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Molecular Phylogenetic Analyses Reveal Undiscovered Monospecific Genera in the tribe Episcieae (Gesneriaceae)

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Abstract—Recent molecular phylogenetic analyses have revealed that many genera in tribe Episcieae of Gesneriaceae are polyphyletic. The strong support from molecular data necessitates name changes for these taxa. In this paper we make the formal transfer of these species. As a result, four monospecific new genera are described to accommodate monophyletic lineages. The option to create monospecific genera is made as opposed to including these species in single, large, morphologically heterogeneous genera. The new genera are ***Christopheria, Lesia, Pachycaulos***, and ***Pagothyra***, and include the species ***Christopheria xantha, Lesia savannarum, Pachycaulos nummularium,*** and ***Pagothyra maculata.***

Keywords—*Christopheria*, *Lesia*, *Pachycaulos, Pagothyra.*

The discipline of molecular systematics has provided botanists with a powerful tool to better understand evolutionary relationships. As a result, it has been a useful means for identifying taxonomic boundaries such that named taxa can now be circumscribed to encompass mutually exclusive evolutionary lineages (monophyly). These lineages may be discovered through phylogenetic analyses of molecular data, but defined by unique morphological synapomorphies. Such analyses have been used to re-define taxa throughout the plant and other kingdoms (Glenn et al. 1996; Pröschold et al. 2001; Beck et al. 2010; Buerki et al. 2010; Fishbein et al. 2010; Ohi-Toma et al. 2010; Su et al. 2010; Queiroz and Lavin 2011) including other members of Lamiales (Albach et al. 2005; O'Leary et al. 2009) and Gesneriaceae (Clark and Zimmer 2003; Clark 2005; Roalson et al. 2005; Boggan et al. 2008; Clark et al. 2011; Wang et al. 2011).

Generic boundaries in the Gesneriaceae have been particularly challenging due to convergence of morphological characters that have traditionally been used to define generic limits (Wiehler 1983; Clark et al. 2012). Phylogenetic analyses derived from molecular data that are independent of the difficulties of morphological convergence have been especially useful to resolve monophyletic groups that can then be examined for morphological characters that unite the species in each particular clade (Clark and Zimmer 2003; Clark 2005; Roalson et al. 2005).

When re-defining generic boundaries, it is imperative that the type species for each genus be included such that names are applied to the correct clades. In a previous molecular phylogenetic analysis of tribe Episcieae of Gesneriaceae, Clark et al. (2012) identified eight para- or polyphyletic genera. While some of these difficulties could easily be accommodated by transferring species to existing genera, there were four species that could not be so easily moved without creating large, morphologically heterogeneous, and geographically disjunct taxa. These species were *Nematanthus savannarum* (C. V. Morton) J. L. Clark, *Episcia xantha* Leeuwenb., *Neomortonia nummularia* (Hanst.) Wiehler, and *Paradrymonia maculata* (Hook. f.) Wiehler. Therefore, we describe herein four new genera to accommodate these species and make the official transfers.

Materials and Methods

Species names, vouchers, and GenBank numbers for all species used in the phylogenetic analyses are enumerated in Clark et al. (2012), as are the methods used to generate the sequences and the phylogenetic analyses. An abbreviated summary is presented here.

The following cpDNA regions were sampled: *trnL-trnF* spacer, *trnL* intron, the *rps16* intron, and the *rpl20-rps12* spacer. The following nrDNA regions were sampled: ITS (ITS1, 5.8S, and ITS2; hereafter referred to as ITS), the low-copy nuclear loci *GCYC*, and two different loci of the nuclear encoded, chloroplast expressed, glutamine synthetase (*ncpGS*1 and *ncpGS*2).

Phylogenetic trees were estimated using maximum parsimony (MP), maximum likelihood (ML), and Bayesian inference (BI). Maximum parsimony analyses were performed using PRAP2 (Müller 2004) in conjunction with PAUP*4.0b10 (Swofford 2002). Bootstrap support (BS) for nodes (Felsenstein 1985) was estimated with 1,000 heuristic replicates using PRAP2.

Maximum likelihood analyses were performed using optimal substitution models suggested by Modeltest 3.6 (Posada and Crandall 1998). The Akaike information criterion (AIC), which allows non-nested models to be evaluated, was used as a selection criterion (Posada and Buckley 2004). The GTR + Γ model was chosen. Analyses of ML were completed using GARLI v0.96 (Zwickl 2006) with 100 bootstrap replicates.

Bayesian inference analyses were completed using MrBayes 3.1.1 (Huelsenbeck and Ronquist 2003) using either a single model across the entire dataset with the models used for ML, or partitioned models using a different model for each of the partitions (each low copy locus, ITS, and cpDNA considered as partitions, see Clark et al. 2012 for specific models for each region).

Results and Discussion

The MP analysis with indels treated as missing data resulted in 48 trees of length 6,411 (consistency index [CI] = 0.59, retention index [RI] = 0.62, rescaled consistency index [RC] = 0.36). The ML analysis resulted in a tree (ln likelihood = −42,751.72118; Fig. 1) of nearly identical topology to the MP strict consensus, with the only differences being the positions of three clades. In the MP analysis the clades containing *Nematanthus* and *Codonanthe, Cobananthus/Alsobia*, and *Episcia* were sequentially sister to the remainder of the Episcieae (Clark et al. 2012). The two BI runs (both with a unique model for each data partition and a single model across all data) produced a majority rule consensus tree in full agreement with the ML analysis and posterior probability values differed between the two runs only by a single point for nodes with posterior probability < 100.

The phylogenetic analyses place *Christopheria xantha* (= *Episcia xantha*), *Pachycaulos nummularium* (= *Neomortonia nummularia*), *Lesia savannarum* (= *Nematanthus savannarum*), and *Pagothrya maculata* (= *Paradrymonia maculata*) outside of the boundaries of the remainder of their genera, which includes the type for

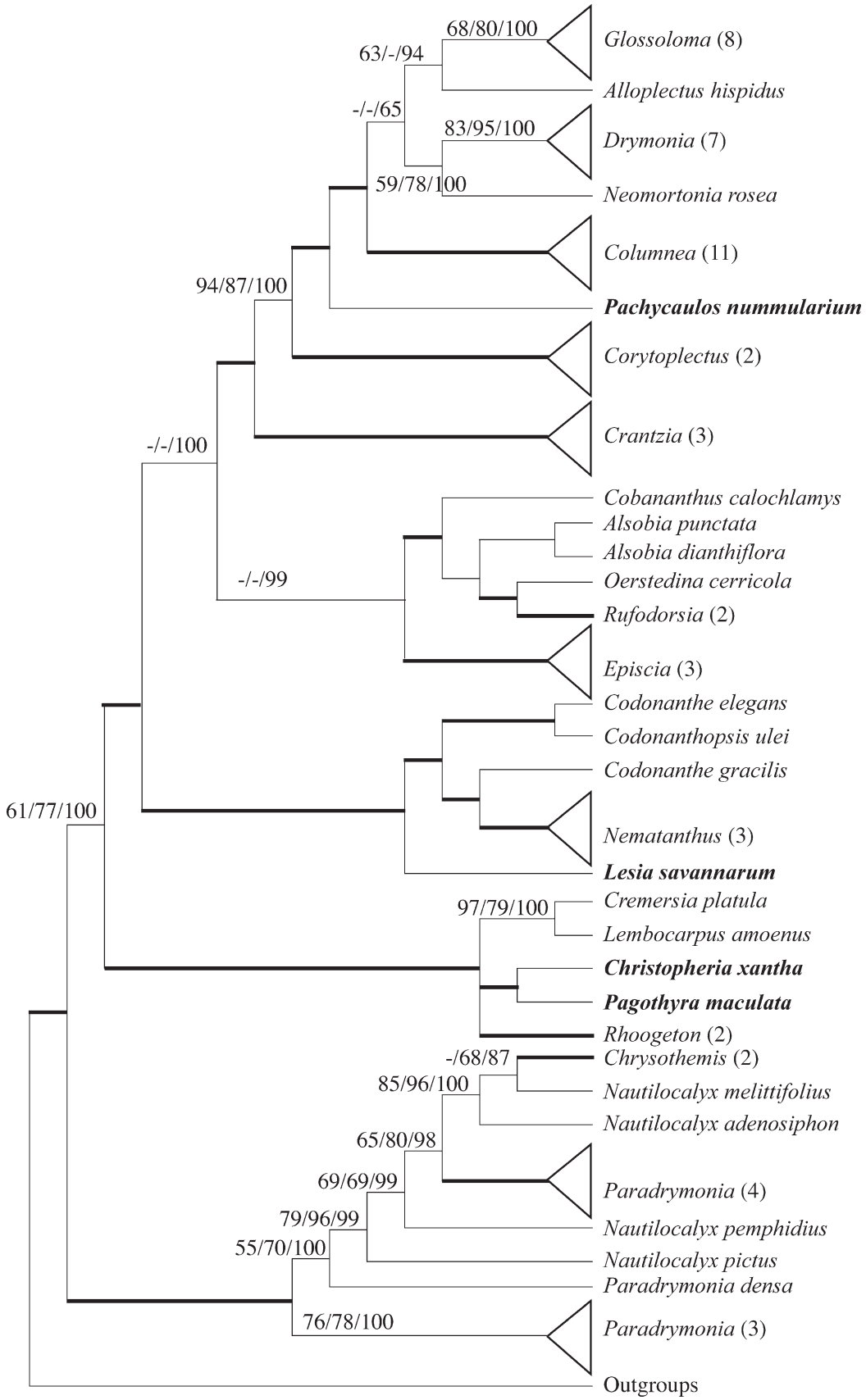

FIG. 1. Majority-rule tree from the Bayesian inference analysis for Episcieae based on cpDNA, ITS, *GCYC*, *ncpGS*1, and *ncpGS*2 using a unique model for each partition (a single model neither altered the topology nor the support). Monophyletic clades of species in the same genus are collapsed and those with three or more species are represented by triangles. The topology from the maximum likelihood analysis (ln likelihood = −42,751.72118) resulted in the same topology shown here. Numbers above branches are maximum parsimony bootstrap/maximum likelihood bootstrap/Bayesian posterior probabilities. Thick bars indicate nodes where support for all three analyses was > 0.95.

each species (note that the type for *Nematanthus, N. corticola* was not sampled here). Neither *Christopheria xantha* nor *Pagothrya maculata* would be best combined into a single genus because the two species are distinct from each other: *P. maculata* is an herbaceous vine without stolons, with a large, bracteate, racemose inflorescence (Fig. 2) and corollas that have a lower lip covering the opening of the throat (Feuillet 2009), whereas *C. xantha* is a terrestrial herb with stolons and an axillary, cymose inflorescence with flowers few to many and a throat never occluded by the lower petal (Fig. 3). Therefore we opt to describe new genera to include these species.

Lesia savannarum was originally described as a member of *Alloplectus* (Morton 1948) and assigned to section *Alloplectus* Hanst. Its geographical distribution was initially known from a few collections from the Guianas, even though section *Alloplectus* was primarily recognized for species in the Andes. Thus, the phylogenetic placement and disjunct distribution of this taxon is not surprising given that it is more closely related to *Nematanthus*, which has its center of diversity in the southeastern Atlantic forests of Brazil.

Pachycaulos nummularium (= *Neomortonia nummularia*) cannot readily be merged into other genera without combining several of the larger genera of the Neotropical Gesneriaceae. This solution would neither be practical nor reflect the evolutionary diversity in this group. The traditionally recognized species of *Neomortonia* (*Pachycaulos nummularium* and *Neomortonia rosea* Wiehler) have never been recovered as monophyletic in any study based on molecular data alone (Clark et al. 2012). It should be noted that the two species were united with morphological data (Clark et al. 2006), but the coding of laterally compressed fruits is erroneous. Further investigation of the orange berries shows that the fruits of *Pachycaulos nummularium* are globose and not laterally compressed (Clark et al. 2012). The results presented here, and in Clark et al. (2012), provide strong support for the separation of the two species in different genera.

Taxonomic Treatment

Christopheria J. F. Smith & J. L. Clark, gen. nov.—TYPE: *Episcia xantha* Leeuwenb.

Creeping, stoloniferous herb with pale yellow corolla.

Terrestrial stoloniferous herb with two stolons per node. Stems decumbent, terete, 5–7 mm diam, internodes ca. 1–2.5 cm long, pilose, nodes with adventitious roots. Leaves opposite, equal to subequal; petiole hirsute, 1–8 cm long; blade bullate, elliptic-ovate, 5–20 × 3–15 cm, papery when dry, apex obtuse to acute, base rounded to subcordate, margin crenate-serrate, adaxial surface green, pilose with impressed veins, adaxial surface tinged with purple to entirely purple, sparsely pilose to glabrous with prominent veins, lateral veins 4–8 per side. Inflorescences axillary, pedunculate, flowers few to many in cymes; peduncle purplish, sparsely pilose to glabrous, 1.5–5 cm long; bracts resembling sepals but smaller in size, 4–8 × 1.2–2 mm; pedicels 3–12 mm long, sparsely pilose or glabrous. Calyx pale green, lobes nearly free, sparsely pubescent on both surfaces, four sepals subequal, obovate, 10–12 × 5–8 mm with 2–5 teeth near the obtuse apex, gradually narrowed toward the base and spreading, dorsal lobe smaller, 9–11 × 2–2.5 mm and curved around the dorsal nectary gland, margin ciliate. Corolla posture oblique relative to calyx, yellow with 4–5 red spots ventrally in throat, 21–26 mm long, 2.5–3 mm diam at the base and 7–10 mm at the throat, not constricted, exterior hirsute at the throat, becoming glabrous at the base, interior partially pubescent with glandular hairs in the throat, limb 17–20 mm wide, lobes subequal, suborbicular, 5 × 6–7 mm, rounded, margin entire, spreading. Androecium of 4 fertile stamens included in the throat; filaments glabrous, curling after anthesis, connate at base and adnate to the corolla; anthers coherent in pairs, suborbicular, 1.2 × 1.2 mm, staminode small, glabrous, 0.5 × 0.1–0.2 mm. Ovary hirsute except glabrous at the base, ovoid, laterally compressed, 3–4 × 2–3 mm, style glabrous, stigma capitate. Nectary a single dorsal gland. Fruit a bivalved capsule, subglobose, laterally compressed, 10 × 6 mm, acute or obtuse, pubescent, color uncertain on specimens. Seeds ellipsoid, ca. 1.0 × 0.3 mm, obliquely striate, light to dark brown. Figure 3.

Additional Specimens Examined—FRENCH GUIANA. Cayenne: route de Kaw, pk 37, *F. Billiet & B. Jadin 7468* (MO); Régina, Mt. Tortue, 11 km WNW of Approuague River, 04°18′N, 52°22′W, *C. Feuillet et al. 10118* (BBS, K, MO, NY, US); Haut Oyapock, ouest de Trois Sauts, Mont Saint Marcel, *J. J. de Granville 1198* (WAG); Montagne de Kaw, bord de chemin, 10 km á l'est du Camp Caïman, *J. J. de Granville 2931* (CAY, WAG); Massif des Emerillons, *J. J. de Granville 3858* (WAG); Monts Bakra, 1.5 km à l'ouest du Pic Coudreau, tête de crique, versant ouest du sommet de 600 m à l'ouest de la savane-roche, 03°18′00″N, 52°57′00″W, *J. J. de Granville 14965* (US); Montagne de Kaw, 04°33′N, 52°10′W, *R. A. A. Oldeman B2376* (US); Route de Kaw, 04°35′N, 52°20′W, *M. F. Prévost 3887* (US); Montagne Trésor, route de Kaw, 04°31′N, 52°45′W, *C. Sastre & D. Bell 8003* (US); Montagne de Kaw, south side of mountain, track between "Camp Caïman" and "Degrad La Lanne," 04°30′N, 52°10′W, *L. E. Skog & C. Feuillet 5658* (US); Montagne de Kaw region, summit plateau, Camp Caïman, 04°33′N, 52°09′W, *L. E. Skog et al. 7086* (US); Kaw Mountains, secondary forest opposite Trésor Voluntary Natural Reserve, 04°32′N, 52°10′W, *J. F. Smith et al. 4116* (CAY, SRP, US). Saint-Laureny du Maroni: Saül, Monts La Fumée, 03°37′N, 53°12′W, *B. Boom & S. Mori 1564* (US); Montagne de l'Inini, Bassin de l'Inini, 03°30′N, 53°30′W, *C. Feuillet 3699* (US); Sources de la Mana, au pied des Monts Galbao, *J. J. de Granville 1605* (CAY, P, US, WAG); Versant nord des Monts Galbao, 10 km WSW de Säul, *J. J. de Granville 1659* (CAY, US, WAG); Saül, Carbet Maïs, *J. J. de Granville 3025* (CAY, WAG); Saül, entre Carbet Maïs et Pic Matecho, *J. J. de Granville 3089* (CAY, WAG); Montagne Bellevue de l'Inini, zone centrale, versant sous le vent, 03°03′N, 53°35′W, *J. J. de Granville et al. 7851* (US); Mont Galbao, Secteur Est, 03°36′N, 53°17′W, *J. J. de Granville et al. 8833* (P, US); Mont Atachi Bacca, région de l'Inini, versant nord, 9 km SE de Gobaya Soula, abords du camp no. 3, 03°33′N, 53°55′W, *J. J. de Granville et al. 10638* (CAY, US); Layon Galbao, région de Saül, 03°37′N, 53°17′W, *M. Hoff & G. Cremers 6634* (US); Saül, Mont Galbao trail, 03°37′N, 53°12′W, *S. A. Mori & C. A. Gracie 18735* (NY, US); same location, *S. A. Mori et al. 19036* (NY), *S. A. Mori et al. 19110* (NY), *S. A. Mori et al. 20920* (NY); Saül, near Eaux Claires, Sentier Botanique, 03°37′N, 53°12′W, *S. A. Mori et al. 22285* (NY); Dorlin, 03°45′N, 53°33′W, *M. F. Prévost 3509* (US).

GUYANA. Potaro-Siparuni: Iwokrama Rainforest Reserve, Karupukari, 04°20′N, 58°48′W, *H. D. Clarke et al. 4214* (NY, U, US); Iwokrama Rainforest Reserve, Iwokrama Mountains, 1–2 km SE of camp at bottom of gorge, 04°20′N, 58°48′W, *H. D. Clarke et al. 4260* (MO, NY, U, US); *S. Mori & S. Heald 24647* (NY, US).

CULTIVATED. *L. E. Skog & M. U. Kopp 7581* (US). *N. Kast s. n.* (SRP), *J. van Veldhuizen 687* (WAG).

Christopheria xantha (Leeuwenb.) J. F. Smith & J. L. Clark, comb. nov. *Episcia xantha* Leeuwenb., Misc. Pap. Landb. Wageningen 19: 241. 1980.—TYPE: FRENCH GUIANA. Cayenne: Montagnes de Kaw 400 m, 4.32 N 52.06 W, *A. J. M. Leeuwenberg 11819* (holotype: WAG-2!, isotypes: CAY, K, MO, P, U).

The description for the species is identical to the genus.

Leeuwenberg (1980) in his description of *Episcia xantha* comments that this is the only known species of *Episcia* with yellow flowers, but states that it is "closely allied to *E. cupreata* (Hook.) Hanst. by the habit and shape and size

Fig. 2. *Pagothyra maculata* (Hook. f.) J. F. Smith & J. L. Clark. A. Racemose inflorescence showing bracts. B. Front view of inflorescence showing inflexed ventral corolla lobe closing flower. C. Lateral view of flowers. D. Euglossine bee (*Eulaema* sp.) shown to forcibly open corolla. (Photo A by Chris Davidson; B–D by Heiko Hentrich).

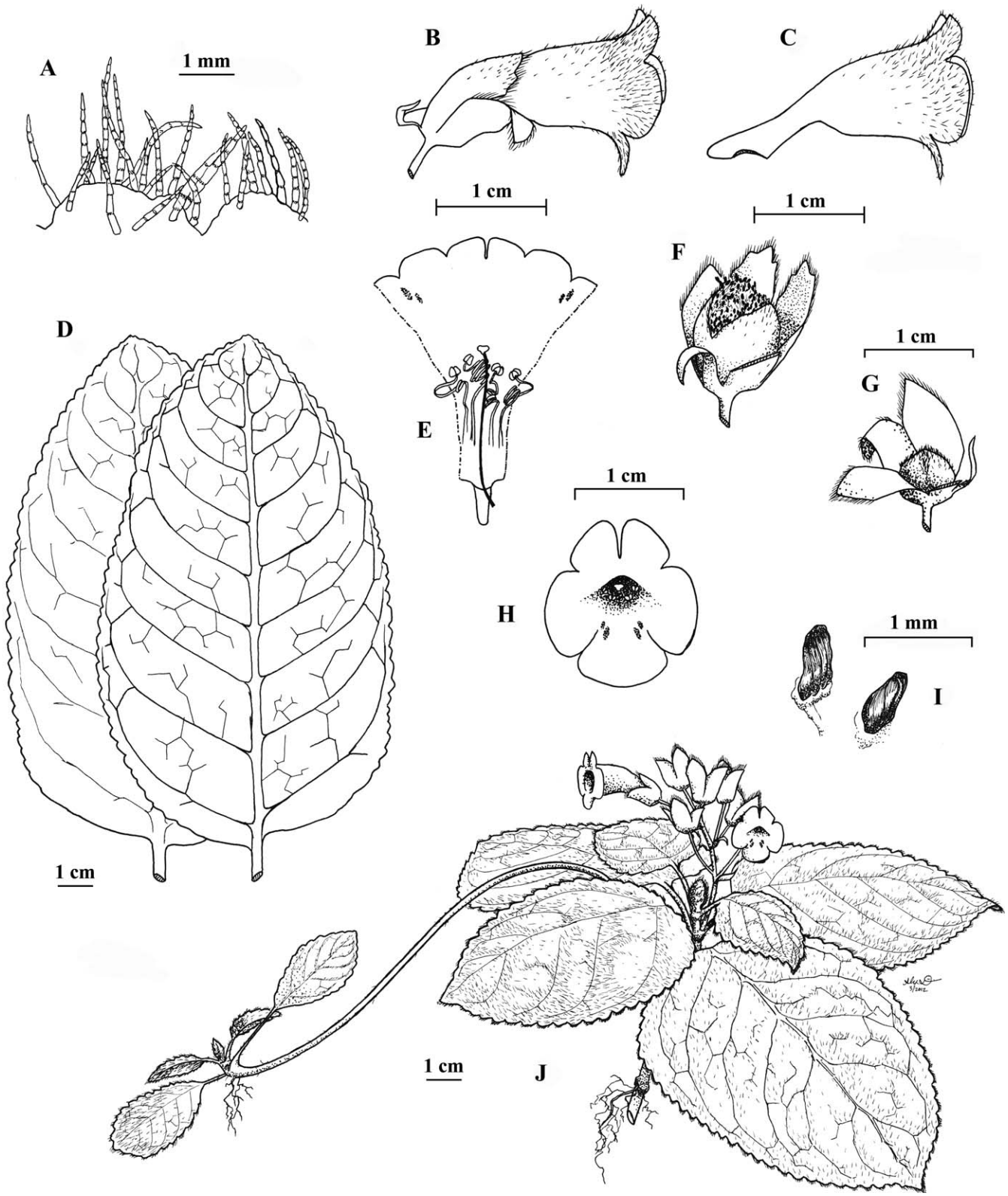

Fig. 3. *Christopheria xantha* (Leeuwenb.) J. F. Smith & J. L. Clark. A. Leaf margin pubescence. B. Lateral view of flower with calyx. C. Lateral view of corolla. D. Abaxial surface of large leaf. E. Lateral view of open flower. F. Mature dehiscing fruit with calyx. G. Immature fruit with calyx. H. Front view of flower. I. Seeds. J. Habit showing stolon. (A from *H. D. Clarke 4260 et al.* (MO); B and C from *C. Sastre & D. Bell 8003, with F. Crozier* (US) and *J. J. de Granville 1659* (WAG); D–G from *J. J. de Granville 1659* (WAG) and *L. E. Skog & M. U. Kopp 7581* (US); H and I from *C. Feuillet 10118 et al.* (MO); J from *L. E. Skog & M. U. Kopp 7581* (US)).

of the flowers." The placement in *Episcia* has not been questioned until this species was included in phylogenetic analyses (Clark et al. 2006, 2012). It is clearly part of a clade of other Guiana Shield endemic Gesneriaceae and is not related to other species of *Episcia*, a Neotropical genus defined by the presence of two stolons per node. Neither is *Christopheria* closely related to the other Neotropical species of Gesneriaceae with stolons, *Alsobia*, albeit typically with only one stolon per node. The placement of *Christopheria* among morphologically divergent species indicates that the character state of stolons is convergent in the Gesneriaceae and independently derived in *Christopheria xantha*.

Many labels for this species note that it is found growing on old logs or epiphytic on dead trunks (Skog and Feuillet 2008). It is likely that this species requires a more open habitat by its presence in early successional forests or light gaps.

Distribution—*Christopheria xantha* is known from forests in French Guiana and Guyana between 50–500 m.

Phenology—Flowering and fruiting specimens are known from March-June and August, presumably also in flower and fruit in July, but no specimens have been seen from this month. Specimens from other times were sterile.

Etymology—The name is derived from the first and last names, respectively, of Christopher Davidson and Sharon Christoph who have provided both logistical and intellectual support to the first author, including the trip to French Guiana where leaf material for this species was collected.

Lesia J. L. Clark & J. F. Smith, gen. nov—TYPE: *Alloplectus savannarum* C. V. Morton.

Epiphytic to terrestrial subshrub to 4 m tall, calyx lobes with dentate margins near base and entire margins near apex, and fruit a bivalved capsule.

Epiphytic or terrestrial subshrub. Stems erect, usually branched, sometimes sparingly so, terete, to 4 m tall, to 0.5 cm in diameter, subwoody, internodes 2–8 cm long, glabrescent proximally, yellow-tomentose or reddish brown with white hairs distally. Leaves opposite, subequal to unequal in a pair; petiole yellow-tomentose, 2–5.5 cm long; blade obliquely oblong-elliptic to broadly elliptic, larger blade 7.5–16 × 3–7 cm, smaller blade 3–5 × 1–2 cm, papery when dry, apex acuminate, base obliquely cuneate, margin serrate, adaxial surface sparsely pilose, abaxial surface hirsute to densely tomentose, lateral veins 6–10 per side. Inflorescences axillary, flowers 1–2 in reduced cymes; pedicels 0.9–1.2 cm long, hirsute to densely tomentose. Calyx lobes nearly free, base of each lobe appressed to adjacent lobe, folded lengthwise with the margin curved inward, erect, both sides hirsute, subequal, ovate, 2–3 × 1–1.25 cm, apex acute, margin dentate at base and entire near apex. Corolla posture oblique relative to calyx, yellow, 2–2.8 cm long, 0.5 cm diam at the base and 0.5 cm wide at the throat, slightly constricted, gibbous basally on upper surface, middle curved, becoming apically ventricose on upper surface, exterior glabrous at base, densely yellow-sericeous towards apex, interior pilose towards apex, limb 0.3–0.4 cm wide, lobes equal, erect, triangular, 0.2 × 0.2 cm wide, margin nearly entire. Androecium of 4 fertile stamens included in the throat; filaments glabrous, connate at the base and adnate to the base of the corolla tube for 3 mm; anthers coherent in pairs, quadrangular, 1 × 1 mm, staminode absent. Ovary densely pilose, ovoid, ca. 0.3 × 0.25 cm, style glabrous, stigma 2-lobed. Nectary a bilobed gland on dorsal surface of ovary. Fruit a bivalved capsule, subglobose, opening to 45 degrees, ca. 1.2 × 1 cm, white, hirsute. Seeds fusiform, 1 × 0.3 mm, longitudinally striate, brownish red. Figure 4.

Additional Specimens Examined—BRAZIL. Amazonas: Between Missao Salesiana and Serra Pirapucú, 01°16′N, 67°54′W, *N. T. Silva & U. Brazão 60860* (NY, UB, US).

COLOMBIA. Amazonas: Río Caqueta, La Pedrera and vicinity, Cerro de la Pedrera, 01°18′S, 69°34′W, *R. E. Schultes & I. Cabrera 16316* (US). Vaupes: Serrania de Taraira, 10 km NW of La Libertad, La Mina, 00°58′S, 69°45′W, *R. Cortés & J. Rodríguez 520* (NY).

GUYANA. Cuyuni-Mazaruni: Upper Mazaruni River region, Karowtipu Mountain, slopes of eastern peak, between camp and peak, 05°45′N, 60°35′W, *B. M. Boom & D. Gopaul 7484* (NY, US); same location, *B. M. Boom & D. Gopaul 7746* (NY, US); Holitipu, trail between camp & airstrip & surrounding area, 05°59′N, 61°03′W, *H. D. Clarke 1072* (CAY, NY, US); Paruima, 9 km W, Ararata scrub area, 05°49′N, 61°08′W, *H. D. Clarke et al. 5312* (NY, US); Paruima, 15 km W, eastern edge of Waukauyengtipu, 05°49′N, 61°11′W, *H. D. Clarke et al. 5616* (US); Wayalayeng Village, falls of the Ataro River above the first escarpment of Mount Maringma, 05°14′25″N, 60°30′58″W, *H. D. Clarke et al. 11448* (NY, US); Mt. Maringma, southern slopes near source of Arabaru River, 05°12′24″N, 60°34′19″W, *H. D. Clarke et al. 11497* (NY, US); plateau below summit escarpment, 07°12′10″N, 60°35′16″W, *H. D. Clarke et al. 11837* (NY, US); Mt. Maringma, slope below sub-summit plateau, 05°12′17″N, 60°34′36″W, *H. D. Clarke et al. 11927* (US); Escarpment slope above Timehri rock paintings, ± 2 km SSW of Maipuri Falls, 05°40′N, 60°17′W, *L. J. Gillespie & D. R. Smart 2864* (US); Between camp 1 and 3 along Waruma Trail, ± 5–10 km upstream of Kako River, 05°18′N, 60°40′W, *W. J. Hahn & D. Gopaul 5313* (NY, US); Pakaraima Mountains, Kurupung-Membaru trail, 2.75 km from Kumarau Falls, 06°05′N, 60°23′W, *B. Hoffman & G. Marco 2111* (NY, US); Pakaraima Mts, 1–4 km NW of Mt. Ayanganna on outer toe slopes of mountain, 05°25′N, 60°00′W, *B. Hoffman & T. Henkel 3316* (US); Mt. Ayanganna, Pakaraima Mountains, 05°23′N, 59°56′W, *B. Maguire et al. 40595* (K, NY, S, U, US); Valley of West Branch, Eping River, 05°58′N, 60°14′W, *T. McDowell & A. Stobey 4025* (US); To plateau S end of Haiamatipu, 05°28′N, 60°32′W, *T. McDowell et al. 4721* (US); Vicinity of Chinoweing Village, 05°32′N, 60°07′W, *J. J. Pipoly et al. 10450* (NY, US); Along Koatse River, ± 2 km W of Pang River, ± 5 hr walk S of Chinoweing, 05°28′N, 60°04′W, *J. J. Pipoly et al. 10609* (NY, U, US); Foothills immediately S of Mt. Ayanganna, ca. 1 km W of Pong Creek, 05°28′N, 60°04′W, *J. J. Pipoly et al. 10673* (NY, US); Ayanganna Plateau, ca. 2 km W of base camp in Koatse River valley, 05°28′N, 60°04′W, *J. J. Pipoly et al. 11003* (BBS, CAY, NY, PORT, U, US); Headwaters of Kangu River, W branch, ca. 4 km NW of E peak of Mt. Ayanganna, first talus slope of plateau, 05°25′N, 60°00′W, *J. J. Pipoly et al. 11027* (CAY, GH, NY, U, US); same location, *J. J. Pipoly et al. 11077* (BRG, CAY, NY, US), *J. J. Pipoly et al. 11092* (BRG, CAY, NY, U, US); Mt. Ayanganna, gorge N of central-eastern side, 05°25′N, 59°57′W, *J. J. Pipoly et al. 11221* (CAY, NY, US); Imbaimadai vicinity, Mazaruni River, at base of tepui, 2 miles from Mazaruni base camp, 05°36′05″N, 60°12′56″W, *K. M. Redden 1339* (US); Pakaraima Mts., Imbaimadai. Karowrieng River, 05°41′21″N, 60°12′35″W, *K. M. Redden et al. 1532* (US); Pakaraima Mts., Mazaruni River, NW of Chi-Chi Falls, along stream between two tepuis, approx. 1.5 km above Base Camp 2, 05°35′49″N, 60°12′49″W, *K. M. Redden et al. 1642* (US); Pakaraima Mts., Mazaruni River, 0.25 miles S of Base Camp 6, 06°02′27″N, 60°39′10″W, *K. M. Redden et al. 1839* (US); Pakaraima Mts., Mazaruni River, just above ABC Falls, trail/track 2.03 miles SW of Base Camp 6 heading east, 06°06′11″N, 60°39′48″W, *K. M. Redden et al. 2023* (US); Upper Mazaruni River basin, Merume Mountains, Porkknocker Camp 2 on Partang River about 19 miles above mouth, *S. S. Tillett et al. 43930* (NY, US). Potaro-Siparuni: Upper Potaro River region, ca 19 mi N of Kopinang village, 05°05′N, 59°49′W, *B. M. Boom & G. J. Samuels 8909* (US); Upper Potaro R., 2 km south of camp, along stream (affluent of Potaro R.), 05°18′05″N, 59°54′40″W, *H. D. Clarke et al. 8920* (SEL, US); Mt. Wokomung, plateau above first of four escarpments, 05°06′36″N, 59°49′14″W, *H. D. Clarke et al. 10194* (US); Kaieteur Plateau, along trail from Plane-landing to Kaieteur Falls, 05°10′N, 59°29′W, *R. S. Cowan & T. R. Soderstrom 1751* (E, MO, NY, US); Kaieteur National Park, between airstrip and escarpment, 05°11′N, 59°29′W, *L. J. Gillespie & H. Persaud* 907 (US); Kaieteur National Park, forest S of guest house, 05°10′N, 59°29′W, *L. J. Gillespie et al. 1263* (B, BPS, CAY, NY, P, US); Kaieteur National Park, headwaters of Korume Creek, 0.5 km N of airstrip, 05°10′N, 59°29′W, *L. J. Gillespie 4299* (US); Kaieteur Falls National Park, 05°10′N, 59°29′W, *W. J. Hahn et al. 3998* (US); Mt. Kopinang, 04°58′N, 59°53′W, *W. J. Hahn et al. 4287* (US); Pakaraima Mts., Mt. Wokomung, Suruwabaru Creek, 2–3 km upstream from juncture with Yuarka River, 05°03′N, 59°54′W, *T. W. Henkel et al. 1248* (MO, NY, US);

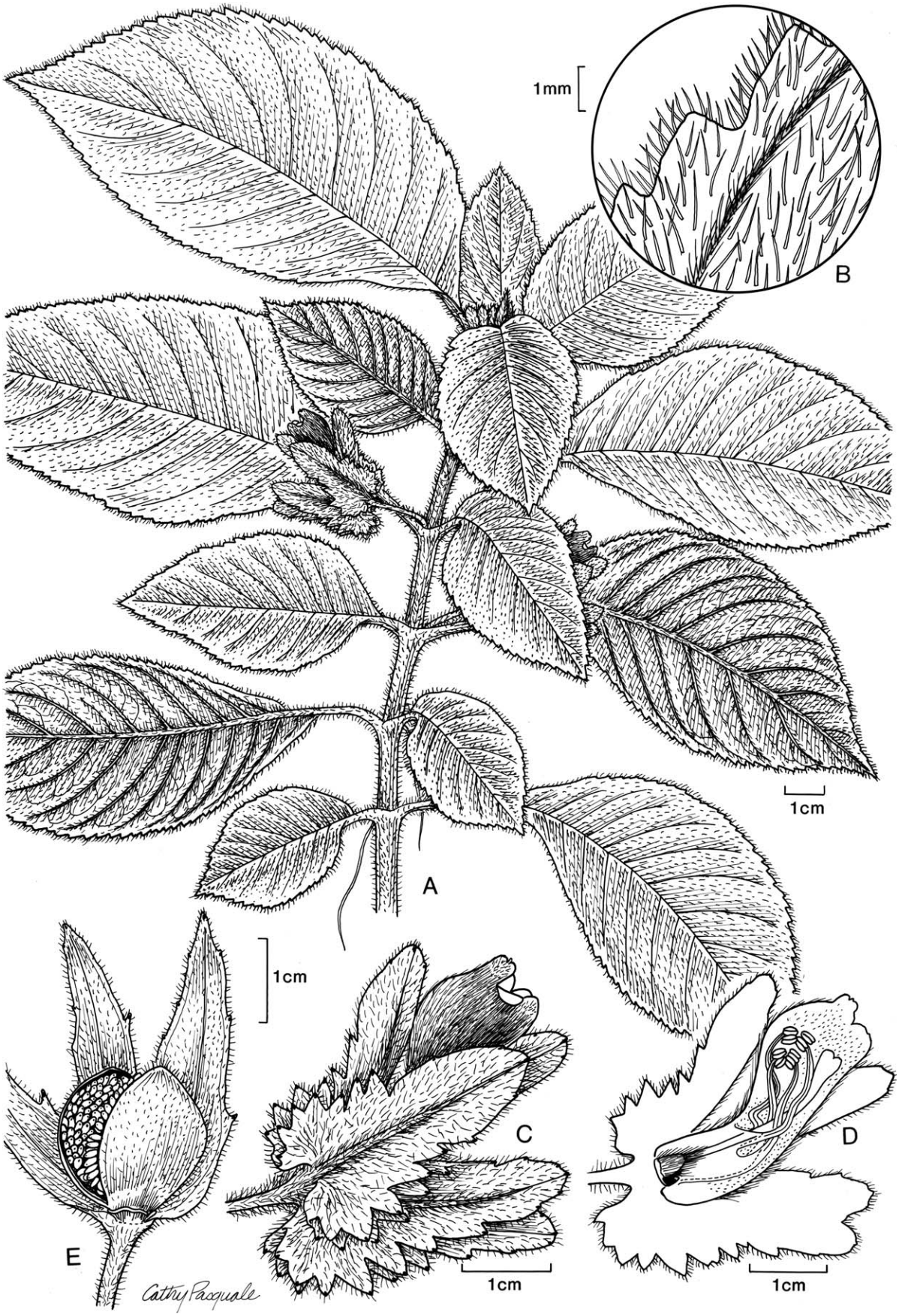

FIG. 4. *Lesia savannarum* (C. V. Morton) J. L. Clark & J. F. Smith. A. Habit. B. Leaf margin. C. Lateral view of flower. D. Flower opened to show gynoecium and androecium. E. Mature fruit (A–D from *Cowan & Soderstron 1751* (US); E from *Tillett et al. 43930* (US)). This illustration was originally published in Skog and Feuillet (2008) and is reprinted with permission from the Flora of the Guianas Consortium.

Pakaraima Mts., Mt. Wokomung, Wusupubaru Creek, 2 km from juncture with Suruwabaru Creek, 05°03′N, 59°53′W, *T. W. Henkel et al. 1345* (MO, NY, US); Kaieteur plateau, W rim of inner gorge, falls to Johnson's Lookout, 05°11′N, 59°28′W, *T. W. Henkel & R. Williams 2409* (NY, U, US); Pakaraima Mts., Mt. Wokomung, W slope on sub-plateau near head of Mo-toy-mabaru Creek, 05°04′N, 59°53′W, *T. W. Henkel et al. 4290* (NY, US); Kaieteur Falls National Park, path just below Johnson's View, 05°10′N, 59°29′W, *C. L. Kelloff et al. 867* (NY, US); Kaieteur Falls, close to the falls and the government house, 05°11′N, 59°29′W, *L. P. Kvist et al. 34* (COL, P, US); Chenapou, Patumona Amerindian village, 50 km upstream from Kaieteur Falls, 05°00′N, 59°34′W, *L. P. Kvist et al. 256* (B, BRG, CAY, US); Tukeit near old government resthouse, 05°13′00″N, 59°27′00″W, *K. Lance et al. 53* (US); Blackwater Creek Camp, NW along rocky river ravine and steep slopes, 05°12′N, 59°10′W, *T. McDowell et al. 4910* (US); Kaieteur Falls National Park, N of Menzie's Landing, 05°11′N, 59°29′W, *J. J. Pipoly & G. Gharbarran 10001* (K, MO, NY, US); Kaieteur Falls National Park, trail to Johnson's View, cliff area proceeding south, on west side of Potaro River, 05°11′N, 59°28′W, *J. J. Pipoly & G. Gharbarran 10169* (NY, U, US).

PERU. Loreto: Prov. Requena, Jenaro Herrera, Río Ucayali, 04°55′S, 73°45′W, *A. Gentry et al. 56258* (MO, US, USM); Prov. Requena, Dtto. de Sapuena, Jenaro Herrera, Río Ucayali, 04°55′S, 73°40′W, *R. Ortiz et al. 106* (US); Vicinity of Iquitos, 03°45′S, 73°15′W, *J. Revilla 3743* (US); Prov. Requena, Jenaro Herrera, 04°50′S, 73°45′W, *R. Vásquez et al. 2175* (US); Prov. Ucayali, Sapuena, Jenaro Herrera (CDJH), 04°55′S, 73°45′W, *R. Vásquez & T. Soto 11899* (US, USM); Prov. Requena, Jenaro Herrera, 04°55′S, 73°45′W, *H. van der Werff et al. 1002* (MO, US).

SURINAM. Sipaliwini: Frederick Top, 2 km SE of Juliana Top, 03°39′N, 56°30′W, *N. Holmgren et al. 54396* (NY-2, US); Wilhelmina Gebergte, upper slopes and summit of Juliana Top, 15 km north of Lucie River, 03°41′N, 56°32′W, *H. S. Irwin et al. 54873* (NY, US); Wilhelmina Gebergte, summit of Frederik Top, 3 km southeast of Juliana Top, 03°39′N, 56°30′W, *H. S. Irwin et al. 54959* (NY, US).

VENEZUELA. Amazonas: Dpto. Atures, Base E del Cerro Cuao, Caño Piedra, 75 km SE de Puerto Ayacucho, 05°05′N, 67°19′W, *A. Fernández et al. 6119* (PORT, US); Cerro Sipapo, Paráque, Savanna Camp and Phelps Camp, *B. Maguire & L. Politi 27735* (NY); Cerro de la Neblina, Río Yatua, Caño Grande SSE of Cumbre Camp, 00°46′N, 66°00′W, *B. Maguire et al. 42525* (NY, US); Dpto. Atures, Base E del Cerro Cuao, Caño Piedra, 75 km al SE de Puerto Ayacucho, 05°05′N, 67°19′W, *E. Sanoja et al. 3027* (PORT, UNELL, US). Bolívar: Slopes along and above Salto El Danto, km 121–122 of Highway 10, La Escalera, 05°57′47″N, 61°23′30″W, *P. E. Berry et al. 6591* (US, VEN); Along road between Santa Elena and El Dorado on the Gran Sabana, 181 km N of Santa Elena, 39 km S of village "km 88," 05°43′N, 61°23′W, *T. B. Croat 54290* (MO, US, VEN); Mun. Gran Sabana, carretera El Dorado - Santa Elena de Uairén, sector La Escalera, approx. 27 km al Sur del sitio "Piedra de la Virgen," 05°54′N, 61°26′W, *O. Huber et al. 12898* (US); Distr. Piar, summit of Amaruay-tepui, south side east half, 05°55′N, 62°13′W, *R. L. Liesner & B. K. Holst 20820* (MO, US, VEN); Sororopan, 05°45′N, 61°43′W, *B. Maguire & J. J. Wurdack 33838* (US); Chimanta Massif, along trail between camp 2 and camp 3, northwestern part of Abacapa-tepui, 05°13′N, 62°15′W, *J. A. Steyermark 74836* (F, MO, NY, US, VEN, WIS); Chimanta Massif, between bluff camp and low promontory N of bluff camp, along W-facing portion of Chimanta-tepui, 05°18′N, 62°10′W, *J. A. Steyermark 75658* (F, MO, NY, US, VEN); Sierra de Lema, cabeceras de Río Chicanán, 80 km (en línea recta) al suroeste de El Dorado, 06°05′N, 62°00′W, *J. A. Steyermark 89416* (US); same location, *J. A. Steyermark 89518* (US); Sierra de Lema, cabeceras de Río Chicanán, 80 km (en línea recta) al suroeste de El Dorado, on summit west of waterfall at headwaters of Río Chicanán above N-facing bluffs, 06°05′N, 62°00′W, *J. A. Steyermark 89620* (US, VEN); Cerro Venamo, Cuyani rain forest, km 117–118 (km 125) old road camp, *H. Wiehler 72421* (SEL, US); Salto El Dante, *H. Wiehler 72424* (SEL, US); Cerro Venamo, Cuyani rain forest, *H. Wiehler 72439* (SEL, US); Between camps 2 and 3, Tirepón-tepui, *J. J. Wurdack 34046* (NY).

Lesia savannarum (C. V. Morton) J. L. Clark & J. F. Smith, comb. nov. *Alloplectus savannarum* C. V. Morton, Bull. Torrey Bot. Club 75: 563. 1948. *Nematanthus savannarum* (C. V. Morton) J. L. Clark, Selbyana 25: 205. 2005.—TYPE: GUYANA. Potaro-Siparuni: Kaieteur Plateau, Wallaba Forest [*Eperua* spp.], 1 May 1944, 05°10′N, 59°29′W, *B. Maguire & D. B. Fanshawe 23127* (holotype: NY!; isotypes: A (photo: US!), BR!, F!, G!, K!, MO (photo: US!), P, U!, UC!, US!, VEN!, W (photo: US!).

Columnea steyermarkii C. V. Morton, Bol. Soc. Venez. Ci. Nat. 23(101): 76. 1962.—TYPE: VENEZUELA. Bolívar: along headwaters of Río Venamo, northern slopes of Cerro La Danta, NW of Cerro Venamo, 1,040 m, 12 Apr 1960, *J. A. Steyermark & S. Nilsson 41* (holotype: US!; isotypes: NY (photo: US!), VEN!).

Columnea calotricha J. D. Smith var. *austroamericana* C. V. Morton, Bol. Soc. Venez. Ci. Nat. 23: 78. 1962.—TYPE: SURINAM. Sipaliwini: Brownsberg Plateau, 6 Sep 1915, *G. Stahel & J. Gonggrijp 122* (holotype: US!).

The description of the species is identical to that of the genus.

The calyx lobes in *Lesia savannarum* are strongly dentate at the base and entire at the apex. Calyx margins such as this are only found in a small group of *Columnea* within section *Pentadenia* (Planch.) Benth., such as *Columnea atahualpae* J. F. Smith & L. E. Skog, *C. isernii* Cuatrec., and *C. lophophora* Mansf. The large subshrub habit (to 4 m tall) is also unusual for any of the members of the tribe Episcieae. The molecular phylogenetic analyses of Clark et al. (2012), summarized in Fig. 1, clearly indicate that *Lesia savannarum* is the sister to the clade that includes *Codonanthe, Codonanthopsis,* and *Nematanthus*. The results presented in Clark et al. (2006) are also congruent with the phylogenetic placement suggested in Clark et al. (2012).

Distribution—The species is known from eastern Colombia to eastern Peru, Brazil (Roraima), Guyana, and Surinam, from 270–1,570 m.

Phenology—Specimens have been collected in fruit and flower throughout the year.

Etymology—The new genus honors Laurence E. Skog (by using his initials L. E. S.), who has made numerous, invaluable contributions to our understanding of Neotropical Gesneriaceae.

Pachycaulos J. L. Clark & J. F. Smith, gen. nov—TYPE: *Hypocyrta nummularia* Hanst.

Pendent herbaceous epiphyte, shoots succulent, corolla hypocyrtoid, and fruit an indehiscent, globose, orange berry.

Pendent epiphytic herb. Stems creeping to decumbent, terete, 5–7 mm diam, internodes ca. 0.5–3.0 cm long, glabrous to sparsely pilose, reddish-brown, nodes commonly with adventitious roots and conspicuous swellings. Leaves opposite, subequal; petiole pilose 3–5(-20) mm long; blades ovate, 1.7–5(–6) × 1–3(–4) cm, firm when dry, apex obtuse to acute, base cuneate to rounded, margin nearly subentire, adaxial surface strigose, abaxial surface sparsely strigose, lateral veins ca. 2–5 per side. Inflorescences axillary, of a single flower; pedicel 12–20 mm long, sparsely pilose. Calyx green, lobes nearly free, sparsely pilose on both surfaces, all lobes subequal, lanceolate, 7–15 × 1.5–5 mm, apex acute, margin entire. Corolla bright red with a yellow limb, 15.5–20(–30) mm long, 2 mm in diam at the base and 2 mm diam at the throat, the base strongly ventricose and up to 15 mm diam in distal third and tapering rapidly to a narrow tube, constricted at the opening, exterior sparsely pilose, interior glabrous, limb 3.4 mm diam, lobes subequal, semi-orbicular, 1.8 × 1.6 mm. Androecium of 4 fertile stamens included in the throat; filaments glabrous, connate at the base and adnate to the base of the corolla; anthers coherent in pairs, quadrangular, ca. 1 × 1 mm. Ovary glabrous, ovoid, 1.7 × 1.4 mm, style glabrous, stigma bilobed. Nectary a dorsal bilobed gland. Fruit a berry, subglobose, laterally compressed, ca. 1 × 1 cm, orange, glabrous. Seeds ellipsoid, ca. 1 × 0.3 mm, striate, brown. Figures 5, 6.

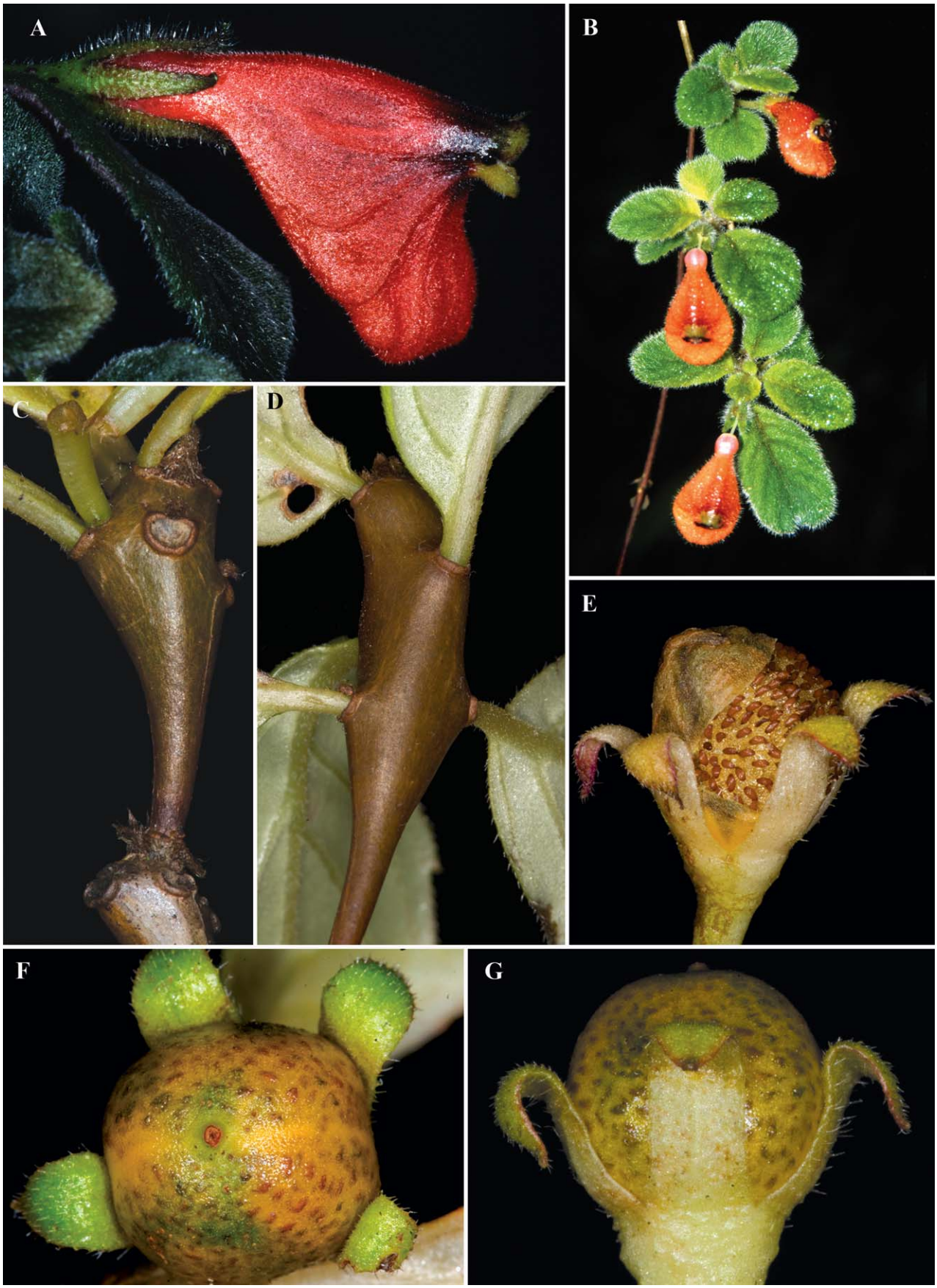

Fig. 5. *Pachycaulos nummularium* (Hanst.) J. L. Clark & J. F. Smith. A. Lateral view of flower. B. Pendent habit. C. Swollen nodes showing leaf scar. D. Swollen nodes. E. Mature fruit showing rupturing berry. F. Dorsal view of mature fruit. G. Lateral view of mature fruit. (Photos A–G by *J. L. Clark*; A. *United States Botanical Research Greenhouse live accession number 1994–522*; B. *J. L. Clark 6284*; C–G. *J. L. Clark et al. 12360*).

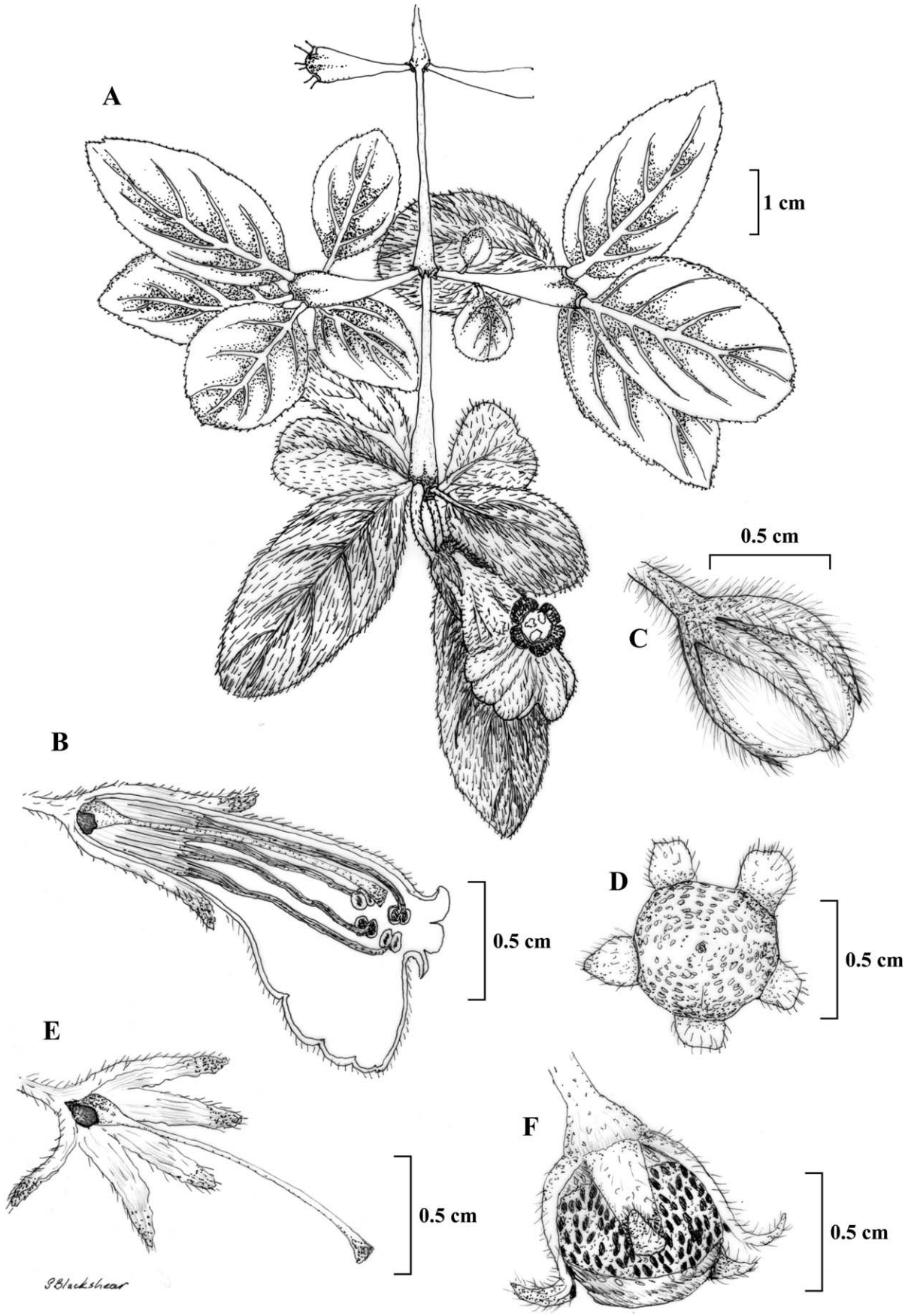

FIG. 6. *Pachycaulos nummularium* (Hanst.) J. L. Clark & J. F. Smith. A. Habit showing swollen nodes. B. Lateral view of flower. C. Lateral view of immature fruit. D. Dorsal view of mature fruit. E. Corolla removed to show calyx and gynoecium. F. Lateral view of mature fruit. (A–F. *J. L. Clark et al. 6248* (US)).

Additional Specimens Examined—COSTA RICA. Unknown Province: del Tablazo, *P. Biolley 10153* (US); *H. Pittier 10354* (US). Alajuela: Camino de San Ramon, *A. M. Brenes 4343* (NY); Concepcion de San Ramon, *A. M. Brenes 14280* (NY); San Isidro de San Ramon, 10°04′46″N, 84°26′30″W, *G. Herrera 65* (US). Puntarenas: Foothills of the Cordillera de Talamanca, in the area of Sitio Coton (Cotonsito), along the road to Sitio Coto Brus, 08°57′N, 82°46′W, *G. Davidse 24618* (MO, US). San José: Cantón de Dota, ca. 3.5 km S of Santa Maria de Dota, in pasture near Cedral, 09°37′22″N, 83°47′45″W, *H. Kennedy et al. 6046* (US); Near Río Parrita Chiquita, 5 km N of Santa Maria de Dota, *R. W. Lent 3913* (MO, NY, PMA, SEL, US); Z. P. Cerros de Escazú, Cedral, Falda noreste del Alto Hierba Buena, 09°50′39″N, 84°06′46″W, *J. F. Morales 119* (MO, US); Z. P. Cerros de Escazú, Aserri, Cerros Escazú-La Carpintera, El Cedral, Alto Hierba Buena, 09°50′30″N, 84°07′35″W, *V. Ramírez 111* (US); Vicinity of Santa Maria de Dota, *P. C. Standley 41562* (US); same location, *P. C. Standley 42399* (US); Near Quebradillas, about 7 km N of Santa Maria de Dota, *P. C. Standley 42971* (US).

ECUADOR. Azuay: Río Patul, along path from El Cajas to Manta Real following Río Patul (2–3 d trek), 02°37′46″S, 79°16′41″W, *J. L. Clark et al. 6248* (AAU, COL, F, K, MO, NY, QCA, QCNE, UNA, US); Cantón Cuenca, road from Cuenca to Guayaquil (vía Molleturo/El Cajas), San Jose de Molleturo, trail from road leading S through small patches of primary forest, 02°42′41″S, 79°28′35″W, *J. L. Clark et al. 9829* (US); Molleturo, al pie del Río Miguir, 02°46′S, 79°24′W, *X. Cornejo & C. Bonifaz 4753* (US). Chimborazo: Cantón Alausi, Parroquia Huigra, headwaters of Sigsig Pamba, Quebrada Huigra Viejo, remnant patch of forest E (2 air-km) of the town of Huigra, 03°17′36″S, 78°59′52″W, *J. L. Clark et al. 7900* (AAU, CAS, COL, E, F, K, MO, NY, QCA, QCNE, SEL, UNA, US, VEN). El Oro: Cantón Zaruma, Parroquia Salvia, 03°41′S, 79°43′W, *C. Bonifaz & X. Cornejo 3675* (US); Cantón Piñas, Buffer zone/border region of Reserva Ecologica Buenaventura, 11 km (air-km) north of the "Entrada la Virgin" on road towards Virón, 03°33′28″S, 79°46′12″W, *J. L. Clark et al. 7983* (QCNE, US); Huertas, 03°36′S, 79°37′W, *X. Cornejo & C. Bonifaz 5966* (US). Guayas: Cantón Santa Elena, Cord. Chongón-Colonche, Bosque Protector Loma Alta, 01°48′S, 80°47′W, *X. Cornejo & C. Bonifaz 5707* (US). Loja: Cantón Macara, road Macara-Catacotcha, 7 km N of Macara, *J. E. Bohlin et al. 1319* (GB, US); Celica-Alamor road, ca. 3 km W of Celica, *G. Harling & L. Andersson 22166* (GB, US); Celica-Zapotillo road, ca. 4 km below Pozul, *G. Harling & L. Andersson 22412* (GB, US). Pichincha: Reserva Floristica-Ecológica "Río Guajalito", km 59 de la carretera Antigua Quito-Santo Domingo de los Colorados, a 3.5 km al NE de la carretera, 00°13′53″S, 78°48′10″W, *J. Jaramillo & E. Grijalva 14645* (NY).

MEXICO. Chiapas: Mt. Pasitar, *E. Matuda 1690* (NY); Reserva de la Biosfera El Triunfo. *M. A. Pérez Farrera 2650* (SRP).

PERU. Cajamarca: Santa Cruz, Dist. Catache, upper Río Zana valley, ca. 5 km above Monte Seco on path to Chorroblanco, *M. O. Dillon et al. 4343* (F, US); Contumazá, *M. O. Dillon et al. 4574* (F, US); Prov. Contumazá, Dpto. Cajamarca, bosque Cachil, *A. Sagástegui & S. Leiva 1505* (NY); Prov. Contumazá, Contumazá – Cascas, *A. Sagástegui et al. 6500* (US); Prov. Contumazá; El Tunel (Cascas - Contumazá), *A. Sagástegui et al. 12643* (MO, US); Santa Cruz, ca. 3 km (by air) ENE Monteseco, *J. Santisteban C. & J. Guevara-B. 10* (F, US); Prov. Contumazá, km 95 on road between Cascas and Contumazá, ca. 15 km S of Contumazá, 07°25′S, 78°50′W, *B. A. Stein & C. Todzia 2032* (MO, NY, US, USM); Contumazá, 12 km from Contumazá on road to Cascas, *B. A. Stein et al. 4040* (US). Piura: Prov. Huancabamba, Canchaque, "Chorro Blanco," *C. Díaz S. et al. 2780* (MO, US); *C. Díaz S. et al. 2870* (US); Prov. Morropón, Dist. Morropón, La Huaca, al E del Puente sobre el Río Noma, camino al bosque del mismo nombre, borde de camino, 05°01′29″S, 79°49′48″W, *I. Sánchez Vega & M. Sánchez Montoya 12764* (US); Prov. Morropón, Dist. Chalaco, Bosque el Diego, caserio Juan Velasco, límite inferior del Bosque, Mijal, 05°03′43″S, 79°43′46″W, *I. Sánchez Vega & M. Sánchez Montoya 12774* (US); Prov. Huancabamba, road from Canchaque to Huancabamba, 05°25′S, 79°35′W, *J. F. Smith & C. Díaz 1700* (US).

CULTIVATED. Orig. Mexico, *L. E. Skog 5511* (US); Smithsonian Institution Dept. of Botany Research Greenhouses, Suitland, Maryland, U. S. A., *L. E. Skog & L. Brothers 8195* (US); *M. H. Stone 1247bis* (US).

Pachycaulos nummularium (Hanst.) J. L. Clark & J. F. Smith, comb. nov. *Hypocyrta nummularia* Hanst., Linnaea 34: 381. 1865. *Columnea nummularia* (Hanst.) Kuntze, Rev. Gen. 2: 472. 1891. *Alloplectus nummularia* (Hanst.) Wiehler, Baileya 18(4): 136. 1972. *Neomortonia nummularia* (Hanst.) Wiehler, Selbyana 5: 63. 1978.—TYPE: COSTA RICA. *H. Wendland 1272* (holotype: GOET!).

Episcia truncicola Brandegee, Univ. Calif. Publ. Bot. 6: 64. 1914.—TYPE: MEXICO. Chiapas: in Sierra del Boquerón, growing on an old log. *Purpus 7008* (holotype: UC, photo!).

The description of the species is identical to that of the genus.

The orange berries in *Pachycaulos nummularia* are globose (Fig. 5E–G), in contrast to the laterally compressed, orange berries in *Neomortonia rosea*. It was previously thought that both of these taxa had laterally compressed berries (Clark et al. 2006). Thus, the only feature that these two taxa share is indehiscent, orange berries. Otherwise, these two species differ based on vegetative and reproductive characters. The molecular phylogenetic analyses of Clark et al. (2012), summarized in Fig. 1, clearly indicate that *Neomortonia* is not monophyletic and that these two morphologically divergent taxa are best treated as separate genera.

Collections from higher elevations (> 2,000 m) from northern Peru and southern Ecuador are distinctive in their larger size. The high-elevation populations have larger leaves (reaching six cm in length) compared to collections from elevations below 2,000 m, where leaves are less than five cm in length. The flowers are also larger (reaching three cm in length) with longer pedicels (to two cm in length). Specimens from below 2,000 m have flowers that are less than two cm in length with pedicels that are typically less than one cm in length. Future studies may delineate the high-elevation collections from southern Ecuador and northern Peru as a distinct species.

Distribution—The species is known from Mexico to northern Peru, from 630–2,700 m.

Phenology—Flowering is known only in July.

Etymology—The generic name reflects swollen or thick stems.

Pagothyra (Leeuwenb.) J. F. Smith & J. L. Clark, comb. nov., *Episcia* section *Pagothyra* Leeuwenb. Acta Bot. Neerl. 7: 312. 1958—TYPE: *Episcia maculata* Hook. f.

Vine, corolla yellow with red-purple spots, lobes of the limb subequal, four round and patent, the fifth concavely inflexed over the corolla opening.

Climbing vine up to 1 m, adhering to host via numerous adventitious roots along stem. Stems attached to host or pendent, terete, 5–12 mm diam, internodes ca. 1–6 cm long, minutely hirsute. Leaves opposite, equal to subequal; petiole densely pilose to glabrous, 1.5–19 cm long; blade elliptic, 7.5–29 × 3.5–12 cm, papery when dry, apex acuminate, base cuneate, rounded, or subcordate, margin serrate, adaxial surface glabrescent to glabrous, abaxial surface sparsely pubescent, denser on veins, lateral veins 4–8 per side. Inflorescences axillary, racemose, bracteate, of three to many flowers, secund, 5–14 cm long; peduncle sparsely pubescent, 1–3 cm long; bracts leafy, short-petiolate to subsessile, 2–6.5 × 1–5.4 cm, green, purple- or red-veined, oblong to ovate, apex acute to obtuse, base cuneate, rounded or subcordate, margin serrate to subentire, sparsely appressed pubescent to glabrous on both surfaces, denser on midrib; pedicels 5–22 mm long, sparsely pubescent. Calyx pale green to purple or with purple veins, lobes nearly free, sparsely appressed pubescent on both surfaces, four subequal sepals lanceolate, 20–40 × 4–7 mm, apex obtuse to acuminate, narrowed toward the base, serrate to crenate at the apex, the fifth sepal smaller by 1/2 than the others, otherwise similar. Corolla posture oblique relative to calyx, yellow (white), marked with bright red, brown, or purple-brown spots, 35–64 mm

long, 4–5 mm diam at the base, 10–18 mm wide at the throat, slightly constricted above the spur, not ventricose, exterior and interior glabrous, spur 5–10 × 3.5–4.5 mm, obtuse, limb ca. 1.5–2.5 cm diam, lobes subequal, suborbicular, 10–12 mm diam, margins entire, four lobes spreading, the ventral lobe folded up over the throat and completely blocking it. Androecium of 4 fertile stamens included in throat; filaments glabrous, distinct from each other, but adnate to the base of the corolla; anthers coherent in pairs, orbicular, ca. 1.2 mm diam, staminode 0.25 mm long, glabrous, without anther. Ovary pubescent, ovoid, 4–5 × 3–4 mm, style glabrous, stigma bilobed. Nectary dorsal, entire, glabrous. Fruit a capsule, subglobose to ovoid, 10–15 × 8–14 mm, greenish white, sparsely pubescent. Seeds subglobose, 0.5–0.7(-1.0) × 0.5–0.7 mm, obliquely striate, brown, borne on long funiculus with small aril. Figure 2.

Additional Specimens Examined—FRENCH GUIANA. Cayenne: Les Nouragues Field Station, Approuague Basin, trail to Saut Pararé and along Crique Cascade near Cascade, *J. F. Smith et al. 4134* (CAY, SRP).

GUYANA. Barima-Waini: Matthews Ridge, Barima River, NW territory, *R. S. Cowan 39337* (US); Portage between Aruau and Yarikita Rivers, 08°00′N, 59°55′W, *A. S. Hitchcock 17601* (US); Upper Kaituma R., 3 km W of Port Kaituma, river & road from start of Jonestown Rd., 07°42′N, 59°54′W, *B. Hoffman & H. Benjamin 525* (US); ± 5 km SW of Sebai Village, on Sebai River, 07°49′N, 59°57′W, *B. Hoffman et al. 615* (US); Along trail between Baramita airstrip toward Millionaire, 07°22′N, 60°28′W, *T. McDowell et al. 4182* (NY, US); Barima River, 15 mi E of Arakaka, just E of Tenapu Creek, 07°37′N, 59°54′W, *J. J. Pipoly et al. 8059* (NY, US). Cuyuni-Mazaruni: near Mazaruni Forest Station, *W. A. Archer 2432* (US); Aurora, helicopter landing site, 0.3 km S of camp, 06°47′N, 59°44′W, *L. J. Gillespie & S. Tiwari 2084* (US). Essequibo Islands-West Demerara: Upper White Creek, near Blue Mountain, 06°35′N, 58°43′W, *T. W. Henkel et al. 1879* (NY, US); Kamuni Creek, Groete Creek, Essequibo River, 06°35′N, 58°25′W, *B. Maguire & D. B. Fanshawe 22826* (F, US). Pomeroon-Supenaam: Pomeroon River, Pomeroon District, *J. S. de la Cruz 3022* (PH, US); same location, *J. S. de la Cruz 3124* (F, PH, US); Pomeroon River, 3 km SW of Kabakaburi Mission village, settlement on Piraka Cr., 07°15′N, 58°45′W, *B. Hoffman & L. Roberts 2839* (NY, US). Potaro-Siparuni: Iwokrama Rainforest Reserve, Karupukari-Annai Road, below summit of unnamed peak, 04°28′14″N, 58°47′16″W, *H. D. Clarke et al. 4181* (US); Kaieteur Falls, Potaro River, 05°10′N, 59°29′W, *J. S. de la Cruz 4395* (F, US, VEN); Potaro, 10 mi S of Potaro landing, 05°10′N, 59°00′W, *A. S. Hitchcock 17397* (US); along North Fork River, 0.5–1.5 km N of Konawark Road, *T. McDowell 4819* (US); Garraway Stream, 102.5 miles on Bartica-Potaro Road, 05°22′25″N, 59°07′21″W, *K. M. Redden et al. 2231* (US). Upper Demerara-Berbice: Mabura region, Ekuk compartment, Holder Falls, 05°20′N, 58°10′W, *R. C. Ek et al. 896* (US); Mabura region, west Pibiri compartment, 6 miles above camp, 05°02′N, 58°38′W, *R. C. Ek et al. 942* (US); Basin of Essequibo River, Haiowa Falls, 05°07′N, 58°49′W, *A. C. Smith 2123* (F, US). Upper Takutu-Upper Essequibo: Maparri R., S bank, 0–6 km from camp at base of waterfall, 03°20′N, 59°15′W, *H. D. Clarke & T. McPherson 1928* (US); Upper Rupununi River, near Dadanawa, 02°45′ N to 02°50′N, 59°31′W, *J. S. de la Cruz 1518* (F, US); same location, *J. S. de la Cruz 1535* (CM, F, US).

VENEZUELA. Delta Amacuro: Dpto. Antonio Diaz, 12 km al S de San José de Amacuro, 08°28′N, 60°27′W, *A. Fernández 3903* (MO, MYF, NY, PORT, US).

Pagothyra maculata (Hook. f.) J. F. Smith & J. L. Clark, comb. nov. *Episcia maculata* Hook. f., Bot. Mag. 116: pl. 7131. 1890. *Paradrymonia maculata* (Hook. f.) Wiehler, Selbyana 5: 57. 1978.—TYPE: Cultivated at Kew Gardens from material collected in Guyana (holotype: K, isotype: K, photographs: BH, NY, U, US!, WAG).

The description of the species is identical to that of the genus.

Pagothyra maculata is unique among Neotropical Gesneriaceae in that the ventral corolla lobe appears to close off access to nectar and thus pollination (Fig. 2B), by blocking access to the corolla throat. The completely occluded throat was noted and illustrated by Hooker (1890). Feuillet (2009) noted that exerting pressure on the apical third of the corolla can cause the ventral lobe to move into "a more classic concave corolla lobe . . . and allows access to the nectar to strong pollinators, possibly carpenter bees." Field observations for a doctoral dissertation by Hentrich (2008) from the University of Ulm (Germany) noted that the corolla remained closed during the entire flowering period (two days) and was forcibly opened by large euglossine bees (*Eulaema* sp.) by pulling down the petals (Fig. 2D). Feuillet (2009) noted that the Asian species *Agalmyla chorisepala* (C. B. Clarke) Hilliard & B. L. Burtt also has a ventral lobe closing the tube that flips open when the flower reaches anthesis.

This species is readily distinct, and although it has been moved from *Episcia* to *Paradrymonia* by Wiehler (1978), is clearly morphologically unique among Gesnerioideae in both its corolla with the ventral lobe covering the throat and the bracteate, pendent, racemose inflorescence.

Distribution—The species is known from forests of French Guiana, Guyana, and Venezuela from near sea level to 500 m. It probably occurs in Surinam, but is not known from there (Feuillet 2009).

Phenology—Specimens have been collected in flower in all months of the year except February; therefore it is likely flowering all year. Fruiting specimens have been collected in December, January, and April, but if it is flowering continually, it is likely to be fruiting continually as well, and may simply be less frequently collected in fruit.

Etymology—*Pagothyra* had been used by Leeuwenberg (1958) to name a section of *Episcia* that included only *E. maculata*. The name is derived from Greek, meaning trap (pago) and door (thyra), to describe the lower, inflexed corolla lobe that covers the opening of the corolla tube.

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