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Morphometrics in the Recurved Corolla Clade of *Burmeistera* (Campanulaceae) Clarifies Species Limits and Identifies a New Species

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Abstract—The genus *Burmeistera* consists mostly of cloud forest species occurring from Guatemala to Peru. Molecular work on this group has revealed previously established subgeneric groupings to be non-monophyletic, while also identifying several monophyletic groups with recognizable synapomorphies. One such monophyletic group is a clade of species with recurved corolla lobes which contains three species: *B. crispiloba*, *B. sodiroana*, and *B. succulenta*. As many as nine names have been recognized previously for these species, though the most recent taxonomic treatments recognize only these three. Additional collections of these species made in the last forty years have uncovered phenotypic variation showing that characters traditionally used to differentiate them no longer do so clearly and suggest the possibility of introgression between them. Here, we report morphometric analyses of herbarium specimens of the recurved corolla clade, using both hierarchical and normal mixture model-based clustering methods to test the current species hypotheses. Our results support the recognition of the three known species plus the newly described *Burmeistera kitrinaima* sp. nov. We provide complete descriptions of all four species, and include photographs, distributions maps, taxonomic discussion, and an identification key.

Keywords—Andes, biodiversity, cluster analysis, hybridization, taxonomy.

Resumen—El género *Burmeistera* consiste principalmente de especies de bosques de neblina desde Guatemala hasta Perú. Trabajo molecular en este grupo ha revelado que los grupos subgenéricos previamente establecidos no son monofiléticos, además ha identificado varios grupos monofiléticos con sinapomorfías reconocibles. Uno de estos grupos monofiléticos es un clado de especies con lóbulos de corola recurvados que contiene tres especies: *B. crispiloba*, *B. sodiroana* y *B. succulenta*. Hasta nueve nombres se han reconocido previamente para estas especies, aunque los tratamientos taxonómicos más recientes reconocen únicamente estas tres. Colecciones adicionales de estas especies realizadas en los últimos cuarenta años han descubierto variación fenotípica demostrando que los caracteres tradicionalmente utilizados para distinguir entre especies ya no lo hacen de manera clara, y sugieren la posibilidad de introgresión entre ellas. Aquí, reportamos análisis morfométricos de especímenes de herbario del clado de corola recurvada, utilizando los métodos de agrupamiento jerárquico y de modelos de mezcla normal para evaluarlas hipótesis actuales de especies. Nuestros resultados respaldan el reconocimiento de las tres especies conocidas, además de una nueva especie recién descrita *Burmeistera kitrinaima* sp. nov. Describimos las cuatro especies en detalle e incluimos fotografías, ilustraciones, mapas de distribución, discusión taxonómica y una clave de identificación.

Palabras claves—Análisis de agrupamiento, Andes, biodiversidad, hibridación, taxonomía.

Burmeistera H.Karst. & Triana (Campanulaceae subfamily Lobelioideae) is a genus of approximately 130 species occurring in Central and South America, the majority of which are found from Costa Rica to Ecuador. Only one species has been described north of Costa Rica, in Honduras and Guatemala (Nash 1976; Lammers and Maas 1998), while two to four species extend from the south of Ecuador into Peru (Stein 1987; Lammers 2007). Roughly half of all species (~57) are found in Colombia, with ~50 in Ecuador, and ~21 along the Cordillera de Talamanca of Panama and Costa Rica (Lagomarsino et al. 2015; Ulloa Ulloa et al. 2017; Mashburn et al. 2021; Muchhala and Mashburn 2021; González 2023). Most inhabit cloud forest ecosystems from 1000 to 3000 m in elevation along either side of the Andes and the Cordillera de Talamanca, often with narrowly restricted ranges (Lagomarsino et al. 2015; Muchhala and Pérez 2015; Uribe-Convers et al. 2017).

Molecular studies (Lagomarsino et al. 2015; Uribe-Convers et al. 2017; Bagley et al. 2020) have shown *Burmeistera* to be monophyletic and have changed our understanding of infrageneric groups within the genus. Wimmer (1943, 1953) originally proposed two groups: *Barbatae*, with barbate anther tips, and *Imberbes*, with glabrous or sparsely pubescent anther tips. Molecular studies have shown the presence/absence of pubescence on anther tips to be homoplastic (Lagomarsino et al. 2014; Uribe-Convers et al. 2017). However, these studies have revealed monophyletic groups within the genus with

identifiable synapomorphies, including a clade of species exhibiting recurved corolla lobes (Uribe-Convers et al. 2017).

The recurved corolla clade (RCC) identified in Uribe-Convers et al. (2017) contained four species: *Burmeistera crispiloba* Zahlbr., *Burmeistera sodiroana* Zahlbr., *Burmeistera succulenta* H.Karst., and *Burmeistera toroensis* Wilbur. However, we have determined that the collection called *B. toroensis* in Uribe-Convers et al. (2017) was misidentified (it does not belong to *B. toroensis*). Instead, this sample may represent a northern extension of *B. succulenta* into Panama. As a result, more recent studies in *Burmeistera* (e.g. Bagley et al. 2020), including the present study, treat the RCC as having three species: *B. crispiloba*, *B. sodiroana*, and *B. succulenta*.

Species in the RCC differ from other *Burmeistera* in the way the unfused portion of the five corolla lobes flare out from the enlarged opening and recurve or scroll back (e.g. Fig. 1B); corolla lobes of other *Burmeistera* are falcate, turning downward and away from the dorsal side of the flower. In *B. sodiroana*, the corolla lobes often flare open and only sometimes curl back, though the curling tip does not often touch the lower part of the corolla (e.g. Fig. 1H). In *B. crispiloba* and *B. succulenta*, however, the curling corolla lobes are much more evident, scrolling back and circling (e.g. Fig. 1B, D). In *B. sodiroana* and sometimes in *B. succulenta*, this curling seems to occur at a later stage of flower maturity, such that not all herbarium specimens clearly exhibit the trait.

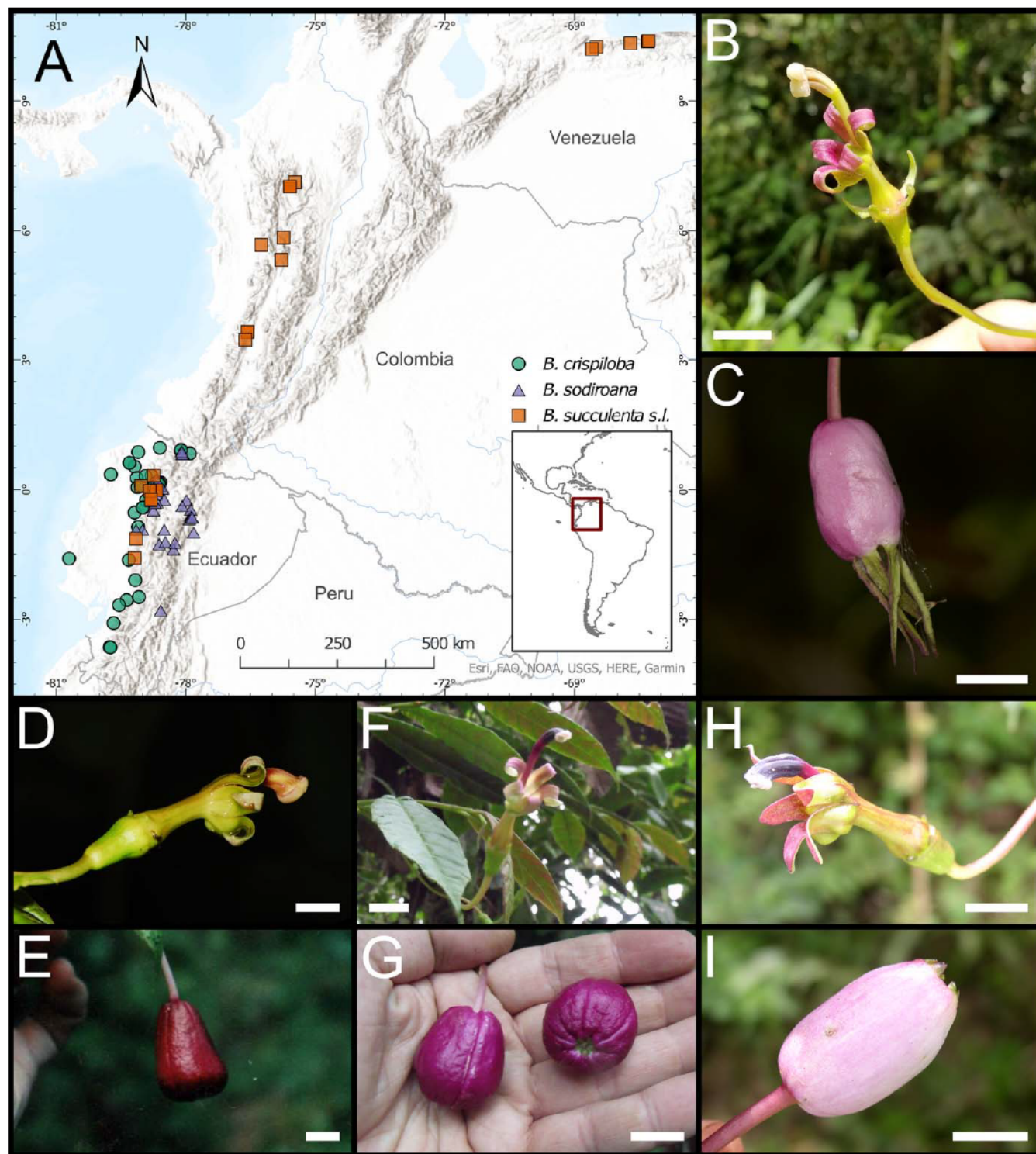


FIG. 1. A. Distribution maps of the three recurved corolla clade species in this study (note that we re-identify most of the Ecuadorian specimens of *B. succulenta* sensu lato as *B. kitrinanima* sp. nov.; see Fig. 7). B, C. *Burmeistera succulenta*. D, E. *Burmeistera crispiloba*. F, G. Putative hybrid morphology, intermediate between *Burmeistera crispiloba* and *Burmeistera sodiroana*. H, I. *Burmeistera sodiroana*. All scale bars indicate 10 mm. Photo credits: B, C, E-I by Nathan Muchala; D by Francisco Tobar.

The three species in the RCC have a varied taxonomic history. Wimmer (1943, 1968) recognized as many as five species and four varieties. Jeppesen (1981), while treating the *Burmeistera* of Ecuador, reduced Wimmer's nine taxonomic entities to three species without varieties. In his treatment, Jeppesen (1981) hypothesized that "the three species *B.*

crispiloba, *B. sodiroana*, and *B. succulenta* may prove to be varieties of one widespread, variable species, but more collections and field observations are necessary, especially in Venezuela and Colombia." In the last 40 yr, increased collections of the RCC throughout its range have allowed us to test this hypothesis; in his treatment, Jeppesen (1981) cited 55

specimens of all three species, while our study of the group makes use of 184.

Of the three species in the current circumscription of the RCC, *B. succulenta* is the most widespread, found from western Venezuela to south-central Ecuador at elevations from 1000 to 2500 m (Fig. 1A). In Ecuador, *B. succulenta* occurs on the west side of the Andes, generally at higher elevations (> 1500 m). *Burmeistera crispiloba* and *B. sodiroana* are restricted to Ecuador: *B. crispiloba* is found west of the Andes from sea level to ca. 1500 m in elevation in the Andean foothills, while *B. sodiroana* occurs on the east and west slopes of the Andes from ca. 1500 to 3000 m in elevation (Fig. 1A). Consequently, *B. succulenta* more often co-occurs with *B. sodiroana* than with *B. crispiloba*.

According to Jeppesen (1981), *B. succulenta* is differentiated from *B. sodiroana* by “the much longer, linear or tongue-shaped sepals.” By extension, this character differentiates *B. succulenta* from *B. crispiloba* as well, as both *B. sodiroana* and *B. crispiloba* are described by Jeppesen as having triangular sepals, 1–2(–4) mm long and 1–2 mm long, respectively (vs. 8–21 mm long in *B. succulenta*). As a result, specimens seeming to occur in this group with long calyx lobes (Jeppesen’s sepals) are consistently ascribed to *B. succulenta*.

The two species endemic to Ecuador, *B. crispiloba* and *B. sodiroana*, can be difficult to differentiate from each other using the characters identified by Jeppesen (1981): leaf size, pedicel length, and hypanthium shape. Increased collections in the last 40 years indicate that these characters are often just as variable within species as among them. In addition, Jeppesen noted that *B. crispiloba* differs from *B. sodiroana* by having a more “slender growth” form. Though this trait is difficult to quantify, it could signify a difference we have noticed between two general habits of *Burmeistera* species: 1) plants with long scandent branches (“slender growth” form), and 2) plants with a bushy, robust form (“shrub-like” form). Generally, species with a slender growth form have distichous phyllotaxy, while plants with a shrub-like form have spiral phyllotaxy (phyllotaxy is described in more detail in the Methods section). This trait is consistent with Jeppesen’s description of the slender form of *B. crispiloba*, which has distichous phyllotaxy, compared to the more shrub-like form of *B. sodiroana*, which has spiral phyllotaxy.

Despite the usefulness of the phyllotaxy character, a number of specimens of these two species remain difficult to differentiate along the intersection of their ranges, at around 1500 m in elevation. Many specimens have phyllotaxy, flower size, and fruit traits similar to *B. crispiloba*, yet leaf shape and flower color traits similar to *B. sodiroana* (Fig. 1). This difficulty is highlighted by the fact that individual specimens (even duplicate specimens deposited at different herbaria) have been identified by different taxonomists as either *B. crispiloba* or *B. sodiroana*. As a result, we hypothesize that *B. crispiloba* and *B. sodiroana* hybridize at the intersection of their ranges.

An additional taxonomic difficulty in the RCC is that many specimens collected in the western Andes of Ecuador without recurved corolla lobes have been identified as *B. succulenta* because of similar vegetative and floral traits. As previously mentioned, the lack of curling corolla lobes could be attributed to the perception that these are collections with immature flowers. However, the fact that these specimens are found only in Ecuador and not throughout the range of *B. succulenta* suggests that they could belong to an

undescribed species that may not be in the RCC. Therefore, it remains to be determined if additional characters can be identified which differentiate these Ecuadorian collections from *B. succulenta* in Colombia and Venezuela.

In this study, we attempt to resolve the taxonomic issues within the RCC of *Burmeistera* using multiple approaches to morphometric analysis as a basis for our decision-making process. Jeppesen’s (1981) taxonomy and species notes form the foundation for the hypotheses tested here. First, we test Jeppesen’s three species hypotheses compared to his alternative hypothesis that the three RCC species could be one widespread variable species. We find reason to support the uniqueness of *B. succulenta* from *B. crispiloba* and *B. sodiroana*, though we also find additional morphological evidence for taxonomic issues within *B. succulenta*. Thus, in the second part of our study we further analyze *B. succulenta* independent of the other two species. Third, we analyze *B. crispiloba* and *B. sodiroana* to explore morphological evidence for our hypothesis of two species with hybridization between them. In each of the three parts, both clustering methods (hierarchical and model-based) are used on the dataset and compared. Finally, because these specimens have historically been misidentified and confused, we produce a key and taxonomic treatment of the species discussed and described in this study.

MATERIALS AND METHODS

Materials—Morphometric analyses were based upon measurements made from 184 herbarium specimens of *Burmeistera* from three herbaria, MO, NY, and QCA, that could be identified as *B. crispiloba*, *B. sodiroana*, or *B. succulenta* using Jeppesen’s (1981) key to the species of Ecuador. Of these, 107 had complete vegetative and floral parts. Characters were averaged from duplicates of each collection, such that one sample per collection was included in the analysis, resulting in 95 samples (37 *B. crispiloba*, 31 *B. sodiroana*, and 27 *B. succulenta*). The morphometric measurements produced in this study are found in the Supplementary Data available on Dryad (Mashburn et al. 2024). All specimens were georeferenced from coordinates on the specimen labels or approximated from label descriptions.

Morphological Characters—A total of 24 morphological characters were measured or observed from corresponding mature parts of each specimen in order to span the vegetative and reproductive variation of the species while allowing enough specimens to have all measurements (Table 1). Of these, 22 were continuous quantitative characters and two were discrete qualitative characters. All measurements were taken in millimeters using either a ruler (for vegetative measurements) or a Tajima 150 mm dial caliper to a tenth of a millimeter precision (for reproductive measurements). Our methods for measuring characters particular to *Burmeistera* are explained in detail below.

Phyllotaxy (distichous vs. spiral) was identified as a previously unused but potentially useful character to differentiate species in this group. We find phyllotaxy to be consistent with Jeppesen’s (1981) use of growth habit descriptors (e.g. “slender”). All *Burmeistera* have alternate phyllotaxy (vs. opposite), as two petioles never arise from the stem at the same node. However, they can be either distichous or spiral. An alternate, distichous phyllotaxy, sometimes called “two-ranked,” is when petioles arise on one plane, consistently alternating 180 degrees on either side of the stem. Meanwhile, spiral phyllotaxy is when the petioles of successive leaves arise at less than 180 degrees, forming a spiral along the stem.

Many *Burmeistera* species exhibit a reduction in the size of the leaf subtending a flower, sometimes termed a bract. To maintain consistency for all species, including those that lack reduced leaves, we refer to these simply as leaves subtending flowers. When flowers are not present, or when older flowers have fallen off, the first leaf subtending a flower can still be determined by the presence of a visible pedicel scar in the axil of the leaf petiole.

In *Burmeistera*, the calyx lobes emerge from a hypanthium tube adnate to the ovary and extend outward. Calyx lobe length is measured from the point the lobes separate from one another at the distal end of the

TABLE 1. List of characters used in morphometric analysis. *Denotes use of character in Phases 1 and 2. **Denotes use of character in Phase 3.

Organ	Quantitative Characters	Organ	Qualitative Characters
Leaf	Shortest petiole length ⁺ Longest petiole length ⁺ Smallest leaf length Smallest leaf width Largest leaf length ^{**} Largest leaf width ^{**} First leaf subtending flower length ⁺ First leaf subtending flower width ⁺ Leaf apex length ⁺ Leaf apex width ⁺	Leaf	Phyllotaxy ^{**}
Flower	Pedicle length at anthesis ^{**} Hypanthium length ^{**} Hypanthium width ^{**} Calyx lobe length ^{**} Calyx lobe width ^{**} Corolla tube width at throat ⁺ Length to dorsal corolla opening ⁺ Length to ventral corolla opening ^{**} Androecium length ^{**} Exsertion length ^{**} Anther tube length ⁺ Anther tube width ⁺	Flower	Strength of corolla curling ^{**}

hypanthium. The five-lobed corolla is fused from the base, from which it narrows slightly into a thin tube (“throat”) before abruptly widening and then separating into the five distinct corolla lobes (see Fig. 1). We measured the distance from the corolla tube base to the ventral edge of the opening (“length to ventral corolla opening”), as well as the distance from the base to the dorsal sinus where the two dorsal lobes separate (“length to dorsal corolla opening”). Five filaments and anthers are fused together into a tube, or androecium, that extends from the ovary, and the androecium length is measured from the base of the corolla tube to the furthest extent of the androecium (including the anther tube) along a straight line following the axis of the androecium. We measured exsertion length as the distance from the ventral opening of the corolla, where the corolla tube expands outward, to the distal tip of the anther tube along the axis of the androecium.

The strength of backwards-curling of the corolla lobes differs among species in the RCC. We recorded corolla curling on all specimens with flowers at anthesis (full maturity), which can be identified from the presence of pollen at the tip of the anther tube and/or the emergence of the stigmas through the anther tube. The corolla does not continue to curl after anthesis, and we consider the strength of corolla curling to be static at and after anthesis. Corolla curling was recorded as a qualitative character with three states. If no curling was visible, this was recorded as “none.” If the corolla curved backward but did not form a circle, this state was termed “curl” (e.g. Fig. 1H). Finally, if the corolla continued to curl backwards to touch itself this was termed “scroll” (e.g. Fig. 1B, D). Morphometric measurements are found in the Supplemental Data which, along with the R Code used for morphometric analysis, is available on Dryad (Mashburn et al. 2024).

Theoretical Framework—Though most new species are described based on differences from known species in both qualitative and quantitative phenotypic characters, the specific rationale used in differentiating new species are often not identified (McDade 1995). Nevertheless, the underlying perception is typically that non-overlapping patterns of morphological variation would indicate the existence of two or more species (Davis and Nixon 1992; Wiens and Servedio 2000; Sites and Marshall 2004), based on the assumption that an evolutionary force is maintaining the morphological differences (Wiens and Servedio 2000; Coyne and Orr 2004). This is the framework we employ in this study. Even with this theoretical understanding, there is continual discussion of how to methodologically establish the presence of “non-overlapping patterns” of morphological characters (Mallet 1995; Wiens and Servedio 2000; Ezard et al. 2010; Zapata and Jiménez 2012; Cadena et al. 2018). Unbiased statistical clustering methods are typically preferred (Sneath and Sokal 1973; Zapata and Jiménez 2012), yet there is little agreement on what clustering methods are appropriate for biological species, and often species taxonomies do not correspond to phenetic clusters (Rieseberg et al. 2006). In this study, we compare two approaches to morphometric clustering. The first is a hierarchical clustering method, reminiscent of a “numerical

taxonomy” approach (Sneath and Sokal 1973), which assumes the presence of nested hierarchical patterns of morphological traits between populations or species. Such approaches have been criticized because gene flow can lead to phenotypic patterns that are not characterized by discrete, mutually exclusive groups (De Queiroz and Good 1997). The second approach uses a multivariate normal mixture model-based clustering method that has been proposed as appropriate for continuous morphological data (Zapata and Jiménez 2012; Cadena et al. 2018).

Data Analysis—We analyzed our data in three phases, starting with samples from the entire RCC in Phase 1, and two unique subsets of samples in Phases 2 and 3 based on our results in Phase 1. In Phase 1, we assigned each specimen to the three species hypotheses given by Jeppesen (1981) for *B. crispiloba*, *B. sodiroana* and *B. succulenta*. Analyses in Phase 1 revealed support for differentiating species rather than combining them into one, but also identified issues within *B. succulenta*. Phase 2 narrows in on *B. succulenta*, while Phase 3 focuses on the two Ecuador-endemic species *B. crispiloba* and *B. sodiroana*. In Phase 3 we wanted to explore our hypothesis that *B. sodiroana* and *B. crispiloba* may hybridize at the intersection of their ranges. Therefore, we placed putatively hybrid specimens in a separate group (“intermediates”) to visualize where they fall in relation to more conservative (*sensu stricto*, i.e. without intermediates) concepts of *B. crispiloba* and *B. sodiroana*.

In Phases 1 and 2, we used ten quantitative and two qualitative characters that are most often used to differentiate *Burmeistera* species (see * characters in Table 1). Of these, leaf length, leaf width, pedicle length, hypanthium length, hypanthium width, and calyx lobe length were specifically used by Jeppesen (1981) to differentiate RCC species. In Phase 3, we explored relationships with a larger set of characters to capture both vegetative and floral variation in the intermediate specimens. There, we show results based on 22 of the 24 characters measured (see + characters in Table 1).

Our first step in Phases 1 and 2 was to perform univariate analysis among taxonomic groups for individual characters to test if species hypotheses can be diagnosed by non-overlapping differences in single-trait measurements. To statistically compare the distributions of the ten qualitative characters between species, we performed a Pairwise Wilcoxon Rank Sum Test, a non-parametric alternative to a paired *t* test. Although a statistical difference between distributions does not show that a trait is diagnostic, it does indicate that the groups have independent distributions of the character being tested. In Phase 3, since we include morphological intermediates, we did not perform univariate analyses; instead, we went directly into multivariate analyses, described below.

In each of the three phases we performed multivariate analyses using two methods to reduce the dimensionality of the data and two methods of clustering. This allowed us compare methods and thus increase the robustness of our taxonomic decisions. The two methods used to reduce dimensionality were principal component analysis (PCA) and factor analysis of mixed data (FAMD). PCA is performed on quantitative data only

(e.g. the ten quantitative characters), while FAMD allows for analysis of data sets containing a mixture of quantitative and qualitative data (e.g. the ten quantitative and two qualitative characters). Effectively, FAMD performs principal component analysis on quantitative variables and multiple correspondence analysis on qualitative variables. In the process of FAMD, both types of variables are normalized to balance their influence on the whole analysis. PCA and FAMD were performed using the functions PCA and FAMD in the R package FactoMineR (Le et al. 2008). The first method of clustering was performed on the results of both the PCA and FAMD. We used a hierarchical clustering on principal components (HCPC) approach (FactoMineR package, function HCPC), which is primarily a hierarchical clustering method, but includes input from a partitioning clustering (k-means) method. PCA and FAMD first reduce the dimensionality of the dataset. HCPC then performs hierarchical clustering using Ward's criterion on the PCA/FAMD dimensions. The resulting hierarchical tree is used to perform an initial clustering. Then, k-means clustering is performed and consolidated with the hierarchical clustering results to improve the initial partitions. In the HCPC function, we set $n_{cp} = -1$, which selects the "optimal" number of clusters without a preselected range. The optimal number is determined by the structure of the hierarchical tree, where clusters include all samples below a branch at a particular partition of the tree. For each partition, an inertia value is calculated as the sum of squared distances from the center of each cluster. The optimal number of clusters is at the partition (n) with the highest relative loss of inertia moving from partition n-1 to partition n (i.e. the "elbow method" where the inertia values plateau on an inertia-curve). We refer to this as "unsupervised clustering" since the algorithm selects the number of clusters best supported by the structure of the hierarchical tree.

The second method of clustering performed was model-based clustering. The model-based method considers the data as coming from one or more Gaussian distributions, thus only quantitative characters were used. The method tests different distribution parameter models to find the best fit for the data. Model-based clustering was performed using the function Mclust in the package mclust (Scrucca et al. 2016). The Mclust function fits a number of models to the data, with each model including different parameters for the shape, volume, and orientation of the data distribution. The models are fit to the data using maximum likelihood, and the best model and number of clusters (k) is selected using the Bayesian information criterion (BIC score), with the highest BIC score (least negative) indicating the model with the best fit. While the Mclust function works on a data frame and not the results of a PCA, the visualization of the Mclust results are shown on a PCA for visual simplification.

RESULTS

Phase 1: Analysis of the Entire recurved Corolla Clade—Jeppesen (1981) suggested several characters that could be useful to differentiate RCC species, including leaf size (length and width), pedicel length, hypanthium size (length and width), and calyx lobe size. Over half of the pairwise trait comparisons among species sensu Jeppesen, (17 of 30, or

56.7%) showed significant differences in the median values of the trait (Fig. 2; Fig. S1). In particular, the distribution of calyx lobe length measurements in *B. succulenta* did not overlap with either *B. crispiloba* or *B. sodiroana* (Fig. 2A). In addition, the distributions of both androecium length (Fig. 2B) and exertion length (Fig. 2C) in *B. succulenta* were bimodal, indicating potential taxonomic issues therein.

Samples of all three species largely overlapped in the PCA with some differentiation at the edges (Fig. 3A). A group of *B. succulenta* samples were separated in the PCA, largely driven by smaller floral measurements. Unsupervised clustering of the PCA results selected three clusters that were not clearly consistent with the current taxonomy (Fig. 3B; Table S1). Cluster 1 contained 16 samples (16.8% of 95), cluster 2 contained 61 samples (64.2%), and cluster 3 contained 18 samples (19.0%). *Burmeistera succulenta* samples were split into clusters 1 (9 of 27) and 3 (18 of 27). The majority of *B. crispiloba* and *B. sodiroana* samples were grouped in cluster 2. Of the 16 samples in cluster 1, five were *B. crispiloba*, two were *B. sodiroana*, and nine were *B. succulenta*. All *B. succulenta* in cluster 1 were from Ecuador, whereas cluster 3 contained one Ecuador and all Colombia and Venezuela samples. In summary, *B. succulenta* was separated into two clusters with a geographical component (Ecuador vs. Colombia/Venezuela), while *B. crispiloba* and *B. sodiroana* were united into a single cluster.

In the FAMD, *B. sodiroana* was more strongly differentiated from the other two species compared to the PCA, driven by differences in phyllotaxy and corolla curling (Fig. 3C). Unsupervised clustering of the FAMD results selected four clusters (Fig. 3D; Table S1). Cluster 2 contained 15 samples (15.8% of 95) and corresponded almost exactly with PCA cluster 1. Cluster 3 contained 18 samples (18.9%) and corresponded exactly with PCA cluster 3. Similar to the PCA, samples of *B. succulenta* were split into two clusters, with all but one Ecuador sample in cluster 2 and the remaining samples in cluster 3. All 28 of the samples in cluster 1 were *B. sodiroana*, while one *B. sodiroana* sample was placed in cluster 2, and two samples were placed in cluster 4. Finally, 32 of the 34 samples in cluster 4 were *B. crispiloba*.

Model-based clustering selected two clusters (Fig. 3E; Fig. S2) with 28 samples in cluster 1 and 67 samples in cluster 2. Unlike the HCPC clustering on the PCA and FAMD results, model-based clustering united 26 of the 27 *B. succulenta*

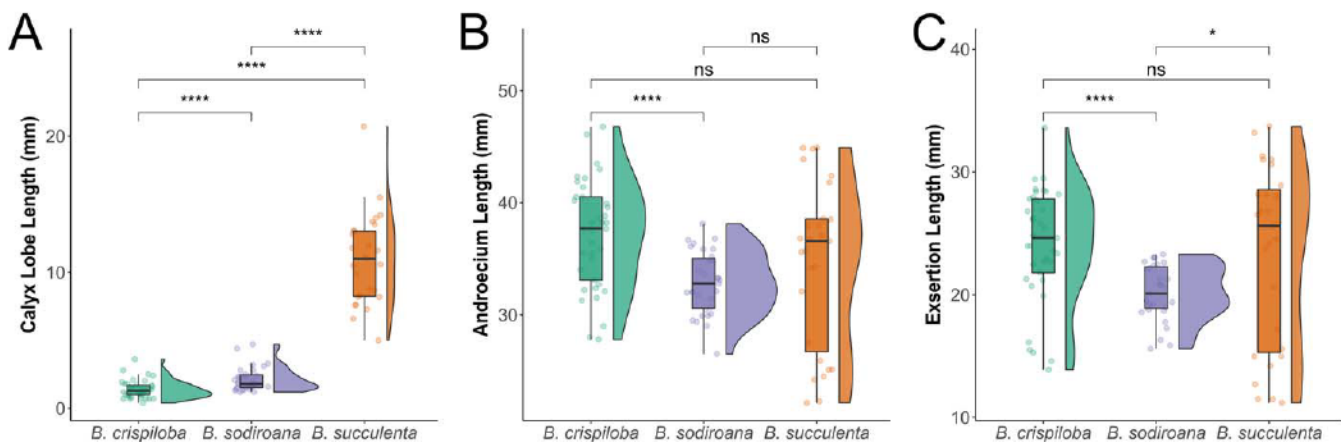


FIG. 2. Univariate comparisons between species concepts sensu Jeppesen for three quantitative traits. A. Calyx lobe length was suggested by Jeppesen (1981) as useful in differentiating *B. succulenta* from *B. crispiloba* and *B. sodiroana*. B, C. Measures of androecium length and exertion length have a bimodal distribution in *B. succulenta*. Significance values were calculated by Pairwise Wilcoxon Rank Sum Tests.

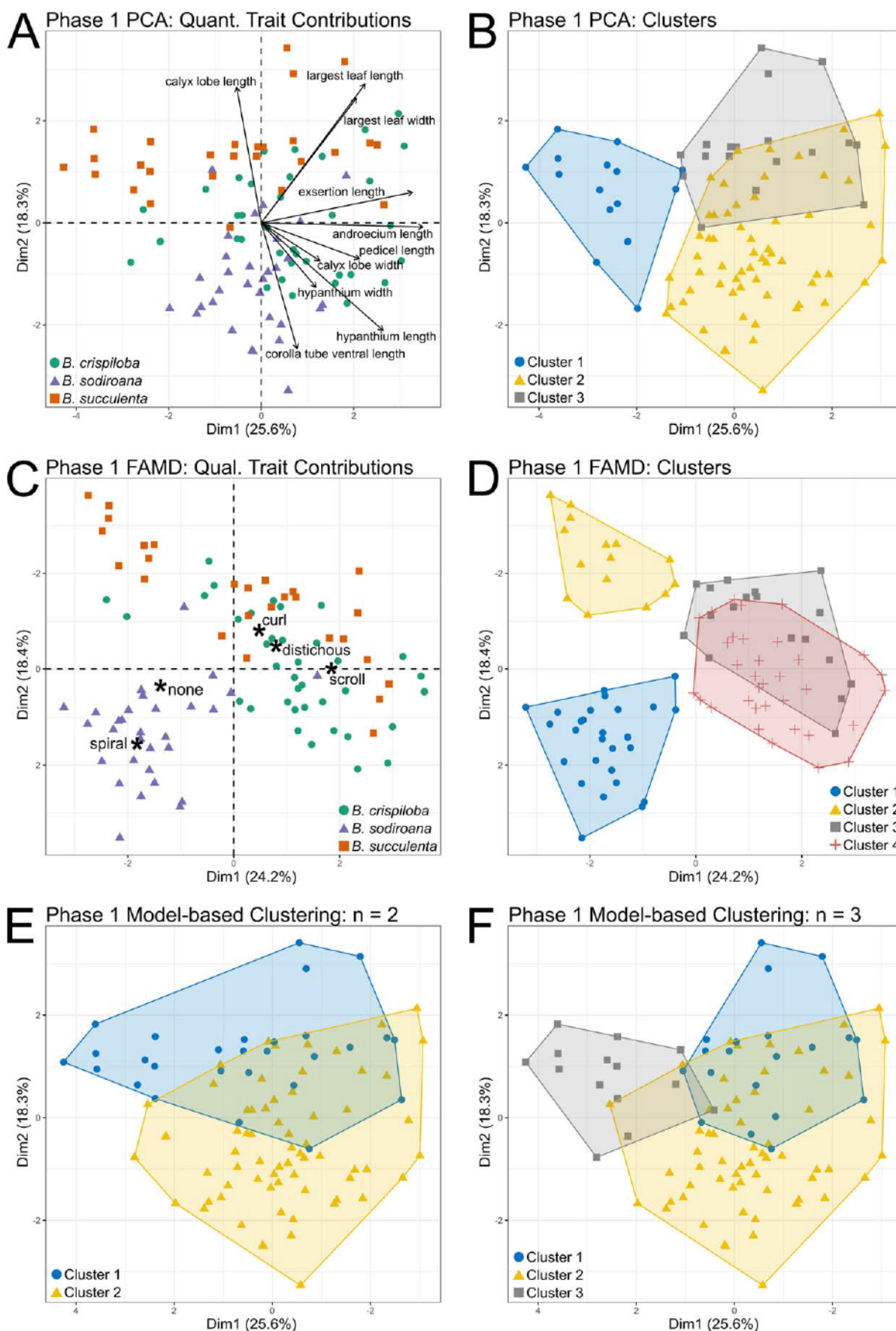


FIG. 3. Results of data dimension reduction and unsupervised clustering methods on the entire dataset of the recurved corolla clade (Phase 1 analysis), with samples colored by assignment to species concepts sensu Jepesen. A, B. PCA of ten quantitative traits; unsupervised clustering performed with HCPC. C, D. FAMD of ten quantitative traits and two qualitative traits with centroids of qualitative traits shown; unsupervised clustering performed with HCPC. E, F. Model-based clustering where $n = 2$ is the optimal number of clusters and $n = 3$ is shown for comparison.

samples into cluster 1 (Fig. 3E; Table S1). Cluster 2 then united *B. crispiloba* and *B. sodiroana* as one group. Model-based clustering at $n = 3$ is also shown (Fig. 3F); at $n = 3$, the Ecuadorian *B. succulenta* was split from the Colombian and Venezuelan samples while the cluster of *B. crispiloba/B. sodiroana* was maintained, similar to the clustering of the PCA results (Fig. 3C). Figures with sample numbers included can be found in the Supplementary Materials (Fig. S2).

Phase 2: Analysis of *B. succulenta*—We transferred all 27 samples of *B. succulenta* into our analysis in Phase 2. Twenty-six of the 27 samples were included in cluster 1 in the model-based clustering method. The one sample not included was grouped with other *B. succulenta* in the clustering of the PCA and FAMD. We elected not to transfer two *B. crispiloba* specimens placed in cluster 1 by model-based clustering, as neither of the HCPC results concurred with this placement.

With the 27 specimens included, we performed both univariate and multivariate analyses in the same manner as in Phase 1, this time comparing the specimens from Ecuador versus those from Colombia and Venezuela (Fig. 4; Fig. S3). Specimens in the two geographic groups did not differentiate in the size of the leaves (Fig. S3) or in calyx lobe length (Fig. 4C). However, the two groups did strongly differentiate in most measures of flower size, with the Ecuadorian samples having shorter pedicels, shorter hypanthia, narrower calyx lobes, shorter androecia, and shorter exertion lengths (Fig. 4).

Principal component analysis of the 27 *B. succulenta* samples showed clear separation between all but one of the Ecuadorian samples and the Colombian and Venezuelan samples (Fig. 5A). This differentiation was largely driven by differences in pedicel length, hypanthium length, calyx lobe width, androecium length, and exertion length. Unsupervised clustering of the PCA results selected four clusters (Fig. 5B; Table S2). Cluster 1 contained nine of 10 Ecuadorian samples, plus one Colombian sample. Cluster 2 contained five samples, all of which are Colombian. Cluster 3 also contained five samples, four from Colombia and one from Ecuador. Cluster 4 contained two Colombian samples and all five Venezuelan samples.

The results of the FAMD visually mirrored those of the PCA, but with slightly more differentiation between geographic groups (Fig. 5C). The differentiation between groups was largely driven by the fact that the Ecuadorian samples did not exhibit the corolla curling/scrolling character, a trait that was present in nearly all Colombian and Venezuelan samples. Unsupervised clustering of the FAMD results selected three clusters (Fig. 5D; Table S2). Cluster 1 contained 10 of 11 Ecuadorian specimens and no Colombian or Venezuelan specimens. This time, the Colombian and Venezuelan specimens were split into two clusters, without much obvious correlation to the clusters found in the PCA results.

Model-based clustering also suggested three clusters (Fig. S4). We share the results of model-based clustering at $n = 2$ (Fig. 5E), to show that at this number of clusters the model-based clustering approach was in accordance with the HCPC on the PCA results pertaining to cluster 1 assignments, with the same nine Ecuadorian specimens and one Colombian specimen (Table S2). At $n = 3$, the Colombian and Venezuelan samples were split into clusters 1 and 2. Cluster 3 contained eight of the 10 Ecuadorian samples plus one Colombian sample. Figures with sample numbers included can be found in the Supplementary Materials (Fig. S4).

Phase 3: Analysis of the *B. crispiloba/B. sodiroana* Complex—In Phase 1, model-based clustering placed 66 of 68 *B. crispiloba* and *B. sodiroana* specimens in one cluster. We transferred all 68 specimens into our analysis in Phase 3, electing to keep the extra two specimens given that they clustered with *B. crispiloba* in both the PCA and FAMD clustering results. In Phase 3, we wanted to see if clustering methods would identify putative intermediate/hybrid samples as a separate cluster from either parental species, *B. crispiloba* s.s. and *B. sodiroana* s.s. A total of 20 intermediate samples were identified a priori as having a mixture of traits associated with either *B. crispiloba* or *B. sodiroana*, including floral and fruit color traits not used in the morphometric analysis. The intermediate group included 14 samples moved from *B. crispiloba* and 6 moved from *B. sodiroana* in Phase 1. The analysis therefore included 23 specimens in *B. crispiloba* s.s., 25 specimens in *B. sodiroana* s.s., and the 20 intermediate specimens.

Principal component analysis showed some differentiation between *B. crispiloba* s.s. and *B. sodiroana* s.s., but without a clear gap between the two (Fig. 6A). Intermediate specimens were largely separated in the PCA and were not placed directly between the two species. The location of most intermediate specimens was driven by larger measures of petiole length and leaf size traits (Fig. 6A). Unsupervised clustering of the PCA selected three clusters (Fig. 6B; Table S3). Of the 35 samples in cluster 1, 25 were *B. sodiroana* s.s., two were *B. crispiloba* s.s., and eight were intermediates. Five of these intermediates were taken from *B. sodiroana*; thus 30 of 35 samples in cluster 1 were originally *B. sodiroana*. Of the 24 samples in cluster 2, 20 were *B. crispiloba* s.s. and four were intermediates taken from *B. crispiloba*. Of the nine samples in cluster 3, seven were intermediates taken from *B. crispiloba*, one was an intermediate from *B. sodiroana*, and one was *B. crispiloba* s.s.

The FAMD results divided the specimens more strongly than the PCA results due to consistent differences between taxa in phyllotaxy and corolla curling (Fig. 6C). Specimens of *B. sodiroana* s.s. typically had spiral phyllotaxy and rarely exhibited noticeable corolla curling on herbarium specimens, while specimens of *B. crispiloba* s.s. typically had distichous phyllotaxy and curling or scrolling corollas. Most intermediate specimens were more strongly pushed into the top-right quadrant of the FAMD compared to the PCA. All intermediate specimens were recorded as having distichous phyllotaxy, though there was a mix of corolla curling characters (six “none”, five “curl”, eight “scroll”). Unsupervised clustering again selected three clusters (Fig. 6D; Table S3). Of the 30 samples in cluster 1, 25 were *B. sodiroana* s.s., two were *B. crispiloba* s.s., and three were intermediates taken from *B. sodiroana*. Of the 24 samples in cluster 2, 21 were *B. crispiloba* s.s. and three were intermediates taken from *B. crispiloba*. Cluster 3 contained 14 samples, all of which were identified as intermediates (11 from *B. crispiloba* and three from *B. sodiroana*). Thus, 60 of 68 samples (88.2%) were placed into clusters that match their a priori identification (Table S3).

Model-based clustering suggested the optimal number of clusters to be one (Fig. S5), consistent with model-based clustering in Phase 1, where *B. crispiloba* and *B. sodiroana* were grouped together (Fig. 3E). Model-based clustering of the dataset at $n = 2$ and $n = 3$ are shown for comparison (Fig. 6E, F). At both $n = 2$ and $n = 3$, *B. crispiloba* and *B. sodiroana* were split into two clusters with some exceptions (Table S3) and an independent group of intermediate specimens was

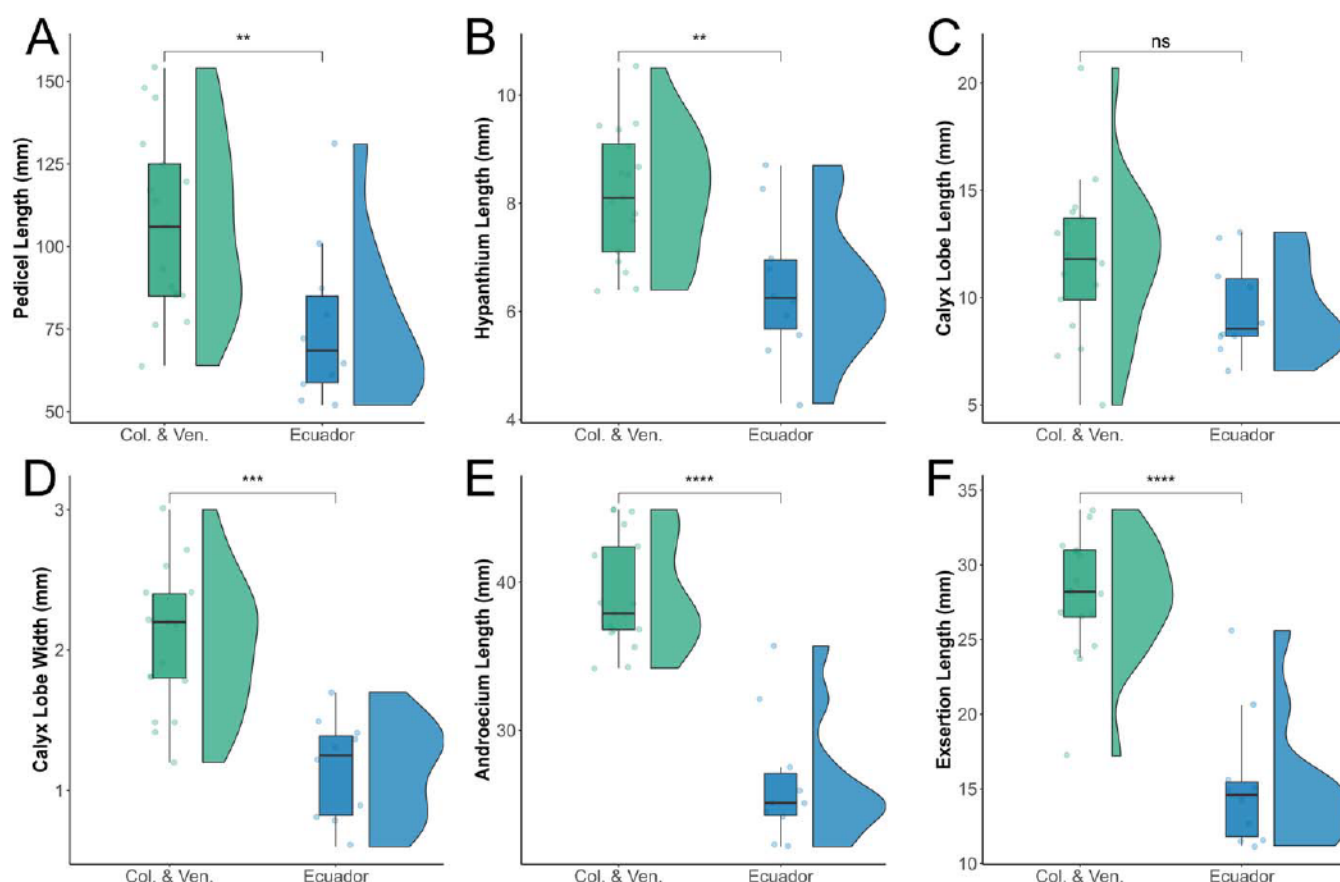


FIG. 4. Univariate comparisons between geographic groups of *B. succulenta* specimens for six quantitative floral traits commonly used in *Burmeistera* taxonomy, showing generally smaller measures of flower size in Ecuadorian samples versus samples from Colombia and Venezuela. Significance values were calculated by Pairwise Wilcoxon Rank Sum Tests.

not identified. Figures with sample numbers included can be found in the Supplementary Materials (Fig. S5).

DISCUSSION

Burmeistera is a taxonomically difficult group; traits are often highly labile, and interspecific hybridization seems common. The recurved corolla clade is no exception, leading to a diversity of species hypotheses. Zahlbruckner (1915) and Wimmer (1943, 1968) described five species and four subspecific varieties within the RCC. Jeppesen (1981) merged these into three species and posited that even these three may in fact be one widespread and variable species (Jeppesen 1981; Lammers 1998). Our morphometric analysis of 95 samples examined traits among Jeppesen's (1981) concepts of the three *Burmeistera* species in the RCC. We performed three phases of analysis, each phase using two different methods of unsupervised clustering. Our intent in using multiple methods was to assess how these different methods might converge or diverge in their conclusions, helping us make more informed decisions about species delimitation. We did not find consistent agreement between all clustering methods, though our findings are largely consistent with Jeppesen's (1981) species hypotheses, with some modifications.

Phase 1: Analysis of the Entire Recurved Corolla Clade—Overall, our analysis of the three RCC species showed Jeppesen's (1981) three species concepts to be broadly cohesive, though this result would be difficult to determine based on

univariate comparisons alone. Diagnostic characters mentioned by Jeppesen were leaf length and width, pedicel length, hypanthium length and width, and calyx lobe length and width. For most of these traits, despite significant differences in the median values of each trait, it is difficult to detect clearly diagnostic differences in these characters (Fig. 2; Fig. S1). Longer calyx lobe length appears to be diagnostic for *B. succulenta* compared to *B. crispiloba* and *B. sodiroana*. This corresponds to our observation that specimens appearing to occur in the RCC with long calyx lobes have regularly been assigned to *B. succulenta*. Even so, we discovered issues within *B. succulenta*, evidenced by bimodal distributions in androecium length and exsertion length. Meanwhile, quantitative characters that clearly differentiate *B. crispiloba* and *B. sodiroana* were difficult to identify.

Though the unsupervised clustering methods used on the RCC did not agree in the number of clusters formed by the data, all three methods did agree that *B. succulenta* is distinct from *B. crispiloba* and *B. sodiroana*. In fact, HCPC on the PCA (three clusters), found greater divergence within *B. succulenta*, which was split into two clusters, than between *B. crispiloba* and *B. sodiroana*, which were united into one cluster (Fig. 3B). This morphological split of *B. succulenta* had a geographic component (Ecuador vs. Colombia/Venezuela). HCPC on the FAMD results also maintained the geographic split of *B. succulenta* samples. Only model-based clustering maintained *B. succulenta* as a unified group at the optimal $n = 2$ (Fig. 3E). Standing alone, model-based clustering would

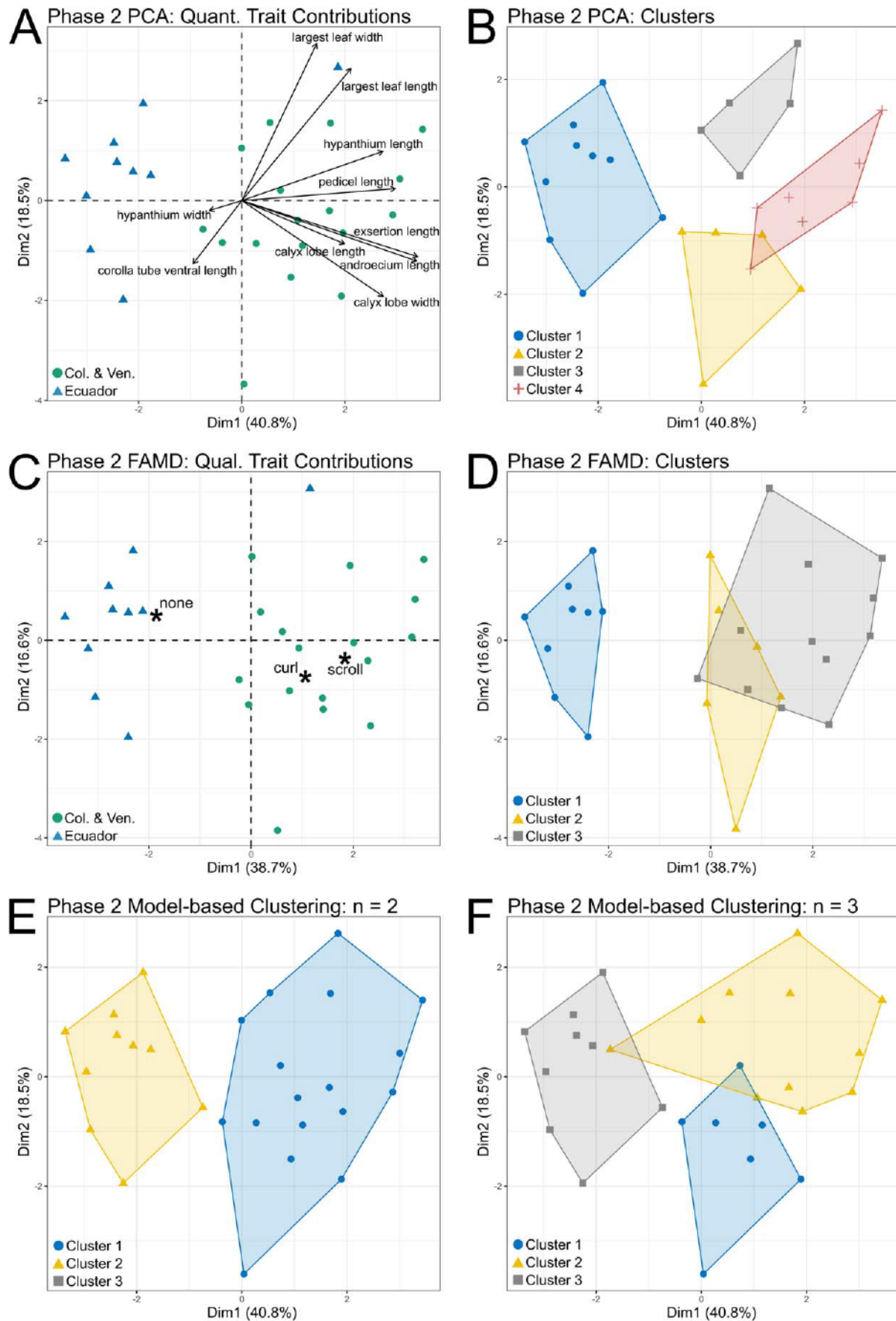


FIG. 5. Results of data dimension reduction and unsupervised clustering methods on 27 *B. succulenta* s.l. samples, colored by geographic origin of collection. A, B. PCA of ten quantitative traits; unsupervised clustering performed with HCPC. C, D. FAMD of ten quantitative traits and two qualitative traits with centroids of qualitative traits shown; unsupervised clustering performed with HCPC. E, F. Model-based clustering where $n = 3$ is the optimal number of clusters; clustering at both $n = 2$ and $n = 3$ shown for comparison.

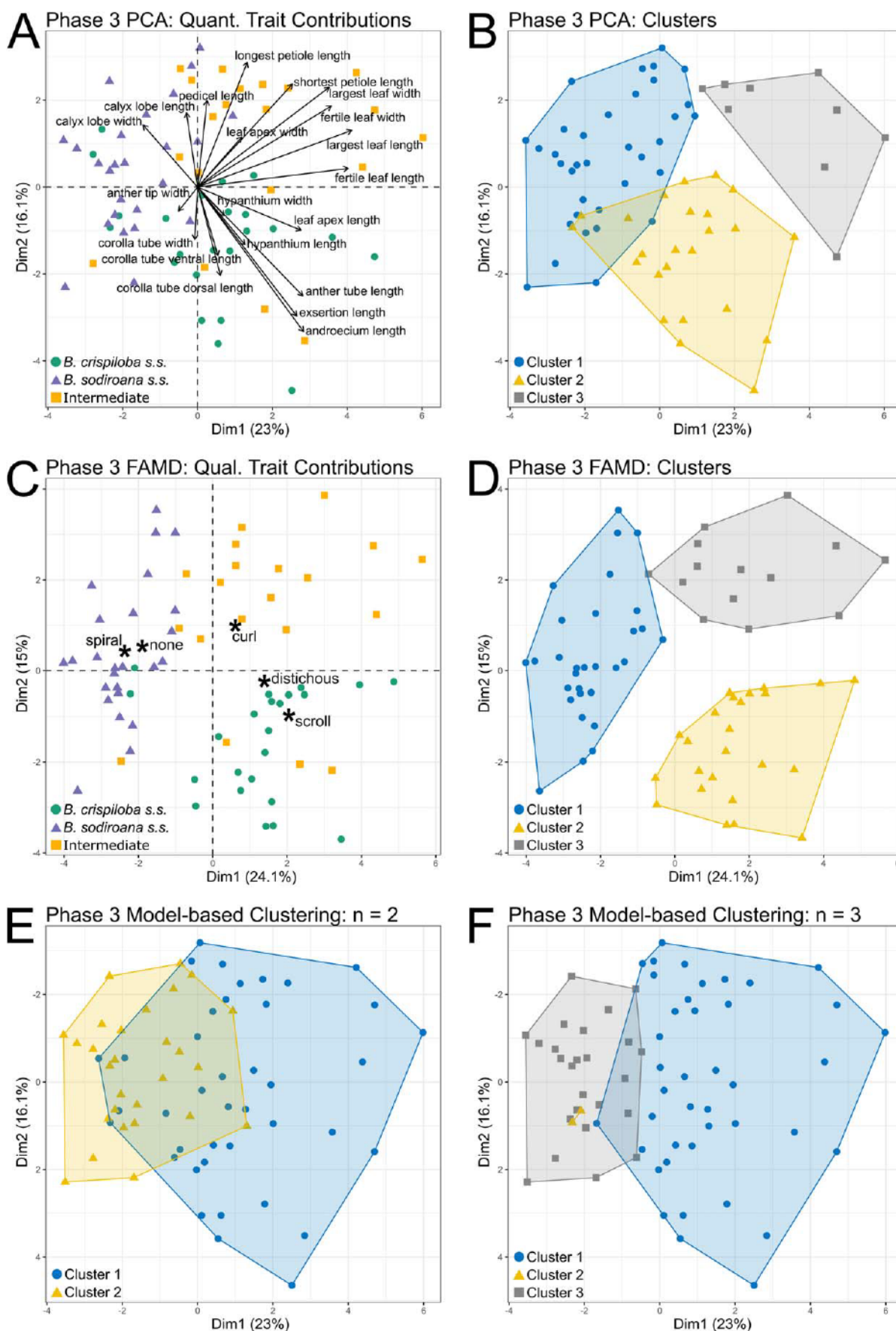


FIG. 6. Results of data dimension reduction and unsupervised clustering methods on 68 *B. succulenta* samples, colored by our a priori placement of samples to *B. crispiloba* s.s., *B. sodiroana* s.s., and intermediate specimens. A, B. PCA of 22 quantitative traits; unsupervised clustering performed with HCPC. C, D. FAMD of 22 quantitative traits and two qualitative traits with centroids of qualitative traits shown; unsupervised clustering performed with HCPC. E, F. Model-based clustering where $n = 1$ is the optimal number of clusters; clustering at both $n = 2$ and $n = 3$ shown for comparison.

suggest that *B. succulenta*, as understood by Jeppesen and successive botanists, is a cohesive species hypothesis based on the morphological data. Nevertheless, our findings of bimodal distributions in flower size characters (Fig. 2) and the unsupervised clustering on the PCA and FAMD, which split *B. succulenta* into two groups, prompted us to analyze *B. succulenta* as a separate dataset in Phase 2.

Clustering attempts on the entire data set also disagreed in how to treat *B. crispiloba* and *B. sodiroana*. Both HCPC on the PCA and model-based clustering combined the two species into one group, while the FAMD clustering separated them (Fig. 3). FAMD incorporated two qualitative measures, phyllotaxy and corolla curling, that were not included in the PCA and model-based clustering. These two qualitative characters would seem to be helpful in differentiating two species that are similar in most quantitative characters. Additionally, we observed that the two species seem to be more similar where their distributions meet, suggesting hybridization as the driving factor behind their morphometric similarity and the inability of certain clustering methods to distinguish them. This hypothesis was tested in more detail in Phase 3.

Phase 2: Analysis of *Burmeistera succulenta*—Standalone analyses of *B. succulenta* samples confirmed the existence of issues in the current species delimitation and supported its separation into two taxonomic entities. The majority of Ecuadorian specimens placed in *B. succulenta* had shorter pedicels, hypanthia, androecium length and exertion length, as well as thinner calyx lobes compared to specimens from Colombia and Venezuela (Fig. 4). Clustering methods consistently found the group of Ecuadorian specimens, one or two samples excepted, to be morphologically distinct. It was, however, unexpected that each clustering method suggested at least three optimal clusters. More sampling of *B. succulenta* samples from Colombia and Venezuela may be necessary to better conclude if the clustering methods are over-splitting the data or finding real differences between samples in these regions. In the meantime, we find sufficient support to describe the Ecuadorian samples previously placed under *B. succulenta* as a new species. This decision is further supported by the presence of bright yellow latex in the *B. succulenta* samples from Ecuador, which is unique compared to the white latex of *B. sodiroana* and *B. succulenta* and the cream-colored latex of *B. crispiloba*. Altogether, it seems apparent that specimens of this new Ecuadorian species were identified as *B. succulenta* because of vegetative similarity and long corolla lobes, and botanists likely considered the recurved corolla character to be absent because the smaller flowers could be considered immature and thus not exhibiting the trait. In fact, the absence of corolla curling in the Ecuadorian samples suggests that this new species may not be part of the recurved corolla clade at all, prompting the inclusion of an Ecuadorian sample in a recent phylogenetic study (Bagley et al. 2020). This study placed the new species outside of the RCC, closely related to other Ecuadorian species such as *B. huacamayensis* Jeppesen and *B. cylindrocarpa* Zahlbr (see Fig. 2 in Bagley et al. 2020). Therefore, both morphological and genetic data support the recognition of the Ecuadorian *B. succulenta* as a new species.

Phase 3: Analysis of the *B. crispiloba*/*B. sodiroana* Complex—Our intent in Phase 3 was to test if intermediate specimens between *B. crispiloba* and *B. sodiroana*, which we hypothesize to be putative hybrids, could be shown to cluster independently of parental species; or if they would be placed

between *B. crispiloba* and *B. sodiroana* and cluster with the parental species. If all specimens clustered as one group, this would suggest that *B. crispiloba* and *B. sodiroana* are in fact a single species. We identified 22 specimens as intermediates/potential hybrids (13 from *B. crispiloba* and nine from *B. sodiroana*) that were not easy to cleanly place in either of the two species.

Model-based clustering suggested that the optimal number of clusters was, in fact, one (Fig. S5). Putative hybrids were not found to be morphologically intermediate (occurring between the parent species), but instead occupied a different portion of the PCA and FAMD (Fig. 6A, C). This suggested that intermediates were not causing the clustering of otherwise morphologically distinct species. However, unsupervised clustering of both the PCA and FAMD results suggested three clusters, with each cluster roughly corresponding to the a priori groups *B. crispiloba* s.s., *B. sodiroana* s.s. and intermediates, lending support to our a priori defined species concepts. As a result, we conclude that *B. crispiloba* and *B. sodiroana* are morphologically distinct species, but that the quantitative traits alone are not sufficient to distinguish them in the model-based clustering method. In addition, though our hypothesis of hybridization can only be proven inconclusively with genomic data, our results here indicate that hybridization between *B. crispiloba* and *B. sodiroana* could be driving novel phenotypic combinations that are not simply intermediate between parental species.

Comments on Clustering Methods—Achieving statistical confidence in decisions of species delimitation based on morphological characters can be a difficult enterprise, requiring a large number of samples and characters (Wiens and Servedio 2000). In addition, species boundaries can be porous, and introgression in hybrid zones can make clean species delimitation difficult (Spasojevic et al. 2014). In such situations, phenotypic data is integral to species delimitation, providing evidence for selection on traits of ecological or evolutionary importance where studies of neutral genetic diversity might find no evidence of selection (Barraclough 2019). Despite this, methods for delimiting species and/or hybrids using phenotypic data lag behind those using genomic data (Cadena et al. 2018), largely due to the dramatic shift towards genomic methods in systematics and an over-reliance upon genomic data to test species concepts (Barraclough 2019). As a result, botanists are provided few guides for species delimitation when attempting to do so using morphological data and statistical clustering methods, resulting in a great diversity of methods employed and/or little congruence between species taxonomies and clustering methods (Rieseberg et al. 2006).

We compared three combinations of dimension reduction and clustering to test species hypotheses in the recurved corolla clade of *Burmeistera*. While our analysis was not intended to be an exhaustive comparative test of the methods themselves, we found differences among them that are worth mentioning. First, model-based clustering appears to be a more conservative test of species boundaries than the modified hierarchical clustering approach. In each of the three phases of our study, model-based clustering suggested the smallest number of clusters. It has been argued that model-based methods are the most appropriate for morphological data given the evolutionary assumptions of polygenic inheritance and random mating (Cadena et al. 2018; Cadena and Zapata 2021). Therefore, the more conservative clustering of

the model-based approach may be an indication that other methods over-split the distribution of morphological data, leading to over-split species concepts. On the other hand, hierarchical clustering, unlike model-based clustering, was able to recover patterns of morphological variation that corresponded to our hypothesis of hybridization between *B. crispiloba* and *B. sodiroana*, suggesting that the conservative nature of the model-based approach may have some limitations. Second, it remains unclear how many specimens are necessary to satisfactorily demonstrate that gaps between clusters indicate different species. For example, the possible over-splitting of *B. succulenta* into three or four clusters (Fig. 5) could be driven by a lack of adequate specimens to properly test the species concepts using both hierarchical and model-based methods. Finally, methods that can incorporate qualitative data, such as FAMD, are able to expose more of the potential variation between species than methods that require quantitative data only. In each phase of our analysis, the inclusion of the phyllotaxy and corolla curling characters strengthened the differentiation between clusters identified in the PCA or model-based methods.

CONCLUSION

Despite imperfect congruence among the clustering methods used in this study, our results largely coincided with the three species hypotheses presented by Jeppesen (1981) and led us to reject his suggestion that they could be one widespread, variable species. Our analysis supported the acceptance of the three names Jeppesen used for species in the recurved corolla clade: *B. crispiloba*, *B. sodiroana*, and *B. succulenta*. While we found *B. succulenta* to be distinct from *B. crispiloba* and *B. sodiroana*, we also identified a new Ecuador endemic species, *B. kitrinaima* sp. nov., among specimens previously identified as *B. succulenta*. The inclusion of *B. kitrinaima* in a recent phylogenetic study showed it to be outside of the RCC. We also showed support for the distinctiveness of *B. crispiloba* and *B. sodiroana*, though we found evidence for a hybrid zone at the intersection of their ranges. Introgression in this hybrid zone may be leading to combinations of morphological traits not seen in either parent species. Given the results of these analyses, we provide an updated key to aid in the correct identification of the three species of the RCC and the new species *B. kitrinaima*, described below.

KEY TO BURMEISTERA SPECIES TREATED IN THIS STUDY

1. Phyllotaxy alternate, spiral; corolla lobes at anthesis flaring outward or recurved but not scrolling; anther tube dark purple. *B. sodiroana*
1. Phyllotaxy alternate, distichous; corolla lobes falcate, not curling, or recurved and scrolling backward; anther tube pale green, yellow, sometimes with a red tinge. 2
 2. Calyx lobes < 3 mm long, deltate. *B. crispiloba*
 2. Calyx lobes > 5 mm long, linear to ligulate. 3
 3. Latex yellow; flowers < 38 mm long; androecium < 27 mm long, exerted < 15 mm from the corolla opening; calyx lobes falcate, not recurved. *B. kitrinaima*
 3. Latex white; flowers > 44 mm long; androecium > 35 mm long, exerted > 23 mm from the corolla opening; calyx lobes recurved, curling or scrolling backward. *B. succulenta*

TAXONOMIC TREATMENT

BURMEISTERA CRISPILOBA Zahlbr., Repert. Spec. Nov. Regni Veg. 13: 528. 1915. TYPE: ECUADOR. Chimborazo, "In silva subtropica vallis Pallatanga," Sep 1891, *L. Sodiro 91/24* (holotype: B [presumed destroyed], isotypes: P [barcode] 00408884 [digital image!], QPLS [bc] 210999 [digital image!], W 1961-0017416 [digital image!], W 1967-0015165 [digital image!]).

Burmeistera montana E. Wimm., Repert. Spec. Nov. Regni Veg. 30: 23, t. 124. 1932. TYPE: ECUADOR. Pichincha, "In silvis montis Corazón ad Cauzacotó," 2000 m, Jul 1882, *L. Sodiro 91/22* (holotype: B [presumed destroyed], isotypes: P [barcode] 00408885 [digital image!], W 1963-0012270 [digital image!]).

Burmeistera succulenta var. *breviloba* E. Wimm., Pflanzenz. 276c: 836. 1968. TYPE: ECUADOR. Pichincha, San Carlos de los Colorados, 150 m, 28 Sep 1935, *A. Schultze-Rhönhof 1929* (holotype: B [barcode] 10 0158362 [digital image!]).

Scandent herbs, up to 5 m long. Latex cream-colored. Stems ca. 4 mm in diameter, green to green tinged violet, glabrous. Leaves alternate, distichous, often reduced in size when subtending a flower, the internodes 10–30 mm long; petioles 5–10 mm long, glabrous, green to green tinged violet; lamina 90–160 × 25–55(–70) mm, where subtending a flower reducing to 55–105 × 15–40 mm, elliptic to oblong-lanceolate, the base attenuate to obtuse, the apex attenuate, the margins shallow callose-dentate to nearly entire, sometimes slightly revolute; upper surface green, glabrous; lower surface green to green tinged violet, glabrous; veins craspidodromous to

campitodromous, the primary vein prominent, raised, the secondary veins thin, slightly raised, the tertiary veins visible. Flowers solitary in the upper leaf axils, 44–58 mm long; pedicels 75–110 mm long at anthesis, 85–110 mm long in fruit, green to green tinged violet, glabrous; hypanthium 9–13 × 5–9 mm, obconical, green to green tinged violet, glabrous; calyx lobes 0.5–2(–3) × 0.5–1.5(–2.5) mm, deltate, green, glabrous, the margin entire, the apex acute, ascending at anthesis; corolla glabrous, entirely green to green tinged violet outside, white to pale blue-green inside; corolla tube 6–8 mm wide basally, the throat narrowing to 2–3 mm wide; corolla lobes lanceolate, strongly scrolling back, the two dorsal lobes 20–25 × 2–4 mm, opening dorsally 15–23 mm from the corolla base, the two lateral lobes 17–18 × 2–3 mm, the ventral lobe ca. 16 × 3 mm, opening ventrally 11–14 mm from the corolla base; androecium 35–48(–57) mm long, exerted 23–30(–44) mm from the ventral opening, the filament tube green to green tinged violet, glabrous to villose distally, the anther tube 8–12 × 2.5–4 mm, green to violet, glabrous to villose basally, all five anther tips glabrous to sparsely pubescent; the style and stigma cream-colored, the stigma lobes densely villose underneath, shortly pubescent on the margin. Fruits ca. 25 × 30 mm, obovoid to pyriform, spongy, inflated, maturing cherry red, rarely pink or violet.

Distribution and Habitat—*Burmeistera crispiloba* is a relatively common terrestrial herb in wet tropical forests of western Ecuador. It can be found at low elevations near the coast, though collections are more common from 500–1500 m in the western foothills of the Andes, and it is sometimes found at elevations up to 2000 m.

Etymology—The specific epithet likely refers to the strongly scrolling/curling (Latin: *crispus*) corolla lobes, a distinctive feature of this species, along with the closely related *B. succulenta*.

Notes—Both *B. crispiloba* and *B. succulenta* exhibit strong scrolling of the corolla lobes at anthesis, in which corolla lobes scroll back multiple times (see Fig. 1). However, *B. succulenta* is differentiated by its longer linear calyx lobes (> 8 mm long), compared with the shorter (< 3 mm long) deltate calyx lobes of *B. crispiloba*.

Specimens intermediate between *B. crispiloba* and *B. sodiroana* suggest that these two species hybridize and introgress where their ranges meet in the western Andes of Ecuador, at around 1500 m in elevation. Many of these intermediate specimens have been collected in and around Maquipucuna Reserve in Pichincha province. *Burmeistera crispiloba* s.s. is differentiated from *B. sodiroana* s.s. in having distichous phyllotaxy (vs. spiral), slightly larger flowers (44–58 mm long vs. 37–42[–48] mm) with corolla lobes scrolling open (vs. flaring or curling), a white to pink anther tube (vs. dark purple anther tube), and cherry red, obovoid to pyriform fruits (vs. white to pink, globose to ellipsoid). Most intermediate specimens exhibit distichous phyllotaxy and have larger flowers and are therefore placed with *B. crispiloba*.

Three specimens from Reserva Ecológica Los Ilinizas in Cotopaxi Province (*Silverstone-Sopkin et al.* 9723 & 9965 and *Ramos et al.* 7305) have flowers similar in many ways to *B. crispiloba*, differing primarily in their much longer exertion length (30.5–44 mm vs. 23–30 mm in “typical” *B. crispiloba*). More collections are needed in the region of this reserve to clarify the status of this group.

Additional Specimens Examined—Ecuador. —AZUAY: Cantón Camilo Ponce Enrique localidad Bella Rica-Villa Rica, 1096 m, [–3.088°, –79.669°], 31 Mar 2010, *Jaramillo* 30276 (QCA). —BOLÍVAR: Hacienda Changuil, sector La 47, 400 m, [–2.1°, –79.167°], 1 Aug 1995, *Bonifaz & Cornejo* 3170 (MO). —CAÑAR: La Troncal, Manta Real, vertientes bajas en la base occidental de los Andes, a 20 km al sureste de La Troncal, 430–650 m, [–2.557°, –79.366°], 25 May 2005, *Vargas & Defas* 5585 (MO). —CARCHI: Alrededores de Maldonado, 90 km al oeste de Tulcán, 1500 m, 5 Sep 1981, *Balslev* 1996 (QCA); Maldonado, banks of small stream just N of the village, 1500 m, 4 Oct 1981, *Werling & Leth-Nissen* 233 (QCA, 2 sheets); Maldonado, Chical trail, 1500 m, 26 Jan 1977, *Boeke* 842 (MO, NY, QCA); Near Maldonado, 1400 m, 30 Jul 1989, *van der Werff & Gudino* 10767 (MO). —COTOPAXI: Cantón Pujilí, Reserva Ecológica Los Ilinizas, Sector II, Sector Sur, sector Chuspitambo, al occidente de Choasilli, 1727 m, [–0.978°, –79.106°], 3 Aug 2003, *Silverstone-Sopkin et al.* 9723 (MO); Cantón Pujilí, Reserva Ecológica Los Ilinizas, Sector II, Sector Sur, sector Chuspitambo, al occidente de Choasilli, 1727 m, [–0.979°, –79.115°], 8 Aug 2003, *Silverstone-Sopkin et al.* 9965 (MO); Cantón Sigchos, Reserva Ecológica Los Ilinizas, ca. 4 km antes de Saguambi, en la vía Triunfo Grande-Las Pampas, 2156 m, [–0.493°, –78.994°], 13 Aug 2003, *Ramos et al.* 7305 (MO); Reserva Otonga, entre Quito y Sto. Domingo, cerca de San Francisco de las Pampas, 1990–2200 m, [–0.417°, –79°], Jun 1997, *Nowicki & Mutke* 1498 (QCA); Tenefuerste, Río Pilaló, km 52–53, Quevado-Latacunga, 750–900 m, 29 Oct 1981, *Dodson & Dodson* 12000 (MO); Tenefuerste, Río Pilaló, km 52–53, Quevado, Latacunga, 750–1300 m, 21 Feb 1982, *Dodson & Gentry* 12782 (MO). —ESMERALDAS: New road under construction from Lita to San Lorenzo, 600–800 m, [0.967°, –78.583°], 11 May 1991, *Gentry et al.* 69965 (MO, NY); Quinindé, Bilsa Biological Station, Mache mountains, 35 km W of Quinindé, 5 km W of Santa Isabel, 400–600 m, [0.35°, –79.733°], 25 Mar 1995, *Clark & Troya* 499 (MO). —EL ORO: Cantón Piñas, parroquia Moromoro, Reserva Ecológica Buenaventura, remnant patch of forest south of Entrada la Virgen, 900–1000 m, [–3.651°, –79.74°], 12 May 2003, *Clark et al.* 7944 (QCA); Piñas, Parroquia El Placer, Reserva Buenaventura, propiedad de la Fundación Jocotoco, recorrido desde la estación hasta el bosque Puma, 1000 m, [–3.645°, –79.763°], 3 Apr 2005, *Vargas et al.* 5171 (MO); West of Piñas 10 km on new road to Sta. Rosa, 950 m, 8 Oct 1979, *Dodson et al.* 9159 (MO). —GUAYAS: Hacienda Botija, ca. 8 km E of Naranjal, 250–350 m, 26 May 2980, *Harling & Andersson* 19471 (NY);

Naranjal, Reserva Ecológica Manglares-Churute, cumbre del Cerro Pancho Diablo, 700 m, [–2.45°, –79.583°], 31 Dec 1991, *Cerón* 17925 (MO). —IMBABURA: 1390 m, [0.301°, –78.783°], 16 Apr 2003, *Muchhala* 207 (QCA). —LOJA: Finca of the Calderón family, taking a trail NE from Mercadillo towards the crest, 1770 m, [–4°, –79.95°], 12 Aug 2000, *Cotton et al.* 1605 (MO, NY). —LOS RÍOS: Río Palenque Science Center, km 56, road Quevedo-Sto. Domingo, 150–220 m, 30 Nov 1978, *Dodson* 7310 (MO). Hacienda Clementina, Cerro Samama, trail between Destacamento Pita and La Torre, 600 m, [–1.5°, –79.317°], 24 Oct 1995, *Knudsen et al.* 459 (QCA). —MANABÍ: Machalilla National Park, San Sebastian, 8–9 km SE of Agua Blanca, 550–730 m, [–1.6°, –80.7°], 19 Jan 1991, *Gentry et al.* 72409 (MO). —PICHINCHA: Along road and trail from Maquipucuna Lodge to Ecología Santa Lucía, 2 km N of Maquipucuna entrance, 1400 m, [0.122°, –78.618°], 15 Mar 2006, *Croat et al.* 95948 (MO); Bosque Integral Otonga, 1676 m, [0.167°, –78.667°], 4 Jul 2002, *Muchhala* 115 (QCA); Cantón Quito, Maquipucuna Biological Reserve, 9 km NE of Nanegal, 1500–1700 m, [0.083°, –79.033°], 2 Feb 1991, *Neill et al.* 9800 (MO); Carretera Quito a La Concordia vía Nono, Mindo, San José de las Minas y Puerto Quito, km 77, 1300 m, 7 Aug 1984, *Dodson et al.* 15196 (MO); Carretera Quito-Puerto Quito, km 113, 10 km al N de la carretera principal, 800 m, [0.083°, –79.033°], 26 May 1984, *Arguello* 507 (MO, NY); Centinela, 12 km oeste de Patricia Pilar que queda en km 45 Santo Domingo a Quevedo, 600 m, 2 Feb 1985, *Dodson & Neill* 15548 (MO, NY); Centinela, Canton Sto. Domingo, 12 km E of Patricia Pilar, along path on ridge line, 600 m, 23 Aug 1978, *Dodson & Embree* 7217 (MO); Centinela, km 12 carretera Patricia Pilar-24 de Mayo, altura de km 47 Santo Domingo-Quevedo, en la cima de las Montañas de Ila, 650 m, 30 Jul 1984, *Dodson et al.* 14661 (MO, NY); Centinela Ridge, 12 km E of Patricia Pilar on road to 24 de Mayo, 600 m, 26 Jun 1985, *Stein & Dodson* 3091 (MO, 2 sheets); Cooperativa Santa Marta #2, along Río Verde, 2 km SE of Sto. Domingo de Los Colorados, 530 m, 5 Feb 1979, *Dodson* 7433 (MO); El Centinela, 12 km E of Patricia Pilar on road between Santo Domingo and Quevedo, 650 m, 15 Jul 1979, *Fallen & Dodson* 858 (MO); From path following ridge line at El Centinela at crest of Montañas de Ila on road from Patricia Pilar to 24 de Mayo at km 12, 600 m, 28 Jul 1979, *Dodson* 5628 (MO); Maquipucuna, 5 km E of Nanegal, transect no. 2, 1630 m, [0.117°, –78.617°], 9 May 1990, *Gentry et al.* 69945 (MO); Maquipucuna Tropical Reserve, northern boundary of reserve, 10 km N of Nanegalito, 1200 m, [0.167°, –78.583°], 2 Dec 1988, *Neill et al.* 8654 (MO); Nanegalito-Tandayapa road, 1890–2400 m, [–0.05°, –78.733°], 7 Nov 1989, *Luteyn & Tirira* 13333 (NY); Old road Santo Domingo-Chiriboga-Quito, ca. 3 km from bridge over Río Pilatón, 1000 m, 17 Mar 1985, *Harling & Andersson* 23062 (NY); Old road from Santo Domingo to Quito, ca. 5 km from paved highway, 1200 m, [–0.25°, –78.917°], 3 May 1985, *Stein et al.* 2686 (MO); Parroquia Nanegal, Cerro Campana, 5–6 km airline E of Nanegal, ridge between Quebrada Cariyacu and Q. Loreto, 1700 m, [0.15°, –78.617°], 1 Sep 1993, *Webster & Paradise* 30017 (MO); Parroquia Puerto Quito, Reserva Forestal de ENDESA, 10 km al norte de Alvaro Pérez Intriago, 650–800 m, [0.05°, –79.117°], 11 Jun 1990, *Cerón & Ayala* 10082 (MO); Quito Cantón, Nanegal, Reserva Biológica Maquipucuna, 1200–1700 m, [0.133°, –78.583°], 20 May 1991, *Tipaz & Quelal* 157 (MO); Quito-Puerto Quito road, 10 km N of km 113, Reserva Forestal ENDESA, Río Silancha, Corporación Juan Manuel Durini, 650–700 m, [0.083°, –79.033°], 18 May 1987, *Daly et al.* 5206 (MO, NY); Reserva de ENDESA, km 113 along Quito-Pto. Quito road, near ENDESA house, 800–1000 m, [0.083°, –79.033°], 16–17 Nov 1989, *Luteyn & Borchsenius* 13363 (MO, NY, QCA); Reserva Forestal de ENDESA, Río Silancha, Corporación Forestal Juan Manuel Durini, km 113 de la carretera Quito-Pto. Quito, faldas occidentales, a 10 km al Norte de la carretera principal, 650–700 m, [0.083°, –79.033°], 26 Mar 1984, *Jaramillo* 6611 (QCA); Reserva Orquideológica El Pahuma, carretera Calacalí-Los Bancos, km 22, 2000 m, [0.028°, –78.631°], 19 Oct 1999, *Rojas et al.* 391 (MO); Road Nono-Pacto-Río Yacuambi, 5–10 km above Nanegalito, 1700 m, [0°, –78.667°], 21 Jul 1980, *Holm-Nielsen et al.* 24419 (MO, NY); West of Santo Domingo de los Colorados 20 km, 1000 m, 30 Oct 1961, *Cazalet & Pennington* 5207 (NY).

Burmeistera kitrinaima Mashburn, Muchhala & C.Ulloa, sp. nov. TYPE: ECUADOR. Pichincha: Bosque Integral Otonga, 2228 m, [–1.418°, –79.012°], 5 Jul 2002, *N. Muchhala* 119 (holotype: QCA [barcode] 27004!).

This new species is distinguished from other *Burmeistera* by the combination of: yellow latex; ovate to ovate-lanceolate leaves without a significant drip tip (< 5 mm long), glabrous or, when present, translucent-tan hairs; ascending, linear,

calyx lobes, > 6 mm long; flowers 29–38 mm long, the androecium exerted 11–15 mm from the ventral opening; and globose, spongy, white fruits ca. 20 × 20 mm.

Scandent herbs, up to 2 m long. Latex yellow. Stems ca. 5 mm in diameter, green to violet, glabrous (rarely villose). Leaves alternate, distichous, the internodes 15–30 mm long; petioles 4–8 mm long, green to violet, glabrous or villose with translucent-cream colored hairs; lamina 50–135 × 20–75 mm, ovate to ovate-lanceolate, widest below the middle, the base obtuse to rounded, the apex attenuate to acuminate, the tip, when distinct, ca. 5 mm long, the margins callose-serrate, the teeth more prominent distally; upper surface dark green, glabrous; lower surface green to violet, glabrous or rarely villose along the primary and secondary veins with translucent-tan hairs with tan spots; venation camptodromous to brochidromous, the primary and secondary veins prominent, raised, the tertiary veins visible. Flowers solitary in the upper leaf axils, 29–38 mm long; pedicels 50–100 mm long at anthesis, 80–105 mm long in fruit, green to violet, glabrous (rarely villose); hypanthium 6–7 × 5–8 mm, obconical, green suffused with violet, glabrous (rarely sparsely villose), the five ridges smooth or slightly raised; calyx lobes 6–13 × 0.5–1.5 mm, ascending at anthesis, linear, violet outside, green suffused with violet inside, glabrous, the margin shallow callose-serrate, the apex acute; corolla green suffused with maroon-violet, glabrous (rarely sparsely villose); corolla tube 5–7 mm wide basally, the throat narrowing to 2–3 mm wide; corolla lobes lanceolate, lighter green inside, the margins smooth, the two dorsal lobes 14–17 × 3–4 mm, opening dorsally 14–18 mm from the corolla base, falcate, the two lateral lobes 10–16 × 3 mm, falcate, the ventral lobe ca. 6 × 2 mm, opening ventrally 11–13 mm from the corolla base; androecium 22–27 mm long, exerted 11–15 mm from the ventral opening, the filament tube green with tan striations, sometimes speckled with violet, glabrous or distally puberulous, the anther tube 5–6 × 3–4 mm, green, violet along the sutures, glabrous, the three dorsal anther tips glabrous to sparsely puberulous, the two ventral anther tips densely villose with white hairs; the style violet, glabrous, the stigma green with a violet margin, the stigma lobes densely villose underneath and along the margin. Fruits ca. 20 × 20 mm, globose, spongy, slightly inflated, white. Figure 7B–E.

Distribution and Habitat—*Burmeistera kitrinaima* has been collected on the western side of the Andes in northern and central Ecuador. Specimens are found as low as 600 m elevation, though most come from high elevation cloud forests from 1,500–2,500 m.

Etymology—The specific epithet is a combination of the Greek *kitrino*, meaning “yellow,” and *aíma*, meaning “blood,” in reference to the unique yellow latex found in this species.

Notes—*Burmeistera kitrinaima* resembles *B. succulenta* in its leaf morphology and ascending calyx lobes, but individuals of *B. kitrinaima* have narrower calyx lobes (0.5–1.5 mm wide vs. 2–5 mm in *B. succulenta*) and shorter flowers (29–38 mm long vs. 45–53 mm long in *B. succulenta*). *Burmeistera huacamayensis* Jeppesen has similar sized flowers as *B. kitrinaima*, but is differentiated in its flattened translucent-white hairs (vs. round and tan, when present, in *B. kitrinaima*), and elliptic leaves with long (10–25 mm) drip tips. Live plants of *B. kitrinaima* can often be differentiated from either *B. succulenta* or *B. huacamayensis* by the presence of yellow latex (vs. white).

Burmeistera kitrinaima and *Burmeistera smaragdi* Lammers share the presence of long, linear to ligulate calyx lobes and small flowers (33–37 mm long in *B. smaragdi*, 29–38 mm in *B. kitrinaima*). *Burmeistera kitrinaima* can be differentiated by the presence of yellow latex (vs. white in *B. smaragdi*), shorter exertion length (11–15 mm vs. 16–17 mm) and larger fruits (ca. 20 × 20 mm vs. ca. 15 × 12 mm).

Specimens of *B. kitrinaima* were often assigned to *B. succulenta* because of morphological similarity, which, despite the absence of curling corolla lobes, would suggest placement of *B. kitrinaima* in the recurved corolla clade of *Burmeistera*. The inclusion of a sample of *B. kitrinaima* in the phylogeny of Bagley et al. (2020) reveals that this species is in fact closely related to *Burmeistera cylindrocarpa* Zahlbr., *B. huacamayensis*, *Burmeistera tenuiflora* Donn.Sm., and *B. smaragdi*, outside of the recurved corolla clade (see Fig. 2 in Bagley et al. 2020).

Additional Specimens Examined—Ecuador. —BOLIVAR: Road Guaranda-Caluma, km 53, 1100 m, [−1.583°, −79.183°], 29 Jul 1996, *Ståhl & Knudsen* 2901 (QCA). —COTOPAXI: Reserva Otonga, entre Quito y Sto. Domingo, cerca de San Francisco de las Pampas, 1990–2200 m, [−0.417°, −79°], Jun 1997, *Nowicki & Mutke* 1479 (QCA). —PICHINCHA: Cantón Quito, nueva carretera Calacalí-Nanegalito, km 20, 1800–2000 m, [0.033°, −78.05°], 19 Jan 1989, *Hurtado et al.* 1419 (MO); Northwest slopes of Volcán Pichincha, Quito-Nono-Mindo road, 5 km N of Mindo, 1500 m, [−0.033°, −78.833°], 29 Apr 1989, *Neill et al.* 8942 (MO); Parroquia Nanegalito, western slopes of Cerro Negro, 2.5–3 km airline NE of Nanegalito, 1900 m, [0.067°, −78.65°], 8 Sep 1993, *Webster et al.* 30455 (MO); Reserva Bellavista, 2215 m, [−0.014°, −78.685°], 11 Jul 2002, *Muchhala* 128 (QCA); Reserva Bellavista, 2229 m, [−0.014°, −78.690°], 12 Jul 2002, *Muchhala* 130 (QCA); Reserva Florística “Río Guajalito,” km 59 de la carretera antigua Quito-Santo Domingo de los Colorados, a 3.5 km al NE de la carretera, estribaciones occidentales del Volcán Pichincha, 1800–2200 m, [−0.231°, −78.803°], 29 Jun 1991, *Jaramillo & Grijalva* 13651 (MO, NY, QCA); Reserva Florística Río Guajalito, Las Palmeras, 1800–2100 m, [−0.233°, −78.817°], May 1997, *Nowicki & Mutke* 1193 (QCA); Reserva forestal ENDESA, corporación forestal Juan Manuel Durini, km 113 de la carretera Quito-Puerto Quito, 600 m, 5 Jun 1986, *Sigcha* 28 (QCA); Reserva Maquipucuna, 1807 m, [−0.098°, −78.624°], 10 Jul 2002, *Muchhala* 125 (QCA); Reserva Río Guajalito, 1900 m, [−0.248°, −78.803°], 19 Jun 2010, *Muchhala* 447 (QCA); Reserva Río Guajalito, on Argentino trail, 2045 m, [−0.239°, −78.804°], 25 Jun 2010, *Muchhala* 454 (QCA); Valle de Lloa y Palmira, faldas SO del Volcán Pichincha 20–29 km del carretero Quito-Lloa-Mindo, 2500–3000 m, [−0.2°, −78.65°], 26 Sep 1987, *Buitrón* 253 (QCA). —SANTO DOMINGO: Near footbridge by Río Quajalito Science Centre, 1802 m, [−0.231°, −78.821°], 26 Oct 2010, *Antonelli* 602 (QCA).

BURMEISTERA SODIROANA Zahlbr., Repert. Spec. Nov. Regni Veg. 13: 534. 1915. TYPE: ECUADOR. Pichincha, “Secus flumen Pilatón”, 900–1600 m, *L. Sodiro* 91/25 (holotype: B [presumed destroyed], isotypes: P [barcode] 00408899 [digital image!], W 1963–0012263 [digital image!]).

Burmeistera succulenta var. *latispala* E.Wimm., syn. nov., Repert. Spec. Nov. Regni Veg. 29: 55. 1931. TYPE: ECUADOR. Tunguruahua: “In sylvis montanum Tunguragua,” Dec. 1857, *R. Spruce* 5119 (holotype: K [barcode] 000250836 [digital image!], isotypes: BM [bc] 000778656, E [bc] 00259141 [digital image!], G [bc] 00236670 [digital image!], G [bc] 00236671 [digital image!], P [bc] 00408902 [digital image!], K [bc] 000250837 [digital image!], W 1889–0004938 [digital image!], W 1889–0132990 [digital image!]).

Burmeistera leucocarpa Zahlbr., Repert. Spec. Nov. Regni Veg. 13: 529. 1915. TYPE: ECUADOR. Pichincha: “In silvis temperatis prope San Florencio et Niebly,” s.d., *L. Sodiro* 91/92 (holotype: B [presumed destroyed], neotype: designated here, ECUADOR. Pichincha: “In reg. subtrop. pr. S. Florencio,” s.d., *Sodiro* 91/21 [neotype, P [barcode] 00408898 [digital image!]).

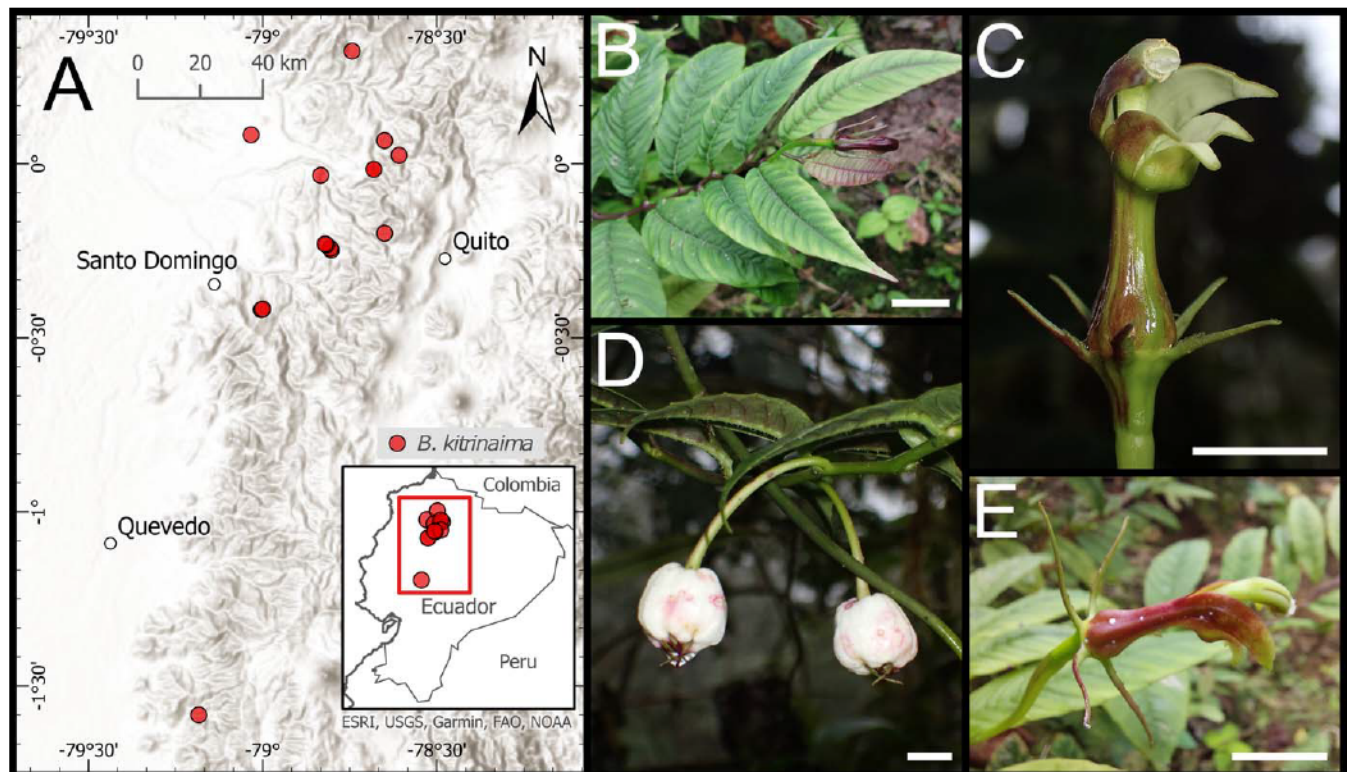


FIG. 7. *Burmeistera kitrinaima* sp. nov. A. Distribution map of specimens used in this study. B. Growth habit and flower bud. C. Flower. D. Fruit. E. Flower. All scale bars indicate 10 mm. Photo credits: B, E by Nataly Lara; C, D by Brandon Cohen.

Burmeistera leucocarpa var. *dentata* E.Wimm., Repert. Spec. Nov. Regni Veg. 30: 25. 1932 TYPE: ECUADOR. Pichincha: "In silvis subtropicis prope Niebly," 1874, L. Sodiro 9 (holotype: W 1967-0015304 [digital image!]).

Scandent herbs, up to 4 m long. Latex white. Stems ca. 7 mm in diameter, green to violet, glabrous. Leaves alternate, spiral (rarely distichous in individuals introgressed with *B. crispiloba*), often bullate, typically reduced in size when subtending a flower, the internodes 20–45 mm long, where flowering 5–10 mm long; petioles 5–10 mm long, green to violet, glabrous; lamina 55–130 × 30–50 mm, where subtending a flower reducing to (20–)30–50(–80) × (5–)15–35 mm, ovate to ovate-lanceolate, the base obtuse to rounded, the apex acuminate to caudate, 2–10 × 2–4 mm, the margins shallow callose-serrate to nearly entire, the teeth and margin sometimes tinged violet; upper surface green to green lightly tinged violet, the primary and secondary veins sometimes lightly tinged violet, glabrous, nitid; lower surface green to green suffused violet, especially along veins, glabrous, nitid; veins camptodromous, diminishing along the margin or terminating in marginal teeth, the primary and secondary veins prominent, raised, the tertiary veins visible. Flowers solitary in the upper leaf axils, 37–42(–48) mm long; pedicels 80–160 mm long at anthesis, 100–165 mm long in fruit, green to violet, glabrous; hypanthium 8–13 × 5–8 mm, abruptly widening distally, obconical to cupuliform, green to violet tinged, glabrous; calyx lobes 1–5(–8) × 1–2 mm, deltate, green, glabrous, the margin green or violet, entire or with few callose-tipped teeth, ascending at anthesis; corolla glabrous, entirely green to green tinged or streaked with maroon-violet; corolla tube 5–6 mm wide basally, narrowing to 2–4 mm wide; corolla

lobes lanceolate, sometimes curled back at anthesis, the interior dark violet, the margins smooth to undulate, the two dorsal lobes 12–14 × 2–4 mm, opening dorsally 14–18 mm from the corolla base, ascending to falcate, the two lateral lobes 10–13 × 2–3 mm, falcate, the ventral lobe ca. 7 × 3 mm, opening ventrally 9–12 mm from the corolla base; androecium 29–32(–36) mm long, exerted 19–20(–23) mm from the ventral opening, the filament tube green basally, becoming dark violet distally, glabrous, the anther tube 6.5–9 × 4–6 mm, dark violet, glabrous, the three dorsal anthers glabrous at the tips, the two ventral anthers densely pubescent; the stigma violet, the stigma lobes fringed with short white hairs along the margin. Fruits ca. 20 × 25 mm, globose to ellipsoid, pendent, fleshy, spongy, white, maturing pink or white tinged with violet.

Distribution and Habitat—*Burmeistera sodiroana* is found on both sides of the Andes of central Ecuador, mostly in Pichincha, Napo, and Tungurahua provinces, although reaching as far south as El Oro and Morona Santiago. It occurs in cloud forests from 1500–3200 m in elevation.

Notes—In his publication of *B. succulenta* var. *latisejala*, Wimmer (1931) noted that his new variety was similar to *B. succulenta* var. *meiophylla*, but even more similar to *B. sodiroana*, except for having slighter longer calyx lobes. Wimmer (1932), Jeppesen (1981), and Lammers (2007) continued to treat var. *latisejala* as a variety or synonym of *B. succulenta*. We find *B. succulenta* var. *latisejala* to be no different from other *B. sodiroana* collections in Ecuador that have slightly larger calyx lobes, including spiral phyllotaxy, curling but not scrolling corolla lobes, and dark purple anthers. We therefore treat *B. succulenta* var. *latisejala* E.Wimm as a new synonym of *B. sodiroana*.

Jeppesen (1981) noted that the type collection of *B. leucocarpa* may be a typographical error in Zahlbruckner (1915). Zahlbruckner cited the specimen *L. Sodiro 91/92*, though Jeppesen was not aware of Sodiro collection numbers exceeding 91/36; Luis Sodiro recorded specimens by his own species numbers instead of collection numbers (Jørgensen & León-Yáñez 1999). Though Zahlbruckner did not cite an herbarium for the holotype, he often worked from Berlin specimens, and Berlin housed many Sodiro collections. Outside of Zahlbruckner (1915), we are not aware of any duplicates of *Sodiro 91/92* belonging to the same gathering. If this collection ever existed, it was likely destroyed in Berlin. Jeppesen (1981) suggested that *Sodiro 91/21* (P) may be an isotype of Zahlbruckner's intended holotype of *B. leucocarpa*. This specimen certainly fits with Zahlbruckner's original species description and occurs near the same town (San Florencio). Finding no evidence that these two specimens are of the same gathering, we consider them distinct and choose *Sodiro 91/21* (P) as a neotype of *B. leucocarpa*.

Burmeistera sodiroana can resemble *B. succulenta* vegetatively but is differentiated by having spiral phyllotaxy (vs. distichous), flowers with smaller calyx lobes (< 5[–8] mm vs. > 8 mm in *B. succulenta*), and corolla lobes that flare outward but do not scroll (vs. scrolling). *Burmeistera sodiroana* and *B. crispiloba* are also very similar, especially because they seem to hybridize and introgress at the intersection of their ranges at about 1500 m in elevation. The taxonomic placement of putative hybrid and introgressed individuals is difficult to resolve. *Burmeistera sodiroana* s.s. is differentiated from *B. crispiloba* s.s. in having spiral phyllotaxy (vs. distichous), slightly smaller flowers (37–42[–48] mm long vs. 44–58) with corolla lobes flaring or curling open (vs. scrolling), and white to pink, globose to ellipsoid fruits (vs. cherry red, obovoid to pyriform).

Additional Specimens Examined—Ecuador. —BOLIVAR: Along road Chillanes-Yaquiubus, 2300 m, 20 Jul 1991, *van der Werff et al.* 12516 (MO). —CAÑAR: El Triunfo, Cañar road, km 50 from El Triunfo, 1500 m, [–2.483°, –79.083°], 20 Jun 1979, *Lajtnant & Molau 15174* (NY). —CARCHI: East of Maldonado 12 km on road to Tulcán, 2230 m, 27 Sep 1979, *Gentry & Shupp 26647* (MO); Tulcán-Maldonado road, 45 km W of Tufiño, 2425 m, 13 Apr 1978, *Luteyn & Lebron-Luteyn 5750* (MO, NY, QCA); West of Tulcán 78–82 km, 2040–2320 m, [0.833°, –78.833°], 8 Jan 1985, *Luteyn & Cotton 10893* (NY); Valle de Maldonado, km 71 on road Tulcán-Maldonado, 2100–2200 m, [0.9°, –78.1°], 20 May 1973, *Holm-Nielsen et al.* 6000 (NY, QCA). —COTOPAXI: Around Pilaló, 2400 m, [–0.95°, –79.033°], 7 Mar 1968, *Holm-Nielsen & Jeppesen 1282* (MO, NY); Cantón Pilaló, camino a la cumbre del Cerro Puchato, 1800–2500 m, [–0.917°, –79.15°], 5 Dec 1987, *Cerón & Villavicencio 2798* (MO); Cantón Sigchos, Campo Alegre, a ca. 20 km al noreste de Sigchos, 2614 m, [–0.584°, –78.793°], 11 Jul 2003, *Ramos et al.* 5814 (MO); Cantón Sigchos, finca de Antonio Tigse, 3060 m, [–0.595°, –78.832°], 18 Jul 2003, *Ramos et al.* 6204 (MO); Carretera Latacunga-Pilaló-Quevedo, 5–10 km al este de Pilaló, 2400–2700 m, [–0.917°, –79°], 23 May 1988, *Cerón et al.* 3830 (MO); Salcedo, Los Llanganates, carretera Salcedo-Tena, km 60, Rancho la Poderosa, descendiendo al Río Mulatos, a 4 km, 2500–2870 m, [–0.95°, –78.233°], 16 Mar 1995, *Vargas & Sandoval 431* (MO). —EL ORO: Quebrada El Mono, entre Piñas y Buenaventura, crece borde de la carretera, 950 m, 28 May 1979, *Escobar 1377* (QCA). —NAPCO: Along E side of R. Chalpi, 1–3 km from confluence with R. Oyacachi, 2600–2800 m, [–0.25°, –77.967°], 23 May 1996, *Ståhl et al.* 2564 (QCA); Along trail between Oyacachi and Pueblo Viejo (Old Oyacachi), 3000 m, [–0.233°, –77.983°], 24 May 1996, *Ståhl et al.* 2578 (QCA); Baeza, forest remnants, 1800–2000 m, 22 Sep 1977, *Maas et al.* 3035 (QCA); Between Tena and Pappalacta, 12 Jan 1981, *D'Arcy 14101* (MO, NY); Between Tena and Pappalacta, 12 Jan 1981, *D'Arcy 14092* (NY); Cantón Quijos, Unión del Río Blanco con Río Quijos, 2680 m, [–0.467°, –78.05°], 12 Jun 1998, *Vargas et al.* 1761 (MO); Cantón Quijos, ca. 4 km W of Cosanga on the Cosanga-Las Caucheras road, between Las Caucheras and SierrAzul, 2200–2250 m, [–0.67°, –77.917°], 12 Feb 2011, *Tepe et al.* 2955 (MO);

Cantón Quijos, Baeza, parte alta del Río Machángara, 2200–2300 m, [–0.467°, –77.9°], 9 May 1990, *Palacios & Freire 4982* (NY); Carretero Papallacta-Baeza, Hacienda Flor del Bosque, [–0.367°, –78.067°], 14 December 1993, *Freire-Fierro & Yáñez 2673* (NY); Cosanga, stream just south of town, [–0.6°, –77.867°], 1 December 1976, *Boeke & McElroy 376* (QCA); Hacienda Antisana, closest town Cuyuja, along banks of Río Quijos (northside), southwest of Quito-Baeza road, 2500 m, 29 Aug 1980, *Sobel & Strudwick 2522* (NY); Lago Agrio-Quito road, km 195, between Cuyuja and Papallacta, 2500 m, [–0.367°, –78.083°], 18 Jun 1985, *Stein 3082* (QCA, MO); Parque Nacional Llanganates, vía Salcedo-Tena, colecciones a lo largo del camino desde Los Carmelos-Río Ana Tenorio al Río Llangoa, bosque de Neblina Montano, 2600–2850 m, [–0.971°, –78.254°], 18 Feb 2015, *Pérez et al.* 8112 (QCA); Private property of William Phillips, ca. 2 hrs. walk from end of road, W of Cosanga, N slopes of Cordillera de Huacamayos, [–0.75°, –77.917°], 12 Dec 1989, *Luteyn & Cabo 13459* (NY, QCA); Quijos, Reserva Ecológica Antisana, Río Aliso, 8 km al suroeste de Cosanga, afluente del Río Aliso, margen derecha a 1 km, 2530 m, [–0.583°, –77.95°], 12 Nov 1998, *Vargas et al.* 3003 (MO); Quito to Baeza, km 92, 1850 m, 30 Jun 1985, *Dodson & Hirtz 15883* (MO); Reserva Yanayacu, collected on trail behind station heading towards Antisana, 2100 m, [–0.588°, –77.88°], 28 Jul 2010, *Muchhala 458* (QCA); Road Baeza-Napo, Cosanga, 20 km S of Baeza, along mule track to 3 km W of the village, 2000–2100 m, [–0.617°, –77.867°], 26 Oct 1976, *Balslev & Madsen 10329* (NY); Road Baeza-Tena, km 24–29 from Baeza, S of Cosanga, 2100–2300 m, [–0.633°, –77.85°], 28 Mar 1979, *Holm-Nielsen 16226* (QCA); Salcedo-Napo road, ca. 56–60 km E of Salcedo, 2926–3060 m, [–0.917°, –78.5°], 23 Nov 1989, *Luteyn & Tirira 13389* (MO, NY, QCA). —PICHINCHA: Along road between Tandayapa and Mindo, 19.5 km from Tandayapa, ca. 5.5 km from Mindo, 1930 m, 16 Dec 1979, *Croat 49392* (MO); Ca. 5 km SW of San José de Niebli, 13 road km N of Calacalí, 2450 m, [0.033°, –78.533°], 1 May 1985, *Stein 2662* (MO); Carretera Quito-San Juan-Chiriboga, Empalme, en el km 69, carretera secundario a 3 km de la carretera a Sto. Domingo de los Colorados, sector Bellavista, 2050 m, 17 Sep 1986, *Zak 1192* (MO); Carretera Sto. Domingo-Quito, 13 km al oeste del paso, Ceja Andina, 3000 m, [–0.433°, –78.633°], 21 Jun 1982, *Balslev 2759* (NY); Cerro Corazón, 2438–2835 m, 5 Jan 1945, *Camp E-1652* (NY); Cerro El Castillo, en el camino desde Guarumos hasta El Castillo, derecho de vía del Oleoducto de Crudos Pesados, 2665 m, [–0.033°, –78.633°], 10 Sep 2001, *Freire-Fierro et al.* 3208 (MO); Cerro Pugi, NW slope of Volcán Pichincha, on ridge crest, 3020 m, 27 Sep 1980, *Bleiwiss 1142* (NY); Nanegalito-Tandayapa road, 1890–2400 m, [–0.067°, –78.733°], 7 Nov 1989, *Luteyn & Tirira 13328* (MO, NY); Reserva Bellavista, 2295 m, [–0.011°, –78.688°], 11 Jul 2002, *Muchhala 129* (QCA); Reserva Orquideológica El Pahuma, carretera Calacalí-Los Bancos, km 22, 2000 m, [0.028°, –78.631°], 26 Oct 1999, *Mantuano et al.* 30 (MO); Road from Chiriboga to Santo Domingo, ca. 5 km W of Chiriboga, 2050 m, 3 May 1985, *Stein et al.* 2683 (MO); Road from Quito-Tandayapa-Mindo, 2355 m, [0.05°, –78.667°], 21 May 1989, *Smith 1975* (MO, NY, QCA); Route Tandayapa-Nanegalito, 2250 m, [0°, –78.667°], 24 Jan 1996, *Billiet & Jadin 6684* (MO); Old road Quito-Santo Domingo, between San Juan and Chiriboga, on steep slopes along road, 2700–2750 m, [–0.283°, –78.667°], 20 Mar 1979, *Lajtnant & Molau 11261* (NY); Old road Quito-Santo Domingo, ca. 3–16 km W of San Juan de Chiriboga, on steep roadside slopes, 2460–3350 m, [–0.283°, –78.75°], 4 Feb 1983, *Luteyn et al.* 8792 (MO, NY); Old road Quito to Santo Domingo via Chiriboga, km 33–35, 2550 m, 3 May 1985, *Stein et al.* 2674 (MO, QCA); Quito-Santo Domingo old road, Las Palmeras, ca. 59 km WSW of Quito, trail and forest along Río Guajalito, 1800–1900 m, [–0.3°, –78.717°], 14 Dec 1990, *Luteyn et al.* 14342 (NY); West slopes of the Cordillera Occidental, above Tandapi, 20–21 km from Alóag on road to Santo Domingo, 2650 m, 7 Feb 1985, *Molau & Öhman 1156* (QCA). —TUNGURAHUA: Cantón Baño, Río Vascun Valley, northern slopes of Volcán Tungurahua, 2500–3200 m, [–1.439°, –78.433°], 27 Apr 2003, *Clark et al.* 7699 & 7715 (QCA); Cordillera de Llanganates valley of Río Sangarinas (Desaguadero), “La Trinca,” at the shore of Río Golpe, 3000 m, 18 Nov 1939, *Asplund 9767* (NY); Cusatagua, Vicinity of Ambato, Mar 1919, *Pachano 177* (NY); Parque Nacional Llanganates, entrando por Baquerizo Moreno hacia el sector de Lagartococha, 3270 m, [–1.2°, –78.472°], 1 Mar 2015, *Pérez et al.* 8409 (QCA); Trail along W slope of Río Ulba Canyon above Hacienda San Antonio, 4 km up Río Ulba from village of Ulba, 2200–2500 m, [–1.417°, –78.367°], 3 Jun 1985, *Stein 2945* (MO); Zona de amortiguamiento del Parque Nacional Llanganates, Machay, Río Verde, colecciones entre Río Machay y Colina San Agustín, 2090 m, [–1.367°, –78.283°], 30–31 Jul 1999, *Vargas et al.* 3712 (MO). —MORONA SANTIAGO: Between Tambo Consuelo and Tambo Cerro Negro, 2590–2895 m, 20–24 Aug 1945, *Camp E-4955* (NY).

BURMEISTERA SUCCULENTA H.Karst. & Triana, *Linnaea* 28: 445. 1856. TYPE: COLOMBIA. Quindío: Nouvelle-Grenade prov. De Mariquita, *crescit circa "El Roble" in monte Quindio, 2000 m, 1851–1857, J. J. Triana 1586* (Lectotype designated by Gleason, 1925: P [barcode!] 00408903 [digital image!]).

Burmeistera succulenta var. *meiophylla* Zahlbr. ex E.Wimm., *Rep. Spec. Nov.* 30: 28. 1932. TYPE: VENEZUELA. Aragua: Tovar, *H. Karsten s.n.* (Lectotype designated here: W 1889–0134874 [digital image!], isolectotype: B, presumed destroyed).

Herbaceous shrubs or scandent herbs, up to 3 m long. Latex abundant, white. Stems ca. 5 mm long, green to violet, glabrous. Leaves alternate, distichous, the internodes 20–50 mm long; petioles 2–6 mm long, green to violet, glabrous; blades 50–150 × 25–60 mm, elliptic, the base obtuse, the apex attenuate to acuminate, the margins shallow callose-serrate to nearly entire, the teeth and margin sometimes tinged violet; upper surface green to green tinged violet, glabrous, nitid; lower surface green to maroon-violet, glabrous; veins camp-todomous, diminishing along the margin or terminating in marginal teeth, the primary and secondary veins prominent, raised, the tertiary veins visible. Flowers solitary in the upper leaf axils, 45–53 mm long; pedicels 60–115 mm long at anthesis, 110–125 mm long in fruit, green to violet, glabrous; hypanthium 7–10 × 4–6 mm, obconical (rarely campanulate), the base often barely distinguishable from the pedicel, abruptly widening distally, green to violet, glabrous; calyx lobes (5–)8–21 × 2–5 mm, ligulate, dark green, often suffused with violet, glabrous, the margin entire or with a few callose-tipped teeth, the apex acute, ascending at anthesis; corolla green to green suffused with maroon-violet outside, light green to violet inside; corolla tube 6–9 mm wide basally, the throat narrowing to 3–5 mm wide; corolla lobes lanceolate, strongly scrolling back, the two dorsal lobes 22–28 × 3–4 mm, opening dorsally 14–17 mm from the corolla base, the two lateral lobes 18–25 × 3–5 mm, opening ventrally 10–12 mm from the corolla base; androecium 37–43 mm long, exerted 27–33 mm from the ventral opening, the filament tube maroon-violet, glabrous, the anther tube 8–10 × 3–4 mm, green to maroon-violet, glabrous, all five anther tips sparsely to densely pubescent; the style violet, the stigma green to violet, the stigma lobes fringed with short white hairs along the margin. Fruits ca. 15 × 20 mm, globose, fleshy, pink to violet.

Distribution and Habitat—*Burmeistera succulenta* is a widespread species, ranging from the western slopes of the Andes in central Ecuador, through Colombia, into northwestern Venezuela. It occurs in cloud forests from 1000–2500 m in elevation.

Notes—*Burmeistera succulenta* was described by Hermann Karsten and José Triana in 1856, just two years after their description of the genus *Burmeistera*. No type specimens were indicated, but the collection locality was given as "*Crescit circa 'El Roble' in monte Quindio, 2000 metr. altitudine.*" Triana's collection at P (*Triana 1586*) seems to have been annotated by himself (the handwriting is the same as on the rest of the label). In his brief synopsis of *Burmeistera*, Gleason (1925) recognized *Triana 1586* from P as the type of *B. succulenta*. Similarly, Wimmer's (1932) monograph of the genus identifies *Triana 1586* as the original specimen, though he did not see it himself ("*spec. orig. in Hb. Paris, non vidi*"). As such, we agree with Gleason's recognition of *Triana 1586* as the

type of *B. succulenta*, and we consider it an unintended lectotypification.

Wimmer (1932) also described *Burmeistera succulenta* var. *meiophylla*, attributing the name to the Austrian-Hungarian botanist Alexander Zahlbruckner, based in Vienna. Wimmer noted that the original specimens were collected by Karsten (*s.n.*) in "Venezuela: Colonia Tovar" and found in Vienna and Berlin. The specimen at Berlin is presumed to be destroyed. The Vienna Karsten specimen W 1889–0134874 shows Zahlbruckner's notation as: "*Sectio Burmeistera: Centropogon succulentus* (Karsten et Tr.) var. *meiophyllus* A.Zahlbr." Above this is Wimmer's notation from 1931: "*Burmeistera succulenta* var. *meiophylla* A.Zahlbr." James L. Luteyn then notated the same specimen in 1989 as an "isotype of *Burmeistera succulenta* var. *meiophylla* A.Zahlbr. ex Wimm." Because Karsten collections are often without numbers, it is difficult to identify duplicates beyond the Vienna and Berlin collections mentioned by Wimmer (1932). Therefore, we have lectotypified the Vienna specimen and presume the Berlin isolectotype to be destroyed.

Burmeistera succulenta is the most widespread species in the recurved corolla clade and currently the only one known from Colombia, Venezuela, and possibly Panama. Most specimens from Ecuador previously identified as *B. succulenta* have been transferred to *B. kitrinaima* sp. nov. Nevertheless, a few Ecuadorian collections remain placed in *B. succulenta*. Vegetatively, *B. succulenta* and *B. kitrinaima* are difficult to differentiate except by the color of the latex (white vs. yellow in *B. kitrinaima*), but they are quite distinct in their reproductive characters. Individuals of *B. succulenta* have wider calyx lobes (2–5 mm vs. 0.5–1.5 mm wide in *B. kitrinaima*) and longer flowers (45–53 mm long vs. 29–38 mm long). In addition, *B. succulenta* exhibits scrolling corolla lobes, a character absent in *B. kitrinaima*.

Burmeistera succulenta is closely related to two other species in the recurved corolla clade: *B. crispiloba* and *B. sodiroana*. Both *B. succulenta* and *B. crispiloba* have similar sized flowers, but *B. succulenta* is easily differentiated by its long (> 8 mm) vs. short (< 3 mm) calyx lobes. *Burmeistera succulenta* can be differentiated from *B. sodiroana* by phyllotaxy (distichous vs. spiral), as well as the calyx lobes, which are long (> 8 mm) in *B. succulenta*, and short (< 5[–8] mm) in *B. sodiroana*.

Additional Specimens Examined—Venezuela. —ARAGUA: Colonia Tovar, 1800–2000 m, Dec 1924, *Allart 479* (NY); Colonia Tovar and vicinity, 1700–2300 m, 1921, *Pittier 9317* (NY); Henry Pittier National Park, trail to Pico Periquito opposite the Biological Station at Rancho Grande, 1000–1200 m, 14 Jan 1978, *Luteyn & Lebrun-Luteyn 5177* (NY). —YARACUY: Cerro La Chapa, selva nublada al norte de Nirgua, 1200–1400 m, 9–10 Nov 1967, *Steyermark et al. 100250* (NY); Cumbre Gamelatal 4.3–11 km N of Salom on road from Salom to Candelaria, 1000–1200 m, [10.25°, –68.492°], s.d., *Mori et al. 14602* (NY); North of Salom 7.5 km, 1200–1300 m, [10.25°, –68.483°], 4 Mar 1982, *Leisner & Steyermark 12386* (NY); Sierra de Aroa, 9 km W of San Felipe air distance, on road 0–3 km NE of road between Cocorote and Aroa, 15 km NW of Cocorote and 1 km SW of Los Cruceros, 1100–1500 m, [10.35°, –68.817°], 4 Apr 1980, *Leisner & González 10048* (NY). Colombia. —ANTIOQUIA: Cordillera Central, ca. 60 km S of Medellín on main hwy. to Manizales, 1350 m, [5.833°, –75.733°], 26 Jan 1986, *Stein & McDade 3303* (NY); Medellín–Cartagena Hwy., turnoff to Briceño, ca. 25 km N of Yarumal, 1800 m, [7.117°, –75.467°], 7 Feb 1986, *Stein & Cogollo 3369* (NY); To 5 km down road to San Fermín de Briceño, W off Pan American Hwy., ca. 25 km N of Yarumal, 1525–1830 m, [7.017°, –75.583°], 26 May 1984, *Luteyn et al. 10750, 10761 & 10773* (NY); To 5 km down road to San Fermín de Briceño, W off Pan American Hwy., ca. 25 km N of Yarumal, 1525–1830 m, [7.017°, –75.583°], 22 May 1988, *Luteyn & Sylva 12418 & 12420* (NY). —CALDAS: San Clemente, edge of woods, 1800–2200 m, 16 Sep 1922, *Pennell 10685* (NY). —CHOCÓ: Ansermanuevo-San José del Palmar road, 2–5 km E of San

José del Palmar, 1200–1500 m, 20 Apr 1979, *Luteyn et al.* 7322 (NY); Ansermanuevo-San José del Palmar road, from Chocó-Valle border W 10 km towards San José del Palmar, 1524–2050 m, [4.667°, –76.417°], 15 May 1984, *Luteyn* 10545 (NY); Bolívar-Quibdó road, ca. 37–40 km W of El Carmen, 671–1360 m, [5.667°, –76.25°], 21–22 May 1984, *Luteyn et al.* 10650 (NY). —VALLE DEL CAUCA: La Cumbre, 1800–2000 m, 7–10 May 1922, *Pennell* 5151 (NY); La Cumbre, 2000–2200 m, 14–19 May 1922, *Pennell & Killip* 5783 (NY); Mpio. La Elvira, Finca Zingara, ca. 25 km W of Cali at km 18, 1600–1700 m, [3.467°, –76.617°], 20 Apr 1989, *Luteyn et al.* 12557 (NY). Ecuador. —AZUAY: Hacienda Yacopiana, on ridge bordering Río Patul, above Sanagüín, 850 m, 2 Jun 1943, *Steyermark* 52805 (NY). BOLÍVAR: Road Echeandía-Guanujo, E of Echeandía, 2400 m, [–1.417°, –79.117°], 8 Jul 1979, *Holm-Nielsen & Andrade* 18581 (MO, NY). —COTOPAXI: Trail from El Corazón to Facundo Vela, 1–3 km S of El Corazón, 1300–1400 m, 17 May 1980, *Harling & Andersson* 19211 (NY).

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AUTHOR CONTRIBUTIONS

NM and BM conceived the study. BM and AT performed measurements and data analysis. All authors contributed to writing and editing the text. BM, NM, and CUU wrote the species descriptions and are authors of the new species.

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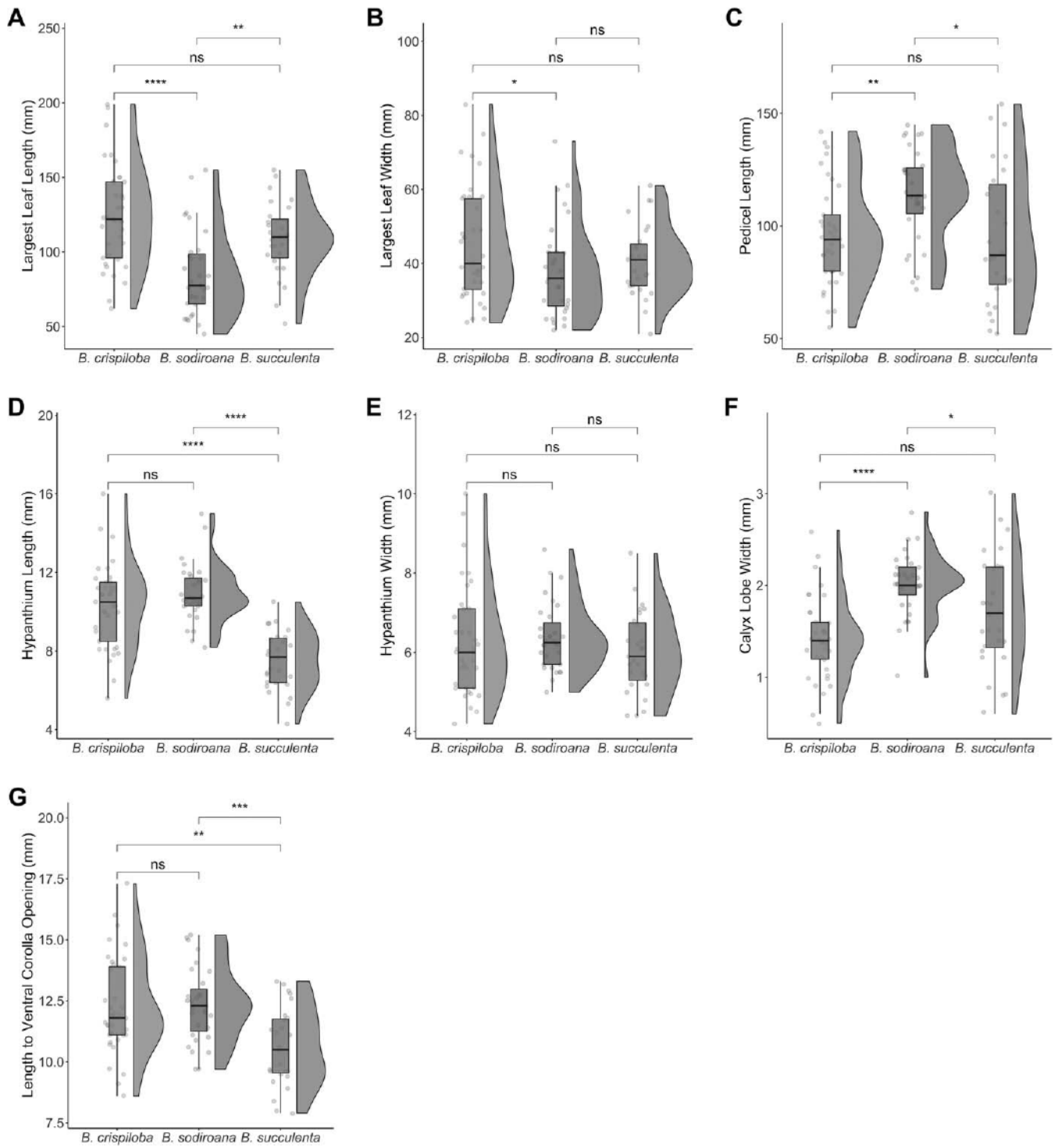


FIG. S1. Univariate comparisons of additional traits measured between *B. crispiloba*, *B. sodiroana*, and *B. succulenta*.

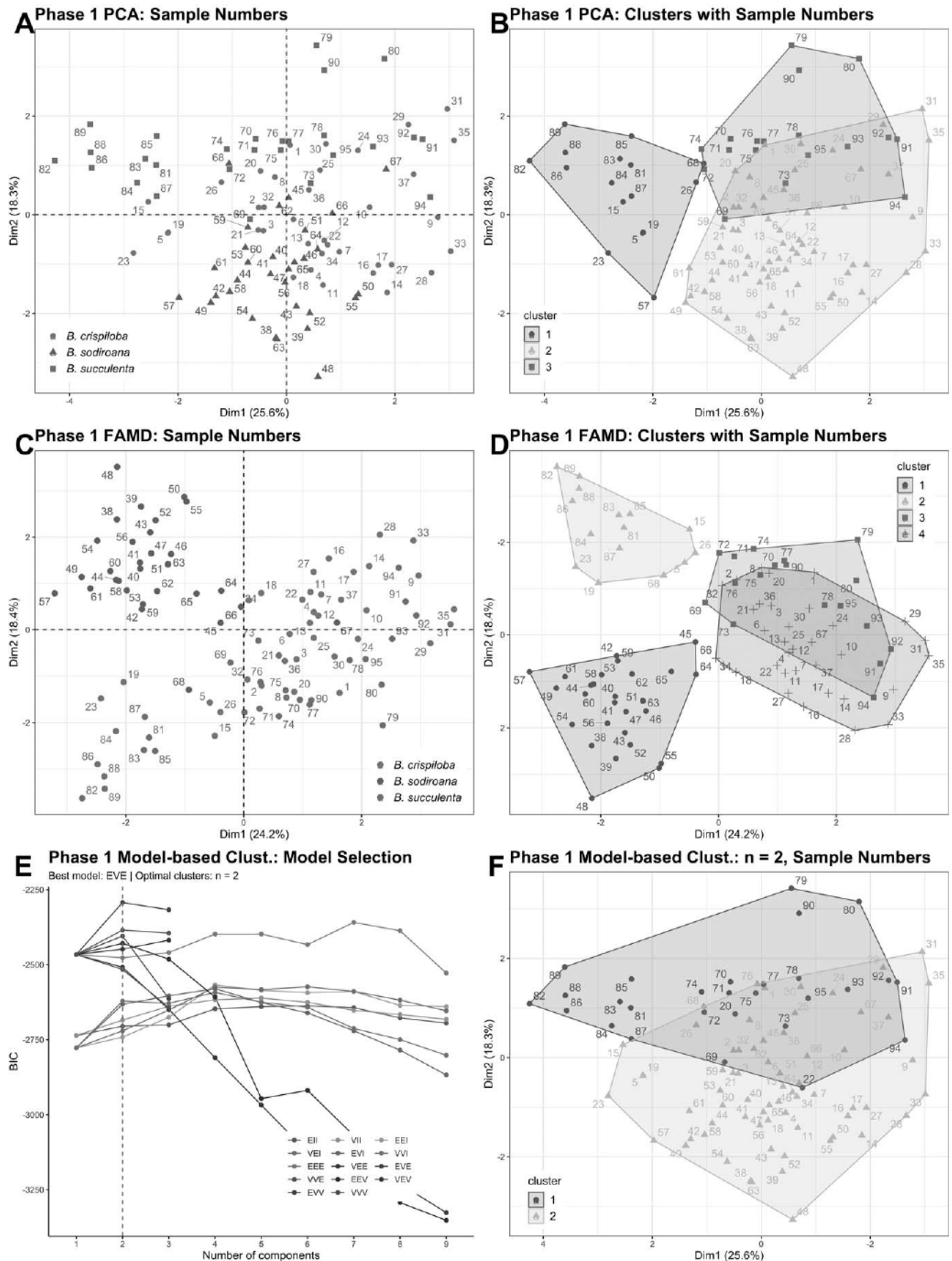


FIG. S2. Results of Phase 1 multivariate analyses with sample numbers included. Sample numbers correspond to numbers in the Supplemental Data. A, B. PCA of ten quantitative traits; unsupervised clustering performed with HCPC. C, D. FAMD of ten quantitative traits and two qualitative traits; unsupervised clustering performed with HCPC. E, F. Model-based clustering where $n = 2$ is selected as the optimal number of clusters.

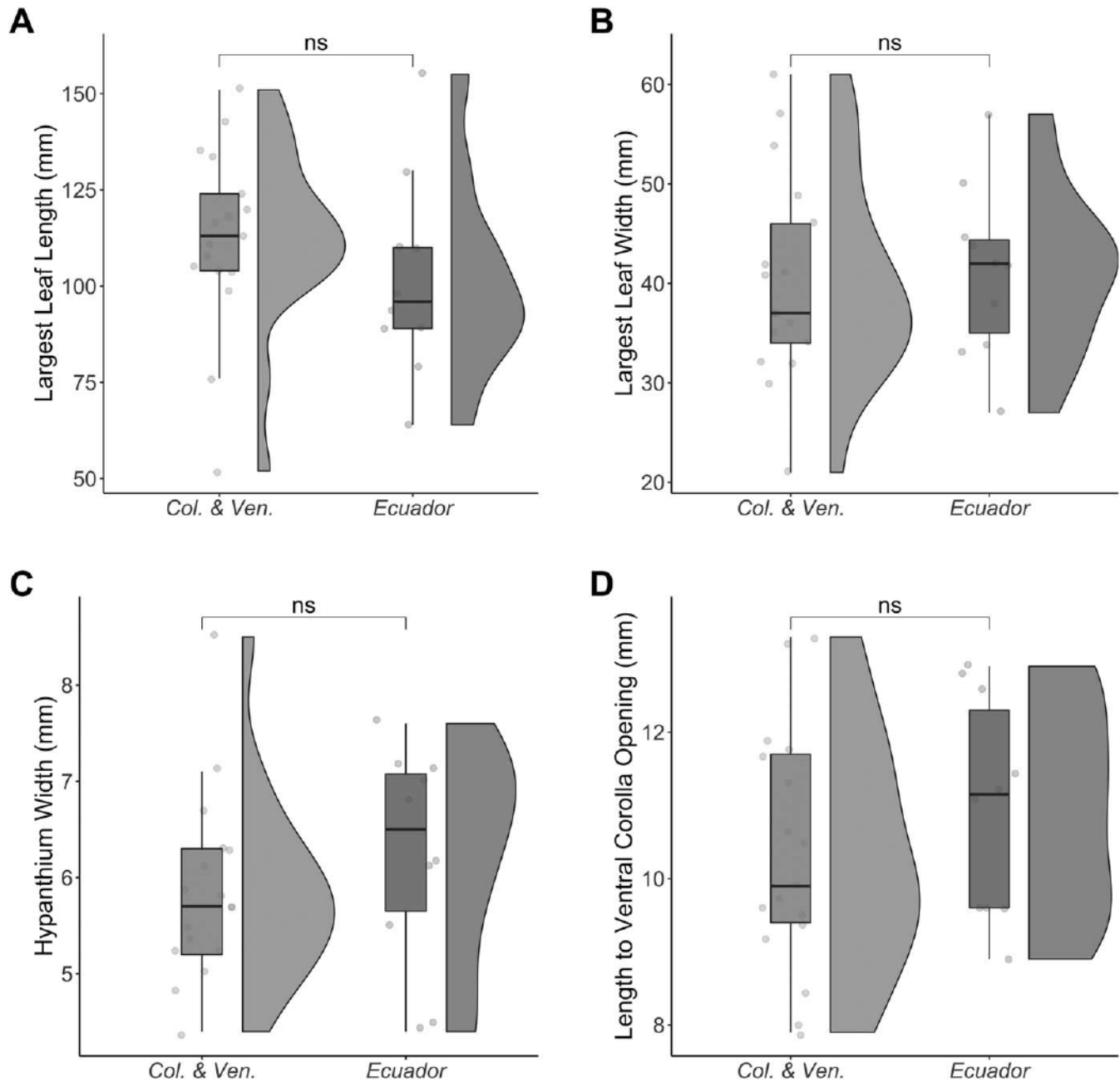


FIG. S3. Univariate comparisons of additional traits measured between geographic groups of *B. succulenta* specimens.

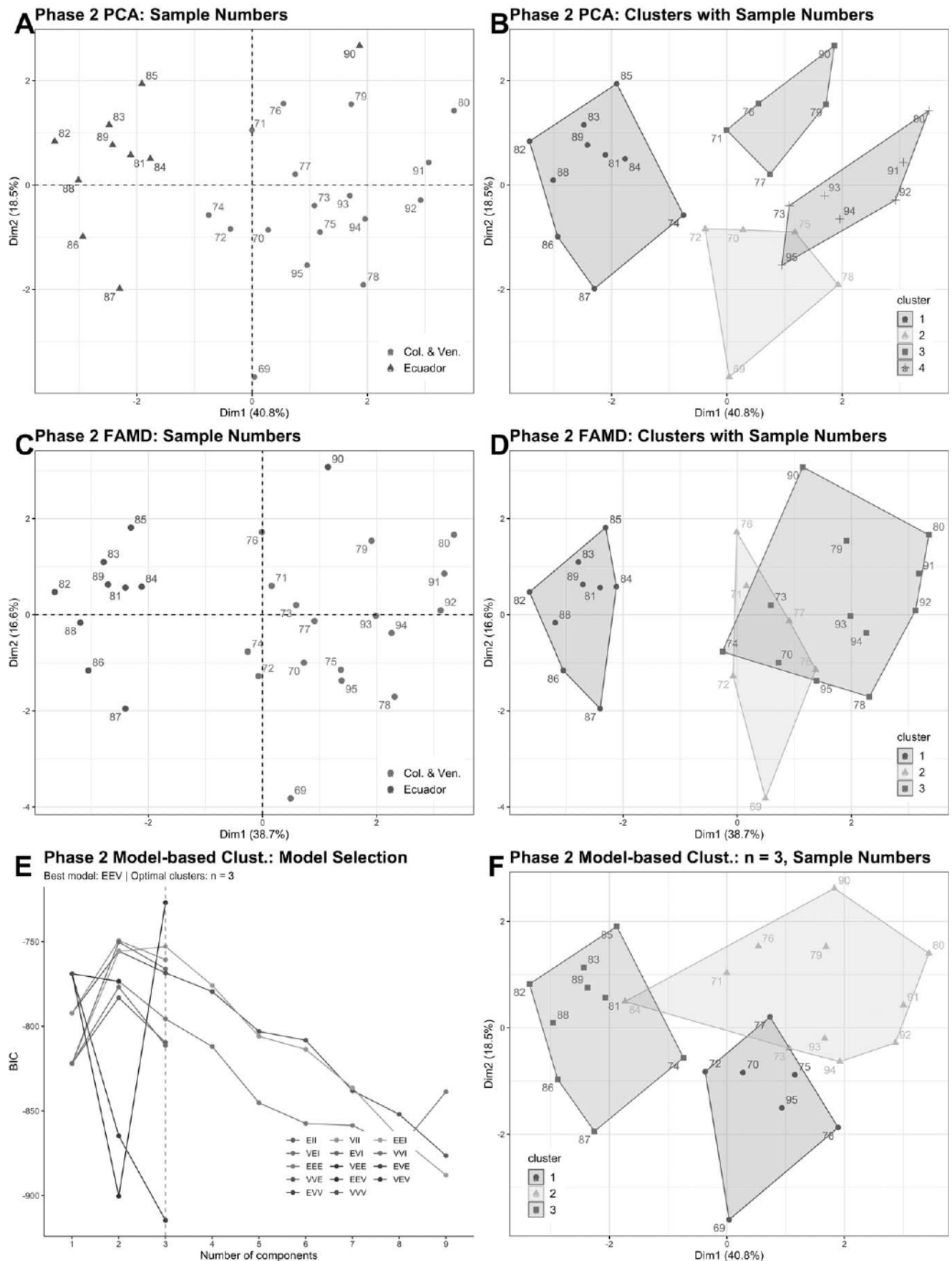


FIG. S4. Results of Phase 2 multivariate analyses with sample numbers included. Sample numbers correspond to numbers in the Supplemental Data. A, B. PCA of ten quantitative traits; unsupervised clustering performed with HCPC. C, D. FAMD of ten quantitative traits and two qualitative traits; unsupervised clustering performed with HCPC. E, F. Model-based clustering where $n = 3$ is selected as the optimal number of clusters.

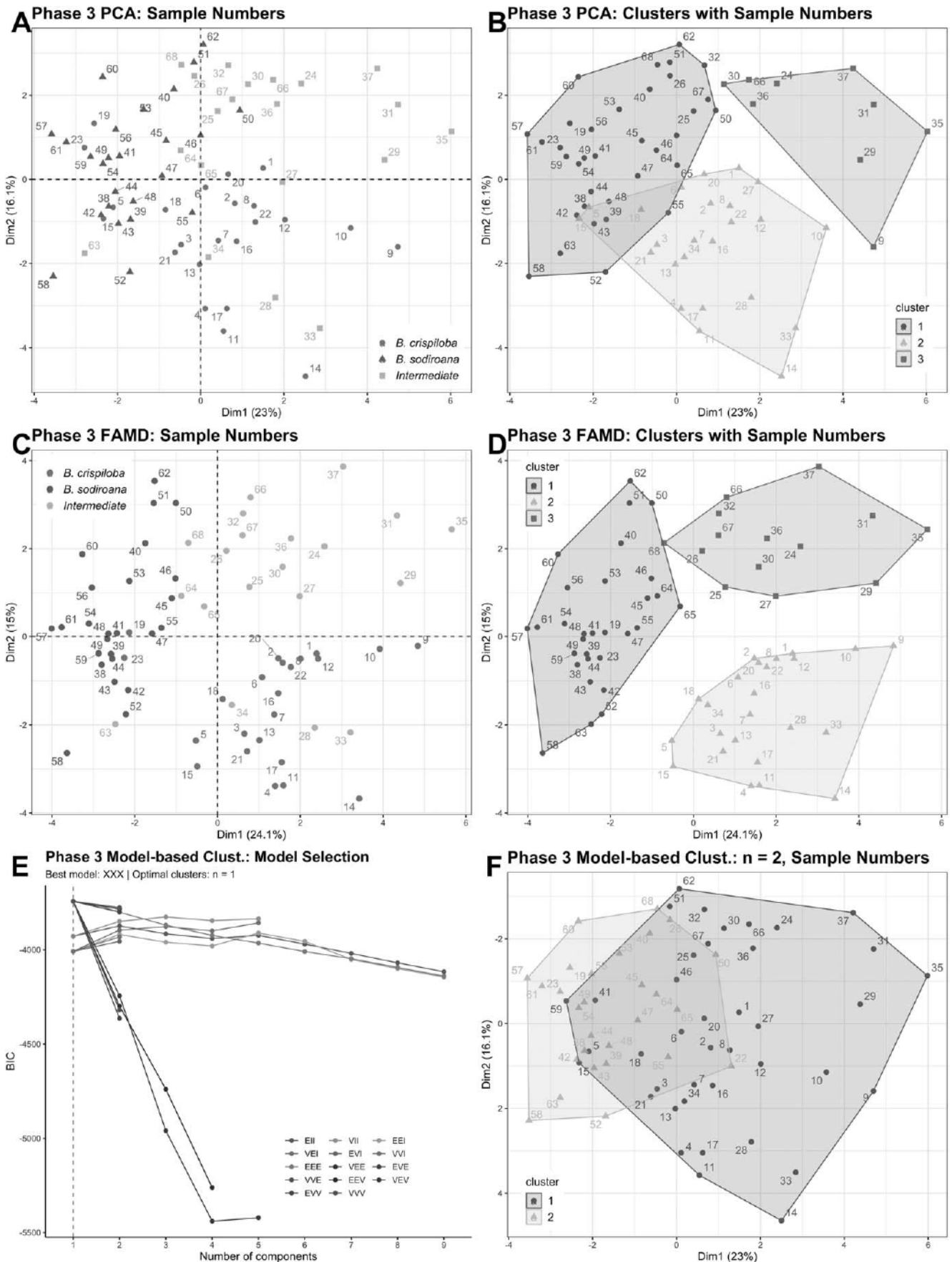


FIG. S5. Results of Phase 3 multivariate analyses with sample numbers included. Sample numbers correspond to numbers in the Supplemental Data. A, B. PCA of 22 quantitative variables; unsupervised clustering performed with HCPC. C, D. FAMD of 22 quantitative variables and two qualitative variables; unsupervised clustering performed with HCPC. E, F. Model-based clustering where $n = 1$ is selected as the optimal number of clusters; clustering at $n = 2$ is shown with sample numbers.

TABLE S1. Placement of each sample into Phase 1 clustering results on the entire RCC dataset.

Sample number	A priori species assignments	Collector	Collection number	Collection country	PCA clusters	FAMD clusters	Model-based Clusters K = 2	Model-based Clusters K = 3
1	<i>B. crispiloba</i>	Muchhala	207	Ecuador	2	4	2	2
2	<i>B. crispiloba</i>	Werling	233	Ecuador	2	4	2	2
3	<i>B. crispiloba</i>	Knudsen	459	Ecuador	2	4	2	2
4	<i>B. crispiloba</i>	Clark	499	Ecuador	2	4	2	2
5	<i>B. crispiloba</i>	Balslev	1996	Ecuador	1	2	2	2
6	<i>B. crispiloba</i>	Stein	2686	Ecuador	2	4	2	2
7	<i>B. crispiloba</i>	Stein	3091	Ecuador	2	4	2	2
8	<i>B. crispiloba</i>	Bonifaz	3170	Ecuador	2	4	2	2
9	<i>B. crispiloba</i>	Daly	5206	Ecuador	2	4	2	2
10	<i>B. crispiloba</i>	Vargas	5585	Ecuador	2	4	2	2
11	<i>B. crispiloba</i>	Jaramillo	6611	Ecuador	2	4	2	2
12	<i>B. crispiloba</i>	Dodson	7217	Ecuador	2	4	2	2
13	<i>B. crispiloba</i>	Dodson	7433	Ecuador	2	4	2	2
14	<i>B. crispiloba</i>	Ceron	10082	Ecuador	2	4	2	2
15	<i>B. crispiloba</i>	van der Werff	10767	Ecuador	1	2	2	2
16	<i>B. crispiloba</i>	Dodson	12000	Ecuador	2	4	2	2
17	<i>B. crispiloba</i>	Luteyn	13363	Ecuador	2	4	2	2
18	<i>B. crispiloba</i>	Dodson	14661	Ecuador	2	4	2	2
19	<i>B. crispiloba</i>	Lojtnant	15174	Ecuador	1	2	2	3
20	<i>B. crispiloba</i>	Dodson	15196	Ecuador	2	4	1	1
21	<i>B. crispiloba</i>	Dodson	15548	Ecuador	2	4	2	2
22	<i>B. crispiloba</i>	Harling	23062	Ecuador	2	4	1	1
23	<i>B. crispiloba</i>	Jaramillo	30276	Ecuador	1	2	2	3
24	<i>B. crispiloba</i>	Muchhala	115	Ecuador	2	4	2	2
25	<i>B. crispiloba</i>	Nowicki	1498	Ecuador	2	4	2	2
26	<i>B. crispiloba</i>	Vargas	5171	Ecuador	1	2	2	3
27	<i>B. crispiloba</i>	Clark	7944	Ecuador	2	4	2	2
28	<i>B. crispiloba</i>	Neill	8654	Ecuador	2	4	2	2
29	<i>B. crispiloba</i>	Neill	9800	Ecuador	2	4	2	2
30	<i>B. crispiloba</i>	Dodson	12782	Ecuador	2	4	2	2
31	<i>B. crispiloba</i>	Luteyn	13333	Ecuador	2	4	2	2
32	<i>B. crispiloba</i>	Harling	19471	Ecuador	2	4	2	3
33	<i>B. crispiloba</i>	HolmNielsen	24419	Ecuador	2	4	2	2
34	<i>B. crispiloba</i>	Webster	30017	Ecuador	2	4	2	2
35	<i>B. crispiloba</i>	Gentry	69945	Ecuador	2	4	2	2
36	<i>B. crispiloba</i>	Gentry	69965	Ecuador	2	4	2	2
37	<i>B. crispiloba</i>	Gentry	72409	Ecuador	2	4	2	2
38	<i>B. sodiroana</i>	Muchhala	129	Ecuador	2	1	2	2
39	<i>B. sodiroana</i>	Pachano	177	Ecuador	2	1	2	2
40	<i>B. sodiroana</i>	Muchhala	458	Ecuador	2	1	2	2
41	<i>B. sodiroana</i>	Bleiweiss	1142	Ecuador	2	1	2	2
42	<i>B. sodiroana</i>	Molau	1156	Ecuador	2	1	2	2
43	<i>B. sodiroana</i>	Smith	1976	Ecuador	2	1	2	2
44	<i>B. sodiroana</i>	Stahl	2578	Ecuador	2	1	2	2
45	<i>B. sodiroana</i>	Stein	2662	Ecuador	2	1	2	2
46	<i>B. sodiroana</i>	Stein	2674	Ecuador	2	1	2	2
47	<i>B. sodiroana</i>	Stein	2683	Ecuador	2	1	2	2
48	<i>B. sodiroana</i>	Tepe	2955	Ecuador	2	1	2	2
49	<i>B. sodiroana</i>	Maas	3035	Ecuador	2	1	2	2
50	<i>B. sodiroana</i>	Stein	3082	Ecuador	2	1	2	2
51	<i>B. sodiroana</i>	Vargas	3712	Ecuador	2	1	2	1
52	<i>B. sodiroana</i>	Ceron	3830	Ecuador	2	1	2	2
53	<i>B. sodiroana</i>	Camp	4955	Ecuador	2	1	2	2
54	<i>B. sodiroana</i>	Perez	8409	Ecuador	2	1	2	2
55	<i>B. sodiroana</i>	Luteyn	8792	Ecuador	2	1	2	2
56	<i>B. sodiroana</i>	Asplund	9767	Ecuador	2	1	2	2
57	<i>B. sodiroana</i>	Balslev	10329	Ecuador	1	1	2	2
58	<i>B. sodiroana</i>	Lojtnant	11261	Ecuador	2	1	2	2
59	<i>B. sodiroana</i>	Luteyn	13328	Ecuador	2	1	2	2
60	<i>B. sodiroana</i>	Luteyn	13389	Ecuador	2	1	2	2
61	<i>B. sodiroana</i>	D'Arcy	14101	Ecuador	2	1	2	2
62	<i>B. sodiroana</i>	Holm-Nielsen	16226	Ecuador	2	1	2	2
63	<i>B. sodiroana</i>	Ceron	2798	Ecuador	2	1	2	2
64	<i>B. sodiroana</i>	Luteyn	5750	Ecuador	2	1	2	2
65	<i>B. sodiroana</i>	Holm-Nielsen	6000	Ecuador	2	1	2	2
66	<i>B. sodiroana</i>	Luteyn	10893	Ecuador	2	4	2	1
67	<i>B. sodiroana</i>	Luteyn	14342	Ecuador	2	4	2	2
68	<i>B. sodiroana</i>	Gentry	26647	Ecuador	1	2	2	2
69	<i>B. succulenta</i>	Stein	3303	Colombia	3	3	1	1
70	<i>B. succulenta</i>	Stein	3369	Colombia	3	3	1	1
71	<i>B. succulenta</i>	Pennell	5151	Colombia	3	3	1	1
72	<i>B. succulenta</i>	Pennell	5783	Colombia	3	3	1	1

(Continued)

TABLE S1. (CONTINUED).

Sample number	A priori species assignments	Collector	Collection number	Collection country	PCA clusters	FAMD clusters	Model-based Clusters K = 2	Model-based Clusters K = 3
73	<i>B. succulenta</i>	Luteyn	10650	Colombia	3	3	1	1
74	<i>B. succulenta</i>	Pennell	10685	Colombia	3	3	1	3
75	<i>B. succulenta</i>	Luteyn	10750	Colombia	3	3	1	1
76	<i>B. succulenta</i>	Luteyn	10761	Colombia	3	3	2	2
77	<i>B. succulenta</i>	Luteyn	10773	Colombia	3	3	1	1
78	<i>B. succulenta</i>	Luteyn	12418	Colombia	3	3	1	1
79	<i>B. succulenta</i>	Luteyn	12420	Colombia	3	3	1	1
80	<i>B. succulenta</i>	Luteyn	12557	Colombia	3	3	1	1
81	<i>B. succulenta</i>	Sigcha	28	Ecuador	1	2	1	3
82	<i>B. succulenta</i>	Muchhala	125	Ecuador	1	2	1	3
83	<i>B. succulenta</i>	Muchhala	128	Ecuador	1	2	1	3
84	<i>B. succulenta</i>	Muchhala	130	Ecuador	1	2	1	3
85	<i>B. succulenta</i>	Muchhala	447	Ecuador	1	2	1	3
86	<i>B. succulenta</i>	Muchhala	454	Ecuador	1	2	1	3
87	<i>B. succulenta</i>	Stahl	2901	Ecuador	1	2	1	3
88	<i>B. succulenta</i>	Neill	8942	Ecuador	1	2	1	3
89	<i>B. succulenta</i>	Jaramillo	13651	Ecuador	1	2	1	3
90	<i>B. succulenta</i>	Harling	19211	Ecuador	3	3	1	1
91	<i>B. succulenta</i>	Allart	479	Venezuela	3	3	1	1
92	<i>B. succulenta</i>	Fendler	731	Venezuela	3	3	1	1
93	<i>B. succulenta</i>	Luteyn	5177	Venezuela	3	3	1	1
94	<i>B. succulenta</i>	Mori	14602	Venezuela	3	3	1	1
95	<i>B. succulenta</i>	Steyermark	100250	Venezuela	3	3	1	1

TABLE S2. Placement of each *B. succulenta* s.l. sample into Phase 2 clustering results.

Sample number	A priori species assignment	Collector	Collection number	Collection country	PCA clusters	FAMD clusters	Model-based clusters K = 2	Model-based clusters K = 3
69	<i>B. succulenta</i>	Stein	3303	Colombia	2	2	1	1
70	<i>B. succulenta</i>	Stein	3369	Colombia	2	3	1	1
71	<i>B. succulenta</i>	Pennell	5151	Colombia	3	2	1	2
72	<i>B. succulenta</i>	Pennell	5783	Colombia	2	2	1	1
73	<i>B. succulenta</i>	Luteyn	10650	Colombia	4	3	1	2
74	<i>B. succulenta</i>	Pennell	10685	Colombia	1	3	2	3
75	<i>B. succulenta</i>	Luteyn	10750	Colombia	2	2	1	1
76	<i>B. succulenta</i>	Luteyn	10761	Colombia	3	2	1	2
77	<i>B. succulenta</i>	Luteyn	10773	Colombia	3	2	1	1
78	<i>B. succulenta</i>	Luteyn	12418	Colombia	2	3	1	1
79	<i>B. succulenta</i>	Luteyn	12420	Colombia	3	3	1	2
80	<i>B. succulenta</i>	Luteyn	12557	Colombia	4	3	1	2
81	<i>B. succulenta</i>	Sigcha	28	Ecuador	1	1	2	3
82	<i>B. succulenta</i>	Muchhala	125	Ecuador	1	1	2	3
83	<i>B. succulenta</i>	Muchhala	128	Ecuador	1	1	2	3
84	<i>B. succulenta</i>	Muchhala	130	Ecuador	1	1	2	2
85	<i>B. succulenta</i>	Muchhala	447	Ecuador	1	1	2	3
86	<i>B. succulenta</i>	Muchhala	454	Ecuador	1	1	2	3
87	<i>B. succulenta</i>	Stahl	2901	Ecuador	1	1	2	3
88	<i>B. succulenta</i>	Neill	8942	Ecuador	1	1	2	3
89	<i>B. succulenta</i>	Jaramillo	13651	Ecuador	1	1	2	3
90	<i>B. succulenta</i>	Harling	19211	Ecuador	3	3	1	2
91	<i>B. succulenta</i>	Allart	479	Venezuela	4	3	1	2
92	<i>B. succulenta</i>	Fendler	731	Venezuela	4	3	1	2
93	<i>B. succulenta</i>	Luteyn	5177	Venezuela	4	3	1	2
94	<i>B. succulenta</i>	Mori	14602	Venezuela	4	3	1	2
95	<i>B. succulenta</i>	Steyermark	100250	Venezuela	4	3	1	1

TABLE S3. Placement of each *B. crispiloba*/*B. sodiroana* sample into Phase 3 clustering results.

Sample number	A priori species assignment	Collector	Collection number	Collection country	PCA clusters	FAMD clusters	Model-based clusters K = 2	Model-based clusters K = 3
1	<i>B. crispiloba</i>	Muchhala	207	Ecuador	2	2	1	1
2	<i>B. crispiloba</i>	Werling	233	Ecuador	2	2	1	1
3	<i>B. crispiloba</i>	Knudsen	459	Ecuador	2	2	1	1
4	<i>B. crispiloba</i>	Clark	499	Ecuador	2	2	1	1
5	<i>B. crispiloba</i>	Balslev	1996	Ecuador	2	2	1	2
6	<i>B. crispiloba</i>	Stein	2686	Ecuador	2	2	1	1
7	<i>B. crispiloba</i>	Stein	3091	Ecuador	2	2	1	1
8	<i>B. crispiloba</i>	Bonifaz	3170	Ecuador	2	2	1	1
9	<i>B. crispiloba</i>	Daly	5206	Ecuador	3	2	1	1
10	<i>B. crispiloba</i>	Vargas	5585	Ecuador	2	2	1	1
11	<i>B. crispiloba</i>	Jaramillo	6611	Ecuador	2	2	1	1
12	<i>B. crispiloba</i>	Dodson	7217	Ecuador	2	2	1	1
13	<i>B. crispiloba</i>	Dodson	7433	Ecuador	2	2	1	1
14	<i>B. crispiloba</i>	Ceron	10082	Ecuador	2	2	1	1
15	<i>B. crispiloba</i>	van der Werff	10767	Ecuador	2	2	1	2
16	<i>B. crispiloba</i>	Dodson	12000	Ecuador	2	2	1	1
17	<i>B. crispiloba</i>	Luteyn	13363	Ecuador	2	2	1	1
18	<i>B. crispiloba</i>	Dodson	14661	Ecuador	2	2	1	3
19	<i>B. crispiloba</i>	Lojtnant	15174	Ecuador	1	1	2	3
20	<i>B. crispiloba</i>	Dodson	15196	Ecuador	2	2	1	1
21	<i>B. crispiloba</i>	Dodson	15548	Ecuador	2	2	1	3
22	<i>B. crispiloba</i>	Harling	23062	Ecuador	2	2	2	1
23	<i>B. crispiloba</i>	Jaramillo	30276	Ecuador	1	1	2	3
24	Intermediate	Muchhala	115	Ecuador	3	3	1	1
25	Intermediate	Nowicki	1498	Ecuador	1	3	1	1
26	Intermediate	Vargas	5171	Ecuador	1	3	2	1
27	Intermediate	Clark	7944	Ecuador	2	3	1	1
28	Intermediate	Neill	8654	Ecuador	2	2	1	1
29	Intermediate	Neill	9800	Ecuador	3	3	1	1
30	Intermediate	Dodson	12782	Ecuador	3	3	1	1
31	Intermediate	Luteyn	13333	Ecuador	3	3	1	1
32	Intermediate	Harling	19471	Ecuador	1	3	1	1
33	Intermediate	HolmNielsen	24419	Ecuador	2	2	1	1
34	Intermediate	Webster	30017	Ecuador	2	2	1	1
35	Intermediate	Gentry	69945	Ecuador	3	3	1	1
36	Intermediate	Gentry	69965	Ecuador	3	3	1	1
37	Intermediate	Gentry	72409	Ecuador	3	3	1	1
38	<i>B. sodiroana</i>	Muchhala	129	Ecuador	1	1	2	3
39	<i>B. sodiroana</i>	Pachano	177	Ecuador	1	1	2	1
40	<i>B. sodiroana</i>	Muchhala	458	Ecuador	1	1	2	3
41	<i>B. sodiroana</i>	Bleiweiss	1142	Ecuador	1	1	1	3
42	<i>B. sodiroana</i>	Molau	1156	Ecuador	1	1	2	3
43	<i>B. sodiroana</i>	Smith	1976	Ecuador	1	1	2	3
44	<i>B. sodiroana</i>	Stahl	2578	Ecuador	1	1	2	3
45	<i>B. sodiroana</i>	Stein	2662	Ecuador	1	1	2	3
46	<i>B. sodiroana</i>	Stein	2674	Ecuador	1	1	1	1
47	<i>B. sodiroana</i>	Stein	2683	Ecuador	1	1	2	3
48	<i>B. sodiroana</i>	Tepe	2955	Ecuador	1	1	2	3
49	<i>B. sodiroana</i>	Maas	3035	Ecuador	1	1	2	3
50	<i>B. sodiroana</i>	Stein	3082	Ecuador	1	1	2	1
51	<i>B. sodiroana</i>	Vargas	3712	Ecuador	1	1	1	1
52	<i>B. sodiroana</i>	Ceron	3830	Ecuador	1	1	2	3
53	<i>B. sodiroana</i>	Camp	4955	Ecuador	1	1	2	3
54	<i>B. sodiroana</i>	Perez	8409	Ecuador	1	1	2	3
55	<i>B. sodiroana</i>	Luteyn	8792	Ecuador	1	1	2	1
56	<i>B. sodiroana</i>	Asplund	9767	Ecuador	1	1	2	3
57	<i>B. sodiroana</i>	Balslev	10329	Ecuador	1	1	2	3
58	<i>B. sodiroana</i>	Lojtnant	11261	Ecuador	1	1	2	3
59	<i>B. sodiroana</i>	Luteyn	13328	Ecuador	1	1	1	3
60	<i>B. sodiroana</i>	Luteyn	13389	Ecuador	1	1	2	3
61	<i>B. sodiroana</i>	D'Arcy	14101	Ecuador	1	1	2	3
62	<i>B. sodiroana</i>	Holm-Nielsen	16226	Ecuador	1	1	1	1
63	Intermediate	Ceron	2798	Ecuador	1	1	2	3
64	Intermediate	Luteyn	5750	Ecuador	1	1	2	3
65	Intermediate	Holm-Nielsen	6000	Ecuador	1	1	2	1
66	Intermediate	Luteyn	10893	Ecuador	3	3	1	1
67	Intermediate	Luteyn	14342	Ecuador	1	3	1	1
68	Intermediate	Gentry	26647	Ecuador	1	3	2	1