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Three new species of *Lycianthes* (Solanaceae) from Panama

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Abstract

Three Panamanian cloud forest species in the genus *Lycianthes* are newly described: *L. coloradensis*, from the Ngäbe-Buglé Comarca; *L. fortunensis* from Chiriquí Province, Veraguas Province, and the Ngäbe-Buglé Comarca; and *L. talamancensis* from Bocas del Toro and Chiriquí provinces. All three species are woody vines with tan, yellow, or orange-brown multangulate-stellate trichomes and entire to nearly entire white to purple corollas. In terms of vegetative morphology and trichome characteristics, *L. coloradensis* most closely resembles *L. purpusii* of Mexico, Guatemala, and Honduras, *L. fortunensis* resembles the widespread *L. multiflora*, and *L. talamancensis* resembles *L. hortulana* of Honduras, El Salvador, and Nicaragua. This article provides species descriptions, maps of geographic distributions, specimen images of each species, and comparison tables of morphological characters used to separate *L. coloradensis*, *L. fortunensis* and *L. talamancensis* from similar species.

Keywords: *Lycianthes*, Solanaceae, Panama, plant taxonomy

Introduction

Lycianthes (Dunal 1852: 29) Hassler (1917: 180) (Solanaceae) includes 150 to 200 species and has a distribution that spans the New World (from Mexico to Argentina and the Caribbean), southeast Asia, China, Japan, and the Pacific (D'Arcy 1991, Hunziker 2001). All members of the genus have a calyx in which the sepals have been truncated into a rim, and in many species five to ten appendages emerge below this rim; this character, combined with poricidal anther dehiscence, allows the genus to be distinguished from similar genera in the Solanaceae (D'Arcy 1986, Hunziker 2001). Calyx appendages are also usually present in *Capsicum* L. (1753: 188), the closest relative of *Lycianthes* (and only other member of tribe Capsiceae), and recent phylogenetic analyses have indicated that *Capsicum* may be nested within *Lycianthes* (Bitter 1919; Guzman *et al.* 2009; Särkinen *et al.* 2013). Therefore, *Lycianthes* may need to be recircumscribed to make it monophyletic.

The genus as a whole was last studied by Georg Bitter (1919), whose monograph included 189 species, subspecies and varieties, divided into subgenera, sections, and series. Bitter placed New World shrubs and vines with furcate to multangulate-stellate trichomes and fruits lacking sclerotic granules within several series: *Virgatae* (Bitter 1919: 360); *Glanduliferae* (Bitter 1919: 380); and *Caribaccolae* (Bitter 1919: 391). Phylogenetic and monographic studies of these series have not yet been completed, and the species included in them may not be closely related. In addition, since Bitter's monograph, many new species with furcate to multangulate-stellate trichomes have been described, none of which have been placed in one of Bitter's series (for example: Dean *et al.* 2019, Standley & Williams 1952, D'Arcy 1973 [1974]).

As part of a project that will provide online species descriptions for all New World *Lycianthes* species at the Solanaceae Source website (<http://solanaceaesource.org/>), we examined herbarium specimens (including types) of all species of *Lycianthes* occurring from Mexico to Panama. It became clear that some of the specimens with multiangulate-stellate trichomes from high elevation cloud forest areas of Panama were undescribed species. Three new Panamanian species, *Lycianthes coloradensis* E. Dean and H. Kang, *Lycianthes fortunensis* J. Poore & E. Dean, and *Lycianthes talamancensis* E. Dean & J. Poore, are described below.

Materials and methods

The species concept used here is a morphological one (Cronquist 1978), and the circumscriptions of the species described here are based solely on data obtained from the examination of herbarium specimens (we did not observe these species in the field). Information on lifeform and floral color were obtained from collector data on specimen labels. This study was part of a much larger study carried out by the first author in which specimens of all *Lycianthes* species of Mexico and Central America were examined, and many species were observed in the field. This background allowed us to determine which species are most similar to the new species described here. To delineate the new species and separate them from similar species, we examined: 68 specimens of the three newly described *Lycianthes* species; 56 specimens of *L. breedlovei* E. Dean (2019: 265); two specimens of *L. dendriticothrix* Bitter (1919: 375); 58 specimens of *L. fredyclaudiae* E. Dean (2019: 268); 71 specimens of *L. furcatistellata* Bitter (1919: 401); 62 specimens of *L. hortulana* Standley & L.O. Williams (1952: 58); 39 specimens of *L. howardiana* D'Arcy (1973 [1974]: 642); 292 specimens of *L. multiflora* Bitter (1919: 361); three specimens of *L. porteriana* D'Arcy (1973 [1974]: 645); and 129 specimens of *L. purpusii* (Brandege (1914: 62)) Bitter (1919: 382). Throughout this work, herbarium specimens are cited with the herbarium code followed by an accession number. If no accession number is cited, none was attached to the specimen (as is the case with many NY specimens). Herbarium codes were obtained from *Index Herbariorum* (Thiers continuously updated). For all the species that we compared in this study (including types), we examined specimens from the following herbaria either in person or as online images: A, BM, BR, C, CAS, DAV, DUKE, ENCB, F, EAP, G, GH, GOET, IEB, K, LD, LL, M, MEXU, MO, NY, TEX, UC, US, W, WIS, and XAL.

If we added coordinates to a cited specimen, they are displayed in brackets. Specimens were georeferenced by using Geolocate, an online software-mapping package (Rios & Bart, 2010), or manually using Google Earth Pro (Sullivan, 2009), and maps were created with the coordinates. We did not calculate conservation assessments for these species, because most of the specimens we examined are between 30 and 50 years old, and we are not familiar with the state of the habitat in which they occur.

Much of the terminology used in this paper follows Radford *et al.* (1974) and Harrington and Durrell (1979); however, some seed surface terms follow Gunn and Gaffney (1974). The terminology used 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, Dean *et al.* 2019). Trichome terms are taken from Roe (1968, 1971) and are illustrated in Fig. 1 of Dean *et al.* (2019). We are defining stellate branching as having more than two branches at a trichome node and dendritic as having only two branches at a trichome node.

Results

Morphology

As in other *Lycianthes* (Dean *et al.* 2017), the upper branches of the species described here are comprised of short sympodial units consisting of two leaves and a flower. These sympodial units emerge either singly (monochasial branching) or in pairs (dichasial branching) beneath the inflorescence of the prior sympodial unit. In some species, the branches at a dichasial branching point diverge widely (with the angle much larger than 90 degrees, sometimes approaching 180 degrees); when this is the case, we are using the term “divaricate” for the branching. These species often exhibit marked zigzagging in their monochasial branching. When the branching is monochasial, the leaf arrangement is usually geminate.

The trichomes in all three species newly described here are multangulate-stellate; however, in *Lycianthes coloradensis* and *L. talamancensis*, some of the three to five primary trichome rays often bear another set of two to three stellate rays, and those can also be rebranched (see Fig. 1A in Dean *et al.* 2019).

The corollas of the three species described here are sympetalous and entire (or nearly so), with five corolla lobes connected by interpetalar tissue. As described for other *Lycianthes* (Dean 2001, Dean *et al.* 2017), the corollas of many *Lycianthes* open and close each day for several days in a row (usually 3 days). Quite a number of specimens of *L. fortunensis* have flowers with fully open, rotate corollas, indicating that the corollas are probably open for a longer time during the day than many species of *Lycianthes*. The corollas on the few specimens we examined of *L. talamancensis* are closed, indicating that they probably only open early in the morning, and we cannot be certain of the

shape of the open corolla. The corollas of *L. coloradensis* range from closed to partially open, appearing campanulate; we are unsure if the open corollas of this species are actually campanulate or if the corollas are partially open on the specimens.

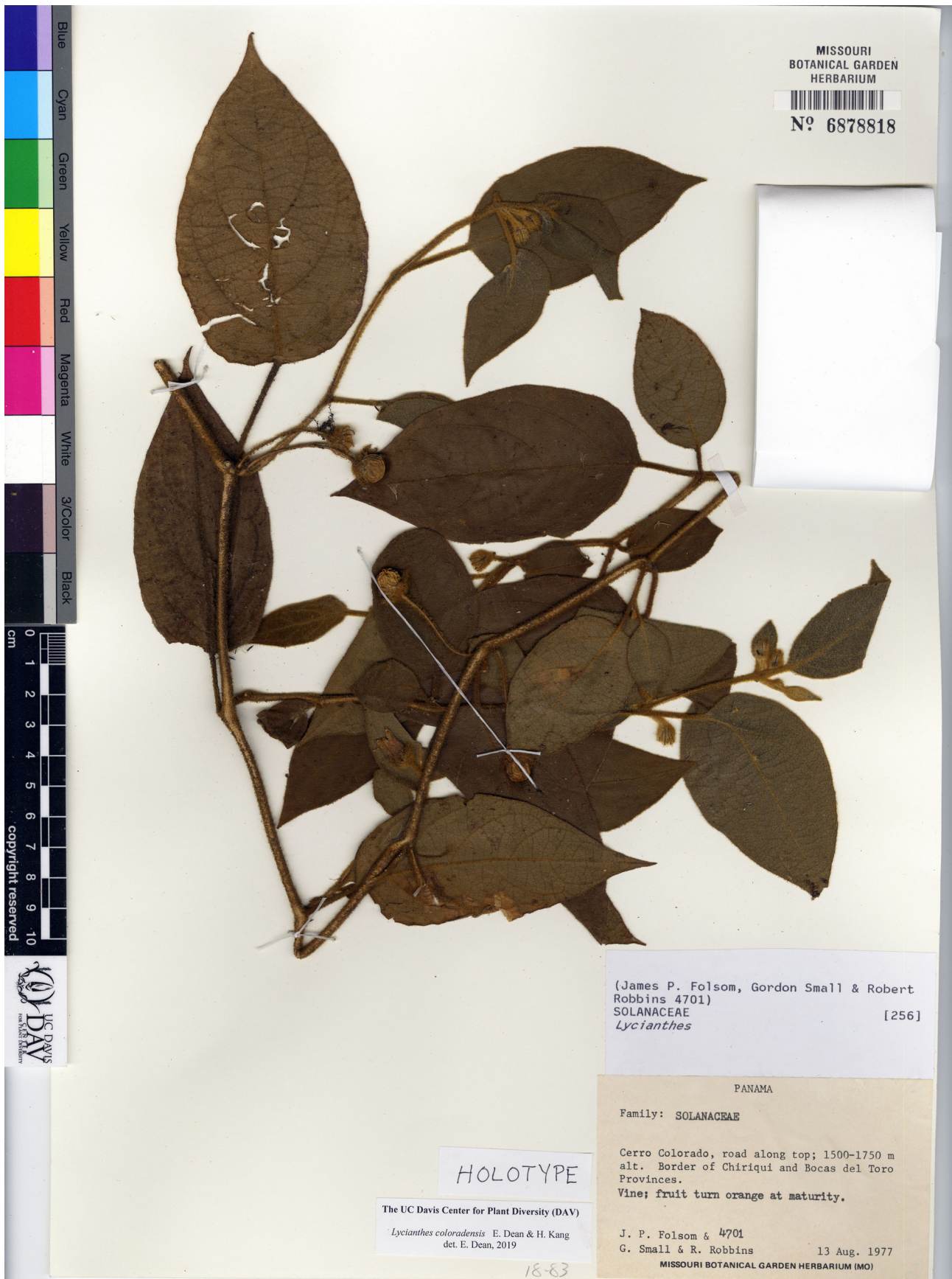


FIGURE 1. Scan of the holotype of *Lycianthes coloradensis*. Image used with permission of the Missouri Botanical Garden Herbarium.

The five stamens of the androecium of the three species described here range from equal (with equal filaments and equal anthers) in *L. talamancensis*, subequal in *L. coloradensis* (with filaments slightly unequal), and unequal (with one filament longer than the other four) in *L. fortunensis*. The stamens in *L. fortunensis* and *L. talamancensis* are completely free of one another, while in *L. coloradensis*, the anthers of adjacent stamens are sometimes connivent at their basal edges.

Species descriptions

1. *Lycianthes coloradensis* E. Dean and H. Kang (Fig. 1).—Type: PANAMA. [Ngäbe-Buglé] Chiriquí: Cerro Colorado, border of Chiriquí and Bocas del Toro provinces, [8.5406, -81.8233], 1500–1750 m, 13 Aug 1977, *J. P. Folsom 4701* (holotype: MO acc. # 6878818; isotype: MO acc. # 2624365)

Diagnosis. Endemic to Panama; most similar to *Lycianthes purpusii*, but differing in often having multangulate-stellate trichomes with rebranched rays (rather than unbranched), shorter calyx appendages to 5.5 mm long in flower and to 6 mm long in fruit (rather than 7–17 mm in flower and to 20 mm long in fruit), subequal stamens with filaments ca. 1.5 mm long (rather having four equal filaments and one longer filament), and smaller fruit to 12 mm long and 15 mm in diameter (rather than 15–30 mm long and 15–30 mm in diameter).

Usually a vine (rarely a shrub), sometimes creeping or low to the ground, to 1 m tall. Indument of pale yellow, orange, or brown, uniseriate, multicellular, simple, dendritically branched or multangulate-stellate, long-stalked, eglandular, spreading trichomes, the rays often rebranched. Stems greenish-tan when young, terete in cross section, not compressed upon drying, becoming woody with age, moderately to densely pubescent with trichomes 0.5–2 mm long, 0.5–1.1 mm in diameter; upper sympodial branching points usually monochasial, sometimes dichasial, not widely divaricate, the sympodial units shallowly zigzagging, the upper sympodial units 1–12 cm long, 2–4 mm in diameter. Leaves of upper sympodia simple, usually paired and unequal in size, the smaller leaf of the pair sometimes not developing, or abscising early, larger ones with blades 7–14 × 2.7–7.5 cm, the smaller ones with blades 3.2–7.5 × 2–4.5 cm, the leaf pairs similar in shape, the blades ovate to elliptic, thick chartaceous, moderately to densely pubescent with trichomes like those of the stem, the primary veins 3–7 on each side of the midvein, the base widely cuneate, truncate, rounded, or slightly cordate, sometimes slightly oblique, the margin entire, usually undulate, the apex acute to acuminate, the petioles 0.5–3 (3.5) cm long. Flowers solitary or in groups of 2–3, axillary, the inflorescence axes moderately to densely pubescent with trichomes to 2 mm long; peduncles absent; pedicels 17–41 mm long and erect to arching in flower, to 40 mm long (probably longer) and erect to arching in fruit; calyx 3–5 mm long, 6–7 mm in diameter, campanulate, moderately to densely pubescent (the surface sometimes obscured) with trichomes like those of the stem, the margin truncate, the 10 linear appendages 2–5.5 mm long emerging ca. 0.5 mm below the calyx margin; fruiting calyx enlarged, widely bowl-shaped, 2–5 mm long, 5–11 mm in diameter, the appendages to 6 mm long; corolla oriented horizontally to ascending, 1.1–1.3 cm long, rotate, nearly entire, the lobes with abundant interpetalar tissue, the adaxial side white (sometimes reported as having green markings on the lobes at the base), the abaxial side of the lobes moderately pubescent with long, shaggy trichomes to 1 mm long; stamens subequal, the filaments ca. 1.5 mm long, glabrous, the anthers 4.5–6 mm long, narrowly oblong to lanceolate, yellow, sparsely pubescent, sometimes one or more of the anthers connivent at the basal edges to the adjacent anther, poricidal at the tips, the pores obovate, dehiscing distally, not opening into longitudinal slits; pistil with glabrous ovary, the style 8–9 mm long, linear, straight to slightly curved, glabrous, the stigma oblong, decurrent down two sides. Fruit a berry, 5–12 mm long, 7–13 mm in diameter, globose to depressed globose, green when immature, orange to red at maturity, glabrous, lacking sclerotic granules. Seeds ca. 30 per fruit, 3–3.75 × 2–2.75 mm, flattened, slightly thickened on edges, circular to depressed ovate in outline, sometimes slightly notched on one side, the center orange to orange-brown, the rim yellow, the surface reticulum with densely arranged cells with wavy cell walls and shallow lumina.

Distribution and habitat:—*Lycianthes coloradensis* is endemic to Panama, originally in Bocas del Toro and Chiriquí provinces, now located in the Ngäbe-Buglé Comarca (Fig. 2), growing in lower montane rainforest, cloud forest, and disturbed primary forest, 1100–2200 m in elevation. Most specimens are from Cerro Colorado on the border of what was originally Bocas del Toro and Chiriquí provinces.

Phenology:—Specimens with flowers have been collected April and May; specimens with mature fruits have been collected March through November. The corollas on flowering specimens are usually closed, indicating that the corollas are not open for an extended time during the day.

Etymology:—This species is named after Cerro Colorado in Panama where this plant has been most heavily collected.

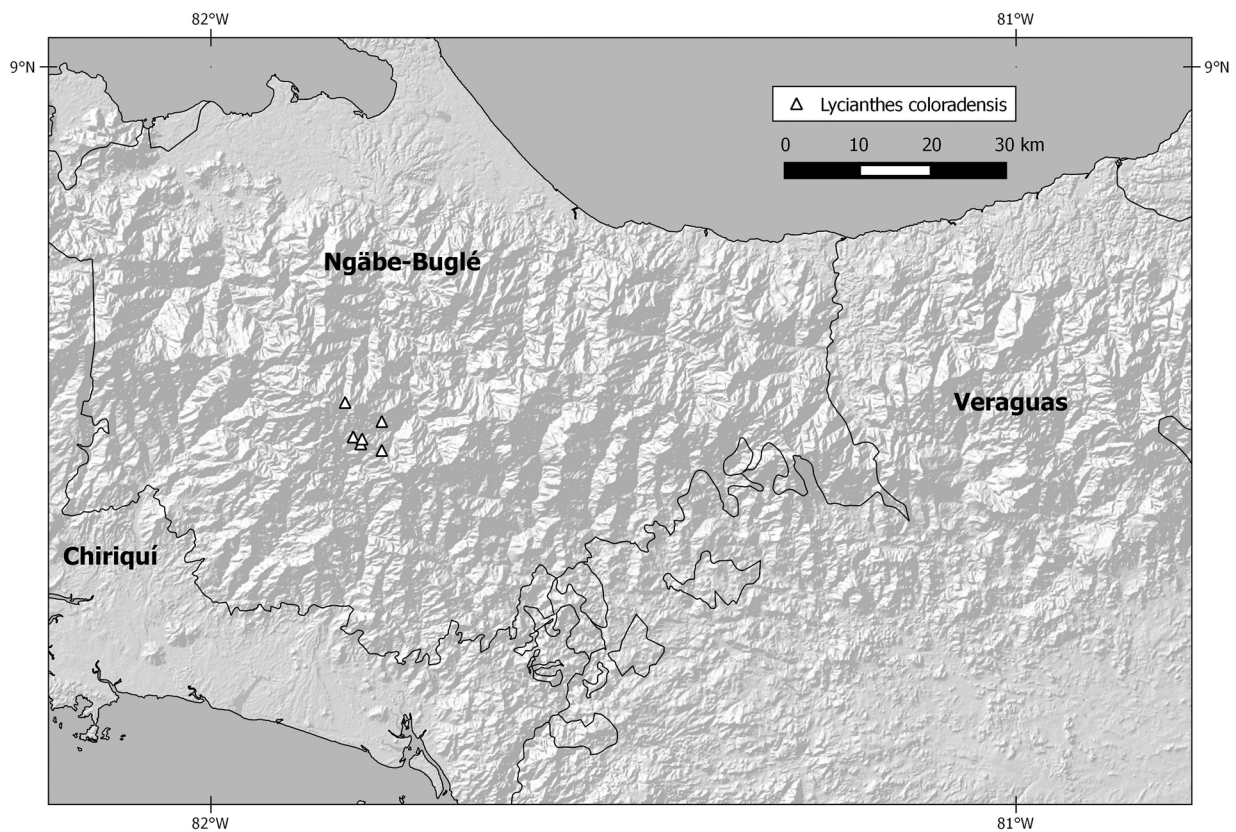


FIGURE 2. Map of the distribution of *Lycianthes coloradensis*.

Notes:—*Lycianthes coloradensis* is most similar to *L. purpusii* of Mexico, Guatemala, and Honduras. Both species are densely pubescent with yellow, orange or brown simple or long-stalked dendritic or multangulate-stellate trichomes, have relatively long pedicels, and entire corollas (Table 1). *Lycianthes coloradensis* differs from *L. purpusii* in usually having the rays of the stellate trichome rebranched (versus rarely rebranched), having much shorter appendages to 5.5 mm in flower (vs. to 17 mm long in flower), and having subequal stamens (vs. unequal) (Table 1). This species is also similar to *L. furcatistellata* of Costa Rica and Panama but differs in having denser pubescence and only having dendritic or multangulate-stellate trichomes on the adaxial leaf surface (vs. mostly simple trichomes in *L. furcatistellata*) (Table 1). It is somewhat similar to the Colombian species *L. dendriticothrix*, only known to the authors from the type material; it differs from that species in having equal stamens (vs. unequal) (Table 1) and coarser trichomes (vs. fine trichomes).

Representative Specimens Examined (paratypes):—PANAMA. Ngäbe-Buglé: Cerro Colorado, mining road 20 mi above bridge over Río San Félix, [8.5597,-81.7878], 2000 m 21 Nov 1979, *T. Antonio 2589* (MO acc. # 3695500); Cerro Colorado, 31.6 km beyond bridge over Río San Félix (10.6 km beyond turnoff to Escopeta), [8.5239,-81.7878], 1690 m, 15 Jul 1976, *Thomas B. Croat 37192* (MO acc. # 2474939); Cerro Colorado: 9.2 mi W of Chamé, along trail E of road which leads down to stream, 8°35'N, 81°50'W [8.5833,-81.8333], 1450–1480 m, 6 Jul 1988, *Thomas B. Croat 69035* (MO acc. # 3624096); N of San Félix at Chiriquí-Bocas del Toro border, on Cerro Colorado copper mine road along continental divide, [8.5406,-81.8233], 5000–5500 ft, 5 May 1975, *S. Mori 5917* (MO acc. # 3673785); Cerro Colorado. 50 km. N of San Félix on the continental divide, [8.5319,-81.8139], 1200–1500 m, 18 Aug 1975, *S. Mori 7870* (MO acc. # 6878822, MO acc. # 3673812); Cerro Colorado, 35.6 km. from Río San Félix bridge, [8.5381,-81.8122], 1690 m, 15 Jul 1976, *G. A. Sullivan 347* (MO acc. # 3698398).

TABLE 1. Comparison of the characteristics of *L. coloradensis* with those of similar species.

Species Name	<i>L. coloradensis</i>	<i>L. purpusii</i>	<i>L. dendriticothrix</i>	<i>L. furcatistellata</i>
Trichomes	Simple or long-stalked dendritically branched to multangulate-stellate, trichomes, the rays of the stellate trichomes often rebranched.	Simple or long-stalked dendritically branched to multangulate-stellate, trichomes, the rays of the stellate trichomes rarely rebranched.	Simple or long-stalked dendritically branched to multangulate-stellate, trichomes, the rays of the stellate trichomes often rebranched.	Simple or long-stalked dendritically branched (rarely multangulate-stellate), trichomes, the rays of the few stellate trichomes not rebranched.
Leaf trichomes	Leaf blades moderately to densely pubescent. The trichomes of the adaxial side rarely simple.	Leaf blades moderately to densely pubescent. The trichomes of the adaxial side rarely simple.	Leaf blades moderately to densely pubescent. The trichomes of the adaxial side rarely simple.	Leaf blades sparsely to moderately pubescent. The trichomes of the adaxial side often simple.
Pedicel length	17–41 mm long in flower, to 40 mm long (probably longer) in fruit.	(4) 8–20 (30) mm long in flower, to 30 mm long in fruit.	22–35 mm long in flower/ unknown in fruit.	15–45 mm long in flower, to 50 mm long in fruit.
Appendage length	2–5.5 mm long in flower, to 6 mm long in fruit.	7–17 mm long in flower, to 20 mm long in fruit.	4.5–8 mm long in flower, unknown in fruit.	1.75–5 mm long in flower, to 7 mm long in fruit.
Corolla	1.1–1.5 cm long, adaxially white, sometimes with green markings on the lobes at the base, glabrous, abaxially moderately pubescent on the lobes.	1.1–1.6 (2) cm long, adaxially white (sometimes reported as pale lilac or purple), glabrous, abaxially moderately pubescent on the lobes.	1–1.9 cm long, adaxially white, glabrous, abaxially sparsely to moderately pubescent on the lobes.	0.9–2.5 cm long, adaxially white to purple with darker purple markings on the lobes, often with a greenish spot at the lobe base, abaxially sparsely to moderately puberulent on the lobes.
Filaments	Subequal, ca. 1.5 mm long.	Unequal, four 1–1.5 mm long, one 4–5 mm long.	Unequal, four 1 mm long, one 4 mm long.	Equal or nearly so, 1–4 mm long.
Anthers	4.5–6 mm long, sometimes one or more of the anthers connivent at the basal edges to adjacent anther.	5–6 mm long, sometimes one or more of the anthers of the short stamens connivent at the edges to adjacent anther.	4–5 mm long, free of one another.	4–6 (7) mm long, free of one another.

Lycianthes fortunensis J. Poore & E. Dean (Fig. 3).—Type: PANAMA. [Ngäbe-Buglé]: Bocas del Toro region of Cerro Colorado, on trails from continental divide, 8°35'N, 81°45'W [8.583,-81.75], 1500 m, 12 Apr 1986, G. McPherson 8848 (holotype: DAV acc. #230777; isotypes: NY, MO acc. # 6866682)

Diagnosis. Endemic to Panama; similar to the widespread Central American species *Lycianthes multiflora* but differing in rounded flower bud tip (rather than pointed tip), elongated, scarious, and lobed calyx margin 0.5–2 mm long in flower (rather than short, non-scarious, non-lobed margin 0.25–0.5 mm long), and a lack of appendages (rather than usually having appendages 1–4 mm long).

Shrub to woody vine, sometimes epiphytic, to 5 m tall. Indument tan to pale yellow-orange, uniseriate, multicellular, sessile to short-stalked, multangulate-stellate, eglandular trichomes, the rays of the stellate trichomes sometimes crisped. Stems drying tan to brown when young, slightly to very compressed when dried, becoming brown and woody with age, moderately to densely pubescent with trichomes 0.1–0.2 (0.5) mm long, 0.25–0.75 mm in diameter, glabrate, with age; upper branching a mixture of dichasial and monochasial, not widely divaricate, the segments shallowing zigzagging, the upper sympodial units 1.6–13 cm long, 2–4 mm in diameter. Leaves of upper sympodia simple, rarely paired and unequal in size, the larger ones with blades 7.6–14.8 × 3.6–7.6 cm, the smaller ones with blades 4.0–9.6 × 2.3–4.4 cm, the leaf pairs similar in shape, the blades ovate to elliptic, chartaceous, sparsely to moderately pubescent with spreading trichomes similar to the stem but to 1 mm in diameter, the trichomes often sessile with the rays appressed to the plant surface, especially on the adaxial side, the trichomes denser on the veins of the abaxial side, the primary veins 3–5 on each side of the midvein, the base cuneate, rounded, or truncate, sometimes oblique, the margin entire, usually irregularly undulate, the apex acute to acuminate, the petioles 0.6–3 (5) cm long. Flowers in groups of 2–20, axillary, the inflorescence axes densely pubescent with sessile trichomes like those of the stem; peduncles usually present, to 3 mm long, or area of pedicel attachment raised into a pad with many attachment scars; pedicels (6) 9–17 mm long and erect in flower, (7) 11–26 mm long and erect in fruit; calyx 2–4 mm long, 3–5 (6) mm in diameter, campanulate, densely pubescent with sessile trichomes like those of the stem, the margin truncate, scarious in texture at the distal half, undulate or lobed, the appendages usually lacking (rarely with small bumps where the appendages would be; fruiting calyx enlarged, bowl shaped, 2–4 mm long, 6–8.5 mm in diameter, the appendages rarely to 0.5 mm



FIGURE 3. Scan of holotype of *Lycianthes fortunensis*. Image used with permission of the UC Davis Center for Plant Diversity.

long; corolla oriented horizontally, 0.8–1.6 cm long, rotate, entire, with abundant interpetalar tissue, adaxially white to light pink or tinged purple, glabrous, abaxially densely puberulent on the lobes, especially at the distal end, this more evident in bud; stamens unequal, the four short filaments 1–1.5 mm long, the one long filament 1.5–2 mm long, glabrous, the anthers 3.5–4 mm long, narrowly ovate to lanceolate, free from one another, yellow, sparsely pubescent on the inner face, poricidal at the tips, the pores ovate, dehiscent distally, not opening into longitudinal slits; pistil with glabrous ovary, the style 6–8 mm long, linear, straight to curved, glabrous, the stigma oblong, decurrent down two sides. Fruit a berry, 7–14 mm long, 8–19 mm in diameter, usually globose to depressed globose, red-orange when mature, glabrous to very slightly pubescent, lacking sclerotic granules. Seeds 45–85 per fruit, 2–3 × 2–3 mm, flattened, circular, triangular, or depressed ovate in outline, sometimes slightly notched, tan to yellow-orange in the center, the margin slightly thickened and of similar or darker color, the surface reticulum smooth to faintly patterned with densely arranged cells with wavy cell walls and shallow lumina.

Distribution and habitat.—*Lycianthes fortunensis* is endemic to Panama in Chiriquí and Veraguas provinces and the Ngäbe-Buglé Comarca (originally in Bocas del Toro Province) (Fig. 4), growing in cloud and premontane forests, often found on slopes or along roads and trails, 730–1645 m in elevation.

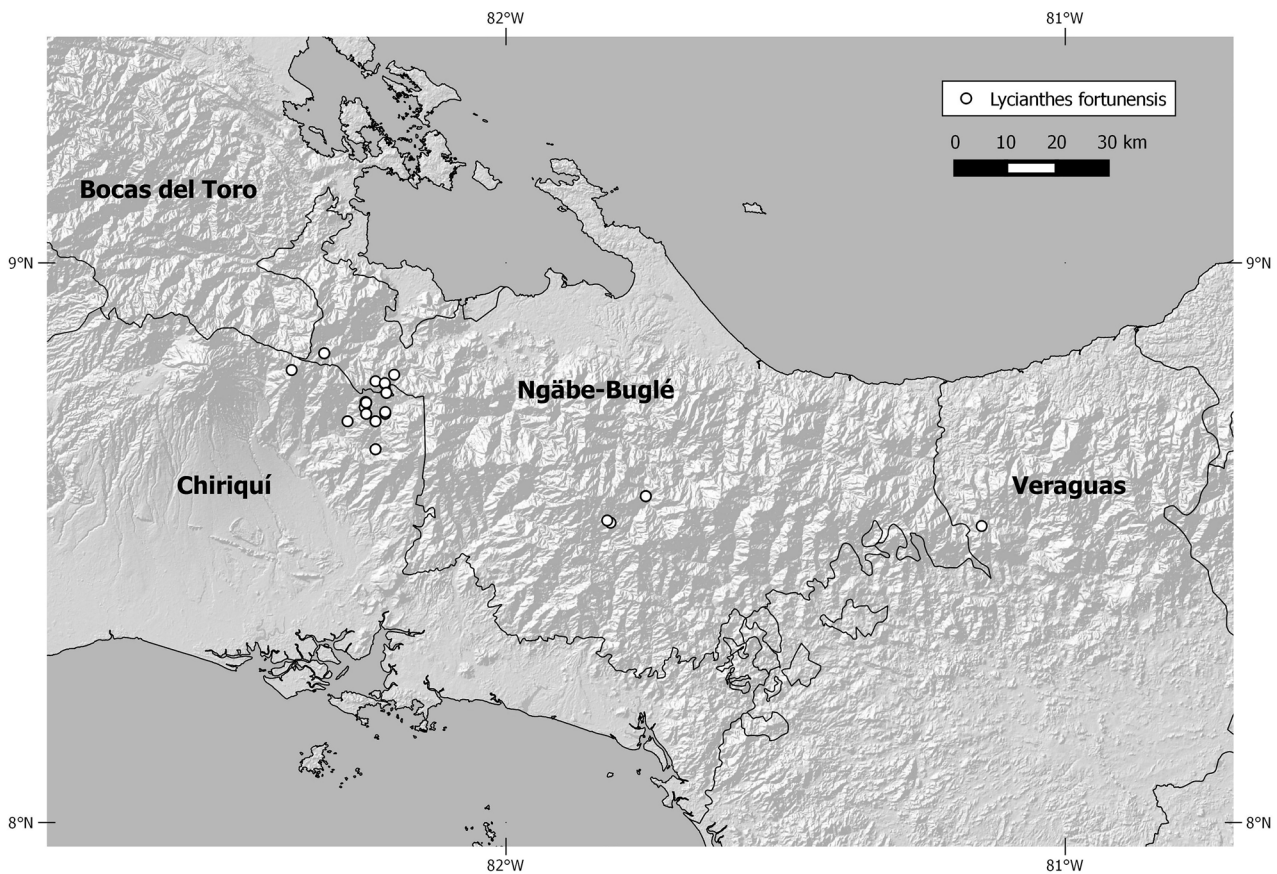


FIGURE 4. Map of the distribution of *Lycianthes fortunensis*.

Phenology.—Flowering specimens have been collected February through April; specimens with mature fruits have been collected January through September.

Etymology.—This species is named for the Fortuna Dam, and resulting Fortuna Reservoir, where this plant has been most frequently collected.

Notes.—*Lycianthes fortunensis* is closely related to *L. multiflora*, which is known from Belize, Nicaragua, Costa Rica, and Panama, and the two other members of the *L. multiflora* complex in Panama, *L. howardiana* and *L. porteriana*. All four species have similar pubescence of sessile to short-stalked multangulate-stellate trichomes with rays that are often crisped and that lie flat on the plant surface, especially on the leaves (Table 2). All four species also share having unequal stamens, a similar leaf shape (ovate to elliptic), and similar leaf texture (chartaceous to subcoriaceous). *Lycianthes fortunensis* differs from the other three in having round to oval flower buds with round tips (rather than conical buds with acute tips) and in lacking appendages (rather than having appendages that are usually

1–4 mm long [in *L. multiflora*] or even longer [to 11 mm in *L. porteriana*]). *Lycianthes fortunensis* also differs from *L. multiflora* and *L. howardiana* in having a prominent, scarious, often lobed calyx margin 0.5–2 mm long, a feature it shares with *L. porteriana* (Table 2).

TABLE 2. Comparison of characteristics of *L. fortunensis* with those of similar species.

Species Name	<i>L. fortunensis</i>	<i>L. multiflora</i>	<i>L. howardiana</i>	<i>L. porteriana</i>
Trichome type	Tan to pale yellow-orange sessile to short-stalked multangulate-stellate trichomes, the rays often appressed to the plant surface, the rays sometimes crisped.	White, grey, pale yellow, or yellow-orange sessile to short-stalked multangulate-stellate trichomes, the rays often appressed to the plant surface, the rays often crisped.	Pale yellow or yellow-orange sessile to stalked multangulate-stellate to geminate-stellate trichomes, the rays often appressed to the plant surface, the rays often crisped.	Light yellow to orange-brown sessile to stalked multangulate-stellate trichomes, the rays often appressed to the plant surface, the rays often crisped.
Bud shape	Buds oval to round, the apex rounded.	Buds conical, the apex acute.	Buds conical, the apex acute.	Buds conical, the apex acute.
Pedicle length	(6) 9–17 mm in flower, (7) 11–26 mm long in fruit.	5–15 mm in flower, to 20 mm in fruit.	5–10 mm in flower, to 15 mm in fruit.	5–15 mm in flower, to 20 mm in fruit.
Calyx margin	Prominent, 0.5–2 mm long, scarious, usually undulate or lobed to bilobed.	Not prominent, 0.25–0.5 mm long, not scarious, not undulate or lobed.	Somewhat prominent, 0.5–1 mm long, not scarious, not undulate or lobed.	Often prominent, 1–3 mm long, often scarious, usually undulate or lobed.
Appendage length	Absent to a very slight raised area in flower, absent or to 0.5 mm in fruit.	(0.5) 1–4 (6) mm long in flower, to 5 mm long in fruit. The appendages rarely lacking.	4–8 mm long in flower, to 12 mm long in fruit.	4–11 mm long in flower, not elongating in fruit.
Inflorescence in fruit	Leaves around the maturing fruits often missing, appearing like a terminal panicle.	Leaves around the maturing fruits often missing, appearing like a terminal panicle.	Leaves around the maturing fruits usually present, not appearing like a terminal panicle.	Leaves around the maturing fruits usually present, not appearing like a terminal panicle.
Corolla	0.8–1.6 cm long, adaxially white to light pink, sometimes tinged purple basally, abaxially densely pubescent on the lobes.	0.8–1.7 cm long, adaxially white to pale violet, abaxially sparsely to densely pubescent on the lobes.	1–2 cm long, adaxially white to lavender, abaxially densely pubescent on the lobes.	0.8–1.7 cm long, adaxially white, abaxially densely pubescent on the lobes.
Anther length	3.5–4 mm long	3–4 mm long	4–5 mm long	4.5–5 mm long
Seed shape	Flattened, circular, triangular or depressed ovate in outline sometimes notched.	Flattened, circular to depressed ovate, sometimes shallowly indented on one side.	Flattened, circular to depressed ovate, not indented on one side.	Seeds not seen.

Representative specimens examined (paratypes):—PANAMA. Chiriquí: NO del campamento de Fortuna (Hornito), sitio de presa, [8.74166,-82.25277], 1000–1200 m, 12 Aug 1976, *M. D. Correa* 2250 (MO acc. # 2792553); along road from Gualaca to Fortuna dam site, 5.9 mi NW of Los Planes de Hornito, 8°43'N, 82°17'W [8.71667,-82.28333], 1370 m, 9 Apr 1980, *T. B. Croat* 49867 (MO acc. # 2885507, NY); Gualaca-Chiriquí Grande, 5.5 mi NW of Los Planes de Hornito, 8°40'N, 82°14'W [8.6667,-82.2333], 1320 m, 29 Mar 1993, *T. B. Croat* 74908 (DAV acc. # 230351, MO acc. # 6866584, NY); between Palo Alto and near Cerro Pate Macho, above Río Palo Alto, NE of Boquete, [8.808333,-82.38333], 5400–7100 ft, 18 Mar 1979, *W. D'Arcy* 12661 (NY); Fortuna Dam area, above Gualaca, 8°45'N, 82°15'W [8.75,-82.25], 3400 ft, 30 Jul 1984, *W. G. D'Arcy* 15855 (DAV acc. # 230353, MO acc. # 3676764, MO acc. # 3695488); Fortuna Dam area, on Kaolin hill, just N of reservoir, [8.75,-82.25], 1100–1400 m, 31 Jul 1984, *W. G. D'Arcy* 15907 (MO acc. # 3695487, NY, MO acc. # 3676764); slope of hill above camp at Fortuna Dam site, [8.7333,-82.216], 1400–1500 m, 14 Sep 1977, *J. Folsom* 5468 (MO acc. # 2628652); Valle del Río Chiriquí, [8.73,-82.16], 24 Mar 1981, *I. Gordon* 194 (MO acc. # 3661098); La Fortuna hydroelectric project, behind camp, [8.730,-82.25], 1300–1400 m, 23 Mar 1978, *B. Hammel* 2238 (DAV acc. # 230774, MO acc. # 6866793, NY); forests behind Vivero Forestal de Boquete, 12 km N of Los Planes de Hornito, IRHE Fortuna Hydroelectric Project, 8°43'N, 82°14'W [8.71667,-82.23333], 1100–1200 m, 17 Jun 1982, *S. Knapp* 5552 (DAV acc. # 230773, MO acc. # 3695491, MO acc. # 6866688); Fortuna Dam area, 8°45'N, 82°15'W [8.75,-82.25], 1200 m, 11 Mar 1985, *G. McPherson* 6783 (DAV acc. # 230778, MO acc. # 6866681, NY); Fortuna Dam region, along Quebrada Arena near continental divide, 8°45'N, 82°15'W [8.75,-82.25], 1050 m, 9 Mar 1986, *G. McPherson* 8746 (DAV acc. # 230783, MO acc. # 3673807, MO acc. # 6878296); on gravel road branching N from main Fortuna Dam-Chiriquí Grande road, 1.1 miles from

junction, 8°47'18"N, 82°14'W [8.7883,-82.2333], 1200 m, 11 Mar 1985, *G. McPherson 6802* (DAV acc. # 230776, MO acc. # 6866685, NY); vicinity of Fortuna Dam, along trail across valley south of lake, 8°45'04"N, 82°15'04"W [8.751,-82.251], 1300–1400 m, 7 Feb 1987, *G. McPherson 10389* (DAV acc. # 230786, MO acc. # 3673800, MO acc. # 6866824); Bocas del Toro-Chiriquí border, Fortuna Dam region, along continental divide trail, 8°45'N, 82°15'W [8.75,-82.25], 1200 m, 16 Jan 1989, *G. McPherson 13551* (MO acc. # 5287728); **Ngäbe-Buglé**: Oleoducto Road, near Continental Divide, Fortuna Dam area, 8°48'N, 82°12'W [8.8,-82.2], 1000 m, 5 Feb 1984, *H. W. Churchill 4578* (MO acc. # 3282255); Cerro Colorado, top, Bocas Road, [8.53583,-81.81], 1500 m, 17–18 Feb 1977, *J. P. Folsom 1733* (MO acc. # 2605590); near headwaters of Río Culebra ca. 5 km ENE of Cerro Pate Macho, [8.8383,-82.325], 5000 ft, 11 Feb 1979, *B. Hammel 6121* (DAV acc. # 230781, MO acc. # 3661198, MO acc. # 5205011); Chiriquí/Bocas del Toro border, along continental divide on trail in Zona Protectora Palo Seco, 8°47.1'N, 82°13'W [8.7833,-82.21667], 1100–1300 m, 11 Aug 2000, *S. Knapp 9183* (MEXU acc. # 1167410, MO acc. # 5601511); Cerro Colorado, c. 12 miles from Camp Chami, 8°35'N, 81°45'W [8.5833,-81.75], 1400–1470 m, 20 Jun 1986, *G. McPherson 9543* (MO acc. # 3673809); Cerro Colorado, 7.2 miles from Camp Chami, Chamel, 8°35'N, 81°45'W [8.783333,-81.75], 1400–1470 m, 21 Jun 1986 *G. McPherson 9586* (DAV acc. # 230782, MO acc. # 3673808, MO acc. # 6866818); Bocas del Toro-Chiriquí border, Fortuna Dam region, on trail along continental divide, 8°46'03"N, 82°12'50"W [8.76750,-82.21389], 1250 m, 10 Mar 1988, *G. McPherson 12289* (DAV acc. # 230787, MO acc. # 3661211, MO acc. # 6866819); Cerro Colorado, 35.6 km. from Río San Félix bridge, [8.5399,-81.82], 1390 m, 15 Jul 1976, *G. A. Sullivan 374* (MO acc. # 3698399); **Veraguas**: along road between Escuela Agrícola and Alto Piedra (above Santa Fe) and Río Dos Bocas, ca 5–8 km from Escuela, [8.53,-81.14944], 730–770 m, 26 Jul 1974, *T. B. Croat 25911* (MO acc. # 3673764).

Lycianthes talamancensis E. Dean & J. Poore (Fig. 5).—Type: PANAMA. Bocas del Toro: Cordillera de Talamanca, 2–5 airline km NW of the peak of Cerro Ehandi on the Costa Rican-Panamanian international border. 9°04'N, 82°51'W [9.0667,-82.8500], 1 and 9 Mar 1984, *G. Davidse 25487* (holotype: MO acc. # 3661181; isotype: MO acc. #6866840)

Diagnosis. Endemic to Panama; closely related to *Lycianthes hortulana* of Honduras, El Salvador, and Nicaragua but differing in having much longer pedicels, 15–22 mm long in flower and 27–35 mm long in fruit (rather than 3–9 mm long in flower and 5–13 mm long in fruit), an entire corolla that is moderately pubescent on the adaxial lobes (rather than shallowly stellate corolla with glabrous adaxial lobes), and longer stamen filaments, 1–2 mm long (rather than 0.5 mm long).

Climbing vine or liana (height not given on any of the specimens). Indument of tan to yellow-orange, uniseriate, multicellular, usually long-stalked, eglandular, multangulate-stellate, spreading trichomes, the primary rays usually 3–6 per whorl, often rebranched, Stems green to light brown when young, slightly to not compressed upon drying, becoming woody with age, densely pubescent with trichomes 0.2–0.5 mm long, 0.5–1.0 mm in diameter; upper sympodial branching points dichasial or monochasial, the branching widely divaricate, the segments shallowly zigzagging to twining, the upper sympodial stem units 2.5–11.3 cm long, 2–4 mm in diameter. Leaves of upper sympodia simple, rarely geminate, the smaller leaf of the pair sometimes not developing, or abscising early, the larger ones with blades 4.5–14 × 3.0–8.6 cm, the smaller ones with blades 3.5–7.7 × 2.1–4.3 cm, the leaf pairs similar in shape, the blades ovate to elliptic, chartaceous, moderately to densely pubescent with trichomes similar to the stem but sessile to short stalked, the pubescence usually denser on the abaxial side of the blade, the primary veins 3–5 on each side of the midvein, the base rounded to truncate, sometimes oblique, the margin entire, usually irregularly undulate, the apex acute to acuminate, the petioles 0.6–3.9 cm long. Flowers in groups of 1–6 (10), axillary, the inflorescence axes densely pubescent with spreading trichomes like that of the stem; peduncles absent; pedicels 15–22 mm long and erect to arching in flower, to 27–35 mm and erect to arching in fruit; calyx 2.5–4 mm long, 4–5 mm in diameter, campanulate, moderately to densely pubescent with spreading trichomes like those of the stem to 0.7 mm in diameter, the margin truncate, the 10 appendages 0.75–3 mm long emerging 0.5–1.0 mm below the prominent, scarious calyx rim; fruiting calyx enlarged, bowl-shaped to rotate, 2–4.5 mm long, 5–9 mm in diameter, the appendages to 4 mm; corolla oriented horizontally, 1–1.8 cm long, campanulate (or not fully open on specimens), entire, with abundant interpetalar tissue, adaxially light violet to purple with center of lobes darker and moderately puberulent, abaxially moderately puberulent on the lobes especially at the distal end, this more evident in bud; stamens equal, the filaments 1–2 mm long, glabrous, the anthers 4–4.5 mm long, narrowly ovate to lanceolate, free from one another, yellow, sparsely pubescent on the inner face, poricidal at the tips, the pores ovate, terminal, dehiscing distally, not opening into longitudinal slits; pistil with glabrous ovary, the style 6–8 mm long, linear, straight to curved, glabrous; stigma truncate,



FIGURE 5. Scan of holotype of *Lycianthes talamancensis*. Image used with permission of the Missouri Botanical Garden Herbarium.

slightly bilobed. Fruit a berry, 7–9 mm long, 6–9 mm in diameter, usually globose to depressed globose, green when immature, color unknown, glabrous to very slightly pubescent, lacking sclerotic granules. Seeds 30–35 per fruit, 3–3.5 × 2.2–2.5 mm, flattened, usually reniform with 0.5–1.0 mm notch on one side, depressed ovate in outline, yellow to orange-brown, the seed margin rougher texture and of similar or lighter color, the surface reticulum with faint pattern formed by densely arranged cells with wavy cell walls and shallow lumina.

Distribution and habitat:—*Lycianthes tamamancesis* is endemic to Panama in Bocas del Toro and Chiriquí provinces (Fig. 6), growing in cloud forest and wet forest, with *Quercus*, *Podocarpus*, *Magnolia*, *Symplocos*, and *Chusquea* understory, 2200–2850 m in elevation.

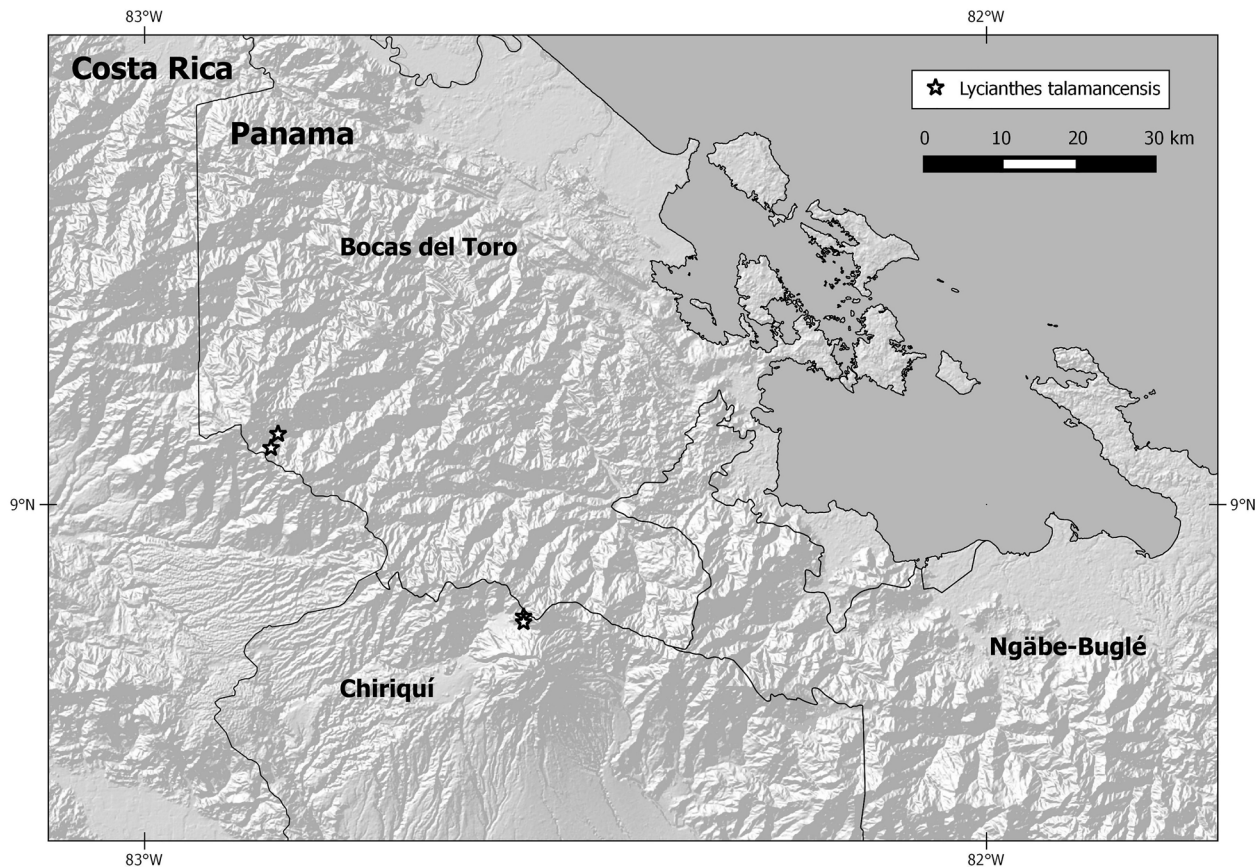


FIGURE 6. Map of the distribution of *Lycianthes tamamancesis*.

Phenology:—Flowering specimens have been collected January through March; specimens with nearly mature fruits (still green, but seeds nearly mature) have been collected January through March.

Etymology:—This species is named after the Cordillera de Talamanca where Senior Missouri Botanical Garden Botanist Gerrit Davidse collected the type specimen.

Notes:—*Lycianthes tamamancesis* is closely related to *L. hortulana*, originally described from the cloud forests of Honduras, and *L. breedlovei*, which occurs in the cloud forests of Chiapas, Mexico. All three species are densely pubescent with stalked, multangulate-stellate trichomes with rebranched rays, have widely divaricate branching, and have seeds that are usually notched on one side (Table 3). *Lycianthes tamamancesis* differs from the other two species in having longer pedicels, 15–22 mm long in flower, 27–35 mm long in fruit (rather than to 9 mm in flower and 13 mm in fruit in *L. hortulana* and to 16 mm long in flower and 25 mm long in fruit in *L. breedlovei*) and entire corollas that are moderately pubescent on the adaxial side (rather than stellate corollas that are glabrous or nearly so in the other two species). We also compared this new species to the common *L. multiflora*, which also occurs in Panama; it differs from this species in trichome type and many other features (Table 3).

Representative specimens examined (paratypes):—**PANAMA. Bocas del Toro:** Cordillera de Talamanca, 6 airline km NW of the peak of Cerro Echandi on the Costa Rican-Panamanian international border, 9°05'N, 82°50'30"W [9.0833, -82.8417], 2450–2600 m, 2–3 Mar 1984, *G. Davidse 25167* (DAV acc. # 230775, MO acc. # 6866842, MO acc. # 3661184, MO acc. # 6866841); **Chiriquí:** Distrito Bugada, Cerro Punta, from STRI house to nearby ridge.

[8.86,-82.55], 2200 m, 25 Jan 1984, *H. Van der Werff* 6366 (MO acc. # 3661117); Distrito Bugada, Cerro Punta, along ridge to watershed to Bocas del Toro, 8°52'N, 82°33'W [8.8667,-82.55], 2200 m, 26 Jan 1984, *H. Van der Werff* 6485 (MEXU acc. # 1356972).

TABLE 3. Comparison of characteristics of *L. talamancensis* with those of similar species.

Species Name	<i>L. talamancensis</i>	<i>L. hortulana</i>	<i>L. breedlovei</i>	<i>L. multiflora</i>
Upper branch characteristics	Dichasial branching widely divaricate, the segments shallowly zigzagging.	Dichasial branching widely divaricate, the segments shallowly zigzagging.	Dichasial branching widely divaricate, the segments shallowly zigzagging.	Dichasial branching not widely divaricate.
Trichome type	Long-stalked, multangulate-stellate trichomes, the straight rays often rebranched.	Stalked, multangulate-stellate trichomes, the straight rays usually rebranched.	Stalked, multangulate-stellate trichomes, the straight rays usually rebranched, sometimes several times.	Sessile to short-stalked, multangulate-stellate trichomes, the rays often crisped, not rebranched.
Pedicle length	15–22 mm long in flower, 27–35 mm long in fruit, erect to arching in both flower and fruit.	3–9 mm long in flower, 5–13 mm long in fruit, erect in both flower and fruit.	9–16 mm long in flower, 10–25 mm long in fruit, erect in both flower and fruit.	5–15 mm long in flower, up to 20 mm long in fruit, erect to arching in both flower and fruit.
Appendage length	0.75–3 mm long in flower, up to 4 mm long in fruit.	1–2 mm long in flower, 2–2.5 mm long in fruit.	1–3 mm in flower, 2–3 mm long in fruit.	(0.5) 1–4 (6) mm in flower, up to 5 mm long in fruit.
Corolla	1.0–1.8 cm long, entire, adaxially light violet to purple, the lobes with darker purple stripes and moderate pubescence, abaxially moderately puberulent.	0.6–1 cm long, shallowly stellate, adaxially white to lilac, the lobes with darker purple stripes and no pubescence, abaxially moderately puberulent.	0.9–1.5 cm long, shallowly stellate, adaxially white to lilac, the lobes with darker purple stripes and just a few scattered trichomes, abaxially usually densely puberulent.	0.8–1.7 cm long, entire, adaxially white to pale violet and glabrous, abaxially sparsely to densely puberulent.
Filaments	Equal, 1–2 mm long.	Equal, 0.5 mm long.	Slightly unequal, four 0.5–1 mm, one 1–2 mm long.	Unequal, four 0.5–1 mm long, one 1.5–2 mm long.
Anthers	4–4.5 mm long, narrowly ovate to lanceolate.	2.5–4 mm long, elliptic.	3–4 mm long, elliptic.	3–4 mm long, elliptic to lanceolate.
Seeds	Flattened, reniform to depressed ovate, usually with 0.5–1.0 mm notch on one side.	Flattened, reniform to depressed ovate, usually with small notch on one side.	Flattened, reniform to depressed ovate, usually with small notch on one side.	Flattened, round to depressed ovate, sometimes shallowly indented on one side, but not notched.

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