A phenetic analysis of the *Bakeridesia integerrima* complex (Malvaceae)

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Abstract. The *Bakeridesia integerrima* complex is a geographically and morphologically variable group consisting of populations that have been variously assigned to *B. integerrima, B. molinae, B. bakeriana*, and *B. subcordata.* Phenetic analyses of morphological data were undertaken to clarify species boundaries within this complex. Ninety-five specimens were placed into one of ten Operational Taxonomic Units (OTUs) and measured for 16 morphological characters and 29 ratios of these characters. Univariate analyses were conducted to examine variation within individual variables, and Canonical Variates Analyses (CVA), and Principal Components Analysis (PCA) were used to examine relationships among the variables. The results presented here show that the *B. integerrima* complex consists of nine morphologically and geographically distinct species, compared to the four previously published species names. One new combination, **B. chittendenii,** is made, *B. subcordata* is synonymized with *B. bakeriana*, and diagnoses are given for five new species: **B. huastecana, B. jaliscana, B. zapoteca, B. parvifolia**, and **B. guerrerensis**.

Key Words: *Bakeridesia*, Malvaceae, phenetic analysis, canonical variates analysis, species complex.

Bakeridesia (Malvaceae) is a genus of tall shrubs native to the seasonally dry forests of Mexico, Central America, and northwestern South America. It differs from most other genera in tribe Malveae in having a lacerate wing (or wing remnant) on the dorsal margin of the mericarp. For this reason, *Bakeridesia galeottii* was segregated from *Abutilon*, which does not have winged fruits (Hochreutiner, 1913). Currently, 14 species of *Bakeridesia* are recognized. *Bakeridesia* has only been revised once, by D. M. Bates in 1973. In that revision, Bates described three new species and transferred several species from *Abutilon* and *Robinsonella* to *Bakeridesia. Bakeridesia,* as currently recognized, is united by the following suite of characters (in addition to the winged mericarps): entire leaves (rarely subentire or slightly sinuate), yellow to orange flowers, height (at maturity) of at least 2 m, glabrous inner mericarp walls, and a base chromosome number of x=15 (Bates & Blanchard, 1970; Donnell et al., 2012).

Bakeridesia integerrima (Hook. f.) D. M. Bates is a highly polymorphic and widely distributed species recognized by Bates (1973). Individuals assigned to this name are found in eastern Mexico (in the states of Tamaulipas, San Luis Potosí and Veracruz), Central America (Honduras and Nicaragua), and northwestern South America (Colombia, Venezuela and Ecuador). Bates's (1973) broad circumscription of *B. integerrima* subsumed and synonymized several previously recognized species, including the Central American *Abutilon chittendenii* Standl. and the South American *A. goudotianum* Triana & Planch. Collections included by Bates in *B. integerrima* vary widely in leaf size (relatively small leaves in central American and some Mexican collections), leaf texture (papery thin in eastern Mexican collections, more coarse-textured in South American collections), pedicel length (generally longer in Central and South American collections), pedicel thickness (noticeably thicker in South American collections), number of flowers per inflorescence (1 or 2 in Mexican and Central American collections, 1–4(–5) in South American ones), and flower color (bright yellow with or without red spots at the

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base of the petal in Mexican collections; yellow with maroon, purple, red or dark-brown spots in South American collections, and usually fully yellow in central American collections). Habitat varies as well, with the Mexican and Central American collections usually found in edge environments (on roadsides and in fence rows) and the South American collections in habitats with less human disturbance such as limestone ridges or along streams. Further complicating matters is the unclear relationship between *B. integerrima* and the other species of section *Minores* D. M. Bates that have fully developed wings on the mericarps: *B. bakeriana* (Rose) D. M. Bates, *B. molinae* D. M. Bates and *B. subcordata* (Hochr.) D. M. Bates. These species intergrade with populations of *B. integerrima* in pedicel length and thickness and number of flowers per inflorescence. For example, the Mexican populations of *B. integerrima* are more similar to *B. molinae* in terms of pedicel thickness than they are to the South American populations of *B. integerrima*. On the other hand, *B. bakeriana* and *B. subcordata* share stout pedicels and the presence of three or more flowers on some infloresences with the South American populations of *B. integerrima*. In the years following Bates's revision, several specimens have been collected in the Oaxacan Isthmus of Tehuantepec that fit somewhat within the broad description of *B. integerrima*, and Fryxell assigned some of these to *B. integerrima* and others to *B. subcordata* in his treatment of Mexican Malvaceae (1988). However, these specimens from Oaxaca appear to intergrade morphologically with *B. subcordata* and somewhat with the South American populations of *B. integerrima*.

Molecular evidence based on ITS sequences further confounds matters, as it suggests that *B. integerrima* is polyphyletic (Donnell et al., 2012), with the eastern Mexican accession included in a strongly supported clade consisting of all the species in eastern Mexico (*B. notolophium, B. ferruginea* and *B. gertrudisensis*). The South American accession of *B. integerrima* was unresolved with regard to all the Mexican species, and it was not found to be sister to any of them in any equally most parsimonious trees. *Bakeridesia bakeriana* was inferred to be sister to *B. amoena* Fryxell, and *B. subcordata* was placed in a moderately supported clade with the "*B. integerrima*" species from the Isthmus of Tehuantepec region.

Because of the considerable overlap in various characters, it is quite difficult to differentiate between these taxa as currently delimited. Phenetic analyses of morphological characters are used here to try to answer the following questions: Is *B. integerrima* a highly polymorphic taxon with no discernable breaks in morphological variation? If so, should *B. integerrima* also include *B. bakeriana, B. molinae*, and *B. subcordata,* as these are quite similar morphologically to certain populations of *B. integerrima*? If there are breaks in the morphological continuity in this complex that may represent species boundaries, which characters (or combinations of characters) are most useful to differentiate between the species? To answer these questions, Canonical Variates Analysis (CVA) and Principal Components Analysis (PCA) were used. CVA works with *a priori* groups of specimens, attempting to achieve maximal separation of such groups based on measured traits, and it also determines which traits are most useful in distinguishing groups. It is therefore well suited to test the validity of previously described taxa. PCA is a complementary method because it uses no *a priori* group assignments of individuals; it creates a new system of axes in which symbols representing the specimens are positioned in such a way that the greatest degree of variation in the data matrix is expressed.

Materials and methods

IDENTIFICATION OF OPERATIONAL TAXONOMIC UNITS

Within the *B. integerrima* complex, a total of ten morphological groups were identified as operational taxonomic units (OTUs) into which specimens were assigned. The OTUs included five named groups (i.e., each such OTU contains the type specimen of at least one name) and five previously unnamed groups (shown in Table I). Assignment of specimens to OTUs was based on both morphology and geographical range (see map in Fig. 1)

Three of the OTUs (7, 9 and 13) require further comment. OTU 7 was initially divided into two groups from the Tehuantepec region—one with what seemed to be smaller leaves and flower parts than the other. However, upon further examination of the specimens, it became apparent that there is a continuum in the sizes of the floral parts of the plants, and that the specimens with smaller leaves were mostly collected in the latter half of

TABLE I

LIST OF OPERATIONAL TAXONOMIC UNITS (OTUS) INCLUDED IN THIS STUDY, THE NAMES WITH WHICH THEY HAVE BEEN ASSOCIATED, THEIR DISTRIBUTIONS, AND NUMBER OF SAMPLES INCLUDED IN THE ANALYSIS. NAMES MARKED WITH AN ASTERISK (*) INDICATE THAT THE OTU INCLUDES THE TYPE SPECIMEN ASSOCIATED WITH THAT NAME.

OTU No.	Associated Name(s)	Distribution	No. samples
1	*Abutilon chittendenii**, *B. integerrima*	Nicaragua, Honduras	6
2	*Abutilon goudotianum** *B. integerrima**	Venezuela, Colombia and Ecuador	13
4	*B. integerrima*	Veracruz, Tamaulipas	21
5	*B. molinae**	Honduras	5
6	*B. bakeriana*	Jalisco, Colima	16
7	*B. integerrima* *B. subcordata*	Oaxaca (Isthmus of Tehuantepec)	10
9	*B. bakeriana** *B. subcordata**	Oaxaca (Tehuacan-Cuicatlán Valley)	11
12	*B. bakeriana*	Colima	3
13	*B. integerrima*	San Luis Potosí	9
14	*B. bakeriana*	Guerrero	1

the dry season (March through May). In the Isthmus of Tehuantepec, the dry season is extremely hot, and it seems that the plants drop most of their vegetative leaves during this time, leaving only the leaves subtending the inflorescences, which are generally smaller. Similarly, the flowers are often smaller but more numerous on specimens collected towards the end of the dry season. Specimens lacking vegetative leaves were excluded from the analysis because many foliar characters were used, and the two groups we had previously recognized were merged into one, referred to here as OTU 7.

OTU 9 includes the type collections of *B. bakeriana* and *B. subcordata,* both found in the same part of the Tehuacán-Cuicatlán Valley of

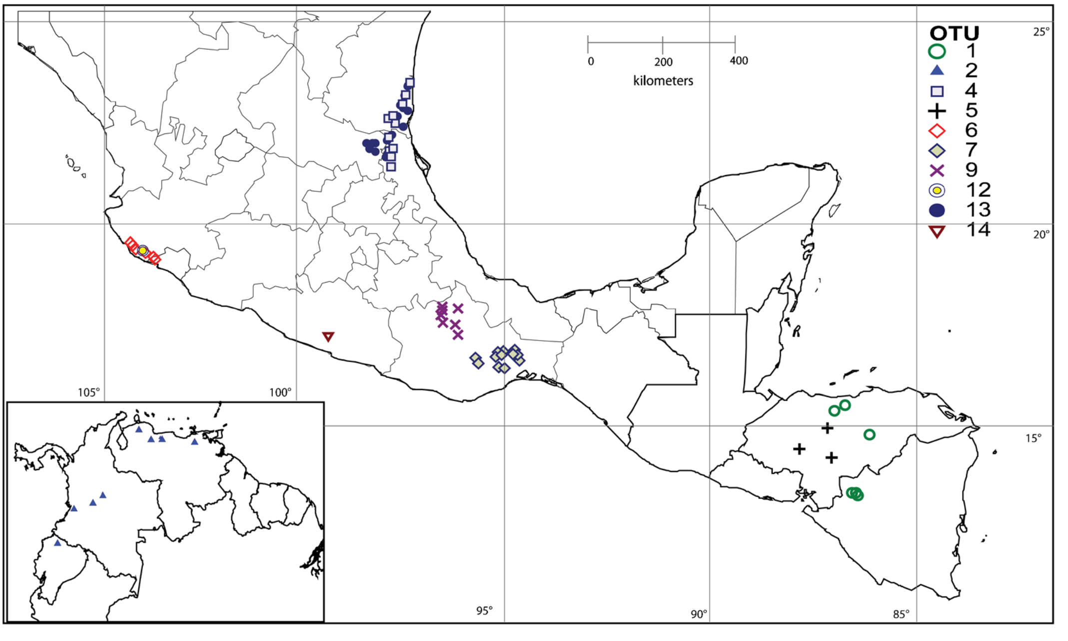

FIG. 1. Map showing distribution of OTUs throughout Mexico, Honduras and Nicaragua (South American distribution shown as inset). Symbols represent all examined collections of each OTU, including those that were not included in the phenetic analyses.

Oaxaca. Initially, separate OTUs were recognized for each of these names. To the *B. subcordata* group, we assigned specimens that corresponded to Bates's concept of that species, i.e., they were relatively short-pedicelled with dense infloresences that appear to be umbel-like due to short internodes between flower clusters. To the *B. bakeriana* group, we assigned specimens from the type locality of that species, which have very long pedicels and internodes. The two groups have similar leaves, calyx lobes, and fruits. *Bakeridesia subcordata* and *B. bakeriana* have only been collected in a small area within the Tehuacán-Cuicatlán Valley, in some cases from the same locality. Thus, the only apparent differences between the two groups are pedicel length and length of internodes between flower clusters, but careful examination of all available specimens revealed that there is intergradation in pedicel length. Specimens assigned to *B. subcordata* display a variety of pedicel lengths, though they are mostly short. However, it appears that the pedicels continue to elongate as the fruits develop. Some specimens appear intermediate between the two groups and were difficult to place in one group or the other. In consideration of the degree of intergradation between the two groups, they were classified as a single group in the analysis, OTU 9. If these two species are merged, the epithet *bakeriana* has nomenclatural priority.

All but one of the specimens representing Group 13 were collected in the Mexican state of San Luis Potosí (SLP). In the exploratory phase of the analysis, the specimens from eastern Mexico were arbitrarily placed in three groups according to state, i.e., separate OTUs were defined for Tamaulipas, Veracruz, and SLP. Preliminary analyses showed no differentiation between the Tamaulipas and Veracruz groups, but the SLP group was consistently found to be distinct from the other two. For this reason, the Tamaulipas and Veracruz specimens (with one exception) were merged into one OTU (4), and the SLP OTU (13) was left separate; one Tamaulipas specimen that appeared to fit better morphologically with the SLP specimens was transferred to OTU 13. Initially, the first author was hesitant to recognize the two groups as distinct because of their geographic proximity. However, the results of the preliminary analyses led to a search for other characteristics that separated OTU 13 from OTU 4, and the two groups were found to differ in flower color, leaf size and bloom time.

Taxonomic Characters

Based on field observations in Mexico and examination of around 700 herbarium specimens, 11 floral and five vegetative characters were identified. To further examine possible relationships between these characters, 29 comparison values, or ratios, were included (characters listed in the Appendix). Some of these characters have been used previously to differentiate species of *Bakeridesia* (Bates, 1973), but others have not. Ninety-five specimens were selected for sampling, with priority given to specimens with all features present and easily accessible. An effort was made to ensure that the range of variation within each OTU was represented. Most characters were measured directly on the specimens. Smaller features, such as pedicel width and number of carpels, were measured under a light microscope with an ocular micrometer. Flowers in which the parts were difficult to measure (e.g., because petals covered the staminal column) were removed from the specimen and rehydrated in a weak solution of dish detergent and water before being dissected and measured. Only specimens with at least one vegetative leaf (i.e., a leaf that does not subtend an inflorescence) were used. Fruit characters, though useful, were not included in the analysis due to a scarcity of specimens with both flowers and mature fruits. Specimens included in the analyses are indicated within "additional specimens examined" for each taxonomic group in the Taxonomy section.

Univariate Analysis

To examine single-trait variation among OTUs, a Kruskal-Wallis One-Way ANOVA on Ranks was performed to test for differences in medians, and a Bonferroni (All-Pairwise) Multiple Comparison Test was used to determine differences in means. Univariate analyses were performed using NCSS 2004 (Hintze, 2005).

Discriminant Analysis

Canonical Variates Analysis was performed using NCSS 2004 (Hintze, 2005). To address potential problems of multicollinearity, variables with R-square values greater than 0.99 were removed through an iterative process. First, the variables with the five highest R-square scores were recorded. Then, these variables were crossreferenced with the variable-variate correlations, and the variable with the least influence on the first two axes was removed from the analysis. The analysis was repeated as needed until no more R-square values above 0.99 remained. This approach was used so that the effect of correlated variables could be reduced while maximizing the number of informative characters included in the analyses.

Because of the large number of OTUs included in this study, a sequential removal approach was used during multiple rounds of analysis to maximize the separation between groups. The analysis was initially run with all of the a priori groups. OTUs that were completely separated from the remaining samples were removed, and the remaining OTUs were re-analyzed. This process was repeated until no further separation was achieved among the remaining OTUs.

Principal Components Analysis

Principal components analysis was conducted using PAST (Hammer et al., 2001) on the dataset that included all characters except those removed due to strong correlations in the discriminant analysis. Both variance-covariance and correlation matrices were used.

Results

Univariate Analysis

Kruskal-Wallis One-way ANOVA indicated that most of the 45 characters had medians that differed significantly among the various OTUs (data not shown). The Bonferroni (All-Pairwise) Multiple Comparisons Test showed that for most of the characters that strongly influenced the first three axes in the CVA and PCA, the means for at least one pair of OTUs differed significantly (Fig. 2). Characters showing no significant differences among OTUs (not included in Fig. 2) were LeafWid, NumCarpels, LobToBl:Leaf Ratio, and LobToBl:Leaf Area (see Appendix for full names of characters). The greatest differences among OTUs were found in the means of the following characters: StamenLn, PedWidMax, PedWidMin, PedLn, LeafBroad:StamCol, and LeafBroad:PedWidMax. Of the OTUs considered to be part of *B. integerrima* in the broad sense (1, 2, 4, 7, and 13), OTU 2 differed significantly from 1, 4 and 13 in five characters (Fig. 2), and from either 1, 4 or 13 in nine additional characters. OTU 7, a group that has sometimes been placed within *B. integerrima*, is significantly different from OTU 2 in six characters (Fig. 2), from OTUs 1, 4 and 13 in four characters (Fig. 2), and from either 1, 4 or 13 in eight additional characters.

Discriminant Analysis

After the removal of correlating variables (those with R-square scores of more than .99), 40 characters remained in the analysis (Table II). The discriminant analysis predicted the a priori placement of 100% of samples assigned to OTUs 1, 7, 9, 12, and 14; in each of the remaining OTUs, the discriminant analysis predicted the a priori placement of at least 80% of samples assigned to a given OTU (Table III).

The CVA of all OTUs yielded two distinct groups: Group A, which consisted of OTUs 2, 6, 9, 12, and 14, and Group B, which contained OTUs 1, 4, 5, 7, and 13 (Fig. 3). Groups A and B were recovered in all combinations of the first three axes, which accounted for 68.8% of the variation. In Group A, one sample of OTU 12 was found to be intermediate between the two groups. However, because all three samples of OTU 12 are from the same collection, it was not possible to change the a priori status of the outlying sample.

To determine if better separation between groups could be achieved when fewer OTUs were included, the CVA was run separately for Group A and Group B. Before A and B could be examined further, we inspected for correlating variables to reduce potential problems of multicollinearity. Using the stepwise procedure described in Materials and methods, the variable sets were independently reduced from the main dataset, as the correlations between variables are likely to change depending on which taxa are examined.

In the CVA of Group A based on a reduced dataset of 26 characters (Table IIB), the first three axes together accounted for 94.9% of the variation (Fig. 4). In axis 1, OTU 14 is separate from the other taxa. When axes 1 and 2 are plotted, OTUs 2, 6 and 9 display good separation, though OTU 2 overlaps with one specimen of OTU 12. However, OTU 12 is well separated from OTU 2 (and all the other taxa) when axes 1 and 3 are plotted. The discriminant analysis of Group A alone predicted the a priori placement of 100% of samples in Group A (data not shown).

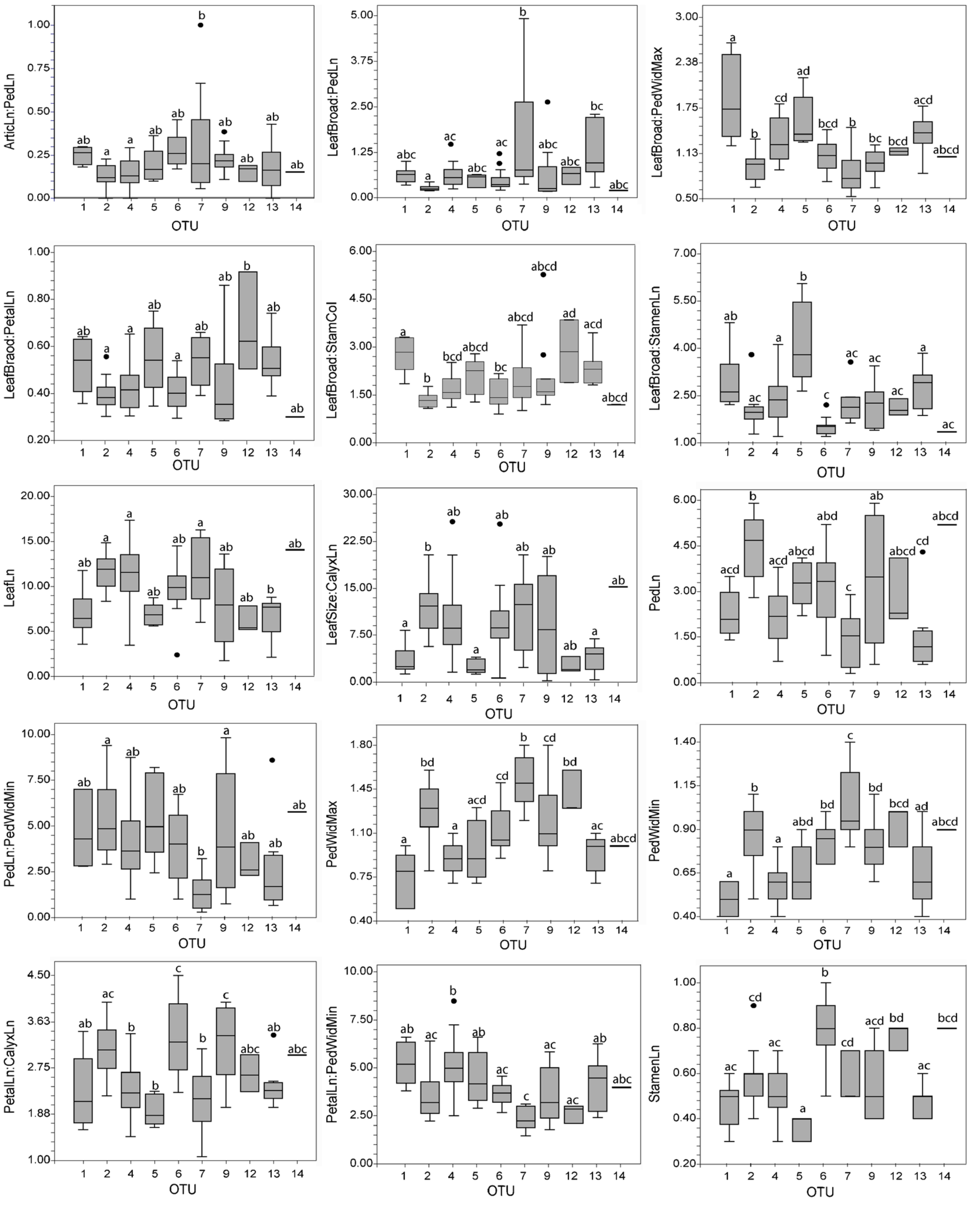

FIG 2. Box plots denoting selected characters that contributed significantly (i.e., in the top five) to any of the first three axes in the CVA or the PCA (not all characters that contributed significantly are shown). Shaded areas represent the values between the 25th and 75th percentile, the internal line represents the median, and the whiskers correspond to non-outlying maximum and minimum values. Outliers (values that are three or more times the interquartile range from the 25th or 75th percentile) are denoted by small dots above or below the whiskers. Letters above boxes indicate similarity or difference of means; if the same letter appears above two OTUs, then their means for that character do not differ significantly, as determined through a Bonferroni (All-wise) Multiple Comparison Test. Abbreviated character names are defined in the Appendix.

TABLE II

CORRELATIONS OF VARIABLES WITH AXES IN FOUR DISCRIMINANT ANALYSES, **A.** ALL OTUS. **B.** GROUP "A". **C.** GROUP "B". **D.** GROUP "B" WITH OTU 7 REMOVED. THE FIVE MOST INFLUENTIAL VARIABLES FOR EACH AXIS ARE SHOWN IN BOLDFACE TYPE. FOR DESCRIPTION OF VARIABLES SEE APPENDIX.

Variable	Variate1	Variate2	Variate3
A. All OTUs			
PedLn	0.192126	0.063779	-0.045386
CalLobLn	-0.189092	0.130405	-0.010278
PerCalyxFr	-0.007576	0.064002	-0.054012
StamenLn	**0.264897**	-0.022539	0.187750
PedWidMax	0.121735	**-0.460634**	-0.030410
PedWidMin	0.162172	**-0.407886**	-0.041747
NumCarpels	0.056502	-0.075895	-0.017655
PetalLn	0.121026	0.126575	0.082939
Pedln:PedWidMin	0.065058	0.160772	-0.045050
CalyxLn:PedWidMax	**-0.237135**	**0.348935**	0.006301
StamCol:PedLn	-0.101556	-0.198734	0.034894
StamCol:CalyxLn	**0.233514**	-0.078676	0.055189
CalLobLn:CalWid	-0.185138	0.186938	-0.039254
StamCol:PedWidMax	0.004304	0.252250	0.107994
StamCol:PedWidMin	-0.063485	0.232367	0.155781
StamCol:StamenLn	-0.078664	0.013970	-0.073816
PetalLn:CalyxLn	**0.288618**	0.021617	0.019020
PetalLn:PedWidMin	-0.094752	**0.318942**	0.086755
LeafLn	0.017182	-0.091959	**0.262737**
LeafWid	0.044049	-0.032558	0.049039
LeafBroad	-0.056115	-0.015617	-0.175798
LfLobeLn	0.036669	-0.075246	0.217571
ArticLn	**0.211168**	0.118045	-0.104408
ArticLn:PedLn	0.012584	-0.072794	-0.077396
ArticLn:PedWidMax	0.111677	0.206008	-0.123632
ArticLn:PedWidMin	0.087469	0.202127	-0.094081
LeafBroad:PedLn	-0.103975	-0.171711	-0.025126
LeafBroad:PedWidMax	-0.160948	**0.323942**	-0.168396
LeafBroad:StamCol	-0.093640	0.005913	-0.194516
LeafBroad:StamenLn	-0.209498	0.070794	**-0.312945**
LeafSize:PedLn	-0.091351	-0.203650	0.108009
LeafSize:PedWidMax	0.000685	0.054882	**0.331260**
LeafSize:PedWidMin	-0.035709	0.060932	**0.357126**
LeafSize:StamCol	-0.013282	-0.106830	0.211129
LeafSize:CalyxLn	0.084953	-0.104417	0.215064
LeafSize:StamenLn	-0.048126	-0.064148	**0.281472**
LeafBroad:PetalLn	-0.099036	-0.102104	-0.182633
LobToBl:LeafBroad	0.044327	-0.041726	0.179315
LobToBl:LeafSize	0.032121	-0.001400	-0.043743
LeafSize:PetalLn	-0.016816	-0.146415	0.251249
B. Group "A"			
PedLn	0.030767	0.017784	-0.217386
CalLobLn	-0.070885	0.075670	0.048913
StamenLn	**-0.187645**	**0.242831**	0.220235
PedWidMax	0.104209	0.055202	0.010944
PedWidMin	0.029669	0.083700	-0.017088
NumCarpels	0.045749	0.042267	-0.140304
PetalLn	-0.080594	0.043347	-0.128836
CalyxLn:PedWidMax	-0.102957	0.023624	-0.075985
StamCol:PedLn	-0.065109	-0.026792	0.099203
StamCol:CalyxLn	-0.052317	0.097098	-0.129582
CalLobLn:CalWid	**-0.150799**	0.003305	0.021130
StamCol:PedWidMax	**-0.127703**	0.098912	-0.156334
StamCol:PedWidMin	-0.064948	**0.100995**	-0.180085
LeafWid	-0.053861	0.015532	**-0.279651**
LeafBroad	0.074365	**0.144307**	**0.246341**

Table II Continued

Variable	Variate1	Variate2	Variate3
ArticLn:PedLn	**-0.172581**	-0.062251	0.226725
ArticLn:PedWidMax	-0.114202	-0.075881	0.023341
LeafBroad:PedWidMax	-0.051228	0.051197	0.148369
LeafBroad:StamCol	0.081024	-0.069805	**0.259464**
LeafBroad:StamenLn	**0.161267**	**-0.125839**	-0.034470
LeafSize:PedLn	-0.086447	0.036932	-0.080176
LeafSize:PedWidMax	-0.069598	-0.027479	-0.213232
LeafSize:StamenLn	0.030332	-0.027880	**-0.322765**
LeafBroad:PetalLn	0.098019	0.013173	**0.227324**
LobToBl:LeafBroad	-0.049805	-0.038318	-0.021811
LobToBl:LeafSize	0.017803	**-0.131714**	0.083223
C. Group "B" only			
PedLn	-0.099067	0.105021	-0.121389
PerCalyxFr	-0.044922	0.102974	-0.050717
StamenLn	0.115764	-0.178597	0.096452
PedWidMax	**0.437043**	0.049047	-0.119243
PedWidMin	**0.346775**	0.058206	-0.076325
NumCarpels	0.063960	0.010266	**0.285685**
CalyxLn:PedWidMax	**-0.217189**	0.035184	0.044758
StamCol:PedLn	0.147970	-0.046199	-0.008213
CalLobLn:CalWid	-0.097473	0.105091	-0.128881
StamCol:PedWidMin	-0.178389	-0.145685	**-0.140490**
StamCol:StamenLn	-0.041756	0.061557	**-0.242022**
PetalLn:CalyxLn	-0.027028	-0.083316	0.067056
PetalLn:PedWidMin	**-0.251363**	-0.084437	0.038490
LeafLn	0.115834	**-0.246224**	-0.063156
LeafBroad	0.000701	0.195372	-0.040647
LfLobeLn	0.109666	**-0.293113**	-0.068359
ArticLn:PedLn	0.102530	0.075203	0.083609
ArticLn:PedWidMin	-0.124088	0.127831	0.091502
LeafBroad:PedLn	0.123840	-0.001231	0.036429
LeafBroad:PedWidMax	**-0.220057**	0.148312	**0.150622**
LeafBroad:StamCol	-0.026177	0.214889	**0.236390**
LeafBroad:StamenLn	-0.090186	**0.276946**	-0.130491
LeafSize:PedLn	0.159406	-0.082700	0.002546
LeafSize:PedWidMax	-0.017558	**-0.351560**	-0.053052
LeafSize:StamCol	0.120389	-0.212835	0.005838
LeafSize:StamenLn	0.053189	**-0.264329**	-0.091277
LeafBroad:PetalLn	0.073170	0.217960	0.037371
LobToBl:LeafBroad	0.058827	-0.246261	-0.044915
LobToBl:LeafSize	-0.030782	0.006941	0.025847
D. Group "B" with OTU 7 removed			
PedLn	-0.022112	-0.129718	**-0.285156**
PerCalyxFr	-0.044117	-0.073721	-0.167994
StamenLn	0.112629	**0.159216**	0.046250
PedWidMax	0.020040	**-0.180487**	0.082384
PedWidMin	-0.009532	-0.139656	0.118122
NumCarpels	-0.050064	**0.250925**	-0.003941
CalyxLn:PedWidMax	-0.017717	0.059217	**-0.234492**
CalLobLn:CalWid	-0.035855	-0.144834	-0.160799
StamCol:PedWidMin	0.135164	-0.050426	-0.164680
StamCol:StamenLn	0.018354	**-0.241379**	-0.151735
PetalLn:CalyxLn	0.031747	0.098971	0.113802
PetalLn:PedWidMin	0.047580	0.094954	-0.155391
LeafBroad	-0.135168	-0.128559	-0.045848
LfLobeLn	**0.296471**	0.069824	-0.041880
ArticLn:PedLn	-0.091341	0.077760	-0.047421
ArticLn:PedWidMin	-0.073847	0.063514	**-0.265064**
LeafBroad:PedLn	-0.040537	0.017297	**0.377651**
LeafBroad:PedWidMax	-0.133840	0.104243	-0.118220
LeafBroad:StamCol	**-0.245998**	0.156134	0.094846
LeafBroad:StamenLn	-0.156651	**-0.218530**	-0.109604

Table II Continued

Variable	Variate1	Variate2	Variate3
LeafSize:PedLn	0.173047	0.067510	0.048825
LeafSize:PedWidMax	**0.278912**	0.114997	**-0.181151**
LeafSize:StamenLn	**0.225619**	0.034164	-0.145829
LeafBroad:PetalLn	-0.165253	-0.067909	0.084469
LobToBl:LeafBroad	**0.227120**	0.067511	0.040584
LobToBl:LeafSize	-0.034436	0.005579	0.169669

In the analysis of the Group B dataset (29 characters; see Table IIC), OTU 7 was recovered as distinct from the other OTUs (1, 4, 5 and 13) (Fig. 5), but the latter four OTUs were not clearly separated. Because greater separation often occurs when outlying taxa are removed from discriminant analyses, OTU 7 was removed. After removing the correlating variables through the same stepwise procedure used in previous analyses, a CVA was performed on the resulting data set of 26 characters (Table IID). With OTU 7 removed, OTUs 1, 4, 5, and 13 were found to be distinct from each other in the plot of CV1 vs. CV2 (Fig. 6). The discriminant analysis predicted the a priori placement of 100% of samples in Group B (data not shown) whether OTU 7 was included or not.

Principal Components Analysis

Results of the principal components analysis of the dataset used in the CVA of all groups (Table IV) were similar to those obtained in the CVA, especially when the correlation matrix was

Table III

Group classification of OTUs by discriminant analysis. Values in each row indicate number of samples and percentage of total of each a priori group predicted in each respective taxon group by the analysis. Note: Discriminant analysis does not recognize missing data. Therefore, three samples from OTU 4 and one from OTU 2 were excluded from the preliminary analysis due to missing ArticLn data. These samples were included, however, in subsequent analyses of smaller data sets, because the variable ArticLn (and consequently any missing data) was removed due to multicollinearity.

Classification by Discriminant Analysis											
OTU	1	2	4	5	6	7	9	12	13	14	Total
1	6 (100%)	0	0	0	0	0	0	0	0	0	6
2	0	11 (92%)	0	0	1 (8%)	0	0	0	0	0	12
4	0	0	18 (95%)	0	0	0	0	0	1 (5%)	0	19
5	0	0	0	4 (80%)	0	0	0	0	1 (20%)	0	5
6	0	1 (6%)	0	0	15 (94%)	0	0	0	0	0	16
7	0	0	0	0	0	10 (100%)	0	0	0	0	10
9	0	0	0	0	0	0	11 (100%)	0	0	0	11
12	0	0	0	0	0	0	0	3 (100%)	0	0	3
13	0	0	0	0	0	1 (12%)	0	0	7 (88%)	0	8
14	0	0	0	0	0	0	0	0	0	1 (100%)	1
Total	6	12	18	4	16	11	11	3	9	1	91

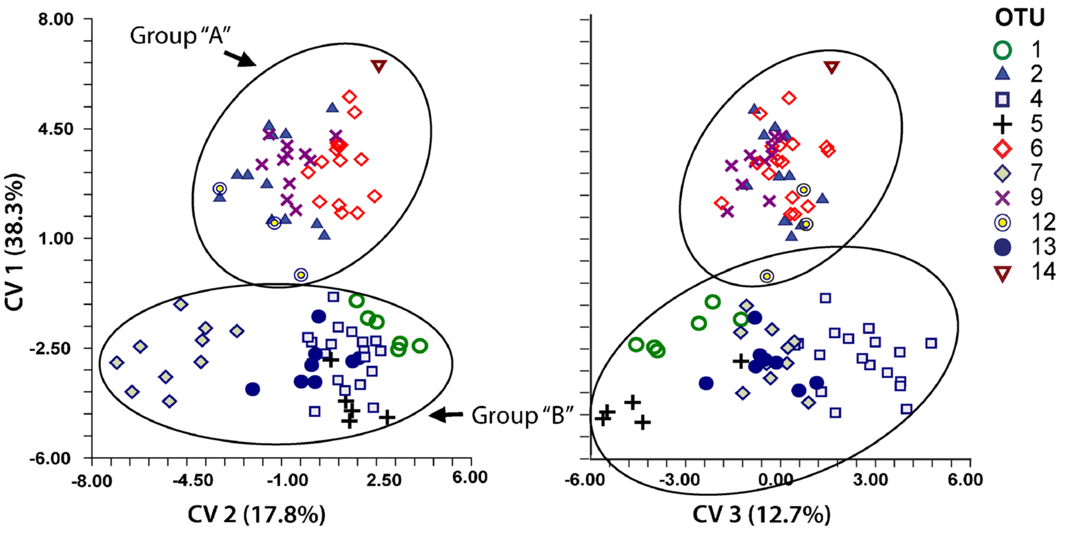

FIG. 3. Results of discriminant analyses of morphological variation with all OTUs included.

used. The variance-covariance matrix did not produce good separation (data not shown), probably because the variables contribute to the results in proportion to their variance. The correlation matrix standardizes all variables and appears to be a better fit for the dataset since raw data were used in addition to ratios. When the first two principal components (accounting for ~43% of the variation) were plotted (Fig. 7A), none of the OTUs were distinct, though OTU 7 overlaps only minimally with other taxa. When the first and third principal components (accounting for ~36% of the variation) are plotted (Fig. 7B), Groups A and B as displayed in the CVA plots can be distinguished fairly easily. Individuals from Group A (OTUs 2, 6, 9, 12, and 14) are concentrated below the axis of principal component 3; those from Group B (OTUs 1, 4, 5, 7, and 13) are concentrated above. When boundaries are drawn around the groups, no specimens from Group A are

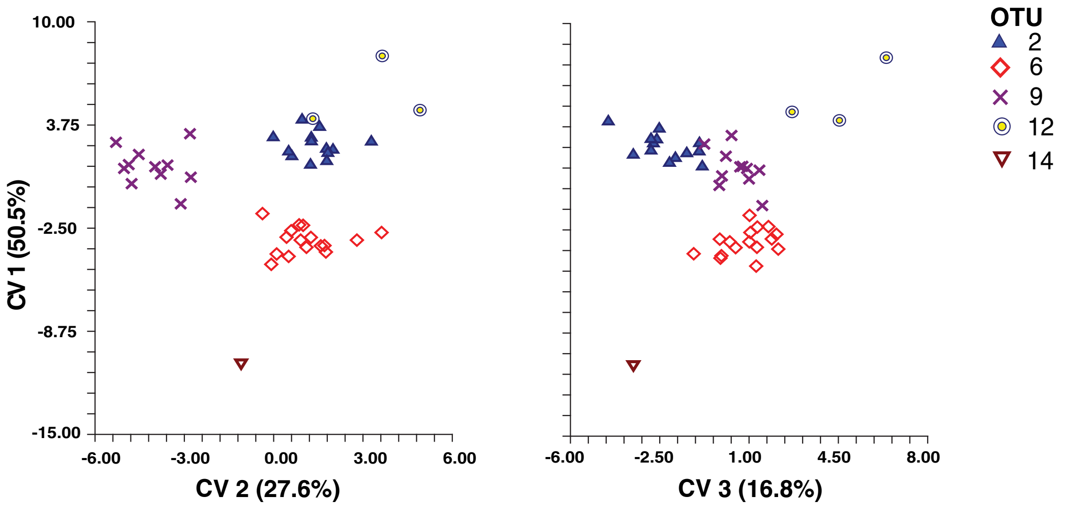

FIG. 4. Results of discriminant analyses of Group "A".

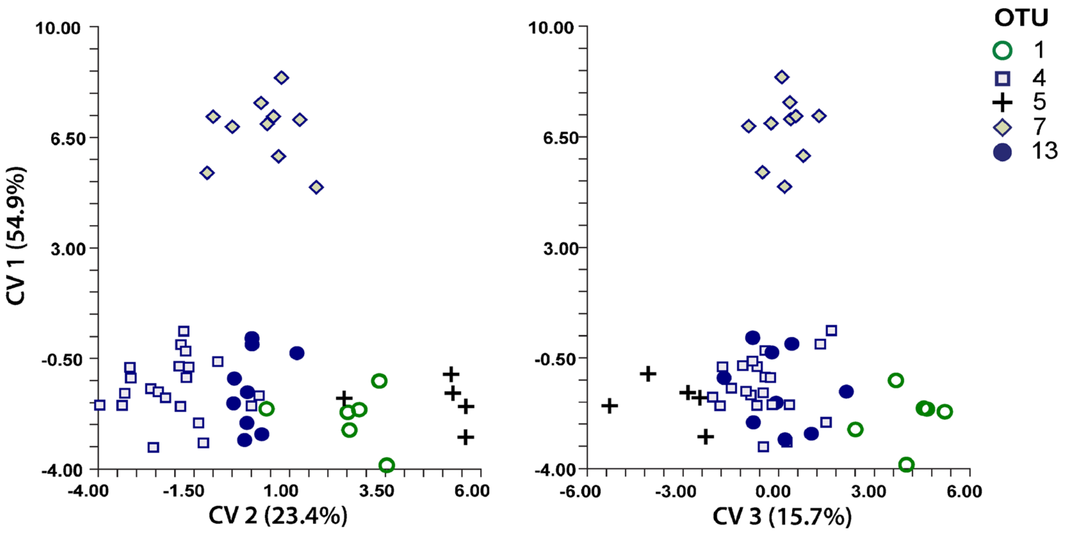

Fig. 5. Results of discriminant analysis of Group "B".

within Group B, and only three specimens from Group B are within Group A (Fig. 7B).

Discussion

Taxonomic Decisions

The OTUs associated with the name *B. integerrima* (1, 2, 4, 7, and 13) do not form a cohesive unit in the CVA or PCA plots. Specifically, the South American individuals (OTU 2) are much more similar to OTUs 6, 9, and 12, none of which have been included in *B. integerrima* by previous authors. These results are consistent with a phylogenetic analysis of molecular data (Donnell et al., 2012), which showed *B. integerrima* to be non-monophyletic due to the separation of the Mexican and South American collections. Although OTU 2 is more similar to OTUs 6, 9, and 12 in the univariate analyses, it forms a separate cluster in the

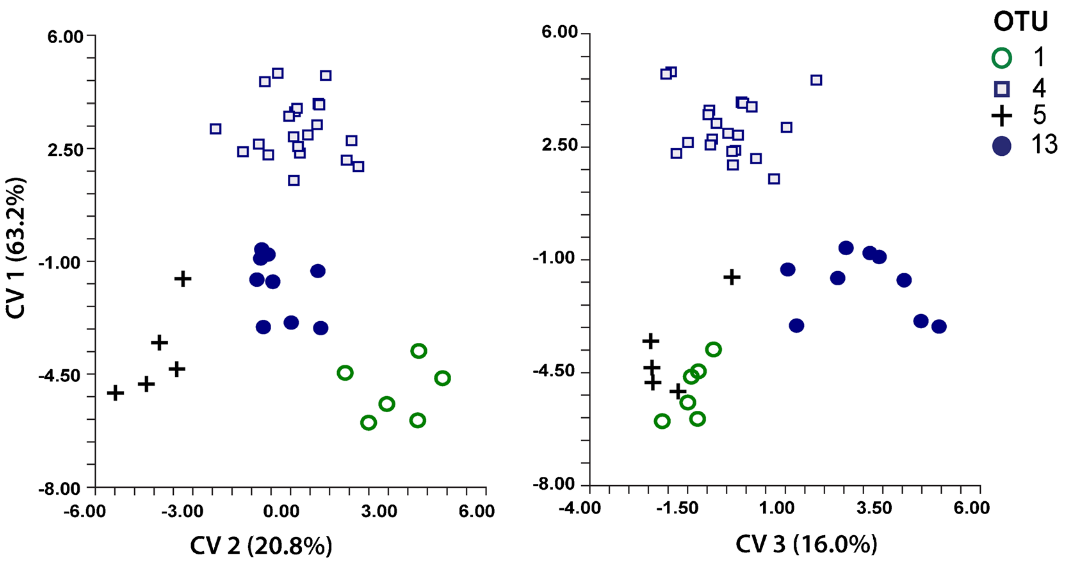

Fig 6. Results of discriminant analysis of Group "B" with OTU 7 removed.

TABLE IV
VARIABLE LOADINGS IN PCA, WITH THE FIVE MOST INFLUENTIAL VARIABLES FOR EACH AXIS SHOWN IN BOLDFACE TYPE. FOR DESCRIPTION OF VARIABLES SEE APPENDIX.

Variable	PC1	PC 2	PC3
PedLn	0.1638	0.1605	-0.1805
CalLobLn	0.00598	0.1526	0.2401
PerCalyxFr	-0.0385	0.05592	0.107
StamenLn	0.09778	-0.06956	**-0.2371**
PedWidMax	-0.05287	**-0.2644**	-0.08648
PedWidMin	-0.006936	**-0.2609**	-0.1252
NumCarpels	-0.007202	-0.03734	-0.04752
PetalLn	0.139	0.1018	-0.1804
Pedln:PedWidMin	0.1414	**0.2599**	-0.06942
CalyxLn:PedWidMax	0.0305	**0.2636**	0.2043
StamCol:PedLn	-0.08225	-0.1964	0.09578
StamCol:CalyxLn	0.06084	-0.0897	**-0.2645**
CalLobLn:CalWid	-0.05143	0.1711	**0.2369**
StamCol:PedWidMax	0.1229	0.2041	-0.03621
StamCol:PedWidMin	0.09253	0.2152	0.03608
StamCol:StamenLn	0.0004975	0.04805	0.07988
PetalLn:CalyxLn	0.06229	-0.05086	**-0.3059**
PetalLn:PedWidMin	0.0684	**0.2615**	0.06668
LeafLn	**0.2737**	-0.08961	0.1408
LeafWid	0.301	-0.09304	0.08845
LeafBroad	-0.174	0.03629	0.08936
LfLobeLn	0.1958	-0.162	0.05259
ArticLn	0.1458	0.1298	**-0.235**
ArticLn:PedLn	-0.03812	-0.1211	-0.02136
ArticLn:PedWidMax	0.1302	0.2165	-0.1371
ArticLn:PedWidMin	0.1257	0.2307	-0.1191
LeafBroad:PedLn	-0.1327	-0.1902	0.1534
LeafBroad:PedWidMax	-0.07075	0.2588	0.1562
LeafBroad:StamCol	-0.1857	0.006081	0.162
LeafBroad:StamenLn	-0.1668	0.0936	0.2174
LeafSize:PedLn	0.05693	-0.211	0.198
LeafSize:PedWidMax	**0.2927**	-0.000359	0.1465
LeafSize:PedWidMin	**0.2709**	0.01869	0.1779
LeafSize:StamCol	**0.2479**	-0.1177	0.1692
LeafSize:CalyxLn	**0.2703**	-0.1427	0.05607
LeafSize:StamenLn	0.2492	-0.07778	0.2098
LeafBroad:PetalLn	-0.2071	-0.04982	0.1722
LobToBl:LeafBroad	0.1261	-0.1493	-0.03117
LobToBl:LeafSize	-0.1411	-0.02313	-0.1312
LeafSize:PetalLn	0.248	-0.1443	0.1756

discriminant analysis (Fig. 4). It also differs from the other OTUs in qualitative characters not included in the analysis. From OTUs 6 and 12 it differs in the structure of the inflorescence: the flower clusters arise directly from leaf axils on mature, lignified shoots in OTU 2, whereas in OTUs 6 and 12, the flower clusters are born on short, non-lignified axillary shoots. From OTU 9, it differs in the amount of pubescence at the base of the staminal column (densely pubescent in OTU 9 vs sparsely pubescent or glabrous in OTU2). Based on the totality of quantitative, qualitative and geographic evidence, OTU 2 is here treated as a separate species. Because the type collection for the basionym, *Sida integerrima*, is an illustration of a cultivated plant supposedly collected in Colombia, the name *B. integerrima* should remain with the South American group.

The Central American specimens (OTU 1) are morphologically distinct from the Mexican collections of "*B. integerrima*" (OTUs 4, 7 and 13) and the Honduran endemic *B. molinae* (OTU 5) in the CVA (Figs. 5, 6). Though the clusters

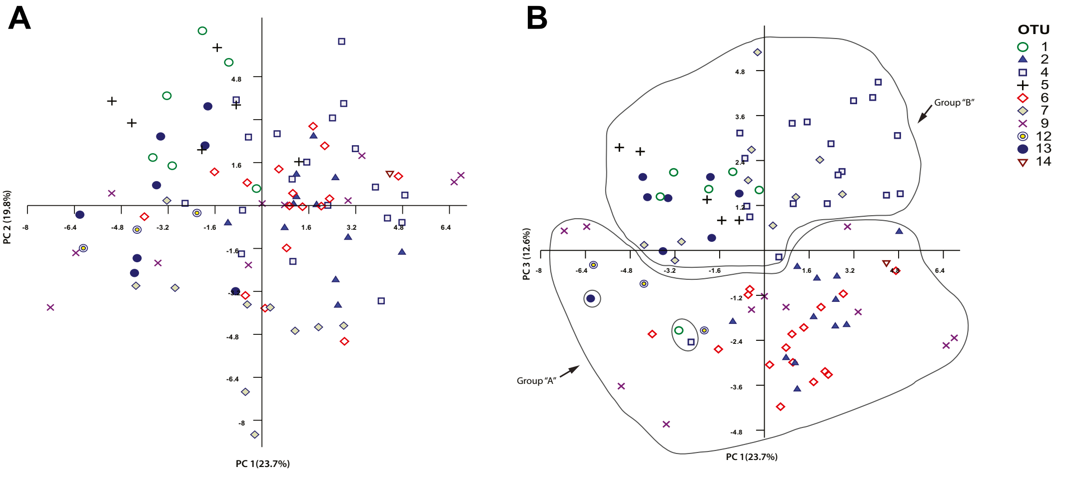

Fig. 7. Results of Principal Components Analysis of a correlation matrix including all OTUs. **A.** Principal components 1 and 2. **B.** Principal components 1 and 3, with outlines drawn around Groups "A" and "B" from Fig. 3. Small circles are drawn around the three specimens of Group "B" that fall within the Group "A" cluster.

representing OTUs 1 and 5 overlap substantially in the PCA, they separate widely in the CVA (CV1 vs CV2 in Fig. 6; CV1 vs CV3 in Fig. 5). Furthermore, these two OTUs are markedly dissimilar in characters that were not used in this analysis, including leaf pubescence (adaxial surface with both sericeous and stellate pubescence in OTU 5 vs stellate pubescence only in OTU 1), stem thickness (twigs of OTU 5 noticeably more slender than OTU 1), and in habitat (OTU 5 has only been collected in riparian zones, whereas OTU 1 prefers edges of seasonally dry forest). Based on these findings, OTU 1 is recognized here as a distinct species, *B. chittendenii* (new combination made in Taxonomy section).

The eastern Mexican specimens associated with the name *B. integerrima* (OTUs 4 and 13) are described below as a new species based on their separation from OTU 2 in the CVA (Fig. 6). A new name is required because the type of *B. integerrima* is part of OTU 2, and OTUs 4 and 13 do not include the types of any other names. The finding that the San Luis Potosí taxon (OTU 13) is distinct from the specimens from Veracruz and Tamaulipas (OTU 4) was a surprise, as the two are morphologically similar and are found in close proximity to each other (Fig. 1). However, they form separate clusters in both the CVA and PCA. The San Luis Potosí group has smaller vegetative leaves and shorter pedicels, blooms in spring, and prefers less disturbed habitats, most often being collected from thorn scrub. The Tamaulipas-Veracruz group has large vegetative leaves (though inflorescence leaves are usually smaller) and generally longer pedicels, blooms in the fall and winter, and is most often collected from roadsides and fencerows. When all the eastern Mexican "*B. integerrima*" specimens were examined (including those that could not be used in the phenetic analyses due to missing flowers or vegetative leaves), several collections from Tamaulipas and Veracruz were identified that fit within the concept of group 13, revealing that 13 is not restricted to the state of San Luis Potosí. However, some specimens cannot be placed easily within either group. For example, some specimens that fit morphologically into OTU 13 have been collected with flowers in December. Further complicating matters, specimens from the same collection may differ in the presence of large vegetative leaves. Leaf size apparently weighed heavily in the separation of groups 4 and 13 in both the CVA and PCA, because four of the five variables in which the two groups differed significantly were leaf length (Fig. 2) and ratios involving leaf size (data not shown). It is possible that the apparent differences in leaf sizes between these two OTUs do not reflect genetic differences but instead are simply a function of collection date and seasonal climate differences. The vast majority of the specimens of both OTUs were collected while in flower.

Specimens of Group 13 (the OTU with smaller leaves) were mostly collected between March and May, which is the end of the dry season; in contrast, the specimens of Group 4 (the OTU with larger leaves) were mostly collected between October and February, during the beginning to middle of the dry season. Furthermore, many specimens of Group 13 had scars where leaves (of unknown size) had abscised. It is possible that leaf abscission occurs progressively through the dry season and that the missing leaves of the Group 13 specimens collected in the spring had been as large as those of the fall-to-winter-blooming Group 4. There is also some uncertainty about how many times per year plants in these groups bloom; it is unclear whether a single plant may be able to bloom in both the fall and spring. Though the results of the phenetic analyses suggest that these two groups should be treated separately, we have decided to maintain them provisionally as a single species (*B. huastecana*, described in the Taxonomy section) due to their sympatric distribution, uncertainty about the number of flowering periods per year, and our suspicion that the ostensible difference in leaf size that heavily influenced their separation in the phenetic analyses might be simply a function of collection date relative to timing of abscission. The situation would be greatly clarified by phenological study of natural populations throughout the year. Molecular analysis of the two groups would also be informative.

The subsuming of *B. subcordata* within *B. bakeriana* (discussed in Materials and methods) is supported by the results presented here. The univariate analyses show that OTU 9 (which includes the types of both names) is highly variable in many characters, but in the CVA, the specimens assigned to OTU 9 clumped together tightly (Fig. 4). In the PCA (Fig. 7), the strong variation among characters caused the specimens of OTU 9 to appear quite dispersed among the other OTUs, but this broad dispersal of individuals is not congruent with previous assignments to *B. subcordata* versus *B. bakeriana*.

Group 6, consisting of specimens from coastal Jalisco and Colima, was previously included in *B. bakeriana* (Group 9) by Bates (1973). However, these collections differ markedly from *B. bakeriana* in habitat and stamen length. OTU 6 has only been collected near sea-level on the Pacific coast, whereas OTU 9 has only been collected inland at elevations above 1000 m. Univariate analyses demonstrate that these two groups differ significantly in stamen length (Fig. 2). In the CVA, Group 6 was found to be distinct from other taxa (Fig. 4), though it was most similar to Groups 2 and 9. Because of the differences in distribution (Fig. 1), habitat, and stamen length, OTU 6 is here recognized as a species distinct from *B. bakeriana* and is briefly described below as a new species, *B. jaliscana.*

The CVA (Fig. 5) provides strong support for the recognition of Group 7 as a distinct taxon. It differs from the other taxa by its combination of relatively short, very thick pedicels, large stipules, large fruits and dense, mostly terminal infloresences. In the CVA, it is one of only two OTUs to separate fully when all taxa are examined together (Fig. 3). It is also the only OTU to approach true separation in the PCA plots, specifically when axes 1 and 2 are examined (Fig. 7A). Based on this evidence, Group 7 is briefly described below as a new species, *B. zapoteca*.

Group 12, comprising three specimens from a single collection made in Colima, is most likely to be confused with Group 6, as it has a similar inflorescence structure (flowers mostly borne on axillary short shoots) and has been collected along the same stretch of highway as specimens of OTU 6. However, these specimens differ from Group 6 in their smaller flowers and fruits and much smaller leaves, and the two groups are well separated in the CVA (Fig. 4). In the univariate analyses, they differ significantly the following character ratios: LeafBroad: StamCol and LeafBroad: PetLn (Fig. 2). In addition, Group 6 has only been collected in bloom in June–July and December–January. In contrast, the sole collection of OTU 12 was collected in flower in March. Though there is only one collection of this taxon, it is sufficiently different from OTU 6 in the size of vegetative and reproductive parts that it is here recognized as a new species, *B. parvifolia*. If future collections show that *B. parvifolia* intergrades morphologically with *B. jaliscana* (OTU 6), the boundaries of *B. jaliscana* can simply be broadened to include *B. parvifolia.* In the meanwhile, We hope that our naming of this taxon as a species will encourage further study of the two taxa.

Group 14, consisting of a single specimen collected in the highlands of Guererro in 1898, is unique within the complex with its combination of long pedicels, long calyx lobes, and large petals; it is also the only taxon in the complex with nodding buds. It does not c luster with any other taxon in the CVA, and morphologically it does not fit in with any other OTU. Because of its distinct suite of characters and its geographical isolation, it is described below as a new species, *B. guerrerensis*.

Utility of Morphological Characters

Bakeridesia species have previously been distinguished by the length of the calyx in flower, the shape of the calyx in bud, the length and relative pubescence of the staminal column, pedicel length, and the degree to which the lacerate margin of the mature fruit is developed (Bates, 1973; Fryxell, 1988). The use of these characters has been sufficient to distinguish most species in the genus. However, within the *B. integerrima* complex, all the taxa have winged mericarps, staminal columns that are pubescent and similar in size, and flower buds of similar shape (generally ovoid). This study revealed several new characters that will be useful for distinguishing species in this group, namely pedicel width, stamen length, and size and shape of non-infloresence leaves. Pedicel width was mentioned qualitatively in the previous revision (Bates, 1973); Bates used the terms "slender", "filiform", and "stout" to describe pedicel thickness in some species descriptions, but the feature was not measured quantitatively as part of his study and it was not used as a distinguishing character in the key to species. Similarly, stamen length was mentioned in species descriptions, but Bates did not recognize it as a useful character for distinguishing species. Previous work also did not emphasize leaf characters as taxonomically useful because the leaves are superficially similar (broadly ovate with cordate bases and mostly entire margins) and appear to intergrade. However, when correlated with other features, characters such as leaf size and leaf breadth can provide insight into species boundaries in the genus. A good example illustrating this point concerns OTUs 1 and 4, both of which have traditionally been included in *B. integerrima*. When the pedicel width at its thickest point (PedWidMax) and leaf breadth (LeafBroad) are used as single variables, they do not differ significantly between OTUs 1 and 4 (data not shown). However when PedWidMax and leaf breadth (LeafBroad) are combined as a ratio, a significant difference in means is revealed (Fig. 2).

Though new characters were discovered, some of the characters traditionally used to distinguish species remain useful in the *B. integerrima* complex, specifically pedicel length and the length of the calyx lobes. Others characters may not be useful for differentiation on their own but provide adequate separation when expressed in relation to another character (e.g., ratio of the length of staminal column to pedicel width, or leaf breadth to stamen length).

Taxonomy

The following list includes all species that are here recognized in the *Bakeridesia intergerrima* complex, with brief descriptions of those that are new. Measurements included in the new species diagnoses are based on all available specimens, not just those used in the phenetic analyses (specimens used in the phenetic analysis are indicated with an asterisk under "Additional specimens examined", unless otherwise noted). All of the species listed below display the following suite of characteristics, which vary elsewhere in the genus: glabrous styles, 3 ovules per carpel and a well-developed lacerate wing on the fruits (though the latter two features are unknown in OTU 14 due to limited material).

Bakeridesia chittendenii (Standl.) Donnell, **comb. nov.** *Abutilon chittendenii* Standl., Trop. Woods. 10: 5. 1927. Type: Honduras. Yoro: Olanchito, dry region, 14 Feb 1927, *S. J. Record & H. Kuylen H. 63* (holotype: US*; isotypes: A, [online image], GH [online image], NY, WIS [online image]). (**OTU 1)**

Additional specimens examined. HONDURAS. Olancho: Matorrales de Quebrada, Jaguitas cerca de Santa María del Real, Valle de Catacamas, 500 m, 29 Apr 1957, *Molina R. 8422* (F, NY). **Yoro:** Município Olanchito, 3 mi W of Olanchito, 15°28'59"N, 86°36'11"W, 200 m, 1 Jul 1994, *Davidse et al. 35493* (MO, MEXU); Near small town of Arenal, Aguán Valley, 320 m, 21 Apr 1983, *Hughes 347* (MO*).

NICARAGUA. Estelí: Cuesta Cucamonga, N of Estelí, 13°15'N, 86°21'W, 800 m, 30 May 1985, *Davidse et al. 30687* (BH, MO); Escuela de Agricultura, 2 km sobre la carretera a la Laguna de Miraflores, "Llano el Duaque", 13°15'N, 86°22'W, 850–870 m, 17 Apr 1981, *Moreno 8360* (MO*, NY), *Moreno 8361* (MO, NY); Ca. km 178.5 on Hwy 1, between Condega and Estelí, ca. Km 167 on Hwy 1, ca 13°19'N, 86°22'W, 640 m, 31 May 1980, *Stevens et al. 17376* (MEXU*, MO*, NY!); 15.8 km N of entrance to Estelí, ca. 13°15'N, 86°22'W, 800–825 m, 31 May 1980, *Stevens et al. 17388* (MO*, NY).

Bakeridesia integerrima (Hook. f.) D. M. Bates, Gentes Herb. 10(5): 467. 1973. *Sida integerrima* Hook. f., Bot. Mag. 74: 4360. 1848. *Abutilon integerrimum* (Hook. f.) Triana & Planch. Ann. Sci. Nat., Bot., ser 4, 17: 182. 1862. Type: Hooker's plate and description (lectotype, designated by Bates, 1973) [not *Funcke 753* (K) nor *Linden 1508* (K) cited by Hooker; see Bates, 1973, p. 470]. (**OTU 2**)

Abutilon aurantiacum Linden, Cat. Pl. Exot. (Linden) 13:11. 1858, nom. nud.

Abutilon aurantiacum Linden ex Turcz., Bull. Soc. Imp. Naturalistes Moscour 31: 204. 1858, nom.illegit. superfl.

Abutilon aurantiacum Linden & Planch., Pl. Columb. (Linden) 1: 44. 1863. Syntypes: Colombia: without definite locality, 1842–1843, *J. J. Linden 1508* (GH*, K, MA [online image]); Venezuela: Carabobo. Prés de Puerto Cabello, 1842–1843, *Funck 753* (not located).

Abutilon goudotianum Triana & Planch. Ann. Sci. Nat., Bot., ser 4, 17: 184. 1862. TYPE: Colombia: Bogotá, entre Tocaima et Magdalena, 1844, *Goudot s.n.* (lectotype, designated by Fryxell, 2002: P-n.v.).

*See Donnell (2012) for an in-depth discussion of the complicated nomenclatural history of *Bakeridesia integerrima.*

Additional specimens examined. COLOMBIA. Cundinamarca: Chocantlá, 1933, *Arbeláez 2157* (US*); Hacienda El Cucharo, between Tocaíma and Pubenza, 350 m, 7 May 1944, *Killip et al. 38282* (US). **Valle de Cauca**: Rio Dagua, W Andes of Calí, 400–1000 m, *Lehmann 5432* (F, NY, US); La Parada, Tocaíma, 500 m, 1851-1857, *Triana s.n.* (K).

ECUADOR. Imbabura: Carretera Salinas-Lita, 1440–1550 m, 25 Feb 1988, *Panero & Gómez 1095* (NY).

VENEZUELA. Aragua: Distrito Giradot, on edge of Cata, 20 Jan 1984, *Fryxell & Burandt 4316* (BH, NY). **Carabobo:** El Palito, Puerto Cabello, 0 m, 4 Jan 1939, *Alston 6063* (NY[2], US); Around El Palito, near Puerto Cabello, 0–30 m, 2 Jul 1913, *Pittier 6431* (NY); Hacienda Taborda, near El Palito, on the road from Valencia to Puerto Cabello, 0–200 m, 31 Dec 1917, *Pittier 7693* (A, GH*, US); Near El Palito, Carabobo, 30 Jan 1928, *Pittier 13063* (A*, F, K*, MO, NY*, US). **Falcón:** Distrito Bolivar, Limestone ridges ca. 100 m W of Cave of Carrizalito, Sierra de San Luis, 1200 m, 19 Oct 1985, *van der Werff & Wingfield 7433* (F*, MO, NY, TEX). **Federal:** 10 km NE of Carayaca, 420 m, 17 Dec 1973, *Davidse 5102* (LL*, MO*, NY*). **Lara:** Duaca, 1893–1894, *Macquerys s.n.* (NY*, US*). **Sucre:** Cumanacoa, 1893, *Macquerys 783* (A, K, NY*, US*).

Bakeridesia huastecana Donnell, **sp. nov.** Type: Mexico. Tamaulipas: ca. 18 km N of Aldama at K55, 600 ft, 30 Oct 1972, *P. Fryxell & D. M. Bates 2189* (holotype: BH [51458]; isotypes: BH [51455], K*, LL*, NY*). **(OTUs 4 and 13)** (Fig. 8)

Leaf blades to 19 cm long and 16 cm broad, usually greatly reduced in size towards shoot apex and in inflorescence. Inflorescences axillary, often on short, sometimes branched shoots, composed of repeating units of 1 or 2 flowers. Flowers not nodding in bud. Calyx lobes not reflexed in flower. Pedicels 0.4–1.1 mm thick and 0.5–3(–4.5) cm long. Stamens 3–7 mm long. Mericarps brittle in texture, 8–11 mm long, the lacerate wing small and deciduous, less than 1 mm broad.

Distribution and ecology.—*Bakeridesia huastecana* is found in the Mexican states of San Luis Potosí, Veracruz and Tamaulipas. It grows in fencerows, along roadsides and on margins of seasonally dry deciduous forest and thorn scrub. It is found at relatively low altitudes, from sea level to 370 m.

Etymology.—The specific epithet refers to La Huasteca, the region of eastern Mexico where the species is most abundant.

Phenology.—*Bakeridesia huastecana* has been collected in flower from September to May.

Additional specimens examined*. MEXICO. San Luis Potosí: Between Tamuín pyramids & Sagrada Familia, Tanquian Município, 29 May 1979, *Alcorn 3108b* (NY, TEX); Km 83 of Tampico-Valles highway, 29 May 1948, *Atchinson 440* (BH); Mante Valles-Tampico Highway, 1 May 1952, *Chapman 3055* (MICH¤, US¤); 11 miles S of Tamuín on road to San Vicente or Tancuayalab, 1 May 1960, *Crutchfield & Johnston 5301-II* (MICH¤, TEX¤); 12 miles SE of Tamuín near Rancho El Fiscal, 400 ft, 18 June 1969, *Fryxell 1081* (MICH, NY, TEX, UC), *Fryxell 1082* (BH, GH, NY); Tampaom tramo de Casa Blanca a Ebano, Município Tamuín, 22°04'N, 98°30'W, 30 m, 24 Feb 1987, *Gutierrez B. 2320* (XAL); Las Palmas, 300 ft, 27 Apr 1894, *Pringle 5768* (GH, US); 3 km al NW de Ébano, 100 m, 22 Jan 1956, *Rzedowski 7077* (MICH¤, TEX¤); Ébano, 30 m, 13 Mar 1960, *Rzedowski 12297* (NY)¤; E of Tamuín near Valles at whitewing dove water holes, 165 ft, 17 May 1949, *Saunders 67* (US). **Tamaulipas**: 13 miles N of Aldama on road to Soto la Marina, 25 Sep 1960, *Crutchfield & Johnston 5713* (MICH, TEX); Between Manuel and Altamira (near Tampico), 27 Sep 1966, *Fryxell 513* (BH, F, NY*); Near Altamira (ca. 60 km N of Tampico) at K92, 12 Mar 1968, *Fryxell 648* (MICH, NY, TEX); Near Altamira (ca. 60 km N of Tampico), 12 Mar 1968, *Fryxell 649* (MICH, NY); Município Soto La Marina, Tepeguaje, 10–20 m, 16 Sep 1981, *Fryxell 3671* (MICH*, NY, TEX*); 11 miles SE of Manuel at K92, 18 Jan 1969, *Fryxell & Bates 834* (BH, NY(2)); Ca. 40 km N of Aldama on side road

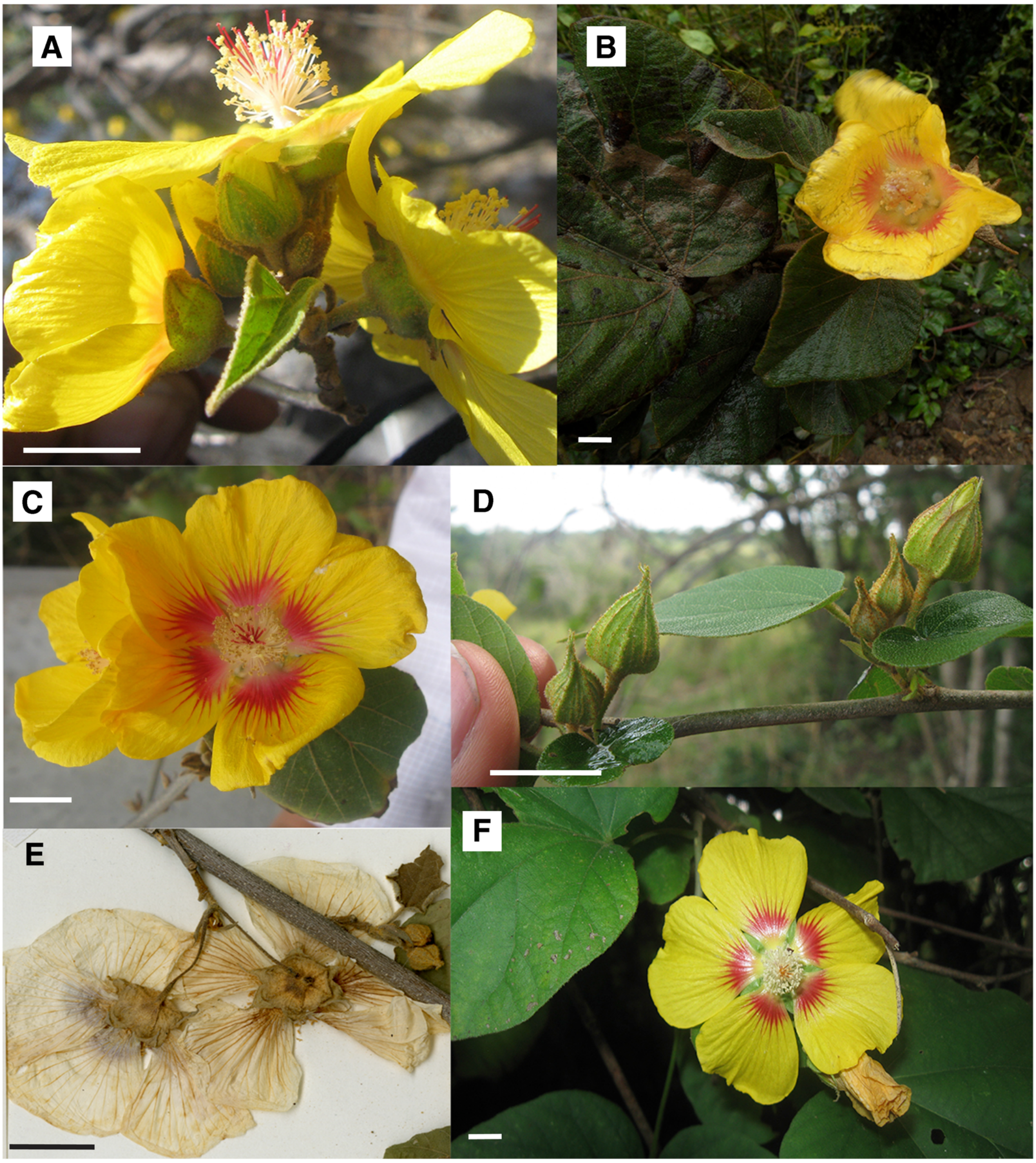

FIG. 8. *Bakeridesia zapoteca* (A–C) and *B. huastecana* (D–F). **A.** Terminal flower cluster; note short, thick pedicels. **B.** Flower and leaves. **C.** Flower. **D.** Buds; compare pedicel length in bud to flowering pedicels in A. **E.** Axillary flower cluster; note slender pedicels (from *Fryxell & Bates 942*, TEX). F. Flowers and leaves. Scale bars represent 1.5 cm. Photos by A. Donnell.

to east, 400 ft, 30 Oct 1972, *Fryxell & Bates 2193* (LH, MICH, MO, NY[*]); 29 km N of Aldama at K65, 1200 ft, 29 Mar 1974, *Fryxell & Magill 2356* (MO[¤], NY); 1 km al N De Esteros, Estación de microondas, Municípío Altamira, 29 Sep 1983, *Hernandez 724* (F); 5 km al oeste del Tepeguaje a lado de la carretera, 0 m, 25 Apr 1986, *Jones 100* (MEX, MO); Rancho de Barberena, 3 Aug 1939, *LeSueur 751* (GH(2), TEX); Rancho Los Alados, Cerro del Metate, 190 m, 25 Dec 1971, *Martínez Ojeda 281* (MEXU, MICH, NY); 18 km al E de Aldama sobre la carretera Aldama-Barra del Tordo, 230 m, 10 Dec 1992, *Mora-Lopez 246* (XAL); Rancho Santa Gertrudis, ca. 90 km NW of Tampico, 3 Dec 1969, *Percival s.n.* (NY); along Mex. 180, 19 mi N of Aldama, 27 May 1971, *Ward 7762* (MICH[*]); Km 93 between Tampico and Manuel, 28 Nov 1967, *Wilson 67-16* (BH, NY[*]). **Veracruz**: El Higo, 10 Apr 1979, *Alcorn 2650* (NY, TEX); Municípío El Higo, Ejido Mundo Raro, 9 km antes de llegar a El Higo, carretera Panuco-Tempoal, 2.5 km del entronque (turnoff) El Higo-Tempoal, 21°45.86'N, 98°21.51'W, 54 m, 26 Jan 2010, *Donnell & R. Madrigal-Chavero 66* (NY*, XAL) & *Donnell & R. Madrigal-Chavero 67* (MEXU*, MO*, NY*, XAL); Municípío Pánuco, camino de terraceria a Las Animas lado derecho de la carretera Panuco-Ebano, antes de la caseta, 22°06'58.7"N, 98°08'02.3"W, 20 m, 27 Jan 2010, *Donnell & R. Madrigal-Chavero 68* (XAL), *Donnell & R. Madrigal-Chavero 69* (NY*, XAL), *Donnell & R. Madrigal-Chavero 70* (XAL); Municípío Pánuco, orilla de la Carretera de Pánuco a Ebano, antés de la caseta, 22°07'40.5"N, 98°08'11.9"W, 27 Jan 2010, *Donnell & R. Madrigal-Chavero 71* (NY*, XAL); Municípío Pánuco, orilla de la carretera Ebano-Estación Manuel, 22°14'56.9"N, 98°22'16.5"W, 48.6 m, 27 Jan 2010, *Donnell & R. Madrigal-Chavero 72* (NY*, XAL); Between Tantoyuca and Tempoal, 15 Apr 1967, *Fryxell 599* (F, MO, NY); 25 miles S of Pánuco, 300 ft, 18 Jan 1969, *Fryxell & Bates 845* (BH[2]*, NY); 26 miles S of Pánuco (2 miles S of El Higo junction), 600 ft, 28 Jan 1969, *Fryxell & Bates 942* (MICH*, NY, TEX); 5 km del entronque al Higo direccion ejido San Andres, Municípío Tempoal, 21°49'N, 98°24'W, 20 m, 10 June 1986, *Gutierrez B. & Montoya 1833* (XAL); Orilla de la colonia "Media Camino" dirección Chicojilote al N de Ébano, Municípío Pánuco, 22°15'N, 98°22'W, 30 m, 13 Jan 1987, *Gutierrez B. 2207* (XAL); 6 km SW del Molina, tramo Panuco-Tempoal, Municípío Pánuco, 22°50'N, 98°20'W, 30 m, 16 Jan 1987, *Gutierrez B. 2292* (XAL); 3 km W of hwy Mex. 105 on road to El Higo, 6 km E of El Higo, Municípío Tempoal, 21°47'N, 98°23'W, 40 m, 25 June 1982, *Nee & Diggs 24621* (F, XAL); 41 km SSW of bridge at Pánuco, along Hwy. 105, Municípío Tempoal, 21°44'N, 98°21'30"W, 50 m, 4 Jan 1981, *Nee et al. 19512* (F); 3 km E of Tamaulipas-Veracruz state line and 3 km S of the Ebano-Tampico highway, 7 km SE of Ebano, Municípío Pánuco, 22°10'N, 98°19'W, 55 m, 7 Mar 1983, *Nee & Taylor 25795* (F, MO, NY, TEX).

***Specimens placed in OTU 4 in the phenetic analysis are indicated by an asterisk; those placed in OTU 13 are indicated by the currency sign. (¤).**

Bakeridesia molinae D. M. Bates, Gentes Herb. 10 (5): 466–467. 1973. Type: Honduras. Tegucigalpa: Río Guarabuquí, terrenos de los indios Xicaques del La Montaña de La Flor, 1800 m, 2 Jun 1950, *A. Molina R. 3049* (holotype: GH; isotypes: EAP [online image] F, US*). **(OTU 5).**

Additional Specimens Examined. HONDURAS. Comayagua: Zona xerofítica de Plan Colorado, 12 km de Comayagua, 700 m, 28 May 1956, *Molina R. 7309* (F*, GH*). **El Paraíso:** Municípío de Morocelí, loc. Quebrada El Carrizal cerca El Plan, ± 2 km al E de El Plan, 17 Feb 2002, *Linares 5701* (MEXU). **Morazán:** Río Guarabuquí, terrenos de los indios Xicaques de Montana de La Flor, 1800 m, 2 June 1950, *Molina R. 3055* (F, GH*, US*).

Bakeridesia jaliscana Donnell, **sp. nov.** Type: Mexico. Jalisco: Coastal plain, 3 miles north of the road junction at the western end of Bahía de Navidad, elevation 50 m or less, 12 Dec 1959, *R. McVaugh & W. N. Koelz 1718* (holotype: MICH*; isotypes: NY*, TEX*). **(OTU 6).** (Fig. 9)

Leaf blades to 17 cm long and 15 cm wide, not greatly reduced in size towards shoot apices and in inflorescence. Inflorescences borne on short-peduncled axillary shoots bearing 1 or more units of 1–4 (usually 2 or 3) flowers, though the flower units sometimes sessile in leaf axils or terminal on woody axillary shoots. Flowers not usually nodding in bud. Calyx lobes not reflexed in flower. Pedicels 0.7–1.5 mm thick and (1–) 1.5–5 cm long. Stamens (5–) 7–10 mm long. Mericarps somewhat rigid in texture, 9–13 mm long, the lacerate wing not early deciduous, 1–1.5 mm broad.

Distribution and ecology.—*Bakeridesia jaliscana* is found only in the coastal regions of the Mexican states of Jalisco and Colima. It grows along roadsides and streambanks, in disturbed deciduous or semidecidous forest and in second-growth thickets. It has been collected from sea level to 135 m.

Etymology.—The specific epithet refers to the Mexican state of Jalisco, where the species is most abundant.

Phenology.—*Bakeridesia jaliscana* has been collected in flower in December, January, June and July.

Additional specimens examined. MEXICO. Colima: Municípío Manzanillo, Sitio 6, 1.8 km en linea recta al SO de La Central, 19°8'4"N, 104°26'29"W, 29 Aug 2002, *Ibarra-Manríquez 5853* (MO); Hills west of Manzanillo Bay, 5 miles west of Santiago, thence 1 mile southwest on road to Peña Blanca, 60 m, 24 Jul 1957, *McVaugh 15724* (BH, IBUG, MICH*, NY). Rocky hills at road-summit, 8 miles west-northwest of Santiago, road to Cihuatlán, Jalisco, 135 m, 25–26 Jul 1957, *McVaugh 15767* (MICH, NY, TEX). **Jalisco:** Municípío La Huerta, Estación de Biología Chamela, 19°30'N, 105°03'W, 9 Jun 1985, *Ayala & Lott 39* (GH*, K, MEXU*, NY*, TEX*, XAL*); Municípío La Huerta, carr. 200, km 34–35, 19 Jan 1985, *Bullock 1551* (LL, MICH*, MO*, NY*, TEX); Municípío La Huerta, Rancho Cuixmala, Arroyo Cajones, along the road to Cumbres 1 from Station 45, 19°26'30"N, 104°59'W, 3 Nov 1991, *Lott 2049* (NY, TEX). Estación de Investigación, Experimentación y Difusión Chamela, Municípío La Huerta, 29 Jul 1981, *Magallanes 3019* (MEXU[2] *, NY*). Municípío La Huerta, Chamela, cerca viva junto al aeropuerto, 7 Jun 1982, *Magallanes 3609* (NY*).

Bakeridesia zapoteca Donnell, **sp. nov.** Type: Mexico. Oaxaca: Municipio de Yautepec, a 6 km al S. de El Camarón, 1090 m, 25 Nov 1977, *A. Delgado S., J. García P. & R. Hernández M. 723* (holotype: NY*; isotype: MO*). **(OTU 7).** (Fig. 8)

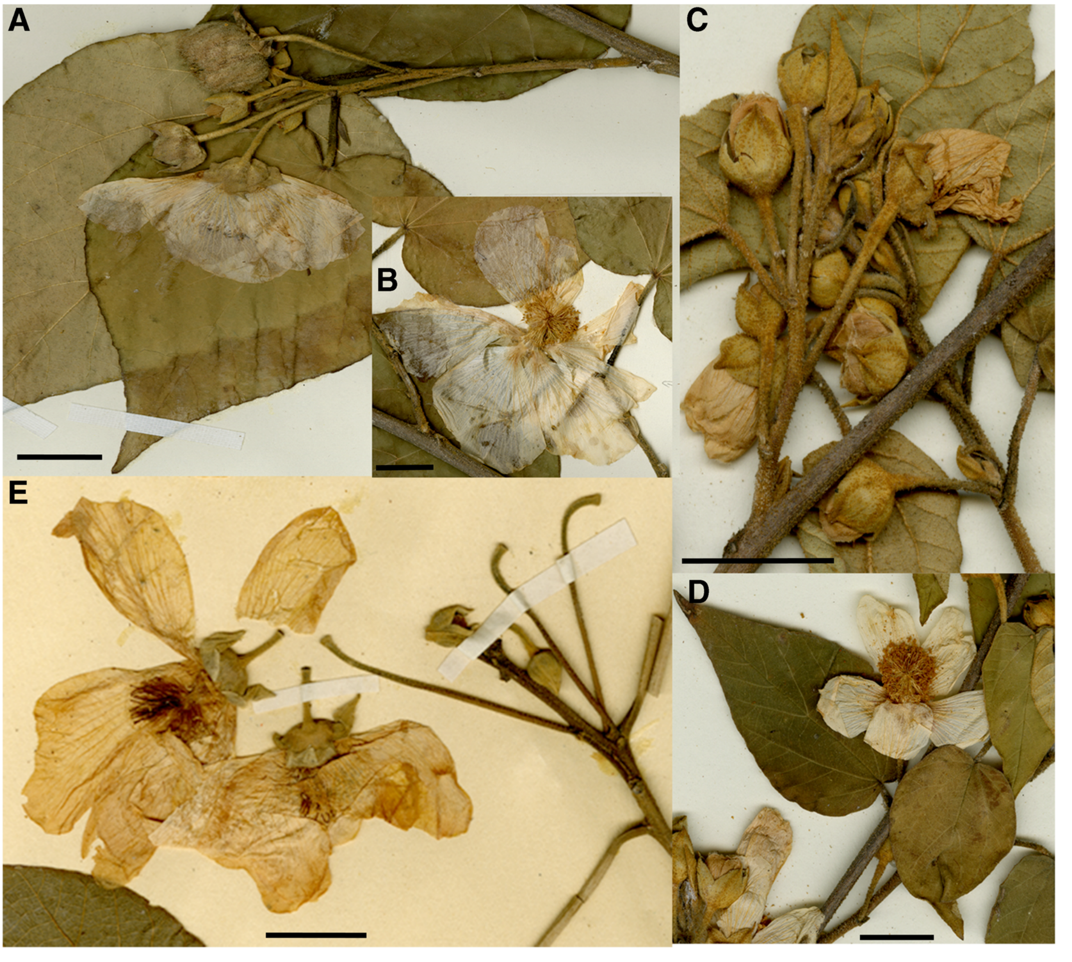

FIG. 9. *Bakeridesia jaliscana* (A–B, from the holotype). *B. parvifolia* (C–D, from the isotype, TEX). *B. guerrerensis* (E, from the holotype). **A.** Inflorescence borne on non-lignified, axillary shoot. **B.** Flower showing relatively long stamens. **C.** Axillary inflorescence showing densely-packed flower clusters and relatively short peduncle; compare to A. **D.** Flower and leaves; note size of petals and leaves relative to A and B. **E.** Terminal inflorescence; note reflexed calyx lobes and nodding flower buds. Scale bars represent 1.5 cm.

Leaf blades to 18 cm long and 16 cm broad, substantially reduced in size in inflorescence, but not towards vegetative shoot apices. Inflorescence dense, composed of tightly packed units of 1–2 (rarely 3) flowers. Flowers not nodding in bud. Calyx lobes not reflexed in flower. Pedicels 1.2–1.9 mm thick and 0.5–3.2 cm long. Stamens (2–)4–7 mm long. Mericarps somewhat rigid in texture, (10–)12–17 mm long, the lacerate wing not early deciduous, 1–2 mm long.

Distribution and ecology.—Bakeridesia zapoteca has only been collected from the Isthmus of Tehuantepec in Oaxaca, Mexico. It can be found in seasonally dry deciduous forest, oak-pine forest and along roadsides at elevations of 230–1300 m.

Etymology.—The specific epithet honors the Zapotec indigenous group, whose culture and language are particularly strong in the Isthmus of Tehuantepec, where *B. zapoteca* is endemic.

Phenology.—Bakeridesia zapoteca has been collected in flower in October–December, February and March, and sprodically in May and June.

Additional specimens examined. MEXICO. Oaxaca: Município Santiago Lachiguiri, Distrito Tehuantepec, recorrido de Crucero Guadalupe a las cuevas, 12.5 km al NE de Santiago Lachiguiri, 16°44'N, 95°31'W, 120 m, 10 May 1991, *Campos V. 3677* (MEXU*); Município Guevea de Humboldt, Distrito Tehuantepec, Guevea de Humboldt (Pueblo Nuevo), 16°47'N, 95°21'W, 655 m, 10 Feb 1994, *Campos V. 5152* (MEXU); Carretera Matias Romero a Juchitán, desviación a Chivela al SW de Matias Romero (km.

1 de camino a Chivela), 260 m, 15 Feb 1982, *Cedillo T. 1069* (MEXU, NY); Munícipio El Barrio de La Soledad, lado del camino de Almoloya a La Laguna, ~3 km de Almoloya 16°47'13.9"N, 95°04'24.4"W, 236 m, 3 Mar 2010, *Donnell & R. Madrigal-Chavero 107* (NY*, XAL); Munícipio El Barrio de La Soledad, al lado del camino de Almoloya a La Laguna, al entronque La Laguna-Basurero, ~4 km de Almoloya 16°47'24.5"N, 95°04'35"W, 250 m, 3 Mar 2010, *Donnell & R. Madrigal-Chavero 108* (NY*, XAL); Munícipio San Bartolo Yautepec, lado de la carretera Tehuantepec-Oaxaca en arroyo temporal (seco), ca. 4.5 km al S de El Camarón, 16°33'04.6"N, 95°59'51.6"W, 957 m, 8 Mar 2010, *Donnell & R. Madrigal-Chavero 114* (XAL); Munícipio San Pedro Totolapan, lado de la carretera Tehuantepec-Oaxaca al SE de San Juan Gracia, cerca a Las Cantiles 16°37'52.8"N, 96°03'21.3"W, 776 m, 8 Mar 2010, *Donnell & R. Madrigal-Chavero 115* (XAL); Munícipio El Barrio de La Soledad, camino pasando el pueblo Almoloya, cerca de tiradero de basura, sobre la carretera, antés del entronque a La Laguna, 28 Dec 2011, *Donnell & R. Madrigal-Chavero 122* (XAL); Municipío El Barrio de La Soledad, pasando Almoloya, entronque al esquina mano derecha, rumba a la cementera Cruz Azul, 28 Dec 2011, *Donnell & R. Madrigal-Chavero 123* (XAL); Munícipio Santiago Lachiguiri, 6.5 km. al NE de Santiago Lachiguiri, al lado del camino, 16°42'49.7"N, 95°31'45.2"W, 3 Jan 2012, *Donnell & H. Gomez-Dominguez 128* (HEM); Munícipio Santiago Lachiguiri, 8 km. al NE de Santiago Lachiguiri, 16°43'31.5"N, 95°51'45"W, 3 Jan 2012, *Donnell & H. Gomez-Dominguez 130* (HEM, NY*); Munícipio El Barrio de la Soledad, Almoloya, ca. 18 km. directo al Sur de Matias Romero, 300 m, 13 Nov 1978, *Koch et al. 78283* (BH, NY*); Cerro Verde, a 1.75 km en línea recta al NE de Nizanda, Munícipio de Asunción Ixaltepec, Distrito de Juchitán, 16°39'14"N, 94°59'7"W, 300 m, 18 Feb 2001, *Pérez-García 2046* (MEXU, MO); Del Mango al Ocotal N a S, Cerro Guiengola, Distrito Tehuantepec, 980 m, 13 Jun 1986, *L. Torres C. 410* (NY); Subida al Cerro Guiengola por la ladera S, Distrito Tehuantepec, 16°21' y 16°30'N, 95°19' y 95°24'W, 6 Nov 1986, *L. Torres C. 699* (MEXU*, NY); "Buenavista", ladera S subiendo por la fábrica de cal, 16°21' y 16°30'N, 95°19' y 95°24'W, 30 Apr 1987, *L. Torres C. 855* (NY, XAL); Cerro Guiengola, 1 km al S de Guevea de Humboldt, Distrito Juchitán, 16 Mar 1983, *R. Torres C. 2513* (F, MEXU, MO, NY*); 8.9 km al N de Lachiguiri, Distrito de Tehuantepec, 10 Dec 1983, *R. Torres C. 4330* (NY); Torre de Microondas de Jalapa del Marquéz, Distrito Tehuantepec, 25 May 1984, *R. Torres C. 5142* (MEXU, NY); Muncípio Tehuantepec, Distrito Tehuantepec, Cerro Guiengola, 11 km al NO de Tehuantepec, 16°21' N, 95°19'W, 26 Oct 1991, *R. Torres C. 14062* (MO*).

Bakeridesia bakeriana (Rose) D. M. Bates, Gentes Herb. 10 (5): 473. *Abutilon bakerianum* Rose, Contr. U.S. Natl. Herb. 5:133. 1897. Type: Mexico. Oaxaca: Tomellin Canyon, 3,500 ft., 1 Dec 1895, *C.G. Pringle 6278* (lectotype designated D. M. Bates [1973: 473]: US; isotypes: A*, AC [online image], BKL [online image], CAS [online image], CM [online image], COLO [online image], F*, E [online image], GH*, GOET [online image], JE [online image], K [online image], MEXU [online image], M [online image], MIN [online image], MO, MSC-n.v., NDG [online image], NY[2], PH [online image], S [online image], UC, US).

Bakeridesia subcordata (Hochr.) D. M. Bates, Gentes Herb. 10 (5): 476. 1973. *Robinsonella subcordata* Hochr., Annuaire Conserv. Jard. Bot. Genéve 21: 449. 1920. Type: Mexico. Oaxaca: Jayacatlán, Mar 1910, *H. H. Rusby s.n.* (holotype: NY). **(OTU 9)**

Additional specimens examined. MEXICO. Oaxaca: 16 km al S de Dominguillo, 29 Aug 1980, *Chiang 1804* (NY); Cuesta Quiotepec, Distrito de Cuicatlán, 1300 m, 16 Jul 1920, *Conzatti 4030b* (MEXU, US). Cuesta inferior de Salomé, Distrito de Cuicatlán, 1300 m, 15 Apr 1937, *Conzatti 5320* (LL*, MICH*); Munícipio San Juan Bautista Cuicatlán, entre la Buena Vista y la brecha antigua que va a San Juan Coyula, pendientes al lado del camino, 17°55'30.9"N, 96°56'54.9"W, 1297 m, 9 Mar 2010, *Donnell & R. Madrigal-Chavero 119* (MEXU, MO, XAL); A 4.3 km en línea recta al NW (285) de San Juan Coyula, sobre brecha, 17°55'30.5"N, 96°57'0.9"W, 1288 m, 8 Jul 2004 *García 452* (IBUG*); Cañon above Dominguillo, 2 Nov 1894, *Pringle 5656* (US*); Jayacatlán, Mar 1910, *Rusby s.n.* (NY); Loma de Buena Vista, 19 km al E de Quiotepec, 17°55'N, 96°56'W, 1300 m, 5 May 1990, *Salinas T. 5419* (MEXU, MO, XAL); 9 km al NE de Santiago Quitepec, brecha a San Juan Coyula, Distrito Cuicatlán, Munícipio San Juan Bautista Cuicatlán, 17°55'22"N, 96°56'35"W, 1239 m, 26 Jan 1995, *Salinas T. 8118c* (MEXU*); Jayacatlán, 4000 ft, 3 Jun 1894, *Smith 24* (GH*, US); Jayacatlán, 4300 ft, 29 July 1895, *Smith 547* (GH*, US*).

Bakeridesia parvifolia Donnell, **sp. nov.** Type: Mexico. Colima: Dry hills, 15–25 km northwest of Santiago, road to Cihuatlán, Jalisco, 50–100 m, 16 Mar 1965, *R. McVaugh 23013* (holotype: NY*; isotypes: TEX*, MICH*). **(OTU 12)** (Fig. 9)

Leaf blades to 8 cm long and 5.5 cm broad, reduced somewhat in size in inflorescences but not towards shoot apices. Inflorescences, composed of several repeating units of 1–4 flowers separated by relatively short internodes. Flowers not nodding in bud. Calyx sometimes reflexed in flower. Pedicels 0.8–1.3 (–1.6) mm thick and 2–4 cm long. Stamens 6–8 mm long. Mericarps somewhat rigid-textured, 5–7 mm long, the lacerate wing early deciduous, less than 1 mm broad.

Distribution and ecology.—*Bakeridesia parvifolia* has only been collected from coastal Colima, Mexico on "dry hills" in deciduous forest between 50 and 100 m above sea level.

Etymology.—The specific epithet is derived from the Latin for small leaves.

Phenology.—*Bakeridesia parvifolia* has only been collected in flower in March.

Bakeridesia guerrerensis Donnell, **sp. nov.** TYPE: Mexico. Guererro: Santa Rosa, prés Aguila, 650 m., 16 Jul 1898, *Eug. Langlassé 249* (holotype: K*; isotype: GH, n.v.). (**OTU 14**) (Fig. 9)

Leaf blades to 16 cm long and 15 cm broad, apparently not reduced in size in inflorescences or towards shoot apices. Inflorescence composed of several units of solitary or paired flowers. Flowers nodding in bud. Pedicels 0.9–1 mm thick and 4.5–5.2 cm long. Calyx lobes reflexed in flower. Stamens 8 mm long. Mericarps unknown.

Distribution and ecology.—*Bakeridesia guerrerensis* has only been collected from the Mexican state of Guerrero at an elevation of 650 m.

Etymology.—The specific epithet refers to the Mexican state of Guerrero, the site of the sole collection of this species.

Phenology.—*Bakeridesia guerrerensis* has been collected in flower in July.

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Appendix

Characters measured for phenetic analysis of the *B. integerrima* complex. All floral characters were measured on the largest flower on the specimen. If the character was not easily accessible on the selected flower, the second largest flower was selected.

A. Raw variables and ratios treated as raw variables (i.e., they are subsequently used in other ratios):

PedLn – length of pedicel (cm)

StamCol – length of staminal column, not including stamen cluster (cm)

CalyxLn – length from base of calyx to apex (cm)

CalLobWid – width of calyx lobe at broadest point (cm)

CalLobLn – length of the calyx lobe (cm)

PerCalyxFr – percentage of the calyx that is free from the tube. Calculated by dividing CalLobLn by Calyx Ln and multiplying by 100.

StamenLn – length of longest stamen (mm)

PedWidMax – width of the pedicel at the broadest point (mm)

PedWidMin – width of the pedicel at the narrowest point (mm)

NumCarpels – number of carpels, inferred from style number.

PetalLn – length of the petal from base to apex (cm)

ArticLn – length from base of flower to articulation on pedicel (cm).

LeafLn – leaf length, measured from leaf base to apex. The value is the average from the two largest vegetative leaves if more than one leaf is present (cm).

LeafWid – leaf width, measured at the widest point on the leaf. The value is the average from the two largest vegetative leaves if more than one leaf is present (cm).

LeafSize – a rough measure of relative leaf size, calculated by multiplying LeafLn by LeafWid and dividing the product by 10

LeafBroad – a measure of relative leaf breadth as a component of leaf shape, calculated by dividing LeafLn by LeafWid.

LfLobeLn – length of leaf lobe. Measured from point where the petiole meets the base of the midrib to the base of the leaf lobe at longest point. The value is the average from the two largest vegetative leaves if more than one leaf is present (cm).

LobToBl – length of leaf lobe relative to blade. Calculated by dividing LfLobeLn by LeafLn (cm).

B. Ratios of variables listed in part A, calculated by dividing first variable by the one following the colon:

PedLn:PedWidMax	LeafBroad:PedLn
Pedln:PedWidMin	LeafBroad:CalyxLn
CalyxLn:PedWidMax	LeafBroad:StamCol
CalyxLn:PedWidMin	LeafBroad:StamenLn
StamCol:PedLn	LeafBroad:PedWidMax
StamCol:CalyxLn	LeafBroad:PedWidMin
StamCol:PedWidMax	LeafBroad:PetalLn
StamCol:PedWidMin	LeafBroad:LobToBl
StamCol:StamenLn	LeafSize:PedLn
CalyxLobLn:CalLobWid	LeafSize:StamCol
PetLn:PedLn	LeafSize:CalyxLn
PetalLn:CalyxLn	LeafSize:StamenLn
PetalLn:PedWidMax	LeafSize:PedWidMax
PetalLn:PedWidMin	LeafSize:PedWidMin
ArticLn:PedLn	LeafSize:PetalLn
ArticLn:PedWidMax	LeafSize:LobToBl
ArticLn:PedWidMin	