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A Taxonomic Revision of the Genus Burmeistera (Campanulaceae) in Ecuador

Brock Mashburn

B.S. Agriculture Science, Truman State University, 2012

A thesis presented to the Graduate School of the University of Missouri – St. Louis in partial fulfillment of the requirements for the degree Master of Science in Biology with an emphasis in Evolution, Ecology and Systematics

> August 2019 St. Louis, Missouri

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Disclaimer

According to Article 30.9 of the International Code of Nomenclature (ICN) for algae, fungi, and plants (Turland et al. 2018), the descriptions of new species presented in this dissertation do not constitute effective publication. Thus, the names proposed are not valid until they are published in an appropriate manner to meet the conditions of effective publication set out by the ICN. The author intends to accomplish this after the completion and submission of the present thesis.

Note on the Formatting of Taxonomic Treatments

The chapters in this thesis are formatted to the standards of the intended journals of publication. Chapter one is intended to be published in the journal Phytotaxa (Phytotaxa 2019). Chapter two is intended to be published in the Annals of the Missouri Botanical Garden (Missouri Botanical Garden Press 2019).

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Chapter One

Morphometric analysis helps clarify species limits within the recurved corolla clade of *Burmeistera* (Campanulaceae), including the description of two new species *Brock Mashburn*^{1*}, *Nathan Muchhala*¹

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ABSTRACT

The genus *Burmeistera* consists of mostly 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. The molecular phylogeny produced by Uribe-Convers et al. (2017) identified four species in the recurved corolla clade (RCC) – *B. crispiloba*, *B. sodiroana*, *B. succulenta*, and *B. toroensis*. As many as ten names for these four species have been recognized previously, though the most recent taxonomic treatments recognize only these four. Hundreds of collections made in the last forty years have uncovered additional phenotypic variation in these species, and provide more data with which to test and describe species boundaries. Observations of these specimens reveal that characters traditionally used to differentiate these species no longer do so clearly, and suggest the possibility of introgression between RCC species. Here, we report morphometric analyses of herbarium specimens of RCC to test the current species understandings. We perform principal component analyses followed by unsupervised clustering analyses to explore grouping tendencies of morphological traits. Our results support the recognition of six species, including two newly described here: *B. kitrinaima* and *B. melanocarpa*. In addition, we conclude that the majority of Ecuadorian specimens previously identified as *B. succulenta* are either *B. kitrinaima* or *B. huacamayensis*, although neither of these two species is in the RCC, nor do they possess recurved corolla lobes. All six species are described in full in the taxonomic treatment. These species descriptions are accompanied by photographs, illustrations, distributions maps, taxonomic discussion, and an identification key to the species treated here. *Key words*: Andes, biodiversity, hybridization, taxonomy, phenetics

INTRODUCTION

Burmeistera Karsten & Triana (1854: 13) (Campanulaceae subfamily Lobelioideae) is a genus of approximately 120 species distributed from Central to South America (Uribe-Convers et al. 2017; Vallejo et al. 2018). The majority of species are found from Costa Rica to Ecuador. Only one species—*Burmeistera virescens* (Benth.) Bentham & Hooker ex Hemsley (1881: 263)—has been described north of Costa Rica, in Honduras and Guatemala (Lammers & Maas 1998; Nash 1976), while two to four species extend from the south of Ecuador into Peru (Lammers 2007; Stein 1987). Roughly half of all species (~60) are found in Colombia, with ~40 in Ecuador and ~21 along the Cordillera de Talamanca of Panama and Costa Rica (Lagomarsino et al. 2015; Vallejo et al. 2018; Venegas et al. 2014). Most species inhabit cloud forest ecosystems from 1000 to 3000 m in elevation along either side of the Andes and the Cordillera de Talamanca, often in narrowly restricted ranges (Lagomarsino et al. 2015; Muchhala & Pérez 2015a; Uribe-Convers et al. 2017).

Burmeistera is sister to two larger Lobelioid genera: *Centropogon* Presl (1836: 48) (~210 species) and *Syphocampylus* Pohl (1831: 104) (~230 species) (Lammers 2007). Aside from *Lobelia* L., these three genera, known collectively as the centropogonid clade, are the largest within Lobelioideae (Lammers 1998). Centropogonid species are distinguished from *Lobelia* (1753: 929) by the entire corolla tubes that are neither fenestrate nor dorsally cleft. Other traits of the clade include corolla lobes that are either monomorphic or dimorphic, fused staminal tubes that almost always extend beyond the corolla, and anther tubes that often bear bunched hairs on the apex (Lagomarsino et al. 2014; Lammers 1998). Species are mostly herbaceous to semi-woody scandent or erect shrubs, though many *Burmeistera* are hemiepiphytic.

The three centropogonid genera have traditionally been distinguished by fruit type: *Siphocampylus* produces capsules while *Centropogon* and *Burmeistera* produce berries (Lagomarsino et al. 2014). *Burmeistera* is further differentiated from *Centropogon* via several synapomorphies: generally ebracteolate pedicels, an inflated corolla opening, a wider fused anther tube and opening, and isodiametric seeds (Lagomarsino et al. 2014; Lammers 1998). Of these, the inflated corolla opening of *Burmeistera* was used early to identify the genus (Karsten 1856; Triana 1854). Molecular studies have confirmed the monophyly of *Burmeistera*, while also revealing extensive paraphyly between *Siphocampylus* and *Centropogon* (Antonelli 2008; Knox et al. 2008; Lagomarsino et al. 2014; Uribe-Convers et al. 2017). The centropogonid clade presents an interesting diversity of pollination syndromes. Molecular work has identified an ancestral shift from hummingbird pollination, found in *Siphocampylus* and *Centropogon*, to bat pollination in *Burmeistera* (Lagomarsino et al. 2017). The morphology of most *Burmeistera* species supports a bat pollination syndrome: an inflated corolla opening, dull flower color, skunky flower odor, and erect pedicels (Muchhala 2006). Still, pollination syndromes among centropogonid genera are somewhat labile, with other independent shifts to bat pollination in *Siphocampylus* and *Centropogon*, and at least two reversions to hummingbird pollination in *Burmeistera* (Lagomarsino et al. 2017; Muchhala 2006). The recent diversification of *Burmeistera*, and its coevolution with pollinators, make the group a fascinating and yet challenging group to study. In particular, taxonomic studies on the group are difficult because of often overlapping and seemingly labile morphological characters, as well as significant morphological variation within widespread species (Lagomarsino et al. 2015; Uribe-Convers et al. 2017).

Initial taxonomic work on *Burmeistera* did not attempt to identify infrageneric groups. Wimmer (1943, 1953) was the first to formally propose two groups, *Barbatae*, with barbate anther tips, and *Imberbes*, with glabrous or sparsely pubescent anther tips. Not only is the nature of the anther tip difficult to discern from herbarium specimens, molecular studies have shown it to be non-monophyletic (Lagomarsino et al. 2014; Uribe-Convers et al. 2017). However, these molecular studies have been instructive in identifying other potential monophyletic groups within the genus. For example, Uribe-Convers et al. (2017) identified three clades with a single apomorphy each: a bibracteate

pedicel clade, an inflated fruit clade, and a recurved corolla clade. To date no alternative infrageneric groupings have been proposed.

The recurved corolla clade (RCC) identified by Uribe-Convers et al. (2017) consists of four species. The authors identified these as Burmeistera crispiloba Zahlbruckner (1915: 528), B. sodiroana Zahlbruckner (1915: 534), B. succulenta Karsten (1856: 445), and B. toroensis Wilbur (1976: 608). However, the sample of B. toroensis used by Uribe-Convers et al. (2017) was misidentified, and its true identity remains unknown. The herbarium material from which the sample was taken was not found in a recent herbarium search. Though this sample is likely a new species from Panama, it cannot be confirmed until the specimen is recovered. Thus, for the sake of our study here, we deal only with the three other species mentioned above. These species differ from other *Burmeistera* in the way the five unfused lobes of the corolla flare out from the enlarged opening and then curl or scroll back; corolla lobes of other *Burmeistera* are falcate, turning downward and away from the dorsal side of the flower (Figure 1). In B. sodiroana, the corolla lobes curl back, though the curling tip does not touch the lower part of the corolla (see Figure 5E). In B. crispiloba and B. succulenta, however, the curling corolla lobes are much more evident, scrolling back and circling multiple times (see Figure 5A). In *B. sodiroana* and sometimes in *B. succulenta*, this curling seems to occur only at a later stage of flower maturity, such that dried specimens with flowers do not always exhibit the trait.

The three currently recognized species in the RCC have an interesting taxonomic history. Wimmer (1943, 1968) recognized six species and three varieties. Jeppesen (1981), dealing only with the *Burmeistera* of Ecuador, reduced Wimmer's nine names to

three species without varieties. Furthermore, in his treatment, Jeppesen hypothesized: "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". Jeppesen (1981) cited 55 specimens of all three species in his treatment, while our study uses 205. Following Jeppesen, Lammers (2007) recognized *B. crispiloba* with two synonyms, *B. sodiroana* with two synonyms, and *B. succulenta* with two synonyms. Clearly each author recognized the morphological diversity of these species, and struggled with how to appropriately deal with the variation. In our study, we use Jeppesen's (1981) species limits for *B. crispiloba*, *B. sodiroana*, and *B. succulenta* as a starting point for our analysis of the recurved corolla clade.

Of the three species in the RCC, *B. succulenta* is the most widespread, found from western Venezuela to Columbia to south-central Ecuador (Figure 2). *Burmeistera crispiloba* and *B. sodiroana* are restricted to Ecuador: *B. crispiloba* is found west of the Andes from sea level to 1500 m in the Andean foothills, while *B. sodiroana* occurs on the east and west slopes of the Andes from 1500 to 3000 m in elevation (Figure 3). Both *B. crispiloba* and *B. sodiroana* can look similar vegetatively and can be difficult to differentiate using the characters identified by Jeppesen (1981). This may be due, in part, to the fact that morphological traits traditionally used to differentiate the two species – leaf size, pedicel length, and hypanthium shape (Jeppesen 1981) – appear just as variable within species as between them. A number of specimens of these two species are especially difficult to differentiate along the intersection of their ranges, at around 1500 m in elevation (Figure 4): they have phyllotaxy, flower size, and fruit morphology traits

similar to *B. crispiloba*, yet leaf shape and flower color traits are similar to *B. sodiroana* (Figure 5). This difficulty is made evident in that individual specimens (even duplicate specimens from the same collection) have been identified by different taxonomists as either *B. crispiloba* and *B. sodiroana*. Given the difficulty in differentiating them, in our study we sometimes refer to this group as the *B. crispiloba / B. sodiroana* complex. Meanwhile, *B. sodiroana* and *B. succulenta* co-occur on both sides of the Andes. These two species are not easily confused with each other, though they each exhibit considerable within-species morphological variation between disjunct populations.

In the present study, we attempt to tease apart and resolve the taxonomic issues within the RCC of *Burmeistera*. First, we test Jeppesen's (1981) hypothesis that the three species may constitute one variable *B. succulenta* complex, finding instead that some traits consistently differentiate *B. succulenta* from the combined *B. crispiloba / B. sodiroana* complex. Second, we perform morphometric analysis on the *B. crispiloba / B. sodiroana* complex to examine whether or not these two species differentiate *morphologically*. Third, we perform further analyses on the morphologically variable *B. succulenta* and *B. sodiroana* to identify potential new species within them. Fourth, and 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

The morphometric analysis and taxonomic revisions in this study are based upon measurements and observations made from 205 herbarium specimens of Burmeistera from the herbaria MO, NY, and QCA. We measured all specimens from these herbaria that could be identified as *B. crispiloba*, *B. sodiroana*, or *B. succulenta* using Jeppesen's key, or that have been regularly identified as these species by taxonomists working on the group. Field observations and photographs from living plants were used, when available, to aid in descriptions of shapes. Of the 205 specimens used, over half had complete flowers, including 41 identified as B. succulenta, 37 as B. sodiroana, 24 as B. crispiloba and 22 unidentified specimens. Of the B. succulenta specimens used, 24 were from Colombia, 17 from Ecuador, and five from Venezuela. A complete list of specimens used in morphometric analyses can be found in Appendix 1. All specimens were georeferenced from coordinates or locations given on the specimen labels. When specimen labels did not provide GPS locations, we approximated these using the label descriptions and Google Maps. When elevation data was not provided, we produced precise elevation data from Google Maps APIs using the R package "googleway" (Cooley 2018).

Morphological Variables

A total of 37 morphological characters were measured or observed from corresponding mature parts of each specimen (Table 1). Of these, 23 were continuous quantitative characters, and 14 were discrete qualitative characters. All quantitative measurements were taken in millimeters. Quantitative vegetative measurements were taken using a ruler, while quantitative reproductive measurements were taken using a Tajima 150 mm dial caliper. Color characters were not recorded because of the inconsistency of label descriptions and color retention on dried herbarium specimens.

Morphological characters were chosen to span the vegetative and reproductive variation of the species, including the characters traditionally used to differentiate the RCC Burmeistera. Phyllotaxy (distichous vs. spiral) was identified as a previously unused but useful character to differentiate species in this group. Phyllotaxy is defined as the arrangement of the leaves on the stem, though more precisely it refers to the arrangement of the petiole attachement on the stem. All Burmeistera have alternate phyllotaxy (vs. opposite), as two leaves never arise from the stem at the same node. However, Burmeistera leaves are either distichous or spiral. An alternate, distichous phyllotaxy, also called "two-ranked," is when leaves are arranged along two columns, consistently alternating 180 degrees on the other side of the stem. Meanwhile, spiral phyllotaxy is when leaves arise at a different point along the stem. Often, herbarium specimens are pressed flat and/or plant stems turn as they grow, making it difficult to identify distichous vs. spiral phyllotaxy. For *Burmeistera*, it is useful to follow the vertical striations of the stem, noting whether alternating leaves arise from the same striation (distichous) or randomly on the stem (spiral).

In addition to phyllotaxy, many *Burmeistera* exhibit a reduction in size of the leaf subtending a flower. Although these leaves could be termed bracts, to maintain consistency for all species, including those without reducing leaves, here we refer to them as fertile leaves. In our species descriptions, however, if this character is present we call them bracts. Thus, we took six measures of leaf size: length and width of the largest sterile leaf, the smallest sterile leaf, and the first fertile leaf distal to a sterile leaf. When

flowers are not present, or when older flowers have fallen off, the first fertile leaf can still be determined by the presence of a visible pedicel scar in the axil of the leaf petiole.

Certain floral traits measured by us are particular to Lobelioid genera, especially *Burmeistera*, and are briefly explained here. For these species, the calyx forms a hypanthium tube adnate to the ovary, from which five calyx lobes extend outward; these sepal-like lobes are variable in length and width. The five-lobed corolla is fused from the base, from which it narrows slightly into a thin tube before abruptly widening and then splitting into the five lobes (see Figure 1). The distance from the base to the ventral edge of the opening is different from the base to the dorsal edge. Five filaments and anthers are fused together into a tube, or androecium, that extends from the ovary. The anther portion of this tube is distinct from the filament portion, thus the anther tube length is a subset of the androecium length. We measured exsertion length as the distance from the ventral widening of the corolla to the tip of the anther tube (Figure 6).

Data Analysis

We analyzed our data in three phases. For the first phase, we conducted univariate and multivariate analyses in the program R (R Core Team 2018) to explore the morphological variation within the RCC. We used univariate methods on the entire dataset to produce descriptive statistics for each taxon. At this stage of the analysis, the taxon groups were made by sorting specimens into the three species concepts given by Jeppesen (1981): *B. crispiloba*, *B. sodiroana* and *B. succulenta*. Even though we were aware of problems with these species delimitations, we first wanted to explore the data from this perspective to reveal the taxonomic issues therein. Given the identification

issues, we call each of these a species complex to highlight the uncertainty within each species (e.g. the *B. succulenta* complex). Initial herbarium work identified seemingly intermediate specimens between *B. crispiloba* and *B. sodiroana*. These specimens were identified, roughly, as having phyllotaxy, floral size, and fruit characters similar to *B. crispiloba*, with leaf shape and flower colors more similar to *B. sodiroana*. In this first stage of our analysis, these intermediate specimens are included in the *B. crispiloba* complex, as this is where many of them have been placed in the past.

We began by testing variables within each species complex for normality using the Shapiro-Wilk's test ('stats' package, function 'shapiro.test', R Core Team 2018). We then analyzed differences among means for each variable per species complex. Means of normally distributed variables were tested using a one-way ANOVA ('stats' package, functions 'lm' and 'aov'), followed by a Tukey test ('stats' package, function 'TukeyHSD') to determine if differences were significant. For variables without a normal distribution, or when outlier measurements could skew means, we applied the Kruskal-Wallis test ('stats' package, function 'kruskal.test'), a non-parametric alternative to a oneway ANOVA. To make pairwise comparisons between species complexes for each variable, we performed a Pairwise Wilcoxon Rank Sum Test ('stats' package, function 'pairwise.wilcox.test'), a non-parametric alternative to a paired t-test. We used the Benjamini-Hochberg Procedure to correct for multiple testing ('p.adjust.method = "BH""). The results of these tests identified characters that differentiate species complexes, as well as characters that may identify morphological variation within species complexes.

The first phase of analyses demonstrated that, among the RCC species, *B.* succulenta is easy to distinguish from *B. crispiloba* and *B. sodiroana*. Therefore, for the second phase of analyses we conducted multivariate analysis on the *B. sodiroana / B. crispiloba* complex, which are much more difficult to differentiate and include the previously-mentioned intermediate specimens. In these analyses we treated intermediate specimens as a separate group to visualize where they fall in relation to more conservative (i.e. without intermediates) concepts of *B. crispiloba* and *B. sodiroana*. We used principal component analysis (PCA) followed by unsupervised cluster analysis (CA) to identify characters differentiating the groups, and to examine the placement of putative hybrids between the two species. PCA was performed using the function 'PCA' in the R package 'FactoMineR' (Le et al. 2008). We chose to retain all components with eigenvalues greater than one.

Unsupervised cluster analysis was performed on the results of the PCA to determine whether, for example, choosing to separate *B. crispiloba* and *B. sodiroana* is statistically supportable, and to analyze the placement of intermediate specimens. We used a hierarchical clustering on principal components (HCPC) approach ('FactoMineR' package, function 'HCPC'), which is a combination of hierarchical and partitioning clustering (k-means) methods on PCA results. The PCA first allows for the reduction in dimensionality of the dataset. HCPC then performs hierarchical clustering using the Ward's criterion on the principal components. 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 'ncp = -1', which allows the clustering algorithm to select the ideal

number of clusters without a preselected range. We refer to this as 'unsupervised clustering' since the algorithm selects the ideal number of clusters.

The first two phases outlined above confirmed the separation of the *B. crispiloba*, *B. succulenta*, and *B. sodiroana* complexes from each other. However, herbarium work and preliminary data analysis identified some taxonomic issues within each of these three complexes. Thus, in the third phase of our study we used the same data analyses as outlined in phases one and two to analyze each of the three species complexes separately in order to clarify these issues.

RESULTS

Univariate Analysis of Recurved Corolla Clade

Six continuous morphological traits can be used in combination to differentiate the three species of the recurved corolla clade: hypanthium length, sepal length, sepal width, androecium length, exsertion length, and anther tube length (Table 2, Figure 7). Of these, Jeppeson (1981) noted only hypanthium length. Shapiro-Wilks normality tests revealed that of these six traits, only hypanthium length is normally distributed. Thus, we used the Pairwise Wilcoxon Rank Sum Test for non-parametric data. Of the 18 pairwise comparisons between species pairs (3 species pairs, 6 variables), 15 showed a significant difference between medians (Table 2). Notably, androecium length, sepal length, and sepal width were significantly different between all pairs.

Despite a fair amount of overlap between *B. crispiloba* and *B. sodiroana* in measurements of these six traits (Figure 7), only hypanthium length does not show a significant difference between means (Table 2). Measurements of intermediate specimens

tend to fall in between these two conservative groups, indicating a need for our second phase of analyses of this complex (described below). *Burmeistera succulenta* shows a large amount of variation in all six measurements, including non-parametric distributions in androecium length, exsertion length, and anther tube length, which is visible in Figure 7. This result, which reveals different clusters in measures of important floral traits, suggests a need for our third phase of analyses to clarify this variation (described below).

Principal Component Analysis and Clustering of the Burmeistera crispiloba / Burmeistera sodiroana Complex

Principal component analysis (PCA) of the *B. crispiloba / B. sodiroana* complex included intermediate and other specimens that are not easy to fit into conservative delimitations of the two species. Correlation analysis between variables led us to remove four variables from the PCA: smallest leaf length, smallest leaf width, corolla tube dorsal length, and androecium length. PCA results in six components with eigenvalues greater than one. These six components include 72.6% of the variance. The first three components explain 53.9% of all variance, 25.5%, 16.5%, and 11.9% respectively. Many variables are significantly associated with the first two dimensions of the PCA. Dimension one has 13 variables that are significantly correlated, while dimension two has 14, and dimension three has 6 (Table 3). The PCA plot in Figure 8A shows that conservative delimitations of *B. crispiloba* and *B. sodiroana* group separately on dimensions one and two, with intermediate specimens in-between or skewed to the top right of the graph. Figure 9 displays the variables that separate these groups in PCA space, thus revealing characters that differentiate the complexes.

Unsupervised clustering selected three clusters from the PCA (Figure 10A) that roughly correspond to our three *a priori* identified groups: a conservative *B. crispiloba*, a conservative *B. sodiroana*, and intermediate specimens (Figure 8A). Cluster A1 (i.e. Cluster 1 of Figure 10A) contains 33 specimens, all of them *a priori* identified as *B. sodiroana*. Cluster A2 contains 28 specimens, 23 of which were *a priori* identified as *B. crispiloba*, and 5 identified as intermediates. Cluster A3 contains 20 specimens, 12 of which were *a priori* identified as intermediates, 5 *B. sodiroana*, and 3 *B. crispiloba*. Variables that significantly describe each cluster for the unsupervised clustering (Figure 10A) are listed in Table 4. Jeppesen's (1981) species concepts identify two species from this complex, *B. crispiloba* and *B. sodiroana*. If the HCPC function is forced to select two clusters, it selects the clusters shown in Figure 10B. In this case, all intermediate specimens and 4 *B. sodiroana* specimens cluster with all *B. crispiloba* specimens.

Further Analysis of the Burmeistera crispiloba Complex

Observations of specimens revealed two individuals that were clustering with *B*. *crispiloba* in Figure 10A because of similar values in three variables: phyllotaxy, strength of corolla curling, and exsertion length. However, these specimens separate from the rest of *B. crispiloba* based on a much longer androecium length (visible as the two longer outlier points in Figure 7, 'Androecium Length,' and 'Exsertion Length'), as well as a different leaf morphology.

Further Analysis of the Burmeistera sodiroana Complex

Collections in this complex are divided into three disjunct geographical regions within Ecuador: 1) eastern Andes, 2) central-western Andes, and 3) northwestern Andes. Further univariate analysis PCA was performed only on these specimens (not shown). Northwestern specimens are differentiated from eastern and central-western specimens by their phyllotaxy (distichous vs. spiral), fruit color (dark violet to "black" vs. white to pale violet), and larger, non-reducing fertile leaves. Both northwestern and eastern groups have shorter androecium lengths than central-western specimens.

Further Analysis of the Burmeistera succulenta Complex

Within the *B. succulenta* complex, specimens were divided into two groups that facilitated analysis: 1) specimens from Ecuador, and 2) specimens from Colombia and Venezuela. Specimens collected in Ecuador have significantly smaller flowers than those collected in Colombia and Venezuela. Univariate analysis of these specimens, focused on floral characters, was performed on these two groups (Figure 11). Calyx lobe length, a character used to differentiate the *B. succulenta* complex from *B. crispiloba* and *B. sodiroana*, does not differ significantly between the two geographic groups in *B. succulenta*. However, androecium length, exsertion length, and anther tube length were all significantly shorter in the Ecuadorian specimens. The group of Ecuadorian specimens was further divided into two groups, one on each side of the Andes, based on differences in androecium length, pubescence, and latex color.

DISCUSSION

In this study we perform several phases of analyses in order to tease apart and resolve multiple taxonomic issues in the recurved corolla clade of *Burmeistera*. Molecular work proposed four species in this clade (Uribe-Convers et al. 2017), though questions about the identity of *B. toroensis* led us to work with the three species recognized by established pre-molecular taxonomic perspectives: *B. crispiloba, B. sodiroana,* and *B. succulenta*. We first confirmed that trait differences distinguish these species complexes from each other. Afterwards, we analyzed each species complex to resolve taxonomic issues identified therein.

Univariate Analysis of Recurved Corolla Clade

Univariate analysis of the three species complexes that make up the recurved corolla clade (RCC) of *Burmeistera* roughly supports Jeppesen's (1981) species delimitations. The widespread *B. succulenta* complex is readily differentiated from the combined *B. crispiloba / B. sodiroana* complex by its long, linear to ligulate sepals that usually extend beyond the corolla opening of flowers at anthesis. However, within the *B. succulenta* complex, measurements of important floral traits vary widely, which indicated a need for further analysis, discussed in a seperate section below.

Unlike the *B. succulenta* complex, the *B. crispiloba* and *B. sodiroana* complexes are more difficult to differentiate from one another. Visual inspection of Figure 7 reveals substantial overlap in many floral measurements, even if statistical tests result in a significant difference between each species for those measures (Table 2). Additionally, the presence of specimens with a mix of traits of the two complexes, occurring at the boundary of their ranges, complicates the clear identification of either species. Away from these intermediate zones, though, the species are more easily differentiated by phyllotaxy, strength of corolla curling, and measurements of androecium length, exsertion length, and anther tube length. Our univariate analyses motivated us to perform further morphometric analysis on a combined *B. crispiloba / B. sodiroana* complex, discussed below.

Principal Component Analysis and Clustering of the Burmeistera crispiloba / Burmeistera sodiroana Complex

Visual analysis of the PCA results suggests support of the separation of a conservative *B. crispiloba* and *B. sodiroana* (Figure 8). Specimens of *B. crispiloba* are distinguished from *B. sodiroana* by having distichous phyllotaxy, a longer anther tube and exsertion length, as well as a stronger degree of corolla curling. Specimens in the *B. sodiroana* group, on the other hand, have spiral phyllotaxy, smaller fertile leaves, wider sepals, a wider anther tips opening, and occur at a higher altitude. Fruit color also helps differentiate the two species: *B. succulenta* have cherry red to maroon mature fruits, while *B. sodiroana* have pale violet fruits, although this trait is not completely consistent. Of these traits, phyllotaxy readily and consistently differentiates the two groups, though it is not a character that was previously used to separate them.

Difficulty arises, however, when examining the intermediate specimens (Figure 5). These specimens always exhibit distichous phyllotaxy, allying them with *B*. *crispiloba*, and, although flower size varies widely, they tend to be larger than those of *B*. *sodiroana* and more similar to *B*. *crispiloba*. On the other hand, leaf morphology and flower colors are much more similar to *B*. *sodiroana*. In addition, fruits of these

intermediates are often described as pink, not quite matching those of *B. crispiloba* or *B. sodiroana*, but in their shape are more similar to *B. crispiloba*. Intermediates are also identifiable by having somewhat larger leaves, which do not diminish in size when subtending flowers (i.e. the 'fertile' leaves), as do those of *B. sodiroana* and *B. crispiloba*. Furthermore, these intermediates occur geographically where hybridization is possible, at the intersection of the ranges of both *B. crispiloba* and *B. sodiroana*. The placement of these specimens in PCA space suggests that they represent introgressed or hybrid individuals; a handful are found in the PCA space of *B. crispiloba*, largely because of the larger size of the flowers of these specimens, but the majority are found between *B. sodiroana* and *B. crispiloba* (Figure 8A).

We employed unsupervised hierarchical clustering on principal components (HCPC) on the combined *B. crispiloba / B. sodiroana* complex to test if our visual analysis could be supported with data-centered cluster analysis. Unsupervised HCPC corroborates our *a priori* defined groups—two species with a third intermediate group— by selecting three clusters that roughly match these *a priori* identified groups (Figure 10A). However, the question remains of what to do taxonomically with these intermediate specimens. In this study, we choose to take a conservative approach by placing these specimens with *B. crispiloba*. We hope to perform future molecular analyses on these species to test three potential hypotheses: 1) that these intermediate specimens a subpopulation of one species (either *B. crispiloba* or *B. sodiroana*) with introgressed genes of the other, due to rare and/or historical gene flow; 2) that these specimens represent recent (possibly first-generation) hybrids which form regularly

between the two species; or 3) that these specimens represent a hybrid species with some reproductive barriers between it and both parental species.

Further analysis of the Burmeistera crispiloba Complex

As discussed above, we choose to place specimens that are morphological intermediates of *B. crispiloba* and *B. sodiroana* with *B. crispiloba*. Intermediate specimens share an important diagnostic trait with *B. crispiloba*, distichous leaf phyllotaxy, and are more similar to *B. crispiloba* in flower size, fruit color and fruit shape. It is a choice that has some statistical merit, as forcing the HCPC function to select two clusters (a conservative approach of maintaining two taxonomic entities) places all of our *a priori* intermediate specimens with *B. crispiloba* (Figure 10B). We have also elected to keep another set of 4 specimens, which all have a comparatively long androecium and exsertion length, grouped with *B. crispiloba*, as they are otherwise very similar to *B. crispiloba* in flower color and strength of corolla curling.

Further Analysis of the Burmeistera sodiroana Complex

Herbarium observations and the three distinct geographic groupings of the *B*. sodiroana complex led us to compare traits between these groups. The three groups include specimens from: 1) eastern Andes, 2) central-western Andes, and 3) northwestern Andes. Specimen measurements revealed that flowers of the eastern group are slightly smaller than those of the central-western group. However, as this is the only trait differentiating these otherwise identical groups, we treat them as one species, *B*. sodiroana. On the other hand, the north-western group differs from the first two in more

characters. In some ways, specimens of northern group are morphologically similar to the intermediate specimens discussed above, with distichous phyllotaxy and larger fertile leaves not reducing. However, the flowers of this north-western group are smaller than those of the western group, rather than larger as are those of the intermediate group. In addition, fruits of the northern group have been described as dark violet to black with a yellow interior, versus the white tinged violet fruits of *B. sodiroana*, and the pinkish-red fruits of putative hybrids. For this reason, we have named this north-western group *Burmeistera melanocarpa* Mashburn.

Further Analysis of the Burmeistera succulenta Complex

Burmeistera succulenta has been understood as a widespread species ranging from Ecuador, through Colombia, into Venezuela. Our analysis initially revealed two distinct morphological groupings within the species, which were also geographically consistent. The two groups are identifiable by flower size, with specimens in Ecuador having a much shorter androecium, exsertion, and anther tube length than those in Colombia and Venezuela. Additionally, these Ecuadorian specimens do not have recurved corollas. A few specimens in Ecuador, though, are identifiable as the Colombian and Venezuelan *B. succulenta*, and these can be seen as the outliers in exsertion length in Figure 11.

The majority of Ecuadorian specimens previously identified as *B. succulenta* cannot be matched with *B. succulenta* because of the difference in floral traits mentioned above. Furthermore, many of these specimens exhibit hairs on the leaves or stems, while *B. succulenta* is entirely glabrous. These specimens can be further divided into two

species that correspond to their geographic distribution within Ecuador: 1) east of the Andes, and 2) west of the Andes. Eastern specimens have stems and undersides of leaves that are villose with flattened, translucent-white anfractuose (ribbon-like) hairs. Flowers are slightly longer, exserted 15–16 mm from the corolla opening, versus 12–15 mm in the western specimens. We have identified these specimens as *B. huacamayensis* Jeppesen, a species not in the recurved corolla clade, from central-eastern Ecuador. Western specimens formerly identified as *B. succulenta* are glabrous to puberulous with tan hairs, and have a trait unique among *Burmeistera*: bright yellow latex (vs. cream to white in most species). Thus, we have named this species Burmeistera kitrinaima Muchhala & Mashburn, from the Greek kitrinos, meaning 'yellow,' and aima, meaning 'blood.' A specimen of *B. kitrinaima* was recently included in a phylogeny of the genus (unpublished), and is placed sister to *B. cylindrocarpa* Zalhbruckner (1915: 533), also not in the recurved corolla clade. Thus, both morphological and molecular data identify these two species as unique from each other and from *B. succulenta*, which both lack recurved corolla lobes and fall outside of the clade of species with this trait.

CONCLUSIONS

Burmeistera is a taxonomically difficult group, and the species in the recurved corolla clade are no exception. Traits are often labile, and traits of taxonomic usefulness are difficult to identify. Those working on the taxonomy of the genus are regularly forced to choose between the recognition of broadly defined species with large amounts of morphological variation, or narrowly defined species with defining traits that are not as clear as they would like. This choice has been made in the history of the RCC with early

authors Zahlbruckner (1915) and Wimmer (1943) describing six species and three subspecific varieties. These species were subsequently synonymized into three, though it was hypothesized that even these three may in fact be one widespread and variable species (Jeppesen 1981; Lammers 1998). Our morphometric analysis of more than twohundred specimens examined traits between Jeppesen's (1981) and subsequent species concepts of three Burmeistera species in the RCC. Our results support the acceptance of the three names Jeppesen used—B. crispiloba, B. sodiroana, and B. succulenta—though in a reduced and clarified form. We identified specimens that were intermediate between B. crispiloba and B. sodiroana and showed, using PCA and Clustering Analysis, that these specimens group independently of B. crispiloba and B. sodiroana. However, we chose to place these intermediates with *B. crispiloba* until molecular work can be used to test hypotheses of gene flow. We identified a new species previously grouped with B. sodiroana: B. melanocarpa. Furthermore, we clarify the definition of B. succulenta, showing that the majority of specimens identified as *B. succulenta* in Ecuador are not *B.* succulenta nor are they in the RCC. Instead, those specimens east of the Andes are identified as B. huacamayensis, while those specimens west of the Andes are identified as a new species: B. kitrinaima. To prevent future confusion, we provide a key to the recurved corolla clade and commonly confused species.

TAXONOMIC KEY

1. Phyllotaxy alternate, spiral 5. <i>B. sodiroana</i>
1. Phyllotaxy alternate, distichous.
2. Calyx lobes more than 5 mm long.
3. Flowers > 45 mm long; androecium > 35 mm long, exserted > 25 mm from the
corolla opening
3. Flowers < 40 mm long; androecium < 30 mm long, exserted < 18 mm from the
corolla opening.
4. Stems and undersides of leaves villose with flattened, translucent-white
anfractuose hairs (rarely glabrous); latex white; leaves elliptic; calyx lobes
ligulate, green; androecium 29-30 mm long, exserted 15-16 mm from the corolla
opening2. B. huacamayensis
4. Stems and undersides of leaves glabrous, (rarely villose with translucent-tan
hairs); latex yellow; leaves ovate to ovate-lanceolate; calyx lobes linear, violet;
androecium 24–27 mm long, exserted 12–15 mm from the corolla
opening
2. Calyx lobes less than 3.5 mm long.
5. Androecium exserted 23–30 mm from the corolla opening; corolla lobes
strongly scrolling back at anthesis; fruits obovoid (rarely globose), cherry red
(rarely pink) 1. <i>B. crispiloba</i>
5. Androecium exserted 20-22 mm from the corolla opening; corolla lobes curled
back (not scrolling) at anthesis; fruits globose, dark violet to black 4. B. melanocarpa

TAXONOMIC TREATMENT

Burmeistera crispiloba Zahlbruckner (1915: 528). TYPE:—ECUADOR. Chimborazo:
"In silva subtropica vallis Pallatango," September 1891, Sodiro 91/24 (holotype, B, destroyed; isotypes, P [barcode] 00408884 digital image!, QPLS [bc] 210999 digital image!, W 1961-0017416 digital image!, W 1967-0015165 digital image!). Figures 12, 18A.

Burmeistera montana Wimmer (1932: 23). TYPE:—ECUADOR. Pichincha: "In silvis montis Corazón ad Cauzacotó," 2000 m, July 1882, *Sodiro 91/22* (holotype, B, destroyed; isotypes, P [barcode] 00408885 digital image!, W 1963-0012270 digital image!)

Burmeistera succulenta var. *breviloba* Wimmer (1968: 836). TYPE:—ECUADOR. Pichincha: San Carlos de los Colorados, 150 m, 28 September 1935, *Schultze-Rhonhof 1929* (holotype, B [barcode] 10 0158362 digital image!)

Scandent herbs, to 5 m long. *Latex* cream to tan. *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; blades, when sterile 90–160 × 25–55(–70) mm, when fertile reducing to $55-105 \times 15-40$ 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 camptodromous, 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– $13 \times 5-9$ mm, obconical, green to green tinged violet, glabrous; calyx lobes ca. 1×2 mm, deltate, green, glabrous, the margin entire, the apex acute, ascending at anthesis; corolla exterior entirely green to green tinged violet, glabrous, the interior white to pale blue-green; corolla tube 6–8 mm wide basally, the throat narrowing to 2–3 mm wide, glabrous; corolla lobes lanceolate, strongly scrolling back, the two dorsal lobes $20-25 \times$ 2–4 mm, opening dorsally 15–23 mm from the corolla base, the two lateral lobes $17-18 \times$ 2-3 mm, the ventral lobe ca. 16×3 mm, opening ventrally 11-14 mm from the corolla base; and roccium 35-48(-57) mm long, exserted 23-30(-44) mm from the ventral opening, the filament tube green to green tinged violet, glabrous to villose distally, the anther tube $8-12 \times 2.5-4$ 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. 30×30 mm, obovoid to pyriform, spongy, inflated, maturing cherry red, rarely white tinged pink or violet.

Distribution and habitat:—A common terrestrial herb in wet tropical forests of western Ecuador. Found at low elevations near the coast, though more common from 500–1500 m in the foothills of the eastern Andes. Sometimes found at elevations up to 2000 m.

Similar species:—Both *B. crispiloba* and *B. succulenta* exhibit the strong scrolling of the calyx lobes at anthesis, in which calyx lobes scroll back multiple times (see Figure 5A). However, *B. succulenta* is differentiated by its longer calyx lobes (8–18 mm long), compared with the shorter (ca. 1 mm long), deltate calyx lobes of *B. crispiloba*. The few specimens of *B. crispiloba* that do not exhibit an obvious reduction of leaf size when flowering can be confused with *B. sodiroana*, however, all specimens of *B. crispiloba* can be readily identified by their distichous phyllotaxy, compared to the spiral phyllotaxy of *B. sodiroana*. In addition, the corollas of *B. crispiloba* scroll more than those of *B. sodiroana*, which simply curl back.

Discussion:—Intermediate specimens between *B. crispiloba* and *B. sodiroana* suggest that these two species hybridize or introgress where their ranges meet in the eastern 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. In this study, intermediate specimens are placed with *B. crispiloba* until molecular work on the group can test hypotheses of gene flow between these species. In addition, 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 exsertion 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.

The specific epithet likely refers to the strongly scrolling/curling (Latin: *crispus*) corolla lobes, a distinctive feature of the species.

Additional Specimens examined:-ECUADOR. Bolívar: Hacienda Changuil, sector La 47, 400 m, 02°06'S 79°10'W, 01 August 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, 02°33'25"S 79°21'59"W, 25 May 2005, Vargas & Defas 5585 (MO). Carchi: Alrededores de Maldonado, 90 km al oeste de Tulcan, 1500 m, 05 September 1981, Balslev 1996 (QCA); Maldonado, banks of small stream just N of the village, 1500 m, 04 October 1981, Werling & Leth-Nissen 233 (QCA); Maldonado, Chical trail, 1500 m, 26 January 1977, Boeke 842 (MO, NY, QCA); Near Maldonado, 1400 m, 30 July 1989, van der Werff & Gudiño 10767 (MO). Cotopaxi: Cantón Pujilí, Reserva Ecológica Los Ilinizas, Sector II, Sector Sur, sector Chuspitambo, al occidente de Choasilli, 1727 m, 00°58'42"S 79°06'22"W, 03 August 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, 00°58'45"S 79°06'53"W, 08 August 2003, Silverstone-Sopkin et al. 9965 (MO); Cantón Sigchos, falda del Cerro Azul, lado sur del Cerro, ca. 1.5 horas de las parcelas, 3297 m, 00°35'53"S 78°50'26"W, 25 July 2003, Ramos et al. 6546 (MO); Cantón Sigchos, Reserva Ecológica Los Ilinizas, ca. 4 km antes de Saguambi, en la vía Triunfo Grande-Las Pampas, 2156 m, 00°29'35"S 78°59'37"W, 13 August 2003, Ramos et al. 7305 (MO); Reserva Otonga, entre Quito y Sto. Domingo, cerca de San Francisco de las Pampas, 1990–2200 m, 00°25'S 79°00'W, June 1997, Nowicki & Mutke 1498 (QCA); Tenefuerste, Río Pilalo, km 52-53, QuevadoLatacunga, 750–900 m, 29 October 1981, Dodson & Dodson 12000 (MO); Tenefuerste, Río Pilalo, km 52–53, Quevado, Latacunga, 750–1300 m, 21 February 1982, Dodson & Gentry 12782 (MO). Esmeraldas: New road under construction from Lita to San Lorenzo, 600-800 m, 00°58'N 78°35'W, 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, 00°21'N 79°44'W, 25 March 1995, Clark & Troya 499 (MO). El Oro: Cantón Pinas, parroquia Moromoro, Reserva Ecologica Buenaventura, remnant patch of forest south of Entrada la Virgin, 900-1000 m, 03°39'03"S 79°44'24"W, 12 May 2003, Clark et al. 7944 (QCA); Pinas, Parroquia El Placer, Reserva Buenaventura, propiedad de la Fondacion Jocotoco, recorrido desde la estacion hasta el bosque Puma, 1000 m, 03°38'41"S 79°45'46"W, 03 April 2005, Vargas et al. 5171 (MO); West of Pinas 10 km on new road to Sta. Rosa, 950 m, 08 October 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, 02°27S 79°35W, 31 December 1991, Cerón 17925 (MO). Imbabura: 1390 m, 00°18.066'N 78°46.979'W, 16 April 2003, Muchhala 207 (QCA). Loja: Finca of the Calderón family, taking a trail NE from Mercadillo towards the crest, 1770 m, 04°00'S 79°57'W, 12 August 2000, Cotton et al. 1605 (MO, NY). Los Ríos: Río Palenque Science Center, km 56, road Quevedo-Sto. Domingo, 150-220 m, 30 November 1978, *Dodson 7310* (MO). Pichincha: Along road and trail from Maquipucuna Lodge to Ecolodge Santa Lucia, 2 km N of Maquipucuna entrance, 1400 m, 00°07'19"N 78°37'06"W, 15 March 2006, Croat et al. 95948 (MO); Bosque Integral Otonga, 1676 m, 00°25.148'S 78°59.567'W, 04 July 2002, Muchhala 115 (QCA);
Cantón Quito, Maquipucuna Biological Reserve, 9 km NE of Nanegal, 1500–1700 m, 00°10'N 78°40'W, 02 February 1991, Neill et al. 9800 (MO); Carretera Quito a La Concordia via Nono, Mindo, San Jose de las Minas y Puerto Quito, km 77, 1300 m, 07 August 1984, Dodson et al. 15196A (MO); Carretera Quito-Puerto Quito, km 113, 10 km al N de la carretera principal, 800 m, 00°05'N 79°02'W, 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, 02 February 1985, Dodson & Neill 15584 (MO, NY); Centinela, Canton Sto. Domingo, 12 km E of Patricia Pilar, along path on ridge line, 600 m, 23 August 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 Mantañas de Ila, 650 m, 30 July 1984, Dodson et al. 14661 (MO, NY); Centinela Ridge, 12 km E of Patricia Pilar on road to 24 de Mayo, 600 m, 26 June 1985, Stein & Dodson 3091 (MO); Cooperativa Santa Marta #2, along Rio Verde, 2 km SE of Sto. Domingo de Los Colorados, 530 m, 05 February 1979, Dodson 7433 (MO); El Centinela, 12 km E of Patricia Pilar on road between Santo Domingo and Quevedo, 650 m, 15 July 1979, Fallen & Dodson 858 (MO); From path following ridge line at El Centinela at crest of Montanas de Ila on road from Patricia Pilar to 24 de Mayo at km 12, 600 m, 28 July 1979, Dodson 5628 (MO); Maquipucuna, 5 km E of Nanegal, transect no. 2, 1630 m, 00°07'N 78°37'W, 09 May 1990, Gentry et al. 69945 (MO); Maquipucuna Tropical Reserve, northern boundary of reserve, 10 km N of Nanegalito, 1200 m, 00°10'N 78°35'W, 02 December 1988, Neill et al. 8654 (MO); Nanegalito-Tandayapa road, 1890–2400 m, 00°03-05'S, 78°44'W, 07 November 1989, Luteyn & Tirira 13333 (NY); Old road Santo Domingo-Chiriboga-Quito, ca. 3 km from bridge over Río Pilatón, 1000 m, 17 March

1985, Harling & Andersson 23062 (NY); Old road from Santo Domingo to Quito, ca. 5 km from paved highway, 1200 m, 00°15'S 78°55'W, 03 May 1985, Stein et al. 2686 (MO); Parroquia Nanegal, Cerro Campana, 5–6 km airline E of Nanegal, rigdge between Quebreda Cariyacu and Q. Loreto, 1700 m, 00°09'N 78°37'W, 01 September 1993, Webster & Paradise 30017 (MO); Parroquia Puerto Quito, Reserva Forestal de ENDESA, 10 km al norte de Alvaro Pérez Intriago, 650–800 m, 00°03'N 79°07'W, 11 June 1990, Cerón & Avala 10082 (MO); Quito Cantón, Nanegal, Reserva Biológica Maquipucuna, 1200–1700 m, 00°08'N 78°35'W, 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, 00°05'N 79°02'W, 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, 00°05'N 79°02'W, 16–17 November 1989, Luteyn & Borchsenius 13363 (MO, NY, QCA); Reserva Forestal de ENDESA, Río Silanche, 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, 00°05'N 79°02'W, 26 March 1984, Jaramillo 6611 (QCA); Reserva Orquideológica El Pahuma, carretera Calacalí-Los Bancos, km 22, 2000 m, 00°01'42"N 78°37'50"W, 19 October 1999, Rojas et al. 391 (MO); Road Nono-Pacto-Río Yacuambi, 5-10 km above Nanelagito, 1700 m, 00°00'N 78°40'W, 21 July 1980, Holm-Nielsen et al. 24419 (MO, NY); West of Santo Domingo de los Colorados 20 km, 1000 m, 30 October 1961, Cazalet & Pennington 5207 (NY). Los Ríos: Hacienda Clementina, Cerro Samama, trail between Destacemento Pita and La Torre, 600 m, 01°30'S 79°19'W, 24 October 1995, Knudsen et al. 459 (QCA). Manabí: Machalilla National Park, San Sebastian, 8–9 km

SE of Agua Blanca, 550–730 m, 01°36'S 80°42'W, 19 January 1991, *Gentry et al. 72409* (MO).

2. Burmeistera huacamayensis Jeppesen, Fl. Ecuador 14: 22, fig. 1B-C. 1981. TYPE:
Ecuador. Napo: Cordillera Guacamayo, slope towards Urcusiqui, 27 Oct. 1939 (fl., fr.),
E. Asplund 9580 (holotype, S-04-899 digital image!; isotype, NY [barcode] 548037!).
Figures 13, 18B.

Scandent herbs, up to 1 m long. Latex white. Stems ca. 4 mm in diameter, terete, green, sometimes with violet striations, glabrous to villose. Leaves alternate, distichous, often bullate, the internodes 15–35 mm long; petioles 2–8 mm long, green, sometimes tinged violet, villose; lamina $55-155 \times 15-30$ mm, elliptic to lanceolate to oblanceolate, the base obtuse, the apex attenuate to caudate, $5-15(-25) \times 1-2$ mm, the margins shallow callose-serrate to crenate, the teeth often intramarginal; adaxial surface green, sometimes lightly tinged violet, glabrous, nitid; abaxial surface green suffused with violet, especially along the veins, villose along the primary vein only or along all veins with flattened, translucent-white anfractuose hairs; venation camptodromous, the secondary veins sometimes terminating in marginal teeth, the primary and secondary veins prominent, slightly raised but flattened, the tertiary veins visible. *Flowers* 33–38 mm long, solitary; pedicels 30–75 mm long at anthesis, 30–90 mm long in fruit, glabrous to sparsely villose, green, sometimes becoming violet distally; hypanthium $5-9 \times 4-8$ mm, obconical, green, glabrous to sparsely villose, the ridges slightly raised; calyx lobes $(5-)7-16 \times 0.5-3$ mm, linear to ligulate, green spotted with violet, glabrous to sparsely villose, the margin entire, the apex acute, ascending to patent at anthesis; corolla green to green tinged maroonviolet, glabrous (rarely very sparsely pubescent); corolla tube 3–4 mm wide basally, the throat narrowing to 2–3 mm wide; corolla lobes lanceolate, lighter green inside, the margins smooth, the two dorsal lobes $11-13 \times 3$ mm, opening dorsally 15–20 mm from the corolla base, slightly falcate, the two lateral lobes $10-11 \times 3-4$ mm, opening ventrally 12–15 mm from the corolla base, slightly falcate; androecium 26–32 mm long, exserted 13–16 mm from the ventral opening, the filament tube green, glabrous basally, glabrous to sparsely villose distally, the anther tube ca. 6×3 mm green, sometimes violet along the sutures, villose basally, the three dorsal anther tips glabrous to sparsely pubescent, the two ventral anther tips densely villose with white hairs; the style and stigma green, the stigma lobes densely pubescent along the margin with short white hairs. *Fruits* ca. 15×20 mm, globose, spongy, slightly inflated, maturing white or pink.

Distribution and habitat:—Known from the eastern Andes of Ecuador in Napo province, with a few collections to the south in Pastaza and Morona Santiago Provinces. Found in high humidity primary forest and along river banks from 900–2300 m in elevation.

Similar species:—*Burmeistera succulenta* has similar calyx lobes to *B. huacamayensis*, but is entirely glabrous, has much longer flowers (45–53 mm vs. 33–38 here), and has not been found in the eastern Andes of Ecuador. *Burmeistera kitrinaima* also has similar calyx lobes, though they are thinner at the base. Most *B. kitrinaima* specimens are glabrous; those with hairs exhibit a similar structure, though they are tan instead of

entirely translucent-white. Additionally, the latex of *B. kitrinaima* is bright yellow (vs. white here).

Discussion:—All known specimens from east of the Andes in Ecuador that have, until now, been identified as *B. succulenta* have now been transferred to *B. huacamayensis*. Notes left on specimens of *D'Arcy 14100* (MO) and *Luteyn 13463* (MO) by Thomas Lammers (UW-Oshkosh) mentioned the inability to key them to species using Jeppesen (1981), and identified the unusual pubescence of the species. Possibly, Lammers was unable to identify these specimens using Jeppesen's (1981) key because of their calyx lobe morphology: Jeppesen's (1981) key identified *B. huacamayensis* as having reflexed or patent calyx lobes, while these specimens have ascending calyx lobes. All but two specimens examined were collected after the publication of Jeppesen's Flora of Ecuador treatment. These specimens have improved our understanding of the morphology species, including calyx lobe position.

Additional Specimens examined:— ECUADOR. Morona Santiago: Gualaquiza Cantón, Cordillera del Cóndor, Cuangos, 20 km east of Gualaquiza, near disputed Peru-Ecuador border, 1500–1600 m, 03°29'S 78°14'W, 17 Jul. 1993, *Gentry 80025* (MO); Trail Kenkuim to Jordán, 15–20 km E of Macas, 1000–1200 m, 02°18'S 77°58'W, 23 Aug. 1996, *Ståhl et al. 2915* (QCA). **Napo:** A 8 km al occidente de Pacto, faldas de Volcán Sumaco, km 40 del carretero Hollín Loreto, partiendo del Campamento Damnificados del Chaco, 1800 m, 00°50'S 77°40'W, 24 Aug. 1989, *Jaramillo et al. 10943B & 10944B* (QCA); Along road between Baeza and Tena ca. 40 km N of

Archidona, 2000 m, 00°41'S 77°41'W, 07 Oct. 1980, Croat 50515 (MO); Archidona Cantón, Parque Nacional Napo-Galeras, Cordillera de Galeras, sendero hacia Huamaní, 1000–1650 m, 00°39'S 77°31'W, 16 Mar. 1997, Alvarez et al. 1619 (MO); Between Tena and Papallacta, 12 January 1981, D'Arcy 14100 (MO); Carretera Cotundo-Coca, 15 km al E de la carretera Baeza-Tena, faldas de Volcán Sumaco, 1300 m, 00°40'S 77°40'W, 13 Feb. 1987, Neill & Palacios 7626 (MO, QCA); Cloud forest 44-45 km by road N of Tena, 1190–1220 m, 00°43'S 77°52'W, 16 Aug. 1978, Webster 23254 (MO); Localidad Codo Alto, en las márgenes del Río Granadilla, 1980 m, 00°03'S 77°49'W, 14 Sep. 1990, Jaramillo et al. 12728 (QCA); North slopes of Cordillera de Guacamayos, ca. 10 km above Cosanga, 2 km below pass, 2150 m, 00°40'S 77°53'W, 27 April 1985, Stein 2641 (MO, QCA); Private property of William Philips, ca. 2 hrs. walk from end of road, W of Cosanga, N slopes of Cordillera de Huacamayos, 2400 m, 00°45'S, 77°55'W, 12 December 1989, Luteyn 13463 (MO, NY, QCA); Reserva Yanayacu, 2100 m, 00°35.3'S 77°52.8'W, 09 August 2002, Muchhala 163 (QCA); Reserva Yanayacu, on stream trail, 2100 m, 00°35.3'S 77°52.8'W, 29 July 2010, Muchhala 462 (QCA); S slope of Cordillera de Guacamayos, new road Cotunda-Coca, 3 to 5 km from turn-off of Baeza-Archidona road, 1150 m, 01°52'S 77°48'W, 11 Jun. 1985, Stein 3062 (MO, NY, QCA); Sierra Azul, Agrícola Industrial Río Aragón, campamento San Fernando, 2250 m, 00°41'S 77°55'W, 20 June 1992, Alvarez et al 515 (MO); Trail down-slope from Lago Agrio-Baeza road, ca. 5 km N of town of Reventador, 1350 m, 00°05'S 77°35'W, 16 Jun. 1985, Stein 3070 (MO, QCA). Pastaza: Cantón Mera, Parroquia Shell, road to Río Anzu and beyond, south of the town Mera, 1450–1550 m, 01°25'45"S 78°05'15"W, 06 May 2003, Clark et al. 7777 (QCA); East 0.4 km on new road to Río Bobonaza, leaving PuyoMacas road at km 15, 1050 m, 01°35'S 77°53'W, 08 Jun. 1985, *Stein 3015* (MO); Hacienda San Antonio de Baron von Humboldt, 2 km al NE de Mera, 1100 m, 01°27'S 78°06'W, 27 Feb.–19 Mar. 1985, *Neill et al. 6089* (MO, NY, QCA); Parque Omaere, Puyo, 900 m, Jul.–Aug. 1996, *Blanc et al. 96-86* (QCA).

3. Burmeistera kitrinaima Muchhala & Mashburn sp. nov. Type:—ECUADOR.
Pichincha: Reserva Florística "Río Guajalito," km 59 de la carretera antique Quito-Santo
Domingo de los Colorados, a 3.5 km al NE de la carretera, estribaciones occidentales del
Volcán Pichincha, 1800–2200 m, 00°13'53"S 78°48'10"W, 29 June 1991, Jaramillo &
Grijalva 13651 (holotype, QCA barcode 195853!; isotypes, MO 5700737!, NY barcode
1185767!). Figures 14, 18C.

Diagnosis:—This new species is distinguished from other *Burmeistera* by the combination of yellow latex, ascending, narrow, linear, calyx lobes, flowers 33–38 mm long, ovate to ovate-lanceolate leaves without a significant drip tip (< 5 mm long), and, when present, translucent-tan hairs.

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 hairs; blades $50-135 \times 20-75$ 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 brochidodromous, the primary and secondary veins prominent, raised, the tertiary veins visible. Flowers 30-34 mm long, solitary in the upper leaf axils; pedicels 50–100 mm long at anthesis, 80–105 mm long in fruit, green to violet, glabrous (rarely villose); hypanthium $6-7 \times 5-8$ mm, obconical, green suffused with violet, glabrous (rarely sparsely villose), the ridges smooth or slightly raised; calyx lobes $6-13 \times$ 0.5-1.5 mm, ascending at anthesis, linear, exterior violet, interior green suffused with violet, 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 $14-17 \times 3-4$ mm, opening dorsally 14-18 mm from the corolla base, falcate, the two lateral lobes $10-16 \times 3$ mm, falcate, the ventral lobe ca. 6×2 mm, opening ventrally 11–13 mm from the corolla base; androecium 24-27 mm long, exserted 12-15 mm from the ventral opening, the filament tube green with tan striations, sometimes speckled violet, glabrous or distally puberulous, the anther tube $5-6 \times 3-4$ 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.

Distribution and habitat:—Known from the western side of the Andes in central Ecuador. Specimens are found as low as 600 m elevation, though most come from high elevation cloud forests from 1500–2500 m.

Etymology:— The name comes from the Greek *kitrino*, meaning 'yellow,' and aima, meaning 'blood,' in reference to the unique bright yellow latex of this species.

Similar species:—This new species 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 (30–34 mm long vs. 45–53 mm long in *B. succulenta*). *Burmeistera huacamayensis* has similar sized flowers as *B. kitrinaima*, however it also has flattened translucent-white hairs (vs. tan, when present, here), and elliptic leaves with long (10–25 mm) drip tips. If live plants are available, *B. kitrinaima* can be differentiated from either *B. succulenta* or *B. huacamayensis* by the presence of yellow latex (vs. white in the latter species).

Discussion:—The inclusion of a sample of *B. kitrinaima* in a recent molecular phylogeny (unpublished) reveals that this species is closely related to *B. cylindrocarpa, Burmeistera tenuiflora* Donnel Smith (1895: 147), and *Burmeistera smaragdi* Lammers (2002: 213).

Additional Specimens examined:—ECUADOR. Bolívar: Road Guaranda-Caluma, km
53, 1100 m, 01°35'S 79°11'W, 29 July 1996, *Ståhl & Knudsen 2901* (QCA). Cotopaxi:
Reserva Otonga, entre Quito y Sto. Domingo, cerca de San Francisco de las Pampas,

1990–2200 m, 00°25'S 79°00'W, June 1997, *Nowicki Mutke 1479* (QCA). Pichincha: Bosque Integral Otonga, 2228 m, 01°25.099'S 79°0.71W, 05 July 2002, Muchhala 119 (OCA); Cantón Ouito, nueva carretera Calacalí-Nanegalito, km 20, 1800–2000 m, 00°02'N 78°03'W, Hurtado et al. 1419 (MO); Northwest slopes of Volcán Pichincha, Quito-Nono-Mindo road, 5 km N of Mindo, 1500 m, 00°02'S 78°50'W, 29 April 1989, Niell et al. 8942 (MO); Parroquia Nanegalito, western slopes of Cerro Negro, 2.5–3 km airline NE of Nanegalito, 1900 m, 00°04'N 78°39'W, 8 September 1993, Webster et al. 30455 (MO); Reserva Bellavista, 2215 m, 00°0.814'S 78°41.083°W, 11 July 2002, Muchhala 128 (QCA); Reserva Bellavista, 2229 m, 00°0.819'S 78°41.418°W, 12 July 2002, Muchhala 130 (QCA); Reserva Florística Río Guajalito, Las Palmeras, 1800–2100 m, 00°14'S 78°49'W, May 1997, Nowicki & Mutke 1193 (QCA); Reserva forestall ENDESA, corporación forestall Juan Manuel Durini, km 113 de la carretera Quito-Puerto Quito, 600 m, 05 June 1986, Sigcha 28 (QCA); Reserva Maquipucuna, 1807 m, 00°5.866'S 78°37.455'W, 10 July 2002, Muchhala 125 (QCA); Reserva Río Guajalito, 1900 m, 00°14.9'S 78°48.2'W, 19 June 2010, Muchhala 447 (QCA); Reserva Río Guajalito, on Argentino trail, 2045 m, 00°14.3611'S 78°48.214'W, 25 June 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, 00°12'S 78°39'W, 26 September 1987, Buitrón 253 (QCA). Santo Domingo: Nearest city Quito, near footbridge by Río Quajalito Science Centre, 1802 m, 00°13'50"S 78°49'15.4"W, 26 October 2010, Antonelli 602 (QCA).

4. Burmeistera melanocarpa Mashburn, sp. nov. TYPE:—ECUADOR. Carchi: Tulcán-Maldonado road, 45 km W of Tufiño, 2425 m, 13 April 1978, Luteyn & Lebron-Luteyn
5750 (holotype, QCA [barcode] 26985!; isotypes, MO 5700007!, NY!). Figures 15, 18D.

Diagnosis:—This new species is distinguished from other *Burmeistera* by its distichous phyllotaxy, elliptic leaves that do not reduce when flowering, flowers with dark violet anther tubes, and fruits maturing dark violet.

Scandent herbs, up to 4 m long. Latex white. Stems ca. 4 mm in diameter, green to violet, glabrous, striate when dry. Leaves alternate, distichous, the internodes 20-40 mm long; petioles 4-11 mm long, green to green suffused with violet, glabrous; blades 60- $160 \times 25-60$ mm, elliptic, the base obtuse, the apex acuminate to caudate, $6-10 \times 1-3$ mm, the margins shallow callose-serrate, sometimes tinged violet; upper surface green to green tinged dark violet, the primary and secondary veins sometimes tinged dark 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, 37–47 mm long; pedicels 100–130 mm long at anthesis, 100–140 mm long in fruit, green to violet, glabrous; hypanthium 10–13 \times 5–7.5 mm, obconical, dark violet, glabrous; calyx lobes 1.5–3 \times 1.5–2.5 mm, deltate, dark violet, glabrous, the margin entire or with few callose-tipped teeth, ascending at anthesis; corolla green streaked with dark violet to entirely maroon-violet, glabrous; corolla tube 5–6 mm wide basally, the throat narrowing to 3-4 mm wide; corolla lobes

lanceolate, the margins smooth, the two dorsal lobes $16-18 \times 3-4$ mm, opening dorsally 16-17 mm from the corolla base, ascending, the two lateral lobes $11-15 \times 3-4$ mm, falcate, the ventral lobe ca. 12×4 mm, opening ventrally 11-14 mm from the corolla base; androecium 33-36 mm long, exserted 20-22 mm from the ventral opening, the filament tube dark violet, glabrous, the anther tube $9-11 \times 4-5$ mm, dark violet, glabrous, all five anther tips sparsely to densely villose; the stigma violet, upper and lower margins barbate. *Fruits* 30×25 mm, globose, pendent, fleshy, spongy, the exterior dark violet, nearly black, the interior yellow.

Distribution and habitat:—Found in a narrow range in the Carchi province of Ecuador, parroquia Maldonado, bordering Colombia. Specimens have been collected in cloud forests from 2100–2700 m in elevation.

Etymology:—The specific epithet comes from the Greek *melas*, meaning 'black, dark,' and *karpós*, 'fruit,' in reference to the unique dark-violet, nearly black, mature fruits.

Similar species:—This species is most similar to *B. sodiroana* in its leaf shape and uniformly dark violet anther tube. However *B. melanocarpa* is differentiated by having distichous phyllotaxy, non-reducing fertile leaves, and dark violet fruits. Some specimens of *B. crispiloba* are vegetatively similar to *B. melanocarpa*. However, *B. melanocarpa* is differentiated by its dark violet fruits (vs. pink to cherry red in *B. crispiloba*), generally smaller flowers (37–47 mm long vs. 44–58 mm long in *B. crispiloba*), and non-reducing fertile leaves. **Discussion:**—Morphological similarity with intermediate specimens of *B. crispiloba / B. sodiroana* suggests this species may also be the result of hybridization or introgression between *B. crispiloba* and *B. sodiroana*. However, no specimens of *B. sodiroana* and very few of *B. crispiloba* have been collected in areas near the narrow distribution of *B. melanocarpa*, where the species seems to be relatively abundant.

Additional Specimens examined:—ECUADOR. Carchi: Espejo, faldas del Cerro Golondrinas Hembra, 2300–2400 m, 00°51'N 78°07'W, 20 August 1994, *Palacios 12757* (MO); East of Maldonado 12 km on road to Tulcán, 2230 m, 27 September 1979, *Gentry* & *Shupp 26647* (MO); Road Tulcán-Maldonado, ca 13 km SE of Maldonado, 2600 m, 01 March 1974, *Harling & Andersson 12384* (MO); Trail from Machinas, 12 km above Maldonado, toward Planada de Chilma, Río Chilma Valley, 2350–2450 m, 00°52'N 78°03'W, 30 May 1985, *Stein 2911* (MO, QCA); Up small mountain SW of Rafael Quindis finca along small stream and descending mountain trail, 1930–2100 m, 00°52'N 78°08'W, 28 November 1987, *Hoover & Wormley 1850* (MO); Valle de Maldonado, km 71 on road Tulcán-Maldonado, 2100–2200 m, 00°54'N 78°06'W, 20 May 1973, *Holm-Nielsen et al. 6000* (NY, QCA); West of Tulcán 62–75 km, 2720–2460 m, 00°50'N 78°50'W, 07 January 1985, *Luteyn & Cotton 10882* (NY); West of Tulcán 78–82 km, 2040–2320 m, 00°50'N 78°50'W, 08 January 1985, *Luteyn & Cotton 10893* (NY). **5.** *Burmeistera sodiroana* Zahlbreckner (1915: 534). TYPE:—ECUADOR. Pichincha: Secus flumen Pilatón, 900–1600 m, *Sodiro 91/25* (holotype, B, destroyed; isotypes, P [barcode] 00408899 digital image!, W 1963-0012263 digital image!). Figures 16, 18E.

Burmeistera succulenta var. latisepala E. Wimm., Repert. Spec. Nov. Regni Veg. 29: 55.
1931, syn. nov. Type: Ecuador. Tunguruahua: In sylvis montanum Tunguragua, Dec.
1857 (fl.), R. Spruce 5119 (holotype, K [barcode] 250836 digital image!; isotypes, K [bc]
250837 digital image!, G [bc] 236671 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, destroyed; neotype, designated here, Ecuador. Pichincha: In reg. subtrop. pr. S. Florencio, s.d., *Sodiro 91/21* [neotype, P [barcode] 408898 digital image!]).

Burmeistera leucocarpa Zahlbr. 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, 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; blades when sterile $55-130 \times 30-50$

mm, when subtending a flower reducing to $(20-)30-50(-80) \times (5-)15-35$ mm, ovate to ovate-lanceolate, the base obtuse to rounded, the apex acuminate to caudate, $2-10 \times 2-4$ 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 long mm in fruit, green to violet, glabrous; hypanthium $8-13 \times 5-8$ mm, abruptly widening distally, obconical to cupuliform, green to violet tinged, glabrous; calyx lobes $1-5 \times 1-2$ mm, deltate, green, glabrous, the margin green or violet, entire or with few callose-tipped teeth, ascending at anthesis; corolla green to green tinged or streaked with maroon-violet; corolla tube 5–6 mm wide basally, narrowing to 2-4 mm wide, glabrous; corolla lobes lanceolate, sometimes curled back at anthesis, the interior dark violet, the margins smooth to undulate, the two dorsal lobes $12-14 \times 2-4$ mm, opening dorsally 14-18 mm from the corolla base, ascending to falcate, the two lateral lobes $10-13 \times 2-3$ mm, falcate, the ventral lobe ca. 7×3 mm, opening ventrally 9–12 mm from the corolla base; androecium 29–32(–36) mm long, exserted 19–20(–23) mm from the ventral opening, the filament tube green basally, becoming dark violet distally, glabrous, the anther tube 6.5–9 \times 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* 25×25 mm, globose, pendent, fleshy, spongy, white, maturing pink or white tinged with violet.

Distribution and habitat:—Found on the 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. Occurs in cloud forests from 1500–3200 m in elevation.

Similar species:—*Burmeistera sodiroana* resembles *B. crispiloba* and *B. melanocarpa*. It is differentiated from both by having spiral phyllotaxy and fruits maturing white tinged with violet (vs. pink, cherry red, or dark violet in the latter species).

Discussion:—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-Yánez 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 other collection *Sodiro 91/92*, though it is possible specimens exist at herbaria with large Sodiro collections, such as QPLS (Ecuador) or SI (Argentina). If this collection ever existed, it was likely destroyed in Berlin in WWII. 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). Thus, 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*.

Additional Specimens examined:—ECUADOR. Azuay: Cantón Camilo Ponce Enrique localidad Bella Rica-Villa Rica, 1096 m, 03°05'16.8"S 79°40'10.8"W, 31 March 2010, Jaramillo 30276 (QCA). Bolívar: Along road Chillanes-Yaquibusu, 2300 m, 20 July 1991, van der Werff et al. 12516 (MO). Cañar: El Triunfo, Cañar road, km 50 from El Triunfo, 1500 m, 02°29'S 79°05'W, 20 June 1979, Løjtnant & Molau 15174 (NY). Cotopaxi: Around Pilalo, 2400 m, 00°57'S 79°02'W, 07 March 1968, Holm-Nielsen & Jeppesen 1282 (MO, NY); Cantón Pilalo, camino a la cumbre del Cerro Puchuato, 1800-2500 m, 00°55'S 79°09'W, 05 December 1987, Cerón & Villavicencio 2798 (MO); Cantón Sigchos, Campo Alegre, a ca. 20 km al noreste de Sigchos, 2614 m, 00°35'03"S 78°47'36"W, Ramos et al. 5814 (MO); Cantón Sigchos, finca de Antonio Tigse, 3060 m, 00°35'43"S 78°49'55"W, 18 July 2003, Ramos et al. 6204 (MO); Carretera Latacunga-Pilaló-Quevedo, 5–10 km al este de Pilaló, 2400–2700 m, 00°55'S 79°00'W, 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, 00°57'S 78°14'W, 2500– 2870 m, 16 March 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). Napo: Along E side of R. Chalpi, 1–3 km from confluence with R. Oyacachi, 2600–2800 m, 00°15'S 77°58'W, 23 May 1996, Ståhl et al. 2564 (QCA); Along trail between Oyacachi and Pueblo Viejo (Old Oyacachi), 3000 m, 00°14'S

77°59'W, 24 May 1996, Ståhl et al. 2578 (QCA); Baeza, forest remnants, 1800–2000 m, 22 September 1977, Maas et al. 3035 (QCA); Between Tena and Pappalacta, 12 January 1981, D'Arcy 14101 (MO, NY); Between Tena and Pappalacta, 12 January 1981, D'Arcy 14092 (NY); Cantón Quijos, Unión del Río Blanco con Río Quijos, 00°28'S 78°03'W, 2680 m, 12 June 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, 00°40'12"S 77°55'01"W, 2200–2250 m, 12 February 2011, Tepe et al. 2955 (MO); Cantón Quijos, Baeza, parte alta del Río Machángara, 00°28'S 77°54W, 2200–2300 m, 9 May 1990, Palacios & Friere 4982 (NY); Carretero Papallacta-Baeza, Hacienda Flor del Bosque, 00°22'S 78°04'W, 14 December 1993, Friere-Fierro & Yánez 2673 (NY); Cosanga, stream just south of town, 00°36'S 77°52'W, 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 August 1980, Sobel & Strudwick 2522 (NY); Lago Agrio-Quito road, km 195, between Cuyuja and Papallacta, 2500 m, 00°22'S 78°05'W, 18 June 1985, Stein 3082 (QCA, MO); Parque Nacional Lllanganates, vía Salcedo-Tena, colecciones a lo largo del camino desde Los Carmelos-Río Ana Tenorio al Río Langoa, bosque de Neblina Montano, 00°58'17"S 78°15'14"W, 2600–2850, 18 February 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, 00°45'S 77°55'W, 12 December 1989, Luteyn & Cabo 13459 (NY, QCA); Quijos, Reserva Ecológica Antisana, Río Aliso, 8 km al suroeste de Cosanga, afluente del Río Aliso, margen derechoa a 1 km, 00°35'S 77°57'W, 2530 m, 12 November 1998, Vargas et al. 3003 (MO); Quito to Baeza, km 92, 1850 m, 30 June 1985, Dodson & Hirtz 15883 (MO); Reserva Yanayacu, collected on trail behind station heading towards Antisana, 2100 m, 00°35.3'S 77°52.8'W, 28 July 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, 00°37'S 77°52'W, 26 October 1976, Balslev & Madsen 10329 (NY); Road Baeza-Tena, km 24-29 from Baeza, S of Cosanga, 00°38'S 77°51'W, 2100-2300 m, 28 March 1979, Holm-Nielsen 16226 (QCA); Salcedo-Napo road, ca. 56–60 km E of Salcedo, 00°55'S 78°30'W, 2926–3060 m, 23 November 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 December 1979, Croat 49392 (MO); Ca. 5 km SW of San José de Niebli, 13 road km N of Calacalí, 2450 m, 00°02'N 78°32'W, 01 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 September 1986, Zak 1192 (MO); Carretera Sto. Domingo-Quito, 13 km al oeste del paso, Ceja Andina, 3000 m, 00°26'S 78°38'W, 21 June 1982, Balslev 2759 (NY); Cerro Corazón, 2438–2835 m, 05 January 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, 00°02'S 78°38'W, 10 September 2001, Friere-Fierro et al 3208 (MO); Cerro Pugsi, NW slope of Volcán Pichincha, on ridge crest, 3020 m, 27 September 1980, Bleiweiss 1142 (NY); Nanegalito-Tandayapa road, 1890–2400 m, 00°03-05'S, 78°44'W, 07 November 1989, Luteyn & Tirira 13328 (MO, NY); Reserva Bellavista, 2295 m, 00°0.67'S 78°41.285'W, 11 July 2002, Muchhala 129 (QCA); Reserva Orquideológica El Pahuma, carretera Calacalí-Los Bancos, km 22, 2000 m, 00°01'42"N 78°37'50"W, 26 October 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, 00°03'N 78°40'W, 21 May 1989, Smith 1975 (MO, NY, QCA); Route Tandayapa-Nanegalito, 2250 m, 00°00'S 78°40'W, 24 January 1996, Billiet & Jadin 6684 (MO); Old road Quito-Santo Domingo, between San Juan and Chiriboga, on steep slopes along road, 2700-2750 m, 00°17'S 78°40'W, 20 March 1979, Løjtnant & 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, 00°15–20'S 78°40–50'W, 04 February 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, 00°18'S 78°43'W, 14 December 1990, Lutevn et al. 14342 (NY); West slopes of the Cordillera Occidental, above Tandapi, 20-21 km from Alóag on road to Santo Domingo, 2650 m, 07 February 1985, Molau & Öhman 1156 (QCA). Tungurahua: Cantón Baño, Río Vascun Valley, northern slopes of Volcán Tungurahua, 2500–3200 m, 01°26'21"S 78°25'58"W, 27 April 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 November 1939, Asplund 9767 (NY); Cusatagua, Vicinity of Ambato, March 1919, Pachano 177 (NY); Parque Nacional Llanganates, entrando por Baquerizo Moreno hacia el sector de Lagartococha, 3270 m, 01°12'01"S 78°28'19"W, 01 March 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, 01°25'S 78°22'W, 3 June 1985, Stein 2945 (MO); Zona de amortiguamiento del Parque Nacional Llanganates, Machay, Río Verde,

colecciones entre Río Machay y Colina San Austín, 2090 m, 01°22'S 78°17'W, 30–31 July 1999, *Vargas et al. 3712* (MO). **Morona Santiago:** Between Tambo Consuelo and Tambo Cerro Negro, 2590–2895 m, 20–24 August 1945, *Camp E-4955* (NY).

6. *Burmesitera succulenta* Karsten & Triana (1856: 445). TYPE:—COLOMBIA. Quindío: Nouvelle-Grenade prov. De Mariquita, crescit circa "El Roble" in monte Quindio, 2000 m, 1851–1857, *Triana 1586* (lectotype, designated here, P barcode 00408903 digital image!). Figures 17, 18F.

Burmeistera succulenta var. *meiophylla* Zahlbr.ex Wimmer (1943: 143) TYPE:— VENEZUELA. Aragua: Tovar, *Karsten s.n.* (lectotype, designated here, COL barcode 000266968; isolectotypes, JE barcode 00000627 digital image!, JE barcode 00000628 digital image!)

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 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, 45–53 mm; pedicels 60–115

50

mm at anthesis, 110–125 mm 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 8–18 × 2–5 mm, ligulate, dark green, often suffused with violet, glabrous, the margin entire or with few callose-tipped teeth, the apex acute, ascending at anthesis; corolla exterior green to green suffused with maroon-violet, interiorly violet; 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, exserted 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. 20 × 20 mm, globose, fleshy, pink to violet.

Distribution and habitat:—A widespread species, ranging from the western slopes of the Andes in central Ecuador, through Colombia, into northwestern Venezuela. This species occurs in cloud forests from 1000–2500 m in elevation.

Similar species:—Vegetatively, some specimens of *B. succulenta* can appear similar to *B. melanocarpa* and *B. sodiroana*, but are easily differentiated by the calyx lobes, which are long (> 8 mm) in *B. succulenta*, and short (< 3 mm) in the other two. Strongly scrolling corolla lobes are present in both *B. succulenta* and *B. crisipiloba*, and the two

species have similar sized flowers. Again, *B. succulenta* is easily differentiated by long vs. short calyx lobes. *Burmeistera kitrinaima* and *B. huacamayensis* can have calyx lobes similar in size to *B. succulenta*, but both are differentiated by their much shorter flowers (30–38 mm long) compared to *B. succulenta* (45–53 mm long), as well as the absence of scrolling corolla lobes.

Discussion:—*Burmeistera succulenta* is the most widespread species in the recurved corolla clade, and currently the only one known from Colombia and Venezuela. The phylogeny of Uribe-Convers et al. (2017) shows *B. succulenta* as sister to *B. crispiloba*.

Selected Specimens examined:—COLOMBIA. Antioquia: Cordillera Central, ca. 60 km S of Medellin on main hwy. to Manizales, 1350 m, 05°50'N 75°44'W, 26 January 1986, *Stein & McDade 3303* (NY); Medellin-Cartagena Hwy., turnoff to Briceño, ca. 25 km N of Yarumal, 1800 m, 07°07'N 75°28'W, 07 February 1986, *Stein & Cogollo 3369* (NY); To 5 km down road to San Fermin de Briceño, W off Pan American Hwy., ca. 25 km N of Yarumal, 1525–1830 m, 07°01'N 75°35'W, 26 May 1984, *Luteyn et al. 10750, 10761 & 10773* (NY); To 5 km down road to San Fermin de Briceño, W off Pan American Hwy., ca. 25 km N of Yarumal, 1525–1830 m, 07°01'N 75°35'W, 22 May 1988, *Luteyn & Sylva 12418 & 12420* (NY). Amazonas: Departamento Río Negro, cerro de La Neblina Camp V, valley north base of Pico Cardona, 1250 m, 00°49'N 66°00'W, 21–24 March 1984, *Leisner & Stannard 16856* (NY). Caldas: San Clemente, edge of woods, 1800–2200 m, 16 September 1922, *Pennell 10685* (NY). Chocó: Ansermanuevo-San José del Palmar road, 2–5 km E of San José del Palmar, 1200–1500 m, 20 April

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, 04°40'N 76°25'W, 15 May 1984, Lutevn 10545 (NY); Bolívar-Quibdó road, ca. 37-40 km W of El Carmen, 671-1360 m, 05°40'N 76°15'W, 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, 03°28'N 76°37'W, 20 April 1989, Luteyn et al. 12557 (NY). ECUADOR. Azuay: Hacienda Yacopiana, on ridge bordering Río Patul, above Sanagüín, 850 m, 02 June 1943, Steyermark 52805 (NY). Bolívar: Road Echeandía-Guanujo, E of Echeandía, 2400 m, 01°25'S 79°07'W, 08 July 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). VENEZUELA. Aragua: Colonia Tovar, 1800–2000 m, December 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 January 1978, Luteyn & Lebron-Luteyn 5177 (NY). Yaracuy: Cerro La Chapa, selva nublada al norte de Nirgua, 1200-1400 m, 9-10 November 1967, Stevermark et al. 100250 (NY); Cumbre Gamelatal 4.3–11 km N of Salom on road from Salom to Candelaria, 1000–1200, 10°15'N 68°29'30"W, s.d., Mori et al. 14602 (NY); North of Salom 7.5 km, 1200–1300 m, 10°15'N 68°29'W, 04 March 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°21'N 68°49'W, 04 April 1980, Leisner & González 10048 (NY).

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Figure 1 The two corolla lobe morphologies in Burmeistera: A) recurved corolla lobes of an individual of the recurved corolla clade (RCC); B) falcate corolla lobes of *Burmeistera* species outside of the RCC. Photographs by Nathan Muchhala.



Figure 2 Distribution map of *B. succulenta* (red circles) as understood previous to our study. The blue diamond in western Panama shows the placement of the specimen identified as *B. toroensis* in Uribe-Convers et al. (2017) (here called *B. sp. Panama*).



Figure 3 Distributions of *B. crispiloba* (blue diamonds) and *B. sodiroana* (red circles) as understood previous to this study.



Figure 4 Geographic locations in northwest Ecuador of the majority of intermediates specimens between *B. crispiloba* and *B. sodiroana* (gold triangles). A few intermediates occur to the southwest along the Andes (not shown). All intermediate specimens occur at the intersection of the ranges of *B. crispiloba* (blue diamonds) and *B. sodiroana* (red circles).


Figure 5 Photographs of flowers and fruits of: A-B) *B. crispiloba*, C-D) Intermediate specimens between *B. crispiloba and B. sodiroana*, and E-F) *B. sodiroana*. Photographs by Nathan Muchhala.

ORGAN	QUANTITATIVE CHARACTERS	ORGAN	QUALITATIVE CHARACTERS
LEAF	Minimum petiole length*	LEAF	Phyllotaxy*
	Maximum petiole length*		Stem pubescence
	Smallest leaf length		Petiole pubescence
	Smallest leaf width		Leaf adaxial surface pubescence
	Largest leaf length*		Leaf abaxial surface pubescence
	Largest leaf width*	FLOWER	Pedicel pubescence
	First fertile leaf (bract) length*		Hypanthium pubescence
	First fertile leaf (bract) width*		Sepal pubescence
	Leaf apex length*		Corolla pubescence
	Leaf apex width*		Strength of corolla curling*
FLOWER	Pedicel length at anthesis*		Filament tube pubescence
	Hypanthium length*		Anther tube pubescence
	Hypanthium width*		Anther tip pubescence
	Calyx lobe length*	Fruit	Fruit type (inflated, not-inflated)
	Calyx lobe width*		
	Corolla tube width at base		
	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*		
Fruit	Mature fruit length		
	Mature fruit width		

Table 1 List of characters used in morphometric analysis. *Denotes use in PCA of *B. crispiloba / B. sodiroana* complex.



Figure 6 Illustration of exsertion length, and important morphological character and ecological trait for pollen placement on bats or hummingbirds. From Fig. 1A, Muchhala (2006).

Pairs	Hypanthium Length	Sepal Length	Sepal Width	Androecium Length	Exsertion Length	Anther Tube Length
B. crispiloba–	0.17	4.1e-09	6.1e-12	4.5e-06	2.6e-07	1.2e-06
B. soairoana B. crispiloba–	1.4e-18	<2e-16	0.00229	0.045	0.668	2.7e-07
B. succulenta	10.15	. 0 1 (0.00000	0.025	0.011	0.16
B. sodiroana– B. succulenta	1.2e-15	<2e-16	0.00029	0.037	0.011	0.16

Table 2 Results of pairwise comparisons using Wilcoxon Rank Sum Test showingadjusted p-values. P-values are adjusted using the Benjamini-Hochberg Procedure.



Figure 7 Boxplots of six traits that can be used in combination to differentiate established species concepts of the *B. crispiloba, B. sodiroana,* and *B. succulenta* complexes.

-	Dimension 1		D	Dimension 2		D	Dimension 3	
	Correlation	P-value		Correlation	P-value		Correlation	P-value
Fertile leaf length	0.8508075	1.25E-24	Maximum petiole length	0.709746	4.09E-14	Hypanthium length	0.7683008	1.47E-17
Largest leaf length	0.8498398	1.60E-24	Pedicel length at anthesis	0.6501474	2.20E-11	Corrolla tube width at throat	0.7560634	9.24E-17
Strength of corolla curling	0.7021146	9.97E-14	Minimum petiole length	0.5709091	1.42E-08	Hypanthium width	0.6921599	3.06E-13
Largest leaf width	0.6759675	1.73E-12	Calyx lobe length	0.5618012	2.70E-08	Anther tip width	0.6430336	4.24E-11
Fertile leaf width	0.6674726	4.10E-12	Largest leaf width	0.5445098	8.59E-08	Exsertion length	0.2936165	6.71E-03
Anther tube length	0.6336748	9.84E-11	Fertile leaf length	0.4745663	5.10E-06	Anther tube length	0.2870767	8.11E-03
Exsertion length	0.5681413	1.73E-08	Calyx lobe width	0.4407165	2.72E-05	C		
Leaf apex length	0.5321926	1.89E-07	Leaf apex width	0.3807938	3.52E-04			
Minimum petiole length	0.4492371	1.82E-05	Phyllotaxy	0.3124279	3.81E-03			
Anther tip width	-0.2545235	1.95E-02	Anther tip width	0.3097539	4.14E-03			
Calyx lobe length	-0.2860429	8.35E-03	Largest leaf length	0.2772067	1.07E-02			
Calyx lobe width	-0.5246961	3.00E-07	Anther tube length	-0.2660133	1.45E-02			
Phyllotaxy	-0.7539857	1.25E-16	Exsertion length	-0.3201409	2.99E-03			
			Strength of corolla curling	-0.4999055	1.29E-06			

Table 3 Correlation of variables to each of the first three dimensions in the PCA of the *B. crispiloba / B. sodiroana* complex.



Figure 8 Scatterplots of PCA results in the *B. crispiloba / B. sodiroana* complex. A) Principal Components 1 & 2. B) Principal Components 1 & 3. C) Principal Components 2 & 3. Red circles are *B. crispiloba*, gold triangles are *B. sodiroana*, and green squares are intermediate specimens. Note that intermediate specimens in A occur roughly inbetween *B. crispiloba* and *B. sodiroana*, while in B they group with *B. crispiloba* specimens, and in C they group with *B. sodiroana* specimens.



Figure 9 Directionality of all variables significantly correlated to Principle Components 1 & 2. Length of the arrows equates to strength of correlation (Table 3).



Figure 10 Results of hierarchical clustering on principal components (HCPC). A) Results of unsupervised clustering with three clusters roughly analogous to *B. sodiroana* (Cluster A1, red), *B. crispiloba* (Cluster A2, green), and intermediate specimens (Cluster A3, blue). B) Results of unsupervised clustering when the function HCPC is forced to select two clusters. Resulting clusters are roughly analogous to traditional concepts of *B. sodiroana* (Cluster B1, red) and *B. crispiloba* (Cluster B2, light blue), since intermediate specimens have regularly been identified as *B. crispiloba*.

Table 4 Variables that describe each cluster. Each variable is shown with the average value of that variable in each the cluster (Mean in Category). Also shown is the overall mean of that variable in the entire dataset (Overall Mean). The p-value relates to a test of the hypothesis: "the 'mean in category' is equal to the 'overall mean'". V-test (Kuiper test) values greater than 1.96 correspond to p-values less than 0.05 (Husson et al. 2010).

Cluster 1	V-test	Mean in	Overall	P-value
		Category	Mean	
phyllotaxy	7.627701	0.81818182	0.3333333	2.39E-14
sepal_wid_mm	4.645018	2.02424242	1.6975309	3.40E-06
sepal_len_mm	2.933369	1.99393939	1.6679012	3.35E-03
anth_tip_wid	2.861155	4.4969697	4.1876543	4.22E-03
pedicel_length_mm	2.565045	112.030303	103.8703704	1.03E-02
fert_leaf_wid	-3.695026	26.6969697	32.1851852	2.20E-04
l_leaf_width_mm	-3.800513	34.36363636	41.3148148	1.44E-04
apex_length	-3.81623	7.78787879	9.4938272	1.36E-04
exsertion_len_mm	-4.297676	20.03636364	23.054321	1.73E-05
anth_tub_1	-5.446656	8.04242424	9.2987654	5.13E-08
l_leaf_length_mm	-5.45694	78.12121212	106.0925926	4.84E-08
fert_leaf_len	-5.893897	55.36363636	79.962963	3.77E-09
cor.curling	-7.012818	0.09090909	0.962963	2.34E-12
Cluster 2	V-test	Mean in Category	Overall Mean	P-value
cor.curling	6.051693	1.821429	0.962963	1.43E-09
anth tub 1	4.538002	10.492857	9.2987654	5.68E-06
exsertion len mm	4.18093	26.403571	23.054321	2.90E-05
apex_length	2.113156	10.571429	9.4938272	3.46E-02
fert_leaf_wid	-2.00633	28.785714	32.1851852	4.48E-02
l_leaf_width_mm	-2.204937	36.714286	41.3148148	2.75E-02
anth_tip_wid	-2.477263	3.882143	4.1876543	1.32E-02
petiole_min_mm	-2.492081	4.464286	4.9753086	1.27E-02
sepal_len_mm	-3.60576	1.210714	1.6679012	3.11E-04
petiole_max_mm	-3.773769	6.464286	7.9259259	1.61E-04
sepal_wid_mm	-3.797193	1.392857	1.6975309	1.46E-04
pedicel_length_mm	-4.186222	88.678571	103.8703704	2.84E-05
phyllotaxy	-4.596964	0	0.3333333	4.29E-06
Cluster 3	V-test	Mean in	Overall	P-value
		Category	Mean	
l_leaf_width_mm	6.762349	59.225	41.3148148	1.36E-11

fert_leaf_wid	6.423107	46	32.1851852	1.34E-10
l_leaf_length_mm	6.336453	153.125	106.0925926	2.35E-10
fert_leaf_len	5.557311	113.55	79.962963	2.74E-08
petiole_min_mm	3.936624	6	4.9753086	8.26E-05
petiole_max_mm	2.591424	9.2	7.9259259	9.56E-03
apex_length	2.017823	10.8	9.4938272	4.36E-02
phyllotaxy	-3.62143	0	0.3333333	2.93E-04



Figure 11 Boxplots showing selected traits of specimens in the *B. succulenta* complex, divided by region of collection (Colombia & Venezuela vs. Ecuador).



Figure 12 A-D. Photographs of *B. crispiloba*. A. Typical flowers with strongly scrolling corolla lobes. B. Flowers with corolla lobes tinged violet. C. Flowers and fruits of an intermediate individual; note the larger leaves, darker flower colors, and the more globose pink fruit. D. Fruits more typical of *B. crispiloba*: obovoid shape and cerese red color. Photographs by Nathan Muchhala.



Figure 13 Burmeistera huacamayensis Jeppesen.



Figure 14 Burmeistera kitrinaima Muchhala & Mashburn.



Figure 15 Burmeistera melanocarpa Mashburn



Figure 16 Burmeistera sodiroana Zahlbr.



Figure 17 Burmeistera succulenta H. Karst. & Triana



Figure 18 A–F Geographic distribution maps. —A. *Burmeistera crispiloba* Zahlbr. —B. *Burmeistera huacamayensis* Jeppesen —C. *Burmeistera kitrinaima* Muchhala & Mashburn —D. *Burmeistera melanocarpa* Mashburn —E. *Burmeistera sodiroana* Zahlbr. —F. *Burmeistera succulenta* H. Karst. & Triana, Ecuadorian distribution.

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Original Identification	Resulting	Herbarium	Senior Collector	Collection	Country
B. crispiloba	B. crispiloba	OCA	Muchhala	207	Ecuador
B. crispiloba	B. crispiloba	QCA	Werling	233	Ecuador
B. crispiloba	B. crispiloba	QCA	Werling	233	Ecuador
B. crispiloba	B. crispiloba	QCA	Knudsen	459	Ecuador
B. crispiloba	B. crispiloba	MO	Clark	499	Ecuador
B. crispiloba	B. crispiloba	NY	Arguello	507	Ecuador
B. crispiloba	B. crispiloba	МО	Arguello	507	Ecuador
B. crispiloba	B. crispiloba	QCA	Boeke	842	Ecuador
B. crispiloba	B. crispiloba	NY	Boeke	842	Ecuador
B. crispiloba	B. crispiloba	МО	Boeke	842	Ecuador
B. crispiloba	B. crispiloba	МО	Fallen	858	Ecuador
B. crispiloba	B. crispiloba	QCA	Balslev	1996	Ecuador
B. crispiloba	B. crispiloba	МО	Stein	2686	Ecuador
B. crispiloba	B. crispiloba	МО	Stein	3091	Ecuador
B. crispiloba	B. crispiloba	МО	Stein	3091	Ecuador
B. crispiloba	B. crispiloba	МО	Daly	5206	Ecuador
B. crispiloba	B. crispiloba	NY	Daly	5206	Ecuador
B. crispiloba	B. crispiloba	NY	Cazalet	5207	Ecuador
B. crispiloba	B. crispiloba	МО	Vargas	5585	Ecuador
B. crispiloba	B. crispiloba	МО	Dodson	5628	Ecuador
B. crispiloba	B. crispiloba	QCA	Jaramillo	6611	Ecuador
B. crispiloba	B. crispiloba	МО	Dodson	7217	Ecuador
B. crispiloba	B. crispiloba	МО	Dodson	7433	Ecuador
B. crispiloba	B. crispiloba	MO	Ceron	10082	Ecuador
B. crispiloba	B. crispiloba	МО	van der Werff	10767	Ecuador
B. crispiloba	B. crispiloba	MO	Dodson	12000	Ecuador
B. crispiloba	B. crispiloba	MO	Luteyn	13363	Ecuador
B. crispiloba	B. crispiloba	NY	Luteyn	13363	Ecuador
B. crispiloba	B. crispiloba	QCA	Luteyn	13363	Ecuador
B. crispiloba	B. crispiloba	MO	Dodson	14661	Ecuador
B. crispiloba	B. crispiloba	NY	Dodson	14661	Ecuador
B. crispiloba	B. crispiloba	MO	Dodson	15548	Ecuador
B. crispiloba	B. crispiloba	MO	Dodson	15548	Ecuador
B. crispiloba	B. crispiloba	NY	Harling	23062	Ecuador
B. crispiloba	B. crispiloba	MO	Gentry	69965	Ecuador
B. crispiloba	B. crispiloba	NY	Gentry	69965	Ecuador
B. crispiloba	B. crispiloba	МО	Bonifaz	3170	Ecuador

Appendix 1. List of specimens with complete flowers used in numerical analyses.

B. crispiloba	B. crispiloba	MO	Dodson	7310	Ecuador
B. crispiloba	B. crispiloba	МО	Dodson	12782	Ecuador
B. crispiloba	B. crispiloba	МО	Ceron	17925	Ecuador
B. crispiloba	B. crispiloba	NY	Harling	19471	Ecuador
B. crispiloba	B. crispiloba	МО	Tipaz	157	Ecuador
B. crispiloba	B. crispiloba	МО	Dodson	15196	Ecuador
B. crispiloba	B. crispiloba	МО	Gentry	72409	Ecuador
B. crispiloba	B. crispiloba	МО	Ramos	7305	Ecuador
B. crispiloba	B. crispiloba	МО	Silverstone-	9151	Ecuador
			Sopkin		
B. crispiloba	B. crispiloba	МО	Dodson	9159	Ecuador
B. crispiloba	B. crispiloba	MO	Silverstone-	9723	Ecuador
B crispiloba	B crispiloba	MO	Sopkin Silverstone-	9965	Ecuador
Diensphood	Di enspricea	1110	Sopkin	<i>,,,</i> ,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,	Louudoi
B. crispiloba	B. crispiloba	MO	Cotton	1605	Ecuador
B. crispiloba	B. crispiloba	NY	Cotton	1605	Ecuador
B. crispiloba	B. crispiloba	MO	Vargas	5171	Ecuador
B. crispiloba	B. crispiloba	QCA	Clark	7944	Ecuador
B. crispiloba	B. crispiloba	QCA	Muchhala	115	Ecuador
B. crispiloba	B. crispiloba	QCA	Nowicki	1498	Ecuador
B. crispiloba	B. crispiloba	МО	Neill	8654	Ecuador
B. crispiloba	B. crispiloba	МО	Neill	9800	Ecuador
B. crispiloba	B. crispiloba	NY	Luteyn	13333	Ecuador
B. crispiloba	B. crispiloba	МО	Webster	30017	Ecuador
B. crispiloba	B. crispiloba	МО	Gentry	69945	Ecuador
B. crispiloba	B. crispiloba	МО	Rojas	391	Ecuador
B. crispiloba	B. crispiloba	МО	Ramos	6546	Ecuador
B. crispiloba	B. crispiloba	МО	Holm-Nielsen	24419	Ecuador
B. crispiloba	B. crispiloba	NY	Holm-Nielsen	24419	Ecuador
B. crispiloba	B. crispiloba	МО	Croat	95948	Ecuador
B. sodiroana	В.	МО	Hoover	1850	Ecuador
	melanocarpa		~ .	• • • •	
B. sodiroana	B.	MO	Stein	2911	Ecuador
B. sodiroana	B.	OCA	Stein	2911	Ecuador
	melanocarpa	X		_,	
B. sodiroana	В.	MO	Luteyn	5750	Ecuador
D. andironna	melanocarpa	NIV	Lutow	5750	Equador
D. Souroana	D. melanocarpa	IN I	Luteyn	5750	Ecuador
B. sodiroana	B.	QCA	Luteyn	5750	Ecuador
	melanocarpa	-	-		

B. sodiroana	B. melanocarpa	NY	HolmNielsen	6000	Ecuador
B. sodiroana	B. melanocarna	QCA	Holm-Nielsen	6000	Ecuador
B. sodiroana	B. melanocarpa	NY	Luteyn	10882	Ecuador
B. sodiroana	B. B.	NY	Luteyn	10893	Ecuador
B. sodiroana	B. melanocarpa	МО	Harling	12384	Ecuador
B. sodiroana	B. melanocarpa	МО	Palacios	12757	Ecuador
B. sodiroana	B. melanocarpa	МО	Gentry	26647	Ecuador
B. sodiroana	B. sodiroana	NY	Pachano	177	Ecuador
B. sodiroana	B. sodiroana	QCA	Boeke	376	Ecuador
B. sodiroana	B. sodiroana	МО	Vargas	431	Ecuador
B. sodiroana	B. sodiroana	QCA	Muchhala	458	Ecuador
B. sodiroana	B. sodiroana	МО	Vargas	1761	Ecuador
B. sodiroana	B. sodiroana	NY	Sobel	2522	Ecuador
B. sodiroana	B. sodiroana	QCA	Stahl	2564	Ecuador
B. sodiroana	B. sodiroana	QCA	Stahl	2578	Ecuador
B. sodiroana	B. sodiroana	NY	FriereFierro	2673	Ecuador
B. sodiroana	B. sodiroana	МО	Stein	2945	Ecuador
B. sodiroana	B. sodiroana	МО	Tepe	2955	Ecuador
B. sodiroana	B. sodiroana	МО	Vargas	3003	Ecuador
B. sodiroana	B. sodiroana	QCA	Maas	3035	Ecuador
B. sodiroana	B. sodiroana	МО	Stein	3082	Ecuador
B. sodiroana	B. sodiroana	QCA	Stein	3082	Ecuador
B. sodiroana	B. sodiroana	МО	Vargas	3712	Ecuador
B. sodiroana	B. sodiroana	NY	Camp	4955	Ecuador
B. sodiroana	B. sodiroana	МО	Palacios	4982	Ecuador
B. sodiroana	B. sodiroana	QCA	Clark	7699	Ecuador
B. sodiroana	B. sodiroana	QCA	Clark	7715	Ecuador
B. sodiroana	B. sodiroana	QCA	Perez	8112	Ecuador
B. sodiroana	B. sodiroana	QCA	Perez	8409	Ecuador
B. sodiroana	B. sodiroana	NY	Asplund	9767	Ecuador
B. sodiroana	B. sodiroana	NY	Balslev	10329	Ecuador
B. sodiroana	B. sodiroana	NY	Luteyn	13389	Ecuador
B. sodiroana	B. sodiroana	МО	Luteyn	13389	Ecuador
B. sodiroana	B. sodiroana	QCA	Luteyn	13389	Ecuador
B. sodiroana	B. sodiroana	NY	Luteyn	13459	Ecuador
B. sodiroana	B. sodiroana	QCA	Luteyn	13459	Ecuador

B. sodiroana	B. sodiroana	NY	D'Arcy	14092	Ecuador
B. sodiroana	B. sodiroana	MO	D'Arcy	14101	Ecuador
B. sodiroana	B. sodiroana	NY	D'Arcy	14101	Ecuador
B. sodiroana	B. sodiroana	MO	Dodson	15883	Ecuador
B. sodiroana	B. sodiroana	QCA	Holm-Nielsen	16226	Ecuador
B. sodiroana	B. sodiroana	MO	Mantuano	30	Ecuador
B. sodiroana	B. sodiroana	QCA	Muchhala	129	Ecuador
B. sodiroana	B. sodiroana	NY	Bleiweiss	1142	Ecuador
B. sodiroana	B. sodiroana	QCA	Molau	1156	Ecuador
B. sodiroana	B. sodiroana	MO	Zak	1192	Ecuador
B. sodiroana	B. sodiroana	NY	HolmNielsen	1282	Ecuador
B. sodiroana	B. sodiroana	MO	HolmNielsen	1282	Ecuador
B. sodiroana	B. sodiroana	NY	Camp	1652	Ecuador
B. sodiroana	B. sodiroana	MO	Smith	1975	Ecuador
B. sodiroana	B. sodiroana	NY	Smith	1975	Ecuador
B. sodiroana	B. sodiroana	QCA	Smith	1975	Ecuador
B. sodiroana	B. sodiroana	MO	Stein	2662	Ecuador
B. sodiroana	B. sodiroana	MO	Stein	2674	Ecuador
B. sodiroana	B. sodiroana	MO	Stein	2683	Ecuador
B. sodiroana	B. sodiroana	NY	Balslev	2759	Ecuador
B. sodiroana	B. sodiroana	MO	Ceron	2798	Ecuador
B. sodiroana	B. sodiroana	MO	Friere Fierro	3208	Ecuador
B. sodiroana	B. sodiroana	MO	Ceron	3830	Ecuador
B. sodiroana	B. sodiroana	MO	Ramos	5814	Ecuador
B. sodiroana	B. sodiroana	MO	Ramos	6204	Ecuador
B. sodiroana	B. sodiroana	MO	Billiet	6684	Ecuador
B. sodiroana	B. sodiroana	MO	Luteyn	8792	Ecuador
B. sodiroana	B. sodiroana	NY	Luteyn	8792	Ecuador
B. sodiroana	B. sodiroana	NY	Lojtnant	11261	Ecuador
B. sodiroana	B. sodiroana	MO	Luteyn	13328	Ecuador
B. sodiroana	B. sodiroana	NY	Luteyn	13328	Ecuador
B. sodiroana	B. sodiroana	NY	Luteyn	14342	Ecuador
B. sodiroana	B. sodiroana	MO	Croat	49392	Ecuador
B. sodiroana	B. sodiroana	QCA	Escobar	1377	Ecuador
B. sodiroana	B. sodiroana	MO	van der Werff	12516	Ecuador
B. sodiroana	B. sodiroana	NY	Lojtnant	15174	Ecuador
B. sodiroana	B. sodiroana	QCA	Jaramillo	30276	Ecuador
B. succulenta	В.	QCA	Muchhala	163	Ecuador
B. succulenta	huacamayensis B. huacamayensis	QCA	Muchhala	462	Ecuador

B. succulenta B. huckmayensis QCA Stein 2641 Ecuador B. succulenta B. NY Luteyn 13463 Ecuador huacamayensis B. MO Luteyn 13463 Ecuador huacamayensis B. MO Luteyn 13463 Ecuador huacamayensis B. QCA Luteyn 13463 Ecuador huacamayensis B. MO D'Arcy 14100 Ecuador huacamayensis B. MO D'Arcy 14100 Ecuador B. succulenta B. kitrinaima QCA Muchhala 119 Ecuador B. succulenta B. kitrinaima QCA Muchhala 128 Ecuador B. succulenta B. kitrinaima QCA Muchhala 130 Ecuador B. succulenta B. kitrinaima QCA Muchhala 147 Ecuador B. succulenta B. kitrinaima QCA Muchhala 147 Ecuador B. succulenta B. kitrinaima QCA Nowicki 1193 Ecuador	B. succulenta	B. huacamavensis	MO	Alvarez	515	Ecuador
B. succulentaB. mudataniaychisisNYLuteyn13463EcuadorB. succulentaB.MOLuteyn13463EcuadorhuacamayensisNOLuteyn13463EcuadorhuacamayensisNOD'Arey14100EcuadorB. succulentaB.MOD'Arey14100EcuadorB. succulentaB. kitrinaimaQCASigcha28EcuadorB. succulentaB. kitrinaimaQCAMuchhala119EcuadorB. succulentaB. kitrinaimaQCAMuchhala125EcuadorB. succulentaB. kitrinaimaQCAMuchhala130EcuadorB. succulentaB. kitrinaimaQCAMuchhala130EcuadorB. succulentaB. kitrinaimaQCAMuchhala447EcuadorB. succulentaB. kitrinaimaQCAMuchhala447EcuadorB. succulentaB. kitrinaimaQCAMuchhala447EcuadorB. succulentaB. kitrinaimaQCAMuchhala447EcuadorB. succulentaB. kitrinaimaQCANowicki1193EcuadorB. succulentaB. kitrinaimaQCANowicki1193EcuadorB. succulentaB. kitrinaimaQCANowicki1479EcuadorB. succulentaB. kitrinaimaQCANowicki1479EcuadorB. succulentaB. kitrinaimaMOJaramillo13651EcuadorB. suc	B. succulenta	B.	QCA	Stein	2641	Ecuador
B. succulenta B. MO Luteyn 13463 Ecuador huacamayensis OCA Luteyn 13463 Ecuador huacamayensis MO D'Arcy 14100 Ecuador huacamayensis MO D'Arcy 14100 Ecuador B. succulenta B. kitrinaima QCA Sigcha 28 Ecuador B. succulenta B. kitrinaima QCA Muchhala 119 Ecuador B. succulenta B. kitrinaima QCA Muchhala 125 Ecuador B. succulenta B. kitrinaima QCA Muchhala 130 Ecuador B. succulenta B. kitrinaima QCA Muchhala 447 Ecuador B. succulenta B. kitrinaima QCA Muchhala 454 Ecuador B. succulenta B. kitrinaima QCA Muchhala 419 Ecuador B. succulenta B. kitrinaima QCA Nowicki 1193 Ecuador B. succulenta B. kitrinaima QCA Nowicki 1479 Ecuador B. succulenta <td< td=""><td>B. succulenta</td><td>B.</td><td>NY</td><td>Luteyn</td><td>13463</td><td>Ecuador</td></td<>	B. succulenta	B.	NY	Luteyn	13463	Ecuador
B. succulentaB. huacamayensisQCALuteyn13463EcuadorB. succulentaB. huacamayensisMOD'Arey14100EcuadorB. succulentaB. kitrinaimaQCASigcha28EcuadorB. succulentaB. kitrinaimaQCAMuchhala119EcuadorB. succulentaB. kitrinaimaQCAMuchhala125EcuadorB. succulentaB. kitrinaimaQCAMuchhala128EcuadorB. succulentaB. kitrinaimaQCAMuchhala130EcuadorB. succulentaB. kitrinaimaQCAMuchhala447EcuadorB. succulentaB. kitrinaimaQCAMuchhala447EcuadorB. succulentaB. kitrinaimaQCAMuchhala447EcuadorB. succulentaB. kitrinaimaQCAMuchhala454EcuadorB. succulentaB. kitrinaimaQCANowicki1193EcuadorB. succulentaB. kitrinaimaQCANowicki1479EcuadorB. succulentaB. kitrinaimaQCAStahl2901EcuadorB. succulentaB. kitrinaimaQCAStahl2901EcuadorB. succulentaB. kitrinaimaMONeill8942EcuadorB. succulentaB. kitrinaimaMOJaramillo13651EcuadorB. succulentaB. kitrinaimaMOJaramillo13651EcuadorB. succulentaB. succulenta <td< td=""><td>B. succulenta</td><td>B.</td><td>МО</td><td>Luteyn</td><td>13463</td><td>Ecuador</td></td<>	B. succulenta	B.	МО	Luteyn	13463	Ecuador
B. succulentaB. huacamayensisMOD'Arcy14100EcuadorB. succulentaB. kitrinaimaQCASigcha28EcuadorB. succulentaB. kitrinaimaQCAMuchhala119EcuadorB. succulentaB. kitrinaimaQCAMuchhala125EcuadorB. succulentaB. kitrinaimaQCAMuchhala128EcuadorB. succulentaB. kitrinaimaQCAMuchhala130EcuadorB. succulentaB. kitrinaimaQCAMuchhala447EcuadorB. succulentaB. kitrinaimaQCAMuchhala447EcuadorB. succulentaB. kitrinaimaQCAMuchhala447EcuadorB. succulentaB. kitrinaimaQCAMuchhala454EcuadorB. succulentaB. kitrinaimaQCANowicki1193EcuadorB. succulentaB. kitrinaimaQCANowicki1419EcuadorB. succulentaB. kitrinaimaQCANowicki1479EcuadorB. succulentaB. kitrinaimaQCAStahl2901EcuadorB. succulentaB. kitrinaimaMOJaramillo13651EcuadorB. succulentaB. kitrinaimaMOJaramillo13651EcuadorB. succulentaB. kitrinaimaMOJaramillo13651EcuadorB. succulentaB. succulentaNYStein3303ColombiaB. succulentaB. succulentaN	B. succulenta	B.	QCA	Luteyn	13463	Ecuador
B. succulentaB. kitrinaimaQCASigcha28EcuadorB. succulentaB. kitrinaimaQCAMuchhala119EcuadorB. succulentaB. kitrinaimaQCAMuchhala125EcuadorB. succulentaB. kitrinaimaQCAMuchhala128EcuadorB. succulentaB. kitrinaimaQCAMuchhala130EcuadorB. succulentaB. kitrinaimaQCAMuchhala447EcuadorB. succulentaB. kitrinaimaQCAMuchhala447EcuadorB. succulentaB. kitrinaimaQCAMuchhala454EcuadorB. succulentaB. kitrinaimaQCAAntonelli602EcuadorB. succulentaB. kitrinaimaQCANowicki1193EcuadorB. succulentaB. kitrinaimaQCANowicki1479EcuadorB. succulentaB. kitrinaimaQCANowicki1479EcuadorB. succulentaB. kitrinaimaQCAStahl2901EcuadorB. succulentaB. kitrinaimaMOJaramillo13651EcuadorB. succulentaB. kitrinaimaMOJaramillo13651EcuadorB. succulentaB. kitrinaimaMOJaramillo13651EcuadorB. succulentaB. kitrinaimaMOJaramillo13651EcuadorB. succulentaB. kitrinaimaMOStein3303ColombiaB. succulentaB. succulentaNY </td <td>B. succulenta</td> <td>B.</td> <td>МО</td> <td>D'Arcy</td> <td>14100</td> <td>Ecuador</td>	B. succulenta	B.	МО	D'Arcy	14100	Ecuador
B. succulentaB. kitrinaimaQCAMuchhala119EcuadorB. succulentaB. kitrinaimaQCAMuchhala125EcuadorB. succulentaB. kitrinaimaQCAMuchhala130EcuadorB. succulentaB. kitrinaimaQCAMuchhala130EcuadorB. succulentaB. kitrinaimaQCAMuchhala447EcuadorB. succulentaB. kitrinaimaQCAMuchhala447EcuadorB. succulentaB. kitrinaimaQCAMuchhala454EcuadorB. succulentaB. kitrinaimaQCAAntonelli602EcuadorB. succulentaB. kitrinaimaQCANowicki1193EcuadorB. succulentaB. kitrinaimaQCANowicki1193EcuadorB. succulentaB. kitrinaimaQCANowicki1419EcuadorB. succulentaB. kitrinaimaQCANowicki1479EcuadorB. succulentaB. kitrinaimaMONeill8942EcuadorB. succulentaB. kitrinaimaMONeill8942EcuadorB. succulentaB. kitrinaimaMOJaramillo13651EcuadorB. succulentaB. kitrinaimaMOJaramillo13651EcuadorB. succulentaB. kitrinaimaMOStein3303ColombiaB. succulentaB. succulentaNYStein3303ColombiaB. succulentaB. succulentaNY	B. succulenta	B. kitrinaima	QCA	Sigcha	28	Ecuador
B. succulentaB. kitrinaimaQCAMuchhala125EcuadorB. succulentaB. kitrinaimaQCAMuchhala130EcuadorB. succulentaB. kitrinaimaQCAMuchhala130EcuadorB. succulentaB. kitrinaimaQCABuitron253EcuadorB. succulentaB. kitrinaimaQCAMuchhala447EcuadorB. succulentaB. kitrinaimaQCAMuchhala454EcuadorB. succulentaB. kitrinaimaQCAAntonelli602EcuadorB. succulentaB. kitrinaimaQCANowicki1193EcuadorB. succulentaB. kitrinaimaQCANowicki1419EcuadorB. succulentaB. kitrinaimaQCANowicki1479EcuadorB. succulentaB. kitrinaimaQCANowicki1479EcuadorB. succulentaB. kitrinaimaMOHurtado1419EcuadorB. succulentaB. kitrinaimaMONeill8942EcuadorB. succulentaB. kitrinaimaMOJaramillo13651EcuadorB. succulentaB. kitrinaimaMOJaramillo13651EcuadorB. succulentaB. kitrinaimaMOStein3303ColombiaB. succulentaB. succulentaMVStein3303ColombiaB. succulentaB. succulentaNYStein3303ColombiaB. succulentaB. succulentaNYP	B. succulenta	B. kitrinaima	QCA	Muchhala	119	Ecuador
B. succulentaB. kitrinaimaQCAMuchhala128EcuadorB. succulentaB. kitrinaimaQCAMuchhala130EcuadorB. succulentaB. kitrinaimaQCABuitron253EcuadorB. succulentaB. kitrinaimaQCAMuchhala447EcuadorB. succulentaB. kitrinaimaQCAMuchhala454EcuadorB. succulentaB. kitrinaimaQCAAntonelli602EcuadorB. succulentaB. kitrinaimaQCANowicki1193EcuadorB. succulentaB. kitrinaimaQCANowicki1419EcuadorB. succulentaB. kitrinaimaQCANowicki1479EcuadorB. succulentaB. kitrinaimaQCANowicki1479EcuadorB. succulentaB. kitrinaimaQCAStahl2901EcuadorB. succulentaB. kitrinaimaMONeill8942EcuadorB. succulentaB. kitrinaimaMOJaramillo13651EcuadorB. succulentaB. kitrinaimaMOJaramillo13651EcuadorB. succulentaB. kitrinaimaMOStein3303ColombiaB. succulentaB. succulentaMOStein3303ColombiaB. succulentaB. succulentaNYStein3303ColombiaB. succulentaB. succulentaNYPennell5783ColombiaB. succulentaB. succulentaNYLu	B. succulenta	B. kitrinaima	QCA	Muchhala	125	Ecuador
B. succulentaB. kitrinaimaQCAMuchhala130EcuadorB. succulentaB. kitrinaimaQCABuitron253EcuadorB. succulentaB. kitrinaimaQCAMuchhala447EcuadorB. succulentaB. kitrinaimaQCAMuchhala454EcuadorB. succulentaB. kitrinaimaQCAAntonelli602EcuadorB. succulentaB. kitrinaimaQCANowicki1193EcuadorB. succulentaB. kitrinaimaQCANowicki1419EcuadorB. succulentaB. kitrinaimaQCANowicki1479EcuadorB. succulentaB. kitrinaimaQCANowicki1479EcuadorB. succulentaB. kitrinaimaQCAStahl2901EcuadorB. succulentaB. kitrinaimaMONeill8942EcuadorB. succulentaB. kitrinaimaMOJaramillo13651EcuadorB. succulentaB. kitrinaimaMOVebster30455EcuadorB. succulentaB. succulentaMOStein3303ColombiaB. succulentaB. succulentaNYStein3369ColombiaB. succulentaB. succulentaNYPennell5151ColombiaB. succulentaB. succulentaNYLuteyn10545ColombiaB. succulentaB. succulentaNYLuteyn10550ColombiaB. succulentaB. succulentaNYLu	B. succulenta	B. kitrinaima	QCA	Muchhala	128	Ecuador
B. succulentaB. kitrinaimaQCABuitron253EcuadorB. succulentaB. kitrinaimaQCAMuchhala447EcuadorB. succulentaB. kitrinaimaQCAMuchhala454EcuadorB. succulentaB. kitrinaimaQCAAntonelli602EcuadorB. succulentaB. kitrinaimaQCANowicki1193EcuadorB. succulentaB. kitrinaimaQCANowicki1419EcuadorB. succulentaB. kitrinaimaQCANowicki1479EcuadorB. succulentaB. kitrinaimaQCANowicki1479EcuadorB. succulentaB. kitrinaimaQCAStahl2901EcuadorB. succulentaB. kitrinaimaMONeill8942EcuadorB. succulentaB. kitrinaimaMOJaramillo13651EcuadorB. succulentaB. kitrinaimaNYJaramillo13651EcuadorB. succulentaB. kitrinaimaMOWebster30455EcuadorB. succulentaB. succulentaMYStein3303ColombiaB. succulentaB. succulentaNYStein3369ColombiaB. succulentaB. succulentaNYPennell5783ColombiaB. succulentaNYLuteyn10545ColombiaB. succulentaNYB. succulentaNYLuteyn10650ColombiaB. succulentaB. succulentaNYLuteyn	B. succulenta	B. kitrinaima	QCA	Muchhala	130	Ecuador
B. succulentaB. kitrinaimaQCAMuchhala447EcuadorB. succulentaB. kitrinaimaQCAMuchhala454EcuadorB. succulentaB. kitrinaimaQCAAntonelli602EcuadorB. succulentaB. kitrinaimaQCANowicki1193EcuadorB. succulentaB. kitrinaimaMOHurtado1419EcuadorB. succulentaB. kitrinaimaQCANowicki1479EcuadorB. succulentaB. kitrinaimaQCAStahl2901EcuadorB. succulentaB. kitrinaimaMONeill8942EcuadorB. succulentaB. kitrinaimaMONeill8942EcuadorB. succulentaB. kitrinaimaMOJaramillo13651EcuadorB. succulentaB. kitrinaimaNYJaramillo13651EcuadorB. succulentaB. kitrinaimaQCAJaramillo13651EcuadorB. succulentaB. kitrinaimaMOWebster30455EcuadorB. succulentaB. succulentaMOStein3303ColombiaB. succulentaB. succulentaNYStein3369ColombiaB. succulentaB. succulentaNYPennell5783ColombiaB. succulentaB. succulentaNYLuteyn10545ColombiaB. succulentaB. succulentaNYLuteyn10650ColombiaB. succulentaB. succulentaNY	B. succulenta	B. kitrinaima	QCA	Buitron	253	Ecuador
B. succulentaB. kitrinaimaQCAMuchhala454EcuadorB. succulentaB. kitrinaimaQCAAntonelli602EcuadorB. succulentaB. kitrinaimaQCANowicki1193EcuadorB. succulentaB. kitrinaimaMOHurtado1419EcuadorB. succulentaB. kitrinaimaQCANowicki1479EcuadorB. succulentaB. kitrinaimaQCAStahl2901EcuadorB. succulentaB. kitrinaimaQCAStahl2901EcuadorB. succulentaB. kitrinaimaMONeill8942EcuadorB. succulentaB. kitrinaimaMOJaramillo13651EcuadorB. succulentaB. kitrinaimaNYJaramillo13651EcuadorB. succulentaB. kitrinaimaQCAJaramillo13651EcuadorB. succulentaB. kitrinaimaMOWebster30455EcuadorB. succulentaB. succulentaMOStein3303ColombiaB. succulentaB. succulentaNYStein3369ColombiaB. succulentaB. succulentaNYPennell5151ColombiaB. succulentaNYPennell5783ColombiaB. succulentaNYLuteyn10545ColombiaB. succulentaNYPennell10685ColombiaB. succulentaNYLuteyn10750ColombiaB. succulentaNY <t< td=""><td>B. succulenta</td><td>B. kitrinaima</td><td>QCA</td><td>Muchhala</td><td>447</td><td>Ecuador</td></t<>	B. succulenta	B. kitrinaima	QCA	Muchhala	447	Ecuador
B. succulentaB. kitrinaimaQCAAntonelli602EcuadorB. succulentaB. kitrinaimaQCANowicki1193EcuadorB. succulentaB. kitrinaimaMOHurtado1419EcuadorB. succulentaB. kitrinaimaQCANowicki1479EcuadorB. succulentaB. kitrinaimaQCAStahl2901EcuadorB. succulentaB. kitrinaimaQCAStahl2901EcuadorB. succulentaB. kitrinaimaMONeill8942EcuadorB. succulentaB. kitrinaimaMOJaramillo13651EcuadorB. succulentaB. kitrinaimaNYJaramillo13651EcuadorB. succulentaB. kitrinaimaQCAJaramillo13651EcuadorB. succulentaB. kitrinaimaQCAJaramillo13651EcuadorB. succulentaB. kitrinaimaMOWebster30455EcuadorB. succulentaB. succulentaMOStein3303ColombiaB. succulentaB. succulentaNYStein3369ColombiaB. succulentaB. succulentaNYPennell5783ColombiaB. succulentaB. succulentaNYLuteyn10545ColombiaB. succulentaB. succulentaNYPennell10685ColombiaB. succulentaB. succulentaNYPennell10685ColombiaB. succulentaB. succulentaNY <td>B. succulenta</td> <td>B. kitrinaima</td> <td>QCA</td> <td>Muchhala</td> <td>454</td> <td>Ecuador</td>	B. succulenta	B. kitrinaima	QCA	Muchhala	454	Ecuador
B. succulentaB. kitrinaimaQCANowicki1193EcuadorB. succulentaB. kitrinaimaMOHurtado1419EcuadorB. succulentaB. kitrinaimaQCANowicki1479EcuadorB. succulentaB. kitrinaimaQCAStahl2901EcuadorB. succulentaB. kitrinaimaMONeill8942EcuadorB. succulentaB. kitrinaimaMOJaramillo13651EcuadorB. succulentaB. kitrinaimaMOJaramillo13651EcuadorB. succulentaB. kitrinaimaNYJaramillo13651EcuadorB. succulentaB. kitrinaimaQCAJaramillo13651EcuadorB. succulentaB. kitrinaimaMOWebster30455EcuadorB. succulentaB. kitrinaimaMOStein3303ColombiaB. succulentaB. succulentaNYStein3303ColombiaB. succulentaB. succulentaNYPennell5151ColombiaB. succulentaB. succulentaNYPennell5783ColombiaB. succulentaB. succulentaNYLuteyn10545ColombiaB. succulentaB. succulentaNYLuteyn10650ColombiaB. succulentaB. succulentaNYPennell10685ColombiaB. succulentaB. succulentaNYLuteyn10750ColombiaB. succulentaB. succulentaNY <td>B. succulenta</td> <td>B. kitrinaima</td> <td>QCA</td> <td>Antonelli</td> <td>602</td> <td>Ecuador</td>	B. succulenta	B. kitrinaima	QCA	Antonelli	602	Ecuador
B. succulentaB. kitrinaimaMOHurtado1419EcuadorB. succulentaB. kitrinaimaQCANowicki1479EcuadorB. succulentaB. kitrinaimaQCAStahl2901EcuadorB. succulentaB. kitrinaimaMONeill8942EcuadorB. succulentaB. kitrinaimaMOJaramillo13651EcuadorB. succulentaB. kitrinaimaMOJaramillo13651EcuadorB. succulentaB. kitrinaimaNYJaramillo13651EcuadorB. succulentaB. kitrinaimaQCAJaramillo13651EcuadorB. succulentaB. kitrinaimaMOWebster30455EcuadorB. succulentaB. succulentaMOStein3303ColombiaB. succulentaB. succulentaNYStein3303ColombiaB. succulentaB. succulentaNYStein3369ColombiaB. succulentaB. succulentaNYPennell5151ColombiaB. succulentaB. succulentaNYPennell5783ColombiaB. succulentaB. succulentaNYLuteyn10545ColombiaB. succulentaB. succulentaNYPennell10650ColombiaB. succulentaB. succulentaNYPennell10650ColombiaB. succulentaB. succulentaNYPennell10650ColombiaB. succulentaB. succulentaNY <td>B. succulenta</td> <td>B. kitrinaima</td> <td>QCA</td> <td>Nowicki</td> <td>1193</td> <td>Ecuador</td>	B. succulenta	B. kitrinaima	QCA	Nowicki	1193	Ecuador
B. succulentaB. kitrinaimaQCANowicki1479EcuadorB. succulentaB. kitrinaimaQCAStahl2901EcuadorB. succulentaB. kitrinaimaMONeill8942EcuadorB. succulentaB. kitrinaimaMOJaramillo13651EcuadorB. succulentaB. kitrinaimaMOJaramillo13651EcuadorB. succulentaB. kitrinaimaNYJaramillo13651EcuadorB. succulentaB. kitrinaimaQCAJaramillo13651EcuadorB. succulentaB. kitrinaimaQCAJaramillo13651EcuadorB. succulentaB. kitrinaimaMOWebster30455EcuadorB. succulentaB. succulentaMYStein3303ColombiaB. succulentaB. succulentaNYStein3303ColombiaB. succulentaB. succulentaNYPennell5151ColombiaB. succulentaB. succulentaNYPennell5783ColombiaB. succulentaB. succulentaNYLuteyn10545ColombiaB. succulentaB. succulentaNYPennell10650ColombiaB. succulentaB. succulentaNYPennell10655ColombiaB. succulentaB. succulentaNYLuteyn10750ColombiaB. succulentaB. succulentaNYLuteyn10750Colombia <tr<tr>B. succulentaB. succulenta<t< td=""><td>B. succulenta</td><td>B. kitrinaima</td><td>MO</td><td>Hurtado</td><td>1419</td><td>Ecuador</td></t<></tr<tr>	B. succulenta	B. kitrinaima	MO	Hurtado	1419	Ecuador
B. succulentaB. kitrinaimaQCAStahl2901EcuadorB. succulentaB. kitrinaimaMONeill8942EcuadorB. succulentaB. kitrinaimaMOJaramillo13651EcuadorB. succulentaB. kitrinaimaNYJaramillo13651EcuadorB. succulentaB. kitrinaimaNYJaramillo13651EcuadorB. succulentaB. kitrinaimaQCAJaramillo13651EcuadorB. succulentaB. kitrinaimaMOWebster30455EcuadorB. succulentaB. succulentaMOStein3303ColombiaB. succulentaB. succulentaNYStein3303ColombiaB. succulentaB. succulentaNYStein3369ColombiaB. succulentaB. succulentaNYPennell5151ColombiaB. succulentaB. succulentaNYPennell5783ColombiaB. succulentaB. succulentaNYLuteyn10545ColombiaB. succulentaB. succulentaNYLuteyn10650ColombiaB. succulentaB. succulentaNYPennell10685ColombiaB. succulentaB. succulentaNYLuteyn10750ColombiaB. succulentaB. succulentaNYLuteyn10761ColombiaB. succulentaB. succulentaNYLuteyn10761ColombiaB. succulentaB. succulentaNY	B. succulenta	B. kitrinaima	QCA	Nowicki	1479	Ecuador
B. succulentaB. kitrinaimaMONeill8942EcuadorB. succulentaB. kitrinaimaMOJaramillo13651EcuadorB. succulentaB. kitrinaimaNYJaramillo13651EcuadorB. succulentaB. kitrinaimaQCAJaramillo13651EcuadorB. succulentaB. kitrinaimaQCAJaramillo13651EcuadorB. succulentaB. kitrinaimaMOWebster30455EcuadorB. succulentaB. succulentaMOStein3303ColombiaB. succulentaB. succulentaNYStein3369ColombiaB. succulentaB. succulentaNYPennell5151ColombiaB. succulentaB. succulentaNYPennell5783ColombiaB. succulentaB. succulentaNYLuteyn7322ColombiaB. succulentaB. succulentaNYLuteyn10650ColombiaB. succulentaB. succulentaNYPennell10685ColombiaB. succulentaB. succulentaNYLuteyn10750ColombiaB. succulentaB. succulentaNYLuteyn10761ColombiaB. succulentaB. succulentaNYLuteyn10761ColombiaB. succulentaB. succulentaNYLuteyn10761ColombiaB. succulentaB. succulentaNYLuteyn10773Colombia	B. succulenta	B. kitrinaima	QCA	Stahl	2901	Ecuador
B. succulentaB. kitrinaimaMOJaramillo13651EcuadorB. succulentaB. kitrinaimaNYJaramillo13651EcuadorB. succulentaB. kitrinaimaQCAJaramillo13651EcuadorB. succulentaB. kitrinaimaMOWebster30455EcuadorB. succulentaB. kitrinaimaMOStein3303ColombiaB. succulentaB. succulentaMYStein3303ColombiaB. succulentaB. succulentaNYStein3369ColombiaB. succulentaB. succulentaNYPennell5151ColombiaB. succulentaB. succulentaNYPennell5783ColombiaB. succulentaB. succulentaNYLuteyn7322ColombiaB. succulentaB. succulentaNYLuteyn10650ColombiaB. succulentaB. succulentaNYLuteyn10650ColombiaB. succulentaB. succulentaNYLuteyn10750ColombiaB. succulentaB. succulentaNYLuteyn10761ColombiaB. succulentaB. succulentaNYLuteyn10761ColombiaB. succulentaB. succulentaNYLuteyn10773Colombia	B. succulenta	B. kitrinaima	MO	Neill	8942	Ecuador
B. succulentaB. kitrinaimaNYJaramillo13651EcuadorB. succulentaB. kitrinaimaQCAJaramillo13651EcuadorB. succulentaB. kitrinaimaMOWebster30455EcuadorB. succulentaB. succulentaMOStein3303ColombiaB. succulentaB. succulentaNYStein3303ColombiaB. succulentaB. succulentaNYStein3369ColombiaB. succulentaB. succulentaNYPennell5151ColombiaB. succulentaB. succulentaNYPennell5783ColombiaB. succulentaB. succulentaNYLuteyn7322ColombiaB. succulentaB. succulentaNYLuteyn10545ColombiaB. succulentaB. succulentaNYLuteyn10650ColombiaB. succulentaB. succulentaNYPennell10685ColombiaB. succulentaB. succulentaNYLuteyn10750ColombiaB. succulentaB. succulentaNYLuteyn10750ColombiaB. succulentaB. succulentaNYLuteyn10761ColombiaB. succulentaB. succulentaNYLuteyn10761ColombiaB. succulentaB. succulentaNYLuteyn10761ColombiaB. succulentaB. succulentaNYLuteyn10773Colombia	B. succulenta	B. kitrinaima	MO	Jaramillo	13651	Ecuador
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•	B. succulenta	B. succulenta	NY	Luteyn	10773	Colombia

B. succulenta	NY	Luteyn	12418	Colombia
B. succulenta	NY	Luteyn	12420	Colombia
B. succulenta	NY	Luteyn	12557	Colombia
B. succulenta	NY	Leisner	16856	Colombia
B. succulenta	MO	Holm-Nielsen	18581	Ecuador
B. succulenta	NY	Holm-Nielsen	18581	Ecuador
B. succulenta	NY	Harling	19211	Ecuador
B. succulenta	NY	Steyermark	52805	Ecuador
B. succulenta	NY	Allart	479	Venezuela
B. succulenta	NY	Luteyn	5177	Venezuela
B. succulenta	NY	Pittier	9317	Venezuela
B. succulenta	NY	Leisner	12386	Venezuela
B. succulenta	NY	Mori	14602	Venezuela
B. succulenta	NY	Steyermark	100250	Venezuela
	 B. succulenta 	B. succulentaNYB. succulentaNYB. succulentaNYB. succulentaMOB. succulentaMOB. succulentaNYB. succulentaNY	B. succulentaNYLuteynB. succulentaNYLuteynB. succulentaNYLuteynB. succulentaNYLeisnerB. succulentaMOHolm-NielsenB. succulentaNYHolm-NielsenB. succulentaNYHarlingB. succulentaNYSteyermarkB. succulentaNYAllartB. succulentaNYLuteynB. succulentaNYLuteynB. succulentaNYLuteynB. succulentaNYMoriB. succulentaNYMoriB. succulentaNYSteyermark	B. succulentaNYLuteyn12418B. succulentaNYLuteyn12420B. succulentaNYLuteyn12557B. succulentaNYLeisner16856B. succulentaMOHolm-Nielsen18581B. succulentaNYHolm-Nielsen18581B. succulentaNYHarling19211B. succulentaNYSteyermark52805B. succulentaNYAllart479B. succulentaNYLuteyn5177B. succulentaNYPittier9317B. succulentaNYMori14602B. succulentaNYSteyermark100250

Province of	Herbarium	Senior	Collection	Original
Collection		Collector	Number	Identification
Cotopaxi	MO	Ramos	6546	Sp.
Cotopaxi	QCA	Nowicki	1498	B. sodiroana
El Oro	QCA	Clark	7944	B. sodiroana
El Oro	MO	Vargas	5171	B. sodiroana
Loja	MO, NY	Cotton	1605	B. sodiroana
Pichincha	MO	Croat	95948	B. sodiroana
Pichincha	QCA	Muchhala	115	B. sodiroana
Pichincha	MO	Neill	9800	B. crispiloba
Pichincha	MO	Gentry	69945	B. crispiloba
Pichincha	MO	Neill	8654	B. sodiroana
Pichincha	NY	Luteyn	13333	B. crispiloba
Pichincha	MO	Webster	30017	B. crispiloba
Pichincha	MO	Rojas	391	Sp.
Pichincha	MO, NY	Holm-Nielsen	24419	B. sodiroana

Appendix 2 List of specimens identified as putative hybrids of *B. crispiloba / B. sodiroana*, showing their province of collection and original identification (on the specimens).

Chapter Two

A TAXONOMIC REVISION OF THE GENUS *BURMEISTERA* (CAMPANULACEAE) IN ECUADOR¹

Brock Mashburn^{1, 3*}, Carmen Ulloa², and Nathan Muchhala³

ABSTRACT

A taxonomic revision of the species of Burmeistera H. Karst. & Triana (Campanulaceae) in Ecuador is presented. Burmeistera is a monophyletic genus of approximately 130 species that occurs from Guatemala to Peru. Most species occur in restricted ranges in mid- to high-elevation cloud forests. Ecuador is second to Colombia in number of species with fifty-two. Twelve new species are recognized and described herein. Three species are newly recorded in Ecuador: Burmeistera asclepiadea Gleason, B. marginata H. Karst., and B. microphylla Donn. Sm. One name is newly placed in synonymy: B. oblongifolia E. Wimm. [=B. pallida (Drake) E. Wimm.]. One synonym is moved: B. succulenta var. latisepala E. Wimm. [=B. sodiroana Zahlbr.]. One name is raised in rank from a variety to a species: B. resupinata var. heilbornii Wimm. [=B. heilbornii (E. Wimm.) Mashburn]. Five names are lectotypified: B. marginata H. Karst., B. millei E. Wimm., B. multiflora Zahlbr., B. succulenta H. Karst & Triana, and B. succulenta var. meiophylla Zahlbr. ex E. Wimm. We provide a taxonomic history of Burmeistera focused on Ecuador, general morphological comments on the genus, and an identification key for all Ecuadorian species. For each of the accepted species, we discuss etymology, geographic distribution, habitat information, diagnostic characters, nomenclatural

comments, and a list of examined specimens. We provide distribution maps for each accepted species, as well as illustrations and photos when available.

¹ This work was developed under the project "Quantifying the roles of pollination and post-pollination barriers in flowering plant speciation: a case study of the diverse Neotropical genus Burmeistera (Campanulaceae)" in the Evolution, Ecology and Systematics Department at the University of Missouri – St. Louis, supported by the National Science Foundation (NSF Grant # 1754802 to N.M.). B.M. thanks Andrea Trigueros for help working with specimens in the herbarium, and Charlotte Taylor and Peter Stevens for valuable advice on the taxonomic process. We thank the Missouri Botanical Garden (MO) for office and working space, and the curators MO, NY, and QCA for access to their herbarium specimens and collection data.

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INTRODUCTION

Burmeistera H. Karst. & Triana is the fourth largest genus of the Campanulaceae subfamily Lobeliodeae with over 130 species (Lammers 2007). Phylogenetic studies consistently confirm the monophyly of *Burmeistera*, and place it sister to two larger Lobelioid genera, *Centropogon* Presl. and *Siphocampylus* Pohl., which have approximately 210 and 230 species, respectively (Antonelli 2008; Knox et al. 2008; Lagomarsino et al. 2014; Lammers 2007; Uribe-Convers et al. 2017). These three genera, known informally as the 'centropogonid clade,' are distinguished from other Lobelioideae by the entire corolla tubes that are neither fenestrate (as in *Lobelia stenocarpa* E. Wimm.) nor dorsally cleft (as in most *Lobelia* species; Lammers 2011). The clade is also identified by corolla lobes that are either monomorphic or dimorphic (the lobes differing in shape and/or color), fused staminal tubes that almost always extend beyond the corolla lobes, and fused anther tubes with bunched hairs on the apex (Lagomarsino et al. 2014; Lammers 1998).

Pre-molecular taxonomies of the centropogonid clade distinguished *Burmeistera*, *Centropogon*, and *Siphocampylus* primarily by fruit type and flower morphology (Gleason 1925; Jeppesen 1981; Lagomarsino et al. 2014). *Siphocampylus* was described as producing capsules, while *Centropogon* and *Burmeistera* produced berries. *Burmeistera* was separated from *Centropogon* by having generally ebracteolate pedicels, and an inflated corolla opening, a wider anther tube opening, and isodiametric seeds (Lagomarsino et al. 2014; Lammers 1998). While phylogenetic studies have upheld the monophyly of *Burmeistera*, they have also shown that *Centropogon* and *Siphocampylus* are extensively paraphyletic (Antonelli 2008; Knox et al. 2008; Lagomarsino et al. 2014), revealing that fruit characters have shifted regularly as the group has evolved.

The genus *Burmeistera* was established in 1854 by Karsten & Triana with the description of the Colombian species *Burmeistera ibaguensis* H. Karst & Triana. The species was published in the book *Nuevos Jeneros i Especies de Plantas para la Flora Neo-Granadina* by José Jerónimo Triana a Colombian botanist, explorer and physician (Triana 1854). Though the book is authored by Triana alone, on page four of the prologue he states, in flowery language not atypical of the time, that German botanist Hermann Karsten is to be attributed with co-authorship of the species described in the chapter entitled *Viaje de Karsten i Triana*. The ambiguity of this co-authorship has led both early and recent taxonomists to treat the genus as *Burmeistera* Triana (Lammers 2007; Moreno & Muchhala 2011; Muchhala & Pérez 2015b; Nash 1976; Stein 1987). It should be noted, however, that Karsten himself treated the genus as *Burmeistera* Karst. et Triana [sic] (Karsten 1856). Interestingly, some early authors, possibly not aware of Triana's 1854 publication, treated the genus as *Burmeistera* Karst. [sic] (Bentham & Hooker 1876; Hemsley 1881).

After the description of the genus, the late 19th century saw the descriptions of a few new species and transfers of species from *Lobelia, Centropogon,* and *Siphocampylus* into *Burmeistera* (Bentham & Hooker 1876; Donnell Smith 1895; Hemsley 1881). Descriptions of new species took off in the early to mid 20th century, as the lobelioids were studied by multiple prolific authors: Austrian botanist Alexander Zahlbruckner (1906, 1915); American botanist Henry A. Gleason (1925); and German botanist Franz Elfried Wimmer (Wimmer 1931, 1932, 1943, 1953, 1956, 1968). Wimmer was the first to propose infrageneric groups in *Burmeistera* (Wimmer 1931). He divided the genus into two subgenera: *Barbatae*, with tufts of hair on the two ventral anther tips and glabrous dorsal anther tips, and *Imberbes*, with anther tips entirely glabrous or each tip equally pubescent. Wimmer's monograph of the genus in 1943 recognized 77 species, and was the only genus-wide treatment.

The latter half of the 19th century continued to see new species discovered and published, though large treatments of the group shifted to country-specific works as floras of these nations were produced: Guatemala (Nash 1976), Costa Rica (Wilbur 1975), Panama (Wilbur 1975, 1981), Ecuador (Jeppesen 1981), and Peru (Stein 1987). More recently, checklists have been produced for various countries, such as Colombia (Bernal et al. 2016), and for the Americas as a whole (Ulloa Ulloa et al. 2017). In the beginning of this century, new species continue to be discovered and described at a rate seemingly unchanged from a century ago (Lagomarsino et al. 2015; Lammers 2002; Muchhala & Lammers 2005; Muchhala & Pérez 2015b; Rodríguez & Solano Peralta 2018; Vallejo et al. 2018; Venegas & González 2012; Venegas et al. 2013, 2014). Recent counts put the number of *Burmeistera* species at approximately 120 (Ulloa Ulloa et al. 2017). With the new species in this treatment, that number will rise to over 130, likely approaching 140 species.

The advent of molecular phylogenetic techniques have shifted our understanding of the relationships and evolutionary history of *Burmeistera*. Though the genus has been confirmed as monophyletic, the infrageneric groups proposed by Wimmer are not (Lagomarsino et al. 2014; Uribe-Convers et al. 2017). Uribe-Convers et al. (2017) identified three clades with a single apomorphy each: a bibracteate pedicel clade, an

inflated fruit clade, and a recurved corolla clade. Otherwise, many morphological traits within *Burmeistera* seem quite labile. As a result, no new infrageneric groupings have been proposed.

In Ecuador, the last country-wide taxonomic treatment of *Burmeistera* was by Stig Jeppesen for the publication of the Flora of Ecuador (Jeppesen 1981), in which he recognized 31 species. Since then, nine new species have been described from Ecuador, most recently *Burmeistera pterifolia* A. F. Vallejo et al., and *Burmeistera draconis* Á. J. Pérez & Muchhala (Vallejo et al. 2018). Our treatment presented here recognizes an additional 12 species newly described in Ecuador, as well as three newly recorded, bringing the total number of species in the country to 52. Collections since 1981 have not only discovered new species, but have also increased our understanding of the geographic and morphological variations of the group. For example, Jeppesen's treatment cited 309 specimens, while this treatment made use of nearly 1000 specimens. In the introduction to his 1981 treatment, Jeppesen stated: "A revision of the genus throughout the area of distribution is badly needed." Consequently, in the taxonomic revision presented here, we aim to improve and clarify the taxonomy and delimitations of the species of *Burmeistera* in Ecuador.

MATERIALS AND METHODS

The physical specimens used in this study come from the following herbaria: the Missouri Botanical Garden, St. Louis, Missouri, USA (MO); the New York Botanical Garden, New York, New York, USA (NY), and Pontificia Universidad Católica del Ecuador, Quito, Ecuador (QCA). When necessary, digital scans specimens were accessed

from the following online herbaria: the University of Gothenburg, Gothenburg, Sweden (GB); the Royal Botanic Gardens, Kew, England (K); the Swedish Museum of Natural History, Stockholm, Sweden (S); Muséum National d'Histoire Naturelle, Paris, France (P); and the Naturhistorisches Museum Wien, Vienna, Austria (W); or from the Global Plants database on JSTOR (JSTOR). Specimens that were studied through digital images are indicated by 'digital image!' in the text. All specimens examined for each species are presented following the species descriptions and relevant discussion. For type specimens, phenological phases are indicated as flowering (fl.) and/or fruiting (fr.). If a type specimen was sterile, no indication is given.

Species understandings and relationships are informed by previous phylogenetic work, but species circumscriptions here are based on the presence of shared morphological features. Every attempt was made to avoid describing species using characters that are considered variable in *Burmeistera* or difficult to perceive in the field or on specimens, such as the presence of minute hairs on vegetative parts, the hairs on the tips of anthers, or natural variation in flower colors. Many species of *Burmeistera* are known from only a few collections. We avoided describing new species from one or a few specimens unless multiple characters were available to differentiate it from similar species. In this way, we avoided the recognition of species differentiated by only a single character.

Plant habit descriptions stem from collector observations on specimen labels and observations in the field. Stem width measurements are taken from the widest available stem material from the species. Vegetative measurements were taken from adult plants, avoiding immature growth at the apex of stems. Floral measurements were taken from

mature flowers at anthesis. The process of drying and pressing specimens sometimes causes *Burmeistera* flowers to open. We attempted to avoid these obvious outliers in measurements of floral size. As *Burmeistera* fruits continue to expand as they mature, we took measurements of fruit size only from the largest fruits available for each species. This was done to avoid writing descriptions that make mature fruits seem extremely variable in size. Hair terminology follows Beentje (2016). Color descriptions on specimen labels vary widely, often depending on the perspective of the collector. We attempted to unify and simplify color descriptions as much as possible, though when descriptions are incompatible, we maintain both. We avoid, as much as possible, the use of color vocabulary that is easily misunderstood. For example, we avoid the use of the term magenta, opting instead to use terms like dark-violet or red-violet as much as possible. We choose to use the term violet here, though collectors often use purple. Violet is a spectral color that has its own wavelength, while purple is a combination of red and blue. Practically, though, our use of violet here encompasses the common term purple.

Geographic distribution maps were produced in the program R (R Core Team 2018), using the packages 'ggplot' (Wickham 2016), 'raster' (Hijmans 2019) 'sf' (Pebesma 2018), and 'tmap' (Tennekes 2018). GPS coordinates were taken as provided on herbarium specimen labels. When none were provided, coordinates were estimated using the directions given on specimen labels and Google Maps (Google).

RESULTS

VEGETATIVE MORPHOLOGY

Ecuadorian *Burmeistera* are generally scandent herbaceous shrubs; they sprawl on existing vegetation without twining, holdfast roots, or the use of tendrils. Stems can reach lengths of six or more meters. Plants often have many-branching shoots coming from the base, and thus are often described as shrubby. Many collections describe plants as epiphytic, though very few *Burmeistera*, if any, actually are. Plants can be perceived as epiphytic because they tend to drop mature leaves, leaving green growth near the apical shoots; thus all that is visible to the collector is vegetative growth emerging from above, unconnected to the ground. It is possible that stems adventitiously root into moist, hummus rich crevices in large plants. Many species are not scandent at all, instead remaining shrubby and close to the ground. These tend to be larger leaved species with reduced bracts, such as *B. racemosa, B. lutosa, B. multiflora,* and *B. brighamioides*.

Burmeistera stems are hollow and generally herbaceous, though sometimes becoming semi-woody and tough. All parts of the plant, but especially the stems, exude latex. In some species this latex can be quite profuse (*B. succulenta*). Latex is often white, cream or tan, rarely bright yellow (*B. kitrinaima*). Stems often twist to adjust leaves, complicating the identification of leaf phyllotaxy (discussed below).

Leaf phyllotaxy is the pattern arrangement of the petiole attachement on the stem. All *Burmeistera* have alternate phyllotaxy (vs. opposite), as two leaves never arise from the stem at the same node. However, *Burmeistera* leaves are either distichous or spiral. An alternate, distichous phyllotaxy, also called "two-ranked," is when leaves are arranged along two columns, consistently alternating 180 degrees on the other side of the stem. Meanwhile, spiral phyllotaxy is when leaves arise at a different point along the stem.

Often, herbarium specimens are pressed flat and/or plant stems turn as they grow, making it difficult to identify distichous vs. spiral phyllotaxy. For *Burmeistera*, it is useful to follow the vertical striations of the stem, noting whether alternating leaves arise from the same striation (distichous) or randomly on the stem (spiral). This is a consistent within species character and, because many vegetative characters on *Burmeistera* are hard to define, we have taken the liberty of using phyllotaxy as a primary diagnostic character for the group.

Leaves of mature Ecuadorian *Burmeistera* are always simple. Leaves of juvenile (pre-reproductive) plants are rarely collected, but field observations predict that many species may be heterophyllous. Leaf petioles are estipulate. They are sometimes decurrent on the stems, causing stems to look slightly winged. Leaf venation varies widely in the group. A few species are readily identifiable with help from their venation: *B. crassifolia*, *B. microphylla*, *B. marginata*, and *B. holm-nielsenii*. Leaf margins are always crenate, dentate, or serrate, never entire, with callose-tipped teeth. Often, the teeth can be quite reduced, making the margin seem nearly entire. In this case teeth are identifiable by the intramarginal callosities of the reduced teeth.

Indumentum types vary widely in *Burmeistera*, from soft, puberulent or villose hairs to tough, callose strigose or hispid hairs. In all but one species, hairs are simple and uniseriate or unicellular. The one exception is *B. arbusculifera*, which has callose, stellate hairs. Hairs are often white, cream, tan, or yellow, though in *B. catula* they are tipped with violet. Indument can appear on any part of *Burmeistera* plants, though most often it is found on the underside of leaves, especially along primary and secondary veins. Only a
few species are entirely glabrous on their vegetative parts: *B. succulenta, B. crispiloba, B. sodiroana,* and *B. melanocarpa*.

REPRODUCTIVE MORPHOLOGY

Burmeistera flowers are always solitary, held on pedicels emerging from the axils of leaves near the apical part of a growing stem. When stems enter a reproductive phase, a flower emerges from the axil of every new leaf. The internodes between leaves may stay the same as when growing vegetatively. In this case, the reproductive stem often shows every stage of the reproductive cycle, with flower buds at the apex, then mature flowers, immature fruits, and mature fruits progressively lower. However, sometimes a growing stem in fertile phase may extend more slowly. In this case, the internodes are more closely packed than when growing vegetatively, and flowers appear bunched apically. Pedicels may be equally long, held perpendicular to the stem, or longer on slightly older flowers, and held upright. This formation causes stems to appear as racemose or corymbose inflorescences.

Leaves subtending flowers are often similar in size to sterile leaves, though they may appear smaller because they are still immature. However, in some species, these leaves are noticeably reduced in size, never reaching the size of mature, sterile leaves. These reduced leaves subtending flowers are sometimes called bracts, depending on the severity and consistency of their reduced size. In some species, these bracts are reduced to only a few millimeters long, and may even be caducous (e.g. *B. multiflora, B. racemiflora*). Ontologically, inflorescences are not terminal. Thus, stems may go through repeated visibly sterile and fertile phases.

Generally speaking, *Burmeistera* with a terrestrial, shrubby habit tend to have larger basal leaves, spiral phyllotaxy, and stems with reduced internodes and bracts. Species with a scandent habit tend to have more uniformly sized leaves, distichous phyllotaxy, and non-reducing internodes or bracts (Knox et al. 2008).

Burmeistera are universally monoecious with perfect flowers. Flowers are zygomorphic, and tend to be colored green to shades of violet. Flowers are held on erect pedicels that hold flowers and fruits upright, away from stems and leaves. In Ecuador, only one species has pedicels with two small, basal bracteoles (*B. formosa*), while the rest are ebracteolate. Ovaries are inferior and surrounded by a hypanthium that emerges from the pedicel. The shape of the hypanthium is obconical, cupuliform, or urceolate. It has 10 ridges that can be prominently raised. Sometimes the hypathium is barely distinguishable from the pedicel (*B. holm-nielsenii*), and this morphology often results in long, narrow fruits. Hypanthium shape is a consistent feature in *Burmeistera* species, and is thus an often used identification character.

The perianth of *Burmeistera* is heterochlamydeouos, with a distinct calyx and corolla, and is 5-merous. The calyx lobes are held ascending, covering the basal portion of the corolla, patent, in a whorled fan-like shape, or reflexed, covering the hypanthium below. They vary widely in size and shape, from reduced, almost non-existent (e.g. *B. crispiloba*), long and linear or ligulate (e.g. *B. smaragdi, B. kitrinaima*), foliaceous (*B. auriculata, B. lingulata, B. borjensis*), to the unique comb-shaped calyx lobes of *B. holm-nielsenii*.

The corolla of *Burmeistera* species is epigynous, emerging from the distal end of the hypanthium, fused basally. This fused section often bulges just above the base, inside

of which the nectaries are held. The corolla tube then narrows noticeably before abruptly expanding again just before the corolla lobes separate from each other. The single ventral lobe separates downward, providing an opening to the interior of the fused corolla tube. The two lateral lobes then separate from the two dorsal lobes further up, before the two dorsal lobes separate from each other. These lobes typically turn downwards, away from the dorsal side of the flower, and are falcate, with the dorsal lobes longer than the lateral and ventral lobes. This shape has been compared to the clenched iron glove of a knight (Jeppesen 1981). In a few species, the corolla lobes curl or scroll backward: *B. crispiloba, B. sodiroana*, and *B. succulenta*.

The five filaments emerge from the flattened top of the ovary, initially separate but quickly fusing to form a hollow connate tube. This tube emerges from corolla, extending along the dorsal plane of the flower. The connate filament tube merges into a connate anther tube. The anther tube is often different from the filament tube in color and indumentum. The anther tube then curves downward, in order to present and receive pollen from the heads of pollinators. The tips of the anther tube are variously hairy, sometimes with tufts of hairs only on the two shorter, ventral anthers, or with no or sparse hairs on all five anther tubes. Many Lobelioids have hairs at the tip of anther tubes, and these serve as a critical part of the pollinator to release pollen (Stein 1992). The widened anther opening in *Burmeistera* possible allows more pollen to be deposited on a pollinator, but has led to a loss of the trigger function. Thus, these hairs are likely a vestigial character (Knox et al. 2008; Stein 1987). Instead the anthers dehisce pollen inwardly, and the emerging style pushes pollen outward as it grows. *Burmeistera* pollen have not been documented.

The ovaries of *Burmeistera* are inferior, often with a flat top. The two ovules are attached via axile placentation in a unilocular ovary. The style grows from the ovary inside the filament and anther tube. At this point, the two stigma lobes are unreceptive and curled inward. As the style grows, it pushes pollen grains out of the anther tube. This is the male phase of the flower. The style then pushes out of the anther tube and the stigma lobes unfurl, presenting a distinct female phase of the flower.

After fertilization, the perianth and style of the flower fall away, leaving the hypanthium, ovary, and persistent calyx lobes. Fruits of *Burmeistera* are berries, in which the outer layer of the ovary becomes fleshy. Fruits are cylindrical, globose, or obovoid. They are rarely hairy, but range widely in color, from green to white, violet, yellow, red, or bright blue. In mature fruits, the fruit wall thickens to varying degrees, becoming spongy. Many species, including an entire clade (Uribe-Convers et al. 2017), produce large, inflated fruits, in which the unilocular interior of the fruit continues to expand with empty space, while the fruit wall remains ca. 1-3 mm thick. Seeds are numerous and small, often sticky, 0.6–1.4 mm long, oblong, ovoid, or fusiform, sometimes slightly flattened, the surface usually longitudinally foveate-reticulate, sometimes striate or isodiametrically foveate-reticulate.

GEOGRAPHIC DISTRIBUTION

Species of the genus *Burmeistera* are distributed in the American tropics from Mexico to Peru. The highest density of species is found from Costa Rica to Ecuador, with

only one species north of this range, in southern Mexico, Honduras, and Guatemala (*B.virescens* (Benth.) Benth. & Hook. f. ex. Hemsl.; Lammers & Maas 1998; Nash 1976), and two to four species south of Ecuador, in northeast Peru (Lammers 2007; Stein 1987). The Huancabamba Depression, an east-west depression that separates the Northern Andes and the Central Andes in northern Peru (see Weigend 2002), represents the southernmost limit of the genus. To the east, the genus reaches into Venezuela. However, all known species are found within Costa Rica, Panama, Colombia, or Ecuador. Just under half of all species (~60) are found in Colombia, with 52 in Ecuador and ~21 along the Cordillera de Talamanca of Panama and Costa Rica (Lagomarsino et al. 2015; Venegas et al. 2014). A handful of species are widespread (e.g. *B. cyclostigmata, B. microphylla*), but the majority of species occur in narrowly restricted ranges.

Within Ecuador, 52 species are known to occur and are described in this treatment. However, a number of unique, but incomplete, specimens with only a few collections suggest that this number will continue to grow. Most species are found in central or northern Ecuador, and diversity drops off significantly south of ca. 02°00'S. This latitude, known as the Girón-Paute Valley, a transversal deep dry valley, is a geographical barrier for plant distribution (see Jørgensen et al. 1995; Paredes-Burneo et al. 2018; Quintana et al. 2017). Only eight species are found south of this line. Roughly one-third of species are found east of the Andes, the other two-thirds occurring west of the Andes and north of ca. 01°00S.

In Ecuador, and throughout its range, *Burmeistera* species are commonly found in wet, medium- to high-altitude cloud forests, from 1000 to 3000 m in elevation. East of the Andes, only a few species (e.g. *B. glabrata, B. refracta, B. pallida*) occur at

elevations lower than 1000 m, at the footsteps of the Amazon rainforest. West of the Andes, more species occupy lower elevations (*B. brachyandra, B. crispiloba, B. cyclostigmata, B. domingensis, B. pacifica*), but even these are still more likely to be found near or above 500 m in elevation. Interestingly, many of these species that occupy this region of Ecuador are found in a disjunct distribution, along the western foothills of the Andes, and again in higher elevation areas along the Pacific coast in the Chongón Colonche and Mache Chindul Ranges. This distribution has led to some morphological variation between geographic groups, likely evidence of incipient speciation.

As in most areas of the world, plant collections in Ecuador are primarily made along roadsides or in reserves accessible by car. This means that many primary forests have not been explored and, due to the often narrow ranges of species, leads us to assume that many more species of *Burmeistera* are still to be discovered in Ecuador. For example, a recent collecting trip in the provinces of Carchi and Pichincha by N. Muchhala and J. Gruhn resulted in the discovery of four new species within three days (*B. catula, B. chrysothrix, B. crocodila,* and *B. velutina*). Collecting trips targeting other poorly collected areas in Ecuador may yield similar results.

TAXONOMIC TREATMENT

Burmeistera H. Karst. & Triana, Nuev. Jen. Esp. 13. 1854. TYPE: *Burmeistera ibaguensis* H. Karst & Triana.

Herbaceous, suffrutescent plants, often scandent, though without twining or tendrils, terrestrial, not epiphytic, though often reported as such. Latex always present, usually white to cream, rarely yellow. *Leaves* cauline, simple, alternate, arranged spirally or distichous. *Flowers* zygomorphic, solitary in upper leaf axils, sometimes crowded apically in corymbiform or racemose bracteate inforescenses. Pedicels most often ebracteolate, erect, holding flowers and fruits away from stems and leaves. Calyx adnate to the ovary forming a hypanthium, this structure cupuliform, urceolate, or obconical, with 10 longitudinal ridges. Calyx lobes five, emerging from the distal end of the hypanthium, small, almost nonexistent, to foliaceous, ascending, patent, or reflexed at anthesis. Corolla epigynous, usually green tinged, spotted, or suffused with red, violet, or maroon violet; the five corolla lobes fused basally, forming a cylindrical tube that is widest at or just above the base, then narrowing before the fused lobes separate; the single ventral lobe separating first, followed by the two lateral lobes, then the two dorsal lobes, the tube abruptly widening where the lobes separate; all five calyx lobes triangular to linear, the ventral and lateral lobes often distended where separating, shorter than the dorsal lobes, all the lobes usually turning downward away from the dorsal side of the flower, though sometimes curling or scrolling backward. Androecium a connate tube, the 5 filaments distinct only near the base, quickly fusing, emerging from the corolla opening; the anthers a connate tube, abruptly curving at the base away from the dorsal side of the flower, oblique and open distally, the anther tips all equally hairy, or the two shorter, ventral anther tips often more densely hairy than the three longer, dorsal anther tips, the anther tips separating and curling back with age or upon drying, the anthers dehiscing inwardly. Gynoecium, the ovary inferior and bilocular, the top often flat,

placentation axile; the style jointed just above the ovary, growing inside the filament tube, pushing pollen from the interior of the anther tube, upon emerging from the anther tube, opening with two lobes, deciduous with the corolla and stamens from the fruit. *Fruits* baccate, globose, obovoid, to cylindrical, often much inflated and filled with air at maturity, the outer wall thin and dry to thick and fleshy, blue, red, yellow, white, or dark violet, though most often green to green tinged with violet or maroon, the calyx lobes persistent in fruit; seeds numerous, small, 0.6–1.4 mm long, oblong, ovoid, or fusiform, sometimes slightly flattened, the surface usually longitudinally foveate-reticulate, sometimes striate or isodiametrically foveate-reticulate.

Species of *Burmeistera* can be distinguished from all other Neotropical Lobelioideae by a unique combination of features, including the entire corolla tubes that are neither fenestrate nor dorsally cleft (as in *Lobelia*), fused staminal tubes almost always extending beyond the corolla, the baccate fruits (not capsules), generally ebracteolate pedicels, the inflated opening where the corolla lobes separate, a wider anther tube opening, the style deciduous with the corolla and androecium, and isodiametric seeds.

TAXONOMIC KEY TO THE SPECIES OF BURMEISTERA IN ECUADOR

1. Phyllotaxy alternate, spiral.

2. Stems and underside of leaves with tan, callose, stellate trichomes with

2. Stems and leaves glabrous or with simple hairs.

3. Mature leaves oblanceolate, over 200 mm long; underside of leaves with yellow to tan hairs.

4. Calyx lobes 2–3 mm long; androecium ca. 72 mm long9. B. brighamioides

4. Calyx lobes 10–15 mm long; androecium 35–37 mm long...... 42. B. racemiflora

3. Mature leaves ovate, elliptic, lanceolate, or, if oblanceolate, not more than 180

mm long; underside of leaves glabrous or with white to cream hairs.

5. Leaves subtending flowers progressively reducing to less than 1/5 the size of mature leaves.

6. Vegetative parts entirely glabrous.

7. Corolla lobes falcate, turning away from the dorsal side of the flower, the

interior green...... 1. B. anderssonii

6. Vegetative parts minutely puberulent to villose, especially on new growth.

8. Corolla glabrous.

9. Leaves and bracts elliptic; plants occurring west of the Andes.

5. Leaves subtending flowers of similar size compared to other immature leaves, not reducing noticeably.

12. Stems and underside of leaves pubescent to villose, hairs visible with the naked eye.

15. Leaves ovate-lanceolate with a long, tapering apex $10-20 \times 0.5-2$ mm, the margin shallow callose-dentate, nearly entire; venation

15. Leaves ovate to elliptic without a long tapering apex, if ovate-lanceolate, the margin irregularly crenate with teeth up to 4 mm long; venation not brochidodromous.

16. Corolla entirely green; fruits ca. 15×15 mm, not inflated; plants occuring west of the Andes.

17. Calyx lobes $10-15 \times 5-9$ mm, foliaceous, lanceolate; fruits maturing yellow

17. Calyx lobes $4-10 \times 1.5-3$ mm, ligulate; fruits red 39. *B. pacifica*

16. Corolla green suffused with violet to entirely violet; if corolla entirely green,

fruits ca. $25-45 \times 25-45$ mm, inflated, and plants occurring east of the Andes.

18. Fruits cylindrical, maturing light blue to blue-violet; plants occurring west of

the Andes17. B. cyclostigmata

18. Fruits globose, inflated, maturing green to maroon-violet; plants occurring

east of the Andes.

21. Corolla green with violet along the margins; calyx lobes $2-3 \times ca. 1 \text{ mm}$,

21. Corolla green spotted or suffused with violet; calyx lobes longer than 4 mm.

22. Leaf margin irregularly serrate, the teeth up to 4 mm long; calyx lobes 11–18

22. Leaf margin crenate or serrate; if serrate and calyx lobes longer than 11 mm,

then the teeth not more than 1 mm long.

24. Leaf margin crenate or serrate, the teeth alternating in size; hypanthium
cupuliform
24. Leaf margin entire or serrate, the teeth uniform in size; hypanthium turbinate.
25. Stem glabrous; the leaf margin serrate, tinged violet; the calyx lobes
ascending at anthesis
25. Stem minutely puberulent, especially on new growth; the leaf margin repand,
not clearly serrate or crenate; the calyx lobes reflexed at anthesis
1. Phyllotaxy alternate, distichous (two-ranked).
26. Leaves thick, coriaceous, the tertiary veins not visible on the underside of the
leaf.
27. Leaves ovate, rarely more than 2× longer than wide 14. <i>B. crassifolia</i>
27. Leaves lanceolate to narrowly elliptic, at least $2.5 \times$ longer than
wide
26. Leaves normal, the tertiary veins visible on the underside of the leaf.
28. Underside of leaves with a strong, submarginal collecting vein, similar in size
to secondary veins.
29. Calyx lobes 15–20 mm long, the margin fimbriate or dentate 25. B. holm-nielsenii
29. Calyx lobes 1–3 mm long, the margine entire
28. Underside of leaves without a strong, connected submarginal collecting vein.
30. Stems and both leaf surfaces covered equally with hairs.
31. Leaves narrowly elliptic to oblanceolate, covered in long, soft, appressed,
translucent-white to violet-tinged articulate hairs
31. Leaves ovate to lanceolate, covered in coarse, stiff, yellow to tan

hairs
30. Stems and both leaf surfaces not entirely covered with hairs.
32. Leaves ovate, mature leaf blades never longer than 40 mm.
33. Flowers pale green tinged pink or pale red, the hypanthium 2–3 mm wide,
narrowly obconical, the calyx lobes ca. 0.5 mm wide, linear, patent to reflexed at
anthesis
33. Flowers green suffused with dark violet, the hypanthium 4–8 mm wide,
broadly obconical to cupuliform, the calyx lobes 3-4 mm wide, ligulate,
ascending to patent at anthesis.
34. Leaf margin sharply serrulate, tinged violet, the androecium ca. 18 mm long,
exserted ca. 11 mm from the corolla opening
34. Leaf margin bluntly serrate to crenate, green, the androecium 30–31 mm long,
exserted 18–19 mm from the corolla opening 4. B. aspera
32. Leaves not ovate, mature leaf blades much longer than 40 mm, or when ovate,
mature leaf blades much longer than 40 mm.
35. Leaf margin pinnatilobate
35. Leaf margin not pinnatilobate.
36. Leaf margin erose, the teeth irregular in size and curved or pointing in
different directions
36. Leaf margin serrate or crenate, the teeth uniform in size.
37. Stems and underside of leaves covered with tan to yellow hairs.
38. Flowers 15–18 mm long, the corolla red, the calyx lobes 4–5 mm long 28. <i>B. jostii</i>

38. Flowers 32–37 mm long, the corolla green to green tinged marron-violet, the		
calyx lobes 15–23 mm long	. 51. B. velutina	
37. Stems and underside of leaves glabrous or, if pubescent, with translusc	ent or	
white hairs.		
39. Calyx lobes 7–9 mm wide, foliaceous, ovate or rhomboid.		
40. Leaves ovate to elliptic, the margin callose-serrate with relatively large	,	
forward pointing, rounded teeth	.5.B. asplundii	
40. Leaves lanceolate, the margin repand-crenate	6. B. auriculata	
39. Calyx lobes less than 5 mm wide, ligulate, linear, or deltate.		
41. Leaves lanceolate.		
42. Calyx lobes 3–5 mm wide, strongly reflexed in bud and at anthesis, gre	een	
heavily suffused with red-violet45.	B. rubrosepala	
42. Calyx lobes 1–2 mm wide, ascending at anthesis, green to green lightly	v tinged	
violet.		
43. Androecium ca. 58 mm long, exserted ca. 36 mm from the corolla		
opening44	4. B. resupinata	
43. Androecium 29–34 mm long, exserted 24–30 mm from the corolla		
opening	.50. B. truncata	
41. Leaves elliptic or ovate.		
44. Calyx lobes less than 3 mm long, deltate.		
45. Leaves narrow, at least $4 \times$ longer than wide, and roccium 26–32 mm lo	ng,	
exserted 17–20 mm from the corolla opening 18. B	. cylindrocarpa	

45. Leaves rarely $4 \times$ longer than wide, if so, androecium greater than 35 mm long, exserted greater than 23 mm from the corolla opening.

Burmeistera anderssonii Jeppesen, Fl. Ecuador 14: 26, fig. 2B. 1981. TYPE: Ecuador.
 Sucumbios: Santa Bárbara-La Bonita road, ca. 2400 m, 05 Mar. 1974 (fl.), *G. Harling & L. Andersson 12511* (holotype, GB [barcode] 0047975 digital image!; isotype, AAU digital image!).

Terrestrial herbaceous shrubs, 1.5 m. *Latex* unknown. *Stems* ca. 7 mm wide, green to cream colored, glabrous, with distinct sterile and fertile zones, the latter with reduced leaves (bracts) and shorter internodes. *Leaves* alternate, spiral, the sterile zone internodes 15–45 mm; petioles 10–20 mm, green tinged violet, glabrous; lamina 70–95 × 28–38 mm, elliptic, the base cuneate, the apex acute, the margin shallow callose-dentate, nearly entire, the teeth often intramarginal, tinged violet; adaxial surface green, glabrous; abaxial surface green, glabrous; venation camptrodromous, the primary and secondary veins prominent, raised but flat, the tertiary veins visible. *Flowers* 36–39 mm, bunched apically with new fertile zone growth, appearing corymbiform or racemose, the bracts initially similar in size to sterile leaves, quickly reducing to 5–6 × 0.5–1.5 mm, caducous or persistent, the internodes 2–11 mm; pedicels 40–50 mm at anthesis, 65–75 mm in fruit, green to violet, glabrous; hypanthium 8–10 × 4–6 mm, narrowly cupuliform, green tinged violet, glabrous, the ridges smooth, faintly visible; calyx lobes ca. 2.5 × 2 mm, deltate,

green tinged violet, glabrous, the margin entire, the apex rounded, ascending to patent at anthesis; corolla green tinged or spotted with red-violet, glabrous; corolla tube 6–7 mm wide basally, bulging just above the base, narrowing to 3.5-4.5 mm; corolla lobes lanceolate, the margins smooth, the two dorsal lobes $14-15 \times 3-4.5$ mm, opening dorsally 14–16.5 mm from the corolla base, slightly falcate, the two lateral lobes $10-11 \times 3.5-4.5$ mm, falcate, the ventral lobe $8.5-9.5 \times 5-5.5$ mm, opening ventrally 7–8 mm from the corolla base; androecium 28–30 mm, exserted 21-22.5 mm from the ventral opening, the filament tube green, sparsely puberulous with white hairs, the anther tube ca. 6×4 mm, green, tinged with violet between the sutures, glabrous, all five anther tips sparsely villose; the style and stigma cream colored. *Fruits* ca. 30×25 mm, globose, inflated, green.

Phenology. This species has been collected with flowers and fruits in March and April.

Distribution. This species has been collected in Sucumbios Province of Ecuador near the border of Colombia, between the towns of Santa Bárbara and La Bonita.

Discussion. Morphologically, *B. andersonii* is closely related to *B. ceratocarpa* and *B. asclepiadea*. It is differentiated from *B. ceratocarpa* by the much smaller bracts. It is differentiated from *B. asclepiadea* by being entirely glabrous on the vegetative parts and by the smaller, narrow bracts, shorter calyx lobes, and larger fruits.

Occurring in a very narrow distribution with few collections recorded. It is interesting that the distribution of *B. asclepiadea* overlaps that of *B. anderssonii*, though it is uncertain if they co-occur. Additional collections in this area are needed.

Additional specimens examined. ECUADOR: **Sucumbíos**: Km 40 from El Carmelo on road towards La Bonita, ca. 5 km below La Alegría, 2350 m, 00°35'N, 77°30'W, 08 Apr. 1979, *Lojtnant et al. 11910* (AAU).

2. Burmeistera arbusculifera Lammers, Novon 12(2): 207–208, fig. 1. 2002. TYPE:
Ecuador. Charchi: Espejo, El Gualtal, Cerro Golondrinas Hembra, 2800 m, 00°51'N,
78°08'W, 21 Aug. 1994 (fl.), *W. Palacios & J. Clark 12465* (holotype OSH [barcode] 30
digital image!; isotypes, MO [bc] 4917512!, QCNE [bc] 131 digital image!).

Herbaceous shrubs to scandent herbs, 2 m. *Latex* white. *Stems* ca. 6 mm wide, green, covered in tan, callose, stellate trichomes with enlarged bases, verrucose on mature growth with only the enlarged bases persisting. *Leaves* alternate, spiral, the internodes 15-25 mm; petioles 3-10 mm, green, verrucose; lamina $25-65 \times 10-25$ mm, ovate to ovate-lanceolate, the base cuneate to rounded, the apex attenuate, the margin callose-serrate, the teeth often intramarginal; adaxial surface green, sometimes tinged violet along the margin, glabrous; abaxial surface white to pale green, covered with tan stellate trichomes, especially on the veins; venation craspidodromous to camptodromous, the primary and secondary veins prominent, slightly raised, the tertiary veins barely visible. *Flowers* ca. 34 mm, solitary in the upper leaf axils; pedicels 20-25 mm at anthesis, 20-30

mm in fruit, green to green suffused with violet, glabrous; hypanthium 7–10 × 4–5 mm, obconical, green, glabrous, the ridges smooth to slightly raised; calyx lobes 7–11 × 2–3.5 mm, ascending to patent at anthesis, reflexed in fruit, lanceolate, green to green suffused with violet, glabrous, the margin shallow callose-serrate with 5–11 teeth, the apex acute; corolla green irregularly blotched with violet, glabrous; corolla tube ca. 6 mm wide basally, the throat narrowing to 2–3 mm; corolla lobes lanceolate, the margins slightly undulate, the two dorsal lobes $11-12 \times 3-4$ mm, opening dorsally 12-13 mm from the corolla base, falcate, the two lateral lobes $9-10 \times 4-5$ mm, slightly falcate, the ventral lobe ca. 8.5×3.5 mm, opening ventrally ca. 7 mm from the corolla base, falcate; androecium ca. 28 mm, exserted ca. 20 mm from the ventral opening, the filament tube green, glabrous, the anther tube ca. 5×3 mm, green, glabrous, the two ventral anther tips sparsely pubescent; the style and stigma cream-colored, the stigma lobes fringed with short white hairs. *Fruits* unknown.

Phenology. This species has been collected with flowers in July and August. Fruits have not been collected.

Distribution. This species is known from only two collections not far from each other in Ecuador. It is found in Carchi province in wet, high elevation elfin forest in the vicinity of Cerro Golodrinas.

Discussion. Though known from only two collections, the distinctive hairs of *B*. *arbusculifera* set it apart from any other species of *Burmeistera*, although certain sections

of *Centropogon* and *Siphocampylus* also have arbusculiform hairs. *Burmeistera arbusculifera* is found geographically close to *B. aspera* (Imbabura province and S Colombia), and shared characters of the species hint at their close relationship: habit, size and shape of leaves, length of pedicels, shape and margin of calyx lobes, and corolla pigmentation. However, *B. arbusculifera* is differentiated by its arbusculiform hairs (vs. simple or articulate in *B. aspera*), obconical hypanthium (vs. cupuliform), slightly shorter androecium length (28 vs. 30–31 mm), and slightly longer exsertion length (20 vs. 18–19 mm). *Burmeistera arbusculifera* can also be confused with *B. knaphusii*, but is differentiated from the latter by the presence of arbusculiform hairs (vs. simple or articulate), leaves 10–25 mm wide (vs. 8-15 mm), calyx lobes 2–3.5 mm wide (vs. 0.5 mm), and corolla tube opening ca. 7 mm from the base (vs. 14–16 mm).

Additional specimens examined: ECUADOR. **Carchi:** Cerro Golondrinas, valley bottom ca. 1.5 km NNE of summit, 2750 m, 00°51'52"N 78°08'10"W, 25 Jul. 1994, *Boyle et al. 3451* (MO).

3. Burmeistera asclepiadea Gleason, Bull. Torrey Bot. Club 52(3): 103. 1925. TYPE:
Colombia. Huila: Balsillas, on Río Balsillas, 2100–2200 m, 3–5 Aug. 1917 (fl., fr.), H. H.
Rusby & F. W. Pennell (holotype, NY [barcode] 467985!).

Herbaceous shrubs to scandent herbs, 3 m. *Latex* white. *Stems* ca. 6 mm wide, green to violet, puberulous with white to gold hairs, especially on new growth, striate when dry, with distinct sterile and fertile zones, the latter with reduced leaves (bracts) and

shorter internodes. *Leaves* alternate, spiral, the sterile zone internodes 25–80 mm; petioles 2–20 mm, green to green tinged violet, puberulous; lamina $90-220 \times 40-70$ mm, ovate to elliptic (often ovate where flowering), the base obtuse to rounded, the apex attenuate, the margin shallow callose-crenate to dentate, sometimes nearly entire, the teeth sometimes intramarginal; adaxial surface green, glabrous; abaxial surface green to tinged violet, especially on the veins, puberulous with short appressed cream to golden colored hairs, especially along the veins; venation camptodromous, the primary and secondary veins prominent, raised, the tertiary veins visible. Flowers 33-37 mm, bunched apically with new growth, appearing racemose, the bracts $10-50 \times 3-30$ mm, progressively reducing in size, the internodes 4–15 mm; pedicels 20–40 mm at anthesis, 20–40 mm in fruit, green to tinged violet, puberulous, becoming more dense distally; hypanthium $4-5 \times 4-5$ mm, cupuliform, green to green tinged violet, puberulous, the ridges smooth; calyx lobes $7-13 \times 2-3$ mm, patent to slightly reflexed at anthesis, lanceolate, green to green suffused with violet, glabrous to sparsely puberulous, the margin shallow callose-dentate with 5–9 blunt teeth, the apex acute; corolla green to green tinged violet, glabrous; corolla tube 5–6 mm wide basally, bulging just above the base, the throat narrowing to 2–3 mm; corolla lobes lanceolate, the interior violet, the margins slightly undulate, the two dorsal lobes $12-13 \times 3-4$ mm, opening dorsally 17-18mm from the corolla base, falcate, the two lateral lobes $8-9 \times 3-4$ mm, falcate, the ventral lobe $5-7 \times 4-5$ mm, opening ventrally 11-13 mm from the corolla base; androecium 27–32 mm, exserted 17–21 mm from the ventral opening, the filament tube green, sparsely puberulous distally with white hairs, the anther tube ca. 5×4 mm, violet, pale green along the sutures, sparsely to densely villose with cream to golden hairs, all

five anther tips glabrous; the style tinged violet, glabrous, the stigma cream colored, the stigma lobes shortly public along the margin. *Fruits* 15×14 mm, globose, fleshy, white to green when immature, maturing maroon-violet.

Phenology. This species has been collected in flower and fruit throughout the year.

Distribution. This species is found along the eastern Andean range in Ecuador and Colombia. The southern edge of its range extends to Napo province, near the city of Tena. To the north, its range extends into the Department of Boyacá in north-central Colombia. It has been collected in humid forests at elevations from 1500 to 2800 m.

Discussion. In Ecuador, *B. asclepiadea* most resembles *B. ceratocarpa*. Both species have large leaves and reduced bracts in defined sterile and fertile zones. However, the two species are readily differentiated using vegetative characters. The leaves of *B. asclepiadea* are ovate, often widest near the base of the lamina, while those of *B. ceratocarpa* are elliptic, widest near the middle, and longer. These differences are especially pronounced in the bracts. In addition, leaves of *B. ceratocarpa* have a more pronounced caudate apex with a falcate drip tip. The apex of *B. asclepiadea* leaves, on the other hand, are attenuate.

Until the current work, *B. asclepiadea* was thought to be restricted to Colombia. In fact, most Ecuadorian specimens now assigned to *B. asclepiadea* were previously identified as *B. ceratocarpa*. In Ecuador, the two species are geographically isolated. *Burmeistera asclepiadea* occurs along the eastern Andean range, coinciding with its

continued distribution in Colombia. Similarly, *B. ceratocarpa* is found in northwest Ecuador on the western side of the Andes, coinciding with where the species is commonly found in Colombia.

Additional specimens examined. COLOMBIA. Cundinamarca: Toquiza, Gazaunta Valley, Cordillera de Heliconia, 15 km NW of Medina, 2435 m, 23 Sep. 1944, Grant 10267 (NY). Huila: Lavaderos, ridge between Río Naranjo and Río Granadillo, 15 km S of San Augustín, 2000–2200 m, 01°44'N 76°17'W, 11 Feb. 1943, Fosberg 20054 (NY). Putumayo: Along highway between Sibundoy and Mocoa, km 90-91, 2500 m, 26 Jan. 1976, Luteyn et al. 5048 (NY). ECUADOR. Napo: Canton El Chaco, márgen derecha del Río Quijos, finca La Ave Brava de Segundo Pacheco, 1800–1900 m, 00°12'S 77°39'W, 07–10 Sep. 1990, Palacios 5347 (MO, NY); Carretera Baeza-Tena, a 17 km de Baeza en la localidad de Logma Playa, 1900–2000 m, 25 Aug. 1990, Jaramillo et al. 12221 (NY, QCA); Carretero San Gabriel-Julio Andrade-Santa Bárbara-La Alegría-La Bonita, collecciones de La Alegría, 2450–2800 m, 29 Dec. 1986, Friere Fierro 505 (QCA); Carretera Quito-Tena via Baeza, km 118, 1800 m, 06 Aug. 1984, Dodson et al. 15154 (MO); Cordillera de Huacamayos, along road from Archidona to Baeza, 46.1 km N of Archidona, 12.2 km S of Cosanga, 34.6 km S of junction of Baeza Road with Papallacta-Lago Agrio Road, 2200 m, 00°41'S 77°53'W, 24 Apr. 2003, Croat et al. 88066 (MO); El Chaco Canton, Proyecto Hidroeléctronico Coca, Punto ST3, margen derecho del Río Quijos, ca. 10 km al sur de Reventador, 1500 m, 00°11'S 77°39'W, 3–5 Oct. 1990, Palacios 5790 (MO); Junction of Baeza-Lago Agrio road with Río Azuela, 1740 m, 20 Oct. 1971, MacBryde 759 (MO); Localidad Codo Alto, sendero Precooperativa Alto

Coca, Sector 5, finca Ave Brava y alrededores, 1980 m, 00°03'S 77°49'W, 08 Sep. 1990, Jaramillo et al 12452 (QCA); Parque Nacional Sumaco-Galeras, southern slope of Sumaco volcano, 1870 m, 00°35'S 77°35'W, 16 Oct. 2005, Homeier & Chinchero 1885 (MO); Private property of William Philips, ca. 2 hrs walk from end of rd., W of Cosanga, N slopes of Cardillera de Huacamayos, 2300 m, 00°45'S 77°55'W, 12 Dec. 1989, Luteyn & Cobo 13466 (NY); Reserva Ecológica Antisana, Cordillera de los Guacamayos, entre camino La Virgen y Río Urcusiqui, oleoducto secundario, compaña Arco, 1775 m, 00°39'S 77°50'W, 14 Dec. 1999, Vargas & Narváez 3213 (MO); Reserva Ecológica Cayambe-Coca, the trail 'De Interpretacion,' north of El Chaco, 1878 m, 00°19.109'S 77°50.664'W, 19 Aug. 2002, Muchhala 177 (QCA); Reserva Ecológica Cayambe-Coca, volcan Reventador, trail between Río Quijos and refugio, 1500 m, 00°05'S 77°37'W, 22 Nov. 1997, Clark 4447 (MO); Reserva Yanacu, 2087 m, 00°36.053'S 77°53.372'W, 8 Aug. 2002, Muchhala 156 (QCA); Trail up Volcán Reventador leaving Logo Agrio-Baeza road at km 100, 1500–1700 m, 00°05'S, 77°35'W, 17 Jun. 1985, Stein 3076 (MO); W of Cosanga 4 km, 2000 m, 11 Feb. 1980, *Harling & Andersson 16465* (NY). Sucumbios: El Reventador, en ambas márgenes del Río Reventador, 1850 m, 06 Oct. 1990, Jaramillo & Grijalva 12893 (NY, QCA); Trail to La Bonita, 1 to 2 km from end of Tulcán-Sta. Bárbara road, ca. 25 km below Sta. Bárbara, 2100–2150 m, 00°35'N 77°30'W, 28 May 1985, Stein 2870 (MO, QCA).

4. Burmeistera aspera E. Wimm., Pflanzenr. IV. 276b (Heft 106): 160. 1943. TYPE:
Colombia. San Pablo: 22 May 1876 (fr.), E. F. André 3365 (holotype, K digital image!).

Scandent herbs, 6 m. *Latex* unknown. *Stems* ca. 6 mm wide, terete, green to violet, glabrous to strigose with tan, often articulate, trichomes, sometimes with a bulbous callose base, or simply collosities irregularly spaced on the stem, denser apically. *Leaves* alternate, distichous, the internodes 5–20 mm; petioles 5–10 mm, green to violet, scabrous; lamina $15-40 \times 10-25$ mm, ovate, the base rounded to subcordate, the apex attenuate, the margin shallow callose-serrate, the teeth often intramarginal, sometimes tinged violet; adaxial surface green, glabrous, nitid; abaxial surface green, often tinged violet, especially along the veins, puberulous to strigose, more densely so along the veins, with short white to tan hairs; venation camptodromous, diminishing along the margin or terminating in marginal teeth, the primary and secondary veins prominent, slightly raised, the tertiary veins visible. Flowers 37–38 mm, solitary in the upper leaf axils; pedicels 31– 39 mm at anthesis, 34–45 mm in fruit, glabrous, green to violet; hypanthium $6-7 \times 4-5$ mm, broadly obconical, violet, glabrous, the ridges raised; calyx lobes $7-9 \times 3$ mm, ascending to patent at anthesis, ligulate, exterior green, basally suffused violet, interior green, glabrous, the margin shallow callose-serrate, undulate, violet, the apex obtuse; corolla green suffused violet, glabrous; corolla tube 6–7 mm wide basally, the throat narrowing to 3–4 mm; corolla lobes lanceolate, the margins smooth, undulate, the two dorsal lobes $13-14 \times 3-4$ mm, opening dorsally 15 mm from the corolla base, slightly falcate, the two lateral lobes $8-9 \times 4$ mm, falcate, the ventral lobe ca. 9×4 mm, opening ventrally 11–12 mm from the corolla base; androecium 30–31 mm, exserted 18–19 mm from the ventral opening, the filament tube green, basally glabrous, distally sparsely villose with white hairs, the anther tube ca. 6×3 mm, green, dark violet along the sutures, glabrous, the three dorsal anthers glabrous, the two ventral anthers villose with

white hairs; the style and stigma unknown. *Fruits* ca. 16×24 mm, broadly globose, not-inflated, fleshy, waxy, white to violet-pink.

Phenology. This species has been collected with flowers and fruits throughout the year.

Distribution. This species occurs in northeast Ecuador, around the meeting place of the provinces Carchi, Imbabura, and Sucumbíos. One specimen has been collected as far south as Morona Santiago province. The species occurs in wet cloud forests at elevations of 2800–3400 m.

Discussion. Though similar in many ways to *B. arbusculifera*, *B. aspera* is mainly differentiated by having simple or articulate strigose hairs, instead of the callose, arbusculiform trichomes in *B. arbusculifera* (see discussion in *B. arbusculifera*). Specimens of *B. arbusculifera* have also been confused with *B. knaphusii*, which shares a similar vegetative habit. *Burmeistera knaphusii* is differentiated by having narrower, lanceolate leaves, 8–15 mm wide (vs. ovate, 10–25 mm wide in *B. aspera*); smaller calyx lobes, $3-7 \times 0.5$ mm (vs. $7-9 \times 3$ mm); and a longer fused corolla tube, opening ventrally 14–16 mm from the corolla base (vs. 11–12 mm).

The one collection of *B. aspera* in Morona Santiago is interesting not only because of its far south disjunct distribution, but also because of its fruit color. This specimen reports fruits that are violet-pink, while all specimens in northeast Ecuador have white fruits. The southern specimen is vegetatively identical to the northern ones, but it was collected without flowers. More collections are needed from this southern distribution of *B. aspera* to determine if other differences occur between the populations.

Additional specimens examined. ECUADOR: **Carchi:** Juilo Andrade-El Carmelo road, km 18, 3200 m, 00°38'N 77°40'W, 16 May 1982, *Luteyn et al. 8415* (NY, QCA). **Imbabura:** Alturas de Cayachupa, ca. 5 km NW of the village of Piñan, 3200 m, 00°34'N 78°28'W, 21 Jun. 1980, *Sperling & Bleiweiss 5157 & 5158* (QCA). **Morona Santiago:** Trail Alao-Huamboya, around and above El Placer, 2850–3400 m, 01°47'S 78°23'W, 08 May 1982, *Øllgaard et al. 38425* (MO, NY). **Sucumbíos:** 8–12 km ESE of Santa Barbara, 2780–2880 m, 00°40'N 77°30'W, 11 Jan. 1985, *Luteyn & Cotton 11004* (NY, QCA); Carretera Sucumbíos-Sta. Bárbara-La Alegría, 2450–2800 m, 29 Dec. 1986, *Jaramillo 9344* (QCA); Playon de San Francisco-El Mirador trail, 07 Jul. 1978, *Boeke & Jaramillo 2390* (NY); SE of El Playón de San Francisco on the slopes of Cerro Mirador, 3300–3700 m, 00°35'N 77°38'W, 28 Dec. 1980, *Holm-Nielsen et al. 29836* (MO).

5. Burmeistera asplundii Jeppesen, Fl. Ecuador 14: 28, fig. 2C-D. 1981. TYPE: Ecuador.
Bolívar: San Jacinto de la Unión, 2500 m, 14 Aug. 1939 (fl.), *E. Asplund 8275* (holotype, S-04-897 digital image!).

Scandent herbs, size unknown. *Latex* white. *Stems* ca. 4 mm wide, pale green, glabrous. *Leaves* alternate, distichous, the internodes 15–35 mm; petioles 7–12 mm, pale green, glabrous; lamina 45–110 × 20–45 mm, ovate-elliptic, the base obtuse to rounded, the apex acuminate, the tip $6-9 \times 3-4$ mm, the margin irregularly serrate, the teeth

rounded with intramarginal callose tips, protruding 1–3 mm, separated 3–7 mm apart; adaxial surface green, glabrous; abaxial surface green tinged violet, glabrous; venation camptodromous to craspedodromous, the primary vein prominent, slightly raised but flat, the secondary and tertiary veins visible. Flowers solitary, not seen mature; pedicels ca. 10 mm, glabrous, pale green; hypanthium ca. 10×7 mm, obconical, green, glabrous, the ridges faintly visible, not raised; calyx lobes ca. 19 × 8 mm, ascending at anthesis, broadly lanceolate, overlapping at the base, green, glabrous, the margin shallow calloseserrate, the teeth rounded, darker colored, the apex obtuse; corolla green, glabrous; corolla tube ca. 7.5 mm wide basally, the throat narrowing to ca. 3.5 mm; corolla lobes lanceolate, the margins undulate, the two dorsal lobes ca. 13×5 mm, falcate, opening dorsally ca. 14.8 mm from the corolla base, the two lateral lobes ca. 10×4 mm, falcate, the ventral lobe ca. 9×4 mm, opening ventrally ca. 11 mm from the corolla base; androecium ca. 25 mm, exserted ca. 14.5 mm from the ventral opening, the filament tube dark colored, glabrous, the anther tube tan, glabrous, the top three anther tips villose, the bottom two anther tips densely villose with white hairs; the style and stigma unkown. Fruits unknown.

Phenology. One specimen collected in August had immature flowers. One specimen collected in October was sterile.

Distribution. Only two specimens are known, both from southeast Bolívar province at elevations of 2500–2900 m.

Discussion. Though rarely collected, this species is distinguished by the depth and irregularity of the marginal teeth, and the large ovate-lanceolate sepals overlapping each other at the base. The shape and color of the leaves may resemble certain specimens of *B*. *latisepala* and *B*. *leucocarpa*, though the marginal teeth of *B*. *asplundii* are more uniquely pronounced. In addition, neither *B*. *leucocarpa* or *B*. *latisepala* have calyx lobes nearly the size of those of *B*. *asplundii*.

Additional specimens examined. ECUADOR. **Bolívar:** Parroquia San Pablo de Atenas, in and around the San José de las Palmas community forest, near km 33 on the Guaranda-Babahoyo highway, in forest along trail, 2839 m, 01°47.441'S, 79°02.699'W, *McDowell 5873* (QCA).

6. Burmeistera auriculata Muchhala & Lammers, Novon 15(1): 177, fig. 1. 2005. TYPE:
Ecuador. Cotopaxi: Bosque Integral Otonga, 00°25.264'S 79°00.779'W, 2233 m, 07 Jul.
2002 (fl.), *N. Muchhala 120* (holotype, QCA!; isotype, MO!).

Scandent herbs, 3 m. *Latex* white. *Stems* ca. 3 mm diam., tan to green, sometimes tinged violet, glabrous to puberulent with white hairs, especially on new growth. *Leaves* alternate, distichous, the internodes 20–30 mm; petioles 10–20 mm, green to green tinged violet, puberulent; lamina 75–140 \times 20–45 mm, lanceolate, the base obtuse, the apex acuminate, the margin shallow callose-dentate to crenate; adaxial surface green, puberulent; abaxial surface violet with pale green primary and secondary veins, puberulent; venation camptodromous, the primary and secondary veins prominent, raised,

the tertiary veins barely visible, tinged violet. Flowers 45-48 mm, solitary in the upper leaf axils; pedicels 70–100 mm at anthesis, 75–150 mm in fruit, green distally tinged violet, puberulent; hypanthium ca. $5-6 \times 5-6$ mm, obconical to narrowly urceolate, tan tinged with violet, puberulent, the ridges smooth; calyx lobes $9-11 \times 7-9$ mm, patent to reflexed at anthesis, foliaceous, rhomboid, pale green, sometimes lightly tinged violet, glabrous to puberulent, the margin sinuate with 7-11 callose-tipped teeth, the apex obtuse; corolla pale green, dorsally lightly tinged with violet, sparsely puberulent; corolla tube 8–10 mm wide basally, bulging just above the base, the throat narrowing to 3–4 mm; corolla lobes ligulate, the margins smooth, the two dorsal lobes ca. $14-18 \times 3-5$ mm, opening dorsally ca. 15-16 mm from the corolla base, arcuate, the two lateral lobes 9-10 \times 3–4 mm, opening ventrally 8–11 mm from the corolla base, falcate; and roccium 40–44 mm, exserted 32–33 mm from the ventral opening, the filament with pale green and tan striations, puberulent, the anther tube dark green to tan, covered with short, appressed, sordid yellow hairs, the top three anther tips glabrous, the bottom two anther tips glabrous or sparsely puberulous with short white hairs; the style and stigma tan, the stigma lobes fringed with short white hairs along the margin. Fruits ca. 35×20 mm, globose, inflated, light green apically fringed with violet.

Phenology. This species flowers throughout the year. The flowers open nocturnally between 1715 and 1800 hr., and last 5 to 6 days (Muchhala & Lammers 2005).

Distribution. This species has been collected in and around the Reserva Integral Otonga at the border of the provinces Cotopaxi and Santo Domingo de los Tsáchilas. Specimens have been collected at elevations from 1400 to 2400 m.

Discussion. Molecular work has placed *B. auriculata* in a clade with other inflated fruit species (Uribe-Convers et al. 2017), sister to *B. truncata*, which occurs in a similarly restricted range as *B. auriculata*, only 30–35 km to the north. The two species are very similar vegetatively, particularly in their long, lanceolate leaf blade. However, *B. auriculata* is differentiated by its shorter and wider calyx lobes $(9-11 \times 7-9 \text{ mm vs. } 9-18 \times 1-2 \text{ mm in } B. truncata)$, longer androecium (40–44 mm vs. 29–39 mm), and longer exsertion length (32–33 mm vs. 24–30 mm). The enlarged calyx lobes of this species are similar in size to those of *B. borjensis*, which is also part of the inflated fruit clade. However, *B. borjensis* has elliptic leaves (vs. lanceolate in *B. auriculata*), a shorter androecium (34–39 mm vs. 40–44 mm), and a shorter exsertion length (24–28 mm vs. 32–33 mm).

Additional specimens examined. ECUADOR: **Cotopaxi:** Cantón Sigchos, Bajo Triunfo Grande, bosque a mano izquierda de vía Triunfo Granda-Las Pampas, 2321 m, 00°30'55"S 78°59'53"W, 09 Aug. 2003, *Ramos et al. 7151* (MO). **Santo Domingo de los Tsáchilas:** Ca. km 36 along road to the southeast from La Aurora (km 7 on Sto. Domingo-Quevedo road), passing through La Reforma, 1450 m, 00°28'S 79°08'W, 24 Jul. 1990, *Øllgaard 98069* (QCA). 7. Burmeistera borjensis Jeppesen, Fl. Ecuador 14: 29, fig. 2E-F. 1981. TYPE: Ecuador.
Napo: Montane forest ridge 1 mile NE of Borja, 1706 m, 20 Aug. 1960 (fl.), P. J. Grubb,
J. R. Lloyd, T. D. Pennington & T. C. Whitmore 1339 (holotype, K [barcode] 250832
digital image!; isotype, NY [bc] 467987!).

Scandent herbs, 3 m. *Latex* white. *Stems* ca. 4 mm wide, tan to green, glabrous. Leaves alternate, spiral, bullate, the internodes 10–25 mm; petioles 10–25 mm, green, glabrous to puberulent with white hairs; lamina $45-135 \times 25-65$ mm, elliptic, the base attenuate to cuneate, the apex attenuate, the margin shallow callose-dentate to serrate, the teeth often slightly irregular in size, sometimes becoming slightly larger and blunted near the apex; the adaxial surface green, glabrous, nitid; the abaxial surface green with lighter primary and secondary veins, minutely puberulent along the veins with white hairs, elsewhere glabrous, nitid; venation camptodromous, the primary and secondary veins prominent, slightly raised but flat, the tertiary veins visible. Flowers 44–50 mm, solitary in the upper leaf axils; pedicels 80–115 mm at anthesis, 80–115 mm in fruit, green to violet, glabrous to puberulent; hypanthium $8-10 \times 5-7$ mm, obconical, green to tan, sometimes tinged violet, glabrous to puberulent, the ridges smooth; calyx lobes $13-19 \times$ 6–13 mm, ascending at anthesis, broadly lanceolate, green speckled with violet, glabrous, the margin shallow callose-serrate, sometimes puberulent, the apex obtuse; corolla green speckled with violet, glabrous to minutely puberulent; corolla tube 7–8 mm wide basally, the throat narrowing to 3–4 mm; corolla lobes ligulate, the margins smooth to undulate, the two dorsal lobes $13-16 \times 3-4$ mm, opening dorsally 17-22 mm from the corolla base, falcate, the two lateral lobes $7-9 \times 3$ mm, falcate, the ventral lobe $7-8 \times 4$ mm, opening

ventrally 11–14 mm from the corolla base; androecium 34–39 mm, exserted 24–28 mm from the ventral opening, the filament tube green tinged violet to entirely dark violet, villose with cream colored hairs, the anther tube ca. 6×5 mm, dark-colored between the sutures, along the sutures pale violet, glabrous to villose basally, sometimes with short, sordid yellow appressed hairs along the sutures, all five anther tips sparsely villose with white hairs; the style tan, glabrous, the stigma lobes tan, pubescent along the margin with short white hairs. *Fruits* ca. 30×25 mm, globose, inflated, green speckled with maroon-violet.

Phenology. This species has been collected in flowers and fruits throughout the year.

Distribution. This species occurs in a narrow distribution in Napo Province, roughly from the vicinity of the village Cosanga in the south to the village El Chaco in the north. Specimens have been collected in wet humid forests from 1700 to 2500 m in elevation.

Discussion. Few species of *Burmeistera* have calyx lobes of similar length and width as *B. borjensis*. The ones that do — *B. auriculata* and some *B. brachyandra* — are easily differentiated. Compared to *B. auriculata*, *B. borjensis* has shorter elliptic leaves with irregular serrations (vs. lanceolate with a shallowly crenate margin), a shorter androecium (34–39 mm vs. 40–44 mm), and a shorter exsertion length (24–28 mm vs. 32–33 mm). *B. borjensis* is differentiated from *B. brachyandra* by its obconical hypanthium (vs. cupuliform), the absence of reduced bracts, and the presence of inflated fruits.

Molecular work (Uribe-Convers et al. 2017) places *B. borjensis* in the inflated fruit clade next to *B. oyacachensis*, with which it shares many characters, including leaf and flower size traits. Vegetatively, the two species differ in the serration of the leaves, especially young leaves: those of *B. borjensis* are irregularly serrate, though with small, similarly sized teeth, while the teeth of *B. oyacachensis* are up to 3×2 mm. The two species also differ in sepal shape. The calyx lobes of *B. borjensis* are broadly lanceolate, significantly widening to 6–13 mm just above the base, then tapering to an obtuse tip. Meanwhile, the calyx lobes of *B. oyacachensis* are ligulate, widest at the base or widening slightly to 3–5 mm just above the base, then tapering continuously to an acute tip.

Additional specimens examined. ECUADOR. Napo: Ca. 16 km NW of Cosanga along trail after road ends near Las Caucheras, 2500 m, 00°35'S 77°51'N, 18 Oct. 1992, *Luteyn et al. 14700* (NY, QCA); Canton Quijos, Yanayacu Biological Station, ca. 5 km W of Cosanga on the Cosanga-Las Caucheras road, Macucoloma trail, 2100 m, 00°36'07.5"S 77°53'00.1"W, 11 Feb. 2011, *Tepe et al. 2948* (MO); Cosanga, carretera Cosanga-El Aliso, a 1 km del partidero hacia El Aliso, 2240 m, 20 Aug. 1990, *Jaramillo 11992* (MO); El Chaco, fincas de la parte Este del Pueblo, 1700–2000 m, 15 Mar. 1991, *Givalanes & Quezada 466* (QCA); Private property of William Philips, ca. 2 hrs walk from end of rd., W of Cosanga, N slopes of Cordillera de Huacamayos, 2300 m, 00°45'S 77°55'W, 12 Dec. 1989, *Luteyn & Cobo 13462* (MO, NY); Quijos Canton, valle del Río Cosanga, 1 km arriba de la union de los Ríos Cosanga y Aliso, 2280 m, 00°37'S 77°54'W, 19 Oct. 1990, *Palacios 6401* (MO, NY); Reserva Ecológica Cayambe-Coca,

the trail 'De Interpretacion,' north of El Chaco, 1778 m, 00°18.95'S 77°50.501'W, 19 Aug. 2002, *Muchhala 176* (QCA); San Franciso de Borja, patch of forest above river behind town, 1700 m, 06 Jul. 1980, *Sobel & Strudwick 2386* (NY); Yanacu Biological Station, 5 km W of Cosanga, Stream Trail, 2100 m, 00°35'09"S 77°53'04"W, 18 Jan. 2009, *Tepe 2610* (QCA).

8. Burmeistera brachyandra E. Wimm., Pflanzenr. IV. 276b (Heft 106): 129. 1943.
TYPE: Ecuador. Esmeraldas: Parroquia de Concepcion, Playa Rica, 105 m, 10 Dec. 1936 (fl., fr.), *Y. Mexia 8432* (holotype W-1967-0015310 digital image!; isotypes, BM [barcode] 947543 digital image!, F [bc] V0052919F digital image!, G [bc] 236657 digital image!, GB [bc] 47976 digital image!, K [bc] 250831 digital image!, MO-1165223!, NY [bc] 467988!, S-05-1874 digital image!, U [bc] 933 digital image!, UC [bc] 644342 digital image!).

Terrestrial herbaceous shrubs, 2 m. *Latex* white. *Stems* ca. 7 mm wide, green to cream colored, glabrous to very sparsely puberulent, with distinct sterile and fertile zones, the latter with reduced leaves (bracts) and shorter internodes. *Leaves* alternate, spiral, the sterile zone internodes 10-40 mm; petioles 10-45 mm, green, glabrous to puberulous with cream colored hairs; lamina $120-250 \times 60-90$ mm, broadly elliptic, the base cuneate, the apex attenuate to acuminate, the margin shallow callose-dentate, basally nearly entire, the teeth sometimes irregular in size, slightly increasing in size toward the apex; adaxial surface green, glabrous; abaxial surface green, puberulent with cream colored hairs; venation camptrodromous, the primary and
secondary veins prominent, raised but flat, the tertiary veins visible. *Flowers* 32–37(–41) mm, bunched apically with new fertile zone growth, appearing racemose, the bracts 30–75 × 15–40 mm, progressively reducing in size, caducous or persistent, the internodes 3–10 mm; pedicels 30–60 mm at anthesis, 30–65 mm in fruit, green, glabrous; hypanthium $5-6 \times 3-6$ mm, cupuliform, green, glabrous, the ridges smooth; calyx lobes $6-7 \times 2-3$ mm, ligulate, green, glabrous, the margin shallow callose-dentate with 7–9 blunt teeth, the apex obtuse, patent at anthesis; corolla entirely green, glabrous; corolla tube 4–6 mm wide basally, narrowing to 2–3 mm; corolla lobes ligulate, the margins smooth, the two dorsal lobes $12-16 \times 2-3$ mm, opening dorsally 12-16 mm from the corolla base, falcate, the two lateral lobes $6-10 \times 2-3$ mm, opening ventrally 10-14 mm from the corolla base, falcate, falcate; androecium 27-31(-35) mm, exserted 15-23 mm from the ventral opening, the filament tube green, glabrous to sparsely puberulous, the anther tube green, glabrous, all five anther tips glabrous; the style and stigma cream colored, the stigma lobes glabrous. *Fruits* ca. 10×10 mm, globose, fleshy, pale green to yellow.

Phenology. This species has been collected in flower and fruit throughout the year.

Distribution. This species has been collected in northwest Ecuador in the provinces of Esmeraldas, northern Manabí, western Carchi, and western Pichincha. It is found in high humidity tropical forests at elevations from 100 to 1350 m.

Discussion. Burmeistera brachyandra is similar to *B. pacifica*, but is differentiated by fruit color (red in *B. pacifica* and pale green to yellow in *B. brachyandra*).

Additional specimens examined. ECUADOR. Carchi: Border area between Prov. Carchi and Esmaraldas, about 20 km past Lita on road Lita-Alto Tambo, 550 m, 24 Jun. 1991, van der Werff 11911 (MO); On plateau above San Marcos de los Coaiqueres, on trail towards Gualpí Bajo, 1000 m, 01°06'N 78°17'W, 07 Feb. 1985, Øllgaard et al. 57355 (QCA); Reserva Entica y Forestal Awá, San Marcos, around the village, 1000 m, 01°05'N 78°15'W, 11 Mar. 1988, Jørgensen 65176 (QCA); San Marcos valley, 600 m, 01°07'N 78°20'W, 20 Nov. 1983, Kvist 48696 (QCA); Trail to Río Gualpi Chico, along ridge line near Awa encampment, 1330 m, 00°58'N 78°16'W, 17 Jan. 1988, Hoover et al. 2516 (QCA); Tulcan Cantón, Parroquia Chical, Sector Gualpí Medio, Reserva Indígena Awá, sendero a San Marcos al norte de la casa communal, 1026 m, 01°02'N 78°16'W, 23–27 May 1992, Tipaz et al. 1039 (MO); Tulcan Cantón, Reserva Etnica Awá, Parroquia El Chical, Sector Gualpí Medio, Río Canumbí, 1150 m, 01°02'N 78°15'W, 19–28 Feb. 1993, Grijalva et al. 466 (MO). Esmeraldas: Along road from Lita-San Lorenzo Hwy to Río San José, departing main highway 44.4 km NW of Río Lita bridge near Lita, 5.3 km N of El Dorado, 0.1 km down road to Río San José, 153 m, 01°04'25"N 78°39'01"W, 14 Oct. 2007, Croat et al. 99821 (MO); Cayapas-Cotacachi area, San Miguel and Santiago River, 100 m, 00°75'N 78°50'W, Jul.-Aug. 1977, Rodriguez-Carrasquero 5580 (MO); Communidad Awá Río Bogota, 11.5 km W of Alto Tambo, 30.5 km W of Río Lita, 3 km by trail to Río Bogota on S side of Lita-San Lorenzo road, 380 m, 00°58'57"N 78°35'58", 15 Sep. 2002, Croat et al. 87524 (MO); Eloy Alfaro Cantón, Reserva Ecológica Cotacachi-Cayapas, Parroquia Luis Vargas Torres, Río Santiago, estero Pote, 250 m, 00°49'N 78°45'W, 23-27 Oct. 1993, Tirado et

al. 504 (MO); Eloy Alfaro, Reserva Ecológica Cotacachi Cayapas, Río Santiago, Angostura, 200 m, 00°49'N 78°45'W, 25 Mar.–5 Apr. 1995, Tirado et al. 940 (MO); Further along trail to Río Mataje, Awá encampment from Río Palaví encampment, 200– 230 m, 01°07'N 78°37'W, 11 Feb. 1988, Hoover et al. 3946 (MO, QCA); Highway from Lita to Alto Tambo, 797 m, 00°54.624'N 78°32.736W, 18 Jul. 2002, Muchhala 142 (QCA); Lita-San Lorenzo Road, 19.1 km E of Río Tululbí, 5.2 km W of El Durango, 0.6 km down gravel road going N to Río Tululbí and crossing Río San José, vicinity of Río San José, 73 m, 01°04'47" N78°38'55" W, 13 Oct. 1999, Croat et al. 83271 (MO); Quininde, carretera vecinal Herrera-Los Manos, cabacera del Río Aguacatal, finca de Francisco Cantos, 550 m, 00°19'30"N 79°46'06"W, 24–26 Feb. 1995, Palacios 13636 (MO); Río Cayapa, Zapallo Grande, 1 km upriver Río Zapallo Grande, a trail on the right bank into the forest, 150 m, 00°49'N 78°55'W, 04 Aug. 1982, Kvist & Asanza 40876 (QCA); Río Cayapa, Zapallo Grande, 500 m upstream the village, 100 m, 00°48'N 78°54'W, 26 Jun. 1982, Kvist & Asanza 40343 (MO, QCA); Río Zapallo Grande, tributary of Río Cayapa, trail 200 m from, and opposite to, the evangelic mission station, 200 m, 00°48'N 79°52'W, 23 Oct. 1982, Barfod 41031 (MO, QCA); Road Lita-San Lorenzo, km 32, 800 m, 00°30'N 78°53'W, 28 Sep. 1991, Øllgaard 99150 (QCA); San Lorenzo, Alto Tambo, Recinto el Dorado, 2 km al noroeste del Recinto, 340 m, 00°55'N 78°36'W, 26 Oct. 1999, Valenzuela et al. 693 (MO); San Lorenzo Canton, Reserva Etnica Awá, Centro Guadualito, 80 m, 01°05'N 78°40'W, 20-29 Jul. 1992, Aulestia et al. 86 (MO); San Lorenzo Canton, Reserva Indígena Awá, Parroquia Ricaurte, Comunidad Balsareño, Río Palabí, 100 m, 01°09'N 78°31'W, 15–29 Apr. 1991, Rubio & Quelal 1314 (MO); Stream bed near Río Palaví Awá encampment, 150–250 m, 01°07'N

78°37'W, 10 Feb. 1988, Hoover et al. 3735 (MO, QCA); Quinindé Cantón, the Mache-Chindul Ecological Reserve, Bilsa Biological Station, Mache mountains, 35 km W of Quinindé, 5 km W of Santa Isabel, 600 m, 00°21'N 79°44'W, 27 Sep. 1996, Clark 2935 (MO). Los Rios: Along road E of Santo Domingo-Quevedo road, beginning 10.5 km N of Patricia Pilar, at Caseria Palmar de Bimbe, 550-575 m, 00°35'00"S 79°12'30"W, 09 Oct. 1983, Croat 57006 (MO); Rio Palenque Field Station, halfway between Quevedo and Santo Domingo de los Colorados, 200 m, 23 Feb. 1974, Gentry 10142 (MO); Rio Palenque Biological Station, km 56 on road Quevedo-Santo Domingo, 150–220 m, 26 Oct. 1974, Dodson 5706 (QCA); Rio Palenque Biological Station, km 56 on road Quevedo-Sto. Domingo, 150-220 m, 02 Oct. 1976, Dodson & Gentry 6469 (MO); Rio Palenque Science Center, km 56 on road Quevedo-Sto. Domingo, 150–220 m, 10 Feb. 1979, Dodson & Duke 7683 (MO). Manabí: Pedernales, Bosque Protector Cerro Pata de Pájaro, 15 km SE of Pedernales, headwaters of Río Vite, 500 m, 00°02'S 79°58'W, 26 Aug. 1998, Neill et al. 11374 (MO); Padernales Cantón, Reserva Ecologica Mache-Chindul, Comunidad Ambacha, vía marginal de la costa Chindul, 250 m, 00°15'N 79°48'W, 25 Mar. 1997, Clark et al. 4148 (MO). Pichincha: Bosque primario de la Reserva Endesa, 10 km al norte del caserío Álvaro Pérez Intriago ubicado en el km 113 de la carretera Quito-Puerto Quito, 600 m, 00°03'N 79°07'W, 08 Jul. 2001, Valenzuela 31 (QCA); Reserva Endesa, km 113 on the road between Quito & Pto. Quito, 9 km N of km 113, 750 m, 00°05'N 79°02'W, 14 Jul. 1986, Croat & Rodriguez 61447 (MO); Reserva de ENDESA, km 113 along Quito-Pto. Quito road, 800–1000 m, 00°05'N 79°02'W, 16–17 Nov. 1989, Luteyn & Borchsenius 13342 (MO, NY, QCA); Reserva Forestal de ENDESA, Río Silanche, Corporación Forestal Juan Manuel Durini, km 113

de la carretera Quito-Pto. Quito, a 10 km al Norte de la carretera principal, 650–700 m, 00°05'N 79°02'W, 26 Apr. 1984, *Jaramillo 6454* (NY, QCA).

9. *Burmeistera brighamioides* Lammers, Novon 12(2): 208, fig. 2. 2002. TYPE: Ecuador. Carchi: Further ascent of Río Verde past stream and waterfall entering from SW and continuing beyond principal drainage stream of large Cerro Golondrinas into drainage streams of medium Golondrinas mountains, 1200 m, 00°52'N 78°07'W, 01 Dec. 1987, *W. S. Hoover 2182* (holotype, MO!).

Terrestrial herbaceous shrubs, 3 m. *Latex* white. *Stems* up to 10 mm wide, thick walled, green, striate when dry, glabrous when mature, new growth villose with cream to tan hairs. *Leaves* alternate, spiral, the internodes 15–40 mm; petioles 20–30 mm, green, glabrous to sparsely puberulous; lamina 135–280 × 55–190 mm, obovate, the base cuneate, the apex attenuate, the margin shallow callose-dentate, the teeth and margin ciliate; adaxial surface green, glabrous to sparsely puberulous; abaxial surface green, guberulous along the veins with appressed hairs; 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, ca. 79 mm; pedicels ca. 60 mm at anthesis, 65–85 mm in fruit, glabrous to very sparsely puberulous, green basally, becoming violet distally; hypanthium 7–8 × 8–9 mm, cupuliform to urceolate, sparsely puberulous, green; calyx lobes 2–3 × 2 mm, deltate, green, densely ciliate with tan hairs, the margin entire or with few callose-tipped teeth, the apex obtuse, ascending at anthesis; corolla green, very sparsely puberulous, though

becoming more dense distally; corolla tube ca. 5.5 mm wide basally, the throat narrowing to ca. 5 mm; corolla lobes lanceolate, the margins smooth, the two dorsal lobes ca. 13×5 mm, opening dorsally ca, 54 mm from the corolla base, falcate, the two lateral lobes ca. 8 \times 6 mm, slightly decurving, the ventral lobe ca. 6×6 mm, opening ventrally ca. 51 mm from the corolla base; androecium ca. 72 mm, exserted ca. 28 mm from the ventral opening, the filament tube green to violet, glabrous, the anther tube ca. 8×4 mm, dark violet, lighter along the sutures, densely villose between the sutures with sordid-yellow hairs, the three dorsal anther tips glabrous, the two ventral anther tips densely villose with cream-colored hairs; the style and stigma unknown. *Fruits* ca. 20 \times 20 mm, globose, fleshy, green to cream.

Phenology. This species has been collected with flowers and flower buds in August, November, and December. Fruits have been collected in August, November, and January.

Distribution. This species has been collected in northern Ecuador, in Carchi Province near the border with Colombia, in and around the Maldonado Parish of Tulcán Canton. Specimens have been collected in wet montane cloud forests at elevations from 1200 to 2700 m.

Discussion. No species of *Burmeistera* is known to have a corolla tube of any length close to *B. brighamioides*. Of the few collections that have been made, only one has a mature flower.

Additional specimens examined. ECUADOR. **Carchi:** Bosque Protector Golondrinas, on path from Moran to lodge, 2598 m, 01°49'15.27"N 79°05'41.503"W, 04 Jul. 2018, *Muchhala & Gruhn 548* (MO); Maldonado-Tulcán, km 21, 2500 m, 25 Nov. 1985, *Besse et al. 2249* (MO); Mira, El Carmen, Cerro Golondrinas, 2000–2400 m, 00°50'N 78°11'W, 18–25 Aug. 1994, *Tirado 1257* (MO); West of Tulcán 62–75 km, 2460–2720 m, 00°50'N 78°05'W, 07 Jan. 1985, *Luteyn & Cotton 10868* (NY).

10. *Burmeistera caelestis* Mashburn, sp. nov. TYPE: Ecuador. Carchi: Espejo, faldas del Cerro Golondrinas Hembra, 2300-2400 m, 00°51'N 78°07'W, 20 Aug. 1994, *W. Palacios 12741* (holotype, MO-5343220!; isotype, NY!).

Herbaceous shrubs to scandent herbs, 2 m. *Latex* white. *Stems* ca. 7 mm wide, terete, green to maroon-violet, sparsely to densely villose with cream to golden hairs. *Leaves* alternate, spiral, bullate, the internodes 7–30 mm; petioles 5–20 mm, green to maroon-violet, villose; lamina $35-150 \times 15-70$ mm, elliptic, the base attenuate to cuneate, the apex attenuate, the margin shallow callose-crenate to dentate; adaxial surface green, sometimes tinged violet, glabrous to very sparsely puberulous; abaxial surface green to green tinged violet, villose with translucent white to golden hairs, especially along the veins; venation camptodromous, the primary and secondary veins prominent, raised but flattened, the tertiary veins visible. *Flowers* 44–52 mm, solitary in the upper leaf axils; pedicels 20–85 mm at anthesis, 40–90 mm in fruit, green to violet, glabrous to sparsely villose; hypanthium 8–12 × 6–9 mm, cupuliform, abruptly widening distally, green to violet, glabrous to sparsely villose, the ridges slightly raised; calyx lobes 1–2 × 2-3 mm, deltate, dark green to maroon-violet, glabrous, the apex obtuse, patent to ascending at anthesis; corolla dark green tinged with violet to entirely maroon-violet; corolla tube 7–9 mm wide basally, the throat narrowing to 3–4 mm; corolla lobes ligulate, the margins smooth, the two dorsal lobes $16-23 \times 3-4$ mm, opening dorsally 10-15 mm from the corolla base, falcate to arcuate, the two lateral lobes $9-13 \times 3-4$ mm, falcate to arcuate, the ventral lobe ca. 11×6 mm, opening ventrally 5–9 mm from the corolla base; androecium 35–40 mm, exserted 26-31 mm from the ventral opening, the filament tube green lightly suffused with violet, glabrous to sparsely villose basally with white hairs, more dense apically, the anther tube green with appressed white hairs along the sutures, all five anther tips sparsely villose; the style and stigma tinged maroon-violet, the stigma lobes sparsely pubescent along the margin with short white hairs. *Fruits* ca. $30 \times 20-25$ mm, cylindrical, not inflated, fleshy, maturing light blue to dark blue tinged with violet.

Etymology. The specific epithet means "sky blue" in reference to the color of the mature fruits.

Phenology. This species has been collected with flowers and fruits throughout the year.

Distribution. This species is found in northern Ecuador, in the provinces of Carchi and Esmeraldas, in humid montane cloud forests. It has been collected at elevations as low as 800 m, though it is more common at elevations of 1800–2400 m.

Discussion. Described from specimens formerly identified as *B. cyclostigmata*, because of the blue fruits. This new species is differentiated from the former based on the presence of golden hairs on the vegetative parts and bullate leaves.

Additional specimens examined. ECUADOR. Carchi: Bosque Protector Cerro Golondrinas, 2030 m, 00°49.676'N 78°06.996'W, Muchhala 136 (QCA); Campamento Machines, road Tulcán-Maldonado, ca 10 km. south east of Maldonado, 2200–2400 m, 28 Nov. 1974, Harling & Andersson 12332 (MO, NY); Espejo, Reserva Golondrinas, El Corazón, recorrido por el sendero a La Cortadera, 2230 m, 00°50'N 78°06'W, 22 Jan. 2004, Vargas et al. 4265 (MO); Espejo, Reserva Golondrinas, El Corazón, sendero a Río El Corazón, 2010 m, 00°50'N 78°08'W, 28 Jan. 2004, Vargas et al. 4382 (MO); From Prima Vera, hike six hours up Río Gualchan drainage to shelter built by Nilo Ortiz, collected mostly along ridge to the north and around camp, 1950 m, 00°49'58"N 78°10'01"W, 07–08 Jun. 1993, Bradford et al. 60 (MO); Mira Cantón, El Carmen, Cerro Golondrinas, 2000–2400 m, 00°50'N 78°11'W, 18–25 Aug. 1994, Tirado et al. 1252 (MO); Mira Canton, norte del Carmen, camino a Chical, 2000–2200 m, 00°17'N 78°13'W, 10 Feb. 1992, Palacios et al. 9709 & 9765 (MO); Mira, El Carmen, Cerro Golondrinas, 2000–2400 m, 00°50'N 78°11'W, 18–25 Aug. 1994, Tirado et al. 1338 (MO); Valle de Maldonado, km 71 on road Tulcán Maldonado, 2100–2200 m, 00°54'N 78°06'W, 20 May 1973, Holm-Nielsen et al. 6039 (NY). Esmeraldas: Canton San Lorenzo, Lita to El Cristal road, on finca of Dr. La Lama, 13.5 km S of Lita, 1220–1350 m, 00°49'N 78°26'W, 02 Nov. 1992, Luteyn et al. 14751 (MO, NY); San Lorenzo

Canton, 10 km suroeste de Lita, subiendo al sector El Cristal, 800 m, 00°48'N 78°30'W, 10 Sep. 1990, *Rubio & Quelal 679* (MO).

11. Burmeistera catula Muchhala & Mashburn, sp. nov. TYPE: Ecuador. Pichincha:
Mashpi Lodge, on 'Jungle Swing' trail, 971 m, 00°09'59.63"N 78°52'54.413"W, 06 Jul.
2018 (fl.), N. Muchhala & J. Gruhn 558 (holotype, MO!).

Herbaceous shrubs to scandent herbs, 2.5 m, vegetative parts entirely villose with long, translucent-white, sometimes violet-tinged, articulate hairs. Latex unknown. Stems ca. 5 mm, yellow-green. *Leaves* alternate, distichous, the internodes 20–30 mm; petioles 10–20 mm, pale green; lamina $130-200 \times 40-65$ mm, narrowly elliptic to oblanceolate, the base attenuate, the apex attenuate to acuminate, the margin callose-dentate, the teeth often alternating small and large in size, spaced 5–10 mm apart; adaxial surface dark green; abaxial surface lighter green; venation camptodromous, the primary vein prominent, raised, the secondary veins only slightly raised, the tertiary veins faintly visible. *Flowers* 44–46 mm, solitary in the upper leaf axils, only 1–3 per stem; pedicels 60–70 mm, yellow-green to dark green, glabrous; hypanthium $15-18 \times 4-5$ mm, turbinate, green, villose (rarely glabrous); calyx lobes $4-8 \times 1-2$ mm, deltate, patent to slightly recurved at anthesis, dark green, the exterior villose, the interior glabrous, the margin entire, the apex acute; corolla dark green, becoming yellow-green distally, villose; corolla tube 5-6 mm wide basally, the throat narrowing to 4-5 mm; corolla lobes lanceolate, the two dorsal lobes $15-16 \times 4-5$ mm, falcate, opening dorsally 14-16 mm from the corolla base, the two lateral lobes $12-14 \times 4-5$ mm, falcate, the ventral lobe 10 $12 \times 4-5$ mm, opening ventrally 8–10 mm from the corolla base; androecium 27–28 mm, exserted 19–20 mm from the ventral opening, the filament tube green, glabrous, the anther tube 6–7 × 5–6 mm, yellow-green, sparsely puberulous between the sutures, the three dorsal anther tips glabrous, the two ventral anther tips densely villose with white hairs; the style and stigma cream-colored, the stigma lobes fringed with short white hairs along the margin. *Fruits* ca. 15 × 8 mm, cylindrical, maturing white.

Etymology. From the Latin *catulus*, meaning 'young dog, puppy' in reference to the unique hairs on the leaves and stems.

Phenology. This species has been collected with flowers and fruits in July.

Distribution. It has been collected in two locations west of the Andes in Ecuador, in the Provinces Los Ríos and Pichincha. It occurs in wet forests from 600 to 950 m in elevation.

Discussion. This species is unique from any other in Ecuador with its long, white appressed hairs on every part of the plant except the pedicel. The narrow hypanthium and cylindrical fruits are reminiscent of *B. huacamayensis* and *B. marginata*.

Additional specimens examined. ECUADOR: **Los Ríos:** Road Patricia Pilar, Montañas de Ila, km 18, N side of Torre de Bijagual, below antenas, 620–680 m, 00°38'S 79°17'W, 28 Feb. 1993, *Øllgaard & Borchsenius 100690* (QCA). **Pichincha:** Mashpi Lodge, next to

scientific station, 951 m, 00°09'59.70"N 78°53'12.343"W, 06 Jul. 2018, *Muchhala & Gruhn 553* (MO); Mashpi Lodge, on road between scientific station and lodge, 951 m, 00°09'59.70"N 78°53'12.343"W, 06 Jul. 2018, *Muchhala & Gruhn 557* (MO).

12. Burmeistera ceratocarpa Zahlbr., Repert. Spec. Nov. Regni Veg. 13: 534. 1915.
TYPE: Colombia. Cauca: Western slopes of Andes of Popayan, 1700–2100 m, 1876–
1881 (fl., fr.), *F. C. Lehmann 5767* (holotype, B, destroyed; isotypes, F [bc] V0052921F digital image!, GH [bc] 32000 digital image!, K [bc] 250857 digital image!, K [bc]
250858 digital image!, NY [bc] 467990 digital image!, S-05-1884 digital image!, W0046733 digital image!).

Burmeistera ceratocarpa Zahlbr. var. dentata E. Wimm., Pflanzenr. IV. 276b: 154. 1943.
TYPE: Colombia. Caldas: Río San Rafael, below Cerro Tatama, 2500–2800 m, 7–11
Sep. 1922 (fl., fr.), F. W. Pennell 10421 (holotype, NY [barcode] 468006!; isotype, BH
[bc] 33003 digital image!).

Herbaceous shrubs to scandent herbs, 3 m. *Latex* white to cream. *Stems* ca. 6 mm wide, green, puberulous with appressed, gold colored hairs, especially on new growth, striate when dry. *Leaves* alternate, spiral, where flowering progressively reducing in size (becoming bracts?); petioles 5–20 mm, green to green tinged violet, puberulous; lamina $100-250 \times 35-80$ mm, where flowering reduced to $10-80 \times 3-35$ mm, elliptic to ovate-lanceolate (narrowly lanceolate where flowering), the base cuneate to rounded, the apex attenuate to acuminate, $5-25 \times 2-3$ mm, the margin shallow callose-crenate to dentate,

often nearly entire, the teeth often intramarginal, sometimes increasing in size toward the apex; adaxial surface green, glabrous; abaxial surface green to tinged violet, especially on the veins, puberulous with short appressed cream to golden colored hairs, especially along the veins; venation brochidodromous, the primary and secondary veins prominent, raised, the tertiary veins visible. Flowers 30–34 mm, solitary, but bunched apically with new growth, appearing racemose; pedicels 20-50 mm at anthesis, 20-50 mm in fruit, green to tinged violet, puberulous, more dense distally; hypanthium $4-5 \times 4-6$ mm, cupuliform, green to tinged violet, puberulous, the ridges smooth or slightly raised; calyx lobes $5-17 \times 1-2$ mm, ligulate, green to green suffused with violet, glabrous to sparsely puberulous, the margin shallow callose-dentate with 5–9 blunt teeth, the apex acute, patent to reflexed at anthesis; corolla pale green to green tinged maroon-violet, glabrous to sparsely puberulous; corolla tube 5–7 mm wide basally, bulging just above the base, narrowing to 2–3 mm; corolla lobes lanceolate, the margins slightly undulate, the two dorsal lobes $14-17 \times 3-4$ mm, opening dorsally 14-17 mm from the corolla base, falcate, the two lateral lobes $7-11 \times 3-4$ mm, opening ventrally 9-11 mm from the corolla base, falcate; androecium 25–29 mm, exserted 16–18 mm from the ventral opening, the filament tube green, glabrous basally, sparsely puberulous distally, the anther tube green suffused with violet, sparsely to densely villose with white to golden colored hairs, the top three anther tips glabrous, the bottom two anther tips villose with white hairs; the style and stigma dark colored, the stigma lobes shortly pubescent along the margin. *Fruits* 7×9 mm, globose, fleshy, maturing violet.

Phenology. This species has been collected with flowers and fruits throughout the year.

Distribution. This species is found in Colombia and Ecuador along the western Andean range. Its northernmost distribution extends into the department of Cordoba in Colombia. In the south, it extends into northern Ecuador, in the province of Carchi. Specimens have been collected at elevations from 1000 to 3000 m.

Discussion. In Ecuador, *Burmeistera ceratocarpa* and *B. asclepiadea* are unique in the combination of distinct sterile and fertile zones, the latter with reduced bracts, and long calyx lobes that are reflexed at anthesis. *B. ceratocarpa* is most similar to *B. asclepiadea*, but is differentiated by its elliptic leaves widest near the middle (vs. ovate, widest at the base in *B. asclepiadea*), and its caudate, falcate leaf apex (vs. attenuate)

Additional specimens examined. COLOMBIA. **Antioquia:** Municipio de Frontino, corregimiento Nutibara, cuenca alta del Río Cuevas, Finca de Tulio Alvarez, 2090 m, 13 Jul. 1987, *Sánchez 1368* (NY); Municipio de Frontino, corregimiento Nutibara, cuenca alta del Río Cuevas, Sitio el Peligro, 1900 m, 23 Nov. 1986, *Sánchez 817* (NY); Municipio Frontino, correg. Nutibara, Nutibara-La Blanquita rd., region of Murrí, Alto de Cuevas, 1700–1800 m, 06°45'N 76°20'W, 19 Apr. 1988, *Luteyn et al. 11990* (NY); Mcpio. Frontino, correg. Nutibara, región de Murrí, Altos de Cuevas, 1500–1800 m, 06°45'N 76°20'W, 16–18 Oct. 1987, *Luteyn et al. 11716* (NY). **Cauca:** El Tambo, in silva primaria ad Munchique, 2300 m, 27 Aug. 1935, *von Sneidern 506* (NY); El Tambo, Las Casita, 1800 m, 26 Jan. 1936, *von Sneidern 593* (NY); La Gallera, Micay Valley, 1400–1500 m, 29–30 Jun. 1922, *Killip 7770* (NY); La Gallera, Micay Valley, open land west of Rio San Joaquin, 1400–1500 m, 29–30 Jun. 1922, Killip 7862 (NY); La Gallera, Micay Valley, 1900–2000 m, 01 Jul. 1922, Killip 7942 (NY); La Gallera, Micay Valley, 2000–2200 m, 01 Jul. 1922, Killip 7955 (NY); Municipio El Tambo, Parque Nacional Natural Munchique, 28 km El Tambo-10 de Julio, 2545 m, 13 May 1991, Betancur & *Churchill 2531* (NY); Parque Nacional Munchique, 1–12 km into park beyond its entrance, 2100–2440 m, 02°40'N 76°50'W, 07 May 1984, Luteyn et al. 10293 (NY); Parque Nacional Munchique, 42–47 km NE of Uribe, 2350–2650 m, 24 Apr. 1979, Luteyn et al. 7425 (NY); Parque Nacional Munchique, 1–12 km into park beyond its entrance, 2100–2440 m, 02°40'N 76°50'W, 07 May 1984, Luteyn et al. 10294 (NY). Nariño: La Planada Biological Reserve, ca. 7 km S of Chucunez, along La Vieja Trail, 1800–1900 m, 01°10'N 77°55'W, 05-06 Aug. 1990, Luteyn & Sylva 13851, 13906 & 13910 (NY); La Planada, 7 km above Chucunes on road between Tuguerres and Ricaurte, 1780 m, 01°05'N 78°01'W, 26 Jul. 1988, Croat 69553 (MO); La Planada, Salazar Finca 7 km above Ricaurte, 1750 m, 01°08'N 77°58'W, 26 Nov. 1981, Gentry et al. 34970 (NY); Municipio de Ricuarte, Reserva Natural La Planada, a 7 km de Chucunés, 1800 m, 27 Sep. 1989, de Benavides 10950 (NY); Municipio de Ricaurte, Reserva Natural La Planada, bosque bajo entre Santa Rosa y la Reserva, 1300–1700 m, 01°14'N 77°58'W, 20 Feb. 1993, Betancour et al. 3939 (NY); Municipio Piedraancha, Corrigimiento Chucunez, Reserva Natural La Planada, camino desde la Reserva hacia Pialapi, 1650-1800 m, 18 May 1991, Betancour et al. 2577 (NY); Reserva Natural La Planada, 01°10'N 77°58'W, 16 Jan. 1991, Benavides 11142 (NY). ECUADOR. Carchi: Along road from El Chical to El Carmen, departing main El Chical to Peñas Blancas road 0.6 km W of bridge over Río Chical, just W of El Chical, 3.3 km S of jct., 1300 m,

00°59'01"N 78°11'37"W, 07 Aug. 2004, *Croat & Hannon 93024* (MO); Cerro Golondrinas, north-facing slope on south side of upper Río Blanco valley, 1750–1800 m, 00°52'N 78°11'W, 06 Feb. 1993, *Boyle & Boyle 1509* (MO); Forest area along slope of mountain ENE of Rafael Quindí's mountain finca and above Río Verde, 1870–2400 m, 00°52'N 78°07'W, 03 Dec. 1987, *Hoover 2272* (MO, QCA); Ridge to NE of Rafael Quindí's mountain finca, 2000 m, 00°52'N 78°08'W, 29 Nov. 1987, *Hoover 2019* (MO); Trail from Untal to Rafael Quindí's Finca, south of Cerro Golondrinas, 1700 m, 00°55'N 78°15'W, 23 Nov. 1987, *Hoover & Wormley 1460* (MO, QCA).

13. *Burmeistera chrysothrix* Muchhala & Mashburn, sp. nov. TYPE: Ecuador. Carchi: Bosque Protector Golondrinas, on path from Moran to lodge, 2750 m, 00°49'11.13"N 78°04'59.663"W, 03 Jul. 2018 (fl.), *N. Muchhala & J. Gruhn 544* (holotype, MO!).

Scandent herbs, 3 m. *Latex* white. *Stems* 4 mm wide, terete, green to violet, densely hispid with yellow to tan colored hairs. *Leaves* alternate, distichous; petioles 4–8 mm, green to violet, densely villose; lamina $25-55 \times 8-25$ mm, narrowly ovate to lanceolate, the base obtuse to rounded, the apex attenuate to acuminate, the margin shallow callose-dentate, the teeth often irregular in size; adaxial surface green, tinged violet when young, the veins sometimes tinged violet, villose; abaxial surface green, sometimes tinged violet, densely villose; venation arcuate, the secondary veins terminating in marginal teeth, the primary and secondary veins prominent, slightly raised, light green to yellow, the tertiary veins visible. *Flowers* 29–30 mm, solitary; pedicels 15– 30 mm at anthesis, 25–30 mm in fruit, villose, green; hypanthium 7–8 × 7 mm, obconical, green to violet, densely villose, the ridges raised; calyx lobes $2-3 \times 1-2$ mm, deltate, green to violet, villose, the margin entire, the apex obtuse, ascending at anthesis; corolla green to green suffused violet, villose; corolla tube 3–4 mm wide basally, narrowing to 2 mm; corolla lobes lanceolate, the margins undulate, the two dorsal lobes $8-11 \times 2-3$ mm, opening dorsally 14 mm from the corolla base, arcuate, the two lateral lobes $4-7 \times 1-3$ mm, opening ventrally 8–9 mm from the corolla base, arcuate; androecium 20–21 mm, exserted 13–14 mm from the ventral opening, the filament tube green spotted violet, glabrous, the anther tube violet, dark green along the sutures, villose with cream colored hairs; the top three anther tips glabrous, the bottom two anther tips densely villose with cream colored hairs; the style and stigma unknown. *Fruits* 25 × 30 mm, globose, inflated, spongy, white, villose.

Etymology. The specific epithet means 'with golden hairs,' from the Greek *chrysos*, gold, and *thrix*, hair.

Phenology. This species flowers and fruits from April to October.

Distribution. Collections of this species are concentrated in the northern Ecuador province of Carchi, near the border with Colombia. The species potentially occurs in southern Colombia as well.

Discussion. This species is potentially related to *B. aspera* and *B. loejtnantii*, as they are quite similar in fruit and flower size. *Burmeistera chrysothrix* differs in its uniformly hispid vegetative surfaces and villose reproductive parts.

Additional specimens examined. ECUADOR. **Carchi:** Bosque Protector Golondrinas, on path from Moran to lodge, 2844 m, 00°49'06.06''N 78°04'34.093''W, 03 Jul. 2018, *Muchhala & Gruhn 542* (MO); Bosque Protector Golondrinas, on path from Moran to lodge, 2704 m, 00°49'03.15''N 78°05'22.883''W, 03 Jul. 2018, *Muchhala & Gruhn 546* (MO); Carretero Tulcán-Tufiño-Maldonado-Chical, km 33–56 de Tufiño, 2000–2900 m, 00°50'N 78°02'W, 23 Apr. 1993, *Friere-Fierro & Andersen 2561* (QCA); Carretero Tulcán-Tufiño-Maldonado, Sector La Pradera, 2340–2640 m, 12 Oct. 1986, *Friere-Fierro 374* (QCA); Road Maldonado-Tulcan, km 24, 2575 m, 04 May 1993, *Borchsenius* 77 (QCA); Tufiño–Maldonado, km 42, 2700 m, 19 Feb. 1995, *Schwerdtfeger 21923* (QCA); Tulcán-Maldonado road, 42 km W of Tufiño, 2425 m, 13 Apr. 1978, *Luteyn & Lebron-Luteyn 5747* (NY).

14. Burmeistera crassifolia (E. Wimm.) E. Wimm., Repert. Spec. Nov. Regni Veg. 30:
33, tab. 125. 1932. Basionym: *Centropogon crassifolius* E. Wimm., Repert. Spec. Nov.
Regni Veg. 19: 389. 1924. TYPE: Ecuador. Esmeraldas: In sylvis tropic. prov.
Esmeraldas, 1905 (fl., fr.), *L. Sodiro 7* (holotype, W-1967-0015269 digital image!).

Burmeistera crassifolia (E. Wimm) E. Wimm. var. *ovatifolia* (E. Wimm) E. Wimm., Repert. Spec. Nov. Regni Veg. 30: 33. 1932. Basionym: *Centropogon crassifolius* E. Wimm. var. *ovatifolius* E. Wimm., Repert. Spec. Nov. Regni Veg. 19: 389. 1924. TYPE: Ecuador. Pichincha: Prope Cauzacoto, s.d. (fl.), *L. Sodiro 91/26* (holotype, B, destroyed; isotype, P [barcode] 00408886 digital image!).

Scandent herbs or epiphytes, 4 m. Latex white to cream. Stems ca. 5 mm wide, terete, green to violet, glabrous to very sparsely puberulous. Leaves alternate, distichous, sometimes reduced in size where flowering; petioles 2–8 mm, green, sometimes tinged violet, glabrous to sparsely puberulous; lamina $50-85 \times 20-55$ mm, where flowering reduced to $20-40 \times 10-20$ mm, ovate to shortly lanceolate, the base obtuse to rounded, the apex attenuate, the margin shallow callose-serrate, sometimes nearly entire, often revolute, often tinged violet, the teeth sometimes intramarginal; adaxial surface green to lightly tinged violet, glabrous; abaxial surface lighter green to tinged violet, puberulous with cream colored hairs, mostly along the primary vein, velutinous; venation arcuate with secondary veins terminating in marginal teeth, the primary vein prominent, the secondary veins only slightly visible or not visible, the tertiary veins not visible. *Flowers* 30–37 mm, solitary; pedicels 30–45 mm at anthesis, 30–60 mm in fruit, glabrous to sparsely villose, green to violet; hypanthium $5-6 \times 4$ mm, obconical, green to speckled violet, glabrous to sparsely villose, the ridges smooth; calyx lobes $9-14 \times 0.5-1$ mm, linear, green spotted with violet, glabrous to sparsely villose, the margin shallow callosedentate, the apex acute, slightly ascending to patent at anthesis; corolla entirely reddish violet or with green and violet striations and blotches, glabrous to sparsely puberuous; corolla tube 4–5 mm wide basally, narrowing to 2–3 mm; corolla lobes lanceolate, the margins smooth, the two dorsal lobes $13-15 \times 3$ mm, opening dorsally 17-18 mm from

the corolla base, ascending to slightly falcate, the two lateral lobes $9-13 \times 3 \,$ mm, opening ventrally 14–15 mm from the corolla base, slightly falcate; androecium 29–32 mm, exserted 13–19 mm from the ventral opening, the filament tube green to violet, glabrous basally, villose distally with white hairs, the anther tube green to violet, villose basally and between the sutures, the top three anther tips glabrous to sparsely pubescent, the bottom two anther tips densely villose with white hairs; the style and stigma green, the stigma lobes densely pubescent along the margin with short white hairs. *Fruits* 12 × 15 mm, globose, slightly inflated, white to pink with violet blotches or striations.

Phenology. Specimens have been collected with flowers and fruits throughout the year.

Distribution. Found in southwestern Colombia and northwestern Ecuador, this species occurs from 100 to 2000 m in elevation. It occurs in wet lowland forests and upland cloud forests.

Discussion. This species is part of a complex of species including the widespread *B*. *microphylla*. This group is defined by the absence of visible tertiary, and often secondary, veins on the underside of the leaf. Dried specimens are characterized by a uniform pale tan on the underside of the leaf. In Ecuador, *B. crassifolia* differs from *B. microphylla* in having ovate to cordate leaves, vs. narrowly lanceolate in *B. microphylla*.

Additional specimens examined. COLOMBIA. **Antioquia:** Mpio. de Frontino, km 13 of road Nutibara-La Blanquita, region of Murrí, Alto de Cuevas, 1990 m, 06°44'N

76°23'W, 06 Nov. 1988, Zarucchi et al. 7223 (MO). ECUADOR. Carchi: Banks of Río Gualpi Chico above encampment by river, 1161 m, 00°58'N 78°16'W, 22 Jan. 1988, Hoover et al. 3543 (MO): Banks of Río Gualpi Chico above encampment by river, 1161 m, 00°58'N 78°16'W, 22 Jan. 1988, Hoover et al. 3544 (QCA); Río Palaví above Awá encampment, 200 m, 00°58'N 78°16'W, 10 Feb. 1988, Hoover et al. 3121 (MO, QCA); Trail along plain above Tobar-Donoso and to Río Guape, 245–400 m, 01°10'N 78°18– 31'W, 19 Feb. 1984, Hoover 1303 (MO); Tulcan Canton, Reserva Etnica Awá, Comunidad de Gualpi Medi, 900 m, 01°01'N 78°16'W, 21 May 1992, *Quelal 659* (MO). Cotopaxi: Bosque Integral Otonga, 1791 m, 00°25.256'S 78°59.834'W, 06 Jul. 2002, Muchhala 121 (QCA). Esmeraldas: Ascending Río Palaví near Awá encampment, 150-250 m, 01°07'N 78°37'W, 09 Feb. 1988, Hoover et al. 3859 (MO, QCA); Canton San Lorenzo, road Lita to El Cristal, on finca of Dr. La Lama, 13.5 km S of Lita, 1220–1350 m, 00°49'N 78°26'W, 13 May 1992, Luteyn et al. 14639 (NY); Canton San Lorenzo, Lita to El Cristal road, on finca of Dr. La Lama, 13.5 km S of Lita, 1220–1350 m, 00°49'N 78°26'W, 02 Nov. 1992, Luteyn et al. 14732 (NY, QCA); Cantón Quinindé, Bilsa Biological Reserve, Reserva Ecológica Mache-Chindul, 35 km W of Quinindé, trail from SW border of reserve to Don Bolivar's home, connecting the road towards Pierdrita and the road towards Mono, 400–600 m, 00°21'N 79°44'W, 21 Aug. 2003, *Clark 8824* (QCA); Km 5–18 on road Lita to Alto Tambo, 650–750 m, 18 Jan. 1987, Dodson et al. 16861 & 16862A (MO); San Lorenzo Canton, Parroquia Alto Tambo, frente finca del Sr. Lalama, a 1.5 km del sector de El Cristal, 650 m, 00°50'N 78°30'W, 13 May 1992, Quelal & Luteyn 522 (MO); Quinindé, Bilsa Biological Station, Mache Mountains, 35 km W of Quinindé, 5 km W of Santa Isabel, 400–600 m, 00°21'N 79°44'W, 11 Oct.

1994, *Clark 178* (MO). Imbabura: Cantón Cotocachi, parroquia García Moreno, Charguayacu Alto, Reserva Los Yaltes, desde la casa hacia arriba por el lindero y luego sendero a la loma y camino, 1550-1705 m, 00°17'39"N 78°41'45"W, 01 May 2017, Pérez et al. 11026 (QCA). Santo Domingo de los Tsáchilas: Carretera Antigua to Santo Domingo de los Colorados, km 72-74, 1800-1900 m, 03 Apr. 1978, Luteyn 5647 (MO, NY, QCA); Collections from path following ridge line at El Centinela at crest of Montanas de Ila on road from Patricia Pilar to 24 de Mayo at km 12, Patricia Pilar is at km 45 on road from Sto Domingo to Quevedo, 600 m, 06 Feb. 1979, Dodson 7361 (MO); Collections from path following ridge line at El Centinela at crest of Montanas de Ila on road from Patricia Pilar to 24 de Mayo at km 12, Patricia Pilar is at km 45 on road from Sto Domingo to Quevedo, 600 m, 06 Apr. 1980, Dodson & Gentry 10304 (MO); Old road from Santo Domingo to Quito, ca. 5 km from paved highway, 1200 m, 00°15'S 78°55'W, 03 May 1985, Dodson & Cook 1985 (MO, NY); Quevedo Canton, Cerro Centinela, el Mirador, a 12 km al este de Patricia Pilar y Centro Científico Río Palenque, 540 m, 00°37'S 79°18'W, 03 Jun. 1990, Rubio & Alverson 397 (MO); Vía Alluriquin-Las Damas, 1670 m, 00°25'08"S 78°59'38"W, 25 Aug. 2012, Pérez 5690 (QCA).

15. Burmesitera crispiloba Zahlbr., Repert. Spec. Nov. Regni Veg. 13: 528. 1915.
TYPE: Ecuador. Chimborazo: In silva subtropica vallis Pallatango, Sep. 1891 (fl.), *L.*Sodiro 91/24 (holotype, B, destroyed; isotypes, P [barcode] 408884 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
(fl.), L. Sodiro 91/22 (holotype, B, destroyed; isotypes, P [barcode] 408885 digital
image!, W-1963-0012270 digital image!).

Burmeistera succulenta Zahlbr. var. *breviloba* E. Wimm., Pflanzenr. 276c: 836. 1968. TYPE: Ecuador. Los Ríos: San Carlos de los Colorados, 150 m, 28 Sep. 1935 (fl.), *A. Schultze-Rhonhof 1929* (holotype, B [barcode] 100158362 digital image!).

Scandent herbs, 5 m. *Latex* white to tan. *Stems* ca. 4 mm, green to green tinged violet, glabrous. *Leaves* alternate, distichous, often reduced in size when subtending a flower, the internodes 10-30 mm; petioles 5-10 mm, glabrous, green to green tinged violet; lamina, when sterile $90-160 \times 25-55(-70)$ mm, when fertile reducing to $55-105 \times 15-40$ mm, elliptic to oblong-lanceolate, the base attenuate to obtuse, the apex attenuate, the margin shallow callose-dentate to nearly entire, sometimes slightly revolute; adaxial surface green, glabrous; abaxial surface green to green tinged violet, glabrous; veins craspidodromous to camptodromous, 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; pedicels 75-110 mm at anthesis, 85-110 mm in fruit, green to green tinged violet, glabrous; hypanthium $9-13 \times 5-9$ mm, obconical, green to green tinged violet, glabrous; how in the upper leaf axies, ascending at anthesis; corolla exterior entirely green to green tinged violet, glabrous, the interior white to pale blue-green; corolla tube 6-8 mm wide basally, the

throat narrowing to 2–3 mm, glabrous; corolla lobes lanceolate, strongly scrolling back, the two dorsal lobes $20-25 \times 2-4$ mm, opening dorsally 15–23 mm from the corolla base, the two lateral lobes $17-18 \times 2-3$ mm, the ventral lobe ca. 16×3 mm, opening ventrally 11-14 mm from the corolla base; androecium 35–48 mm, exserted 23–30 mm from the ventral opening, the filament tube green to green tinged violet, glabrous to villose distally, the anther tube $8-12 \times 2.5-4$ 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. $30 \times$ 30 mm, globose, spongy, inflated, maturing white tinged with red-violet, to entirely pink or cerese red.

Distribution. A common and wide-ranging terrestrial herb in wet tropical forests of western Ecuador. Found at low elevations near the coast, though more common from 500–1500 m in the foothills of the eastern Andes. Sometimes found at elevations up to 2000 m.

Discussion: Both *B. crispiloba* and *B. succulenta* exhibit the strong scrolling of the calyx lobes at anthesis, in which calyx lobes scroll back multiple times (see Figure 5A). However, *B. succulenta* is differentiated by its longer calyx lobes (8–18 mm long), compared with the shorter (ca. 1 mm long), deltate calyx lobes of *B. crispiloba*. The few specimens of *B. crispiloba* that do not exhibit an obvious reduction of leaf size when flowering can be confused with *B. sodiroana*, however, all specimens of *B. crispiloba* can be readily identified by their distichous phyllotaxy, compared to the spiral phyllotaxy of *B. sodiroana*. In addition, the corollas of *B. crispiloba* scroll more than those of *B. sodiroana*, which simply curl back.

Intermediate specimens between *B. crispiloba* and *B. sodiroana* suggest that these two species hybridize or introgress where their ranges meet in the eastern 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. In this study, intermediate specimens are placed with *B. crispiloba* until molecular work on the group can test hypotheses of gene flow between these species. In addition, 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 exsertion 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. **Bolívar:** Hacienda Changuil, sector La 47, 400 m, 02°06'S 79°10'W, 01 August 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, 02°33'25"S 79°21'59"W, 25 May 2005, Vargas & Defas 5585 (MO). **Carchi:** Alrededores de Maldonado, 90 km al oeste de Tulcan, 1500 m, 05 September 1981, Balslev 1996 (QCA); Maldonado, banks of small stream just N of the village, 1500 m, 04 October 1981, Werling & Leth-Nissen 233 (QCA); Maldonado, Chical trail, 1500 m, 26 January 1977, Boeke 842 (MO, NY, QCA); Near Maldonado, 1400 m, 30 July 1989, van der Werff & Gudiño 10767 (MO). **Cotopaxi:** Cantón Pujilí,

Reserva Ecológica Los Ilinizas, Sector II, Sector Sur, sector Chuspitambo, al occidente de Choasilli, 1727 m, 00°58'42"S 79°06'22"W, 03 August 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, 00°58'45"S 79°06'53"W, 08 August 2003, Silverstone-Sopkin et al. 9965 (MO); Cantón Sigchos, falda del Cerro Azul, lado sur del Cerro, ca. 1.5 horas de las parcelas, 3297 m, 00°35'53"S 78°50'26"W, 25 July 2003, Ramos et al. 6546 (MO); Cantón Sigchos, Reserva Ecológica Los Ilinizas, ca. 4 km antes de Saguambi, en la vía Triunfo Grande-Las Pampas, 2156 m, 00°29'35"S 78°59'37"W, 13 August 2003, Ramos et al. 7305 (MO); Reserva Otonga, entre Quito y Sto. Domingo, cerca de San Francisco de las Pampas, 1990–2200 m, 00°25'S 79°00'W, June 1997, Nowicki & Mutke 1498 (QCA); Tenefuerste, Río Pilalo, km 52-53, Quevado-Latacunga, 750–900 m, 29 October 1981, Dodson & Dodson 12000 (MO); Tenefuerste, Río Pilalo, km 52–53, Quevado, Latacunga, 750–1300 m, 21 February 1982, Dodson & Gentry 12782 (MO). Esmaraldas: New road under construction from Lita to San Lorenzo, 600–800 m, 00°58'N 78°35'W, 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, 00°21'N 79°44'W, 25 March 1995, Clark & Troya 499 (MO). El Oro: Cantón Pinas, parroquia Moromoro, Reserva Ecologica Buenaventura, remnant patch of forest south of Entrada la Virgin, 900-1000 m, 03°39'03"S 79°44'24"W, 12 May 2003, Clark et al. 7944 (QCA); Pinas, Parroquia El Placer, Reserva Buenaventura, propiedad de la Fondacion Jocotoco, recorrido desde la estacion hasta el bosque Puma, 1000 m, 03°38'41"S 79°45'46"W, 03 April 2005, Vargas et al. 5171 (MO); West of Pinas 10 km on new road to Sta. Rosa, 950 m, 08 October 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, 02°27S 79°35W, 31 December 1991, Cerón 17925 (MO). Imbabura: 1390 m, 00°18.066'N 78°46.979'W, 16 April 2003, Muchhala 207 (QCA). Loja: Finca of the Calderón family, taking a trail NE from Mercadillo towards the crest, 1770 m, 04°00'S 79°57'W, 12 August 2000, Cotton et al. 1605 (MO, NY). Los Ríos: Hacienda Clementina, Cerro Samama, trail between Destacemento Pita and La Torre, 600 m, 01°30'S 79°19'W, 24 October 1995, Knudsen et al. 459 (QCA); Río Palenque Science Center, km 56, road Quevedo- Sto. Domingo, 150–220 m, 30 November 1978, Dodson 7310 (MO). Manabí: Machalilla National Park, San Sebastian, 8–9 km SE of Agua Blanca, 550–730 m, 01°36'S 80°42'W, 19 January 1991, Gentry et al. 72409 (MO). Pichincha: Along road and trail from Maquipucuna Lodge to Ecolodge Santa Lucia, 2 km N of Maquipucuna entrance, 1400 m, 00°07'19"N 78°37'06"W, 15 March 2006, Croat et al. 95948 (MO); Bosque Integral Otonga, 1676 m, 00°25.148'S 78°59.567'W, 04 July 2002, Muchhala 115 (QCA); Cantón Quito, Maquipucuna Biological Reserve, 9 km NE of Nanegal, 1500–1700 m, 00°10'N 78°40'W, 02 February 1991, Neill et al. 9800 (MO); Carretera Quito a La Concordia via Nono, Mindo, San Jose de las Minas y Puerto Quito, km 77, 1300 m, 07 August 1984, Dodson et al. 15196A (MO); Carretera Quito-Puerto Quito, km 113, 10 km al N de la carretera principal, 800 m, 00°05'N 79°02'W, 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, 02 February 1985, Dodson & Neill 15584 (MO, NY); Centinela, Canton Sto. Domingo, 12 km E of Patricia Pilar, along path on ridge line, 600 m, 23 August 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 Mantañas de Ila, 650 m, 30 July 1984, Dodson et al. 14661 (MO, NY); Centinela Ridge, 12 km E of Patricia Pilar on road to 24 de Mayo, 600 m, 26 June 1985, Stein & Dodson 3091 (MO); Cooperativa Santa Marta #2, along Rio Verde, 2 km SE of Sto. Domingo de Los Colorados, 530 m, 05 February 1979, Dodson 7433 (MO); El Centinela, 12 km E of Patricia Pilar on road between Santo Domingo and Quevedo, 650 m, 15 July 1979, Fallen & Dodson 858 (MO); From path following ridge line at El Centinela at crest of Montanas de Ila on road from Patricia Pilar to 24 de Mayo at km 12, 600 m, 28 July 1979, Dodson 5628 (MO); Maquipucuna, 5 km E of Nanegal, transect no. 2, 1630 m, 00°07'N 78°37'W, 09 May 1990, Gentry et al. 69945 (MO); Maquipucuna Tropical Reserve, northern boundary of reserve, 10 km N of Nanegalito, 1200 m, 00°10'N 78°35'W, 02 December 1988, Neill et al. 8654 (MO); Nanegalito-Tandayapa road, 1890–2400 m, 00°03–05'S, 78°44'W, 07 November 1989, Luteyn & Tirira 13333 (NY); Old road Santo Domingo- Chiriboga-Quito, ca. 3 km from bridge over Río Pilatón, 1000 m, 17 March 1985, Harling & Andersson 23062 (NY); Old road from Santo Domingo to Quito, ca. 5 km from paved highway, 1200 m, 00°15'S 78°55'W, 03 May 1985, Stein et al. 2686 (MO); Parroquia Nanegal, Cerro Campana, 5-6 km airline E of Nanegal, rigdge between Quebreda Cariyacu and Q. Loreto, 1700 m, 00°09'N 78°37'W, 01 September 1993, Webster & Paradise 30017 (MO); Parroquia Puerto Quito, Reserva Forestal de ENDESA, 10 km al norte de Alvaro Pérez Intriago, 650–800 m, 00°03'N 79°07'W, 11 June 1990, Cerón & Ayala 10082 (MO); Quito Cantón, Nanegal, Reserva Biológica Maquipucuna, 1200–1700 m, 00°08'N 78°35'W, 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, 00°05'N 79°02'W, 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, 00°05'N 79°02'W, 16– 17 November 1989, Luteyn & Borchsenius 13363 (MO, NY, QCA); Reserva Forestal de ENDESA, Río Silanche, 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, 00°05'N 79°02'W, 26 March 1984, Jaramillo 6611 (QCA); Reserva Orquideológica El Pahuma, carretera Calacalí-Los Bancos, km 22, 2000 m, 00°01'42"N 78°37'50"W, 19 October 1999, Rojas et al. 391 (MO); Road Nono-Pacto-Río Yacuambi, 5–10 km above Nanelagito, 1700 m, 00°00'N 78°40'W, 21 July 1980, Holm-Nielsen et al. 24419 (MO, NY); West of Santo Domingo de los Colorados 20 km, 1000 m, 30 October 1961, Cazalet & Pennington 5207 (NY).

16. Burmeistera crocodila Muchhala & Mashburn, sp. nov. TYPE: Ecuador. Carchi:
Bosque Protector Golondrinas, on path from Moran to lodge, 2750 m, 00°49'11.13"N
78°04'59.663"W, 03 Jul. 2018 (fl., fr.), *N. Muchhala & J. Gruhn 545* (holotype, MO!).

Scandent herbs, 1 m. *Latex* white. *Stems* ca. 3 mm wide, green tinged violet, glabrous, nitid, zig-zag. *Leaves* alternate, distichous; petioles 8–12 mm, green to violet, glabrous basally, becoming villose near the lamina, especially underneath, with white hairs; lamina $60-85 \times 20-35$ mm, narrowly ovate to elliptic, the base obtuse to rounded, the apex acuminate, $5-10 \times 1-2$ mm, the margin shallow callose-serrate, the teeth intramarginal; adaxial surface green tinged violet, glabrous, nitid; abaxial surface green

tinged violet to entirely violet, villose with white hairs; venation pinnate, the secondary veins terminating in marginal teeth or in a thin submarginal collecting vein, the primary vein prominent, raised, the secondary veins slightly raised, the tertiary veins barely visible or not visible. Flowers 36-37 mm, solitary; pedicels 60-85 mm at anthesis, 80-110 mm in fruit, green tinged violet, glabrous; hypanthium ca. 6×6 mm, obconical, green to violet, puberulent, the ridges smooth; calyx lobes $9-10 \times 1-2$ mm, ligulate, green to violet, glabrous, the margin shallow callose-serrate, the apex obtuse, ascending to patent at anthesis; corolla pale green suffused maroon-violet, glabrous; corolla tube 5– 7 mm wide basally, narrowing to 3–4 mm; corolla lobes lanceolate, the margins smooth, the two dorsal lobes $15-16 \times 4-5$ mm, opening dorsally 18–20 mm from the corolla base, slightly falcate, the two lateral lobes $10-12 \times 5-6$ mm, opening ventrally 11-14 mm from the corolla base, falcate; and roccium 29–31 mm, exserted 15–18 mm from the ventral opening, the filament tube green with violet striations, glabrous, the anther tube green with violet along the sutures, glabrous, the top three anther tips glabrous, the bottom two anther tips pubescent with white hairs; the style and stigma unknown. Fruits 25×30 mm, globose, inflated, the exterior violet, the interior white.

Etymology. The specific epithet is in reference to the reptiles in the family *Crocodylidae*, as the leaves of this species are reminiscent of the scales of a crocodile's back.

Phenology. This species has been collected with flowers and fruits in July.

Distribution. This species is narrowly restricted to northwestern Ecuador in Carchi province, near the border with Colombia. It possibly occurs in southwester Colombia as well.

Discussion. This species similar to *B. resupinata* and *B. heilbornii*, but is differentiated by its much smaller flowers.

Additional specimens examined. ECUADOR. **Carchi:** Bosque Protector Golondrinas, on path from Moran to lodge, 2782 m, 00°49'08.09"N 78°04'54.093"W, 03 Jul. 2018, *Muchhala & Gruhn 543* (MO); Sendero desde 0.3–0.5 km WNW de la Cabaña Las Orquídeas (ubacada a 0.14 km W de la intersección con la carretera El Placer-Morán, km 19) hasta el Río El Moran entrado por el km 19 NW desde El Salado, 2719 m, 00°46'38.8"N 78°03'29.6"W, 22 Nov. 2011, *Buenaño et al. 152* (QCA); SE of Maldonado 9–10 km on road to Tulcan, 2480–2550 m, 00°51'N 78°02'W, 27 Jul. 1983, *Thompson & Rawlins 901* (NY); Tulcán-Maldonado road, 41–45 km W of Tufiño, 2500– 2700 m, 13 Apr. 1978, *Luteyn & Lebron-Luteyn 5745* (NY); West of Tulcán 62–75 km, 2460–2720 m, 00°50'N 78°05'W, 07 Jan. 1985, *Luteyn & Cotton 10881* (MO, NY, QCA).

17. Burmeistera cyclostigmata Donn. Sm., Bot. Gaz. 20(7): 291. 1895. TYPE: Costa
Rica. Cartago: Estrella, 1340 m, Apr. 1888, J. J. Cooper 5845 (holotype, GH [barcode]
31994 digital image!; isotypes, K [bc] 329698 digital image!, G [bc] 236837 digital
image!).

Burmeistera cerasifera Zahlbr., Repert. Spec. Nov. Regni Veg. 13: 532. 1915. TYPE: Colombia. Cauca: in planitie partis inferioris fluminis Rio Dagna, ad marginem sylvarum densium, 100–300 m, 14 Jul. 1883 (fl.), *F. C. Lehmann 2934* (holotype, G [barcode] 236658 digital image!; isotype, BM [bc] 947544 digital image!).

Burmeistera suerrensis (Donn. Sm.) E. Wimm., Repert. Spec. Nov. Regni Veg. 30: 14, tab. 124. 1932. Basionym: *Burmeistera cyclostigmata* Donn. Sm. var. *suerrensis* Donn. Sm., Bot. Gaz. 24(6): 394. 1897. TYPE: Costa Rica. Limón: Suerre, Llanos de Santa Clara, 900 m, Feb. 1896 (fl.), *J. Donnell Smith 6623* (holotype, US [barcode] 623982 digital image!; isotypes, G [bc] 236834 digital image!, GH [bc] 31995 digital image!, M [bc] 189976 digital image!).

Burmeistera suerrensis (Donn. Sm.) E. Wimm. var. almirantensis E. Wimm., Repert.
Spec. Nov. Regni Veg. 30: 14, fig. 26, tab. 124. 1932. TYPE: Panama. Bocas del Toro:
Regio circa Almirante, Jan.–Mar. 1928 (fl., fr.), *G. P. Cooper 234* (holotype, F not seen; isotypes, NY [bc] 467984!, M not seen).

Burmeistera millei E. Wimm., Repert. Spec. Nov. Regni Veg. 30: 15, fig. 12, tab. 123. 1932. TYPE: s.l., s.d., *L. Mille 32* (lectotype, designated here, W-1967-0015306 digital image!; isolectotype, Q not seen).

Burmeistera mindoana E. Wimm. Repert. Spec. Nov. Regni Veg. 30: 27, tab. 124. 1932. TYPE: Ecuador: Pichincha: In sylv. sutrop. vallis Mindo, Apr. 1900 (fl.), *L. Sodiro 17* (holotype, W-1961-0016773 digital image!).

Herbaceous shrubs to scandent herbs, 5 m. *Latex* white. *Stems* ca. 8 mm wide, terete, green to maroon-violet, glabrous to puberulent with white hairs. Leaves alternate, spiral, the internodes 5–40 mm; petioles 7–30 mm, green to maroon-violet, glabrous to puberulent; lamina 40–150 \times 20–70 mm, elliptic, the base attenuate to cuneate, the apex attenuate, the margin irregularly shallow callose-crenate, sometimes appearing erose; adaxial surface green, sometimes tinged maroon-violet, glabrous; abaxial surface green to green tinged maroon-violet, glabrous to puberulent, especially along the primary vein, nitid; venation camptodromous, the primary and secondary veins prominent, raised, the tertiary veins visible. *Flowers* 42–57 mm, solitary in the upper leaf axils; pedicels 55–70 mm at anthesis, 60–80 mm in fruit, green to maroon-violet, glabrous; hypanthium $6-10 \times$ 4–8 mm, turbinate to cupuliform, abruptly widening distally, green to maroon-violet, glabrous, the ridges smooth to slightly raised; calyx lobes $2-7 \times 0.5-2$ mm, deltate to ligulate, green to maroon-violet, glabrous, the margin shallow callose-dentate, undulate, the apex acute, patent at anthesis; corolla green to red to maroon-violet, sometimes tinged blue-green, glabrous; corolla tube 5–9 mm wide basally, the throat narrowing to 2–5 mm; corolla lobes ligulate, the margins smooth, the two dorsal lobes $19-25 \times 3-7$ mm, opening dorsally 14–22 mm from the corolla base, falcate to arcuate, the two lateral lobes $11-15 \times 3-4$ mm, falcate to arcuate, the ventral lobe ... opening ventrally 13-16 mm from the corolla base; and roecium 37–49 mm, exserted 24–35 mm from the ventral

opening, the filament tube green to tinged violet, villose with white hairs, more dense apically, the anther tube green to maroon-violet, glabrous to puberulent with appressed white hairs, all five anther tips sparsely villose; the style and stigma tinged violet, the stigma lobes shortly pubescent along the margin with white hairs. *Fruits* $20-25 \times 15-20$ mm, cylindrical, green to white when immature, maturing light blue to blue-violet.

Phenology. This species has been collected with flowers and fruits throughout the year.

Distribution. A wide ranging species, found from Costa Rica to central Ecuador at lower elevations generally under 1000 m.

Discussion. Burmeistera cyclostigmata is unique from other *Burmeistera* in its sky blue fruits. However, in the north of its range, most fruits are described as violet. Only in Colombia and Ecuador do many collectors describe the fruits as blue. The new species *B. caelestis* also exhibits blue fruits and is surely a close relative of *B. cyclostigmata*. However, *B. caelestis* occurs in a narrow range at much higher altitudes in Ecuador, and is differentiated by having villose vegetative parts (vs. glabrous or sparsely puberulent here) and shorter, ovate, bullate leaves.

Selected specimens examined. COLOMBIA. **Nariño:** La Planda, 7 km above Chucunes on road between Tuquerres and Ricaurate, along trail to summit of hill behind Centro de Científicos, 1780 m, 01°05'N 78°01'W, 28 Jul. 1988, *Croat 69643* (NY); La Planada Biological Reserve, ca. 7 km S of Chucunez, along trail opposite the posada, 1800-1900 m, 01°10'N 77°55'W, 09 Aug. 1990, Luteyn & Sylva 13959 (NY); Mpio. de Tumaco, Corregimiento de la Guayacana, a 10 km Guayacana, 320 m, 08 Oct. 1988, de Benavides 10410 (NY); Mpio. de Tumaco, localidad Guayacana, 300 m, 20 Mar. 1988, de Benavides 9367 (NY); Mun. Tumaco, 80 km from Tumaco along road to Pasto, Guayacana, 19 Jul. 1984, Balick et al. 1666 (NY); Reserva Natural La Planada, a 7 km de Chucunés, 1800 m, 01°10'N 77°58'W, 14 Nov. 1987, de Benavides 8863 (NY). Chocó: Bolívar-Quibdó rd., ca. 37–40 km W of El Carmen, 671–1360 m, 05°40'N 76°15'W, 21– 22 May 1984, Lutevn et al. 10668 (NY); S ridge of Cerro Mecana, 710–880 m, 06°15'N 77°19'W, 08 Jan. 1984, Juncosa 1768 (NY). Valle del Cauca: Ad pa. El Tambo, La Costa, 800 m, 31 Jul. 1936, von Sneidern 913 (NY); Municipio Dagua, corregimiento El Queremal, antigua vía Cali-Buenaventura km 22, 1284 m, 03°31'29"N 76°44'31"W, 04 Jan. 2014, Salinas & Perdomo 965 (NY); Old road Cali-Buenaventura, km 36-38, Finca Las Elsas, 1320–1500 m, 10 Mar. 1979, Luteyn & Lebron-Luteyn 7003 (NY). COSTA RICA. Alajuela: Monteverde Reserve, El Valle trail, 1600 m, 10°20'N 84°50'W, 27 Oct. 1985, Haber & Bello 3222 (MO). Cartago: South of Bonilla Arriba 1–2 km, or 11–12 km N of Santa Cruz on slope of Volcan Turrialba, 1450–1500 m, 09 Mar. 1978, Utley 6002 (MO). Guanacaste: La Cruz Canton, N Caribbean slope of Cerro Cacao, E to near Río Las Haciendas, Prov. Alajuela boundary, Cordillera de Guanacaste, 1150–1400 m, 10°57'N 85°27'W, 14 Aug. 2007, Grayum et al. 12730 (MO). Heredia: Between Quebrada Tigre and east fork of Río Sardinal, ca 9 km SW of Las Horquetas, route crossing several branches of Río Sardinal, 600 m, 10°17'N 84°02'W, 02 Feb. 1985, Grayum et al. 5062 (MO). Limón: Cantón de Talamanca, P. N. de Cardillera de Talamanca, margen opuesta union Queb. Kuisa con Río Lori, entre Ujarrás y San José

Cabécar, 1800 m, 09°21'38"N 83°13'55"W, 21 Mar. 1993, Fernández 770 (MO).

Puntarenas: Dry steep bank of roadway about 11 km west of Monteverde, 08 May 1971, Wilbur 14265 (MO). San José: West of San Isidro 13–16 km along road to Dominical, 900 m, 05 Mar. 1987, Utley 5986 (MO). ECUADOR. Azuay: Jesús María-Molleturo, about 12 km from Guayas border, 1200 m, 16 Jul. 1977, Boeke & Loyola 2177 (MO, NY). Cañar: Cañar, Parroquia Chontamarca, communidad Yanayacu, base occidental de los Andes, 950 m, 02°26'05"S 79°13'53"W, 02 Aug. 2005, Vargas & Defas 6169 (MO); Guayaquil, Cuenca road, ca. 10 km E of Cochencai, 1970–2000 m, 26 Jan. 1981, Gentry et al. 30817 (MO); La Troncal, Manta Real, a 20 km al sureste de La Troncal, 800 m, 02°33'35"S 79°20'51"W, s.d., Vargas & Defas 5792 (MO). Carchi: Along trail leading to Tobar Donoso from San Marcos, 660 m, 01°07'N 78°20'W, 01 Mar. 1983, Barfod 41576 (MO, NY, QCA); Border area between Prov. Carchi and Esmeraldas, about 7 km past Lito on road Lita-Alto Tambo, 550 m, 00°53'N 78°29'W, 27 Jun. 1991, van der Werff et al. 12062 (MO); Collections from forest area along trail from Rafael Quindí's house to his mountain finca, 1890 m, 00°52'N 78°08'W, 28 Nov. 1987, Hoover & Wormley 1898 (MO); Plateau above San Marcos de los Coaiqueres, on trail towards Gualpí Bajo, 1000 m, 01°06'N 78°17'W, 07 Feb. 1985, Øllgaard et al. 57254 (QCA); San Marcos, 600 m, 01°08'N 78°20'W, 08 Jul. 1983, Thompson et al. 768 (NY); Trail from Rafael Quindí's mountain finca to Río Verde and short distance up Río Verde, 1890 m, 00°52'N 78°08'W, 28 Nov. 1987, Hoover & Wormley 1860 (MO, QCA); Tulcan Canton, Reserva Etnica Awá-Camumbí, 1700–1900 m, 00°53'N 78°16'W, 20–29 Jul. 1991, Quelal et al. 244 (MO); Tulcan Canton, Reserva Indígena Awá, Comunidad San Marcos, 25 km al NW de El Chical, parroquia Maldonado, 1500 m, 01°06'N 78°14'W,
16-30 Nov. 1990, Rubio et al. 995 (MO); Tulcan Canton, Reserva Indígena Awá, Sector El Baboso, camino a Lita, 700 m, 00°49'N 78°21'W, 03 Oct. 1991, Tipaz & Rubio 334 (MO); Tulcan Canton, Reserva Indígena Awá, Comunidad San Marcos, 25 km al NW de El Chical, parroquia Maldonado, 1500 m, 01°06'N 78°14'W, 16–30 Nov. 1990, Rubio et al. 995 (NY); Tulcan, Reserva Etnica Awá, Parroquia El Chical, Centro San Marcos, 750 m, 01°06'N 78°14'W, 20-30 Apr. 1993, Méndez et al. 258 & 293 (MO); Tulcan, Reserva Indígena Awá, Comunidad Gualpi Alto, parroquia Chical, 1800 m, 01°02'N 78°14'W, 15–18 Jun. 1991, Rubio et al. 1567 (MO). Cotopaxi: Forest remnants E of San Francisco de Pampas, 1600 m, 00°25'S 78°58W, 29 Jul. 1991, Øllgaard 99128 (QCA); Reserva Ecológica Los Ilinizas, sector Brasil, acceso desde La Carmela, 1480 m, 00°40'37"S 79°05'09"W, 13 Jul. 2003, Silverstone-Sopkin et al. 9124 (MO); Reserva Ecológica Los Ilinizas, Sector II, Sector Sur, sector Paleseco, al occidente de Choasillí, 00°58'34"S 79°06'58"W, 12 Aug. 2003, Silverstone-Sopkin 10081 (MO). El Oro: Along trail from Sambotambo, following headwaters of Río Moro Moro, south of Buenaventura at and along highway to Portovelo, 1035–1800 m, 29 Aug. 1943, Stevermark 54222 (NY); Cantón Piñas, Parroquia Moromoro, Reserva Ecológica Buenaventura, remnant patch of forest south of Entrada la Virgin, 900–1000 m, 03°39'03"S 79°44'24"W, 12 May 2003, *Clark* 7934 (QCA); In the Moro-Moro region, about 21 miles west of Portovelo, 1035– 1280 m, 07 Oct. 1944, Camp E-611 (NY); Pinas, Parroquia El Placer, Reserva Ecológica Buenaventura, propiedad de la Fundación Jocotoco, recorrido desde la Cripta de la Virgen hasta la salida a la carretera de Moromoro, sendero Tapaculo de El Oro, 1080 m, 03°39'55"S 79°44'22"W, 05 Apr. 2005, Vargas et al. 5206 (MO); West of Pinas 11 km on new road to Sta. Rosa, 850 m, 08 Oct. 1979, Dodson et al. 9068 (MO). Esmeraldas:

Awá Reserve, community of Mataje, 200 m, 01°15'N 78°40'W, 23 Jan. 1993, Beck et al. 1776 (NY, QCA); Eloy Alfaro, Reserva Ecológica Cotacachi-Cayapas, Charco Vicente, Río San Miguel, 200 m, 00°43'N 78°53'W, 20–31 Sep. 1993, *Tirado et al.* 455 (MO); Eloy Alfaro, Reserva Ecológica Cotacachi-Cayapas, Parroquia Luis Vargas Torres, Río Santiago, Estero Angostura, 250 m, 00°49'N 78°45'W, 08-14 Dec. 1993, Tirado et al. 727 (MO); Highway from Lita to Alto Tambo, 792 m, 00°54.468'N 78°32.54'W, 18 Jul. 2002, Muchhala 145 (QCA); In secondary forest near Lita, 30 Jul. 1963, Játiva & Epling 618 (MO, NY); Km 5–18 on road Lita to Alto Tambo, 650–750 m, 18 Jan. 1987, Dodson et al. 16848 (MO); Lita, 600 m, 20 May 1987, van der Werff et al. 9519 & 9572 (MO); Lita-San Lorenzo road, 10–20 km NW of Lita, 800 m, 00°55'N 78°35'W, 12 May 1991, Gentry et al. 70078A (NY); Lita-San Lorenzo road, 18 km W of Río Lita Bridge on old road below Lita, 6.6 km W of bridge over Río Chuchubí, site near Alto Tambo, 425 m, 00°52'11"N 78°27'16"W, 10 Jul. 1998, Croat et al. 82609 (MO); Lita, trail to village, 1000 m, 20 Jul. 1964, Játiva & Epling 838 (NY); Mataje, entre el Estero Molina-Heda. Montero Riera, S. Marco, 140 m, 07 Sep. 1991, Jaramillo 13784 (MO, NY); Mun. de Lita, road from Lita to San Lorenzo, 5 km N of Lita, 650 m, 08 May 1987, Acevedo & Daly 1648 (NY); Río Cayapa, Zapallo Grande, in front of the village a trail was followed into the forest, 100 m, 00°48'N 78°55'W, 01–02 Aug. 1982, Kvist & Asanza 40771 (MO); San José, km 321 along railroad from Ibarra to San Lorenzo, 350 m, 01°00'N 78°00'W, 03 May 1982, Boom 1312 (NY, QCA); San José, km 321 along railroad from Ibarra to San Lorenzo, 350 m, 01°00'N 78°00'W, 04 May 1982, *Boom 1346* (NY) San Lorenzo Cantón, Alrededores de Mataje, 200 m, 01°13'N 78°33'W, 23 Jan. 1999, Cueva et al. 285 (MO); San Lorenzo Canton, Alto Tambo, a 15 km al oeste de Lita, 400 m,

00°50'N 78°32'W, 09 Sep. 1990, Rubio & Ouelal 701 (MO); San Lorenzo Canton, carretera Lita-Alto Tambo-La Punta, 400 m, 01°00'N 78°35'W, 06 Feb. 1991, Gudiño & Moran 1292 (MO, NY); San Lorenzo Canton, Parroquia Mataje, Reserva Etnica Awá, Centro Mataje, 200 m, 01°08'N 78°33'W, 21 Sep. 1992, Aulestia et al. 558 (NY); San Lorenzo Cantón, Reserva Etnica Awá, Parroquia Ricaurte, Centro Pambilar, 500 m, 01°08'N 78°36'W, 21 Jan. 1993, Aulestia & Aulestia 1045 (MO); San Lorenzo Canton, Reserva Indígena Awá, Cañon del Río Mira, 10 km al oeste de Alto Tambo, Comunidad La Union, 250 m, 01°02'N 78°26'W, 16–26 Mar. 1991, Rubio et al. 1172 (MO); San Lorenzo Canton, Ricaurte, Reserva Indígena Awá, 300 m, 01°10'N 78°32'W, 19–24 Oct. 1992, Tipaz et al. 2129 (MO); San Lorenzo, Reserva Etnica Awá, Parroquia Alto Tambo, Centro de la Unión, Cañón del Río Mira, 250 m, 00°52'N 78°26'W, 22 Mar. 1993, Aulestia & Aulestia 1257 (MO); San Lorenzo, Territorio Indígena Awá, Centro Mataje, 500 m W of Río Mataje, 150 m, 01°13'00"N 78°34'01"W, 15 Nov. 2000, Neill et al. 12916 (MO); San Lorenzo, Territorio Indígena Awá, Mataje village, 200 m, 01°11'40"N 78°34'25"W, 16 Feb. 2000, Neill et al. 12484 (MO); Trail from Awá encampment at the Río Palaví to Awá encampment at Matahe, ca. 2 km, 150–250 m, 01°07'N 78°37'W, 09 Feb. 1988, Hoover et al. 3712 (MO); Ventanas, km 319, Quito-S. Lorenzo road, 100 m, 06 Jul. 1964, Játiva & Epling 645 (MO, NY); Zapallo Grande, a mixed black and Cayapa Amerindian community along Río Cayapa, 200 m, 00°48'N 78°54'W, 11–15 Oct. 1983, Barfod et al. 48102 (MO). Imbabura: Along railroad tracks 0.5 km E of Lita, 600 m, 00°50'N 78°27'W, 13 Aug. 1983, *Boom 2579* (NY); Carretero Lita-Alto Tambo, km 6, 500 m, 00°51'N 78°27'W, 25 Jul. 1992, Friere-Fierro et al. 2352 (NY); Cotacachi, Parroquia García Moreno, Reserva Biológica Los Cedros, sendero Estación-Y de

Bracilargo, 1470 m, 00°18'30"N 78°46'47"W, 31 Oct. 2005, Vargas et al. 6427 (MO); Railroad line from Lita to 2 km above, 812 m, 01 Sep. 1982, D'Arcy 14875 (MO); Road along tip of river valley S of Lita, 800–850 m, 03 Sep. 1982, D'Arcy 14898 & 14906 (MO); Pichincha: Along road from Pacto to San Miguel de Los Bancos, between Bellavista and Cielo Verde, Imbabura, 9.8 km E of Pacto, 3.7 km E of La Delicia, 1617 m, 00°09'40"N 78°49'22"W, 07 Sep. 2007, Croat & Ferry 98394 (MO); Trail along Río Chictoa, tributary of Río Pilatón, 2-8 km NE of Quito-Santo Domingo road, 11 km W of Tandapi, 1500–1600 m, 27 Oct. 1974, Gentry et al. 12129 (NY). PANAMA: Bocas del Toro: Oleoducto Road, near Continental Divide, Fortuna Dam area, 1000 m, 08°48'N 82°12'W, 05 Feb. 1984, Churchill et al. 4571 (MO). Chiriquí: Fortuna Dam region, along Quebrada Arena near continental divide, 1050 m, 08°45'N 82°15'W, 09 Mar. 1986, McPherson 8749 (MO). Coclé: Cerro Pilon, 5 km NE of El Valle, 800–1045 m, 14 Jun. 1975, Mori et al. 6624 (MO). Colón: Donoso Distrito, site of proposed copper mine, MPSA, 70 m, 08°53'14"N 80°38'47"W, 06 Dec. 2009, *McPherson 21170* (MO). Darién: NE slope of Summit Cerro Sapo, approach from Garachiné, 975 m, 08 May 1979, *Hammel 7273* (MO). Panamá: High point of ridges S of Ipetí, 5–6 hours walk from Chocó Village, Serrania de Maje, 650–800 m, 08°45'N 77°30'W, 31 Mar. 1982, Knapp et al. 4516 (MO). Veraguas: Vicinity of Escuela Agricultura, Alto Piedra near Santa Fe, 0.3 mi beyond the fork in the road near the school, toward Atlantic slope along trail to top of Cerro Tute, 975–1040 m, 26 Jan. 1980, Antonio 3479 (MO).

18. Burmeistera cylindrocarpa Zahlbr., Repert. Spec. Nov. Regni Veg. 13: 533. 1915.TYPE: Ecuador. Pichincha: In declivibus occidentalibus Andium Quitensium prope

Angui, 1800 m, Nov. 1880 (fl.), *F. C. Lehmann 192* (holotype, B, destroyed; isotypes, BM [barcode] 947551 digital image!, G [bc] 236660 digital image!, W-1898-0000635 digital image!).

Scandent herbs, 2 m. *Latex* white. *Stems* ca. 4 mm wide, terete with a raised ridge along either side of the stem connecting the petioles, green tinged violet, glabrous. Leaves alternate, distichous; petioles 4–11 mm, green tinged violet, glabrous; lamina $80-160 \times$ 10–35 mm, oblong to oblanceolate, the base attenuate, the apex acuminate, $10-15 \times 0.5-$ 1 mm, the margin shallow callose-serrate, the teeth sometimes intramarginal; adaxial surface green, lighter along the primary and secondary veins, sometimes tinged violet, glabrous; abaxial surface green, sometimes tinged violet, glabrous; venation camptodromous, the secondary veins sometimes terminating in marginal teeth, the primary vein prominent, raised, the secondary veins thin, slightly raised, the tertiary veins barely visible. *Flowers* 35–43 mm, solitary; pedicels 40–50 mm at anthesis, 50–70 mm in fruit, glabrous, green tinged violet; hypanthium $9-10 \times 4-5$ mm, obconical, green tinged violet, glabrous, the ridges slightly raised; calyx lobes $1-2 \times 1-2$ mm, deltate, green to violet, glabrous, the margin entire, the apex obtuse, ascending at anthesis; corolla green to maroon-violet, glabrous; corolla tube 4–5 mm wide basally, narrowing to 2–3 mm; corolla lobes lanceolate, the margins undulate, the two dorsal lobes $13-15 \times 3-4$ mm, opening dorsally 16–20 mm from the corolla base, falcate, the two lateral lobes $9-10 \times$ 3-5 mm, opening ventrally 10-12 mm from the corolla base, falcate; and roccium 26-33mm, exserted 17–20 mm from the ventral opening, the filament tube green, puberulous with white hairs, the anther tube green, tan between the sutures, glabrous between the

sutures, with appressed white hairs along the sutures, otherwise glabrous or sparsely puberulous, the top three anther tips sparsely pubescent, the bottom two anther tips more densely villose with white hairs; the style and stigma unknown. *Fruits* 19×13 mm, cylindrical to obovoid, fleshy, white when immature, maturing pink to pale violet.

Phenology. This species has been collected with flowers and fruits from June to December.

Distribution. This species is occurs in the eastern Andean range of Ecuador in Pichincha Province and the northeast corner of Santo Domingo de los Tsáchilas Province. Specimens have been collected at elevations from 1500 to 2200 m.

Discussion. This species is similar to *B. auriculata* and *B. truncata* in having long narrow leaves. However, *B. cylindrocarpa* is differentiated as having small, deltate calyx lobes, vs. the much longer ones in the aforementioned species. The calyx lobes and leaves of *B. cylindrocarpa* are similar to *B. crispiloba*, but the flowers of *B. cylindrocarpa* are much smaller than those of *B. crispiloba*, and do not have scrolling corolla lobes.

Additional specimens examined. ECUADOR. **Pichincha:** Parroquia Nanegal, Maquipucuna area, Cerro Sta. Lucia, Cerro Campana, ca. 6 km airline E of Nanegal, 1800 m, 00°8.5'N 78°37.5'W, 20 Jul. 1990, *Webster & Bonning 28325* (QCA); Quito-Santo Domingo old road, Las Palmeras, ca. 59 km WSW of Quito, Pablo Feret trail above Río Guajalito, 1900-2000 m, 00°18'S 78°43'W, *Luteyn & Berg 14356* (NY); San Miguel de los Bancos Cantón, Nanegalito-Mindo road, 16.5 km SSW of Nanegalito, 1500 m, 00°01'14"S 78°24'23"W, 21 Jul. 1998, *Croat 82781A* (MO). **Santa Domingo de los Tsáchilas:** Las Palmeras, along old road Sto. Domingo-Quito, ca. km 59, 2200 m, 00°13'S 78°48'W, 18 Nov. 1989, *Luteyn & Borchsenius 13368* (NY); Las Palmeras, old road Quito-Sto. Domingo, km 59, trail leaving to the south, just opposite sign saying "Estacion científico Río Guajalito, 1970 m, 00°16'S 78°50'W, 01 Dec. 1989, *Borchsenius 91439* (NY); Reserva Río Guajalito, 2000 m, 00°13'W 78°48'W, 21 Jul. 2000, *Muchhala 25* (QCA); Reserva Florística-Ecológica Río Guajalito, km 59 de la carretera antigua Quito-Sto Domingo de los Colorados, 3.5 km al NE de la carretera, estribaciones occidentales del Volcán Pichincha, 1800-2200 m, 00°13'53"S 78°48'10"W, 14 Aug. 1985, *Jaramillo & Zak 8096* (MO); Reserva Río Guajalito, collected on Argentino trail, 1978 m, 00°14.7101'S 78°48.0976'W, 25 Jun. 2010, *Muchhala 452* (QCA).

19. Burmeistera domingensis Jeppesen, Fl. Ecuador 14: 20, fig. 1A. 1981. TYPE:
Ecuador. Pichincha: Virgin forest along Rio Toachi near Santo Domingo, 700 m, 03 Aug.
1962 (fl., fr.), *C. Játiva & C. Epling 317* (holotype, UC [barcode] 1450527 digital
image!).

Herbaceous shrubs to scandent herbs, 2 m. *Latex* white. *Stems* ca. 5 mm wide, green to green tinged violet, puberulous with cream colored hairs, especially dense apically on new growth, striate when dry. *Leaves* alternate, spiral, the internodes 10-30 mm; petioles 5–20 mm, green to green tinged violet, puberulous; lamina $(30-)65-120 \times$

(10–)35–65 mm, broadly elliptic, the base cuneate, the apex attenuate, the margin shallow callose-dentate, the teeth often somewhat irregular, slightly increasing in size toward the apex; adaxial surface green, glabrous; abaxial surface green, puberulent along the veins with cream colored hairs; venation arcuate, the secondary veins dispersing near the margin and terminating in marginal teeth, the primary and secondary veins prominent, raised, the tertiary veins visible. Flowers 31-36 mm; pedicels 40-55 mm at anthesis, 40-85 mm in fruit, green suffused violet, puberulous basally, sparsely puberulous to glabrous distally; hypanthium $4-6 \times 2-4$ mm, cupuliform, green, glabrous to sparsely puberulous, the ridges smooth; calyx lobes $5-8 \times 1-3$ mm, ligulate, green, sometimes fringed violet, glabrous, the margin serrate with many callose tipped teeth, the serrations irregular, the teeth sometimes violet, ciliate, the apex acute, ascending at anthesis; corolla green streaked and spotted with violet to entirely tinged violet, puberulous with white hairs; corolla tube 3–6 mm wide basally, narrowing to 2–3 mm; corolla lobes ligulate, the margins smooth to undulate, the two dorsal lobes $11-12 \times 2-3$ mm, opening dorsally 13-14 mm from the corolla base, falcate, the two lateral lobes ca. 7×2 mm, opening ventrally 9–11 mm from the corolla base, falcate; androecium 26–29 mm, exserted 16–18 mm from the ventral opening, the filament tube green, sparsely to densely puberulous with white hairs, the anther tube green, glabrous, the top three anther tips glabrous, the bottom two anther tips glabrous or sparsely puberulous with short white hairs; the style and stigma tinged violet, the stigma lobes glabrous. Fruits ca. 8×8 mm, globose, fleshy, dark red.

Phenology. This species has been collected with flowers and fruits throughout the year.

Distribution. Found in central-western Ecuador at lower elevations in remnant forest patches.

Discussion. Vegetatively, this species is easily confused with *B. pacifica*, as they both have broadly elliptic leaves with irregularly serrate margins. Both species also have red fruits. However, the flowers of *B. domingensis* are small and violet, while those of *B. pacifica* are much longer and entirely green.

Additional specimens examined. **Guayas:** In wet forest east of Manglar Alto, 100–300 m, *Haught 3102* (NY). **Manabí:** Cord. De Chongón, Parque Nacional Machalilla, S of San Sebastian, C. Josse ha plot, 500–600 m, 01°35'S 80°41'W, 24 Mar. 1993, *Øllgaard 100778* (QCA); Jama, 28 km south of Pedernales as the crow flies, 3.5 km SW of the town Camarones, off trail NW of Pertextaxto Gutierrez's house, 500–550 m, 00°07'42"S 80°09'47"W, 27 Nov. 1999, *Delinks 490* (MO). **Santo Domingo de los Tsáchilas:** Alluriquin, along small river 5 km S from the village, 1000 m, 19 Oct. 1981, *Werling & Leth-Nissen 444* (QCA); Refugio de Vida Silvestre Pasochoa, 901 m, 00°19.58'S 78°56.558'W, 22 Jun. 2002, *Muchhala 102* (QCA); Río Pilatón valley, Quito to Santo Domingo de los Colorados, Tinalandia, 13 km E of Santo Domingo, along small stream S of highway, 750 m, 00°20'S 79°02'W, 20 Jun. 1987, *Hammel & Wilder 16068* (MO); Road La Unión del Toachi-San Franciso de las Pampas, km 3, 1100–1200 m, 19 Mar. 1985, *Harling & Andersson 23154* (NY); Santo Domingo de los Colorados to Quito, ca. 12 km E of Santo Domingo, 700 m, 00°20'S 79°02'W, 06 Dec. 1986, *Hammel & Trainer* 15887 (MO); West of Santo Domingo de los Colorados 20 km, 305 m, 24 Oct. 1961, Cazalet & Pennington 5139 (NY).

20. Burmeistera draconis Á. J. Pérez & Muchhala, Phytotaxa 362(3): 267, fig. 3A–D.
2018. TYPE: Ecuador. Zamora Chinchipe: Nudo de Sabanilla, east slope ca. 5 km from pass on road Yangana-Valladolid, 2700 m, 04 Apr. 1985 (fl., fr.), *G. Harling & L.*Andersson 23645 (holotype, QCA not seen; isotypes, G not seen, MO-5679296!, NY
[barcode] 1185765!).

Herbaceous shrubs to scandent herbs, 5 m. *Latex* cream colored. *Stems* 8–15 mm wide, green, puberulent, velutinous. *Leaves* alternate, spiral; petioles 7–15 mm, green tinged violet, puberulent; lamina $30-80 \times 10-30$ mm, elliptic, the base cuneate, the apex attenuate to acuminate, $5-15 \times 2-3$ mm, the margin irregularly callose-crenate, the teeth $0.25-4 \times 0.25-2$ mm, the large teeth separated by 3–8 mm with 1–5 small teeth between; adaxial surface green, glabrous; abaxial surface violet, puberulent with white hairs; venation pinnate, the secondary veins sometimes terminating in marginal teeth, the primary and secondary veins prominent, raised, the tertiary veins dark violet. *Flowers* 44–45 mm, solitary; pedicels 50–70 mm at anthesis, 65–75 mm in fruit, green, glabrous, nitid; hypanthium $10-11 \times 8-10$ mm, broadly obconical to cupuliform, green, glabrous, the ridges smooth; calyx lobes $4-5 \times 2$ mm, deltate, green, glabrous, the margin callose-dentate, the apex acute, ascending at anthesis; corolla pale green lightly suffused with violet, glabrous; corolla tube 7–8 mm wide basally, narrowing to 2–3 mm; corolla lobes ligulate, the margins undulate, the two dorsal lobes $14-16 \times 3-4$ mm, opening dorsally

16–18 mm from the corolla base, falcate, the two lateral lobes 9–10 × 3–4 mm, opening ventrally 11–12 mm from the corolla base, falcate; androecium 35–39 mm, exserted 22–23 mm from the ventral opening, the filament tube green to tinged violet, very sparsely puberulous, the anther tube green with violet along the sutures, glabrous, all the anther tips glabrous to very sparsely pubescent; the style and stigma cream colored, the stigma lobes shortly glabrous along the margin. *Fruits* 30 × 55 mm, globose, inflated, pale green lightly suffused maroon-violet.

Phenology. Flowers and fruits have been observed throughout the year.

Distribution. Found in southwest Ecuador in Zamora Chinchipe Province in wet forests between 2400 and 2700 m in elevation.

Discussion. This species has been placed in a clade of inflated fruit species, many of which occur on the western edge of the Andes (unpublished data). *Burmeistera draconis* is an extreme south collection of this group. It is most similar to another species in the inflated fruit clade, *B. pallida*, which also extends into Peru. Both *B. draconis* and many specimens of *B. pallida* have irregularly crenate margins. In *B. draconis*, these bidentate margins are significantly more pronounced.

Additional specimens examined. NONE.

21. *Burmeistera erosa* Mashburn, sp. nov. TYPE: Ecuador. Carchi: Forest and ridge area above Río Verde and ridge flanking medium Cerro Golondrinas, 2070–2430 m, 00°52'N 78°07'W, 04 Dec. 1987 (fl., fr.), *W. S. Hoover 2301* (holotype, QCA [barcode] 26701!; isotype, MO-3751825!).

Scandent herbs, 4 m. Latex cream colored. Stems 3 mm wide, green, puberulent, terete, zig-zag. Leaves alternate, distichous; petioles 7–9 mm, green, puberulent; lamina $120-185 \times 20-55$ mm, lanceolate, the base cuneate to obtuse, the apex acuminate to caudate, the apex $25-30 \times 0.5-2$ mm, the margin callose dentate, the teeth irregular in spacing, size, and direction, the callose tips puberulous; adaxial surface green tinged pale violet, glabrous; abaxial surface pale violet, puberulent along the veins with short white hairs; venation brochidodromous, the primary and secondary veins prominent, raised, the tertiary veins visible, sometimes raised. *Flowers* solitary, 25–28 mm; pedicels 15–34, puberulent, green; hypanthium $6-7 \times 1-2$ mm, tubular, the base barely distinguishable from the pedicel, abruptly widening to 2.5–3 mm distally, green, puberulent; calyx lobes $1-1.5 \times 1$ mm, deltate, green, puberulent, the margin entire, ascending at anthesis; corolla pale green, sometimes lightly tinged violet, sparsely puberulent; corolla tube 2–3 mm wide basally, narrowing to 2–2.5 mm; corolla lobes ligulate, the margins smooth, the two dorsal lobes 7×1.5 mm, opening dorsally 10–11 mm from the corolla base, falcate, the two lateral lobes $3-4 \times 2$ mm, opening ventrally 8-9 mm from the corolla base, falcate; androecium 18–19 mm, exserted 11 mm from the ventral opening, the filament tube green, densely puberulent with white hairs, the anther tube green, lighter along the

sutures, all the anther tips glabrous or with very few white hairs; the style and stigma green, the stigma lobes glabrous. *Fruits* (immature?) ca. 6×4 mm, green.

Etymology. The specific epithet is in reference to the erose margin of the leaves of this species.

Phenology. This species has been collected with flowers and fruits in December.

Distribution. Known only from a narrow distribution in Carchi Province of northwest Ecuador.

Discussion. This species is likely closely related to *B. holm-nielsenii* and *B. marginata*. It is easily differentiated, however, by its irregularly dentate (erose) leaf margin and much smaller flowers.

Additional specimens examined. ECUADOR. **Carchi:** Espejo, El Gualtal, faldas de Cerro Golondrina Hembra, 2450 m, 00°51'N 78°07'W, 21 Aug. 1994, *Palacios 12682* (MO); Further ascent of Río Verde past stream and waterfall entering from SW and continuing beyond principal drainage stream of large Cerro Golondrinas into drainage streams of medium Golondrinas mountains, 1200 m, 00°52'N 78°07'W, 01 Dec. 1987, *Hoover 2156* (MO, QCA). 22. Burmeistera formosa (Wimm.) Jeppesen, Fl. Ecuador 14: 22. 1981. Basionym: Centropogon formosus Wimm., Repert. Spec. Nov. Regni Veg. 22: 200. 1926. TYPE: Ecuador: s.l., s.d. (fl., fr.), L. Mille 20 (holotype, W 1967-0015575 digital image!).

Terrestrial herbaceous shrubs, 2 m. Latex unkown. Stems ca. 7 mm wide, tan, villose with yellow-tan to cream-colored hairs, terete. Leaves alternate, spiral, the internodes 10–22 mm; petioles 7–16 mm, green, villose; lamina $60-100 \times 30-50$ mm, elliptic, often broadest just above the middle, the base cuneate, the apex acute, the margin shallow-callose crenate, slightly revolute; adaxial surface dark green, glabrous to puberulous along the main veins; abaxial surface green to green tinged with violet, puberulous along the veins; venation camptodromous, the primary and secondary veins prominent, raised, the tertiary veins visible, sometimes slightly raised. *Flowers* solitary in the upper leaf axils, 47–48 mm; pedicels ca. 100 mm, with two small basal bracteoles, entirely glabrous to sparsely puberulous basally, tan; hypanthium $7-8 \times 8-9$ mm, cupuliform to urceolate, green to tan, glabrous to sparsely puberulous; calyx lobes $1-2 \times$ 1-2 mm, deltate, green, glabrous to sparsely puberulous, the margin shallow callosedentate, ascending at anthesis; corolla green to green suffused with maroon-violet, glabrous; corolla tube 5–6 mm wide basally, narrowing to 3–4 mm; corolla lobes ligulate, comparatively short, the margins smooth, the two dorsal lobes $9-10 \times 2.5-3$ mm, falcate, opening dorsally ca. 30 mm from the corolla base, the two lateral lobes $7-8 \times 2.5-3$ mm, falcate, the ventral lobe $6-7 \times 2.5-3$ mm, opening ventrally ca. 25 mm from the corolla base; androecium ca. 41 mm, exserted 15–16 mm from the ventral opening, the filament tube green, glabrous, the anther tube ca. 8×4.5 mm, green, sparsely puberulent, the three dorsal anther tips glabrous to sparsely public public public exactly white hairs; the style and stigma unknown. *Fruits* ca. 22×28 mm, globose, not inflated, fleshy, maturing white.

Phenology. The sole collection of this species was made with flowers and fruits, though a date was not recorded.

Distribution. No geographic location is given on the sole collection of this species.

Discussion. Flowers are similar to *B. brighamioides* in the broadly cupuliform hypanthium and long fused corolla tube, but the flower of *B. formosa* are still much small than those of *B. brighamioides*.

Additional specimens examined. NONE.

23. Burmeistera glabrata (Kunth) Benth. & Hook. f., Gen. Pl. 2: 547. 1876. Basionym: Lobelia glabrata Kunth, Nov. Gen. Spec. 3: 307, tab. 270. 1818. Siphocampylus glabratus (Kunth) G. Don, Gen. Hist. 3: 702. 1834. Centropogon glabratus (Kunth)
Planch. & Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1857: 157.
1857. TYPE: Colombia. Bogotá: Crescit prope Santa Fe de Bogota, 1360 m, s.d. (fl.), A. Humboldt & A. Bonpland s.n. (holotype, P [barcode] 671027 digital image!).

Burmeistera subcrenata E. Wimm., Pflanzenr. IV. 276b (Heft 106): 160. 1943. TYPE:
Ecuador. Napo: Zatzayacu, 400–500 m, 22–28 Mar. 1935 (fl., fr.), Y. Mexia 7081
(holotype, W-0046736 digital image!; isotypes, UC [bc] 743241 digital image!, US [bc] 146955 digital image!).

Herbaceous shrubs to scandent herbs, 2 m. Latex white. Stems ca. 5 mm wide, green to dark violet, glabrous, sometimes minutely puberulent with white hairs on new growth. Leaves spiral; petioles 7–22 mm, green to green tinged violet, glabrous to minutely puberulent; lamina $35-150 \times 15-70$ mm, elliptic, the base attenuate, the apex attenuate, the margin shallow callose-dentate, the teeth often tinged violet; adaxial surface green, often with violet margins, glabrous, nitid; abaxial surface green to dark violet, minutely puberulent along the primary and secondary veins, elsewhere glabrous, nitid; venation camptodromous, the primary vein prominent, slightly raised but flat, the secondary and tertiary veins visible. *Flowers* 39–47 mm; pedicels 60–90 mm at anthesis, 65–95 mm in fruit, glabrous, green to dark violet; hypanthium $5-7(-10) \times 4-6$ mm, obconical, green to dark violet, glabrous, the ridges smooth; calyx lobes $8-15 \times 3-6$ mm, deltate to lanceolate, green to green suffused with violet, glabrous, the margin shallow callose-serrate, the teeth tinged violet, the apex acute, ascending at anthesis; corolla green to dark violet, sometimes green spotted with violet, glabrous; corolla tube 5–6 mm wide basally, narrowing to 3–4 mm; corolla lobes lanceolate, the margins smooth, the two dorsal lobes $12-18 \times 4-6$ mm, falcate, opening dorsally 15-20 mm from the corolla base, the two lateral lobes $8-9 \times 4-5$ mm, falcate, the ventral lobe $8-9 \times 4-5$ mm opening ventrally 9–13 mm from the corolla base; androecium 31–39 mm, exserted 19–27 mm

from the ventral opening, the filament tube green to distally tinged violet, puberulous to villose with white hairs, the anther tube tan, yellow to violet along the sutures, puberulent between the sutures with appressed white to yellow hairs, all five anther tips sparsely pubescent with white hairs; the style tan, glabrous, the stigma lobes tan, tinged violet along the margin, glabrous above, villose below, fringed with short white hairs. *Fruits* ca. 30×25 mm, globose, inflated, green to green suffused with violet.

Phenology. Specimens have been collected with flowers and fruits throughout the year.

Distribution. This commonly collected species occurs in Napo province from the region around the city Tena in the south, into Sucumbíos Province in the north. Collections have been made from 1000 to 3200 m in elevation.

Discussion. This widespread species is also quite variable, especially in the size of its calyx lobes. It is a major species in the inflated fruit clade identified by Uribe-Convers et al. (2017). It is difficult to differentiate from some closely related species, such as *B. refracta*. A character traditionally used is the ascending calyx lobes of *B. glabrata* versus the reflexed calyx lobes of *B. refracta*. While this character seems to hold up well for the majority of herbarium specimens, field observations have revealed it to not be an entirely consistent character.

Additional specimens examined. ECUADOR. **Carchi:** Valle de Maldonado, km 53 on the road Tulcán-Maldonado, 3150–3250 m, 00°50'N 78°03'W, 19 May 1973, *Holm-Nielsen*

et al. 5854A (NY);Valle de Maldonado, km 53 on the road Tulcán-Maldonado, 3150– 3250 m, 00°50'N 78°03'W, 17–18 May 1973, *Holm-Nielsen et al. 5590* (NY).

Imbabura: Reserva Siempreverde, Páramo de Urcusiqui, 3200–3600 m, 00°22'39"S 78°25'45"W, 07 Jul. 2012, Pérez et al. 5550 (QCA); Siempre Verde Cloud Forest Reserve, Arriba Trail, upslope just beyond flag marking 3060 m elevation and before elfin forest, 3060 m, 00°21'54.72"N 78°24'44.28'W, 21 May 2016, Jones 11192 (QCA); Vía Mariano Acosta-Palmira-Tambo-Nueva América, Nueva América-Río Pisque-Cruce a Potrerillos, 3048–3170 m, 29 Dec. 1979, Jaramillo 1664 (QCA). Napo: 3 km este del Caserío de Huamaní, al norte de la carretera Hollín-Loreto, 1200 m, 00°43'S 77°36'W, 17 Sep. 1988, Hurtado & Alvarado 312 (MO); 8 km rio abajo de Puerto Misahualli, por el Rio Napo y 1.5 km al sur, 450 m, 01°04'S 77°36'W, 18–30 May 1985, Palacios et al. 426 (MO); 16 km from Tena-Baeza road on road to Coca, 1300 m, 00°42'S 77°44'W, 20 Sep. 2001, Gustafsson et al. 450 (QCA); 150 m al noroeste del Caserío de Huamaní, márgen derecha de la carretera Hollín-Loreto, 1200 m, 00°43'S 77°36'W, 09 Sep. 1988, Hurtado & Neill 231 (MO); Along new road from Pangayacu to Loreto, 10.6 km E of main N/S road between Baeza and Tena, departing main road 23.7 km N of Archidona, 1285 m, 00°47'S 77°41'W, 30 Apr. 1984, Croat 58791 (MO, QCA); Along road between Baeza and Lago Agria, 72.5 km W of Lago Agria, 1166 m, 19 Dec. 1979, Croat 49523 (MO, NY); Along road between Baeza and Tena, 5.7 km S of Baeza, 1780 m, 00°31'S 77°52'W, 30 Apr. 1984, Croat 58744 (QCA); Along road between Coca and Archidona, between Loreto and Narupa, 40.1 km east of Narupa at main Baeza-Tena Hwy., 00°43'03"S 77°38'01"W, 07 Oct. 2007, Croat et al. 99454 (MO); Along road between Lago Agrio and Baeza, at km 74.5, 1220 m, 00°00'N 77°20'W, 06 Oct. 1980, Croat

50448 (MO); Archidona Canton, Comunidad de Pacto Sumaco, alrededores del pueblo, 1550 m, 00°40'09"S 77°35'47"W, 01 May 1997, Alvarez et al. 2100 (MO); Archidona Canton, Merced de Jondachi, km 28, 1300 m, 00°44'S 77°47'W, 24 Nov. 1992, Palacios 10504 (MO, QCA); Archidona, Reserva de Biósfera Sumaco, 1160 km, 00°49'39"S 77°33'47"W, 26 Feb. 2003, Cevallos 36 (MO); Archidona, Reserva de Biósfera Sumaco, Cordillera de Galeras, Bosque Protector de la Comunidad Mushullacta, 1160 m, 00°49'39"S 77°33'47"W, 28 Feb. 2003, Farfán & Neill 453 (MO); Archidona, Reserva Ecologica Antisana, Comunidad Shamato, entrado por km 21-Shamato, plot 1, 1700 m, 00°43'S 77°49'W, 24 Apr. 1998, Clark et al. 5133 (MO, NY); Baeza-Tena road, 5 km S of Cosanga, 1975–2225 m, 09 Jan. 1979, Luteyn & Lebrón-Luteyn 6717 (NY); Baeza-Tena Road, 25–28 km S of bridge in Cosanga, 1375–1460 m, 10 Jan. 1979, Luteyn & Lebrón-Luteyn 6746 (MO, NY, QCA); Baeza-Tena road, km 40 from Baeza, 1900 m, 00°43'S 77°46'W, 29 Mar. 1979, Løjtnant & Molau 11502 (QCA); Baeza-Tena Road, Hacienda Guacamayos ca. 3 km S of Cosanga, 2000 m, 06 Feb. 1980, Harling & Andersson 16302 (NY); Baeza-Tena Road on the southern slopes of Cordillera de Guacamayos, 1800 m, 09 Nov. 1980, Harling & Andersson 16429 (QCA); Baeza-Tena Road, southern slope of Cordillera de Guacamayos, above Jondachi, 1500 m, 07 Feb. 1980, Harling & Andersson 16328 (NY); Between Archidona & Jondache, 26 Oct. 1939, Asplund 9657 & 9531 (NY, QCA); Between Tena and Papallacta, 12 Jan. 1981, D'Arcy 14092 (MO); Borde de la carretero en el km 17 de la vía Loreto-Río Hollín, 1100 m, 00°43'S 77°40'W, 14 Jul. 2001, Salazar & Carrera 33 (QCA); Canton Archidona, carretera Hollín-Loreto, km 17, cerca del Río Hollín, 1100 m, 00°41'S 77°41'W, 14–22 Feb. 1989, Hurtado & Shiguango 1644 & 1671 (MO); Cantón Archidona, carretera

Hollín-Loreto, km 25, faldas al sur del Volcán Sumaco, Comunidad Challua Yacu, 1100 m, 00°43'S 77°36'W, 17 Dec. 1988, Hurtado 1201 (MO); Cantón Archidona, carretera Hollín-Loreto, Río Huataraco, dos horas a pié por bosque primario desde la aldea de Guagua Sumaco, transectos Hd1 y Hd2 para censo de mamíferos, 800–1000 m, 00°43'S 77°32'W, 23–30 Aug. 1989, Cerón & Factos 7628 (MO); Canton Archidona, faldas al sur del Volcán Sumaco, carretera Hollín-Loreto, km 31, Comuna Challua Yacu, 1200 m, 00°43'S 77°36'W, 15–17 Nov. 1988, Alvarado 48 (MO); Canton Archidona, faldas al sur del Volcán Sumaco, carretera Hollín-Loreto, km 31, Comuna Challua Yacu, 1200 m, 00°43'S 77°36'W, 06–07 Jan. 1989, Alvarado 116 (MO); Canton Archidona, faldas al sur del Volcán Sumaco, carretera Hollín-Loreto, km 50, Comuna Huahua Sumaco, 1000 m, 00°43'S 77°34'W, 29-30 Apr. 1989, Hurtado et al 2019 (MO); Canton Archidona, faldas al sur del Volcán Sumaco, carretera Hollín-Loreto, km 50, Comuna Huahua Sumaco, 1000 m, 00°43'S 77°34'W, 18–21 May 1989, Hurtado & Alvarado 2155 (MO); Canton El Chaco, Codo Sinclair, 650 m, 00°08'S 77°27'W, 16–20 Sep. 1990, Palacios 5699 (MO, NY); Canton El Chaco, márgen derecha del Río Quijos, Finca La Ave Brava de Segundo Pacheco, 1800-1900 m, 00°12'S 77°39'W, 7-10 Sep. 1990, Palacios 5362 (MO, NY); Canton Loreto, Parroquia San Vicente de Huaticocha, Comunidad Santa Rosa de Arapino, Bloque 19 Triton, Pozo Santa Rosa, 600 m, 00°58' 77°40'W, 15 Aug. 1997, Freire et al. 2291 (MO); Canton Tena, Cardillera de los Huacamayos, localidad Pigui Yacu (Verde Yacu) Río Cushillo Yacu (Río Grande se origina en la cabecera de Sisahua), las colecciones se hicieron en Pigui Yacu, 1600 m, 00°48'S 78°07'W, 29 Dec. 1995, Jaramilla & Tapia 18561 (QCA); Carretera Hollín-Loreto-Coca, Comunidad Chaluayacu, km 25, 1200 m, 00°45'S 77°40'W, 23 Dec. 1988, Cerón et al. 5766 (MO);

Carretera Hollín-Loreto-Coca, entre Avila y el Río Pucuno, 800 m, 00°39'S 77°22'W, 10 Dec. 1987, Cerón et al. 2857 (MO); Carretera Hollín-Loreto-Coca, km 45, canchones de damnificados del torremoto de marzo de 1987, 1200 m, 00°43'S 77°35'W, 23 Jul. 1988, Hurtado & Mena 128 (MO); Carretera Hollín-Loreto-Coca, km 45, Río Pucuno, 1100 m, 00°40'S 77°40'W, 10 Dec. 1987, Neill et al. 8066 (MO); Carretera Coca-Loreto, entre la Comuna 10 de Agosto y el río Pinguillo, 1000 m, 00°43'S 77°28'W, 20 Oct. 1988, Cerón & Iguago 5294 (MO); Carretera Hollín-Loreto, km 25, Centro Challuayacu, en trocha hacia la zona del Guagua Sumaco, 1230 m, 00°43'S 77°40'W, 10–19 Nov. 1988, Hurtado & Alvarado 895, 986 & 1142 (MO); Carretera Hollín-Loreto, km 32, 8 km al W de Guamaní, arriba del Rí0 Guamaní, 1200 m, 00°43'S 77°38'W, 20 Sep. 1988, Neill et al. 8637 (MO); Carretera Hollín-Loreto, km 40, 5 km al oeste del Caserío de Huamani, faldas del volcan Sumaco, 1200 m, 00°43'S 77°36'W, 07 Sep. 1988, Hurtado et al. 153 (MO); Carretera Hollín-Loreto, km 40–50, 1200 m, 00°43'S 77°36'W, 10–22 Oct. 1988, Hurtado 584, 585, 703, 726 & 786 (MO); Carretera Quito-Tena via Baeza, km 118, 1800 m, 06 Aug. 1984, Dodson et al. 15147 (MO); Cercanías de Archidona, 610 m, 00°56'S 77°50'W, 13 Jan. 2001, Prieto 25 (QCA); Cloud forest 44–45 km by road N of Tena, 1188–1220 m, 00°43'S 77°52'W, 16 Aug. 1978, Webster 23234 (MO); Cerro Antisana, Montane forest 1 mi E of Borja, 1524 m, 17 Aug. 1960, Grubb 1296 (NY); Cordillera de Guacamayos, 2000 m, 10 Mar. 1993, Schwerdtfeger 18 (QCA); Cordillera de Guacamayos, 2000 m, 12 Mar. 1995, Schwerdtfeger 31209 (QCA); Cosanga, Reserva Ecológica Antisana, Guacamayos Ridge, Mirador de la Virgen, 7.7 km E of Cosanga, 2250 m, 00°37'25"S 77°58'25"W, 29 Jan 2009, Tepe 2676 (QCA); Cosanga, stream just south of town, 1940 m, 01 Dec. 1976, Boeke & McElroy 357 (NY); Hollin-Loreto road,

15.5–40 km E of jct. with Baeza-Puyo road, 1100–1160 m, 00°51'S 77°40'W, Luteyn & Sylva 14650 (NY, QCA); De la carretera entre Reventador y Lumbaqui, 10 km al sur, Río Tigre, 800 m, 00°05'S 77°24'W, 06 Dec. 1986, Neill 7533 & 7536 (MO); East upper slopes of Corillera de Guacamayos, 11–13 km S of Cosanga on the Baeza-Tena road, 2100-2200 m, 00°40'S 77°52'W, 22 Dec. 1987, Molau & Erkisen 2142 (QCA); Huamani Centro Calluhua Yacu, 31 km E of Tena-Baeza Road, on new road to Coca, 1150 m, 00°40'S 77°40'W, 24 Dec. 1988, Gentry et al. 64174 (MO); Junction of Baeza-Lago Agrio Road with Río Azuela, 1740 m, 03 Mar. 1972, Dwyer & MacBryde 9638 (MO, QCA); Km 2, carretera nueva Cotundo-Coca, 1130 m, 05 Aug. 1984, Dodson et al. 15039 (MO); Km 71, Baeza-Lago Agrio, 1550 m, 24 Nov. 1983, Besse et al. 1913 (MO); Localidad Codo Bajo, 660 m, 00°03'S 77°15'W, 17 Sep. 1990, Jaramillo et al. 12763 (QCA); Loreto, 500 m al sur de la carretera a Campo Alegre, carretera Hollín-Loreto-Coca, bloque 19, línea sísmica 4, helipuerto 4, compañía Triton, 450 m, 00°36'S 77°20'W, 20–22 Jan. 1996, Vargas et al. 623 (MO, QCA); Loreto, faldas del volcán Sumaco, al oeste de Avila Viejo, bloque 19, línea sísmica 8, compañía Triton, 850 m, 00°37'53"S 77°27'46"W, 15 Feb. 1996, Friere & Cerda 71 (MO, QCA) & 119 (MO); Loreto, Parque Nacional Sumaco Napo-Galeras, Matorral de Bambú, bloque 19, línea sísmica 22, compañía Triton, 500 m, 00°47'S 77°28'W, 25 Mar. 1996, Friere & Cerda 236 (MO); North slopes of Cordillera de Guacamayos, ca. 10 km above Cosanga, 2 km below pass, 2150 m, 00°40'S 77°53'W, 27 Apr. 1985, Stein 2640 (MO, QCA); On Narupa-Loreto road, at the Rio Hollin Cascada, descending stairs to waterfall, on side path on right, 2250 m, 00°41.9'S 77°43.8'W, 16 May 2013, Muchhala 516 (QCA); Orellana, zona de amortiguamiento del Parque Nacional Sumaco, líneas sísmicas de la

compañía petrolera Amoco, 400 m, 00°29'S 77°21'W, 09 Nov. 1996, *Revelo 118* (MO); Quijos Canton, carretera Tena-Baeza, 00°15'S 77°55'W, 15 Jan. 1991, Gudiño & Zak 1252 (MO, QCA); Rainforest along banks of Río Hollín, ca. 11.5 km E on road to Loreto, S of Vulcán Sumaco, 1000 m, 00°40'S 77°40'W, 31 Jul. 1990, Webster & Richardson 28498 (MO, QCA); Reserva Biológica Jatun Sacha, Río Napo, 8 km abajo de Misahuallí, 450 m, 01°04'S 77°36'W, 17 Jan.-06 Feb. 1987, Cerón 823 (MO); Reserva Biológica Jatun Sacha, Río Napo, 8 km abajo de Misahuallí, 450 m, 01°08'S 77°30'W, 02 Oct. 1986, Palacios 1302 (MO); Reserva Ecológica Cayambe-Coca, Cordillera de los Guacamayos, trail from the Virgen de los Guacamayos, 2265 m, 00°38.481'S 77°50.487'W, 10 Aug. 2002, Muchhala 116 (QCA); Reserva Wildsumaco, collected behind workers bathroom, near Benavides Trail, 1450 m, 00°38'S 77°25'W, 27 May 2010, Muchhal 442 (QCA); Reserva Wildsumaco, on Benavides Trail, near lodge, 1450 m, 00°38'S 77°25'W, 27 May 2010, Muchhala 441 (QCA); Road Baeza-Tena, 8 km from Baeza, 1800–1900 m, 00°31'S 77°50'W, 28 Oct. 1976, Balslev & Madsen 10401 (NY, QCA); Road Baeza-Tena, km 21, past Cosanga, 2000 m, 02 Sep. 1993, Borchsenius 166 (QCA); Road Baeza-Tena, km 24–29 from Baeza, S of Cosanga, 2100–2300 m, 00°38'S 77°51'W, 28 Mar. 1979, Holm-Nielsen 16228 (NY, QCA); Road Baeza-Tena, km 40 from Baeza, 1900 m, 00°43'S 77°46'W, 29 Mar. 1979, Holm-Nielsen 16279 (MO, NY, QCA); Road between Lago Agrio and Baeza, km 85 to 90, 2 to 5 km N of Reventador Village, 1400 m, 00°05'S 77°35'W, Stein 2624 (MO, QCA) & 2625 (QCA); Road Cotundo-Loreto, ca. 38 km from junction with road Baeza-Tena, 1250 m, 00°53'S 77°39'W, 18 Jul. 1990, Øllgaard 98037 (QCA); Santa Barbara-La Bonita rd., trail towards La Bonita, ca. 25–28 km S of Santa Barbara, along Rio Chingual, 2133–2347 m,

00°35'N 77°30'W, 17 May 1982, Luteyn et al. 8456 (NY, QCA); Sinangue-'Zona de Reserva Ecológica Cayambe-Coca'-Chuscuyacu-'Comuna Quichua'-Río Due, carretera Lago Agrio-Quito, zona de partida km 65 camino de herradura hasta Chuscuyacu, 13 Jul. 1980, Jaramillo & Coello 3043 & 3067 (QCA); South slope of Cordillera de Guacamayos, new road Cotunda-Coca, 3 to 5 km from turn-off of Baesa-Archidona road, 1150 m, 01°52'S 77°48'W, 11 Jun. 1985, Stein 3065 & 3067 (MO, QCA); Vía Hollín-Loreto, a 3 km después del Río Hollín, 1200 m, 00°52'S 77°43'W, 16 Jan. 1989, Palacios 3834 (MO). Pastaza: Villano, pozo petrolero Villano 2 de ARCO, al sur del Río Lliquino, 400 m, 01°28'S 77°27'W, 28 Aug. 1997, Alvarez et al. 2173 (MO). Sucumbios: 21 km below Santa Barbara, 2400 m, 28 May 1985, Stein 2874 (MO, QCA); Cantón Gonzalo Pizarro, 3 km al NO del caerío Gonzalo Pizarro, en la margen derecho del Río Dué, 750 m, 00°03'N 77°22'W, 27 Jan. 1992, Yánez et al. 979 (QCA); Collecciones en el sector Nor Oeste de la Cascada San Rafael, 1300 m, 11 Oct. 1990, Jaramillo et al. 13148 (QCA); El Reventador, en ambas márgenes del Río El Reventador, 1850 m, 06 Oct. 1990, Jaramillo & Grijalva 12884 (QCA); Gonzalo Pizarro, ca. 2 km SE of town, 710 m, 00°01'02.1"S 77°23'42.5"W, 01 Nov. 2010, Persson & Alvarado 1673 (QCA); Gonzalo Pizarro Canton, Bosque Protector Los Cedros, cuena del Río Tigre, 1000 m, 00°05'S 77°25'W, 17 Mar. 1992, *Tipaz et al. 723* (MO); Pizarras, 1 hr upstream from Sinangue on Río Aguarico, 700 m, 00°12'S 77°30'W, 24 Oct. 1996, Ståhl et al. 3265 (QCA); Road from Quito to Lago Agrio, 17 km W of Lumbaque, 73 km W of Lago Agrio, 1200 m, 9–10 Mar. 1983, *Pipoly 6364* (MO, NY); San Rafael, ca. 48 km NE of El Chaco, 1400 m, 00°06'S 77°35'W, 09 May 1996, Ståhl et al. 2457 (QCA); Santa

Barbara-La Bonita road, 14–16 km E of Santa Barbara, 2650–2700 m, 00°40'N 77°30'W, 17 May 1982, *Boom 8439* (NY).

24. Burmeistera heilbornii (E. Wimm.) Mashburn, comb. et stat. nov. Basionym:
Burmeistera resupinata var. heilbornii Wimm., Pflanzenr. IV. 276b: 140. 1943. TYPE:
Ecuador. Pichincha: Ad viam inter Alaspungo et Gualca, 22 May 1920 (fl., fr.), O.
Heilborn 712 (holotype, S-04-900 digital image!; isotypes, BM [barcode] 947546 digital
image!; US [bc] 146954 digital image!).

Scandent herbs, 3 m. *Latex* white. *Stems* ca. 3 mm wide, terete, zigzag, green to violet, glabrous to sparsely puberulous around the petioles. *Leaves* alternate, distichous; petioles 4–8 mm, green to violet, sparsely villose; lamina 45–95 × 15–40 mm, ovate to ovate-lanceolate, the base obtuse to rounded, the apex caudate, $10-20 \times 1-4$ mm, the margin shallow callose-serrate, the teeth often intramarginal; adaxial surface green, glabrous; abaxial surface green, sometimes tinged violet, villose along the primary and secondary veins, sometimes sparsely so, with appressed white hairs; venation pinnate, the secondary veins terminating connecting to a submarginal collecting vein 0.5–1 mm below the margin, the primary and secondary veins prominent, flat, the tertiary veins visible. *Flowers* ca. 61 mm, solitary; pedicels ca. 27 mm at anthesis, 27–30 mm in fruit, glabrous, smooth; calyx lobes $5-6 \times 1-2$ mm, ligulate, green, glabrous, the margin shallow callose-serrate with 2-3 teeth, the apex obtuse, ascending at anthesis; corolla green, glabrous, nitid; corolla tube ca. 8 mm wide basally, narrowing to ca. 3 mm; corolla lobes ligulate,

the margins smooth, the two dorsal lobes ca. 26×5 mm, opening dorsally ca. 21 mm from the corolla base, falcate, the two lateral lobes 17×6 mm, opening ventrally ca. 14 mm from the corolla base, falcate; androecium ca. 51 mm, exserted ca. 37 mm from the ventral opening, the filament tube green, glabrous, the anther tube green, lighter along the sutures, sparsely pubescent dorsally with long, appressed, white hairs, all the anther tips glabrous; the style green, glabrous, the stigma green, the stigma lobes barbate. *Fruits* 34 \times 18 mm, oblong, inflated, pink to pale violet.

Phenology. This species has been collected with flowers and fruits throughout the year.

Distribution. This species occurs in northwest Ecuador in the Provinces of Imbabura and Pinchincha. It is found in cloud forests at elevations of 2600–3100 m.

Discussion. Burmeistera heilbornii is most similar to *B. resupinata* and *B. crocodila*. In fact, *B. heilbornii* was, until now, considered to be a variety of *B. resupinata*. However the two species are readily differentiated, as the leaves of *B. heilbornii* are broadly ovate, while those of *B. resupinata* are narrowly lanceolate. It is also differentiated from *B. crocodila* by its much larger flowers.

Additional specimens examined. ECUADOR. **Imbabura:** Carretera Cotacachi-San Luis de La Delicia-Apuela, collecciones en San Luis de La Delicia, 2600–3000 m, 06 Dec. 1986, *Friere-Fierro 472* (QCA); Cotacachi, Plaza Gutierrez, Sector Tabla Chupa, 3000 m, 00°13'N 78°25'W, 18 Jan. 1992, *Tipaz & Gudiño 1212* (MO); Cotacachi, Parroquia

Plaza Gutierrez, Tabla Chupa, arriba de Apuela, 2300–3000 m, 00°20'N 78°30'W, 12 May 1992, *Tipaz et al. 985* (MO); NW of Laguna Cuicocha 22.3 km, on road to Apuela, 3045 m, 00°18'N 78°21'W, 18 Nov. 1988, *Dorr & Barnett 6186* (MO, NY, QCA); Sector San Luis de la Delicia, 2600–3000 m, 06 Dec. 1986, *Jaramillo 9259* (QCA); Via Apuela-Cotocachi, 2900–3100 m, 00°18'N 78°23'W, 14 Feb. 1989, *Palacios & van der Werff 3769* (MO). **Pichincha:** Quito, Hacienda Tanlahua, a 10 km al norte de San Antonio de Pichincha, Loma Monte Redondo, 2850 m, 00°06'N 78°29'W, 06 Aug. 1994, *Vargas et al. 226* (MO).

25. Burmeistera holm-nielsenii Jeppesen, Fl. Ecuador 14: 35, fig. 3F-G. 1981. TYPE:
Ecuador. Carchi: Valle de Maldonado, km 71 on road Tulcán–Maldonado, steep forested slopes, alt. 2100–2200 m, 00°54'N 78°06'W, 20 May 1973 (fl.), *L. Holm-Nielsen, S. Jeppesen, B. Løjtnant & B. Øllgaard 6037* (holotype, AAU digital image!; isotypes, K [barcode] 250830 digital image!, NY [bc] 467993!, QCA [bc] 26893 digital image!, S-05-1894 digital image!).

Scandent herbs, 3 m. *Latex* white to cream. *Stems* 6 mm wide, green to violet, glabrous to puberulous around petioles, terete. *Leaves* alternate, distichous; petioles 10–15 mm, green, glabrous to sparsely puberulous; lamina 70–140 \times 30–55 mm, elliptic, the base cuneate to rounded, the apex attenuate to acuminate, the margin denticulate to fimbriate-denticulate, the margin sometimes tinged violet, the teeth callose tipped, puberulous; adaxial surface green to green suffused violet, glabrous to sparsely and irregularly puberulous with white hairs; abaxial surface green to green suffused violet, the green suffused violet, su

puberulous along the veins with short white to cream colored hairs; secondary veins arcuate, connecting to a prominent submarginal collecting vein, the primary and secondary veins prominent, raised, the tertiary veins visible, sometimes raised. Flowers solitary, 45–53(-60) mm; pedicels 90–160 mm at anthesis, 110–160 mm in fruit, glabrous to puberulous, green to violet; hypanthium $10-20(-25) \times 1-1.5$ mm, tubular, the base barely distinguishable from the pedicel, abruptly widening distally to 4–6 mm, green to violet, puberulent; calyx lobes $15-20 \times 1-1.5$ mm, linear, green to violet, puberulent, the margin dentate to fimbriate, the teeth up to 1 mm long, 1-2 mm apart, the apex obtuse, ascending at anthesis; corolla green to green suffused violet, puberulent; corolla tube 4–7 mm wide basally, narrowing to 4–5 mm; corolla lobes lanceolate, the interior pale maroon-violet, the margins smooth, the two dorsal lobes $11-12 \times 3$ mm, opening dorsally 14-15(-18) mm from the corolla base, falcate, the two lateral lobes 6-7 \times 3 mm, opening ventrally 7–11 mm from the corolla base, falcate; and roccium 26–31(– 34) mm, exserted 18–24 mm from the ventral opening, the filament tube green to violet, puberulent, the anther tube green, the distal end sometimes tinged violet, glabrous, the top three anthers glabrous or with a few hairs at the tips, the bottom two anthers sparsely pubescent with white hairs; the style green tinged violet, glabrous, the stigma green, the stigma lobes pubescent underneath, the lobe margins barbate with short white hairs. *Fruits* 20×5 mm, narrowly cylindrical, violet.

Phenology. This species has been collected with flowers and fruits throughout the year.

Distribution. This species is found in a narrow distribution in northwest Ecuador in Carchi province, near the border with Colombia. It occurs in high elevation cloud forests from 1900 to 2600 m in elevation.

Discussion. Burmeistera holm-nielsenii is most similar to *B. marginata*, as both have a prominent submarginal collecting vein and denticulate leaf margins. However, *B. holm-nielsenii* is readily differentiated by the presence of long, comb-shaped calyx lobes, while the calyx lobes of *B. marginata* are small and deltate.

Additional specimens examined. ECUADOR. Carchi: Campamento Machines, road
Tulcán-Maldonado, ca. 10 km SE of Maldonado, 2200–2400 m, 28 Feb. 1974, Harling &
Andersson 12335 (MO); Espejo, Cerro Golondrinas, 2450 m, 00°51'N 78°07'W, Aug.
1994, Palacios 12773 (MO); Espejo, Reserva Golondrinas, El Corazón, el sendero a La
Cortadera hasta El Mirador, 2390 m, 00°50'N 78°06'W, 23 Jan. 2004, Vargas et al. 4329
(MO); Maldonado-Tulcán road, ca. km 20, 2400–2600 m, 07 Oct. 1981, Werling & LethNissen 354 (QCA); Mira Canton, norte del Carmen, camino a Chical, 2000–2200 m,
00°17'N 78°13'W, 10 Feb. 1992, Palacios et al. 9730 (MO); Trail from Machinas, 12 km
above Maldonado, toward Planada de Chilma, Río Chilma Valley, 2350–2450 m,
00°52'N 78°03'W, 30 May 1985, Stein 2905 (MO, QCA); Trail from Rafael Quindí's
mountain finca to Río Verde and short distance up Río Verde, 1890 m, 00°52'N
78°08'W, 28 Nov. 1987, Hoover & Wormley 1890 (MO); Tulcan Canton, arriba de
Maldonado, frontera con Colombia, Sitio Chilmá, 2000 m, 00°51'N 78°02'W, 20 May

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1991, *Palacios & Rubio 7227* (MO); Tulcán-Maldonado road, 42 km W of Tufiño, 2425 m, 13 Apr. 1978, *Luteyn & Lebron-Luteyn 5748* (NY).

26. Burmeistera huacamayensis Jeppesen, Fl. Ecuador 14: 22, fig. 1B-C. 1981. TYPE:
Ecuador. Napo: Cordillera Guacamayo, slope towards Urcusiqui, 27 Oct. 1939 (fl., fr.), *E. Asplund 9580* (holotype S-04-899 digital image!, isotype NY [barcode] 548037!).

Scandent herbs, 1 m. *Latex* white. *Stems* ca. 4 mm wide, terete, green, sometimes with violet striations, glabrous to villose. Leaves alternate, distichous, often bullate, the internodes 15–35 mm; petioles 2–8 mm, green, sometimes tinged violet, villose; lamina $55-155 \times 15-30$ mm, elliptic to lanceolate to oblanceolate, the base obtuse, the apex attenuate to caudate, $5-15(-25) \times 1-2$ mm, the margin shallow callose-servate to crenate, the teeth often intramarginal; adaxial surface green, sometimes lightly tinged violet, glabrous, nitid; abaxial surface green suffused with violet, especially along the veins, villose along the primary vein only or along all veins with flattened, translucent-white anfractuose hairs; venation camptodromous, the secondary veins sometimes terminating in marginal teeth, the primary and secondary veins prominent, slightly raised but flattened, the tertiary veins visible. *Flowers* 33–38 mm, solitary; pedicels 30–75) mm at anthesis, 30-90 mm in fruit, glabrous to sparsely villose, green, sometimes becoming violet distally; hypanthium $5-9 \times 4-8$ mm, obconical, green, glabrous to sparsely villose, the ridges slightly raised; calyx lobes $5-7-16 \times 0.5-3$ mm, linear to ligulate, green spotted with violet, glabrous to sparsely villose, the margin entire, the apex acute, ascending to patent at anthesis; corolla green to green tinged maroon-violet, glabrous

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(rarely very sparsely pubescent); corolla tube 3–4 mm wide basally, the throat narrowing to 2–3 mm; corolla lobes lanceolate, lighter green inside, the margins smooth, the two dorsal lobes $11-13 \times 3$ mm, opening dorsally 15–20 mm from the corolla base, slightly falcate, the two lateral lobes $10-11 \times 3-4$ mm, opening ventrally 12–15 mm from the corolla base, slightly falcate; androecium 26–32 mm, exserted 13–16 mm from the ventral opening, the filament tube green, glabrous basally, glabrous to sparsely villose distally, the anther tube ca. 6×3 mm green, sometimes violet along the sutures, villose basally, the three dorsal anther tips glabrous to sparsely pubescent, the two ventral anther tips densely villose with white hairs; the style and stigma green, the stigma lobes densely pubescent along the margin with short white hairs. *Fruits* ca. 15×20 mm, globose, spongy, slightly inflated, maturing white or pink.

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

Distribution. Known from the eastern Andes of Ecuador in Napo province, with a few collections to the south in Pastaza and Morona Santiago Provinces. Found in high humidity primary forest and along river banks from 900–2300 m in elevation.

Discussion. Burmeistera succulenta has similar calyx lobes but is entirely glabrous, has much larger flowers, and has not been found in the eastern Andes of Ecuador. *Burmeistera kitrinaima* also has similar calyx lobes, though thinner at the base. Most *B. kitrinaima* specimens are glabrous; those with hairs exhibit a similar structure, though with tan instead of entirely translucent-white. Additionally, the latex of *B. kitrinaima* is bright yellow (vs. white here).

All known specimens from east of the Andes in Ecuador that have, until now, been identified as *B. succulenta* have now been transferred to *B. huacamayensis*. Notes left on specimens of *D'Arcy 14100* (MO) and *Luteyn 13463* (MO) by Thomas Lammers (UW-Oshkosh) mentioned the inability to key them to species using Jeppesen (1981), and identified the unusual pubescence of the species. All but two specimens examined were collected after the publication of Jeppesen's Flora of Ecuador treatment.

Additional specimens examined. ECUADOR. **Morona Santiago:** Gualaquiza Cantón, Cordillera del Cóndor, Cuangos, 20 km east of Gualaquiza, near disputed Peru-Ecuador border, 1500–1600 m, 03°29'S 78°14'W, 17 Jul. 1993, *Gentry 80025* (MO); Trail Kenkuim to Jordán, 15–20 km E of Macas, 1000–1200 m, 02°18'S 77°58'W, 23 Aug. 1996, *Ståhl et al. 2915* (QCA). **Napo:** A 8 km al occidente de Pacto, faldas de Volcán Sumaco, km 40 del carretero Hollín Loreto, partiendo del Campamento Damnificados del Chaco, 1800 m, 00°50'S 77°40'W, 24 Aug. 1989, *Jaramillo et al. 10943B & 10944B* (QCA); Along road between Baeza and Tena ca. 40 km N of Archidona, 2000 m, 00°41'S 77°41'W, 07 Oct. 1980, *Croat 50515* (MO); Archidona Cantón, Parque Nacional Napo-Galeras, Cordillera de Galeras, sendero hacia Huamaní, 1000–1650 m, 00°39'S 77°31'W, 16 Mar. 1997, *Alvarez et al. 1619* (MO); Between Tena and Papallacta, 12 January 1981, *D'Arcy 14100* (MO); Carretera Cotundo-Coca, 15 km al E de la carretera Baeza-Tena, faldas de Volcán Sumaco, 1300 m, 00°40'S 77°40'W, 13 Feb. 1987, *Neill & Palacios 7626* (MO, QCA); Cloud forest 44–45 km by road N of

Tena, 1190-1220 m, 00°43'S 77°52'W, 16 Aug. 1978, Webster 23254 (MO); Localidad Codo Alto, en las márgenes del Río Granadilla, 1980 m, 00°03'S 77°49'W, 14 Sep. 1990, Jaramillo et al. 12728 (QCA); North slopes of Cordillera de Guacamayos, ca. 10 km above Cosanga, 2 km below pass, 2150 m, 00°40'S 77°53'W, 27 April 1985, Stein 2641 (MO, QCA); Private property of William Philips, ca. 2 hrs. walk from end of road, W of Cosanga, N slopes of Cordillera de Huacamayos, 2400 m, 00°45'S, 77°55'W, 12 December 1989, Luteyn 13463 (MO, NY, QCA); Reserva Yanayacu, 2100 m, 00°35.3'S 77°52.8'W, 09 August 2002, Muchhala 163 (QCA); Reserva Yanayacu, on stream trail, 2100 m, 00°35.3'S 77°52.8'W, 29 July 2010, Muchhala 462 (QCA); S slope of Cordillera de Guacamayos, new road Cotunda-Coca, 3 to 5 km from turn-off of Baeza-Archidona road, 1150 m, 01°52'S 77°48'W, 11 Jun. 1985, Stein 3062 (MO, NY, QCA); Sierra Azul, Agrícola Industrial Río Aragón, campamento San Fernando, 2250 m, 00°41'S 77°55'W, 20 June 1992, Alvarez et al 515 (MO); Trail down-slope from Lago Agrio-Baeza road, ca. 5 km N of town of Reventador, 1350 m, 00°05'S 77°35'W, 16 Jun. 1985, Stein 3070 (MO, QCA). Pastaza: Cantón Mera, Parroquia Shell, road to Río Anzu and beyond, south of the town Mera, 1450–1550 m, 01°25'45"S 78°05'15"W, 06 May 2003, Clark et al. 7777 (QCA); East 0.4 km on new road to Río Bobonaza, leaving Puyo-Macas road at km 15, 1050 m, 01°35'S 77°53'W, 08 Jun. 1985, Stein 3015 (MO); Hacienda San Antonio de Baron von Humboldt, 2 km al NE de Mera, 1100 m, 01°27'S 78°06'W, 27 Feb.–19 Mar. 1985, Neill et al. 6089 (MO, NY, QCA); Parque Omaere, Puyo, 900 m, Jul.–Aug. 1996, *Blanc et al.* 96-86 (QCA).

27. *Burmeistera ignimontis* E. Wimm., Repert. Spec. Nov. Regni Veg. 30: 17, tab. 124, fig. 21A. 1932. TYPE: Ecuador. Tunguragua: In sylvis vulc. Tugurahua, 1904 (fl.), *L. Sodiro ed. L. Mille 5 p. parte* (holotype, W-1967-0015302 digital image!).

Burmeistera cuyujensis Jeppesen, Fl. Ecuador 14: 32, fig. 3B-C. 1981. TYPE: Ecuador. Napo: Valley of Río Papallacta, Cuyuja, 2400–2500 m, 23 Sep. 1939 (fl.), *E. Asplund 8796* (holotype, S-04-898 digital image!; isotype NY [barcode] 345552!).

Burmeistera ignimontis E. Wimm. var. *ovalis* (E. Wimm.) E. Wimm., Pflanzenr. IV. 276b: 131. 1943. Basionym: *Burmeistera ovalis* E. Wimm., Repert. Spec. Nov. Regni Veg. 30: 18, tab. 124, fig. 21B. 1932. TYPE: Ecuador. Tuguragua: In sylvis vulcani Tungurahua, 1904 (fl.), *L. Sodiro ed. L. Mille 5 pro parte* (holotype, W-1967-0015301 digital image!).

Scandent herbs, 3 m. *Latex* white. *Stems* ca. 5 mm wide, tan to green suffused with violet, glabrous. *Leaves* alternate, spiral, bullate; petioles 8–18 mm, green suffused with violet, glabrous; lamina $45-90 \times 20-40$ mm, elliptic, the base cuneate, the apex attenuate to acuminate, the tip $5-8 \times 1-2$ mm, the margin shallow callose-serrulate, sometimes tinged violet; adaxial surface green, rarely tinged violet, glabrous, nitid, the primary vein often gold or tinged violet; abaxial surface green, rarely tinged violet, with gold to violet tinged primary and secondary veins, glabrous to sparsely pilose along the veins with translucent white to golden hairs, often more dense on marginal teeth; venation semicraspidodromous, the primary and secondary veins prominent, strongly

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raised, the tertiary veins visible. *Flowers* 40–51 mm; pedicels 70–100 mm at anthesis, 70–100 mm in fruit, green suffused with violet, glabrous; hypanthium $6-13 \times 6-11$ mm, cupuliform to broadly urceolate, green to tan, sometimes tinged violet, glabrous to sparsely pilose, the ridges smooth; calyx lobes $12-18(-28) \times 3(-6)$ mm, ligulate, green suffused with violet, glabrous, the margin shallow callose-serrate, the teeth sometimes fringed with trichomes, the apex acute, ascending to reflexed at anthesis; corolla green to green tinged maroon-violet, glabrous; corolla tube 7-10 mm wide basally, bulging just above the base, narrowing to 3-5 mm; corolla lobes ligulate, the margins smooth to undulate, the two dorsal lobes $12-17 \times 3-5$ mm, opening dorsally 16-18 mm from the corolla base, falcate, the two lateral lobes $7-10 \times 3-4$ mm, falcate, the ventral lobe 7-10 \times 3–5 mm opening ventrally 10–12 mm from the corolla base; and roccium 34–40 mm, exserted 24–27 mm from the ventral opening, the filament tube green tinged violet to entirely dark violet, glabrous to sparsely villose with white hairs, the anther dark colored between the sutures, along the sutures pale violet and covered with short, sordid yellow appressed hairs, especially basally, all five anther tips sparsely villose with white hairs; the style tan, glabrous, the stigma lobes tan, pubescent along the margin with short white hairs. *Fruits* ca. 40×35 mm, globose, inflated, green, sometimes tinged maroon-violet.

Phenology. Flowers and fruits have been collected throughout the year.

Distribution. Found at high elevations in Napo Province of Ecuador, near Papallacta and Cuyuja. It occurs in cloud forests at elevations of 2400 to 3200 m.

Discussion. Burmeistera ignimontis is differentiated from similar species such as *B. glabrata, B. oyacachensis*, and *B. borjensis* by the broadly elliptic leaves with an irregularly serrate margin and the presence of long calyx lobes that are widest near the base but not overlapping.

Additional specimens examined. ECUADOR. Cotopaxi: Cantón Salcedo, Sector Las Cramelas, cerca al Río Mulatos, km 59 vía Salcedo-Napo, 2650–2750 m, 01°03'S 78°09'W, 22 Jul. 1987, Cerón & Rojas 1797 (MO). Napo: Along road between Quito and Baeza, at km 198, along stream, 2980 m, 00°18'S 78°10'W, 02 Oct. 1980, Croat 50277 (NY, MO); Baeza-Quito road, ca. 0.5 km E of Río Chalpi Grande, 2750 m, 00°22'11"S 77°04'55"W, 25 Feb. 2011, Tepe 3057 (MO, QCA); Between Cuyuja and Papallacta, 10 km E of Papallacta on road to Baeza, 2800-2900 m, 00°21'S 78°01'W, 05 Jun. 1973, Holm-Nielsen et al. 6846 (NY, QCA); Chalpi Grande, 50 km de la vía al Tena, 2800 m, 00°21'48"S 78°04'59"W, 12 Sep. 2010, Sandoya-Sánchez et al. 566 (QCA); Cuyuja, along muletrack passing through montane forest S of Rio Papallacta, 2500–2600 m, 00°23'S 77°58'W, 01 Nov. 1976, Balslev & Madsen 10525 (NY, QCA); Este de Papallacta 9 km, 2700-3000 m, 00°21'S 78°02'W, 08 May 1991, Yánez et al. 159 (QCA); North of Cuyuja 7 km, 11 km south of Papallacta on road between Pifo and Baeza, 2650 m, 20 Jul. 1987, McDade et al. 1126 (NY); Papallacta, 2 km al norte de la población en borde del carretero, 2700 m, 08 May 1983, Jaramillo 5312 (QCA); Parque Nacional Llanganates, vía Salcedo-Tena, colecciones a lo largo del camino desde Los Carmelos-Río Ana Tenorio al Río Langoa, 2600–2850, 00°58'17"S 78°15'14"W, 18 Feb. 2015, *Pérez 8146* (QCA); Private property near the confluence of Rio Chalpi and Rio
Papallacta, east of the Guango PUCE land, 2600 m, 00°20'S 78°05'W, 14 Aug. 2004, *Muchhala 233, 234 & 235* (QCA); Salcedo-Napo road, ca. 56–60 km E of Salcedo, 2926–3060 m, 00°55'S 78°30'W, 23 Nov. 1989, *Luteyn & Tiriraa 13391* (NY, QCA); Salcedo (San Miguel) to Salcedo-Napo road, km 55, 3105 m, 04 Feb 1977, *Boeke 902* (MO, NY); Tena Cantón, Parque Nacional Llanganates, vía Salcedo-Tena, km 55–60, Río Anatenorio, 3015 m, 00°58'S 78°15'W, 17 Sep. 1998, *Vargas et al. 2520* (MO).

28. Burmeistera jostii Muchhala & Mashburn, sp. nov. TYPE: Ecuador. Tungurahua: Baños, Parque Nacional Llanganates, Cordillera Sacha Llanganates, summit ridge, overlooking Amazon lowlands to east, Río Zuñac watershed to west, 2740 m, 01°21'50"S 78°07'32"W, 28 Nov. 2001, D. Neill, L. Jost, J. Caranqui & E. Toapanta 13469 (holotype, MO-5945905!).

Scandent herbs, 0.5 m. *Latex* unknown. *Stems* ca. 3 mm wide, tan, basally glabrous, scaly, nitid, apically strigose with yellow to tan hairs. *Leaves* alternate, distichous, the internodes 5–10 mm; petioles 3–6 mm, tan, strigose; lamina 25–70 × 10–22 mm, elliptic, the base cuneate, the apex attenuate, the margin callose-serrate; adaxial surface dark green, glabrous; abaxial surface lighter green, strigose with yellow to tan hairs; venation craspedodromous, the primary vein slightly raised, the secondary veins barely visible, the tertiary veins not visible. *Flowers* 1618 mm, solitary in the upper leaf axils; pedicels 15–20 mm, green to tan, strigose; hypanthium 3–4 × 3–4 mm, green to tan, strigose, the ridges slightly raised; calyx lobes 4–5 × 0.5–1 mm, linear, patent to reflexed at anthesis, green, strigose; corolla red, sparsely pilose with tan hairs, membranous,

drying translucent; corolla tube 3–4 mm wide basally, the throat narrowing to 2–3 mm; corolla lobes lanceolate, the margins smooth, the two dorsal lobes ca. 11×5 mm, opening dorsally ca. 11 mm from the corolla base, ascending further than the androecium, the two lateral lobes ca. 11×5 mm, slightly falcate, the ventral lobe ca. 9×4 mm, opening ventrally ca. 5 mm from the corolla base; adroecium 13–14 mm, exserted ca. 7 mm from the ventral opening, the filament tube pale green, villose with white hairs, the anther tube pale-green, glabrous, the three dorsal anther tips glabrous, the two ventral anther tips sparsely pubescent with white hairs; style and stigma unknown.

Etymology. This species is named after Lou Jost, mathematician, conservationist, and orchid taxonomist, who helped discover the species.

Phenology. This species has been collected with flowers in November.

Distribution. This species is known only from the type location, in Llanganates National Park is Tungurahua Province of Ecuador. It occurs in wet, high elevation cloud forest.

Discussion. This species is unique among *Burmeistera*, especially those in Ecuador, because of its very small red flowers. It is perhaps related to *B. rostrata* Jeppesen, which occurs in southern Colombia, and also has very small flowers with a membranous corolla that dries translucent. The flowers of *B. rostrata*, however, are green with very thin corolla lobes.

Additional specimens examined. This species is known only from this specimen, though it is possible other collections exist at QCNE.

29. *Burmeistera kitrinaima* Muchhala & Mashburn, sp. nov. TYPE: Ecuador. Pichincha: Reserva Florística "Río Guajalito," km 59 de la carretera antique Quito-Santo Domingo de los Colorados, a 3.5 km al NE de la carretera, estribaciones occidentales del Volcán Pichincha, 1800–2200 m, 00°13'53"S 78°48'10"W, 29 Jun. 1991 (fl., fr.), *J. Jaramillo & E. Grijalva 13651* (holotype, QCA [barcode] 195853!; isotypes, MO-5700737!, NY [bc] 1185767).

Scandent herbs, 2 m. *Latex* white to yellow. *Stems* ca. 5 mm wide, green to violet, glabrous (rarely villose). *Leaves* alternate, distichous, the internodes 15–30 mm; petioles 4–8 mm, green to violet, glabrous or villose with translucent-cream hairs; lamina 50–135 \times 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 margin callose-serrate, the teeth more prominent distally; adaxial surface dark green, glabrous; abaxial surface green to violet, glabrous or rarely villose along the primary and secondary veins with translucent-cream hairs with tan spots; venation camptodromous to brochidodromous, the primary and secondary veins prominent, raised, the tertiary veins visible. *Flowers* 30–34 mm, solitary in the upper leaf axils; pedicels 50–100 mm at anthesis, 80–105 mm in fruit, green to violet, glabrous (rarely villose); hypanthium 6–7 \times 5–8 mm, obconical, green suffused with violet, glabrous (rarely sparsely villose), the

ridges smooth or slightly raised; calyx lobes $6-13 \times 0.5-1.5$ mm, ascending at anthesis, linear, exterior violet, interior green suffused with violet, 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; corolla lobes lanceolate, lighter green inside, the margins smooth, the two dorsal lobes $14-17 \times 3-4$ mm, opening dorsally 14-18 mm from the corolla base, falcate, the two lateral lobes $10-16 \times 3$ mm, falcate, the ventral lobe ca. 6×2 mm, opening ventrally 11-13 mm from the corolla base; androecium 24-27 mm, exserted 12-15 mm from the ventral opening, the filament tube green with tan striations, sometimes speckled violet, glabrous or distally puberulous, the anther tube $5-6 \times 3-4$ mm, green, violet along the sutures, glabrous, the three dorsal anther tips glabrous to sparsely puberulous, 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.

Etymology. The name comes from the Greek κ itpivo, meaning 'yellow,' and α iµ α , meaning 'blood,' in reference to the unique bright yellow latex of this species.

Phenology. This species has been collected with flowers throughout the year, and with fruits from June to October.

Distribution. This species is known from the western side of the Andes mostly in the Ecuadorian province of Pichincha, but also in Bolívar, Carchi, Cotopaxi, and Santo

Domingo. It has been found as low as 600 m elevation, but it occurs mostly in high humidity cloud forests from at elevations from 1500 to 2500 m.

Discussion. Resembles *B. succulenta*, but *B. kitrinaima* has narrower calyx lobes, much smaller flowers, and ovate-lanceolate leaves (vs. elliptic). *Burmeistera huacamayensis* has similar sized flowers, however, it also has wider calyx lobes, flattened translucent-white hairs (vs. cream colored, when present, here), and elliptic leaves with long (10–25 mm) drip tips.

The inclusion of a sample of *B. kitrinaima* in a recent molecular phylogeny (unpublished) reveals that this species is closely related to *B. cylindrocarpa*, *B. tenuiflora*, and *B. smaragdi*.

Additional specimens examined. ECUADOR. **Bolívar:** Road Guaranda-Caluma, km 53, 1100 m, 01°35'S 79°11'W, 29 July 1996, *Ståhl & Knudsen 2901* (QCA). **Carchi:** Espejo, El Gualtal, faldas de Cerro Golondrina Hebra, 2450 m, 00°51'N 78°07'W, 21 August 1994, *Palacios 12672* (MO); Maldonado-Tulcán road, ca. km 20, 2400–2600 m, 7 October 1981, *Werling & Leth-Nissen 346* (QCA); Forest area along slope of mountain ENE of Rafael Quindí's mountain finca and above Río Verde, 00°52'N, 78°07'W, 1870–2400 m, 3 Dec. 1987, *W.S. Hoover 2264* (MO). **Cotopaxi:** Reserva Otonga, entre Quito y Sto. Domingo, cerca de San Francisco de las Pampas, 1990–2200 m, 00°25'S 79°00'W, June 1997, *Nowicki Mutke 1479* (QCA). **Pichincha:** Bosque Integral Otonga, 2228 m, 01°25.099'S 79°0.71W, 05 July 2002, *Muchhala 119* (QCA); Cantón Quito, nueva carretera Calacalí-Nanegalito, km 20, 1800–2000 m, 00°02'N 78°03'W, *Hurtado et al.*

1419 (MO); Northwest slopes of Volcán Pichincha, Quito-Nono-Mindo road, 5 km N of Mindo, 1500 m, 00°02'S 78°50'W, 29 April 1989, Niell et al. 8942 (MO); Parroquia Nanegalito, western slopes of Cerro Negro, 2.5–3 km airline NE of Nanegalito, 1900 m, 00°04'N 78°39'W, 8 September 1993, Webster et al. 30455 (MO); Reserva Bellavista, 2215 m, 00°0.814'S 78°41.083°W, 11 July 2002, Muchhala 128 (QCA); Reserva Bellavista, 2229 m, 00°0.819'S 78°41.418°W, 12 July 2002, Muchhala 130 (QCA); Reserva Florística Río Guajalito, Las Palmeras, 1800–2100 m, 00°14'S 78°49'W, May 1997, Nowicki & Mutke 1193 (QCA); Reserva forestall ENDESA, corporación forestall Juan Manuel Durini, km 113 de la carretera Quito-Puerto Quito, 600 m, 05 June 1986, Sigcha 28 (QCA); Reserva Maquipucuna, 1807 m, 00°5.866'S 78°37.455'W, 10 July 2002, Muchhala 125 (QCA); Reserva Río Guajalito, 1900 m, 00°14.9'S 78°48.2'W, 19 June 2010, Muchhala 447 (QCA); Reserva Río Guajalito, on Argentino trail, 2045 m, 00°14.3611'S 78°48.214'W, 25 June 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, 00°12'S 78°39'W, 26 September 1987, Buitrón 253 (QCA). Santo Domingo de los Tsáchilas: Nearest city Quito, near footbridge by Río Quajalito Science Centre, 1802 m, 00°13'50"S 78°49'15.4"W, 26 October 2010, Antonelli 602 (QCA).

30. *Burmeistera knaphusii* Lammers, Novon 12(2): 212, fig. 5. 2002. TYPE: Ecuador. Carchi: Forest area along slope of mountain ENE of Rafael Quindí's mountain finca and above Río Verde, 00°52'N, 78°07'W, 1870–2400 m, 03 Dec. 1987, *W. S. Hoover 2276* (holotype MO [barcode] 3751826!).

Scandent herbs, 6 m. Latex unknown. Stems ca. 3 mm wide, terete, green, villose or strigose with white to tan colored trichomes, sometimes the trichomes with a bulbous callose base, or callosities irregularly spaced on the stem. *Leaves* alternate, distichous, the internodes 5–20 mm; petioles 3–4 mm, green to violet, villose or strigose; lamina 25–40 \times 8–15 mm, narrowly ovate to lanceolate, the base obtuse to rounded, the apex attenuate to acuminate, the margin shallow callose-serrate to crenulate, the teeth intramarginal; adaxial surface green, glabrous to sparsely villose; abaxial surface green, sometimes tinged violet when young, villose with white to tan hairs, especially along the primary vein; venation camptodromous, the primary and secondary veins prominent, slightly raised, the tertiary veins visible. *Flowers* 28–36 mm, solitary in the upper leaf axils; pedicels 10–17 mm at anthesis, 13–17 mm in fruit, villose, green; hypanthium $3-4 \times 2-3$ mm, obconical, green, glabrous, smooth; calyx lobes $3-7 \times 0.5$ mm, linear, green to tinged pale red-violet, glabrous, the margin shallow callose-dentate with 2-3 blunt teeth, the apex acute, patent to reflexed at anthesis; corolla pale pink to violet, glabrous; corolla tube ca. 3 mm wide basally, the throat narrowing to ca. 2 mm; corolla lobes lanceolate, the margins smooth, the two dorsal lobes $8-13 \times 3-4$ mm, opening dorsally 18-20 mm from the corolla base, falcate, the two lateral lobes $5-7 \times 3$ mm, falcate, the ventral lobe ca. 4×3 mm, opening ventrally 14–16 mm from the corolla base; and roccium 28–33 mm, exserted 12–20 mm from the ventral opening, the filament tube green, glabrous, the anther tube ca. 3×3 mm, green, glabrous, the three dorsal anther tips sparsely villose, the two ventral anther tips more densely villose with white hairs; the style green, glabrous, the stigma green, the stigma lobes barbate. Fruits ca. 7×8 mm, globose, not-inflated, white.

Phenology. This species has been collected flowering in December and July, and fruiting in April.

Distribution. This species is found in a narrow distribution in northern Ecuador along the border of Colombia, in Canton Tulcán of Carchi province. Specimens have been collected from 900 to 2400 m in elevation.

Discussion. Though it resembles *B. aspera* and *B. arbusculifera* in habit, *B. knaphusii* is readily differentiated from both species by leaf size and shape, sepal lobe size, and corolla tube length (see discussion in *B. aspera* and *B. arbusculifera*).

Additional specimens examined. ECUADOR. **Carchi:** Cerro Golondrinas, valley bottom ca. 1 km NNE of summit, 2740 m, 00°15'38"N 78°08'14"W, 20 Jul. 1994, *Boyle et al. 3333* (MO); Forest and ridge area above Río Verde and ridge flanking medium Cerro Golondrinas, 2070–2430 m, 00°52'N 78°07'W, 04 Dec. 1987, *Hoover 2322* (MO); Tulcan, Reserva Etnica Awá, Parroquia El Chical, Centro San Marcos, 900–1100, 01°06'N 78°14'W, 20–30 Apr. 1993, *Méndez et al. 382* (MO).

31. Burmeistera lingulata Mashburn, sp. nov. TYPE: Ecuador. Carchi: Tulcan Canton,
Reserva Indígena Awá, Comunidad San Marcos, 25 km al NW de El Chical, parroquia
Maldonado, 1500 m, 01°06'N 78°14'W, 16–30 Nov. 1990 (fl., fr.), D. Rubio, C. Quelal
& J. Pai 905 (holotype, MO-6370917!).

Scandent herbs, 1.5 m. Latex white. Stems 4–6 mm wide, tan to green, glabrous, striate when dry. *Leaves* alternate, spiral, the internodes 10–40 mm; petioles 15–30 mm, green to brown, glabrous to sparsely puberulent; lamina $50-180 \times 15-65$ mm, elliptic, the base attenuate, the apex attenuate, the margin shallow-callose dentate, sometimes nearly entire; adaxial surface green, glabrous; abaxial surface green, puberulent, especially along the main veisn, with soft white hairs; venation camptodromous, the primary and secondary veins prominent, raised, the tertiary veins visible. *Flowers* solitary in the upper leaf axils, 44–45 mm; pedicels 75–105 mm, glabrous, green; hypanthium $4-6 \times 4-5$ mm, cupuliform, green, glabrous; calyx lobes $10-15 \times 5-9$ mm, foliaceous, lanceolate, green, glabrous, the margin shallow callose-serrate, slightly ascending to patent at anthesis; corolla pale green (rarely tinged red), glabrous; corolla tube ca. 5 mm wide basally, the throat narrowing to ca. 2 mm; corolla lobes ligulate, the margins smooth, the two dorsal lobes $13-14 \times 3-4$ mm, arcuate, opening dorsally 20-21 mm from the corolla base, the two lateral lobes $6-8 \times 3-4$ mm, arcuate, the ventral lobe $4-5 \times 3-4$ mm, opening ventrally ca. 16 mm from the corolla base; androecium 39–41 mm, exserted 25–27 mm from the ventral opening, the filament tube green, glabrous, the anther tube ca. 5×4 mm, green, glabrous, all five anther tips glabrous to sparsely pubescent; the style and stigma glabrous. Fruits ca. 15×15 mm, globose, not inflated, fleshy, maturing yellow (rarely reddish-tan).

Etymology. The specific epithet comes from Latin, meaning 'like a little tongue.'

Phenology. This species has been collected with flowers and fruits throughout the year.

Distribution. Found at middle elevation in Carchi and Esmeraldas Provinces of Ecuador. It occurs in wet forests from 380 to 1200 m in elevation.

Discussion. Before the description of this species, specimens of *B. lingulata* were often identified as *B. glabrata*, due to the tongue-like shape of the calyx lobes. This species is differentiated from *B. glabrata* by having yellow fruits that do not inflate at maturity. In this sense, *B. lingulata* is similar to *B. brachyandra*. However, *B. lingulata* has much larger calyx lobes and flowers than *B. brachyandra*, nor does it exhibit bracts when flowering.

Additional specimens examined. ECUADOR. **Carchi:** Border area between Prov. Carchi and Esmeraldas, about 20 km past Lita on road Lita-Alto Tambo, 550 m, 24 Jun. 1991, *van der Werff et al. 11911* (MO); Plateau above San Marcos de los Coaiqueres, on trail towards Gualpí Bajo, 1000 m, 01°06'N 78°17'W, 07 Feb. 1985, *Øllgaard et al. 57355* (QCA); Reserva Etnica y Forestal Awá, San Marcos, 1000 m, 01°05'N 78°15'W, 11 Mar. 1988, *Jørgensen et al. 65176* (QCA); San Marcos valley, 600 m, 01°07'N 78°20'W, 20 Nov. 1983, *Kvist et al. 48696* (QCA); Tulcan Canton, Parroquia Chical, Sector Gualpi medio, Reserva Indígena Awá, sendera a San Marcos al norte de la casa communal, 1026 m, 01°02'N 78°16'W, 23–27 May 1992, *Tipaz et al. 1039* (MO); Tulcan Canton, Reserva Etnica Awá, Parroquia El Chical, Sector Gualpí Medio, Río Canumbí, 1150 m, 01°02'N 78°15'W, 19–28 Feb. 1993, *Grijalva et al. 466* (MO). **Esmeraldas:** Along road between Lita and San Lorenzo, vicinity of Alto Tambo, 6.6 km NW of railroad tracks in Alto Tambo, 684 m, 00°57'34"N 78°37'36"W, 22 Feb. 2005, *Croat 95181* (MO); Communidad Awá Río Bogota, 11.5 km W of Alto Tambo, 30.5 km W of Río Lita, 3 km by trail to Río Bogota on S side of Lita-San Lorenzo road, 380 m, 00°58'57"N 78°35'58"W, 15 Sep. 2002, *Croat et al. 87524* (MO); Highway from Lita to Alto Tambo, 797 m, 00°54.624'N 78°32.736'W, 18 Jul. 2002, *Muchhala 142* (QCA); Mun. Lita, Río Lita and tributaries, affluent of Río Mira, 120 km NW of Ibarra, 14 km WNW of Lita, 600 m, 00°52'N 78°29'W, 07 May 1987, *Daly & Acevedo 5145* (NY); Road Lita-San Lorenzo, km 32, 800 m, 00°30'N 78°53'W, 28 Sep. 1991, *Øllgaard 99150* (QCA);

32. Burmesitera loejtnantii Jeppesen, Fl. Ecuador 14: 23, fig. 1D. 1981. TYPE: Ecuador.
Carchi: Valle de Maldonado, km 53 on the road Tulcán-Maldonado, 3150–3250 m,
00°50'N 78°03'W, 19 May 1973 (fl., fr.), L. Holm-Nielsen, S. Jeppesen, B. Løjtnant & B.
Øllgaard 5838 (holotype, AAU digital image!; isotypes, K [barcode] 250829 digital
image!, NY [barcode] 467997!, S-05-1904 digital image!).

Herbaceous shrubs, 1.5 m. *Latex* unkown. *Stems* green suffused with violet, glabrous to sparsely verrucose, appearing winged because of persistent decurrent petiole bases, these bases strigose. *Leaves* alternate, distichous; petioles 4–6 mm, green suffused with violet, strigose; lamina $25-40 \times 10-25$ mm, ovate to ovate-lanceolate, the base obtuse to rounded, the apex attenuate, the margin callose-serrate; adaxial surface green with violet margins to green suffused with violet, glabrous, nitid; abaxial surface light green suffused with violet, strigose with tan colored trichomes; venation

craspidodromous, the primary vein prominent, raised, the secondary veins thin, slightly raised, the tertiary veins visible. *Flowers* solitary, ca. 22 mm; pedicels 10–15 mm at anthesis, 25–30 mm in fruit, green to green tinged violet glabrous, distally sparsely vertucose; hypanthium ca. $6-9 \times 6-8$ mm, cupuliform, green suffused with violet, glabrous to sparsely strigose; calyx lobes ca. $6-8 \times 4$ mm, ligulate, glabrous, green suffused with violet, the margin callose-serrate, the apex acute, ascending to patent at anthesis; corolla exterior dorsally green suffused with violet, ventrally violet, the interior lighter colored; corolla tube ca. 5 mm wide basally, narrowing to c. 3 mm, glabrous; corolla lobes ligulate, the two dorsal lobes ca. 7×3 mm, opening dorsally ca. 12 mm from the corolla base, the two lateral lobes ca. 4×2 mm, opening ventrally at ca. 7 mm from the corolla base; androecium ca. 18 mm exserted ca. 11 mm from the ventral opening, the filament tube green, puberulous distally with white hairs, the anther tan lightly suffused with violet, glabrous, the top three anther tips glabrous, the bottom two anther tips villose; the style and stigma unkown. Fruits ca. 15×15 mm, globose, fleshy, maturing white suffused with violet.

Phenology. This species has been collected with flowers and fruits in May.

Distribution. Only known from one location in Carchi Province of northwest Ecuador, at ca. 3200 m in elevation.

Discussion. This species was described, and is still only known, from the type collection. It is likely closely related to *B. aspera*, but is differentiated by its larger flowers. Additional specimens examined. NONE.

33. *Burmeistera lutosa* E. Wimm., Repert. Spec. Nov. Regni Veg. 29: 56, t. 115, fig. 2. 1931. TYPE: Ecuador. Guayas: Guayahil, s.d., *Hall 26* (holotype, K [barcode] 250839 digital image!).

Herbaceous terrestrial shrubs, 3 m. Latex white to cream. Stems ca. 8 mm wide, green to violet, puberulous with white hairs, velutinous, striate when dry. *Leaves* alternate, spiral, often reduced in size where flowering; petioles 10-50 mm, green tinged violet, puberulent; lamina $90-210 \times 60-80$ mm, where flowering reduced to $50-70 \times 15-$ 25 mm, elliptic, the base cuneate, the apex attenuate, the margin shallow callose-dentate, sometimes nearly entire basally, the teeth often increasing in size toward the apex; adaxial surface green, glabrous; abaxial surface green, puberulous with appressed cream colored hairs, especially dense along the veins; venation camptodromous, the secondary veins sometimes terminating in marginal teeth, the primary and secondary veins prominent, raised but flattened, the tertiary veins visible. Flowers 27-28(-32) mm, solitary, bunched apically with new growth; pedicels 25–45 mm at anthesis, 30–50 mm in fruit, green, villose; hypanthium $4-6 \times 4-5$ mm, cupuliform, green, villose, the ridges smooth; calyx lobes $7-9 \times 2-3$ mm, lanceolate, green, villose, the margin shallow callose-dentate, the apex acute, reflexed at anthesis; corolla green (rarely tinged pink or violet basally), villose; corolla tube 4-6 mm wide basally, narrowing to 2-3 mm; corolla lobes lanceolate, the margins undulate, the two dorsal lobes $7-15 \times 4-5$ mm, opening

dorsally 14–17 mm from the corolla base, falcate, the two lateral lobes 6–10 × 3–4 mm, opening ventrally 10–11 mm from the corolla base, falcate; androecium 22–26 mm, exserted 12–15 mm from the ventral opening, the filament tube green, glabrous basally, glabrous to sparsely puberulous distally, the anther tube green, villose with cream colored hairs, the top three anther tips glabrous, the bottom two anther tips villose with white hairs; the style and stigma cream colored, the stigma lobes villose along the margin. *Fruits* 7 × 9 mm, globose, fleshy, pale green to violet, villose.

Phenology. This species has been collected with flowers and fruits throughout the year.

Distribution. Burmeistera lutosa occurs in northwest Ecuador in the Provinces Carchi and Pinchincha in mid to high elevation rainforests.

Discussion. Burmeistera lutosa is most similar to *B. multiflora*, though it is differentiated from the latter by its densely pubescent leaves, new growth, and flowers, and larger flowers.

Additional specimens examined. ECUADOR. **Carchi:** Above Maldonado 9 km on road to Tulcán, 2200–2250 m, 00°53'N 78°03'W, 30 May 1985, *Stein 2902* (MO); Along road from El Chical to San Marcos, via Peñas Blancas and Quinshul, 9 km W of Quinshul, at end of road owing to cave off road, 1150 m, 01°00'02" 78°12'34"W, 14 Oct. 2012, *Croat et al. 104266* (MO); Along trail between the Coaiquer AWA Amerindian communities San Marcos and San Antonio, located along the trail before Gualpi Bajo, 900–1100 m,

01°08'N 78°22'W, 25 Nov. 1983, Kvist et al. 48957 (QCA); Approx. 6 km above Maldonado, just below Puente de Palo, 2275 m, 00°54'N 78°06'W, 23 May 1993, Boyle & Bradford 1873 (MO); Further ascent of Río Verde approaching headwaters of river at base of Cerro Golondrinas stopping at point where prominent stream with waterfall enters from SW, 1900 m, 00°52'N 78°07'45"W, 30 Nov. 1987, Hoover 2128 (MO); Mira Canton, norte del Carmen, Camino a Chical, 2000–2200 m, 00°17'N 78°13'W, 10 Feb. 1992, Palacios et al. 9707 (MO); Reserva Golondrinas, El Corazón, recorrido por el sendero a La Cortadera, 2230 m, 00°50'N 78°06'W, 22 Jan. 2004, Vargas et al. 4269 (MO); Trail from Machinas (12 km above Maldonado) toward Planada de Chilma, Río Chilma Valley, 2350–2450 m, 00°52'N 78°03'W, 30 May 1985, Stein 2907 (MO); Trail to Río Gualpi Chico, along ridge line near AWA encampment, 1330 m, 00°58'N 78°16'W, 17 Jan. 1988, Hoover 2516 (MO, QCA); Valle de Maldonado, km 71 on road Tulcán-Maldonado, 2100–2200 m, 00°54'N 78°06'W, 20 May 1973, Jeppesen 6038 (NY). Pichincha: Quito-Santo Domingo old road, ca. 2–4 km from the road in area called "Bella Vista" at km 69 of old road, 2400 m, 00°13'S 78°51'W, 13 Nov. 1992, Lutevn et al. 14775 (NY); Quito-Santo Domingo old road, Las Palmeras, ca. 59 km WSW of Quito, Pablo Forest trail above Río Guajalito, 1900–2000 m, 00°18'S 78°43'W, 16 Dec. 1990, Lutevn & Berg 14358 (NY); Reserva Florística Ecológica Río Guajalito, km 59 de la carretera antigua Quito-Sto. Domingo de los Colorados, a 3.5 km al NE de la carretera, estribaciones occidentales del Volcán Pichincha, 1800-2200 m, 00°13'53"S 78°48'10"W, 22 May 1992, Jaramillo & Grijalva 14777 (NY).

34. *Burmeistera marginata* H. Karst., Linnaea 28: 445. 1856. TYPE: Colombia. Cauca: vicinity of the village 'Consata' on mount Quindio, alt. 1350 m, 1851–1857 (fl.), *J. J. Triana 1585* (lectotype, designated here, P [barcode] 408889 digital image!).

Scandent herbs, 3 m. *Latex* unknown. *Stems* 5 mm wide, green, puberulent, terete. *Leaves* alternate, distichous; petioles 7–10 mm, green, puberulent; lamina $130-200 \times 40-$ 70 mm, elliptic, the base cuneate, the apex attenuate to acuminate, the margin shallow callose-denticulate, sometimes nearing entire; adaxial surface green to green tinged violet, velutinous; abaxial surface green to green tinged violet, velutinous, puberulent along the veins with short white to cream colored hairs; secondary veins connecting to a prominent submarginal collecting vein, the primary and secondary veins prominent, raised, the tertiary veins visible, sometimes raised. *Flowers* solitary, 52–55 mm; pedicels 120–160 mm at anthesis, 120–180 mm in fruit, puberulent, green, in places lightly tinged violet; hypanthium $17-20 \times 1.5$ mm, tubular, the base barely distinguishable from the pedicel, abruptly widening to 4–5 mm distally, green tinged or spotted violet, puberulent; calyx lobes $1.5-3.5 \times 1-2$ mm, deltate, green, the apex tinged violet, puberulent, the margin entire, ascending at anthesis; corolla green to tinged violet, puberulent; corolla tube 4 mm wide basally, narrowing to 3 mm; corolla lobes ligulate, the interior pale green, the margins tinged violet, smooth, the two dorsal lobes $12-15 \times 2.5$ mm, opening dorsally 14–15 mm from the corolla base, arcuate, the two lateral lobes $7-8 \times 3$ mm, opening ventrally 9 mm from the corolla base, arcuate; androecium 33–35 mm, exserted 25–26 mm from the ventral opening, the filament tube green, dorsally tinged violet, densely puberulent, the anther tube green, along the anther sutures lighter green with

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short, white, appressed hairs, all the anther tips glabrous or with very few white hairs; the style and stigma green, the stigma lobes puberulent above, the lobe margins barbate with short white hairs. *Fruits* unknown.

Phenology. This species has been collected with flowers in May and July.

Distribution. This species was previously only known from southwest Ecuador. This is the first record of its occurrence in northwest Ecuador in Esmeraldas province. It occurs in wet forests from 800 to 1400 m in elevation.

Discussion. Burmeistera marginata is most similar to *B. holm-nielsenii*, though it is readily differentiated by its small, deltate calyx lobes, versus the long, comb-like calyx lobes of *B. holm-nielsenii*.

Additional specimens examined. ECUADOR. Esmeraldas: Km 12, Cristal, Lita-Buenos Aires, edge of Cotacachi Cayapas Reserva Ecologica, 20 Jul. 1988, *Dodson 17645* (MO); Lita-San Lorenzo road, 10–20 km NW of Lita, 800 m, 00°55'N 78°35'W, 12 May 1991, *Gentry et al. 70106* (MO) & *70113* (NY).

35. Burmeistera microphylla Donn. Sm., Bot. Gaz. 25: 146. 1898. TYPE: Costa Rica.
San José: La Palma, 1500 m, Nov. 1897, *C. Wercklé 11600* (holotype, US [barcode]
146946 digital image!).

Burmeistera aurobarbata (E. Wimm.) E. Wimm., Repert. Spec. Nov. Regni Veg. 30: 35.
1932. Basionym: *Centropogon aurobarbatus* E. Wimm., Repert. Spec. Nov. Regni Veg.
19: 251. 1924. TYPE: Costa Rica. Heredia: Barba, s.d. (fl.), *A. C. Brade 2315* (holotype, B destroyed; isotype BR [barcode] 696995 digital image!).

Burmeistera aurobarbata (E. Wimm) E. Wimm. var. cuspidata E. Wimm., Pflanzenr. IV.
276b (Heft 69): 151. 1943. TYPE: Costa Rica. Heredia: Vera Blanca de Sarapiqui,
Nordabhang der Zendtral-Kordillere, zwischen den Vulkanen Poás und Barba, 1800 m,
Oct. 1937, A. F. Skutch 3372 (holotype, designated here, S-14-25146 digital image!).

Burmeistera aurobarbata (E. Wimm) E. Wimm. var. *valde-cuspidata* Seuss., Bot. Jahrb. Syst. 72(2): 287. 1942. TYPE: Costa Rica. Heredia: Vara Blanca, 25 Dec. 1931 (fl., fr.), *W. Kupper 256* (holotype, M [barcode] 189975 digital image!; isotype, M [bc] 189974 digital image!)

Scandent herbs. *Latex* unknown. *Stems* ca. 3 mm wide, terete, green to violet, glabrous. *Leaves* alternate, distichous, thick, coriaceous, the internodes 10-40 mm; petioles 3–6 mm, green, sometimes tinged violet, glabrous; lamina $45-110 \times 15-30$ mm, narrowly ovate to lanceolate, the base cuneate to obtuse, the apex attenuate, the margin shallow callose-serrate, sometimes nearly entire, the teeth sometimes intramarginal; adaxial surface dark green, glabrous; abaxial surface lighter green to tinged violet, glabrous, velutinous??; venation arcuate with secondary veins terminating in marginal teeth, the primary vein prominent, the secondary veins only slightly visible or not visible,

the tertiary veins not visible. Flowers 34–39 mm, solitary; pedicels 60–100 mm, glabrous, green to violet; hypanthium $5-6 \times 5-6$ mm, obconical, green to violet, glabrous, the ridges smooth; calyx lobes $5-13 \times 1-2$ mm, ligulate, slightly ascending to patent at anthesis, green to violet, glabrous, the margin shallow callose-dentate, the apex acute; corolla green to cream spotted or suffused with maroon-violet, glabrous; corolla tube 4–5 mm wide basally, the throat, narrowing to 2–3 mm; corolla lobes lanceolate, the margins smooth, the two dorsal lobes $10-12 \times 3-4$ mm, opening dorsally ca. 20 mm from the corolla base, falcate, the two lateral lobes $8-9 \times 3-4$ mm, falcate, the ventral lobe ca. 7×4 mm, opening ventrally 15–18 mm from the corolla base; and roccium 28–32 mm, exserted 13–14 mm from the ventral opening, the filament tube pale green, glabrous basally, puberulous distally with white hairs, the anther tube pale green, puberulous basally and between the sutures, the three dorsal anther tips glabrous to sparsely pubescent, the two ventral anther tips densely villose with white hairs; the style and stigma cream-colored, the stigma lobes pubescent along the margin with short white hairs. Fruits not seen.

Phenology. This species has been collected with flowers and fruits throughout the year.

Distribution. Widely distributed in mid-elevation rainforests from Costa Rica to Peru.

Discussion. This species is closely related to *B. crassifolia* with the thick, coriaceous leaves and not visible secondary and tertiatry veins. It is differentiated from *B. crassifolia* by the thinner lanceolate leaves, rather than ovate or cordate.

Two of these specimens from Ecuador were previously undetermined, as they do not quite match *B. crassifolia*. The third Ecuadorian specimen has been identified as *B. microphylla* and later as *B. crassifolia*. *Burmeistera microphylla* is a diverse species along its range. Previously, it was described in Costa Rica, Panama, and Peru, a distribution that is possible, but difficult to believe. We have called these specimens *B. microphylla* because they seem to go with the *B. microphylla* from Peru better than the *B. crassifolia* from northeast Ecuador. *Burmeistera microphylla* and *B. crassifolia* are clearly part of a clade of thick leaved *Burmeistera* that ranges from Costa Rica to Peru. Other thick leaved species have been described in Colombia, (e.g. *B. reclinata*). More work is necessary on this clade to better understand its species and distribution.

Additional specimens examined. ECUADOR. **Morona Santiago:** Cordillera Cutucú, ridge ascending into central Cutucú, 1430–1495 m, 02°40'S 78°00'W, 17 Nov.–05 Dec. 1944, *Camp E-1168* (NY); Parque Nacional Sangay, Lagunas de Sardinayacu, sendero desde la laguna Enmascarado hacia la laguna Comandante, 1750–1980 m, 02°03'27"S 78°13'09", 23 Jan. 2015, *Pérez et al. 8086* (QCA); Road Santa Susana de Chiviasa-Panecillo, km 3.5, 1300 m, 02°55'S 78°04'W, 21 Nov. 1997, *Øllgaard & Navarrete 2707* (QCA). PERU. **San Martín:** Prov. Ríoja, ca. 100 km W of Ríoja on road to Pedro Ruiz, 2 km E of Puente Río Nieva, border between Amazonas and San Martín Departments, 2000 m, 05°47'S 77°39'W, 16 Feb. 1985, *Stein & Todzia 2198* (MO, NY). **36.** *Burmeistera multiflora* Zahlbr., Repert. Spec. Nov. Regni Veg. 13: 530. 1915. TYPE: Ecuador. Pichincha: Quito, Nanegal, s.d., *H. Karsten s.n.* (lectotype, designated here, W-0046734 digital image!).

Herbaceous shrubs to scandent herbs, 4 m. Latex white. Stems ca. 12 mm wide, green to violet, puberulent with white to tan colored hairs, with distinct sterile and fertile zones, the latter with reduced leaves (bracts) and shorter internodes. *Leaves* alternate, spiral, the internodes 10–50 mm; petioles 10–60 mm, green to green tinged violet, puberulent; lamina $80-180 \times 40-90$ mm, elliptic to oblance late, the base cuneate, the apex attenuate, the margin shallow callose-crenate to dentate, sometimes nearly entire, the teeth often intramarginal, sometimes increasing in size near the apex; adaxial surface green, glabrous to very sparsely puberulent; abaxial surface green to green tinged violet, puberulent with white to tan colored hairs, especially along the veins; venation brochidodromous, the primary and secondary veins prominent, raised, the tertiary veins visible. Flowers 21–30 mm, bunched apically with new fertile zone growth, appearing racemose, the bracts ca. 3×0.5 mm, caducous, the internodes 1–6 mm; pedicels 20–60 mm at anthesis, 20-65 mm in fruit, green to green tinged violet, puberulent; hypanthium $3-6 \times 2-4$ mm, cupuliform, green to green tinged violet, puberulent, the ridges smooth to slightly raised; calyx lobes $2-4 \times 1-2$ mm, deltate, green, sometimes tinged violet along the margin and at the apex, puberulent, somewhat revolute, the margin shallow callosedentate with 1–3 blunt teeth, the apex obtuse, patent to slightly ascending at anthesis; corolla green, rarely green tinged violet, glabrous to sparsely puberulent; corolla tube 4-5 mm wide basally, bulging just above the base, narrowing to 2-3 mm; corolla lobes

lanceolate, the margins undulate, the two dorsal lobes $8-12 \times 2-3$ mm, opening dorsally 8-13 mm from the corolla base, falcate, the two lateral lobes $5-6 \times 2-3$ mm, opening ventrally 5-10 mm from the corolla base, falcate; androecium 16-24 mm, exserted 11-18 mm from the ventral opening, the filament tube green to green lightly tinged violet, glabrous to puberulent, the anther tube green, lighter along the sutures, glabrous, all five anther tips glabrous or very sparsely pubescent; the style and stigma cream colored, the stigma lobes shortly pubescent along the margin. *Fruits* ca. 13×13 mm, globose, fleshy, green to white to peach.

Etymology. The specific epithet is in reference to the way in which the flowers bunch apically into a corymb-like inflorescence.

Phenology. This species has been collected with flowers and fruits throughout the year.

Distribution. This species is found in northwest Ecuador from Carchi to Santo Domingo. It is a relatively common mid-elevation forest species.

Discussion. Burmeistera multiflora is most similar with *B. lutosa*, with which it cooccurs. *Burmeistera multiflora* is differentiated by having much smaller flowers, and glabrous to minutely puberulent stems and leaves, vs. the densely pubescent in *B. lutosa*.

Zahlbruckner named three syntypes, one (Sodiro 91/27) which was deposited at Berlin and likely destroyed, the other deposited at Kew (André 3088). Wimmer (1943) treated the Karsten collection in Vienna to be the original specimen, which makes sense given that Zahlbruckner worked from Vienna, though he still cited the others. Thus, to make it official, we designate here the Karsten collection from Vienna as the lectotype.

Additional specimens examined. ECUADOR. Carchi. Cantón Tulcán, along road from El Chical to Gualchán, vicinity km 12 marker, 12 km S of main El Chical-Peñas Blancas Road, 1906 m, 00°53'27"N 78°13'13"W, 19 Aug. 2013, Croat et al. 104984 (MO); Cerro Golondrinas, upper Río Pablo drainage, north side of valley, just above river on steep slope, 1730–1760 m, 00°52'N 78°10'W, 14 Apr. 1993, Boyle et al. 1663 (MO); Espejo Cantón, nueva vía El Carmen-Chical, 2200 m, 00°15'13"N 78°13'50"W, 14 May 2009, Palacios 16724 (MO); Espejo, Reserva Golondrinas, recorrido de la Estación Santa Rosa por el sendero hasta el Cerro Golondrinas, parte baja, 2100 m, 00°49'N 7°07'W, 26 Jan. 2004, Vargas et al. 4493 (MO); Railroad from Ibana to San Lorenzo, km 78, Río Blanco, 1400–1500 m, 14 Dec. 1961, Dodson & Thien 1614 (MO); SE side of Quebrada Mongon, 1200–1400 m, 00°52'N 78°16'W, 21 Jan. 1988, *Hoover et al. 2985* (QCA); Southeast trail, primary forest in Gualpi Chicó area of Awá reserve, near encampment, 1330 m, 00°58'N 78°16'W, 19 Jan. 1988, *Hoover et al. 2768* (MO, QCA); South on main trail from camp, away from Pylus, for 1/12 mi from camp East down to Río Gualpi Chico, 1100 m, 00°58'N 78°16'W, 21 Jan. 1988, *Hoover et al. 3006* (QCA); Trail along Awá border, to Mongon Creek to W of encampment and ascending creek Gualpi Chico area, 1161–1258 m, 00°58'N 78°16'W, Hoover et al. 3306 (MO); Trail from Rafael Quindí's mountain finca to Río Verde and short distance up Río Verde, 1890 m, 00°52'N 78°08'W, 28 Nov. 1987, Hoover & Wormley 1881 (MO). Cotopaxi: Cantón Sigchos, Orillas del Río Illinazas, 2280 m, 00°34'49"S 78°47'22"W, 14 Jul. 2003, Ramos et al.

5994 (MO). Esmeraldas: Mun. Lita, Río Lita and tributaries, affluent of Río Mira, 120 km NW of Ibarra, 14 km WNW of Lita, 600 m, 00°52'N 78°29'W, 07 May 1987, Daly & Acevedo 5146 (NY); Road Lita-Urbina, km 38.8, 450–500 m, 00°47'N 78°35'W, 12 Jan. 1991, Øllgaard et al. 98671 (QCA); San Lorenzo Canton, Reserva Indígena Awá, Cañon del Río Mira, 10 km al oeste de Alto Tambo, Comunidad La Union, 250 m, 01°02'N 78°26'W, 16–26 Mar. 1991, Rubio et al. 1204 (MO); San Lorenzo, San Franciso, Recinto Durango, Valle de la Virgen, 2 km al suroeste de la carretera Lita-San Lorenzo, 500 m al noroeste del Río Bogota, 385 m, 00°59'N 78°36'W, 20 Oct. 1999, Valenzuela & Friere 584 (MO). Imbabura: Along road from Otovalo to Selva Alegre, 38 km W of Cambugan, 15 km E of Selva Alegra, 1773 m, 00°16'49"N 79°30'55"W, 24 Aug. 2004, Croat & Ferry 93971 (MO); Cotacachi Canton, Parroquia Apuela, Sector Cuellage, 1600 m, 00°15'N 78°25'W, 10 Jul. 1992, Tipaz & Aulestia 1659 (MO); Cotacachi Canton, Plaza Gutierrez, Sector Tabla Chupa, 3000 m, 00°13'N 78°25'W, 18 Jun. 1992, Tipaz & *Gudiño 1186* (MO); Cotacachi, Hacienda La Florida, 1900–2500 m, 00°23'S 78°28'W, 27 Aug. 1992, Alvarez & Castro 596 (MO). Pichincha: Along road between Pacto and Cielo Verde on Río Guayabamba, 10.2 km SW of Pacto, 34.8 km SW of Armenia junction with Nanegalito-Pto. Quito Hwy., 1619 m, 00°09'42"N 78°41'23"W, 25 Mar. 2006, Croat et al. 96375 (MO); Maquipucuna Biological Field Station, ca. 5 km E of Nanegalito and ca. 25 km N of Quito, 1400–1700 m, 00°08'N 78°35'W, 02 Feb. 1991, Moran & Rohrbach 5216 (MO); Maquipucuna Tropical Reserve, western slopes of Andes, northern boundary of reserve, 10 km N of Nanegalito, 1200 m, 00°10'N 78°35'W, 02 Dec. 1988, Neill et al. 8649 (MO); Parroquia Nanegal, Maquipucuna area, Cerro Sta. Lucia (Cerro Campana), ca. 6 km airline E of Nanegal, 1700 m, 00°8.5'N

78°37.5'W, 20 Jul. 1990, Webster & Castro 28323 (MO); Quito Canton, Nanegal,
Reserva Biológica Maquipucuna, 1200–1700 m, 00°08'N 78°35'W, 20 May 1991, *Tipaz*& Quelal 196 (NY); Quito, Reserva Orquideológica El Pahuma, carretera Calacalí-Los
Bancos, km 22, 2000 m, 00°01'42"N 78°37'50"W, 26 Oct. 1999, Mantuano et al. 10
(MO); Quito, Reserva Orquideológica El Pahuma, carretera Calacalí-Los Bancos, km 22, 2000 m, 00°01'42"N 78°37'50"W, 26 Oct. 1999, Mantuano et al. 10
(MO); Quito, Reserva Orquideológica El Pahuma, carretera Calacalí-Los Bancos, km 22, 2000 m, 00°01'42"N 78°37'50"W, 19 Oct. 1999, Nicolalde et al. 339 (MO); Quito, vía a
Nanegalito, 2350 m, 00°04'49"S 78°37'00"W, 20 Mar. 2001, Montenegro et al. 224
(MO); Reserva Forestal La Favorita, 2.4 km from main Quito-Chiriboga-Santo Domingo
road, departing main road 0.7 km S of village of Chiriboga, 1800–1830 m, 00°12'S
78°47'W, 15 Feb. 1992, Croat 72135 (MO); Road Quito-Nono-Pacto, between Nono and
Tandayapa, 2000 m, 00°01'S 78°38'W, 24 Mar. 1979, Holm-Nielsen 16128 (NY); Santo
Domingo de las Tsáchilas: Around Río Quajalito Science Centre, 2013 m, 00°14'06.8"S
78°48'42.1"W, 26 Oct. 2010, Antonelli 606 (QCA).

37. *Burmeistera melanocarpa* Mashburn, sp. nov. TYPE: Ecuador. Carchi: Tulcán-Maldonado road, 45 km W of Tufiño, 2425 m, 13 April 1978, *J. L. Luteyn & M. L. Lebrón-Luteyn 5750* (holotype, QCA barcode 26985!; isotypes, MO 5700007!, NY!).

Scandent herbs, 4 m. *Latex* white. *Stems* ca. 4 mm, green to violet, glabrous, striate when dry. *Leaves* alternate, distichous, the internodes 20–40 mm; petioles 4–11 mm, green to green suffused with violet, glabrous; lamina $60-160 \times 25-60$ mm, elliptic, the base obtuse, the apex acuminate to caudate, $6-10 \times 1-3$ mm, the margin shallow callose-serrate, sometimes tinged violet; adaxial surface green to green tinged dark violet,

the primary and secondary veins sometimes tinged dark violet, glabrous, nitid; abaxial 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, 37–47 mm; pedicels 100–130 mm at anthesis, 100–140 mm in fruit, green to violet, glabrous; hypanthium $10-13 \times 5-7.5$ mm, obconical, dark violet, glabrous; calyx lobes $1.5-3 \times 1.5-2.5$ mm, deltate, dark violet, glabrous, the margin entire or with few callose-tipped teeth, ascending at anthesis; corolla green streaked with dark violet to entirely maroon-violet, glabrous; corolla tube 5–6 mm wide basally, the throat narrowing to 3-4 mm; corolla lobes lanceolate, the margins smooth, the two dorsal lobes $16-18 \times 3-4$ mm, opening dorsally 16-17 mm from the corolla base, ascending, the two lateral lobes $11-15 \times 3-4$ mm, falcate, the ventral lobe ca. 12×4 mm, opening ventrally 11–14 mm from the corolla base; androecium 33–36 mm, exserted 20–22 mm from the ventral opening, the filament tube dark violet, glabrous, the anther tube $9-11 \times$ 4–5 mm, dark violet, glabrous, all five anther tips sparsely to densely villose; the stigma violet, upper and lower margins barbate. Fruits 30×25 mm, globose, pendent, fleshy, spongy, the exterior dark violet, nearly black, the interior yellow.

Etymology. Named for the unique dark violet, nearly black, mature fruits.

Phenology. This species has been collected with flowers and fruits throughout the year.

Distribution. Found in a narrow range in the Carchi province of Ecuador, parroquia of Maldonado, bordering Colombia. Specimens have been collected in cloud forests from 2100–2700 m in elevation.

Discussion. This species is most similar to *B. sodiroana* in its leaf shape and uniformly dark violet anther tube. However *B. melanocarpa* is differentiated by having distichous phyllotaxy, non-reducing fertile leaves, and dark violet fruits. Some specimens of *B. crispiloba* that are potential hybrids with *B. sodiroana* are vegetatively similar to *B. melanocarpa*. However, *B. melanocarpa* is differentiated by its dark violet fruits and smaller flowers.

Morphological similarity with *B. crispiloba / B. sodiroana* hybrids suggests this species is the result of hybridization between *B. crispiloba* and *B. sodiroana*. However, no specimens of *B. sodiroana* and very few of *B. crispiloba* have been collected in areas near the narrow distribution of *B. melanocarpa*, where the species seems to be relatively abundant.

Additional Specimens examined. ECUADOR. **Carchi:** Espejo, faldas del Cerro Golondrinas Hembra, 2300–2400 m, 00°51'N 78°07'W, 20 August 1994, *Palacios 12757* (MO); East of Maldonado 12 km on road to Tulcán, 2230 m, 27 September 1979, *Gentry* & *Shupp 26647* (MO); Road Tulcán-Maldonado, ca 13 km SE of Maldonado, 2600 m, 01 March 1974, *Harling & Andersson 12384* (MO); Trail from Machinas, 12 km above Maldonado, toward Planada de Chilma, Río Chilma Valley, 2350–2450 m, 00°52'N 78°03'W, 30 May 1985, *Stein 2911* (MO, QCA); Up small mountain SW of Rafael Quindis finca along small stream and descending mountain trail, 1930–2100 m, 00°52'N 78°08'W, 28 November 1987, *Hoover & Wormley 1850* (MO); Valle de Maldonado, km 71 on road Tulcán-Maldonado, 2100–2200 m, 00°54'N 78°06'W, 20 May 1973, *Holm-Nielsen et al. 6000* (NY, QCA); West of Tulcán 62–75 km, 2720–2460 m, 00°50'N 78°50'W, 07 January 1985, *Luteyn & Cotton 10882* (NY); West of Tulcán 78–82 km, 2040–2320 m, 00°50'N 78°50'W, 08 January 1985, *Luteyn & Cotton 10893* (NY).

38. Burmeistera oyacachensis Jeppesen, Fl. Ecuador 14: 40. 1981. TYPE: Ecuador.
Napo: In silvis Andibus orientalibus prope Oyacachi, Feb. 1900 (fl., fr.), L. Sodiro 91/29
(holotype, P [barcode] 00408895 digital image!).

Scandent herbs. *Latex* cream colored. *Stems* ca. 4 mm wide, green, glabrous, nitid, striate when dry. *Leaves* alternate, spiral; petioles 10-25 mm, green, glabrous; lamina $40-60 \times 20-25$ mm, elliptic, the base obtuse, the apex acuminate, $5-10 \times 2-3$ mm, the margin irregularly callose-dentate, sometimes tinged violet, the teeth $0.25-3 \times 0.25-2$ mm, the large teeth separated by 3-5 mm with 1-3 small teeth between; adaxial surface green, glabrous; abaxial surface lighter green with tan colored veins, glabrous; venation camptodromous, the secondary veins sometimes terminating in marginal teeth, the primary and secondary veins prominent, raised, the tertiary veins visible. *Flowers* 44–47 mm, solitary; pedicels 40-55 mm at anthesis, 70-85 mm in fruit, green, glabrous, nitid; hypanthium $8-9 \times 8-9$ mm, broadly obconical, green to violet, glabrous, the ridges smooth; calyx lobes $11-18 \times 3-5$ mm, ligulate, green suffused violet, especially on the margin, glabrous, the margin callose-serrulate, the apex acute, ascending at anthesis;

corolla pale green tinged violet, glabrous; corolla tube 6–7 mm wide basally, narrowing to 3–4 mm; corolla lobes ligulate, the margins undulate, the two dorsal lobes $14-15 \times 2-3$ mm, opening dorsally 16–17 mm from the corolla base, falcate, the two lateral lobes 8–9 \times 4 mm, opening ventrally ca. 11 mm from the corolla base, falcate; androecium 35–37 mm, exserted 24–26 mm from the ventral opening, the filament tube green to tinged violet dorsally, glabrous, the anther tube green with violet along the sutures, glabrous, all the anther tips sparsely villose; the style and stigma cream colored, the stigma lobes shortly pubescent along the margin. *Fruits* 25 \times 15 mm, globose, inflated, pale green with maroon-violet blotches.

Phenology. This species has been collected with flowers and fruits in February, August, September, and December.

Distribution. This species is found in a narrow distribution in Napo Province of Ecuador on the east side of the Andes. It occurs in wet cloud forests at 2800 to 3100 m in elevation.

Discussion. B. oyacachensis is part of the inflated fruit clade of *Burmeistera*, and is thus closely related to *B. borjensis*, with which it shares a similar flower morphology. However, *B. oyacachensis* is differentiated by having bilobate leaf margins and non-overlapping calyx lobes, compared to the serrate leaf margins and overlapping calyx lobes of *B. borjensis* *Additional specimens examined.* ECUADOR. **Napo:** Oyacachi, sendero que conduce a el Chaco, 3096 m, 00°10'S 78°07'W, 05 Sep. 1998, *Moreno 111* (QCA); Reserva Ecológica Cayambe-Coca, road from Oyacachi to El Chaco, 2995 m, 00°13.099'S 78°02.631'W, 17 Aug. 2002, *Muchhala 171* (QCA); Río Oyacachi, Sector Nono, path between Oayacachi and El Chaco, near the abandoned village, Huasipamba, 2800 m, 00°13'S 78°02'W, 23 Dec. 1996, *Clark et al. 3591* (MO).

39. Burmeistera pacifica Mashburn, sp. nov. TYPE: Ecuador. Manabí: Montecristi,
Cerro Montecristi, carretera Manta-Jipijapa, entrada por Montecristi o El Chorrillo, 300–
600 m, 01°02'S 80°41'W, 11–12 Nov. 1995 (fl., fr.), *T. Núñez, S. Sandoval & J.*Machuca 340 (holotype, MO-5343243!).

Terrestrial herbaceous shrubs, 1.5 m. *Latex* unknown. *Stems* ca. 4 mm wide, yellow-green, glabrous. *Leaves* alternate, spiral, the internodes 5–40 mm; petioles 20–50 mm, green, sometimes tinged violet, glabrous; lamina $60-170 \times 25-75$ mm, elliptic, the base cuneate, the apex acute to attenuate, the margin shallow callose-serrate, sometimes nearly entire; adaxial surface green, puberulent along the veins; abaxial surface lighter green, glabrous; venation camptodromous, the primary vein prominent, raised, the secondary veins slightly raised, the tertiary veins visible. *Flowers* 47–50 mm, solitary in the upper leaf axils; pedicels 55–95 mm, glabrous, yellow-green, rarely tinged violet; hypanthium 6–8 × 4–7 mm, cupuliform to urceolate, yellow-green, glabrous, the ridges smooth; calyx lobes 4–10 × 1.5–3 mm, ligulate, ascending to patent at anthesis, green, glabrous, the margin shallow callose-dentate, the apex acute; corolla green, glabrous;

corolla tube 3–6 mm wide basally, the throat narrowing to 2–3 mm; corolla lobes ligulate, the margins smooth, the two dorsal lobes $16-20 \times 3-4$ mm, opening dorsally ca. 20 mm from the corolla base, falcate, the two lateral lobes $9-10 \times 3-4$ mm, falcate, the ventral lobe ca. 9×3 mm, opening ventrally 15–17 mm from the corolla base; androecium 38–43 mm, exserted 24–26 mm from the ventral opening, the filament tube green, glabrous to sparsely villose with white hairs, the anther tube green, glabrous, all five anther tips glabrous to sparsely pubescent; the style and stigma cream-colored, glabrous. *Fruits* ca. 15×15 mm, globose, fleshy, not inflated, red.

Etymology. The specific epithet is in reference to the geographic occurrence of this species, along the Pacific coast of Ecuador.

Phenology. This species has been collected with flowers and fruits from September to February.

Distribution. Burmeistera pacifica is found in western Ecuador in Manabí Province in remaining low elevation forests.

Discussion. This species is most similar to *B. domingensis* in leaf margin serration and fruit color and size, but *B. pacifica* has much longer green flowers, vs. the smaller violet flowers of *B. domingensis*. *Burmeistera pacifica* differes from B. brachyandra in the red vs. yellow fruits.

Additional specimens examined. ECUADOR. **Manabí:** Cantón Jipijapa, Parroquia Jipijapa, Cerro Montecristi, 1 km W of the town of Montecristi, 550 m, 01°03'05.2"S 80°39'42.5"W, 29 Jan. 2001, *Clark et al. 6195* (QCA); Cerro Monte Cristi, 550 m, 08 Sep. 1963, *Escuela 330* (MO); Parque Nacional Machalli, San Sebastian, 08 Feb. 1994, *Cornejo 1215* (MO); Machalilla, San Sebastian, 550–700 m, 01°36'S 80°42'W, 22 Nov. 2004, *Muchhala 241* (QCA).

40. Burmeistera pallida (Drake) E. Wimm., Repert. Spec. Nov. Regni Veg. 30: 50. 1932.
Basionym: *Centropogon pallidus* Drake, Journ. Bot. (Morot) 3: 239. 1889. TYPE:
Ecuador. Loja: Saraguro, 24 Jan. 1886 (fr.), *H. Poortmann 333* (holotype, P [barcode]
408896 digital image!).

Burmeistera ramosa E. Wimm., Repert. Spec. Nov. Regni Veg. 30: 16, t. 124, f. 17. 1932. TYPE: Peru. Amazonas: Stromgebiet des Maranon, Santiago-Mündung am Pongo de Manseriche, ca. 77°30'W, 10 Dec. 1924, *G. Tessmann 4725* (holotype, B destroyed, F [photo negative number] 9073 digital image!; isotype, G [barcode] 236668 digital image!, NY [bc] 468004!).

Burmeistera oblongifolia E. Wimm., Brittonia 8: 108. 1955, syn. nov. TYPE: Ecuador. Camp E-4925 (holotype not named; isotypes F-1447922 digital image!, K [barcode] 250838 digital image!, MICH [bc] 1111448 digital image!, NY [bc] 467998!, US [bc] 146948 digital image!). *Burmeistera ramosa* E. Wimm. var. *campii* E. Wimm., Brittonia 8: 108. 1955. TYPE: Ecuador. Morona Santiago: Oriente, Cordillera Cutucú, ca. 02°40'S 78°W, on banks of Río Ontza, 1400 m, *W. H. Camp E-1177* (holotype, MICH [barcode] 1111446 digital image!; isotypes, NY [bc] 468005 digital image!, US [bc] 146953 digital image!).

Herbaceous shrubs to scandent herbs, 2 m. Latex white. Stems ca. 4 mm wide, glabrous to puberulent, velutinous, green to green tinged violet. *Leaves* alternate, spiral; petioles 8–15 mm, glabrous to puberulent, green to green tinged violet; lamina $60-160 \times$ 25–60 mm, elliptic, the base attenuate, the apex attenuate, the margin shallow callosedentate, the teeth on mature leaves rounded and irregular in size, often alternating large (up to 4×3 mm) and short; adaxial surface glabrous, green; abaxial surface puberulent with clear to white hairs, especially on the veins, green to green suffused violet; venation camptodromous, the primary vein prominent, raised, the secondary veins thin, slightly raised, the tertiary veins visible. *Flowers* solitary, 40–44 mm; pedicels 40–60 mm at anthesis, 40–60 mm in fruit, glabrous to puberulent, green; hypanthium $4-6 \times 4-7$ mm, cupuliform, glabrous to sparsely puberulent, green to green tinged violet; calyx lobes 4–9 \times 1–2 mm, ligulate to lanceolate, glabrous to puberulent, green to green suffused with violet, the margin shallow callose-dentate, undulate, the apex acute, slightly ascending to reflexed at anthesis; corolla exterior entirely green to grean lightly suffused with violet, glabrous to puberulent, the interior pale green; corolla tube 6–8 mm wide basally, narrowing to 3–4 mm; corolla lobes ligulate, the two dorsal lobes $17-20 \times 4-5$ mm, opening dorsally at 15–18 mm from the corolla base, the two lateral lobes $10-12 \times 4-5$ mm, the ventral lobe ca. 11×6 mm, opening ventrally at 8–14 mm from the corolla base; androecium 35–38 mm, exserted 24–29 mm from the ventral opening, the filament tube green with pale violet striations, villose distally with white hairs, the anther tube green with violet along the sutures, puberulent with appressed cream to yellow hairs, all five anther tips glabrous to sparsely villose with long white hairs; the style tinged violet, sparsely puberulous, the stigma lobes tan, puberulent, along the margin shortly pubescent. *Fruits* ca. 27×27 mm, globose, inflated, green to green suffused with violet.

Phenology. This species has been collected with flowers and fruits throughout the year.

Distribution. Widely distributed in low to medium elevation forests in southwest Ecuador, in the Provinces of Morona Santiago and Zamora Chinchipe.

Discussion. Similar to *B. draconis* and *B. refracta*, this species is recognizable often by the strongly crenate margin with irregularly sized teeth. However, at the north end of its range these teeth dimish in size and become more sharp, dentate.

In Ecuador this species has been known more commonly as B. ramosa, while in Peru is has been called B. pallida. Looking at the types, these are clearly the same thing. Though both species were described in Burmeister by Wimmer at the same time (1932), the name 'pallida' takes priority because it comes from the older basionym *Centropogon pallidus*.

Additional specimens examined. ECUADOR. **Cañar:** North slope of canyon of Río Paute, across from Campamento Guarumales, trail to Estacion Hydrometrica Quebrada Molino, 1650–1850 m, 02°33'S 78°33'W, 21 May 1985, Stein 2847 (MO, QCA);

Morona Santiago: 6 km E of Limón on road under construction to La Unión, 1300 m, 23 Apr. 1985, Harling & Andersson 24492 (QCA); 8 km E of Limón on road under construction to La Unión, 1300 m, 22 Apr. 1985, Harling & Andersson 24452 (QCA); 9-10 km southeast of San Juan Bosco, 1540–1600 m, 27 Jan. 1981, Gentry et al. 30893 (MO); Along new road Mendez-Morona, km 55–62, 800 m, 23 Aug. 1989, van der Werff & Gudiño 11411 (MO); Between Santa Susana de Chiviaza and Caseríos El Panecillo and Las Orquideas, 6-7 km N of Chiviaza, 1300-1400 m, 03 Mar. 1993, Harling & Ståhl 26916 (QCA); Cordillera de Cutucu, road Mendez-Morona, 800 m, 03 Feb. 1989, van der Werff & Palacios 10367 (MO); Finca de Don Lucho, Domono, on main path in forest, 1160 m, 02°12.9'S 78°07.2'W, 01 May 2010, Muchhala 435 (QCA); From end of road in consruction Limón-La Unión, horse trail to Caserío El Pescado, km 1–3, 1300 m, 28 Feb. 1993, Harling & Ståhl 26782 (MO, QCA); Gualaquiza-Limon, General Plaza, road, ca. 7 km S of Tucumbatza, 1650 m, 03°17'S 78°30'W, 17 May 1985, Stein 2803 (MO, QCA); In the vicinity of Macuma, path Macuma-Río Cusutcaime, ca. 50 km north east of Macas, 27 Mar. 1973, Lugo 3746 (QCA); In the vicinity of Macuma, path Macuma-Río Cusutcaime, ca. 50 km north east of Macas, 29 Mar. 1973, Lugo 3782 (QCA); Limon Indanza, Región de la Cordillera del Cóndor, al oeste del Río Zamora, cerca la población de Santa Susana de Chiviaza, en la loma arriba de la población, 1560 m, 02°55'22"S 78°22'18"W, 24 Feb. 2006, Morales & Reyes 1678 (MO); Limon General Plaza-Cuenca road, ca. 3 km above Plan de Milagro, 1900–2000 m, 03°00'S 78°30'W, 18 May 1985, Stein 2816 (MO, QCA); Morona Canton, Cordillera de Cutucú, vertiente occidental, en la base del la Cordillera, Parroquia Sevilla, Centro Shuar Guadalupe, 1100 m, 02°21'10"S

78°05'12"W, 23–28 Mar. 2009, Kajekai 1591 (MO); Morona, Cordillera del Cutucú, Asociación Shuar Sevilla, Comunidad Angel Ruby, pie de la cordillera, 1064 m, 02°21'41"S 78°02'24"W, 26 Mar. 2002, Suin et al. 1299 (MO); Morona, Cordillera del Cutucú, Centro Shuar Angel Roubi, 2000 m, 02°32'S 78°01'W, 02 Feb. 2002, Toasa & Nicolalde 8788 (MO); Morona, Cordillera del Cutucú, Centro Shuar Angel Roubi, 2000 m, 02°32'S 78°01'W, 02 Feb. 2002, Nicolalde et al. 1064 (MO); Morona, Cordillera del Cutucú, Centro Shuar Uunsuants/Trnaskutuku, 650 m, 02°32'S 77°54'W, 19 Jan. 2002, Palacios et al. 15617 (MO); Near Plan de Milagro on road to Gualaceo, 1800 m, 03°01'S 78°29'W, 15 Jul. 1996, Ståhl & Knudsen 2880 (QCA); Parque Nacional Sangay, Lagunas de Sardinayacu, sendero desde el refugio 1 hacia la laguna Chimerella, 1400–1500 m, 02°05'54"S 78°09'19"W, 17 Jan. 2015, Pérez et al. 7833 (QCA); Parque Nacional Sangay, Lagunas de Sardinayacu, sendero desde el refugio 2 hacia el refugio 3, 1400– 1750 m, 02°05'54"S 78°09'19"W, 19 Jan. 2015, Pérez et al. 7916 (QCA); Plan de Milagro, intersection of Cuenca-Limon-Gaulaquiza roads, ca. 5 km S of intersection on road to Indaza, 1650 m, 03°00'S 78°30'W, 17 May 1985, Stein 2809 (MO, QCA); Región de la Cordillera del Condór, Centro Shuar Chimius, 330–500 m, 03°06'25"S 78°03'13"W, 04 May 2006, Wisum & Kajekai 491 (MO); Río Macuma near Cerro Macuma, 16 Dec. 1976, McElroy 30 (QCA); Road from Indanza to Limon, General Plaza, ca. 4 km below, N, Plan de Milagro toward Limon, 1450 m, 03°00'S 78°25'W, 18 May 1985, Stein 2821 (QCA); Road from Limon, General Plaza, to Cuenca, 2800 m, 03°00'S 78°30–40'W, 19 May 1985, Stein 2838 (MO); Road from Plan del Milagro to 10-15 km past San Juan Bosco, 1590 m, 03°0-10'S 78°50'W, 01 Jun. 1989, Smith 2089 (QCA); Road Limón, General Plaza, to Macas, ca. km 25 from Limón, 700 m, 28 Mar.
1974, Harling & Andersson 12922 (MO, NY); Shuinia Nait, small mountain ridge ca. 8 km SE of Misión Bomboiza, 900-1000 m, 03°30'S 78°33'W, 24 Apr. 1973, Holm-Nielsen 4400 (NY, QCA); Tambo Chontal to Tambo Consuelo, eastern slope of the cordillera, valley of the rios Negro and Chupianza, on the trail from Sevilla de Oro to Mendez, 1737–2439 m, 16 Dec. 1944, *Camp E-1587* (NY); Tiwintza, Región de la Cordillera de Cutucú, al norte del Río Santiago, Centro Shuar Yapapas, Cerro Kinku Naint, sector Napintsa, 580 m, 02°59'53"S 78°09'32"W, 05 Nov. 2005, Morales et al. 1486 (MO); Tumbes, 17–18 km N of Gualaquiza on road to Indanza, 1700–1800 m, 17 Apr. 1985, Harling & Andersson 24229 (MO, QCA). Zamora Chinchipe: 10 km E of Paquisha, 1400-1500 m, 13 Apr. 1985, Harling & Andersson 24104 (NY, QCA); Along road to Romerillao Alto from Zamora, 19.1 km E of Río Bombuscaro in Zamora, 6.3 km E of La Pituca, 1203 m, 04°10'04"S 78°56'10"W, 20 Jul. 2004, Croat 91560 (MO); El Pangui, Cordillera del Cóndor, cresta de la Cordillera, en la frontera Ecuador-Perú, 1 km al sur del destacemento military Cóndor Mirador, 2000 m, 03°38'32"S 78°23'36"W, 15 Dec. 2000, Montenegro et al. 173 (MO); Entrance of the Quimi Valley, ca. 1 km from mining camp, 950 m, 03°31'41"S 78°25'33"W, 02 Nov. 2004, van der Werff et al. 19185 (MO); Palanada, Región de la Cordillera del Cóndor, sector sur, Parroquia San Francisco de Vergel, Playones, Cuenca alta del Río Vergel, 1900 m, 04°43'01"S 78°57'47"W, 10 Mar. 2005, Quizhpe et al. 914 (MO); Parque Nacional Podocarpus, entrada por el sector del Río Bombuscaro, 1000–1100 m, 27 Mar. 2015, Zapata et al. 321 (QCA); Parque Nacional Podocarpus, entrada por el sector del Río Bombuscaro, 900–1000 m, 04°06'53.5"S 78°57'58.9"W, 30 Mar. 2015, Pérez 8500 (QCA); Pichicutza, sendero hacia el Hito, 1000-1200 m, 18 Oct. 1991, Jaramillo 14057 (QCA); Valley of Río

Waiwaime, near mouth at Río Quime, 1000 m, 03°33'40"S 78°27'47"W, 22 Sep. 2007, *Croat & Ferry 99010 & 99029* (MO); Yantzaza, Cordillera del Cóndor, carretera desde Los Encuentros hacia el Cerro Machinaza, sendero a Las Peñas, 1400 m, 03°43'15"S 78°29'48"W, 20 Jul. 2005, *Quizhpe 1632* (MO).

41. *Burmeistera pterifolia* A. F. Vallejo, Á. J. Pérez & Muchhala, Phytotaxa 362(3): 264, fig. 1. 2018. TYPE: Ecuador. Pichincha: Cantón Quito, Parroquia Nanegal, Santa Lucia Cloud Forest Reserve, on 'Loop Trail,' near where it joins the principal trail, 00°07'06.5"N, 78°36'30.5"W, ca. 2000 m, 05 Jun. 2016 (fl., fr.), *A. F. Vallejo 1* (holotype, QCA [bc] 236942!; isotype, MO!).

Terrestrial herbaceous shrubs, ca. 1 m. *Latex* white. *Stems* 4 mm wide, pale green, hispidulous. *Leaves* alternate, distichous, chartaceous; petioles 5–11 mm, green, hispidulous; lamina 55–130 × 15–35 mm, lanceolate, the base rounded to truncate, the apex acute, the margin pinnatilobate; adaxial surface green, glabrous; adaxial surface green, glabrous; abaxial surface tinged violet, the veins light green, hispidulous; venation brochidodromous, the primary and secondary veins prominent, raised, the tertiary veins visible. *Flowers* 34–41 mm, solitary in the upper leaf axils; pedicels 25–65 mm, hispidulous, green to green tinged maroon-violet; hypanthium 5.8–6.1 × 3.8–4.7 mm, cupuliform, green to green tinged maroon-violet, hispidulous, the ridges smooth; calyx lobes $13-15 \times 2-2.5$ mm, ligulate, ascending to patent to slightly reflexed at anthesis, green, hispidulous, the margin shallow callose-dentate, lightly tinged maroon-violet, the apex acute; corolla green to green suffused with red-violet, hispidulous; corolla tube ca.

6.5 mm wide basally, bulging just above the base, the throat narrowing to 2–3 mm; corolla lobes ligulate, the margins smooth, the two dorsal lobes $11-15 \times 2-3$ mm, opening dorsally ca. 20 mm from the corolla base, falcate, the two lateral lobes $9-10 \times 2-3$ mm, falcate, the ventral lobe ca. 9×3 mm, opening ventrally 6.5–8 mm from the corolla base; androecium 28–35 mm, exserted ca. 17 mm from the ventral opening, the filament tube pale green, villose with white hairs, the anther tube ca. 7×3 mm green along the sutures, violet between the sutures, glabrous, all five anther tips pubescent; the style and stigma pale green. *Fruits* ca. 30×25 mm, globose to ovoid, inflated with 2 mm thick fleshy walls, maturing pale green to white.

Phenology. Flowers and fruits are observed throughout the year, but are more abundant from June to July.

Distribution. This species is endemic to the foothills of the Andes in northwestern Ecuador. It is only known from its type locality in Santa Lucia Cloud Forest Reserve in Pichincha Province. It grows in cloud forests between 1870–2000 m in elevation.

Discussion. In Ecuador, *B. pterifolia* is most similar to *B. truncata*, *B. rubrosepala*, and *B. auriculata* in their truncate leaves. However, none of these other species have the unique pinnatilobate margin of *B. pterifolia*.

Additional specimens examined. ECUADOR. Pichincha: Cantón Quito, Parroquia Nanegal, Santa Lucia Cloud Forest Reserve, on 'Loop trail' near where it joins the principal trail, 2000 m, 00°07'06.5"N 78°36'30.5"W, 21 Jul. 2014, *Muchhala 522 & 523* (QCA).

42. Burmeistera racemiflora Lammers, Brittonia 50(2): 258, fig. 8. 1998. TYPE:
Ecuador. Carchi: Tulcan Canton, Chical, Reserva Étnica Awá-Camumbi, 00°53'N,
78°16'W, 1700–1900 m, 00°53'N 78°16'W, 20–29 Jul. 1991, *C. Quelal, C. Aulestia & F. Nastacuáz 218* (holotype, F-2165235 digital image!; isotypes, AAU digital image!, MO4899115!, NY [barcode] 328788!, QCNE [bc] 132 digital image!).

Terrestrial herbaceous shrubs, 4 m. *Latex* white. *Stems* ca. 7 mm wide, green to tan colored, puberulous with appressed tan colored trichomes, with defined sterile and fertile zones, the latter with progressively reducing leaves (bracts) and shorter internodes. *Leaves* alternate, spiral, the internodes 25–40 mm; petioles 5–10 mm, green, puberulous; lamina 140–250 × 70–100 mm, obovate, the base attenuate, the apex acuminate, the margin shallow callose-serrate, basally nearly entire, the teeth sometimes irregular in size, slightly increasing in size toward the apex; adaxial surface green, glabrous; abaxial surface green, puberulous with appressed tan colored trichomes, especially along the veins; venation camptrodromous, the primary and secondary veins prominent, raised but flat, the tertiary veins visible. *Flowers* 40–42 mm, occurring only in a defined fertile zone, appearing racemose, the bracts progressively reducing to ca. 25 × 4 mm, caducous or persistent, the internodes 5–15 mm; pedicels ca. 45 mm at anthesis, 65–75 mm in fruit, green to tan colored, puberulous; hypanthium 5–7 × 5–6 mm, cupuliform, green, puberulous, the ridges smooth; calyx lobes 10–15 × 2–5 mm, lanceolate, green,

puberulous, the margin shallow callose-dentate, the apex obtuse, ascending at anthesis; corolla green, glabrous to very sparsely puberulous; corolla tube ca. 6 mm wide basally, narrowing to ca. 4 mm; corolla lobes ligulate, the margins smooth, the two dorsal lobes ca. 16×5 mm, opening dorsally 21–22 mm from the corolla base, falcate, the two lateral lobes ca. 9×5 mm, opening ventrally 17–19 mm from the corolla base, falcate; androecium 35–37 mm, exserted 17–19 mm from the ventral opening, the filament tube green, glabrous, the anther tube green, puberulent with appressed cream colored hairs, the top three anther tips glabrous, the bottome three anther tips densely pubescent with white hairs; the style and stigma dark colored, glabrous. *Fruits* ca. 10×13 mm, globose, fleshy.

Phenology. Flowers and fruits have been collected in July and November.

Distribution. This species is endemic to Ecuador and is only known from Carchi Province at elevations of 800 to 1900 m.

Discussion. Burmeistera racemiflora is similar to other *Burmeistera* species with significantly reduced bracts, such as *B. anderssonii*, *B. multiflora*, and *B. brachyandra*. However, *B. racemiflora* is differentiated by its larger flowers and longer calyx lobes.

Additional specimens examined. ECUADOR. Carchi: El Pailon, ca. 45 km below Maldonado along a foot path to Tobar Donoso, 800 m, 29 Nov. 1979, *Madison & Besse* 7145 (AAU digital image). **43.** *Burmeistera refracta* E. Wimm., Repert. Spec. Nov. Regni Veg. 30: 11, tab. 124, fig. 19. 1932. TYPE: Ecuador. In Andibus Ecuadorensibus, 1857–59 (fl., fr.), *R. Spruce 5376* (holotype, W-1889-0132993 digital image!; isotypes, BM [barcode] 778658 digital image!, G [bc] 236666, G [bc] 236667 digital image!, K [bc] 250834 digital image!, K [bc] 250835 digital image!, W-1889-0004940 digital image!).

Herbaceous shrubs to scandent herbs, 3 m. *Latex* white. *Stems* ca. 4 mm wide, green suffused with violet, puberulent with clear to white hairs, especially on new growth, velutinous. *Leaves* alternate, spiral; petioles 10–20 mm, green tinged violet, puberulent; lamina $65-150 \times 25-55$ mm, elliptic, the base attenuate, the apex attenuate, the margin shallow callose-dentate to crenate, the teeth often intramarginal; adaxial surface green, glabrous, nitid; abaxial surface green suffused with violet, puberulent, the veins often darker violet; venation camptodromous, the primary vein prominent, raised, the secondary veins slightly raised, the tertiary veins barely visible??. Flowers 37–44 mm; pedicels 50–75 mm at anthesis, 50–75 mm in fruit, puberulent, green, sometimes tinged violet; hypanthium $4-5 \times 4-5$ mm, cupuliform, sometimes narrowly so, green, puberulent, the ridges smooth; calvx lobes $7-13 \times 2-3$ mm, ligulate, green suffused with violet, puberulent, the margin shallow callose-serrate, the apex obtuse, patent to reflexed at anthesis; corolla entirely pale green to green suffused with maroon-violet, especially dorsally, puberulent; corolla tube 4–6 mm wide basally, narrowing to 2–4 mm; corolla lobes lanceolate, the margins smooth, the two dorsal lobes $15-17 \times 4-5$ mm, opening dorsally 16–20 mm from the corolla base, falcate, the two lateral lobes $8-10 \times 3-5$ mm, falcate, the ventral lobe $8-9 \times 4-5$ mm opening ventrally 9-15 mm from the corolla base; androecium 33–40 mm, exserted 22–27 mm from the ventral opening, the filament tube tan to pale green, sparsely to densely villose distally with white hairs, the anther tube pale green to tan between the sutures, glabrous to puberulent basally with appressed white to yellow hairs, all five anther tips glabrous to sparsely pubescent with white hairs; the style tan, glabrous, the stigma tan, glabrous. *Fruits* ca. 30×30 mm, globose, inflated, green, sometimes tinged maroon-violet.

Phenology. This species has been collected with flowers and fruits throughout the year.

Distribution. This is a common species in mid- to high-elevation forests in Pastaza Province.

Discussion. Burmeistera refracta is placed in the inflated fruit clade of *Burmeistera*. It is both closely related to and geographically close to *B. glabrata*, from which it is differentiated by having calyx lobes that are reflexed at anthesis, versus ascending in *B. glabrata*.

Additional specimens examined. ECUADOR. **Tungurahua:** Baños-Mera road, ca. 30 km from Mera, 1200 m, 01°25'S 78°15'W, 27 Mar. 1983, *Lawesson 43301* (QCA); Bosque Protector de Machay, trail to the Machay waterfalls, 1524 m, 01°23.869'S 78°16.967'W, 27 Jun. 2002, *Muchhala 110* (QCA); Bosque Protector de Machay, trail to the Machay waterfalls, 1598 m, 01°23.796'S 78°16.969'W, 27 Jun. 2002, *Muchhala 112* (QCA); Chashaurco, 18 Mar. 1969, *Lugo 806* (NY, QCA); Colleciones a lo largo de la vía Río

Negro-La Estancia, 4.8 km, y sendero al Río Encanto 500 m, 1600–1800 m, 01°27'04"S 78°13'37"W, 25 Feb. 2012, Pérez & Vallejo 5243 (QCA); Quebreda Estansia, a small tributary of Rio Pastaza, below Baños, 2 km above confluence of Río Tojo, 1220 m, 09 Jan. 1945, Fosberg 22479 (NY); Rio Negro, at the bridge at the W entrance to the village, 1200 m, 17 Jul. 1967, Sparre 17660 (NY, QCA); Roadside between Ambato and Baños, 10 Jan. 1981, D'Arcy 14004 & 14006 (NY); Trail 2 km E of Río Topo, ca. 31 km E of Baños on road to Puyo, 1250-1450 m, 01°25'S 78°10'W, Stein 2978 (MO, QCA); Trail to waterfall at confluence of Río Verde and Río Pastaza, ca. 14 km E of Baños, 1500 m, 01°22'S 78°17'W, 01 Jul. 1985, Stein & Tucker 3099 (MO); Vía Baños-Puyo, colecciones a lo largo de la quebrada y cauce del Río Verde, 1593 m, 07 Mar. 2006, Pérez & Moscoso 2692 (QCA). Morona Santiago: Arapicos, 800-900 m, 01 Apr. 1981, Lugo 5908 (MO, NY); Parroquia Cumandá, 24 Apr. 1969, Lugo 1179 (MO). Pastaza: 1-4 km N of Puyopungu, 24 Sep. 1976, Lugo 4992 (MO, NY); 1–5 km N of Mera, 1100– 1200 m, 07 Mar. 1980, Harling & Andersson 17030 (NY); 5 km al NE de Mera, carretera al Rio Ansu, 1200 m, 01°26'S 78°06'W, 02 Mar. 1985, Neill et al. 5912 (MO, NY, QCA); 9.4 km E of Topo, 1300 m, 21 Jan. 1971, MacBryde 149 (MO, QCA); About 4 km NW of Canelos, 650 m, 01°33'S 77°45'W, 08 Mar. 1997, *Ståhl et al. 4363* (QCA); About 5 km east of town Río Negro, 1350 m, 17 Jan. 1973, Humbles 6119 (NY); Along road between Puyo and Baños, 2.7 km W of Mera, 4.6 km W of Shell, 1110 m, 01°27'S 78°50'W, 05 May 1984, Croat 59086 (MO, QCA); Along road between Puyo and Baños, 3 km W of Mera, 1160 m, 23 Dec. 1979, Croat 49720 (MO); Along road between Puyo and Baños, 4 km W of Mera, 24 Dec. 1979, Croat 49729 (MO); Along road between Puyo and Baños, 11.9 km W of Shell, 3.9 km W of Mera, 1100 m, 01°27'S 78°50'W, 05

May 1984, Croat 59095 (MO, QCA); Baños Puyo road, 7.6 km E of Río Negro, 1340 m, 01°30'S 78°10'W, 01 May 1992, Luteyn & Friere-Fierro 14572 (NY, QCA); Between Mera and Río Negro, 27 km from Puyo on the road to Baños, 1 km N of the road, 1300– 1400 m, 01°25'S 78°11'W, 14 Jan. 1988, Molau et al. 2476 (MO, NY, QCA); Canelos, 06 Nov. 1974, Lugo 4486 (MO); Canton Mera, 1400 m, 01°27'54"S 78°07'58"W, 15 Feb. 1996, Jaramillo 18831 & 18755 (QCA); Canton Mera, Parroquia Shell, road to Río Anzu and beyond, south of the town Mera, trail heading north from road, 1350–1450 m, 01°23'15"S 78°03'12"W, 06 May 2003, Clark et al. 7760, 7791 & 7796 (QCA); Carretera Baños-Shell Mera, 10 km antes de Shell Mera, cerca del Rio Magayacu, 1123 m, 01°27'S 78°07'W, 28 Jun. 1992, Friere-Fierro 2225 (QCA); Colonia 24 de Mayo, ca. 18-20 km from Puyo, 13 Sep. 1968, Lugo 414 (MO); Colonia Játiva, 10-12 km from Mera, 04 Jul. 1968, Lugo 94 (MO); Colonia Játiva, ca. 7 km N of Mera, 1200–1300 m, 05 Mar. 1980, Harling & Andersson 16931 (NY, QCA); Mera, 16 Apr. 1940, Lugo 202 (MO); Mera, 10 Apr. 1955, Asplund 18295 (MO); Mera, road and muletracks to approx.. 4 km N of the village along Río San Jorge and Río Tigre, 1200 m, 01°35'S 77°53'W, 01– 02 Sep. 1976, Øllgaard & Balslev 9129 (NY); Mera Canton, Along road between Puyo and Baños, along creek ca. 5 km W of Mera, 1100 m, 01°26'S 78°08'W, 07 Mar. 1992, Croat 72840 (MO); Mera-Río Anzu road, ca. 5.4–10 km along road, 1400–1450 m, 01°23'S 78°07'W, 06 Oct. 1992, Luteyn & Sylva 14675 (NY, QCA); Near Puyo, 17 Feb. 1953, Prescott 869 (NY); On the bank of Río Pastaza, in the vicinity of Puyopungu, 01 Oct. 1976, Lugo 5086 (NY); Parayacu, ca. 10 km east of Canelos, 08 Nov. 1974, Lugo 4549 (MO, QCA); Pindo, ca. 3.5 km N on Río Pindo road, 1100 m, 01°25'S 78°05'W, 07 Jun. 1985, Stein 3007 (MO, QCA); Pindo, ca. 6 km east of Mera, 15 Jun. 1972, Lugo

2403 (MO, QCA) & 2414 (NY); Puyo-Puerto Napo Road, San José ca. 17 km NE of
Puyo, 800 m, 10 Mar. 1980, *Harling & Andersson 17140* (NY); Río Pastaza, a 20 km del
Puyo en la vía Puyo-Baños, 1100 m, Jul.–Aug. 1996, *Blanc et al. 96-818* (QCA); Road
Puyo-Puerto Napo, ca. 12 km north of Puyo, 03 Dec. 1974, *Lugo 4726* (NY); Shell-Mera, 1000 m, 01°30'S 78°03'W, 21 Mar. 1985, *Neill 6175* (MO, NY); Trail towards Coloniá
24 de Mayo, 2.5 km W on road departing main Puyo-Tena road at km 9, 1050 m, 01°25'S 77°58'W, 03 Jul. 1985, *Stein & Tucker 3120* (MO); Trail up quebrada 3.5 km W of Mera on road to Baños, 1200 m, 01°27'S 78°09'W, 04 Jun. 1985, *Stein 2985* (MO, QCA); Vía Puyo-Fátima, 900 m, Jan. 1995, *Palacios 13468* (MO); Westlich Mera, 1400 m, 02 Feb. 1934, *Schimpff 695* (MO).

44. Burmeistera resupinata Zahlbr., Repert. Spec. Nov. Regni Veg. 13: 530. 1915.
TYPE: Ecuador. Pichincha: In silvis prope Guanaxa, 1000 m, Jun. 1883 (fr.), *L. Sodiro* 91/20 (holotype, B, destroyed; isotype, P [barcode] 408897 digital image!).

Scandent herbs, 4 m. *Latex* unknown. *Stems* ca. 4 mm wide, terete, green tinged violet, glabrous, nitid. *Leaves* alternate, distichous; petioles 4–12 mm, green tinged violet, glabrous, slender; lamina 70–90 × 10–25 mm, lanceolate, the base obtuse, the apex acuminate to caudate, $15-30 \times 1-2$ mm, the margin shallow callose-serrate to crenate, the teeth often intramarginal; adaxial and abaxial surfaces green, lighter green along the primary vein, glabrous; venation pinnate with secondary veins terminating in a thin submarginal collecting vein 0.5 mm from the margin, the primary vein prominent raised, the secondary veins thin, the tertiary veins barely visible. *Flowers* ca. 69 mm, solitary;

pedicels 40–43 mm at anthesis, 40–43 mm in fruit, glabrous, green; hypanthium 8–10 × 5–8 mm, obconical, green, glabrous to sparsely puberulent, the ridges smooth; calyx lobes $2-5 \times 1$ mm, ligulate, green tinged violet, glabrous, the margin entire, the apex acute, ascending at anthesis; corolla green with violet tinged margins, glabrous to sparsely puberulent; corolla tube ca. 7 mm wide basally, narrowing to ca. 3 mm; corolla lobes ligulate, the margins smooth, the two dorsal lobes ca. 28×3 mm, opening dorsally ca. 32 mm from the corolla base, arcuate, the two lateral lobes ca. 18×3 mm, opening ventrally ca. 23 mm from the corolla base, arcuate; androecium ca. 58 mm, exserted ca. 36 mm from the ventral opening, the filament tube green tinged violet, glabrous, the anther tube green with violet along the sutures, glabrous, the top three anther tips glabrous to sparsely pubescent, the bottom two anther tips villose with white hairs; the style and stigma green, the stigma lobes densely pubescent along the margin with short white hairs. *Fruits* 25 × 15 mm, globose, bright pink.

Phenology. Flowers and fruits have been collected April to July.

Distribution. This species is narrowly distributed in Pichincha Province of Ecuador, in forests at elevations from 1000 to 2500 m.

Discussion. This species is most similar to *B. heilbornii*, which which is shares many floral traits. However, *B. heilbornii* is differentiated by having narrowly lanceolate leaves, versus the broadly ovate leaves of *B. heilbornii*.

Additional specimens examined. ECUADOR. **Pichincha:** Cantó Quito, Parroquia Nono, El Pahuma Orchid Reserve, 17 km E of Nanegalito, trail from La Guarida del Oso to Sendero de Los Yumbos, 2200–2650, 00°00'S 78°38'W, 10 Apr. 2003, *Clark 7666* (QCA); Reserva Orquideológica El Pahuma, Parroquia Nono, carretero Calacalí-Nanegalito, km 30, sendero hacia Río Alambí, 2460 m, 00°01'N 78°37'W, 19 Dec. 1996, *Friere et al. 1339* (MO); Reserva Pahuma, the Los Llumbos trail, 2300 m, 00°01'N 78°38'W, 14 Jul. 2004, *Muchhala 223* (QCA); Reserva Pahuma, the Oso trail, before Los Llumbos trail, 2300 m, 00°01'N 78°38'W, 12 Jul. 2003, *Muchhala 219* (QCA); Valley of Rio Pilatón, Garretas, 2500 m, 04 Nov. 1939, *Asplund 9691* (MO, NY, QCA).

45. Burmeistera rubrosepala (E. Wimm) E. Wimm., Repert. Spec. Nov. Regni Veg. 30:
10, t. 123. 1932. Basionym: *Centropogon rubrosepalus* E. Wimm., Repert. Spec. Nov.
Regni Veg. 19: 252. 1924. TYPE: Ecuador. Pichincha: Quito, s.d. (fl.), *H. Karsten s.n.*(holotype, W-0046703 digital image!).

Scandent herbs, 3 m. *Latex* unknown. *Stems* ca. 5 mm, green to violet, glabrous. *Leaves* alternate, distichous, the internodes 35–50 mm; petioles 10–20 mm, green to violet, glabrous; lamina $85-100 \times 30-45$ mm, broadly lanceolate, the base rounded, the apex attenuate, the margin callose-dentate to crenate, repand, the teeth irregular in size, blunt; adaxial surface dark green, glabrous; abaxial surface lighter green tinged violet, glabrous; venation camptodromous, the primary vein prominent, raised, the secondary and tertiary veins visible. *Flowers* 34–36 mm, solitary in the upper leaf axils, only 1–3 per stem; pedicels 80–85 mm at anthesis, green tinged violet, glabrous; hypanthium 5–6

× 5–6 mm, cupuliform, green, glabrous; calyx lobes 7–8 × 3–5 mm, strongly reflexed in bud and at anthesis, covering the hypanthium, lanceolate, green suffused with red-violet, glabrous, the margin callose-serrate, the apex acute; corolla red-violet with yellow tips; corolla tube 6–7 mm wide basally, bulging just above the base, the throat narrowing to 4– 5 mm; corolla lobes comparatively short, deltate, the two dorsal lobes 9–10 × 4–5 mm, falcate, opening dorsally 13–14 mm from the corolla base, the two lateral lobes 2–3 × 2– 3 mm, falcate, the ventral lobe 1–2 × 2–3 mm, opening ventrally 6–7 mm from the corolla base; androecium 28–30 mm, exserted 21–22 mm from the ventral opening, the filament tube lightly tinged violet, puberulent distally, the anther tube 4–5 × 3–4 mm, maroon-violet, glabrous, all five anther tips sparsely villose; the style and stigma creamcolored, the stigma lobes fringed with short white hairs along the margin. *Fruits* globose, inflated, green tinged with red.

Phenology. This species has been collected with flowers in July.

Distribution. This species is found in cloud forests northwest of Quito, in Pichinca Province of Ecuador. Specimens have been collected at elevations around 2300 m.

Discussion. This species is closely related to *B. truncata* and *B. auriculata*, sharing the lanceolate leaf shape with a crenate margin. *Burmeistera rubrosepala* is differentiated from *B. truncata* by its more irregularly shaped marginal teeth and its strongly reflexed dark red calyx lobes (vs. ascending in *B. truncata*). *Burmeistera rubrosepala* differentiated from *B. auriculata* by its thinner calyx lobes and shorter flowers.

Despite occurring in an a well collected area of Ecuador, it is interesting that relatively few collections of *B. rubrosepala* are represented in major herbaria. This species occurs just to the north of its two closest relatives, *B. truncata* and *B. auriculata* and is sister to these two species. *Burmeistera truncata* occurs ca. 35 km to the southeast of *B. rubrosepala*, while *B. auriculata* occurs ca. 25 km southeast of *B. truncata*. Despite their close geographic and phylogenetic relationships, each species is recognizable by its unique calyx lobe traits. Interestingly, these three species are sister to *B. quercifolia*, which is only known from Costa Rica.

Additional specimens examined. ECUADOR. **Pichincha:** Pahuma, the Los Llumbos trail, 2300 m, 00°01'N 78°38'W, 15 Jul. 2004, *Muchhala 221* (QCA, digital image) & *Muchhala 222* (QCA, MO); Quito, s.d., *Jameson 536* (W, digital image).

46. Burmeistera sierrazulensis Muchhala & Mashburn, sp. nov. TYPE: Ecuador. Napo:
Private property of William Philips, ca. 2 hr walk from end of road, W of Cosanga, N slopes of Cordillera de Huacamayos, 2300 m, 00°45'S 77°55'W, 12 Dec. 1989 (fl., fr.), J.
L. Luteyn & S. Cobo 13464 (holotype, NY [barcode] 1185857!; isotype, QCA [bc] 26736!).

Scandent herbs, 1 m. *Latex* unknown. *Stems* 5 mm wide, thick-walled, green to tinged violet, puberulent, striate when dry. *Leaves* alternate, spiral; petioles 15–20 mm, slender, green to tinged violet, puberulent; lamina $35-70 \times 15-25$ mm, elliptic, the base cuneate to obtuse, the apex attenuate, the margin shallow callose-serrate, sometimes

tinged maroon-violet; adaxial surface green, glabrous to sparsely puberulent, nitid; abaxial surface green, puberulent along the veins with short white to cream colored hairs; venation camptodromous, diminishing along the margin or terminating in marginal teeth, the primary and secondary veins prominent, raised, the tertiary veins visible. Flowers 42-43 mm, solitary, but often with many flower buds bunched apically; pedicels 40–65 mm at anthesis, 65–85 mm in fruit, puberulent, green to tinged violet; hypanthium $6-7 \times 4-5$ mm, obconical, patent at anthesis, green to tinged violet, puberulent; calvx lobes $2-3 \times 1$ mm, deltate, green, puberulent, the margin shallow callose-dentate, the apex acute, the margin and apex violet; corolla pale green, sometimes lightly tinged violet, especially on the margins, puberulent, ascending to patent at anthesis; corolla tube 5–6 mm wide basally, narrowing to 2–3 mm; corolla lobes ligulate, the margins smooth, the two dorsal lobes $11-13 \times 2-3$ mm, opening dorsally 15-16 mm from the corolla base, arcuate, the two lateral lobes $7-8 \times 2-3$ mm, opening ventrally 9-10 mm from the corolla base, arcuate; androecium 31–36 mm, exserted 23–27 mm from the ventral opening, the filament tube green, basally sparsely puberulous with appressed white hairs, distally becoming villose, the anther tube green, tinged violet along the sutures, with very short white and yellow appressed hairs, all the anther sparsely villose with white hairs; the style green, sparsely villose, the stigma green, puberulent. Fruits 45 × 45 mm, inflated, globose, green suffused with maroon-violet.

Etymology. The species is names after its known area of occurrence, in the SierrAzul Nature Reserve in Napo Province.

Phenology. This species has been collected with flowers and fruits in December, March and May.

Distribution. This species is known only from its type location in Napo Province, Ecuador. It occurs in cloud forests at elevations from 2000 to 2300 m.

Discussion. Burmeistera sierrazulensis is part of the inflated fruit clade of *Burmeistera*, and is thus closely related to *B. glabrata*, *B. oayacachensis*, *B. ignimontis*, and *B. borjensis*. However, it is easily differentiated by its uniformly green flowers with violet only along the margins, and the small, deltate calyx lobes.

Additional specimens examined. ECUADOR. **Napo:** Private property of William Philips, ca. 2 hr walk from end of road, W of Cosanga, N slopes of Cordillera de Huacamayos, 2300 m, 00°45'S 77°55'W, 12 Dec. 1989, *Luteyn & Cobo 13465* (NY, QCA); Quijos, Sierra Azul, Agrícola Industrial Río Aragón, alrededores del Campamento Estero Chico, 2500 m, 00°41'S 77°56'W, 25 Mar. 1992, *Alvarez et al. 224* (MO); Quijos, Sierra Azul, Agrícola Industrial Río Aragón, Campamento Aragón, 2050 m, 00°38'S 77°54'W, 28 Mar. 1992, *Alvarez & Proaño 258* (MO); Quijos, Sierra Azul, Agrícola Industrial Río Aragón, Campamento San Fernando, 2250 m, 00°41'S 77°55'W, 03 May 1992, *Alvarez et al. 439* (MO).

47. Burmeistera smaragdi Lammers, Novon 12(2): 213–214, fig. 6. 2002. TYPE:
Ecuador. Esmeraldas: Quinindé, Bilsa Biological Station, Montañas de Mache, 35 km W

of Quinindé, 5 km W of Santa Isabel, road between station and the SE Ridge Trail, 400– 600 m, 00°21'N 79°44'W, 19 Sep. 1994 (fl.), *M. S. Bass & N. Pitman 22* (holotype, OSH [barcode] v-0000033 digital image!; isotypes, MO-5187650!; QNCE [bc] 133 digital image!).

Scandent herbs, 1 m. Latex white. Stems ca. 6 mm wide, terete, green to maroonviolet, glabrous to villose, especially around the petioles. *Leaves* alternate, distichous; petioles 3–6 mm, green, villose with white hairs; lamina $75-150 \times 35-45$ mm, elliptic, the base cuneate, the apex attenuate, the margin shallow callose-serrate to crenate, the teeth often intramarginal; adaxial surface green, glabrous; abaxial surface green, villose along the primary vein with appressed white hairs, elsewhere glabrous; venation arcuate, the secondary veins terminating in marginal teeth, the primary vein prominent, raised, the secondary veins thin, the tertiary veins barely visible. *Flowers* 33–37 mm, solitary; pedicels 55–80 mm at anthesis, 80–100 mm in fruit, glabrous, green, sometimes tinged violet distally; hypanthium $6-8 \times 4-6$ mm, obconical, green, sometimes tinged violet, glabrous, the ridges slightly raised; calyx lobes $10-18(-28) \times 1-3$ mm, ligulate, green, glabrous, the margin shallow callose-serrate, the apex acute, ascending at anthesis; corolla light green to maroon-violet, glabrous; corolla tube 4–6 mm wide basally, narrowing to 2–3 mm; corolla lobes lanceolate, the margins smooth, the two dorsal lobes $11-14 \times 2-3$ mm, opening dorsally 15-17 mm from the corolla base, falcate, the two lateral lobes $9-10 \times 3$ mm, opening ventrally 11-12 mm from the corolla base, falcate; androecium 27–29 mm, exserted 16–17 mm from the ventral opening, the filament tube green, glabrous basally, villose distally, the anther tube green, villose basally, otherwise

glabrous or sparsely puberulous, the top three anther tips glabrous to sparsely pubescent, the bottom two anther tips more densely pubescent with white hairs; the style and stigma green, the stigma lobes pubescent along the margin with short white hairs. *Fruits* ca. $15 \times$ 12 mm, globose, fleshy, white.

Phenology. This species flowers and fruits throughout the year.

Distribution. A somewhat common species occurring in low to mid elevation forests in northwest Ecuador and southwest Colombia.

Discussion. Burmeistera smaragdi is closely related to *B. velutina*, *B. cylindrocarpa* and *B. huacamayensis*. It is differentiated from these by its white latex, uniformly green calyx lobes, and glabrous pedicel, hypanthium, calyx lobes, and corolla.

Additional specimens examined. ECUADOR. **Carchi:** Near Lita, 600 m, 19 May 1987, *van der Werff 9481* (MO); N of San Marcos along trail leading to Río San Juan, 660 m, 01°07'N 78°20'W, 18 Jan. 1983, *Barfod 41463* (MO, QCA); Plateau above San Marcos de los Coaiqueres, on trail towards Gualpí Bajo, 1000 m, 01°06'N 78°17'W, 07 Feb. 1985, *Øllgaard et al. 57258* (QCA). **Esmeraldas:** A 5 km de Alto Tambo, 650–690 m, 00°51'N 78°31'W, 11 May 2003, *Pérez 972* (QCA); Along road between Lita and San Lorenzo, 2.4 km N of El Durango, 41.4 km N of Gasolinera San Lorenzo, 424 m, 01°00'36''N 78°36'48''W, 19 Jul. 2000, *Croat et al. 84184* (MO); Along road between Lita and San Lorenzo, vicinity of Alto Tambo, 6.6 km NW of railroad tracks in Alto Tambo, 684 m, 00°57'34"N 78°37'36"W, 22 Feb. 2005, Croat 95182 (MO); Estación Biológica Bilsa, Cordillera de Mache-Chindul, 500-600 m, 00°20'N 79°43'W, 30 Sep. 2006, Pérez et al. 2903 (QCA); Highway from Lita to Alto Tambo, 799 m, 00°54.624'N 78°32.836'W, 18 Jul. 2002, Muchhala 143 (QCA); Km 8, Lita-Altotambo, 740 m, 19 Jul. 1988, Dodson & Gentry 17508 (MO); Quininde, Bilsa Biological Station, Mache Mountains, 35 km W of Quinindé, 5 km W of Santa Isabel, 400–600 m, 00°21'N 79°44'W, 13 Sep. 1994, Clark & Adnepos 27 (MO); Quininde, Bilsa Biological Station, Mache Mountains, 35 km W of Quinindé, 5 km W of Santa Isabel, 400–600 m, 00°21'N 79°44'W, 21 Nov. 1994, Clark & Bergman 302 (MO); Quininde, Bilsa Biological Station, Montañas de Mache, 20 km NW of Quinindé and 3 km W of Santa Isabela, 600 m, 00°22'N 79°45'W, 24 Sep. 1994, Abbott 15243 (MO); Quininde, carretera Herrera-El Páramo (Sta. Isabel), Estación Biológica Bilsa, 850 m, 00°21'36"N 79°42'40"W, 18 Feb.-05 Mar. 1995, Palacios 13614 (MO); Quininde, the Mache-Chindul Ecological Reserve, Bilsa Biological Station, Mache mountains, 35 km W of Quinindé, 5 km W of Santa Isabel, 500 m, 00°21'N 79°44'W, 24 Sep. 1996, Clark 2902 (MO); Reserva Bilsa, on the Red trail, 644 m, 00°20.486'N 79°42.443'W, 08 Apr. 2003, Muchhala 205 (QCA); Road from Lita to El Cristal, 1150 m, 00°50.24'N 78°28.99'W, 19 Jul. 2002, Muchhala 147 (QCA); Road Lita-San Lorenzo, km 34.4, 650 m, 00°52'N 78°31'W, 28 Sep. 1991, Øllgaard 99166 (QCA); Road Lita-Urbina, km 30, 500 m, 00°47'N 78°32'W, 12 Jan. 1991, Øllgaard et al. 98701 (QCA); San Lorenzo Canton, Río Negro, a 2 km de El Placer, 500 m, 00°55'N 78°35'W, 20 Feb. 1991, *Palacios 6929* (MO). Manabí: Cantón Pedernales, Cerro Pata de Pájaro a 10 km al este de Pedernales rancho de la familia Arroyo, 300–700 m, 00°01'N 79°57'W, 05 Mar. 1997, Vargas et al. 1231 (MO).

48. *Burmeistera sodiroana* Zahlbr., Repert. Spec. Nov. Regni Veg. 13: 534. 1915. TYPE: Ecuador. Pichincha: Secus flumen Pilatón, 900–1600 m, s.d. (fl.), *L. Sodiro 91/25* (holotype, B, destroyed; isotypes, P [barcode] 408899 digital image!, W 1963-0012263 digital image!).

Burmeistera succulenta var. latisepala E. Wimm., Repert. Spec. Nov. Regni Veg. 29: 55.
1931, syn. nov. Type: Ecuador. Tunguruahua: In sylvis montanum Tunguragua, Dec.
1857 (fl.), R. Spruce 5119 (holotype, K [barcode] 250836 digital image!; isotypes, K [bc]
250837 digital image!, G [bc] 236671 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, destroyed; neotype, designated here, Ecuador. Pichincha: In reg. subtrop. pr. S. Florencio, s.d., *Sodiro 91/21* [neotype, P (barcode) 408898 digital image!]).

Burmeistera leucocarpa Zahlbr. 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, 4 m. *Latex* white. *Stems* ca. 7 mm, green to violet, glabrous. *Leaves* alternate, spiral, often bullate, often reduced in size when subtending a flower, the internodes 20–45 mm, where flowering 5–10 mm; petioles 5–10 mm, green to violet, glabrous; blades when sterile $55-130 \times 30-50$ mm, when subtending a flower reducing to $(20-)30-50(-80) \times (5-)15-35$ mm, ovate to ovate-lanceolate, the base obtuse to rounded, the apex acuminate to caudate, $2-10 \times 2-4$ mm, the margin shallow callose-servate 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; pedicels 80–160 mm at anthesis, 100–165 mm in fruit, green to violet, glabrous; hypanthium $8-13 \times 5-8$ mm, abruptly widening distally, obconical to cupuliform, green to violet tinged, glabrous; calyx lobes $1-5 \times 1-2$ mm, deltate, green, glabrous, the margin green or violet, entire or with few callose-tipped teeth, ascending at anthesis; corolla green to green tinged or streaked with maroon-violet; corolla tube 5–6 mm wide basally, narrowing to 2-4 mm, glabrous; corolla lobes lanceolate, sometimes curled back at anthesis, the interior dark violet, the margins smooth to undulate, the two dorsal lobes $12-14 \times 2-4$ mm, opening dorsally 14–18 mm from the corolla base, ascending to falcate, the two lateral lobes 10– $13 \times 2-3$ mm, falcate, the ventral lobe ca. 7×3 mm, opening ventrally 9–12 mm from the corolla base; and roccium 29-32(-36) mm, exserted 19-20(-23) mm from the ventral opening, the filament tube green basally, becoming dark violet distally, glabrous, the anther tube $6.5-9 \times 4-6$ 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* 25×25 mm, globose, pendent, fleshy, spongy, white, maturing pink or white tinged with violet.

Phenology. This species has been collected with flowers and fruits throughout the year.

Distribution. Found on the 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. Occurs in cloud forests from 1500–3200 m in elevation.

Discussion. Burmeistera sodiroana resembles *B. crispiloba* and *B. melanocarpa*. It is differentiated from both by having spiral phyllotaxy, shorter flowers with a dark violet anther tube, and fruits maturing white tinged with violet.

Jeppesen (1981) noted that the type collection of *B. leucocarpa* may be a typographical error in Zahlbruckner (1915). Zahlbruckner cited the specimen *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). 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), no evidence exists of the collection *Sodiro 91/92*. If this collection ever existed, it was likely destroyed in Berlin in WWII. Jeppesen (1981) hypothesized 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). Thus, here, following Jeppesen, we have officially designated *Sodiro 91/21* (P) as the neotype of *B. leucocarpa*.

Additional Specimens examined. ECUADOR. Azuay: Cantón Camilo Ponce Enrique localidad Bella Rica-Villa Rica, 1096 m, 03°05'16.8"S 79°40'10.8"W, 31 March 2010, Jaramillo 30276 (QCA). Bolívar: Along road Chillanes-Yaquibusu, 2300 m, 20 July 1991, van der Werff et al. 12516 (MO). Cañar: El Triunfo, Cañar road, km 50 from El Triunfo, 1500 m, 02°29'S 79°05'W, 20 June 1979, *Løjtnant & Molau 15174* (NY). Cotopaxi: Around Pilalo, 2400 m, 00°57'S 79°02'W, 07 March 1968, Holm-Nielsen & Jeppesen 1282 (MO, NY); Cantón Pilalo, camino a la cumbre del Cerro Puchuato, 1800– 2500 m, 00°55'S 79°09'W, 05 December 1987, Cerón & Villavicencio 2798 (MO); Cantón Sigchos, Campo Alegre, a ca. 20 km al noreste de Sigchos, 2614 m, 00°35'03"S 78°47'36"W, Ramos et al. 5814 (MO); Cantón Sigchos, finca de Antonio Tigse, 3060 m, 00°35'43"S 78°49'55"W, 18 July 2003, Ramos et al. 6204 (MO); Carretera Latacunga-Pilaló-Quevedo, 5–10 km al este de Pilaló, 2400–2700 m, 00°55'S 79°00'W, 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, 00°57'S 78°14'W, 2500-2870 m, 16 March 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). Napo: Along E side of R. Chalpi, 1–3 km from confluence with R. Oyacachi, 2600–2800 m, 00°15'S 77°58'W, 23 May 1996, *Ståhl et al. 2564* (QCA); Along trail between Oyacachi and Pueblo Viejo (Old Oyacachi), 3000 m, 00°14'S 77°59'W, 24 May 1996, Ståhl et al. 2578 (QCA); Baeza, forest remnants, 1800–2000 m,

22 September 1977, Maas et al. 3035 (QCA); Between Tena and Pappalacta, 12 January 1981, D'Arcy 14101 (MO, NY); Between Tena and Pappalacta, 12 January 1981, D'Arcy 14092 (NY); Cantón Quijos, Unión del Río Blanco con Río Quijos, 00°28'S 78°03'W, 2680 m, 12 June 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, 00°40'12"S 77°55'01"W, 2200–2250 m, 12 February 2011, Tepe et al. 2955 (MO); Cantón Quijos, Baeza, parte alta del Río Machángara, 00°28'S 77°54W, 2200–2300 m, 9 May 1990, Palacios & Friere 4982 (NY); Carretero Papallacta-Baeza, Hacienda Flor del Bosque, 00°22'S 78°04'W, 14 December 1993, Friere-Fierro & Yánez 2673 (NY); Cosanga, stream just south of town, 00°36'S 77°52'W, 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 August 1980, Sobel & Strudwick 2522 (NY); Lago Agrio-Quito road, km 195, between Cuyuja and Papallacta, 2500 m, 00°22'S 78°05'W, 18 June 1985, Stein 3082 (QCA, MO); Parque Nacional Lllanganates, vía Salcedo-Tena, colecciones a lo largo del camino desde Los Carmelos-Río Ana Tenorio al Río Langoa, bosque de Neblina Montano, 00°58'17"S 78°15'14"W, 2600–2850, 18 February 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, 00°45'S 77°55'W, 12 December 1989, Luteyn & Cabo 13459 (NY, QCA); Quijos, Reserva Ecológica Antisana, Río Aliso, 8 km al suroeste de Cosanga, afluente del Río Aliso, margen derechoa a 1 km, 00°35'S 77°57'W, 2530 m, 12 November 1998, Vargas et al. 3003 (MO); Quito to Baeza, km 92, 1850 m, 30 June 1985, Dodson & Hirtz 15883 (MO); Reserva Yanayacu, collected on trail behind station heading towards Antisana, 2100 m,

00°35.3'S 77°52.8'W, 28 July 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, 00°37'S 77°52'W, 26 October 1976, Balslev & Madsen 10329 (NY); Road Baeza-Tena, km 24-29 from Baeza, S of Cosanga, 00°38'S 77°51'W, 2100-2300 m, 28 March 1979, Holm-Nielsen 16226 (QCA); Salcedo-Napo road, ca. 56–60 km E of Salcedo, 00°55'S 78°30'W, 2926–3060 m, 23 November 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 December 1979, Croat 49392 (MO); Ca. 5 km SW of San José de Niebli, 13 road km N of Calacalí, 2450 m, 00°02'N 78°32'W, 01 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 September 1986, Zak 1192 (MO); Carretera Sto. Domingo-Quito, 13 km al oeste del paso, Ceja Andina, 3000 m, 00°26'S 78°38'W, 21 June 1982, Balslev 2759 (NY); Cerro Corazón, 2438–2835 m, 05 January 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, 00°02'S 78°38'W, 10 September 2001, Friere-Fierro et al 3208 (MO); Cerro Pugsi, NW slope of Volcán Pichincha, on ridge crest, 3020 m, 27 September 1980, Bleiweiss 1142 (NY); Nanegalito-Tandayapa road, 1890–2400 m, 00°03-05'S, 78°44'W, 07 November 1989, Luteyn & Tirira 13328 (MO, NY); Reserva Bellavista, 2295 m, 00°0.67'S 78°41.285'W, 11 July 2002, Muchhala 129 (QCA); Reserva Orquideológica El Pahuma, carretera Calacalí-Los Bancos, km 22, 2000 m, 00°01'42"N 78°37'50"W, 26 October 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, 00°03'N 78°40'W, 21 May 1989, Smith 1975 (MO, NY, QCA); Route Tandayapa-Nanegalito, 2250 m, 00°00'S 78°40'W, 24 January 1996, Billiet & Jadin 6684 (MO); Old road Quito-Santo Domingo, between San Juan and Chiriboga, on steep slopes along road, 2700-2750 m, 00°17'S 78°40'W, 20 March 1979, Løjtnant & 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, 00°15–20'S 78°40–50'W, 04 February 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, 00°18'S 78°43'W, 14 December 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, 07 February 1985, Molau & Öhman 1156 (QCA). Tungurahua: Cantón Baño, Río Vascun Valley, northern slopes of Volcán Tungurahua, 2500–3200 m, 01°26'21"S 78°25'58"W, 27 April 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 November 1939, Asplund 9767 (NY); Cusatagua, Vicinity of Ambato, March 1919, Pachano 177 (NY); Parque Nacional Llanganates, entrando por Baquerizo Moreno hacia el sector de Lagartococha, 3270 m, 01°12'01"S 78°28'19"W, 01 March 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, 01°25'S 78°22'W, 3 June 1985, *Stein 2945* (MO); Zona de amortiguamiento del Parque Nacional Llanganates, Machay, Río Verde, colecciones entre Río Machay y Colina San Austín, 2090 m, 01°22'S 78°17'W, 30-31

July 1999, *Vargas et al. 3712* (MO). Morona Santiago: Between Tambo Consuelo and Tambo Cerro Negro, 2590–2895 m, 20–24 August 1945, *Camp E-4955* (NY).

49. *Burmesitera succulenta* H. Karst & Triana, Linnea 28: 445. 1856. TYPE: Colombia. Quindío: Nouvelle-Grenade prov. De Mariquita, crescit circa 'El Roble' in monte Quindio, 2000 m, 1851–1857 (fl.), *J. J. Triana 1586* (lectotype, designated here, P barcode 00408903 digital image!).

Burmeistera succulenta H. Karst & Triana var. meiophylla Zahlbr. ex E. Wimm. (1943:
143) TYPE:—VENEZUELA. Aragua: Tovar, Karsten s.n. (lectotype, designated here,
COL barcode 000266968; isolectotypes, JE barcode 00000627 digital image!, JE barcode
00000628 digital image!).

Herbaceous shrubs or scandent herbs, 3 m. *Latex* abundant, white. *Stems* ca. 5 mm, green to violet, glabrous. *Leaves* alternate, distichous, the internodes 20–50 mm; petioles 2–6 mm, green to violet, glabrous; lamina 50–150 × 25–60 mm, elliptic, the base obtuse, the apex attenuate to acuminate, the margin shallow callose-serrate to nearly entire, the teeth and margin sometimes tinged violet; adaxial surface green to green tinged violet, glabrous, nitid; abaxial surface green to maroon-violet, glabrous; 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, 45–53 mm; pedicels 60–115 mm at anthesis, 110–125 mm 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 $8-18 \times 2-5$ mm, ligulate, dark green, often suffused with violet, glabrous, the margin entire or with few callose-tipped teeth, the apex acute, ascending at anthesis; corolla exterior green to green suffused with maroon-violet, interiorly violet; corolla tube 6–9 mm wide basally, the throat narrowing to 3–5 mm; corolla lobes lanceolate, strongly scrolling back, the two dorsal lobes $22-28 \times 3-4$ mm, opening dorsally 14–17 mm from the corolla base, the two lateral lobes $18-25 \times 3-5$ mm, opening ventrally 10-12 mm from the corolla base; androecium 37-43 mm, exserted 27-33 mm from the ventral opening, the filament tube maroon-violet, glabrous, the anther tube $8-10 \times 3-4$ 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. 20×20 mm, globose, fleshy, pink to violet.

Phenology. This species has been collected with flowers and fruits throughout the year.

Distribution. A widespread species, ranging from the western slopes of the Andes in central Ecuador, through Colombia, into northwestern Venezuela. Occurs in cloud forests from 1000–2500 m in elevation.

Discussion. Vegetatively, some specimens of *B. succulenta* can appear similar to *B. melanocarpa*, and *B. sodiroana*, but are easily differentiated by the calyx lobes: long (> 8 mm) in *B. succulenta*, and short (< 3 mm) in the other two. Strongly scrolling corolla

lobes are both present in *B. succulenta* and *B. crisipiloba*, and the two species have similar sized flowers. Again, *B. succulenta* is easily differentiated by long vs. short calyx lobes. Both *B. araneosa* and *B. anfractuosa* can have calyx lobes similar in size to *B. succulenta*, but are both differentiated by their much shorter flower length and androecium length compared to *B. succulenta*.

Burmeistera succulenta is the most widespread species in the recurved corolla clade, and currently the only one known from Colombia and Venezuela. The phylogeny of Uribe-Convers et al. (2017) shows *B. succulenta* as sister to *B. crispiloba*, and this makes sense morphologically, given their shared floral characters. The description of *B. anfractuosa* and *B. araneosa* in this paper potentially changes this relationship. It is interesting to observe that *B. crispiloba* shares many floral traits with *B. succulenta*, minus the long calyx lobes, while *B. anfractuosa* and *B. araneosa* share the long calyx lobes of *B. succulenta*, but have flowers that are much reduced, among other changes.

Selected specimens examined. COLOMBIA. Antioquia: Cordillera Central, ca. 60 km S of Medellin on main hwy. to Manizales, 1350 m, 05°50'N 75°44'W, 26 January 1986, *Stein & McDade 3303* (NY); Medellin-Cartagena Hwy., turnoff to Briceño, ca. 25 km N of Yarumal, 1800 m, 07°07'N 75°28'W, 07 February 1986, *Stein & Cogollo 3369* (NY); To 5 km down road to San Fermin de Briceño, W off Pan American Hwy., ca. 25 km N of Yarumal, 1525–1830 m, 07°01'N 75°35'W, 26 May 1984, *Luteyn et al. 10750, 10761 & 10773* (NY); To 5 km down road to San Fermin de Briceño, W off Pan American Hwy., ca. 25 km N of Yarumal, 1525–1830 m, 07°01'N 75°35'W, 26 May 1984, *Luteyn et al. 10750, 10761 & 10773* (NY); To 5 km down road to San Fermin de Briceño, W off Pan American Hwy., ca. 25 km N of Yarumal, 1525–1830 m, 07°01'N 75°35'W, 26 May 1984, *Luteyn et al. 10750, 10761 & 10773* (NY); To 5 km down road to San Fermin de Briceño, W off Pan American Hwy., ca. 25 km N of Yarumal, 1525–1830 m, 07°01'N 75°35'W, 26 May 1984, *Luteyn et al. 10750, 10761 & 10773* (NY); To 5 km down road to San Fermin de Briceño, W off Pan American Hwy., ca. 25 km N of Yarumal, 1525–1830 m, 07°01'N 75°35'W, 22 May 1988, *Luteyn & Sylva 12418 & 12420* (NY). Amazonas: Departamento Río Negro, cerro de La

Neblina Camp V, valley north base of Pico Cardona, 1250 m, 00°49'N 66°00'W, 21–24 March 1984, Leisner & Stannard 16856 (NY). Caldas: San Clemente, edge of woods, 1800–2200 m, 16 September 1922, Pennell 10685 (NY). Chocó: Ansermanuevo-San José del Palmar road, 2–5 km E of San José del Palmar, 1200–1500 m, 20 April 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, 04°40'N 76°25'W, 15 May 1984, Luteyn 10545 (NY); Bolívar-Quibdó road, ca. 37–40 km W of El Carmen, 671– 1360 m, 05°40'N 76°15'W, 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, 03°28'N 76°37'W, 20 April 1989, Lutevn et al. 12557 (NY). ECUADOR. Azuay: Hacienda Yacopiana, on ridge bordering Río Patul, above Sanagüín, 850 m, 02 June 1943, Steyermark 52805 (NY). Bolívar: Road Echeandía-Guanujo, E of Echeandía, 2400 m, 01°25'S 79°07'W, 08 July 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). VENEZUELA. Aragua: Colonia Tovar, 1800–2000 m, December 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 January 1978, Luteyn & Lebron-Luteyn 5177 (NY). Yaracuy: Cerro La Chapa, selva nublada al norte de Nirgua, 1200–1400 m, 9–10 November 1967, Stevermark et al. 100250 (NY); Cumbre Gamelatal 4.3-11 km N of Salom on road from Salom to Candelaria, 1000–1200, 10°15'N 68°29'30"W, s.d., Mori et al. 14602 (NY);

North of Salom 7.5 km, 1200–1300 m, 10°15'N 68°29'W, 04 March 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°21'N 68°49'W, 04 April 1980, *Leisner & González 10048* (NY).

50. Burmeistera truncata Zahlbr., Repert. Spec. Nov. Regni Veg. 13: 531. 1915. TYPE:
Ecuador. Pichincha: Andes Quitenses, in descensu a Canzacato ad S. Florencio, Dec.
1882 (fl.), L. Sodiro 91/23 (holotype, B, destroyed; isotypes, P [barcode] 408908 digital
image!; W-0046735 digital image!).

Scandent herbs, 2 m. *Latex* white. *Stems* ca. 5 mm wide, green tinged violet, puberulent, velutinous. *Leaves* alternate, distichous; petioles 8–22 mm, green to tinged violet, puberulent; lamina 75–150 × 25–45 mm, lanceolate, the base obtuse to rounded, the apex attenuate to acuminate, $15-30 \times 1-3$ mm, the margin shallow callose-serrate to crenate, the teeth often intramarginal; adaxial surface green, lighter along the primary vein, sometimes tinged violet, glabrous to sparsely puberulent; abaxial surface green, often tinged violet, puberulent with white hairs; venation brochidodromous, the primary vein prominent, raised, the secondary veins slightly raised, the tertiary veins visible. *Flowers* 36–43 mm, solitary; pedicels 35–85 mm at anthesis, 65–90 mm in fruit, green to tinged violet, puberulent; hypanthium 5-7 × 4–5 mm, cupuliform (rarely obconical), green to violet, puberulent, the ridges smooth; calyx lobes 9–18 × 1–2 mm, ligulate, green to violet, puberulent, the margin entire, the apex obtuse, ascending at anthesis;

corolla pale green, sometimes spotted or tinged with violet, puberulent; corolla tube 4–6 mm wide basally, narrowing to 3–4 mm; corolla lobes ligulate, the margins undulate, the two dorsal lobes $12-18 \times 3-6$ mm, opening dorsally 13-15 mm from the corolla base, arcuate, the two lateral lobes $5-8 \times 2-4$ mm, opening ventrally 5–10 mm from the corolla base, arcuate; androecium 29–39 mm, exserted 24–30 mm from the ventral opening, the filament tube green, villose with white hairs, the anther tube violet along the sutures, between the sutures covered with appressed short yellow hairs, all the anther tips sparsely villose with white hairs; the style and stigma cream colored, the stigma lobes shortly pubescent along the margin. *Fruits* 45 × 35 mm, globose, inflated, green to reddish violet.

Phenology. This species has been collected with flowers and fruits throughout the year.

Distribution. Found only in Pichincha Province of Ecuador in wet cloud forests from 1500 to 2500 m in elevation.

Discussion. This species is closely to *B. auriculata* and *B. rubrosepala*, but is easily differentiated by the ascending ligulate calyx lobes.

Additional specimens examined. ECUADOR. **Pichincha:** Along old road from Quito to Santo Domingo de los Colorados, 19 km S of San Juan, 15 km NE of Chiriboga, 1710 m, 00°17'S 78°43'W, 12 Oct. 1980, *Croat 50609* (MO); Below Chiriboga, on Quito-Santo Domingo road, 1800 m, 01 Apr. 1942, *Haught 3210* (NY); Cantón Quito, Chiriboga, en la carretera vieja Quito-Sto. Domingo, Reserva Forestal La Favorita, Minist. de

Agricultura, 1600–1800 m, 00°12'S 78°47'S, 05 Dec. 1989, Cerón et al. 7940 (MO); Carretera antigua Quito-San Juan ± Chiriboga-Empalme-Sto. Domingo de los Colorados, km 55, sector denominado Guajalito, 2000–2300 m, 20 Sep. 1986, Zak 1258 (MO); Carretera Antiqua from Quito to Santo Domingo de los Colorados, km 46-54, 1980-2100 m, 08 Jan. 1979, Luteyn & Lebron-Luteyn 6702 (NY); Carretera Quito-Aloag-Santo Domingo de los Colorados, km 94, sector La Esperie, 1350–1800 m, 20 Nov. 1987, Zak & Jaramillo 3003 (MO); Km 68 Quito-Santo Domingo, 2100 m, 27 Sep. 1980, Dodson et al. 10552 (MO); New road from Quito to Santo Domingo, 1900 m, 24 Jun. 1985, Stein & Dodson 3089 (MO); Quito-Santo Domingo old road, Las Palmeras, ca. 59 km WSW of Quito, Pablo Feret trail above Río Guajalito, 1900–2000 m, 00°18'S 78°43'W, 16 Dec. 1990, Luteyn & Berg 14362 (MO, NY); Quito-Santo Domingo old road, Las Palmeras, ca. 59 km WSW of Quito, trail and forest along Río Guajalito, 1800–1900 m, 00°18'S 78°43'W, 14 Dec. 1990, Luteyn et al. 14354 (NY); Reserva Florística-Ecológica Río Guajalito, km 59 de la carretera antigua Quito-Sto. Domingo de los Colorados, a 3.5 km al NE de la carretera, 1800–2200 m, 00°13'53"S 70°48'10"W, 27 Dec. 1990, Grijalva 553 (NY); Reserva Florística-Ecológica Río Guajalito, km 59 de la carretera antigua Quito-Sto. Domingo de los Colorados, a 3.5 km al NE de la carretera, 1800-2200 m, 00°13'53"S 70°48'10"W, 09 Aug. 1991, Jaramillo & Grijalva 13684 (MO, NY); Reserva Florística-Ecológica Río Guajalito, km 59 de la carretera antigua Quito-Sto. Domingo de los Colorados, a 3.5 km al NE de la carretera, 1800–2200 m, 00°13'53"S 70°48'10"W, 17 Jan. 1992, Jaramillo & Grijalva 14547 (MO, NY); Trail going from the new Santo Domingo-Quito road into disturbed montane forest on steep slopes, 1700-2000 m, 01°21'S 78°42'W, 11 Dec. 1983, Kvist & Barfod 49070 (MO).

51. Burmeistera velutina Muchhala & Mashburn, sp. nov. TYPE: Ecuador. Pichincha: Mashpi Lodge, on 'Palma Caminante' path, 1047 m, 00°09'47.59"N 78°52'26.823"W, 06 Jul. 2018 (fl.), *N. Muchhala & J. Gruhn 556* (holotype, MO!).

Herbaceous shrubs to scandent herbs, 6 m. Latex unknown. Stems ca. 4 mm wide, yellow-green, villose with yellow-tan to cream-colored hairs. *Leaves* alternate, distichous, the internodes 15–25 mm; petioles 5–10 mm, green, villose; lamina $80-135 \times$ 25–35 mm, narrowly elliptic, the base attenuate, the apex attenuate to acuminate, the margin shallow callose-dentate, nearly entire, the teeth intramarginal; adaxial surface dark green, glabrous; abaxial surface lighter green, villose, especially along the main veins; venation camptodromous, the primary vein prominent, raised, the secondary veins only slightly raised, the tertiary veins faintly visible. Flowers 32–37 mm, solitary in the upper leaf axils; pedicels 65–95 mm, green, villose, especially distally; hypanthium 7–11 \times 4–6 mm, turbinate, the base barely distinguishable from the pedicel, green, villose; calyx lobes $15-23 \times 0.5-1.5$ mm, linear, strongly patent at anthesis, green, the exterior villose, the interior glabrous, the margin callose-serrate, the apex acute; corolla green to green tinged maroon-violet, villose; corolla tube 5–6 mm wide basally, the throat narrowing to 3–4 mm; corolla lobes lanceolate, the two dorsal lobes $12-15 \times 3-4$ mm, falcate, opening dorsally 14–15 mm from the corolla base, the two lateral lobes $8-9 \times 3-$ 4 mm, falcate, the ventral lobe $7-8 \times 3-4$ mm, opening ventrally 11-12 mm from the corolla base; androecium 25–29 mm, exserted 15–17 mm from the ventral opening, the filament tube green, sparsely puberulous with white hairs, the anther tube ca. 5×4 mm,

green, violet along the sutures, sparsely puberulous between the sutures, all five anther tips glabrous to sparsely puberulous; the style and stigma cream-colored, the stigma lobes fringed with white hairs along the margin. *Fruits* ca. 10×7 mm, cylindrical, not inflated, maturing white.

Etymology. The specific epithet comes from the term *velutinous*, in reference to the soft hairs found all over the plant.

Phenology. This species has been collected with flowers and fruits in July.

Distribution. Known only from the type locality in Pichincha Province. It occurs at ca. 1000 m in elevation.

Discussion. This species is closely related to *B. smaragdi* and *B. kitrinaima*, but is differentiated by the yellow villose hairs that cover the vegetative and reproductive parts of the plant.

Additional specimens examined. ECUADOR. Pichincha: Mashpi Lodge, on 'Palma Caminante' path, 1034 m, 00°09'53.81"N 78°52'25.743"W, 06 Jul. 2018, *Muchhala & Gruhn 552* (MO); Mashpi Lodge, on 'Palma Caminante' path, 1031 m, 00°09'47.89"N 78°52'27.553"W, 06 Jul. 2018, *Muchhala & Gruhn 554* (MO); Mashpi Lodge, on 'Palma Caminante' path, 1035 m, 00°09'47.05"N 78°52'27.273"W, 06 Jul. 2018, *Muchhala &* *Gruhn 555* (MO); Mashpi Lodge, on road to lodge, at start of 'Copal' trail, 978 m, 00°09'59.69"N 78°52'37.653"W, 06 Jul. 2018, *Muchhala & Gruhn 549* (MO);

52. Burmeistera zamorensis Muchhala & Á.J. Pérez, Novon 24(1): 36–38, fig. 1. 2015.
TYPE: Ecuador. Zamora Chinchipe: Reserva Tapichalaca, 04°29.629'S 79°07.825'W,
2478 m, 13 Nov. 2010 (fl.), *N. Muchhala 467* (holotype, QCA-206843!).

Scandent herbs, 2 m. Latex cream colored. Stems ca. 3 mm wide, green to violet, glabrous, striate when dry. *Leaves* alternate, spiral; petioles 10–25 mm, slender, green to green tinged violet, glabrous; lamina $55-95 \times 25-50$ mm, ovate-lanceolate, the base cuneate to obtuse, the apex acuminate to caudate, $10-20 \times 0.5-2$ mm, the margin shallow callose-dentate, appearing nearly entire, especially basally; adaxial surface green, glabrous; abaxial surface maroon-violet with pale green veins, glabrous; venation brochidodromous, the primary and secondary veins prominent, the primary vein raised, the secondary veins only slightly, the tertiary veins barely visible but becoming more visible when dry. Flowers ca. 29 mm; pedicels 40-55 mm at anthesis, 50-70 mm in fruit, green tinged violet, glabrous; hypanthium $4-5 \times 4-5$ mm, cupuliform, green, glabrous, the ridges smooth; calyx lobes $3-4 \times 1-2$ mm, deltate, green, sometimes tipped violet, glabrous, the margin callose-serrate with 3-7 teeth, the teeth sometimes violet, the apex acute, ascending to patent at anthesis; corolla light green lightly suffused with violet, glabrous; corolla tube ca. 5 mm wide basally, bulging just above the base, narrowing to 2–3 mm; corolla lobes ligulate, violet inside, the margins smooth, the two dorsal lobes ca. 13×3 mm, opening dorsally ca. 13 mm from the corolla base, falcate, the two lateral
lobes $6-7 \times 2$ mm, opening ventrally ca. 6 mm from the corolla base, falcate; androecium 23–24 mm, exserted ca. 17 mm from the ventral opening, the filament tube maroon-violet tinged, puberulous with cream colored hairs, the anther tube dark blue-violet, lighter along the sutures, covered with short, appressed, sordid yellow hairs, the top three anther tips glabrous, the bottom two anther tips glabrous or sparsely puberulous with short white hairs; the style and stigma cream colored, the stigma lobes fringed with short white hairs along the margin. *Fruits* ca. 15×15 mm, globose, inflated, with fleshy walls ca. 3 mm thick, light green suffused with maroon-violet.

Phenology. This species has been collected in flowers and fruits throughout the year.

Distribution. Found in southeast Ecuador in Zamora Chinchipe province. It occurs in high elevation cloud forests from 1800–2700 m.

Discussion. Burmeistera zamorensis is unique from other *Burmeistera* species in Ecuador in the combination of ovate-lanceolate leaves with a long drip tip, brochidodromous venation, and short deltate calyx lobes.

Additional specimens examined. ECUADOR. **Zamora Chinchipe:** Cantó Nangaritza, Sector Pachicutza, colecciones en el sendero hacia el Hito, 950–1800 m, 04 Dec. 1990, *Jaramillo & Grijalva 13312* (QCA); Cantón Palanda, Reserva Tapichalaca, colecciones a lo largo del sendero de las Tangaras, 2500 m, 04°29'41"S 79°07'53"W, 05 Aug. 2015, *Pérez et al. 9118* (QCA); Cantón Palanda, Reserva Tapichalaca, colecciones a lo largo del sendero de las Tangaras, 2470–2600 m, 04°29'43"S 79°07'55"W, 21 Jun. 2016, *Pérez et al. 7142* (QCA); Parque Nacional Podocarpus, road Yangana-Valladolid, just S of the pass, Nudo de Sabanilla, 2700 m, 04°27'S 78°08'W, 14 Feb. 1989, *Øllgaard & Madsen 90540* (QCA); Road from Loja to Zumba, S side of Nudo de Sabanilla Pass, border of Loja Province, 2460 m, 04°30'S 79°10'W, 11 May. 1985, *Stein & D'Alessandro 2745* (MO). LITERATURE CITED

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Figure 1. Burmeistera asclepiadea



Figure 19 Burmeistera aspera



Figure 20 Burmeistera borjensis



Figure 21 Burmeistera brighamioides



Figure 22 Burmeistera caelestis



Figure 23 Burmeistera chrysothrix



Figure 24 Burmeistera crassifolia



Figure 25 Burmeistera crocodila



Figure 26 Burmeistera cyclostigmata



Figure 27 Burmeistera cylindrocarpa



Figure 28 Burmeistera domingensis



Figure 29 Burmeistera draconis



Figure 30 Burmeistera erosa



Figure 31 Burmeistera glabrata



Figure 32 Burmeistera heilbornii



Figure 33 Burmeistera holm-nielsenii



Figure 34 Burmeistera huacamayensis



Figure 35 Burmeistera ignimontis



Figure 36 Burmeistera kitrinaima



Figure 37 Burmeistera knaphusii



Figure 38 Burmeistera lingulata



Figure 39 Burmeistera loejtnantii



Figure 40 Burmeistera lutosa



Figure 41 Burmeistera marginata



Figure 42 Burmeistera microphylla



Figure 43 Burmeistera multiflora



Figure 44 Burmeistera melanocarpa



Figure 45 Burmeistera oyacachensis


Figure 46 Burmeistera pacifica



Figure 47 Burmeistera pallida



Figure 48 Burmeistera racemiflora



Figure 49 Burmeistera refracta



Figure 50 Burmeistera resupinata



Figure 51 Burmeistera sierrazul



Figure 52 Burmeistera smaragdi



Figure 53 Burmeistera sodiroana



Figure 54 Burmeistera succulenta



Figure 55 Burmeistera truncata



Figure 56 Geographic distribution maps



Figure 57 Geographic distribution maps



Figure 58 Geographic distribution maps



Figure 59 Geographic distribution maps



Figure 60 Geographic distribution maps



Figure 61 Geographic distribution maps



Figure 62 Geographic distribution maps



Figure 63 Geographic distribution maps



Figure 64 Geographic distribution maps