'ta Mesté, 2470 m, 12 Feb 1992, *M. González E. 1752* (MEXU553984); Mpio. Motozintla de Mendoza, a 6 Km de Motozintla, Cerro Mozotal, 3058 m, 15 Jul 2009, *J. Jonapa 150* (MEXU1415571); Mt. Pasitar, 30 Dec 1936, *E. Matuda 255* (MEXU97741; MO1278555; NY); Mpio. Siltepec, Fraylesca, 2000 m, 3 Mar 1945, *E. Matuda 5259* (CAS720382, MEXU82117); Sierra Madre de Chiapas, Saxchanal, 2000 m, 11 May 1948, *E. Matuda 17812* (MEXU82113); Sta. Rosa, Escuintla, 25 May 1948, *E. Matuda 17852* (CAS-DS655454, MEXU445162); Mpio. Chamula, Cerro Zontehuitz, NE of San Cristóbal de Las Casas, 9000–9400 ft, 25 Jun 1962, *G. Webster 11741* (DAV48953).

4. *Lycianthes stephanocalyx* (Brandege (1917: 374) Bitter (1922: 315) (Figs. 5, 7, 11). *Solanum stephanocalyx* Brandege (1917: 374). Type: MEXICO. Veracruz: Zacuapan, Jul 1915, *Purpus 7519* (holotype: UC barcode UC-178649!; isotypes, GH barcode GH00077535 [digital photo!], MO825716!, NY barcode 00139030 [digital photo!]).

Lycianthes symphyandra Bitter (1919: 430). *Solanum symphyandrum* (Bitter (1919: 430)) C.V.Morton (in Lundell 1940: 27). Type: MEXICO. Veracruz: Mirador, 1842, *Liebmann 1456* (lectotype [designated by Dean and Reyes (2018)]: C barcode C10022133 [digital photo!]).

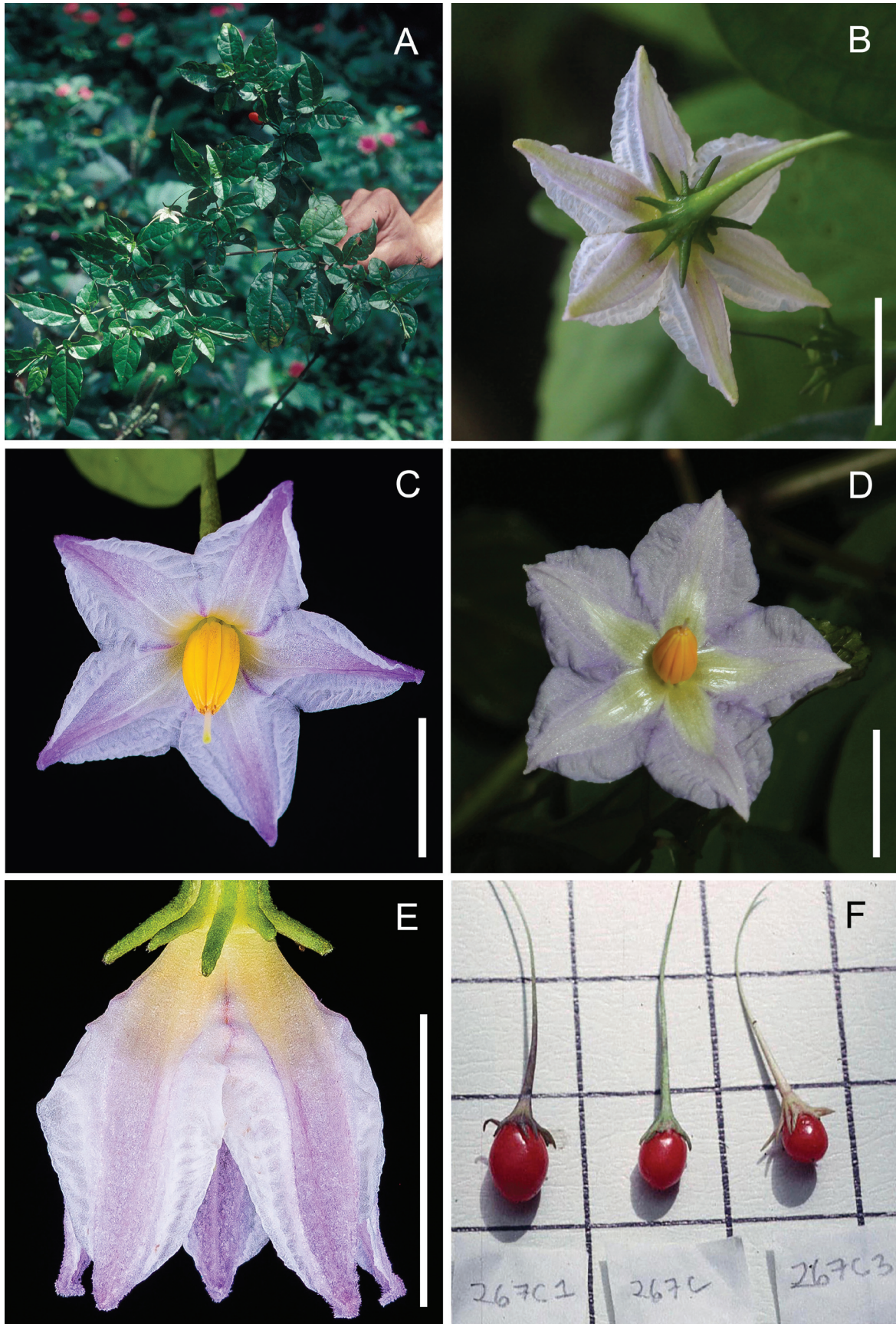


FIGURE 11. *Lycianthes stephanocalyx*. A. Habit showing branch, leaves, and flowers (field photograph of *Dean 265*). B. Calyx (field photograph of *Amith 1953*). C. Corolla and stamens (greenhouse plant of *Dean 265*). D. Corolla and stamens (field photograph of *Amith 2315*). E. Closed corolla (greenhouse plant of *Dean 265*). F. Fruits (field photograph of *Dean 267*; sides of squares on grid equal 2 cm). All scale bars equal 5 mm.

Solanum solitarium S.F.Blake (1922: 21). *Lycianthes solitaria* (S.F. Blake (1922:21)) Standley (1927: 15). Type: GUATEMALA. Izabal: Río Mojanales, 17 May 1919, S. F. Blake 7489 (holotype: US barcode 00027803 [digital photo!]).

Lycianthes luisana Standley (1940: 101). Type: MEXICO. San Luis Potosí: Tamazunchale, Jul 1937, M. Edwards 913 (holotype: F barcode 0072917F (F918327) [digital photo!]; isotypes: ARIZ barcode ARIZ-BOT-0005035 [digital photo!], CAS barcode 0003290 [digital photo!], MO barcode 503464 [digital photo!]).

Solanum hondurensis C.V.Morton (in Lundell 1940: 26). *Lycianthes hondurensis* (C.V.Morton (in Lundell 1940: 26)) Standley & Steyermark (1943: 18)., Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 18. 1943. Type: BELIZE, El Cayo District, Chalillo Crossing, 15 Jul 1936, C. Lundell 6512 (holotype: US barcode 00027603 [digital photo!]; isotypes: LL barcode 00372878!, MICH barcode 1109936 [digital photo!]).

Perennial herb to climbing shrub, erect, often recumbent with age, to 2 (3) m tall, dying back to rhizomes. Indument of small, white, multicellular, simple, eglandular, curved, appressed-antrorse trichomes that often flatten upon drying. Stems green when young, compressed and ribbed when dried, becoming woody with age; upper sympodial branching points mono- or dichasial, the upper sympodial units (1.5) 3.4–13 cm long, 1–3 mm in diameter, difoliate, sparsely pubescent with appressed-antrorse trichomes 0.1–0.6 mm long. Leaves of upper sympodia usually geminate, unequal in size, the larger ones with blades 3.5–15 × 1.5–6.2 cm, the smaller ones 0.7–6.5 (10.5) × 0.5–3.1 (5) cm, the geminate leaf pairs usually similar in shape, the blades ovate (sometimes narrowly), elliptic, or obovate, chartaceous to thick chartaceous, glabrous to sparsely pubescent with trichomes like those of the stems 0.1–0.6 mm long, the primary veins on the large leaves 3–6 on each side of midvein, the base truncate, cuneate, or attenuate, sometimes oblique, the margin entire to wavy, the apex acute to acuminate, the petioles absent or (0.1) 0.2–0.9 (2) cm long. Flowers solitary, axillary, the axes glabrous to sparsely pubescent with appressed-antrorse trichomes to 0.25 mm long; peduncles absent; pedicels 12–45 mm and arching to deflexed in flower, to 53 mm long and deflexed in fruit; calyx 1.5–3 (4) mm long, 3–4 mm in diameter, obconic to campanulate, glabrous to sparsely pubescent with trichomes similar to those of the stem, the margin truncate, the 10 spreading to reflexed appendages 1.5–5 mm long, emerging 0.5 mm below rim; fruiting calyx usually accrescent, widely campanulate to bowl-shaped, 1.5–4 mm long, 3–8 mm in diameter, the appendages 2–8 mm long, spreading; corolla pendant, (0.5) 0.7–1.4 cm long, campanulate to reflexed, stellate, lobed 1/3 to 2/3 of the way to the base (lobes shallow on first day that the flower opens, becoming deeper each subsequent day that the flower opens), with interpetalar tissue, white to light purple, glabrous; stamens equal, the filaments 1–1.5 mm long, glabrous, the anthers 4.5–7 mm long, lanceolate, connate, yellow, the pores round, dehiscing upward; pistil with glabrous ovary, the style (6) 8.5–9 mm, linear, straight, glabrous, the stigma truncate. Fruit a berry, 3–10 (17) mm long, 3–9 (12) mm diameter, spherical to ovoid, red, glabrous. Seeds 7–60 per fruit, (1.5) 2–3 mm × 1.5–2 mm, flattened, depressed ovate in outline, tan to orange, the surface reticulum with a serpentine pattern with shallow lumina, the walls lacking protruding fibrils.

Vernacular names:—Tomatillo, arrete de la virgin, flor de mariposa (Standley 1940). Masan ay (from herbarium specimen *Marco Leonti* 71).

Distribution:—*Lycianthes stephanocalyx* is known from Mexico (states of San Luis Potosí, Querétaro, Hidalgo, Veracruz, Oaxaca, Chiapas), Guatemala, Belize, and Honduras (and possibly further south in Central America) (Fig. 6), near rivers or waterfalls, in gorges, or on the sides of canyons in tropical rainforest, deciduous forest, semideciduous forest, high evergreen forest, and cloud forest, sometimes in coffee plantations or disturbed forest at elevations of 30–1050 m.

Phenology:—Flowering May to September. Fruiting September to December. Possibly flowering and fruiting throughout the year in some locations. In the field, the first author observed that the corollas are open in the very early morning and closed by late morning.

Notes:—*Lycianthes stephanocalyx* differs from the other three Mexican species included by Bitter in series *Piliferae* in being a rhizomatous herb (that can sometimes produce above-ground woody growth) with white stellate flowers and connivent to connate anthers (Fig. 11). Its closest relatives are not yet fully known, but preliminary data from the Bohs laboratory at the University of Utah place it near other species with equal stamens and stellate corollas such as *Lycianthes heteroclita* (Sendtner 1846: 193) Bitter (1919: 494) and *L. geminiflora* (M. Martens & Galeotti) (Martens & Galeotti (1845: 142)) Bitter (1919: 497).

Representative Specimens Examined—**BELIZE.** Belize: Mile 33 1/2 beyond Hattieville, Rich Woods Farm, 6 Jul 1972, J. Dwyer 10112 (MO2825959); El Cayo: 37 Miles Section, Humming Bird Highway, 5 Nov 1955, P. Gentle 8928 (LL, MO3342047, NY). **Toledo:** Trail from Columbia Forest Station to Esperanza, 2 to 4 miles west of San José road, 600–1100 ft, 13 Jun 1973, A. Gentry 8159 (MO3698371);

GUATEMALA. Huehuetenango: Sierra de los Cuchumatanes, between Xoxlac and Nucapuxlac, 1650–2500 m, 17 Jul 1942, *J. Steyermark 48960* (NY). **Izabal:** Mohanal, trail from Espiritu Santo to Las Playitas, 10–18 May 1919, *H. Pittier 8532* (NY). **Petén:** Dolores, bordering Río Mopan, in clearing 6 km SE, 29 Jun 1961, *E. Contreras 2566* (MO3237313);

HONDURAS. Atlántida: Near San Francisco, 2 May 1970, *F. Barkley 40239* (DAV123359); vicinity of La Ceiba, near the Congrejal River, foothills back of Ceiba, 5 Jul 1938, *T. Yuncker 8193* (MO1194194, NY). **Copán:** 4 miles NE of Santa Rita, 700 m, 28 Aug 1975, *A. Molina R. 30832* (MO2581340); **Cortés:** Aldea de Corinto y alrededores frontera con Guatemala, 55 km al O de Puerto Cortés, 9–11 Aug 1975, *C. Nelson 2824* (MO5194219);

MEXICO. Chiapas: Mpio. Ocosingo, Restaurante la Escondida, en la 11 de Julio, camino a Palenque, 163 m, 12 Jun 2002, *G. Aguilar 1380* (DAV220025); Mpio. Ocosingo, a 12 km al NW del crucero de Bonampak, 299 m, 12 Feb 2003, *G. Aguilar 5584* (DAV220026); Mpio. Barriozábal, along road from Berriozábal to Las Maravillas, ca. 1.4 km south of the town of Efraín A Gutiérrez, remnant of tall forest called La Mata Café, 1005 m, 12 Sep 2017, *E. Dean 9529* (DAV225277); vicinity of Palenque ruins, 200 m, 3 Jul 1969, *B. Marcks 967* (MO3278608); Mpio. Ocosingo, 5 km al S de Campamento COFOLASA, el cual está a 24 km al SE de Crucero Corozal, camino Palenque-Boca Lacantum, 220 m, 24 Sep 1984, *E. Martínez S. 7847* (NY); Mpio. Ocosingo, a 6.4 km al SSE de Nuevo Guerrero, 380 m, 9 Aug 2002, *E. Martínez S. 35582* (MEXU1151976); Mpio. Ocosingo, 5 km al S de Frontera Echeveria, sobre la orilla del Río Usumacinta, 80 m, 4 Dec 1984, *E. Martínez S. 9121* (MEXU593934, MO4246504); Mpio. Ocozocoautla, on road to Malpaso, 20 mi NW of Ocozocoautla, 1700 ft, 16 Aug 1972, *G. Webster 17907* (DAV81395). **HIDALGO:** Twelve miles south of Tamazunchale, 5 Jul 1947, *F. Barkley 7261* (MEXU173896); Mpio. Chapulhuacán, 53 km al noreste de Zimapan, 1000 m, 7 Nov 1979, *R. Hernández M. 3898* (MEXU290182); Mpio. Chapulhuacán, 3 km al noreste de Chapulhuacán, 900 m, 7 Nov 1979, *R. Hernández M. 3905* (MEXU285525); Mpio. Chapulhuacán, near Chapulhuacán, km 340 of highway, 20 Aug 1943, *C. Lundell 12407* (LL barcode 00227034, LL barcode 00227038). **Oaxaca:** 15 km north of Valle Nacional along road to Oaxaca City, 150 m, 5 Jan 1982, *D. Breedlove 56697* (MEXU843331, MO3657654); alrededores de las bombas de auxilio de la presa de Temascal, 22 Sep 1984, *E. Cabrera C. 7237* (MEXU1423433); Mpio. Santa María Jacatepec, en el poblado La Joya, del ejido Corriente Ancha, 150 m, 17 Jul 1990, *J. I. Calzada 15416* (MEXU1169703; MEXU1221247); Mpio. Santa María Jacatepec, al NO del poblado La Joya parcela de Melquiades, 22 Jun 1990, *J. I. Calzada 15636* (MEXU1223118); Distrito Tehuantepec, Mpio. Santa María Guienagati, 3 km al norte de Santa María Guienagati, carretera a Guevea de H., 460 m, 27 Aug 1991, *A. D. Campos V. 3849* (MEXU932503, MEXU1163915); Distrito Tuxtepec, presa Temascal, camino a los vertederos, 90 m, 8 Sep 1985, *L. Cortes 30* (MEXU927219); same location and date, *L. Cortes 40* (MEXU1237410); Distrito Tuxtepec, Mpio. Soyaltepec, 500 m al SE del vertedor de la presa Temascal, 70 m, 24 Nov 1986, *L. Cortes 572* (MEXU571639, MO5074257); Distrito Tuxtepec, Mpio. Soyaltepec, 4 km al sur de la Hidroeléctrica Temascal, 60 m, 22 Aug 1986, *L. Cortes A. 390* (MEXU1138771); Distrito Tuxtepec, Mpio. Soyaltepec, Cerro Verde al sureste de Temascal, 300 m, 19 Aug 1987, *L. Cortes A. 974* (MEXU1194594); Mpio. Santa María Chimalapa, Paso Lagarto (Huacatapac) del Río del Corte ca. 5 km al N de Sta. María, 180 m, 16 Aug 1984, *H. Hernández G. 350* (NY); hacia Cerro de la Bola Tuxtepec, 16 Sep 1947, *F. Miranda 4248* (MEXU72979); Mpio. Soyaltepec, Presa Temascal, 150 m, 10 Aug 1981, *C. Ramos s.n.* (MEXU1361259). **Puebla:** Road (575) Cuetzalan to San Antonio Rayón [Santiago Yancuictalpan], 592 m, 10 Nov 2014, *P. Acevedo-Rodríguez 16044* (DAV218009); Sierra Nororiental de Puebla, Mpio. Cuetzalan del Progreso, Tacuapan, just before the main road into town starts going up toward the church, 312 m, 9 Sep 2014, *J. Amith 2134* (DAV217977). **Querétaro:** Mpio. Landa, 2 km al sureste de Neblinas, Río Tancuilin, 610 m, 12 Jun 1990, *H. Rubio 1953* (DAV218509, IEB193314); Mpio. Landa, 2 km al sureste de Neblinas, Río Tancuilin, 610 m, 12 Sep 1990, *H. Rubio 1954* (DAV218498, IEB193315); 74 miles north of Zimapan, 22 Aug 1957, *U. Waterfall 14257* (BRIT). **San Luis Potosí:** San Antonio, 7 Sep 1978, *J. Alcorn 1649* (TEX barcode 00227035); Tamazunchale (Poistapa), 12 Jul 1937, *M. Edwards 520* (TEX127864); same location, 22 Jul 1937, *M. Edwards 913* (WIS); Tamazunchale, 175 m, Jul 1937, *C. Lundell 7096* (NY); 7 miles E of Xilitla, 3000 ft, 18 Jul 1963, *R. McGregor 886* (LL barcode 00227032); Tamasopo, 400–500 m, 8–9 Aug 1934, *F. Pennell 17998* (NY). **Tabasco:** Mpio. Tenosique, a orillas del Chinilkija en el ejido Linda Vista, 2 Aug 1990, *M. Magaña 2299* (MEXU717293). **Veracruz:** Mpio. Atoyac, Cerro La Perla, 3 km al sureste de Miraflores, 900 m, 17 May 1985, *R. Acevedo R. 92* (IEB114872, MEXU552762); Mpio. Atoyac, La Joya a 1.5 km aproximadamente al NW del rancho de Santa Rosa, 600 m, 20 Jun 1985, *R. Acevedo R. 207* (MEXU931200); Mpio. Atoyac, Vara Negra, 3 km al nor-noroeste de Atoyac, 650 m, 17 Jul 1985, *R. Acevedo R. 287* (IEB114871, MEXU931117); Mpio. San Andrés Tuxtla, Laguna Encantada, 8 km al N de San Andrés Tuxtla, 22 Nov 1986, *J. I. Calzada 12988* (MEXU702836); ca. 6 miles S of Acayucan, 1 mile W of Sayula de Alemán, 90 m, 3 Jul 1977, *T. Croat 40020* (MO2597731, MO5287741); about 4 rd miles from cuota road to Veracruz (hwy 150), along old rd 150 between Orizaba and Fortín, N side of rd, 3600 ft, 26 Sep 1991, *E. Dean 265* (DAV162814); Mpio

Coetzala, along old stone rd between Coetzala and Cuichapa, about 1–1.5 km from Coetzala, 2300 ft, 26 Sep 1991, *E. Dean* 267 (DAV162815, MEXU1195821); Mpio. Coetzala, 3 km WNW of Cuichapa on road to Coetzala, 1.5 km SE of Coetzala, 550–700 m, 3 Jul 1982, *G. Diggs* 2716 (BRIT); Mpio. Cuichapa, 400 m al N de los Xúchiles, 565 m, 5 Jul 1990, *F. Fernández C.* 98 (MEXU1376035); Mpio. Ixtaczoquitlán, Cerro Buenavista, 1335 m, 3 Oct 1995, *B. Juárez L.* 861 (MEXU1347519, MEXU1441604); Mpio. Santiago Tuxtla, Acahual, 30 m, 10 Jul 1967, *G. Martínez C.* 1448 (MEXU140796, MEXU140797, MO2085644); Mpio. San Andrés Tuxtla, Salto de Eyipantla, 5 km by air S of San Andrés Tuxtla, 150 m, 4 Dec 1981, *M. Nee* 23,611 (MEXU785058, MO3339989); Mpio. Ixtaczoquitlán, 5 km SW of Fortín, 1050 m, 7 Dec 1981, *M. Nee* 23847 (MEXU712875); Misantla-Veracruz, Aug 1912, *C. Purpus* 5952 (MO5384119); Zacuapan, Jul 1915, *C. Purpus* 7519 (MO825716, US884631); Mpio. Amatlán de los Reyes, 400 m al sureste del puente del Río Negro en La Patrona, 700 m, 19 Sep 1990, *F. Ramón* 246 (IEB114876, WIS); Mpio. Zontecomatlán, 6 km en línea recta al sureste de Zontecomatlán, ejido Cabellete, 800–1100 m, 8 Sep 2000, *A. Rincón G.* 1869 (IEB237724, MEXU1358399); Mpio. San Andrés Tuxtla, por la carretera cerca Máquina Vieja y Salto de Agua, al norte de San Andrés, 10 Nov 1975, *G. Shapiro* 218 (MEXU234651); Mpio. Santa Rosa, Los Tuxtlas, 14 Sep 1974, *M. Sousa* 4442 (MEXU164958); Mpio. Sotapan, Benito Juárez a la orilla del camino rumbo Pop soj nas, 600 m, 6 Jul 1999, *M. Leonti* 71 (MEXU988765); Mpio. Tlapacoyan, Río Zordo, 200 m, 11 Aug 1981, *F. Ventura* 18934 (MEXU776567).

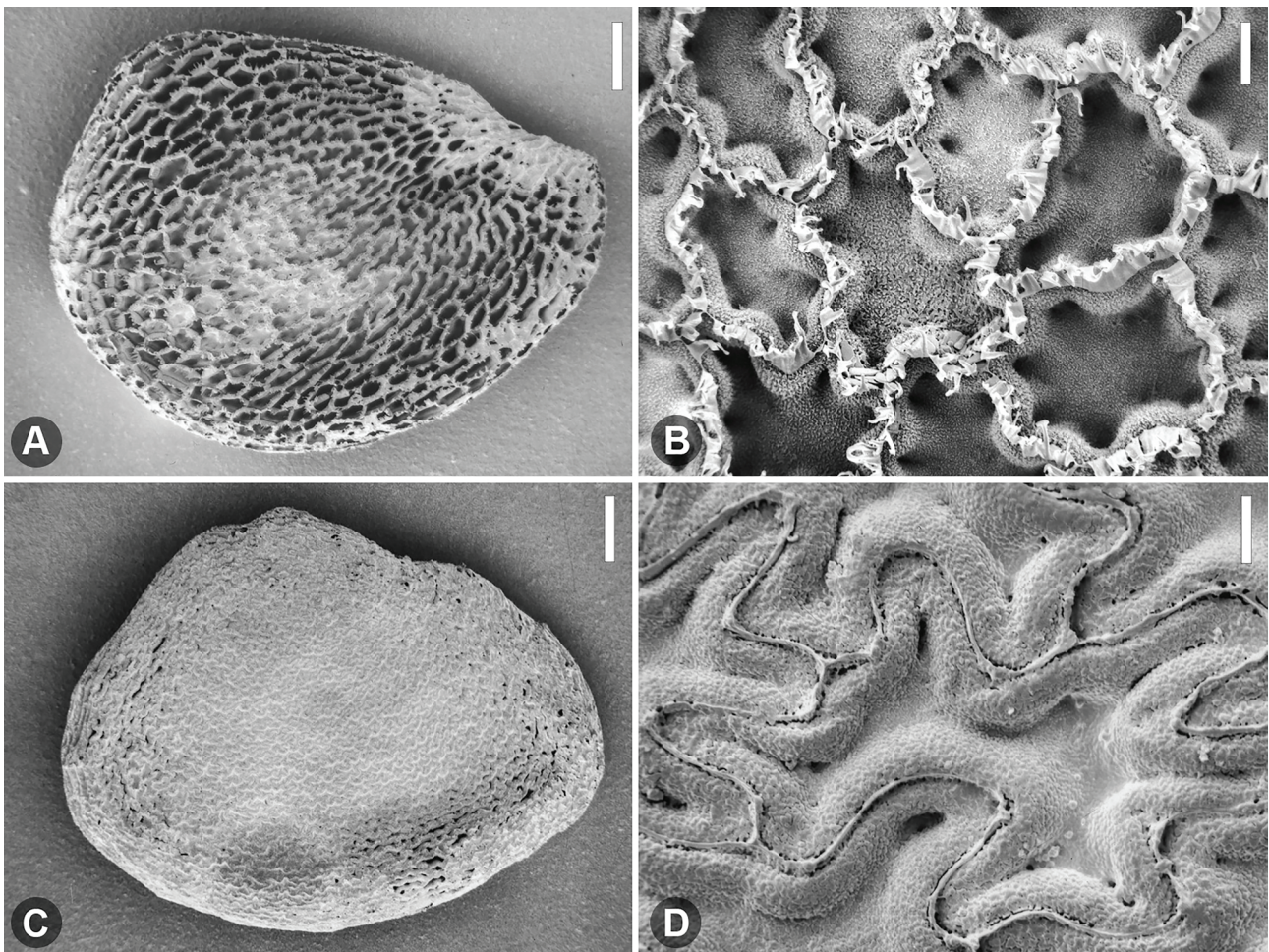


FIGURE 12. Digested seeds and seed surfaces of *Lycianthes pilifera* (A and B, from San Francisco Botanical Garden) and *Lycianthes stephanocalyx* (C and D, *Dean* 265, DAV). Scale bars: A: 351 microns; B: 62 microns; C: 277 microns; D: 14 microns.



FIGURE 13. Seeds of A. *Lycianthes caeciliae* (Dean 10030, DAV), B. *Lycianthes quichensis* (Breedlove 11485, CAS), and C. *Lycianthes coffeifolia* (Luteyn 9011, NY). Scale bars equal 1 mm.

Discussion

After examining the morphological characteristics and distributions of the species placed into series *Piliferae* by Georg Bitter, we believe that series *Piliferae*, as originally circumscribed, is an unnatural group that unites species with disparate ecology, life forms, floral structure, and fruit and seed characteristics. It is doubtful that *L. stephanocalyx* and *L. coffeifolia* are closely related to *L. caeciliae*, *L. pilifera* and *L. quichensis*, but it is likely that the three latter, which share similar habitats, elevational ranges, floral color patterns, and seed size and coloration, are closely related to each other. Ongoing phylogenetic studies of *Lycianthes* based on sequence data (currently being carried out in the Bohs laboratory at the University of Utah) will provide more insight into the relationships within the genus and allow future workers to divide *Lycianthes* into more natural groups. It is possible that additional species will be included in the final *Piliferae* clade, such as *L. beckneriana* D'Arcy (1973: 635), another high elevation cloud forest species with unlobed corollas and equal stamens that occurs in Panama and Costa Rica (Bohs 2015). Therefore, we do not recircumscribe series *Piliferae* here as a smaller group (i.e., one containing only *L. caeciliae*, *L. pilifera*, and *L. quichensis*).

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