

## RE-ESTABLISHMENT OF *AECHMEA LAXIFLORA* (BROMELIACEAE, BROMELIOIDEAE) BASED ON MORPHOLOGICAL AND PHYLOGENETIC EVIDENCE, WITH NOTES ON ITS GEOGRAPHICAL DISTRIBUTION

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### Abstract

**Background:** Previous phylogenetic analyses suggested that *Aechmea bracteata* is not a monophyletic species, being each variety an individual lineage within the *Aechmea bracteata* complex.

**Hypothesis:** A phylogenetic analysis based on molecular data and a morphological analysis will provide evidence to support the taxonomic recognition of *A. bracteata* var. *pacifica* as a distinct species.

**Studies species:** *A. bracteata* var. *bracteata*, *A. bracteata* var. *pacifica* and related species.

**Study site and dates:** Mexico to Northern South America; 17 populations from Southeastern and Western Mexico. Analyses were performed between 2021 and 2023.

**Methods:** A linear morphometric analysis was conducted with 85 herbarium specimens testing 28 quantitative and three qualitative variables. Potential diagnostic traits were reviewed in living specimens. A phylogenetic analysis was performed with two nDNA markers (*ETS* and *g3pdh*) and one cpDNA marker (*trnL-F*). A total of 373 records were projected into biogeographical provinces of the Neotropics.

**Results:** The morphometric analysis allowed to separate each variety into a group, also, nine of the evaluated traits resulted statistically significant through a univariate analysis. Five additional diagnostic traits from the inflorescence and leaves were recognized. According to nDNA both taxa present reciprocal monophyly, however, cpDNA groups *A. bracteata* var. *pacifica* with Central American species, showcasing a potential hybrid origin. Geographically, the Sierra Madre del Sur acts as a barrier between both taxa.

**Conclusions:** Due to the gathered evidence is possible to recognize *A. bracteata* var. *pacifica* as an endemic species to Mexico, reestablishing the basionym *A. laxiflora*.

**Keywords:** *Aechmea bracteata* complex, Bromelioideae, endemic species, species delimitation, taxonomy.

### Resumen

**Antecedentes:** Análisis filogenéticos previos sugirieron que *Aechmea bracteata* no es una especie monofilética, siendo cada variedad un linaje individual dentro del complejo *Aechmea bracteata*.

**Hipótesis:** Un análisis filogenético basado en datos moleculares y un análisis morfológico proporcionarán evidencia para respaldar el reconocimiento taxonómico de *A. bracteata* var. *pacifica* como una especie distinta.

**Especies estudiadas:** *A. bracteata* var. *bracteata*, *A. bracteata* var. *pacifica* y especies relacionadas.

**Sitio de estudio y fechas:** México hasta el norte de Sudamérica; 17 poblaciones del sureste y occidente de México. Los análisis se realizaron entre 2021 y 2023.

**Métodos:** Se realizó un análisis morfométrico lineal con 85 especímenes de herbario evaluando 28 variables cuantitativas y tres cualitativas. Se revisaron potenciales caracteres diagnósticos en especímenes vivos. Se realizó un análisis filogenético con dos marcadores de ADNn (*ETS* y *g3pdh*) y uno de ADNcp (*trnL-F*). Se proyectaron un total de 373 registros en provincias biogeográficas del Neotrópico.

**Resultados:** El análisis morfométrico permitió separar cada taxón en un grupo, además, nueve de los caracteres evaluados resultaron estadísticamente significativos mediante un análisis univariado. Se reconocieron cinco caracteres diagnósticos adicionales de la inflorescencia y las hojas. Según el ADNn ambas variedades presentan monofilia recíproca, sin embargo, el ADNcp agrupa a *A. bracteata* var. *pacifica* con especies centroamericanas, mostrando un potencial origen híbrido. Geográficamente, la Sierra Madre del Sur actúa como una barrera entre ambos taxones.

**Conclusiones:** Debido a la evidencia recopilada es posible reconocer a *A. bracteata* var. *pacifica* como especie endémica de México, restableciendo el basiónimo *A. laxiflora*.

**Palabras clave:** Bromelioideae, Complejo *Aechmea bracteata*, delimitación de especies, especie endémica, taxonomía.

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**A***echmea bracteata* (Sw.) Griseb. is an epiphytic (occasionally saxicolous) tank forming bromeliad known by having a wide geographical distribution, occurring from northern Mexico to northern Colombia and Venezuela (Smith & Downs 1979, Utley & Burt-Utley 1994, Ramírez *et al.* 2004, Espejo-Serna & López-Ferrari 2018).

This species consists of two varieties (Smith & Downs 1979), the populations found alongside the Gulf of Mexico, the Yucatan Peninsula, Chiapas, eastern Oaxaca, Central America and northern South America belong to the typical variety of the species, *Aechmea bracteata* var. *bracteata*. On the other hand, the populations found alongside the Pacific slopes of Mexico, have been described as *Aechmea bracteata* var. *pacifica* Beutelsp. (Beutelspacher 1971, Smith & Downs 1979, Ramírez *et al.* 2004). The main differences between both varieties are found on the inflorescence, being described for *A. bracteata* var. *pacifica* a thin inflorescence up to 90 cm tall with primary bracts up to 10 cm in length, and distributed across the inflorescence to the apex, contrasting with *A. bracteata* var. *bracteata*, which is known for having inflorescences up to 2 meters tall, primary bracts varying from 10 to 24 cm in length, and a distribution of the primary bracts up to the middle portion of the inflorescence (Beutelspacher 1971, Smith & Downs 1979).

During the XIX century, a taxon named *Aechmea laxiflora* Benth. (*non Aechmea laxiflora* (Baker) Mez, *nom. illeg.*) was described from a specimen collected near Acapulco, Guerrero, Mexico (*Sinclair s.n.*, K) (Benthham 1846), however, this taxon was considered a synonym for *A. bracteata* by Smith (1958), and later, as a synonym for *A. bracteata* var. *pacifica* (Smith & Downs 1979), and being considered as it ever since; however, no further explanation for synonymy proposals is given in the aforementioned publications.

Sass & Specht (2010) performed an analysis of 150 species of *Aechmea* and allied genera based on the combination of three nuclear DNA markers (*ETS*, *g3pdh* and *rpb2*) and one chloroplast DNA marker (*trnL-F*) in order to assess their monophyly and analyze the biogeographic history of Core Bromelioids. In this analysis, most of the species or varieties were represented only by one individual; *Aechmea bracteata* var. *bracteata* and *A. bracteata* var. *pacifica* were found to be part of a clade with *Aechmea dactylina* Baker, *Aechmea pittieri* Mez, and *Aechmea pubescens* Baker. This clade was named as Central American Clade II due to all the included species occur in Central America, even though some of them have a wider distribution that includes Mexico (*A. bracteata* var. *bracteata* and *A. bracteata* var. *pacifica*) and northern South America (*A. bracteata*, *A. pubescens* and *A. dactylina*). However, *A. bracteata* turned out to be non-monophyletic, being the specimen of *A. bracteata* var. *pacifica* part of a clade, with an unidentified *Aechmea* specimen; that is sister to the rest of the species from the Central American Clade II, whereas *A. bracteata* var. *bracteata* is part of a clade that includes *A. pittieri*, *A. dactylina*, two unidentified *Aechmea* specimens, and *A. pubescens*, which was retrieved as the sister species of the *A. bracteata* var. *bracteata* specimen.

Later, Ramírez-Díaz (2019) performed a phylogenetic analysis in order to assess the phylogenetic position of Mexican and Central American distributed Bromelioids. This work included a phylogenetic analysis with the same markers used by Sass & Specht (2010) but with a higher number of species (210 spp.), as well as individual analyses for nDNA markers (*agt1* and *g3pdh*) and cpDNA markers (*rpl32-trnL* and *ycf1*) with fewer species but with several specimens per taxa to test the monophyly of various clades and species complexes. All the analyses by Ramírez-Díaz (2019) retrieved the monophyly of the Central American Clade II (*sensu* Sass & Specht 2010). According to the nDNA evidence by Ramírez-Díaz (2019), *A. bracteata* var. *bracteata* (four sampled individuals) and *A. bracteata* var. *pacifica* (three sampled individuals) possessed reciprocal monophyly, being each taxa recovered as monophyletic with respect to each other (Kizirian & Donnelly 2004); however, according to cpDNA evidence, *A. bracteata* var. *pacifica* seems to be more related to *A. pittieri* and *A. pubescens* (Ramírez-Díaz 2019), but this relationship is not well supported since the topology shows low resolution.

The species of the *Aechmea bracteata* complex share a similar morphology being epiphytic tank-forming bromeliads with ligulate to broadly triangular leaf blades, serrate margins, lax inflorescence arrangement, axis, and branches with white indument, red peduncle and primary bracts, and yellow (*A. bracteata* var. *bracteata* and *A. bracteata* var. *pacifica*), white (*A. dactylina*) or purple (*A. pittieri* and *A. pubescens*) flowers. Most of these species are native to Central America, although some of them possess wider geographical distribution ranges, occurring in Mexico and northern South America (Sass & Specht 2010, Ramírez-Díaz 2019). Both phylogenetic analyses by Sass & Specht

(2010) and Ramírez-Díaz (2019) do not support *Aechmea bracteata* as a monophyletic species, since its varieties seem to represent independent lineages within the *A. bracteata* complex.

This study aims to provide from different sources of evidence the monophyly of the varieties of *A. bracteata*, as well as providing evidence of *A. bracteata* var. *pacifica* as a distinct species by 1) comparing the morphology of *A. bracteata* var. *bracteata* and *A. bracteata* var. *pacifica* through a morphometric analysis of herbarium specimens and analyzing potential diagnostic traits in living specimens, 2) re-assessing the monophyly of *A. bracteata* by sampling several individuals from different populations of each variety, and 3) inferring which geographical areas could represent barriers between the distribution of these taxa.

## Materials and methods

*Specimen revision.* Specimens identified as *Aechmea bracteata*, *A. bracteata* var. *bracteata*, and *A. bracteata* var. *pacifica*, and housed at the herbaria CHIP, CICY, HGOM, HUAP, IBUG, INIF, MICH, UADY, UAMIZ, UASLP UJAT, XAL, and ZEA (acronyms follow Thiers 2023 and count. updated) were studied and digitized with a scale for further analysis. Also, previously digitized specimens were included from the following herbaria: MEXU (IBdata: [www.ibdata.abaco3.org](http://www.ibdata.abaco3.org)), NY ([sweetgum.nybg.org/science/vh/](http://sweetgum.nybg.org/science/vh/)), MO (Tropicos: [www.tropicos.org](http://www.tropicos.org)), and the ones included in Red de Herbarios del Noreste de México ([herbanwmex.net](http://herbanwmex.net)). We obtained a total of 373 herbarium specimens (331 for *A. bracteata* var. *bracteata* and 42 for *A. bracteata* var. *pacifica*), including the type specimens for both varieties and that of *A. laxiflora*. Type specimens were retrieved from JSTOR Global Plants ([plants.jstor.org](http://plants.jstor.org)).

*Linear morphometric analysis.* 82 herbarium specimens ([Supplementary material 1](#)) selected from across the distribution of *Aechmea bracteata* were studied for the morphometric analysis. The specimens used for this analysis were chosen because they were complete (leaves and inflorescence) with well-preserved vegetative and floral structures. In addition, the holotypes for *Aechmea bracteata* (*W. Houston, s.n.*, BM), *Aechmea laxiflora* (*Sinclair, s.n.*, K), and the isotype of *A. bracteata* var. *pacifica* (*C. R. Beutelspacher 51*, US) were included, obtaining a total of 85 specimens. Each specimen was measured using the ImageJ version 153q software (Schneider *et al.* 2012).

A total of 28 quantitative characters were measured considering inflorescence and leaf structures. Characters, used abbreviations, detailed information on how the measures were taken and the number of structures averaged is shown on [Table 1](#). For the characteristics related to the inflorescence, this structure was sectioned into thirds, each referred to as basal, middle and an upper portion.

To test the separation of both taxa into different groups, an exploratory cluster analysis with an UPGMA algorithm was performed using a Gower distance matrix considering the coefficient of cophenetic correlation as an indicator of the goodness of fit for the obtained classification. Additionally, to the quantitative traits, the Gower matrix allows the inclusion of qualitative data, which were codified as follows:

Ramification of the basal spikes of the inflorescence

0 = no ramifications, 1 = two ramifications, 2 = three ramifications, 3 = four or more

Margin of the peduncle bracts

0 = entire, 1 = serrate

Margin of the primary bracts

0 = entire, 1 = serrate

Subsequently, for each of the quantitative traits, the normality of the data sets was evaluated through a Shapiro-Wilk test. After determining the distribution of the data for each character, Student's T tests were performed for the characters with a normal distribution, and Mann-Whitney tests for characters that lack normality. To detect which characters were statistically different between taxa, an alpha value of  $P < 0.05$  was established and adjusted with the Bonferroni correction. Since primary bracts are absent on the upper portion of *A. bracteata* var. *bracteata*, the characters regarding these structures (LPRBU, WPRBU, LWPRBU) were excluded from the normality tests.

**Table 1.** Measured characters and used abbreviations.

Morphological character	Abbreviation	Description	Number of individual structures averaged
Inflorescence length	IFL	Measured from the first branch to the apex excluding the peduncle	-
Inflorescence branch length from the basal portion (average)	IBLB		
Inflorescence branch length from the middle portion (average)	IBLM		
		Measured from the base of branch to their apex	Two per inflorescence portion
Inflorescence branch length from the upper portion (average)	IBLU		
Length of the peduncle bracts (average)	LPB	Measured from the base to the apex of the two peduncle bracts closer to the inflorescence	
Width of the peduncle bracts (average)	WPB	Measured from the widest part of the two peduncle bracts closer to the inflorescence	The two peduncle bracts closer to the inflorescence
Length/width proportion of the peduncle bracts (average)	LWPB	Dividing the length and the width of each peduncle bract measured	
Length of the primary bracts from the basal portion (average)	LPRBB		
Length of the primary bracts from the middle portion (average)	LPRBM		
		Measured from the base to the apex	Two per inflorescence portion
Length of the primary bracts from the upper portion (average)	LPRBU		
Width of the primary bracts from the basal portion (average)	WPRBB		
Width of the primary bracts from the middle portion (average)	WPRBM	Measured from the widest part of the primary bract	Two per inflorescence portion
Width of the primary bracts from the upper portion (average)	WPRBU		
Length/width proportion of the primary bracts from the basal portion (average)	LWPRBB		
		Dividing the length and the width of each primary bract measured	Two per inflorescence portion
Length/width proportion of the primary bracts from the middle portion (average)	LWPRBM		
Length/width proportion of the primary bracts from the upper portion (average)	LWPRBU	Dividing the length and the width of each primary bract measured	Two per inflorescence portion

Re-establishment of *Aechmea laxiflora* (Bromeliaceae)

Morphological character	Abbreviation	Description	Number of individual structures averaged
Length of the floral bracts (average)	LFB	Measured from the base to the apex of the dorsoventrally flattened floral bracts	
Width of the floral bracts (average)	WFB	Measured from the widest part of the dorsoventrally flattened floral bracts	Five selected across the whole inflorescence
Length/width proportion of the floral bracts (average)	LWFB	Dividing the length and the width of each floral bract measured	
Leaf sheath length	LSL	Measured from the base of the leaf sheath to before the base of the leaf blade	
Leaf sheath width	LSW	Measured from the middle portion of the leaf sheath	one
Leaf sheath length/width proportion	LSLW	Dividing the length and the width of the leaf sheath	
Leaf blade length	LBL	Measured from the base of the leaf blade to the apex	
Leaf blade width	LBW	Measured at the middle portion of the leaf blade	one
Leaf blade length/width proportion	LBLW	Dividing the length and the width of the leaf blade	
Length of the spines (average)	LS	From the base (the widest part of the spine) to the tip	Five selected along the leaf blade
Space between the spines (average)	SS	Measuring the distance from the end of the base of the spine to the beginning of another one along the leaf blade	Five selected along the leaf blade
Fruit diameter (average)	FD	Measuring a line across the fruit	Five arbitrarily selected

Additionally, to identify the statistical significance of each taxon being different, using only the statistically significant characters, a one-way permutated multivariate analysis (PERMANOVA) was performed with 9,999 permutations using a Euclidean similarity index, with an alpha value of  $P < 0.05$  and a subsequent Bonferroni correction. All the analyses were performed according to the classification algorithm UPGMA in the software PAST 4 version 4.10 (Hammer *et al.* 2001).

For each of the quantitative morphological characters that turned out to be statistically significant, boxplots were made with R (R core Team 2022) using the package ggplot2 (Wickham 2016), to visualize their ranges and distribution of the data obtained.

*Living specimens' revision.* To study potential diagnostic traits that are usually not available in herbarium specimens, living specimens cultivated at the Regional Botanical Garden “Roger Orellana” (Centro de Investigación Científica de Yucatán, A. C. (CICY)) and private collections, as well as field specimens and photographic records were analyzed, reviewing 21 individuals of *A. bracteata* var. *bracteata* and 15 of *A. bracteata* var. *pacifica* (specimens were deposited at CICY and UADY herbaria). This information was complemented with the information available in the

protologues and the descriptions available in Flora Neotropica (Smith & Downs 1979, Beutelspacher 1971). The suggested terminology by Scharf & Gouda (2008) was used for the morphological descriptions.

*Taxonomic sampling for the phylogenetic analysis.* All the species belonging to the *Aechmea bracteata* complex (*sensu* Ramírez-Díaz 2019) were analyzed in this study (*A. bracteata* var. *bracteata*, *A. bracteata* var. *pacifica*, *A. pubescens*, *A. pittieri*, and *A. dactylina*).

Fresh foliar tissue from *A. bracteata* var. *bracteata*, *A. bracteata* var. *pacifica*, *A. pittieri* and *A. pubescens* was obtained from wild and cultivated specimens; for both varieties of *A. bracteata*, tissues were obtained from specimens of different localities of their distribution in order to obtain representation of different populations. In addition, *Aechmea aquilega* (Salisb.) Griseb. was included as an outgroup rooting due to its phylogenetical position on previous analyses (Sass & Specht 2010, Ramírez-Díaz 2019), additionally, sequences of *A. aquilega*, *A. dactylina*, *A. pittieri*, and *A. pubescens* were retrieved from GenBank, obtaining a total of 23 terminals, having nine for *A. bracteata* var. *bracteata*, eight for *A. bracteata* var. *pacifica*, two for *A. pittieri*, two for *A. pubescens*, one for *A. dactylina* and one for *A. aquilega* (Table S3).

*DNA extraction.* Collected leaf tissue was frozen in liquid nitrogen and stored between -20 and -80 °C for later use. The DNA was extracted with the silica gel DNA extraction protocol described by Echevarría-Machado *et al.* (2005), with the following modifications: adding 1 g of leaf tissue, 100 mM of Tris-HCl (pH8) to the lysis buffer, and 5 µl β-mercaptoethanol to the previously mixed lysis buffer, additionally, centrifuge repetitions per minute (RPM) were adjusted, utilizing 14,000 RPM. Finally, DNA quality was verified through electrophoresis with agarose gel with TBE 0.5x at a 1 % concentration.

*Sequence sampling and PCR amplification.* The regions selected were two nuclear genes: the nuclear ribosomal external transcribed spacer (*ETS*) and the region between the 8<sup>th</sup> and the 10<sup>th</sup> exons of glyceraldehydes-3-phosphate-dehydrogenase (*g3pdh*), and one chloroplast region: the *trnL* intron and the *trnL-trnF* intergenic spacer (*trnL-F*). The previously mentioned regions were selected due to their variability, the resolution and statistical support values obtained in previous studies (*i.e.*, Sass & Specht 2010, Ramírez-Díaz 2019).

PCR amplification was performed from genomic DNA with Invitrogen (Carlsband, California) or Qiagen (Germantown, Maryland) Taq polymerase. The PCR conditions and their primers are shown on Table 2. After performing the PCR reaction, the quality and the approximate size of the PCR products was verified in an electrophoresis with an agarose gel with TBE 0.5x at a 1 % concentration. After checking their quality, the products were sent to Macrogen (South Korea) for sequencing with the Sanger method. All the obtained sequences were deposited in GenBank (Table S3).

*Sequence alignment and phylogenetic reconstruction.* Sequence assembling and editing was performed in Sequencher version 4.1 (Gene Codes Corporation [www.genecodes.com](http://www.genecodes.com)). The matrix assembling and manual edition was performed utilizing BioEdit version 7.0.5.3 (Hall 1999), while the alignment was performed using the algorithm MUSCLE (Edgar 2004) on the software MEGA version 11.0.13 (Tamura *et al.* 2021). The evaluation of the most adequate nucleotide substitution model for each region, according to the Akaike Information Criteria, was analyzed with the software JModelTest version 2.1.7 (Guindon & Gascuel 2003, Darriba *et al.* 2012), where the selected nucleotide substitution model for the *ETS* and *trnL-F* regions were GTR + G, while for the *g3pdh* region was HKY + I.

For the phylogenetic analyses, Bayesian Inference (BI) and Maximum Likelihood (ML) analyses were performed. For the BI analysis the phylogenetic reconstruction was carried out with MrBayes version 3.2.5 (Ronquist & Huelsenbeck 2003) in the CIPRES portal 2.0 (Miller *et al.* 2010) with four independent Markov Chain analysis consisting of 1,000,000 generations with a sampling frequency of 1,000 generations, discarding the 25 % as burn-in. While for the ML analysis, 1,000 Bootstrap replicates were performed in the MEGA 11 (Tamura *et al.* 2021) software. Individual analyses were performed for each marker, as well as a concatenated analyses for both nDNA markers, and a concatenated analysis of all nDNA and cpDNA evidence.



## Re-establishment of *Aechmea laxiflora* (Bromeliaceae)

**Table 2.** Amplified regions, details of primers and amplification conditions for the regions used in this analysis. References: 1) Sass & Specht (2010), 2) Ramírez-Díaz (2019), 3) Baldwin & Markos (1998), 4) Aguirre-Santoro *et al.* (2016), 5) Barfuss *et al.* (2005).

Gene region	Primers	PCR conditions	References
<i>ETS</i>	F' GTT TCG GCC TCC CAG TCT AGC	97 °C × 1 min, 40 cycles (97 °C × 10 sec, 55 °C × 30 sec, 72 °C × 20 sec, with the addition of 4 sec each consecutive cycle) 72 °C × 7 min	1,2,3,4
	R' CAA CCA GGT AGC ATG TCC TTT G		
<i>g3pdh</i>	F' CAT CTA GCA AGG ACT GGA GAG G	94 °C × 3 min, 35 cycles (95 °C × 1 min, 54 °C × 1 min, 64 °C × 1 min), 72 °C × 5 min	1,2,4
	R' GCT GAA GAT ACC TGC TGT CAC C		
<i>trnL-F</i>	F' CGA AAT CGG TAG ACG CTA CG	94 °C × 2 min, 29 cycles (94 °C × 30 sec, 52 °C × 40 sec, 72 °C × 40 sec) 72 °C × 5 min	1,2,4,5
	R' ATT TGA ACT GGT GAC ACG AG		

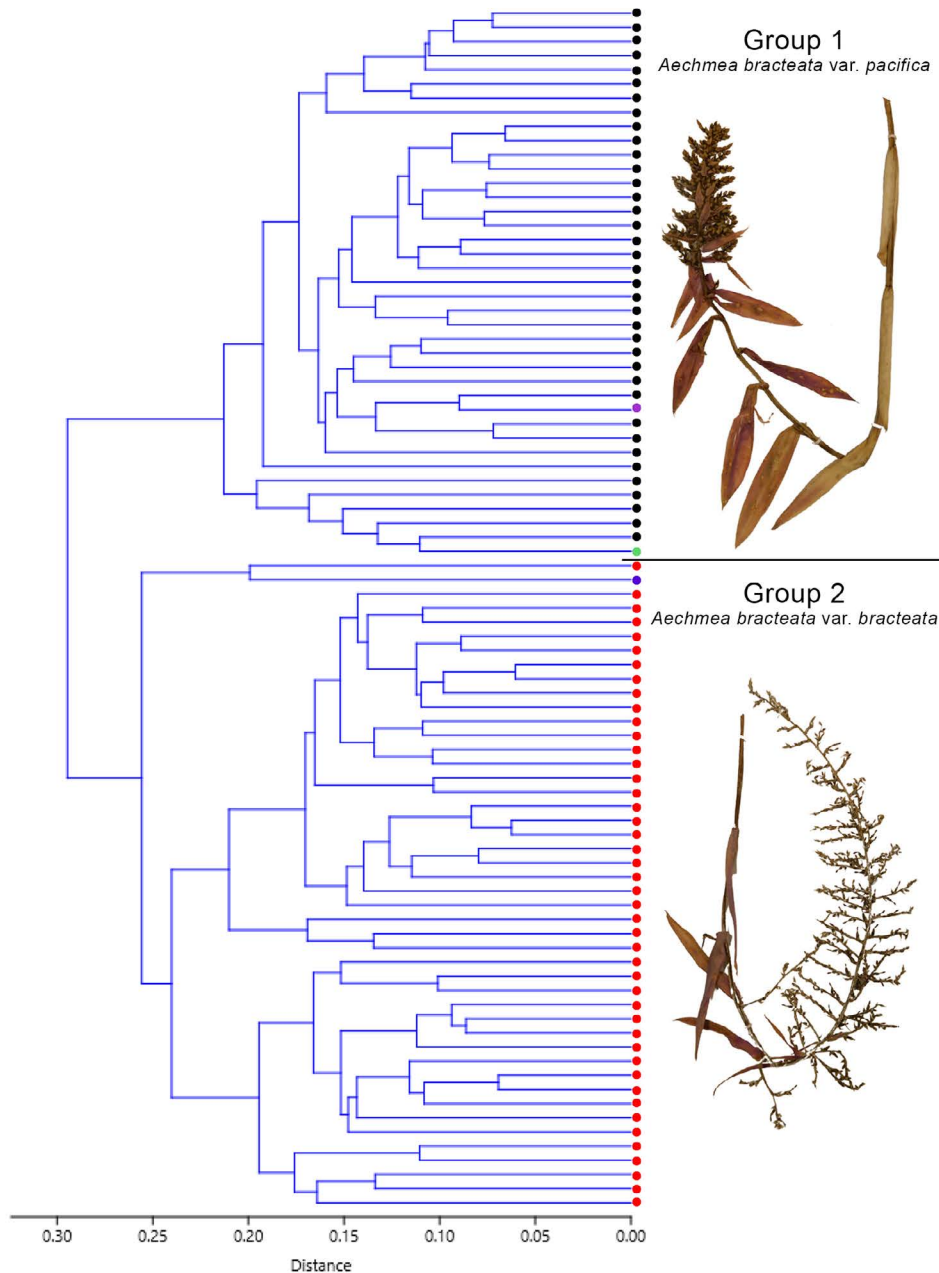
A topological comparison was carried out between the phylograms obtained from the concatenated and individual analyses to detect topological inconsistencies, considering as inconsistencies those nodes whose values are less than 70 BS and 0.70 PP (Mason-Gamer & Kellogg 1996, Barber *et al.* 2007). The phylograms were edited using the platform Interactive Tree of Life (<https://itol.embl.de/>) (Letunic & Bork 2021).

*Geographic distribution map.* Distribution records were obtained from the collection sites from the 373 herbarium specimens. For specimens without coordinates, these were georeferenced with Google Earth (Google Earth 2023) considering the information provided in the herbarium labels. In addition, the data was complemented with accessions from the Global Biodiversity Information Facility (GBIF 2022). After reviewing and determinate which taxa, the herbarium specimens belonged to, data bases of the coordinates were made. The distribution map was generated with QGIS version 3.30 (QGIS Development Team 2023), projecting the coordinates on a layer of the biogeographic provinces for the Neotropics (Morrone *et al.* 2022) from Mexico to northern South America.

## Results

*Linear morphometric analysis.* The dendrogram obtained by the conglomerate analysis resulted into two groups (Figure 1) with a cophenetic correlation coefficient of 0.764. According to the position of the included nomenclatural types of each taxon, group 1 represents a cluster that can be characterized as *A. bracteata* var. *pacifica*, in which the type specimen of *A. laxiflora* is included; as for group 2, is composed merely of the typical variety of *A. bracteata* where the holotype of the species belongs.

As for the qualitative morphological traits included in the data sets, the most variable character between both taxa was the number of secondary branches on the basal branches of the inflorescence. Out of the 45 evaluated herbarium specimens of *A. bracteata* var. *bracteata*, 23 had four or more secondary branches, whilst the rest had two or no secondary branches, as for the 37 specimens of *A. bracteata* var. *pacifica*, 19 of the evaluated specimens did not have secondary branches, 14 had two secondary branches, and only three had 3 or more secondary branches in the basal branches of the inflorescence. For the peduncle and primary bracts margin there was no variation, except for three specimens of *A. bracteata* var. *bracteata* that possessed a serrate margin, the rest of the specimens for both taxa showed entire margins.



**Figure 1.** Dendrogram resulting from the cluster analysis of the Gower distance matrix. Group 1 *A. bracteata* var. *pacifica*, black circles; purple circle: isotype; green circle: *A. laxiflora* type specimen; Group 2 *A. bracteata* var. *bracteata*, red circles; dark purple circle: *A. bracteata* holotype. Herbarium specimens of the photographs: *A. bracteata* var. *pacifica* J. P. Pinzón & J. J. Ancona 339 (UADY); *A. bracteata* var. *bracteata* M. Soto David *et al.* 6 (UADY).

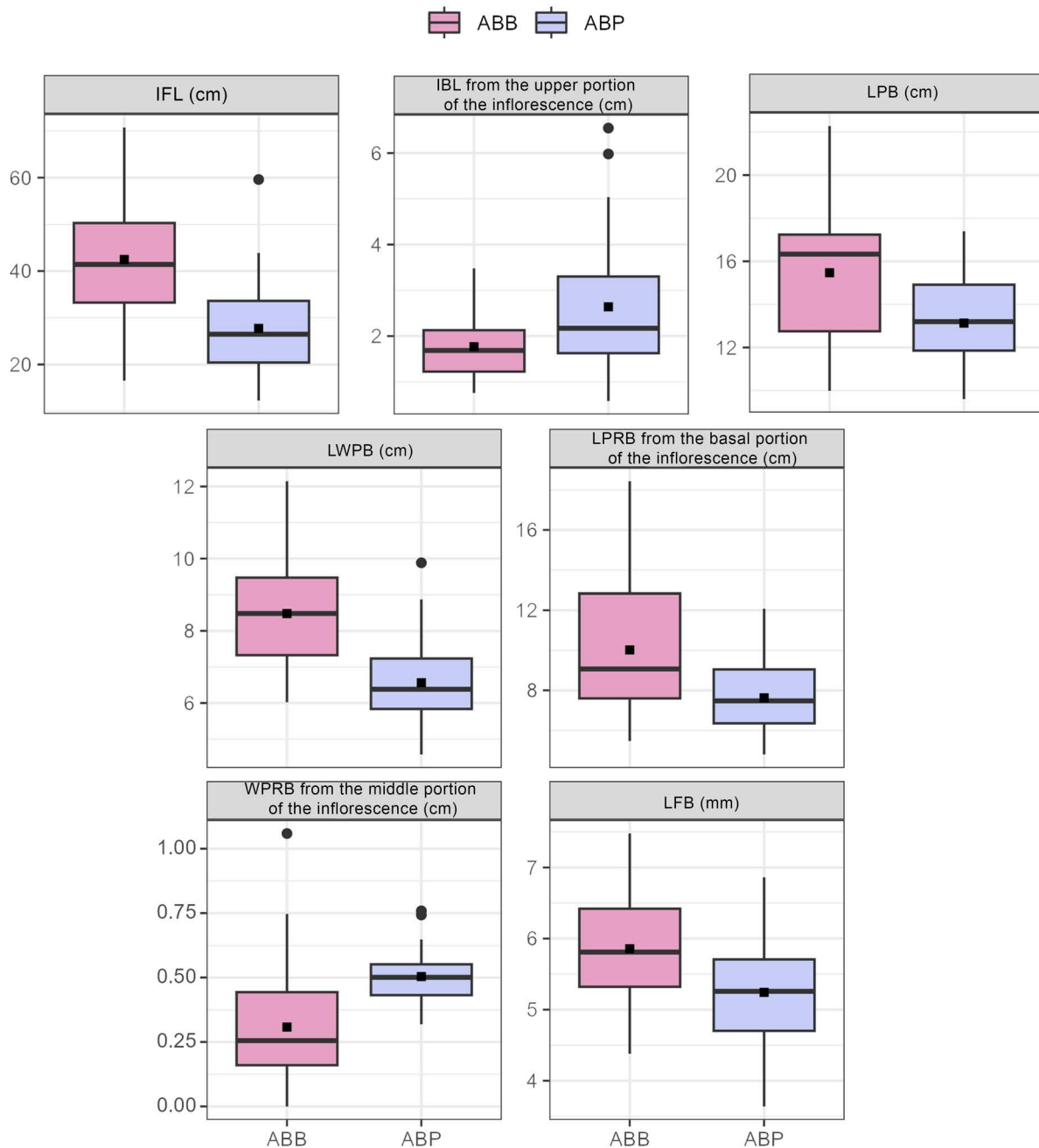
Out of the 25 quantitative characters analyzed, according to the Shapiro-Wilk's tests, 14 of them turned out to be normally distributed, whereas 11 did not ([Table S1](#)). For the parametric character analyses (Student's *T* test), the alpha value with the Bonferroni correction was of  $P < 0.038$  whilst for the non-parametric character analyses (Mann-Whitney test) the obtained value was  $P < 0.004$ . Seven characters resulted as statistically significant between the two varieties of *A. bracteata*, such as IFL, IBLU, LPB, LWPB, LPRBB, WPRBM, and the LFB ([Figure 2](#)). P values of the Student's *T* and Mann-Whitney tests are provided in [Table S2](#).



Re-establishment of *Aechmea laxiflora* (Bromeliaceae)

Regarding the one-way PERMANOVA analysis with the statistical significant data sets, *A. bracteata* var. *bracteata* and *A. bracteata* var. *pacifica* represent two different groups with statistical significance, since a *P* value of 0.0001 and a *F* value of 31.19 were obtained.

*Living specimens' revision.* In addition to the differences on the inflorescence size and the distribution of the primary bracts (Figures 3A, 4A), there are some other morphological traits that provide elements to diagnose both taxa that are usually lost or hard to identify in herbarium specimens.



**Figure 2.** Boxplots diagrams for the statistical significant morphological characters according to the univariate analyses. ABB = *Aechmea bracteata* var. *bracteata*; ABP = *Aechmea bracteata* var. *pacifica*.

The morphology of the corolla and the floral bracts shows differences between both taxa. The corolla, for *A. bracteata* var. *pacifica* is usually wider (2-3 mm), compared to the typical variety where it is narrower (1.5-1.8 mm), regarding the petals, in *A. bracteata* var. *bracteata* they are pale yellow while the petals of *A. bracteata* var. *pacifica* are bright yellow colored (Figures 3B, 4B). As for the floral bracts, in *A. bracteata* var. *bracteata* they are ovate to elliptic and acuminate, while in *A. bracteata* var. *pacifica*, these tend to be ovate-triangular and apiculate (Figures 3E, 4E).

Additionally, differences can be appreciated during the ripening process of the fruits. In *A. bracteata* var. *bracteata* the exocarp is provided with a white punctuated indument, shortly after fertilization, during the widening and maturation of the fruit the exocarp presents a green coloration, and the persistent sepals a rufous red coloration; after the fruit ripens the sepals acquire a purple coloration and the exocarp becomes bluish black (Figure 3C). In the other hand, the fruits of *A. bracteata* var. *pacifica* possess a stellate white indument, after fertilization, the exocarp presents a yellowish green coloration as well as the persistent sepals; when the fruit matures, both structures acquire a black coloration (Figure 4C).

Furthermore, in the vegetative structures other differences can be noticed. The leaf blades in *A. bracteata* var. *bracteata* possess are coriaceous, parallelodromous trichomes abaxially, a ligulate to triangular shape, with spines from the leaf margin being uncinata to antrorse (Figure 3D). In contrast, leaf blades of *A. bracteata* var. *pacifica* are more flexible, with less and irregularly distributed trichomes abaxially, and has ligulate to broadly triangular leaf blades with antrorse spines (Figure 4D).

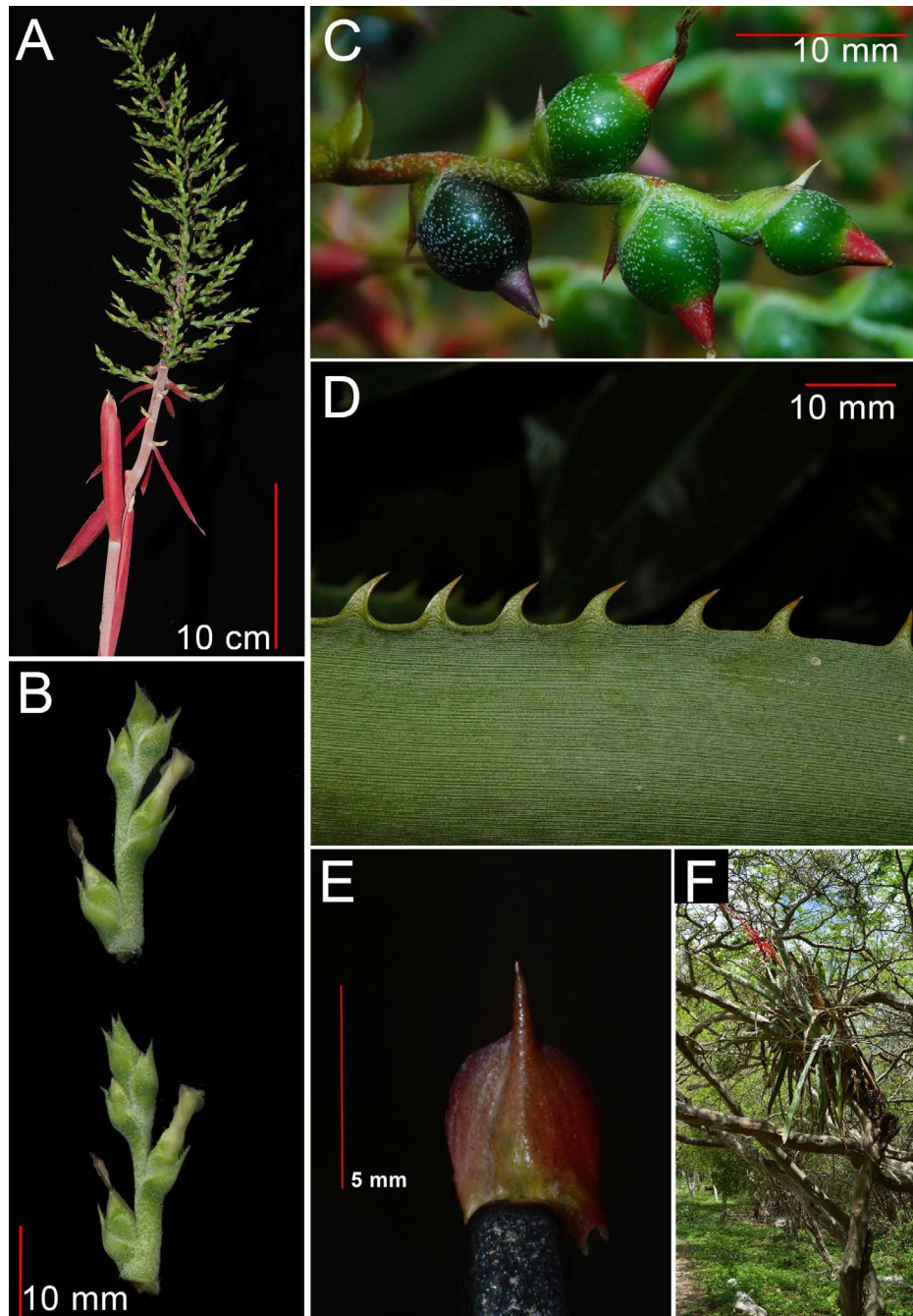
*Phylogenetic analysis.* For the 23 terminals included in this analysis, size, variability, and informative levels of the data sets for each region and combined are shown in Table 4. From this data we can identify that *ETS* possessed the higher values of informativity whilst *trnL-F* resulted in the least informative region.

While analyzing the markers individually and combined in the BI and ML, topologies with different resolution levels and statistical support values were obtained. Regarding the observed topological incongruences, these were distinguished as soft incongruences, mostly due to the phylogenetic position of the individuals within the clades for both varieties of *A. bracteata*.

In the analyses performed for the nDNA markers (Figure 5) both varieties of *A. bracteata* show reciprocal monophyly with high statistical support (PP: 1, BS: 98), their clade is divided into two subclades, one conformed solely of the typical variety of the species (PP: 1, BS: 99), and the other composed by *A. bracteata* var. *pacifica* (PP: 0.99, BS: 94). For the rest of the species of the complex, a clade containing *A. pittieri*, *A. pubescens* and *A. dactylina* was retrieved with a high statistical support (PP: 1, BS: 100). The monophyly of *A. pittieri* (PP: 1, BS: 100) and *A. pubescens* (PP: 1, BS: 100) was retrieved, however, the phylogenetic position of *A. dactylina* could not be determined due to topological incongruences on its position on the BI and ML analyses as well as low statistical support. Individual phylogenetic analyses of *ETS* and *g3pdh* are shown in Figures S1 and S2, respectively.

Contrary to the results obtained with nuclear DNA regions, the BI and ML analyses for chloroplast region *trnL-F* (Figure 6), showed a low phylogenetic resolution, resulting in a polytomy with two main clades: a polytomy including *A. bracteata* var. *pacifica* variety as well as *A. pittieri* and *A. pubescens*, with a higher statistical support (PP: 0.99, BS: 84), and a polytomy composed of the majority of the *A. bracteata* var. *bracteata* sampled specimens (PP: 0.76, BS: 64). However, three of the sampled specimens of *A. bracteata* var. *bracteata* (663, 664 and 665) appeared collapsed at the base of the tree.

In the resulting phylogram obtained from the concatenated matrix of the two nDNA and the cpDNA markers (Figure 7), the topology is identical to that obtained from the nDNA markers analysis, but with slightly lower statistical values. In this analysis with the three markers, both varieties of *A. bracteata* showed reciprocal monophyly (PP: 1, BS: 87), the subclade conformed by *A. bracteata* var. *bracteata* showed high statistical support (PP: 1, BS: 99), whereas the subclade conformed by *A. bracteata* var. *pacifica* showed a high PP value but a low BS support (PP: 0.99, BS: 72). The remaining species of the complex formed their own clade with a high statistical support (PP: 1, BS: 99). The monophyly of *A. pittieri* (PP: 1, BS: 86) and *A. pubescens* (PP: 1, BS: 92) was retrieved, however, the phylogenetic position of *A. dactylina* could not be determined either in this concatenated analysis due to low statistical support and topological incongruences on its position on the BI and ML analyses.



**Figure 3.** *Aechmea bracteata* (Sw.) Griseb. var. *bracteata* A. Inflorescence. B. Inflorescence branches. C. Fruits in different maturation stages. D. Detail of the leaf blade spines. E. Floral bract. F. Habitat. Photographs: Mauricio Soto David (A-D) and Claudia Ramírez-Díaz (E-F).

*Geographic distribution.* Based on the georeferenced collection sites reported on herbarium records, two population groups are distinguished, each one corresponding to a variety of *A. bracteata* (Figure 8). According to the obtained data, these varieties are not sympatric. Our results show that the distribution of *Aechmea bracteata* var. *pacifica* is restricted to Mexico, from the south of Sinaloa to western Oaxaca, occurring in the biogeographic province of the Pacific Lowlands with some records in transition areas with the Sierra Madre del Sur province.

**Table 3.** Morphological characters with statistically significant values.

<b>T-Student</b>		
<b>Morphological character</b>	<b>T</b>	<b>P</b>
IFL	5.5872	3.2529E-07
LPB	3.1666	0.0024244
LWPB	5.566	6.4336E-07
LFB	3.5185	0.00071078
<b>Mann-Whitney</b>		
<b>Morphological character</b>	<b>Z</b>	<b>P</b>
IBLU	2.8839	0.0039273
LPRBB	3.5938	0.00032585
WPRBM	4.8688	1.228E-06

**Table 4.** Size, variability, and information levels of the analyzed data sets. Abbreviations: CS: Conserved sites; VS: Variable sites.

<b>Matrix</b>	<b>Size (pb)</b>	<b>CS (%)</b>	<b>VS (%)</b>	<b>Terminals</b>
<i>ETS</i>	474	405 (85.44 %)	65 (13.71 %)	22
<i>g3pdh</i>	1,024	863 (85.44 %)	117 (11.42 %)	21
<i>trnL-F</i>	911	869 (95.38 %)	30 (3.29 %)	21
Nuclear ADN ( <i>ETS</i> + <i>g3pdh</i> )	1,498	1,268(84.64 %)	182 (12.14 %)	23
DNA evidence	2,409	2,137 (88.70 %)	212 (8.80 %)	23

Meanwhile, *A. bracteata* var. *bracteata* possesses a wider distribution from Mexico to northern Colombia and Venezuela, being found throughout various Neotropical biogeographic provinces. In Mexico this taxon occurs in the Veracruz Province, the Yucatan Peninsula, some localities in transitional areas with the Sierra Madre Oriental, a small portion within the Chiapas Highlands, and Pacific Lowlands in the region of the Isthmus of Tehuantepec. In Central America it is found in the biogeographic provinces of Mosquito, Pacific Lowlands, Guatuso-Talamanca and Punta Arenas-Chiriquí, and in South America, records were found in the provinces of Guajira, Magdalena, and the Venezuelan Province. Records were not found in the Chocó-Darién and Cauca provinces.

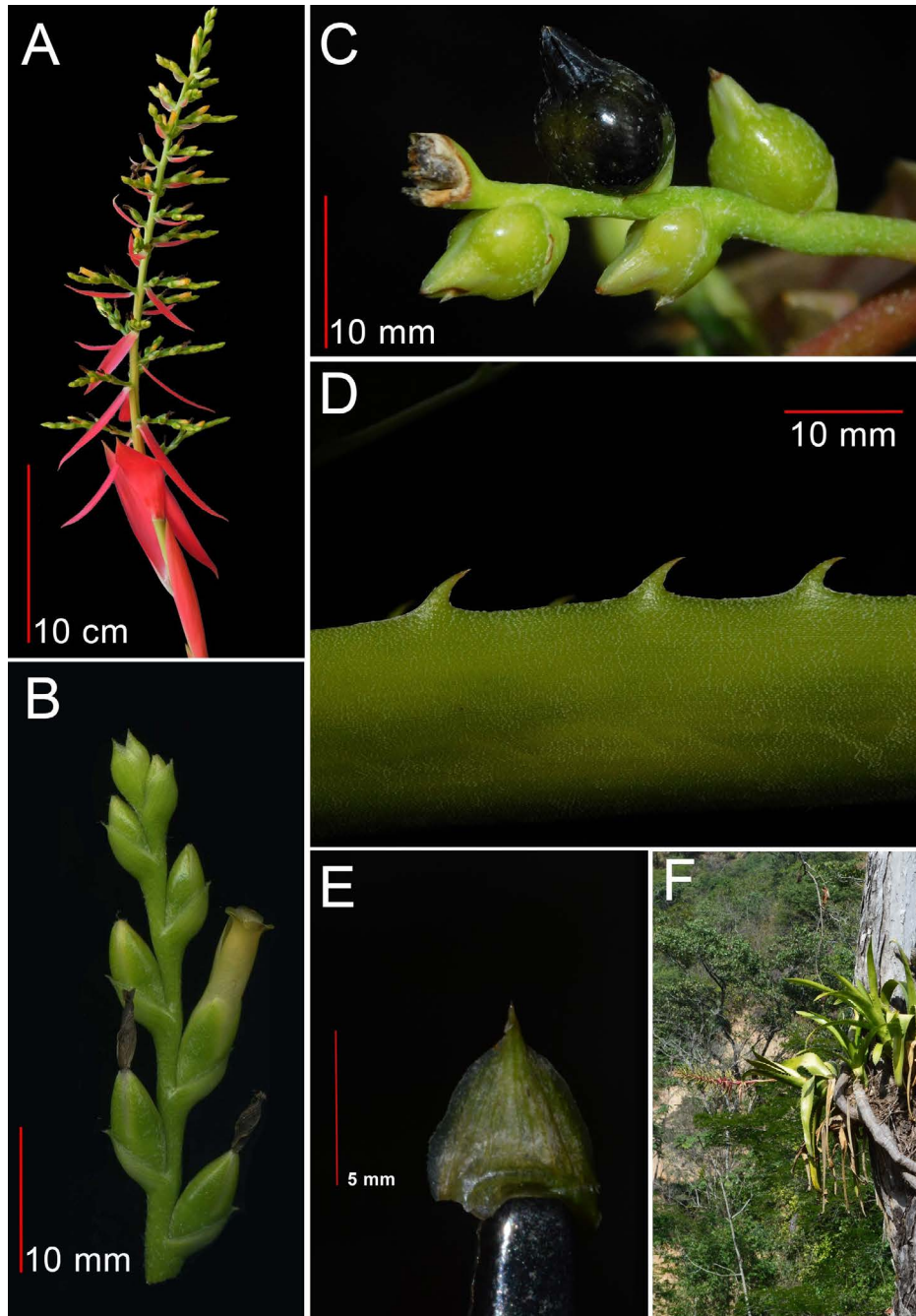
## Discussion

*Morphometry and morphology of A. bracteata.* Different kinds of linear and geometrical morphometric analyses have resulted useful to study the Bromeliaceae family, allowing to elucidate, validate, recognize new taxa, or change the taxonomic status of varieties and synonyms (*e.g.*, Wendt *et al.* 2000, Hornung-Leoni & Sosa 2008, Ferreira *et al.* 2009, de Faria *et al.* 2010, Pinzón *et al.* 2011, Castello & Galetto 2013, Guarçoni *et al.* 2017, Neves *et al.* 2018, González-Rocha *et al.* 2018, Martínez-García *et al.* 2022). In this study, the morphometric cluster analysis grouped the individuals into two clusters, each corresponding to a variety of *A. bracteata*, according to the characters previously recognized by Beutelspacher (1971) and Smith & Downs (1979). In addition, the PERMANOVA analysis showed that both groups are statistically different.

Among the morphological characters that showed differences between both groups in the univariate analyses, are the IFL, IBLU, LPB, LWPB, LPRBB, WPRBM and LFB.

According to the original description for *A. bracteata* var. *pacifica* by Beutelspacher (1971), the inflorescence in this variety is shorter than the typical variety of the species. Although the description mentions that such structure

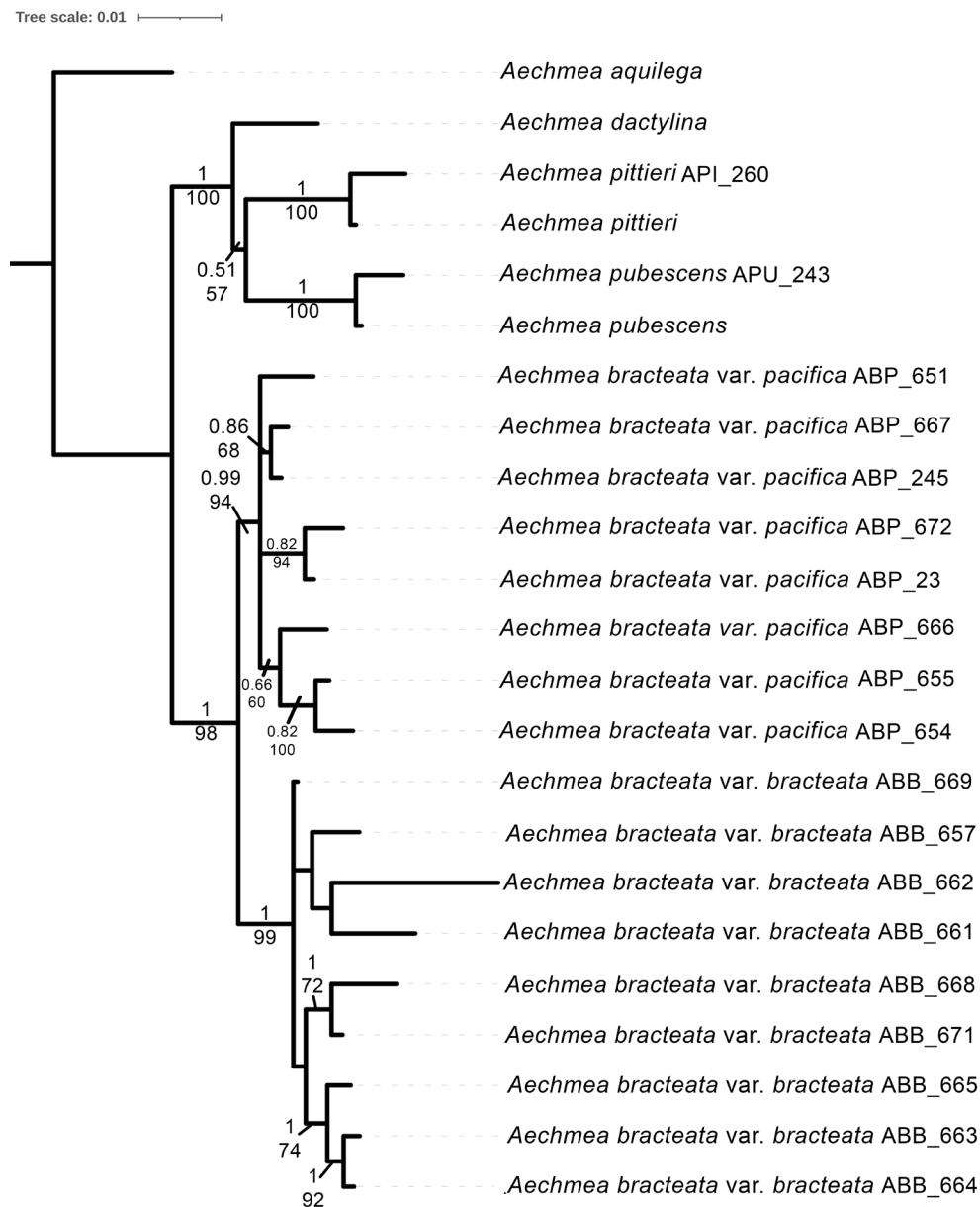




**Figure 4.** *Aechmea bracteata* var. *pacifica* Beutelsp. (*Aechmea laxiflora* Benth.). A. Inflorescence. B. Secondary inflorescence branches. C. Fruits in different maturation stages. D. Detail of the leaf blade spines. E. Floral bract. F. Habitat. Photographs: Mauricio Soto-David (A-D) and Claudia Ramírez-Díaz (E-F).

size is up to 90 cm (probably including the peduncle), despite not including the peduncle in the herein study, the obtained data for the IFL resulted in *A. bracteata* var. *pacifica*, having a tendency to possess a smaller size range ([12.3-] 20.1-33.6 [-43.9] cm) in comparison to *A. bracteata* var. *bracteata* ([16.5-] 33.5-50.5 [-70.7] cm).

As to the LPRB, the values obtained for *A. bracteata* var. *pacifica* were close to the description by Beutelspacher (1971), in which it is said that these structures are larger, being up to 10 cm in length, smaller than the ones on the typical variety, in the present study. For the LPRB of the basal portion of the inflorescence the obtained range was



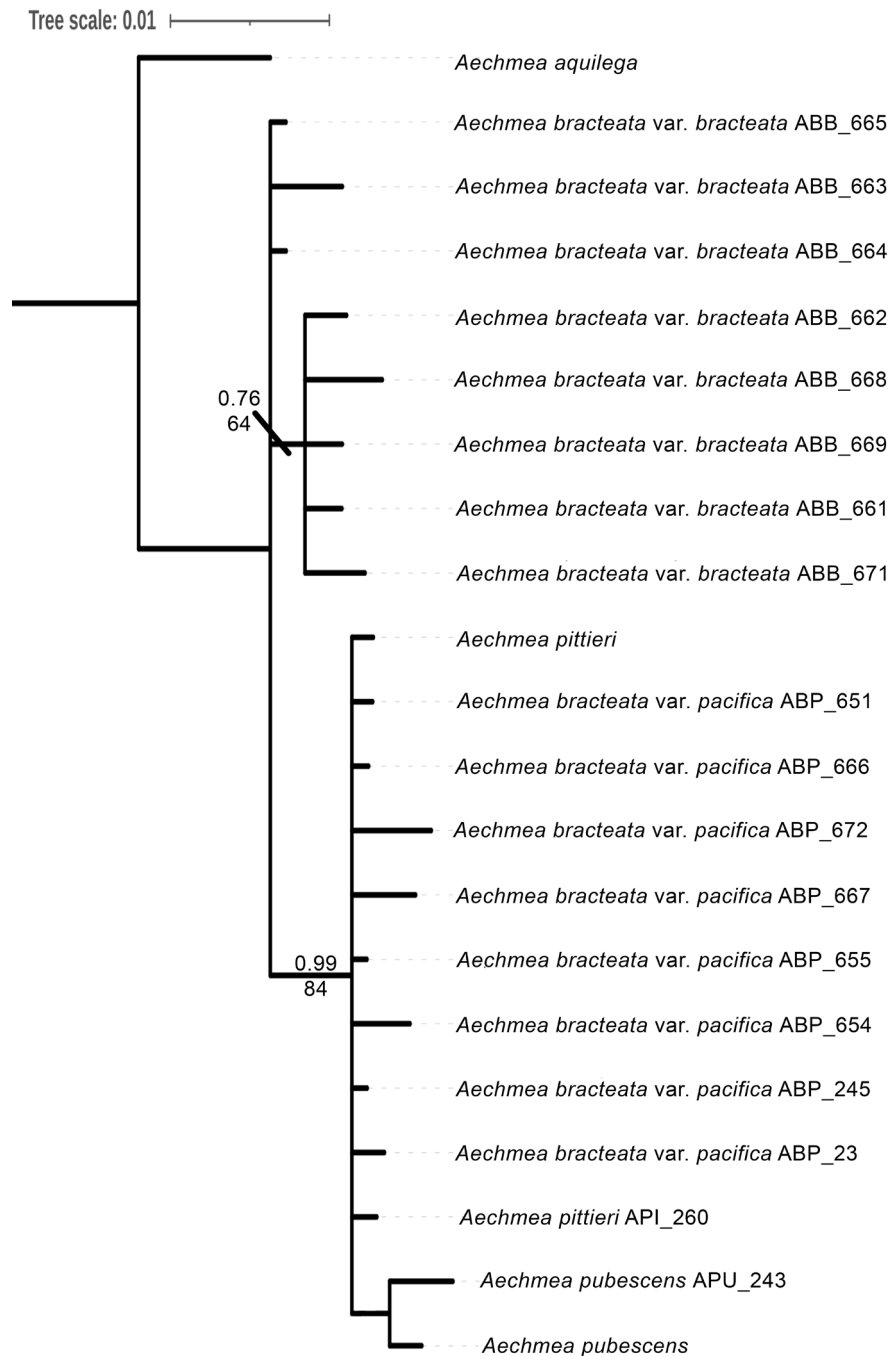
**Figure 5.** Majority Rule Consensus tree from a Bayesian Inference analysis of the *Aechmea bracteata* complex with evidence of nuclear DNA markers (*ETS* and *g3pdh*). Above the branches: Posterior Probability; below the branches: Bootstrap from a Maximum Likelihood analysis. PP values above 0.50 and BS values above 50 are shown.

(4.8-) 6.3-9 (-11.9) cm, contrasting with the range obtained for *A. bracteata* var. *bracteata* (5.5-) 7.5-12.9 (-18.4) cm, indicating a higher variation and size of this structure.

Moreover, according to the same description, it is mentioned that the branches of the inflorescence have a regular longitude, being almost of the same size across the whole inflorescence which is up to 6 cm (Beutelspacher 1971). The specimens analyzed in the present study showed some concordance with the description of *A. bracteata* var. *pacifica*, as the obtained range of the IBL was (0.5-) 1.6-6.9 (-10.6) cm long, contrasting with *A. bracteata* var. *bracteata* in which IBL range was (0.7-) 1.2-12.4 (-23.6) cm long, being larger than those observed for *A. bracteata* var. *pacifica*.



Re-establishment of *Aechmea laxiflora* (Bromeliaceae)



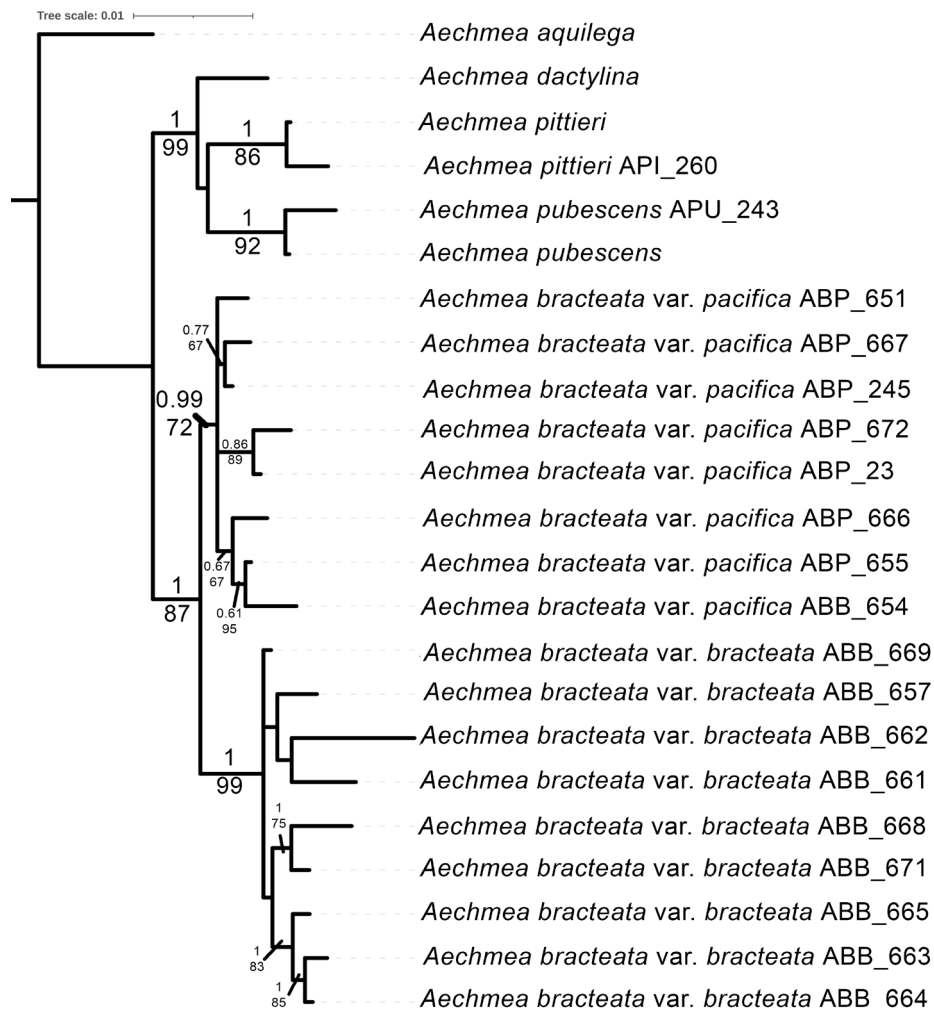
**Figure 6.** Majority Rule Consensus tree from a Bayesian Inference analysis of the *Aechmea bracteata* complex with evidence of chloroplast DNA marker *trnL-F*. Above branches: Posterior Probability; below the branches: Bootstrap from a Maximum Likelihood analysis. PP values above 0.50 and BS values above 50 are shown.

According to the cluster analysis, the type specimen of *A. laxiflora* is placed within the *A. bracteata* var. *pacifica* group, supporting the fact that both taxa belong to the same entity as proposed by the synonymy of Smith & Downs (1979).

In addition to morphometric analyses, some of the qualitative characters observed in living specimens are useful for the differentiation between taxa. According to the observed traits, *A. bracteata* var. *bracteata* has green fruits with persistent red sepals when immature, and after ripening, the berry turns bluish black and the persistent sepals acquire a purple col-

oration, while *A. bracteata* var. *pacifica* has yellowish green fruits and when ripe they turn black as well as the persistent sepals. In previous studies, fruit and floral characteristics, among others, have been used to provide further support for the characterization and delimitation between closely related taxa within the subfamily Bromelioideae (e.g., Leme 1997, 1998, 2000, 2007, Leme *et al.* 2017). These traits were not revised until the herein study for species of the *A. bracteata* complex.

*Phylogenetic relationships.* According to the phylogenetic analysis by Sass & Specht (2010), which is based on the concatenation of three nDNA markers (*g3pdh*, *ETS* and *rpb2*) and one from cpDNA (*trnL-F*); the *Aechmea bracteata* complex represents a monophyletic group with high statistical support (PP: 1, BS: 99) and its composed by both varieties of *A. bracteata*, *A. pubescens*, *A. dactylina*, and *A. pittieri*, as well as three unidentified samples. Even though our analysis and Sass & Specht (2010) analysis are congruent with *A. bracteata* not being a monophyletic species, the topology of the clade is different than the herein obtained, positioning *A. bracteata* var. *pacifica* in a clade with an undetermined specimen (*Aechmea* sp.) as the sister clade of the rest of the complex. Regarding *A. bracteata* var. *bracteata*, in Sass & Specht (2010) its phylogenetic position is as the sister species of *A. pubescens*. However, it is possible that the differences among the topology of Sass & Specht's (2010) analysis and ours, rely on the inclusion of three undetermined specimens (which were excluded in our analysis), and the inclusion of the *rpb2* sequences in their analysis.



**Figure 7.** Majority Rule Consensus tree from a Bayesian Inference analysis of the *Aechmea bracteata* complex with the concatenated evidence of two markers of the nDNA (*ETS* and *g3pdh*) and the cpDNA marker (*trnL-F*). Above the branches: Posterior Probability; below the branches: Bootstrap from a Maximum Likelihood analysis. PP values above 0.50 and BS values above 50 are shown.

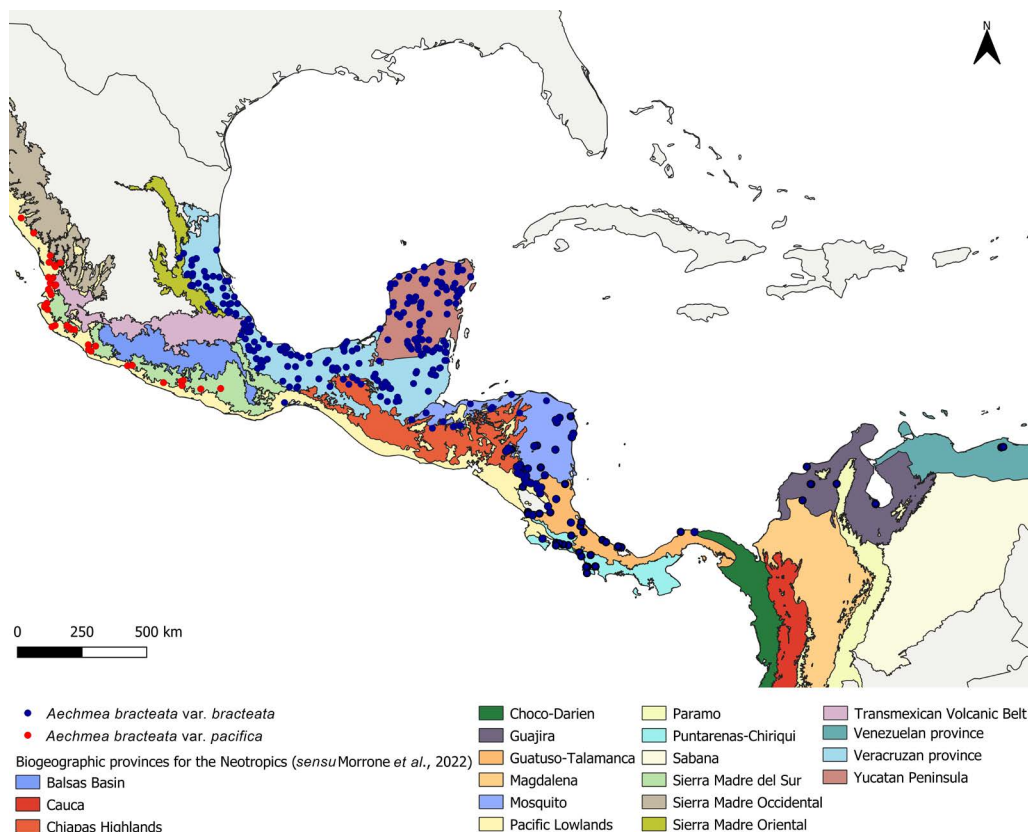
On the other hand, the obtained results by Ramírez-Díaz (2019) in a consensus analysis for two nDNA markers (*agt1* and *g3pdh*), are congruent with the results in the present publication, since *A. bracteata* var. *bracteata* and *A. bracteata* var. *pacifica* also showed to be reciprocally monophyletic (PP: 0.85, BS: 87), with high statistical values for *A. bracteata* var. *bracteata* (PP: 0.90, BS: 86.2) but lower statistical support values for *A. bracteata* var. *pacifica* (not shown). In our analysis with *ETS* and *g3pdh* markers (nDNA), the node support for both taxa being reciprocally monophyletic was higher (PP: 1, BS: 98), as well as the statistical support for the clades conformed by individuals of each taxa (for *A. bracteata* var. *bracteata* PP: 1, BS: 99; for *A. bracteata* var. *pacifica* PP: 0.99, BS: 94).

Regarding the cpDNA evidence obtained by Ramírez-Díaz (2019) with the markers *rpl32-trnL* and *ycf1*, the *Aechmea bracteata* complex presented a polytomy with high PP value (0.99) but with low BS value (not shown), *A. pittieri* and *A. pubescens* appeared collapsed towards the base of the polytomy, while *A. bracteata* var. *pacifica* presented a polytomy by its own (PP: 0.99, BS: 77.3). Concerning *A. bracteata* var. *bracteata*, the individuals sampled by Ramírez-Díaz formed a clade with a high BS value (98.6) but a low PP value (not shown). In the herein study, the phylogenetic tree obtained with the cpDNA marker *trnL-F*, showed some congruence with the results obtained by Ramírez-Díaz, however, the specimens of *A. bracteata* var. *pacifica* grouped in a polytomy with *A. pittieri* and *A. pubescens* (PP: 0.99, BS: 84), whereas many of the *A. bracteata* var. *bracteata* specimens conformed an independent polytomy but with low statistical support (PP: 0.76, BS: 64) and others appear collapsed at the base of the tree. The difference among the obtained topology and the one obtained by Ramírez-Díaz (2019) might be due to the low resolution of the *trnL-F* marker and the low differentiation in the sequences among the sampled species and individuals. However, in both cases, cpDNA evidence suggests that the monophyly of *A. bracteata* as a single species is not supported.

Due to the topological inconsistencies regarding the phylogenetic position of *A. bracteata* var. *pacifica*, and considering that in angiosperms the inheritance of nDNA is biparental, whereas the inheritance of cpDNA is uniparental, mostly maternal, and highly conserved due to its slow molecular evolution and low mutation rates (Small *et al.* 2004, Robbins & Kelly 2023), it can be hypothesized that the origin of this taxon might be due to potential events of ancestral hybridization, introgression and/or incomplete lineage sorting (Barber *et al.* 2007, Kim & Donoghue 2008, Jabaily & Systma 2010). Incongruences between nDNA and cpDNA evidence has been constantly observed in Bromeliaceae, suggesting that phenomena such as hybridization, introgression and incomplete lineage sorting have been of importance to the diversification of bromeliads and are present in several groups within the family (*e.g.*, Jabaily & Sytsma 2010, Schulte *et al.* 2010, Palma-Silva *et al.* 2011, Versieux *et al.* 2012, Krapp *et al.* 2014, Goetze *et al.* 2017, Mota *et al.* 2019, Ancona *et al.* 2022), being observed mostly in taxa resulting from a recent adaptative radiation in which the lineages experiment a process of diversification into various ecological niches in a short time period (Goetze *et al.* 2017). However, to determine whether these events influenced the evolutionary history of *A. bracteata* var. *pacifica*, studies involving population genetics, phylogenetic networks, phylogeographic analyses and ancestral area estimation could address this more explicitly.

**Geographic distribution.** *Aechmea bracteata* var. *pacifica* is distributed mainly over the biogeographic province of the Pacific Lowlands and some transitional areas with Sierra Madre del Sur. This variety, according to the reviewed herbarium specimens and Flores-Argüelles *et al.* (2023), occurs in riparian forests, low and medium deciduous to sub-deciduous forests, oak forests, and pine-oak forests, at elevations lower than 1,250 m asl, with a distribution that forms a strip from southern Sinaloa to western Oaxaca.

As previously mentioned, *A. bracteata* var. *pacifica* has been collected in the southern slope of the Sierra Madre del Sur at elevations below 1,250 m asl. This may be due to the presence of transition areas, divisions and ravines across the Sierra Madre del Sur caused by the mouths of rivers towards the Pacific Ocean (Santiago-Alvarado *et al.* 2016). In the rest of the region the elevation can be higher than 3,500 m asl with temperate climates, or on the slope facing the Balsas Basin, there are dry climates with xeric scrubs (Espinosa *et al.* 2008, Santiago-Alvarado *et al.* 2016), environmental conditions that represent a geographical barrier for this taxon.



**Figure 8.** Geographic distribution of the varieties of *Aechmea bracteata* projected over the Biogeographic Provinces of the Neotropics.

Other geographic limitations and barriers for the distribution of *A. bracteata* var. *pacifica* are the Sierra Madre Occidental to the north, and the Trans Mexican Volcanic Belt. These provinces represent mountainous chains with elevations above 1,000 m asl and reaching elevations up to 3,000 m, with warm to temperate and semi cold climates (Espinosa *et al.* 2008, González-Elizondo *et al.* 2012, Gámez *et al.* 2012, Morrone 2014).

On the other hand, *Aechmea bracteata* var. *bracteata* is found throughout the Veracruz province, the Yucatan Peninsula, in low elevation points in the eastern slope of the Sierra Madre Oriental, Mosquito, Guatuso-Talamanca, Puntarenas-Chiriquí, some projections of the Pacific Lowlands, the provinces of Guajira, Magdalena and the Venezuelan Province. This taxon is found in sites from sea level to 1,000 m of elevation, occurring in low to medium deciduous and sub-deciduous forests, semi-evergreen forests, medium and high evergreen forests, and savannas. Likewise, it is found in areas with tropical sub-humid and even semi-arid climates such as the north of the Yucatan Peninsula (Espinosa *et al.* 2008, Muchoney *et al.* 2000).

Within the Sierra Madre Oriental, this taxon occurs in areas below 1,000 m asl, in transitional areas with the Veracruz Province, growing in the eastern slope where different types of jungle and forest ecosystems are favored by humidity (Espinosa *et al.* 2008, Suárez-Mota *et al.* 2017). On the other hand, most of this province acts as one of the geographical barriers that limit the distribution of this taxon due to high altitudes and the dry slope in the west portion (Espinosa *et al.* 2008, Suárez-Mota *et al.* 2017).

Other barriers to the distribution of *A. bracteata* var. *bracteata* include the Trans Mexican Volcanic Belt, the northern and eastern portions of the Sierra Madre del Sur, and the Chiapas Highlands, all of them composed of mountains with elevations greater than the requirements that the taxon seems to have. Regarding the Chiapas Highlands, it is possible that it is due to this mountain chain that *A. bracteata* var. *bracteata* does not occur in the southern portions of Guatemala and Honduras, and El Salvador, being found only in the Caribbean slope up to Nicaragua.

The Chocó-Darién and Cauca provinces interrupt the distribution of *A. bracteata* var. *bracteata*. This is probably because the Chocó-Darién is an area of high humidity and precipitation (8,000 to 13,000 mm) (Fagua *et al.* 2019). In the case of the Cauca province, this province consists of the western and central mountain ranges of Colombia (Kattan *et al.* 2004, Morrone 2014). This coincides with the reports published by Aguirre-Santoro & Betancur (2008), where *A. bracteata* is only reported for areas that belong to the biogeographical provinces of Magdalena and Guajira. Likewise, *A. bracteata* has not been reported for the Chocó-Darién region (*e.g.*, Cárdenas-López 2003).

In Mexico both taxa are found in the state of Oaxaca, however, there are no sympatric areas in their distribution. This could be due to the presence of the Sierra Madre del Sur and the Balsas Basin in central Oaxaca, where the elevational ranges vary between 1,500 to 2,000 m, having cooler temperatures (Ortiz *et al.* 2004, Trejo 2004). *Aechmea bracteata* var. *bracteata* is found in the Tehuantepec isthmus region, which is a low elevation area with warm humid and sub-humid climates (Ortiz *et al.* 2004, Trejo 2004). Whereas *A. bracteata* var. *pacifica* is reported for the west of the state, near the locality of Villa de Putla de Guerrero, at 730 m (*A. Espejo, A. R. López-Ferrari, J. Ceja & A. Mendoza R. 6794 CICY; UAMIZ*), a region which possesses a warm sub-humid climate. However, considering the elevational distribution of this taxon, it could be found at minor elevations in areas with the same type of climate.

*Re-establishment of Aechmea laxiflora Benth.* According to the gathered evidence, it is suggested that both varieties of *Aechmea bracteata* can be treated under the unified species concept proposed by De Queiroz (2005, 2007) which primary property establishes that a species is the segment of a population that have evolved separately conforming its own lineage. It can be considered that both varieties represent their own lineage, since nDNA evidence separates them with reciprocal monophyly, although cpDNA evidence groups *A. bracteata* var. *pacifica* in a polytomy with the Central American species of the complex, possibly due the low variability of the analyzed region.

De Queiroz (2007) also proposes that the traits considered by other species concepts serve as secondary or contingent properties that could be or not be acquired through the evolution of the populations. The secondary criteria include intrinsic reproductive isolation, monophyly, exclusive coalescence, diagnosability, deficits of genetic intermediates, and ecological divergence (De Queiroz 2007). For the studied taxa, some of the contingent properties that can be considered are the capability of being identified through their morphology (by qualitative and quantitative methods), their reciprocal monophyly (according to nDNA), and their disjunct geographical distribution, that also serve as an extrinsic reproductive barrier. However, it is not possible to determine if they somehow differ ecologically or possess intrinsic reproductive barriers because those approaches were not considered in the present study.

Due to the gathered evidence, it is possible to elevate to a specific level both taxonomic entities. According to the grouping of the specimens and nomenclatural types included in the morphometric cluster analysis, and the obtained results of the phylogenetic analyses, it is suggested that the circumscription of *Aechmea bracteata* is restricted to the populations previously considered as the typical variety of the species. The populations restricted to the Pacific slopes of Mexico (from Sinaloa to western Oaxaca), includes the collections and nomenclatural types of *A. bracteata* var. *pacifica* and *A. laxiflora*. Considering that and the fact that they share morphological traits, we propose to reestablish the name *Aechmea laxiflora* and turn *A. bracteata* var. *pacifica* into its synonym.

Since *Aechmea laxiflora* has a restricted geographic distribution alongside the Pacific Slopes of Mexico, it is possible to recognize it as an endemic species to Mexico. This elevates the number of species from the genus *Aechmea* reported for Mexico from ten, and the endemic species number from three (Espejo-Serna & López-Ferrari 2018, Flores-Argüelles *et al.* 2020) to eleven and four, respectively (Table 5).

*Aechmea bracteata* (Sw.) Griseb. Fl. Brit. W. I.: 592. 1864.

*Bromelia bracteata* Sw., Prodr.: 56. 1788. Type: Mexico, Veracruz, 1731, *W. Houston, s.n.* (holotype: BM).

*Aechmea schiedeana* Schltdl., Linnaea 18: 437-439. 1845 “1844”. Type: Mexico, Veracruz, Hacienda de la Laguna, without collection date, *Schiede & Deppe, s.n.* (holotype: B, destroyed).

*Hoplophytum bracteatum* (Sw.) K. Koch, Wochenschr. Vereines Beförd. Gartenbaues Königl. Preuss. Staaten 3: 306. 1860.

*Hohenbergia bracteata* (Sw.) Baker in: Saunders, Refug. bot. 4: sub t. 284, no. 3. 1871.

*Aechmea barleei* Baker, Gard. Chron. n.s., 20: 102. 1883. Type: Belize, British Honduras, 1877, *Barlee s.n.* (holotype: K).

*Aechmea isabellina* Baker, J. Bot. 28: 305. 1890. Type: Guatemala, Izabal, boca del Polochic, April 1889, *J. Donnell Smith 1824* (holotype: US).

**Table 5.** *Aechmea* species reported for Mexico (References: Ramírez *et al.* 2004, Espejo-Serna *et al.* 2005, López-Ferrari *et al.* 2011, Espejo-Serna & López-Ferrari 2018, Flores-Argüelles *et al.* 2020).

Species of <i>Aechmea</i> reported for Mexico	General distribution	Distribution in Mexico
<i>Aechmea aenigmatica</i> López-Ferr., Espejo, Ceja & A. Mend	Endemic to Mexico	Oaxaca
<i>Aechmea bracteata</i> (Sw.) Griseb.	Mexico, Central America and Northern Colombia and Venezuela	Campeche, Chiapas, Hidalgo, Puebla, Querétaro, Quintana Roo, San Luis Potosí, Tabasco, Tamaulipas, Veracruz, and Yucatán
<i>Aechmea bromeliifolia</i> (Rudge) Baker	Southeastern Mexico and Central America to Brasil and Argentina	Campeche and Quintana Roo
<i>Aechmea laxiflora</i> Benth.	Endemic to Mexico	Colima, Guerrero, Jalisco, Michoacán, Nayarit, Oaxaca, and Sinaloa
<i>Aechmea lueddemanniana</i> (K. Koch) Brongn. ex Mez	Mexico to Panama	Chiapas, Oaxaca, and Veracruz
<i>Aechmea magdalenae</i> (André) André ex Baker	Mexico, Central America, Colombia and Ecuador	Chiapas, Oaxaca, and Veracruz
<i>Aechmea matudae</i> L.B. Sm.	Endemic to Mexico	Chiapas
<i>Aechmea mexicana</i> Baker	Mexico, Central America, Colombia and Ecuador	Chiapas, Oaxaca, Puebla, San Luis Potosí, and Veracruz
<i>Aechmea novoae</i> Flores-Arg., López-Ferr. & Espejo	Endemic to Mexico	Jalisco
<i>Aechmea nudicaulis</i> (L.) Griseb.	Mexico, Central America, Northern South America and the Antilles	Chiapas, Puebla, and Veracruz
<i>Aechmea tillandsioides</i> (Mart. ex Schult. & Schult. F.) Baker	Mexico, Central America and Northern South America	Campeche, Chiapas, Oaxaca, Quintana Roo, Tabasco, and Veracruz

**Description.** Plants epiphytic, rarely saxicolous herbs, from 50 cm to over 2 m when flowering, polycarpic, funnelform rosette. Leaves erect to recurved, coriaceous; leaf sheaths 13-26 × 10-16 cm, elliptic to obovate, adaxially pardus lepidote, abaxially green, lepidote, coriaceous; leaf blades 26-123 × 3-9 cm, ligulate to broadly triangular, green on both sides but sometimes red when growing exposed, slightly lepidote adaxially, densely lepidote abaxially, parallelodromous trichomes, conspicuous veining, serrate margins; spines 2-7 × 1-3 mm long, decreasing its size gradually towards the leaf blade apex, straight to uncinat, antrorse, green with yellowish tips. Inflorescence terminal, usually the basal spikes twice-branched and the rest once-branched, occasionally completely once-branched, erect or curved, paniculated; peduncle, 46-67 (-95) cm long, 2-9 mm in diameter, cylindrical, erect to curved, green or red colored axis, covered with white floccose indument; peduncle bracts 9-22 × 1-2 cm, broadly elliptic to lanceolate, acute, imbricated, entire margin, bright red colored, alternate phyllotaxis; fertile portion of the inflorescence 16-70 cm long, erect to curved, green to red colored axis, covered with white indument; spikes 0.4-7 cm long, ca. 30



to over 100, decreasing in size towards the apex, alternate phyllotaxis, green or red colored axis covered with white floccose indument; secondary spikes, 1-4 cm, alternate phyllotaxis, green or red colored axis covered with white floccose indument; primary bracts along the inflorescence up to the middle portion of the inflorescence and decreasing in size, 3-21 × (0.30-) 0.40-2 cm in the basal portion, 1-7 (-10) × 0.1-0.6 (-1) cm in the middle portion, generally absent in the upper portion towards the apex, lanceolate to linear, acute, margin entire to minutely serrated, bright red, glabrous; floral bracts 4-7 × 1-5 mm, ovate to elliptic, acuminate, with a small spine in the apex, white indument abaxially, glabrous adaxially, green to red, apical spine green or red to pale brown. Flowers 10-13 × 2-2.5 mm, sessile, appressed to the spike rachis; sepals 3-4 × 2-2.5 mm, triangular, slightly acuminate, free, glabrous, smooth, coriaceous, green with hyaline margins; corolla tubular, actinomorphic, 5-8 × 1.5-1.8 mm; petals 5-8 × 2-2.5 mm, oblanceolate, acute, slightly incurved, hyaline margins, free, glabrous on both surfaces, pale yellow, scaled crenated appendages; stamens 6, 3 attached to each one of the petals and the other 3 attached to the ovary, free, shorter than the petals, white filaments, dorsoventrally flattened, 3-5 mm long; anthers 1-1.1 mm long, oblong, monothecal, subbasifixed, yellow; pollen yellow; style 6-8 mm long, erect, inserted, white to pale yellow, cupulate stigma; ovary 3-4 × 3-3.5 mm, oblong, green, floccose white lepidote. Berry 7-8 × 6-7 mm, globose, green when immature, bluish-black when mature, floccose to dotted white lepidote; persistent sepals, red when the fruit is immature, purple when mature; seeds 3.2-3.8 × 1-1.6 mm long, cuneiform, light brown to reddish-brown, covered with mucilage.

*Distribution and ecology.* *Aechmea bracteata* occurs from Mexico (alongside the slopes of the Gulf of Mexico, from southern Tamaulipas to the Yucatan Peninsula; and eastern Oaxaca and Chiapas) to northern Colombia and Venezuela. This species occurs in oak forests, riparian forests, tropical deciduous forests, tropical sub-deciduous forests, tropical sub-evergreen forests, mangroves, seasonally flooded savannahs, and secondary vegetation from sea level to ca. 1,000 m asl (according to herbarium records, Ramírez *et al.* 2004, Espejo-Serna *et al.* 2005).

*Phenology.* This species has been collected flowering and fructifying almost all year long, however, flowering occurs most commonly from October to May, while fructification mostly occurs from January to August.

*Etymology.* Not specified in the protologue, however, “*bracteata*” might be a reference to the inflorescence bracts this species possesses.

*Taxonomic notes.* Initially being described as *Bromelia bracteata* by Swartz (1788) from a specimen collected in Veracruz, Mexico (Houston, *W. s.n.*, BM), and later transferred to the genus *Aechmea* Ruiz & Pav. by Grisebach (1864), *Aechmea bracteata* possess a considerable taxonomic history due to various taxa described from various populations during the XIX century. Among the taxa considered as synonyms of *A. bracteata*, *Aechmea schiedeana* Schldl. was described based on a specimen collected from Veracruz, Mexico (Schiede & Deppe, *s.n.*, B, destroyed). Although its type specimen is declared as destroyed, it is due to its geographic origin and characteristics mentioned on its protologue, such as the leaf size and margin, the parallelodromous trichomes, the size of the inflorescence, branches and primary bracts, and the floral bracts having a “piercing point” (Schlechtendal 1845); that is possible to infer its identity as *A. bracteata*. Other synonyms known for *A. bracteata* are *A. barleei* Baker and *A. isabellina* Baker, both described in Central America, in the countries of Belize (*Barlee, s.n.*, K (photo, US)), and Guatemala (*J. D. Smith 1824*, US), respectively (Baker 1883, 1890). However, the descriptions for each of the previously mentioned taxa, match with the morphology of *A. bracteata*, regarding their type specimen’s collection sites, these belong to the known geographical distribution of *A. bracteata*, supporting the synonymy initially proposed by Smith (1958) and Smith & Downs (1979).

Regarding, *Aechmea regularis* Baker, a taxon which has been previously considered as a synonym of *A. bracteata* in other publications (*i.e.*, Smith 1958, Smith & Downs 1979); it was described from a specimen allegedly collected in South Brazil (*Weir, s.n.*, K) and is described to have white petals (Baker 1879). Due to disagreement with the known distribution and petal color described for *A. bracteata*, *A. regularis* will not be treated as a synonym in this publication.

*Specimens examined.* [Supplementary material 2.](#)

*Aechmea laxiflora* Benth., Bot. Voy. Sulphur [Bentham] 173. 1846. Type: Mexico, Guerrero: Acapulco, without collection date, *Sinclair s.n.*, (holotype K).

*Hohenbergia laxiflora* (Benth.) Baker, Refug. Bot. 4: sub t. 284, no. 7. 1871.

*Aechmea bracteata* var. *pacifica* Beutelsp. Cact. Suc. Mex. 16: 44, f. 26-27. 1971. Type: Mexico, Guerrero, Mun. Manilinaltepec, El Rincón, 45 km de Chilpancingo camino a Acapulco, 26 March 1971, C. R. Beutelspacher *s.n.* (holotype, MEXU)

*Description.* Plants epiphytic, rarely saxicolous herbs, from 50 cm to less than 2 m when flowering, polycarpic, funnellform rosette. Leaves, recurved to erect, flexible, coriaceous; leaf sheaths 13-26 × 9-15 cm, elliptic, adaxially red-brown lepidote, abaxially yellowish green, lepidote, coriaceous; leaf blades 39-96 × 2-9 cm, ligulate to broadly triangular, slightly lepidote adaxially, lepidote with irregularly distributed trichomes abaxially, flexible coriaceous, yellowish green both sides, inconspicuous veining, serrate margins; spines 3-7 mm long, decreasing its size gradually towards the leaf blade apex, uncinat, antrorse, yellowish green with pale brown tips. Inflorescence terminal, usually once-branched, rarely twice-branched at the basal spikes, erect or curved, paniculate; peduncle 39-67 cm long, 3-6 mm in diameter, cylindrical, erect to slightly curved, green to red colored axis, with thin white indument; peduncle bracts 9-17 × 1-2 cm, broadly elliptic, attenuate, imbricated, entire margin, pinkish red colored, alternate phyllotaxis; fertile portion of the inflorescence 12-43 (59) cm long, erect to curved, green to red axis with thin white indument; spikes 0.5-8 cm long, ca. 20 to over a 100, decreasing in size towards the apex, alternate phyllotaxis, green colored axis covered with thin white indument; secondary spikes 2-8 cm long, green colored axis covered with thin white indument; primary bracts along the whole inflorescence decreasing in size towards the apex, 4-12 × 0.50-2 cm in the basal portion, 1-5 × 0.30-0.75 cm in the middle portion, 0.98-2 × 0.20-0.55 cm in the superior portion, lanceolate to linear, acute, entire margin, pinkish red colored, glabrous on both sides; floral bracts 3-6 × 2-5 mm, ovate-triangular, apiculate, cucullate, green, glabrous on both surfaces, smooth. Flowers distichous, ca. 10 × 3 mm, sessile, appressed to the spike rachis; sepals 3-5 × 2-3 mm, obovate, rounded apex, free, asymmetric, coriaceous, green with hyaline margins, glabrous on both surfaces, smooth; corolla tubular, actinomorphic, 5-6 × 2-3 mm; petals 8-9 × 2-4 mm, oblanceolate, bright yellow, hyaline margin, free, glabrous on both surfaces, scaled crenated appendages inserted at the base, slightly incurved towards its apex, apiculate to slightly acuminate; stamens 6, 3 attached to each one of the petals and the other 3 attached to the ovary, free, shorter than the petals, inserted, white filaments, dorsoventrally flattened, 6-7 mm long; anthers 1.4-1.7 mm long, oblong, monothechal, sub basifixed, yellow, pollen yellow; style 8-9 mm long, erect, inserted, yellow, cupulate stigma; ovary 3-4 × 3-3.6 mm oblong, green, scarcely white-lepidote. Berry 7.5-8 × 6-7 mm, globose, yellowish green when immature, black when mature; persistent sepals, coloration before and after maturation is the same as the fruit; seeds 3.2-3.3 × 1-1.4 mm, fusiform, reddish brown, covered with mucilage.

*Distribution and ecology.* *Aechmea laxiflora* is endemic to western Mexico, from southern Sinaloa to western Oaxaca. This species occurs in oak forests, pine-oak forests, riparian forests, tropical deciduous forests, and tropical sub-deciduous forests from sea level to ca. 1,250 m asl (according to herbarium records, Flores-Argüelles *et al.* 2023).

*Phenology.* According to the examined herbarium specimens, *A. laxiflora* can be found flowering and fructifying almost all year long, however, flowering occurs most commonly from September to July, while fructification mostly occurs from January to April.

*Etymology.* Not specified in the protologue, but probably named because of the lax arrangement of the inflorescence branches.

*Taxonomic notes.* This taxon was considered initially as a synonym for *A. bracteata* by Smith (1958), but after *A. bracteata* var. *pacifica* was described (Beutelspacher 1971), *A. laxiflora* was proposed as a its synonym (Smith & Downs 1979), however this proposal was not explicitly justified in such publication.

*Additional specimens examined.* [Supplementary material 3](#).

## Supplementary material

Supplemental material for this article can be accessed here: <https://doi.org/10.17129/botsci.3389>

## Acknowledgements

The present publication is part of the results of the first author's bachelor's degree thesis project. The authors would like to thank the staff of the Molecular Laboratory at CICY for their support with the molecular work, specially to Matilde Ortiz-García and Jaime Muñoz-López; Pablo Carrillo-Reyes (IBUG) for collecting leaf tissue and sharing photographic records; Francisco Hernández-Najarro (CHIP) for helping with field work, specimen collection, and sharing herbarium records; Israel Acosta-Rosado (XAL) for sharing the herbarium database and digitalizing specimens; Juan Tun-Garrido, Juan Javier Ortiz-Díaz and Juan José Ancona-Aragón (all at UADY) for supporting field-work to collect foliar tissue and specimens; Geovani Palma-Pech (UADY) for the support in incorporating specimens to the UADY herbarium; Germán Carnevali Fernández-Concha and Silvia Hernández-Aguilar (both at CICY) for their support on the revision of herbarium specimens; Clarisa Jiménez Bañuelos (CICY) who kindly allowed the study of cultivated specimens at CICY's botanical garden. Last but not least, the authors would like to thank the editor section and two reviewers for their comments that allowed to improve this publication.

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**Associate editor:** Eduardo Ruiz Sánchez

**Author contributions:** MSD analyzed the data, performed the analyses, interpreted the results, and wrote the manuscript, JPP and IMRM designed the study, assisted in the performance of the analyses, the interpretation of the data and fieldwork, CJRD assisted on the design of the study, provided foliar tissue and helpful information for the development of the project, NR assisted on obtaining the sequences used in the phylogenetic analyses and field work. All authors have contributed substantially with ideas and revisions to previous versions of the manuscript.

**Supporting Agencies:** Centro de Investigación Científica de Yucatán, A. C. (CICY) for providing the CADE scholarship (Project: 1041300004) to the first author.

**Conflicts of interest:** The authors declare that there is no conflict of interest, financial or personal, in the information, presentation of data and results of this article.