

road to Jitotol, *Breedlove 23100* (DS); Mpio. San Andrés Larrainzar, ca. summit of Chuchil Ton, NE of Bochil, *Breedlove 26764* (DS, LL, MICH-2, MO); Mpio. Tenejapa, in the Paraje Kurus Ch'en, *Breedlove 28219* (DS, MO, RSA, TEX); Mpio. Tenejapa, at Moel Ch'en near Tenejapa Center, *Breedlove 42891* (CAS, MO, TEX); Mpio. of Rayón, in the Selva Negra, 10 km above the Rayón Mezcalapa along the road to Jitotol, *Breedlove & Keller 49339* (CAS); 12 km N of Jitotol along a side road to an oil well, *Breedlove & Thorne 21441* (DS); Mpio. Pueblo Nuevo Solistahuacán, ca. Rincón Chamula, *Clarke 293* (DS, TEX); Mpio. Pueblo Nuevo Solistahuacán, Clínica La Yerbabuena, *Heath et al. 2186* (CAS); 3 km N of Pueblo Nuevo Solistahuacán, *Lathrop 5282* (DS); 5 mi SE of Pueblo Nuevo Solistahuacán, on Pemex Road, *Lathrop 6531* (DS); 16 km N of Pueblo Nuevo Solistahuacán between Rincón Chamula and Rayón, *Lathrop & Thorne 7392* (DS); Rincón Rayón (Selva Negra), *MacDougal 6022* (DS); Mpio. Yajalón, camino a la punta del Cerro Ventana, *Méndez T. 6694* (MO); Mpio. Pueblo Nuevo Solistahuacán, 3 km NW of Pueblo Nuevo Solistahuacán, *Mill 705* (DS, RSA); Mpio. Pueblo Nuevo Solistahuacán, en Reserva Natural Yerbabuena, frente a la Clínica Yerbabuena, 2 km NW de Pueblo Nuevo Solistahuacán, *Reyes G. 1661* (BM, IEB, MO); Jitotol Ridge of the Northern Highlands, ca. 15 km N of Pueblo Nuevo Solistahuacán, *Thorne & Lathrop 40419* (DS, RSA); Jitotol Ridge of the Northern Highlands, Mpio. Pueblo Nuevo Solistahuacán, 3 km NW of Pueblo Nuevo Solistahuacán, *Thorne & Lathrop 41753* (DS); Mpio. Rayón, Jitotol Ridge of the Northern Highlands, 9 mi NW of Pueblo Nuevo Solistahuacán, along the road between Rincón Chamula and Rayón, *Thorne & Lathrop 46603* (RSA); Mpio. Pueblo Nuevo Solistahuacán, Jitotol Ridge of the Northern Highlands, 3 km NW of Pueblo Nuevo Solistahuacán, *Thorne & Lathrop 46753* (RSA); vicinity of Pueblo Nuevo Solistahuacán, 125 km NE of Tuxtla Gutiérrez, *Tillet 636-50* (RSA).—OAXACA: roadside 2–5 km SW of Totontepec on road from Totontepec to Tamazulapan Mixe, *Benz et al. 614a* (WIS); Atlantic slope of mountains, along road between Ixtlán and Valle Nacional, *Breckon & Christman 674* (WIS-2); 6.5 km E of the Mitla to Choapan road along road to Zacatepec, N slope of Cerro Zempoaltepetl, *Breedlove & Ahmeda 64713* (CAS); on the NNE slope of Cerro Humo Chico, *Breedlove & Mahoney 72425* (CAS, RSA); along Oaxaca–Tuxtepec road, Hwy 175 between Km 130 and 140 beyond Cerro Pelón, *Carlson 4157* (F, RSA); along Hwy 175 between Valle Nacional and Oaxaca, 17–19 mi above bridge at Valle Nacional, *Croat & Hannon 65582* (MO); Km 75 on Mex Hwy 175 from Tuxtepec to Oaxaca, *Holmes 4566* (NY); Dto. Villa Alta, Sierra de Juárez, camino de Calpulalpan a Talea, a 10 km al N de la desviación a Yalina, *Lorence 4229* (CAS, MO); Dto. Ixtlán, Sierra de Juárez, Ruta 175 a 10 km NE de Cerro Pelón, *Lorence 4241* (MEXU, MO); Oaxaca to Tuxtepec, Km 105, 9 Apr 1964, *MacDougal s.n.* (MEXU); Km 108 Oaxaca to Tuxtepec hwy, *MacDougal 34220* (US); Mpio. Totontepec, Dto. Mixe, 5.5 km S of Totontepec on road to Mixistlán, *Martin 186* (MEXU, MO); Mpio. Totontepec, Dto. Mixe, Cerro La Mitra a 5 km de Totontepec, *Ramírez G. 775* (MEXU, MICH, MO, RSA, TEX); 19.1 km N de Yacochi, en el camino a San Andrés Yaa, Dto. Mixe, *Torres C. 7114* (MEXU-2, MO, RSA, TEX); Mpio. Totontepec, Dto. Mixe, 1 km N de la desviación a Villa Alta, la cual se encuentra 7.5 km S de Totontepec, *Torres C. 11768* (MEXU, RSA, WIS); 30.4 mi N of Ixtlán de Juárez, at pass as it drops down to gulf slopes, Oaxaca–Tuxtepec road, *Turner 80A-52* (TEX).

*Cobaea biaurita* is most closely related to *C. scandens*, from which it can be easily distinguished by its deltate calyx lobes, which are 7–18 mm wide, whereas *C. scandens* has circular or broadly ovate calyx lobes, which are (16–) 19–32 mm wide. *Cobaea biaurita* also has longer filaments (62–75 mm vs. 41–59 mm) and styles [(47–) 55–80 mm vs. 41–56 mm].

A few collections from Chiapas near Jitotol and Pueblo Nuevo Solistahuacán have longer and narrower calyx segments than typical specimens of *C. biaurita* (*Clarke 293*, *Breedlove 23100*, *Breedlove 49339*, *Heath et al. 2186*, *Lathrop 5282*, *Lathrop & Thorne 7392*, *MacDougal 6022*, *Thorne & Lathrop 40419*, *Thorne & Lathrop 41753*, *Thorne & Lathrop 46603*, *Tillet 636-50*), and some of those lack the characteristically auriculate bases on the lower leaflets. The calyx segments range from 34–39 mm long and 7–9 mm wide, whereas those of the typical specimens range from 26–34 (–37) mm long and 10–18 mm wide. Among the typical specimens, the trend is for the longer calyx segments to be the widest. For example, the specimen that has calyx segments 37 mm long has a calyx width of 18 mm. Thus, the calyx segments of typical material may approach those of the atypical material in length, but are nonetheless twice as wide when they do. Because one intermediate (*Thorne & Lathrop 46753*) with calyx segments 39 mm long and 12 mm

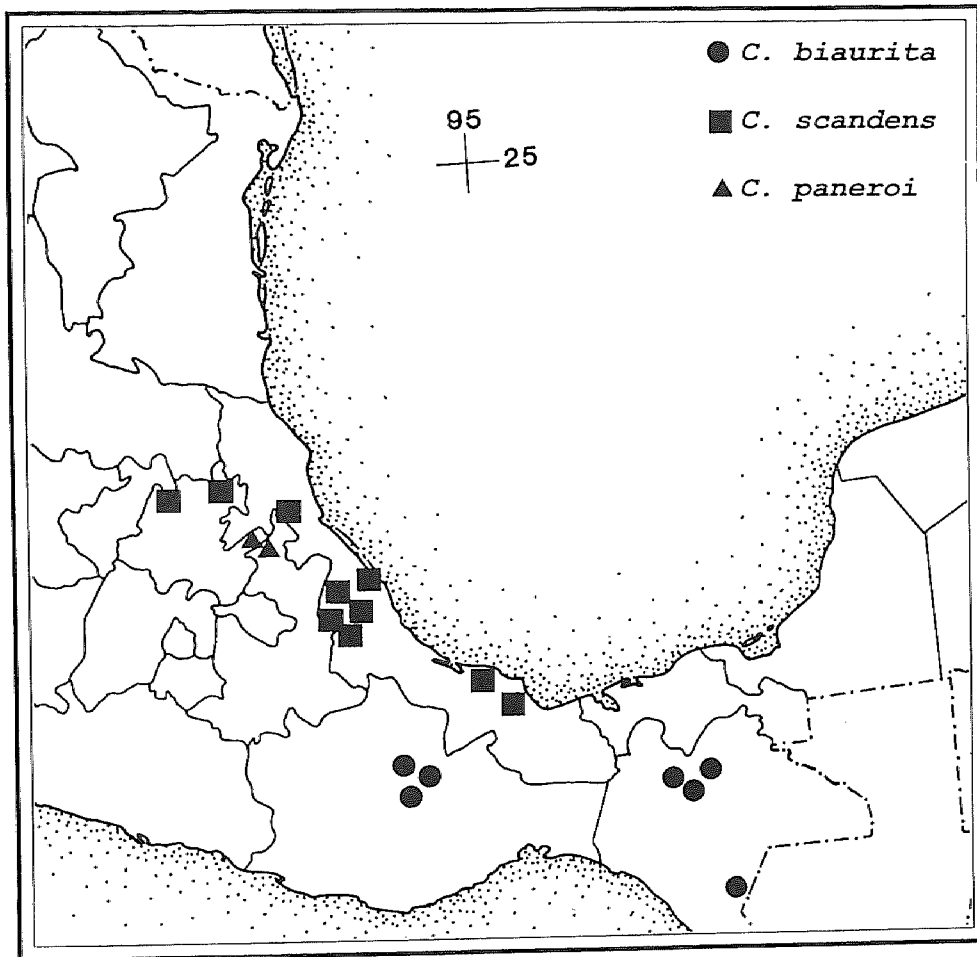


FIG. 18. Distribution of *Cobaea biaurita*, *C. scandens*, and *C. paneroi*.

wide, as well as a typical specimen (*Lathrop 6531*), have been found in the same area, and the two forms are similar in all other respects, the form with longer, narrower calyces is here included in *C. biaurita*.

Some unusual specimens of *C. scandens* from the state of Veracruz, Mexico, have been confused with *C. biaurita* in the *Flora of Veracruz* (Nash 1979; see discussion of *C. scandens*, no. 6, below). The calyx segments of these specimens are more similar to those of *C. biaurita* than in typical representatives of *C. scandens*, but are ovate, whereas those of *C. biaurita* are deltate. All of the specimens cited in *Flora of Veracruz* as *C. biaurita* are either *C. scandens* or *C. stipularis*. I have seen no specimens of *C. biaurita* from Veracruz.

See the discussion under *C. pringlei* (no. 2) for characters that separate that species from *C. biaurita* and *C. trianae*, all of which are morphologically very similar, and for the reasons that Rzedowski et al. (1995) and Rzedowski and Calderón de Rzedowski (1995) placed *C. biaurita* in synonymy under *C. stipularis*.

6. *Cobaea scandens* Cavanilles, Icon. 1: 11. 1791. *Rosenbergia scandens* (Cavanilles) House, Muhlenbergia 4: 23. 1908.—TYPE: tab. 16 in Cavanilles's *Icones*, 1791 (lectotype, here designated.)  
*Cobaea lasserii* Pittier, Bol. Soc. Venez. Cienc. Nat. 4: 346 ('lasserii'). 1938.—TYPE: VENEZUELA. Distrito Federal: near Los Castillitos, 1600 m, May 1938, *Lasser 1* (holotype: VEN!).

Stems slender, woody, glabrous or rarely minutely villous at the nodes. Leaves green, usually suffused with purple, with 6 leaflets; rachis 47–67 mm long, glabrous or puberulent along the channel; petiolules 4–11 mm long, glabrous or puberulent along the channel; blades 44–115 mm long, 20–65 mm wide, glabrous, margins minutely ciliate; upper and middle leaflet pairs broadly elliptic to ovate, base rounded to acuminate, apex acute to acuminate; basal pair elliptic, unequally auriculate, the margin not long-ciliate. Inflorescence of 1–3 flowers; bracts fully to partly expanded, or sometimes abscised at maturity, with 6 leaflets. Peduncles (1.0–) 3.0–6.6 cm long, glabrous or puberulent basally. Pedicels 13.4–23.0 cm long, glabrous, tightly curved at the apex in fruit. Calyx segments 20–32 mm long, (16–) 19–32 mm wide, green, chartaceous, circular to very broadly ovate, apex rounded to emarginate or rarely broadly acute, margins plane, glabrous or minutely ciliate, puberulent adaxially except near the midvein, glabrous abaxially. Corollas pale green, turning deep purple with age, chartaceous, lobes puberulent externally but sometimes only near the margin, glabrous except for the long-villous annulus internally; tube 39–43 mm long, 33–49 mm wide, campanulate, widest at the apex; lobes 14–21 mm long, much shorter than the tube, 22–32 mm wide, depressed-ovate or sometimes approaching broadly deltate, apex rounded, inrolled at the margin, imbricate, not wrinkled in bud. Filaments 41–59 mm long, adnate basally for 8–13 mm, positioned ventrally, bent basally, sharply curved at the apex, becoming undulate after dehiscence; anthers 9–12 mm long, 1.5–2.5 mm wide, yellow, orange, or purple, lanceolate, straight in bud, sometimes curved but not twisted after dehiscence, introrse. Styles 41–56 mm long; style branches 3–5 mm long, flattened, papillae long, occurring on adaxial surface only (type I stigmas). Fruit 59–67 mm long, maculate. Seeds 35–45 per fruit, 16–20 mm long, 10–13 mm wide, furnished with scales; wings 2–3 mm wide. Chromosome number:  $2n = 52$ . Figs. 8, 9F.

Illustrations. Cavanilles (1791: tab. 16, 17); Jacquin (1809: tab. 87); Peter (1891: fig. 19); Brand (1907: fig. 6); Grant (1959: fig. 19); Meeuse (1961: fig. 83); Grant and Grant (1965: figs. 41, 42); Steyermark and Huber (1978: fig. 254A); Nash (1979: fig. 1); Ippolito and Suarez (1998: fig. 2).

Phenology. Collected in flower and fruit year-round.

Distribution (Fig. 18). Mexico (Veracruz and closely adjacent areas of Hidalgo and Puebla; probably adventive in Chiapas, Oaxaca, México, and Michoacán), and introduced in Jamaica, Costa Rica, Guatemala, Bolivia, Colombia, Ecuador, Peru, and Venezuela; wet forests along the forest edge or in openings; 900–1650 (–3000) m.

REPRESENTATIVE SPECIMENS. **Jamaica.** PORTLAND: near road between Section and Hardwar Gap, *Anderson & Sternberg 3021* (TEX); N slope of Hardwar Gap, Port Royal Mts, *Thorne & Proctor 48262* (RSA-2).

**Mexico.** HIDALGO: along Hwy 105 between Pachuca and Tampico, 18–23 mi S of Huejutla. 20°59'N, 98°31'W, *Croat & Hannon 65983* (CAS, MO); Puerto del Zopilote, ca. Km 329 on Hwy between Santa Ana and Chapulhuacán, *Moore 3393* (GH, UC).—PUEBLA: Mpio. Teziutlán, ca. the town of Teziutlán, *Dodds 59* (MICH); Mpio. Chichiquila, camino Tízapa–Chichiquila, *Márquez et al. JM-135* (IEB, WIS-2); San Pedro, *Nicolas 44* (G-6).—MÉXICO: Dist. of Temascaltepec, Nanchititla, *Hinton 4111* (G, TEX).—MICHOCÁN: Zitácuaro–El Sedano, *Hinton 11945* (TEX).—VERACRUZ: Mpio. San Andrés Tuxtla, lado W de Cerro Mastagaga, ca. 13 km

al NE de San Andrés Tuxtla, *Beaman 5601* (F, MEXU); Orizaba, *Botteri 150* (GH); Orizaba, *Botteri 294* (F-2, GH-2, UC, US); Orizaba, *Botteri & Stunichast 1371* (MICH, US); congregación de Ixtapan, en la Sierra de Chiconquiaco, Tonayán, *Calzada 2100* (F, MEXU); Mpio. Banderilla, al N de Banderilla, Rancho La Martinica, *Calzada 7863* (MEXU); Mpio. Juchique de Ferrer, El Cerro de Villa Rica, ca. de Mundo Nuevo, *Castillo C. & Cortez 1858* (WIS); Mpio. Alto Lucero, La Piedra Cuata entre Plan de las Hayas y Tierra Blanca, *Castillo C. & Vázquez 1366* (F); Mpio. Tepetzintla, Sierra Otontepec, *Castillo C. et al. 2529* (F); Mpio. Calahualco, Barranca de Atotonilco, entre Jamapa y Atotonilco, *Cházaro & Oliva 3291* (WIS); Mpio. Páz de Enríquez, 1 km N of Páz de Enríquez, 8 km (by air) SW of Yecuatlá, on road to Misantla, *Diggs & Nee 2827* (BR, CAS, F, GH, MICH, TEX); Mpio. Naolinco, carretera Xalapa a Naolinco, desviación a Tonayán, *Fay & Hernández 738* (AAU); Ixtotenó a 5 km de Atzalan camino a Tlapacoyan, *Lot 220* (GH-2, MEXU); Mpio. Naolinco, 10.6 mi N of turnoff at 140 on road to Misantla, 2.9 mi S of Naolinco, *Luckow 3047* (TEX); Salto del Gato, 4 km NE de Jalapa, Banderilla, *Márquez & Dorantes 158* (F, MEXU, MO); 2 km al SE de Dos Pocitos, camino a Ixtapan, Tonayán, *Márquez R. et al. 467* (F, NY-2, W, WIS); Cerro Punta Coscomat [Coscomatepec?], *Matuda 1505* (MEXU, MICH); Orizaba, *Müller 634* (NY); Mpio. Soteapan, along trails to base of Volcán Santa Marta, 0–3 km E of village of Santa Marta, *Nee et al. 24664* (F, WIS); Sta. Rita, Sierra de Chiconquiaco, *Nevling & Gómez-Pompa 15* (F, GH); 500 m después de la desviación al Ingenio La Concepción, Jilotepec, *Ortega 312* (F); 2 km después de la desviación al Ingenio La Concepción, Jilotepec, *Ortega 340* (F, IEB, MEXU, MO-2); Mpio. Xalapa, Parque Ecológico Fco. Javier Clavijero, *Ortega O. 1511* (F); El Esquilón, cerca de Jilotepec, *Ramos 355* (CAS, MEXU, US); Banderillas Temascaltepec, *Rosas R. 536* (F, GH); Jalapa, *Smith 1873* (F, MEXU, MICH, NY, UC); El Vija, Santiago Tuxtla, *Sousa 2587* (CAS); entre Tequila y San Andrés Tenejapa, S. A. Tenejapa, *Vázquez T. 507* (F, MEXU, NY-2, WIS); Mpio. Atzalan, ca. del panteón, *Ventura A. 11* (CAS, IEB, MO); Mpio. Nautla, La Unión, *Ventura A. 3591* (DH, MICH, TEX); Mpio. Jilotepec, Esquilón, *Ventura A. 5753* (LL); Mpio. de Naolinco, Agua Santa, *Ventura A. 11030* (CAS, MO); valley NW of La Perla (vicinity of Orizaba) along river, *Weaver et al. 1738* (F-2, GH, MICH); Cerro de Macuiltepetl, Xalapa, *Zola B. 394* (F, MEXU, UC); Vista Hermosa, Jilotepec, *Zola B. 563* (F, MEXU-2). U.S.A. TEXAS: cultivated at the University of Texas greenhouses, *Prather 1269* (TEX).

**Costa Rica.** CARTAGO: along a stream that crosses the road to San Gerardo, on the NE edge of Cot, *Prather 1578* (TEX). **Guatemala.** EL QUICHÉ: 0.5 mi NW of Nebaj, *Proctor 25399* (TEX).

**Bolivia.** LA PAZ: Coroico, *Badcock 848* (AAU). **Colombia.** ANTIOQUIA: Mpio. Medellín, Corregimiento Santa Helena, SE de Medellín, Vía Rionegro, Km 6–15 de Medellín, *Callejas & Escobar 7363* (TEX). **Ecuador.** BOLÍVAR: along road Chillanes–El Tambo, *van der Werff et al. 12508* (TEX).—CARCHI: Tulcán–Quito road, 114 km from Tulcán, *Boeke 872* (TEX).—NAPO: Quijos Cantón, Carretera Tena–Baeza, *Gudiño & Zak 1253* (TEX).—TUNGURAHUA: In Baños opposite Hotel Sangay, *Tollsten 126* (GB, S). **Peru.** CAJAMARCA: Prov. Cutervo, alrededores de Gruta San Andrés, *Mostacero et al. 1704* (AAU, F-2, TEX).—PASCO: 2–5 km N of Oxapampa on road to Pozuzo, *Gentry & Smith* (AAU); Prov. Oxapampa, Mallampampa, 26 km SW of Huancabamba, *Smith & Canne 5873* (AAU, TEX). **Venezuela.** TRUJILLO: just S of Valera in the Andean foothills along the road to Mérida, *Prather 1582* (TEX).

The circular or very broadly ovate calyx segments of *C. scandens* distinguish it from all other species. It is the sister taxon to *C. biaurita*; characters distinguishing the two taxa are discussed under *C. biaurita*, no. 5.

Determining the native distribution of *C. scandens* is a difficult task, because the species is so widely cultivated and naturalized. Nearly all of those specimens that are not identifiable as cultivated or escaped material are from the Mexican state of Veracruz, but a few are from adjacent states. I have also seen a few specimens from the states of Chiapas, Oaxaca, México, and Michoacán, which are not clearly marked as cultivated, but which were collected in fencerows, roadsides, or other disturbed habitats, or from areas where *C. scandens* is cultivated. This suggests to me that these plants might be naturalized or adventive. Thus it seems that the native range of *C. scandens* includes Veracruz and closely adjacent areas in the states of Hidalgo and Puebla; the morphological variation seen among collections from this region encompass nearly all of the variability of *C. scandens*. Collections from other areas are relatively uniform and are very similar to cultivated plants.

Nash (1979) treated some unusual specimens of *C. scandens* from Veracruz (*Botteri*

150, Matuda 1505, Sousa 2587, Weaver et al. 1738, and Vázquez 507) as *C. biaurita*. Nearly all of these are from an area near Volcán Orizaba. They are unusual in that the calyx lobes are not as wide and are broadly acute, as opposed to rounded or emarginate. Also, a few of them have a mucro on the calyx that is 3–5 mm long, whereas the mucro on typical calyces is 1–2 mm long. In other features they resemble typical *C. scandens*. The calyces on these specimens are very variable, which may indicate introgression from either *C. stipularis* or *C. paneroi*, both of which occur nearby. *Cobaea minor* occurs on Volcán Orizaba as well, but it is unlikely that the unusual specimens could be the result of hybridization between *C. minor* and *C. scandens*, because the atypical specimens do not resemble *C. minor* in any way. The only remaining specimen (Hernández & Trigos 809) that Nash cited as *C. biaurita* is *C. stipularis*.

The type of *C. lasseri* falls clearly within the circumscription of *C. scandens*. The flower is somewhat smaller than those of most specimens of *C. scandens* but is similar to a naturalized form that is common in Venezuela, especially in the Andean region, and is no smaller than in occasional collections from Mexico.

The description and plate in the protologue were based on specimens grown in the Madrid Botanical Garden. There exists in MA one undated sheet that may be from the living material upon which Cavanilles based the description and illustration (Garilleti 1993), but Cavanilles did not annotate the sheet, and the specimen may have been collected from the garden at a later time, as were two other sheets labeled "Cavanilles Typi" (photos: TEX! IEB!). There are two flowers on the undated sheet, and one of them is clearly tetralogical, having ten corolla lobes, and does not fit the original description or illustration. Because there is no clear indication that this specimen is original material and because the specimen does not fit the original description in some regards, I designate excellent plate as the lectotype.

*Cobaea scandens* is widely cultivated in North and South America, Europe, Asia, Africa, and New Zealand. It has become naturalized in Central America, northern South America, Jamaica, some parts of Mexico, New Zealand, and the Philippines. In Mexico the leaves of *C. scandens* are used to make a tea used as a cough suppressant (García R. 1988; de la Rosa 1983).

7. *Cobaea paneroi* Prather, Brittonia 48: 116. 1996.—TYPE: MEXICO. Hidalgo: Mpio. Tenango de Doria, 5 km NE de Tenango de Doria, 1690 m, 5 Jul 1979, Hernández M. 3332 (holotype: MEXU!; isotypes: MEXU! MO!).

Stems slender, woody, villous at the nodes. Leaves, green suffused with purple, with 6 leaflets; rachis 28–61 mm long, sparsely puberulent especially along the channel; petiolules 2–7 mm long, puberulent along the channel; blades 46–103 mm long, 23–44 mm wide, puberulent along the veins abaxially, margins minutely ciliate; upper and middle pairs obovate to elliptic to broadly elliptic, base acuminate to rounded; basal pair obovate, base truncate to slightly cordate, the margins not long-ciliate. Inflorescence a solitary flower; bracts poorly developed or abscised at maturity, with 4–6 leaflets. Peduncles 1–4 cm long, puberulent. Pedicel 7–14 cm long, puberulent, especially at the base, slightly bent at the apex in fruit. Calyx segments 20–27 mm long, 14–16 mm wide, green, chartaceous, ovate to lanceolate, long-acuminate, margins plane, glabrous or minutely ciliate, puberulent in a broad zone near the margin adaxially, sparsely puberulent abaxially. Corolla greenish white, tinted with purple or purple throughout, chartaceous, puberulent especially towards the apex externally with some long trichomes near

the base; tube 35–38 mm long, 33–36 mm wide, campanulate, widest at the apex; lobes 15–18 mm long, much shorter than the tube, 23–25 mm wide, broadly ovate, apex rounded, inrolled at the margin, imbricate, not wrinkled in bud. Filaments 45–55 mm long, adnate basally for 3–5 mm, positioned ventrally, bent basally, sharply curved at the apex, becoming undulate after dehiscence; anthers 7–9 mm long, 1–2 mm wide, yellow(?), lanceolate, straight in bud, not twisted after dehiscence, introrse. Styles 40–45 mm long; style branches 4–5 mm long, flattened, papillae long, occurring on adaxial surface only (type I stigmas). Fruit 45–55 mm long, maculate. Seeds many per fruit, 10–15 mm long, 7–12 mm wide, furnished with scales; wings 1–2 mm wide. Chromosome number unknown. Figs. 10A, 19.

Phenology. Collected in flower in February, July, and October, and in fruit in July.

Distribution (Fig. 18). Mexico (Hidalgo and adjacent Puebla); montane cloud forests; 1200–1700 m.

ADDITIONAL SPECIMENS EXAMINED. **Mexico.** HIDALGO: Mpio. Tenango de Doria, 9 km E de Tenango de Doria, hacia Tutotepec, *Hernández M. 5536* (MEXU, MO).—PUEBLA: along Hwy 130 about 5 km by road S from Xicotepec de Juárez, *Dieterle 3642* (MICH).

*Cobaea paneroi* is distinguished from all other species in the genus by its long-acuminate calyx segments. In addition, it can be distinguished from all other North American species of sect. *Cobaea* by the base of its lowermost leaflets, which are exauriculate.

**Cobaea** section **Pachysepalae** Prather, sect. nov.—TYPE: *Cobaea pachysepala* Standley.

Lobi corollae acuti vel acuminati. Sepala coriacea zona angustissima pubescentiae in pagina adaxiali. Filamenta villosa ca. 1–2 cm sub apice.

Inflorescence erect, with at least two bracts; pedicels 17.0–22.5 (–27.5) cm long. Calyx segments coriaceous, densely puberulent near the margin adaxially, zone of puberulence 0.5–2.0 mm wide. Corolla lobes broadly ovate to very broadly ovate, shorter than the tube, apices acute to acuminate. Filaments villous at the base and about 1–2 cm below the apex. Style branches flattened, reflexed, not twisted, with rounded apices; papillae long, covering only the adaxial surface (type I stigmas). Ovary with at least two ovules per locule.

Section *Pachysepalae* is monotypic. *Cobaea pachysepala* has many characters that attest to its close relationship with the species of sect. *Cobaea*, but it is placed in a monophyletic lineage with sect. *Rosenbergia* in the molecular analysis. It can be easily distinguished from all other species of *Cobaea* by the patch of villous pubescence near the apex of the filaments. *Cobaea pachysepala* occurs in Guatemala and the Mexican state of Chiapas.

**8. *Cobaea pachysepala*** Standley, Contr. U.S. Natl. Herb. 17: 456. 1914.—TYPE: GUATEMALA. Sacatepéquez: Volcán de Agua, 15 Feb 1905, 9000 ft, *Kellerman 4395* (holotype: US!, photo: MICH!; isotype: MICH!).

*Cobaea tomentulosa* Standley, Contr. U.S. Natl. Herb. 17: 457. 1914. *Cobaea pachysepala* f. *tomentulosa* (Standley) D. N. Gibson, Fieldiana: Botany 31: 354. 1968.—TYPE: GUATEMALA. Quetzaltenango: ca. Zunil, 2340–2400 m, 20 Jan 1896, *Nelson 3683* (holotype: US!, photo: MICH!; isotype: GH!).

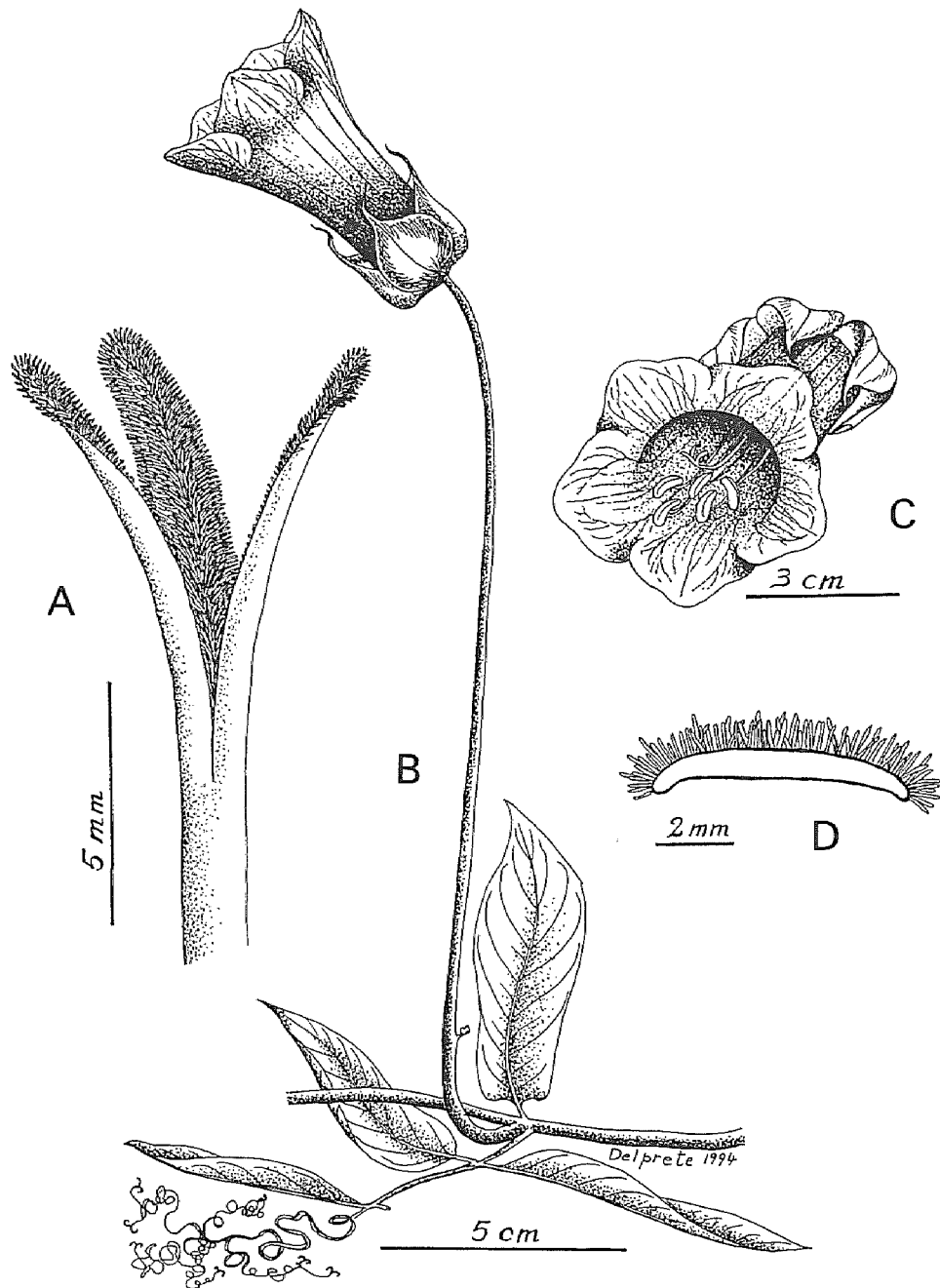


FIG. 19. *Cobaea paneroi*. A. Distal portion of style and style branches. B. Portion of the habit. C. Flower. D. Cross section of a style branch; the lower part of the diagram is the abaxial surface. (Based on Hernández 3332, MEXU.)

Stems slender, woody, puberulent along the internodes, sometimes only sparsely so, villous at the nodes. Leaves green, often suffused with purple, with 6 leaflets; rachis 42–62 mm long, puberulent, sometimes only sparsely so; petiolules 4–11 mm long, puberulent; blades (35–) 60–90 mm long, 13–35 mm wide, pubescent on abaxial surface, especially along the veins, sometimes along the veins adaxially, rarely glabrous, margins minutely ciliate; upper and middle leaflet pairs elliptic, base rounded to acute, apex acute to acuminate; basal pair usually long-ciliate at the base. Inflorescence of 1–5 flowers; bracts usually fully expanded, sometimes only poorly so or abscised at maturity, with 6 leaflets. Peduncles 3.7–9.7 cm long, usually puberulent, rarely glabrous. Pedicels 17.0–22.5 (–27.5) cm long, puberulent, especially at the base and the apex, tightly curved at the apex in fruit. Calyx segments 18–33 mm long, 3–8 mm wide, green, coriaceous, lanceolate to lanceolate-ovate, apex acute to acuminate, margins plane, minutely ciliate, puberulent in a very narrow zone just inside the margin adaxially, glabrous to densely puberulent abaxially. Corollas green to yellowish green or whitish green, chartaceous, puberulent, especially near the apex, sometimes with long trichomes at the base externally, puberulent internally on the upper lobes or glabrous, with a long-villous annulus; tube 38–45 mm long, 30–41 mm wide, campanulate or rarely narrowly campanulate, widest at the apex; lobes 11–22 mm long, much shorter than the tube, 14–24 mm wide, broadly to very broadly ovate, apex acuminate or sometimes acute, sometimes inrolled at the margin, imbricate, not wrinkled in bud. Filaments 46–62 mm long, adnate basally for 7–9 mm, positioned ventrally, bent basally, sharply curved at the apex, becoming undulate after dehiscence; anthers 6–7 mm long, 2–3 mm wide, brown or purplish brown, lanceolate, straight in bud, twisted after dehiscence, introrse. Styles 48–57 (–68) mm long; style branches 2–4 mm long, flattened, papillae long, occurring on the adaxial surface only (type I stigmas). Fruit 50–66 mm long, emaculate. Seeds 22–32 per fruit, 22–25 mm long, 12–13 mm wide, lacking scales; wings 2–6 mm wide. Chromosome number unknown. Fig. 10B.

Illustration. Standley (1914: plate 29).

Phenology. Collected in flower from September to March, and in fruit from December to March.

Distribution (Fig. 20). Mexico (Chiapas) and Guatemala; montane cloud forests and rocky volcanic slopes with mesic but sparse vegetation; 2000–3000 m.

ADDITIONAL SPECIMENS EXAMINED. **Mexico.** CHIAPAS: Mpio. Motozintla de Mendoza, SW side of Cerro Mozotal, 11 km NW of the junction of the road to Motozintla along the road to El Porvenir and Siltepec, *Breedlove 41763* (CAS, F, MICH, MO, NY, RSA, TEX); Mpio. Motozintla de Mendoza, high ridge with Evergreen Cloud Forest near Niquivil at the junction with a small side ridge to Cerro Boquerón, *Breedlove 42780* (DS, MO, RSA, TEX); on ridge NE of Cerro Boquerón on road from El Rosario to Niquivil, *Breedlove 65782* (CAS); Mpio. Motozintla de Mendoza, SW side of Cerro Mozotal, 11 km NW of the junction of the road to Motozintla along the road to El Porvenir and Siltepec, *Breedlove & Almeda 58121* (CAS); Mpio. Siltepec, ridge above Siltepec on the road to Huixtla, *Breedlove & Almeda 58350* (CAS, LL, MO, NY); Mpio. Jaltenango, El Triunfo Reserve, trail NNW from El Triunfo camp to Palo Gordo camp, 1 km from El Triunfo camp, *Hampshire et al. 489* (BM); Mt. Ovando, *Matuda 447* (MICH-2, MO, US); along the road from Route 190 to El Porvenir, 17.1 km W of the junction with Route 190 and 2.3 km E of the junction with the road to Motozintla de Mendoza, *Prather 1081* (TEX); 19.8 km SE of Motozintla de Mendoza on road to Niquivil, *Prather 1083* (TEX).

**Guatemala.** CHIMALTENANGO: montañas de Chichavac Tecpan, *García S. 1449* (F); "Chickory bei Tecpan Guatem." [Chichavac Tecpan?], *Seler & Seler 2293* (GH, NY); Chichavac, *Skutch 230* (GH, MICH, US); Volcán de Acatenango, above Las Calderas, *Standley 61810* (F); region of Los Positos, above Las Calderas, *Standley 80198* (F), *Standley 80271* (F).—GUATEMALA: without specific locality, *Aguilar 457* (F).—QUETZALTENANGO: on the NW slope of Volcán Zunil 6–8 km S of Zunil along road to Fuentes Georginas, *Breedlove & Almeda 64850* (CAS); 15.3 km S of Zunil on 9S in route to Retalhuleu, *Prather 1522* (TEX); along road above



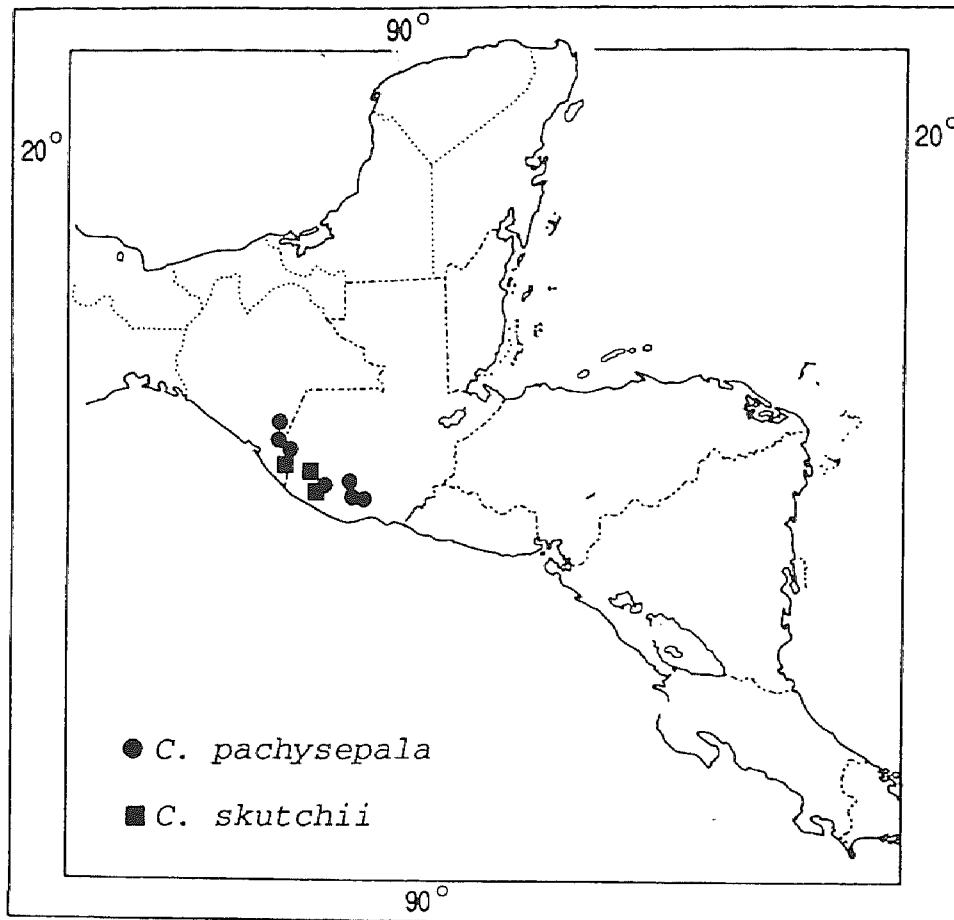


FIG. 20. Distribution of *Cobaea pachysepala* and *C. skutchii*.

Santa María de Jesús, *Standley 84850* (F); ca. Fuentes Georginas, slopes of Volcán de Zunil, *Standley 85858* (F); Volcán Zunil, *Steyermark 34674* (F-2).—SACATEPÉQUEZ: without specific locality, *Hunnewell 14792* (GH); Volcán de Agua, *Maxon & Hay 3747* (US); Volcán de Agua, ca. 1 km below Santa María de Jesús along road from Antigua, *Prather 1504* (TEX); Volcán de Agua, above Santa María de Jesús, *Standley 65144* (F).—SAN MARCOS: slopes of barrancas, tributary to and bordering Río Vega, between San Rafael at NE portion of Volcán Tacaná and Guatemala-Mexico line, *Steyermark 36373* (F).

*Cobaea pachysepala* is sister taxon to sect. *Rosenbergia*. Morphologically it is more similar to the species of sect. *Cobaea*, sharing a number of symplesiomorphic character states, such as the flattened style branches with long papillae covering only the adaxial surface (type I stigmas), and the filaments that are bent basally and sharply curved apically so that all five stamens are positioned in the ventral portion of the tube. *Cobaea pachysepala* differs from all species of sect. *Cobaea* in having villous trichomes near the apex of the filament and having acuminate or sharply acute corolla lobes.

Forms of *C. pachysepala* that have densely pubescent calyx segments have been segregated as *C. tomentulosa*, but the variation is continuous between the two forms, and the pubescent form occurs sporadically throughout the range of the species. The width of the calyx segments is also highly variable, tending to be wider in Guatemala (especially the departments of Chimaltenango and Guatemala) and narrower in Chiapas.

**Cobaea** section **Rosenbergia** (Oersted) Peter in Engler and Prantl, Nat. Pflanzenfam. IV(3a): 44. 1891. *Rosenbergia* Oersted, Vidensk. Meddel. Dansk. Naturhist. Foren. Kjøbenhavn 1856: 30. 1856.—TYPE: *Rosenbergia gracilis* Oersted [= *Cobaea gracilis* (Oersted) Hemsley].

*Cobaea* section *Aschersoniophila* Brand, Helios 21: 88. 1904.—TYPE: *Cobaea aschersoniana* Brand.

Inflorescence erect, with at least two bracts; pedicels (8.2–) 10.5–37 cm long. Calyx segments membranous or chartaceous, variously pubescent adaxially, zone of pubescence broader than 2.0 mm. Corolla lobes broadly ovate to deltate to linear, longer or shorter than the tube, apices rounded to acute to clawed. Filaments villous only at the base. Style branches terete, spreading in an irregular fashion but not reflexed, usually twisted, with acute apices; papillae short, covering nearly the entire surface (type II stigmas). Ovary with at least two ovules per locule.

The circumscription of sect. *Rosenbergia* that I propose here is broader than in other treatments (Peter 1891; Brand 1907; Grant 1959); it includes *C. aschersoniana* (which has historically been placed in the monotypic sect. *Aschersoniophila*), along with several species which were historically placed in sect. *Cobaea*. All of the species of sect. *Rosenbergia* have style branches that are terete and have short papillae covering nearly their entire surface (type II stigmas). This derived type of style branch is not found in the other sections, and thus is a synapomorphy by which the section can be distinguished.

Two species of sect. *Rosenbergia* occur in Guatemala and the state of Chiapas, Mexico, and one is endemic to Guatemala. Two species are endemic to southern Central America (Costa Rica and Panama), and four are endemic to South America. *Cobaea lutea* has disjunct populations in Mexico, Guatemala, El Salvador, Honduras, and Peru.

**9. *Cobaea skutchii*** I. M. Johnston, J. Arnold Arb. 19: 128. 1938. —TYPE: GUATEMALA. Quezaltenango: Palmar, 1221 m, 14 Oct 1934, *Skutch 1456* (holotype: GH!).

Stems slender, woody, puberulent, especially at the nodes. Leaves green, with 2–4 leaflets, one upper pair and sometimes the basal pair absent; rachis 23–25 mm long, puberulent, sometimes only sparsely so; petiolules 10–15 mm long, sparsely puberulent; blades 41–95 mm long, 17–33 mm wide, glabrous, margins minutely ciliate; upper and middle leaflet pairs elliptic, base cordate, apex acute to acuminate; basal pair (if present) similar to upper pair, the margins not long-ciliate at the base. Inflorescence of 1–3 flowers; bracts fully expanded, with 4 leaflets, the basal pair absent. Peduncles 3.5–10.7 cm long, puberulent, especially near the apex. Pedicels (10.5–) 19.0–26.5 cm long, glabrous or puberulent at the base and apex, slightly coiled at the apex in fruit. Calyx segments 14–20 mm long, 5–11 mm wide, yellowish green, sometimes with purple margins and veins, chartaceous, ovate to lanceolate, apex acute to acute-acuminate, margins undulate,

glabrous or minutely pubescent, especially at the base, puberulent adaxially in a narrow zone near the margin, or sometimes only near the apex, glabrous abaxially. Corollas green or greenish yellow, chartaceous, puberulent externally, especially at the apex of the tube and the base of the lobes, sometimes with a few long trichomes near the base of the tube, glabrous except for the long-villous annulus internally; tube 17–21 mm long, (16–) 20–24 mm wide, campanulate, widest below the apex; lobes 7–10 mm long, shorter than the tube, 9–11 mm wide, deltate, apex acute to rounded-acute, not inrolled at the margin, barely imbricate, wrinkled in bud. Filaments 28–35 mm long, adnate basally for 3–4 mm, emergent, not bent basally, not curved at the apex, coiling after dehiscence; anthers 4.0–7.5 mm long, 1–3 mm wide, yellow, lanceolate, straight in bud, twisted after dehiscence, versatile. Styles 36–48 mm long; style branches 4.5–6.0 mm long, terete, papillae short, covering nearly the entire surface (type II stigmas). Fruit 33–45 mm long, maculate. Seeds 6–15 per fruit, 18–24 mm long, 8–13 mm wide, lacking scales; wings 2–6 mm wide. Chromosome number unknown. Figs. 10C, 21.

Phenology. Collected in flower and fruit from August to February.

Distribution (Fig. 20). Mexico (Chiapas) and Guatemala (western central highlands); montane cloud forests; 1200–1800 m.

ADDITIONAL SPECIMENS EXAMINED. Mexico. CHIAPAS: Finca "La Vega de Guadalupe," Unión Juárez, 24 Nov 1961, *MacDougall s.n.* (US-3); Mpio. Unión Juárez, Talquián Chico, 8 km N de Unión Juárez, *Ventura & López 4965* (CAS, MO, TEX), *Ventura & López 3046* (IEB).

Guatemala. QUETZALTENANGO: Zunil, *Johnston 1891* (F); 11.4 km NE of Colomba on rd to San Juan, *Prather 1526* (TEX); 15.9 km NE of Colomba on road to San Juan, *Prather 1527* (TEX); above Mujuliá, between San Martín Chile Verde and Colomba, *Standley 85652* (F); along Quebrada San Gerónimo, Finca Pirineos, lower south-facing slopes of Volcán Santa María, between Santa María de Jesús and Calahuaché, *Steyermark 33388* (F).—SAN MARCOS: 16 km from Colomba on road to San Juan, *Madison 658* (GH).

*Cobaea skutchii* is the sister taxon to the clade composed of *C. aschersoniana*, *C. gracilis*, and *C. penduliflora*. It can be easily distinguished from all these taxa by its short deltate corolla lobes (v. linear corolla lobes). *Cobaea skutchii* is similar to *C. lutea* but can be distinguished from that taxon by its undulate calyx margins, a character state that is unique to this species.

10. *Cobaea aschersoniana* Brand, *Helios*. 21: 87. 1904. *Rosenbergia aschersoniana* (Brand) House, *Muhlenbergia* 4: 25. 1908.—TYPE: COSTA RICA. Prov. Heredia: forêts de la Esmeralda (Barbu), 2000 m, Nov 1892, *Biolley 1326* (distributed by Pittier & Durand as No. 7178) (lectotype, here designated: G!; isolectotypes: BR-2! G! US!).

Stems woody, villous. Leaves green, with 6 leaflets; rachis 30–73 mm long, villous; petiolules 5–9 mm long, villous; blades 56–98 mm long, 22–31 mm wide, long-pubescent, especially on the veins abaxially, margins ciliate, at least minutely so; upper and middle leaflet pairs elliptic to obovate, base rounded to truncate to acute, apex acute to acuminate; basal pair similar to upper pairs, the margins long-ciliate at the base. Inflorescence of 1–2 flowers; bracts fully expanded, with 6 leaflets. Peduncles 5.8–14.5 cm long, villous. Pedicels 13.5–19.5 cm long, villous, more densely so at the base, coiled at the apex in fruit. Calyx segments 24–39 mm long, 4–8 mm wide, green, chartaceous, lanceolate, apex acute, margins plane and long-ciliate, puberulent adaxially in a narrow zone near the margin, or sometimes only near the apex, villous abaxially. Corollas green, chartaceous,

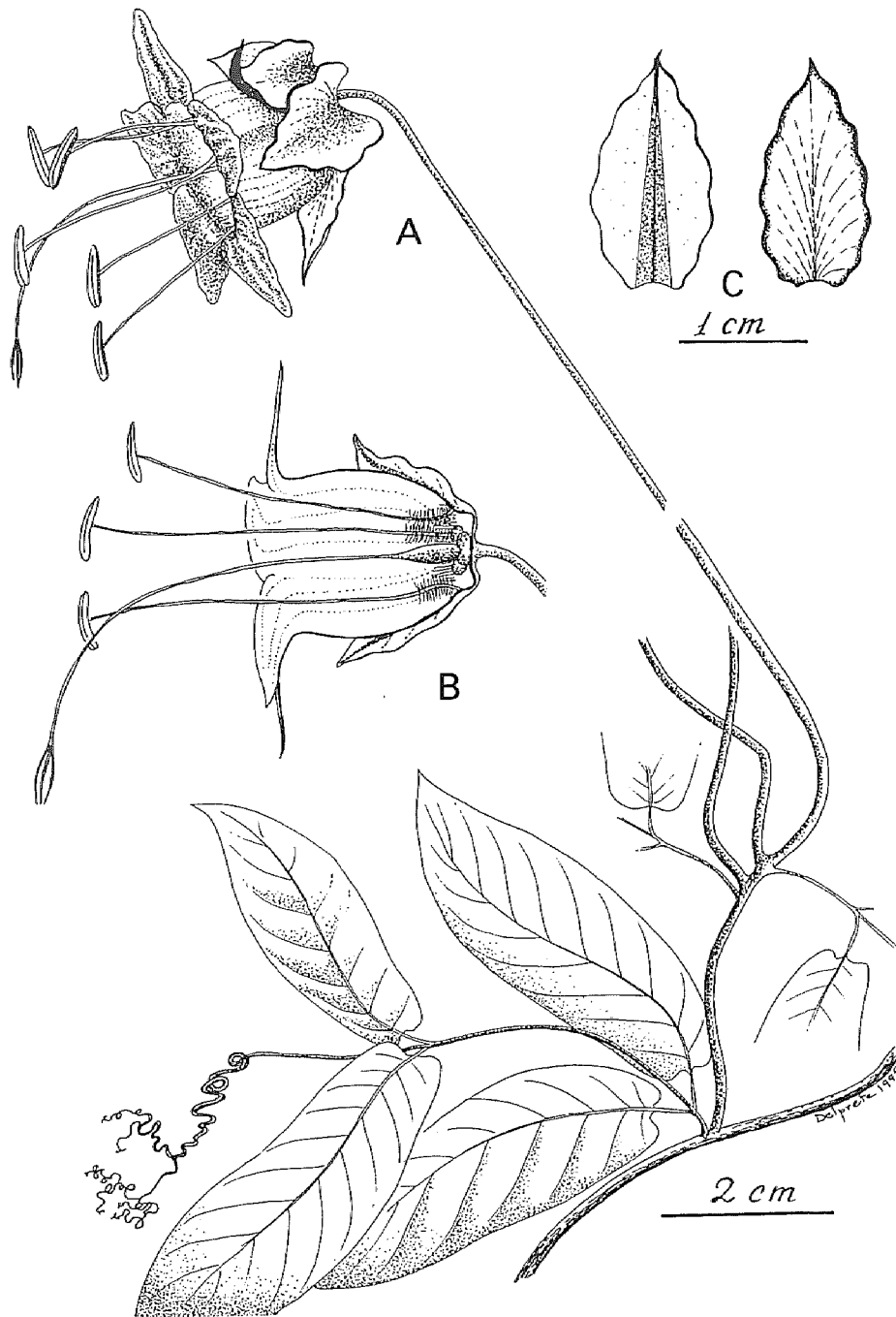


FIG. 21. *Cobaea skutchii*. A. Flower and portion of habit. B. Cut-away flower showing stamen insertion and nectary. C. Calyx segment, adaxial surface on left, with darker region along midvein representing glabrous areas, abaxial surface on right. (Drawn from field-taken photographs of *Prather 1526, TEX.*)

usually with scattered long trichomes on the lower half of the tube, short trichomes throughout, most dense externally at the upper portion of the tube and lower portion of the lobes, glabrous except for the long-villous annulus internally; tube 25–35 mm long, 19–26 mm wide, campanulate, widest below the apex; lobes (27–) 38–59 mm long, less than twice as long as the tube, 11–18 mm wide near the base, 3–6 mm wide at the middle of lobes, basally broad, with a long linear tip, apex usually minutely clawed, not inrolled at the margin, barely imbricate, wrinkled in bud. Filaments (58–) 77–92 mm long, adnate basally for 3–6 mm, emergent, not bent basally or only slightly so, not curved at the apex, coiling after dehiscence; anthers 9–13 mm long, 2–3 mm wide, yellowish green, lanceolate, straight in bud, twisted after dehiscence, versatile. Styles (58–) 70–95 mm long; style branches 6–8 mm long, terete, papillae short, covering nearly the entire surface (type II stigmas). Fruit 45–60 mm long, emaculate. Seeds 9–18 per fruit, 22–29 mm long, 9–13 mm wide, lacking scales; wings 3–10 mm wide. Chromosome number unknown. Figs. 1B, 10D.

Additional illustrations. Brand (1904: fig. 2); Brand (1907: fig. 7A); Ippolito and Suarez (1998: fig. 1); Prather and Jansen (1998: fig. 1B).

Phenology. Collected in flower from November to May, and in fruit from January to May.

Distribution (Fig. 22). Costa Rica; steep banks of streams or on cliffs in cloud forests; 1800–2800 m. Standley (1914) and Austin (1971) suggested that the species might also occur in Panama, but they did not cite any specimens from that country and I saw none.

ADDITIONAL SPECIMENS EXAMINED. **Costa Rica.** CARTAGO: San Gerardo, 5 km NW crater Irazú, Gómez 19894 (BM, GB, GH, MO, TEX); bord du ruisseaux, pres des chalêts de Turrialba, Pittier 867 (BR, US); on the steep slopes of a wooded arroyo on the S slopes of Volcán Irazú, 15.6 km below the summit and 11.3 km below the turnoff to Hacienda Coliblanco, Prather 1577 (TEX); El Roble, Stork 2387 (F, MICH).—SAN JOSÉ: Pan American Highway, high country S of Cartago, 15 Jan 1946, Bangham s.n. (A); Pan Am Highway, ca. 15 km SW of Cerro de la Muerte, Jan 1974, Poppleton s.n. (MO, RSA); ca. Finca La Cima, above Los Lotes, N of El Copey, Standley 42610 (US); bordes du Río Pedregoso au Copey, Tonduz 12217 (US-2, W); San Rafael, Coronado, Valerio 1368 (F, BR).—Province, locality, and date unknown: Warszewicz 2 (G).

*Cobaea aschersoniana* is the sister taxon to the lineage comprising *C. gracilis* and *C. penduliflora*, and is morphologically similar to these two species and to *C. aequatoriensis*. All of them have corollas with long, linear tips, but *C. aschersoniana* can be easily distinguished from the others by the base of its lobes, which are slightly imbricate and broad, abruptly narrowing to the linear tip. The corolla lobes of the other three species are never imbricate and are narrow even at the base. *Cobaea aschersoniana* is also very similar to *C. lutea*. Its stems, pedicels, and calyx segments are villous, and its corolla lobes are (27–) 38–59 mm long; in *C. lutea* the stems, pedicels, and calyx segments are glabrous to puberulent, but never villous (though the margins of the calyx segments may be long-ciliate), and the corolla lobes are 13–30 mm long.

Brand cited two specimens in his protologue, Pittier & Durand 7178 (=Biolley 1326) in the Boissier Herbarium (now in G), and Warszewicz 2, in B (destroyed). Photos of the B specimen are deposited in F!, GH!, and MO!. A duplicate of Warszewicz 2 is extant in G, but was not annotated by Brand. Because Brand saw and annotated one of the Biolley specimens, now at G, it is selected as the lectotype. There are no mature flowers on the sheet that Brand annotated, but it is clearly referred to *C. aschersoniana* by the densely villous calyx of a flower bud. The remaining sheet deposited in G has mature flowers, but I cannot be certain it is original material, because Brand did not annotate it.

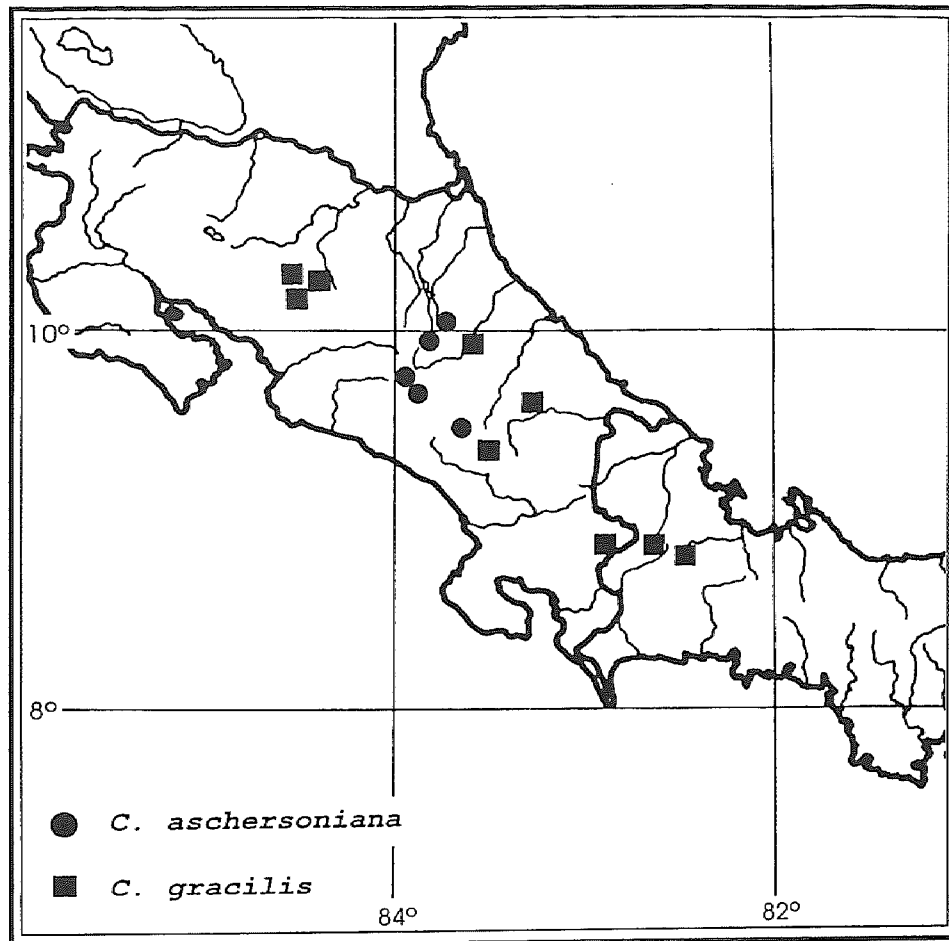


FIG. 22. Distribution of *Cobaea aschersoniana* and *C. gracilis*.

11. *Cobaea gracilis* (Oersted) Hemsley, Garden (London 1871–1927) 17: 353. 1880.  
*Rosenbergia gracilis* Oersted, Vidensk. Medd. Naturh. For. Kjøbenhavn 31.  
 1856.—TYPE: COSTA RICA. Vicinity of Naranjo, 1845–1848, *Oersted* 6600 (lectotype, here designated: C!; isolectotypes: C-2! F! NY!).  
*Cobaea panamensis* Standley, Contr. U.S. Natl. Herb. 17: 452. 1914.—TYPE:  
 PANAMA. Chiriquí: Cerro de La Horqueta, 1200–1700 m, 18 Mar 1911, *Pittier*  
 3270 (holotype: US!; isotype: US!).

Stems woody, puberulent at the nodes, occasionally along the internodes, rarely glabrous. Leaves green, with 4–6 leaflets; rachis (20–) 42–58 mm long, glabrous or pubescent along the channel; petiolules 6–12 mm long, puberulent, especially along the channel, rarely glabrous; blades 50–93 mm long, 21–33 mm wide, glabrous or sometimes

pubescent along the abaxial veins, margins minutely ciliate; upper and middle leaflet pairs elliptic to obovate, base truncate to rounded, apex acuminate; basal pair similar to upper pairs, the margins not long-ciliate at the base. Inflorescence of 1–5 flowers; bracts fully expanded, with 2–6 leaflets. Peduncles 1–8 cm long, glabrous or puberulent, especially at the base and apex. Pedicels 13–28 cm long, puberulent at the apex, or rarely glabrous, curved at the apex in fruit. Calyx segments 20–30 mm long, 3–5 mm wide, green, chartaceous, lanceolate, apex acute, margins plane, usually ciliate with long or short trichomes, rarely glabrous, puberulent adaxially near the apex and in a narrow band about 1 mm from the margin, glabrous or puberulent near the base abaxially. Corollas green, often suffused with purple, chartaceous-membranous, glabrous below constriction at the apex of nectar chamber externally but pubescent with long or short trichomes above, thinning towards the apex, glabrous internally except for the long-villous annulus; tube 12–19 mm long, 10–19 mm wide, campanulate, widest at the apex; lobes 29–60 mm long, more than twice as long as the tube, 3–9 mm wide near the base, 1–3 mm wide at the middle of the lobes, linear, apex usually minutely clawed, not inrolled at the margin, not imbricate, wrinkled in bud. Filaments (60–) 80–95 mm long, adnate basally for 4–8 mm, reflexed, not bent basally, not curved at the apex, coiling after dehiscence; anthers 8–11 mm long, 2–3 mm wide, purple, lanceolate, straight in bud, twisted after dehiscence, versatile. Styles 88–127 mm long; style branches 4–12 mm long, terete, papillae short, covering nearly the entire surface (type II stigmas). Fruit 32–68 mm long, emaculate. Seeds 9–18 per fruit, 23–28 mm long, 9–13 mm wide, lacking scales; wings 2–5 mm wide. Chromosome number unknown. Figs. 1C, 10E.

Additional illustrations. Oersted (1863: plate 15); Standley (1914: plate 27, as *C. panamensis*); Standley (1914: plate 28); Austin (1971: fig. 1).

Phenology. Collected in flower and fruit from December to August.

Distribution (Fig. 22). Costa Rica and Panama; growing along streams, in openings, or occasionally climbing into the canopy of wet forests or cloud forests; 1000–3000 m.

ADDITIONAL SPECIMENS EXAMINED. **COSTA RICA.** ALAJUELA: Los Angeles de San Ramón, *Brenes 13626* (F-2, NY-2); 1 km SE of La Balsa de San Ramón, *Grayum et al. 6340* (MO); San Miguel Oeste Naranjo, carretera Bernardo Soto en los márgenes de Río Grande entrando frente al Km 45, *Herrera Ch. 388* (BM, MO); 12 km NNW of San Ramón by road on way to San Lorenzo, 1 km S of Balsa, *Liesner & Judziewicz 14898* (MO, WIS); 12 km NNW of San Ramón en route to La Tigra, 1 km S of Balsa, *Prather 1579* (TEX); Cantón Alfaro Ruiz, 4 mi S of Zarcero, *Smith 14* (US); San Antonio de Zarcero, Cantón Alfaro Ruiz, *Smith 304* (F, US); La Piña de Zarcero, *Smith A680* (F, MO-2); Cantón Alfaro Ruiz, Bella Vista de Zarcero, *Smith 1593* (MO, NY-2), 4 mi S of Zarcero, Cantón Alfaro Ruiz, *Smith 1948-9* (US).—**CARTAGO:** along Río Grande de Orosí, W side, between suspension bridge and point opposite mouth of Quebrada Casa Blanca, Tapantí, *Grayum & Jacobs 3790* (BM, MO); Cerro Cruces above Río Reventazon, *Lent 2480* (F, MO); Zapote, *Polakowsky 395* (BM).—**GUANACASTE:** Río Chiquito, Tilarán Arenal, Zona Monteverde, *Haber & Bello 8252* (MO).—**PUNTARENAS:** Surá river, by road above La Tigra, *Hazlett 5023* (F); Piedra del Convento, *Pittier & Durand 3974* (BR-2).—**Province, locality, and date unknown:** *Endrés s.n.* (BM); *Endrés 82* (W); *Warszewicz 1* (G). **PANAMA.** CHIRIQUÍ: ca. 8 km W of Cerro Punta in the vicinity of Las Nubes, *Almeda & Nakai 3517* (CAS, F, MO); festooning fencerow across Río Chiriquí Viejo from town of Cerro Punta, *D'Arcy & D'Arcy 6574* (MO); Alto Respinga, above Cerro Punta, *D'Arcy 10697* (MO); District Boquete, Bajo Chorro, *Davidson 396* (F, GH, MO, US); above Cerro Punta, *Folsom et al. 2055* (BM, MO); along Río Caldera (Boquete region), and on slope to the E, ca. 3.5 km NW of Bajo Mono, *Grayum 6469* (BM); 3 km NW of Cerro Punta, along dirt road en route to Las Nubes region, *Hammel 1358* (BM, MO); 3 km below ridge on road from Cerro Punta to Alto Respinga, *Prather 1576* (TEX); valley of the upper Río Chiriquí Viejo, vicinity of Monte Lirio, *Seibert 290* (F, MO); along trail to Alta Respinga above town of Cerro Punta, *Skog 4009* (MO, RSA); vicinity of Boquete, Finca Collins, *Siern et al. 2050* (MICH, MO, US-2); NE of Cerro Punta about 3 km from the main road along the road to Las Cumbres, *Taylor 3338* (F, MO); Río Chiriquí Viejo valley, between El Volcán and Cerro Punta, *White 12* (GH, MO, NY, US).

*Cobaea gracilis* is the sister species to *C. penduliflora* of Venezuela. The two are morphologically very similar, but *C. gracilis* has anthers that are only 8–11 mm long and lacks long trichomes at the base of the lowermost leaflet pair, whereas *C. penduliflora* has anthers 11–15 mm long and the margin of the lowermost leaflet pair is long-ciliate basally.

Austin (1971) suggested that *C. panamensis* might be only a geographic variant of *C. gracilis* but did not place *C. panamensis* in synonymy, because he had not seen the type of *C. gracilis*. In the protologue of *C. panamensis*, based solely on the holotype, Standley (1914) stated that he did not see any specimens of *C. gracilis* and evidently relied on Oersted's (1856) protologue for the description of *C. gracilis*, which also was based solely on the type collection. The holotype of *C. panamensis* and the type collection of *C. gracilis* are different in the characters that Standley used to separate the two taxa (corolla color and pubescence of the calyx margin). Those specimens, however, are representative of extreme forms of a continuum of variation in the two characters over the range of *C. gracilis*, as defined here.

Lectotypification of *C. gracilis* is required, because there are three extant sheets of the type collection at C. One sheet is particularly well-preserved and is apparently the sheet from which most of the details of the original illustration were taken; it is designated the lectotype.

- 12. *Cobaea penduliflora*** (Karsten) Hooker f., Curtis's Bot. Mag. 95: tab. 5757. 1869.  
*Rosenbergia penduliflora* Karsten, Fl. Columb. 1: 27. 1858.—TYPE: VENEZUELA. Distrito Federal [?]: vicinity of Caracas, 1000 m, collector unknown (holotype: not located).  
*Cobaea hookeriana* Standley, Contr. U.S. Natl. Herb. 17: 451. 1914.—TYPE: Plate 5757 of Curtis's *Botanical Magazine*, vol. 95, 1869.

Stems woody, puberulent or villous at the nodes. Leaves green, with 6 leaflets; rachis 49–60 mm long, sparsely puberulent or glabrous; petiolules 3–7 mm long, puberulent or sometimes only slightly so; blades 40–110 mm long, 19–50 mm wide, sparsely puberulent on veins, margins minutely ciliate; upper and middle leaflet pairs obovate to elliptic, base acute to cordate, apex acute to acuminate; basal pair similar to upper pairs, the margin long-ciliate at the base. Inflorescence of 2–4 flowers; bracts fully expanded or occasionally abscised when mature, with 4–6 leaflets. Peduncles 3.8–10.7 cm long, puberulent at the apex and sometimes at the base. Pedicels 16.5–30.0 cm long, puberulent at the base and apex, curved along length and bent at the apex in fruit. Calyx segments 25–29 mm long, 4–7 mm wide, green, chartaceous, lanceolate, apex acute, margins plane, ciliate with minute trichomes, puberulent adaxially in a narrow zone about 1 mm from the margin, sometimes nearly glabrous, glabrous or sparsely puberulent near the base abaxially. Corollas green, sometimes suffused with purple, chartaceous, glabrous below the constriction at the apex of the nectar chamber externally but pubescent with long or short trichomes above, thinning towards the apex, glabrous internally except for the long-villous annulus; tube 13–18 mm long, 10–14 mm wide, campanulate, widest at the apex; lobes 42–62 mm long, more than twice as long as the tube, 4–7 mm wide near the base, 1.5–3.0 mm wide at the middle, linear, apex usually clawed, not inrolled at the margin, not imbricate, wrinkled in bud. Filaments 50–95 mm long, adnate basally for 4–12 mm, reflexed, not bent basally, not curved at the apex, coiling after dehiscence; anthers 11–15 mm long, 2–3 mm wide, greenish purple, linear-lanceolate, straight in bud, sometimes twisted after dehiscence, versatile. Styles 110–125 mm long; style branches 6.5–7.0 mm



long, terete, papillae short, covering nearly the entire surface (type II stigmas). Fruit 31–43 mm long, emaculate. Seeds 9–18 per fruit, 20–26 mm long, 10–13 mm wide, lacking scales; wings 2–8 mm wide. Chromosome number unknown. Fig. 10F.

Illustrations. Karsten (1858: tab. XIV); Hooker (1869: tab. 5757); House (1880); Brand (1907: fig. 8); Standley (1914: plate 20); Steyermark and Huber (1978: fig. 254B, as *C. hookeriana*).

Phenology. Collected in flower and fruit year-round.

Distribution (Fig. 23). Lowlands of Ecuador, Amazon Basin in Peru, and forests of the wet coastal mountains of Venezuela; 100–1400 m.

ADDITIONAL SPECIMENS EXAMINED. **Ecuador.** EL ORO: road Zaracay–Las Piedras, *Harling et al. 15637* (GB).—GUAYAS: Belao [Balao?], *Eggers s.n.* (F); Hacienda Trípoli, ca. 60 km SE of Guayaquil, *Haught 2880* (F, S, US); Playa Río Grande, San Ignacio, *Holmgren 77* (S); Guayaquil, *Pavón [Tafalla?] s.n.* (G-2, BM).—Province unknown: Jct. of the provinces of Guayas, Cañar, Chimborazo, and Bolívar, foothills of the western cordillera near the village of Bucay, *Camp E-3663* (AAU, US). **Peru.** CAJAMARCA: Prov. Santa Cruz, Dist. Catache, upper Río Zaña valley, ca. 5 km above Monte Seco on path to Chorro Blanco, *Dillon et al. 4363* (F).—SAN MARTÍN: prope Tarapoto, *Spruce 4353* (BM, BR, G-3, K-2, W). **Venezuela.** ARAGUA: prope coloniam Tovar, *Fendler 468* (F, G-2, GH, K, MO, NY-2).—DISTRITO FEDERAL: between La Guaira and Río Grande, *Curran & Haman 983* (GH, NY); Caracas, Apr 1867, *Ernst s.n.* (K); Caracas [but from plants cultivated at Kew], Dec 1868, *Ernst s.n.* (K); La Guaira–Caracas, *Kuntze 1361* (F, NY-2); en las márgenes del Río Chacarti, *Lasser 66* (VEN); Río Chacaíto, *Lasser 640* (US, VEN); Cerro Naiguatá, 7 km E de Hacienda Cocuizal (Tanques de Electricidad de Caracas), en la Quebrada Frontina, al lado de sendero, arriba del pueblo de Naiguatá, 7 Feb 1967, *Manara s.n.* (US, VEN); Parque Nacional El Avila, Quebrada Laja Urupal, entre Las Adjuntas y Loma Serrano, 23 Apr 1976, *Manara s.n.* (NY, VEN); Parque Nacional El Avila a un km E de los tanques de la E de C, 25 Feb 1977, *Manara s.n.* (F); Cordillera de La Costa, NE de Caracas, ruta Los Castillitos–El Rincón, sobre La Cordillera, *Morillo & Manara 773* (F, NY); camino El Rincón–Las Tunitas, SE de Maiquetía, vertiente N de la Cordillera de la Costa, *Morillo & Manara 1041* (VEN); around Caracas, Chacaíto Gorge, at the intake, *Pittier 10335* (GH, NY, US, VEN); Parque Nacional El Avila, Laja Urupal, between Quebrada Las Adjuntas and Loma Serrano, ca. 1–2 km from park headquarters, *Prather 1580* (TEX); between Caracas and La Guaira, *Rose & Rose 21705* (GH, US); Cerro Naiguatá, laderas pendientes del lado del mar que miran hacia el Norte, arriba del pueblo de Naiguatá, vecindad de Quebrada Frontina, 5 km al Suroeste de los tanques de la Electricidad de Caracas (Cocuizal), *Steyermark 91816* (F, NY, US, VEN); Caracas, *van Landsberge 215* (S).—FALCÓN: El Chorro, arriba de la chapa, *Flora Falcón Proyecto (HW, ES) 383* (MO); just below El Chorro along the road to the waterfall, between Currimagua and Coro, in Parque Nacional Sierra de San Luis, *Prather 1581* (TEX); Sierra de San Luis entre Currimagua y San Luis, *Steyermark 99090* (NY, US, VEN).—MIRANDA: El Hatillo, *Aristeguieta 3028* (VEN); Petare, *Moritz 230* (BM); La Providencia, *Pittier 13613* (F, MO, NY, US, VEN); Parque Nacional El Avila: vertiente sur, NNE de Caucaguita, a lo largo de la quebrada Tacamahaca (afluente de la quebrada El Encantado), *Steyermark et al. 113978* (NY, VEN).—YARACUY: Sierra de Aroa, 8 km NW of Cocorote on road to Aroa, 8 km SE of Los Cruceros, *Liesner & González 10114* (MO, VEN). "Western South America," 1885, *Pearce s.n.* (BM).

*Cobaea penduliflora* is very similar to *C. gracilis*, and the two are sister taxa. Distinguishing characters are discussed under *C. gracilis* (no. 11).

The description and especially the illustration in Karsten's protologue of *Rosenbergia* [= *Cobaea*] *penduliflora* differed considerably from those in *Curtis's Botanical Magazine* (Hooker 1869). Standley (1914) had no herbarium material of the species available for comparison and was apparently misled by the differences between the two illustrations and descriptions. He based *C. hookeriana* on the description and illustration in *Curtis's Botanical Magazine*, and typified the name with the plate. The illustration in *Curtis's Botanical Magazine* was drawn from garden-grown plants at Kew that were raised from seeds sent by A. Ernst from Caracas, Venezuela. It seems most likely that a modest amount of artistic license was taken in preparing the illustration, which was not uncommon at the time, as documented by others (Turner & Andrews 1986).

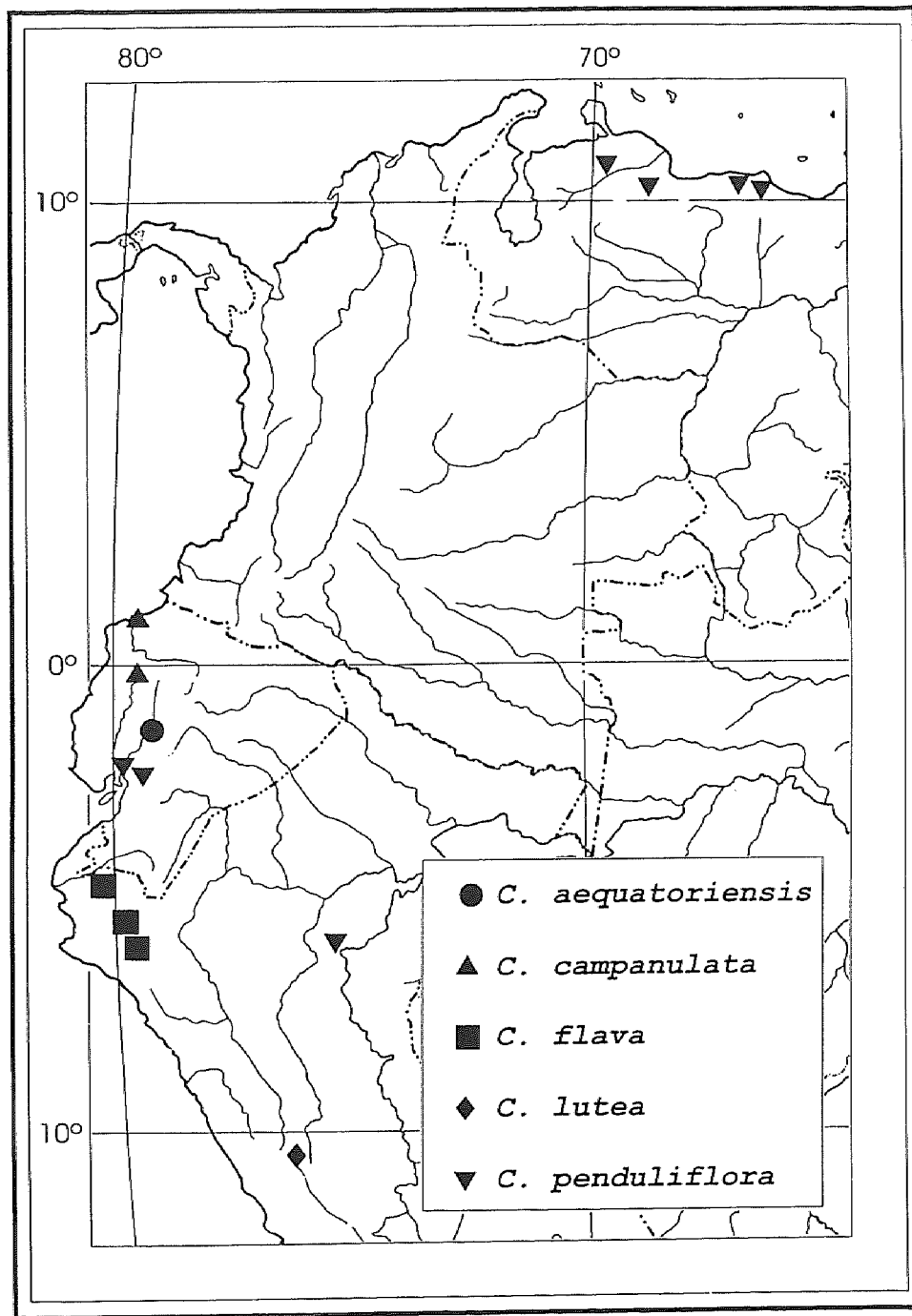


FIG. 23. Distribution of *Cobaea aequatoriensis*, *C. campanulata*, *C. flava*, *C. lutea*, and *C. penduliflora*. For the range of *C. lutea* in Central America, see Fig. 26; for its range in Mexico, see Fig. 27.

Pittier (1936), who had a great deal of experience with the Venezuelan flora, discussed this problem in detail and concluded that *C. hookeriana* is synonymous with *C. penduliflora*. I concur, for the following reasons: 1) no herbarium specimens have ever been associated with *C. hookeriana* and in examining all available material from Venezuela, I have not been able to locate any that match Standley's description; 2) type material of both taxa are said to be from the vicinity of Caracas, an area that is botanically well-known; 3) Hooker presumably saw the living material on which the illustration in *Curtis's Botanical Magazine* was based and the illustration in the protologue of *C. penduliflora*, but did not suggest that the two showed different species; 4) a herbarium specimen, with flowers, labeled "ex horte Kew 12/1868, Ernst. Caracas," at K is unquestionably identifiable as *C. penduliflora*. This specimen is most likely a part of the same material from which the illustration in *Curtis's Botanical Magazine* was prepared; it is one of only two specimens associated with Ernst (the second is a single fruit labeled "Caracas, Ernst . . . [illegible] . . . 4/67" and is likely the original collection). The date "12/1868" on the flowering specimen corresponds precisely with the information given by Hooker (1869) that the material flowered in the Palm House at Kew in December 1868.

The type of *C. penduliflora* is unknown. Most of Karsten's types were his collections, but Hooker (1869) indicated that Fendler had "discovered" the species, and the earliest collection I have seen is indeed *Fendler 468*. The location of Karsten's types is unknown, and there is no indication that Karsten saw Fendler's collection.

The epithet is a misnomer; the flowers are pendulous only if there are no structures to which the tendrils of the bracts may attach to support the inflorescence. Unfortunately, all illustrations of the species, except for the excellent figure by Manara in *Flora del Avila* (Steyermark & Huber 1978), perpetuate the original error.

13. *Cobaea aequatoriensis* Asplund, Svensk Bot. Tidskrift 48: 550. 1954.—TYPE: ECUADOR. Chimborazo: Prov. Tungurahua, ca. Huigra, ca. 1200 m, 10 Jul 1939, *Asplund 7739* (holotype: S; isotypes: G! S! US!).

Stems woody, glabrous or puberulent at the nodes. Leaves green, with 6 leaflets; rachis 45–72 mm long, glabrous or sparsely puberulent, especially along the channel; petiolules 7–14 mm long, glabrous to puberulent; blades 50–130 mm long, 18–58 mm wide, glabrous or inconspicuously puberulent along the veins, margins minutely ciliate; upper and middle leaflet pairs elliptic to elliptic-obovate, base truncate to cordate, apex rounded to acute to acuminate; basal pair similar, the margins long-ciliate at the base. Inflorescence of 1–5 flowers; bracts fully to poorly developed, with 6 leaflets. Peduncles 5.5–12.2 cm long, puberulent to sparsely pubescent with occasional long trichomes near the apex. Pedicels 30–37 cm long, villous, slightly curved along the length in fruit. Calyx segments 17–29 mm long, 4–7 mm wide, green, chartaceous, lanceolate to lanceolate-ovate, apex acute, margins plane, long-ciliate, glabrous or nearly so adaxially except for a band of whitish puberulence along the upper 2–3 mm of the midvein, sparsely villous abaxially. Corollas green, chartaceous, glabrous basally, sparsely villous above externally, glandular-puberulent on the upper tube and lower lobe, thinning towards the apex, glabrous internally except for the long-villous annulus; tube 9–13 mm long, 17–20 mm wide, campanulate, widest at the apex; lobes 26–45 mm long, more than twice as long as the tube, 6–8 mm wide near the base, 2–5 mm wide at the middle, linear, apex erose, not inrolled at the margin, not imbricate, wrinkled in bud. Filaments 30–47 mm long, adnate basally for 6–10 mm, reflexed, not bent basally, not curved at

the apex, coiling after dehiscence; anthers 10–13 mm long, 2–3 mm wide, brownish purple, lanceolate, straight in bud, twisted after dehiscence, versatile. Styles 45–55 mm long; style branches 8–10 mm long, terete, papillae short, covering nearly the entire surface (type II stigmas). Fruit 35–42 mm long, emaculate. Seeds 9–18 per fruit, 17–20 mm long, 11–13 mm wide, lacking scales; wings 1–3 mm wide. Chromosome number unknown. Fig. 11A.

Illustration. Asplund (1954: fig. 1).

Phenology. Collected in flower and fruit in July and August.

Distribution (Fig. 23). Ecuador; tropical deciduous forest; 1200–1500 m.

ADDITIONAL SPECIMENS EXAMINED. **Ecuador**. CHIMBORAZO: Km 16.7 on the road to Huigra, *Panero & Clark 2918* (CAS, MEXU, MO, QCA, QCNE, RSA, TEX, US); vicinity of Huigra, mostly on the Hacienda de Licay, *Rose et al. 22273* (BM, F, G, GH-2, MO-3, S, US-2); Hacienda de Licay near Río Chanchan, hill N of Huigra on old road from Guayaquil to Riobamba, trail starting from railroad track ca. 1 km to E of town and up-hill to stream crossing, *Smith 2054* (QCNE, WIS-2).

*Cobaea aequatoriensis* is sister taxon to a clade composed of *C. campanulata* and *C. flava*, from which it can be easily distinguished by its long, linear corolla lobes and reflexed filaments. *Cobaea aequatoriensis* shares these character states with *C. gracilis* and *C. penduliflora*. The densely long-ciliate calyx segments of *C. aequatoriensis* readily distinguish it from *C. gracilis* and *C. penduliflora*.

14. ***Cobaea flava*** Prather, *Brittonia* 48: 114. 1996.—TYPE: PERU. Piura: Prov. Ayavaca: valley of the river Quirós, 1500 m, May 1912, *Weberbauer 6397* (holotype: GH!; isotypes: F! G! US-2!).

Stems herbaceous, glabrous or occasionally pubescent with long scattered trichomes, especially at the nodes. Leaves green, with 6 leaflets; rachis 25–53 mm long, glabrous; petiolules 3–6 mm long, glabrous; blades 37–85 mm long, 16–49 mm wide, pubescent along the veins abaxially, margins minutely ciliate; upper and middle leaflet pairs elliptic to obovate, base acuminate to cordate, apex acute to acuminate, basal pair similar to upper pairs except the margins long-ciliate at the base. Inflorescence of 1–5 flowers, bracts fully expanded, with 6 leaflets. Peduncles 6.7–11.0 cm long, glabrous. Pedicels 10.5–16.0 cm long, pilose with scattered long trichomes, especially at the base and apex, sometimes curved along the length in fruit. Calyx segments 18–23 mm long, 4–6 mm wide, green, membranous, lanceolate to slightly oblanceolate, acute to acuminate, the margins ciliate with both long and short trichomes, sometimes tomentulose adaxially near the apex, with a few long scattered trichomes abaxially. Corollas light yellow or white, membranous, glabrous externally near the base, increasingly glandular-puberulent towards the apex, glabrous internally except for the long-villous annulus; tube 30–40 mm long, 17–29 mm wide, funnelform to narrowly campanulate, widest at the apex; lobes 11–17 mm long, much shorter than the tube, 10–15 mm wide, broadly ovate, apex rounded, emarginate, not inrolled at the margin, imbricate, wrinkled in bud. Filaments 23–34 mm long, adnate basally for 8–14 mm, positioned ventrally, slightly bent basally, slightly curved at the apex, neither coiling nor becoming undulate after anther dehiscence; anthers 4.0–8.5 mm long, 1–2 mm wide, yellow, narrowly lanceolate, straight in bud, twisted after dehiscence, introrse. Styles 28–43 mm long; style branches 3.5–7.0 mm long, terete, papillae short, covering nearly the entire surface

(type II stigmas). Fruit 32–47 mm long, emaculate. Seeds 9–15 per fruit, 9–13 mm long, 6–8 mm wide, lacking scales; wing 1–2 mm wide. Chromosome number unknown. Figs. 11B, 24.

Phenology. Collected in flower and fruit from April to June.

Distribution (Fig. 23). Peru; lower montane forests of the western Andes; 1000–1500 m.

ADDITIONAL SPECIMENS EXAMINED. **Peru.** CAJAMARCA: Prov. Contumazá, corlós arriba de Cascas, *Sagástegui et al.* 4364 (F).—PIURA: Prov. Huancabamba, Distrito Canchaque, Chorro blanco, *Díaz S. & Baldeón* 2469 (AAU, F, MO, NY); Prov. Ayavaca, arriba de los Caracuchos (Sullana–Ayavaca), *López et al.* 7705 (US); Prov. Huancabamba, immediately W of Canchaque, *Stork* 11395 (GH, UC); Prov. Ayavaca, W slopes of Andes below Frias, *Weberbauer* 6425 (F, G, GH, US).—TUMBES: Cerros de Amotape, Quebrada Los Conejos and adjacent ridge, ca. 25 km SE of Cherrelique, *Gentry & Díaz S.* 58300 (MO, TEX).

*Cobaea flava* closely resembles its sister taxon, *C. campanulata*. Both have rounded, emarginate corolla lobes and anthers that are clustered ventrally in the corolla. They are different in that *C. flava* has pedicels that are sparsely pilose with long hairs, especially near the base and apex; yellow corollas that are membranous when dry; and stamens that are included within the corolla. *Cobaea campanulata* has pedicels that may be puberulent with very short hairs but are never pilose; corollas that are green to greenish yellow with purple or red streaks and are chartaceous, but not membranous; and stamens that are exerted from the corolla.

There has been a great deal of taxonomic confusion concerning three taxa in South America, *C. campanulata*, *C. flava*, and *C. lutea*. Three of the collections of *C. flava* cited above (*Weberbauer* 6397, *Weberbauer* 6425, *Stork* 11395) were cited as the only vouchers of *C. campanulata* in *Flora of Peru* (Gibson 1967) and one of them (*Díaz S. & Baldeón* 2469) was cited as the only voucher of *C. lutea* in the *Catalogue of the Flowering Plants and Gymnosperms of Peru* (Brako & Zarucchi 1993). *Cobaea campanulata* is apparently endemic to Ecuador, even though many treatments and floras cite it as occurring in Peru or Chile (see discussion under *C. campanulata*, no. 15).

*Cobaea lutea* is present in central Peru (*Woytkowski* 7330; MO-2, S, UC), but I have seen no collections of the species from northern Peru, where *C. flava* is found, nor from Ecuador, where *C. campanulata* is found. The type of *C. lutea* may be from Ecuador, and Dodson and Gentry (1978) mistakenly referred some collections of *C. campanulata* to *C. lutea* (see discussion of *C. campanulata*, no. 15). *Cobaea flava* and *C. campanulata* differ from *C. lutea* by their ovate corolla lobes with rounded, emarginate apices, short (5–7 mm) style branches, and anthers that are clustered at the ventral side of the corolla. *Cobaea lutea* has deltate, acute corolla lobes; longer style branches [(8–) 10–13 mm]; and anthers that are held erect from the corolla.

*Cobaea flava* is named for its distinctive corolla color. It is the only species of the genus with yellow flowers, though two other species have greenish yellow flowers. The specific epithet of *C. lutea* implies the presence of a yellow corolla, but the species is misnamed; it consistently has green flowers.

15. *Cobaea campanulata* Hemsley, Garden (London 1871–1927) 17: 352. 1880. *Rosenbergia campanulata* (Hemsley) House, Muhlenbergia 4: 24. 1908.—TYPE: ECUADOR. Esmeraldas: Atacames, Dec 1836, *Barclay* 747 (holotype: K!; isotypes: K! BM!).

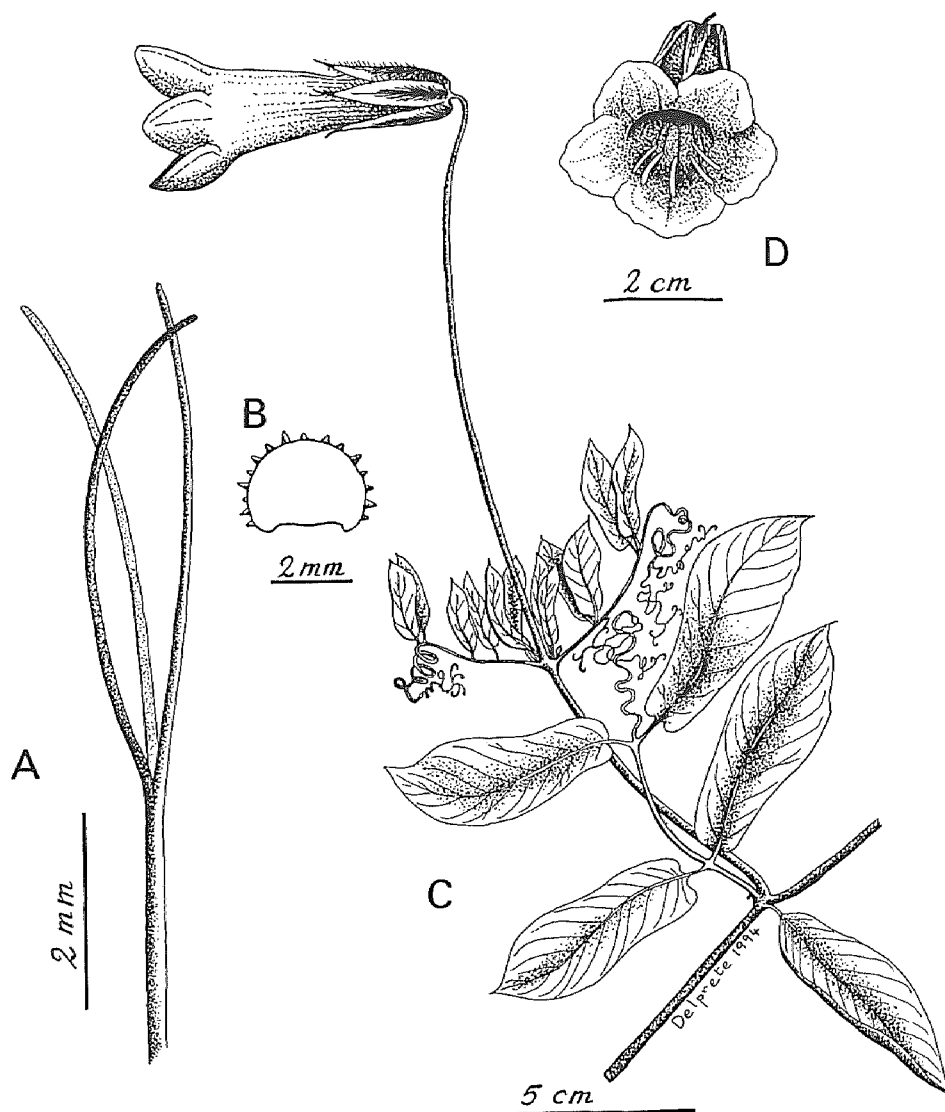


FIG. 24. *Cobaea flava*. A. Distal portion of style and style branches. B. Cross section of style branch; the lower part of the diagram is the abaxial surface. C. Portion of the habit. D. Front view of the flower. (Based on: Stork 11395, GH.)

Stems herbaceous, glabrous. Leaves green, with 6 leaflets; rachis 32–64 mm long, glabrous; petiolules 3–12 mm long, glabrous; blades 32–129 mm long, 16–54 mm wide, glabrous except for the minutely ciliate margins; upper and middle leaflet pairs elliptic to obovate, base acuminate to cordate, apex acute to acuminate; basal pair similar to upper pairs except the margins often long-ciliate at the base. Inflorescence of 2–5 flowers; bracts fully expanded or occasionally poorly developed, with 4 leaflets. Peduncles 3.0–8.7 cm long, sparsely puberulent at the base and the apex, sometimes slightly so along length. Pedicels 20–28 cm long, sparsely puberulent at the base and apex, slightly undulate along

the length in fruit. Calyx segments 17–26 mm long, 4–6 mm wide, green, membranous, lanceolate, apex acute, with a narrow band of tomentose pubescence adaxially, minutely and evenly puberulent abaxially. Corollas green to greenish yellow with purple streaks, membranous, glabrous externally near the base, increasingly puberulent with glandular trichomes towards the apex, eglandular-pubescent at sinuses, glabrous internally except for the long-villous annulus; tube 24–30 mm long, 20–26 mm wide, campanulate, widest at the apex; lobes 11–19 mm long, much shorter than the tube, 11–16 mm wide, ovate, apex rounded, not inrolled at the margin, imbricate, wrinkled in bud. Filaments 32–50 mm long, adnate basally for 4–6 mm, positioned ventrally, slightly bent at the base, slightly curved at the apex, coiling after dehiscence; anthers 4.5–5.5 mm long, 1–2 mm wide, yellow, narrowly oblong to lanceolate, straight in bud, not twisted after dehiscence, versatile. Styles 41–50 mm long; style branches 3–5 mm long, terete, papillae short, covering nearly the entire surface (type II stigmas). Fruit 50–56 mm long, emaculate. Seeds 4–12 per fruit, 19–22 mm long, 8–10 mm wide, lacking scales; wings 2–6 mm wide. Chromosome number unknown. Figs. 11C, 25.

Additional illustration. Dodson and Gentry (1978: fig. 235A, as *C. lutea*).

Phenology. Collected in flower in February, July, August, and December, and in fruit in February, July, and December.

Distribution (Fig. 23). Ecuador; rainforests; 200–400 m.

ADDITIONAL SPECIMENS EXAMINED. **Ecuador.** LOS RÍOS: Río Palenque Field Station halfway between Quevedo and Santo Domingo de los Colorados, *Gentry 9931* (MO), *Gentry 10149* (MO, NY), *Gentry 10216* (MO, NY); El Centro Científico Río Palenque, Km 47 on road Santo Domingo de los Colorados–Quevedo, *Knudsen & Tollsten 109* (GB, QCNE, S); Km 56 Quevedo to Sto. Domingo, *McMahon 4235* (US); Río Palenque Field Station, 1 km from entrance, ca. 600 m from station guest house, *Panero & Clark 2998* (CAS, MEXU, QCA, QCNE, RSA, TEX, US); Río Palenque Field Station, *Webster 22941* (DAV).—PICHINCHA: ca. 10 km down the Río Baba, entrance road at Km 7, Santo Domingo to Quito, *Dodson et al. 3833* (AAU, F, GH).—Province unknown: locality unknown, *André 469* (F, K), *André 470* (K).

*Cobaea campanulata* is very similar to its sister taxon, *C. flava*. Characters by which to distinguish them, and to distinguish these taxa from *C. lutea*, are discussed under *C. flava* (no. 14).

The location given on the label of the isotype at BM is Atacames, Esmeraldas, and that given on the two K sheets is Atacames, Peru. It is clear, then, that the collection is from Atacames, Prov. Esmeraldas, in Ecuador, as Hemsley (1880) recognized in the protologue. When Brand (1907) stated that *C. campanulata* was from “Nord-Chile: Atacama,” he evidently confusing Atacames, Ecuador, with the Atacama Desert in Chile. This error was repeated in House (1908), Standley (1914), Grant (1959), and Gibson (1967). No specimens of *C. campanulata* from Chile have been seen by me nor cited in the literature.

*Cobaea campanulata* was known from only two collections until several workers collected it at the Río Palenque Science Center in Ecuador within the last 30 years. The specimens were mistaken for *C. lutea* by Dodson and Gentry (1978). All the specimens, or duplicates thereof, cited by them as *C. lutea*, have been examined by me and are *C. campanulata*. Because the illustration and description of *C. lutea* in Dodson and Gentry (1978) were compiled from only the specimens they cite, they describe *C. campanulata* well. Some specimens of *C. flava* from Peru have been treated as *C. campanulata*, which has led to mistaken reports of the latter in Peru (Gibson 1967; Brako & Zarucchi 1993).

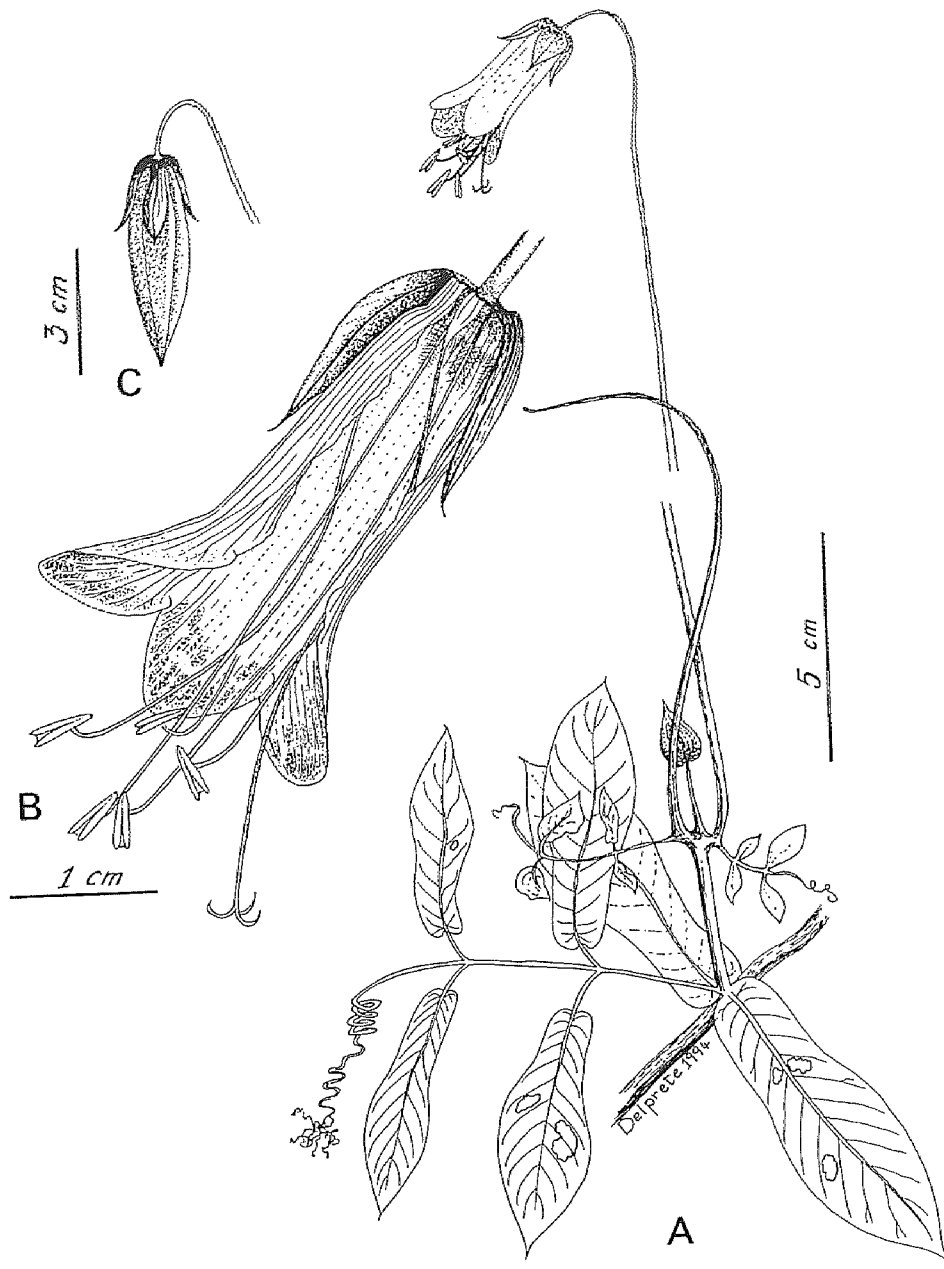


FIG. 25. *Cobaea campanulata*. A. Portion of the habit. B. Flower, part of calyx and corolla removed. C. Fruit. (Based on: Panero & Clark 2998, TEX.)



16. *Cobaea lutea* D. Don, Edinburg Phil. J. 10: 112. 1824. *Cobaea macrostema* Pavón ex D. Don, Edinburg Phil. J. 10: 112. 1824, pro syn. *Cobaea macrostema* Pavón ex Hooker, Curtis's Bot. Mag. 67: tab. 3780. 1840, nom. superfl. *Cobaea acuminata* DC. ex Hooker, Curtis's Bot. Mag. 67: tab. 3780. 1840, pro syn. *Rosenbergia macrostoma* (Pavón ex Hooker) House, Muhlenbergia 4: 24. 1908.—TYPE: ECUADOR. Quito: Guayaquil[?], *Tafalla s.n.* [?] (holotype: not located; isotypes: BM! G-2!).
- Cobaea villosa* Standley, Contr. U.S. Natl. Herb. 17: 454. 1914. *Cobaea lutea* f. *villosa* (Standley) D. N. Gibson, Fieldiana: Botany 31: 354. 1968.—TYPE: EL SALVADOR. San Salvador: vicinity of San Salvador, *Renson 213* (holotype: US!; isotype: NY!).
- Cobaea viorna* Standley, Contr. U.S. Natl. Herb. 17: 453. 1914. *Cobaea lutea* f. *viorna* (Standley) D. N. Gibson, Fieldiana: Bot. 31: 354. 1968.—TYPE: GUATEMALA. San Marcos: between El Rodeo and Malacatán, 420–1050 m, 20 Jan 1895, *Nelson 3745* (holotype: US!; isotype: US!).
- Cobaea steyermarkii* Standley, Field. Mus. Bot. 22: 271. 1940.—TYPE: GUATEMALA. San Marcos: Volcán Tajumulco, ca. El Porvenir, 1300–2000 m, 14 Mar 1940, *Steyermark 37759* (holotype: F!).

Stems usually slender, woody, glabrous or puberulent at the nodes. Leaves green, rarely suffused with purple, with 6 leaflets; rachis 23–70 mm long, glabrous or puberulent along the channel; petiolules 3–7 mm long, puberulent, especially at the base; blades 24–110 mm long, 11–60 mm wide, glabrous or puberulent along the veins, margins minutely ciliate and sometimes long-ciliate at the base; upper and middle leaflet pairs elliptic to elliptic-oblongate, rarely obovate, base acute to truncate to cordate, apex acute to acuminate; basal pair similar, the margins long-ciliate at the base. Inflorescence of 1–5 flowers; bracts fully expanded, with 6 or rarely 4 leaflets. Peduncles (2.3–) 6.3–10.0 (–15.0) cm long, glabrous or puberulent at the base and apex. Pedicels (8.2–) 14.3–25.0 cm long, glabrous or puberulent at the base and apex, tightly coiled in fruit. Calyx segments 19–28 mm long, 3.5–8.0 mm wide, green, rarely suffused with red or purple, chartaceous, lanceolate to lanceolate-ovate, apex acute to acuminate, margins plane, minutely ciliate and sometimes long-ciliate, puberulent adaxially near the apex and in a narrow zone about midway between the margin and midvein, decreasing below, glabrous abaxially. Corollas green, rarely greenish yellow or suffused with purple or red, chartaceous, puberulent or sometimes villous externally on the upper tube and the base of the lobes, decreasing above, glabrous below, glabrous internally except for the long-villous annulus; tube 17–37 mm long, 19–35 mm wide, campanulate, widest below the apex; lobes 13–30 mm long, less than twice as long as the tube, 10–18 mm wide, broadly ovate, narrowing to an acuminate to long-acuminate apex, not inrolled at the margin, barely imbricate, wrinkled in bud. Filaments 34–80 mm long, at least some reaching 58 mm, adnate basally for 4–9 mm, emergent or slightly reflexed, not curved at the apex, both becoming undulate and coiling after dehiscence; anthers 7–14 mm long, 1.5–2.5 mm wide, yellow, linear to lanceolate, straight in bud, twisted after dehiscence, versatile. Styles 65–78 (–90) mm long; style branches 8–13.5 mm long, terete, papillae short, covering nearly the entire surface (type II stigmas). Fruit 20–58 mm long, emaculate. Seeds 6–21 per fruit, 16–21 mm long, 11–12 mm wide, lacking scales; wings 2–4 mm wide. Chromosome number unknown. Figs. 1D, 2, 6, 11D.

Additional illustrations. W. J. Hooker (1840: tab. 3780); Gibson (1970: fig. 15); Chickering (1973: fig. 21, as *C. villosa*; mistakenly cited as fig. 13 in the text).

Phenology. Collected in flower and fruit from June to February.

Distribution (Figs. 23, 26, 27). Mexico (Chiapas, Colima, Guerrero, and Jalisco), Guatemala, El Salvador, Honduras, and Peru (Pasco); cloud forests, semi-deciduous forests, and forested foothills of the Pacific Coastal regions of North and South America; 300–2200 (–3000) m.

ADDITIONAL SPECIMENS EXAMINED. **Mexico.** CHIAPAS: Mpio. Cacahoatán, 1–2 km S of Cacahoatán, *Breedlove & Ahmeda 47758* (CAS, MO, NY), *Breedlove & Smith 31572* (DS, MO, RSA, TEX); along the road from the Mexico/Guatemala border to Cacahoatán, 2.7 km S of Cacahoatán, *Prather 1080b* (TEX); Mpio. Cacahoatán, Unión, *Ventura & López 470* (BM, G, NY); Mpio. Cacahoatán, Unión Roja, orilla de camino, *Ventura & López 2955* (IEB, RSA).—COLIMA: Mpio. Comala, Rancho El Jabalí, 22 km (airline) NNW of Colima in the SW foothills of the Volcán de Colima, canyon above Lago El Jabalí, *Sanders 10360* (CAS); Mpio. Comala, Rancho El Jabalí, 22 km (airline) N of Colima in the SW foothills of the Volcán de Colima, from the Jabalí main gate to Hac. San Antonio along the road to Comala, *Sanders 11946* (CAS); Mpio. Comala, Rancho El Jabalí, 22 km (airline) NNW of Colima in the SW foothills of the Volcán de Colima, margins of Lago Epazote, *Vázquez 442* (CAS).—GUERRERO: Dto. Montes de Oca, San Antonio, *Hinton 11671* (F, GH, K, MO, NY, RSA, UC, US); along Route 134 between Ciudad Altamirano and the intersection with Route 200, 19.2 km N of San Antonio, *Prather 1220* (TEX); same original locality, flowering voucher grown in University of Texas greenhouse, *Prather 1272* (TEX).—JALISCO: Sierra de Manantlán Biosphere Reserve, near Colima boundary, zone of permanently cultivated areas intercalated with extensive chaparral, right below SE edge of Cerro Toxín in bottom of Arroyo Pitahayas, 1 km NE of Toxín, barely N of Puerto de Toxín—La Loma crossroads, along El Sauz—San Pedro Toxín rd, 13 km (airline distance) NNE of Minatitlán, 39 km due NW of Colima, *Cochrane et al. 12268* (MSC, WIS-2); Mpio. Zapotitlán, Rancho El Jabalí, 22 km (airline) N of Colima in the SW foothills of the Volcán de Colima, La Joya area, N of the airstrip and S of Arroyo Santa Cruz, E of Cerro El Campanario, *Sanders 11666* (CAS).—State unknown: locality unknown, *Sessé et al. 5026* (F).

**Costa Rica.** ALAJUELA: Calera de San Ramón, *Brenes 6468* (F, NY; see discussion below). **El Salvador.** AHUACHAPÁN: locality unknown, *Padilla 415* (US).—LA LIBERTAD: Mpio. Antiguo Cuscatlán, Laderas de la Laguna, *Berendsohn & Stevens 1221* (F, MO).—SAN SALVADOR: City of San Salvador, *Bernoulli 25* (K, NY); Tonacatepeque, *Calderón 231* (US); locality unknown, *Dammann & Co. 72* (K); city of San Salvador, *Seiler 720* (F); ca. San Salvador, *Standley 19162* (GH, NY, US); ca. Tonacatepeque, *Standley 19479* (GH, NY, US); ca. San Salvador, *Velasco 8882* (GH, US-2).—SAN VICENTE: roadside overlooking valley of San Vicente, 49 km E of San Salvador, *Carlson 639* (F).—Department unknown: locality unknown, *Choussy 80* (US). **Guatemala.** CHIMALTENANGO: locality unknown, *Alameda & Johnson 183* (F).—CHIQUMULA: divide on the railway above El Rincón, *Standley 74671* (F, NY); llanos around Ipala, *Steyermark 30318* (F); Montaña Nonojá, 3–5 mi E of Camotán, *Steyermark 31727* (F-2).—ESCUINTLA: common about Escuintla, Nov 1860, *Hayes s.n.* (GH); above Palín, *Standley 59857* (ECON, F), Finca Monterrey, Volcán de Fuego, *Standley 64538* (F, NY).—GUATEMALA: San José Pinula, 24 km de la entrada por carretera a El Salvador por camino de tierra que pasa por granja experimental del Ejército, pasada bifurcación a San José Pinula, *Cabrera et al. 82.426a* (MO); along slopes of Lago de Amatitlán, below Morán, *Steyermark 52149* (F).—JALAPA: Laguna de Ayarza, *Heyde & Lux 3987* (G-2, GH, K, MO, US-2).—JUTIAPA: on CA1, 3.2 km E of the junction with CA8, en route to city of Jutiapa, *Prather 1011* (TEX); same original locality, flowering voucher grown in University of Texas greenhouse, *Prather 1273* (TEX); ca. Jutiapa, *Standley 75081* (F), *Standley 75550* (F); ca. San José Acatempa, *Standley 77570* (F); ca. El Molino, *Standley 78487* (F).—QUETZALTENANGO: prope "Sunil" [Zunil?], *Hartweg 543* (BM, G-2, K-2, NY, W-2); 4.3 km S of the village of Zunil along the toll road "CITO" en route to Retalhuleu, *Prather 1080a* (TEX); same original locality, flowering voucher grown in University of Texas greenhouse, *Prather 1274* (TEX); ca. 3 km N of Zunil on "CITO" toll road, in small ravine on the NW side of the road, *Prather 1507* (TEX); ca. 1 km N of Zunil on "CITO" toll road, *Prather 1514* (TEX); locality unknown, *Vaght 286* (US).—RE-TALHULEU: Río Coyote, along road 4 km W of Retalhuleu, *Standley 87494* (F).—SACATEPÉQUEZ: Pachatá, near San Lucas, *Anderson 4609* (F, MO); ca. 20 km W of Guatemala City on road to Antigua (Carretera Nacional 14), near dirt road to San Miguel Milpas Altas, *Davidson 3275* (F, RSA, UC); Antigua, *Hunnewell 17215* (GH); Volcán Agua, *Molina 21065* (F, GH, NY); Volcán Agua, between Sta. María de Jesús and San Juan Obispo, *Molina R. & Molina 24901* (F, MO-2, US); Finca Sta. Teresa of Sta. Lucía Milpas Altas, *Molina R. & Molina 27092* (F, MICH, US); 2 km E of Parras, ca. 9 km NW of Antigua en route to Chimaltenango, *Prather 1501* (TEX); 3.7 km from Antigua on road to Santa María de Jesús, *Prather 1503* (TEX); Volcán de Fuego, Alotemango, Sep

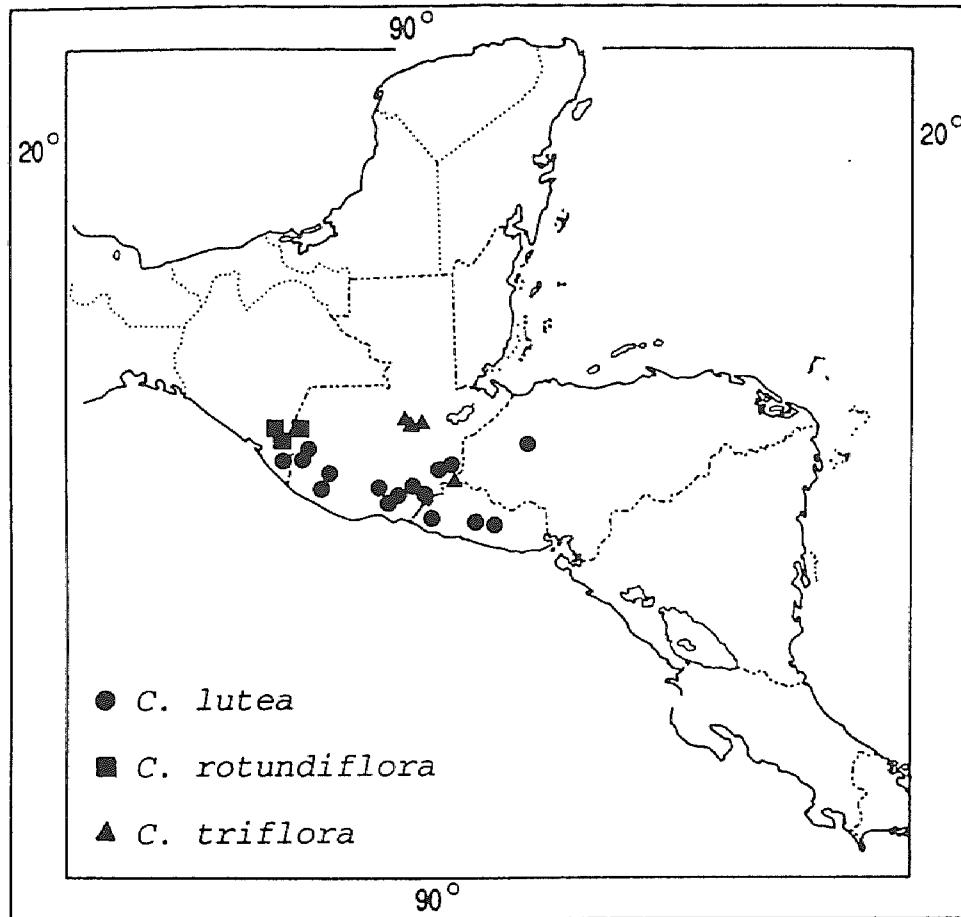


FIG. 26. Distribution of *Cobaea rotundiflora* and *C. triflora*, and of *C. lutea* in Central America. For the range of *C. lutea* in South America, see Fig. 23; for its range in Mexico, see Fig. 27.

1873, *Salvin s.n.* (K), Apr 1874, *Salvin s.n.* (W); San Lucas, *Seler & Seler 2452* (GH, NY, US); Volcán de Agua, N of Santa María de Jesús, *Standley 59393* (F-2); ca. Pastores, *Standley 59939* (F); Volcán Agua, above Sta. María de Jesús, *Webster et al. 12835* (DAV-2, F, MO, TEX).—SANTA ROSA: on Dept. Jutiapa border, ca. 1/2 km W of fork of Jutiapa–Villa Nuevo, E of Culiapa, 27 Dec 1975, *Iltis G-46* (WIS); along CA1, 16.2 km E of Culiapa, *Prather 1010* (TEX); along CA1 ca. 3 km W of the junction of CA1 and CA8, E of Culiapa, *Prather 1022* (TEX); same original locality, flowering voucher grown in University of Texas greenhouses, *Prather 1270* (TEX); along road SE of Barberena, *Standley 77748* (F); ca. Culiapa, *Standley 77979* (F).—Department unknown: on a journey from Guatemala [City] to Chiquimula, *Hayes 41* (GH, US); locality unknown, *Heyde 240* (US-2); Villa de Guadalupe, *García S. 1387* (F). **Honduras.** SANTA BÁRBARA: 10 km W de Lago Yojoa, *Clewell & Hazlett 3853* (MO).

**Peru.** PASCO: Villa Rica, *Woytkowski 7330* (MO-2, S, UC).

*Cobaea lutea* closely resembles *C. rotundiflora* and *C. triflora*. From these it can be easily distinguished by its acuminate corolla lobes and its long-exserted stamens. In South America it has been confused with *C. campanulata* and *C. flava*. Characters which

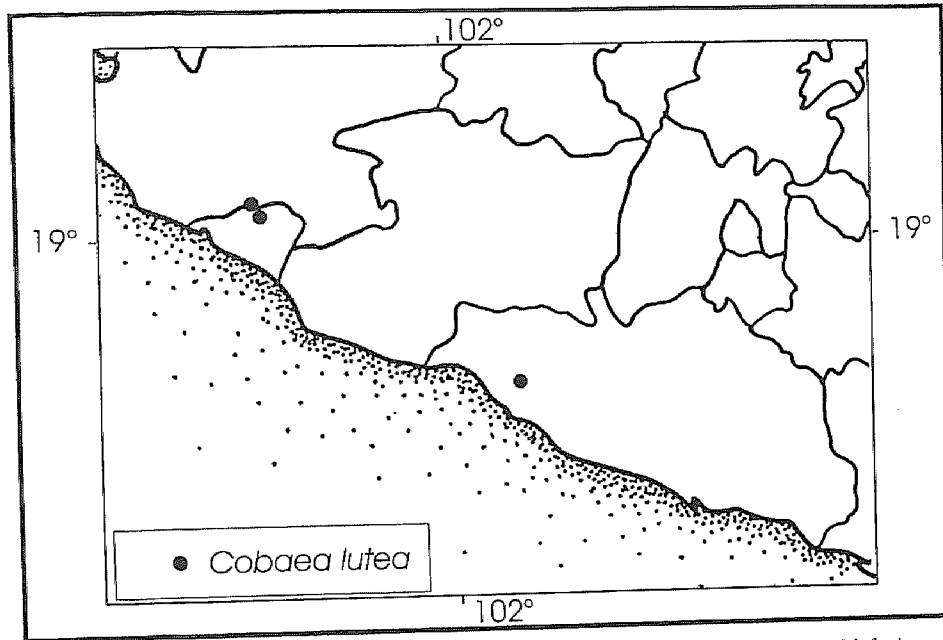


FIG. 27. Distribution of *Cobaea lutea* in Mexico. For its range in Central America, see Fig. 26; for its range in South America, see Fig. 23.

distinguish these taxa are discussed under *C. flava* (no. 14). *Cobaea lutea* also resembles *C. aschersoniana* (no. 10); character states distinguishing the two species are given in the discussion of the latter species.

The length of the corolla lobes, length and position of the stamens, and pubescence of the calyx segments are highly variable over the range of *C. lutea*. This variation is partitioned mainly among, rather than within, populations and is probably at least partly the result of the (facultatively?) autogamous nature of the species. Three segregates have been described, which do not deserve recognition: *C. steyermarkii*, *C. villosa*, and *C. viorna*. *Cobaea steyermarkii* is based on a teratological form that I have observed in the field and in the greenhouse. In this form the development of the corolla is arrested at about 1–2 cm, but the stamens continue to grow, sometimes to their typical length. The flower on the holotype has long since been destroyed, but from the description and the morphological information from the remaining type material it is clear that *C. steyermarkii* is a synonym of *C. lutea*. Gibson (1968) reduced both *C. villosa* and *C. viorna* to forms of *C. lutea*. I believe that recognition of these taxa as varieties, subspecies, or species is not warranted, because the characters in which they differ from *C. lutea* are vestiture characters, and there is little geographic cohesion to these characters. The vestiture characters might even be misleading, because there is a tendency for the long-villous hairs to break off in more mature flowers or older specimens. It may be, however, that detailed field work may uncover patterns of variation in this species that are useful to recognize as formal taxa.

*Cobaea lutea* has a very confusing nomenclatural history. In his very brief protologue, Don (1824) cited in synonymy the manuscript name *C. macrostema* Pavón. Most later authors ignored Don's name and applied Pavón's. W. J. Hooker (1840) was the first

to validate *C. macrostema*; he provided a complete description and Latin diagnosis, as well as an illustration. Bentham and Hooker (1845) cited "Pav. in Hook." as the authority of *C. macrostoma*, creating an orthographic error of *C. macrostema*. Brand (1907) repeated the orthographic error but attributed the name to "Pav. ex Don," as well as proposing the new combination, *C. macrostoma* var. *triflora* (Donn. Sm.) Brand [= *C. triflora*]. House (1880) repeated the orthographic error and made the new combination "*Rosenbergia macrostoma* (Pav.) House." All five authors who used the epithet "*macrostema*" or its orthographic variant cited *C. lutea* in synonymy. Standley (1914) was the first to recognize that Don's name has priority.

The type of *C. lutea* was said by Don to be "*in Herb. Pavón nunc Mus. Lamb.*" The Lambert collection was auctioned to various buyers in 1842 and the ultimate disposition of many of the lots is unknown (McVaugh 1987), but I was able to locate four sheets that are presumably from the Pavón material sent to Lambert, three at G and one at BM. Among the three G sheets, one has an inflorescence and flower of *C. lutea*, one has an inflorescence, fruit, and immature flower (in the envelope) of *C. penduliflora*, and the third has fruits of both species, *C. lutea* on the left (with the diagnostic coiled pedicels) and two of *C. penduliflora* on the right (with very long pedicels characteristic of *C. penduliflora* from western South America). All three of these sheets are labeled "Fl. Huayaquil Herb. Pavón" and on each the word "Huayaquil" is struck out; on the mixed sheet "Guatemala" is written in its place. The material from BM has a flower of *C. lutea* and is labeled "Fl. Huayaquil Herb. Pavón." Thus, Don may have examined a mixed collection composed of Tafalla material from Guayaquil (*C. penduliflora*) and Sessé and Mociño material from Guatemala (*C. lutea*). Don's description, although brief, clearly describes the taxon known today as *C. lutea*, because he states that the corolla is small and the upper stamen is long-exserted. The corolla of *C. penduliflora* is larger than that of *C. scandens* (the only other species described at the time) and the five stamens of *C. penduliflora* are equally exserted; some forms of *C. lutea* have one or two lower stamens that are much reduced in length. If there were no mature flowers of *C. penduliflora* among the specimens available to Don, he may not have realized there was material from two species. In the protologue Don states that the type was Tafalla material from Guayaquil but later told Hooker that the material was probably from Mexico (W. J. Hooker 1840). *Cobaea lutea* is otherwise unknown from Ecuador but is common in parts of Mexico; *C. penduliflora* has been collected from the region of Guayaquil. The holotype of *C. lutea* may be one of the two flowering specimens cited above, or it may be among material that I did not locate.

A specimen from the province of Alajuela, Costa Rica, *Brenes 6468*, has a corolla in the packet which is identifiable as *C. lutea*, but the pedicel of the fruits are not tightly coiled as in *C. lutea*. *Cobaea lutea* is otherwise unknown from Costa Rica. The pedicels resemble those of *C. gracilis*, which was abundant in Alajuela in the past, though I was unable to locate any *Cobaea* populations in that area in 1995. It seems likely that the specimen may be *C. gracilis*, and a corolla of *C. lutea* was mistakenly placed in the packet.

The specific epithet is a misnomer. When describing the species Don, who saw only dried specimens, was under the mistaken impression that the flowers were yellow.

17. *Cobaea rotundiflora* Prather, *Brittonia* 48: 117. 1996.—TYPE: MEXICO. Chiapas: Mpio. Motozintla de Mendoza, SW side of Cerro Mozotal, steep canyon 11 km NW of the junction of the road to Motozintla along the road to El Porvenir and Siltepec, 2100 m, 21 Nov 1976, *Breedlove 41647* (holotype: TEX!; isotypes: DS! MO! RSA!).

Stems herbaceous, villous at the nodes. Leaves green, with 6 leaflets; rachis 40–85 mm long, sparsely puberulent; petiolules 6–12 mm long, puberulent; blades 35–80 mm long, 15–33 mm wide, puberulent along the veins abaxially or sometimes glabrous, margins minutely ciliate, upper and middle leaflet pairs obovate to elliptic to ovate, base acute to slightly cordate, apex acute to acuminate; basal pair similar to upper pairs except the margins long-ciliate at the base. Inflorescence of 1–4 flowers; bracts fully expanded, with 6 leaflets. Peduncles 6.5–12.0 cm long, puberulent at the base and along the length, villous at the apex. Pedicels 17–29 cm long, villous at the base with long trichomes, nearly glabrous along length, puberulent at the apex, slightly undulate in fruit. Calyx segments 24–33 mm long, 8–12 mm wide, green, suffused with brown or red in center, chartaceous, broadly lanceolate, apex acute, margins plane, ciliate with both long and short trichomes, essentially glabrous adaxially, pilose to villous or rarely glabrous abaxially. Corollas yellowish green or occasionally yellow, chartaceous, externally eglandular-villous or rarely glabrous at the base and throat, increasingly glandular-puberulent towards the apex, glabrous internally except for the long-villous annulus; tube 21–28 (–36) mm long, 22–30 mm wide, campanulate, widest below the apex; lobes 10–13 (–17) mm long, much shorter than the tube, 11–17 mm wide, deltate, apex acute, not inrolled at the margin, imbricate, wrinkled in bud. Filaments 27–29 mm long, adnate basally for 4–9 mm, positioned ventrally, slightly bent basally, slightly curved at the apex, coiling after dehiscence; anthers 7.5–8.0 mm long, ca. 1.5 mm wide, yellow, narrowly oblong, straight in bud, twisted after dehiscence, introrse. Styles 42–49 mm long; style branches 5–7 mm long, terete, papillae short, covering nearly the entire surface (type II stigmas). Fruit 34–39 mm long, emaculate. Seeds 10–15 per fruit, 14–18 mm long, 8–10 mm wide, lacking scales; wing 2–6 mm wide. Chromosome number unknown. Figs. 11E, 28.

Phenology. Collected in flower and fruit from November to February.

Distribution (Fig. 26). Mexico (Chiapas) and adjacent Guatemala; cloud forests and tropical deciduous forests; (975–) 1900–2800 m.

ADDITIONAL SPECIMENS EXAMINED. **Mexico.** CHIAPAS: Mpio. Motozintla de Mendoza, 45–50 km NE of Huixtla along road to Motozintla, *Breedlove & Smith 22689* (DS, F, LL, MICH, MO); Mpio. Motozintla de Mendoza, 45–50 km NE of Huixtla along road to Motozintla, *Breedlove & Thorne 31096* (DS, MO, TEX); Mpio. Motozintla de Mendoza, Rancho Nuevo, 6 km al SE de El Rosario, bosque, ladera de cerro, *Vennura & López 4255* (IEB, MO).

**Guatemala.** HUEHUETENANGO: along Central American Hwy 1, ca. 1.6 km E of the Mexico/Guatemala border at Cuahtémoc and La Mesilla, *Prather 960* (TEX); same original locality, flowering voucher grown in University of Texas greenhouse, *Prather 1268* (TEX).

*Cobaea rotundiflora* is similar to *C. triflora* of Alta and Baja Verapaz, Guatemala, in having similarly sized corollas, styles that exceed slightly the corolla, and anthers that are withdrawn after dehiscence by coiling. *Cobaea rotundiflora* differs in its pilose pedicels; pilose to villous calyx segments that are 8–12 mm wide; and corollas that are 22–30 mm wide at the apex of the tube, and lack purple pigmentation. *Cobaea triflora* has puberulent pedicels; puberulent, and sometimes long-ciliate, but never pilose, calyx segments that are 5–7 mm wide; and corollas that are 18–21 mm wide at the apex of the tube and are suffused with purple pigmentation. *Cobaea rotundiflora* is also similar to *C. lutea*; characters distinguishing them are discussed under *C. lutea* (no. 16).

Plants grown from seed collected in Guatemala (*Prather 960*, TEX) are atypical in that they lack any pubescence externally near the base of the corolla and on the abaxial side of the calyx segments, though the margins are ciliate as in the other specimens. In all

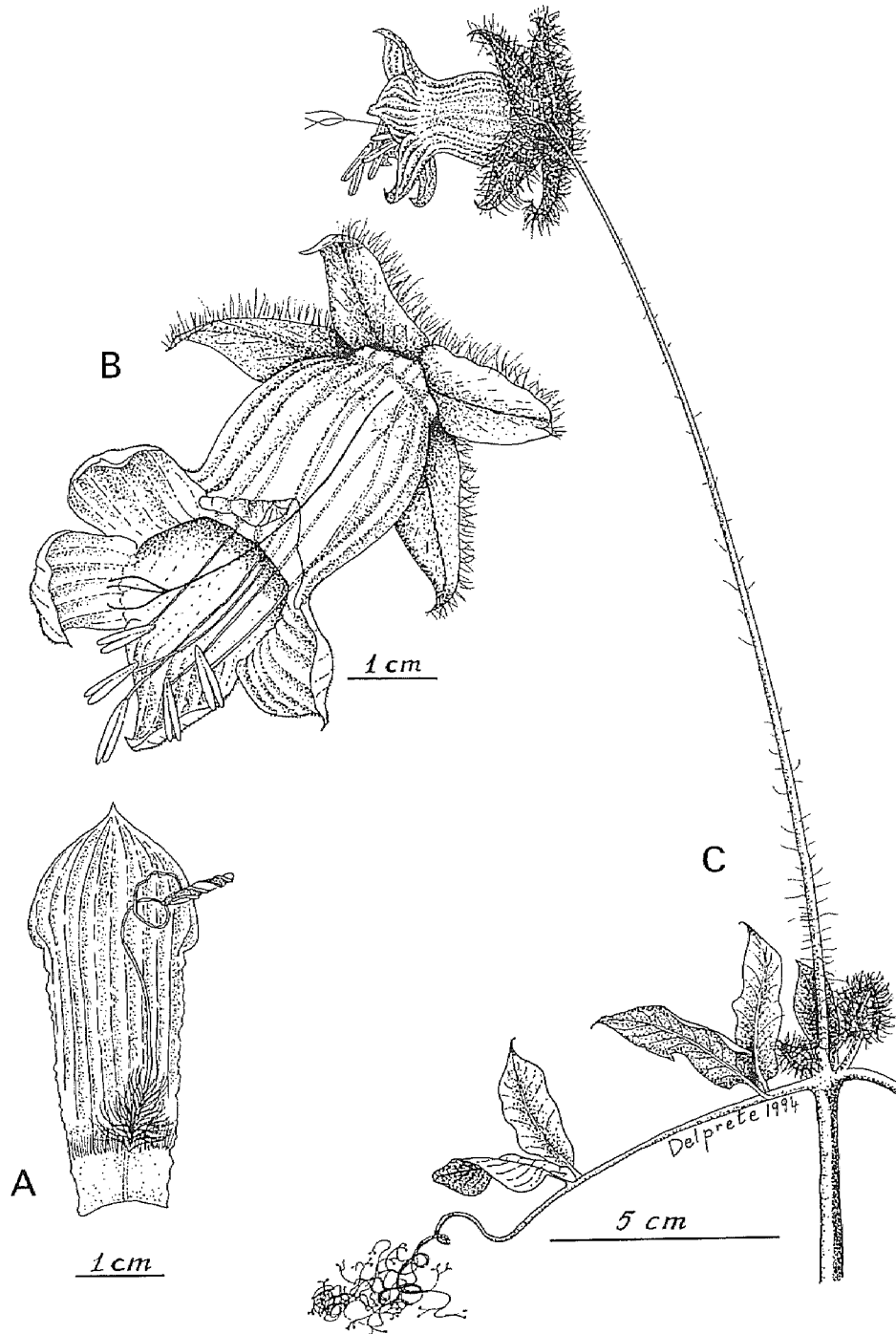


FIG. 28. *Cobaea rotundiflora*. A. Corolla segment showing internal pubescence and post-dehiscence stamens. B. Flower. C. Portion of the habit. (Drawn from living material grown from seeds of *Prather 960*, TEX.)

other aspects they are similar to the specimens from Chiapas. The original collection was of fruits only; the plants were collected during the dry season and the above-ground parts were dead.

- 18. *Cobaea triflora*** Donnell Smith, Bot. Gaz. 13: 75. 1888. *Cobaea macrostoma* var. *triflora* (Donnell Smith) Brand in Engler, Pflanzenreich IV. 150 (Heft 27): 26. 1907. *Rosenbergia triflora* (Donnell Smith) House, Muhlenbergia 4: 25. 1908.—TYPE: GUATEMALA. Alta Verapaz: ca. Coban, 1290 m, Dec 1886, *Türkheim 204* (holotype: US!; isotype: GH! K! MO! US!).

Stems slender, woody, puberulent, especially at the nodes. Leaves green, with 6 leaflets; rachis 35–40 mm long, puberulent, especially along the channel; petiolules 7–8 mm long, glabrous to puberulent; blades 44–121 mm long, 14–43 mm wide, glabrous, margins minutely ciliate; upper and middle leaflet pairs elliptic to elliptic-oblongate, base acute to truncate to rounded, apex acuminate; basal pair similar, the margins minutely ciliate, sometimes sparsely long-ciliate, especially at the base. Inflorescence of 1–5 flowers; bracts fully expanded, with 4–6 leaflets, when 4 the basal pair rudimentary. Peduncles 4.1–14.7 cm long, puberulent at the apex. Pedicels 19–28 cm long, puberulent at the base and apex, coiled in fruit. Calyx segments 23–25 mm long, 5–7 mm wide, green with purple markings, chartaceous, lanceolate-ovate, apex attenuate, margins plane, minutely ciliate, puberulent adaxially near the apex, especially on the midvein, puberulent at the base abaxially. Corollas green or greenish yellow, suffused with purple, chartaceous, puberulent on the upper portion of the tube and the lobes externally, glabrous except for the long-villous annulus internally; tube 20–31 mm long, 17–24 mm wide, campanulate, widest below the apex; lobes 8–11 mm long, much shorter than the tube, 10–13 mm wide, ovate, apex erose and rounded, not inrolled at the margin, imbricate, wrinkled in bud. Filaments 25–39 mm long, adnate basally for 3–7 mm, positioned ventrally, slightly curved at the apex, coiling after dehiscence; anthers 5–9 mm long, 1.5–2.0 mm wide, yellow, lanceolate, straight in bud, twisted after dehiscence, introrse. Styles 38–48 mm long; style branches 3–7 mm long, terete, papillae short, covering nearly the entire surface (type II stigmas). Fruit 38–57 mm long, emaculate. Seeds 6–12 per fruit, 19–21 mm long, 9–12 mm wide, lacking scales; wings 1–4 mm wide. Chromosome number unknown. Fig. 11F.

Phenology. Collected in flower from October to April, and in fruit in March and December.

Distribution (Fig. 26). El Salvador (Santa Ana) and Guatemala (Alta Verapaz and Baja Verapaz); openings of pine-sweetgum forests; 1300–2100 m.

ADDITIONAL SPECIMENS EXAMINED. **El Salvador.** SANTA ANA: on Cordillera Miramundo, mountain of Montecristo, *Molina R. et al. 16875* (F, NY, US, W). **Guatemala.** ALTA VERAPAZ: 9 km W of Tamahú, *Harmon & Dwyer 4293* (BM-2, MO); Finca Mocca, *Johnson 142* (US); above Tamahú, *Standley 70957* (F); mountains E of Tactic, on road to Tamahú, *Standley, 71296* (F); near Tactic, above the bridge across Río Frío, *Standley 90307* (F); along Río Chio about 2–4 km SW of Cobán, *Williams et al. 40360* (F, MO, NY, US); trailside in forest, aldea Candelaria, San Juan Chamelco, *Wilson 40895* (F).—BAJA VERAPAZ: Panzal, *von Türkheim 3932* (US-2).

*Cobaea triflora* is very similar to *C. rotundiflora* (no. 17), and characters by which they differ are discussed under *C. rotundiflora*. It is also similar to *C. lutea* from which it can be distinguished by its apically rounded corolla lobes and stamens that are positioned



ventrally and are exerted only a short distance beyond the corolla. *Cobaea lutea* has acuminate corolla lobes, and stamens that are emergent and long-exserted.

The three specimens that Brand (1907) cited as *C. lutea* var. *triflora* are each a different species: *Türckheim 204* is indeed *C. triflora*, *Seler & Seler 2293* is *C. pachysepala*, and *Heyde & Lux 3987* is *C. lutea*. Given Brand's treatment of these discordant elements as a single species, it is understandable that he considered *C. triflora* a variety of *C. lutea*.

One unusual collection (*Molina et al. 16875*) from the department of Santa Ana, El Salvador, appears to be *C. triflora*. It has purplish green corollas and rounded corolla lobes, but there are no mature flowers on any of the specimens I saw, and it is difficult to determine this material. If it is indeed *C. triflora*, the population from which it came is disjunct approximately 120 km from the nearest known population.

#### ACKNOWLEDGMENTS

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## APPENDIX 1

## VOUCHERS FOR THE QUANTITATIVE ANALYSES OF POLLEN MORPHOLOGY OF COBAEA

<i>C. aequatoriensis</i> : Panero & Clark 2918, TEX.	<i>C. paneroi</i> : Hernández 3332, MEXU.
<i>C. aschersoniana</i> : Bangham s.n., AA.	<i>C. penduliflora</i> : Morilla & Manara 773, NY.
<i>C. biaurita</i> : Torres C. 7114, TEX.	<i>C. pringlei</i> : Peterson 1260, TEX.
<i>C. campanulata</i> : Dodson 3833, GH.	<i>C. rotundiflora</i> : Breedlove 41647, TEX.
<i>C. flava</i> : Weberbauer 6425, GH.	<i>C. scandens</i> : Hinton 11945, LL.
<i>C. gracilis</i> : Smith 304, US.	<i>C. skutchii</i> : Standley 85652, F.
<i>C. lutea</i> : Standley 59857, ECON.	<i>C. stipularis</i> : Prather 924, TEX.
<i>C. minor</i> : Cházaro & Camarillo 3948, WIS.	<i>C. trianae</i> : Panero & Clark 3044, TEX.
<i>C. pachysepala</i> : Breedlove 42780, CAS.	<i>C. triflora</i> : Johnson 142, US.

## APPENDIX 2

## STUDIES OF BREEDING SYSTEMS OF COBAEA

For the first three species the denominator is the number of self-pollinations made by hand; the numerator is the number of those pollinations that produced fruits. For the last two species the denominator is the number of unmanipulated flowers scored, and the numerator is the number of those setting fruits. The percentages are total percent fruit set per treatment combined over all plants of a species. All collection numbers are the author's; vouchers are deposited at TEX.

- C. pringlei*: 1300 (2 plants, 48/50); 96%.  
*C. scandens*: 1269 (2 plants, 61/64); 95%.  
*C. stipularis*: 924 (1 plant, 23/23); 926 (2 plants, 34/36); 97%.  
*C. lutea*: 1010 (3 plants, 24/24); 1011 (2 plants, 8/21); 1022 (2 plants, 22/31); 1080a (3 plants, 35/43); 1080b (3 plants, 32/41); 1220 (2 plants, 58/74); 76%.  
*C. rotundiflora*: 960 (3 plants, 80/83); 96%.

## NUMERICAL LISTS OF SPECIES

- |                              |                                  |
|------------------------------|----------------------------------|
| 1. <i>Cobaea minor</i>       | 10. <i>Cobaea aschersoniana</i>  |
| 2. <i>Cobaea pringlei</i>    | 11. <i>Cobaea gracilis</i>       |
| 3. <i>Cobaea stipularis</i>  | 12. <i>Cobaea penduliflora</i>   |
| 4. <i>Cobaea trianae</i>     | 13. <i>Cobaea aequatoriensis</i> |
| 5. <i>Cobaea biaurita</i>    | 14. <i>Cobaea flava</i>          |
| 6. <i>Cobaea scandens</i>    | 15. <i>Cobaea campanulata</i>    |
| 7. <i>Cobaea paneroi</i>     | 16. <i>Cobaea lutea</i>          |
| 8. <i>Cobaea pachysepala</i> | 17. <i>Cobaea rotundiflora</i>   |
| 9. <i>Cobaea skutchii</i>    | 18. <i>Cobaea triflora</i>       |

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