

RESEARCH PAPER

A morphometric and taxonomic study of *Anthurium augustinum* complex (Araceae), endemic to the Brazilian Atlantic Forest

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The *Anthurium augustinum* (Araceae) complex (including *A. augustinum* K. Koch & Lauche, *A. hatschbachii* E. G. Gonç., *A. jureianum* Cath. & Olaio, *A. laucheanum* K. Koch, *A. lhotzkyanum* Schott, *A. lucidum* Kunth, *A. maximiliani* Schott and *A. parvum* N.E.Br.) is endemic to the Brazilian Atlantic Forest. Some of these taxa are strictly endemic, with only the type population known, and may occur in sympatry. These species share a leaf morphology in which the blade is deflexed at the petiole insertion and is usually cordate, or rarely rounded at the base due to congenital fusion of the basal lobes. Taxonomic delimitation of the species in this group is difficult because of overlap in diagnostic characters such as deflexed leaf blade, cordate, rounded or semi-oval leaf base and campodromous venation. The objective of the study was to test whether these taxa could be recognized using leaf morphometrics. Elliptic Fourier analysis was carried out on a sample of 257 individuals in 12 natural populations. The results of multivariate analyses indicated that in various comparisons, leaf shape was not diagnostic due overlap of variation within and between populations of different species. Consequently, we propose that *A. laucheanum*, *A. lhotzkyanum* and *A. maximiliani* should be regarded as synonyms of *A. augustinum*, and that the following five species be recognized in this complex: *A. augustinum*, *A. hatschbachii*, *A. jureianum*, *A. lucidum* and *A. parvum*. We also formally designate two neotypes (*A. laucheanum*, *A. maximiliani*), one lectotype (*A. augustinum*) and one epitype (*A. augustinum*).

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1 Introduction

The use of a taxonomic species concept, such as that defined by Gregg (1950), makes it inevitable that the delimitation of taxa by classical qualitative methods is subjective, since the limited number of specimens in herbaria only partially reflects the full morphological

variation found in nature (Stace 1989). Experimental taxonomy, biosystematics and morphometrics are areas of biological science which developed in response to dissatisfaction with this situation, by attempting to minimize subjectivity through quantifying organismal variation (Sneath & Sokal 1973; Stace 1989; Bernadello et al. 1995).

Morphometrics has been used in various ways for the delineation of taxonomic species. In particular geometric morphometrics, or shape biometry, focusses exclusively

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on variation in the shape of organisms or organismal structures, after removing the effects of variation in size, position and orientation (Bookstein 1991; Monteiro & Reis 1999). In this approach, two major types of data are used; 1) landmark configurations, which consist of a set of homologous points on a structure (Bookstein 1991; Monteiro & Reis 1999), and 2) outline configurations – when the biological structure does not have a sufficient number of identifiable landmarks, the shape can be described by a sequence of points along the outline of the structure of interest, without requiring biological correspondence (i.e. homology) between the points (Premoli 1996; McLellan & Endler 1998; Rumpunen & Bartish 2002). The outline of a structure such as a leaf blade can thus be captured as a set of non-homologous points and in practice these are generally the coordinates of the pixels that delineate the structure's outline in a digital image. These data sets, each representing a contour, can be used in various ways to generate statistical shape variables (Monteiro & Reis 1999). Elliptic Fourier Analysis (EFA) was developed by Kuhl & Giardina (1982) and is particularly useful for the study of shapes in which clearly homologous landmarks are either absent or very few (Monteiro & Reis 1999). EFA uses outline configuration data to generate Fourier coefficient shape variables for further multivariate analysis, with the added advantage that the Fourier coefficients can be used to reconstruct the original outlines to a level of precision that depends only on the number of pixels used in the original digitization of the leaf image (Rohlf & Archie 1984).

The first published morphometric study in Araceae was that of Ray (1992), in which he proposed a combination of outline and landmark analysis in the description of leaves of *Syngonium podophyllum* Schott. Landmarks were used in a study of *Montrichardia linifera* (Arruda) Schott to assess allometric effects and outline morphological patterns at population and species levels (Silva et al. 2012).

In the genus *Monstera* Adans., 1,695 leaves at three different ontogenetic stages from 20 natural populations of three taxa were studied with EFA by Andrade et al. (2008). Using data from adult leaves, multivariate analyses showed that the populations of the three taxa were grouped according to the currently accepted taxonomy, confirming that despite its high morphological variability, adult leaf outline can be a useful specific and infraspecific taxonomic marker in *Monstera*. Multivariate morphometric analysis applied to the taxonomy of *Monstera* taxa occurring in the State of Bahia resulted in the recognition of a new subspecies, *Monstera adansonii* Schott subsp. *blanchetii* (Schott) Mayo & I. M. Andrade (Mayo & Andrade 2014). EFA morphometrics was also used to discriminate five species of *Heteropsis* Kunth in a study in central Amazonia by Soares et al. (2011).

In *Anthurium* Schott, EFA was used in a study of *A. pentaphyllum* (Aubl.) G. Don var. *pentaphyllum* and *A. sinuatum* Benth. ex Schott (Andrade et al. 2010), based on 1,120 leaflets from 15 populations, that compared morphological variability of populations in Amazonia, isolated forest fragments in Northeast Brazil and the Atlantic Forest of Brazil. The results showed that the two species could be distinguished by their leaflet outline shapes.

Anthurium is the largest genus of Araceae, with approximately 950 species (Boyce & Croat 2011 onwards). Of these, approximately 130 occur in Brazil (Coelho & Temponi 2013). The delimitation of species in the genus is based primarily on vegetative morphological characters (Mayo et al. 1997), such as leaf color and consistency, presence of punctate glands on the leaf surface, type of venation, petiole length and cross-sectional shape, cataphyll morphology and internode length (Croat & Sheffer 1983; Coelho et al. 2009; Temponi & Coelho 2011). The current taxonomy includes species complexes in which taxa are difficult to distinguish. This situation may reflect both active evolutionary diversification (Carlsen & Croat 2013) and phenotypic plasticity, but paucity of precise geographical and ecological information from natural populations is also a factor in the resulting taxonomic and nomenclatural difficulties (Coelho & Mayo 2007). In this context, classical taxonomy alone is often insufficient to resolve certain taxonomic problems and the quantitative approach of morphometric analysis can be a valuable tool in comparing the closely related and highly variable taxa characteristic of species complexes.

The *Anthurium augustinum* complex, as defined here, currently comprises eight taxa: *A. augustinum* K. Koch & Lauche, *A. hatschbachii* E. G. Gonçalves, *A. jureianum* Cath. & Olai, *A. laucheanum* K. Koch, *A. lhotzkyanum* Schott, *A. lucidum* Kunth, *A. maximiliani* Schott and *A. parvum* N.E.Br. The complex includes all Brazilian species with deflexed leaf blades, cordate or rounded or semi-oval leaf bases and camptodromous venation. In Brazil, this combination of vegetative characters is exclusive to the *Anthurium* sect. *Urospadix* clade (Temponi 2006; Carlsen & Croat 2013), to which the *Anthurium augustinum* complex belongs. Anatomical and molecular characters used in a study of the phylogeny of *Anthurium* sect. *Urospadix* also indicate that there is a close phylogenetic relationship between these species (Temponi 2006). The complex is endemic to the Brazilian Atlantic Forest (Temponi 2006; Stehmann et al. 2009; Coelho & Temponi 2013), more precisely, to a narrow strip of the Atlantic Forest located between Santa Catarina and Rio de Janeiro states (see Fig. 1).

In this study, the *Anthurium augustinum* complex was investigated using leaf morphometrics to compare the morphological variation within and between the compo-

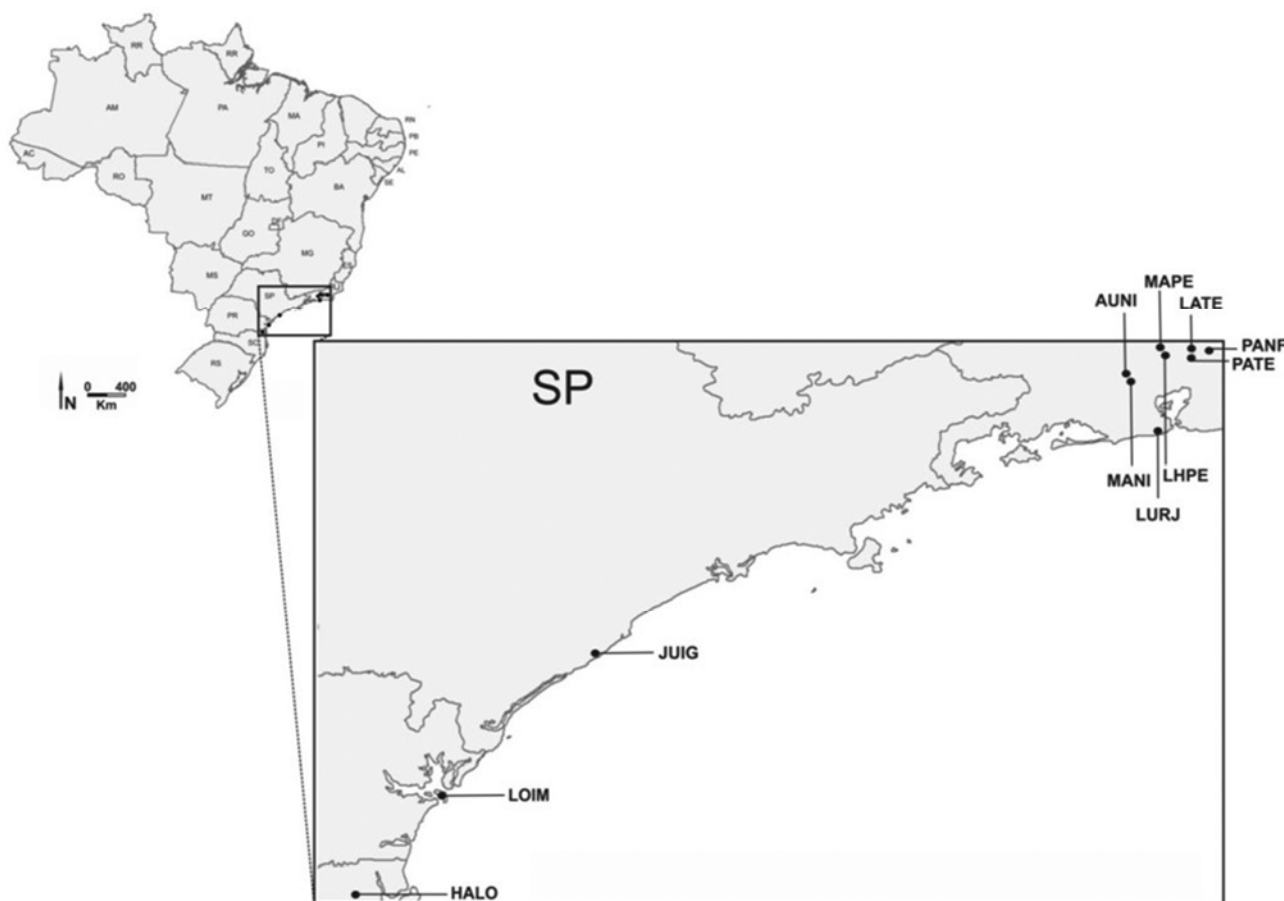


Figure 1. Geographical location of populations sampled in this study, including all taxa belonging to the *Anthurium augustinum* complex in southern and southeastern Brazil. Population codes: AUNI (*Anthurium augustinum*); HALO (*A. hatschbachii*); JUIG (*A. jureianum*); LATE (*A. laucheanum*); LHPE and LHTE (*A. lhotzkyanum*); LURJ (*A. lucidum*); MANI and MAPE (*A. maximiliani*); PANF and PATE (*A. parvum*); LOIM (*A. loefgrenii*).

nent species. Leaves were used due to their greater availability and also because leaf shape is one of the most commonly used characters for species identification in *Anthurium*. Furthermore, leaf outline shape is at least partially determined genetically; e.g. as Kessler & Sinha (2004) have shown, a series of genetically mediated processes are involved in establishing leaf blade shape, which therefore makes the latter significant from a taxonomic viewpoint (Andrade et al. 2008).

In this context, the objective of the present study is to test whether or not the species belonging to the *A. augustinum* complex can be distinguished morphologically using quantitative descriptions of leaf outline shape as a surrogate for their morphological delimitations.

2 Material and methods

2.1 Sampling

Collections were made between July 2011 and August 2012 in four states (Paraná, Rio de Janeiro, Santa

Catarina and São Paulo), belonging to the South and Southeast regions of Brazil (Table 1, Fig. 1). Two hundred fifty-seven specimens from 12 natural populations belonging to eight taxa were sampled (Table 1, Fig. 2), *A. augustinum* (one population); *A. hatschbachii* (one population), *A. jureianum* (one population); *A. laucheanum* (one population); *A. lhotzkyanum* (two populations); *A. lucidum* (one population); *A. maximiliani* (two populations); *A. parvum* (two populations). Besides these, one population of *A. loefgrenii* Engl. was sampled to enable comparison of the morphological variation in the *A. augustinum* complex with that in a species belonging to a different group.

In each population only one leaf was sampled from each individual and thus the sample size was limited by the population size. The abaxial side of each adult leaf was photographed at an angle of 90 degrees, using a Sony Cybershot digital camera (14.1 megapixels).

The sampling area of this study covered the entire geographical distribution of the taxa (Temponi 2006; Coelho & Temponi 2013). The sampling effort aimed at

Table 1. Populations sampled in this study for all taxa included in the *Anthurium augustinum* complex, including location with coordinates, number of samples, and specimen voucher information.

Taxon	Population	Code	Coordinates	Voucher	Number of samples
<i>Anthurium augustinum</i> K. Koch & Lauche	Nova Iguaçu – RJ	AUNI	22°33'41" S, 43°28'60" W	L. G. Temponi, et al. 1052	25
<i>Anthurium hatschbachii</i> E. G. Gonçalves	Joinville – SC	HAJO	26°12'43" S, 48°57'28" W	A. P. Cardozo, et al. 63	20
<i>Anthurium jureianum</i> Cath. & Olaio	Iguape – SP	JUIG	24°32'42" S, 47°13'50" W	A. P. Cardozo, et al. 60	23
<i>Anthurium laucheanum</i> K. Koch	Teresópolis – RJ	LATE	22°26'57" S, 42°59'22" W	L. G. Temponi, et al. 1025	32
<i>Anthurium lhotzkyanum</i> Schott	Teresópolis – RJ	LHTE	26°26'54" S, 43°00'48" W	L. G. Temponi, et al. 1031	21
	Petrópolis – RJ	LHPE	22°24'35" S, 43°12'35" W	A. P. Cardozo et al. 33	22
<i>Anthurium loefgrenii</i> Engl.	Ilha do Mel – PR	LOIM	25°30'36" S, 48°20'19" W	A. P. Cardozo, et al. 31	24
<i>Anthurium lucidum</i> Kunth	Rio de Janeiro – RJ	LURJ	22°58'5,6" S, 43°15'25" W	L. G. Temponi, et al. 1050	27
<i>Anthurium maximiliani</i> Schott	Nova Iguaçu – RJ	MANI	22°34'34" S, 43°27'59" W	L. G. Temponi, et al. 1051	12
	Petrópolis – RJ	MAPE	22°24'35" S, 43°12'35" W	A. P. Cardozo, et al. 34	7
<i>Anthurium parvum</i> N.E.Br	Nova Friburgo – RJ	PANF	22°25'37" S, 42°31'48" W	A. P. Cardozo, et al. 43	24
	Teresópolis – RJ	PATE	22°25'37" S, 42°31'48" W	L. G. Temponi, et al. 975	20
Total number of samples					257

finding and recollecting the type locality populations of each species, which was possible for *Anthurium lhotzkyanum*, *A. lucidum*, *A. jureianum* and *A. maximiliani*. However, for *Anthurium augustinum*, *A. laucheanum* and *A. parvum* this was not possible because the locations of the types were given only in very general terms, “Rio de Janeiro province”, “tropical Brazil” and “Rio de Janeiro” respectively. In the case of *Anthurium hatschbachii*, although the type population is known to have been located at Guaratuba, Paraná state, we did not succeed in finding it there, but instead at a locality nearby.

In general, the ranges of these species are restricted to only a few localities. *Anthurium augustinum* occurs only in the municipality of Nova Iguaçu in the Tinguá Biological Reserve, and *A. lucidum* is known only from the municipality of Rio de Janeiro in the Tijuca Forest National Park; both these municipalities are in the state of Rio de Janeiro. The species *A. laucheanum*, *A. lhotzkyanum*, *A. maximiliani* and *A. parvum* occur in different municipalities, but all in the mountainous region of Rio de Janeiro state. *Anthurium jureianum* is endemic to the Juréia Ecological Station, municipality of Iguape,

São Paulo state. Although *A. hatschbachii* occurs on the border of Paraná and Santa Catarina, the only population found was in the Serra de Araçatuba, in Paraná state.

Voucher specimens of each population were prepared and deposited in the herbaria of the Botany Department of the Universidade Federal do Paraná (UPCB) and Universidade Estadual do Oeste do Paraná (UNOP) (Table 1).

2.2 Morphometric analysis

2.2.1 Digitizing outlines and elliptic Fourier analysis (EFA)

The qualitative leaf shape terminology used here follows that of the standardized descriptions of *Anthurium* species given by Croat & Bunting (1979). Leaf blade images were edited and standardized with the aid of ImageJ software (Rasband 2004) and were approximately aligned to avoid any possible undesirable effects caused by extreme differences in orientation which could mask shape variation (Monteiro & Reis 1999). Digitization of

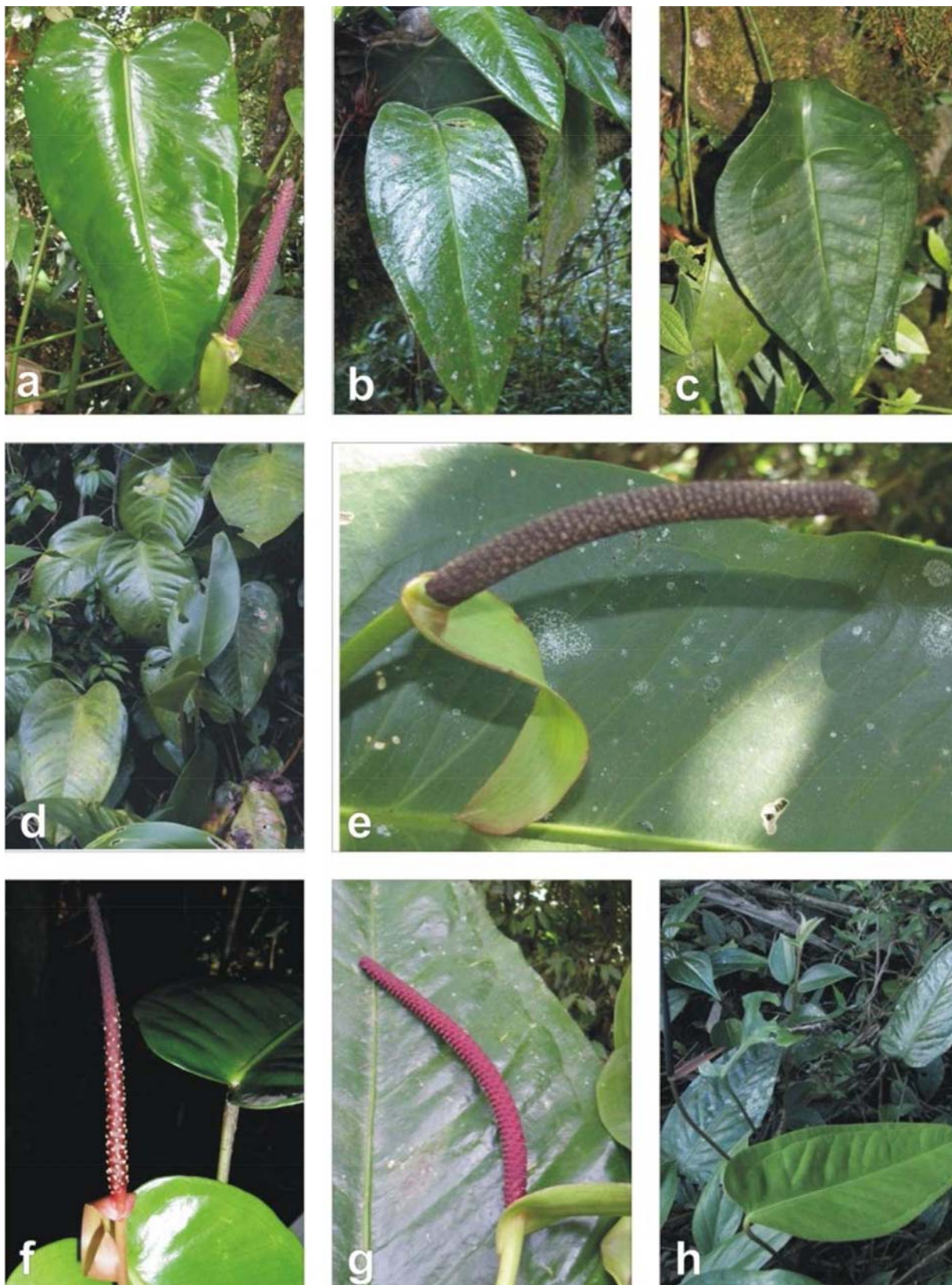


Figure 2. Species of the *Anthurium augustinum* complex: (a) *A. augustinum*; (b) *A. hatschbachii*; (c) *A. jureianum*; (d) *A. laucheanum*; (e) *A. lhotzkyanum*; (f) *A. lucidum*; (g) *A. maximiliani*; (h) *A. parvum*.

leaf outlines was carried out using the TpsDig program (Rohlf 2004). To permit standardization of the location, size and orientation of the outlines, two landmarks were used, one at the base and another at the apex of the midrib (landmarks (LM) 1 and 2 respectively) (Bookstein 1991). The digitization demarcated a sequence of points (captured as x and y coordinates) that mapped the outline of each leaf, using the junction of the petiole and the leaf blade (LM1) as the starting point for digitizing.

Elliptic Fourier analysis (EFA) was carried out using the program Morpheus et al. (Slice 1998) according to methodology of Andrade et al. (2008). Standardization of size and alignment of the contours was performed using the “Bookstein superimposition” option, based on landmarks 1 and 2. Twenty harmonics (ellipses) were chosen to obtain a sufficient number of shape variables (Fourier coefficients) to adequately represent the original leaf outlines. Each ellipse has four parameters (Fourier coefficients), resulting in a matrix consisting of 80 columns (Fourier coefficients) and 257 rows (leaves sampled). From this matrix of Fourier coefficients the mean shapes of each population were computed and reconstructed visually. The Fourier coefficient matrix was then subjected to multivariate analyses in order to compare shape variation of populations and species.

2.2.2 Data analysis

Multivariate analyses were conducted using the PAST software (Hammer et al. 2001). Principal Component Analysis (PCA) was used to generate a smaller number of new independent shape variables (i.e. orthogonal PC axes) that described more than 90% of the total variation in the original data.

Canonical Variate Analysis (CVA) was carried out to quantify the variability within and between the populations studied, using eigenanalysis to find axes representing linear combinations of the shape variables that give maximum separation between the populations (Monteiro & Reis 1999).

Similarity relationships among populations and species were tested using Non-Parametric Multivariate Analysis of Variance (NP-MANOVA), which is analogous to MANOVA. It calculates the probability that the computed test values (representing the distance between each pair of populations) are due entirely to chance – i.e. that they belong to the same population (Monteiro & Reis 1999). This analysis was performed with 10,000 permutations.

The mean of the PCA shape variables for each of the 12 populations was used to calculate the Euclidean distance between the centroids of each population using Principal Coordinate Analysis (PCoA). The same procedure was used to find the Euclidean distance between the centroids of each taxon.

Cluster analysis was carried out with Unweighted Pair-Group Method using Arithmetical Averages (UPGMA)

(Sneath & Sokal 1973). Euclidean distances were computed between the population mean values of the principal component shape variables computed from the matrix of 80 elliptic coefficients. In these analyses, bootstrap was computed with 999 permutations.

3 Results

3.1 Shape variation

Based on the mean leaf shape of each population (Fig. 3), species ranged from ovate to broadly ovate (Croat & Bunting 1979) in *Anthurium jureianum* (Fig. 3c), to slightly cordate in populations of *A. parvum* (Panf and Pate) (Fig. 3j–k), to cordate with the well-developed posterior lobes in all other populations, except for *A. loefgrenii* (LOIM) (Fig. 3l) which has lanceolate leaves.

The most divergent mean shape within the *A. augustinum* complex was that of the JUIG population (*A. jureianum*), which does not have posterior lobes and in which the leaf is peltate. In fact, it is clear from the venation pattern that the leaf in this species is fundamentally cordate but has undergone congenital fusion of the posterior lobes (Fig. 2c). In all other species within the complex, mean shapes are similar to each other, and individuals have ovate to broadly ovate leaves with posterior lobes that range from slightly to well-developed (Fig. 3). The sinus between the posterior lobes is arcuate in most populations, except in the HAJO population (*A. hatschbachii*), where it tends to be triangular (Fig. 3b).

3.2 Principal component analysis

Principal component analysis showed that the first six shape variables, namely the principal components (PCs), generated from the Fourier coefficient matrix, represented 97.6% of the total variance (Table 2). The largest amount of variation in the data set occurs in PC 1 axis (Fig. 4) and accounts for about 71% of the total variance in the data set (Table 2). The PC 1 and PC 3 axes clearly separate the 257 individuals into three groups: a group in the second quadrant formed by the LOIM population (*Anthurium loefgrenii*), a group in the fourth quadrant formed by the JUIG population, and a group composed of the remaining populations in the central part of the plot (Fig. 4b). These shape variables, namely the principal components (PCs), were used in other multivariate analyses as described by Yoshioka et al. (2004); Andrade et al. (2010) and Soares et al. (2011).

3.3 Interpopulation diversity

In the Canonical Variate Analysis (CVA), the first two canonical axes explain 62% and 21% of the variation

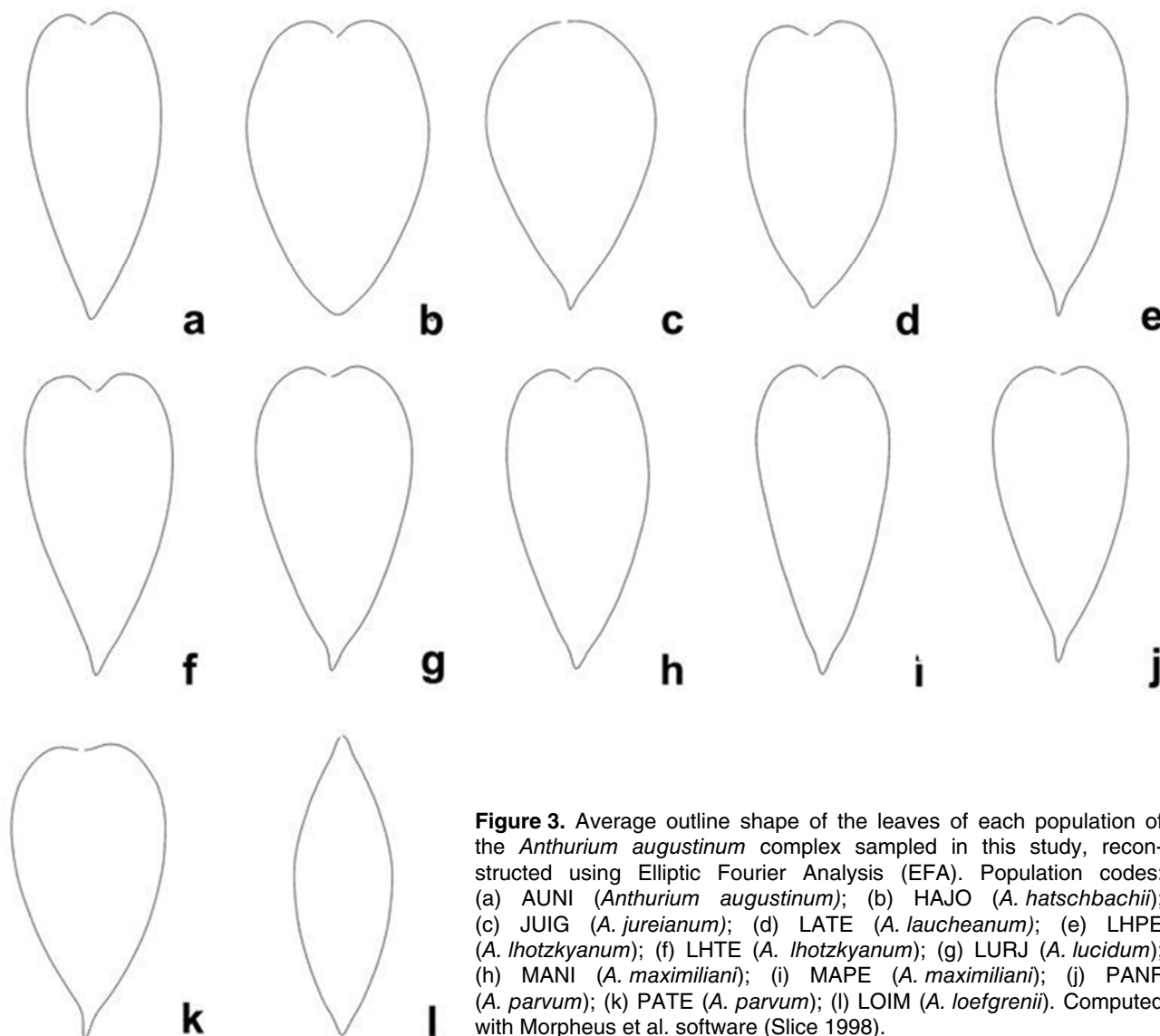


Figure 3. Average outline shape of the leaves of each population of the *Anthurium augustinum* complex sampled in this study, reconstructed using Elliptic Fourier Analysis (EFA). Population codes: (a) AUNI (*Anthurium augustinum*); (b) HAJO (*A. hatschbachii*); (c) JUIG (*A. jureianum*); (d) LATE (*A. laucheanum*); (e) LHPE (*A. lhotzkyanum*); (f) LHTE (*A. lhotzkyanum*); (g) LURJ (*A. lucidum*); (h) MANI (*A. maximiliani*); (i) MAPE (*A. maximiliani*); (j) PANF (*A. parvum*); (k) PATE (*A. parvum*); (l) LOIM (*A. loefgrenii*). Computed with Morpheus et al. software (Slice 1998).

respectively. The twelve populations form three groups within this space (Fig. 5) similar to the PCA results. The LOIM (*Anthurium loefgrenii*) population is clearly separated in the third quadrant and the JUIG population (*A. jureianum*) in the fourth quadrant where as all other populations form a cluster in the center of the space of the first two CVs (Fig. 5).

A CV plot including only populations belonging to the third central group showed that several other populations occupy fairly distinct positions in the CV space; the separation of the HAJO population (*A. hatschbachii*) toward the left side of CV1 is the most notable (Fig. 6). Interpopulation distance was obtained by NP-MANOVA, and demonstrated that 79% of population pairs are sig-

Table 2. First six principal components of *Anthurium augustinum* complex.

Principal Component	Eigenvalues	% Variance	% of Cumulative Variance
PC 1	0.00600439	71.67	71.67
PC 2	0.00105823	12.63	84.31
PC 3	0.000494383	5.90	90.21
PC 4	0.000309416	3.6934	93.90
PC 5	0.000240528	2.8711	96.77
PC 6	7.67421E-05	0.91605	97.69

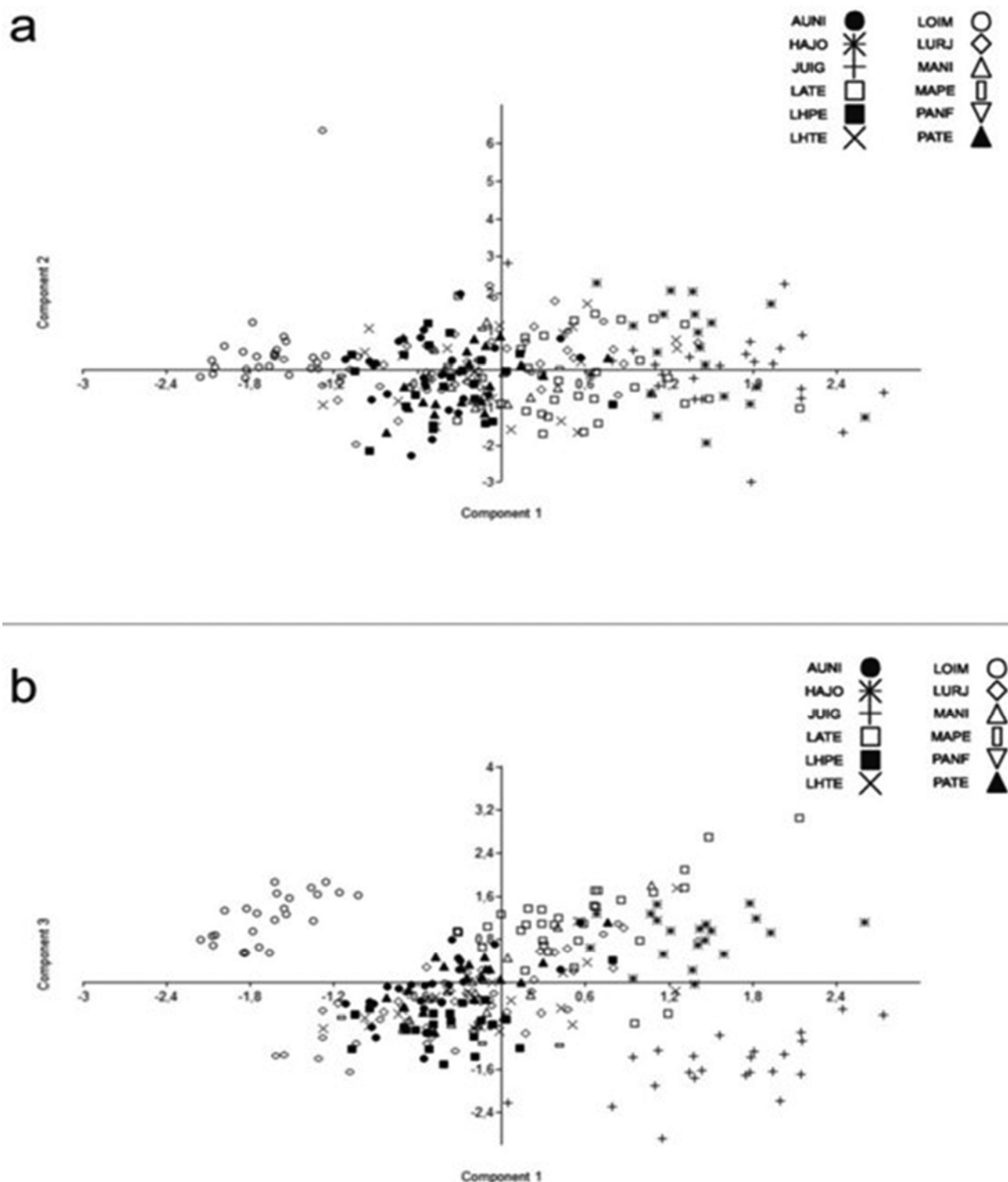


Figure 4. Ordination of scores on the first three axes of a principal component analysis (PCA) based on a matrix of 80 elliptic Fourier coefficients of leaves from populations in the *Anthurium augustinum* complex. (a) distribution of variation in leaf shape on PC1 and PC2 axes; (b) distribution of variation in leaf shape on PC1 and PC3 axes. Population codes: AUNI (*Anthurium augustinum*); HAJO (*A. hatschbachii*); JUIG (*A. jureianum*); LATE (*A. laucheanum*); LHPE and LHTE (*A. lhotzkyanum*); LURJ (*A. lucidum*); MANI and MAPE (*A. maximiliani*); PANF and PATE (*A. parvum*); LOIM (*A. loefgrenii*). Computed with PAST software (Hammer et al. 2001).

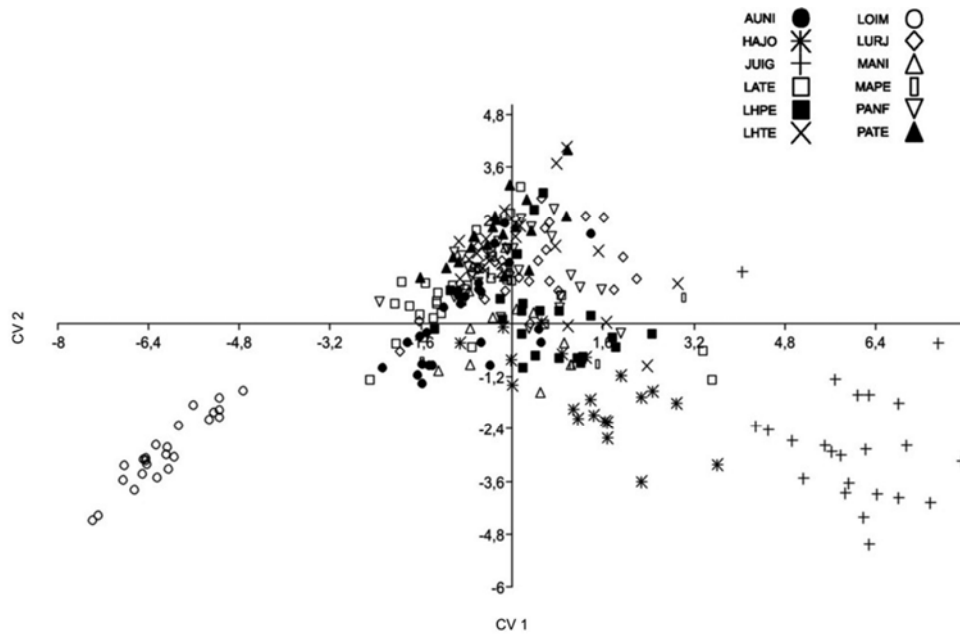


Figure 5. Ordination of scores on the first two canonical axes of a canonical variate analysis (CVA) of populations in the *Anthurium augustinum* complex, using six shape variables (i.e. principal component scores on six axes) derived from a matrix of 80 elliptic Fourier coefficients. Population codes: AUNI (*Anthurium augustinum*); HAJO (*A. hatschbachii*); JUIG (*A. jureianum*); LATE (*A. laucheanum*); LHPE and LHTE (*A. lhotzkyanum*); LURJ (*A. lucidum*); MANI and MAPE (*A. maximiliani*); PANF and PATE (*A. parvum*); LOIM (*A. loefgrenii*). Computed with PAST software (Hammer et al. 2001).

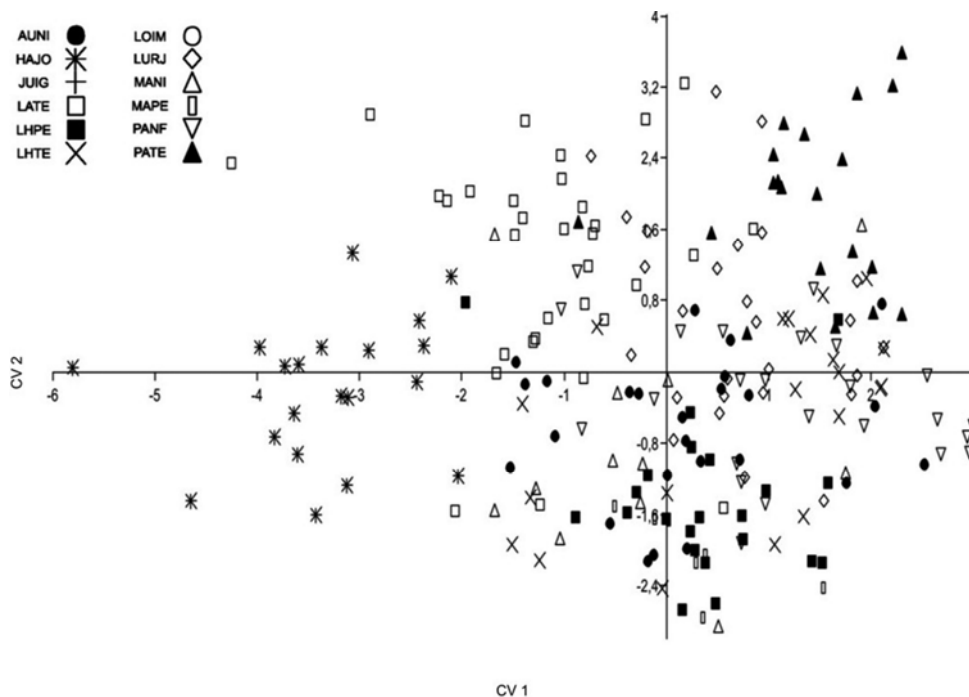


Figure 6. Ordination of scores on the first two canonical axes of a canonical variate analysis (CVA) of the most similar populations in the *Anthurium augustinum* complex (i.e. excluding the JUIG (*A. jureianum*) and LOIM (*A. loefgrenii*) populations). The CVA used a matrix of six shape variables (i.e. principal component scores on six axes) derived from 80 elliptic Fourier coefficients. Population codes: AUNI (*Anthurium augustinum*); HAJO (*A. hatschbachii*); LATE (*A. laucheanum*); LHPE and LHTE (*A. lhotzkyanum*); LURJ (*A. lucidum*); MANI and MAPE (*A. maximiliani*); PANF and PATE (*A. parvum*). Computed with PAST software (Hammer et al. 2001).

Table 3. Similarity between 12 populations of the *Anthurium angustinum* complex based on six shape variables namely principal components (PCs), derived from the elliptic Fourier analysis matrix. The values p -values (probability that two groups are similar) are derived from non-parametric MANOVA implemented in PAST, with 10,000 permutations. See Table 1 for population codes.

Popu- lation	AUNI	HAJO	JUIG	LATE	LHPE	LHTE	LOIM	LURJ	MANI	MAPE	PANF	PATE
AUNI	–											
HAJO	0.0000	–										
JUIG	0.0000	0.0000	–									
LATE	0.0000	0.0000	0.0000	–								
LHPE	n.s.	0.0000	0.0000	0.0000	–							
LHTE	n.s.	0.0000	0.0000	0.0000	0.0396	–						
LOIM	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	–					
LURJ	0.0132	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	–				
MANI	n.s.	0.0000	0.0000	0.0000	n.s.	n.s.	0.0000	0.0066	–			
MAPE	n.s.	0.0000	0.0000	0.0000	n.s.	n.s.	0.0000	0.0000	n.s.	–		
PANF	n.s.	0.0000	0.0000	0.0000	0.0000	n.s.	0.0000	n.s.	n.s.	n.s.	–	
PATE	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0066	0.0000	0.0000	0.0000	–

n.s. = not significant

nificantly different ($p < 0.05$) (Table 3). The other 21% showed no significant differences ($p \geq 0.05$), and these all involved populations of *A. angustinum*, *A. Ihotzky-*

num, *A. lucidum*, *A. maximiliani* and *A. parvum* (PANF population).

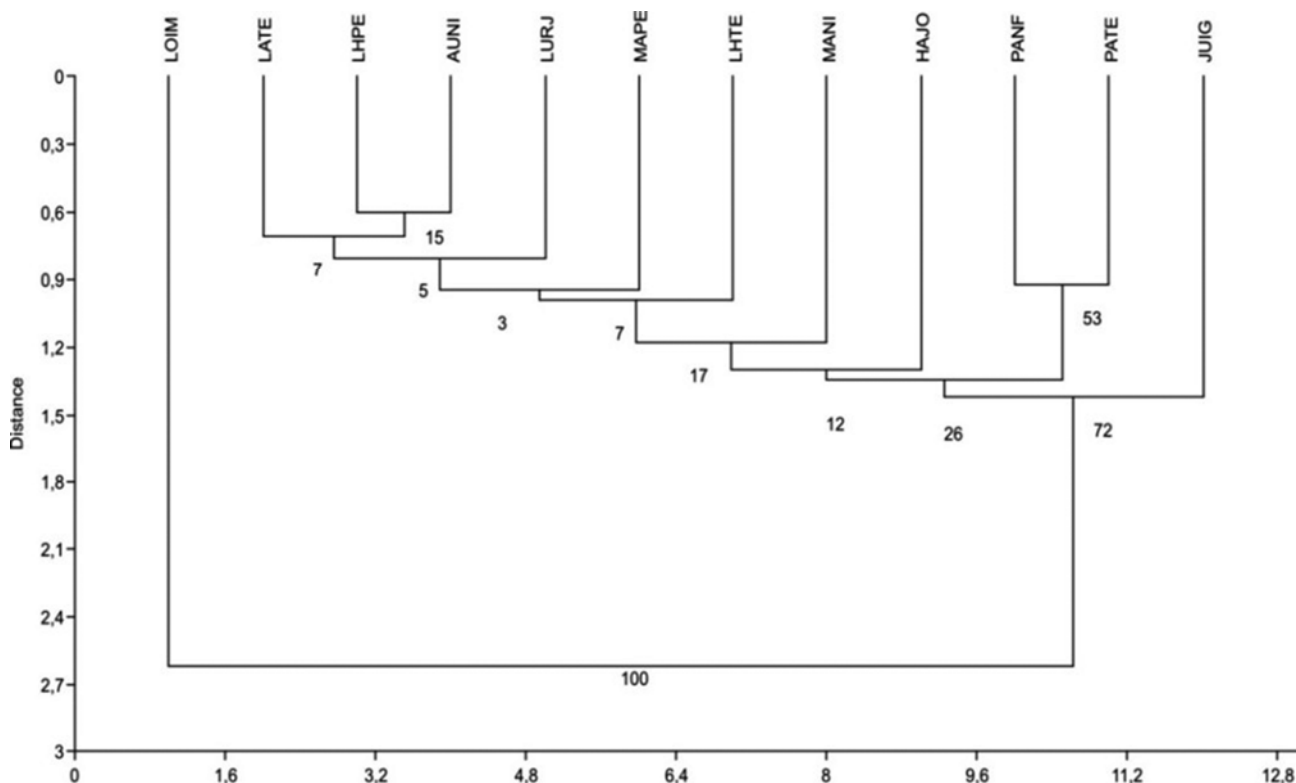


Figure 7. UPGMA dendrogram showing the phenetic relationships among 12 populations of the *Anthurium angustinum* complex, using a matrix of the population mean principal component scores from a principal component analysis (PCA) of 80 elliptic Fourier coefficients. Numbers below each branch represent bootstrap support values (999 replicates). Computed with PAST software (Hammer et al. 2001).

NP-MANOVA analysis also revealed that JUIG (*A. jureianum*), HAJO (*A. hatschbachii*), LATE (*A. laucheanum*), LOIM (*A. loefgrenii*) and PATE (*A. parvum*) populations are highly differentiated with p -values ≤ 0.0002 when compared with any other population (Table 3).

In UPGMA, LOIM (*A. loefgrenii*) and JUIG (*A. jureianum*) populations were isolated, populations of *A. parvum* (PATE and PANF) formed a separate cluster, and the remaining populations formed a larger group (Fig. 7).

The NP-MANOVA analysis (Fig. 3) showed that the two populations of *Anthurium lhotzkyanum* (LHTE and LHPE) were significantly different ($P = 0.0396$), and in the UPGMA cluster analysis these two populations formed a group which included populations of other taxa (Fig. 7). The two populations of *Anthurium maximiliani* (MANI, MAPE) were not significantly different under NP-MANOVA nor were they significantly different from the AUNI population of *A. augustinum*. Despite this similarity, these three populations are grouped together with populations of other species. Conversely, the two populations of *A. parvum* (PANF, PATE) are not significantly different in NP-MANOVA but form a unique group in the UPGMA cluster analysis (Fig. 7).

Distances computed among the nine species by NP-MANOVA showed four significant population-pairwise differences – *A. hatschbachii*, *A. laucheanum*, *A. jureianum* and *A. loefgrenii* – in all comparative pairs (data not shown). These results are similar to those in the NP-MANOVA carried out with populations.

In PCoA, five groups were recognized: *A. hatschbachii*, *A. jureianum*, *A. lucidum*, *A. loefgrenii* and a larger grouping including the other species (*A. augustinum*, *A. lhotzkyanum*, *A. laucheanum*, *A. maximiliani* and *A. parvum*) (Fig. 8).

4 Discussion

Image-based leaf morphometrics has been used in large-scale studies to investigate the relationship between phenotypic polymorphism and evolutionary biological trends (Lexer et al. 2009). In the case of *Anthurium*, studies of leaf shape variation have potential in attempting to understand the phenotypic plasticity at the species level (Coelho & Mayo 2007), especially since the characters used to delimit species are mostly vegetative (Temponi 2006; Coelho et al. 2009).

In CVA it was possible to verify the clear distinction of the following three populations belonging to three different species, demonstrating the efficiency of the method in discriminating taxa outside the *A. augustinum* complex: the LOIM population (*Anthurium loefgrenii*) with lanceolate leaf blades (Fig. 3l, Fig. 5); the JUIG popula-

tion (*A. jureianum*) with a peltate, basally rounded leaf blade (Fig. 2c, Fig. 3c, Fig. 5); and the HAJO population (*A. hatschbachii*) (Fig. 6) with a cordate leaf blade (Fig. 2b, Fig. 3b). These populations and taxa are also significantly different from all the others according to the results of NP-MANOVA (Table 3), PCoA (Fig. 8) and cluster analysis (Fig. 7).

For the remaining species in the *Anthurium augustinum* complex, interpopulation distances tested with NP-MANOVA showed significant differences in 79% of population-pairs, even though there was overlap between most of the sampled populations. A large overlap in leaf shape between populations was also observed in *A. pentaphyllum* and *A. sinuatum* (Andrade et al. 2010), and must be related to the high phenotypic variation that is common in the genus *Anthurium* (Coelho & Mayo 2007). Our analysis indicated that of the nine populations that overlap most in the CVA (AUNI, LATE, LHPE, LHTE, LURJ, MANI, MAPE, PANF, PATE), (Figs. 5 and 6) three (LATE (*A. laucheanum*), LURJ (*A. lucidum*), and PATE (*A. parvum*)) differ significantly from the other populations (Table 3). PCoA also indicated that *A. lucidum* exhibits leaf outline shapes which are distinct from the other taxa (Fig. 8) and UPGMA confirmed this distinction (Fig. 9).

Cluster analysis also suggests that the leaf shape of *A. parvum* is distinct from the other taxa (Fig. 9). Both populations of *A. parvum* (PANF and PATE) appear closely related in the UPGMA cluster analysis (Fig. 7), although they were considered significantly different in the NP-MANOVA (Table 3). A different approach using traditional systematics might help to resolve this apparent conflict, by bringing into consideration other character combinations. This type of analysis was also useful in differentiating specimens of *Heteropsis* (Araceae) in Amazonia (Soares et al. 2011).

Given that a species cannot be defined only by the shape of its leaf outline, the results obtained in morphometric analyses should be combined with characters recognized as important in the classical taxonomy of the group. In this context, *A. hatschbachii*, *A. jureianum*, *A. lucidum* and *A. parvum* indeed have unique characteristics within the complex. The presence of glandular punctate leaf blades differentiates *A. hatschbachii* (HAJO population) from all other species of the *A. augustinum* complex (Gonçalves 2011). *A. jureianum* is distinct in having peltate leaf blades, which is consistent with the significant differences found in all our morphometric analyses. *A. lucidum* differs in having i) only 1–2 basal veins, while the remaining species have 3–5, ii) gray-green leaf blades (green in the other species) and iii) white pollen (yellow pollen in the other species), and geographically in being restricted to the Tijuca Forest of Rio de Janeiro. *A. parvum* differs from other species of the complex by its slender stem with a maximum

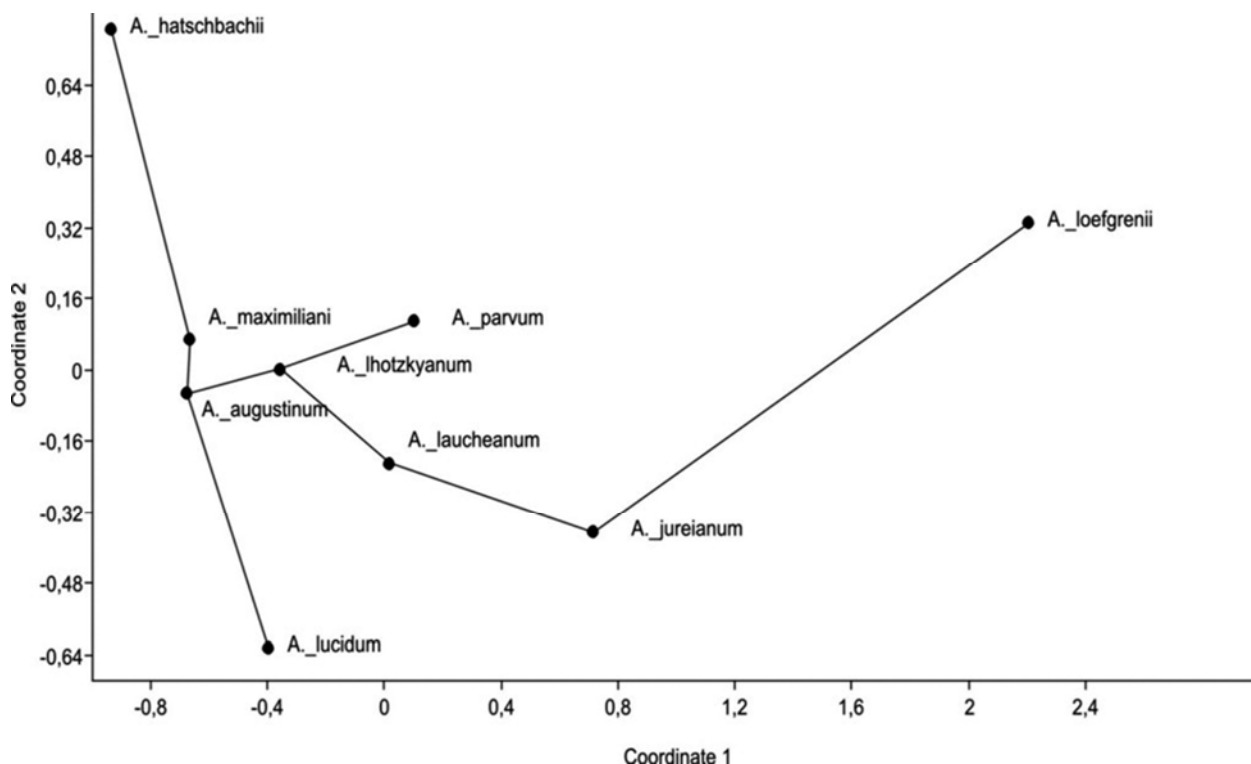


Figure 8. Relative similarity of mean population leaf outlines using principal coordinate analysis (PCoA). Based on a matrix of Euclidean distances between the centroids (mean principal component scores from a PCA of 80 elliptic Fourier coefficients) of each sampled taxon in the *A. angustum* complex. Computed with PAST software (Hammer et al. 2001).

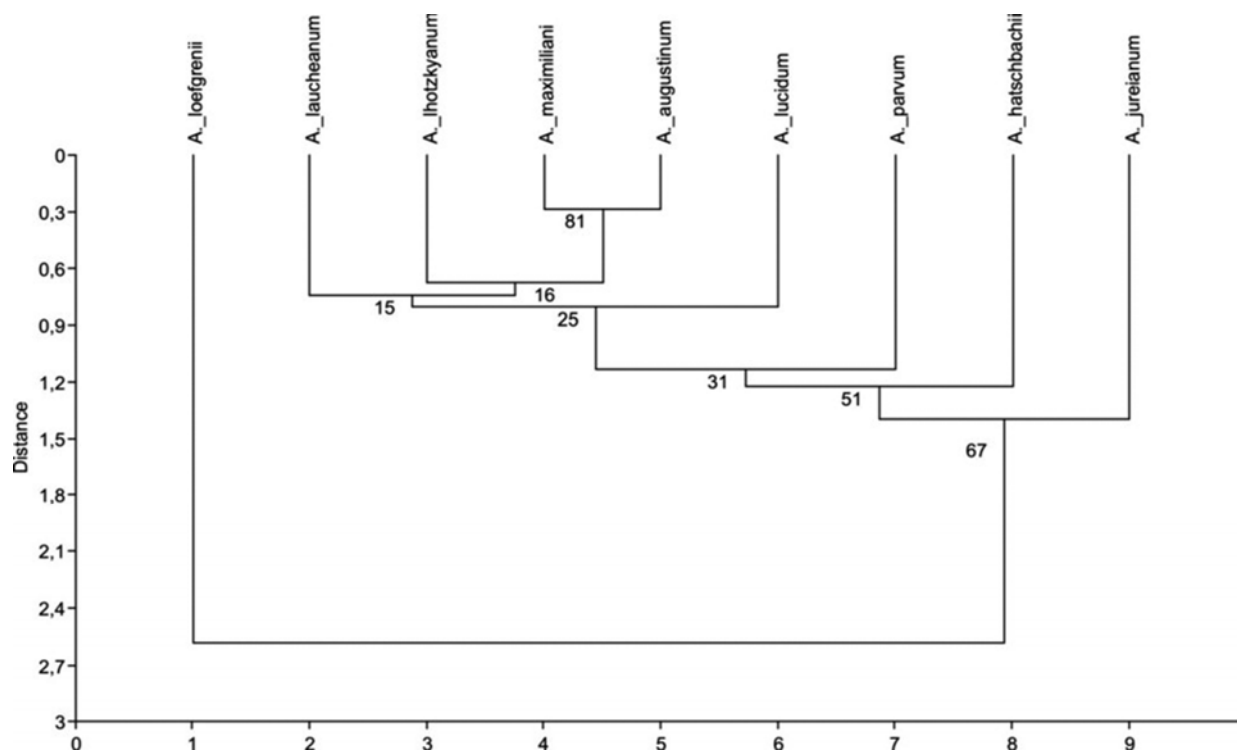


Figure 9. UPGMA dendrogram showing phenetic relationships among the nine taxa analyzed in the *Anthurium angustum* complex, using the means of each population obtained from the principal component analysis (PCA) based on the elliptic Fourier analysis matrix. Numbers below each branch represent bootstrap support values (999 replicates).

height of 5 cm, a completely vinaceous peduncle up to 22 cm long, and insculpted leaf veins.

In contrast, NP-MANOVA revealed that the leaf outline shapes of the AUNI (*A. augustinum*), LATE (*A. laucheanum*), LHPE and LHTE (*A. lhotzkyanum*) and MANI and MAPE (*A. maximiliani*) populations are highly similar. The close relationship of these populations was further confirmed by cluster analysis, although for *A. laucheanum* this positioning is only partially supported (Fig. 7, Fig. 9). Moreover, *A. augustinum*, *A. laucheanum*, *A. lhotzkyanum* and *A. maximiliani* share the presence of marcescent cataphylls, 3–5 basal veins, yellow pollen, and lack glandular punctations in the leaf blade. As shown by UPGMA cluster analysis, these taxa are closely related phenetically (Fig. 9). The absence of diagnostic features for any of these taxa individually reinforces the argument for their close relationship.

5 Taxonomic conclusions

Although morphometric analyses demonstrate overlap in leaf outline shape between taxa in the *A. augustinum* complex, results from NP-MANOVA, CVA, UPGMA and PCoA clearly indicate the distinction of *A. jureianum*, *A. lucidum*, *A. hatschbachii* and *A. parvum*. Each taxon moreover presents several other unique characteristics that differentiate it from the other taxa of the complex. Conversely, when comparing the descriptions of the remaining four taxa, *A. augustinum*, *A. laucheanum*, *A. lhotzkyanum* and *A. maximiliani*, no features were found to clearly distinguish them (Koch 1855; Koch 1857; Schott 1860; Schott 1862) and all morphometric analyses suggested their close relationship within a single species.

We therefore recognize five species within this complex, named as *A. augustinum*, *A. lucidum*, *A. hatschbachii*, *A. jureianum* and *A. parvum*. As a consequence, the names *A. laucheanum* K. Koch, *A. lhotzkyanum* Schott and *A. maximiliani* Schott are proposed here as synonyms of *A. augustinum* K. Koch & Lauche, the oldest validly published name.

6 Nomenclature of *Anthurium augustinum*

6.1 Accepted name and synonyms

Anthurium augustinum K. Koch & Lauche, Index Seminum Horti Berolinense (B) 1855: 7 (1855). Type: cultivated at Berlin Botanical Garden, unknown origin, 1855, *K. Koch s.n.* (B). Lectotype (designated here): 30 Aug 1878, *N. E. Brown s.n.* (K). Epitype (designated here): cultivated in Munich and Berlin botanic gardens, origi-

nally from Brazil, “prov. Rio de Janeiro”, *A. Engler’s Araceae Exsiccatae* No. 190 (K, B iso-epitype).

= *Anthurium laucheanum* K. Koch, Allgemeine Gartenzeitung. 24: 191. 1857, **syn. nov.** Type: cultivated at Berlin Botanical Garden, received by Augustin’s garden nursery in Potsdam from the de Jonghe nursery in Brussels, origin unknown, 1857, *K. Koch s.n.* (B†). Neotype (designated here): cultivated at Berlin Botanical Garden, originally from Brazil, “Patria: Brasilia tropica”, 1883–1884, *A. Engler’s Araceae Exsiccatae* No. 164 (K).

= *Anthurium lhotzkyanum* Schott, Prodrum Systematis Aroidearum. 491. 1860, **syn. nov.**

Type: Brazil, Rio de Janeiro, summit of the Serra dos Orgaos, September 1831, *Lhotzky s.n.* (G).

= *Anthurium maximiliani* Schott, Bonplandia (Hannover) 10: 5. 1862, **syn. nov.** Type (†):

Brazil. Rio de Janeiro, Petropolis, 1860, *Erzherzog [Archduke] Ferdinand Maximilian 764*

(W †). Neotype (designated here): Schott Icones Aroideae no. 3516 (W).

6.2 Typification of *A. augustinum* K. Koch & Lauche

The original description of Koch and Lauche gives no information on the plant’s origin, but since it was published in the Appendix to the Berlin Botanical Garden Seed List for 1855, it was evidently a plant cultivated in that garden. Koch (1857: 190) published another description of his plant in which he added more details of the inflorescence, reported as immature in the original description.

In his description of the species, Schott (1860: 489) gives the citation “Patria ... ? – v. exempl. viva a Lauchio communicata.” This can be interpreted as “Origin unknown. I have seen a living specimen sent by Lauche”, which suggests that a clone of the Berlin type was being cultivated by Schott at the Schönbrunn Garden in Vienna, of which Schott was Director at that time. Schott Icon. Aroid. no. 604 (original at the Natural History Museum, Vienna [W]; microfiche seen Schott 1984) is a colour drawing depicting leaves and young inflorescences which is very probably based on the same type clone sent to Schott by Lauche; This drawing bears a determination label in Engler’s handwriting as follows “*Anthurium* (Parabasium) *trinervium* Kunth B. Augustinum Engl.” This is the name Engler used for Koch’s species in the *Flora brasiliensis* treatment (Engler 1878: 95), where he notes that “Non omnino certus sum, num hujus plantae patria revera sit Brasilia, quum specimina tantum in horto botanico Berolinensi culta viderim, quae ex Brasilia originem ducere dicuntur”, which could be

translated as “I am not entirely certain whether this plant is truly from Brazil, since I have seen only specimens cultivated in the Berlin botanic garden which it is said, originated from Brazil”. Thus at this stage, it seems highly probable that Engler’s concept of *A. augustinum* was based primarily on Koch’s living type plant cultivated in Berlin, although Engler also cites a specimen of Olfers. In the following year, Engler (1879: 154) cites the specimen *Glaziou 9028* from the Rio de Janeiro region. And, by the time of his next revision (Engler 1898: 409), he had seen other Glaziou specimens as well (*Glaziou 16517, 16518*).

Engler’s *Araceae Exsiccatae No. 190* (Engler 1883, 1884), determined as *A. augustinum*, has the label citation “Specimina sicca ex horto bot. regis Monacensi et Berolinensi” (“dried specimens from the royal botanic gardens at Munich and Berlin”) and the origin is given as “Brasilia, prov. Rio de Janeiro”. Duplicates of this plant exist both at B and K, the latter consisting of an inflorescence and a leaf, the former of two leaves. It is possible that the cultivated plants from which these dried specimens were prepared were also from the type clone plant, which may have been distributed from Berlin to Munich as well as to Vienna. However, given that Engler now seems sure of the origin of the species, it is more likely that Engler’s specimens labelled as *Araceae Exsiccatae No. 190* were made from more recent collections, probably *Glaziou 9028*, cultivated at Berlin and Munich; Glaziou began collecting activity in Brazil in 1861 (Urban 1906).

At Kew, there is also a pencil drawing of a single inflorescence and a fragment of a spadix in an envelope, which are said to be from Koch’s type at Berlin, taken by N. E. Brown during his visit there in 1878. Brown has written on the envelope “Fragment of spadix of *C. Koch’s* specimen of *A. augustinum*, *C. Koch*”. On the sheet itself, Brown has written “*A. augustinum*, *C. Koch* outline of inflorescence in *C. Koch’s* Herbarium (the type!). There is at this date nothing but 1 perfect and 1 broken inflorescence in his Herbarium no leaf. N. E. Brown Aug 30th 1878”. Although this spadix fragment, supported by Brown’s drawing, is inadequate for a complete taxonomic understanding of the name *A. augustinum* K. Koch & Lauche, it should be regarded as authentic and therefore cannot be ignored for the purposes of typification. This sheet at K can be considered as protologue material and we therefore select it as the lectotype, meaning that a neotype cannot be proposed (McNeill et al. 2012). In order to clarify the taxon concept we have also selected as epitype the duplicate of Engler’s *Araceae Exsiccatae No. 190* at K, because it has a complete inflorescence and a leaf; this makes the duplicate at B an iso-epitype.

6.3 Typification of *Anthurium laucheanum* K. Koch

Koch’s original description includes the following information on the origin of his living plant: “A smaller species with cordate and coriaceous leaves, which the garden nursery of Augustin received from de Jonghe in Brussels.”

Schott’s treatment in the *Prodromus* (Schott 1860: 514) is very brief and terminates with no specimen citation, merely a laconic “*C. Kch.*”, which must be interpreted to mean that Schott had seen no authentic specimen and based his description on Koch’s original publication. However, it is clear from his earlier descriptions that Engler (1878: 95; 1879: 155) studied cultivated living plants, very probably Koch’s, but he cites no specimens, stating only “Probably originating from Brazil, introduced into European gardens”.

Engler (1884) distributed numbers 101–200 of his specimen series “*Araceae exsiccatae et illustratae*” (Engler 1883) to various herbaria, among which No. 164 is of *A. laucheanum*. The label of the duplicate specimen sent to K (in September 1884) has the information “*Patria: Brasilia tropica Specimina sicca ex horti regis botan. Berolinensi 1883/84.*” Although no collector is named, the known provenance of Brazil makes it likely that this is a specimen made from a Glaziou living collection rather than a voucher of Koch’s type clone at the Berlin Botanic Garden.

At K there is also a series of specimens of a plant cultivated at Kew, both named as *A. laucheanum* and labelled by N. E. Brown (who evidently made the voucher specimens for the herbarium) as “*Rio Janeiro Glaziou (No. 34 on label)*”, the earliest (and smallest) of which was cultivated at Kew on 3rd November 1882, i.e. predating Engler’s distribution. It is possible, though unverifiable, that these Kew specimens are of the same clone as Engler’s “*Araceae exsiccatae et illustratae*” no. 164. Glaziou’s living collections were distributed around the major botanic gardens of Europe and both Kew and Berlin must have cultivated many of the same Glaziou collections. In his next revision Engler (1898: 410) cited two Glaziou specimens (*Glaziou 11641* and *16505*), but in his final revision in *Das Pflanzenreich* (Engler 1905: 161–162) he cited only *Glaziou 16505*.

Also at K there is a sheet with pencil impressions of K. Koch’s type specimen showing three views of the same leaf and a single inflorescence. These were made by N. E. Brown at the Berlin Herbarium (B) and annotated by him as “*Anthurium laucheanum*, *C. Koch* impressions of type specimen in *C. Koch’s* Herbarium Aug 21st 1878”. Since this sheet has no actual specimen material it cannot be designated as a lectotype since in itself it was not part of the protologue, despite representing the type specimen. In the absence of material of the

protologue, no lectotype can be proposed, rather a neotype is appropriate. We have therefore selected the K duplicate of Engler's "Araceae exsiccatae et illustratae" no. 164 as neotype rather than Brown's sheet of pencil impressions, since the plant is more mature and consists of an actual specimen. Brown's impressions of the type nevertheless remain critically important in the interpretation of the taxon concept since they are direct evidence of the type plant. This approach is consistent with that adopted when proposing Schott's *Icones Aroideae* as neotypes rather than lectotypes, on the argument that a drawing of the type specimen cannot be regarded as part of the protologue unless there is clear evidence that it was used by the author at the time of description, a view previously taken by Grayum (1996) and Coelho & Mayo (2007).

6.4 Typification of *Anthurium maximiliani* Schott

Schott (1862) cited the holotype as "Hab. in Provincia Sebastianopolitana ad Petropolim (Archidux Ferd. Maximilianus)." ["Occurring in the Province of Rio de Janeiro at Petropolis (Archduke Ferdinand Maximilian)"]. The aroid collections of Archduke Ferdinand Maximilian of Austria were made by Franz Maly, the botanist-gardener who participated in Maximilian's 1859–1860 expedition to Brazil (Urban 1906; Riedl-Dorn 1992); the expedition reached Petropolis near Rio de Janeiro in 1860. Schott's *Icones Aroideae* (Schott 1984) includes eight illustrations of this species, of which seven are water-colour drawings of living specimens cultivated by Schott at Schönbrunn Imperial Gardens near Vienna (Coelho & Mayo 2007) and one is a pencil drawing of a herbarium specimen. The latter (Icon No. 3516) is certainly of a field collected voucher specimen of the plant later cultivated at Schönbrunn and has label data with the collector's number: "E.F.M. Petropolis 764" ("E.F.M." stands for "Erzherzog [Archduke] Ferdinand Maximilian"). There can be little doubt that all eight of these illustrations represent the type collection. The herbarium specimen, however, was lost with the rest of Schott's Araceae herbarium during the Second World War (Riedl & Riedl-Dorn 1988). For nomenclatural purposes we selected the coloured Icon No. 3516 as neotype, because it combines leaf and floral characters in one plate. However, all the others should be included in the taxonomic interpretation. Peyritsch (1879: p. 7, plates 4, 5) published two of these Schott *Icones* of *A. maximiliani* and a full description in *Aroideae Maximilianae*, a magnificently produced taxonomic treatment of the aroids collected during Maximilian's expedition. The Maly-Maximilian collection from Petrópolis was still the only known specimen of the species at the time of Engler's last monograph of the genus (Engler 1905).

6.5 Notes on the type of *Anthurium lhotzkyanum* Schott

Schott's original description cites the holotype as "Brasil. Lhotzky. – v. sicc. specim. spontan. a Lhotzkyo lectum in Herb. D.C." (translated as "Brazil. *Lhotzky s.n.* – I have seen in de Candolle's herbarium [at G] a dried specimen collected in the field by Lhotzky"). Engler (1878; 1879; 1898; 1905) consistently cited this specimen, which in his final revision, in *Das Pflanzenreich*, is given as "Rio de Janeiro, Serra dos Orgãos (Lhotzky – Herb. De Candolle).

The drawing of the type specimen in Schott's *Icones Aroideae*, No. 623 (Schott 1984) has the following label data, taken presumably from the specimen label: "In sylvis primaevae summae Serra dos Orgãos Sept. 31 Lhotzky Herb. de Candolle".

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