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Three New Gesneria Species (Gesneriaceae) Support Parc National Pic Macaya (Haiti) as an Important Biodiversity Hotspot

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Abstract—The Caribbean Islands are a biodiversity hotspot characterized by a high taxonomic diversity and endemicity, suggesting that many species have yet to be discovered. Unfortunately, many of these undescribed species may go extinct before they are described because of the drastic habitat loss in these oceanic islands. In this study, we describe three new plant species of Gesneria (Gesneriaceae) that are endemic to the Massif de la Hotte in southwest Haiti, a region recently affected by extensive deforestation. Elliptical Fourier analyses of leaf shapes and DNA sequencing of five nuclear genes were used to support the species delimitations. Gesneria flava is a tall shrub with large yellow flowers, leafy sepals, and rugose leaves. Gesneria × cornuta is a hybrid between Gesneria bicolor and the newly described Gesneria flava and is morphologically intermediate between its parents. Its hybrid origin is further supported by the presence of alleles from both parents for all five nuclear genes sequenced. Finally, Gesneria radiata is a saxicolous herb with radially symmetrical corollas. The three new species described here are limited to a single mountain range in the Caribbean, the Massif de la Hotte. These recent discoveries reflect the high endemicity of this region and exemplify the urgency to conserve the remaining primary forest of Haiti in order to protect its biodiversity.

Keywords—Massif de la Hotte, elliptical Fourier analysis, morphometry, Rhytidophyllum, taxonomy.

The Caribbean Islands form a biodiversity hotspot characterized by a high density of species per area, a high degree of endemism, and significant loss of primary forests (Myers et al. 2000). Between 2 and 3% of all plant and vertebrate species of the world are unique to this region (Myers et al. 2000). Local endemicity is important in this region, in particular in Hispaniola where it is frequent to observe species that are restricted to a single mountain range. For instance, 19 of the 35 species of *Miconia* sect. *chaenopleura* found in Hispaniola are endemic to a single mountain range (Judd 2007).

Within Hispaniola, the biodiversity of Haiti is particularly vulnerable because of the pace at which the primary forest is lost in this country. Hedges and Cohen (2018) estimated that primary forest cover in Haiti has decreased from 4.4% of total land area in 1988 to only 0.32% in 2016. Such primary forest loss suggests important species extinction given the high local endemism in Haiti (Skean 1993; Acevedo-Rodríguez and Strong 2008; Huber et al. 2010; Hedges and Cohen 2018) and that the loss of endemic species parallels that of primary forests (Hedges and Cohen 2018).

The flora of Haiti, although very rich, has not been thoroughly studied (reviewed in Acevedo-Rodríguez and Strong 2008) despite occasional efforts (e.g. Ekman 1928; Judd 1987, 2007). Taxonomic surveys were general and few taxonomists have investigated specific plant genera or families. Yet, when such work has been conducted, it has often resulted in the description of several new species, as for the Melastomataceae genera *Mecranium* (Skean 1993) and *Miconia* (e.g. Judd 2007; Judd et al. 2014; Majure et al. 2014). This high degree of endemism combined with the only modest collecting and taxonomic efforts undertaken so far, strongly suggests that there remain new species to be described in the primary forests of Haiti.

We recently performed three field trips in the Massif de la Hotte and the Massif de la Selle in Southern Haiti to study the systematics, pollination, and evolution of Gesneriaceae species (Clark 2015; Lambert et al. 2017; Joly et al. 2018; Faure and Joly 2020). We report here three new species of *Gesneria* from the Parc National Pic Macaya that were discovered during these research expeditions.

Materials and Methods

Criteria for Species Delimitation—As a general guideline for species delimitation, we followed the unified species concept assuming that species represent independently evolving lineages (De Queiroz 2007). In this study, species are delimited mostly using morphological information, although decisions are also informed by phylogenetic analyses of multiple genes and seed germination rates. At the morphological level, individuals are considered to belong to different species when there is a sufficient gap in the morphological variation between species compared to intraspecific variation that suggest a lack of genetic exchange between those entities.

Plant Material—Most of the material utilized in this study came from three field trips in Haiti, but we also studied herbarium specimens from FLAS, NY, S, and US. We visited the Massif de la Hotte and the Massif de la Selle in May 2014 and January 2015. We returned to the Massif de la Hotte in January 2018. Herbarium specimens were used to measure and score morphological characters, and species descriptions were supplemented from field notes and photographs. All specimens collected by the authors and used in this research were legally collected in collaboration with the Les Cayes Botanical Garden.

Seed Germination—A minimum of 100 seeds per plant were placed on wet filtered paper in a glass petri dish to estimate germination rates. Germination rates were estimated after two weeks, which is when the majority of seeds had reached the cotyledon stage.

Leaf Morphometry—To aid species delimitation, we performed elliptical Fourier analyses of leaf shape. We took photographs of herbarium specimens and selected one suitably spread leaf from each specimen for analyses (see Table 1). The background was masked and the contrast adjusted to have a clear demarcation of the leaf. Morphometric analyses were performed with the Momocs package (version 1.4.0, Bonhomme et al. 2014) in the R statistical software (R Core Team 2022). Images were imported in R and converted to outlines. We determined the number of harmonics to use for the elliptical Fourier analysis as the number for which the sum of harmonic power was greater than 99%. We extracted the Fourier coefficients for nine harmonics using two smoothing iterations

Table 1. Voucher specimens used in this study. An asterisk indicates that the sample was included in both the morphometric and molecular study and a double asterisk indicates that the sampled was only used in the molecular study.

Species	Vouchers
G. bicolor	HAITI: Massif de la Hotte: Lambert 2014–001* (MT 194020, 194021); Lambert 2014–002 (MT 00194022)*; Clark 14321 (NY 2647383); Clark 14364 (NY 2647384); Clark 14494 (NY 2647417); Skean 2466 (FLAS 217397); Franz 6 (FLAS 177975); Joly s.n. dna1325**.
G. cornuta	HAITI: Massif de la Hotte: Joly 1115 (MT); Joly 1116 (MT)*; Joly 1117 (MT); Joly 1125 (MT)*; Joly 1110 (MT)*; Clark 14493 (NY 2647412).
G. ekmanii	HAITI: Massif de la Hotte: Ekman S11–12402 (S); Ekman R-7524 (S); Joly 1118 (MT); Massif de la Selle: Lambert 2014–018 (MT 194044); Lambert 2014–020 (MT 194046, 194047); Lambert 2014–024 (MT); Clark 14517 (NY 2647406); Clark 14525 (NY 2647407); Judd 4437 (FLAS 177961, 177962).
G. flava	HAITI: Massif de la Hotte: Lambert 2014-007 (MT)*; Lambert 2014-009 (MT 194029)*; Lambert 2014-010 (MT 194030, 194031)*; Joly 1127 (MT)*; Joly 1119 (MT)*; Joly 1120 (MT); Judd 3475 (US 325978; FLAS 117970); Skean 2522 (FLAS 217396).
R. auriculatum	HAITI: Massif de la Hotte: <i>Lambert 2014–014</i> (MT 194038, 194039)**.

and harmonics were normalized for size and rotation using the first harmonic. We checked visually that the normalization did not result in bad alignments. We then performed a principal component analysis (PCA) on the Fourier coefficients to highlight differences between specimens. Only the principal components that cumulatively represented 95% of the variance were further considered. The data and R scripts were deposited in Dryad (Joly et al. 2022).

DNA Sequencing—To test if one of the species described was of hybrid origin, we sequenced the putative hybrid and parent species (see Table 1) for five single copy nuclear genes: CYCLOIDEA, GAPDH, UF3GT, F3H, and CHI. DNA amplification and sequencing are described elsewhere (Joly et al. 2018). We aligned sequences from both directions for each individual into contigs and manually checked the sequences for evidence of polymorphisms in the chromatograms that would suggest allelic variation. The polymorphic nucelotides identified were coded using the ambiguity codes from the International Union of Pure and Applied Chemistry (IUPAC). We then aligned all sequences with MAFFT (Katoh and Standley 2013) using the L-INS-i settings and then phased the individual sequences to obtain allelic sequences using seqphase (Flot 2010) and Phase (Stephens et al. 2001). A sequence of Rhytidophyllum auriculatum Hook. was included as the outgroup following Joly et al. (2018). Phylogenies for all markers were reconstructed using RAxML (Stamatakis 2014) using the GTRGAMMA nucleotide substitution model. The NCBI accession numbers and DNA alignments and sequences were deposited in Dryad (Joly et al. 2022).

RESULTS

Overview of the New Species—To facilitate the description of the results, we first provide a brief overview of the newly described species. Species delimitation was based on all the information gathered and presented in the results. The complete taxonomic description can be found below.

Gesneria flava differs mainly from other species by its large pale yellow flowers with wide and long leafy-looking sepals (Fig. 1). Its leaves are similar to *G. ekmanii* (but see below) except for the adaxial surface that is covered by numerous stiff hairs that make the surface very rough. The abaxial leaf surface of *G. flava* is unique because of its rugose surface relative to the flat surface in other congeners.

Gesneria \times cornuta is intermediate in morphology between G. flava and G. bicolor (Fig. 2). It has large curved flowers with various shades of reds and yellows (Fig. 2C, D). The petioles are smaller than those of G. flava, the leaves are more symmetric than those of G. bicolor, and the size and shape of calyx lobes are intermediate between G. bicolor and G. flava and is a good diagnostic character. The adaxial leaf surface is covered with numerous small hairs but the surface is not as rough as that of G. flava.

Gesneria radiata differs by the presence of white corollas that are radially symmetrical and an obligate lithophytic habit (Fig. 3).

A New Combination—While studying the species of Gesneria from Haiti, it became evident to also present a new combination. Here we formally propose the new combination Gesneria bicolor for Rhytidophyllum bicolor given that a previous phylogenetic analysis clearly showed that this species strongly groups within a monophyletic Gesneria clade according to the phylogenetic analysis of five single copy nuclear genes (Joly et al. 2018).

Seed Germination—The following germination rates were observed: *G. bicolor (Joly 1134)* = 0.875% (n = 136 seeds), *G. flava (Joly 1119)* = 0.254% (n = 228), *G.* × *cornuta (Joly 1110)* = 0% (n = 534).

Morphometry—We performed a leaf morphometric analysis for two reasons. First, we wanted to test whether the leaf shapes of *G.* × *cornuta* were intermediate between those of *G. flava* and *G. bicolor*. Second, we wanted to test if the leaf shapes of *G. flava* and *G. ekmanii* could be distinguished.

The first nine Fourier harmonics represented more than 99% of the sum of harmonic power. The first four principal components of the principal component analysis (PCA) represented more than 95% of the morphological variance, with the first component representing by far the largest portion with 78.2% of the variance. This first axis represented variation from lanceolate to ovate leaves, the second represented curvature in the leaf main axis, which mostly characterize variation present in *G. bicolor*, the third axis broadly represents leaf variation from ovate to obovate, and the fourth axis represents minor variation in bilateral leaf asymmetry (Fig. 4).

Three groups can be distinguished along the first PC: one that consists of the species *G. bicolor* with narrow leaves, a second that is intermediate and that consists of individuals from *G. × cornuta*, and a last group that comprises two species recognized here, *G. flava* and *G. ekmanii*. The leaves of these last two species can be differentiated along the third PC: *G. ekmanii* has relatively obovate leaves whereas those of *G. flava* are more oval. The leaves of the type specimens of *G. ekmanii* fall within the cloud of points formed by the *G. ekmanii* individuals that we sampled (Fig. 4).

Phylogenetic Analyses—The fact that $G. \times cornuta$ is intermediate in morphology between G. flava and G. bicolor persuaded us to further test if it was a hybrid between these latter species. Initial phylogenetic analyses indicated that all allelic sequences recovered from $G. \times cornuta$ grouped with G. flava and G. bicolor in a phylogenetic analysis of the whole genus (not shown). We thus only analyzed the sequences of these three species here. The alleles of G. bicolor and G. flava

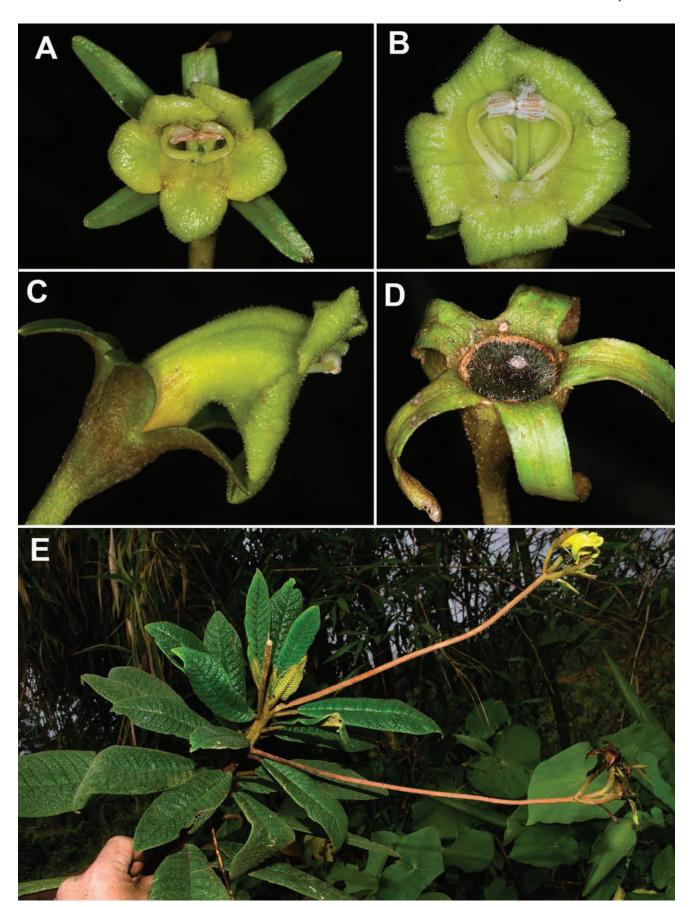


Fig. 1. Gesneria flava. A. Front view of corolla and sepals. B. Front view of corolla. C. Lateral view of flower. D. Immature fruit. E. Habit. Photos of J.L. Clark 14460 (A, B, C, D) and J.L. Clark 14492 (E).

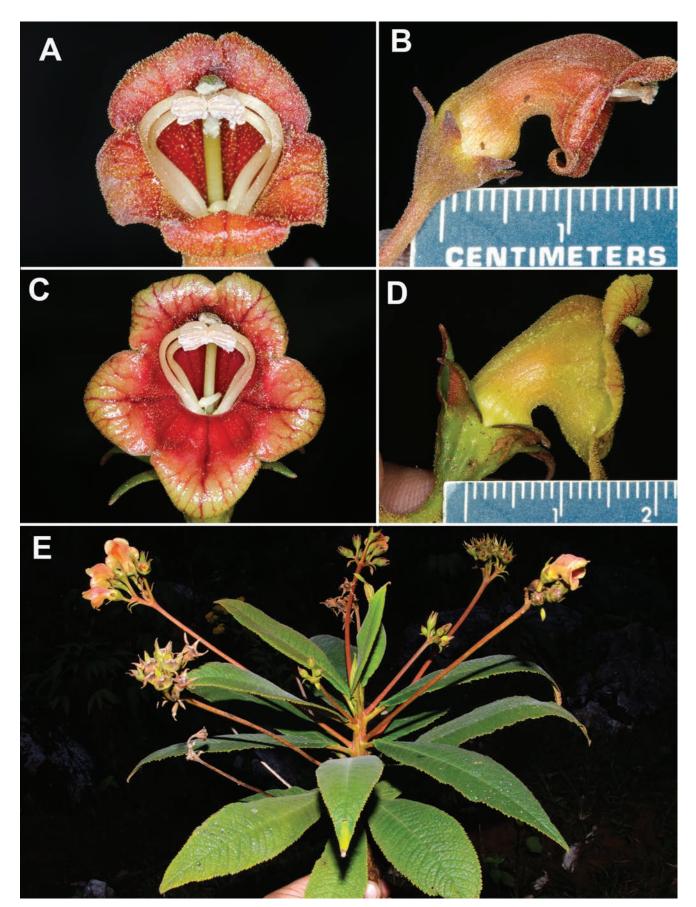


Fig. 2. Gesneria bicolor. A. Front view of corolla of G. bicolor. B. Lateral view of flower of G. bicolor. C–E. Gesneria × cornuta. C. Front view of corolla of Gesneria × cornuta. D. Lateral view of flower of Gesneria × cornuta. E. Habit of Gesneria × cornuta featuring the broadly ovate leaf blades. Photos of J.L. Clark 14321 (A, B) and J.L. Clark 14494 (C, D, E).

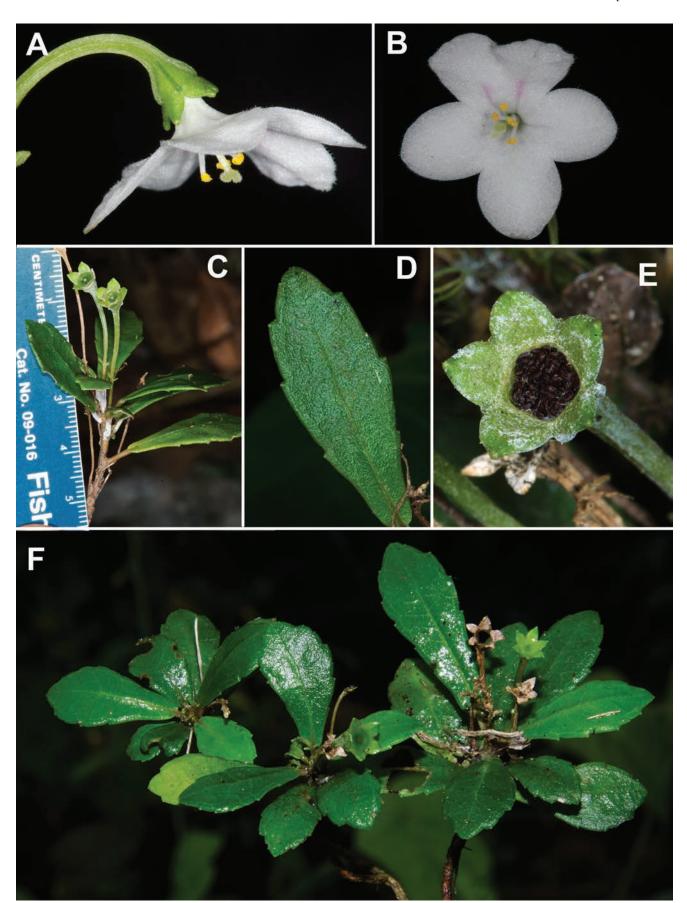


Fig. 3. Gesneria radiata. A. Lateral view of flower. B. Front view of corolla. C. Habit. D. Upper surface of leaf. E. Mature bivalved capsule. F. Habit. Photos of J.L. Clark 14465 (A–E) and J.L. Clark 14491 (F).

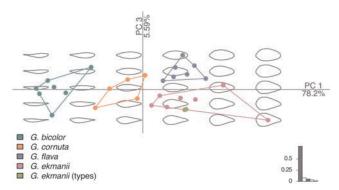


Fig. 4. Elliptical Fourier analysis of the leaf shapes of the species described in this study and *Gesneria ekmanii* (including the type specimens) that have leaves with a shape similar to *G. flava*.

formed distinct groups for all genes with the exception of *UF3GT* for which one allele of *G. bicolor* was identical to *G. flava* sequences (Fig. 5). These gene phylogenies suggest that *G. bicolor* and *G. flava* form distinct species and that there is none or very little gene flow between them.

In contrast, all individuals of $G. \times cornuta$ had one allele identical to G. bicolor sequences and another identical to G. flava sequences, strongly supporting a hybrid origin of $G. \times cornuta$ (Fig. 5). Some intraspecific variation was observed among individuals of $G. \times cornuta$ for GAPDH and UF3GT. Interestingly, some alleles from $G. \times cornuta$ were not observed in the two putative parents, opening the

question as to whether this variation occurred in G. × cornuta after its origin or if it is due to distinct origins from individuals of G. bicolor and G. flava but that these specific alleles were not sampled in the present study.

DISCUSSION

We present three new species of Gesneria from the Parc Pic Macaya in Haiti and a new species combination. The new species are morphologically distinct, based on floral and vegetative characters, and are genetically distinct as well (Fig. 5; Joly et al. 2018, where G. flava is referred to as G. sp. nov). Gesneria flava is distinct from other species of Gesneria by its floral morphology. Its leaves are also distinctive because of the rugose abaxial leaf surfaces, although we note that they are relatively similar in shape to those of G. ekmanii. Interestingly, the type specimen of G. ekmanii comes from the Massif de la Hotte, the same locality as G. flava, but the vast majority of the G. ekmanii specimens represented in herbaria are from the Massif de la Selle, located some 100 km east and isolated from the Massif de la Hotte by lowlands. Because the type specimen of G. ekmanii did not bear flowers and because of its vegetative similarity with the G. flava specimens, we performed a morphometric analysis to see if the two species could be distinguished. The Fourier analysis showed that G. flava and G. ekmanii can be differentiated by their leaf shapes and that the type specimens of G. ekmanii from the Massif de la Hotte group with the specimens of G. ekmanii from the Massif de la

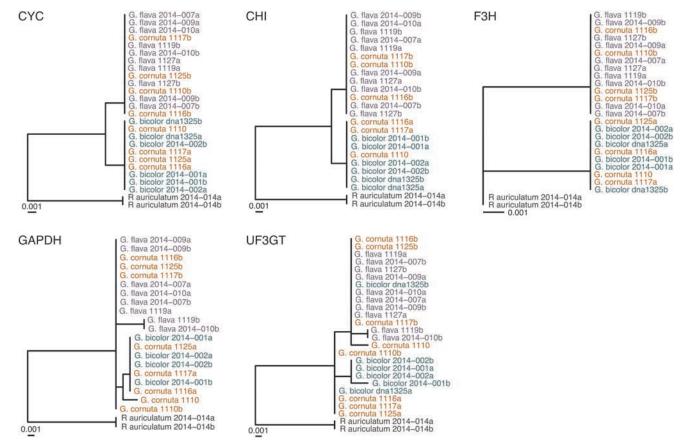


Fig. 5. Gene genealogies for five single copy nuclear genes. All phylogenies were rooted using *Rhytidophyllum auriculatum* (not shown). The numbers after the species names refer to the collection numbers (see Table 1) and they are followed by a random letter to differentiate the alleles present in each individual

Selle. Finally, specimens of *G. ekmanii* were collected during a 2018 research expedition to the Massif de la Hotte (*S. Joly 1118* (MT)), supporting the distinct nature of these two species and a broadly distributed distribution of *G. ekmanii* in Massif de la Hotte (Haiti), the Massif de La Selle (Haiti), and the Sierra de Neiba (DR). The morphometric analyses presented here and the phylogenetic data from Joly et al. (2018, where *G. flava* is referred to as *G.* sp. nov) strongly support that *G. flava* and *G. ekmanii* are distinct species.

Gesneria × *cornuta* is unique because our data suggests that it is of hybrid origin between *G. flava* and *G. bicolor*. Its flowers (Fig. 2A-D) and leaves (Fig. 4) are intermediate between G. flava and G. bicolor. Our molecular data suggest that it possesses allelic sequences that belong to both species for all genes sequenced. This, combined with the phylogenetic results supporting G. flava and G. bicolor forming distinct groups in the genealogies for four out of the five genes studied, strongly supports a hybrid origin for $G. \times cornuta$. The seeds of G. \times cornuta collected in the field were found to all be sterile, which contrasts with the germination rates for G. flava (25%) and G. bicolor (88%). Because germination rates can be affected by several factors, these estimates do not confirm that all $G. \times cornuta$ plants are sterile. However, given that it is likely a hybrid between two relatively distant species (given the genetic distinction observed), it seems possible. If it were the case, it would suggest that most $G. \times cornuta$ individuals found in nature would be F1 hybrid individuals. The sterility of F1 hybrids would also imply that this hybrid species, which is common in the park, has to be maintained via constant hybridization events. This is somewhat surprising given the relative scarcity of G. flava. In contrast, G. bicolor is one of the most abundant shrubs in this region of the park where it was observed frequently along ravines and in disturbed areas. Yet, the perennial nature of these shrubs certainly allows individuals to persist for many years, contributing to the maintenance of population numbers. In summary, given the amount of evidence for a hybrid origin of $G. \times cornuta$, it is designated as a nothospecies.

Implication for Conservation—The fact that three new species of Gesneriaceae are endemic to the Massif de la Hotte (we haven't found them in two trips in the neighbor Massif de la Selle) is consistent with previous reports of high local plant endemism of the Caribbean region and suggests that many more plant species have yet to be described. Whether these species will be described before they go extinct is another urgent question. The Parc Pic Macaya is located to the southwest of Haiti, in the Massif de la Hotte, and represents the highest concentration of primary forest in Haiti. The Massif de la Hotte is a region of exceptional plant diversity that harbors 37 endemic taxa of Miconia (Melastomataceae) and 19 endemic species of Pilea (Urticaceae) (Judd 2019). Nevertheless, the designation of a National Park in the 1980s has not stopped deforestation. And the overhaul of the main road leading to the park in 2018 is likely to jeopardize its biodiversity. If the highest parts of the park are better protected (Pic Macaya culminates at 2347 m) the buffer zone with the most intense human activities and deforestation is also the habitat where we find the greatest diversity of flowering plants. This hardwood karst cloud forest, called "rak bwa" in Creole, is also the region of highest diversity in Gesneriaceae. Most Caribbean Gesneriaceae species occur between 800 m and 1500 m. Within the Caribbean, the Massif de la Hotte is currently the region with the highest known species diversity for

TABLE 2. Gesneriaceae species in the Parc Pic Macaya or its vicinity. Asterisks indicate endemic taxa in the Massif de la Hotte mountain range.

Species

Besleria lutea L.
Bellonia spinosa Sw.
Columnea scandens L.
Columnea domingensis (Urb.) B.D.Morley
Gesneria sp. indet.
Gesneria aspera Urb. & Ekman
Gesneria bicolor (Rub.) Simon Joly & J.L.Clark*
Gesneria × cornuta Simon Joly*
Gesneria cubensis (Decne.) Baill.
Gesneria ekmanii Urb.
Gesneria flava Lambert, Simon Joly & J.L.Clark*
Gesneria fruticosa (L.) Kuntze
Gesneria radiata J.L.Clark & Cinea*
Gesneria reticulata (Griseb.) Urb.

Gesneria viridiflora (Decne.) Kuntz subsp. acrochordonanthe L.E.Skog* Rhytidophyllum auriculatum Hook.

Gesneriaceae with 14 species and one subspecies, including six endemics (Table 2), while there are ca. 84 species in total in the whole Caribbean region (Clark et al. 2019). The only other Caribbean region that compares with a similarly high level of Gesneriaceae diversity is El Yunque de Baracoa in eastern Cuba with ten gesneriad species, including two endemics. We hope that better describing and characterizing the species of this region will bring more attention to Pic Macaya as well as more resources to protect this important biodiversity hotspot.

TAXONOMIC TREATMENT

Gesneria flava Lambert, Simon Joly & J.L.Clark, sp. nov. Type: Haiti. Département du Sud: Massif de la Hotte, Parc National Pic Macaya, forested area near Ville Fromon, 18°19′11′′N, 74°00′41′′W, 986 m, 13 Jan 2015, J.L. Clark, W. Cinea, I. Henrys, M. Despagne & M. Sturla 14465 (holotype: MT!; isotypes: B, E, FLAS, G, K, MO, NY!, P, SEL!, UNA, US!).

Differs from other species by flowers with a relatively large uniformly pale yellow corolla and wide elongate green sepals. Its elliptic, oblanceolate to obovate leaves are similarly shaped to those of *G. ekmanii* but tend to be more obovate. The leaf adaxial surface is covered with numerous small stiff hairs making the surface very rough, while the abaxial leaf surface is rugose, which contrasts to the smooth surface of *G. ekmanii*.

Evergreen shrub up to 5 m tall, generally few-branched; bark brown to brown-red colored, corky at base, many verrucose vertical lenticels toward apex. Apex resinous. Leaves alternate; petioles 1.2–3.8 cm long, brown to reddish, sometimes green for young leaves; blades elliptic or oblanceolate or obovate, 11–30 cm long, 3–8 cm wide, coriaceous, base cuneate to rounded, apex acute, margin serrulate; adaxial surface shiny green, hispid with numerous small thick and spiky trichomes, abaxial surface light green, rugose and resinous; major veins prominent with few trichomes, resinous, and lightly verrucose, tertiary veins reticulate with few trichomes. Inflorescences axillary, 1–4 flowered cymous; peduncles 12.5–27 cm long, light brown or reddish-brown, lightly resinous; pedicels 0.5–4.4 cm long, green, sometimes reddish at the base; flowers gynandrous; calyx lobes 5, leafy looking,

1.2–2.2 cm long, 4–6 mm wide at base, apex rounded to acute, margin smooth or serrulate, green, curled during anthesis; corolla campanulate with a constriction near the base, pale yellow, 6–7 mm wide at the base, 19–21 mm wide at corolla opening, pilose with glandular trichomes; lobes 5, margin entire, upper lobes 6–7 mm long and 7–8 mm wide, lateral lobes 5–7 mm long and 7–8 mm wide, basal lobes 5–6 mm long and 6–8 mm wide; staminal filaments 10–12 mm long, white, glabrous, fused at circa 1 mm of the corolla base; 4 oblong coherent anthers, circa 3 mm long, 1.5–2.0 mm wide; staminode circa 5 mm long; pollen white; ovary inferior, disc 5-angled, annular, 5–6 mm long, 5–6 mm wide, green; style circa 12 mm long, glabrous, stigma stomatomorphic. Capsule turbinate, 7–10 mm long, 6–9 mm wide, brown, with persistent calyx lobes. Seeds 0.74–1.02 mm long, obovate, striate and sometimes slightly angulate.

Distribution and Habitat—*Gesneria flava* is a relatively rare endemic to the Massif de la Hotte in Southwest Haiti. It grows in primary to disturbed broadleaved forest over limestone (rak bwa) at altitudes of 950 to 1500 m.

Etymology—The name of the species is a reference to the yellow color of its flowers.

Additional Specimens Examined—Haiti. —DEPARTMENT SUD: Massif de la Hotte, Parc National Pic Macaya, Bois Formond, Butte de karst à l'est du chemin menant vers Formon. À quelques centaines de mètres de Formond, 997 m, 18.319789°N, 74.008137°W, 15 May 2014, Lambert, Joly & Merizier 2014-009 (MT); Massif de la Hotte, Parc National Pic Macaya, Bois Formon, Butte de karst à l'est du chemin menant vers Formond. À quelques centaines de mètres de Formond, 1015 m, 18.318873°N, 74.009327°W, 15 May 2014, Lambert, Joly & Merizier 2014-010 (MT); Massif de la Hotte, Parc National Pic Macaya, Bois Formon, in Rakbwa, 1012 m, 18.31901°N, 74.00919°W, 24 January 2018, Joly et al. 1119 (MT); Massif de la Hotte, Parc National Pic Macaya, Bois Formon, in Rakbwa, 1012 m, 18.31901°N, 74.00919°W, 24 January 2018, Joly et al. 1120 (MT); Massif de la Hotte, Parc National Pic Macaya, Bois Formon, in Rakbwa at the top of a hill, 1101 m, 18.32034°N, 74.01727°W, 27 January 2018, Joly, Bilbao & Beljean 1127 (MT); Massif de la Hotte, Parc National Pic Macaya, Fond Bleu, dry river on southern slopes of Morne Formon, near Ville Formon, 1528 m, 18°20′59′′N, 74°1'22''W, 12 January 2015, Clark et al. 14443 (MT, NY, SEL, US); Massif de la Hotte, Parc National Pic Macaya, forested area near Ville Formon, 957 m, 18°19'17''N, 74°0'32''W, 42 January 2015, Clark, Cinea & Sturla 14492 (MT, NY, SEL, US); Massif de la Hotte, Parc National Pic Macaya, Bois Formon, to the south of Morne Formon, 950-1050 m, 23 January 1984, Judd 3475 (US); Massif de la Hotte, Macaya Biosphere Reserve, Bwa Deron, along S edge at cliffs, 1100–1200 m, 9 August 1989, Skean & McMullen 2522 (FLAS).

Conservation—Gesneria flava is endemic to the lower slopes of Pic Macaya. The high rates of deforestation throughout Haiti and recent increase in human activities inside the park are factors that risk the remaining extant forest. Therefore, this new species is likely to be categorized as Critically Endangered (CR) according to the IUCN Red List criteria (IUCN 2012, 2019) for restricted geographic range (B1 a,b,c + B2 a,b,c).

Gesneria × cornuta Simon Joly, nothosp. nov. Type: Haiti. Département du Sud: Massif de la Hotte, Parc National Pic Macaya, Morne Cavalier, 1106 m, 25 Jan 2018, Joly & Faure 1125 (holotype: MT!).

Natural hybrid between *G. flava* and *G. bicolor*. Similar to *G. bicolor*, but with larger flowers that have the shape of a cornucopia and longer calyx lobes. Petioles smaller than *G. flava* and leaf more symmetric than the asymmetric leaves of *G. bicolor*. The adaxial leaf surface is covered with numerous small hairs but the surface is not as rough as that of *G. flava*. Overall relatively intermediate in characters between *G. bicolor* and *G. flava*.

Evergreen shrub up to 3 m high, generally few-branched; bark brown to brown-red colored, corky at base, many

verrucose vertical lenticels toward apex. Apex resinous. Leaves alternate; petioles 0.4–1.2 cm, brown to reddish, sometimes green for young leaves; blades oblanceolate, symmetric to slightly asymmetric, 11-19 cm long, 2-5 cm wide, coriaceous, base cuneate, apex acute, margin serrulate; adaxial surface shiny green and hispidulous, abaxial surface light green, rugose with no trichomes; Major veins prominent, resinous and lightly verrucose with few trichomes; tertiary veins reticulate with few trichomes. Inflorescences axillary, 1-6 flowered cymous; peduncles 15-30 cm long and 0.2-0.3 cm wide, brown to reddish; pedicels 1–3 cm long, green with some red at the base; flowers gynandrous; calyx lobes 5, leafy looking, 7-10 mm long, 3-4 mm wide at base, apex acute, margin smooth or serrulate, green with frequent red at the tip; corolla campanulate with constriction near base, yellow and red, 21–23 mm long and 16–19 mm wide at corolla opening; lobes 5, margin entire; staminal filaments circa 20 mm long, white, glabrous; 4 coherent anthers oblong, circa 25 mm long, 1.5 mm wide; staminode present; pollen white; ovary inferior, 4-6 mm long, 4-8 mm wide, green; style circa 20 mm long, stigma stomatomorphic. Capsule turbinate, circa 7 mm long, 7 mm wide, brown. Seeds 0.8–1 mm long, obovate, striate and sometimes slightly bent.

Additional Specimens Examined—Haiti. —Department Sud: Massif de la Hotte, Parc National Pic Macaya, Forested area near Ville Formon, 957 m, 18.3214° N, 74.0089° W, 14 January 2015, Clark 14493 (NY); Massif de la Hotte, Parc National Pic Macaya, Bois Formon, in Rakbwa, 996 m, 18.31891° N, 74.00809° W, 21 January 2018, Joly, Faure & Honnete 1110 (MT); Massif de la Hotte, Parc National Pic Macaya, Morne Cavalier, Rakbwa on a slope, 1186 m, 18.32427° N, 74.02701° W, 22 January 2018, Joly & Faure 1115 (MT); Massif de la Hotte, Parc National Pic Macaya, Morne Cavalier, Rakbwa on a slope, 1199 m, 18.32595° N, 74.02484° W, 22 January 2018, Joly & Faure 1116 (MT); Massif de la Hotte, Parc National Pic Macaya, Morne Cavalier, Rakbwa on a slope, 1199 m, 18.32595° N, 74.02484° W, 22 January 2018, Joly & Faure 1117 (MT).

Distribution and Habitat—This relatively infrequent species is endemic to the Massif de la Hotte in Southwest Haiti. It grows in disturbed broadleaved forest on limestone (rak bwa) at altitudes between 1000 to 1200 m. It grows in the same areas with *Gesneria bicolor*.

Biology—This species is a natural interspecific hybrid between *Gesneria bicolor* and *Gesneria flava*. All seeds evaluated failed to germinate, suggesting it may not be able to reproduce sexually.

Etymology—The name of this species refers to its large curved flowers that have the shape of a cornucopia.

Conservation—Gesneria \times cornuta is endemic to the lower slopes of Pic Macaya. The high rates of deforestation throughout Haiti and recent increase in human activities inside the park are factors that risk the remaining extant forest. Therefore, this new species is likely to be categorized as Critically Endangered (CR) according to the IUCN Red List criteria (IUCN 2012, 2019) for restricted geographic range (B1 a,b,c + B2 a,b,c).

Gesneria radiata J.L.Clark & Cinea, sp. nov. Type: Haiti. Département du Sud: Massif de la Hotte, Parc National Pic Macaya, Bwa Formon, in rak bwa on hills in vicinity of village Formon, 18°19′11′′N, 74°00′41′′W, 986 m, 13 Jan 2015, J.L. Clark, W. Cinea, I. Henrys, M. Despagne & M. Sturla 14465 (holotype: US!; isotypes: MT! NY! SEL!).

Differs from all other congeners by the presence of uniformly white radially symmetrical corollas and an obligate lithophytic habit.

Lithophytic stout herb with erect shoots, up to 10 cm tall, rarely branched at base; stems suffrutescent, brownish red.

Leaves alternate; petioles 0.2–0.4 cm long, light green; blades oblanceolate to obovate, 2.5-3.5 cm long, 1.0-1.5 cm wide, coriaceous, base rounded, apex acute, margin with 3-5 serrations clustered near apex; adaxial surface shiny green, glabrous, abaxial surface light green, glabrous, secondary venation suppressed when live, more prominent when dry. Inflorescence reduced to single axillary flowers; remnant old flowers persistent at base, 1-3 mature flowers near apex; peduncles 3–5 mm long with a pair of reduced bracts subtending pedicels; pedicels nodding during anthesis and erect with mature fruits, with five elongate prominent wings that initiate ca. 5 mm above base, becoming prominent near apex, 1.6 cm long, green. Flowers protandrous; calyx lobes 5, equal in size and shape, uniformly light green, 13-16 mm long, 10-15 mm wide at base, apex acute, margin entire, spreading to truncate at anthesis; corolla truncate and nearly radially symmetrical, lobes fused in a shallow tube, upper lobes slightly fused at base, other lobes nearly free, uniformly white, each lobe 4-5 mm wide at the base, 4-6 mm long, margins of corolla lobes with small pilose trichomes. Androecium with filaments 2.5-3.5 mm long, white, glabrous, adnate for ca. 1 mm at base of corolla tube; 4 oblong free anthers, ca. 2 mm long, 1.5–2.0 mm wide; staminode not observed; pollen yellow; ovary inferior; disc and gynoecium not observed. Fruit a bivalved capsule, subglobose to avoid, splitting broadly and cup-shaped, 7-10 mm long, 6-9 mm wide, with persistant calyx lobes. Seeds numerous, reddish-brown, 0.4–0.8 mm, fusiform to subglobose, spirally striate.

Additional Specimens Examined—Haiti. —DEPARTMENT SUD: Massif de la Hotte, Parc National Pic Macaya, Forested area near Ville Formon. Broad-leaved wet forest on exposed limestone referred to locally as "rak bwa," 957 m, 18°19′17′′N, 74°0′32′′W, 14 Jan 2015, J.L. Clark, W. Cinea & M. Sturla 14491 (MO, MT, NY, SEL, US).

Distribution and Habitat—Gesneria radiata is an obligate lithophyte that is endemic to the Massif de la Hotte in Southwest Haiti. It is located on exposed vertical limestone in shaded forests referred to locally as "rak bwa" near the village of Ville Formon, ca. 950–1000 m. This rare species was only observed in two adjacent populations throughout three expeditions to the region.

Etymology—The name of this species refers to its radially symmetrical flowers.

Conservation—Gesneria radiata is geographically limited to two adjacent populations on the lower slopes of Pic Macaya. The high rates of deforestation throughout Haiti and recent increase in human activities inside the park are factors that risk the remaining extant forest. Therefore, this new species is likely to be categorized as Critically Endangered (CR) according to the IUCN Red List criteria (IUCN 2012, 2019) for restricted geographic range (B1 a,b,c + B2 a,b,c).

Gesneria bicolor (Urb.) Simon Joly & J.L.Clark, comb. nov. Rhytidophyllum bicolor Urb., Arkiv för Botanik 17(7): 56. 1921.
 Holotype: Haiti, Département du Sud, Morne de la Hotte, 800 m, 11 June 1917, E. L. Ekman H 193 (S S-R-7527!).

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AUTHOR CONTRIBUTIONS

All authors planned and performed field work, with the logistics being supervised by WC. SJ, FL, and JLC measured specimens, described the species, and wrote the first draft of the manuscript. SJ performed the morphometric and DNA analyses. All authors critically edited and reviewed the manuscript.

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