Phaseolus costaricensis, a New Wild Bean Species (Phaseolinae, Leguminosae) from Costa Rica and Panama, Central America

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ABSTRACT. During a review of *Phaseolus* undertaken by the senior author to clarify the variability of the *P. coccineus* L. species complex, a few herbarium specimens of what appeared to be a new species from Costa Rica and Panama were encountered. Subsequent field collecting by the junior author confirmed this opinion, and the new taxon is hereby named and described. Its probable relationships and the part it may have played in the early evolution of the economically important pulses such as the common bean, scarlet runner bean, and "polyanthus" bean are discussed.

As a result of an in-depth review of the genus *Phaseolus*, originally begun by the senior author to clarify the variability of the *P. coccineus* L. species complex, and the fieldwork subsequently carried out by the junior author (Debouck et al., 1989), a large vining wild bean growing in the montane forests of Costa Rica appears to be new to science. As described and discussed below, it shares many morphological traits with wild *P. vulgaris* L. and wild *P. dumosus* Macfadyen (= *P. polyanthus* Greenman; see Schmit & Debouck, 1991, for discussion) and will therefore be grouped with these two species to form the section *Phaseolus* in a monograph currently in preparation.

Phaseolus costaricensis Freytag & Debouck, sp. nov. TYPE: Costa Rica. Provincia de San José: San Isidro El General, 3 km SE de Copey, orillas del Río Pedregosa, 9°37′N, 83°55′W, 1800–2080 m, 14 Jan. 1987, *Debouck, Araya Villalobos, Ocampo Sánchez & González Ugalde 2135* (holotype, US; isotypes, BR, CR, UC). Figures 1–4.

Species *P. dumoso* maxime similis, sed bracteolis saepe ovatis, floribus puniceis alis amplectibus et legumine adulto recto 10 cm longo helvo-alutaceo tomentoso differt. Occurrit in sylvis udis pinetis nebulosisque Costa Ricae et Panamae.

Seedling large from epigeal germination, the hypocotyl 1.7 cm long, the epicotyl 2.2 cm long, the stipules united; next internode very long to 12 cm or more; primary leaves opposite, simple, the petiole 3 cm long, stipels present, the blade broadly rounded-ovate, 8 cm long, 7.5 cm wide near the base, the base auriculate, the tip acuminate and not apiculate, membranous, nearly glabrous. *Root* fibrous, extensive, not penetrating deeply into soil. *Plant* a perennial, woody, large, shrubby vine; stems stout, terete, striate-angled, 3–4 mm diam., corky and knobby on basal portions, reflexed pubescent with short and long, fine, strigose, hispid and uncinate, whitish hairs, younger stems densely short white reflexed strigose; internodes 12–16 cm long; stipules triangular-lanceolate, 6 mm long, 3 mm wide, 5- to 7-nerved, acute, thin, sparsely brownish strigose. *Leaves* medium to large, trifoliolate, including the first true leaf on main stem; petioles stout, rounded canaliculate, 2.5–8–16 (smallest–mode–largest) cm long, tawny-villous to hirtellous; rachises 5.5 cm long; stipels 6 mm long, 2.5 mm wide, the lower triangular-ovate, 8- to 10-nerved, acute, the upper oblong-linear, slightly falcate, 5 mm long, 1–1.5 mm wide; pulvini 5–6 mm long, densely yellowish to tawny brown and long strigose; terminal leaflets broadly ovate to oblong-ovate, 4–7–11 cm long, 4.5–12 cm wide at about ⅓ from base, nearly obtuse to short acute, apiculate, the main veins prominently whitish below, secondary veins inconspicuous, upper surface sparsely pubescent, below sparsely to densely yellow strigose to nearly tomentose; lateral leaflets similar and slightly inequilateral. *Inflorescence* a very long raceme, 10–38–87 cm long, much ex-

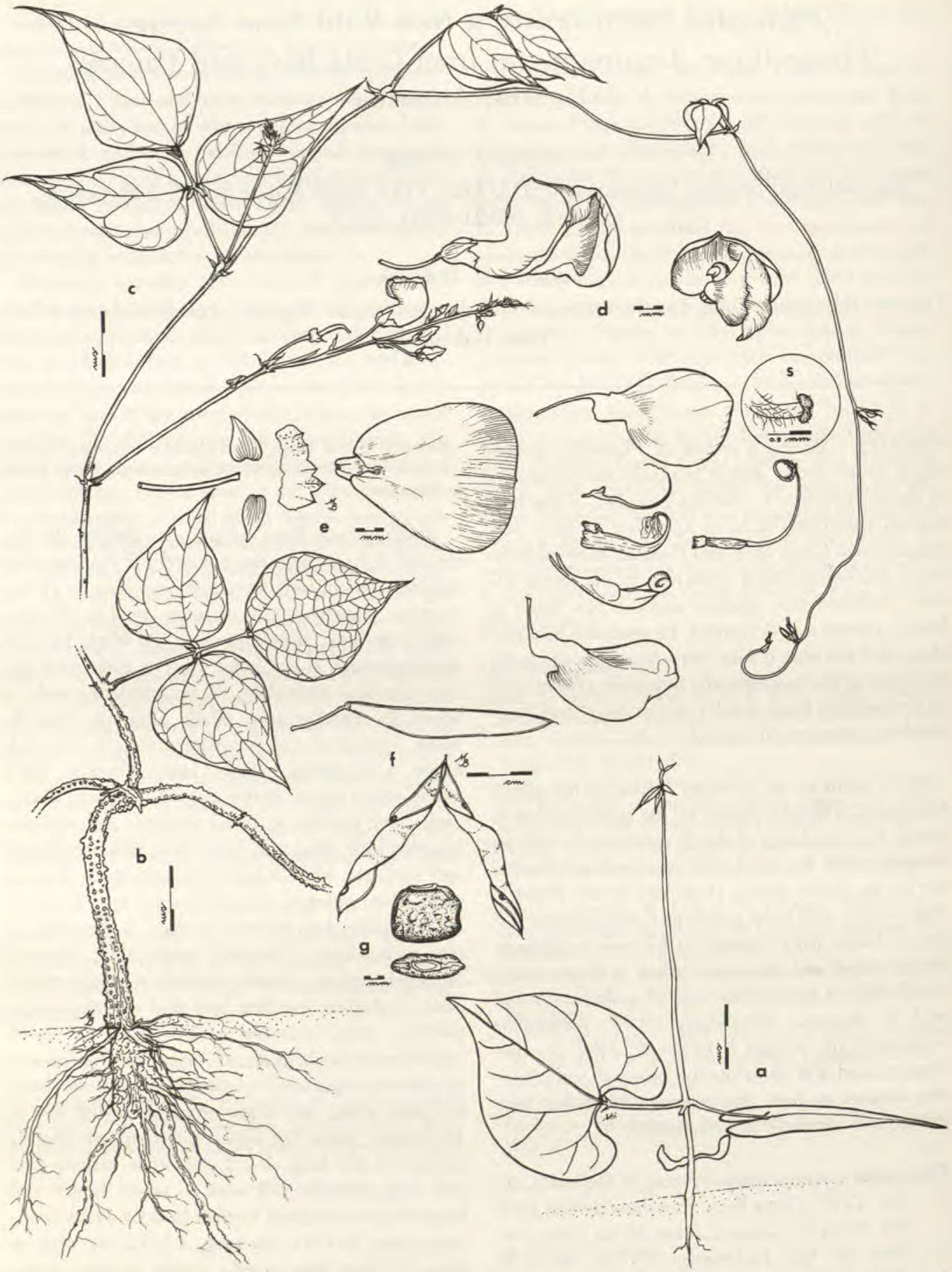
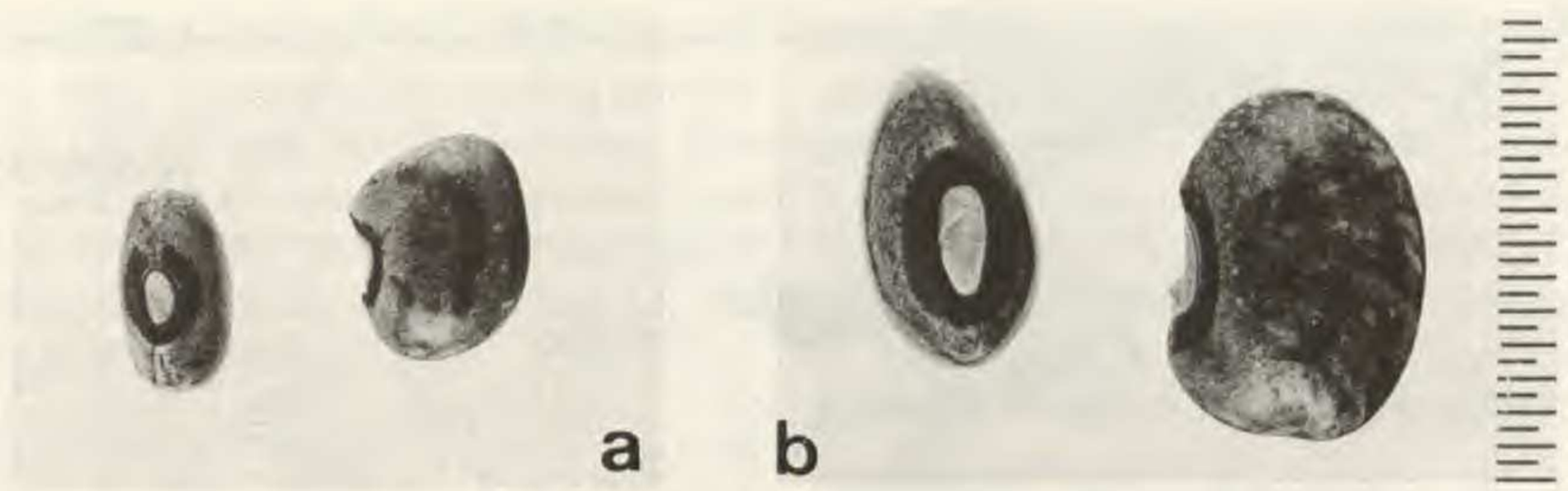


Figure 1. *Phaseolus costaricensis* Freytag & Debouck. —a. Seedling. —b. Lower stem and root. —c. Habit. —d. Flower, front view. —e. Dissected flower: s, view of stigma. —f. Green and dry mature pod. —g. Seed: lateral view and view from hilum. All drawings are from plants grown in the greenhouse at USDA-TARS, Mayagüez, Puerto Rico, of seed from the type collection (*Debouck et al. 2135*) from near Copey, San Isidro El General, San José, Costa Rica, except f and g, which are from the paratype collection *Debouck et al. 2128* from near Herradura, San Isidro El General, San José, Costa Rica.



Figures 2, 3. —2 (top). Close-ups of seeds in lateral views and views from hilum of: —a. *P. costaricensis* (*Debouck et al. 2132*) from Providencia, San Isidro El General, San José, Costa Rica. —b. *P. vulgaris* (*Debouck et al. 2097*), from Tabarca, San José, Costa Rica. —c. *P. dumosus* (*Debouck & Soto 1631*) from Panajachel, Sololá, Guatemala. —d. *P. coccineus* (*Debouck & Vásquez 2437*) from Miramundo, Jalapa, Guatemala. Scale given in millimeters. —3 (bottom). *Phaseolus costaricensis* in its natural habitat: *Debouck & Araya Villalobos 2093*, found close to the Cuesta Chinchilla, Cot, Cartago, Costa Rica. Arrows mark the showy deep fuchsia blossoms and pods.

ceeding leaves; peduncle 11–18–41 cm long; rachis stout, 3–15–46 cm long, hirtellous with tawny hairs, glabrate below with many flowering nodes to 30 or more spaced 2–5–30 mm apart on axis; primary bracts broadly rounded to ovate-lanceolate, 5–12 mm long, 1.5–8 mm wide, 3- to 12-nerved, acute, thin to hyaline, heavily white strigose below, glabrous within, somewhat persistent; pedicel stout, 6–7 mm long, becoming 16–18 mm long at mature pod, sparsely minute white uncinate. *Bracteoles* of-

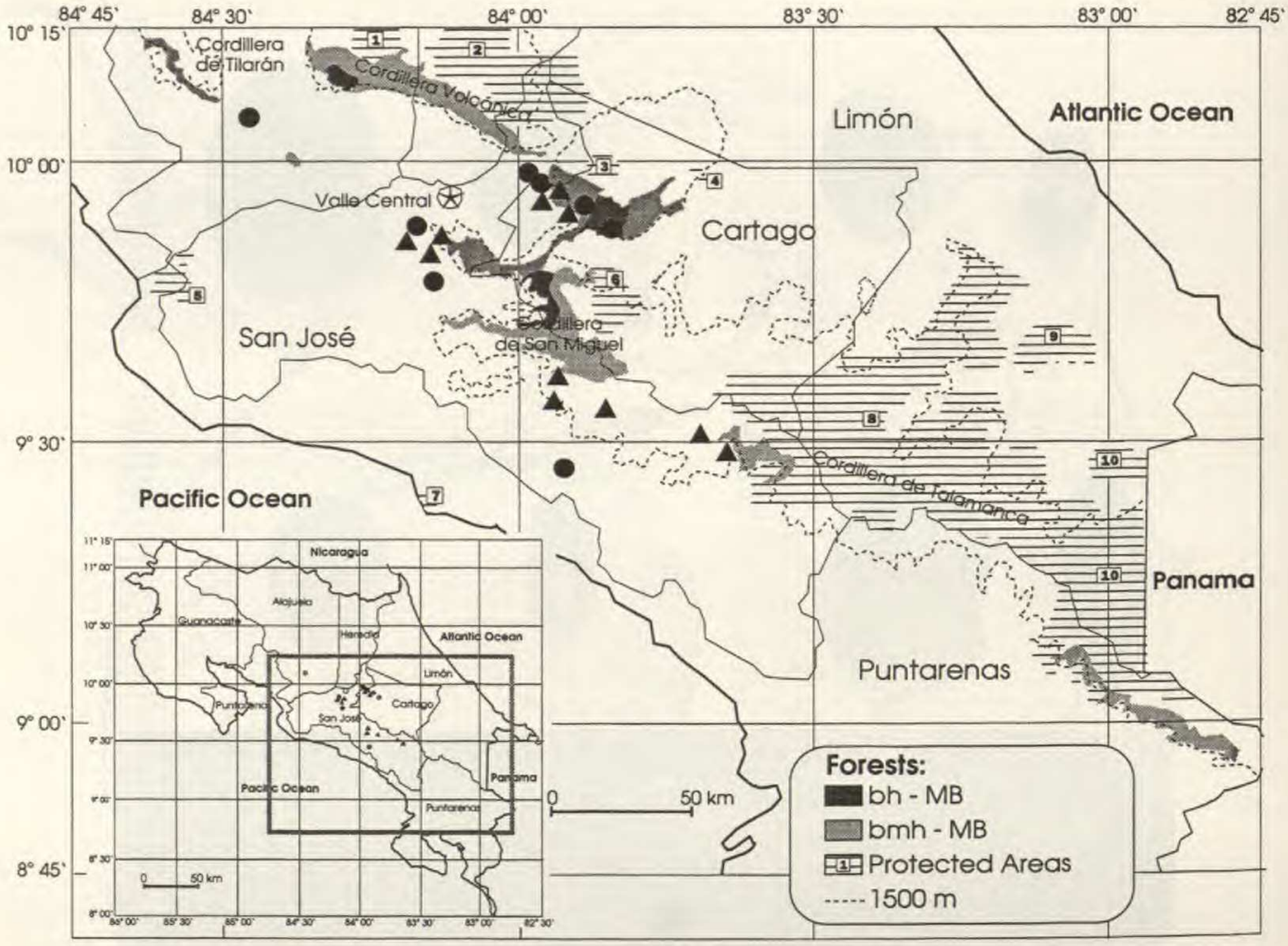


Figure 4. Distribution map for *Phaseolus costaricensis* in Costa Rica. Round spots correspond to herbarium voucher specimens, while triangles correspond to germ plasm collections (including herbarium specimens). The star refers to the capital city of San José. Dark shaded areas correspond to remnants of vegetation type "Bosque húmedo" (bh-MB), while light shaded areas correspond to the wetter variant "Bosque muy húmedo" (bmh-MB), both in the Montano Bajo domain (after the map by Tosi, 1969). Horizontally lined areas refer to protected areas, as follows: —1. Parque Nacional Volcán Poás. —2. Parque Nacional Braulio Carrillo. —3. Parque Nacional Volcán Irazú. —4. Monumento Nacional Guayabo. —5. Reserva Biológica Carara. —6. Refugio Nacional de Fauna Silvestre Tapantí. —7. Parque Nacional Manuel Antonio. —8. Parque Nacional Chirripó. —9. Reserva Biológica Hitoy Cereré. —10. Parque Nacional La Amistad. (After map published by Editorial Heliconia, Anonymous, 1987.)

ten rounded ovate to elongate-acuminate to linear, 5–8–9 mm long, 2.5–4–8 mm wide, acuminate, sparsely white hirsute to strigose on outside, glabrous within, purplish. *Flower* large, dark pink or lilac to purple, very numerous, in racemes of 2–5; calyx campanulate, 5–6 mm long, with a small knob at base, pubescent, the two upper lobes united into one emarginate scarcely developed, 1 mm long, 6 mm wide, the 3 lower lobes subequal, dentate-acute, 2 mm long, 2.5 mm wide, the center one slightly longer, sparsely weak, white, short strigose, the mouth of the calyx oblique; standard dark pink or lilac to purple, broadly rounded-obovate, cupped, 18 mm long, 14–15 mm wide, emarginate, reflexed, 8 mm to bend, somewhat thickened at flexure, lateral edges recurved with a spur at lower edge 1 mm long, claw poorly developed, 0.5 mm long, auricles 3 mm long, 2 mm wide and nectariferous, inserted 3–4 mm from base; wings lilac to purple, broadly rounded, cupped and clasping, unequal, spreading laterally, 23 mm long, claw 6–8 mm long, 0.5 mm wide, blade 13–16 mm long, 10–11 mm wide, spur well developed, nearly round, 1.5–2.5 mm long; keel tubular, straight, claws divided 4 mm, 5 mm more to flexure and 6 mm more to terminal 1¾ tight coils of 3.5 mm diam.; vexillary stamen claw 1.5 mm long to geniculate knob developed into a thin sheath 2 mm long, 1.5 mm wide, the thickened portion 7 mm long to filament; stamen tube straight, ridges not developed; basal collar 1.5–2 mm long, denticulate; ovary straight, 10 mm long covered by fine white pubescence, 6 or fewer ovules; style 10–12 mm long with a terminal thickened coil 3 mm diam.; stigma terminal, capitate, 0.75 mm long. *Pod* when young, straight, flat, broad, about 3 times longer than broad, yellow-brown tomentose, becoming sparsely strigose; the mature pods straight, 10 cm long, 13 mm wide, 7–

10 mm thick; beak strong, 7 mm long, recurved; 4–6 seeds. *Seeds* squarish ovate, rounded and flattened, 10–11.6 mm long, 8.3–9.4 mm wide, 3.8–5.1 mm thick, brown and black speckled and streaked on brown and tan, a black ring around hilum; hilum oblong oval, 4.2 mm long, 1.8 mm wide; lens medium raised.

Geographic distribution. This species seems to be restricted to remnants of the humid (bh-MB) and rain (bmh-MB) montane forests in the mountainous ranges of the Cordillera de San Miguel and Cordillera de Talamanca of Costa Rica (Provinces of Alajuela, Cartago, and San José), and extending into the slopes of volcanoes Chiriquí and Barú in the Macizo Volcánico de Chiriquí in the provinces of Boquete and Chiriquí of western Panama (see Fig. 4).

Ecology. The large vines of up to 3–6 m long are often climbing and sprawling over shrubs (*Dahlia,* Compositae, Solanaceae) and trees, and are found in sunny openings in humid montane forest (*Alnus, Erythrina*) and montane rainforest with bamboo and numerous epiphytes (ferns, orchids, aralias, and bromeliads) (see Fig. 3). These habitats correspond to "Vegetación de las tierras frías," according to Gómez Pignataro (1986), and to "Bosque muy húmedo premontano" and "Bosque húmedo montano bajo," according to Bolaños and Watson (1993), with a dry season of about 2–4 months.

Phaseolus costaricensis is rarely found with *P. dumosus* (*Debouck et al. 2121*), *P. xanthotrichus* Piper (*Debouck & Villalobos 2101*), and *P. tuerckheimii* Donnell-Smith (*Debouck et al. 2125, Debouck et al. 2129*). It is most frequent and abundant in relatively undisturbed habitats and inaccessible areas, at 1400–2100 m, the majority being found at 1600–1800 m, often abundant on steep slopes, and rarely found in disturbed cut-over or burnt-over areas, coffee plantations, or pastures. It is found growing on dark brown soils derived from lavas, volcanic ash, or metamorphic schists, with high organic content and rocky, very moist soils often near streams or riversides. We have found damage by angular leaf spot, anthracnose, lacebugs, thrips, and weevils.

Although some populations might be included in the protected areas "Parque Nacional Chirripó" and "Parque Nacional La Amistad" (see Fig. 4), most will not, since the ecology of *P. costaricensis* matches with zones of most human settlements in Costa Rica with pastures, coffee, and flowers for export, where most deforestation has occurred (Boucher et al., 1983; Sader & Joyce, 1988).

Ethnobotany and common names. Phaseolus costaricensis apparently is not eaten, but is known by rural inhabitants under the names "frijol de montaña" (around Cot, Provincia de Cartago, Costa Rica) and "cubá de venado" (south of Alajuelita). It is to be noted that the name "cubá" is generally used in Costa Rica for cultivated varieties of both *P. coccineus* L. (D. G. Debouck, pers. obs., 1987; P. C. Standley, 1937) and *P. dumosus* Macfadyen (G. F. Freytag, pers. obs., 1969).

Discussion. This species is named in honor of Costa Rica, the country in which it is most widely distributed.

Because of its strong climbing, perennial habit, gross morphology, allogamy, and its very showy inflorescences, *Phaseolus costaricensis* has often been confused with *P. coccineus,* namely in the *Flora of Panama* (Lackey & D'Arcy, 1980) and in the last taxonomic treatment of that group (under *P. coccineus* subsp. *formosus* (Kunth) Maréchal, Mascherpa & Stainier (in Delgado Salinas, 1988)), from which it differs by the dark pink or fuchsia flower color, the large and long primary bracts, the ovate bracteoles, the epigeal germination and fibrous roots, and by a basic difference in inflorescence type. The inflorescence type of most *Phaseolus* species is that of a reduced raceme (pseudoraceme)—similar to most Phaseoleae as pointed out by Lackey (1981) and Debouck (1983) and as is the case with *P. dumosus* and *P. coccineus.* However, *P. costaricensis* often seems to produce a raceme or panicle with several to many lower lateral branches, especially on the larger inflorescences, similar to some populations of *P. lunatus* L., *P. maculatus* Scheele, *P. polystachyus* (L.) Britton, Sterns & Pogg, and other related, more or less woody *Phaseolus* species. Many of these traits may be difficult to evaluate on herbarium specimens of incomplete vegetative and flowering material. *Phaseolus costaricensis* has also been confused with *P. tuerckheimii* Donnell-Smith, an identification given on some herbarium specimens, from which it differs by having much less tawny pubescence; large, long and broad bracts and bracteoles; differences in details of flower structure, especially the considerably larger standard and wings; and in having longer and wider pods with 4–6 seeds.

Results from cpDNA analysis confirm the placement of *Phaseolus costaricensis* close to *P. vulgaris* and *P. dumosus,* perhaps in the same section as the latter two taxa, since *P. costaricensis* shares several cpDNA polymorphisms with them (Schmit et al., 1993). In this study, *P. costaricensis* was located in the same group as a wild common bean of Chiquimula, Guatemala, and two weedy forms of *P. dumosus* of Cauca, Colombia; the wild ancestral form

of *P. dumosus* fell in another close group, together with a wild common bean population of Chimborazo, Ecuador. It has been shown recently (Kami et al., 1995) that the wild common bean populations of southern Ecuador and northern Peru are close to the ancestral lineage of *P. vulgaris* prior to its separation into the two major gene pools (Gepts, 1988; Khairallah et al., 1992).

Phaseolus costaricensis crosses naturally with *P. dumosus* in the field (D. G. Debouck, pers. obs., 1987), though very rarely, since *P. dumosus* is an introduced plant in Costa Rica and can also be crossed with *P. vulgaris* (H. Bannerot, pers. comm., 1989), in both cases as pollen parent. It may be that flower structure, similar in *P. dumosus* and *P. costaricensis* except for the spreading wings of the former and the nearly vertical, clasping wings of the latter (similar to those of *P. coccineus*), and the highly nectariferous standards (also found in *P. coccineus* and *P. striatus* Brandegee) are responsible in large part for the attraction of pollinators. Field observations show *P. costaricensis* is visited by hummingbirds and carpenter bees.

The following specimen was determined by the collectors to be an obvious hybrid, probably with *P. dumosus*, found at the same location: COSTA RICA. **San José:** al pie de la Piedra de Aserrí, 1.5 km E de Aserrí, 9°52′N, 84°7′W, 1560 m, 11 Jan. 1987, *Debouck et al. 2114* (US).

Evidence has been presented elsewhere (Llaca et al., 1994; Schmit et al., 1993) about a proposed origin for *Phaseolus dumosus* that would have a cpDNA genome similar to the one of *P. vulgaris*, and a nuclear genome similar to the one of *P. coccineus*. Although different, the mtDNA genome of *P. dumosus* would be closer to that of *P. vulgaris* than that of *P. coccineus* (Hervieu et al., 1994). It is still premature to conclude that *P. costaricensis* is the cytoplasm donor parent to *P. dumosus*, but there is little doubt that the present novel species should be included in any further phylogenetic study including the three bean cultigens *P. vulgaris*, *P. coccineus*, and *P. dumosus*.

Paratypes. COSTA RICA. **Alajuela:** Tres Ríos and Ochomogo, vicinity of San Ramón, Dec. 1912, *Brenes 18* (GH). **Cartago:** Cot, Cuesta Chinchilla, 1.2 km SW de Cot (también en barranco del Río Páez cerca de Cot), 9°54′N, 83°53′W, 1650 m, 7 Jan. 1987, *Debouck et al. 2093* (BR, CR, US); Tres Ríos, Cerro de la Carpintera, 2 km S de San Vicente, 3 km SE de Tres Ríos, 9°53′N, 83°58′W, 1600 m, 11 Jan. 1987, *Debouck et al. 2118* (CR, US); Tres Ríos, cerca de la planta eléctrica María del Rosario, 3 km NE de Dulce Nombre, 9°57′N, 83°57′W, 1750 m, 11 Jan. 1987, *Debouck et al. 2119* (BR, CR, MICH, US); N of Cartago, Río Reventado, 1950 m, 11 Dec. 1984, *Khan et al. 957* (CR); Cartago, San Ramón de Tres Ríos, 20 Feb. 1959, *Rodríguez 595* (CR). **San José:** San Isidro de Coronado, 1400–1600 m, 1 Dec. 1937–1 Jan. 1938, *Allen 555* (F, GH, MO); Río Herradura, tributary of Río Chirripó del Pacífico, NW of Canaán, General Valley, 9°29′N, 83°37′W, 1600 m, 29 Dec. 1969, *Burger & Liesner 7097* (F, MO); Aserrí, 2 km SW de Aserrí, 0.2 km después de Km 13 de Ruta 4, 9°51′N, 84°6′W, 1470 m, 8 Jan. 1987, *Debouck et al. 2095* (BR, CR, UC, US); Alajuelita, potreros arriba de San Antonio, al pie del cerro San Miguel, 9°52′N, 84°7′W, 1620 m, 8 Jan. 1987, *Debouck et al. 2102* (BR, CR, US); Aserrí, 1.5 km E de Aserrí, al pie de la Piedra, 9°52′N, 84°7′W, 1590 m, 11 Jan. 1987, *Debouck et al. 2116* (BR, CR, COL, US); Santa María, 1.8 km E de Sta. María a Copey, frente Quebrada Salta, orilla del Río Pirris, 9°40′N, 83°57′W, 1660 m, 12 Jan. 1987, *Debouck et al. 2122* (BR, CR, COL, MICH, US); San Isidro El General, 0.8 km S de Pueblo Nuevo, orillas del Río Buenavista, near San Isidro El General, 9°26′N, 83°40′W, 1550 m, 13 Jan. 1987, *Debouck et al. 2126* (CR, US); San Isidro El General, al pie de la Fila Villarevia, orillas del Río Blanco, 2 km N de Herradura, 9°30′N, 83°37′W, 1690 m, 13 Jan. 1987, *Debouck et al. 2128* (BR, CR, MICH, SI, US, WIS); San Isidro El General, 1 km N de Providencia, orillas del Río Brujo, 9°34′N, 83°51′W, 1990 m, 14 Jan. 1987, *Debouck et al. 2132* (BR, CR, US); barranco entre Aserrí y Tarbaca, 1150 m, 25 Nov. 1964, *Jiménez 2581* (F); below Cerro Pico Blanco, 4 km S of Escazú, 9°52′N, 84°8′W, 1900 m, 12 Dec. 1976, *Lent 3966* (F); vicinity of El General, 1560 m, Dec. 1936, *Skutch 2990* (GH, MO); La Cruz de Alajuelita, 1810 m, 22 Dec. 1935, *Solis 392* (F, MO); between Aserrí and Tarbaca, 1200–1700 m, 6 Dec. 1925, *Standley 41362* (F). PANAMA. **Boquete:** Bajo Mono, 1400 m, 3 Apr. 1938, *Davidson 496* (F, GH, MO). **Chiriquí:** valley of the Río Chiriquí Viejo, near New Switzerland, 1800–2000 m, 6–14 Jan. 1939, *Allen 1397* (EAP, MO); Methodist Camp near Nueva Suissa, 19 Feb. 1971, *Croat 13508* (F, MO); Río Chiquero, 22 Mar. 1977, *D'Arcy 11005* (MEXU, MO); N of Volcán City, valley of R. Chiriquí Viejo, 1600–1700 m, 9 Dec. 1966, *Duke 9019* (MO); Nueva Suissa near Audubon Society Cabin, 1750 m, 12 Sep. 1972, *Gentry 5986* (F, MO); Finca Lérida to Peña Blanca, 1750–2000 m, 9 July 1940, *Woodson et al. 313* (MO, US); Casita Alta, Volcán de Chiriquí, 1500–2000 m, 28 June–2 July 1938, *Woodson et al. 918* (GH, MO, NA, US).

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