

Cybianthus Subgenus Conomorpha

Species by Floristic Complex

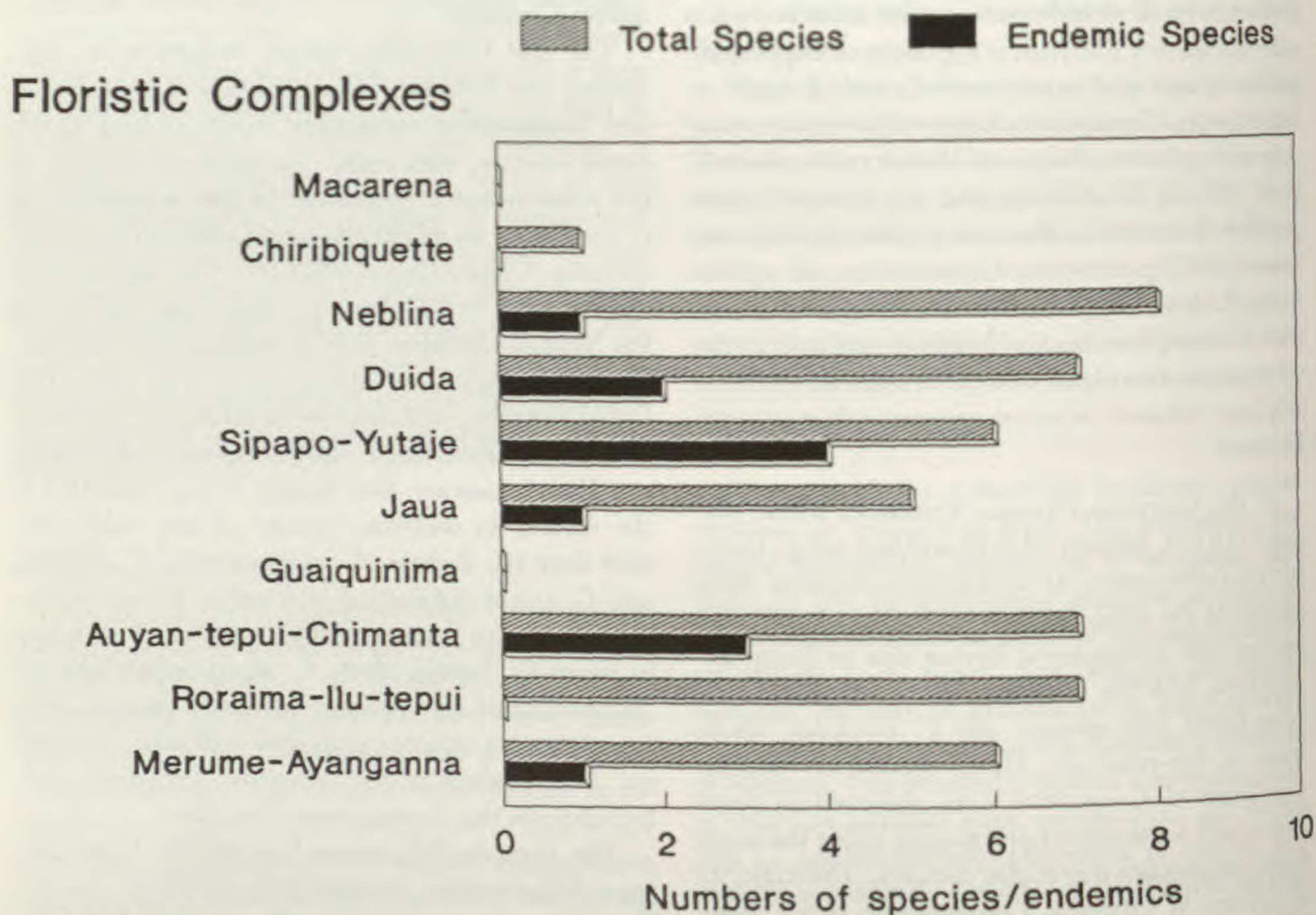


FIGURE 1. Species of *Cybianthus* subgenus *Conomorpha* (A. DC.) Agostini, found in the Guayana Floristic Province: total species vs. endemics per floristic complex (sensu Maguire, 1979). Complexes listed from top to bottom proceed from west to east across South America. Note that Chiribiquette and Macarena complexes belong to the Trans-Río Negro, Colombian Guayana Subprovince; Neblina, Duida, Sipapo-Yutajé, Jaua, and Guaiquinima complexes belong to the Río Caroní-Río Negro Subprovince; Auyán-tepui-Chimantá, Roraima-Illú-tepui, and Merume-Ayanganna complexes belong to the Guyana-Pakaraima-Venezuelan Gran Sabana Subprovince.

exploration is needed in the Macarena, Chiribiquette, and Guaiquinima complexes to determine if the low representation of subgenus *Conomorpha* is biogeographically significant, or if it is merely a collecting artifact.

TAXONOMIC CONCEPTS AND NOTES ON KEYS

My species concept follows that of Wiley (1978, 1981), who defined a species as follows: "An evolutionary species is a single lineage of ancestor-descendant populations which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate." My subspecies concept (Pipoly, 1987) defines a subspecies as follows: "groups of populations within a single lineage of ancestor-descendant populations that show variation by unique combinations of ple-

siomorphies, or homoplastic apomorphies, correlated with biogeography and/or ecology. This rank is primarily used to convey information regarding variation in the life histories of these populations and character state differences hypothesized to be the result of this variation. The subspecific rank in no way attempts to predict speciation events."

The keys are artificial and designed to expedite identification of herbarium specimens. The numbers appearing before the taxa refer to the respective position of the species in the key, and any correlation with phylogenetic relationship is coincidental. Quantitative and qualitative data presented in keys and descriptions for floral parts and bracts were taken from organs rehydrated from herbarium specimens by boiling in water. Measurements from these range from 10% to 15% greater than those measurements taken directly

from dried material. Data regarding stem diameters, inflorescence rachises, pedicels, leaf, and fruit shape were taken from dried herbarium specimens.

A description of the genus *Cybianthus* and a key to its subgenera are provided below. This description, along with that of subgenus *Conomorpha*, includes features found in the taxon as a whole, including those species occurring outside the Guayana Floristic Province.

***Cybianthus* Martius, Nov. Gen. Sp. Pl. 3: 87.**

1831, nom. cons. TYPE SPECIES: *Cybianthus penduliflorus* Martius, Nov. Gen. Sp. Pl. 3: 87. 1831.

Terrestrial or epiphytic, monoaxial or polyaxial shrubs or trees to 15 m tall. Architectural development by Rauh's Corner's, or Aubréville's Models (Hallé et al., 1978). Roots positively geotropic or diageotropic. Branchlets glabrous, glandular-granulose, dendroid- and stellate-tomentose, ferrugineous- or ferruginous stipitate-lepidote. Leaves sessile or petiolate, alternate, subopposite or pseudoverticillate, the venation camptodromous or acrodromous, the petioles canaliculate, pulvinate, or absent. Inflorescence axillary, a simple, condensed or spicate raceme (the flowers sessile to subsessile), a panicle with racemose branches, or an indeterminate umbel. Flowers functionally unisexual or bisexual, 3-6(-7)-merous. Staminate flowers with pistillode conic, lageniform, turbinate or irregularly shaped, vestigial, hollow or bearing sterile placenta, rarely absent. Pistillate flowers with staminodes morphologically similar to the stamens but reduced in size, at times producing abortive pollen. Calyx patelliform, crateriform, cotyliform, or cupuliform, the lobes imbricate, valvate, or somewhat contorted, basally connate $\frac{1}{5}$ - $\frac{2}{3}$ their length, abaxially glabrous, glandular-granulose, or with translucent or ferruginous lepidote scales, adaxially glabrous. Corolla cupuliform, campanulate, rotate or subrotate, the lobes basally connate $\frac{1}{5}$ - $\frac{3}{4}$ their length, abaxially glabrous, glandular-granulose along the margins, or with ferruginous lepidote scales, adaxially glabrous or glandular-granulose. Stamens adnate to corolla tube at least $\frac{2}{3}$ their length, the filaments variously connate to form a tube, the staminal tube adnate to the corolla tube or at times developmentally fused with it (the stamens thus appearing epipetalous), bearing fleshy lobes alternate with the anthers or not, the anthers ovate, widely ovate, or triangular, basifixed or dorsifixed, apically acute, rounded, emarginate or minutely apiculate, basally cordate, erect or dorsally recurved, dehiscent by confluent apical pores or

by wide to narrow longitudinal slits; pollen tricolporate, psilate; pistil obnapiform, umbonate, or turbinate, the ovary glabrous or sparsely to densely translucent glandular-lepidote, the style glabrous, the stigma capitate, capitate-lobate or punctiform, the placenta free-central, carnosose, umbonate to subglobose, the ovules campylotropous, (1-)2-5(-7), uni- or biseriate. Fruit drupaceous, 1(-2)-seeded, the endosperm translucent, nonstarchy, the embryo small, linear, flexuous, erect or curved, longitudinal or transverse, the cotyledons not well developed.

A neotropical genus of 150 species, *Cybianthus* is a conspicuous element of the Guayana Highland, inhabiting tepui summit savannas, gallery, talus slope, lowland igapó, várzea, moist and wet forest formations throughout the Guayana Shield. Its species may always be found near watercourses, and many apparently sympatric species are separated ecologically by life zone rather than elevation.

The genus is cladistically defined by the unique glandular granules at the corolla lobe and tube junction (Pipoly, 1987). For practical purposes of identification, the combination of axillary racemes, spikes or racemose panicles, and filaments that are shorter than the corolla, connate at least $\frac{1}{4}$ their length, and adnate to the corolla at least $\frac{1}{3}$ its length allows for easy recognition.

In the Guayana Highland, there are 40 species in five subgenera. A key to the subgenera of the Guayana Floristic Province is provided below.

KEY TO SUBGENERA OF *CYBIANTHUS* IN GUAYANA

- 1a. Corolla cupuliform to campanulate; anthers longer than wide, usually distally recurved in anthesis, mostly apically acute or minutely apiculate.
 - 2a. Branchlets and calyx ferruginous stipitate-lepidote; calyx lobe margin glabrous (except in *C. apiculatus*); abaxial corolla surface mostly glabrous along the margin I. *Conomorpha*
 - 2b. Branchlets and calyx stellate and/or dendroid tomentose; calyx lobe margin glandular-ciliate; abaxial corolla surface always glandular-granulose along the margin II. *Laxiflorus*
- 1b. Corolla rotate to subrotate; anthers wider than long, always erect, apically rounded or emarginate.
 - 3a. Petioles abruptly swollen basally; anthers versatile, longitudinally dehiscent III. *Weigeltia*
 - 3b. Petioles not abruptly swollen basally or absent; anthers basifixed, poricidally dehiscent.
 - 4a. Leaves apically mucronate, the petioles absent, the margins scarious, the venation acrodromous, the bases au-

riculate; staminal tube merely adnate to the corolla tube IV. *Grammadenia*

- 4b. Leaves apically not mucronate, the petioles present, the margins opaque, the venation camptodromous, the bases attenuate, acute or cuneate; staminal tube developmentally fused to the corolla tube, the stamens thus appearing epipetalous V. *Cybianthus*

I. **Cybianthus** Martius subg. **Conomorpha** (A. DC.) Agostini, Acta Biol. Venez. 10: 150. 1980. *Conomorpha* A. DC., Trans. Linn. Soc. London, Bot. 17: 102. 1834; *Conomorpha* sect. *Euconomorpha* Miquel, Stirp. Surinam. Select. 111. 1850; *Conomorpha* subg. *Euconomorpha* (Miquel) Mez, in Engler, Pflanzenr. IV, 236: 254. 1902. TYPE SPECIES: *Cybianthus oblongifolius* (A. DC.) Agostini (lectotype, selected by Agostini, Acta Biol. Venez. 10: 151. 1980).

Conomorpha sect. *Aconomorpha* Miquel in Martius, Fl. Bras. 10: 304. 1856. TYPE SPECIES: *Conomorpha heterantha* Bentham (lectotype, selected by Agostini, Acta Biol. Venez. 10: 151. 1980).

Terrestrial shrubs or trees. Bark smooth or fissured, brown or beige, rarely with significant amounts of cork (*C. quelchii*). Trunk distinguishable, leptocaulous, the growth dynamics following Rauh's or rarely (*C. fabiolae*) Aubréville's Architectural Model. Branchlets thin to moderately thick, terete or ridged, densely to moderately covered with ferrugineous stipitate-lepidote scales, the scales at times appressed, rarely glabrescent (*C. quelchii*, *C. apiculatus*). Leaves alternate, petiolate, covered with ferrugineous stipitate-lepidote scales, often glabrescent above; petioles canaliculate, marginate, or rarely winged. Inflorescence axillary, racemose, spicate or paniculate, the panicles with racemose branches, rarely a solitary flower; inflorescence bract small, lanceolate, early caducous; rachis erect or lax, straight or rarely tortuous, ferrugineous stipitate-lepidote; floral bracts deltate,

lanceolate or ovate, ferrugineous stipitate-lepidote, inserted at the base of the pedicel; pedicels terete, at times clavate in fruit, erect, apically recurved, pendent, or nodding, at times accrescent in fruit, rarely absent. Flowers unisexual, rarely bisexual, dimorphic, (3-)4-5(-6)-merous, the plants dioecious or rarely polygamous; calyx cotyliform, cupuliform, crateriform, or patelliform, the lobes valvate, the margin entire, rarely crenulate or erose; corolla campanulate to cupuliform, rarely subrotate (*C. apiculatus*), or deeply rotate (*C. crotonoides*), the lobes erect or reflexed, valvate or imbricate, ferrugineous stipitate-lepidote or glabrous without, at times with a narrow line of glandular granules along the margin, glandular-granulose within, epunctate or the punctations conspicuous, not prominent, brown or translucent, the margins entire or rarely crenulate, glabrous or rarely glandular-granulose; staminodes resembling stamens but reduced in size, the tube conspicuous or inconspicuous, adnate to the corolla, lobate or elobate, the anthers ovate or triangular-ovate, usually recurved distally, rarely erect, the apex acute or apiculate, rarely rounded, the apiculum dorsally, rarely proximally recurved or erect, the base cordate, dorsifixed from near base to subversatile, the connective punctate or not; pistillode conic to lageniform, rarely absent, translucent-lepidote, hollow; pistil obnapiform, rarely conic, the ovary globose, lobed or with an apical apophysis (*C. huberi*, *C. holstii*), the style short, the stigma capitate-lobate, 2-3-lobed or punctiform; placenta cupuliform or cotyliform, the ovules 2-4. Fruit subglobose, 1(-2)-seeded.

Cybianthus subg. *Conomorpha* contains 38 species, 21 of which have been collected in the Guayana Highland. All species are readily distinguishable by their autapomorphic ferrugineous stipitate-lepidote scales (Pipoly, 1987), which are always present on the branchlets.

KEY TO SPECIES OF *CYBIANTHUS* SUBGENUS *CONOMORPHA*

- 1a. Leaves mostly less than 3 cm long (rarely to 3.5 cm in *C. huberi*), up to 2 cm wide.
 2a. Inflorescence 2(-3)-flowered, at times 1-flowered; leaves smooth above; anthers rounded to emarginate apically.
 3a. Trunk orthotropic, the branches plagiotropic; leaves chartaceous, apically obtuse to rounded, the margins flat; petioles 2-4 mm long; calyx chartaceous; pedicels 5-10 mm long 1. *C. fabiolae*
 3b. Trunk and branches orthotropic; leaves coriaceous or cartilaginous, apically acute or abruptly acuminate, the margins revolute; petioles 5-10 mm long; calyx coriaceous; pedicels 0-4.5 mm long.
 4a. Leaves coriaceous, apex abruptly acuminate; flowers sessile; calyx deeply crateriform, 1.9-2.4 mm long 2. *C. huberi*
 4b. Leaves cartilaginous, apex acute; flowers on pedicels 3-4.5 mm long; calyx cotyliform, 0.8-1.2 mm long 3. *C. julianii*

- 2b. Inflorescence 4-9-flowered; leaves scrobiculate above; anthers apiculate to cuspidate apically.
- 5a. Leaf blades nitid above; flowers carnose; staminate corolla 2.7-2.9 mm long; pistillate corolla 1.9-2.2 mm long; stamens 1.6-1.7 mm long, the free portion of the filaments flat, less than 0.1 mm long; staminodes 1.0-1.3 mm long, the free portion of the filaments flat, 0.1-0.2 mm long; stigma capitate, 2-lobed 4. *C. steyermarkianus*
- 5b. Leaf blades dull above; flowers coriaceous; staminate corolla 2.0-2.3 mm long; pistillate corolla 2.4-2.8 mm long; stamens 1.4-1.5 mm long, the free portion of the filaments terete, 0.1 mm long; staminodes 1.8-2.1 mm long, the free portion of the filaments terete, 0.2-0.3 mm long; stigma not capitate, 3-4-lobed 5. *C. wurdackii*
- 1b. Leaves mostly 3.1-24 cm long, (1.5-)2.1-8.5 cm wide.
- 6a. Inflorescence paniculate or spicate.
- 7a. Inflorescence paniculate.
- 8a. Branchlets 5-12 mm diam.; leaves coriaceous.
- 9a. Branchlets stiff, not subsucculent, the bark creamish white; inflorescence a simple panicle, the branches racemose; leaf apices acuminate.
- 10a. Branchlets terete, prominently furrowed, moderately adpressed-lepidote, without lenticels; leaves smooth above, the margins flat; pedicels 2-3 mm long; calyx patelliform, coriaceous, the lobes oblate to suborbicular; corollas 3.0-3.5 mm long, apically cucullate 6. *C. plowmanii*
- 10b. Branchlets angular, densely lepidote, prominently lenticellate; leaves scrobiculate above, the margins revolute; pedicels 0.5-1.0 mm long; calyx cupuliform, carnose, the lobes ovate-triangular to deltate; corollas 2.3-2.7 mm long, apically flat 7. *C. amplus*
- 9b. Branchlets subsucculent, the bark yellowish brown; inflorescence tripinnately paniculate; leaf apices rounded, obtuse, truncate, or emarginate 8. *C. quelchii*
- 8b. Branchlets 2-3 mm diam.; leaves membranaceous to chartaceous.
- 11a. Leaves to 5(-6) cm wide, abruptly acuminate apically; petioles canaliculate, marginate only distally; inflorescence to 8 cm long; pedicels erect.
- 12a. Leaf margin revolute; calyx cotyliform, carnose; corolla carnose 9. *C. punctatus*
- 12b. Leaf margin flat; calyx subcupuliform, chartaceous; corolla chartaceous 14. *C. guyanensis*
- 11b. Leaves 5-7 cm wide, apically acute; petioles marginate along entire length; inflorescence 8-15 cm long; pedicels curved upward 10. *C. cardonae*
- 7b. Inflorescence spicate.
- 13a. Flowers subsessile (pedicels 0.2-0.6 mm long); calyx deeply cupuliform, carnose, the lobes proximally curved; corolla lobes not keeled.
- 14a. Leaves pustulate above; inflorescence (2-)6-16 cm long; corolla lobe apex flat; anthers erect 11. *C. lepidotus*
- 14b. Leaves smooth above; inflorescence 0.8-1.0 cm long; corolla lobe apex cucullate; anthers distally recurved 12. *C. sipapoensis*
- 13b. Flowers sessile; calyx crateriform, coriaceous, the lobes erect to spreading; corolla lobes prominently keeled.
- 15a. Leaves membranaceous 6-9.5 cm long, (1.5-)2.2-3.5 cm wide, scrobiculate above; petioles 1.2-1.5 cm long; corolla coriaceous; anthers proximally recurved, the apex apiculate, glabrous; pistil sessile 13. *C. holstii*
- 15b. Leaves coriaceous, 2.5-3.5(-4) cm long, 1.2-1.9 cm wide, smooth above; petioles 0.5-1.0 cm long; corolla carnose; anthers erect, the apex rounded, glandular-papillate; pistil on a carnose disc 2. *C. huberi*
- 6b. Inflorescence racemose.
- 16a. Staminate corolla 2-2.5 mm long; staminate calyx 0.7-1.1 mm long; pistillate calyx 0.8-1.2 mm long.
- 17a. Leaves elliptic, 7-20 cm long, apices acuminate; corolla membranaceous or chartaceous; fruit 4-7 mm diam. when dried.
- 18a. Branchlets 2-3 mm diam., the bark beige; leaves smooth above, the margins flat; petioles 0.5-2.0 cm long; pedicels to 1 mm long; corolla campanulate; fertile and sterile anthers strongly recurved dorsally, the apical portion of the sterile anthers tightly twisted 14. *C. guyanensis*
- 18b. Branchlets 3.5-4.5 mm diam., the bark reddish brown; leaves pustulate above, the margins revolute; petioles 2-3 cm long; pedicels 2-3.5 mm long; corolla rotate, the lobes reflexed, perpendicular to the tube in anthesis; fertile and sterile anthers slightly recurved dorsally, the apical portion of the sterile anthers straight 15. *C. roraimae*
- 17b. Leaves obovate-spathulate, 4-5 cm long, apices obtuse to rounded; corolla carnose, glandular-granulose within; fruit 7-8 mm diam. 16. *C. breweri*
- 16b. Staminate corolla 2.5-3.7 mm long; staminate calyx 1.1-1.5 mm long; pistillate calyx 1.1-1.7 mm long.

- 19a. Calyx cotyliform; corolla glabrous or glandular-ciliate along the margins; staminal tube conspicuous, chartaceous or carnose, opaque.
- 20a. Leaves membranaceous, long-acuminate apically, smooth above; petioles (1-)1.3-1.7(-2.3) cm long; pedicels 0.6-1.0 mm long; calyx without scales, the margin glandular-ciliate; corolla lobe apex cucullate; staminal tube carnose, costate, elobate, the free portion of the filaments as long as the anthers; fruit 4-7 mm diam. 17. *C. apiculatus*
- 20b. Leaves chartaceous to coriaceous, rounded to acute apically, pustulate above; petioles 0.5-1.1 cm long; calyx sparsely lepidote, the margin glabrous; corolla lobe apex flat; staminal tube chartaceous, terete, bearing lobes to 0.1 mm long alternating with the filaments, the free portion of the filaments shorter than the anthers; fruit 3-3.5 mm diam. 18. *C. agostinianus*
- 19b. Calyx cupuliform; corolla glandular-granulose along the margins; staminal tube inconspicuous, membranaceous, hyaline.
- 21a. Leaves smooth above, the margins flat; petioles 0.1-0.2 cm long; inflorescence tortuous; staminate corolla 3.5-3.7 mm long, pistillate corolla 2.7-3.5 mm long 19. *C. spathulifolius*
- 21b. Leaves scrobiculate or pustulate above, the margins revolute; petioles 0.9-1.3 cm long; inflorescence straight; staminate corolla 2.5-3.0 mm long, pistillate corolla 1.9-3.3 mm long.
- 22a. Leaves pustulate above, moderately lepidote below, the scales not overlapping; pedicels erect, less than 1 mm long; calyx lobes longer than broad; staminate corolla 2.7-3.0 mm long, pistillate corolla 3.0-3.3 mm long, the lobes flat; free filaments shorter than the anthers; fruit verruculose, 6-8 mm diam. ... 20. *C. maguirei*
- 22b. Leaves scrobiculate above, densely lepidote below, the scales overlapping; pedicels nodding, 1-3 mm long; calyx lobes broader than long; staminate corolla 2.5-2.7 mm long, pistillate corolla 1.9-2.0 mm long; free filaments longer than the anthers; fruit smooth, 4.5-5.0 mm diam. when dried 21. *C. crotonoides*

1. *Cybianthus fabiolae* Pipoly, sp. nov. TYPE: Guyana. Cuyuni-Mazaruni Region No. VIII, Mazaruni Subregion No. VIII-2: Mt. Ayan-ganna, summit of E plateau, 5°24'N, 59°57'W, 1,350-1,380 m, elfin forest on cliffs dominated by *Bonnetia roraimae*, 11 Mar. 1987 (pist. fl, fr), Pipoly, Gharbarran, Samuels & Chin 11120 (holotype, US; isotypes, AAU, B, CAY, COL, F, FDG, G, GH, L, MO, NY, P, VEN). Figure 2.

Quoad filamenta staminum tubi manifeste punctata, antheras non apiculatas suberectas vel ventraliter recurvatasque, folia obovato-spathulata, ad *C. dussium* valde affinis, sed ab ea pedicellis gracilibus 4-10 (non crassis, 1.5-2.5) mm longis inflorescentisque reductis (1-)2-floris (non racemosis, plus quam 3-floris) praeclare differt. Species haec allopatricos *C. steyermarkiano* et *C. wurdackii* simulans, sed ab eis filamentis punctatis (non epunctatis) Aubrevillei (nec Rauhii) architectura statim distinguitur.

Treelet to 2.5 m tall, 2 cm diam.; trunk monopodial, orthotropic, the growth rhythmic, the branching pseudoverticillate, the branches modular, with rhythmic growth, plagiotropic by apposition (Aubréville's Model); branchlets terete, 1.5-2.0 mm diam., densely lepidote at first, glabrescent, with only scattered scales persistent. Leaves broadly obovate-spathulate, chartaceous, 1.3-2.0 cm long, 0.9-1.2 cm wide, apex obtuse to rounded,

base cuneate, slightly decurrent on the thin petiole, midrib depressed on the upper surface, prominent below, nerves 5-7 pairs, inconspicuous above, somewhat conspicuous below on older leaves, prominently black punctate above, densely lepidote at first, but glabrescent above, moderately lepidote below, the scales not impressed, the margin entire, punctate, flat; petiole canaliculate, 0.2-0.4 cm long, densely lepidote. *Staminate inflorescence*: a reduced, 2-flowered raceme (appearing umbelliform) or at times 1-flowered; rachis, pedicels, and calyces densely stipitate-lepidote, the margins often overlapping; peduncle 0.5-1.5 cm long; floral bracts lanceolate, 1.0-1.5 mm long, 0.3-0.5 mm wide, apex acute, densely lepidote below, the margin entire; pedicel terete, 5-10 mm long. Flowers pendent, 4-5-merous; calyx patelliform, chartaceous, 0.7-1.1 mm long, the tube 0.1-0.3 mm long, the lobes subdeltate, 0.6-0.8 mm long, 0.7-1.0 mm wide, apex acute, densely stipitate-lepidote without, the margins of the scales overlapping, glabrous within, the margin glabrous, subentire to crenulate; corolla subcotyliform, chartaceous, 2.1-2.3 mm long, the tube 0.3-0.6 mm long, the lobes erect, slightly concave, narrowly ovate, 1.6-1.8 mm long, 0.9-1.1 mm wide, apex rounded, sparingly glandular-granulose within and along margin only at apex, sparingly lepidote without apically, prominently black punctate and punctate-lineate without,

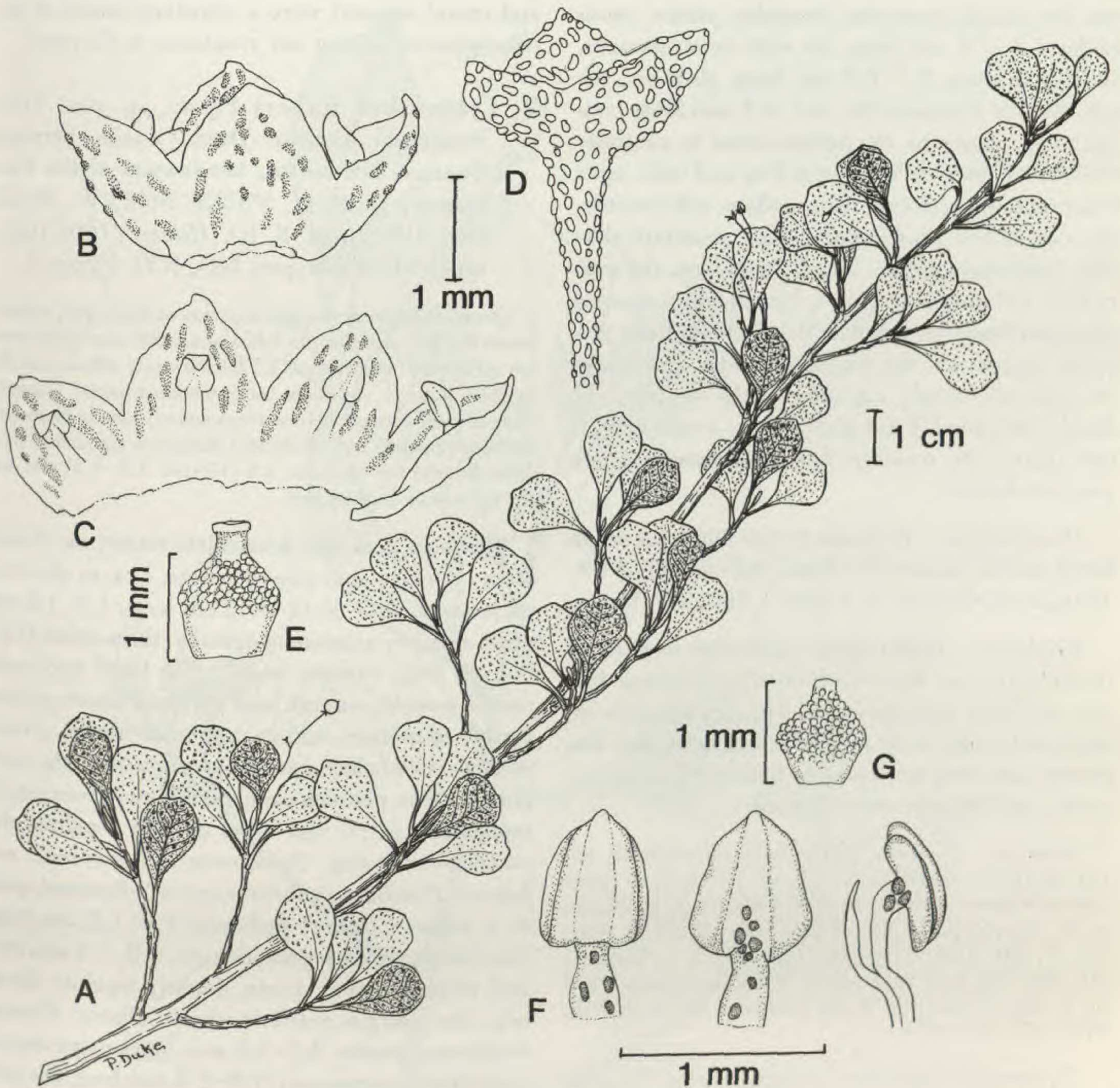


FIGURE 2. *Cybianthus fabiolae* Pipoly.—A. Habit, showing short shoots.—B. Staminate corolla.—C. Opened pistillate corolla, showing suberect to proximally recurved anthers.—D. Pistillate calyx.—E. Pistil.—F. Anther, ventral, dorsal, and lateral views, showing punctate filaments and connective.—G. Pistillode, showing punctiform stigma. (A, C, D, and E, from the holotype; B and F, from Pipoly et al. 11112.)

the margin regular, entire; stamens 1.6–1.9 mm long, the tube inconspicuous, membranaceous, 0.4–0.5 mm long, the apically free filaments 0.5–0.7 mm long, flat, prominently punctate, the anthers suberect to proximally recurved, ovate, 0.7–0.9 mm long, 0.5–0.6 mm wide, apex truncate to emarginate, base cordate, subversatile, the connective prominently black punctate; pistillode globose, 1.0–1.1 mm long, the ovary 0.7–0.8 mm long, 0.8–0.9 mm wide, densely translucent glandular-lepidote, the style 0.3–0.4 mm long, glabrous, stigma punctiform. *Pistillate inflorescence*: a reduced, 2-flowered raceme (appearing umbelliform), 1.5–2.0 cm long, axis sparingly lepidote; peduncle 1.0–1.5 mm long; floral bracts ovate,

0.7–1.0 mm long, 0.4–0.5 mm wide, sparingly lepidote adaxially; pedicels terete, 5.0–5.5 mm long, densely lepidote. Flowers pendent, 4- or 5-merous; calyx subcotyliform, chartaceous, 0.7–0.9 mm long, the tube 0.2–0.3 mm long, the lobes widely ovate to deltate, 0.6–0.8 mm long, 0.6–1.0 mm wide, apex rounded, sparingly lepidote without, glabrous within, punctations dark brown, not prominent, the margin entire to crenulate; corolla subcotyliform, chartaceous, 1.9–2.0 mm long, the tube 0.5–0.6 mm long, the lobes broadly ovate, 1.5–1.6 mm long, 1.3–1.5 mm wide, apex rounded, sparingly glandular-granulose within apically, sparingly lepidote medially at apex without, prominently black punctate and punctate-lineate with-

out, the margin somewhat irregular, entire; staminoles 1.5–1.8 mm long, the tube inconspicuous, membranaceous, 0.7–0.9 mm long, glabrous, the apically free filaments flat, 0.4–0.5 mm long, conspicuously punctate, the anthers erect to ventrally recurved, deltate, 0.4–0.5 mm long and wide, apex truncate to emarginate, base cordate, subversatile, the connective prominently black punctate dorsally; pistil obnapiform, 1.4–1.5 mm long, the ovary 0.9–1.0 mm long, 0.9–1.2 mm diam., densely glandular-lepidote, the style 0.1–0.2 mm long, glabrous, epunctate, the stigma capitate, 3–4-lobed, the placenta deeply cupuliform, the ovules 2–3, deeply imbedded. Fruit globose, ca. 5 mm long, 3 mm diam., the exocarp thin, prominently black punctate-lineate.

Distribution. Endemic to the elfin and scrub forest on the uppermost slopes and summit of Mt. Ayanganna, Guyana, at 1,350–1,380 m elevation.

Ecology. *Cybianthus fabiolae* occurs in thickets in zones between *Bonnetia roraimae* forests and large rock outcrops. The treelets grow on hummocks and rarely exceed 2.5 m in height. The flowers and fruit are pendent beneath the leaf rosettes, and no odor was detected.

Paratypes. GUYANA. CUYUNI-MAZARUNI REGION, NO. VIII, MAZARUNI SUBREGION VIII-2: Mt. Ayanganna, upper cliffs of E flank, 1,380 m, 11 Mar. 1987 (stam. fl), Pipoly et al. 11112 (FDG, NY, US), 11117 (B, CAY, FDG, NY, P, PH, TEX, US), (fr) 11135 (CAY, F, FDG, L, NY, PH, US), on E flank above Thompson Camp, 1,370 m, 8 Aug. 1960 (pist. fl, fr), Tillett et al. 45056 (F, FDG, NY, US, VEN).

Cybianthus fabiolae is unique within *Cybianthus* because its morphogenesis follows Aubréville's Model (Hallé et al., 1978). This architectural model is defined by a monopodial, orthotropic trunk with rhythmic growth, producing pseudovercillate tiers of branches that are modular, with plagiotropic growth by apposition. In this type of growth, the terminal meristems are evicted by sylleptic branches, which function as short shoots because no elongation occurs. The short shoots produce rosettes of leaves, and the small, axillary inflorescences are pendent beneath them. *Cybianthus fabiolae* can most readily be confused with *C. wurdackii*, but can immediately be distinguished from it by the architectural model, the punctate filaments, the emarginate or truncate anthers, the subcotyliform corolla, umbelliform inflorescence, and long pedicels.

I dedicate this species to my wife, Fabiola Monje-Pipoly, whose patience, hard work, enthusiasm,

and moral support were a constant source of encouragement during our residence in Guyana.

2. *Cybianthus huberi* Pipoly, sp. nov. TYPE: Venezuela. Bolívar: Dtto. Cedeño, Serranía Guanay, NE sector, headwaters of Río Paraguaza, 1,700 m, 5°55'N, 66°23'W, 20–28 Oct. 1985 (pist. fl, fr), *Huber 11005* (holotype, VEN; isotypes, MO, NY). Figure 3.

Quoad inflorescentias spiciformias reductasque, calyces crateriformes, corollarum lobos abaxaliter carinatos erectos ad apicem cucullatos, *C. holstii* arcte affinis, sed illa ab hac laminis coriaceis (non membranaceis) staminodiorum tubi conspicui (nec inconspicui) lobulis filamentis alterans praeditis (nec destitutis) filamentis glandulosis (nec eglandulosis) fructibusque 5.5–10 (nec 4.0–4.5) mm diametris statim cognoscitur.

Shrub to 3 m tall; branchlets terete, ca. 3 mm diam., densely appressed-lepidote. Leaves obovate, coriaceous, (2.5–)3.0(–3.5) cm long, 1.2–1.9 cm wide, abruptly acuminate apically, the acumen 0.3–0.7 cm long, cuneate basally, the blade decurrent on the petiole, smooth and glabrous above at maturity, epunctate, midrib depressed above, prominently raised below, nerves inconspicuous, the margin revolute; petioles canaliculate and prominently marginate, 5–10 mm long, densely lepidote, the scales overlapping. *Staminate inflorescence*: unknown. *Pistillate inflorescence*: a 2-flowered spike or a solitary flower; peduncle 1.0–1.2 cm long; floral bracts chartaceous, deltate, 0.8–1.1 mm long and wide, the apex acute, densely lepidote abaxially, the margin entire; pedicels absent. Flowers 4-merous, sessile, 2.7–3.0 mm long; calyx deeply crateriform, coriaceous, 1.9–2.4 mm long, the tube 1.3–1.6 mm long, the lobes very broadly triangular, 0.5–0.9 mm long, 1.1–1.4 mm wide, acute, medially keeled, prominently brown punctate, lepidote along the margins, the margins irregular, entire; corolla cupuliform, carnose, 2.3–2.7 mm long, the tube 0.4–0.6 mm long, the lobes oblong, erect, keeled medially, 1.9–2.1 mm long, 0.4–0.6 mm wide, apically rounded and cucullate, glabrous and prominently orange punctate without, glandular-granulose within the margin entire, glandular-granulose; staminodial tube conspicuous, carnose, 0.5–0.7 mm long, bearing lobes alternate with the filaments to 0.1 mm long, the tube and filaments eglandular, the apically free filaments less than 0.1 mm long, the anthers subsessile, erect, ovate, 0.9–1.1 mm long, 0.6–0.7 mm wide, apex rounded and rufous glandular-papillate, dorsifixed ca. ¼ from base, the connective prominently punctate dorsally; pistil above a carnose disc, obnapiform.

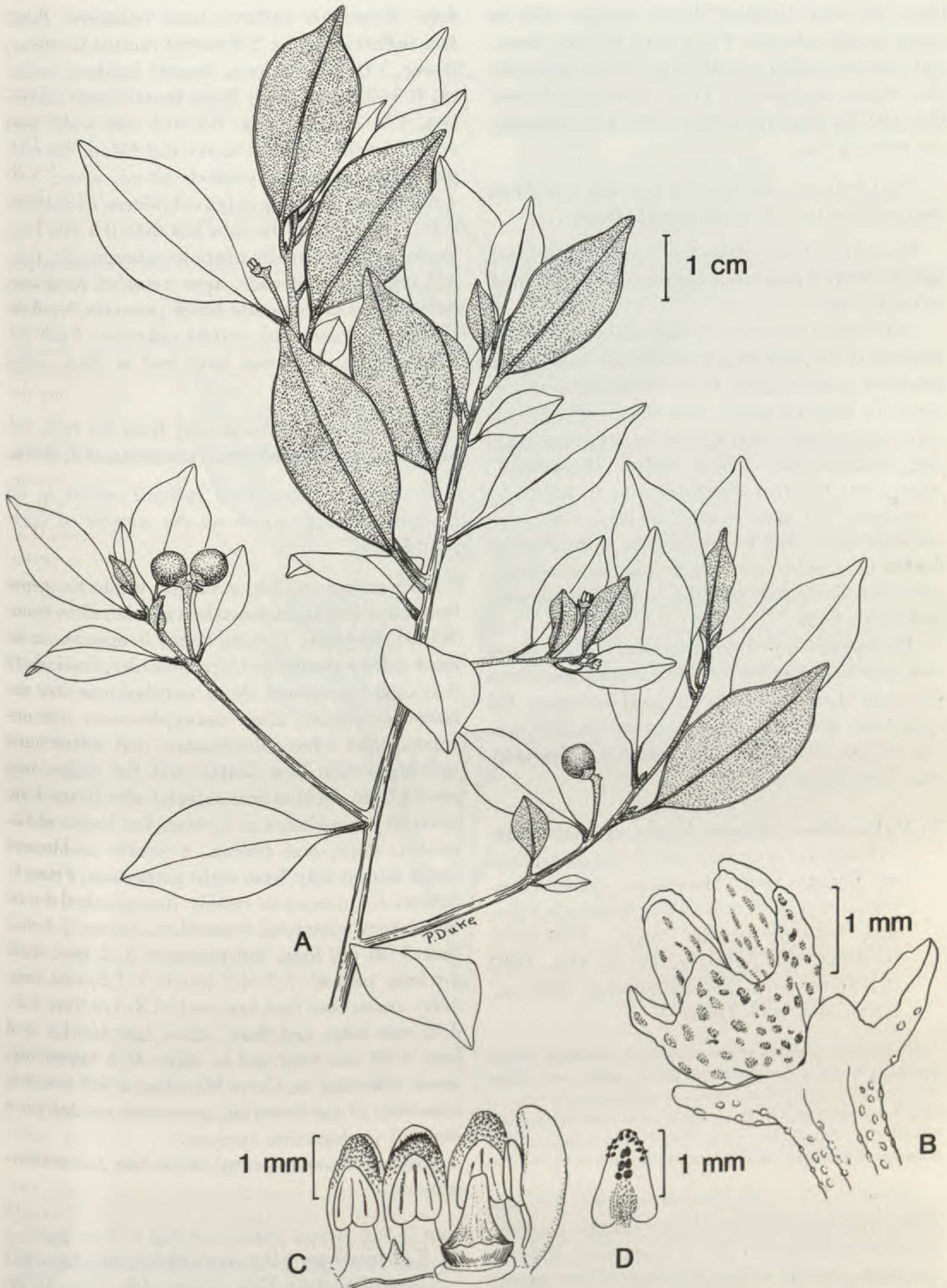


FIGURE 3. *Cybianthus huberi* Pipoly.—A. Habit.—B. Inflorescence, with one flower removed.—C. Opened pistillate flower, showing cucullate corolla lobes, and apophysate ovary with disc below.—D. Dorsal view of sterile anther, showing punctate connective and glandular-papillate thecae. (From the holotype.)

form, the ovary 4-lobed, deeply costate, with an upper apophysate rim, 1 mm long, 1.3 mm diam., glabrous, the style truncate, prominently punctate, the stigma punctiform. Fruit depressed-globose, 0.5–1.0 cm long and in diam., black at maturity, the exocarp thin.

Distribution. Known only from the type, from Serranía Guanay, at 1,700 m elevation.

Ecology. *Cybianthus huberi* is a scrub forest species growing near low, inundated areas and small watercourses.

Cybianthus huberi is unique within the genus because of its pistil on a carnose disc and, within subgenus *Conomorpha*, by its rufous-papillate anthers. Its reduced spike, crateriform calyces, carinate corolla lobes, and apically apophysate ovary are synapomorphies with *C. holstii*. However, *C. huberi* may be easily separated from *C. holstii* by coriaceous (not membranaceous) leaves, the conspicuous lobate (not inconspicuous, elobate) staminal tube, subsessile anthers (not on short, apically free filaments), pistil on a disc (not sessile), and larger fruit.

This species is dedicated to Otto Huber, friend and preeminent authority on the vegetation of the Guayana Highland and neotropical savannas. His collections and their accompanying detailed ecological data have greatly increased our understanding of the Guayana flora.

3. *Cybianthus julianii* Pipoly, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Depto. Atabapo, Cerro Marahuaca, cumbre, central portion of SE mesa, along Quebrada Yekuna, tributary of Río Negro, 3°40'30"N, 65°26'20"W, 2,560 m, 10–12 Oct. 1983 (fr), *Steyermark 129448* (holotype, VEN; isotypes, MO, NY). Figure 4.

Ob laminas plicatas secus marginem revolutas subtus dense lepidotas *C. crotonoideo* arcte similis, sed ab ea laminis cartilagineis (non coriaceis) inflorescentiis uni- vel bifloris (non racemis largis), calycis lobis suborbicularibus ad apicem obtusis (non ovatis ad apicem rotundatis) fructibusque luteis (non atris) praeclare distat.

Shrub to 1.5 m tall; branchlets terete, 2–3 mm diam., appressed-lepidote. Leaves elliptic to oblanceolate, cartilaginous, 2.6–3.1 cm long, 0.8–1.4 cm wide, apically acute to subacuminate, prominently pellucid punctate above and below, densely lepidote below, the scales not overlapping, the midrib depressed above, prominently raised below, the leaf plicate, the margin revolute; petioles canaliculate, 0.5–0.7 cm long, densely appressed-lepi-

dote. *Staminate inflorescence*: unknown. *Pistillate inflorescence*: a 2-flowered raceme or solitary flower, 1.0–2.0 cm long, densely lepidote; peduncle 0.5–0.7 mm long; floral bracts linear-lanceolate, 1.9–2.5 mm long, 0.3–0.5 mm wide, apex acute, densely lepidote above and below, the margin entire, glabrous; pedicels terete, erect, 3.0–4.5 mm long. Fruiting calyx cotyliform, coriaceous, 0.8–1.2 mm long, the tube less than 0.1 mm long, the lobes very broadly ovate to suborbicular, 0.8–1.2 mm long and wide, apex rounded to obtuse, densely and prominently black punctate, lepidote, the margin crenulate; corolla unknown. Fruit yellow, globose, 2–3 mm long and in diam. when dried.

Distribution. Known only from the type, collected on Cerro Marahuaca, Amazonas, at 2,560 m.

Ecology. *Cybianthus julianii* occurs at the margins of boggy areas on the summit of Cerro Marahuaca.

Cybianthus julianii is unique within the genus because of its cartilaginous leaves and yellow fruits. Within subgenus *Conomorpha*, it appears to be most closely related to *C. crotonoides*, from which it is easily separated by its cartilaginous (not coriaceous) leaves, 2(not many)-flowered inflorescence, calyx lobes suborbiculate (not deltate) and apically obtuse (not acute), and the yellow (not black) fruit. *Cybianthus julianii* also bears a superficial resemblance to *Cybianthus laetus* of Colombia, Peru, and Bolivia, a poorly understood taxon known only from eight gatherings. From *C. laetus*, *C. julianii* is readily distinguished by its terete (not subterete) branchlets, leaves 2.6–3.1 (not 3–8) cm long, inflorescence 1–2 (not 2–3) cm long, pedicels 3.0–4.5 (not 0.9–1.5) mm long, calyx coriaceous (not carnose), 0.8–1.2 (not 1.2–1.8) mm long, and fruit yellow (not black), 2–3 (not 5–8) mm long and in diam. It is hoped that more collecting on Cerro Marahuaca will result in collection of the flowering specimens needed for a detailed phylogenetic analysis.

The species is dedicated to the late Julian Steyermark.

4. *Cybianthus steyermarkianus* (Agostini) Agostini, *Acta Biol. Venez.* 10: 156. 1980. *Conomorpha steyermarkiana* Agostini, *Acta Bot. Venez.* 2: 283. 1967. TYPE: Venezuela. Bolívar: Cerro Auyán-tepui, cumbre, 2,100 m, without date, (stam. fl), *Cardona 2723* (holotype, VEN; isotype, NY). Figure 5.



FIGURE 4. *Cybianthus julianii* Pipoly.—A. Habit, showing two-flowered racemes. (From the holotype.)

Shrub to 4 m tall; branchlets terete, 2.5–3 mm diam., densely lepidote, at times glabrescent. Leaves suborbicular, obovate, or elliptic, stiffly coriaceous, (1.2–)1.5–2.5 cm long, 1.0–1.7 mm wide, apically rounded to obtuse, basally acute to obtuse, decurrent on the petiole, nitid and scrobiculate, densely lepidote when young, glabrescent above, densely to sparingly lepidote below, midrib depressed above,

prominent below, nerves 6–12 pairs, the margin prominently revolute, often inrolled; petioles canaliculate, 0.5–1.0 cm long, densely or sparingly lepidote. *Staminate inflorescence*: a simple, erect raceme, 5–9-flowered, 0.7–3 cm long, the axis and pedicels densely lepidote; peduncle 0.3–1.5 cm long; pedicels 1.5–3.5 mm long; floral bracts narrowly elliptic, 1.0–1.5 mm long, 0.4–0.6 mm

wide, apically acute, densely lepidote adaxially, the margin entire. Flowers pendent, 4-merous; calyx cupuliform, 0.9–1.2 mm long, the tube 0.2–0.3 mm long, the lobes triangular, carnose, 0.7–0.8 mm long, 0.6–0.7 mm wide, tapering to a rounded apex, sparingly lepidote without, inconspicuously pellucid or orange punctate, the margin entire, lepidote; corolla campanulate, 2.7–2.9 mm long, the tube 0.8–0.9 mm long, the lobes elliptic, broadly elliptic or ovate, carnose, 2.0–2.2 mm long, 1.2–1.4 mm wide, apically rounded, glabrous, sparingly lepidote without, pellucid or orange punctate; stamens 1.6–1.7 mm long, adnate 1.2–1.4 mm to the corolla tube, the tube 0.8–1.4 mm long, inconspicuous, elobate, the apically free filaments less than 0.1 mm long, the anthers erect, dorsifixed near the base, ovate, 0.5 mm long, 0.4–0.5 mm wide, apex apiculate, base cordate, the connective pellucid or orange punctate; pistillode clavate, 1.2–1.4 mm long, hollow, translucent glandular-lepidote, the style elongate, the stigma punctiform. *Pistillate inflorescence*: a simple, erect raceme, 5–9-flowered, 0.7–3 cm long, the axis and pedicels densely lepidote; peduncle 0.3–1.5 cm long; pedicels 1.5–3.5 mm long; floral bracts narrowly elliptic, 1.0–1.5 mm long, 0.4–0.6 mm wide, apically acute, densely lepidote adaxially, the margin entire. Flowers pendent, 4-merous; calyx cupuliform, 0.9–1.2 mm long, the tube 0.2–0.3 mm long, the lobes triangular, carnose, 0.7–0.8 mm long, 0.6–0.7 mm wide, tapering to a rounded apex, sparingly lepidote without, inconspicuously pellucid or orange punctate, the margin entire, glabrous, lepidote; corolla campanulate, carnose, 1.9–2.2 mm long, the tube 0.4–0.5 mm long, the lobes elliptic to broadly elliptic, 1.6–1.7 mm long, 0.9–1.1 mm wide, the apex obtuse, rounded or attenuate to a rounded tip, glabrous, sparingly lepidote outside, pellucid or orange punctate; staminodes 1.0–1.3 mm long, adnate 0.6–0.8 mm to the corolla tube, the tube 0.4–0.7 mm long, elobate, the apically free filaments 0.1–0.2 mm long, the anthers erect, dorsifixed near the base, ovate, 0.5–0.6 mm long, 0.4–0.5 mm wide, apex apiculate, base cordate, the connective pellucid or orange punctate; pistil obnapiform, 1.2–1.4 mm long, the ovary 0.6–0.7 mm long and in diam., densely glandular-lepidote, the style elongate, 0.5–0.6 mm long, ca. 0.2 mm diam., glabrous, epunctate, the stigma capitate, 2-lobed; the placenta cotyliform, the ovules 3, naked. Fruit not seen.

Distribution. Endemic to the tepuis of the Chimantá Massif, located in the eastern portion of the state of Bolívar, from 2,000 to 2,300 m elevation.

Ecology. *Cybianthus steyermarkianus* grows in cracks along the upper edges of narrow, deep canyons (zanjones) and in rocky outcrops near the edge of savannas on the summits of the tepuis of the Chimantá Massif. It is subject to high winds and rain in the evening hours, and high levels of sunlight and radiation during the day.

Specimens examined. VENEZUELA. BOLIVAR: Dto. Piar, Macizo del Chimantá, N sector, Abacapa-tepui, NW summit, 2,125–2,300 m, 13 Mar. 1953 (fr), *Steyermark* 74934 (BM, F, MO, NY, US, VEN); Acopán-tepui, sector NE, headwaters of Río Yunek, 1,950 m, 8–11 Feb. 1985 (stam. fl), *Pipoly et al.* 7187 (F, MO, NY, PH, TEX, US, VEN), 7162 (MO, NY, US, VEN); summit, Apacará-tepui, 2,450–2,500 m, 26 June 1953 (pist. fl, fr), *Steyermark* 75899 (NY, US, VEN), S base of upper cliffs of Apacará-tepui, 2,200 m, 30 Jan.–1 Feb. 1983 (stam. fl), *Steyermark et al.* 128435 (F, MO, MYF, NY, US, VEN), 30 Jan.–1 Feb. 1983 (stam. fl), *Huber & Steyermark* 6990 (MO, NY, VEN); Aprada-tepui, 2,460–2,500 m, 25 Feb. 1978 (fr), *Steyermark et al.* 115888 (MO, NY, VEN); Chimantá-tepui, Río Tirica, Caño Grillo, 7–9 Feb. 1983 (ster.), *Steyermark et al.* 128920 (MO, NY, VEN); NW cumbre, Churi-tepui (Muru-tepui), 2,300–2,350 m, 3 Feb. 1953 (stam. fl), *Wurdack* 34299 (NY); S-central section, wide valley between the NE border of Torono-tepui and the central section of Chimantá-tepui, 2,100 m, 11–15 Feb. 1985 (stam. fl), *Pipoly et al.* 7293 (MO, MYF, NY, TEX, US, VEN); Torono-tepui, summit, 2,165–2,180 m, 9 Feb. 1955 (fr), *Steyermark & Wurdack* 660 (BM, F, MO, NY, US, VEN), summit, N-facing slopes above Caño Mojado, 2,030–2,150 m, 21 Feb. 1955 (pist. fl), *Steyermark & Wurdack* 1035 (NY, VEN).

Cybianthus steyermarkianus is most closely related to *C. wurdackii*, an apparently sympatric species, but is easily separated by its epunctate, revolute-inrolled leaf margins, branchlets 2.5–3 (not 3–3.5) mm diam., nitid (not dull) upper leaf surface, and carnose (not coriaceous) flowers. For a discussion of ecological differences, see *C. wurdackii*.

5. ***Cybianthus wurdackii*** Agostini ex Pipoly, sp. nov. TYPE: Venezuela. Bolívar: Macizo del Chimantá, Churi(Muri)-tepui, NW summit, 2,250–2,300 m, 26 Jan. 1953 (stam. fl), *Wurdack* 34240 (holotype, VEN; isotypes, COL, F, NY, S, US). Figure 6.

Quoad filamenta anthera breviora, folia parva obovata vel late elliptica, species haec sympatrico *C. steyermarkiano* praeclare affinis sed florum staminatorum corolla 2.0–2.2 (non 2.7–2.9) mm longa, extusque lepidota (nec glabra), staminibus 1.4–1.5 (nec 1.6–1.7) mm longis et tubo staminali conspicuo (nec inconspicuo) statim separabilis.

Treelet to 3 m tall; branchlets terete, 3.0–3.5 mm diam., densely lepidote at first, glabrescent, the bark smooth, not ridged. Leaves obovate-spathulate, coriaceous, 1.5–2.4 cm long, 0.8–1.4 cm wide, apex obtuse to rounded, rarely appearing

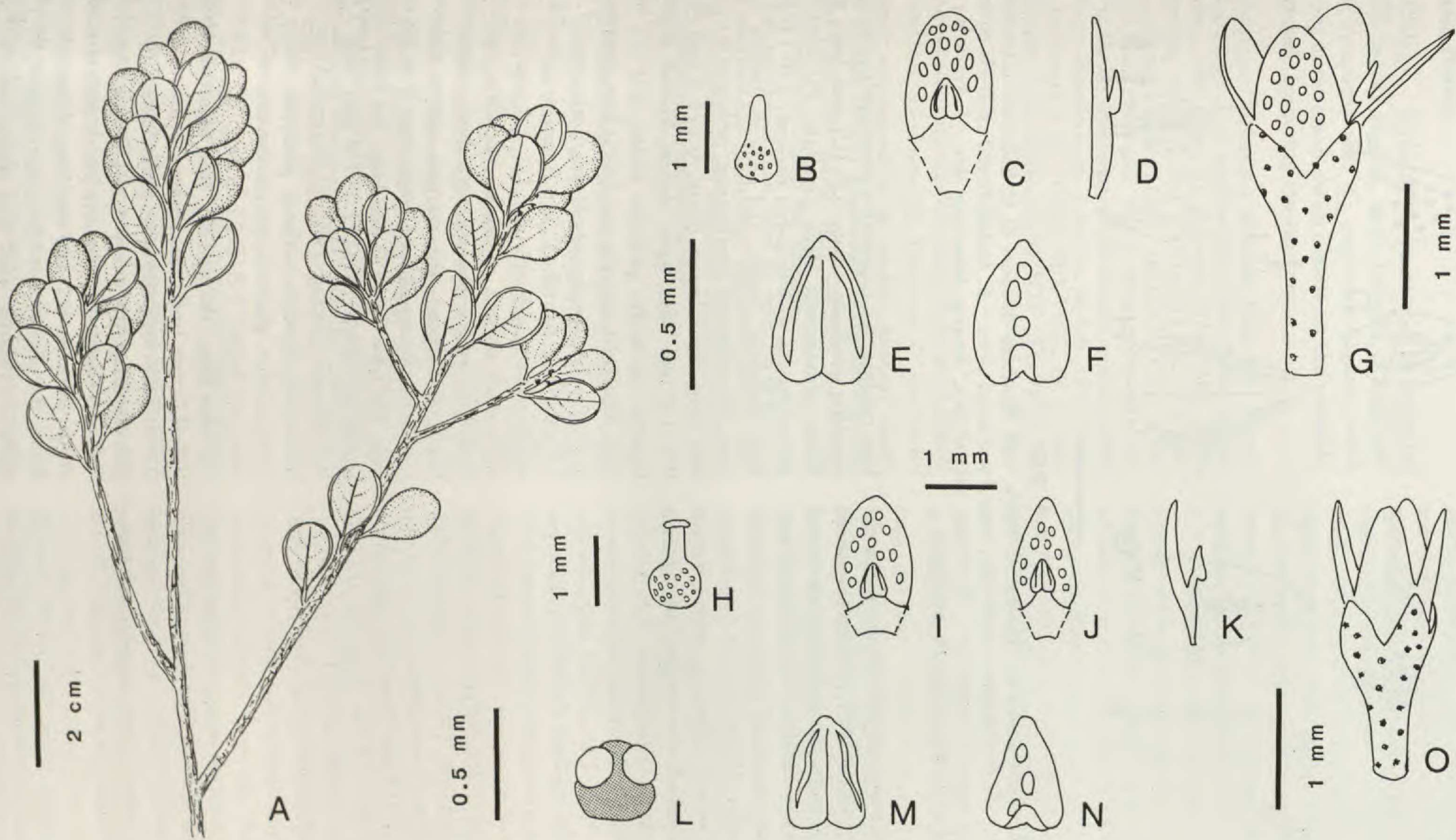


FIGURE 5. *Cybianthus steyermarkianus* (Agostini) Agostini.—A. Habit.—B. Pistillode.—C. Ventral view, pistillate corolla lobe.—D. Lateral view, pistillate corolla lobe.—E. Anther, ventral view.—F. Anther, dorsal view, showing punctate connective.—G. Staminate flower.—H. Pistil, showing capitate stigma.—I, J. Staminate corolla lobes, ventral view.—K. Staminate corolla lobes, lateral view.—L. Placenta, showing naked ovules.—M. Sterile anther, ventral view.—N. Sterile anther, dorsal view, showing punctate connective.—O. Pistillate flower. (A-G, from holotype; H-O, from *Steyermark* 75899.)

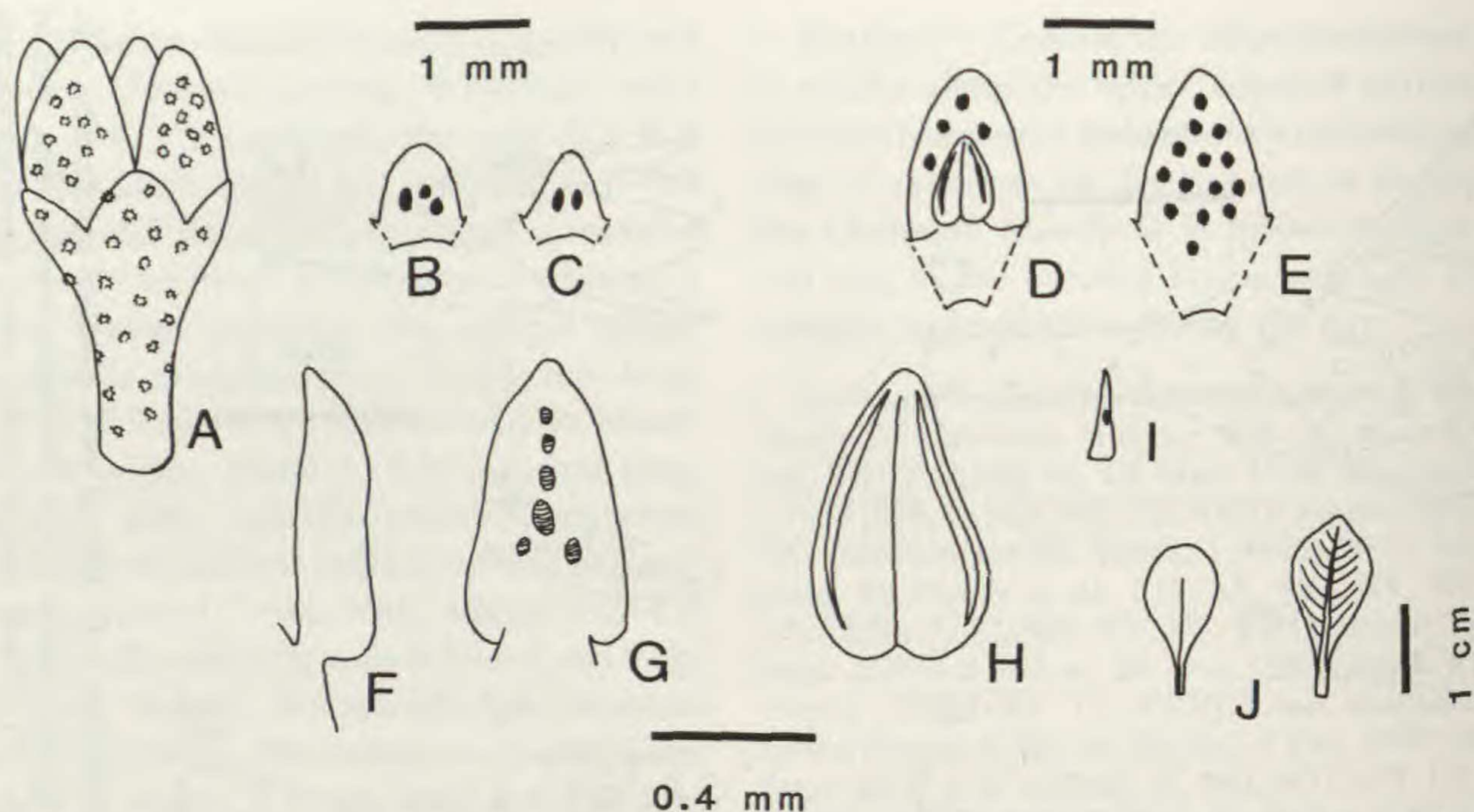


FIGURE 6. *Cybianthus wurdackii* Agostini ex Pipoly.—A. Staminate flower.—B, C. Staminate calyx lobes, showing punctations.—D, E. Staminate corolla lobe, ventral and dorsal views.—F. Anther, lateral view.—G. Anther, dorsal view, showing punctate connective.—H. Anther, ventral view, showing dehiscence slits.—I. Pistillode.—J. Leaf, adaxial and abaxial views. (From the holotype.)

subacute, base cuneate, slightly decurrent on the petiole, midrib depressed above, prominently raised below, nerves 6–8 pairs, inconspicuous above and below, upper surface wrinkled, at first densely lepidote, then scrobiculate and sparingly lepidote, densely lepidote below, the scales sunken, not overlapping, inconspicuously pellucid punctate, except prominently so beneath the margin, the margin entire, revolute; petioles canaliculate, 0.3–0.7 mm long, densely lepidote. *Staminate inflorescence*: a 4–7-flowered raceme, 1.0–2.0 cm long, the peduncle, rachis, and pedicels densely lepidote; peduncle 0.6–0.8 mm long; floral bracts ovate, 0.5–1.0 mm long, 0.2–0.4 mm wide, apex acute, densely lepidote adaxially, the margin entire; pedicels terete, 1.5–1.8 mm long. Flowers 4-merous, nodding; calyx cupuliform, coriaceous, 0.8–1.0 mm long, the tube 0.1–0.2 mm long, the lobes ovate to broadly ovate, 0.7–0.9 mm long, 0.5–0.7 mm wide, apex obtuse, rarely rounded, somewhat cucullate medially and keeled, sparingly lepidote without, glabrous within, conspicuously black punctate, the margin entire, glabrous; corolla cupuliform, coriaceous, 2.0–2.3 mm long, the tube 0.6–0.7 mm long, the lobes ovate, 1.3–1.4 mm long, 1.0–1.2 mm wide, apex rounded, sparingly lepidote without, glabrous within, conspicuously black punctate, the margin entire, glabrous; stamens 1.4–1.5 mm long, the tube conspicuous, chartaceous, 0.7–0.8 mm long, without lobes, the apically free filaments 0.1 mm long, epunctate, terete, the anthers erect, ovate, 0.7–0.8 mm long, 0.4–0.5 mm wide, apex apiculate to cuspidate, the apiculum erect,

base cordate, the connective prominently punctate dorsally; pistillode conic, 0.8–0.9 mm long, glabrous, prominently black punctate. *Pistillate inflorescence*: a 4–9-flowered raceme, 1.0–1.6 mm long, peduncle, rachis, and pedicels densely lepidote, the scales not overlapping; peduncle 0.3–0.6 mm long; floral bracts ovate, 0.7–1.5 mm long, 0.9–1.0 mm wide, apex obtuse, keeled, densely lepidote adaxially; pedicels terete, 3.0–3.5 mm long. Flowers 4-merous, nodding at first, then erect in fruit; calyx deeply cupuliform, coriaceous, 1.2–1.5 mm long, the tube 0.5–0.6 mm long, the lobes widely ovate to suborbicular, 1.1–1.2 mm long and wide, apex obtuse, somewhat cucullate, medially keeled, sparingly lepidote, with three conspicuous black punctations, the margins entire, glabrous; corolla deeply cupuliform, coriaceous, 2.4–2.8 mm long, the tube 0.9–1.0 mm long, the lobes suborbicular to widely ovate, 1.4–1.8 mm long, 1.6–2.0 mm wide, dorsally reflexed, somewhat concave, moderately lepidote without, glabrous within, the margin entire, glabrous; staminodes resembling stamens but larger, 1.8–2.1 mm long, the tube 0.9–1.0 mm long, the apically free filaments terete, 0.2–0.3 mm long, the anthers ovate to deltate, 0.6–0.7 mm long and wide; pistil obnapiform, 1.8–2.1 mm long, the ovary 1.1–1.2 mm long, 1.3–1.4 mm diam., prominently black punctate, glabrous, the style 0.7–0.9 mm long, epunctate, glabrous, the stigma 3–4-lobed, not capitate, the placenta cotyliform, with 3–4 naked ovules. Fruit depressed-globose, 4–6 mm long, 6–8 mm wide, the exocarp thin, prominently punctate.

Distribution. Endemic to the Auyán-tepui-Chimantá Floristic Complex (Maguire, 1979) in eastern Bolívar.

Ecology. *Cybianthus wurdackii* is restricted to the heavily shaded, moist bottoms of zanjones. It is sympatric with *C. steyermarkianus*, which thrives in the small shrub islands on the summits, frequently bordering the canyons.

Paratypes. VENEZUELA. BOLIVAR: Dtto. Piar, Kamar-kaibaray-tepui, E of Auyán-tepui, 2,400–2,500 m, 25–26 Mar. 1987 (stam. fl), *Delascio 13146* (MO, VEN); Ptari-tepui, summit, 2,360–2,420 m, 23 Feb. 1978 (pist. fl), *Steyermark et al. 115657* (MO, NY, VEN), 2,300 m, 26 Mar. 1987 (pist. fl, fr), *Holst 3600* (MO, US, VEN); Macizo del Chimantá, NE section, central portion of Murey-(Eruoda-)tepui, 2,500 m, 24 Feb. 1978 (stam. fl), *Steyermark et al. 115785* (MO, VEN), 15–17 Mar. 1986 (pist. fl, fr), *Huber 11590* (MYF, NY, VEN); Sarven-tepui, 1,750–1,850 m, 19 Jan. 1953 (stam. fl), *Wurdack 34189* (NY, US, VEN).

Cybianthus wurdackii seems to be most closely related to *C. steyermarkii*. However, *C. wurdackii* is easily recognized by its smaller, lepidote staminate corolla, shorter staminodes, a conspicuous staminal tube, and leaves that are dull above and merely revolute along the margin.

The species is dedicated to John Wurdack of the Smithsonian Institution, explorer of the Guayana and preeminent authority on the systematics of neotropical Melastomataceae.

6. *Cybianthus plowmanii* Pipoly, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Depto. Río Negro, Cerro de la Neblina, Venezuelan-Brazilian border, vic. Camp 6, on ridge 3.5 km W of Pico Zuloaga, 0°53'N, 65°56'W, 2,000 m, 13–15 Apr. 1984 (stam. fl), *Thomas & Plowman 3048* (holotype, VEN; isotypes, F, MO, NY, US). Figure 7.

Quoad folia supra dense atro-punctata, laminarum nervulos utrinque conspicuos, inflorescentiam paniculatam ad *C. amplum* valde affinis sed ab ea corollae lobis plicatis (nec planis) ad apicem cucullatum (nec planum) asymmetricis (nec symmetricis) manifeste atro- (nec brunneo-) punctatis, antherisque ad apicem apiculatos (nec acutos) atque ventraliter (nec dorsaliter) curvatis facile cognoscitur.

Shrub or tree to 8 m tall; branchlets terete, 0.7–1.2 mm diam., stiff, the bark creamish white, prominently furrowed, without lenticels, moderately adpressed-lepidote, at times glabrescent. Leaves oblanceolate to obovate, coriaceous, (5.5–)9.3–24 cm long, (4.5–)5.5–7.5(–8.5) cm wide, apically acuminate, the acumen subacute, 0.3–1.8 cm long, the base cuneate, decurrent on the petiole, costa

depressed above, prominently raised below, secondary nerves prominent above and below, nitid above, pallid below, the surface smooth above, with scattered appressed-lepidote scales below, not conspicuously punctate, the margin essentially flat, regular, entire; petioles prominently marginate, thick, (1.4–)1.8–2.5 cm long, 2–4 mm diam., lepidote at first, early glabrescent. *Staminate inflorescence:* a panicle, rarely appearing almost racemose, (1.5–)3.5–5.5 cm long, the rachis densely lepidote; bracts linear-lanceolate, 1.1–1.5 mm long, 0.3–0.5 mm wide, plicate, apically acuminate, the margin entire, glabrous; pedicels 2.1–3.0 mm long. Flowers 4-merous, erect; calyx patelliform, coriaceous, 1.2–1.3 mm long, the tube 0.2–0.3 mm long, the lobes widely ovate to suborbicular, 1.0–1.1 mm long and wide, apex obtuse to rounded, lepidote, medially thick and rugose without, densely and prominently black punctate, the margin irregular, entire; corolla campanulate, carnose, 3.0–3.5 mm long, translucent, the tube 0.9–1.1 mm long, the lobes widely ovate, asymmetric, reflexed at anthesis, 2.0–2.4 mm long, 1.4–1.6 mm wide, plicate, obtuse to rounded apically, cucullate, minutely red lepidote and glandular-granulose within, basally red lepidote and glandular-granulose near the margin without, veins 4, black, conspicuous, prominently black punctate without apically, the margin entire, glandular-granulose; stamens 2.7–3.0 mm long, the tube conspicuous, carnose, 1.2–1.3 mm long, translucent, epunctate, elobate, the apically free filaments 1.0–1.2 mm long, flat, the anthers ovate, erect, 1.4–1.6 mm long, 0.8–0.9 mm wide, apiculate, the apiculum ventrally recurved perpendicular to the anther, the base cordate, glabrous, the connective prominently black punctate, the slits extremely wide, not confluent; pistillode conic, 1.2–1.3 mm long, 0.5 mm diam., the ovary translucent-lepidote. *Pistillate inflorescence:* paniculate, at times poorly formed, appearing racemose in fruit; 3.5–8.0 cm long, the rachis densely lepidote; floral bracts linear-lanceolate, 1.1–1.3 mm long, 0.5–0.6 mm wide, sparsely lepidote, plicate, early caducous, the margin entire, glabrous; pedicel erect, (1.0–)2.0–3.0(–4.0) mm long, moderately punctate, terete, thickening in fruit. Flowers 4-merous; calyx patelliform, coriaceous, 1.0–1.2 mm long, the tube short, 0.1–0.2 mm long, the lobes appearing free, suborbicular, 0.7–0.8 mm long, 1.2–1.3 mm wide, apex rounded to obtuse, essentially glabrous, medially thick and rugose, prominently black punctate, the margin irregular, entire, lepidote; corolla rotate, 3.0–3.2 mm long, the tube 0.5–0.7 mm long, the lobes highly reflexed at anthesis, touching the pedicels,

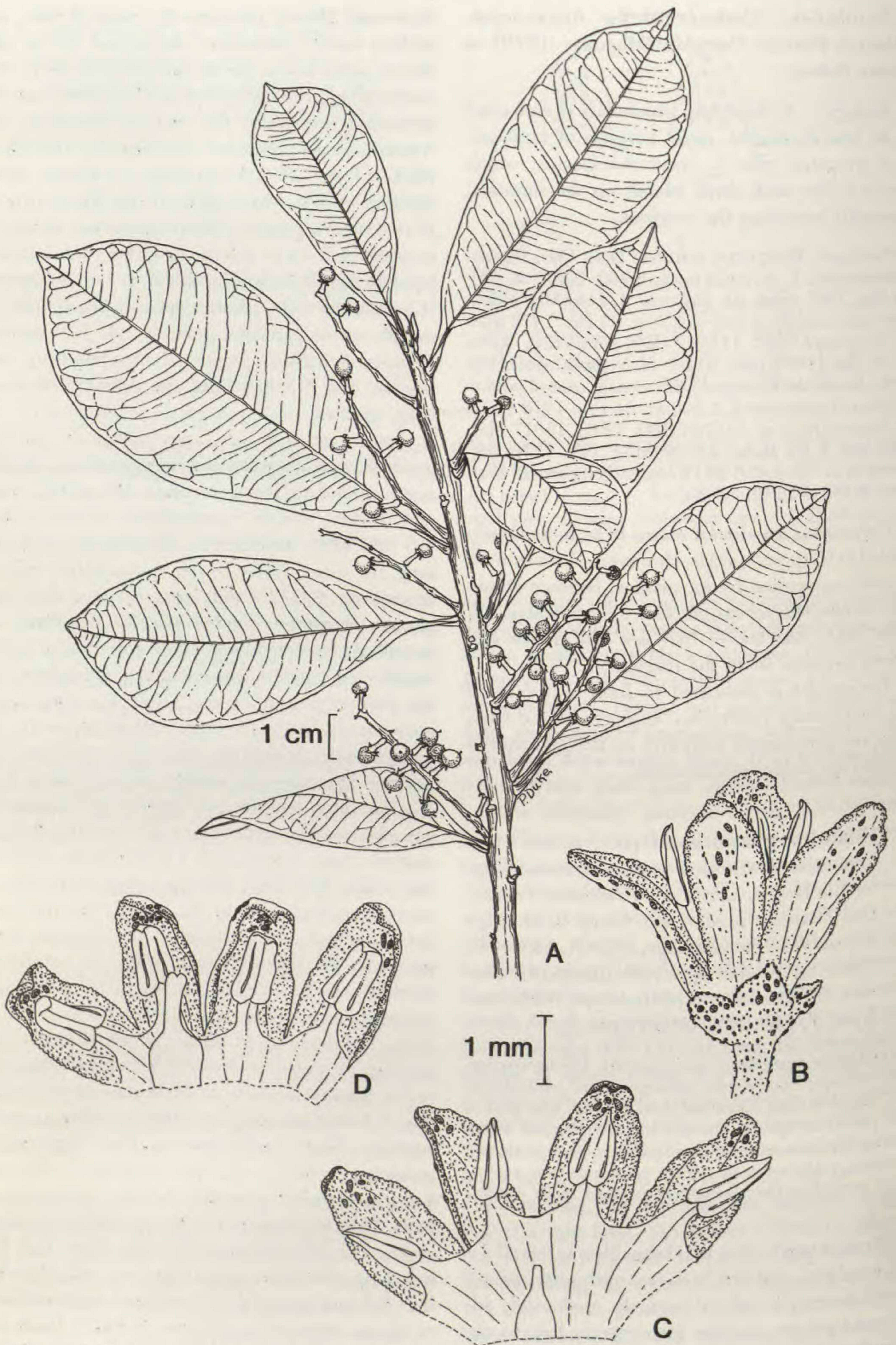


FIGURE 7. *Cybianthus plowmanii* Pipoly.—A. Habit.—B. Staminate flower, showing plicate corolla lobes, calyx, and corolla punctations and erect anther with proximally recurved apiculum.—C. Opened staminate flower, showing cucullate corolla lobes and punctations.—D. Opened pistillate flower, showing pistil with 2-lobed stigma. (A, from Thomas & Plowman 3048; B and C, from holotype; D, from Thomas & Plowman 3069.)

ovate, 2.5–2.8 mm long, 1.7–1.8 mm wide, asymmetric, apically cucullate, minutely red lepidote and glandular-granulose within, basally red lepidote and glandular-granulose near the margin without, the veins 4, conspicuous, prominently black punctate apically without; staminodes 2.6–2.9 mm long, the tube prominent, carnose, 0.8–1.0 mm long, translucent, the apically free filaments 0.8–1.0 mm long, the anthers dorsifixed ca. $\frac{1}{3}$ from base, erect, narrowly ovate, 1.0–1.2 mm long, apiculate, the apiculum ventrally recurved, perpendicular to anther, base nearly cordulate, appearing obtuse, the connective darkened, epunctate but with a prominent translucent callosity and appearing verrucose; pistil obnapiform, 2.0–2.2 mm long, the ovary terete, 1.0–1.2 mm long, 1.3–1.5 mm wide, glabrous, black punctate, the style terete, ca. 0.9 mm long, epunctate, the stigma capitate, 2-lobed, the placenta bilobed, bearing 2 deeply imbedded ovules. Fruit depressed-globose, ca. 0.5–0.8 cm long, 0.7–1.0 cm diam., prominently punctate, verrucose, exocarp thin.

Distribution. Restricted to cloud and scrub forests of Cerro de la Neblina and the environs of Serra Aracá, the latter a satellite tepui in Amazonas, Brazil, at elevations to 2,000 m.

Ecology. *Cybianthus plowmanii* occurs on outcrops in exposed areas, in small shrub islands. It appears to be locally common, but the populations are few and infrequently encountered.

Paratypes. VENEZUELA. AMAZONAS: Depto. Río Negro, Cerro de la Neblina, Venezuelan–Brazilian border, vic. Camp 6, on ridge 3.5 km W of Pico Zuloaga, 2,000 m, 13–15 Apr. 1984 (fr), *Thomas & Plowman 3060* (F, NY, US, VEN), (pist. fl), 3069 (F, US, VEN), Camp VII, 29 Nov. 1984 (pist. fl), *Anderson 13386* (MICH, NY, VEN), S slopes of Cañon Grande, 1,900 m, 29 Nov. 1984 (pist. fl), *Croat 59409* (MO, VEN), E escarpment, Caño Grande below Cumbre Camp, 1,200–2,200 m, 27 Dec. 1957 (fr), *Maguire et al. 42533* (F, NY—3 sheets, US, VEN), 1,730–1,850 m, 31 Jan. 1985 (fr), *Nee 30663* (MO, NY, US, VEN). BRAZIL. AMAZONAS: Rio Cuieras, 50 km upstream, farm of Sr. Caldez, [near Serra Aracá], 3 Apr. 1974 (fr), *Campbell et al. P21820* (INPA, MG, NY, US).

Cybianthus plowmanii is most easily confused with *C. amplus* in the western limit of Guayana. However, the terete branchlets, flat leaf margins, branchlets without lenticels, asymmetric, plicate, and apically cucullate corolla lobes with prominent black punctations easily distinguish *C. plowmanii* from *C. amplus*.

Preliminary data obtained from phylogenetic analysis (Pipoly, unpublished) reveals that *C. peruvianus*, *C. amplus*, and *C. plowmanii* form a

clade defined by staminal and staminodial tube longer than the corolla tube. From there, *C. peruvianus* and *C. plowmanii* form a clade defined by asymmetric corolla lobes. *Cybianthus peruvianus* is defined by its unique linear-lanceolate anthers, while *C. plowmanii* is distinguished by its plicate corolla lobes. *Cybianthus amplus* is defined by its angulate, lenticellate branchlets.

7. *Cybianthus amplus* (Mez) Agostini, Acta Biol. Venez. 10: 151. 1980. *Conomorpha ampla* Mez in Engler, Pflanzenr. IV, 236: 257. 1902. TYPE: Brazil. Bahia: without locality, without date (stam. fl), *Sellow 653* (lectotype, here designated, K; isolectotype, fragment at F). Figure 8.

Conomorpha macrophylla Martius, Herb. Fl. Bras. 260. 1837. TYPE: Colombia. Comisaría de Vaupés: Dtto. Japurense, Serra do Araracoara, (pist. fl, fr), *Martius s.n.* (lectotype, here designated, M; isolectotypes, M—4 sheets).

Conomorpha utiarityi Hoehne, Relat. Commiss. Linhas Telegr. Estraté. Matto Grosso Amazonas, Ann. 5, Bot. 6: 64. 1915. TYPE: Brazil. Matto Grosso [Rondônia]: Salto de Utiarity, Rio Papagio, June 1909 (stam. fl), *Hoehne 2111* (holotype, R).

Shrub or small tree to 7 m tall; branchlets angular, 5–8 mm diam., the bark longitudinally ridged, creamish white, conspicuously lenticellate, densely lepidote. Leaves elliptic or obovate, coriaceous, 8–23 cm long, 4–12 cm wide, apex abruptly acuminate, the acumen to 1 cm, basally obtuse to acute, decurrent on the petiole, midrib depressed above, prominently raised below, nerves 24–40 pairs, inconspicuous or slightly raised above, more conspicuous below, upper surface scrobiculate, densely lepidote at first, glabrescent, the lower surface densely lepidote, the scales not overlapping, sparingly pellucid punctate, the margin revolute, epunctate; petioles marginate, 1.0–3.5 cm long, densely lepidote. *Staminate inflorescence*: a racemose panicle, with 1–6(–8) branches, branching from near the base, 2.5–8.0 cm long; peduncle, axis, and branches densely lepidote; peduncle 0.1–0.5 cm long; pedicels 0.5–1.0 mm long; floral bracts ovate, triangular, or ovate-triangular, 0.6–1.0 mm long, 0.4–0.6 mm wide, apex acute, densely lepidote adaxially, the margin entire. Flowers 4(–5)-merous, white; calyx cupuliform, carnose, 0.7–1.1 mm long, the tube 0.2–0.4 mm long, the lobes triangular, deltate, or deltate-ovate, 0.5–0.8 mm long, 0.5–0.9 mm wide, the apex rounded or attenuate to a rounded tip, sparingly pellucid or brown punctate, sparingly lepidote medially, the margin entire, often densely lepidote; corolla cam-

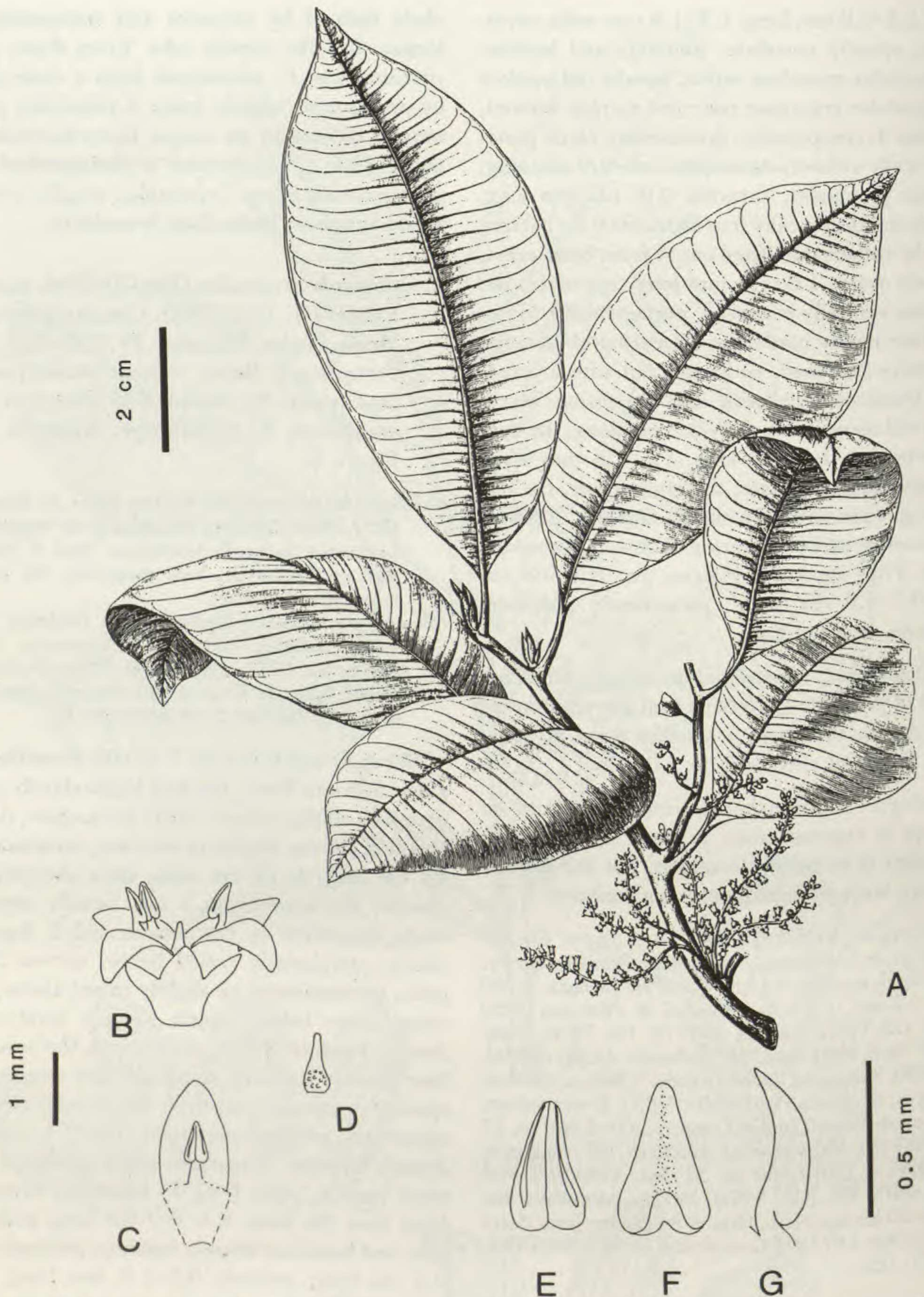


FIGURE 8. *Cybianthus amplus* (Mez) Agostini.—A. Habit.—B. Staminate flower.—C. Staminate corolla lobe, ventral view.—D. Pistillode.—E. Anther, ventral view.—F. Anther, dorsal view, showing darkened connective.—G. Anther, lateral view. (A, modified from Miquel, 1856, fig. 47; B-G, from Maguire & Wurdack 34861.)

panulate, carnose, 2.3–2.7 mm long, the tube 0.8–1.1 mm long, the lobes elliptic to ovate, 1.5–2.0 mm long, 0.8–1.2 mm wide, apex rounded, flat, sparsely lepidote without, glandular-granulose within and without submarginally, inconspicuously pellucid or brown punctate along the margins, the

margin entire, glandular-granulose; stamens 1.7–2.2 mm long, adnate 0.8–1.3 mm to the corolla, the tube inconspicuous, hyaline, 0.8–1.3 mm, elongate, the apically free filaments 0.1–0.3 mm long, flat, the anthers triangular to ovate-triangular, dorsifixed less than $\frac{1}{4}$ from base, 0.5–0.8 mm long,

0.3–0.4 mm wide, dorsally recurved, apex acute, base cordate, the connective inconspicuously brown punctate; pistillode elongate, subconic, 1.0–1.4 mm long, hollow, translucent glandular-lepidote basally. *Pistillate inflorescence*: a racemose panicle, with 1–5 branches, branching from near the base, 2.5–8.0 cm long; peduncle, axis, and branches densely lepidote; peduncle 0.1–0.5 cm long; pedicels 0.5–1.0 mm long; floral bracts ovate, triangular, or ovate-triangular, 0.6–1.0 mm long, 0.4–0.6 mm wide, apex acute, densely lepidote adaxially, the margin entire. Flowers 4(–5)-merous, white; calyx cupuliform, carnose, 0.7–1.1 mm long, the tube 0.2–0.4 mm long, the lobes triangular, deltate, or deltate-ovate, 0.5–0.8 mm long, 0.5–0.9 mm wide, the apex rounded or attenuate to a rounded tip, sparingly pellucid or brown punctate, sparingly lepidote medially, the margin entire, often densely lepidote; corolla campanulate, 2.3–2.7 mm long, the tube 0.8–1.1 mm long, the lobes elliptic to ovate, 1.5–2.0 mm long, 0.8–1.2 mm wide, apex rounded, flat, sparsely lepidote without, glandular-granulose within, and without in the marginal zone, inconspicuously pellucid or brown punctate along the margins, the margin entire, glandular-granulose; staminodes 1.7–2.2 mm long, adnate 0.8–1.3 mm to the corolla, the tube inconspicuous, hyaline, 0.8–1.3 mm, elobate, the apically free filaments 0.1–0.3 mm long, flat, the anthers triangular to ovate-triangular, dorsifixed less than $\frac{1}{4}$ from base, 0.5–0.8 mm long, 0.3–0.4 mm wide, dorsally recurved, apex acute, base cordate, the connective inconspicuously brown punctate; pistil obnapiform, 1.3–2.0 mm long, the ovary 0.7–1.2 mm long, 0.7–1.1 mm diam., glandular-lepidote, the style thick, 0.5–0.7 mm long, the stigma capitate, elobate, the placenta cotyliform, bearing 3 ovules, the ovules imbedded except at the apices. Fruit globose, 5–11 mm long, 6–12 mm diam., endocarp smooth or rugose, aril scanty, adnate to seed, embryo curved, 4 mm long.

Distribution. Colombia, Venezuela, Brazil, and Peru, at elevations below 1,100 m.

Ecology. *Cybianthus amplus* occurs in lowland, mostly seasonally inundated forests (várzea and igapó). It is a gap and forest margin species, and as such, thrives in areas of moderate disturbance.

Representative specimens examined. COLOMBIA. VAUPES: Cerro del Varador, Raudal Alto (Mariapire), right margin, 250 m, 3 Feb. 1953 (pist. fl), *Fernández 2056* (COL); Río Apaporis, Raudal de Jirijirimo, below mouth of Kanarari, 250 m, 25–26 Nov. 1951 (stam. fl), *García-Barriga 13715* (COL, US), 100 m, 15 Mar. 1952 (stam.

fl), *Schultes & Cabrera 15928* (COL, GH, US); near mouth of Río Piraparana, Río Apaporis, 20 June 1952 (fr), *Schultes & Cabrera 16794* (COL, ECON, MO, US); along tributary of Río Macu Parana, 1–8 June 1970 (ster.), *Silverwood-Cope 3* (AMES). VENEZUELA. TERRITORIO FEDERAL AMAZONAS: 0.5–3 km N of San Carlos de Río Negro, ca. 20 km S of confluence of Río Negro and Brazo Casiquiare, 120 m, 19 Nov. 1977 (stam. fl), *Liesner 3692* (MO, NY, VEN), 5 May 1979 (fr), *Liesner 7220*, (stam. fl bud), 7221 (MO, NY, VEN), 16 May 1979 (stam. fl), *Liesner 7468* (MO, VEN), 115 m, 17 Sep. 1975 (stam. fl), *Berry 1373* (MO, VEN); 15 km SW of Sta. Bárbara del Río Orinoco, 120 m, 26 June 1979 (stam. fl), *Huber 3861* (US, VEN); Río Cunucunuma, Caño Culebra, 1,000–1,100 m, 18 Nov. 1950 (pist. fl, fr), *Maguire et al. 29508* (NY, VEN); Cerro Duida, SE slopes along Caño Negro, 350–1,095 m, 25–26 Aug. 1944 (stam. fl), *Steyermark 57984* (F, NY, VEN); Sabana Grande, between Esmeralda and Cerro Duida, 175 m, 24 Mar. 1953 (stam. fl), *Maguire & Wurdack 34861* (COL, F, K, NY, S, U, US, VEN); Capibuará, alto Casiquiare, 120 m, 27 May 1942 (fr), *Williams 15574* (A, F, G, RB, US, VEN); Cerro Curiche, Tama-tama, without date (stam. fl), *Maguire 43662* (NY, VEN); vic. of N Cerro Vinilla, 30 km SSW of Ocamo, jct. of Río Orinoco, (stam. fl), *Steyermark et al. 130400* (MO, VEN); middle part of Río Baría, 80 m, 29 June 1984 (pist. fl), *Davidse & Miller 26773* (MO, VEN); Cerro Neblina Camp IV, 15 km NNE of Pico Phelps, N branch of river canyon, 780 m, 15–18 Mar. 1984 (stam. fl), *Liesner 16637* (MO, VEN). BOLIVAR: mid-basin, Río Paragua, near Minas de Manaima, 300 m, 13 June 1987 (fr), *Stergios 10284* (MO, PORT, US, VEN); Sierra Ichún, Salto Ichún, 27 Dec. 1961 (stam. fl), *Steyermark 90249* (VEN). BRAZIL. AMAZONAS: Yútica, left bank of Rio Vaupés, 15 Nov. 1952 (fr), *Romero-Castañeda 3536* (COL, GH, INPA, MO, NY, US).

Cybianthus amplus is most closely related to *C. plowmanii*, an endemic species of Cerro de la Neblina, and *C. peruvianus*, a western Amazonian species, but differs by its flat, symmetric, pellucid or brown punctate corolla lobes, leaves with revolute margins, the terete, lenticellate branchlets, and the acute anthers dorsally recurved.

Cybianthus amplus is a forest margin species and the only member of the subgenus that tolerates disturbance. Individuals growing in shady areas have longer leaves and longer, more highly branched panicles. Individuals growing in more open areas have thicker, obovate leaves with more prominently revolute margins. This variation has resulted in taxonomic overdescription. The type of *Conomorpha macrophylla* Martius represents populations with long, elliptic leaves, and narrowly campanulate flowers. It is otherwise identical to the other populations. Likewise, the type of *Conomorpha utiarietyi* Hoehne differs only by the widely elliptic leaves and petioles at the longer end of the continuum, and the slightly larger and more broadly campanulate flowers.

8. *Cybianthus quelchii* (N. E. Brown) Agostini, Bol. Soc. Venez. Ci. Nat. 22(132-133): 388. 1976. *Ardisia quelchii* N. E. Brown, Trans. Linn. Soc., Bot. 2, ser. 6: 46. 1901. *Weigeltia quelchii* (N. E. Brown) Mez, Pflanzenr. IV, 236: 288. 1902. TYPE: Venezuela [Guyana]. Summit of Mt. Roraima, 2,860 m, autumn 1808 (stam. fl), *McConnell & Quelch 665* (holotype, K). [Steyermark (1981) reported that McConnell and Quelch arrived at the summit of Roraima from the Venezuelan side.]

Conomorpha depressa Steyermark, Fieldiana, Bot. 28(3): 458. 1953. TYPE: Venezuela. Bolívar: Carrao-tepui, 2,470-2,500 m, 7 Dec. 1944 (fr), *Steyermark 60898* (holotype, F; isotype, NY).

Shrub or tree to 5 m tall; branchlets terete, subsucculent, 0.5-1.2 cm diam., the bark yellowish brown, without lenticels, densely and minutely ferruginous stipitate-lepidote at first, early glabrescent, densely black punctate and punctate-lineate. Leaves elliptic, oblanceolate, obovate, orbicular to obovate, coriaceous, (3.5-)4.5-11.5(-13) cm long, (2.0-)3.0-4.0(-6.0) cm wide, apex rounded, obtuse, truncate or emarginate, base acute, acuminate, or somewhat cuneate, not decurrent on the petiole, nitid and densely black punctate above and below, the midrib planer above, prominently raised and black punctate-lineate below, nerves 16-26 pairs, not usually conspicuous above, conspicuous below, the margin flat, punctate-lineate; petioles flat above, rounded below, (0.3-)1.0-1.5(-2.0) cm long, densely lepidote at first, glabrescent. *Staminate inflorescence*: a tripinnate panicle, 2.7-10 cm long, the peduncle, rachis, and pedicels lepidote at first, glabrescent; peduncle 1.2-2.3 cm; secondary branchlet bracts ovate-spathulate, membranaceous, 2.3-2.5 mm long, 1.2-1.3 mm wide, apex obtuse, prominently black punctate, sparsely lepidote, the margin entire, flat, the petioles to 0.2 mm long; floral bracts ovate, 0.9-1.1 mm long, 0.3-0.5 mm wide, apex acute, densely lepidote, the margin erose, irregular, sometimes denticulate, glabrous; pedicels terete, 0.1-0.5 mm long. Flowers 4-5-merous, erect; calyx cotyliform, carnose, 1.1-1.4 mm long, the tube 0.3-0.5 mm long, the lobes suborbicular to obovate, 0.8-1.1 mm long, 0.9-1.3 mm wide, apex obtuse, hyaline, densely and prominently black punctate medially, essentially glabrous, but sometimes with a few lepidote scales, the margin erose, irregular, often denticulate, glabrous; corolla campanulate, chartaceous, 2.9-3.0 mm long, the tube 0.6-0.9 mm long, the lobes ovate, reflexed, 1.9-2.2 mm long, 1.0-1.2 mm wide, ovate, the apex obtuse, prominently cu-

cullate, glabrous without, densely glandular-granulose above staminal tube and apically along margin within, prominently black punctate and rugose without, the margin regular, entire except crenulate apically, glabrous; stamens 2.4-2.8 mm long, the filaments basally swollen and connivent to form an inconspicuous tube 0.5-0.7 mm long, terete and adnate to the corolla lobe 0.6-0.8 mm above tube, then apically free for 0.6-0.8 mm, ventrally recurved, terete, epunctate, the anther oblong to ovate, dorsifixed less than $\frac{1}{4}$ from base, 0.8-1.2 mm long, 0.5-0.6 mm wide, dorsally recurved, apex apiculate, the apiculum erect, base subcordate, the connective black punctate at apex at point of insertion; pistillode lageniform, 0.9-1.1 mm long, ca. 0.5 mm diam., densely black punctate, the style and stigma not differentiated. *Pistillate inflorescence*: a tripinnate panicle, (1.0-)1.5-2.7(-4.0) cm long, peduncle, rachis, and pedicels lepidote at first, glabrescent; peduncle 0.7-2.0 mm long; secondary branchlet bracts ovate-spathulate, membranaceous, 2.2-2.3 mm long, 1.0-1.3 mm wide, apex obtuse, prominently black punctate, sparsely lepidote, the margin entire, flat, the petioles to 0.2 mm long; floral bracts ovate, 1.0 mm long, 0.5 mm wide, apex acute, densely lepidote, the margin irregular, denticulate, glabrous; pedicels terete, 0.1-0.5 mm long. Flowers 4-merous, erect; calyx deeply cupuliform, carnose, 0.9-1.1 mm long, the tube 0.3-0.5 mm long, the lobes orbicular to obovate, 0.3-0.5 mm long, 0.4-0.7 mm wide, apex obtuse, hyaline, sparsely glandular-papillate and ferruginous lepidote, densely and prominently black punctate medially, essentially glabrous, the margin irregular, denticulate, glabrous; corolla campanulate, carnose, translucent, 2.5-3.0 mm long, the tube 0.5-0.7 mm long, the lobes obovate to suborbicular, reflexed, 1.7-2.1 mm long, 1.9-2.3 mm wide, the apex rounded to emarginate, prominently cucullate, glabrous without, densely glandular-granulose with and apically along margin within, prominently black punctate and punctate-lineate, the margin entire, irregular, glabrous; stamens 2.1-2.3 mm long, the tube inconspicuous, 0.5-0.7 mm long, the apically free filaments 0.9-1.1 mm long, ventrally recurved, subterete, epunctate, the anther erect, ovate, 0.5-0.7 mm long, 0.5-0.8 mm wide, dorsifixed less than $\frac{1}{4}$ from base, apex apiculate, the apiculum erect, base deeply cordate, the connective black punctate at apex at point of insertion; pistil obnapiform, 2.0-2.3 mm long, 0.4-0.5 mm diam., densely translucent-lepidote, the style 0.4-0.5 mm long, the stigma capitate, not lobed, 0.2 mm long, the placenta cupuliform, with 3-4 exposed ovules.

Fruit globose, 0.7–0.8 mm long, 0.9–1.2(–2.0) cm diam., exocarp thick, purple-black, juicy, edible, black punctate. *Bisexual inflorescence*: as in pistillate, but stamens 2.3–2.5 mm long, the tube 0.3–0.5 mm long, the filaments adnate to the corolla lobe 0.5–0.6 mm above tube, then apically free for 1.1–1.3 mm, the anther as in staminate flowers, but 0.8–0.9 mm long; pistil ellipsoid, 2.0–2.3 mm long, 1.1–1.4 mm diam., the style almost obsolete, the stigma capitate, 0.3 mm long, the placenta deeply cupuliform, with 2–3 exposed ovules. Fruit depressed-globose, 0.4–0.5 mm long, 0.5–0.7 mm wide, densely and prominently black punctate, exocarp thin, black, with little juice.

Distribution. Endemic to the Guayana Shield, known from most portions thereof, except Tafelberg and Macarena. It occurs at elevations from 1,150 to 2,330 m.

Ecology. *Cybianthus quelchii* is a conspicuous tree in gallery forests and dense thickets surrounding bogs on the plateaus of tepuis. It is frequently associated with *Archytaea multiflora* (Theaceae) and is one of the taller trees of the shrub islands growing on water-saturated soils. It is not a component of the cloud/elfin forest formations occurring in less exposed areas, nor is it present in the scrub formations in savannas.

This species is sexually labile, but it appears that polygamous individuals are rare (Tillett *et al.* 45689). Flowering occurs throughout the year on new growth, and within a given population there are usually some individuals in flower. During an inventory on the summit of Serra Aracá I observed that there are more staminate than pistillate individuals per population. In gallery forests studied on Chimantá Massif and Serra Aracá, flowers of this species produced a notable musklike odor and small dipterans were seen visiting the flowers. In populations bordering bogs on the summit of Muri-tepui, no odor was detectable in the flowers.

Specimens examined. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Depto. Río Negro, Cerro de la Neblina, plateau, NW range, summit N of base camp along Río Mawarinuma, affluent of Río Baría, 1,880 m, 7–8 Feb. 1984 (bud), Luteyn & Steyermark 9442 (MO, NY, TEX, VEN), (fr), 9482 (MO, NY, TEX, US, VEN), upper basin of Cañon Grande above Salto Grande, 13 Dec. 1957 (fr), Maguire *et al.* 42366 (F, MO, NY, S, US, VEN), S rim of upper basin, (fr), Maguire *et al.* 42373 (F, MO, NY, US, VEN), ridge at Brazil/Venezuela divide, 26 km ENE of Neblina Base Camp, 2,000 m, 15 Apr. 1984 (pist. fl), Plowman & Thomas 13598 (F, MO, NY, US, VEN); Depto. Atures, Serranía Sipapo, summit, S section, 17 Feb. 1981 (stam. fl), Steyermark *et al.* 124531 (MO, VEN). BOLIVAR: Roraima, without date (ster.), Schom-

burgk *s.n.* (K); Dtto. Piar, Aparman-tepui, E of Auyán-tepui, 2,150 m, 23 Mar. 1987 (fr), Delascio 13032 (MO, VEN), westernmost of 4 tepuis in Aparaman range, 2,100 m, 27 Mar. 1987 (fr), Holst 3699 (MO, US, VEN); Auyán-tepui, Jan. 1949 (stam. fl), Cardona *s.n.* (US, VEN), summit, NE section, N of Camarata, 1,950 m, 28 Feb. 1978 (stam. fl), Steyermark 116183 (F, MO, NY, US, VEN); Macizo del Chimantá, summit, Acopán-tepui, 2,200 m, Oct. 1947 (fr), Cardona 2266 (US, VEN), SSE sector, SE plateau, headwaters of Río Arauai, 14–16 Feb. 1984 (stam. fl), Luteyn *et al.* 9482 (AAU, MO, MYF, NY, S, US, VEN), NE plateau, headwaters of Río Yunek, 1,950 m, 8–11 Feb. 1985 (pist. fl), Pipoly *et al.* 7163 (MO, MYF, NY, PH, TEX, US, VEN), SE sector, central–SE section of Churí-tepui, 10–12 Feb. 1984 (bud), Huber & Colella 8964 (MYF, NY, VEN), 4 Feb. 1955 (stam. fl), Steyermark & Wurdack 402 (F, MO, NY, U, US, VEN), central section, Chimantá-tepui, Upper Falls, Río Tirica, 2,150 m, 17 Feb. 1955 (bisex. fl, fr), Steyermark & Wurdack 920 (F, MO, NY, US, VEN), central–S section, large valley between NE border of Torono-tepui and central section, Chimantá-tepui, 2,100 m, 11–15 Feb. 1985 (stam. fl), Pipoly *et al.* 7256 (MYF, NY, TEX, US, VEN), Torono-tepui, summit, between base and upper falls and drop to escarpment, 1,895–1,910 m, 23 Feb. 1955 (stam. fl), Steyermark & Wurdack 1088 (F, MO, NY, US, VEN); summit, Cerro Guaiquinima NE section, near cliffs, headwaters of NE branch of Río Carapo, 1,490–1,500 m, 25 May 1974 (bud), Steyermark *et al.* 117322 (F, MO, NY, US, VEN); Dtto. Heres, Cerro Marutaní, summit, along Río Carla, affluent of Río Paragua at headwaters, 1,200 m, 11–12, 14 Jan. 1981 (bud), Steyermark *et al.* 123866, 123906 (MO, NY, US, VEN); near Venezuelan–Brazilian frontier, 1,420 m, 13 Jan. 1981 (bud), Steyermark *et al.* 123993, (fr), 124023 (MO, NY, US, VEN); Ptari-tepui, SW-facing shoulder, 2,000–2,200 m, 2 Nov. 1944 (fr), Steyermark 59797 (F, NY, VEN), vic. “Miss Kathy Camp,” mesa between Ptari- and Sororopán-tepui, 1,615 m, 15–17 Nov. 1944 (fr), Steyermark 60240 (F, NY, VEN); summit of Mt. Roraima, NW portion, NNW of summit camp, 2,620–2,740 m, 27 Sep. 1944 (stam. fl), Steyermark 58842 (F, NY, VEN); Toromeru, NW of Parupa, 1,200 m, 14 Dec. 1984 (fr), Kral 72045 (MO, NY, US, VDB). GUYANA. Upper Mazaruni River Basin, Mt. Ayanganna, shoulder E flank above Thompson Camp, 1,418–1,525 m, 10 Aug. 1960 (polygamous), Tillett *et al.* 45609 (F, FDG, MO, NY, S, US); Haieka savanna, E side of Haieka River, 4 km E of Chinoweing village, 740 m, 21 Aug. 1960 (stam. fl), Tillett *et al.* 45219 (F, FDG, MO, NY, US, VEN). BRAZIL. AMAZONAS: plateau of Serra Aracá, S side of N mountain, 1,150–1,250 m, 11 Feb. 1984 (stam. fl), Pipoly *et al.* 6695 (INPA, MG, MO, NY, PH, TEX, US, VEN), 14 Feb. 1984 (stam. fl), 6700, (ster.), 6701, 6706 (CM—2 sheets, INPA, MG, MO, NY, PH, TEX, US, VEN), plateau, N massif, 1,400 m, 20 Feb. 1984 (pist. fl), Prance, Pipoly, *et al.* 29194 (INPA, MG, MO, NY, US). TERRITORIO DO RORAIMA: Serra do Sol (Uei-tepui), 2,333 m, 28 Dec. 1954 (pist. fl), Maguire 40396 (F, MO, NY, S, US, VEN); Serra dos Surucucus, upper slopes of Serra Parima, S of Auaris, 1,400–1,520 m, 10 Feb. 1969 (pist. fl), Prance *et al.* 9820 (F, INPA, K, MG, NY, S, U, US).

Cybianthus quelchii was placed in subgenus *Weigeltia* by Agostini (1971, 1980), but its campanulate corolla, with anthers distally recurved,

indicate it shares common ancestry with the *Microconomorpha-Stapfia-Laxiflorus-Conomorpha* clade illustrated by Pipoly (1987). These synapomorphies, combined with its ferruginous lepidote scales on the branchlets and leaves, indicate that it is a member of subgenus *Conomorpha*. Despite the fact that the scales of the branchlets are often early caducous, they are the same type of scale found in the other members of the subgenus, not like the furfuraceous scales encountered in subgenus *Weigeltia*. Also, the anthers are dorsifixed less than $\frac{1}{4}$ from the base, rather than versatile, as are all the members of subgenus *Weigeltia*.

This species is extremely variable throughout its range and often forms stands at the edge of bogs, or in gallery forests along watercourses on summits. Individuals occurring at the edges of bogs often have smaller leaves and larger inflorescences, while those of the gallery forests have correspondingly larger leaves and more compact inflorescences. The bark is extremely corky, and the wood is strong and flexible. The fruit is juicy, with a slightly tart, cherrylike flavor at maturity.

The type of *Conomorpha depressa* Steyermark represents populations in the eastern section of the state of Bolívar, which are notable only for their larger-than-average fruits. However, individuals from Cerro de la Neblina (*Luteyn & Steyermark 9442*) have the largest fruits known thus far, reaching 2 cm diam. It is not known whether the individuals from which fruits were collected on Neblina are pistillate or bisexual.

9. *Cybianthus punctatus* (Mez) Agostini, Acta Biol. Venez. 10: 155. 1980. *Conomorpha punctata* Mez, in Engler, Pflanzenr. IV. 236: 260. 1902. TYPE: Venezuela [Guyana]. Bolívar: Roraima, 1842–1843 (stam. fl), *Schomburgk 554* (lectotype, here designated, G; isotypes, BM, F, K, P, W). Figure 9.

Conomorpha sessilis A. C. Smith, Bull. Torrey Bot. Club 67: 294. 1940. TYPE: Venezuela. Bolívar: Roraima, vic. Arabupu, Arabupu River, Dec. 1938 (stam. fl), *Pinkus 55* (holotype, NY; isotypes, F, GH, S, US).

Shrub or small tree to 3 m tall; branchlets terete, 2.0–2.5 mm diam., densely lepidote. Leaves elliptic, narrowly elliptic, or elliptic-obovate, membranaceous to chartaceous, 7.5–10(–15) cm long, 2.5–4.5 cm wide, apex acuminate, the acumens 0.5–1.0 cm long, base acute, decurrent, midrib depressed above, prominently raised below, nerves 12–18 pairs, slightly raised above and below, upper surface whitish, sparsely and eglandular scrobic-

ulate and densely lepidote when young, glabrescent, sparsely lepidote below, the margin revolute; petioles canaliculate, prominently winged, 1.0–2.2 cm long, densely lepidote. *Staminate inflorescence*: a somewhat pyramidal panicle with 3–7 lateral branches, 3.5–5.5 cm long, 2.5–3.5 cm broad, the peduncle, axis, branches, and pedicels densely lepidote; peduncle 0.3–1.5 cm long; pedicels terete, 1.0–1.5 mm long; floral bracts triangular to ovate-triangular, 0.5–0.7 mm long, 0.3–0.4 mm wide, apex acute, densely lepidote abaxially, the margin entire. Flowers (4–)5(–6)-merous; calyx cotyliform, carnos, 0.9–1.0 mm long, the tube 0.2–0.3 mm long, the lobes triangular, 0.7–0.9 mm long, 0.5–0.6 mm wide, apex attenuate to a rounded tip, brown punctate near the margin, the margin lepidote, entire; corolla campanulate, carnos, 2.0–2.5 mm long, the tube 0.7–0.9 mm long, the lobes ovate or broadly ovate, 1.3–1.6 mm long, 0.9–1.1 mm wide, reflexed, apically rounded or attenuate to a rounded tip, sparsely glandular-granulose without, densely glandular-granulose apically within, conspicuously brown punctate toward the margin, brown punctate-lineate medially, the margin entire, glabrous; stamens 1.7–2.0 mm long, adnate ca. 0.8 mm to the corolla tube, the staminal tube conspicuous, chartaceous, 0.8–1.0 mm long, elobate, the apically free filaments flat, 0.1–0.2 mm long, the anthers ovate-triangular, erect, 0.9–1.0 mm long, dorsifixed ca. $\frac{1}{4}$ from base, apex apiculate, the apiculum erect, cordate basally, the connective prominently brown punctate; pistillode lageniform, 1.2–1.5 mm long, ca. 0.4 mm diam., hollow, translucent glandular-lepidote basally. *Pistillate inflorescence*: a bipinnate or poorly formed panicle with 3–5 lateral branches, 2.0–4.5 cm long, 1.5–2.5 cm broad, the peduncle, axis, branches, and pedicels densely lepidote, the scales superposed; peduncle 0.6–0.8 cm long; pedicels terete, 2.7–3.8 mm long; floral bracts triangular to ovate-triangular, 0.5–0.7 mm long, 0.3–0.4 mm wide, apex acute, densely lepidote abaxially, the margin entire. Flowers 5-merous; calyx cotyliform, carnos, 0.9–1.0 mm long, the tube 0.2–0.3 mm long, the lobes deltate, 0.7–0.9 mm long, 0.7–0.9 mm wide, apex attenuate to a round tip, brown punctate near the margin, the margin lepidote, entire; corolla not seen. Fruit globose, 0.3–0.4 mm long and in diam. when dried, the exocarp verrucose.

Distribution. Endemic to the northeastern section of Pantepuí (sensu Mayr & Phelps, 1967) in the Auyán-tepui-Chimantá Complex of the Guyana Pakaraima–Venezuelan Gran Sabana Sub-

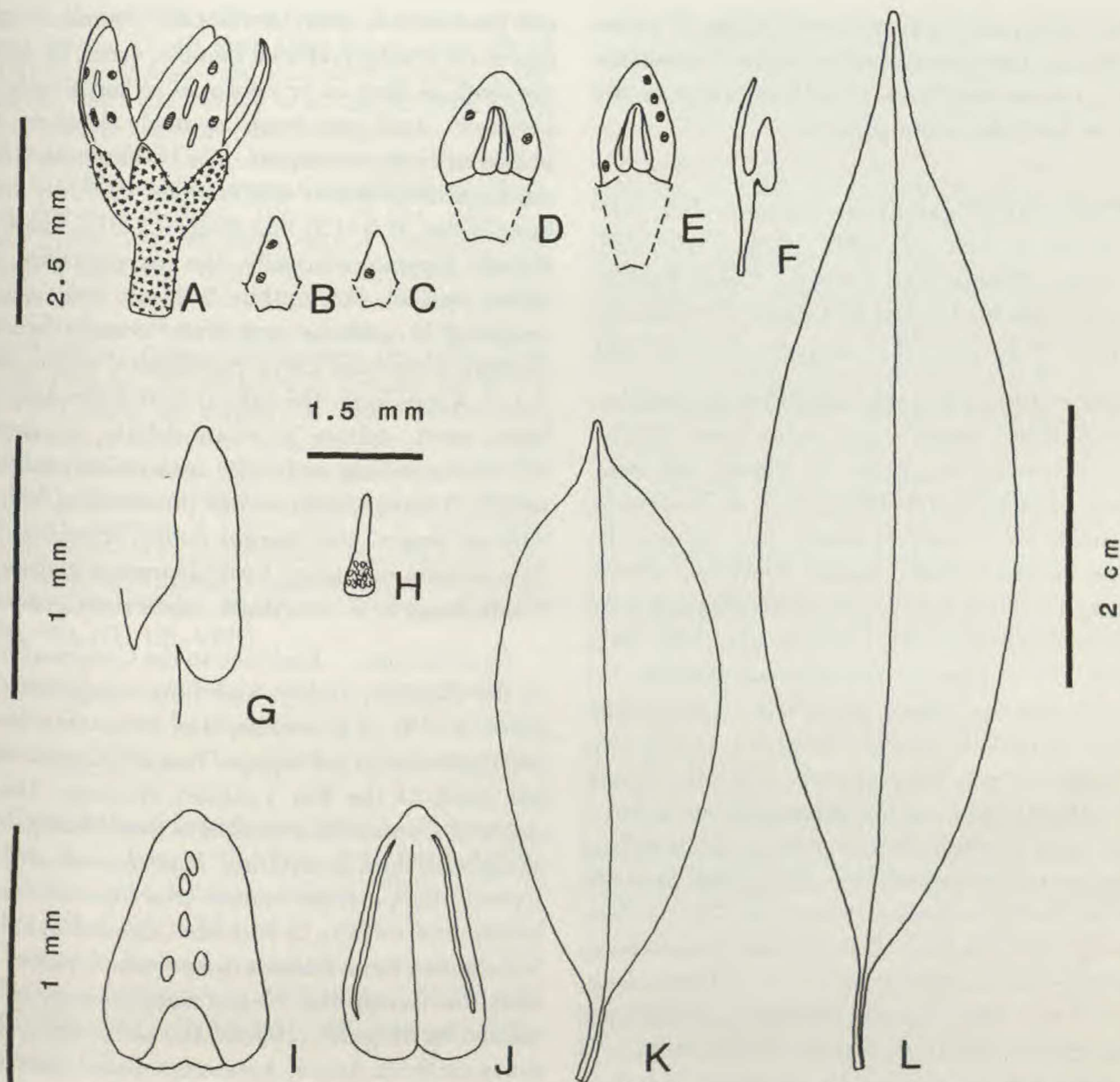


FIGURE 9. *Cybianthus punctatus* (Mez) Agostini.—A. Staminate flower.—B, C. Staminate calyx lobes, ventral view.—D, E. Staminate corolla lobes, ventral view.—F. Staminate corolla lobe, lateral view.—G. Anther, lateral view, showing erect habit.—H. Pistillode.—I. Anther, dorsal view, showing punctate connective.—J. Anther, ventral view.—K, L. Leaves. (A–K, from *Pinkus* 55; L, from *Forest Dept. Brit. Guiana* WB331-5757.)

province of Maguire (1979), at 1,000–1,400 m elevation.

Ecology. *Cybianthus punctatus* is an infrequently encountered element of cloud forests on talus slopes. Very little is known of its life history.

Specimens examined. VENEZUELA. BOLIVAR: Dto. Piar, descent from Salto Hacha, upper basin of Río Purpur, along trail to Urimán, 850–1,100 m, (fr), *Davidse & Huber* 22955 (MO, VEN); Gran Sabana, tributary of Río Kukenán, S of Mt. Roraima, 1,005–1,065 m, 2 Oct. 1944 (stam. fl), *Steyermark* 59122 (F, NY, VEN); Kavanayén, forests of Oparuma, 1,400 m, 28 May 1946 (stam. fl), *Lasser* 1836 (K, US, VEN); Arabapu, Mt. Roraima, 1,400 m, 13 Dec. 1938 (stam. fl), *Forest Dept. Brit. Guiana* P49-282 (BRG, K); Ayavoparú, 10 km SW of Wadacapiapué, 1,100 m, without date, *Hernández* 358 (NY, VEN). GUYANA. Wabuwak Kanuku Mts., Dec. 1948 (stam. fl), *Forest Dept. Brit. Guiana* WB331-5757 (NY).

Within Guayana, *C. punctatus* may be most easily confused with *C. cardonae*, but is easily distinguished by its leaves 7.5–10(–15) cm long, (2.5–)3.5–4.5 cm wide, with acuminate apices, petioles canaliculate and winged, pedicels erect, and corolla carnosose with reflexed lobes.

In sterile condition, *C. punctatus* may be confused with the sympatric *C. roraimae* and *C. lepidotus*. From *C. roraimae*, *C. punctatus* may be recognized by its branchlets 2.0–2.5 mm diameter, membranaceous to chartaceous leaves with upper surfaces shallowly eglandular scrobiculate, the nerves 12–18 pairs, and the petioles winged, 1.0–2.2 cm long. From *C. lepidotus*, *C. punctatus* is more difficult to separate, but may still be recognized by its leaves membranaceous to chartaceous, with nerves 12–18 pairs, and acute leaf bases, which are decurrent on the petiole. It appears that

the two species are separated ecologically, *C. punctatus* being a talus forest species, while *C. lepidotus* occurs in protected cloud/elfin forest areas on the edges of the taller tepui summits.

10. *Cybianthus cardonae* Agostini, Bol. Soc. Venez. Ci. Nat. 22: 386. 1976. TYPE: Venezuela. Bolívar: Alto Paragua, Cerro Tabareupá, 500 m, 1 July 1944 (stam. fl), *Cardona 1081* (holotype, VEN; isotypes, F, NY, US).

Shrub or tree to 8 m tall; branchlets subangular, 2–4 mm diam., densely lepidote, at times glabrescent. Leaves widely elliptic to elliptic, subcoriaceous to coriaceous, 10–18 cm long, 5–7 cm wide, apex acute or short-acuminate, base acute, decurrent on the petiole, midrib depressed above, prominently raised below, nerves 30–50 pairs, conspicuous above and below, densely glandular-scribbulate above, densely ferruginous lepidote below, the margin entire, epunctate, subrevolute; petioles marginate distally, squarrose proximally, 1.5–2.0(–3.0) cm long, densely lepidote. *Staminate inflorescence*: a lax pyramidal to subpyramidal panicle, erect, 8–15 cm long, about as long as the leaves, the peduncle 1–2 cm long, sparsely lepidote, the branches 5–6, racemose, 20–55-flowered, 2.5–10 cm long; floral bracts chartaceous, narrowly ovate, apex acute, 0.6–1.0 mm long, 0.1–0.2 mm wide, densely lepidote adaxially, the margin entire, glabrous; pedicels terete, thin, 1–3 mm long, apically recurved in anthesis and fruit, densely lepidote. Flowers 4-merous, whitish yellow; calyx cupuliform, chartaceous, 1.1–1.4 mm long, the tube 0.2–0.4 mm long, the lobes erect, deltate to ovate-deltate, symmetric, 0.7–0.9 mm long and wide, apex acutely rounded, with 2–6 conspicuous orange punctations, with few lepidote scales, the margin entire, irregular, lepidote; corolla campanulate, membranaceous, 2.5–3.1 mm long, the tube 0.8–1.0 mm long, the lobes ovate to ovate-elliptic, united ca. $\frac{1}{3}$ length, 1.8–2.2 mm long, 0.9–1.4 mm wide, somewhat reflexed in anthesis, apex obtuse to rounded, symmetric, sparsely lepidote without, glandular-granulose apically within, glabrous without, inconspicuously pellucid punctate; stamens 2.1–2.2 mm long, the tube 0.9–1.0 mm long, inconspicuous, hyaline, elobate, the apically free filaments 0.2–0.5 mm long, terete, glabrous, the anthers lanceolate, dorsifixed ca. $\frac{1}{4}$ length, dorsally curved, 0.9–1.0 mm long, 0.2–0.3 mm wide, apex acute, base cordate, the connectives prominently brown punctate dorsally; pistillode conic, 1.5–1.7 mm long, 0.5–0.6 mm diam., the ovary lepidote, hollow, the style glabrous, the stig-

ma punctiform when developed. *Pistillate inflorescence*: a subpyramidal panicle, erect, (6–)8–10 cm long, as long as or subequal to leaf length, the peduncle 1–2 cm long, sparsely lepidote, the branches 5–6, racemose, 12–15-flowered, 2.5–4 cm long; floral bracts chartaceous, narrowly ovate, apex acute, 0.6–1.0 mm long, 0.1–0.2 mm wide, densely lepidote adaxially, the margin entire, glabrous; pedicels terete, thin, 1–3 mm long, apically recurved in anthesis and fruit, densely lepidote. Flowers 4-merous; calyx cupuliform, chartaceous, 1.1–1.4 mm long, the tube 0.2–0.4 mm long, the lobes erect, deltate to ovate-deltate, symmetric, 0.7–0.9 mm long and wide, apex acutely rounded, with 2–6 conspicuous orange punctations, with few lepidote scales, the margin entire, irregular, lepidote; corolla unknown. Fruit depressed-globose, 4–6 mm long, 5–7 mm diam. when dried, smooth.

Distribution. Endemic to the Guayana Shield, in the Neblina, Duida, and Jaua complexes (Maguire, 1979). It is notable that it has thus far not been collected in the Sipapo-Yutajé Complex, which lies north of the Río Ventuari drainage. The absence of *Cybianthus cardonae* from Guaiquinima, along with data from other Myrsinaceae and Clusiaceae, support the notion that the affinities of Guaiquinima's flora lie with the Guyana Pakaraima-Venezuelan Gran Sabana Subprovince, rather than with the Caroní-Río Negro Subprovince, as postulated by Maguire (1979). The occurrence of this taxon on Serra Aracá, Amazonas, Brazil, once again reinforces the notion that Aracá's flora is intimately related to that of the Neblina and Duida complexes. It occurs in the region at 80–1,800 m altitude.

Ecology. *Cybianthus cardonae* is a conspicuous element of the cloud/elfin forest of the summit edge, near a large waterfall on the southern side of the northern mountain of Serra Aracá. These small patches of cloud and elfin forest located on plateau edges are floristically as well as physiognomically distinct from the more extended cloud forests below elfin forest formations on smaller, protruding plateaus scattered over the broad, principal plateaus of the tepuis. It appears that the pistillate flowers are ephemeral, as a number of fruiting specimens were seen and collected, while the pistillate corolla remains unknown. In the rest of its range, *C. cardonae* is infrequently encountered in small, elfin cloud forests in protected areas at the edge of steep cliffs on tops of the tepuis.

Specimens examined. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Depto. Río Negro, Cerro de la Neblina, S face of Pico Phelps Massif, 1,550–1,650 m, 13 Apr. 1984 (stam. fl), Gentry & Stein 46610 (MO, NY, VEN).

Camp IV, 15 km NNE of Pico Phelps, N branch of river canyon, 780 m, 15–18 Mar. 1984 (fr), *Liesner 16678* (MO, VEN); Cerro Aracamuni, summit, Proa Camp, 1,400 m, 26 Oct. 1987 (fr), *Liesner et al. 22486* (MO, VEN), 2 Nov. 1987 (fr), 22760 (MO, VEN); Depto. Atabapo, Cerro Duida, 1,000 m, Jan.–Feb. 1969 (stam. fl), *Fariñas et al. 371* (VEN), saddle between Cerros Duida and Marahuaca, near base of Duida, 100 m, 27 Oct. 1988 (fr), *Liesner 25496* (MO, US, VEN), 28 Oct. 1988 (fr), *Liesner 25533* (MO, US, VEN); Cerro Marahuaca, slopes, "sima," 1,200 m, 16 Oct. 1988 (fr), *Liesner 24964* (MO, VEN); Cerro Huachamacari, E slope, 600–700 m, 3 Nov. 1988 (fr), *Liesner 25772* (MO, US, VEN). BOLIVAR: Río Orinoco, 30 km below la Urbana, 80 m, 14 Mar. 1949 (stam. fl), *Maguire & Politi 29071* (NY, VEN); Meseta de Jaua, Cerro Jaua, summit, 1,750–1,800 m, 22 Feb. 1974 (stam. fl), *Steyermark et al. 109300* (US, VEN). BRAZIL. AMAZONAS: plateau of Serra Aracá, S side of N mountain, 1,150–1,250 m, 17 Feb. 1984 (stam. fl), *Pipoly et al. 6704* (INPA, MG, MO, NY, US, VEN), plateau of N massif, N summit, 1,600 m, 23 Feb. 1984 (stam. fl), *Prance, Pipoly, et al. 29429* (INPA, K, MG, MO, NY, US, VEN).

Cybianthus cardonae may be confused with *C. punctatus* but may be separated by its acute leaves, recurved pedicels, and the membranaceous corolla.

11. ***Cybianthus lepidotus*** (Gleason) Agostini, *Bol. Soc. Venez. Ci. Nat.* 22: 388. 1976. *Conomorpha lepidota* Gleason, *Bull. Torrey Bot. Club* 58: 446. 1931. TYPE: Venezuela. Territorio Federal Amazonas: summit of Mt. Duida, 1,500 m, Aug. 1928–Mar. 1929 (pist. fl), *Tate 741* (holotype, NY; isotype, US). Figure 10.

Conomorpha curvivenia Gleason, *Bull. Torrey Bot. Club* 58: 444. 1931. TYPE: Venezuela. Territorio Federal Amazonas: Mt. Duida, 1,260 m, Aug. 1928–Mar. 1929 (stam. fl), *Tate 927* (holotype, NY; isotype, US).

Conomorpha lepidota Gleason f. *acutata* Steyermark, *Fieldiana, Bot.* 28(3): 465. 1953. TYPE: Venezuela. Territorio Federal Amazonas: Cerro Duida, 2 Dec. 1944 (fr), *Steyermark 58265* (holotype, F; isotype, NY).

Shrub or small tree to 6 m tall; branchlets terete, 2–2.5 mm diam., densely lepidote. Leaves elliptic to narrowly elliptic, chartaceous to coriaceous, (3.1–)5–15 cm long, 1.6–6 cm wide, apically acuminate, the acumen 0.3–2.0 cm long, basally acute to obtuse, midrib depressed above, prominently raised below, nerves 24–28, inconspicuous above and below, pustulate and densely lepidote above at first, glabrescent, densely lepidote below, the scales not overlapping, inconspicuously pellucid punctate, the margin entire, subrevolute to revolute; petioles thin, marginate, 1.0–2.5 cm long, densely lepidote. *Staminate inflorescence*: a spike, rarely two subsessile spikes, (2–)6–16 cm long, 8–15-flowered,

peduncle, pedicels, and axis densely lepidote, the scales not overlapping; peduncle (0.2–)0.5–0.8 mm long; floral bracts ovate to widely ovate, chartaceous, 0.5–0.6 mm long, 0.3–0.4 mm wide, apex acute, densely lepidote adaxially, the margin entire, glabrous. Flowers (4–)5-merous; calyx cupuliform, carnos, 0.9–1.2 mm long, the tube 0.2–0.4 mm long, the lobes deltate to ovate-triangular, 0.6–0.8 mm long and wide, apex acute or acuminate, rarely obtuse, attenuate to a rounded tip, conspicuously brown punctate, the margin entire, lepidote; corolla cupuliform, carnos, 1.5–2.5 mm long, the tube 0.5–1.0 mm long, the lobes ovate to broadly ovate, 1.2–1.7 mm long, 0.7–0.9 mm wide, apex attenuate to a round, cucullate tip, at times with a few, scattered lepidote scales without, glabrous without, glandular-granulose within over the entire surface, punctations brown, submarginal, the margin entire, glabrous; stamens 1.5–1.6 mm long, adnate 0.5–1.0 mm to corolla tube, the staminal tube 0.3–0.4 mm long, carnos, bearing lobes alternating with the apically free filaments 0.1–0.2 mm long, the filaments flat, 0.3–0.4 mm long, erect, glabrous, the anthers dorsifixed less than ¼ from base, ovate-triangular, 0.6–0.7 mm long, 0.4–0.5 mm wide, apex attenuate to a rounded tip, basally cordate, slightly dorsally reflexed, the connective epunctate; pistillode lageniform, 1.1–1.2 mm long, hollow, costate basally, sparingly translucent lepidote, pellucid-punctate. *Pistillate inflorescence*: a spike, (2–)6–16 cm long, 6–10-flowered, peduncle, pedicels, and axis densely lepidote, the scales not overlapping; peduncle 0.6–0.8 mm long; floral bracts ovate to widely ovate, chartaceous, 0.5–0.6 mm long, 0.3–0.4 mm wide, apex acute, densely lepidote adaxially, the margin entire, glabrous. Flowers 5-merous; calyx cupuliform, carnos, 0.9–1.2 mm long, the tube 0.2–0.4 mm long, the lobes deltate to ovate-triangular, carnos, 0.6–0.8 mm long and wide, apex acute or acuminate, rarely obtuse, attenuate to rounded tip, conspicuously brown punctate, the margin entire, lepidote; corolla cupuliform, carnos, 1.5–2.5 mm long, the tube 0.5–1.0 mm long, the lobes ovate to broadly ovate, 1.2–1.7 mm long, 0.7–0.9 mm wide, apex attenuate to a round, cucullate tip, at times with a few, scattered lepidote scales without, glabrous without, glandular-granulose within over the entire surface, punctations brown, submarginal, the margin entire, glabrous; staminodes 1.2–1.3 mm long, adnate 0.5–1.0 mm to corolla tube, the staminal tube 0.5–0.6 mm long, carnos, bearing lobes alternating with the apically free filaments 0.1–0.2 mm long, the filaments flat, 0.3–0.4 mm long, erect, glabrous, the anthers dorsifixed less than ¼ from base,

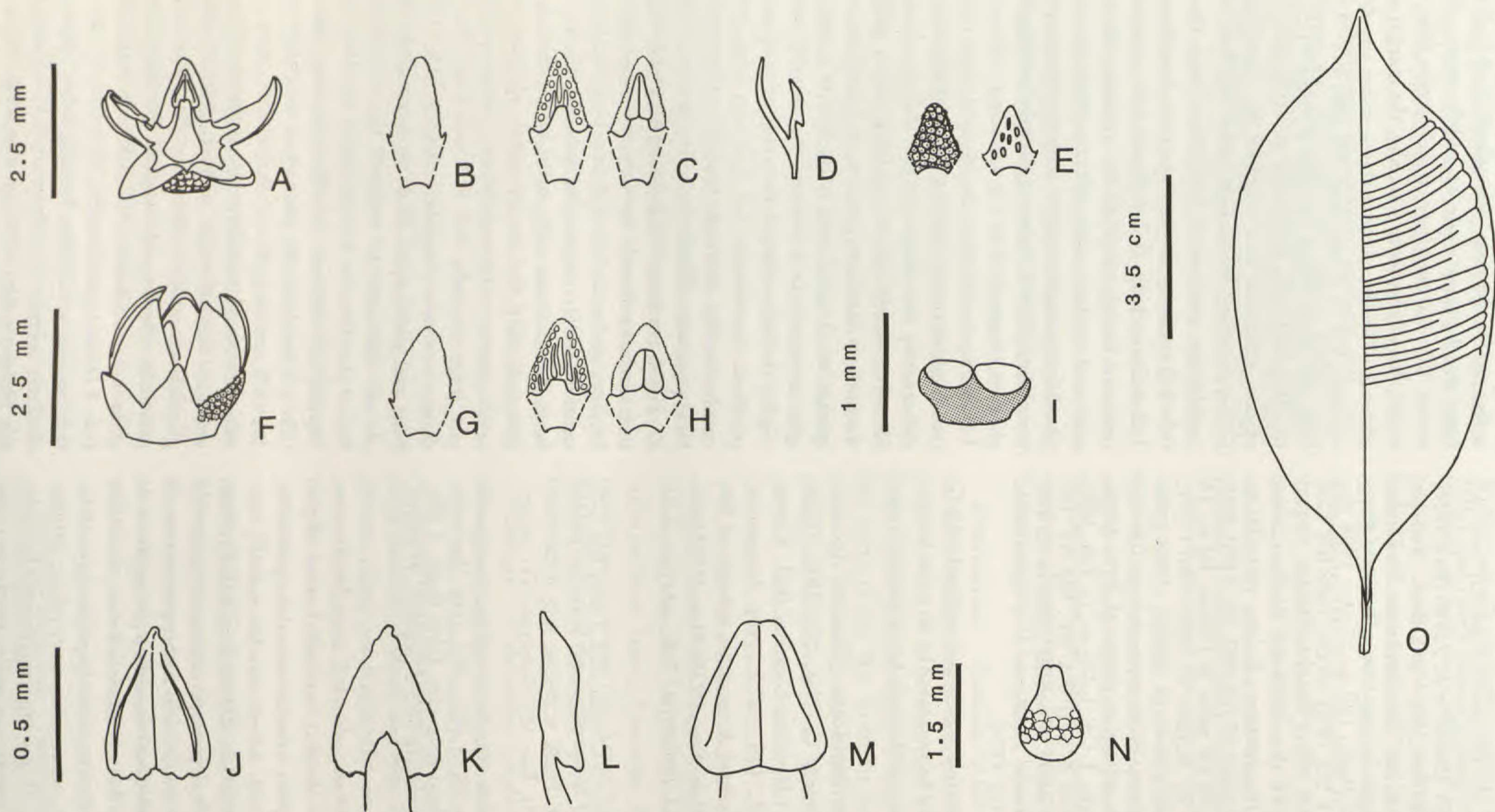


FIGURE 10. *Cybianthus lepidotus* (Gleason) Agostini.—A. Staminate flower, showing pistillode and conspicuous staminal tube.—B. Staminate corolla lobe, dorsal view.—C. Staminate corolla lobe, showing glandular granules, punctations, and anther habit.—D. Staminate corolla lobe, lateral view.—E. Staminate calyx lobe, dorsal and ventral views.—F. Pistillate flower.—G. Pistillate corolla lobe, dorsal view.—H. Pistillate corolla lobe, showing glandular granules, punctations, and anther habit.—I. Placenta, showing two naked ovules.—J. Anther, ventral view.—K. Anther, dorsal view.—L. Anther, lateral view.—M. Sterile anther, ventral view.—N. Pistil.—O. Leaf. (A–E, J–L, from *Steiermark* 74900; F–I, M, N, from holotype; O, from *Tate* 927.)

deltate, 0.7–0.8 mm long and wide, apex attenuate to a rounded tip, basally cordate, slightly dorsally reflexed, the connective epunctate; pistil pyriform, 1.4–1.5 mm long, the ovary 1–1.2 mm diam., the style not differentiated, the stigma punctiform, the placenta patelliform, bearing 2(–3) naked ovules. Fruit globose, purple at maturity, 0.5–1.0 cm long, 0.6–1.0 cm diam., the endocarp smooth, the embryo curved, 3.5–4.0 mm long.

Distribution. Guayana Highland of Venezuela and sandstone formations in Bolivia, 600–2,300 m in Venezuela, 850–950 m in Bolivia.

Ecology. *Cybianthus lepidotus* is restricted to large cloud forest formations in transition zones between sandstone and diabasic intrusions. It is often associated with species of *Erythroxylum*, which are also edaphic endemics. It is interesting to note that, in populations on Serra Aracá, I did not observe any flowering individuals less than 2 m in height. This is rather unusual in *Cybianthus*, where precocious flowering is frequent (Pipoly, 1981, 1983b, 1987). The cloud forest in which *C. lepidotus* was encountered was notably wetter and colder than the cloud/elfin forest in which *C. cardonae* had been found. The forest was located on a small plateau arising from the principal plateau of the mountain and was dominated by *Perissocarpha*. The soils were extremely wet, yet well-drained, humus with deep leaf litter.

Specimens examined. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Depto. Atabapo, below Salto Los Monos on tributary of headwaters of Río Iguapo, 1,500–1,600 m, 11 Mar. 1985 (stam. fl), *Liesner 18537* (MO, NY, VEN); Cerro Huachamacari, E slope, 600–700 m, 3 Nov. 1988 (fr), *Liesner 25744* (MO, US, VEN), (stam. fl), 25745 (MO, US, VEN); Depto. Río Negro, Cerro de la Neblina, Camp VII, S slopes of Cañon Grande, 1,770–1,850 m, 30 Nov. 1984 (pist. fl, fr), *Croat 59505* (MO, NY, VEN), 7 Feb. 1985 (stam. fl), *Renner 2088* (US, VEN); Cerro Yaví, 2,200 m, 1 Mar. 1947 (stam. fl), *Phelps & Hitchcock 32* (NY, VEN), 1,800 m, (stam. fl), *Phelps & Hitchcock 174*; Cerro Parú, summit, 2,000 m, 4 Feb. 1951 (stam. fl), *Cowan & Wurdack 31221* (NY), (fr), 31342 (NY). BOLIVAR: Chimantá Massif, above middle falls of Río Tirica, 1,925 m, 5 Feb. 1955 (stam. fl), *Steyermark & Wurdack 501* (NY, VEN), Amurít-tepui (W sector of Acopán-tepui), 1,950 m, 2–5 Feb. 1983 (ster.), *Steyermark et al. 128734* (MO, NY, US, VEN), summit of Apacará-tepui, 2,125–2,300 m, 23 Mar. 1953 (stam. fl), *Steyermark 74900* (MO, NY, VEN), slope below summit, 2,000–2,150 m, 20 June 1953 (stam. fl), *Steyermark 75185* (MO, NY, VEN), wide valley in the SE sector of Apacará-tepui, 2,150 m, 6–9 Feb. 1985 (pist. fl), *Huber et al. 8882* (NY, US, VEN); Meseta de Jaua, Cerro Jaua, 1,922–2,100 m, 22 Mar. 1967 (pist. fl, fr), *Steyermark 98704* (VEN). BRAZIL. AMAZONAS: plateau of N massif of Serra Aracá, cloud forest of uppermost plateau, 1,600 m, 22 Feb. 1984

(stam. fl), *Prance, Pipoly, et al. 29239* (F, INPA, MG, MO, NY, US), 23 Feb. 1984 (stam. fl), 29247 (F, INPA, K, MG, MO, NY, US), S side of N plateau, 1,150–1,250 m, 14 Feb. 1984 (stam. fl), *Pipoly et al. 6703* (INPA, K, MG, MO, NY, RB, US, VEN). BOLIVIA. LA PAZ: Prov. Nor Yungas, valley of Río Coroico, Sacramento, 10 km NE of Chuspipata on Coroico Rd., 27 Jan. 1984 (ster.), *Gentry & Solomon 44668* (MO), 4 km NE (above) Inaburara, 13.5 km above San Pedro, 1,530–1,560 m, 22 Jan. 1984 (stam. fl), *Gentry & Solomon 44407* (MO); Prov. Larecaja, Maipiri, 6 Nov. 1926–28 Feb. 1927 (stam. fl), *Buchtien 1758* (HBG, NY, US), Copacabana, 10 km S of Maipiri, 850–950 m, 8 Oct.–15 Nov. 1939 (fr), *Krukoff 10987* (A, K, MICH, MO, NY, UC, US).

Cybianthus lepidotus, restricted to sizeable cloud forests in transition zones between sandstone and diabasic intrusions, is most easily recognized by its long, lax spikes. When sterile, it may be confused with *C. roraimae*, but may be easily distinguished by the branchlets 2–2.5 (not 3.5–4.5) mm in diameter. It may also be confused with *C. punctatus* and *C. cardonae*. For a discussion of the differences between these taxa in sterile condition, see *C. cardonae*.

The area of Bolivia in which this species has been collected is of biogeographic interest because it also supports several other Guayana Highland taxa in the Ericaceae and Clusiaceae. It is interesting that *Krukoff 10987* is identical, both qualitatively and quantitatively, to specimens of *C. lepidotus* from Cerro Duida.

12. *Cybianthus sipapoensis* Pipoly & Agostini, *Ernstia* 50: 36. 1988. TYPE: Venezuela. Territorio Federal Amazonas: Cerro Sipapo, along middle of Caño Negro, 1,600 m, 6 Jan. 1949 (stam. fl), *Maguire & Politi 28181* (holotype, VEN; isotypes, F, LL, NY). Figure 11.

Shrub to small tree; branchlets terete, 2.5–3 mm diam., densely ferruginous lepidote; leaves chartaceous, narrowly obovate, 9–13 cm long, 3.5–4.5 cm wide, apically subacuminate to acuminate, basally acute, midrib depressed above, prominently raised below, nerves 30–40 pairs, reticulate, conspicuous above and below, pellucid-punctate, sparsely lepidote and smooth above, glabrescent, moderately lepidote below, the margin entire, subrevolute; petioles canaliculate, 1.3–1.6 cm long. **Staminate inflorescence:** a condensed spike, 0.8–1.0 cm long, 5–8-flowered; floral bracts ovate to ovate-triangular, ca. 1 mm long, 0.8–1.2 mm wide, apex acute, pellucid-punctate, moderately lepidote below, the margin irregular, entire, glabrous; pedicels absent, rarely to 0.3(–0.6) mm long, sparsely lepidote. Flowers 2.5–3.3 mm long; calyx deeply cupuliform, carnos, 1.4–1.6 mm long, the tube

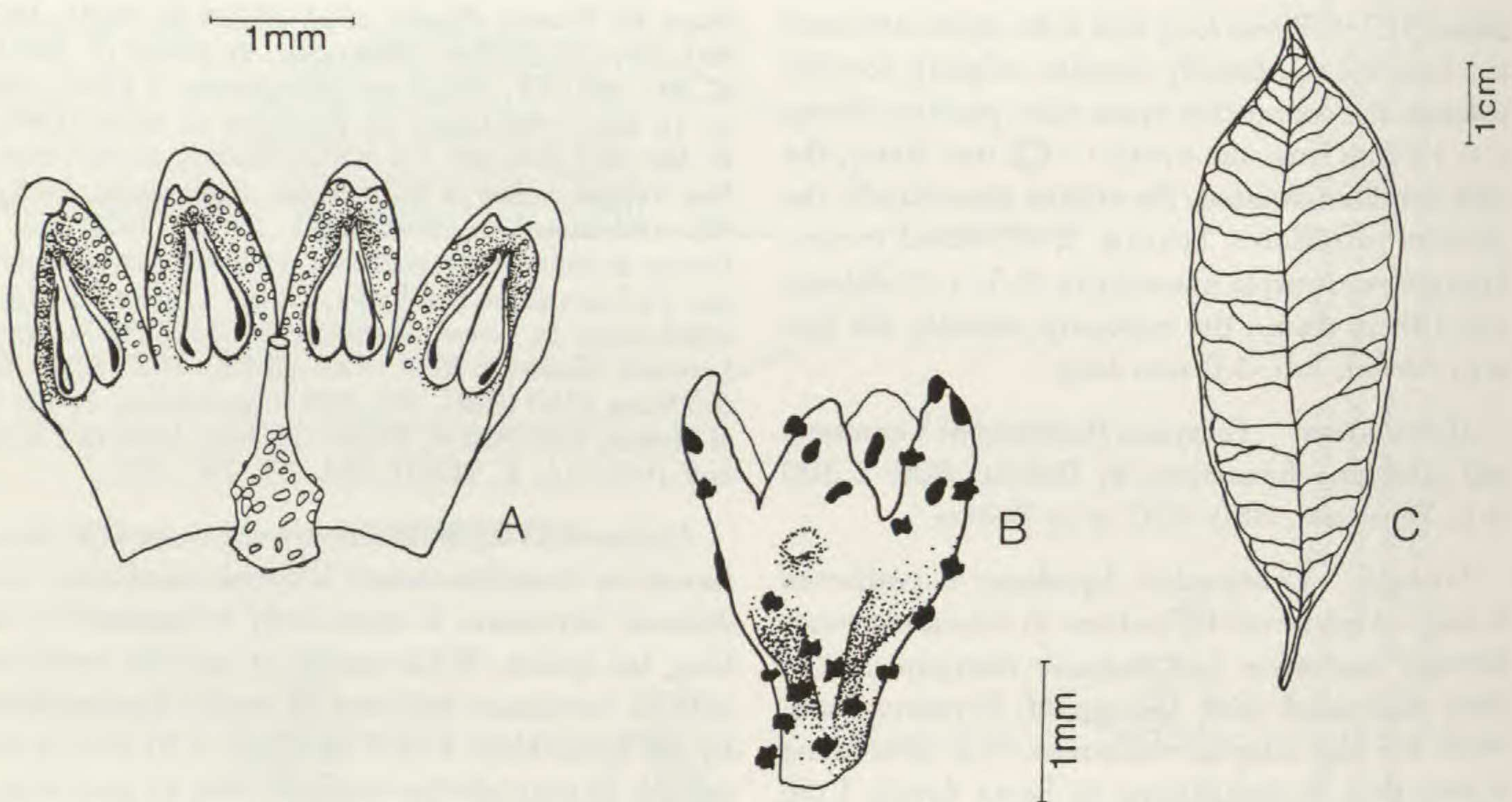


FIGURE 11. *Cybianthus sipapoensis* Pipoly & Agostini.—A. Opened staminate flower, showing cucullate corolla lobes, glandular granules, fused staminal tube, and pistillode.—B. Staminate calyx, showing lepidote scales.—C. Leaf, abaxial view. (From holotype.)

0.6–0.8 mm long, the lobes deltate or ovate-triangular, ca. 1.0 mm long, 0.8–1.2 mm long, apex acute, sparsely lepidote, conspicuously brown punctate, the margin irregular, entire; corolla cupuliform, carnose, 2.4–3.2 mm long, the tube 1.2–1.5 mm long, the lobes erect, ovate-triangular, 1.4–1.8 mm long, 0.9–1.1 mm wide, apex acute or subacute, cucullate, glabrous and sparsely lepidote without, densely glandular-granulose within and along the margin, pellucid-punctate; stamens 0.8–1.0 mm long, the tube 1.3–1.8 mm long, developmentally fused to the corolla, the anthers dorsally recurved, sessile, ovate-triangular, 0.8–1.1 mm long, 0.6–0.8 mm wide, apex long-attenuate, glabrous, prominently brown punctate dorsally; pistillode lageniform or obovoid, ca. 1.5 mm long, the ovary 0.8 mm long, 0.5 mm diam., translucent lepidote, the style ca. 0.8 mm long, prominently brown punctate. *Pistillate inflorescence*: unknown. Fruit unknown.

Distribution. Endemic to Cerro Sipapo (Paraque), 1,600 m. Known only from the type.

Ecology. *Cybianthus sipapoensis* is apparently restricted to cloud forests on steep slopes.

Cybianthus sipapoensis is easily recognized by the condensed spicate inflorescence and the ap-

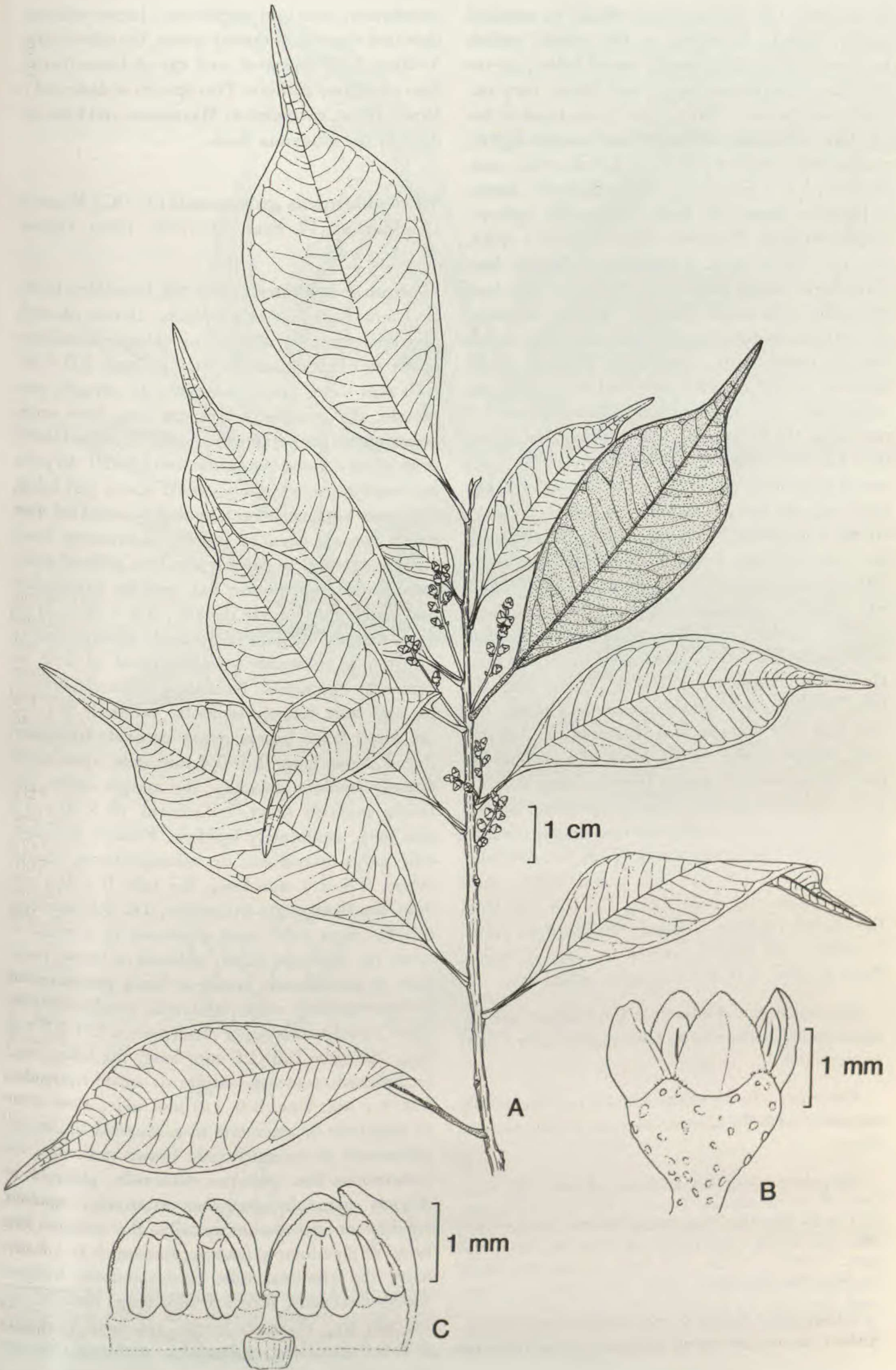
parently epipetalous sessile anthers. It may be confused with *C. spathulifolius*, but is easily separated by its leaves chartaceous (not coriaceous), with subrevolute (not flat) margins, and with petioles 1.3–1.6 (not 0.1–0.2) cm long, the petals erect (not tortuous), and the anthers sessile (not on filaments 0.3–0.4 mm long).

13. *Cybianthus holstii* Pipoly, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Depto. Ature, W side of valley of Río Coro-Coro, 8 km NNW of settlement of Yutajé, 500–1,000 m, 26 Feb. 1987 (pist. fl, fr), *Liesner & Holst 21418* (holotype, VEN; isotypes, MO, US). Figure 12.

Quoad inflorescentias spiciformes reductasque, calyces crateriformes, corollarum lobos abaxialiter carinatos erectos ad apicem cucullatosque pistillum apophysatum, *C. huberi* arcte affinis, sed illa ab hac laminis membranaceis (nec coriaceis) staminodii tubos inconspicuos (nec conspicuos) lobulis filamentis alterans destitutis (nec praeditis) antheris glabris eglandulosisque (nec rufo-papillosis brunneo-glandulosisque) fructibusque 4.0–4.5 (nec 5.5–10) mm diametris statim distinguitur.

Shrub to 2 m tall; branchlets thin, fragile, 1.5–2 mm diam., terete, densely stipitate-lepidote. Leaves obovate, membranaceous, 6.0–9.5 cm long (1.5–)2.2–3.5 cm wide, abruptly caudate apically,

FIGURE 12. *Cybianthus holstii* Pipoly.—A. Habit.—B. Pistillate flower, showing crateriform calyx.—C. Opened pistillate flower, showing apophysate ovary and subsessile sterile anthers. (From holotype.)



the acumen 1.6–4.0 cm long, obtuse to rounded basally, slightly decurrent on the petiole, midrib depressed above, prominently raised below, nerves very fine, conspicuous above and below, very minutely scrobiculate above, moderately lepidote below, the scales along the midrib and margin slightly overlapping, pellucid-punctate; petioles thin, canaliculate, 1.2–1.5 cm long, ridged abaxially, densely lepidote toward the base. *Staminate inflorescence*: not seen. *Pistillate inflorescence*: a spike, 0.5–1.5(–2) cm long, 5–8-flowered, densely lepidote; floral bracts deltate, ca. 0.9–1.1 mm long and wide, apex acute, densely lepidote abaxially, the margin irregular, entire, glabrous; pedicels absent or rarely to 0.1 mm long. Flowers 4(–5)-merous, sessile or subsessile; calyx crateriform, coriaceous, 1.7–2.1 mm long, the tube ca. 1.0 mm long, the lobes very widely triangular, erect, 0.7–1.1 mm long, 1.1–1.5 mm wide, the apex rounded, prominently black punctate without, lepidote near the margin, the margin entire, glabrous; corolla cupuliform, coriaceous, 2.5–2.8 mm long, the tube 0.5 mm long, the lobes oblong, erect, 2.0–2.3 mm long, 0.7–1.1 mm wide, apex rounded, cucullate, strongly carinate without, pellucid punctate apically and along margin without, glandular granulate only along margin within, the margin entire, glabrous; staminodes 2.0 mm long, the tube inconspicuous, membranaceous, elobate, 0.5 mm long, the apically free filaments ca. 1.0 mm long, adnate to the corolla lobes, the anthers appearing epipetalous, ovate, 0.8 mm long, 0.5 mm wide, recurved distally, apically apiculate, the apiculum recurved ventrally, the base deeply cordate; pistil sessile, apophysate, costate, 1.8–2.1 mm long, the ovary 1.4–1.6 mm long and in diam., glandular-lepidote, the style short, 0.2–0.3 mm long, the stigma capitate, 2-lobed, the placenta cubic, 2-ovulate, the ovules covered by flaps of tissue. Fruit globose, 4.0–4.5 mm diam. when dry.

Distribution. Endemic to the Guanay and Yutajé complex, in forests on talus slopes under 1,000 m elevation.

Ecology. *Cybianthus holstii* is infrequently encountered in the margins of cloud forests on talus slopes.

Paratypes. VENEZUELA. Depto. Atures, Río Coroco, W of Serranía de Yutajé, 9 km N of settlement, 600 m, 26 Feb. 1987 (pist, fl, fr), *Holst & Liesner 3185* (MO, US, VEN), Caño Yutajé, right branch, Río Manapiare, 1,400 m, 9 Feb. 1987 (pist. fl), *Maguire 35097* (F, MO, NY, US, VEN).

Cybianthus holstii is most closely related to *C. huberi* but can be easily separated from it by the

membranaceous (not coriaceous) leaves with caudate (not short-acuminate) apices, the inflorescence 5–8(not 1–2)-flowered, and the glabrous (not rufous papillate) anthers. This species is dedicated to Bruce Holst, specialist in Myrtaceae and keen student of the Guayana flora.

14. *Cybianthus guyanensis* (A. DC.) Miquel in Martius, Fl. Bras. 10: 298. 1856. Figures. 13, 14.

Shrub or small tree to 8 m tall; branchlets terete, 2–3 mm diam., densely lepidote. Leaves narrowly obovate, narrowly elliptic, or oblong, membranaceous to chartaceous, 8–20 cm long, 2.0–3.5(–6.0) mm wide, apex acuminate to abruptly acuminate, the acumen 0.5–2 cm long, base acute, decurrent on the petiole, the midrib depressed above, prominently raised below, nerves (15–)20–40 pairs, inconspicuous or slightly raised above and below, the upper surface smooth or slightly wrinkled when dried, densely lepidote at first, glabrescent, lower surface sparsely to densely lepidote, pellucid-punctate, the margin entire, flat; petioles canaliculate and slightly marginate distally, 0.5–1.9(–2.3) cm long, densely lepidote. *Staminate inflorescence*: a raceme, a subsessile pseudoverticil of 2–3 racemes, or a panicle 2–8 cm long; peduncle, branches, and axis densely lepidote; peduncle 0.1–0.5 cm long; floral bracts ovate or ovate-triangular, 0.6–1.2 mm long, 0.3–0.4 mm wide, apex acute, densely lepidote abaxially, the margin entire, glabrous; pedicels erect, cylindrical, (0.3–)0.5–1.0 mm long, moderately lepidote. Flowers 4–5-merous; calyx cotyliform or subcupuliform, chartaceous, 0.8–1.1 mm long, the tube 0.2–0.4 mm long, the lobes ovate-triangular, 0.6–0.8 mm long, 0.5–0.7 mm wide, apex attenuate to a round or acute tip, inconspicuously pellucid or brown punctate, or prominently brown or black punctate, the margin lepidote, entire, glabrous; corolla campanulate, membranaceous or chartaceous, 2.0–2.6 mm long, the tube 0.6–1.0 mm long, the lobes erect or reflexed-recurved, elliptic or ovate-triangular, 1.2–1.7 mm long, 0.6–1.0 mm wide, apex acute to attenuate or attenuate to a rounded tip, inconspicuously or conspicuously brown punctate, the punctations few, glabrous externally, glabrous or densely glandular-granulate internally, sparsely lepidote or glabrous externally, the margins glabrous or glandular-granulate; stamens 1.1–1.8 mm long, the staminal tube inconspicuous, hyaline, membranaceous, 0.6–1.1 mm long, elobate, the apically free filaments terete, recurved ventrally, 0.2–0.9 mm long, eglandular, glabrous, the an-

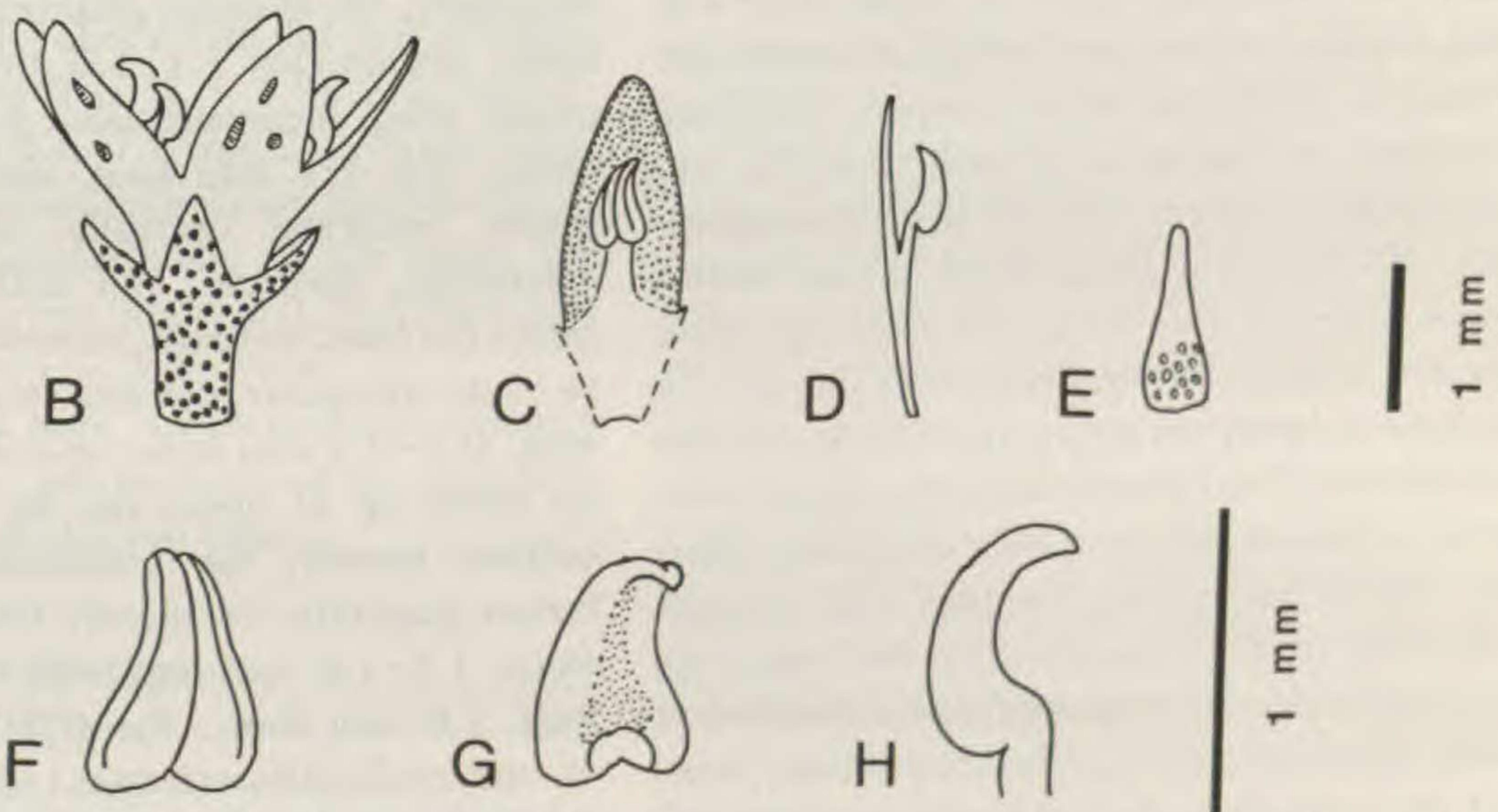


FIGURE 13. *Cybianthus guyanensis* (A. DC.) Miquel subsp. *guyanensis*.—A. Habit.—B. Staminate flower.—C. Staminate corolla lobe, showing elongate apically free filament and tortuous anther.—D. Staminate corolla lobe, lateral view.—E. Pistillode.—F. Anther, ventral view.—G. Anther, dorsal view, showing darkened connective.—H. Anther, lateral view. (A, modified from Miquel, 1856, fig. 49; B–H, from holotype.)

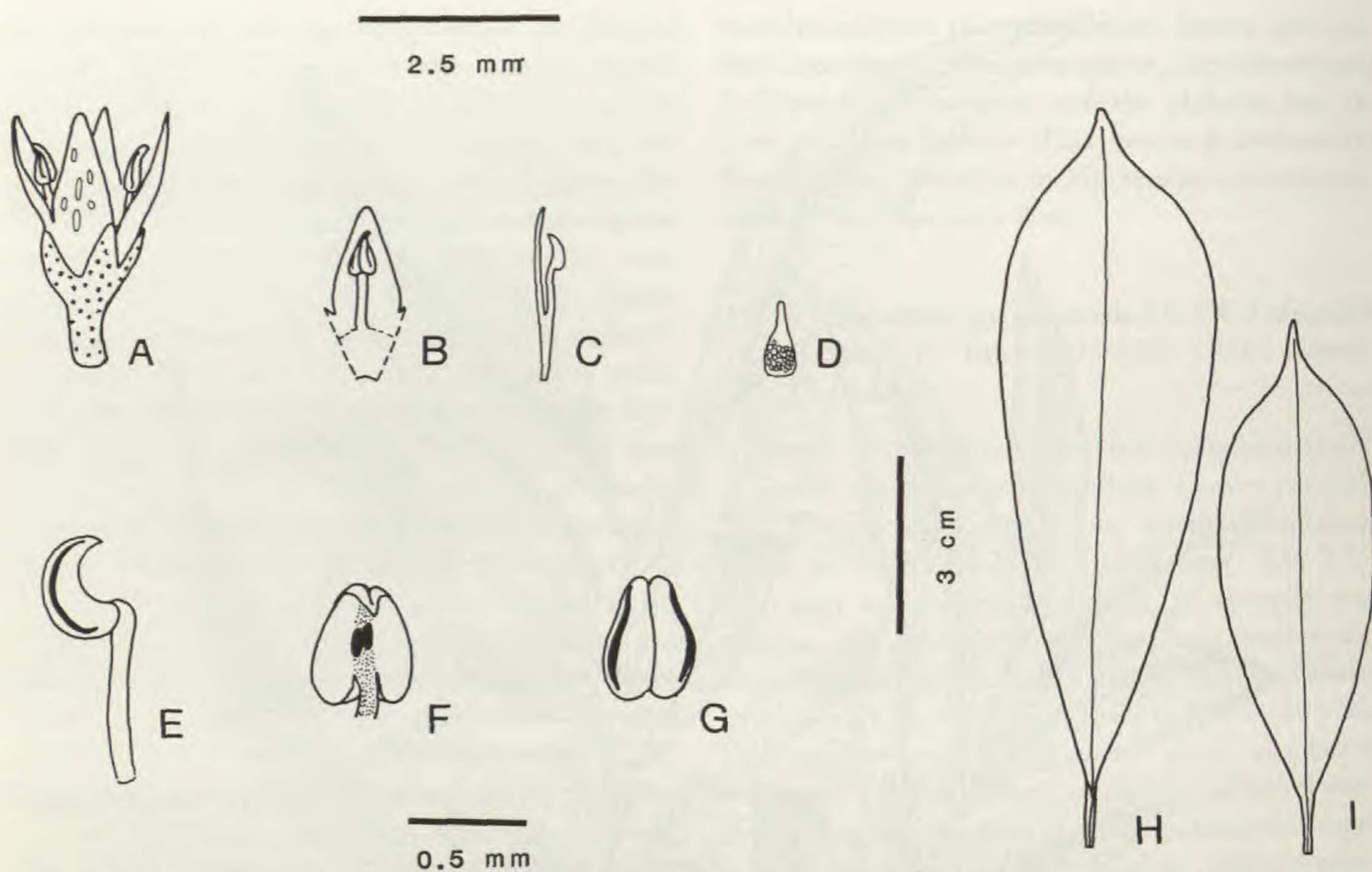


FIGURE 14. *Cybianthus guyanensis* (A. DC.) subsp. *multipunctatus* (A. DC.) Pipoly.—A. Staminate flower.—B. Staminate corolla lobe, ventral view, showing elongate apically free filament and tortuous anther.—C. Staminate corolla lobe, lateral view.—D. Pistillode.—E. Anther and filament, lateral view, showing wide dehiscence slit.—F. Anther, dorsal view, showing darkened and punctate connective.—G. Anther, ventral view.—H, I. Leaves. (A–G, from Pinkus 252; H, I, from Sagot 1031.)

thers dorsifixed just above the base, narrowly triangular, ovate, or ovate-triangular, dorsally recurved, 0.5–0.8 mm long, 0.3–0.4 mm wide, apiculate or attenuate to an acute tip at apex, the tip dorsally recurved, cordate basally, the connective inconspicuously brown punctate, or merely darkened; pistillode lageniform or conic, 0.9–1.4 mm long, basally translucent lepidote, the style not differentiated, the stigma not developed. *Pistillate inflorescence*: a raceme or panicle 2.5–8.0 cm long; peduncle, branches, and axis densely lepidote; peduncle 0.1–0.2 cm long; floral bracts ovate-triangular, 0.6–1.2 mm long, 0.3–0.4 mm wide, apex acute, densely lepidote abaxially, the margin entire, glabrous; pedicels terete, (0.3–)0.5–1.0 mm long, moderately ferruginous lepidote. Flowers 4–5-merous; calyx cotyliform or subcupuliform, chartaceous, 0.8–0.9 mm long, the tube 0.2–0.4 mm long, the lobes ovate-triangular, 0.6–0.8 mm long, 0.5–0.7 mm wide, apex attenuate to a rounded or acute tip, inconspicuously pellucid or brown punctate, or prominently brown or black punctate, the margin lepidote, entire, glabrous; corolla campanulate, membranaceous or chartaceous, 2.0–2.6 mm long, the tube 0.6–1.0 mm long, the lobes erect

or reflexed-recurved, elliptic or ovate-triangular, 1.2–1.7 mm long, 0.6–1.0 mm wide, apex acute to attenuate or attenuate to a rounded tip, conspicuously brown punctate, the punctations few, glabrous externally, glabrous or densely glandular-granulose internally, sparsely lepidote or glabrous externally, the margins glabrous or glandular-granulose; staminodes 1.1–1.8 mm long, the staminodial tube inconspicuous, hyaline, membranaceous, 0.6–1.1 mm long, elobate, the filaments terete, recurved ventrally, 0.2–0.9 mm long, eglandular, glabrous, the anthers dorsifixed just above the base, tortuous, narrowly triangular, ovate, or ovate-triangular, dorsally recurved, 0.5–0.8 mm long, 0.3–0.4 mm wide, apiculate or attenuate to an acute tip at apex, the tip dorsally recurved, cordate basally, the connective inconspicuously brown punctate, or merely darkened; pistil pyriform, 1.4–1.6 mm long, the ovary 0.7–0.8 mm long, 1.0 mm diam., the style 0.7–0.8 mm long, or not well differentiated, the stigma capitate, 2-lobed, the placenta cotyliform, the ovules 2, naked. Fruit 0.5–0.6 cm long, 0.4–0.7 cm diam., exocarp thin to moderately thick, black, inconspicuously pellucid-punctate.

Distribution. *Cybianthus guyanensis* occurs from Venezuela (Amazonas and Bolívar) to Brazil (Amazonas and Pará), Guyana, Surinam, and French Guiana, from 80 to 1,000 m.

Ecology. *Cybianthus guyanensis* grows in lowland Amazonian igapó forests and montane forests. For more detailed discussion, see comments under each subspecies.

Preliminary phylogenetic analysis (Pipoly, unpublished) revealed that *C. guyanensis* is most closely related to *C. pseudoicacoreus* by the synapomorphic undulate anticlinal cell walls, sessile inflorescence, pyriform pistil, and tortuous anthers of the staminodes. *Cybianthus pseudoicacoreus* may only be distinguished from *C. guyanensis* by its cupuliform, although deeply divided (not subcupuliform) calyx, the staminate corolla 2.8–3.2 (not 2–2.6) mm long, with the tube 1.2–1.8 (not 0.6–1.0) mm long. Further study may prove that *C. pseudoicacoreus* is best treated as another subspecies of *C. guyanensis*.

In his dissertation, Agostini (1971) recognized *C. guyanensis* as a distinct species and considered it most closely related to *C. peruvianus* and *C. amplus*. He separated it from those species by the combination of oblong-elliptic leaf blades, the short filaments, the corolla 2.3–2.6 mm long, with lobes internally glandular-granulose, the inconspicuous staminal tube, and the pedicels 0.5–1.0 mm long. The description provided here, based on many more collections, considerably alters the aforementioned quantitative characters. For a discussion of relationships among these species, see *C. plowmanii*.

In Guayana, *C. guyanensis* may be confused with *C. roraimae*, but is easily separated by the branchlets 2–3 (not 3.5–4.5) mm diam., leaves smooth (not pustulate) above with flat (not revolute) margins, the petioles (1.0–)1.5–1.9(–2.3) (not 2–3) cm long, pedicels 0.5–1.0 (not 2–3.5) mm long, corolla campanulate (not subrotate), the lobes erect to spreading (not perpendicular to the tube), the anthers distally recurved (not erect), and the sterile anthers apically tortuous (not erect).

As circumscribed here, *C. guyanensis* consists of two subspecies, *C. guyanensis* subsp. *guyanensis* and subspecies *multipunctatus*.

dular-granulose within and along margins; stamens 1.5–1.8 mm long, the tube 0.9–1.1 mm long, the apically free filaments shorter than the anthers, 0.2–0.4 mm long, the anthers narrowly triangular to ovate-triangular, the apex apiculate, dehiscent by narrow, introrse slits; plants of igapó forests 14a. subsp. *guyanensis*

1b. Petioles 0.5–1.0 cm long; leaves slightly asymmetric, the acumen 0.5–1.0 cm long; calyx cotyliform, the lobes attenuate to a rounded apex; corolla membranaceous, the tube 0.6–0.7 mm long, the lobes distally reflexed-recurved, 1.2–1.6 mm long, 0.6–0.8 mm wide, apically acute, glabrous; stamens 1.1–1.4 mm long, the tube 0.6–0.8 mm long, the apically free filaments longer than the anthers, 0.6–0.9 mm long, the anthers ovate, the apex acute, dehiscent by wide, sublatrorse slits; plants of premontane forests on lateritic and sandstone substrates 14b. subsp. *multipunctatus*

14a. *Cybianthus guyanensis* (A. DC.) Miquel subsp. *guyanensis*. Figure 13.

Conomorpha guyanensis A. DC., Ann. Sci. Nat. 2 ser. 16: 92. 1841. *Peckia guyanensis* (A. DC.) O. Kuntze, Rev. Gen. 2: 402. 1891. *Conomorpha peruviana* var. β *guyanensis* (A. DC.) Mez in Engler, Pflanzenr. IV, 236: 262. 1902. TYPE: Venezuela. Bolívar [Guyana]: *sine loc.*, 1898 (stam. fl), *Schomburgk* 975 (holotype, G-BOIS; isotypes, BM, F, G, GH, K, L, P, US, W).

Conomorpha heterantha Bentham ex Miquel in Martius, Fl. Bras. 10: 304. 1856. TYPE: Brazil. Prov. Rio Negro, Barra, Dec. 1850–Mar. 1851 (pist. fl), *Spruce* 1041 (lectotype, here designated, M).

Shrub or small tree to 5 m tall. Leaves oblong to narrowly elliptic, symmetric, membranaceous to chartaceous, 9–20 cm long, 3–5.5 cm wide, apex acuminate, the acumen 1–2 cm long, nerves 20–40 pairs; petioles canaliculate and winged, (1.0–)1.5–1.9(–2.3) cm long, densely lepidote. **Staminate inflorescence:** a panicle 2–8 cm long; peduncle 0.2–0.5 cm long; floral bracts ovate, 0.7–0.8 mm long, 0.3–0.4 mm wide; pedicels 0.5–1.0 mm long. Flowers 4–5-merous; calyx subcupuliform, 0.8–1.2 mm long, the tube 0.3–0.4 mm long, the lobes subdeltate, 0.6–0.8 mm long, 0.5–0.6 mm wide, apex attenuate to an acute tip, inconspicuously pellucid or brown punctate, the margin lepidote, entire, glabrous; corolla chartaceous, 2.3–2.6 mm long, the tube 0.8–1.0 mm long, the lobes erect to spreading, elliptic, 1.6–1.7 mm long, 0.9–1.0 mm wide, apex attenuate to a rounded tip, inconspicuously brown punctate, glabrous externally, densely glandular-granulose internally, sparsely lepidote externally, the margins glandular-granulose; stamens 1.5–1.8 mm long, the staminal tube 0.9–1.1 mm long, the filaments shorter than the anthers, 0.2–0.4 mm long, the

KEY TO GUAYANA SUBSPECIES OF *CYBIANTHUS GUYANENSIS*

1a. Petioles (1.0–)1.5–1.9(–2.3) cm long; leaves symmetric, apical acumen 1–2 cm long; calyx subcupuliform, the lobes attenuate to an acute apex; corolla chartaceous, the tube 0.8–1.0 mm long, the lobes erect to spreading, 1.6–1.7 mm long, 0.9–1.0 mm wide, apically rounded, glan-

anthers narrowly triangular to ovate-triangular, 0.5–0.8 mm long, 0.3–0.4 mm wide, dehiscent by narrow introrse slits, apex apiculate, the tip dorsally recurved, cordate basally, the connective merely darkened; pistillode conic, 1.2–1.4 mm long. *Pistillate inflorescence*: a panicle 2.5–8.0 cm long; peduncle 0.2–0.5 cm long; floral bracts ovate, 0.7–0.8 mm long, 0.3–0.4 mm wide; pedicels 0.5–1.0 mm long. Flowers 4–5-merous; calyx subcupuliform, 0.8–1.1 mm long, the tube 0.3–0.4 mm long, the lobes subdeltate, 0.6–0.8 mm long, 0.5–0.6 mm wide, apex attenuate to an acute tip, inconspicuously pellucid or brown punctate, the margin lepidote, entire, glabrous; corolla campanulate, chartaceous, 2.3–2.6 mm long, the tube 0.8–1.0 mm long, the lobes erect or spreading, elliptic, 1.6–1.7 mm long, 0.9–1.0 mm wide, apex attenuate to a round tip, inconspicuously brown punctate, glabrous externally, densely glandular-granulose internally, sparsely lepidote externally, the margins glandular-granulose; staminodes 1.5–1.8 mm long, the staminodial tube 0.9–1.1 mm long, elobate, the filaments 0.2–0.4 mm long, narrowly triangular, or ovate-triangular, dorsally recurved, 0.5–0.8 mm long, 0.3–0.4 mm wide, apex apiculate, the tip dorsally recurved, cordate basally, the connective merely darkened; pistil pyriform, 1.4–1.6 mm long, the ovary 0.7–0.8 mm long, 1.0 mm diam., the style 0.7–0.8 mm long, the stigma capitate, 2-lobed, the placenta cotyliform, the ovules 2, naked. Fruit 0.5–0.6 cm long, 0.4–0.7 cm diam., exocarp thin to moderately thick, black, inconspicuously pellucid punctate.

Distribution. Venezuela and Brazil (Amazonas and Pará), at altitudes of 80 to 1,000 m. It is assumed that the type (*Schomburgk* 975) was collected in Venezuela rather than Guyana. Steyermark (1981) discussed the fact that the Schomburgk collections were probably Venezuelan.

Ecology. Subspecies *guyanensis* is restricted to inundated black water forests (igapó) in lowland Amazonia on white sands. It is apparently infrequent and is known from only 11 gatherings. Label data indicate that it grows on the banks of smaller streams and is shade tolerant.

Representative specimens examined. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Depto. Río Negro, lower part of Río Baría, 80 m, 22–23 July 1984 (fr), *Davidse* 27605 (MO, NY, VEN); Río Baría, near Río Marawinuma, 9 May 1984 (fr), *Thomas et al.* 3450 (NY, US, VEN), (fr), 3412 (NY, US, VEN); upper Río Baría, 9 May 1984 (fr), *Gentry & Stein* 47291 (MO, NY, US, VEN). BRAZIL. AMAZONAS: vic. Barra, Apr. 1851 (pist. fl, fr), *Spruce* 1150 (F, K, LD), (stam. fl), *Spruce s.n.* (F, LD, M); 10 km upstream from jct. of Rios Cuieiras and

Branquinho, 7 Apr. 1974 (stam. fl), *Campbell et al.* P21936 (A, C, F, INPA, K, MICH, MO, NY, P, US).

Subspecies *guyanensis* may be distinguished from subspecies *multipunctatus* by the longer petioles (1.0–)1.5–2(–2.3) cm long, the corolla chartaceous (not membranaceous), with tube 0.8–1 (not 0.6–0.7) mm long, the lobes glandular-granulose within and along margins (not glabrous), 1.6–1.7 (not 1.2–1.6) mm long, 0.9–1.0 (not 0.6–0.8) mm wide, apically free filaments shorter than (not longer than) the anthers, and narrowly triangular (not ovate) anthers.

The type specimen of *Conomorpha heterantha* is pistillate, and therefore has shorter pedicels, stamens much shorter than the petals, and a broadly conic ovary. The feature that gave rise to the specific epithet, the heteromerous perianth, occurs frequently within the genus and is not constant among the specimens examined.

14b. *Cybianthus guyanensis* (A. DC.) Miquel in Martius subsp. ***multipunctatus*** (A. DC.) Pipoly, comb. et stat. nov. *Cybianthus multipunctatus* A. DC., Ann. Sci. Nat. 2 ser. 16: 94. 1841. *Conomorpha multipunctata* (A. DC.) Miquel, Stirp. Surinam. Select. 111. t. 34. 1850. TYPE: French Guiana. Cayenne, *Martin s.n.* (holotype, P not seen). Figure 14.

Shrub or small tree to 8 m tall; branchlets terete, 2–3 mm diam., densely lepidote. Leaves narrowly obovate to narrowly elliptic, asymmetric, chartaceous, or rarely membranaceous, 8–12(–15) cm long, 2.0–3.5(–6) cm wide, apex acuminate to abruptly acuminate, the acumen 0.5–1 cm long, nerves 15–30 pairs; petioles canaliculate, 0.5–1.0 cm long, densely lepidote. *Staminate inflorescence*: a raceme or rarely a subsessile pseudoverticel of 2–3 racemes, 2.5–5.0 cm long; peduncle 0.1–0.2 cm long; floral bracts ovate-triangular, 0.6–1.2 mm long, 0.3–0.4 mm wide, apex acute; pedicels (0.3–)0.5–1.0 mm long. Flowers 4-merous; calyx cotyliform, chartaceous, 0.9–1.0 mm long, the tube 0.2–0.3 mm long, the lobes ovate-triangular, 0.7–0.8 mm long, 0.5–0.7 mm wide, apex attenuate to a rounded tip, prominently brown or black punctate; corolla membranaceous, 2.0–2.5 mm long, the tube 0.6–0.7 mm long, the lobes reflexed-recurved, ovate-triangular, 1.2–1.6 mm long, 0.6–0.8 mm wide, apex acute to attenuate, dehiscent by wide, sublatrorse slits, conspicuously brown punctate, the punctations few, glabrous externally and internally; stamens 1.1–1.4 mm long, the staminal tube 0.6–0.8 mm long, the filaments 0.6–0.9 mm long, the anthers ovate, 0.5–0.7 mm

long, 0.3–0.4 mm wide, attenuate to an acute tip at apex, the connective brown punctate, inconspicuous; pistillode lageniform, 0.9–1.0 mm long. *Pistillate inflorescence*: a raceme 2.5–5.0 cm long; peduncle 0.1–0.2 cm long; floral bracts ovate-triangular, 0.6–1.2 mm long, 0.3–0.4 mm wide; pedicels (0.3–)0.5–1.0 mm long. Flowers 4-merous; calyx cotyliform, 0.8–0.9 mm long, the tube 0.1–0.2 mm long, the lobes ovate-triangular, 0.6–0.7 mm long, 0.5–0.7 mm wide, apex attenuate to a rounded tip, prominently brown or black punctate; corolla membranaceous, 1.8–1.9 mm long, the tube 0.5–0.8 mm long, the lobes reflexed-recurved, ovate-triangular, 1.0–1.4 mm long, 0.6–0.8 mm wide, apex acute to attenuate, conspicuously brown punctate, the punctations few, glabrous externally and internally; staminodes 0.9–1.0 mm long, the staminal tube 0.2–0.3 mm long, the filaments 0.7–0.8 mm long, the anthers ovate, 0.4–0.5 mm long, 0.3–0.4 mm wide, attenuate to an acute tip at apex, pistil pyriform, 1.4–1.5 mm long, the ovary ca. 0.8 mm long, the style not well differentiated, the stigma capitate, 2-lobed, the placenta cotyliform, the ovules 2, naked. Fruit 0.5–0.6 cm long, 0.4–0.5 cm diam., the exocarp thick, black, inconspicuously pellucid-punctate.

Distribution. Venezuela (Bolívar), Guyana, Surinam and French Guiana, Brazil (Pará), 25–1,000 m elevation.

Ecology. Subspecies *multipunctatus* is found on lateritic and sandstone formations in the Guianas and eastern Venezuela. In Brazil, it has been collected on Serra do Cachimbo (*Prance et al.* P24999), a sandstone mountain that is known to contain a number of tepui elements, such as *Cybianthus spicatus* (HBK) Agostini, *C. fulvopulverulentus* subsp. *magnoliifolius* (Mez) Pipoly, *Clusia sessilis* Klotzch ex Engler, and *Clusia melchiori* Gleason.

Specimens examined. VENEZUELA. BOLIVAR: Morichal, 2 km E of Río Orinoco between Río Horeda and Cerro Gavilan (Cerro Carichana), 100 m, 17 Dec. 1955 (fr), *Wurdack & Monachino* 39940 (F, MO, NY, US). GUYANA. UPPER DEMARARA: Mabura Hill, 100–200 m, 16 Sep. 1986 (ster.), *Pipoly & Boyan* 8515 (BRG, FDG, NY, US); Moraballi Creek, Essequibo River, 30 Nov. 1938 (fr), *Davis* 2764 (BM, FDG, K, NY, P, S, U), (stam. fl), *Forest Dept. Brit. Guiana* D601-2764 (BM, FDG, K, NY, U); Eagle Mt., 500–700 m, 27 Jan. 1943 (pist. fl), *Forest Dept. Brit. Guiana* F1158-3894 (FDG, K, NY); Kaieteur Plateau, 1 May 1944 (fr), *Maguire & Fanshawe* 23122 (F, FDG, G, GH, IAN, NY, S, US, VEN), vic. Kaieteur Falls, and along W rim of Potaro Gorge, 450 m, 14 Feb. 1962 (pist. fl), *Cowan & Soderstrom* 1860 (F, FDG, NY, US), forest along trail from airstrip to Kaieteur Falls, 450 m, 27 Feb. 1962 (pist. fl),

Cowan & Soderstrom 1988 (F, FDG, K, NY, US); 65 mi., Bartica–Potaro Rd., 28 Nov. 1947 (fr), *Forest Dept. Brit. Guiana* F2790-5589 (FDG, K, NY, U), 10 mi., 14 Mar. 1948 (stam. fl), *Forest Dept. Brit. Guiana* F2803-5602 (FDG, K, NY, RB, U, VEN); Upper Mazaruni River, 22 Sep. 1922 (fr), *De La Cruz* 2045, (fr), 2168 (CM, F, FDG, GH, MO, NY), Kamakusa, 15 Dec. 1922 (pist. fl), *Lang & Persaud* 374 (BFG, F, FDG, K, NY), Coomaka, Nov. 1924 (fr), *Persaud* 199 (F, FDG, K, NY), Makreba Falls, Kurupung River, 25 Feb. 1939 (stam. fl), *Pinkus* 252 (BR, DUKE, G, GH, M, MO, RB, S, VEN), Mt. Ayanganna, 762 m, 3 Aug. 1960 (fr), *Tillett et al.* 45017 (F, NY, P, S, U, VEN); Upper Rupununi River, near Dadanawa, without date (fr), *De La Cruz* 1706 (CM, F, FDG, GH, MO, NY); without locality, *Appun* 836 (K); without locality, Dec. 1890 (stam. fl), *Jenman* 6220 (BRG, K). SURINAM. Hendriktop, 1,080 m, 14 Mar. 1922 (fr), *Boschwezen Surinam* 5662 (BBS, U); ad fl. Carouany, Feb. 1844 (stam. fl), *Kappler* 1729 (BM, P, S, U, W); in mountains called Nassau, 2 Mar. 1949 (stam. fl), *Lanjouw & Lindeman* 2661 (BBS, NY, U), Nassaugbergette, line 13, 550 m, 5 Jan. 1955 (fr), *Lindeman & Cowan* 7000 (BBS, U), along Marwoijne River, 400–550 m, 14 Mar. 1955 (fr), *Maguire et al.* 40805 (BBS, NY, US, VEN). FRENCH GUIANA. Karouany, 1857 (stam. fl), *Sagot* 1031 (BM, G, K, P, S, W); Montagne de Kaw, 275 m, 11 Dec. 1954 (fr), *Cowan* 38722 (CAY, NY, U, US, VEN); Montagnes de la Trinité, sommet Nord, 350 m, 10 Jan. 1984 (stam. fl), *de Granville et al.* 5813 (BR, CAY, G, MG, NY, U, US), Inselberg NW, 450 m, 17 Jan. 1984 (stam. fl), *de Granville et al.* 5899 (CAY, NY, U), (stam. fl), 6087 (BR, CAY, G, NY, P, U); Montagnes Bellevue de l'Inini, 650 m, 15 Aug. 1985 (fr), *de Granville et al.* 7511, 7521 (B, BR, CAY, MG, MO, NY, P, U); Zone centrale, 600 m, 29 Aug. 1985 (fr), *de Granville et al.* 7834 (B, BM, BR, CAY, F, G, GOET, INPA, MG, MO, NY, P, U); Saül, 220 m, 22 June 1988 (ster.), *Gentry et al.* 63081 (CAY, MO, NY), La Fumée Mt., Antenne Est, 300 m, 18 May 1986 (fr), *Mori & Pennington* 18050 (CAY, MO, NY). BRAZIL. PARA: Serra do Cachimbo, BR 163, Cuiabá–Santarém Hwy., km 823, 570 m, 7 Nov. 1977 (stam. fl), *Prance et al.* 24999 (F, INPA, MG, NY, RB, US).

Subspecies *multipunctatus* may be distinguished from subspecies *guyanensis* by the filaments 0.7–0.8 (not 0.2–0.4) mm long, the corolla glabrous (not densely glandular-granulose within), and the petioles 0.5–1.0 (not 1.0–2.3) cm long. It is restricted to the Guianas, the easternmost portion of Guayana, and the Serra do Cachimbo.

15. *Cybianthus roraimae* (Steyermark) Agostini, *Acta Biol. Venez.* 10: 155. 1980. *Conomorpha roraimae* Steyermark, *Fieldiana, Bot.* 28(3): 468. 1953. TYPE: Venezuela. Bolívar: Mt. Roraima, ledge along SW-facing side, from bluffs to summit, 2,255–2,620 m, 27 Sep. 1944 (pist. fl), *Steyermark* 58759 (holotype, F; isotype, NY). Figure 15.

Shrub or small tree to 5 m tall, the bark reddish brown; branchlets terete, 3.5–4(–4.5) mm diam.,

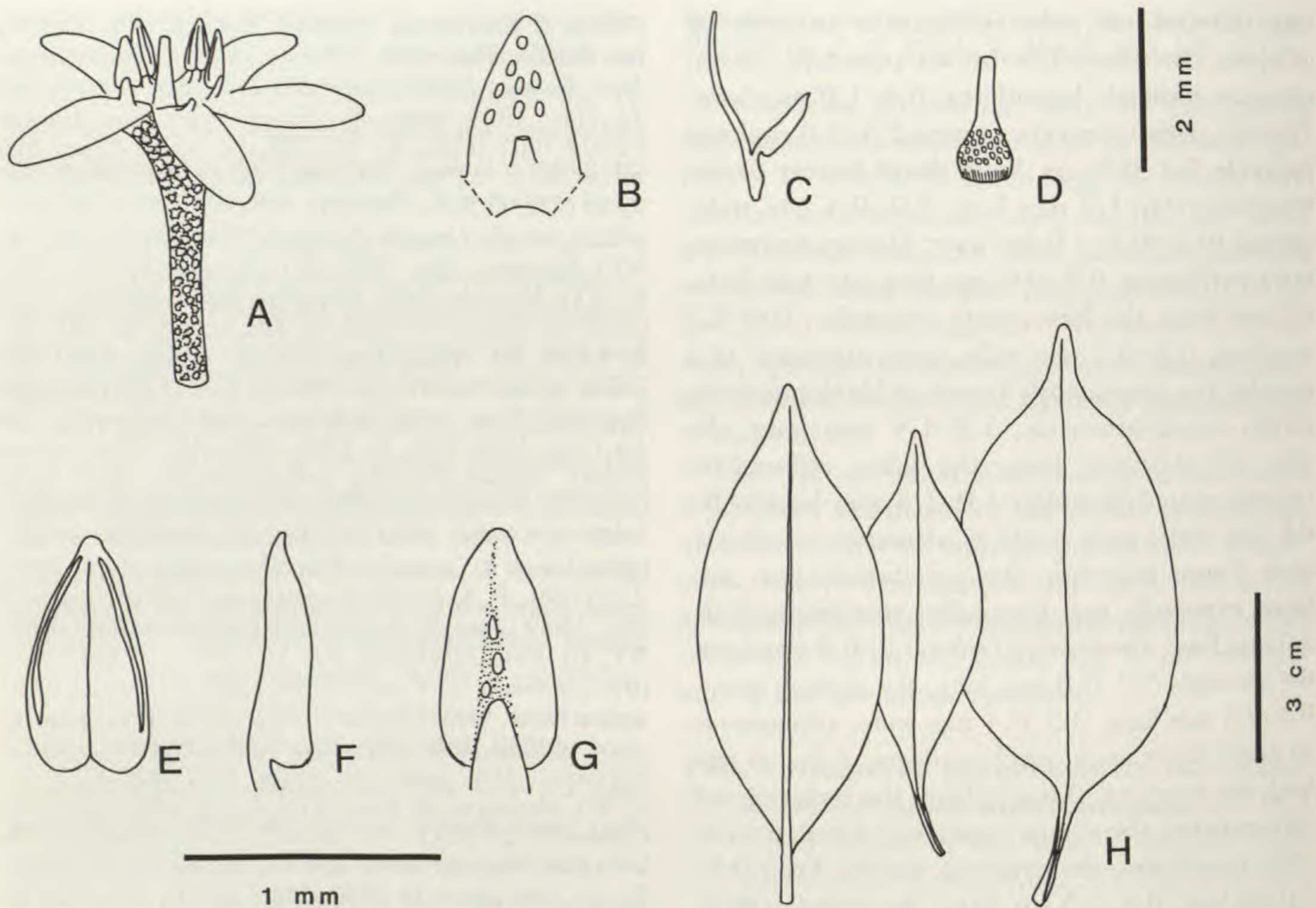


FIGURE 15. *Cybianthus rorimae* (Steyermark) Agostini.—A. Staminate flower.—B. Staminate corolla lobe, ventral view, showing pellucid punctations.—C. Staminate corolla lobe, lateral view showing anther habit.—D. Pistillode.—E. Anther, ventral view.—F. Anther, lateral view.—G. Anther, dorsal view showing darkened connective and pellucid punctations.—H. Leaves. (A–D, from Maguire 33464; E–G, from Wurdack 34259; H, left to right, from Maguire 33464, Wurdack 34270, and Steyermark 58765.)

densely lepidote. Leaves elliptic, coriaceous, 7–11 cm long, 2.5–4.5 cm wide, apex acuminate, the acumen 1.0–1.5 cm long, base rounded to obtuse, decurrent on the petiole, the midrib depressed above, prominently raised below, the nerves 26–30 pairs, conspicuous above and below, the upper surface pustulate, the lower surface densely lepidote, inconspicuously pellucid-punctate, the margin entire, epunctate, revolute; petioles marginate, 2–3 cm long, densely lepidote. *Staminate inflorescence*: a raceme, rarely a sessile pseudoverticil of 2–3 racemes, 5–8 cm long; peduncle, axis, branches, and pedicels densely lepidote; peduncle 0.5–2.5 cm long; floral bracts ovate to broadly ovate, 0.5–1.0 mm long, 0.5–0.8 mm wide, apex acute, densely lepidote abaxially, the margin entire, glabrous; pedicels terete, 2.0–3.5 mm long. Flowers nodding, (4–)5-merous, 2.1–2.4 mm long; calyx shallowly cotyliform, carnose, 0.7–0.9 mm long, the tube 0.3–0.4 mm long, the lobes deltate to subdeltate, 0.5–0.7 mm long, 0.5–0.8 mm wide, the apex rounded or attenuate to a rounded tip, epunctate or with a few, inconspicuous pellucid punctations, densely lepidote externally, the margin entire, lep-

idote; corolla rotate, membranaceous, 2.0–2.3 mm long, the tube 0.3–0.4 mm long, the lobes ovate, highly reflexed (perpendicular to the tube) in anthesis, apex attenuate to a rounded tip, glabrous without and within, the punctations pale brown or yellow, inconspicuous, the margin entire, glabrous; stamens 1.7–1.8 mm long, the staminal tube inconspicuous, hyaline, elobate, 0.4–0.6 mm long, the filaments flat, 0.3–0.4 mm long, epunctate, glabrous, the anthers dorsifixed near the base, ovate-triangular, 0.8–1.0 mm long, 0.4–0.6 mm wide, attenuate to an apiculate tip, the apiculum erect, slightly recurved dorsally, the connective dorsally brown or yellow punctate, the punctations not prominent; pistillode lageniform, 1.2–1.5 mm long, the base glandular lepidote with dark scales. *Pistillate inflorescence*: a raceme, rarely 2 racemes from a common peduncle, 5–8 cm long; peduncle, axis, branches, and pedicels densely lepidote; peduncle 0.5–2.5 cm long; floral bracts ovate to broadly ovate, 0.5–1.0 mm long, 0.5–0.8 mm wide, apex acute, densely lepidote abaxially, the margin entire, glabrous; pedicels terete, erect, 2.0–3.5 mm long. Flowers (4–)5-merous, 2.1–2.4 mm

long; calyx shallowly cotyliform, carnose, 1.0–1.1 mm long, the tube 0.2–0.3 mm long, the lobes very widely ovate, 0.8–0.9 mm long, 1.1–1.3 mm wide, the apex rounded or attenuate to a rounded tip, epunctate or with a few, inconspicuous pellucid punctations, densely lepidote externally, the margin entire, lepidote; corolla not seen. Fruit globose, wine-purple, 0.5–0.6 cm long, 0.4–0.5 cm diam. when dried.

Distribution. Endemic to the Auyán-tepui-Chimantá Complex (sensu Maguire, 1979), from 1,140 m to 2,600 m.

Ecology. *Cybianthus roraimae* occurs in cloud forests on talus slopes. Only a few of the fruiting collections also bear pistillate flowers, implying that the latter are ephemeral in this species, as they are in others of subgenus *Conomorpha* and throughout subgenus *Laxiflorus* (Pipoly, 1983a).

Specimens examined. VENEZUELA. BOLIVAR: Mt. Roraima, ledge along SW-facing side, 2,250–2,620 m, 27 Sep. 1944 (fr), *Steyermark* 58765 (NY), 2,000 m, Dec. 1909 (fr), *Ule* 8724 (L, K); Ilú-tepui, W-facing slopes, 2,100–2,400 m, 17 Mar. 1952 (fr), *Maguire* 33464 (GH, NY, VEN), 21 Mar. 1952 (pist. fl, fr), 33504 (NY); NW slopes of Churi-tepui (Muru-tepui), 2,050 m, 29 Jan. 1953 (stam. fl), *Wurdack* 34259 (K, NY, US, VEN), 30 Jan. 1953 (fr), 34270 (F, K, NY, US, VEN).

Cybianthus roraimae is unique within the genus in its purple flowers and rotate corollas. The densely lepidote pedicels and calyx lobes are reminiscent of *C. crotonoides*, which is easily separated by its overlapping (not merely adjacent) scales on the abaxial corolla surface and the longer calyx and corolla. In sterile condition, it may be confused with *C. cardonae*, *C. punctatus*, or *C. lepidotus*. Differences with those species are discussed under *C. cardonae*.

16. *Cybianthus breweri* Agostini, Bol. Soc. Venez. Ci. Nat. 22: 384. 1976. TYPE: Venezuela. Bolívar: Meseta de Jaua, Cerro Guanacoco, summit, 1,450 m, 3 Mar. 1974 (stam. fl), *Steyermark et al.* 109754 (holotype, VEN).

Shrub or small tree to 3 m tall; branchlets terete, 3.5–5 mm diam., densely lepidote, glabrescent. Leaves obovate-spathulate to narrowly obovate-spathulate, coriaceous, 4–5 cm long, 1.5–2 cm wide, apically obtuse to rounded, at times abruptly short-acuminate, the acumen to 0.4 cm, base cuneate, pustulate above, sparsely lepidote below, midrib somewhat depressed above, prominently raised below, nerves inconspicuous above and below, inconspicuously pellucid punctate, the margin

entire, epunctate, revolute; petioles canaliculate, 0.4–0.6 cm long, sparsely lepidote. *Staminate inflorescence:* a raceme 1–3 cm long, 8–16-flowered; peduncle 0.2–0.4 cm long; floral bracts deltate, carnose, 1.5 mm long and wide, apex acute, densely lepidote abaxially, the margin entire, glabrous; pedicels terete, 2.0–3.0 mm long, erect. Flowers 4–5-merous; calyx cupuliform, carnose, 0.7–1.0 mm long, the tube 0.2–0.3 mm long, the lobes deltate to subdeltate, 0.5–0.7 mm long, 0.5–0.7 mm wide, apex acute, densely and prominently orange punctate, the margin entire, glabrous; corolla campanulate, ca. 2 mm long, the lobes sparsely lepidote without, densely glandular-granulose within; stamens ca. 1.5 mm long, the tube prominent, carnose, ca. 0.3 mm long, lobate, the lobes ca. 0.1 mm long, the anthers ovate-triangular, ca. 1.0–1.2 mm long, 0.5–0.6 mm wide, apex acute, base cordate, recurved distally, prominently punctate dorsally; pistillode conic, ca. 2.3 mm long, densely glandular-lepidote. *Pistillate inflorescence:* a raceme 1–3 cm long, 5–12-flowered; peduncle 0.2–0.4 cm long; floral bracts carnose, deltate, 1.5–1.6 mm long and wide, apex acute, densely lepidote abaxially, the margin entire, glabrous; pedicels terete, 2.5–3.0 mm long, erect. Flowers 4–5-merous; calyx cupuliform, carnose, 0.7–1.0 mm long, the tube 0.2–0.3 mm long, the lobes deltate to subdeltate, 0.5–0.7 mm long, 0.5–0.7 mm wide, apex acute, densely and prominently orange punctate, the margin entire, glabrous; corolla not seen. Fruit depressed-globose, 0.7–0.8 cm diam., the exocarp thin, conspicuously pellucid-punctate.

Distribution. Endemic to the Meseta de Jaua, 1,400–2,100 m.

Ecology. *Cybianthus breweri* occurs in gallery forests and thickets at the margins of savannas.

Specimens examined. VENEZUELA. BOLIVAR: Meseta de Jaua, Cerro Jaua, summit, 1,922–2,100 m, 22–27 Mar. 1967 (fr), *Steyermark* 97931 (VEN), 1,750–1,800 m, 22–28 Feb. 1974 (fr), *Steyermark et al.* 109296, 109393, 109660 (VEN), 1,850–1,920 m, 4 Mar. 1974 (fr), *Steyermark et al.* 109820 (VEN); Meseta de Jaua, Cerro Sarisariñama, 1,400 m, 16–18 Feb. 1974 (fr), *Steyermark et al.* 109162 (VEN).

Cybianthus breweri may be distinguished by its coriaceous, obovate-spathulate leaves with inconspicuous secondary veins, and deltate calyx lobes with orange punctations.

17. *Cybianthus apiculatus* (Steyermark) Agostini, Acta Biol. Venez. 10: 168. 1980. *Conomorpha apiculata* Steyermark, Fieldiana, Bot.

28(3): 456. 1953. TYPE: Venezuela. Territorio Federal Amazonas: Cerro Duida, SE-facing slopes along Caño Negro (tributary of Caño Iguapo), 305–1,095 m, 25–26 Aug. 1944 (fr), *Steyermark 57986* (holotype, F; isotypes, NY, VEN).

Shrub or small tree, to 3 m tall; branchlets thin, terete, 2–3 mm diam., densely lepidote at first, the scales not appressed, early glabrescent. Leaves membranaceous, translucent, elliptic to narrowly oblanceolate, asymmetric, (8–)10–17.5(–20) cm long, (2.0–)3–4(–5.9) cm wide, apically acuminate, the acumen (0.8–)1.5–1.9(–2.2) cm long, basally acuminate to acuminate-attenuate, decurrent on the petiole, nitid, smooth and glabrous above, pallid and densely orange lepidote below, the midrib depressed above, prominently raised below, lateral nerves 12–15, prominent above and below, the margin irregular, subrevolute at first, then flat at maturity, prominently punctate-lineate; petioles thin, marginate, and deeply canaliculate, (1–)1.3–1.7(–2.3) cm long. Prophylls 2, often persistent, chartaceous, elliptic, (1–)1.3–1.5(–2) cm long, 0.5–0.6 cm wide, apex acute, base acute, decurrent on the petiole; petiole thin, marginate, and deeply canaliculate, 0.2–0.4 cm long. *Staminate inflorescence*: a raceme, (0.6–)1.5–4.5(–6.2) cm long, lax, the rachis glandular-papillate and lepidote; floral bracts deltate, 0.8–1.1 mm long and wide, apex subulate, densely lepidote; pedicels terete, thin, 0.6–1.0 mm long, basally lepidote and glandular-papillate. Flowers 4–6-merous; calyx membranaceous, cotyliform, 1.3–1.5 mm long, unequally divided, translucent, the tube 0.3–0.4 mm long, the lobes hyaline, ovate to widely ovate, 0.9–1.2 mm long, 0.7–1.3 mm wide, apex acute, densely and prominently black punctate within and without, glabrous without, with a few glandular papillae at base within, lepidote scales absent, the margin erose, glandular-ciliate; corolla subrotate, chartaceous, translucent, 2.8–3.0 mm long, the tube 0.9–1.1 mm long, the lobes suborbicular to very broadly ovate, 1.8–2.2 mm long and wide, apex rounded, cucullate, glabrous without, densely glandular-granulose within except for a small (0.1 mm) marginal zone, densely and prominently black punctate and punctate-lineate, the margin entire, glabrous; stamens 2.6–3.0 mm long, the tube carnosose, costate, 0.9–1.1 mm long, densely rufous glandular-granulose, without lobes, the apically free portion of the filaments terete, 0.6–1.2 mm long, ventrally recurved, the anthers ovate to widely ovate, 0.9–1.2 mm long, 0.6–0.8 mm wide, apex acute to rounded, the base cordulate, dorsally re-

curved, dorsifixed just above the base, slits very wide, glandular-papillate dorsally, the connective prominently black punctate; pistillode absent. *Pistillate inflorescence*: a simple raceme 2.0–4.5 cm long, erect; floral bracts linear-subulate, membranaceous, 0.6–0.8 mm long, 0.2–0.3 mm wide, apically attenuate, the margin entire, glabrous; pedicels terete, in fruit 1.2–2.3 mm long, incrassate. Flowers 4–5-merous; fruiting calyx subcotyliform, 1.1–1.3 mm long, the tube 0.2–0.3 mm long, the lobes deltate to subdeltate, 0.9–1.3 mm long, 0.9–1.2 mm wide, apex rounded, medially and dorsally thickened, the margin erose, glandular-ciliate; corolla not seen; pistil pyriform, basally lepidote, persistent stigma capitate. Fruit ovoid, (0.5–)0.6–1.0 cm long, (0.3–)0.4–0.7 cm wide, the exocarp thin, rugulose, prominently black punctate.

Distribution. *Cybianthus apiculatus* is currently known only from the southernmost region of Territorio Federal Amazonas in Venezuela, including Cerros Neblina, Duida, and Marahuaca, and also from Mt. Ayanganna in Guyana.

Ecology. *Cybianthus apiculatus* occurs in mixed evergreen moist forest on talus slopes, where various species of *Dicymbe*, *Eperua*, and other legume species dominate. It specifically grows along the banks of black water streams in somewhat open, exposed areas, and has relatively few individuals per hectare, based on my observations in Guyana.

Specimens examined. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Depto. Atabapo, slopes of Mt. Duida, 1,000 m, Aug. 1928–Apr. 1929 (fr), *Tate 901* (NY, US); Cerro Marahuaca, SE-facing slopes, headwaters of Río Iguapo, S section of SE range, 1,560 m, 13–14 Oct. 1983 (stam. fl), *Steyermark 129612* (MO, VEN), (stam. fl), *129683* (CAS, MO, NY, VEN), below Salto Los Monos, on tributary of headwaters of Río Iguapo, 1,500–1,600 m, 20 Oct. 1988 (stam. fl), *Liesner 25121* (MO, US, VEN); Sima Camp, S-central portion along branch of Caño Negro, 21–22 Feb. 1985 (stam. fl), *Steyermark & Holst 130492* (MO, NY, US, VEN), upper Río Yameduaka, 1,225 m, 17–18 Feb. 1985 (pist. fl), *Liesner 17606* (MO, US, VEN), (fr), *17819* (MO, US, VEN); Depto. Río Negro, Cerro de la Neblina, trail S from Camp V, 1,200–1,300 m, 12 Apr. 1984 (fr), *Gentry & Stein 46557* (MO, NY, VEN), Camp V, valley at N base of Pico Cardona, 1,250 m, 21–24 Mar. 1984 (stam. fl), *Liesner & Stannard 16896* (MO, NY, VEN), between Camps II and IV, 8 Nov. 1957 (fr), *Maguire et al. 42000* (F, NY—2 sheets, US, VEN), GUYANA. CUYUNI-MAZARUNI REGION VIII, MAZARUNI SUBREGION VIII-2: Ayanganna Plateau, 2 km W of base camp in Koatse River Valley, 3 Mar. 1987 (ster.), *Pipoly et al. 10940* (CAY, FDG, NY, US), (fr), *11000* (FDG, NY, US), Mt. Ayanganna, along base, NE side, 800–900 m, 1 Aug. 1960 (stam. fl), *Tillett et al. 44959* (F, FDG, NY, US, VEN).

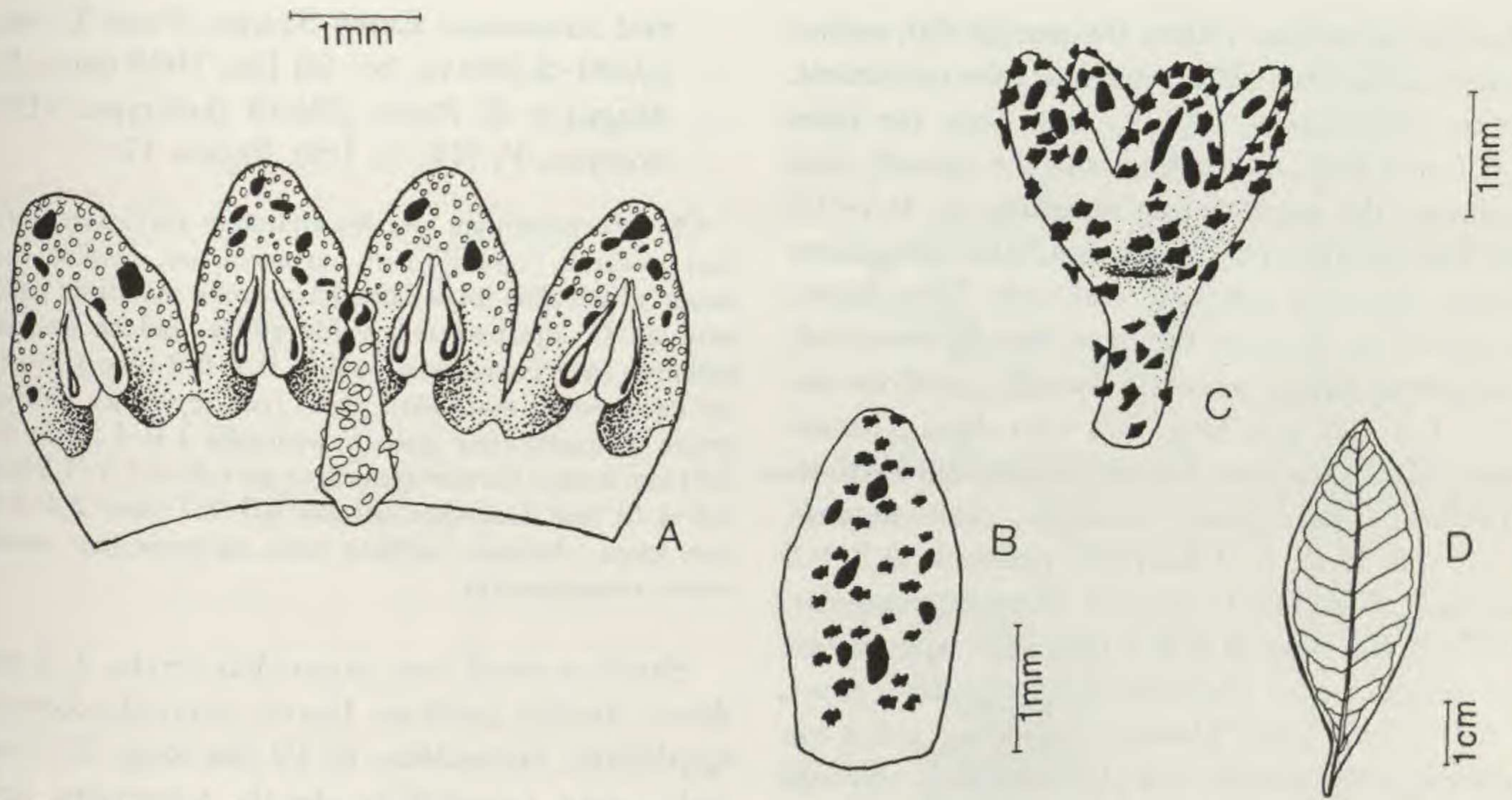


FIGURE 16. *Cybianthus agostinianus* Pipoly.—A. Opened staminate flower, showing prominent punctations, glandular granules, lobate staminal tube, and pistillode.—B. Staminate corolla lobe, dorsal view, showing lepidote scales and punctations.—C. Staminate calyx.—D. Leaf. (From holotype.)

Agostini (1980) placed *Cybianthus apiculatus* in subgenus *Cybianthus* on the basis of fruiting specimens available to him from Steyermark collections. In fruit, the simple raceme, with glandular-papillate rachis and subcotyliform calyx, indicated placement in that group. On the other hand, Agostini (1971) placed the Guyana populations (based on *Tillett et al.* 4459) in a new section, "Intermedius," on the basis of the lepidote branches and calyx with erose, glandular-ciliate margins.

Close examination revealed no qualitative differences between the Venezuelan and Guyanese collections. This species is here transferred to subgenus *Conomorpha* because the lepidote scales that define the subgenus are found on its branches. The anther morphology is entirely consistent with subgenus *Conomorpha* rather than *Cybianthus*, because the anthers are distally recurved (not erect), dorsifixed (not basifixed), and longitudinally (not poricidally) dehiscent. Because the erose and glandular-ciliate calyx lobe margin is a plesiomorphic character state (Pipoly, 1987), and the lepidote scales are homologous to those found in the rest of the subgenus, it is more parsimonious to hypothesize one reversal than to define a new infrageneric taxon on the basis of a homoplasy.

18. *Cybianthus agostinianus* Pipoly, *Ernstia* 50: 33. 1988. TYPE: Venezuela. Territorio Federal Amazonas: Cerro Huachamacari, vic. summit camp, 1,800 m, 10 Dec. 1950 (fr),

Maguire et al. 30006 (holotype, VEN; isotypes, F, LL, NY, US). Figure 16.

Shrub or small tree to 4 m tall; branchlets, petioles, inflorescence rachis, and pedicels densely ferruginous lepidote; branchlets terete, 3–4 mm diam. Leaves narrowly elliptic, elliptic, or rarely elliptic-obovate, chartaceous to coriaceous, 4.6–11.5 cm long, 2–3 cm wide, apically rounded to acute, basally acute, midrib depressed above, prominently raised below, nerves 15–40 pairs, somewhat conspicuous above and below, minutely pustulate above, sparsely to densely lepidote below, the margin flat, entire, epunctate, revolute; petioles canaliculate, 0.5–1.1 cm long, moderately lepidote. *Staminate inflorescence*: a simple, erect raceme, 1.5–3 cm long, 5–12-flowered; peduncle 0.2–0.5 mm long; floral bracts ovate or elongate-triangular, 0.7–1.1 mm long, 0.3–0.5 mm wide, apex acute, the margin entire, glabrous; pedicels terete, erect, 1.5–4.5 mm long. Flowers 4-merous; calyx cotyliform, chartaceous, 1.2–1.4 mm long, the tube 0.2–0.3 mm long, the lobes triangular or deltate, 1.0–1.1 mm long, 0.8–1.1 mm wide, apex acute, prominently black punctate, sparsely lepidote without, the margin irregularly dentate or undulate, glabrous; corolla campanulate, membranaceous, 2.6–2.8 mm long, the tube 0.6–0.7 mm long, the lobes elliptic, 1.9–2.0 mm long, 1.3–1.4 mm wide, erect, apex flat, rounded, prominently black punctate, sparsely lepidote without, sparsely

glandular-granulose within, the margin flat, entire, hyaline, glandular-ciliate; staminal tube prominent, terete, chartaceous, 0.6–0.7 mm long, the lobes to 0.1 mm long, alternating with the apically free filaments; the apically free filaments ca. 0.4–0.5 mm long, prominently brown punctate, the anthers deltate, 0.8–0.9 mm long and wide, apex acute, dorsifixed ca. $\frac{1}{3}$ from the base, distally recurved, prominently brown punctate dorsally; pistillode clavate, 1.4–1.6 mm long, 0.4 mm diam., prominently black punctate, densely translucent lepidote. *Pistillate inflorescence*: a simple, erect raceme, 1.5–3 cm long, 5–9-flowered; peduncle 0.2–0.5 mm long; floral bracts ovate or elongate-triangular, 0.9–1.3 mm long, 0.3–0.5 mm wide, apex acute, the margin entire, glabrous; pedicels terete, erect, 1.5–4.5 mm long. Flowers 4-merous; calyx cotyliform, chartaceous, 1.2–1.4 mm long, the tube 0.2–0.3 mm long, the lobes triangular or deltate, 0.9–1.2 mm long, 0.8–1.1 mm wide, apex acute, prominently black punctate, sparsely lepidote without, the margin irregularly dentate or undulate, glabrous; corolla not seen. Fruit subglobose, 3.0–3.5 mm diam., the exocarp moderately thick, inconspicuously pellucid punctate.

Distribution. Endemic to Cerros Duida and Huachamacari at 1,700–2,660 m.

Ecology. *Cybianthus agostinianus* grows in rocky, open areas where strong winds produce xeric effects. Label data imply that the species is locally common between rocks on the summits of Marahuaca and Huachamacari.

Specimens examined. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Depto. Atabapo, Cerro Huachamacari, elfin forest, vic. summit camp, 1,800 m, 10 Dec. 1950 (fr), *Maguire et al.* 30102, 30103 (NY, VEN), summit, SW side of center, 2,660 m, 23 Oct. 1988 (stam. fl), *Liesner* 25276 (MO, VEN), SE slopes, below Salto Los Monos on tributary of headwaters of Río Iguapo, 1,500–1,600 m, 20 Oct. 1988 (fr), *Liesner* 25108 (MO, VEN), slopes, "sima area," 1,200 m, 16 Oct. 1988 (fr), *Liesner* 24941 (MO, VEN); Cerro Duida, summit, 1,700–1,900 m, 1 Sep. 1944 (fr), *Steyermark* 58153 (F, NY, US), (stam. fl), *Steyermark* 59164 (F, NY, US), summit, slopes of Ridge 25, 26 Nov.–16 Dec. 1928 (fr) *Tate* 435, 874 (NY).

Cybianthus agostinianus is unique within the subgenus for the prominently black punctate calyx and corolla. It is named in honor of the late Getulio Agostini, formerly of the Universidad Central de Venezuela, perceptive student of the genus, who suggested I take up a revision of the group.

19. *Cybianthus spathulifolius* Agostini ex Pi-poly, sp. nov. TYPE: Venezuela. Territorio Fed-

eral Amazonas: Cerro Sipapo, S and E rims, 2,000–2,200 m, 26–28 Jan. 1949 (stam. fl), *Maguire & Politi* 28658 (holotype, VEN; isotypes, F, NY, S, US). Figure 17.

Ob inflorescentiam condensatamque tortuosam calycem profunde cupuliformem carnosumque, corollam carnosam et corollae lobos cucullatos atque manifeste punctatos ad *C. sipapoensem* valde affinis, sed ab ea foliis coriaceis (nec chartaceis) petiolis 0.1–0.2 (nec 1.3–1.6) cm longis secus marginem planis (nec revolutis), inflorescentia racemosa (nec spicata) pedicellis 1.0–1.5 (nec 0–0.6) mm longis, florum staminatorum calyce 1.1–1.2 (nec 1.4–1.6) mm longoque corolla 3.5–3.7 (nec 2.4–3.2) mm longa, denique corollae lobis tortuosis (nec rectis) statim recognoscitur.

Shrub or small tree; branchlets terete, 3–4 mm diam., densely lepidote. Leaves narrowly obovate-spathulate, coriaceous, 8–19 cm long, 3–7 mm wide, apex rounded to shortly acuminate, base truncate to subcuneate, decurrent on the petiole, the midrib depressed above, prominently raised below, nerves 30–60 pairs, conspicuous above and below, smooth and densely lepidote above at first, glabrescent, densely lepidote below, inconspicuously pellucid-punctate, the margin entire, epunctate, flat; petioles 0.1–0.2 cm long, densely lepidote. *Staminate inflorescence*: a tortuous axillary raceme, rarely several subsessile racemes from a common peduncle, 2–4 cm long, the peduncle, axis, and pedicels densely to sparingly lepidote; peduncle to 0.1 cm long; floral bracts depressed-ovate, carnosae, 0.6–0.8 mm long, 0.7–1.0 mm wide, apex rounded to acute, densely lepidote abaxially, the margin entire, glabrous; pedicels terete, 1.0–1.5 mm long, erect. Flowers 4(–5)-merous; 3.6–3.8 mm long; calyx deeply cupuliform, carnosae, 1.1–1.2 mm long, the tube 0.3–0.4 mm long, the lobes deltate to subdeltate, 0.7–0.8 mm long, 0.7–0.8 mm wide, apex obtuse, rarely rounded, prominently orange punctate above, brown punctate below, the margin entire, at times lepidote; corolla tubiform, carnosae, 3.5–3.7 mm long, yellowish brown; the tube 1.3–1.5 mm long, the lobes elliptic, erect, tortuous, 2.1–2.5 mm long, 1.1–1.4 mm wide, apex attenuate to a subacute to rounded tip, glabrous without, densely glandular-granulose within, prominently orange and brown punctate, the margin irregular, entire, densely glandular-granulose; stamens 3.8–3.9 mm long, the staminal tube inconspicuous, membranaceous, hyaline, 1.3–1.5 mm long, elobate, the filaments 0.1–0.3 mm long, adnate, 1.7–2.0 mm long, flat, glabrous, epunctate, the anthers narrowly triangular, 1.1–1.2 mm long, 0.3–0.4 mm wide, apex apiculate, the apiculum distally recurved, base cordate,

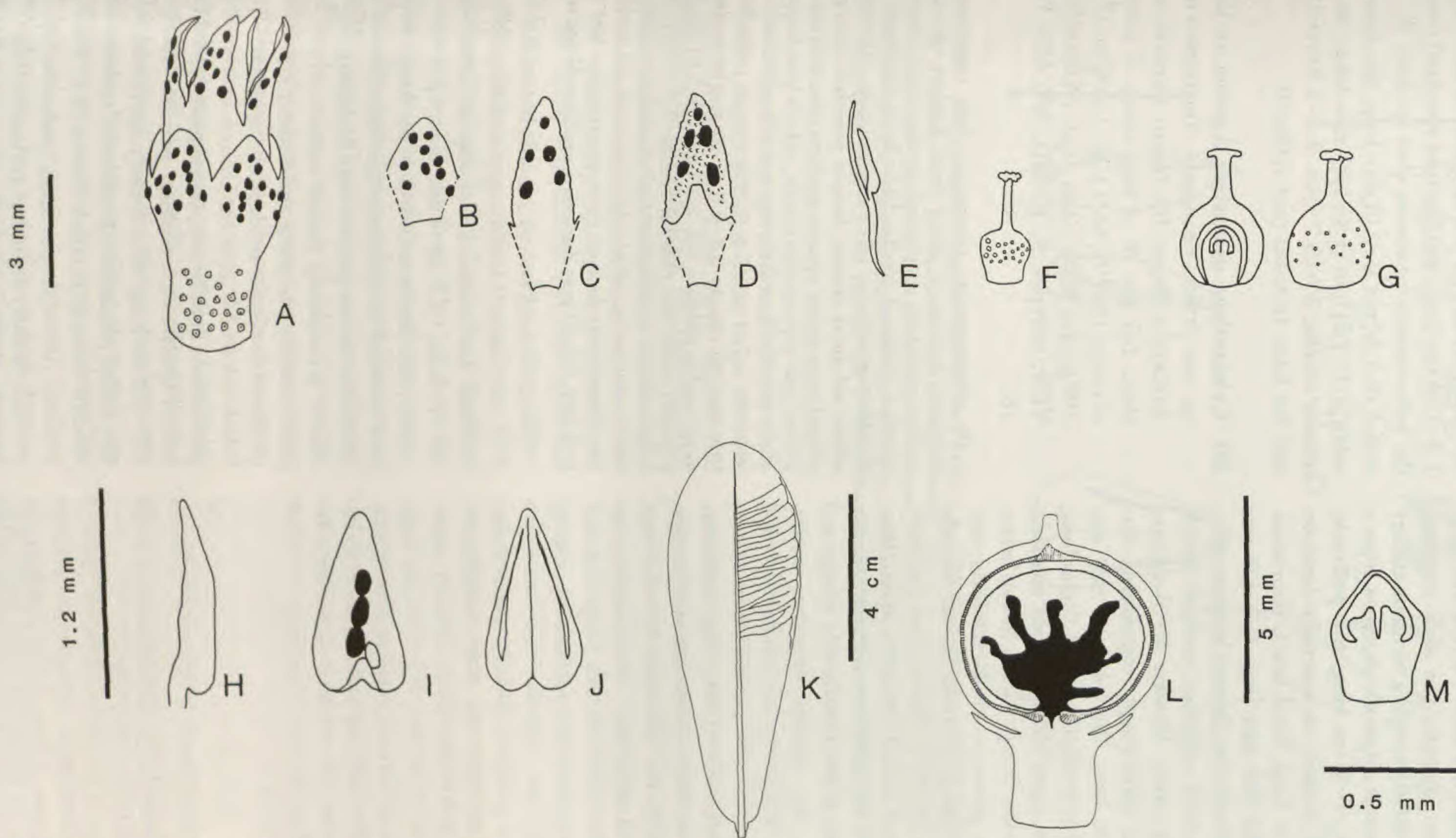


FIGURE 17. *Cybianthus spathulifolius* Agostini ex Pipoly.—A. Staminate flower.—B. Staminate calyx, ventral view, showing punctations.—C. Staminate corolla lobe, dorsal view.—D. Staminate corolla lobe, ventral view, showing punctations and glandular granules.—E. Staminate corolla lobe, lateral view.—F. Pistillode.—G. Pistil, in longisection and entire.—H. Anther, lateral view.—I. Anther, dorsal view, showing pellucid and black punctate connective.—J. Anther, ventral view.—K. Leaf.—L. Fruit longisection, showing lobed endosperm.—M. Placenta showing buried ovules. (A-E and H-K, from holotype; F, L, and M, from *Maguire & Politi 28461*.)

the connective prominently brown punctate dorsally; pistillode obnapiform, 1.4–1.5 mm long, the ovary 0.2–0.4 mm long, 0.3–0.5 mm wide, densely translucent lepidote, the style 1.0–1.2 mm long, prominently brown punctate, the style capitate, elobate. *Pistillate inflorescence*: a tortuous axillary raceme, rarely several subsessile racemes from a common peduncle, 1–3 cm long, the peduncle, axis, and pedicels densely to sparingly lepidote; peduncle to 0.1 cm long; floral bracts depressed-ovate, carnose, 0.6–0.8 mm long, 0.7–1.0 mm wide, apex rounded to acute, densely lepidote abaxially, the margin entire, glabrous; pedicels terete, 1.5–2.5 mm long, erect. Flowers 4(–5)-merous; 2.8–3.6 mm long; calyx deeply cupuliform, carnose, 1.5–1.6 mm long, the tube 0.6–0.8 mm long, the lobes ovate to elliptic, 0.8–1.0 mm long, 0.8–0.9 mm wide, apex obtuse, rarely rounded, prominently punctate, orange above, brown below, the margin entire, glabrous; corolla tubiform, carnose, 2.7–3.5 mm long, yellowish brown; the tube 0.9–1.0 mm long, the lobes elliptic, erect, tortuous, 1.7–2.0 mm long, 0.7–1.0 mm wide, apex attenuate to a rounded tip, glabrous without, densely glandular-granulose within, prominently orange and brown punctate, the margin irregular, entire, densely glandular-granulose; staminodes 0.9–1.0 mm long, the staminal tube inconspicuous, membranaceous, hyaline, 1.0–1.1 mm long, with lobes to less than 0.1 mm long alternating with the apically free filaments, the filaments 0.3–0.4 mm long, flat, glabrous, epunctate, the anthers ovate to ovate-triangular, 0.8–0.9 mm long, 0.3–0.4 mm wide, apex attenuate to a rounded tip, the tip dorsally recurved, base cordate, the connective prominently brown punctate dorsally; pistil obnapiform, 1.6–1.8 mm long, the ovary subglobose, 0.8–0.9 mm long, 0.8 mm diam., densely translucent lepidote, the style thin, 0.6–0.8 mm long, glabrous, prominently brown punctate, the stigma capitate, 2(–3)-lobed, the placenta cylindrical below, the apex obconic, the ovules 2–3, buried within. Fruit subglobose, 0.6–0.7 cm long, 0.7–0.8 cm diam., when dried.

Distribution. Endemic to Cerro Sipapo and the nearby Orinoco area, at 1,600–2,200 m.

Ecology. *Cybianthus spathulifolius* is a scrub forest species, occurring along cliffs.

Paratypes. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Cerro Sipapo, S Basin, 2,000–2,160 m, 26–28 Jan. 1949 (stam. fl), *Maguire & Politi* 28668 (NY); Río Cuao, Río Orinoco, upper E Basin, 1,600–1,850 m, 20 Jan. 1949 (pist. fl, fr), *Maguire & Politi* 28461 (NY).

Cybianthus spathulifolius appears to be closely related to the apparently sympatric *C. sipapoensis*, but may be easily distinguished by the coriaceous (not chartaceous) leaves with petioles 0.1–0.2 (not 1.3–1.6) cm long, and flat (not revolute) margins, the inflorescence racemose (not spicate), the pedicels 1.0–1.5 (not 0–0.6) mm long, the staminate calyx 1.1–1.2 (not 1.4–1.6) mm long, the staminate corolla 3.5–3.7 (not 2.4–3.2) mm long, and the lobes tortuous (not reflexed).

20. *Cybianthus maguirei* Agostini ex Pipoly, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Depto. Río Negro, Cerro de la Neblina, 6.5 km W of base camp, S extension of range, 0°47'N, 66°11'W, 1,600 m, 18 Apr. 1984 (pist. fl, fr), *Stein et al.* 1616 (holotype, VEN; isotypes, F, K, MO, NY, US). Figure 18.

Ob inflorescentiam racemosam folia coriacea secus marginem revoluta et subter dense lepidota calycem cupuliformem tubum staminalem inconspicuum membranaeumque hyalinum corollae lobos secus marginem dense glandulari-granulosos, ad *C. crotonoideum* valde et arcte affinis, sed ab ea laminis desuper pustulatis (non scrobiculatis) atque subter squamis lepidotis adiacentis (nec marginibus ipsis superpositis) indutis, calycis lobis longioribus quam latioribus (nec latioribus quam longioribus), corolla staminata 2.7–3 (nec 2.5–2.7) mm longa, pedicello recto (non nutanti) necnon 0.4–0.6 (1–3) mm longo insidens, atque corolla pistillata 3.0–3.3 (nec 1.9–2.0) mm longa, pedicello recto (nec nutanti) necnon 0.6–1.0 (1–3) mm longo insidens, apicibus corollae staminatae pistillataeque lobis rectis (nec cucullatis) filamentis antheris brevioribus (nec longioribus) denique fructu verruculoso (nec laevi), 6–8 (nec 4.5–5) mm diametro praeclare distinguitur.

Shrub or small tree to 2 m tall; branchlets terete, 2–3 mm diam., densely appressed-lepidote, glabrescent. Leaves obovate or elliptic, coriaceous, 4–9.5 cm long, (2.3–)3–4 cm wide, apex short-acuminate, the acumens 0.4–0.6 cm long, attenuate to a rounded or subacute tip, base obtuse, short-decurrent on the petiole, midrib slightly depressed above, prominently raised below, nerves 24–30 pairs, densely pustulate and densely lepidote, then glabrescent above, moderately appressed-lepidote below, the scales adjacent but not overlapping, the punctations dark brown, inconspicuous, the margin entire, epunctate, revolute; petioles canaliculate, 1.0–1.2 cm long, thin, densely appressed-lepidote, the scales persistent. *Staminate inflorescence*: a straight raceme, rarely a cluster of 2–3 subsessile racemes 1.5–2.0 cm long; peduncle, axis, and pedicels densely lepidote; peduncle 0.2–0.3 mm long; floral bracts deltate or ovate, 0.5–1.0 mm long, 0.8–1.0 mm wide, apex acute, densely lep-

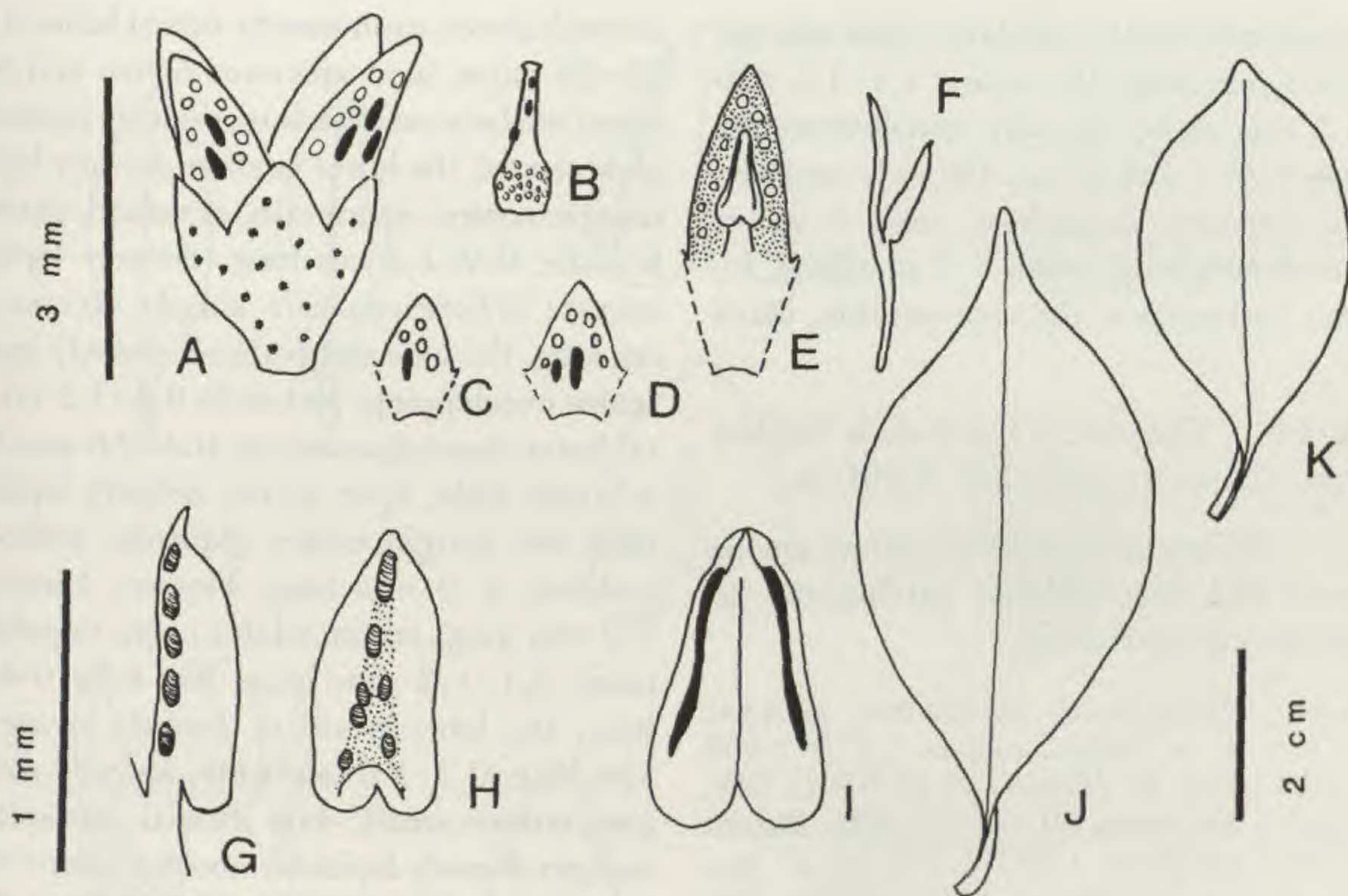


FIGURE 18. *Cybianthus maguirei* Agostini ex Pipoly.—A. Staminate flower, showing pellucid and black punctations.—B. Pistillode.—C, D. Staminate calyx lobes, ventral view.—E. Staminate corolla lobe, ventral view.—F. Staminate corolla lobe, lateral view.—G. Anther, lateral view, showing ventrally curved apiculum and erect habit.—H. Anther, dorsal view, showing darkened and punctate connective.—I. Anther, ventral view, showing apically confluent dehiscence slits.—J, K. Leaves. (A-I, from *Maguire 37042*; J, from *Maguire 37197*; K, from *Silva 60919*.)

idote abaxially, the margin entire, glabrous; pedicels terete, erect, 0.4–0.6 mm long. Flowers 4-merous, 2.8–3.1 mm long; calyx cupuliform, chartaceous, 1.0–1.5 mm long, the tube 0.4–0.5 mm long, the lobes ovate-triangular to deltate, 0.8–0.9 mm long, 0.4–0.7 mm wide, attenuate to an acute tip, prominently punctate and punctate-lineate, the distal punctations red, the proximal punctate-lineations black, the margin entire, densely lepidote; corolla campanulate, chartaceous, 2.7–3.0 mm long, the tube 0.9–1.2 mm long, the lobes erect, ovate, 1.6–1.9 mm long, 0.9–1.2 mm wide, flat, apex attenuate to acute tip, prominently punctate, the submarginal punctations red, the medial ones black, sparsely lepidote without except densely so along the margin, densely glandular-granulose within, densely glandular-granulose near margin without, the margin entire, densely glandular-granulose; stamens 2.1–2.4 mm long, the staminal tube inconspicuous, membranaceous, 0.9–1.2 mm long, hyaline, elobate, the apically free filaments flat, 0.1–0.3 mm long, sparsely brown punctate, the anthers ovate, 0.9–1.0 mm long, 0.4–0.5 mm wide, slightly recurved distally, apex apiculate, the apiculum somewhat recurved proximally, the base cordate, glabrous, the connective dark and prominently separating the thecae; pistillode obturbinate, 1.4–1.5 mm long, the ovary not well differ-

entiated from the style, the base densely translucent glandular-lepidote. *Pistillate inflorescence*: a straight, simple, reduced raceme, 0.4–1.0 cm long; peduncle, rachis, and pedicels densely appressed-lepidote; peduncle 0.5–1.0 mm long; floral bracts triangular, 1.0–1.5 mm long, 0.3–0.5 mm wide, apex attenuate, densely lepidote, the margin entire, regular, glabrous; pedicels terete, 0.6–1.0 mm long; calyx cupuliform, 1.3–1.7 mm long, the tube 0.2–0.4 mm long, the lobes elliptic, 1.0–1.4 mm long, 0.3–0.6 mm wide, apex attenuate, medially thickened, plicate, prominently black punctate and punctate-lineate, moderately stipitate-lepidote except densely so along the margin, the margin entire, regular; corolla campanulate, chartaceous, 3.0–3.3 mm long, the tube 1.2 mm long, the lobes erect, oblong, 2.0–2.2 mm long, 0.7–1.4 mm wide, apex rounded to obtuse, sparsely lepidote medially without except densely so along the margin, glandular-granulose within and near margin without, prominently black punctate and punctate-lineate, the margin densely glandular-granulose; staminodes 2.3–2.6 mm long, the tube inconspicuous, hyaline, membranaceous, 1.0 mm long, the free apical portion of the filaments completely adnate to corolla lobes, 0.5–0.7 mm long, brown punctate, the anthers ovate, 0.9–1.1 mm long, 0.5–0.6 mm wide, apex acute, base deeply cordate, the con-

nective prominently black punctate; pistil obniform, 2.1–2.3 mm long, the ovary 1.1–1.3 mm long, ca. 1.5 mm diam., densely translucent-lepidote, the style 0.9–1.1 mm long, the style capitate, 2-lobed, the placenta subglobose, with 4 naked ovules. Fruit depressed-globose, 4–5 mm long, 6–8 mm diam., verruculose, the exocarp thin, black punctate.

Distribution. Endemic to Cerro de la Neblina and adjacent mountains, at 1,300–2,000 m.

Ecology. *Cybianthus maguirei* grows among *Heliamphora* and Bromeliaceae patches on the summit of Cerro de la Neblina.

Paratypes. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Cerro de la Neblina, summit, 1,700–2,000 m, 4 Jan. 1954 (stam. fl), *Maguire et al.* 37042 (NY, VEN), 10 Jan. 1954 (stam. fl), 37197 (NY). BRAZIL. AMAZONAS: Serra Pirapuçu, 1,300–1,700 m, 27 Jan. 1966 (stam. fl), *Silva & Brazão* 60919 (INPA, NY, VEN).

Cybianthus maguirei is most closely related to *C. crotonoides*, a species endemic to the eastern state of Bolívar. *Cybianthus maguirei* is easily distinguished, however, by its leaves pustulate above, densely lepidote below, calyx lobes longer than broad, pedicels less than 1 mm long, flowers erect, longer corolla, apically free portion of the filaments shorter than the anthers, and finally, the larger fruit with verruculose exocarp.

It is a pleasure to dedicate this species to the late Bassett Maguire, former Curator Emeritus of the New York Botanical Garden, specialist in neotropical Clusiaceae and authority on Guayana floristics.

21. *Cybianthus crotonoides* (R. M. Schomb. ex Mez) Agostini, *Acta Biol. Venez.* 10: 153. 1980. *Conomorpha crotonoides* R. M. Schomb. ex Mez in Engler, *Pflanzenr.* IV, 236: 262. 1902. TYPE: Venezuela. Bolívar [Guyana]: Roraima, 1842–1843 (stam. fl), *Schomburgk* 681 (1027) (lectotype, here designated, G-DEL; isolectotypes, K, P, W). [It should be noted that Steyermark (1981) determined that all of Richard Schomburgk's "Guyana-Roraima" collections were actually made within the borders of Venezuela.] Figure 19.

Shrub to 4 m tall; branchlets terete, thin, 2–3 mm diam., densely lepidote. Leaves elliptic to obovate-elliptic, coriaceous, 3.1–6 cm long, 1.0–2.5 cm wide, apically acute or short-acuminate, base acute, decurrent on the petiole, midrib slightly de-

pressed above, prominently raised below, the nerves 22–26 pairs, inconspicuous above and below, the upper surface scrobiculate, densely lepidote at first, glabrescent, the lower surface densely lepidote, the margin entire, epunctate, revolute; petioles canaliculate, 0.9–1.3 cm long, densely lepidote. *Staminate inflorescence*: a simple raceme, 2.0–3.5 cm long, the axis and pedicels densely lepidote, the scales overlapping; peduncle 0.6–1.2 cm long; floral bracts linear-lanceolate, 0.3–0.6 mm long, 1.5–3.5 mm wide, apex acute, densely lepidote adaxially, the margin entire, glabrous; pedicels terete, nodding, 1–3 mm long. Flowers 4-merous, 2.6–2.9 mm long, cream-white; calyx cupuliform, carnosose, 1.1–1.2 mm long, the tube 0.4–0.5 mm long, the lobes ovate or broadly ovate, 0.5–0.8 mm long, 0.7–1.0 mm wide, apically rounded, the punctations small, dark brown, conspicuous, the margin densely lepidote; corolla campanulate, carnosose, 2.5–2.7 mm long, the tube 1.0–1.1 mm long, the lobes ovate to elliptic, 1.5–1.6 mm long, 1.1–1.2 mm wide, the apex attenuate to a rounded, cucullate tip, densely to sparingly lepidote medially without, glandular-granulose within, the margin irregular, finely crenulate, densely glandular-granulose; stamens 1.9–2.1 mm long, the staminal tube inconspicuous, hyaline, membranaceous, ca. 0.1 mm long, elobate, the apically free filaments 1.2–1.3 mm long, adnate to the corolla lobes, flat, epunctate, glabrous; the anthers ovate, 0.8–0.9 mm long, 0.6–0.7 mm wide, apex apiculate, the apiculum distally recurved, base cordate, the longitudinal slits thin, dorsifixed just above the base, the connective prominently brown punctate ventrally; pistillode pyriform, 1.3–1.4 mm long, the ovary ca. 0.3–0.4 mm long and in diam., densely translucent lepidote, the style ca. 0.9–1.0 mm long, prominently brown punctate, glabrous. *Pistillate inflorescence*: a simple raceme, 2.0–3.5 cm long, the axis and pedicels densely lepidote, the scales overlapping; peduncle 0.6–1.2 cm long; floral bracts ovate, 0.3–0.6 mm long, 1.3–2.7 mm wide, apex acute, densely lepidote adaxially, the margin entire, glabrous; pedicels terete, erect, 1–3 mm long. Flowers 4-merous, 2.0–2.1 mm long, cream-white; calyx cupuliform, carnosose, 1.1–1.2 mm long, the tube 0.4–0.5 mm long, the lobes ovate-triangular, 0.5–0.8 mm long, 0.7–1.0 mm wide, apically rounded, inconspicuously pellucid-punctate, the margin densely lepidote; corolla campanulate, carnosose, 1.9–2.0 mm long, the tube 1.0–1.1 mm long, the lobes ovate to elliptic, 0.7–0.8 mm long, 0.2–0.4 mm wide, the apex attenuate to a round, cucullate tip, densely to sparingly lepidote medially without, glandular-granulose within,

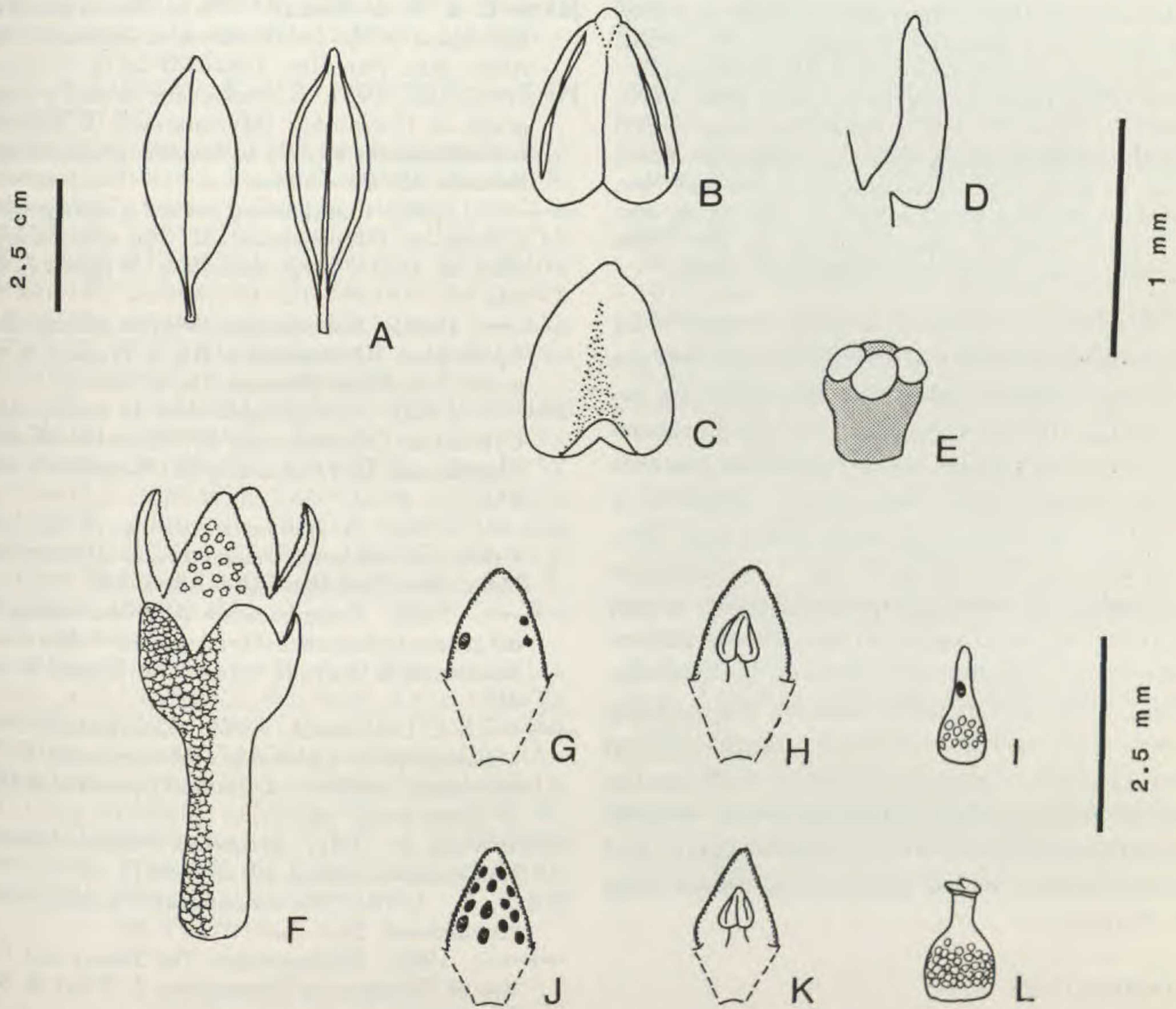


FIGURE 19. *Cybianthus crotonoides* (R. M. Schomb. ex Mez) Agostini.—A. Leaf, adaxial and abaxial views.—B. Anther, ventral view showing apiculum.—C. Anther, dorsal view showing darkened connective.—D. Anther, lateral view.—E. Placenta, showing naked ovules.—F. Staminate flower.—G. Staminate corolla lobe, dorsal view showing punctations.—H. Staminate corolla lobe.—I. Pistillode.—J. Pistillate corolla lobe, dorsal view showing punctations.—K. Pistillate corolla lobe, ventral view.—L. Pistil. (A–D and F–I, from *Cardona 2721*; E and J–L, from *Steyermark 59902*.)

the margin irregular, finely crenulate, densely glandular-granulose; staminodes 1.3–1.5 mm long, the staminodial tube inconspicuous, hyaline, membranaceous, ca. 0.1 mm long, elobate, the filaments 0.7–0.8 mm long, adnate to the corolla lobes, apically free for 0.1–0.2 mm, flat, epunctate, glabrous; the anthers ovate, 0.6–0.7 mm long, 0.5–0.6 mm wide, apex apiculate, the apiculum distally recurved, base cordate, dorsifixed just above the base, the longitudinal slits thin, the connective prominently brown punctate ventrally; pistil obnapiform, 1.6–1.8 mm long, the ovary 0.9–1.1 mm long and in diam., densely translucent glandular-punctate, the style short, 0.5–0.6 mm long, 4.5–5.0 mm diam., glabrous, epunctate, the stigma capitate and lobulate, the lobules ca. 2–3, the placenta subglobose, bearing 3–4 naked ovules. Fruit 3.5–4.5 mm long, 4.5–5.0 mm diam., purple-black at maturity, exocarp smooth.

Distribution. Endemic to Venezuela, state of Bolívar, 1,800–2,500 m.

Ecology. *Cybianthus crotonoides* grows in *Bonnetia roraimae* formations on the summits of various tepuis in the Auyán-tepui-Chimantá Floristic Complex (Maguire, 1979). It is notable that it occurs in the fissures of tall columns of rocks.

Specimens examined. VENEZUELA. BOLIVAR: Aparamán-tepui, 2,150 m, 22 Mar. 1987 (fr), *Holst 3487* (MO, US, VEN), (pist. fl, fr), *Holst 3497* (MO, US, VEN); Auyán-tepui, 2,100 m, Jan. 1949 (stam. fl), *Cardona 2721* (NY, VEN), 1,850 m, without date (stam. fl), *Pannier & Schwabe s.n.* (VEN), *Tate 1171* (NY, VEN), upper slopes of Auyán-tepui, 2,300 m, Apr. 1956 (stam. fl), *Vareschi & Foldats 4844* (VEN), summit of S portion, 2,050–2,300 m, 15 May 1964 (stam. fl), *Steyermark 93936* (F, NY, US, VEN); Camarcaibarai-tepui, summit, 2,400 m, 26 Mar. 1987 (pist. fl), *Holst 3624* (MO, US, VEN), SW-facing shoulder, 1,800–1,825 m, 22–24 May 1986 (stam. fl), *Steyermark et al. 132022* (MO, US,

VEN); summit of Carrao-tepui, 2,470–2,500 m, 7 Dec. 1944 (pist. fl, fr), *Steyermark 60890* (F, NY, VEN); Murisipán-tepui, E of Auyán-tepui, 2,400–2,500 m, 25–26 Mar. 1987 (stam. fl), *Delascio 13063* (MO, VEN), second of 4 tepuis W to E in Apamarán range, 2,300 m, 26 Mar. 1987 (stam. fl), *Holst 3533* (MO, US, VEN); Ptari-tepui, along base of S-facing bluffs, 2,410 m, 6 Nov. 1944 (stam. fl), *Steyermark 59902* (F, NY, VEN); summit, Tereké-Yurén, W edge, 2,135 m, 26 May 1986 (pist. bud), *Liesner et al. 21118* (MO, US, VEN).

Cybianthus crotonoides is easily recognized by its coriaceous, revolute, acuminate leaves, that are so densely punctate below that the scales are superposed by their margins. It is most closely related to *C. maguirei* because of the subglobose placenta bearing naked ovules. However, *C. maguirei* is defined by its wide longitudinal dehiscence slits, which are apically confluent, and *C. crotonoides* is defined by its dense indument of lepidote scales, which overlap each other on the abaxial surface of the leaves, corolla, and calyx, on the pedicels, rachis, stem, and petioles, and by the nodding flowers, *Cybianthus crotonoides* shares several other characters with *C. maguirei* such as the inconspicuous, hyaline, membranaceous staminal and staminodial tube, the cupuliform calyx, and the corolla lobes densely glandular-granulose along the margin.

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Numbers listed in parentheses refer to species number as cited in text.

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EVOLUTIONARY BIOLOGY OF *James Aronson*²
ACACIA CAVEN
(LEGUMINOSAE,
MIMOSOIDEAE):
INFRASPECIFIC VARIATION
IN FRUIT AND SEED
CHARACTERS¹

ABSTRACT

Six varieties are recognized in *Acacia caven* (Leguminosae, Mimosoideae; *Acacia* subg. *Acacia*, subsection *Polyseriae*), based on herbarium studies of vegetative characters, population-level studies of fruit and seed characters, and a map of the species' distribution and morphological variation patterns in southern South America. Two new varieties are described. Ecological and evolutionary aspects of carpological variations are discussed, and a framework is established for further studies in this and related species.

Within the huge pantropical genus *Acacia* Miller, subgenus *Acacia* sensu Vassal (= series *Gummiferae* Bentham, excluding *Faidherbia albida* (Del.) A. Chev.) appears to be a natural phyletic unit (Bentham, 1842; Pedley, 1986; Vassal, 1972). Its members occur primarily in the thornscrub and savannas of the Neotropics (ca. 50 species) and Africa (ca. 115 species) (Guinet & Vassal, 1978; Ross, 1979; Vassal, 1981; Rico Arce, 1984), but there are also 5–10 endemic species in western and northern Australia. The South American members of this subgenus (ca. 15 species) are among the least well known, despite the recent revision of the genus *Acacia* in Argentina by Cialdella (1984).

Although most abundant and variable in the warm temperate to subtropical biogeographical region known as the Chaco (Hueck & Seibert, 1972; Cabrera & Willink, 1973), one member of subgenus *Acacia*, *A. caven* (Molina) Molina, appears to have spread relatively recently into other biogeographical regions in northern Argentina, east-

ern Bolivia, western Paraguay, southern Brazil, Uruguay, and central Chile. This paper attempts to clarify infraspecific taxonomy of the species and set the stage for ecological, biogeographical, and other studies of *A. caven* and related species.

HISTORICAL SYSTEMATIC TREATMENT

Acacia caven was originally described (as *M. caven*) from central Chile by Molina (1782), who considered it very similar to *A. farnesiana* (L.) Willd., a species described over 29 years previously and widely cultivated in Italy and France during the eighteenth and nineteenth centuries. Unfortunately, leaflet size (and "a shorter pod") was the basis on which Bentham (1875: 502) separated the two taxa, thereby paving the way for subsequent authors, e.g., Kuntze (1898), Arechavaleta (1901), Hassler (1909), Spegazzini (1923), and Clos (1930), to lump the two together. By contrast, Hooker & Arnott (1830), Wight & Arnott (1834),

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Arata (1891), Burkart (1952, 1967, unpublished), Tortorelli (1956), Vassal (1972), Lombardo (1982), Cialdella (1984), Rodriguez et al. (1984), and Bernardi (1984) maintained separation of the two taxa on the basis of length to width ratio and anatomy of the pods, pericarp striations, length and pubescence of petioles, size of leaflets, and other morphological characters. Only Spegazzini (1923) and Cialdella (1984) treated *A. caven* in detail.

POSITION WITHIN SUBGENUS *ACACIA*

The small subsection *Polyseriae* (Vassal, 1972) is considered evolutionarily advanced compared to the far larger subsection *Uniseriae*, which contains all other members of the subgenus. *Acacia caven* and *A. farnesiana* are the only South American members of this subsection (*A. erioloba* E. Mey and *A. sphaerocephala* Cham. et Schldl. are the sole African and Mesoamerican representatives). Species of subsection *Polyseriae* have two, rarely three, rows of seeds per pod, as compared to only one row per pod in subsection *Uniseriae* (Vassal, 1972). This character led Wight & Arnott (1834) to propose the segregate genus *Vachellia*, a proposition accepted by Spegazzini (1923) but rejected by most subsequent workers. Many modern workers consider the subsection unnatural (D. Seigler & J. Ebinger, pers. comm.). Yet, it should be noted that indehiscent (or tardily dehiscent) pods are a diagnostic trait cited by Vassal (1972) for subsection *Polyseriae*, and that the group corresponds in part to the subseries *Summibracteatae* defined by Bentham (1875: 499) on the basis of floral as well as carpological characters.

INFRASPECIFIC TREATMENT

Cialdella (1984) recognized four varieties within *Acacia caven*. Three of these were characterized by pod size and shape (vars. *caven*, *microcarpa*, and *stenocarpa*) and corresponded to "forms" recognized by Spegazzini (1923) under *Vachellia farnesiana*. The fourth, *A. caven* variety *dehiscens* Burkart ex Cialdella, recognized the unusual populations with dehiscent pods in the hills between Córdoba and San Luis, Argentina. Three more of Spegazzini's (1923) "forms," characterized by short peduncles, small anthers, and large leaflets, respectively, were rejected by Burkart (unpublished) and Cialdella (1984). Furthermore, Burkart labeled several specimens var. *macrocarpa* or var. *sphaerocarpa*, but never prepared formal descriptions for them. Typical fruit types of the six putative varieties are shown in Figure 1.

HABITAT AND DISTRIBUTION

Acacia caven is one of the most widespread arboreal species of extra-tropical South America, occurring ca. 37°–18°S in six countries, where it is variously known as "espino," "espinillo," "aromita," and "churqui" (Fig. 2). It is a natural component of the deciduous thorn forest in all but the driest areas of the Chaco. This region covers more than 1,000,000 km² between 15° and 35°S in north-central Argentina, adjacent parts of Bolivia, a tiny portion of Mato Grosso, Brazil, and nearly half of Paraguay (Ragonese & Castiglioni, 1970; Cabrera & Willink, 1973; Ramella & Spichiger, 1989). Outside of the Chaco, it is considered invasive.

Like some other widespread acacias, e.g., *A. nilotica* (L.) Willd., *A. farnesiana*, *A. macracantha* Humbl. & Bonpl. ex Willd., and *A. karroo* Hayne, *A. caven* shows remarkable climatic tolerance and ecological adaptability, as well as a propensity to invade disturbed habitats. In central Chile, encroachment by *A. caven* affects over 2,000,000 ha, including natural ecosystems in the semiarid and subhumid portions of the mediterranean climate zone (Parsons, 1976; Fuentes et al., 1989; Ovalle et al., 1990). It occurs from sea level to nearly 3,200 m at its northern limits in central Bolivia. In Argentina and Chile it rarely occurs above 1,200 m, and in Bolivia it is sparse above 1,900 m. Freezing temperatures would appear to be a limiting factor. For unknown reasons, *A. caven* does not occur in close proximity to the sea. It occurs not only in diverse continental-climate areas but also in the mediterranean-climate region in Chile, both in seasonally inundated plains and on very dry slopes or inselbergs. Preferring open cow pastures or abandoned fields, it also enters clearings in various types of natural vegetation wherever livestock roam. Although usually seen as a much-coppiced shrub 1–3 m tall, *A. caven* can attain 8–10 m in height, with DBH of 80 cm, when left uncut in deep soils (Ovalle, 1986; pers. obs.).

REPRODUCTIVE BIOLOGY

Similar to several Australian and African acacias, *A. caven* possesses both hermaphroditic and masculine flowers, and thus should be considered an andromonoecious species (Spegazzini, 1923; Burkart, 1967; León et al., in prep.). These flowers occur in varying proportions, both within and among populations, possibly in response to changes in water availability (León et al., in prep.). *Acacia caven* seems to be largely allogamous, as more than 50 individuals tested have proven to be highly self-

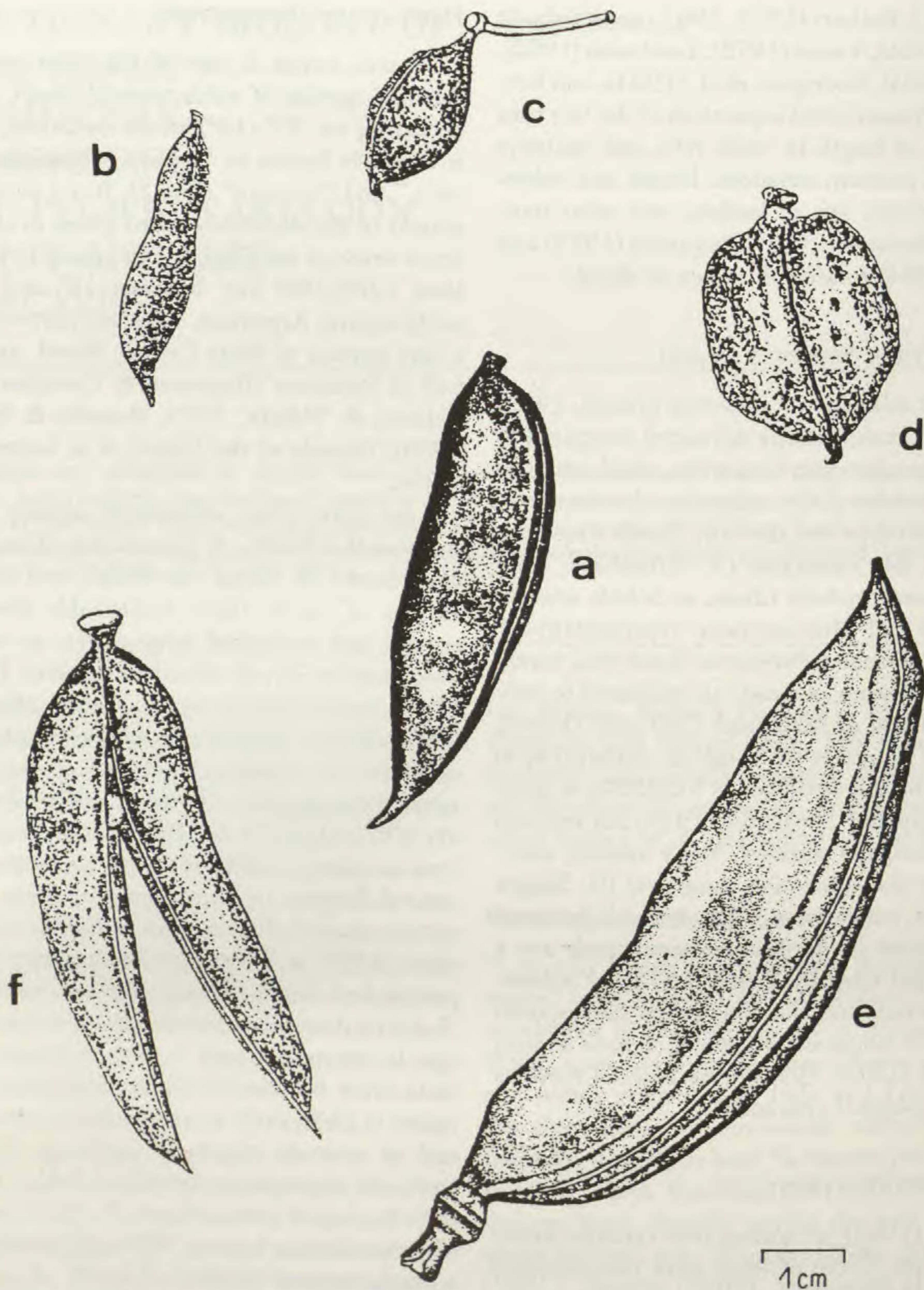


FIGURE 1. Typical fruits of the six varieties of *Acacia caven*.—a. Variety *caven* Burkart 29343.—b. Variety *stenocarpa* Krapovickas 983.—c. Variety *microcarpa* Rojas 7697.—d. Variety *sphaerocarpa* Tressans & Radovancich 3539.—e. Variety *macrocarpa* Burkart 17577.—f. Variety *dehiscens* Burkart 15730. All drawings life size.

incompatible, both in an Argentinian population near Córdoba (A. Anton, pers. comm.) and a Chilean population near Santiago (Peralta et al., in press). Pollination appears to be achieved—at least in central Chile—by small, crawling beetles, especially *Actylus trifaciatus* (Peralta et al., in press) rather than or in addition to, honey bees: the latter pollinator group is the most common for the genus (Arroyo, 1981).

SEED DISPERSAL

Most *Acacia caven* pods float in water, and some seeds are presumably dispersed in this fashion. For this reason, it has been suggested that its primary habitat within the Chaco was near seasonally active waterways, where it is often seen today (C. Saravia Toledo, pers. comm.). At the same time, most varieties of *A. caven* seem adapted for long-dis-

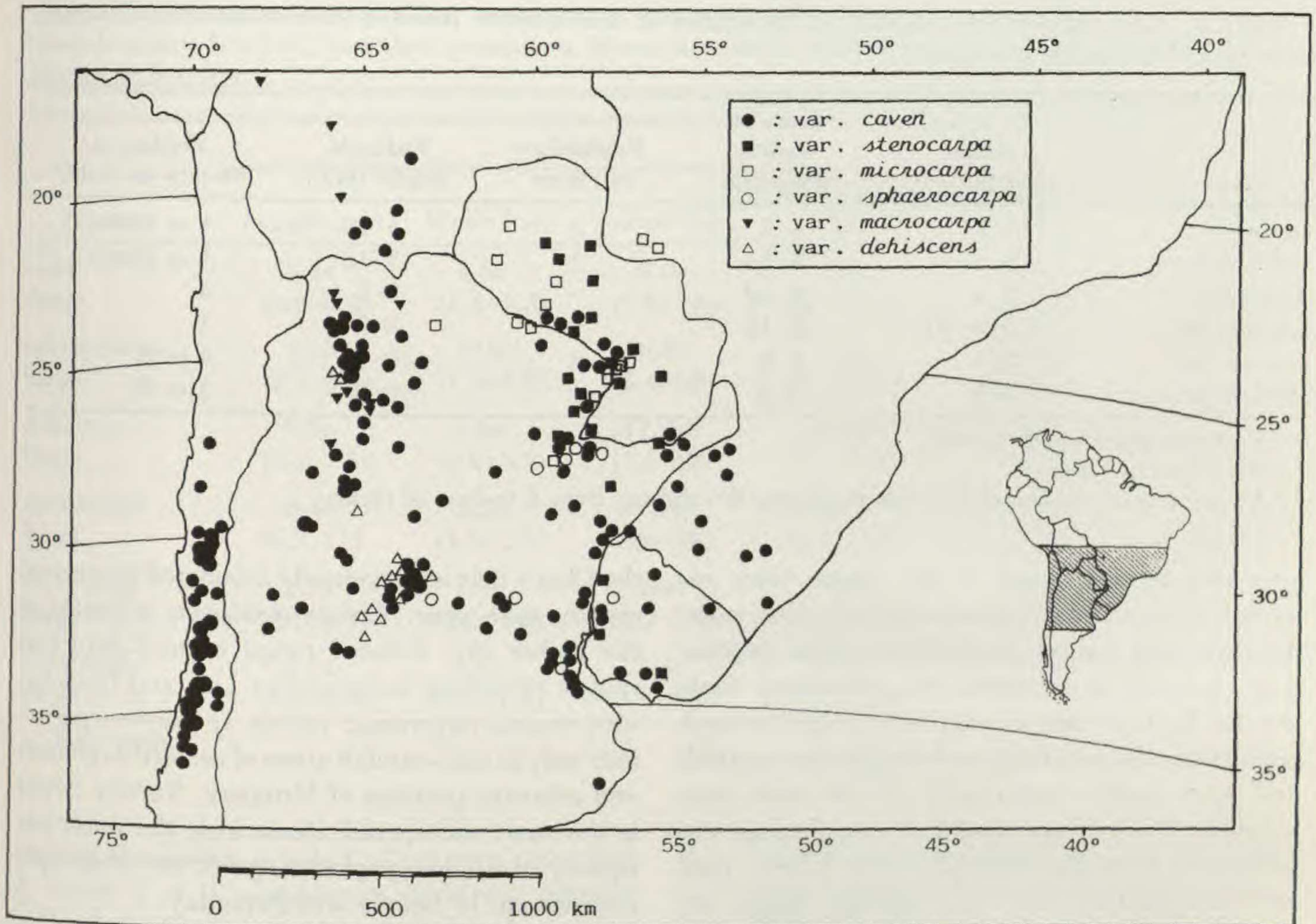


FIGURE 2. Continental distribution of *Acacia caven* in southern South America. Each point represents a single field collection.

tance dispersal by mega-vertebrates. In prehistoric times, there were numerous large animals such as camelids, stegomastodons, notoungulates, edentates, and giant sloths in the Chaco (Bucher, 1987). At present, domestic livestock are undoubtedly the most important agents of dispersal (Gutierrez & Armesto, 1981). Medium-sized birds such as "charata" (*Ortalis canicollis*), and "corzuela" (*Mazama americana*, *M. rufa*), as well as tapir (*Tapirus terrestris*), guanaco (*Lama guanicoe*), and sury (*Rhea americana*) are all probable dispersers of seed (C. Saravia Toledo, pers. comm.).

CYTOLOGY AND PALYNOLOGY

Chromosome numbers for *Acacia caven* have been recorded as $2n = 26$ (Castronovo, 1945) and $2n = 26, 52$ (Atchison, 1948). Similarly variable numbers occur in the closely related *A. farnesiana*, which is said to have $2n = 52, 104$ (Atchison, 1948). Pollen is shed in relatively large polyads consisting of ca. 32 grains (Caccavari, 1970; Heusser, 1971; Peralta et al., in press). Exceptions are Rojas 7694 (SI) (var. *microcarpa*) with 16 grains and Aronson 7977 (MO, SGO) (var. *macrocarpa*)

with 48 grains (Guinet & Aronson, unpublished data).

MATERIALS AND METHODS

FRUITS AND SEEDS

Collections of seeds and pods were made at 49 sites covering the current range of distribution of *Acacia caven*. In addition, more than 750 herbarium fruit-bearing specimens of *A. caven* were compared for carpological and vegetative traits. Several fruit (pod) and seed characters appeared relatively constant within populations, and the three largest fruit samples from populations of each of the six putative varieties were selected for analysis. A total sample of 80 pods from each of five or more individuals was sufficient to represent each population, since the addition of further pods failed to alter the generalized variance (Tatsuoka, 1971; Farrell & Ashton, 1978). Only ripe pods free of bruchid damage were used. Voucher specimens for each population are deposited at herbaria in Chile (CONC, SGO), at Kew (K), and in Missouri (MO).

Length and width of 80 fully ripe pods per population were measured, and pod volume was