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EVOLUTION OF THE CARIBBEAN SPECIES OF *COLUMNNEA* (GESNERIACEAE) WITH AN EMPHASIS ON THE JAMAICAN SPECIES

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Premise of research. Biogeography has improved understanding of evolution and diversification of organisms on both continental and island systems. One complicated island group in terms of geological history and biogeographic pattern is the Caribbean island system. A comparison across taxonomic groups does not result in overarching patterns for this group of islands. *Columnnea* has the greatest number of species endemic to the Caribbean for any genus in Gesneriaceae that is not mostly endemic to the Caribbean with 16 species. Thirteen of these species are found on Jamaica, the remaining three each endemic to Cuba, Hispaniola, and Puerto Rico. In addition, populations of *Columnnea sanguinea* and *Columnnea scandens* are known from both mainland and multiple Caribbean islands. We investigate the pattern of evolution in Caribbean species of *Columnnea* and attempt to explain the large number of species found on the island of Jamaica relative to the other islands. We explicitly test whether Caribbean species of *Columnnea* are monophyletic and whether the 13 species endemic to Jamaica are a monophyletic group. This genus can help understand biogeographic patterns and modes of speciation in the Caribbean.

Methodology. We sampled all Caribbean species of *Columnnea* using DNA sequence data and phylogenetic methods to understand the pattern of diversity to determine whether multiple or single introductions could explain the diversity on the Caribbean islands.

Pivotal results. The Caribbean species do not form a monophyletic group. The Jamaican species are monophyletic, and the endemic Cuban species, *Columnnea tincta*, is sister to 12 of the Jamaican species, with *Columnnea pubescens* sister to *C. tincta* + remaining Jamaican species. Most Jamaican species share similar corolla morphologies to section *Columnnea*. Although never recovered as part of section *Columnnea*, approximately unbiased tests cannot reject a sister group relationship of the Jamaican/Cuban endemic clade to section *Columnnea* but can reject inclusion in section *Columnnea*.

Conclusions. The high diversity of *Columnnea* in the Caribbean is due to the disproportionate number of species on Jamaica, but there is no obvious explanation for the radiation on this island, despite considering island size, topography, pollinators, and dispersers. The large number of species could be attributed to over-splitting on Jamaica, but even if a narrower concept were followed, and four of the species were combined as varieties of *Columnnea hirsuta* as earlier taxonomy had predicted, the number of morphologically distinctive species would still be nine and much greater than that of the other islands. Our data also indicate that *C. hirsuta* sensu lato is not monophyletic.

Keywords: diversification, island biogeography, key innovation, speciation, topography, *Columnnea*.

Online enhancement: supplemental figure.

Introduction

The distribution of biological diversity across the planet, including how it got to be where it is and why it persists there,

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has been a puzzle facing naturalists that precedes the theory of natural selection (Humboldt 1805; Schouw 1823; Brongniart 1828; Swainson 1835; Darwin 1839; Sclater 1858) and has continued to the present day (Huxley 1868; Wallace 1860, 1869, 1876, 1880; MacArthur and Wilson 1963, 1967; Carlquist 1965; Brundin 1972; Raven and Axelrod 1974; Platnick and Nelson 1978; Rosen 1978; Nelson and Platnick 1981; Ronquist and Cannatella 1997; Ree and Smith 2008; Yu et al. 2010; Matzke 2013). The insights that arose after proposing evolution

by natural selection clearly drove the study of biogeography into more specific questions. The advancement of island biogeography theory (MacArthur and Wilson 1963, 1967; Carlquist 1965) and molecular systematics (Hillis and Moritz 1990), coupled with new analytical tools (Ronquist and Cannatella 1997; Ree and Smith 2008; Yu et al. 2010; Matzke 2013), has resolved many questions that puzzled the first naturalists about why species are where they are and how they came to have that distribution.

In the past 20–25 years there has been a growing interest in the evolution of biological diversity on islands using phylogenetic approaches. Major advancements in our understanding of the origins and evolution of the Hawaiian flora have occurred with a new and better understanding that this group of isolated volcanic islands has also been biologically isolated, with fewer source introductions for many groups than had previously been assumed (Baldwin et al. 1990, 1991; Givnish et al. 1995; Gillespie and Croom 1995; Tarr and Fleischer 1995; Gemmill et al. 2002; Cronk et al. 2005; Clark et al. 2008), and that speciation and diversification within the islands has been the explanation for the tremendous diversity. The distance from source populations on Hawaii certainly matches MacArthur and Wilson's (1963, 1967) prediction that diversity on the island would result from few colonizers. Other islands not as isolated as the Hawaiian chain have also been the focus of studies on evolutionary biogeography, and they include New Zealand (Trewick 1997; Wagstaff and Garnock-Jones 1998; von Hagen and Kadereit 2001; Winkworth et al. 2002; Woo et al. 2011), Madagascar (Buerki et al. 2008; Callmander et al. 2016; Gostel et al. 2016, 2016; Bauret et al. 2017), and New Caledonia (Smith et al. 2007; Swenson et al. 2007; Ladiges and Cantrill 2007; Woo et al. 2011).

The present distance from the mainland and size of islands has been critical for interpreting many of the patterns seen with island biodiversity (MacArthur and Wilson 1963, 1967). However, geological advances have allowed even greater interpretation of patterns than MacArthur and Wilson (1963, 1967) could have predicted. Knowledge that some islands were parts of continents, that others are volcanic in origin, that none have been the same size or distance from mainlands throughout their existence, and that some have been completely submerged during their histories has altered how we interpret the evolution of biological diversity in island systems (Cracraft 1973; Raven and Axelrod 1974; Molnar et al. 1975; Iturralde-Vinent and MacPhee 1999; Campbell and Landis 2003; Yoder and Nowak 2006; Grandcolas et al. 2008; Heads 2008; Whitaker et al. 2008).

A group of islands where biogeography has clearly benefited from a better understanding of geology is the Caribbean (Iturralde-Vinent and MacPhee 1999). The geological history of this group of islands is complicated and unlikely to be completely resolved at present. However, better knowledge of the origins of many of the islands and their histories of connections in the past has greatly enhanced our ability to interpret distributions of the biota, mainland sources, and likelihood that evolution and diversification took place in situ. The concept of GAARlandia (Iturralde-Vinent and MacPhee 1999), where the Greater Antilles and Aves Ridge were once connected to mainland South America, has been an important explanation for much of the diversity in the Caribbean islands, and even when patterns do not match the GAARlandia hypothesis it is an important null model against which to test. The biogeography of

the Caribbean reflects the complexity of the geology, fluctuating sea levels, and proximity of subsets of the islands to North America, Central America, and South America. The Antilles are a major wintering ground for many Nearctic migrants (Wunderle and Waide 1993) as well as being a flyway for some bird species that migrate from South America to North America and back, although most studies indicate that the flights are made without any stopovers (SELVA 2017).

The Gesneriaceae are diverse in the Neotropics in general (Weber et al. 2013), with a large diversity in the Caribbean. Four genera are mostly endemic to the Caribbean (*Gesneria*, *Rhytidophyllum*, *Pheidonocarpa*, and *Bellonia*; Skog 1976; Roalson et al. 2008; Weber et al. 2013; Möller and Clark 2013), but an additional 13 genera have at least one to five species on the Caribbean islands (excluding the Old World-introduced *Saintpaulia ionantha* H. Wendl.) with *Columnnea* having 18 species distributed among the islands (Acevedo-Rodriguez and Strong 2017), 16 of which are endemic to a single island (Morley 1974). The remaining two species, *Columnnea sanguinea* and *Columnnea scandens*, are relatively widespread and found on multiple islands as well as mainland areas (Morley 1974; Acevedo-Rodriguez and Strong 2017). The endemic species are *Columnnea ambigua* from Puerto Rico, *Columnnea domingensis* endemic to Hispaniola, *Columnnea tinctoria* endemic to Cuba, and 13 species endemic to Jamaica (*Columnnea argentea*, *Columnnea brevipila*, *Columnnea fawcettii*, *Columnnea grisebachiana*, *Columnnea harrisii*, *Columnnea hirsuta*, *Columnnea hispida*, *Columnnea proctorii*, *Columnnea pubescens*, *Columnnea repens*, *Columnnea rutilans*, *Columnnea subcordata*, and *Columnnea urbanii*). The large number of species of *Columnnea* can in part be explained by the fact that *Columnnea* is the most species-rich genus of Gesneriaceae in the Neotropics, but the high diversity of *Columnnea* in Jamaica is an anomaly. Aside from the four genera mostly endemic to the Caribbean, *Besleria*, another large Neotropical genus in terms of the number of species, follows *Columnnea* with five species distributed in the Caribbean. All but *Besleria lutea* are endemic to the Lesser Antilles, and *B. lutea* is found on many Caribbean islands of both the Greater and Lesser Antilles as well as South America (Acevedo-Rodriguez and Strong 2017).

Based on previously published phylogenetic analyses, the five Caribbean species of *Columnnea* that have been sampled are in three different clades (Smith et al. 2013; Schulte et al. 2014, 2015). *Columnnea ambigua* and *C. domingensis* are sister to each other and included in section *Angustiflorae*. This section was described by Schulte et al. (2014) to include the species that Smith (1994) had included in section *Stygnanthe*, but Smith's (1994) section *Stygnanthe* was not recovered as monophyletic (Smith et al. 2013). Both sections *Angustiflorae* and *Stygnanthe* are characterized by relatively small corollas with a radial to subradial limb (fig. 1A). Although most morphological traits in the species of the two sections have a broad degree of overlap, the ratio of corolla tube to corolla lobe can be diagnostic for the two sections. *Columnnea grisebachiana* has a corolla similar to that of the species of these two sections and a corolla-tube-to-lobe ratio that would place the species in section *Angustiflorae* (fig. 1D), but preliminary unpublished results from Schulte et al. (2014) did not place *C. grisebachiana* in this section. *Columnnea scandens* (fig. 1G) is included in section *Columnnea* and is the type species for the genus. This clade is distinctive in having a long corolla tube that is strongly bilaterally symmetrical with

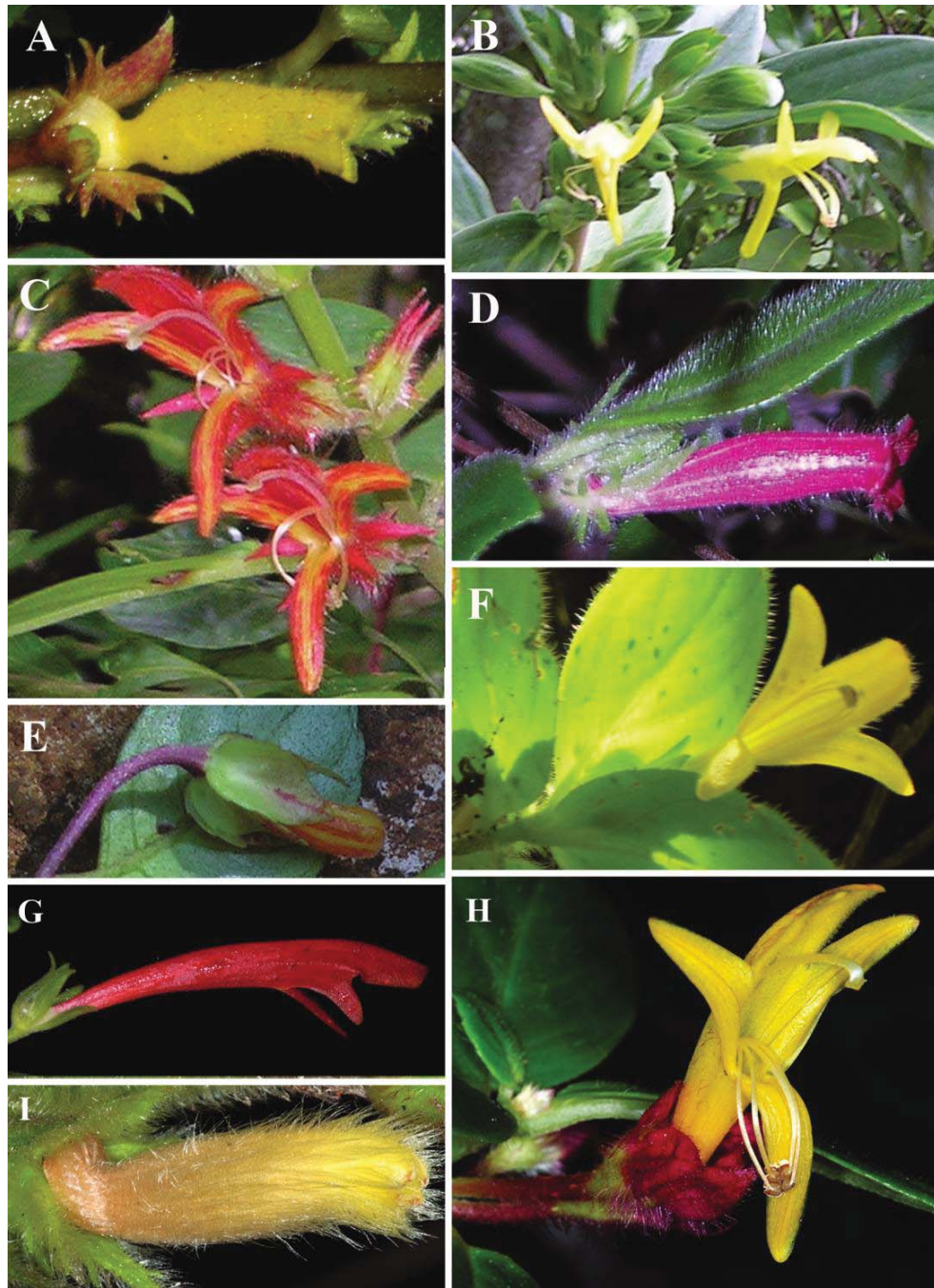


Fig. 1 Images of Caribbean species of *Columnea*. A, *Columnea ambigua* from Puerto Rico. B–F, Jamaican endemic species. B, *Columnea argentea*. C, *Columnea fawcettii*. D, *Columnea grisebachiana*. E, *Columnea repens* (in bud). F, *Columnea urbanii*. G, *Columnea scandens*. H, *Columnea tincta* from Cuba. I, *Columnea sanguinea*. Photographs B–F by J. F. Smith and G–I by J. L. Clark.

the upper two corolla lobes connate and forming a galea, two lateral corolla lobes, and a fifth lower lobe that is often reflexed backward from the corolla opening (fig. 1G). This section has been supported as monophyletic in many previous studies (Smith et al. 2013; Schulte et al. 2014, 2015).

The endemic Jamaican species of *Columnea* were originally described in three genera—*Alloplectus*, *Pterygoloma*, and *Columnea*—with a complicated history of moving several of the species across the three genera. *Columnea repens* was initially described as *Alloplectus repens* Hook., transferred to *Ptery-*

goloma (*P. repens* [Hook.] Hanst.), then treated as *Columnnea* section *Pterygoloma* (Fritsch 1894), and eventually moved to the genus *Ortholoma* (Wiehler 1973). *Columnnea pubescens* followed a nearly reverse path, having been initially described as *Pterygoloma* (*P. pubescens* Griseb.), then to *Alloplectus* (*A. pubescens* [Griseb.] Fawc.), to *Ortholoma* (Wiehler 1973), and to *Trichantha* (Wiehler 1975). Finally, *C. grisebachiana* was initially described as *Pterygoloma*, transferred to *Alloplectus* (*A. grisebachiana* [Kuntze] Urb.) and to section *Pterygoloma* (Morley 1974), to *Ortholoma* (Wiehler 1973), and to *Trichantha* (Wiehler 1975). All three species were eventually transferred to *Columnnea* (or back) and considered members of section *Ortholoma* within *Columnnea* (Kvist and Skog 1992), although section *Ortholoma* was considered artificial because it was not monophyletic (Smith et al. 2013). As mentioned above for *C. grisebachiana*, *C. pubescens* and *C. repens* have relatively small corolla tubes and radial to subradial limbs (fig. 1D, 1E). In contrast, the remaining 10 species of *Columnnea* endemic to Jamaica all have corollas that match the morphology seen in section *Columnnea* (fig. 1B, 1C, 1F, 1G) and have traditionally been placed in this section without controversy (Morley 1974; Wiehler 1983). The circumscription of these 10 species has varied over time, with five of the currently recognized species all considered varieties or forms of *C. hirsuta* (*C. faucettii*, *C. harrisii*, *C. proctorii*, and *C. urbanii*). If a more conservative species concept were followed, combining these five species into one, there would still be nine species on Jamaica alone. Smith et al. (2013) included two Jamaican endemic species in their analyses: *C. brevipila* from section *Columnnea* and *C. repens* from section *Ortholoma*. The two species were sister to each other, implying that the Jamaican endemic species may not be part of two different sections and instead may form a monophyletic group. Insufficient taxon sampling at that time prevented further investigation of this hypothesis.

In the present study, we use molecular phylogenetic analyses to investigate the evolution of *Columnnea* species in the Caribbean with a focus on the large number of species in Jamaica. Many previous studies that have elucidated the biogeography of other taxonomic groups in the Caribbean have recovered a variety of patterns with dispersals from North, Central, and South America; multiple independent introductions of genera into different islands; a single introduction; or a combination of parts of the above (Hedges and Burnell 1990; Seutin et al. 1994; Salzman and Judd 1995; Peck 1997; Schubart et al. 1998; Fritsch 2003; Fritsch and McDowell 2003; Negron-Ortiz and Watson 2003; Joseph et al. 2004; Santiago-Valentin and Olmstead 2004; Hedges 2006; Heinicke et al. 2007; Acevedo and Strong 2008; Roalson et al. 2008; Roncal et al. 2008; Van Ee and Berry 2009; Crews and Gillespie 2010; Gauthier 2010; Oneal et al. 2010; Rodríguez et al. 2010; Matos-Moraví et al. 2014; Irimia et al. 2015; Weaver et al. 2016). Like the geology of the region, the biota also exhibit a complicated evolutionary history.

Material and Methods

Taxon Sampling

We sampled all species of *Columnnea* native to the Caribbean. *Columnnea scandens*, *Columnnea repens*, *Columnnea brevipila*, *Columnnea ambigua*, and *Columnnea domingensis* had been in-

cluded in prior studies (Smith et al. 2013, 2017, 2018; Schulte et al. 2014, 2015). Fieldwork in Jamaica in 2012 allowed us to sample an additional population of *C. repens* as well as all other endemic Jamaican species except *Columnnea subcordata*, which was obtained from living material at the Botanical Garden in Geneva, and *Columnnea pubescens*. Despite several days of searching in the Blue Mountains and John Crow Mountains region of Jamaica, we were unable to relocate *C. pubescens* in 2012, but subsequent fieldwork by K. C. St. E. Campbell in 2018 in the John Crow Mountain region of the Blue and John Crow Mountains area resulted in the collection of *C. pubescens*. We included species from other clades in the genus that had been published previously (appendix; Smith et al. 2013; Schulte et al. 2014, 2015) as well as all available accessions of *Columnnea minor*, as this species had been shown to be sister to the two sampled individuals of Jamaican *Columnnea* species in previous analyses (Smith et al. 2013). Total sampling for this analysis is 123 individuals of *Columnnea*, comprising 83 species. All analyses were rooted using four species of *Glossoloma* as the outgroup (appendix).

DNA Extraction, Amplification, and Sequencing

DNA was extracted from all samples using Qiagen Plant DNeasy mini kits (Qiagen, Valencia, CA), following the manufacturer's instructions, with the exception that incubation of the samples at 60°C was extended to 2 hr. Amplification of internal transcribed spacer, *rps16* intron, *trnS-trnG* spacer, *psbA-trnH* spacer, *trnQ-rps16* spacer, and *rpl32-trnL_{UAG}* used the primers and methods of Schulte et al. (2014). We also sampled external transcribed spacers here using the primers of Baldwin and Markos (1998). Successful amplifications were determined by viewing aliquots on 1% agarose gels stained with ethidium bromide and viewed under ultraviolet illumination. All successful amplifications were purified using Exo-SAPit (Affymetrix, Cleveland, OH) and shipped to GeneWiz (Plainfield, NJ) for sequencing in both directions. Chromatograms were downloaded from the GeneWiz site and edited, and consensus sequences were generated from both strands using Phy-DE (Müller et al. 2010).

Phylogenetic Analyses

Sequences were aligned for each of the seven regions separately, generating indels to keep homologous sequences aligned. Ambiguous sequences and large portions of missing data were removed from the ends of all regions, and a concatenated data set for all seven regions was generated and used as the basis for all phylogenetic analyses.

Maximum parsimony (MP) and MP bootstrap (MPBS) were evaluated using PRAP2 (Müller 2004) in conjunction with PAUP* (Swofford 2002). To verify that cpDNA and nrDNA sampled regions were generating the same tree, separate MP analyses were run of the five cpDNA regions and two nrDNA regions. Maximum likelihood (ML) was assessed using RaxML (Stamatakis 2006) on the CIPRES Science Gateway (Miller et al. 2010) under the default GTR+G+I model and allowing bootstrapping to stop automatically. Consensus trees were generated and viewed in MEGA 7 (Kumar et al. 2016). The best fit model for DNA evolution was determined using jmodeltest 2.1.7 (Darriba et al. 2012) on the CIPRES Science Gateway (Miller et al.

2010). The best model was incorporated into the DNA data set and analyzed with MrBayes 3.2 (Ronquist et al. 2012) on the CIPRES Science Gateway (Miller et al. 2010) both with and without the Beagle library, as inclusion of the library in some analyses may yield spurious results. Majority-rule consensus trees of the output were generated in PAUP*, and effective sample size (ESS) values were estimated in Tracer (Rambaut et al. 2014).

To test the strength of the support for relationships that were not recovered in the best trees, approximately unbiased (AU) tests in CONSEL (Shimodaira and Hasegawa 2001; Shimodaira 2002) were conducted comparing the best trees with constrained trees. Constraint trees included (1) all of the Jamaican/Cuban endemic (JCE) species of *Columnnea* sister to the clade containing species of *Columnnea* section *Columnnea*, (2) including the JCE species of *Columnnea* within section *Columnnea* as part of a polytomy, (3) constraining the JCE clade to be sister to each of the five clades that comprise the polytomy in section *Columnnea* (fig. 2), (4) constraining all endemic Caribbean species as monophyletic, (5) constraining all Caribbean species of *Columnnea* as monophyletic, (6) constraining *Columnnea sanguinea* as monophyletic, both where the cultivated sample and the Caribbean samples fall in the unconstrained trees, and (7) constraining a monophyletic *Columnnea hirsuta* s. l. that made *Columnnea hirsuta*, *Columnnea fawcettii*, *Columnnea harrisii*, *Columnnea proctorii*, and *Columnnea urbanii* as monophyletic with a polytomy of the species.

Results

Sequencing

DNA extraction was successful for all samples, although some regions did not amplify for all individuals (appendix), resulting in 346 new sequences generated for this study. An inversion was present in some individuals for *psbA-trnH*, and this was inverted to match the sequences of the majority of samples prior to analyses.

Phylogenetic Analysis

All three methods of analysis resulted in trees that were nearly identical and fully compatible with each other for the concatenated data from the seven regions. The greatest resolution was in the Bayesian inference (BI) trees and the lowest in the MP trees. Maximum parsimony resulted in 138 trees, length = 1585, consistency index (CI) = 0.5408, retention index (RI) = 0.8518, and rescaled consistency index (RC) = 0.5283. Analyses of cpDNA and nrDNA separately did not result in any conflicting relationships between the two analyses. The model GTR+G was selected by jmodeltest, and this model was implemented in the BI analyses. Results from the two independent runs were in full agreement in terms of topology and differed by only one or two posterior probability points. Topologies and support did not differ regardless of whether the Beagle library was included. The ESS values were 3188 and 2684, respectively, for the two runs. The BI tree is presented in figure 2 with MPBS, MLBS, and BIPP values shown for all nodes. Clades for species with multiple sampled individuals are collapsed. Figure S1 (available online) has all samples. Support for relationships along the backbone of the

tree remains low, but the monophyly of all species (except *Columnnea sanguinea*; see “Discussion”) that included more than a single individual is strongly to maximally supported, and several clades receive strong to maximal support from at least one analysis (figs. 2, S1).

A monophyletic (but not supported) section *Angustiflorae* and a monophyletic (supported in all analyses) section *Columnnea* were recovered. All Jamaican species were recovered as monophyletic with maximal support from all analyses with *Columnnea tincta* from Cuba sister to the Jamaican species except for *Columnnea pubescens* that is sister to *C. tincta* + 12 Jamaican species (fig. 2). A clade comprising *Columnnea rubricalyx*, *Columnnea dissimilis*, *Columnnea pulchra*, *Columnnea fimbriicalyx*, *Columnnea herthae*, and *Columnnea minutiflora* is sister to the JCE species, but this relationship is not supported (fig. 2). Caribbean species of *Columnnea* were not recovered as monophyletic with *Columnnea scandens* in section *Columnnea*; *Columnnea ambigua* and *Columnnea domingensis* sister to each other in section *Angustiflorae*; and two accessions of *C. sanguinea* from Hispaniola and Cuba sister to each other but not monophyletic with one other accession of *C. sanguinea* from a cultivated collection with unknown natural provenance (fig. 2; appendix).

Testing Alternative Topologies

The AU tests could not reject the sister group relationship of the JCE clade to section *Columnnea* ($P = 0.359$). However, all other relationships of JCE to section *Columnnea* were rejected, including the JCE clade in section *Columnnea* as a fourth clade in the polytomy (fig. 2; $P = 0.031$) or as sister to any of the clades within section *Columnnea* (fig. 2; $P < 0.001$). The AU tests also rejected the monophyly of all endemic Caribbean species of *Columnnea* ($P = 0.05$ if *C. ambigua* and *C. domingensis* are sister to the unconstrained topology of the JCE clade, $P < 0.001$ if the JCE clade is sister to the unconstrained placement of *C. ambigua* and *C. domingensis*), the monophyly of all Caribbean species of *Columnnea* ($P < 0.0001$), and the monophyly of *C. sanguinea* whether the two Caribbean species were placed with the unconstrained placement of the cultivated individual ($P < 0.001$) or with the cultivated individual placed with the unconstrained placement of the Caribbean individuals ($P < 0.001$). A monophyletic *Columnnea hirsuta* s. l. such that *C. hirsuta*, *Columnnea fawcettii*, *Columnnea harrisii*, *Columnnea proctorii*, and *Columnnea urbanii* was monophyletic was also rejected ($P < 0.001$).

Discussion

Caribbean Biogeography

Columnnea fits a general pattern in Caribbean biogeography with multiple independent introductions into the islands and with populations of species found on the islands that exist in mainland populations as well (Seutin et al. 1994; Negrón-Ortiz and Watson 2003; Fritsch 2003; Joseph et al. 2004; Santiago-Valentin and Olmstead 2004; Roncal et al. 2008; Van Ee and Berry 2009; Rodríguez et al. 2010). Our data indicate a minimum of four independent introductions into the Caribbean: (1) *Columnnea ambigua* and *Columnnea domingensis*, (2) *Columnnea*

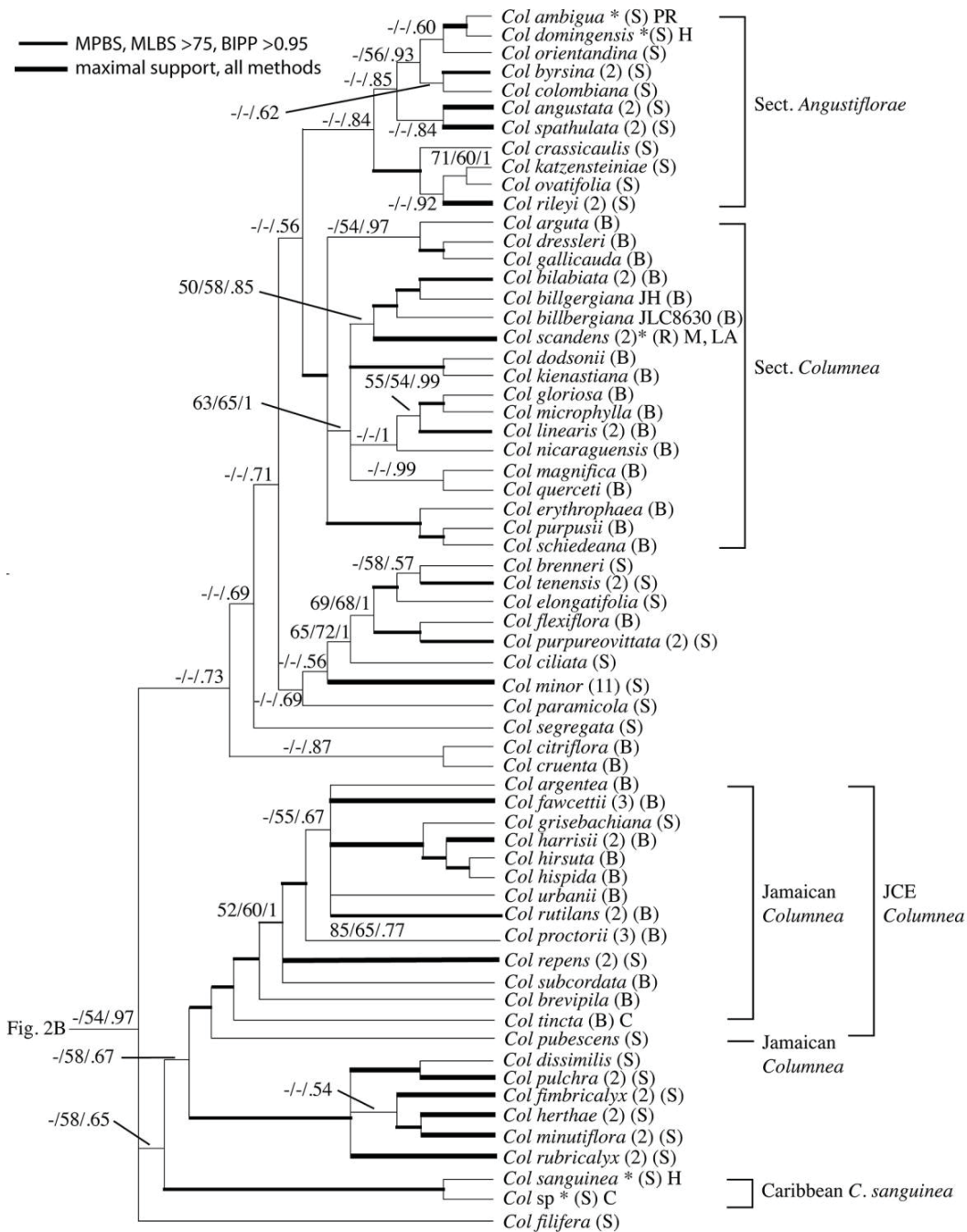


Fig. 2 Majority-rule consensus tree derived from Bayesian inference. Values on branches are maximum parsimony bootstrap/maximum likelihood bootstrap/Bayesian posterior probabilities. Branches supported in all three analyses are those with thick black lines. Letters in parentheses after names indicate corolla morphology as subradial (S), bilateral (B), or hypocyrtoid (H), a morphology with a narrow opening and strongly ventricose corolla tube. Caribbean and Jamaican species are marked with brackets to the right of the tree, as are sections *Angustiflorae* and *Columnea*, which are discussed in the text. JCE refers to the Jamaican/Cuban endemic species. Other species with Caribbean distributions are marked with asterisks. Specific islands are indicated other than the Jamaican species to indicate Cuba (C), Hispaniola (H), Lesser Antilles (LA), mainland (M), and Puerto Rico (R).

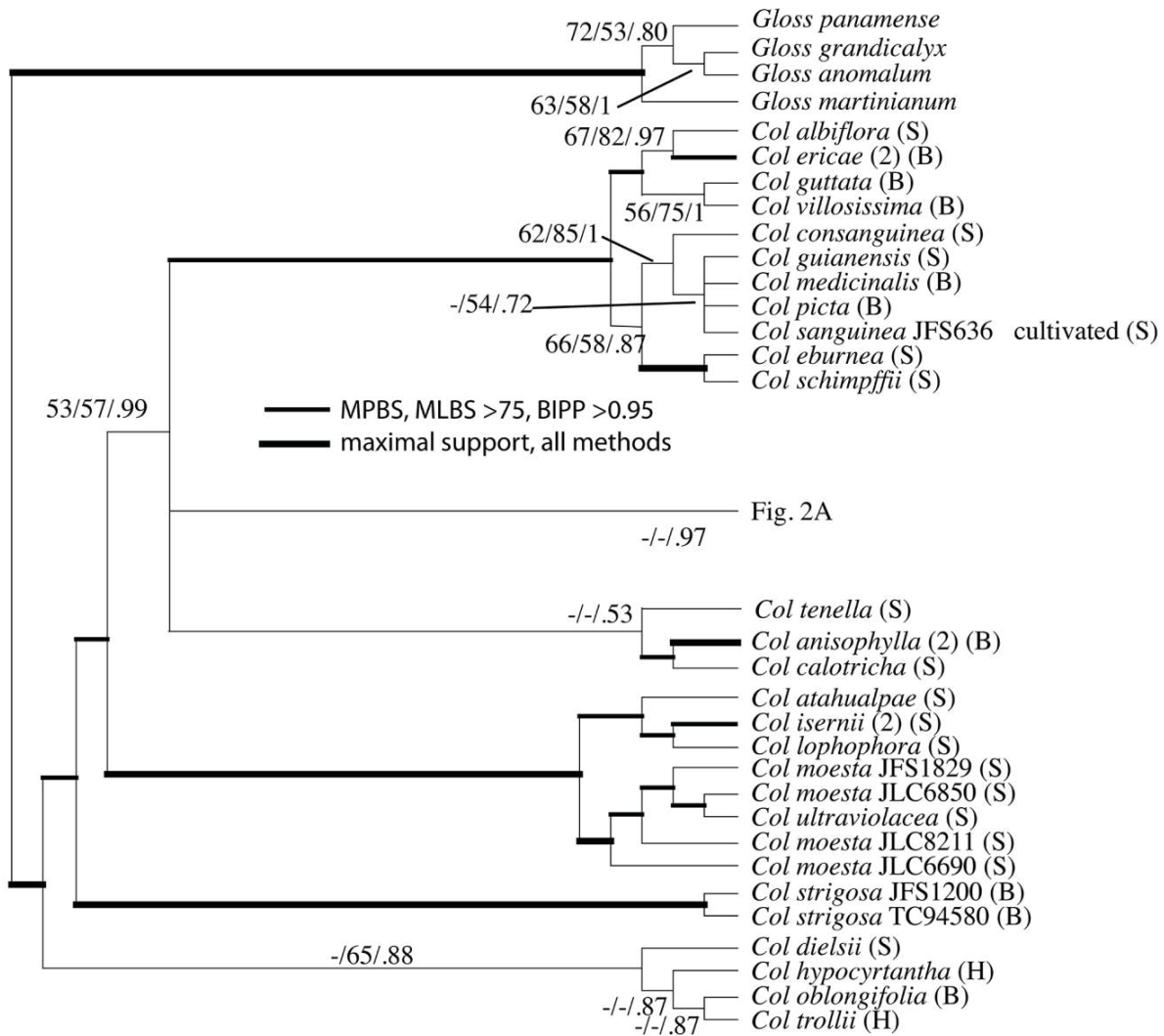


Fig. 2 (Continued)

sanguinea, (3) *Columnnea scandens*, and (4) the JCE species (fig. 2).

The inclusion of *C. sanguinea* from Hispaniola and an unvouchered specimen from Cuba implies that the Cuban collection is also *C. sanguinea*, and it is likely that a single introduction into the Caribbean occurred for this species. However, the lack of a voucher for the one specimen creates uncertainty surrounding this determination, as well as the fact that these two are not monophyletic with one other collection of *C. sanguinea* derived from cultivated material presumably with a mainland provenance (fig. 2). These results imply that the Caribbean *C. sanguinea* may be evolutionarily distinct from those of the mainland populations, but we also cannot preclude that the cultivated accession of *C. sanguinea* may have resulted from inter-specific crosses with other cultivated species. Further sampling will be essential to verify this. Two samples of *C. scandens* are

recovered as sister to each other, one from the island of Martinique, the other from cultivation, again presumably from a mainland source. Although *C. scandens* is clearly monophyletic, the sampling of this species from only one Caribbean island cannot preclude that independent multiple introductions have occurred. Further sampling and analyses at the population level would be essential to resolve this.

Our current data do not allow us to fully test the source populations of the introductions of the endemic species due to poor support on those parts of the tree. Both *C. ambigua* and *C. dominicensis* are sister to each other and together are within section *Angustiflorae* (fig. 2; Schulte et al. 2014, 2015). Nearly all members of section *Angustiflorae* are from South America, with a few individuals of *Columnnea angustata* recorded from Central America. Therefore, it is almost a certainty that the ancestor to these two species would have been from mainland

South America, with an introduction to either Puerto Rico where *C. ambigua* is endemic or Hispaniola where *C. domingensis* is endemic, with a subsequent migration from one to the other adjacent island.

The origin of the JCE clade is more complicated than *C. ambigua*/*C. domingensis* in that the JCE clade is recovered in all analyses as sister to a clade including *Columnnea dissimilis* (fig. 2) but is not supported. If the topology is correct, the species in the *C. dissimilis* clade are known primarily from Colombia and Ecuador; therefore, a South American origin for JCE would be likely. However, as AU tests cannot preclude the sister group relationship to section *Columnnea*, and the shared corolla morphologies between these two clades argues for common ancestry, we cannot eliminate a Central American ancestor for the JCE clade.

Monophyly of Jamaican Species and Relationships within the Clade

The data provide strong support for a single ancestral introduction into Jamaica for *Columnnea* (fig. 2). Single ancestral introductions in Jamaica are known for several other taxa and include *Anolis* (lizards; Hedges and Burrell 1990), *Selenops* (spiders; Crews and Gillespie 2010), land crabs (Schubart et al. 1998), *Limia* (fish; Weaver et al. 2016), and the plant genus *Erithallis* (Negrón-Ortiz and Watson 2003). However, many other studies have demonstrated multiple introductions into the island, often because of a single or few widespread species also found on other islands or the mainland and which include the plant genera *Rochefortia* (Irimia et al. 2015) and *Croton* (Van Ee and Berry 2009) as well as *Myarchus* flycatchers (Joseph et al. 2004).

Relationships within the clade are not all strongly supported, but many of them are. First, in all instances where multiple individuals were sampled, all species are recovered as monophyletic (fig. 2). Previous taxonomic treatments had considered *C. fawcettii*, *Columnnea harrisii*, *C. proctorii*, and *C. urbanii* all to be members of a more broadly circumscribed *C. hirsuta* (Urban 1901). This broader concept of *C. hirsuta* was not recovered as a monophyletic group that would exclude species not previously considered to be conspecific, and a constrained broader concept of *C. hirsuta* could be rejected with AU tests. This provides additional reassurance that the 13 species on Jamaica are evolutionarily distinct and that the greater number of species on the island do not represent simply a taxonomic anomaly.

Stearn (1968) used the Jamaican species of *Columnnea* to demonstrate phenetic relationships of the species using 51 cytological, biochemical, anatomical, and macroscopic morphological characters in a phenetic analysis. The resulting dendrogram also included several hybrid individuals, but ignoring these, Stearn (1968) recovered a clade of *Columnnea rutilans*, *C. hirsuta*, and *C. fawcettii* in a polytomy; another polytomy of *C. proctorii*, *Columnnea subcordata*, and *C. urbanii*; and a third clade of *C. harrisii* sister to the sister pair of *Columnnea brevipila* and *Columnnea argentea*. These three clades were monophyletic in a polytomy. He also recovered *Columnnea grisebachiana*, *Columnnea pubescens*, and *C. ambigua* (all then treated as species of *Alloplectus*) as a polytomy with *Columnnea hispida* as sister. Finally, all three clades were in a polytomy with *Columnnea repens* (called *Columnnea jamaicensis*). Despite this study using a fairly large

number of characters and being one of the earliest to use any form of phylogenetic analysis in Gesneriaceae, the resulting phenetic topology is in complete disagreement with the results of the molecular analyses presented here.

Classification of the JCE Clade

Although no single analysis recovered the Jamaican clade as a part or sister to section *Columnnea*, the AU tests cannot exclude the possibility that they may be sister to section *Columnnea* but do exclude the inclusion of the JCE clade within section *Columnnea* (fig. 2). The corolla of *Columnnea tinctoria* is nearly identical to that of *C. urbanii* or *C. proctorii* (fig. 1H; Morley 1974), and its sister relationship to the Jamaican species except *C. pubescens* implies an ancestral origin for this corolla form. A possible explanation is that an ancestor dispersed to Jamaica with subsequent dispersal to Cuba as likely occurred with *C. ambigua*/*C. domingensis*. Although 10 of the 13 species on Jamaica share a corolla morphology with section *Columnnea* and have been traditionally considered members of this clade (Morley 1974, 1976; Wiehler 1983), the inclusion of the remaining three species would alter the characters defining section *Columnnea* because the radial to subradial corollas of *C. grisebachiana*, *C. pubescens*, and *C. repens* would not share the feature that defines section *Columnnea*: a bilabiate corolla with a galea and long nonventricose corolla tube (Morley 1976; Wiehler 1983). Therefore, we do not propose including members of the JCE within section *Columnnea*, and a new section will be essential to encompass these species.

Higher Diversity in Jamaica Compared with Other Islands

A recent analysis of diversification rates and the potential processes that drive those rates across the entire Gesneriaceae (Roalson and Roberts 2016) demonstrated that floral form and color in New World Gesneriaceae are important factors in increased rates of diversification. Roalson and Roberts (2016) found mixed results that epiphytism could increase rates of diversification. Our present study focuses on part of a single genus within the family, but *Columnnea* species are mostly assumed to be hummingbird pollinated and most species are epiphytic (Wiehler 1983). Roalson and Roberts (2016) demonstrated that tribe Columneinae (*Alloplectus*, *Columnnea*, *Drymonia*, *Glossoloma*, and *Neomortonia*) had the fourth-highest diversification and fifth-highest speciation rate among the eight groups compared. The scale of their study compared with the present one makes generalizations between the two difficult, and here we attempt to explain the higher rate of diversification found on Jamaica in comparison to other Caribbean islands.

The greater number of species of *Columnnea* found in the Caribbean compared with other nonendemic genera of Gesneriaceae is the result of the 13 endemic species on Jamaica. The high number of species on this island is somewhat puzzling, especially since other taxonomic groups have reduced diversity on Jamaica compared with diversity on other islands (Lavin and Matos 2008; Acevedo-Rodríguez and Strong 2017). The puzzle is why there is such a large number of *Columnnea* species on Jamaica. Knowing that the Jamaican species represent a single introduction to the island, factors relating to propagule pressure to ex-

plain higher diversity (such as proximity to mainland areas) are not valid explanations. Island biogeography theory predicts that larger islands are expected to harbor more species. Jamaica is the third-largest island in the Caribbean, and yet only two species of *Columnea* are known from Cuba and Hispaniola: *C. sanguinea* found on both islands and the mainland, and one endemic species on each island. Additionally, Jamaica was either nearly completely or completely submerged at the time GAARlandia provided a connection to South America (Iturralde-Vinent and MacPhee 1999), although both Cuba and Hispaniola would have been part of this connection.

The age of islands may provide an explanation, with older islands having longer times for speciation and divergence to occur. Although the block that Jamaica occupies likely collided with the Guatemala-Yucatan platform in the Paleocene, the island was likely completely submerged in the middle to late Eocene and remained submerged until the late Miocene (Buskirk 1985; Iturralde-Vinent and MacPhee 1999; Graham 2003). Thus, although there may have been a chance for biotic exchange with Central America in the Paleocene, any endemic biota would have been eliminated in the Miocene and all endemic taxa would have to have evolved within a 25–5 myr time frame. In contrast, Cuba and Hispaniola had portions of both islands emergent consistently during that time period (Buskirk 1985; Iturralde-Vinent and MacPhee 1999; Graham 2003). Thus, it appears that the geological history of Jamaica does not help to explain the higher number of endemic species of *Columnea* found there compared with other Caribbean islands.

Topography can also affect rates of species diversification (Richerson and Lum 1980; Kruckeberg 1986; Steinbauer et al. 2016), especially if elevation gradients generate distinct and isolated climates or populations. Although most species of *Columnea* that have been investigated have similar climatic requirements (Schulte et al. 2015), isolated populations could lead to diversification and speciation (Schulte et al. 2015). Jamaican species have some overlap in their distributions but are largely allopatric (Morley 1972). Jamaica is certainly more mountainous than Cuba, with the highest elevation at Blue Mt. Peak (2256 m) and several other elevations above 2100 m. The geology of the island also varies with the Central mountains' igneous origins and metamorphic rock with karst limestone hills in the Cockpit country (Arden 1975). In contrast, Cuba has less topographic diversity with the Sierra Maestra and the highest peak of Pico Turquino (1974 m). The combination of flat to rolling hills and large swaths of serpentine soils in Cuba (Borhidi 1991) has created large barriers (Berazaín Iturralde 2001) and isolated areas where *Columnea* would typically diversify. The mountains and lack of serpentine soils in Jamaica are more similar to Andean forests in South America and therefore more conducive for the diversification of *Columnea*. Although the more varied topography of Jamaica compared with Cuba may be an explanation for the greater diversity of *Columnea* in Jamaica, it does not suffice to explain that diversity in comparison to Hispaniola. Hispaniola has five major mountain ranges: Cordillera Central, Cordillera Septentrional, Massif du Nor, Sierra de Bahoruco, and Sierra de Neiba. Two of these ranges have peaks higher than any found in Jamaica (Pico Duarte = 3175 m, and Pic la Selle = 1680 m; Latta et al. 2010). Thus, if topographic variation were a single explanation for diversification in Caribbean *Columnea*, one would expect greater diversification on Hispaniola.

The bilaterally symmetric flaring corolla (fig. 1) found in 10 of the 13 endemic species of *Columnea* on Jamaica could also be a key innovation for this group, allowing greater diversification (Givnish and Sytsma 2000). A shift from marine to terrestrial habitat has been the major explanation for a rapid radiation of crabs in Jamaica (Schubart et al. 1998). It is possible that a similar key innovation in *Columnea* may be the corolla. It is not clear, at present, how this may have acted as a key innovation. Presumably, the larger opening allows for a greater number of hummingbird visitors, but it is unclear how this may have promoted greater diversity. Additionally, because we cannot reject the sister group relationship between the Jamaican species and section *Columnea* (the second-largest section in the genus in terms of number of species), it is possible that the Jamaican species inherited this trait from a common ancestor with shifts to a subradial corolla occurring in three of the species. However, similar corollas are found in *C. scandens* of section *Columnea*, and there has not been substantial diversification in this lineage in the Caribbean. Even more compelling against the argument that the corolla is a key innovation is the sister relationship of *C. tincta* to 12 of the Jamaican endemic species. *Columnea tincta* shares a corolla morphology (fig. 1H) with most of the endemic Jamaican species, and as sister to all but *C. pubescens*, the lineages are the same age. However, the Jamaican lineage diverged into 12 species, whereas *C. tincta* is the only endemic species of *Columnea* on Cuba.

A final possible explanation may be genetic isolation if there were a greater number of pollinators or dispersers on Jamaica that might generate reproductive barriers between species. Little is known about dispersal or pollination in *Columnea* in general (Morley 1971, 1974; Schulte et al. 2015) and even less about the Jamaican species, although the data that do exist point to hummingbirds as primary pollinators (Morley 1971, 1974), and the flowers clearly fit a hummingbird pollination syndrome (Proctor et al. 1996). Jamaica is home to four different species of hummingbird (three if the red-billed and black-billed streamertails are considered subspecies; Downer and Sutton 1990). Three of these are endemic to the island, and the Vervain hummingbird on Jamaica is considered an endemic subspecies. Although this is a larger number of hummingbirds on Jamaica in comparison to Hispaniola (three species; Latta et al. 2010) and Cuba (two species; Garrido and Kirkconnell 2000), it seems unlikely that the one to two additional species on Jamaica are sufficient to drive speciation to this level. Speciation by isolation by hummingbirds is even less likely when we consider that the Jamaican species were some of the first documented cases of natural interspecific hybridization in the genus (Morley 1971, 1976). Thus, it seems unlikely that four species of birds would have effectively driven isolation to bring about 13 endemic species of plants.

Even less is known about dispersal in *Columnea*. Blake and Loiselle (1992) documented seeds of *Besleria columneoides* Hanst. and *Drymonia pilifera* Wiehler in feces of migratory thrushes. *Columnea* species have fleshy fruits similar to those of *Besleria* and *Drymonia*; therefore, it is likely that these birds would be likely consumers of *Columnea* fruits as well. There are 10 species of thrush on Jamaica, 11 on Cuba, and nine on Hispaniola. Therefore, again it seems unlikely that if thrushes are primary dispersers of *Columnea* fruits, the numbers on Jamaica would have an impact.

Another unusual trait regarding the Jamaican species of *Columnnea* is the degree of sequence divergence that is (1) shared among all species such that the clade is maximally supported as monophyletic in all analyses, a result not seen in other clades that presumably have had a longer time to diverge in comparison to the limited age of an emergent Jamaica, and (2) the sequence divergence found within the clade. Although not all relationships are well supported, there are four clades among 12 species (excluding *C. pubescens* and *C. tincta*) that have strong to maximal support in all analyses, and the sister relationship of *C. hirsuta* to *C. hispida* is strongly supported with MLBS (89) and BIPP (1.0) but is just short of being supported with MPBS (72). In comparison, with 17 out of ca. 75 species of section *Columnnea* sampled, there are seven interspecific nodes with support and only two nodes supported in section *Angustiflorae* (fig. 2). This larger number of nonhomoplastic phylogenetically informative characters for the Jamaican species, despite the short geological time frame for divergence on Jamaica, im-

plies rapid divergence with what would likely have been small populations such that mutations would become fixed for the lineages in a short time period (Bush et al. 1977; Slatkin 1987; Charlesworth and Charlesworth 1997).

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Appendix

Species, voucher specimens, and GenBank accession numbers for all accessions included in phylogenetic analyses. Data are in the order, taxon, voucher, herbarium, collection locality, and GenBank accession numbers for: *rpl32-trnL_{UAG}* spacer, *trnQ-rps16* intron, *rps16* intron, *trnS-G* spacer, *trnH-psbA* spacer, ITS, and ETS. Numbers in bold are new for this study, NA = not available.

Ingroup: *C. albiflora* L. P. Kvist & L. E. Skog, *J. L. Clark & J. Rea 8015*, UNA, Ecuador, KF005812, KF006030, KF005921, JQ953700, DQ211219, DQ211111, **MK326129**. *C. ambigua* (Urb.) B. D. Morley, *J. Smith 3701*, SRP, cultivated originally Puerto Rico, KF005814, KF006032, KF005923, JQ953713, KF005641, JQ953789, **MK326130**. *C. angustata* (Wiehler) L. E. Skog, *J. F. Smith 1433*, WIS, Colombia, KF005815, KF006033, KF005924, KF006136, KF005642, KF005726, **MK326131**. *C. angustata* (Wiehler) L. E. Skog, *J. L. Clark 8627*, UNA, Panama, KF005816, KF006034, KF005925, KF006137, NA, KF005727, **MK326132**. *C. anisophylla* DC., *J. L. Clark & J. Rea 8019*, UNA, Ecuador, KF005819, KF006037, KF005926, KF006141, KF005646, KF005728, **MK326134**. *C. anisophylla* DC., *E. Tepe 1081*, SRP, Panama, KF005817, KF006035, KF005927, KF006138, KF005643, KF005729, **MK326133**. *C. argentea* Griseb., *J. F. Smith et al. 10047*, SRP, Jamaica, **MK326237**, **MK326352**, **MK326086**, **MK326313**, **MK326276**, **MK326047**, **MK326135**. *C. arguta* C. V. Morton, *J. Harrison & L. Harrison 685*, SRP, Panama, **MK326238**, **MK326353**, **MK326087**, **MK326314**, NA, **MK326048**, **MK326136**.

C. atahualpae J. F. Smith & L. E. Skog, *J. L. Clark et al. 8000*, UNA, Ecuador, KF005821, KF006038, KF005930, KF006142, KF005647, KF005732, **MK326137**. *C. bilabiata* Seem., *J. L. Clark et al. 11157*, UNA, Ecuador, KF005822, KF006039, KF005931, KF006143, KF005648, KF005733, **MK326139**. *C. bilabiata* Seem., *J. F. Smith et al. 10896*, COL, Colombia, **MK326239**, **MK326354**, **MK326088**, **MK326315**, **MK326277**, **MK326049**, **MK326138**. *C. billbergiana* Beurl., *J. L. Clark 8630*, US, Panama, **MK326240**, **MK326355**, **MK326089**, **MK326316**, **MK326278**, **MK326050**, **MK326140**. *C. billbergiana* Beurl., *J. Harrison & L. Harrison 683*, SRP, Panama, **MK326241**, **MK326356**, **MK326090**, **MK326317**, NA, **MK326051**, **MK326141**. *C. brenneri* (Wiehler) B. D. Morley, *J. F. Smith 3385*, SRP, Ecuador, KF005823, KF006040, KF005932, KF006144, KF005649, KF005734, **MK326142**. *C. brevipila* Urb., *J. F. Smith 10058*, SRP, Cultivated, originally from Jamaica, KF005825, KF006042, KF005934, KF006146, KF005651, KF005736, **MK326143**.

C. byrsina (Wiehler) L. P. Kvist & L. E. Skog, *J. F. Smith 3408*, SRP, Ecuador, KF005826, KF006043, KF005935, JQ953714, KF005652, KF005737, **MK326144**. *C. byrsina* (Wiehler) L. P. Kvist & L. E. Skog, *J. L. Clark & O. Meija 6291*, UNA, Ecuador, KF005827, KF006044, KF005936, KF006148, KF005653, KF005738, **MK326145**. *C. calotricha* Donn. Sm., *J. F. Smith et al. 4117*, SRP, French Guiana, KF005828, KF006045, KF005937, KF006149, KF005654, KF005739, **MK326146**. *C. ciliata* (Wiehler) L. P. Kvist & L. E. Skog, *J. L. Clark et al. 7508*, UNA, Ecuador, KF005829, KF006046, KF005938, KF006150, **MK326279**, KF005740, **MK326147**. *C. citriflora* L. E. Skog, *J. L. Clark 10053*, UNA, cultivate, originally from Panama, KF005830, KF006047, KF005939, KF006151, KF005655, KF005741, **MK326148**. *C. colombiana* (Wiehler) L. P. Kvist & L. E. Skog, *J. F. Smith 1126*, WIS, cultivated at SEL, KF005832, KF006049, KF005941, KF006153, KF005657, KF005743, **MK326149**. *C. consanguinea* Hanst., *E. Tepe 1082*, SRP, Panama, KF005833, KF006050, KF005942, KF006154, KF005658, KF005744, **MK326150**. *C. crassicaulis* (Wiehler) L. P. Kvist & L. E. Skog, *J. L. Clark 8859*, US, cultivated, KF005834, KF006051, KF005943, KF006155, KF005659, KF005745, **MK326151**. *C. cruenta* B. D. Morley, *J. F. Smith 8606*, SRP, Cultivated, KF005835, KF006052, KF005955, KF006156, KF005660, KF005746, **MK326152**. *C. dielsii* Mansf., *J. F. Smith 1989*, WIS, Ecuador, KF005836, KF006053, KF005945, KF006157, KF005661, KF005747, NA. *C. dissimilis* C. V. Morton, *E. Tepe 1070*, SRP, Panama, KF005837, KF006054, KF005946, KF006158, KF005662, KF005748, **MK326153**. *C. dodsonii* Wiehler, *B. Stewart s. n.*, SRP, Cultivated, KF005838, KF006055, KF005947, KF006159, KF005663, KF005749, **MK326154**. *C. domingensis* (Urb.) B. D. Morley, *L. Hahn 445*, SRP, Dominican Republic, KF005839, KF006056, KF005948, JQ953715, KF005664, JQ953790,

MK326155. *C. dressleri* Wiehler, J. L. Clark & L. Espinosa 8559, US, Panama, MK326242, MK326357, MK326091, MK326318, MK326280, MK326052, MK326156. *C. eburnea* (Wiehler) L. P. Kvist & L. E. Skog, J. L. Clark et al. 6353, US, Ecuador, KF005840, KF006057, KF005949, KF006160, KF005665, KF005750, MK326157. *C. elongatifolia* L. P. Kvist & L. E. Skog, J. L. Clark et al. 10015, US, Cultivated, originally from Ecuador, KF005841, KF006058, KF005950, KF006161, KF005666, KF005751, MK326158. *C. ericae* Mansf., J. L. Clark et al. 6920, UNA, Ecuador, KF005842, KF006059, KF005951, KF006162, KF005667, KF005752, MK326160. *C. ericae* Mansf., E. Tepe 1570, SRP, Ecuador, KF005818, NA, KF005928, KF006139, KF005644, KF005730, MK326159. *C. erythrophaea* Decne. ex Houliet, J. F. Smith 3727, SRP, Cultivated, KF005843, KF006060, KF005952, KF006163, KF005668, AF543246, MK326161. *C. fawcettii* (Urb.) C. V. Morton, J. F. Smith et al. 10040, SRP, Jamaica, MK326243, MK326358, MK326092, MK326319, MK326281, MK326053, MK326162. *C. fawcettii* (Urb.) C. V. Morton, J. F. Smith et al. 10042, SRP, Jamaica, MK326244, MK326359, MK326093, MK326320, MK326282, MK326054, MK326163. *C. fawcettii* (Urb.) C. V. Morton, J. F. Smith et al. 10044, SRP, Jamaica, MK326245, MK326360, MK326094, MK326321, MK326283, MK326055, MK326164. *C. filifera* (Wiehler) L. P. Kvist & L. E. Skog, J. L. Clark et al. 7140, UNA, Ecuador, KF005844, KF006061, KF005954, KF006165, KF005669, KF005753, MK326165. *C. fimbriicalyx* L. P. Kvist & L. E. Skog, J. L. Clark et al. 7395, UNA, Ecuador, KF005845, KF006062, KF005955, KF006166, KF005670, KF005754, MK326167. *C. fimbriicalyx* L. P. Kvist & L. E. Skog, J. L. Clark et al. 10429, UNA, Ecuador, MK326246, MK326361, MK326095, MK326322, MK326284, MK326056, MK326166. *C. flexiflora* L. P. Kvist & L. E. Skog, J. L. Clark et al. 6968, UNA, Ecuador, KF005846, KF006063, KF005956, KF006167, KF005671, KF005755, MK326168. *C. gallicauda* Wiehler, J. L. Clark 6283, UNA, cultivated, KF005847, KF006064, KF005957, KF006168, KF005672, KF005756, MK326169. *C. gloriosa* Sprague, J. L. Clark et al. 9921, UNA, Ecuador, KF005848, KF006065, KF005958, KF006169, KF005673, KF005757, MK326170. *C. grisebachiana* Kuntze, J. F. Smith et al. 10041, SRP, Jamaica, MK326247, MK326362, MK326096, MK326323, MK326285, MK326057, MK326171. *C. guianensis* C. V. Morton, J. F. Smith 3711, SRP, Guyana, KF005849, KF006066, KF005959, JQ953718, KF005674, JQ953791, MK326172. *C. guttata* Poepp., J. L. Clark & L. Jost 6974, UNA, Ecuador, KF005850, KF006067, KF005960, KF006170, KF005675, KF005759, MK326173. *C. harrisii* (Urb.) Britton ex C. V. Morton, J. L. Clark 6278, US, Cultivated, originally from Jamaica, MK326249, MK326364, MK326098, MK326325, MK326287, MK326059, MK326175. *C. harrisii* (Urb.) Britton ex C. V. Morton, J. F. Smith et al. 10055, SRP, Jamaica, MK326248, MK326363, MK326097, MK326324, MK326286, MK326058, MK326174. *C. berthae* Mansf., J. L. Clark et al. 4960, UNA, Ecuador, KF005852, KF006070, KF005961, KF006172, KF005676, KF005760, MK326176. *C. berthae* Mansf., J. L. Clark et al. 7113, UNA, Ecuador, KF005853, KF006069, KF005963, KF006173, KF005677, KF005761, MK326177. *C. hirsuta* Sw., J. F. Smith et al. 10057, SRP, Jamaica, MK326250, MK326365, MK326099, MK326326, MK326288, MK326060, MK326178. *C. hispida* Sw., J. F. Smith et al. 10054, SRP, Jamaica, MK326251, MK326366, MK326100, MK326327, MK326289, MK326061, MK326179. *C. hypocyrtantha* (Wiehler) J. F. Smith & L. E. Skog, J. L. Clark & E. Rodriguez 6741, US, Bolivia, KF005854, KF006071, KF005964, KF006174, KF005679, KF005762, MK326180. *C. isernii* Cuatr., J. L. Clark et al. 6253, UNA, Ecuador, KF005857, KF006074, KF005967, KF006177, DQ211220, AF543247, MK326182. *C. isernii* Cuatr., J. F. Smith 2010, WIS, Ecuador, KF005856, KF006073, KF005966, KF006176, KF005681, KF0057645, MK326181. *C. katzensteiniae* (Wiehler) L. P. Kvist & L. E. Skog, J. L. Clark et al. 7625, UNA, Ecuador, KF005858, KF006075, KF005968, KF006178, KF005683, KF005766, MK326183. *C. kienastiana* Regel, J. F. Smith et al. 10931, COL, Colombia, MK326252, MK326367, MK326101, MK326328, MK326290, MK326062, MK326184. *C. linearis* Oerst., J. L. Clark 6274, US, Cultivated, originally from Costa Rica, MK326254, MK326369, MK326103, MK326330, MK326292, MK326064, NA. *C. linearis* Oerst., no voucher, NA, Cultivated, MK326253, MK326368, MK326102, MK326329, MK326291, MK326063, NA. *C. lophophora* Mansf., J. L. Clark et al. 7888, US, Ecuador, KF005860, KF006076, KF005969, KF006179, KF005684, KF005767, MK326185. *C. magnifica* Klotzsch ex Oerst., J. F. Smith 8602, SRP, Cultivated, KF005861, KF006078, KF005971, KF006181, KF005685, KF005769, MK326186. *C. medicinalis* (Wiehler) L. E. Skog & L. P. Kvist, J. F. Smith 1972, WIS, Ecuador, KF005862, KF006079, KF005972, KF006164, KF005686, KF005770, MK326187. *C. microphylla* Klotsch & Hanst., J. L. Clark 6261, UNA, cultivated, KF005863, KF006080, KF005973, KF006182, KF005687, KF005771, MK326188. *C. minor* (Hook.) Hanst., J. L. Clark 2934, SRP, Ecuador, KF005864, KF006081, MK326107, KF006183, KF005688, KF005772, NA. *C. minor* (Hook.) Hanst., J. L. Clark et al. 6220, US, Ecuador, MK326258, MK326373, MK326108, MK326334, MK326296, MK326068, NA. *C. minor* (Hook.) Hanst., J. L. Clark & O. Mejia 6289, US, Ecuador, MK326259, MK326374, MK326109, MK326335, MK326297, MK326069, NA. *C. minor* (Hook.) Hanst., J. L. Clark & E. Folleco 8504, US, Ecuador, MK326260, MK326375, MK326110, MK326336, MK326298, MK326070, NA. *C. minor* (Hook.) Hanst., J. L. Clark et al. 9647, UNA, Ecuador, MK326261, MK326376, MK326111, MK326337, MK326299, MK326071, NA. *C. minor* (Hook.) Hanst., T. Croat 94778, MO, Ecuador, KF005866, KF006084, KF005975, KF006185, KF005690, KF005774, NA. *C. minor* (Hook.) Hanst., O. H. Marín-Gómez 260, COL, Colombia, MK326262, MK326377, MK326112, MK326338, MK326300, MK326072, NA. *C. minor* (Hook.) Hanst., J. F. Smith et al. 10839, COL, Colombia, MK326255, MK326370, MK326104, MK326331, MK326293, MK326065, NA. *C. minor* (Hook.) Hanst., J. F. Smith et al. 10872, COL, Colombia, MK326256, MK326371, MK326105, MK326332, MK326294, MK326066, NA. *C. minor* (Hook.) Hanst., J. F. Smith et al. 10932, COL, Colombia, MK326257, MK326372, MK326106, MK326333, MK326295, MK326067, NA. *C. minor* (Hook.) Hanst., B. Stewart s. n., SRP, Cultivated, KF005865, KF006082, KF005974, KF006184, KF005689, KF005773, NA. *C. minutiflora* L. P. Kvist & L. E. Skog, J. L. Clark et al. 7092, US, Ecuador, KF005868, KF006086, KF005977, KF006187, KF005692, KF005776, MK326190. *C. minutiflora* L. P. Kvist & L. E. Skog, J. L. Clark et al. 10832, UNA, Ecuador, KF005867, KF006085, KF005976, KF006186, KF005691, KF005775, MK326189. *C. moesta* Poepp., J. F. Smith 1829, WIS, Bolivia, KF005870, KF006084, KF005979, KF006189, KF005694, KF005778, MK326191. *C. moesta* Poepp.,

J. L. Clark & M. Zeballos 6850, UNA, Bolivia, KF005872, KF006089, KF005981, KF006191, KF005695, KF005779, **MK326193**. *C. moesta* Poepp., *J. L. Clark & D. Barrientos* 6690, US, Bolivia, KF005871, KF006088, KF005980, KF006190, DQ211242, DQ211123, **MK326192**. *C. moesta* Poepp., *J. L. Clark et al.* 8211, UNA, Peru, KF005873, KF006091, KF005982, KF006192, KF005696, KF005780, **MK326194**. *C. nicaraguensis*, *J. L. Clark et al.* 10023, US, Cultivated, **MK326263**, **MK326378**, **MK326113**, **MK326339**, **MK326301**, **MK326073**, NA. *C. oblongifolia* Rusby, *J. F. Smith* 1721, WIS, Bolivia, KF005874, KF006092, KF005983, KF006193, KF005697, KF005781, **MK326195**. *C. orientandina* Mansf., *J. L. Clark et al.* 9885, UNA, Ecuador, KF005876, KF006094, KF005985, KF006195, KF005699, KF005783, **MK326196**. *C. ovatifolia* L. P. Kvist & L. E. Skog, *J. F. Smith* 1921, WIS, Ecuador, KF005877, KF006091, KF005986, KF006196, KF005700, KF005784, **MK326197**. *C. paramicola* (Wiehler) L. P. Kvist & L. E. Skog, no voucher USBRG94529, NA, Cultivated, KF005878, KF006095, KF005987, JQ954064, DQ211224, DQ211113, **MK326198**. *C. picta* H. Karst., *T. Croat* 94956, MO, Ecuador, KF005879, KF006096, KF005988, KF006197, KF005701, KF005785, **MK326199**. *C. proctorii* Stearn, *J. F. Smith et al.* 10048, SRP, Jamaica, **MK326264**, **MK326379**, **MK326114**, **MK326340**, **MK326302**, **MK326074**, **MK326200**. *C. proctorii* Stearn, *J. F. Smith et al.* 10052, SRP, Jamaica, **MK326265**, **MK326380**, **MK326115**, **MK326341**, **MK326303**, **MK326075**, **MK326201**. *C. pubescens* (Griseb.) Kuntze, *K. Campbell et al.* 17.05.18, IJ, Jamaica, **MK326266**, **MK326381**, NA, **MK326342**, NA, **MK326077**, **MK326203**. *C. pulchra* (Wiehler) L. E. Skog, *J. L. Clark* 6265, US, cultivated, KF005880, **MK326382**, KF005990, KF006198, DQ211225, KF005786, **MK326205**. *C. pulchra* (Wiehler) L. E. Skog, no voucher, NA, Cultivated, KF005881, KF006097, KF005989, KF006199, KF005702, KF005787, **MK326204**. *C. purpureovittata* (Wiehler) B. D. Morley, *J. L. Clark et al.* 11448, UNA, Peru, KF005882, KF006098, KF005991, KF006200, KF005703, KF005788, **MK326207**. *C. purpureovittata* (Wiehler) B. D. Morley, *J. F. Smith s. n.*, SRP, Cultivated, KF005855, KF006072, KF005965, KF006175, KF005680, KF005763, **MK326206**. *C. purpusii* Standl., *A. Rincon et al.* 2302, XAL, Mexico, KF005883, KF006099, KF005992, JQ953719, KF005704, JQ953792, **MK326208**. *C. querceti* Oerst., *J. L. Clark* 10047, US, Cultivated, originally from Costa Rica, **MK326267**, **MK326383**, **MK326116**, **MK326343**, **MK326304**, **MK326078**, **MK326209**. *C. repens* (Hook.) Hanst., *J. F. Smith* 8605, SRP, Cultivated, originally from Jamaica, KF005884, KF006100, KF005993, KF006201, KF005705, KF005790, **MK326211**. *C. repens* (Hook.) Hanst., *J. F. Smith et al.* 10056, SRP, Jamaica, **MK326268**, **MK326384**, **MK326117**, **MK326344**, **MK326305**, **MK326079**, **MK326210**. *C. rileyi* (Wiehler) *J. F. Smith, J. F. Smith* 1944, WIS, Ecuador, KF005885, KF006101, KF005994, KF006202, KF005706, KF005791, **MK326212**. *C. rileyi* (Wiehler) *J. F. Smith, J. L. Clark* 6263, US, Ecuador, KF005886, KF006102, KF005995, KF006203, DQ211250, AF543239, **MK326213**. *C. rubricalyx* L. P. Kvist & L. E. Skog, *J. L. Clark et al.* 11034, UNA, Ecuador, KF005887, KF006103, KF005997, KF006204, KF005707, KF005792, **MK326214**. *C. rubricalyx* L. P. Kvist & L. E. Skog, *T. Croat* 95236, MO, Ecuador, KF005888, KF006104, KF005996, KF006205, KF005708, KF005793, **MK326215**. *C. rutilans* Sw., *J. F. Smith et al.* 10046, SRP, Jamaica, **MK326269**, **MK326385**, **MK326118**, **MK326345**, **MK326306**, **MK326080**, **MK326216**. *C. rutilans* Sw., *J. F. Smith et al.* 10053, SRP, Jamaica, **MK326270**, **MK326386**, **MK326119**, **MK326346**, **MK326307**, **MK326081**, **MK326217**. *C. sanguinea* (Pers.) Hanst., *L. A. Hahn et al.* 410, SRP, Dominican Republic, **MK326272**, **MK326388**, **MK326121**, **MK326348**, **MK326309**, **MK326083**, **MK326224**. *C. sanguinea* (Pers.) Hanst., *J. F. Smith* 636, WIS, cultivated, KF005889, KF006105, KF005998, KF006206, KF005709, KF005794, **MK326218**. *C. scandens* L., *J. L. Clark & S. G. Clark* 6541, UNA, Martinique, KF005890, KF006106, KF005999, KF006207, KF005711, KF005792, **MK326219**. *C. scandens* L., *J. L. Clark & J. Katzenstein* 8879, US, Cultivated, **MK326271**, **MK326387**, **MK326120**, **MK326347**, **MK326308**, **MK326082**, **MK326220**. *C. schiedana* Schldtl., *J. F. Smith* 288, WIS, Cultivated, originally from Mexico, KF005891, KF006107, KF006000, KF006208, KF005712, KF0057967, **MK326221**. *C. schimpffii* Mansf., *J. F. Smith* 8603, SRP, Cultivated, originally from Ecuador, KF005892, KF006109, KF006001, KF006209, KF005713, KF005797, **MK326222**. *C. segregata* (B. D. Morley) Wiehler, *J. L. Clark et al.* 10029, UNA, cultivated, KF554378, KF006108, KF006002, KF006210, KF005714, KF554337, **MK326223**. *C. spathulata* Mansf., *J. L. Clark et al.* 7485, UNA, Ecuador, KF005894, KF006111, KF006004, KF006212, KF005716, KF005799, **MK326226**. *C. spathulata* Mansf., *J. F. Smith* 1853, WIS, Ecuador, KF005893, KF006110, KF006003, KF006211, KF005715, KF005798, **MK326225**. *C. strigosa* Benth., *T. Croat* 94580, MO, Ecuador, KF005896, KF006113, KF006006, KF006213, KF005718, KF005801, **MK326228**. *C. strigosa* Benth., *J. F. Smith* 1200, WIS, Venezuela, KF005895, KF006112, KF006005, KF006214, KF005717, KF005800, **MK326227**. *C. subcordata* C. V. Morton, no voucher IPEN # XXOG20110726, NA, Cultivate, originally from Jamaica, **MK326273**, **MK326389**, **MK326122**, **MK326349**, **MK326310**, **MK326084**, **MK326229**. *C. tenella* L. P. Kvist & L. E. Skog, *M. Amaya Marquez & J. F. Smith* 603, COL, Colombia, KF005897, KF006114, KF006007, KF006215, KF005719, KF005802, **MK326230**. *C. tenensis* Wiehler, *J. L. Clark et al.* 9500, UNA, Ecuador, KF005899, KF006116, KF006009, KF006217, KF005721, KF005803, **MK326232**. *C. tenensis* Wiehler, *J. F. Smith & R. W. Dunn* 3374, SRP, Ecuador, KF005898, KF006115, KF006008, KF006216, KF005720, KF005804, **MK326231**. *C. tincta*, *J. L. Clark* 15062, UNA, Cuba, **MK326274**, **MK326390**, **MK326123**, **MK326350**, **MK326311**, NA, **MK326233**. *C. trollii* Mansf., *J. F. Smith* 1723, WIS, Bolivia, KF005899, KF006117, KF006010, KF006218, KF005722, KF005805, **MK326234**. *C. ultraviolacea* *J. F. Smith & L. E. Skog, J. L. Clark & V. Velaz* 6603, UNA, Bolivia, KF005900, KF006118, KF006011, KF006219, KF005723, KF005806, **MK326235**. *C. urbanii* Stearn, *J. F. Smith et al.* 10045, SRP, Jamaica, **MK326275**, **MK326391**, **MK326124**, **MK326351**, **MK326312**, **MK326085**, **MK326236**.

Outgroup: *Glossoloma anomalum* *J. L. Clark, J. F. Smith* 3418, SRP, Ecuador, KF005912, KF006128, KF006021, KF006224, NA, AF543225, **MK326125**. *Glossoloma grandicalyx* (*J. L. Clark & L. E. Skog*) *J. L. Clark, J. F. Smith* 3417, SRP, Ecuador, KF005913, KF006129, KF006024, JQ953708, DQ211205, AF543218, **MK326126**. *Glossoloma martinianum* (*J. F. Smith*) *J. L. Clark, J. L. Clark* 6101, US, Ecuador, KF005914, KF006130, KF006022, JQ953709, DQ211209, AF543228, **MK326127**. *Glossoloma panamense* (*C. V. Morton*) *J. L. Clark, L. E. Skog et al.* 7641, US, cultivated, KF005915, KF006131, KF006023, JQ953710, DQ211202, DQ211102, **MK326128**.

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