# RESEARCH PAPER

# A morphometric and taxonomic study of *Monstera* (Araceae) in Bahia, Brazil

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A taxonomic revision is presented of the three taxa of *Monstera* (Araceae) recognized for Bahia State, Brazil:— *M. adansonii* subsp. *blanchetii* (stat. nov.), *M. adansonii* subsp. *klotzschiana* (stat. nov.) and *M. praetermissa*; a fourth taxon, not so far recorded from the state, *M. adansonii* subsp. *laniata* (stat. nov.), is distinguished from subsp. *blanchetii*. The two highly variable subspecies of *Monstera adansonii* were further investigated by morphometric study of herbarium specimens. These two taxa were distinguished using principal coordinates analysis (classical multidimensional scaling) and linear discriminant analysis; the most important diagnostic characters are stigma length and width, stigmatophore length, style apex size and leaf perforation number. Discrimination on leaf characters alone was over 90% successful — subsp. *blanchetii* differs most significantly from subsp. *klotzschiana* in higher values for perforation number and leaf base angle. Descriptions, illustrations, geographical and conservation status information and a key to the taxa are provided. Two neotypes are proposed (*M. maximilianii* Engl., *M. klotzschiana* Schott) and discussions of the typifications are provided.

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# 1 Introduction

Monstera adansonii Schott is a highly variable and widespread species in tropical America. The last attempt at a complete taxonomic treatment was by Madison (1977), who recognized three infraspecific taxa, var. adansonii centred on the Caribbean region, var. laniata (Schott) Madison from Central America to Amazonia and var. klotzschiana (Schott) Madison from the Guianas and eastern Amazonia to southeastern Brazil (we treat these taxa as subspecies in the present study). Madison recognized and discussed the great morphological variability of M. adansonii across its geographical range and conjectured that this had resulted from hybridization between the three varieties and introgression with other species of Section Monstera.

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Monstera adansonii subsp. klotzschiana (Schott) Mayo & I. M. Andrade is the common taxon in the Brazilian Atlantic forest region and in eastern Amazonia including the Guianas. It occurs in montane humid forest refuges and gallery forests throughout dry Northeast Brazil and has also been recorded in gallery forests in Central-West Brazil (Gonçalves 2004). Various studies of Brazilian populations of this taxon have been made in recent decades. Andrade & Mayo (1998) investigated the shoot morphology in a population in Recife, Pernambuco, and in a later paper (Andrade et al. 2007) patterns of genetic diversity in populations ranging from French Guiana to São Paulo state were examined with AFLP molecular markers. Andrade et al. (2008) studied the comparative morphology of leaf outlines using Elliptic Fourier Analysis (EFA) of these same populations. A series of very interesting ecological studies have been carried out on populations of subsp. klotzschiana in the Atlantic Forest of São Paulo state (Cerezini 2009; Marquitti 2009; Martin 2009; Martin et al. 2009; Bogiani et al. 2010; Henning 2010; Vieira 2010; Lemos et al. 2011; Consolmagno 2012; Francisco et al. 2012; Romelli et al. 2012; Sanchez et al. 2012). There are also several recent taxonomic studies of Araceae in Brazil's Atlantic Forest which include records, descriptions and illustrations of *M. adansonii* or *M. adansonii* subsp. *klotzschiana* (Temponi et al. 2005; Temponi & Garcia 2006; Pontes et al. 2010; Pontes & Alves 2010; Pontes & Alves 2011; Temponi 2012; Andrade et al. 2013). Hitherto, however, there has been no specific study of this taxon for the state of Bahia.

Mayo (1983: 210) reported a second subspecific taxon of *M. adansonii* (as var. *laniata* (Schott) Madison) from the Atlantic Forest of southern Bahia. Further collections of this plant have since been made and determined as var. *laniata* and have extended its known range in northeastern and eastern Brazil to Espírito Santo and Pernambuco; we recognize it here as *M. adansonii* subsp. *blanchetii* (Schott) Mayo & I.M. Andrade and describe it in detail for Bahia for the first time.

The main objective of this study was to make a detailed characterization of the two commonest taxa of Monstera in Bahia, M. adansonii subsp. blanchetii and subsp. klotzschiana, using both traditional and morphometric approaches, and to investigate and clarify those morphological distinctions between them which can be used for practical taxonomic identification. A secondary objective was to employ a traditional morphometric approach (i.e. using linear measurements, Claude 2008) to the comparison of leaf and floral characters between taxa at and below species level; this has not been done before in Monstera. We chose to restrict our study to the state of Bahia for two reasons: first because most collections of subsp. blanchetii are from there, and second because previous studies (Andrade et al. 2007, 2008) indicate considerable heterogeneity in subsp. klotzschiana within Brazil, and it seemed preferable to us in a preliminary study of this kind to compare material of the two taxa from the same relatively local region.

# 2 Materials and methods

## 2.1 Samples

The study was based mainly on herbarium collections at the CEPEC, G and K herbaria (Thiers 2013) and a background of field collection and observation by the authors in northeastern and southeastern Brazil, eastern Amazonia and French Guiana. All specimens cited have been seen unless otherwise indicated.

The specimen citations ("Material examined") are arranged as follows: municipalities (municipios) are listed in alphabetical order and after each municipality name, specimens occurring there are listed in alphabetical order of the first collector's name. Only speci-

mens from the state of Bahia are cited. The phenological phase of specimens is indicated in the specimen citations by the following abbreviations:—st: vegetative parts only; prefl.: prefloral stage; fl.: female or male anthesis; postfl.: postfloral but pre-fruiting stage; immfr.: immature fruiting stage; fr.: mature fruiting stage.

#### 2.2 Taxonomic analysis

The taxonomic study was carried out in two phases. First a classical semi-intuitive taxonomic analysis of characters was undertaken, in which specimens were separated into groups mainly using the following easily visible characters: abundance and pattern of leaf perforations (few to many; one to two series; not reaching leaf margin to rupturing it), colour of dried leaf (greenish brown to dark or blackish brown), colour contrast between the dried petioles and cataphylls and the leaf blade tissue (no contrast, petioles and cataphylls distinctly paler), degree of prominence of style apex (prominent and narrowed to flattened), and stigma shape (short and elliptic to long and linear). Taxon descriptions were drafted for the resulting groups, using a larger range of descriptive morphological characters based on the work of previous taxonomists (e.g. Engler & Krause 1908; Madison 1977; Bunting 1975, 1980; Grayum 2003; Gonçalves & Temponi 2004), with some additional information based on our own examination of living plants in the field and in cultivation.

The second phase consisted of a morphometric analysis to investigate quantitatively the delimitation of the three taxa. However, due to the few complete specimens available of M. praetermissa E. G. Gonç. & Temponi, this phase consisted essentially of the quantitative differentiation of the two subspecies of M. adansonii. For this purpose, only specimens which included both vegetative and reproductive parts were used, as well as a small number which though lacking fertile parts, had unambiguous information in the label data concerning the critical characters of the style apex, and hence allowed identification using the most important diagnostic features employed in phase 1. The morphometric analysis thus functioned as a "reality check" on the semiintuitive classical approach rather than as the primary procedure for classification (sensu Gordon 1999) of the individuals.

# 2.2.1 Morphological characters

#### 2.2.1.1 Taxon descriptions

Terms describing the angles at the leaf apex and base such as "acute" and "obtuse" etc. refer to the angle made by the leaf margin with the midrib on each side of the leaf blade separately rather than the overall angle of the apex or base. Perforation number refers to the total

number of perforations in the leaf blade. The number of primary lateral veins refers to the number observed on the wider side of the leaf. The term "interprimary field" refers to that area of leaf lamina lying between two adjacent primary lateral veins (in the same half-lamina) and the leaf margin.

The stigmatophore is a structure which, as far as we are aware, has not been recognized hitherto in morphological descriptions of the genus *Monstera*. It comprises that part of the apex of the stylar region of the gynoecium which supports the stigma. In *M. adansonii* subsp. *blanchetii* (Fig. 1i), and *M. praetermissa* (Fig. 2) the stigmatophore is hardly differentiated but in subsp. *klotzschiana* the apex of the stylar region is extended as a short conical structure bearing the stigma at its tip (Fig. 3c–e).

#### 2.2.1.2 Morphometric variables

Digital images of all specimens were made using a Ricoh CX2 digital camera mounted on a camera stand. Nineteen characters (variables) which could easily be observed on herbarium specimens were selected and recorded for morphometric analysis from the images using ImageJ software. All linear measurements were recorded in centimetres. Some of these were not used directly, but instead as the source of fourteen derived variables, such as sums, averages or differences, bringing the total number of variables dealt with to 33. Detailed descriptions are given in Table 1 and illustrated definitions are provided in a PowerPoint file ("Monstera characters defined.pptx"), available at the CATE Araceae website (Haigh 2013).

The set of 15 characters used directly in the analyses is given in Tables 2 and 3, and combines observed characters and derived variables. Some specimens had two leaves and/or inflorescences and wherever possible measurements were made on all organs available. Many specimens in the CEPEC and K herbaria were duplicates of the same collections, but these were all measured, making the total number of collections used less than the total number of individual organs. If there was doubt as to whether an inflorescence and a leaf belonged to the same shoot, they were recorded as separate individuals.

The three derivative matrices used for analysis were drawn from the raw matrix (Raw\_Data\_Matrix\_Final.xlsx; 70 individuals, 19 characters) and in the process some characters (Peduncle\_length, Spathe\_length, mean\_pistil\_length and mean\_pistil\_width\_at\_style\_apex) were deleted because of the large number of missing data. Rows and columns were then deleted where missing data occurred to form a matrix combining vegetative and reproductive characters (Maximum\_Characters\_Final.xlsx; 37 individuals, 15 characters), a matrix containing only vegetative characters (Vegetative Final.xlsx;

45 individuals, 8 characters) and a matrix containing only reproductive characters (Reproductive\_Final.xlsx; 58 individuals, 7 characters). These three matrices and the raw matrix are available online at the *CATE Araceae* website (Haigh 2013).

# 2.2.2 Morphometric analysis

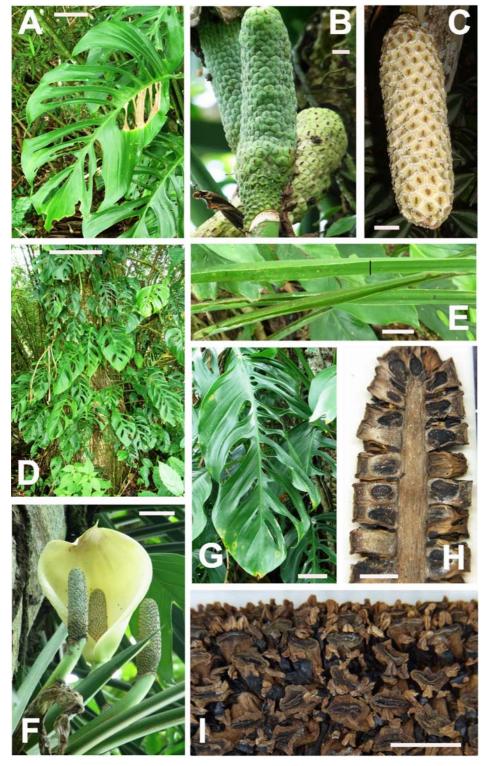
Analyses were carried out using the freeware statistics packages PAST version 2.17c (Hammer et al. 2001) and R version 3.0 (R Core Team 2013). The quantitative morphological variables for *M. adansonii* subsp. *blanchetii* and subsp. *klotzschiana* are described statistically (Tables 2, 3) using PAST for the mean, standard deviation, coefficient of variation, the Shapiro-Wilk test for normality and a non-parametric permutation *t* test (9,999 replicates) for equality of means. The non-parametric Fligner-Killeen test was used for testing homogeneity of variances, as implemented in R (e.g. Crawley 2007: 293).

Principal Coordinates Analysis (PCoA), as implemented in PAST with Euclidean distances between individuals, was used to explore the patterns of phenetic relationship between individuals. The distinctions between subspp. *blanchetii* and *klotzschiana* (identified using the classical taxonomic procedure described above) were then investigated further using linear discriminant analysis (LDA) as implemented in PAST, from which a vector of loadings was obtained for each character indicating their relative importance in the discrimination of the two taxa. The LDA procedure also provided a "leave-one-out" cross-evaluation test.

Because of the mixture of different measurement scales – leaves versus pistils – angle measurements and integer quantitative data, PCoA and LDA were carried out using variables standardized to z-values, i.e. so that each value x was transformed by subtracting the variable vector mean and dividing by the variable standard deviation:  $z = (x - \text{mean}) \div (\text{s.d.})$ , where mean and s.d. refer to the variable values over all rows.

#### 2.3 Conservation status

Preliminary conservation status assessments within the state of Bahia were made for all species using the Geocat online tool (http://www.geocat.kew.org/), which uses range size (EOO: extent of occurrence; AOO: area of occupancy) estimated from the geographical coordinates of plant records (Rivers et al. 2011). We obtained latitude and longitude coordinates from GPS data or we estimated them from maps and Google Earth; the resulting data matrix is thus only provisional. Species known from less than five localities are assessed as Data Deficient (DD). The auto-value option was used for computing AOO.



**Figure 1.** Monstera adansonii subsp. blanchetii. a. Highly asymmetric mature leaf blade. b. Immature fruiting spadix. c. Mature fruiting spadix. d. Habit. e. Petiole sheaths showing non-deciduous sheaths. f. Flowering inflorescence with post-floral inflorescences. g. Less asymmetric mature leaf blade. h. Immature fruiting spadix in longitudinal section (Harley et al. 18300). i. Flowering spadix seen in surface view, showing exposed stamens, flattened style apices and elongated stigmas (Hatschbach 48765). a–g: population in grounds of the Centro de Pesquisas do Cacau (CEPEC) near Itabuna, corresponding to that represented by Hage 2233. Scale bars: A = 5 cm; B = 1 cm; C = 1 cm; D = 40 cm; E = 3 cm; E = 3 cm; E = 3 cm; E = 5 cm; E = 5



**Figure 2.** Monstera praetermissa. a. Mature leaf (Serra da Copioba, Bahia state, alcohol preserved). b. Inflorescence at anthesis (Linhares, Espírito state); note blackened marcescent petiole sheath to right of inflorescence. Scale bars: a = 5 cm; b = 2 cm.

# 3 Results

## 3.1 Morphometric study

Comparison of individual characters. Tables 2 and 3 show univariate statistics of the quantitative morphometric variables for the two subspecies of *M. adansonii*: those for M. praetermissa are not included because of the small sample of only two individuals. Test results for normality (Shapiro-Wilks), homogeneity of variances (Fligner-Killeen) and equality of means are also given. Boxplots of the variables are given in Figs. 4 and 5 and here the results for M. praetermissa and "maximilianii" are included for visual comparison but with sample sizes of only two and four respectively they are no more than rough indications. These results showed that a majority of variables were normally distributed and had consistent variances when compared individually between the two subspecies of M. adansonii. There was a marked overall difference in the coefficients of variation between vegetative and reproductive characters, with the latter being on average half as variable as the former.

With untransformed variables the following vegetative characters differed significantly between subspp. *blanchetii* and *klotzschiana*: leaf length (leaf\_length), the height of the widest point of the leaf (midrib\_maxwidth), the difference in width between the two halves of the leaf

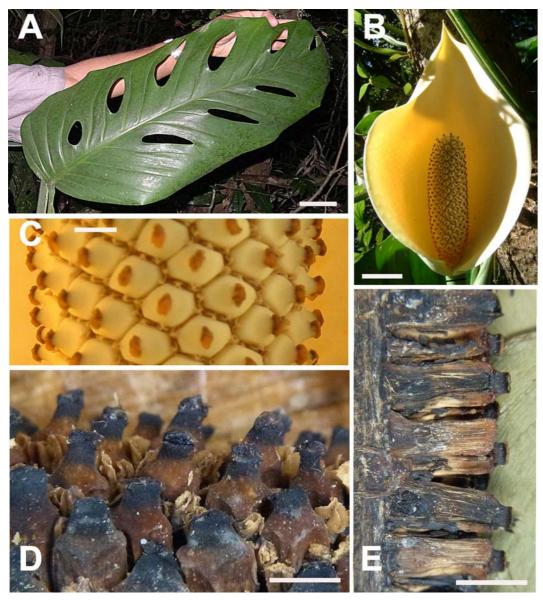
blade (lateral\_asymmetry), the angle of the leaf base (mean\_leafbase\_angle) and the number of leaf perforations (leaf\_perforations\_total\_number), the latter two being the strongest differences (Tables 1 and 2, Fig. 4).

The significantly different reproductive characters (untransformed data) between these two taxa were: spadix width (mean\_spadix\_width), length of style apex (mean\_style\_apex\_plan\_length), stigma length (mean\_stigma\_length), stigma width (mean\_stigma\_width) and stigmatophore height (mean\_stigmatophore height), the strongest being spadix width, stigma length and stigmatophore height (Tables 1, 3, Fig. 5).

#### 3.1.1 Principal coordinate analysis (PCoA)

The principal coordinate analyses of standardized data (Figs. 6A–C) showed a clear distinction between the two subspecies of *M. adansonii* in all three matrices. The two specimens of *M. praetermissa* grouped closer to those of subsp. *blanchetii* (Figs. 6A–C) and the four specimens of the "maximilianii" subgroup of subsp. *blanchetii* (see commentary to the taxonomic treatment of the latter) lay intermediate between the two subspecies in Fig. 6C (reproductive characters) – the lack of complete leaves of these specimens excluded them from the matrices with vegetative variables.

In the plot of the first two principal coordinates, it is noticeable that subsp. *klotzschiana* is more variable in



**Figure 3.** *Monstera adansonii* subsp. *klotzschiana*. A. Mature leaf blade (photo courtesy of Alex Popovkin, Bahia, Brazil). B. Flowering inflorescence (from Recôncavo Baiano). C. flowers with stamens beginning to emerge (living material from Recôncavo Baiano). D. flowers at anthesis showing stigmas and elongated stigmatophores (dried material, *Harley et al. 16571*). E. flowers at recent post-anthesis in longitudinal section showing stigmatophores (dried material, *Mattos-Silva et al. 2712*). Scale bars: A = 5 cm; B = 3 cm; C = 0.2 cm; D = 0.2 cm; E = 0.5 cm.

reproductive characters (Fig. 6C), while in the other two plots (Fig. 6A–B) the two subspecies are similar in variability. This could reflect greater drying distortions in the more elongated flowers of subsp. *klotzschiana* rather than a significant real difference.

## 3.1.2 Linear discriminant analysis (LDA)

With combined and reproductive variables, the linear discriminant analysis showed a very clear distinction between the two subspecies of *M. adansonii* (Fig. 7A, 7C); *M. praetermissa* and the "maximilianii" subgroup of

subsp. *blanchetii* were not included because of the very small samples. With only vegetative characters there was some overlap (Fig. 7B). The LDA implementation in PAST uses a cut-off point at zero (midpoint between the means of the two groups) and classifies the individuals accordingly. The percentage of correctly classified individuals using this method was 95.35% correct for vegetative matrix and 100% for the other two matrices (Table 4). In the "leave-one-out" cross-evaluation, changes only occurred in the vegetative analysis – the omission of any of the specimens *Hage 2233 CEPEC*,

Table 1. Characters used as quantitative variables in the morphometric analyses

Leaf length (cm) [Leaf\_length]

Leaf widest width (cm) [leaf\_maxwidth, Leaf\_maxwid\_Left, Leaf\_maxwid\_Right]

Midrib widest width (cm)
[midrib\_maxwidth, Midrib\_maxwid\_Left,
Midrib\_maxwid\_Right]

Longitudinal asymmetry (cm) [longit\_asymmetry]

Lateral asymmetry (cm) [lateral\_asymmetry]

Leaf perforations: total number [Leaf perforations\_total\_number] Leaf base angles (degrees) [Leaf\_base\_angle\_left (Lbal), Leaf\_base\_angle\_right (Lbar), leaf\_base\_asymmetry, mean\_leafbase\_angle]

Peduncle length (cm) [Peduncle\_length]

Spathe length (cm) [Spathe length]

Leaf length is measured along the midrib, i.e. without considering the basal extension of posterior lobes (if these are present), starting at the petiolemidrib junction and terminating at the tip of the leaf, including the Vorläuferspitz (the ultimate extension of the leaf tip). In ImageJ, this length is measured using the segmented linear measuring tool which allows the user to measure along a curve using a series of segments.

Leaf widest width is measured separately on each side of the lamina (Leaf\_maxwid\_Left, Leaf\_maxwid\_Right) and the two measurements then summed (leaf\_maxwidth). This is because leaves are usually asymmetric with one side broader than the other, and with the point of maximum width differing in position along the midrib. The segmented linear measuring tool in ImageJ was used.

Midrib widest width is measured from petiole insertion to the point corresponding to widest width of the leaf blade on each side (Left and Right). Because of the bilateral asymmetry in *Monstera* leaves, the Left and Right measured segments are usually of different lengths; midrib\_maxwidth is calculated as the mean of these two measurements.

Longitudinal asymmetry expresses the difference in the widest point of each half-lamina along the midrib axis. This is represented by the absolute value of the difference in cm between Midrib\_maxwid\_Left and Midrib maxwid Right:—

longit\_asymmetry = abs (Midrib\_maxwid\_Left - Midrib\_maxwid\_Right)
Lateral asymmetry expresses the difference in the widest with of each
half-lamina. This is represented by the absolute value of the difference
in cm between Leaf\_maxwid\_Left and Leaf\_maxwid\_Right: lateral\_asymmetry = abs (Leaf\_maxwid\_Left - Leaf\_maxwid\_Right)
Leaf perforations are counted throughout the leaf blade, not just on one side.

The angle of the leaf base on each side of the lamina is measured using the ImageJ angle tool.

"Left" and "right" are defined as visualized from the abaxial side of the leaf with the leaf apex at the top of the figure (the powerpoint shows adaxial side with the leaf apex oriented basally). The angle is measured using the midrib as reference axis. The dimensionless variable leaf\_base\_asymmetry is calculated as: –

 $abs(Lbal - Lbar)) \div (Lbal + Lbar).$ 

The mean of Lbal and Lbar is the variable mean\_leafbase\_angle.

The peduncle length is measured from the most basal point of insertion of the spathe (i.e. on the ventral side of the spathe base) to the base of the subtending leaf sheath – this base of the peduncle is usually difficult to estimate because it is normally hidden by the petiole sheath – if the node is visible where the subtending leaf is inserted on the stem, this is the most reproducible landmark to use when the peduncle base is hidden (although, the insertion node of the subtending leaf may also not be very clear and has to be estimated by eye).

Spathe length is measured from the very tip pf the spathe to the most basal part of the spathe insertion on the peduncle – the spathe insertion is usually oblique. Spathe width is hard to measure consistently from herbarium specimens – even in a living specimen it would be necessary to decide whether to measure the cross-sectional arc or a projection of it into two dimensions (e.g. from a 2-D image). The spathe width changes markedly as it unfurls to full male anthesis and few specimens have this stage. Even when they do, the distortions created by pressing and drying make width as measured so variable as to be unreliable for an analysis.

#### Table 1. (Continued)

Spadix length (cm) [Spadix\_length]

Spadix width (cm) [Spadix\_width]

Pistil length (cm) [Pistil\_length]

Pistil width at style apex (cm) [Pistil\_width\_at\_style\_apex]

Style apex plan length (cm) [Style\_apex\_plan\_length]

Style apex plan width (cm) [Style\_apex\_plan\_width]

Stigma length (cm) [Stigma\_length] Stigma width (cm) [Stigma\_width]

Stigmatophore height (cm) [Stigmatophore\_height]

Spadix length (cm) is measured from tip to the base on the ventral side, i.e. nearest to most basal point of the spathe insertion; spathe insertions are usually oblique with the lowest point of the spathe insertion on the ventral side, i.e. the side where the spathe gapes open. In cases where there is a spadix stipe, this measured segment would not include any portion of the stipe.

Spadix width (cm) is measured in three places, estimated by eye, at points 25%, 50% and 75% along the spadix length.

The pistil (gynoecium) length could only be measured in herbarium specimens in which the spadix had been cut longitudinally before drying. Three flowers were measured in each spadix, selecting where possible those cut more-orless through the centre, or those remaining uncut which provided a lateral view.

The pistil (gynoecium) width at the style apex could only be measured in herbarium specimens in which the spadix had been cut longitudinally before drying or when a clear lateral view was possible. Shrinkage at the style apex is less strongly marked than at the level of the ovary because of the presence of abundant trichosclereids in the stylar region. Three flowers were measured in each spadix.

The style apex plan length and width are dimensions as seen from vertically above the pistil and refer to the exposed apex of the stylar region of the pistil (gynoecium). The length is measured along the axis of the stigma furrow (compitum), sometimes hard to see in sub-circular stigmas (e.g. in some individuals of ssp. *klotzschiana*), and the width is perpendicular to this axis. Three to five flowers were measured in each spadix.

Stigma length and width are measured along the long axis of the stigma as seen from above, and along the axis perpendicular to it. Three to five flowers were measured in each spadix

The stigmatophore is that part of the style apex which is raised up from the level at which the upper margins of the pistils meet on the spadix surface, and which carries the stigma. The stigmatophore is usually more-or-less conical and its presence is characteristic of ssp. *klotzschiana*. The height is measured from the upper margin of the stylar region to the base of the stigma. It can only be measured with acceptable accuracy in dried specimens when cut longitudinally or is visible laterally on a non-crushed part of the spadix. Three to five flowers were measured in each spadix.

See Powerpoint file "Monstera characters defined.pptx" at the *CATE Araceae* website (Haigh 2013) for an illustrated version of these definitions. Terms given in square brackets are the variable names as used in the matrices.

Nadruz\_1204\_CEPEC\_inflo1 or Vinha\_64\_CEPEC lowered the proportion of correctly classified individuals to 93.02%, while the omission (individually) of Hatchbach\_63302\_CEPEC, Pinheiro\_2033\_CEPEC or Vinha\_85\_CEPEC increased the correct classification value to 97.67%. All of the specimens which altered the percentage of correctly classified individuals were of subsp. blanchetii, suggesting less stability in the variable correlations in this taxon.

In the analysis of standardized combined vegetative and reproductive data, subsp. *blanchetii* was discriminated from subsp. *klotzschiana* most strongly by low values of stigmatophore height, and high values of stigma length and leaf length (Table 4); the latter distinc-

tion must be treated with caution given the tendency by collectors with such large-leaved plants to avoid leaves that will not fit on a herbarium sheet. In addition, the sample sizes in this analysis are lower than in the other two.

With vegetative characters only, subsp. blanchetii was discriminated from subsp. klotzschiana most, in decreasing order of importance, by higher numbers of leaf perforations, wider leaf base angle and shorter leaf length (Table 4); this opposite weighting for leaf length resulted from a larger sample of individuals and confirms its unreliability.

The matrix of reproductive characters only (with the largest sample sizes) discriminated subsp. *blanchetii* 

**Table 2.** Statistics of vegetative morphometric quantitative variables for *Monstera adansonii* subspp. *blanchetii* and *klotzschiana* 

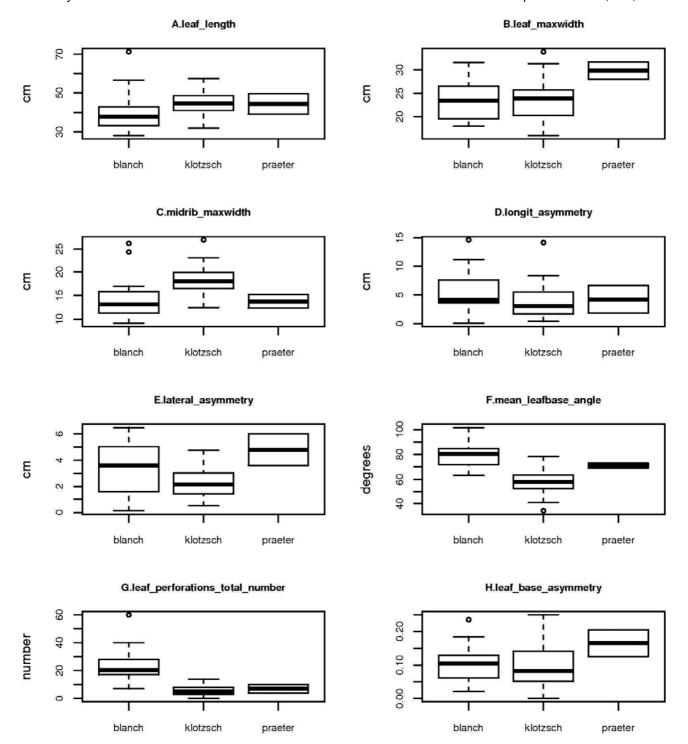
quantitative variable	taxon (subspecies of Monstera adansonii)	sample size	mean	standard deviation	coeffi- cient of variation	normality (Shapiro-Wilk test) p (normal)	equal variances (Fligner- Killeen test) p (equal)	equal means (permutation t test, 9,999 replicates) p (equal)
Leaf_length	blanchetii klotzschiana	18 25	39.56 44.90	10.58 6.19	26.75 13.79	0.004591** 0.8388 n.s.	0.2422 n.s.	0.044*
leaf_maxwidth	blanchetii klotzschiana	18 25	23.55 23.71	4.19 4.33	17.80 18.26	0.3786 n.s. 0.831 n.s.	0.939 n.s.	0.9091
midrib_maxwidth	blanchetii klotzschiana	18 25	14.26 18.11	4.64 3.25	32.52 17.96	0.006289** 0.561 n.s.	0.6114 n.s.	0.003**
longit_asymmetry	blanchetii klotzschiana	18 25	5.64 3.94	3.47 3.21	61.43 81.41	0.04974* 0.001771**	0.8701 n.s.	0.101
lateral_asymmetry	blanchetii klotzschiana	18 25	3.45 2.34	1.90 1.19	55.14 50.76	0.5253 n.s. 0.4097 n.s.	0.01916*	0.0246*
mean_leafbase_angle	blanchetii klotzschiana	18 25	79.43 57.84	9.84 10.43	12.39 18.03	0.6815 n.s. 0.9951 n.s.	0.9327 n.s.	0.0001***
Leaf_perforations_ total_number	blanchetii klotzschiana	18 25	23.06 5.44	12.47 3.42	54.10 62.81	0.01909* 0.2481 n.s.	0.001031**	0.0001***
leaf_base_asymmetry	blanchetii klotzschiana	18 25	0.10 0.09	0.06 0.06	53.95 65.69	0.4804 n.s. 0.0426*	0.09169 n.s.	0.608

Analyses made with PAST (Hammer et al. 2001) and R (R Core Team 2013). See Table 1 for explanation of quantitative variables.

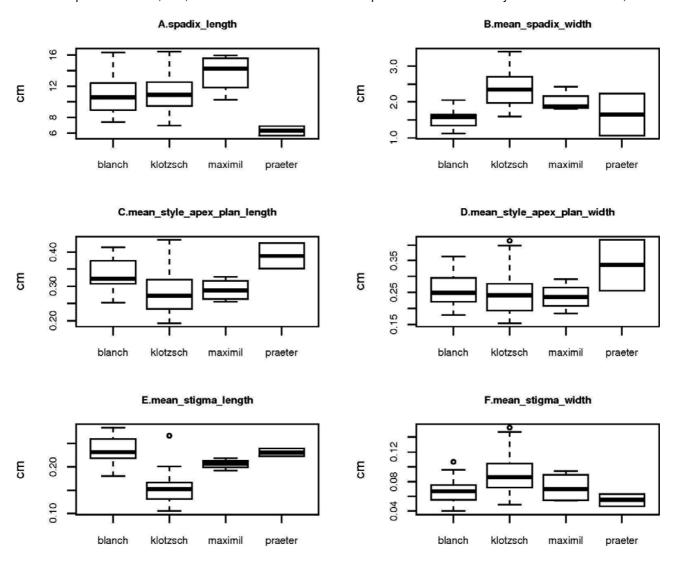
**Table 3.** Statistics of reproductive morphometric quantitative variables for *Monstera adansonii* subspp. *blanchetii* and *klotzschiana* 

quantitative variable	taxon (subspecies of <i>Monstera</i> adansonii)	sample size	mean	standard deviation	coeffi- cient of variation	normality (Shapiro-Wilk test) p (normal)	equal variances (Fligner- Killeen test) $\rho$ (equal)	equal means (permutation t test, 9,999 replicates) p (equal)
Spadix_length (cm)	blanchetii klotzschiana	21 31	10.96 11.18	2.37 2.50	21.58 22.37	0.5862 n.s. 0.6961 n.s.	0.9579 n.s.	0.7552 n.s.
mean_spadix_width (cm)	blanchetii klotzschiana	21 31	1.53 2.37	0.24 0.48	15.56 20.31	0.458 n.s. 0.173 n.s.	0.002698**	0.0001***
mean_style_apex_ plan_length (cm)	blanchetii klotzschiana	21 31	0.33 0.28	0.04 0.06	12.64 22.17	0.6988 n.s. 0.2393 n.s.	0.08109 n.s.	0.0027**
mean_style_apex_ plan_width (cm)	blanchetii klotzschiana	21 31	0.26 0.25	0.05 0.07	19.56 28.01	0.6394 n.s. 0.01683*	0.2755 n.s.	0.4716 n.s.
mean_stigma_length (cm)	blanchetii klotzschiana	21 31	0.24 0.15	0.03 0.03	13.29 20.71	0.3251 n.s. 0.00371**	0.1543 n.s.	0.0001***
mean_stigma_width (cm)	blanchetii klotzschiana	21 31	0.07 0.09	0.02 0.02	27.19 26.30	0.6504 n.s. 0.05062 n.s.	0.4445 n.s.	0.0004***
mean_stigmatophore_ height (cm)	blanchetii klotzschiana	21 31	0.05 0.12	0.01 0.02	26.01 18.57	0.0157* 0.8756 n.s.	0.04216*	0.0001***

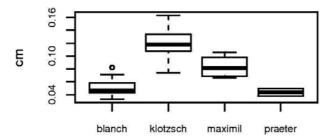
Analyses made with PAST (Hammer et al. 2001) and R (R Core Team 2013). See Table 1 for explanation of quantitative variables.



**Figure 4.** Boxplots of untransformed vegetative variables. A. Leaf length. B. Leaf widest width. C. Distance from leaf base of widest leaf width. D. Distance along midrib between points of widest width of each half-lamina. E. Difference between the widest widths of each half-lamina. F. Mean angle of divergence from the midrib of the two leaf base margins. G. Total number of perforations in the leaf lamina. H. Difference in leaf base angle divided by the combined angle. See Table 1 for details of the variable definitions.



G.mean stigmatophore height



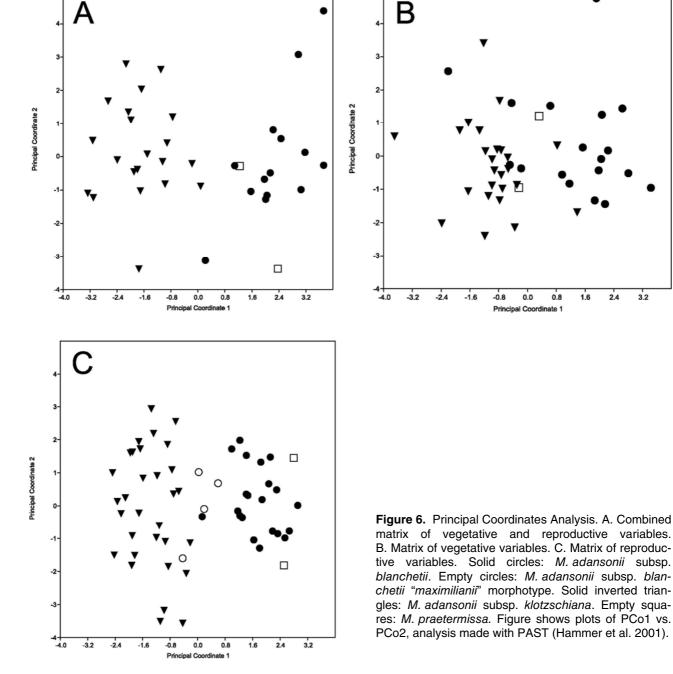
from subsp. *klotzschiana* most, in decreasing order of importance, by high values of stigma length, low values of stigmatophore height, and low values of spadix width (Table 4).

#### 3.1.3 Diagnostic characters

The identification of *M. praetermissa* is relatively easy in vegetative specimens with the characters given in the

**Figure 5.** Boxplots of untransformed reproductive variables. A. Spadix length. B. Mean spadix width. C. Mean length (in sense of spadix axis) of style apex seen from above. D. Mean width (perpendicular to spadix axis) of style apex seen from above. E. Mean stigma length. F. Mean stigma width. G. Mean height of stigmatophore. See Table 1 for details of the variable definitions.

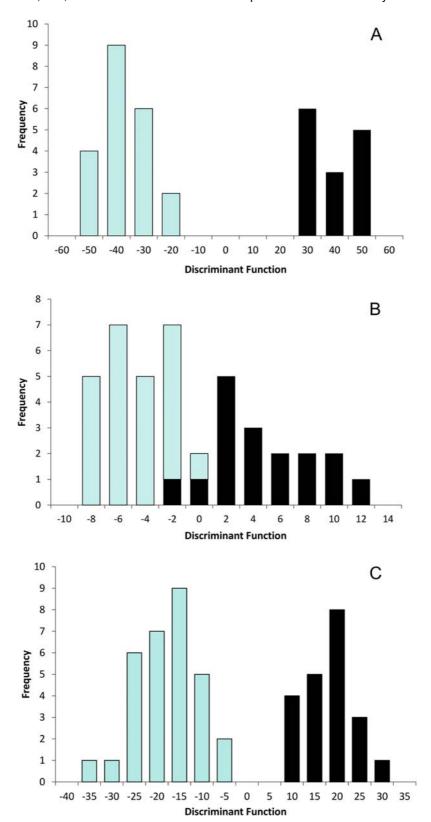
key below and particularly in living material, using the colours and ornamentation of the internodes. In dried specimens the best character is the deciduous petiole sheath, which rapidly decomposes in young leaves into blackened membranaceous fragments which eventually slough off completely. In fertile material, spadix size and fruit colour are the best diagnostic characters to separate it from the two subspecies of *M. adansonii*.



The identification of subsp. *blanchetii* and subsp. *klotzschiana* is also quite straightforward when flowers are available, stigma length, stigmatophore height and spadix width being the strongest diagnostics. However, when only leaves are present identification is not quite as simple because there is overlap in all characters (Fig. 4).

Discriminating the two subspecies with leaf material using the original untransformed characters produced the same result in the cross-evaluation procedure of PAST as for standardized variables. It is possible to use

the discriminant function (Table 5) calculated from the untransformed vegetative matrix to assign a new leaf specimen to one of the subspecies. The vector of character values from the new specimen is vector multiplied (inner product) by the vector of discriminant function coefficients and the offset value is then subtracted; this can be done using the R code available at the *CATE Araceae* website (Haigh 2013). Using our data matrix we computed values for the two leaves of the type specimen of *M. blanchetii*. With better samples of the two taxa, this tool could be further tested and refined.



**Figure 7.** Linear Discriminant Analysis in *Monstera adansonii* subspecies carried out with three different data matrices. A. Combined matrix of vegetative and reproductive variables. B. Matrix of vegetative variables. C. Matrix of reproductive variables. Light bars: subsp. *klotzschiana*. Black bars: subsp. *blanchetii*. Analysis made with PAST (Hammer et al. 2001).

Table 4. Linear Discriminant Analysis of standardized variables

	vegetative and reproductive variables combined	vegetative variables	reproductive variables	
sample size subsp. blanchetii	14	18	21	
sample size subsp. klotzschiana	21	25	31	
offset constant	6.06914	0.085452	2.56367	
Hotelling's t <sup>2</sup>	715.9	113.52	513.59	
F	27.479	11.767	64.565	
p (same)	9.96E-10	7.69E-08	4.75E-21	
% correctly classified	100	95.35	100	
variables	discriminant function coefficients	discriminant function coefficients	discriminant function coefficients	
Leaf_length	7.9975	-1.9948		
eaf_maxwidth	-3.6888	0.51996		
midrib_maxwidth	-2.2428	1.2175		
ongit_asymmetry	3.4158	-0.27022		
ateral_asymmetry	-0.11377	1.4646		
mean_leafbase_angle	-0.56716	2.3237		
Leaf_perforations_total_number	3.9938	4.2795		
eaf_base_asymmetry	1.7061	0.65382		
Spadix_length	0.58008		2.3298	
mean_spadix_width	-2.4069		-6.1068	
mean_style_apex_plan_length	-3.0079		-2.6606	
mean_style_apex_plan_width	3.9022		2.2169	
mean_stigma_length	20.898		9.8531	
mean_stigma_width	-3.0312		-2.7265	
mean_stigmatophore_height	-23.414		-8.1919	

Analyses made with PAST (Hammer et al. 2001). See Table 1 for explanation of quantitative variables.

Table 5. Linear Discriminant Analysis of original variables, vegetative characters only

character (variable)	discriminant function coefficients	character (variable) values for <i>Blanchet s.n.</i> (type specimen of <i>M. adansonii</i> subsp. <i>blanchetii</i> )			
		Leaf 1	Leaf 2		
leaf_length	-0.23455	28.542	35.298		
leaf_maxwidth	0.11986	16.271	25.519		
midrib_maxwidth	0.28685	10.208	13.94		
longit_asymmetry	-0.080717	4.895	0.23		
lateral_asymmetry	0.89267	4.289	4.877		
mean_leafbase_angle	0.16093	62.495	66.431		
Leaf_perforations_total_number	0.35892	18	8		
leaf_base_asymmetry	11.031	0.168	0.109		
offset constant	17.0027				
calculation of discriminant function value for Leaf 1 $ 2.985821 = -(0.23455 \cdot 28.542) + (0.11986 \cdot 16.271) + (0.28685 \cdot 10.2086 + (-0.080717 \cdot 4.895) + (0.89267 \cdot 4.289) + (0.16093 \cdot 62.495) + (0.3589 + (11.031 \cdot 0.168) - 17.0027 $					

Analyses made with PAST (Hammer et al. 2001) and R (R Core Team 2013).

#### 4 Taxonomic conclusions

# 4.1 Key to the species of Monstera in Bahia\*

- 1. Internodes smooth, dark to mid green with numerous white dots, 1–4 cm diam. in adult plants. Petiole sheath with erect to convolute margins, remaining mostly intact and green. Spadix 6.2–16.4 cm long. Berries white when mature.
- 1'. Internodes minutely rugulose-verruculose, the verruculae concolorous with the rest of the epidermis, up to 1.2 cm diam. in adult plants. Petiole sheath quickly marcescent into brown-black membranaceous fragments which are eventually deciduous. Spadix 5.7–6.9 cm long. Berries yellow to orange when mature. . . . praetermissa
- \* measurements made in dried material
- \*\* mean of angles made by leaf base margin to the midrib on each side of the leaf blade.

#### 4.2 Taxon treatments

#### 4.2.1 Monstera adansonii Schott

Over its whole geographic range, Monstera adansonii is distinguished from other species (Madison 1977 and our own observations) by the following characters: stem 1-6 cm thick; internodes green with numerous, minute whitish dots; leaf blades of attached juvenile shoots not flattened against the host tree bark; adult leaf blade with entire margins and usually (but not always) perforated; secondary lateral veins parallel to each other and to primaries; peduncle 9-22 cm long, shorter than the leaves, equalling or exceeding the length of the flowering spadix but not more than twice as long; spathe pale yellow to cream coloured to white; flowering spadix cream to white, 8-13 cm long; fruiting spadix green, becoming white (or yellow to intensely yellow according to Madison 1977), 10-17 cm long, 2-4 cm thick; seeds 5-10 mm long.

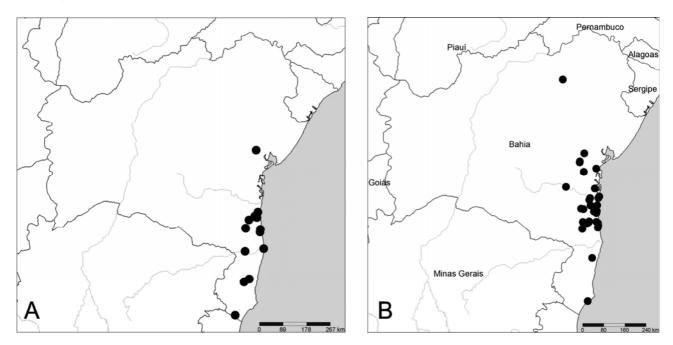
# 4.2.1.1 *Monstera adansonii* Schott subsp. *blanchetii* (Schott) Mayo & I.M. Andrade, stat. nov.

≡ *Monstera blanchetii* Schott, Prodr. Syst. Aroid.: 367 (1860). Type: Brazil, Bahia, *J. S. Blanchet s.n.* (G holotype; W drawing Schott Icon Aroideae No. 2226).

= Monstera maximilianii Engl. in C. F. P. von Martius & auct. suc. (eds.), Fl. Bras. 3(2): 113 (1878). Neotype (designated here): Pencil drawing at the Natural History Museum of Vienna, of a specimen previously preserved (now presumed destroyed) in the Vienna (W) herbarium with the label data "E.F.M. Bahia 754". Schott Icon Aroideae No. 2328 (W drawing; K photo).

Figs. 1, 8A.

HABIT. Hemi-epiphyte, root climber with distichous leaves. STEM. Juvenile plant: internodes 2-4.5 cm long, ellipsoid in cross section, dull to lustrous dark to mid green with numerous tiny white dots or short striae which are hardly visible in very juvenile plants; anchor roots in patches just below nodes. Adult plant: internodes 1-3 × 1-3.5 cm, ellipsoid to subcircular in cross section, dull darkish green with white dots or short striae, leaf scars straw-coloured; anchor roots emerging all along internode on side appressed to host trunk, ca. 0.15 cm diam., wiry, blackish-brown, feeder roots solitary at nodes, up to 0.55 cm diam. Petiole. Juvenile plant: 5-10.5 cm long (including geniculum) when blade entire, to ca. 19 cm long when blade perforated, similar in colour and markings to internodes; sheath margins erect. Adult plant: 30-64 cm long (including geniculum), similar in colour and markings to internodes, distinctly paler than blade and ± straw-coloured when dried, free petiole sulcate with angled margins, distinct basal geniculum present, apical geniculum 3-4 cm long, 1.2-1.3 cm deep, sulcate with angled margins; sheath reaching geniculum or just below, apex obtuse to rounded, auriculate or not, margins erect, one side broader than the other, entire, remaining green, quite often the extreme margin withers or becomes somewhat darker. LEAF BLADE. Juvenile plant: in smaller shoots  $3.5-15 \times 1.8-6.5$  cm, broadly to narrowly ovate, unequal, often falcate, apex narrowly acuteacuminate, base rounded to subcordate on wider side, acute to subacute on narrower side, non-perforate or with up to  $6 \pm$  elliptic perforations; in larger, climbing juvenile shoots 15-27 × 8.8-11 cm, ovate, unequal, apex acute to subacute, hardly acuminate, base truncate to emarginate or subcordate on wider side, subacute to rounded on narrower side, lustrous dark green above,



**Figure 8.** *Monstera adansonii*. Maps of subspecies distribution in Bahia state. A. subsp. *blanchetii*. B. subsp. *klotz-schiana*. Made with SimpleMappr (www.simplemappr.net).

paler and lustrous below, midrib and primary lateral veins impressed above and concolorous with blade, below prominent and whitish, perforations 5-16, in 1-2 series on each side, usually in single series on each side, larger perforations elliptic to irregularly elongated, extending from near the midrib to the leaf margin and some breaking through it, smaller perforations ± circular, adjacent to midrib, usually fewer. Adult plant: 28-71  $\times$  18-31.5 cm, 1.2-2.3 times longer than wide, usually ovate less often oblong-ovate, hardly to strongly unequal, not falcate to strongly falcate, apex acute, subacute, obtuse or rounded, cuspidate to shortly acuminate at extreme apex, base subacute to truncate, emarginate or subcordate on wider side, subacute, rounded or truncate on narrower side, mean of angles on each side 63-102°, margins curving to form a short wedge at petiole insertion, dark green, lustrous to glossy above, paler and duller below, midrib sulcate and major veins impressed above, prominent and distinctly paler below, primary lateral veins (9-)10-14(-20) on wider side, the lowermost 3-4 veins being very close together; perforations (7-)17-40(-60), most commonly between 15 and 33, roughly elliptic, ovate or very elongated, sometimes distorted, in 1-2 series in each half of the blade, the larger, more elongated perforations usually extending from near midrib to near leaf margin, often reaching and breaking through it, the smaller more circular perforations lying near the midrib, interprimary fields with 0-3 perforations, most often with only 1, in more perforated leaves the interprimary fields contain

1 elongated major perforation reaching leaf margin and 1-2(-3) minor perforations forming a group next to midrib. INFLORESCENCE. 1-4 in each floral sympodium; prophylls and cataphylls of floral sympodium paler than leaf blade when dried, 9-24 cm long; peduncle (10-)12.7-23.4, same colour and markings as petiole, elliptic in cross-section; spathe 13.5-17 cm long, about as wide as long when opened out, inflated-orbicular, opening widely at anthesis with somewhat revolute margins, whitish cream, slightly green tinged externally where more exposed to light, 0.7-1.2 times as long as peduncle; spadix  $7.4-16.3 \times 1.1-2.5$  cm, 4.8-10.3(-12.8)times longer than diam., 0.5-1.1 times as long as peduncle, 0.5-0.6 times as long as spathe, cylindrical to somewhat clavate, whitish cream at anthesis, becoming dull pale green or even slightly blueish-green in the postfloral phase, basal 1-2 cm usually rather narrower; fertile gynoecia with flattened polygonal style apex  $0.25-0.58 \times 0.18-0.63$  cm when seen from above, stigma 0.18-0.28 × 0.04-0.1 cm, linear, oriented longitudinally, sessile to subsessile, stigmatophore 0.03-0.08 cm high, flowers of basal portion sterile, glandular with stylar region somewhat narrowed. INFRUCTESCENCE. Immature fruits green, white when mature with very pale yellowish style apex and darker stigma remains.

Common Names: banana de macaco, costela de adão, imbé.

Habitat and Distribution: Climbing to 10 m on tree trunks in well-developed secondary forest and on trees and

fences in cacau plantations. Brazil: Bahia, Espírito Santo and Pernambuco states. Altitude: 0–100 m.

Phenology: flowering from October to April, fruiting throughout the year.

Preliminary conservation status assessment within Bahia: Extent of Occurrence: Near Threatened (NT); Area of Occupancy: Least Concern (LC). Based on 27 specimens from 19 localities.

Etymology: The subspecies epithet honours the Swiss botanist Jacques Samuel Blanchet (1807–1875), the collector of the type specimen, who made very extensive collections of Bahian plants in the period 1828–1856.

## Commentary:

Typification of Monstera blanchetii Schott

The holotype of M. blanchetii Schott consists of three elements: a leaf which bears the label "Dracontium pertusum Bahia. Blanchet", a second leaf which has no collector's label, but instead a determination label in Schott's handwriting which reads "Neguaguam Monstera Adansonii S." (i.e. "certainly not Monstera Adansonii Schott"), and a sheet with a spadix and the remains of a spathe inside a paper capsule, with the label "M. pertusa". Schott's (1860) description mentions only vegetative characters, and his citation reads "Brasilia. Bahia. Blanchet. - vid. s. f. in Herbar. D.C.", indicating that he had seen a dried leaf in the de Candolle herbarium. However, Schott's drawing of this collection by Oberer (Schott Icon No. 2226) includes all three of these elements, with a detail showing the flattened style apex of one of the flowers, confirming that he studied all the material. While, strictly speaking, the holotype sheet is the one with the label giving collector and locality, the other two sheets also form part of the same collection and are essential to its taxonomic interpretation.

The Schott Icones Aroideae (see Riedl 1965; Nicolson 1984; Schott 1984; Nadruz Coelho & Mayo 2007) also include drawings of collections made by the expedition of Archduke Ferdinand Maximilian of Austria to Brazil in 1859-1860 (Riedl-Dorn 1992). Schott Icon No. 2225 is a pencil drawing by Nickelli of two leaves with the data "Ilheos 753"; this drawing is determined only as Monstera, although included in the catalogue (Nicolson 1984) under Monstera blanchetii. It seems likely that the citation by Engler & Krause (1908: 106) "Blanchet n. 753 -Herb. De Candolle ..." is a mistake in which this Schott Icon was confused with the type of M. blanchetii, the latter having no collection number. Schott Icones Nos. 3666, 36667 (sic!) and 3668 are magnificent coloured drawings by Liepoldt, respectively of an inflorescence, a leaf seen from the abaxial side, and the same leaf from the adaxial side; they are determined as "Monstera Blanchetiana" in Schott's own hand. There can be little doubt that these represent a cultivated specimen of a different Maximilian collection from Ilhéus, also depicted in Schott Icon 2227 with the data "E.F.M. Ilheos 759". Schott's understanding of *M. blanchetii* was thus based on reproductive as well vegetative morphology. Schott Icon No. 3666 shows the floral morphology in detail, with the flattened style apices and very short stigmatophores of the fertile flowers and also the more conical style apices of the sterile glandular flowers at the spadix base.

Typification of *Monstera maximilianii* Engl.

Engler's (1878: 113) original description was based on a single specimen "Habitat in prov. Bahia: Expeditio archiducis Maximiliani!", later cited by Engler & Krause (1908: 102) as at the Vienna herbarium: "Bahia (Exped. des Erzherzogs Maximilian – Kais. Herb. Wien)". This specimen no longer exists but the pencil drawing Schott Icon No. 2328 corresponds well to Engler's description, particularly in the non-fenestrate leaf blade and the data on the drawing: "E.F.M. Bahia 754"; we therefore designate this drawing as the neotype. It seems likely that this collection came from the region of Ilhéus, since the plant depicted in Schott Icon No. 2225, made by the same expedition and with "Ilheos" as the locality, is numbered as 753.

Taxonomic status of Monstera maximilianii Engl.

The neotype drawing of M. maximilianii shows gynoecia with a flattened style apex and reduced stigmatophore, thus resembling subsp. blanchetii; however, the leaf is entire, with no perforations, and is recorded by Engler as relatively large, at 50 cm long. The combination of larger leaf blade and flattened style apex was observed in several specimens referred by us to subsp. blanchetii (Amorim 2369, Gonçalves 417, Harley 17920), but these differ from the type of *M. maximilianii* in having leaf blades with well over 9 perforations (precise figures could not be obtained as these specimens show only half the leaf blade). These three modern collections appear intermediate between the two subspecies; the stigmatophore is shorter (mean = 0.08 cm, s.e. 0.009) than in subsp. klotzschiana (mean = 0.12 cm, s.e. 0.004), but longer than in subsp. blanchetii (mean = 0.05 cm, s.e. 0.003) and significantly different in all pairwise combinations. This intermediate condition is confirmed in a PCoA of standardized data of floral characters, in which these specimens lie between the two subspecies. We have nevertheless assigned them to subsp. blanchetii pending further study.

Distinguishing subsp. blanchetii from subsp. laniata.

In the Atlantic forest of Bahia state in northeast Brazil, herbarium specimens we recognize as subsp. *blanchetii* have long been identified as *M. adansonii* var. *laniata* (Schott) Madison (e.g. Andrade et al. 2008, Andrade & Mayo 2010). One of the main conclusions of the present study is that these two taxa are sufficiently distinct to

merit the taxonomic recognition of subsp. *blanchetii* and we also reclassify var. *laniata* as subsp. *laniata* (Schott) Mayo & I. M. Andrade (see below for nomenclatural formalities).

The Bahian material we have studied matches the type of *M. blanchetii* Schott (1860: 367), which is a J.S. Blanchet collection from "Bahia", according to the label. In his revision of *Monstera*, Madison (1977) reduced this name to a synonym of *M. adansonii* but did not assign it to one of his three varieties, leaving its status uncertain at the infraspecific level.

As we have not undertaken a detailed study of the very widespread and variable subsp. laniata, we based our understanding of this taxon mainly on Grayum's (2003) treatment for Costa Rica, the type locality of Tornelia laniata Schott, and on field studies carried out in 2004 in French Guiana at the localities Cayenne, Montravel and Fort Diamant. Grayum lays most emphasis on the presence of a deciduous petiole sheath (also used by Madison 1977 as diagnostic for his var. laniata), the rather thinly coriaceous leaf, the presence or not of leaf perforations, highly variable ecology including dry forest habitat and the usually rather unequal leaf base. Additionally he describes the spathe as internally white, rather than cream or yellowish cream, and the peduncle as almost always longer than the flowering spadix. Grayum's taxon concept of subsp. laniata corresponds in most details to the French Guiana populations we studied. The only character which seems to differ is the persistence of the petiole sheath, which in the Guiana material is mostly persistent and not clearly and regularly deciduous.

The Bahian plants we recognize as *Monstera adansonii* subsp. *blanchetii* share with subsp. *laniata* a broadly ovate leaf blade, linear sessile stigmas, flattened style apices and a preference for more open habitats. They differ however in essentially persistent leaf sheaths, more coriaceous leaf blades, the presence of more numerous and irregularly sized leaf perforations and the cream-coloured internal surface of the spathe. Molecular (AFLP) data from Bahian populations of subsp. *blanchetii* (I.M. Andrade, unpublished data) also clearly separate them from French Guiana populations of subsp. *laniata*.

#### Material examined:

Brazil. Bahia. Belmonte: Fazenda Boa Vista, 16 Apr 1975, fl., *T.S. Santos 2963* (CEPEC 11053). Cachoeira: Estação da Mata (Barragem Bananeiras), Oct 1980, postfl., *Grupo Pedra do Cavalo 807* (CEPEC 32913). Ilhéus: 1860, *F. Maly in Archduke Ferdinand Maximilian of Austria 759* (represented by drawings, Schott Icones Aroideae Nos. 2227, 3666, 36667 (sic!), 3668); Área do CEPEC (Centro de Pesquisas do Cacau), 5 Mar 1981, prefl., postfl., *J.L. Hage & E.B. Santos 530* (CEPEC 23826, K 000302968); Área do CEPEC (Centro de Pes-

quisas do Cacau), 20 Jan 1982, prefl., fl., J.L. Hage & E.B. Santos 1605 (CEPEC 27908, K 000302969); Área do CEPEC (Centro de Pesquisas do Cacau), 8 Feb 1988, prefl., fl., immfr. J.L. Hage 2233 (CEPEC 42008, K 000302933); Campus da Universidade Estadual de Santa Cruz (UEC), 18 Jan 1996, st., L.A. Mattos-Silva et al. 3221 (CEPEC 70930); Área do CEPEC (Centro de Pesquisas do Cacau), 18 Apr 1991, st., S.J. Mayo et al. 756 (CEPEC 50467, K 000302904); Campus da Universidade Estadual de Santa Cruz (UEC), 14 Jun 2006, postfl., J.L. Paixão 984 (CEPEC 118571); Área do CEPEC (Centro de Pesquisas do Cacau), 14 Dec 1988. st., T.S. Santos 4462 (CEPEC 44373, K 000302904); Castelo Novo, margem da Lagoa Encantada, 14 Feb 1968, postfl., S.G. Vinha 64 (CEPEC 3502). Itamarajú: Serra de Itamarajú, Morro Pescoço, 11 Feb 2007, fl. fr., A.M. Amorim et al. 6838 (CEPEC 115904). Itapé: Fazenda Estreito D'água, 20 Oct 1972, prefl. fl. postfl., R.S. Pinheiro 2033 (CEPEC 9028, K 000302966). Itapebi: Rodovia BR-101, próximo de Itapebi, 14 Aug 1995, postfl., G. Hatschbach et al. 63302 (CEPEC 68305). Jussari: RPPN Serra do Teimoso, 9 Apr 1998, postfl., A.M. Amorim et al. 2369 (CEPEC 81956); perto da Serra do Teimoso, Fazenda Santo Antônio de Cima, 11 May 1991, st., S.J. Mayo et al. 811 (CEPEC 50633, K 000302932); Jussari para Palmira, Fazenda Teimoso, 14 Feb 2004, st., P. Fiaschi et al. 1929 (CEPEC 101436). Mucuri: Rodovia BR-101, Rio Mucuri, 9 Nov 1984, fl., G. Hatschbach & J.M. Silva 48765 (CEPEC 42366, K 000302970). Porto Seguro: Parque Nacional de Monte Pascoal, 13 Jan 1977, prefl. fl., R.M. Harley et al. 17920 (CEPEC 19737, K 000302939); Parque Nacional de Monte Pascoal, 21 Mar 1968, st., S.G. Vinha & T.S. Santos 85 (CEPEC 3672). Una: between Pedras and Una, opposite CEPLAC experimental station, 26 Jan 1977, fl. immfr., R.M. Harley et al. 18300 (CEPEC 19751, K 000302962); Estrada que leva a entrada da Reserva Biológica de Una, 7 May 1996, postfl., M. Nadruz & J. Lima 1204 (CEPEC 69427). Uruçuca: 9.4 km do trevo de Uruçuca no sentido Uruçuca-Itabuna, 1 Mar 2000, postfl., E.G. Gonçalves et al. 417 (CEPEC 84388).

# 4.2.1.2 Monstera adansonii Schott subsp. klotzschiana (Schott) Mayo & I.M. Andrade, stat. nov.

■ Monstera klotzschiana Schott, Oesterr. Bot. Wochenbl. 4: 419 (1854). ■ Monstera pertusa var. klotzschiana (Schott) Engl. in C. F. P. von Martius & auct. suc. (eds.), Fl. Bras. 3(2): 113 (1878). ■ Monstera pertusa f. klotzschiana (Schott) Voss, Vilm. Blumengärtn. ed. 3, 1: 1178 (1895). ■ Monstera adansonii Schott var. klotzschiana (Schott) Madison, Contr. Gray Herb. 207: 40 (1977). Neotype (designated here): Pencil drawing at the Natural History Museum of Vienna, of a specimen of

a plant cultivated at the Berlin Botanical Garden as "Dracontium pertusum" and previously preserved (now presumed destroyed) in the Berlin (B) herbarium with the label name "Heteropsis fenestrata KI." Schott Icon Aroideae No. 2268 (W drawing; K photo). Figs. 3, 8B.

HABIT. Hemi-epiphyte, root climber with distichous leaves. Stem. Juvenile plant: internodes  $0.6-5 \times 0.8-1$  cm; anchor roots in clusters below nodes, terrestrial, climbing or flagelliform. Adult plant: internodes 0.5-3.5 x 1.5-4 cm, elliptic in cross section, lustrous, dark green with numerous paler green minute dots, smooth; anchor roots distributed along the internode on side adjacent to host trunk, feeder roots solitary per node, up to 1.8 cm diam.; continuation shoot starting with prophyll and two cataphylls. Petiole. Juvenile plant: sheath extending to petiole apex and auriculate apically, margins involute to convolute. Adult plant: 20-47.5 cm long (including geniculum), epidermis darkish green, densely covered with numerous tiny whitish-green dots, when dried similar in colour to leaf blade, apical geniculum 1-3.5 cm long, 2 cm deep, prominent, sulcate and winged on margins above; sheath extending to geniculum and auriculate apically, margins erect to convolute, remaining intact and green. LEAF BLADE. Juvenile plant: 12-38 x 3-14.2 cm, usually narrowly to broadly elliptic, sometimes ovate or oblong, unequal, often falcate, apex acute or acuteacuminate, base acute; perforations 0-4, usually absent, seen only in larger juvenile leaves (>25 cm long). Adult plant:  $28.5-65 \times 11.5-26.5$  cm, 1.2-2.6 times longer than wide, ovate, oblong, elliptic, sometimes narrowly so, usually ± unequal but not strongly so, apex acute to obtuse or rounded and shortly cuspidate, base often ± equal, usually acute on each side, sometimes rounded to truncate, mean of angles on each side 34-78°, rich glossy green to dark green above, slightly paler and less glossy below, midrib sulcate and major veins impressed above, prominent and distinctly paler below, primary lateral veins 9-12(-14); perforations 0-9(-14), always more numerous in the wider half-lamina, approximately elliptic, often extending for less than half the width of one half-lamina, but sometimes almost as wide as the halflamina, arising ± distant or adjacent to midrib and usually terminating within the margin, sometimes extending almost to margin but not breaking through; usually in a single series located ± centrally in each half-lamina, sometimes with one to a few ± circular, small perforations next to the midrib, interprimary fields always with no more than 1 perforation. INFLORESCENCE. 1-3 in each floral sympodium, prophylls and cataphylls of floral sympodium similar in colour to leaf blade when dried, 16-25 (-44) cm long; peduncle 6.6-23.2(-31.1) cm, up to 2 cm diam. elliptic in cross-section, same colour and markings as petiole; spathe 11.7-21.4 cm long, 0.6-1.7 times as long as peduncle, usually slightly longer than wide, broadly ellipsoid to inflated-orbicular, opening widely at anthesis with somewhat revolute margins, cream-coloured, paler internally and often greenish- or yellowishtinged externally; spadix  $6.2-16.4 \times 1.4-3.1(-3.4)$  cm, 3.1-5.8(-6.8) times longer than diam., 0.4-1.1 times as long as peduncle, 0.3-0.7 times as long as spathe, subcylindric, white to cream, becoming green in postfloral phase; fertile gynoecia with distinctly raised and conical style apex  $0.18-0.44 \times 0.15-0.41$  cm when seen from above, stigma  $0.10-0.18(-0.27) \times 0.05-0.15$  cm, orange at female anthesis, elliptic, borne on distinct stigmatophore 0.07-0.16 cm high, flowers of basal portion sterile and glandular. INFRUCTESCENCE. Immature infructescence off-white, old stigmas prominent, mature berries white.

Common Names: banana de macaco, costela de adão, sapata rota.

Habitat: Climbing to 2–15 m on small to large tree trunks in shade of humid, usually secondary, forest and cacau plantations; forms non-flowering terrestrial populations with juvenile morphology in shaded forest.

Distribution: tropical South America. Brazil: Acre, Alagoas, Amazonas, Amapá, Bahia, Ceará, Espírito Santo, Mato Grosso, Minas Gerais, Pará, Paraíba, Paraná, Pernambuco, Rio de Janeiro, Santa Catarina, São Paulo states (Andrade & Mayo 2013); also in French Guiana, Guyana, Suriname, Venezuela, Bolivia, Peru (eMonocot Portal 2013; Madison 1977; WCSP 2013). Altitude: 0–1,050 m.

Phenology: flowering from December to April, fruiting throughout the year.

Preliminary conservation status assessment within Bahia: Extent of Occurrence: Least Concern (LC); Area of Occupancy: Least Concern (LC). Based on 46 specimens from 37 localities.

Etymology: The subspecies epithet honours the German botanist and mycologist Johann Friedrich Klotzsch (1805–860), author of an important early paper on the genus *Pistia* and sometime Director of the Berlin Botanical Garden.

# Commentary:

Typification of *Monstera klotzschiana* Schott.

In the original published treatment of *Monstera klotzschiana* Schott (1854), the only specimen cited is given as a "synonym" with no indication of its origin: "Synonym: *Dracontium pertusum Hort. Berol. (in Herb. G. Berol.)*". The citation indicates a herbarium specimen prepared from a plant cultivated in the Berlin Botanic Garden under the name *Dracontium pertusum* and preserved in the Berlin Herbarium (B), where it is no longer to be found. Schott Icon No. 2268, a drawing by Oberer in the Schott Icones Aroideae et Reliquiae (for micro-

fiche edition, see Schott 1984, Nicolson 1984), corresponds to the type citation, since the data in the right-hand side of the drawing (which we interpret as that of the specimen label – see Nadruz Coelho & Mayo 2007 for further details in interpreting data on the Schott Icones) is: – "Heteropsis fenestrata KI. sic. in Hrb. G. Berol. Dracontium pertusum Hrt. Berol.". This information includes, critically, a link to Klotzsch in the (unpublished) label name "Heteropsis fenestrata KI." The flowers on the spadix are drawn in a rather stylized way but appear to have more-or-less developed stigmatophores. We therefore designate Schott Icon No. 2268 as the neotype of *Monstera klotzschiana* Schott (following the approach of Nadruz Coelho & Mayo 2007).

Schott (1860: 366–367) redescribed *M. klotzschiana* and gave a different specimen citation: "Brasilia Luschnath. – *v.s. in Herb. G. Berol. et Horti Bot. Petrop.*". All subsequent treatments include this collection. Engler (1878: 114–115) cites "*in prov. Rio de Janeiro: Luschnath*!" under his treatment of *M. pertusa* var. *klotzschiana* (Schott) Engl., and in his treatment of the same taxon for *Das Pflanzenreich* (Engler & Krause 1908: 105) he adds "Herb. Berlin"; the Berlin duplicate no longer exists. Madison (1977: 40) cited Bernhard Luschnath's collection as: "Brazil, Rio de Janeiro, *Luschnath s.n.* (holotype B, *non vidi*; isotype LE)." Since the Luschnath specimen cannot be linked to Schott's original 1854 description, it must be disregarded as the type, despite this history.

## Material examined:

Brazil. Bahia. Almadina: Serra do Corcovado, 4 Sep 2011. fr., M.M. Coelho et al. 403 (CEPEC 134119). Amargosa: Serra do Timbó, 27 Jan 2007, immfr., D. Cardoso et al. 1650 (CEPEC 119974); Próximo à "Jacubinha", 22 Dec 2010, postfl., R.O. Perdiz et al. 179 (CEPEC 121837). Arataca: Parque Nacional da Serra das Lontras, 3 Jul 2011, fr., P. Leitman et al. 294 (CEPEC 133203); Serra das Lontras, 31 Mar 2006, fl., J.L. Paixão et al. 956 (CEPEC 111321). Barro Preto: Serra da Pedra Lascada, 29 Jul 2004, immfr., A.M. Amorim et al. 4209 (CEPEC 107062). Camacã: RPPN Serra Bonita, 28 Oct 2005, immfr., A.M. Amorim et al. 5385 (CEPEC 110429); RPPN Serra Bonita, 25 Apr 2008, prefl. postfl., A.M. Amorim et al. 7312 (CEPEC 122987); RPPN Serra Bonita, 9 Dec 2006, st., R.A.X. Borges et al. 359 (CEPEC 114859); RPPN Serra Bonita, 9 Nov 2005, immfr., Paixão et al. 639 (CEPEC 129944); Fazenda Serra Bonita, 1 Feb 2004, prefl. fl., W.W. Thomas et al. 13761 (CEPEC 102146). Camamu: Rodovia BA-650, Camamu-Travessão, 22 Feb 2000, postfl., J.G. Jardim et al. 2758 (CEPEC 88619). Castro Alves: Pedra Branca, Serra da Gibóia, 8 Dec 1992, st., M.A. Nadruz & S.J. Mayo 841 (K 000302915). Ilhéus: Parque Municipal de Boa Esperança, 25 May 2001, st., L.C.B. Costa et al. 198 (CEPEC 91498); Distrito de Castelo Novo, Rodovia BA-001 trecho Ilhéus-Itacaré, 17 Sep 1995, st., C.S. Florêncio 40 (CEPEC 67341); Campus da Universidade Estadual de Santa Cruz (UESC), 14 Mar 1996, immfr., L.A. Mattos-Silva et al. 3408 (CEPEC 75881); Rio do Engenho, Fazendo Theobroma, 13 Jan 2002, fl., B.R. Santos 4518 (CEPEC 100038); Mata de Esperança, 17 Sep 1994, st., W.W. Thomas et al. 10520 (CEPEC 63327). Itacaré: ca. 8 km SW of Itacaré, 31 Jan 1977, st., R.M. Harley et al. 18446 (CEPEC 19744, K 000302937); Praia da Ribeira, 20 Apr 1989, postfl. immfr., L.A. Mattos-Silva et al. 2712 (CEPEC 45127, K 000302934); km 3 na rodovia que liga a Rodovia BR-101 a Itacaré, 24 Apr 1991, postfl. immfr., S.J. Mayo et al. 766 (CEPEC 50460, K 000302923); 2-3 km ao sul de Itacaré, 25 Apr 1991, postfl. immfr., S.J. Mayo et al. 772 (CEPEC 50444, K 000302923). Jequié: road to Serra dos Brejos, 6 Feb 2004, W.W. Thomas et al. 13897 (CEPEC 102945). Jussari: Serra do Teimoso, Fazenda Teimoso, 18 May 1991, st., S.J. Mayo et al. 843 (CEPEC 50645, K 000302916); Serra do Teimoso, 10 Feb 1998, fl., W.W. Thomas et al. 11801 (CEPEC 79524). Nova Viçosa: Costa Atlântica, 8 Dec 1984, fl., G. Hatschbach & J.M. Silva 48740 (K 000302944). Porto Seguro: km 12 da rodovia Porto Seguro a Eunápolis, 4 Apr 1972, fl., A. Eupunino 260 (CEPEC 8430, K 000302935). Senhor do Bonfim: Serra da Jacobina, 1 Mar 1974, prefl. fl., R.M. Harley et al. 16571 (CEPEC 11042, K 000302946). Tancredo Neves: ca. 14.1 km de Tancredo Neves, 12 Sep 2005, postfl., A.M. Amorim et al. 5213 (CEPEC 110257). Ubaitaba: km 5 a 15 da rodovia BR-101 ao sul de Ubaitaba, 18 Nov 1971, T.S. Santos 2196 (CEPEC 8095). Una: 4 km N of Comandatuba. 25 Jan 1977. st... R.M. Harley et al. 18267 (CEPEC 19269, K 000302945); 6 km E of Una, along old road to Pedras, 26 Jan 1977, fl., R.M. Harley et al. 18274 (CEPEC 19746, K 000302942); Reserva Biológica do Mico-Leão (IBAMA), 28 Jul 1994, st., J.G. Jardim et al. 524 (CEPEC 62019); área vizinha a Reserva Biológica Una, 7 May 1996, st., M.A. Nadruz et al. 1196 (CEPEC 69407); Serra Javi, 10 Mar 1986, fl., T.S. Santos et al. 4224 (CEPEC 39425). Uruçuca: Serra Grande, 6 May 1996, st., M.A. Nadruz et al. 1194 (CEPEC 69408). Valença: estrada de Valença para Guaibim, 26 Jun 2004, fr., P. Fiaschi et al. 2362 (CEPEC 100545).

# 4.2.2 *Monstera praetermissa* E.G.Gonç. & Temponi, Brittonia 56: 72

Type: Brazil, Bahia, município de Una, 8.8 km east of BR-101 on road to São José and Una. 15°08′ S, 39°15′ W, 28 Oct 1993, *W.W. Thomas, J. Jardim, S. Sant'Ana 10179* (holotype CEPEC not seen, isotype K 000400560).

Fig. 2 (See also Andrade et al. 2013, Fig. 4c–d for populations in Ceará state).

HABIT. Hemi-epiphyte, root climber. STEM. Juvenile plant: internodes 2-3 x ca. 0.5 cm, elliptic in section, flattened against substrate, exposed side rather dark green and lustrous, minutely rugulose-verruculose, the verruculae concolorous with the rest of the epidermis, new branching shoots starting with ca. 4 black-marcescent cataphylls clasping stem. Adult plant: internodes ca. 3 x 1.2 cm, similar in colour and texture to juvenile stem. PETIOLE. Juvenile plant: 11-24 cm long, shorter than blade, smooth, green, lustrous, free petiole and geniculum sulcate above with angled margins; sheath up to threequarters as long as whole petiole, margins very rapidly marcescent and deciduous, withering to brown-black membranaceous fragments. Adult plant: 31-37 cm long, geniculum 2-3 cm long; sheath always turning blackbrown membranaceous and marcescent, reaching almost to geniculum. LEAF BLADE. Turning dark brown when dried. Juvenile plant: 19.5-40 x 7-19.5 cm, narrowly ovate to ovate, strongly unequal, falcate, apex acute-acuminate, base acute to subacute on each side, or truncate to subacute on wider side and acute on narrower side, dull to glossy dark green above, paler and lustrous-glossy below with whitish stomata, main veins concolorous and impressed above, midrib paler than blade below, major veins prominent below, blade softly coriaceous; perforations 0-5, usually absent in leaves narrower than 5 cm, elliptic or sometimes distorted, starting next to midrib and larger ones usually extending to the leaf margin, interprimary fields always with no more than 1 perforation. Adult plant:  $38-50 \times 18.5-$ 32 cm, 1.4-1.6 times longer than wide, ovate to broadly ovate, strongly unequal, falcate, apex acute-acuminate. base truncate on wider side, acute on narrower side, rather dark glossy green above, paler and lustrous below, primary lateral veins 5-8 on wider side, impressed and concolorous above, prominent and paler than blade below, forming inconspicuous submarginal collective vein, fine venation reticulated; perforations ca. 4-10, narrowly elliptic, most extending for the entire width of the half-lamina, starting usually very close to midrib and terminating at leaf margin, very often breaking through to form an irregularly pinnatisect leaf, at least on one side; in a single series, interprimary fields always with no more than 1 perforation. INFLORESCENCE. 1-3 in each floral sympodium, prophylls and cataphylls of floral sympodium similar in colour to leaf blade when dried, ca. 11 cm long; peduncle 8-13 cm long; spathe 8.4-8.5 cm long, 0.6-0.8 times as long as peduncle, at anthesis broadly ellipsoid and opening widely, creamy yellow to yellow or orange; spadix  $5.7-6.9 \times 1.1-2.2$  cm, 3.1-5.3 times longer than diam., 0.5-0.6 times as long as peduncle, ca. 0.7 times as long as spathe, cylindric, yellow or cream yellow at anthesis; fertile gynoecia with flattened polygonal style apex 0.35-0.43 × 0.26-0.42 cm when seen from above, stigma  $0.22-0.24 \times 0.05-$  0.06 cm, linear, oriented longitudinally, sessile to subsessile, stigmatophore 0.04–0.05 cm high. INFRUCTESCENCE. Cylindric, erect, mature fruits yellow to orange.

Common Names: none recorded.

Habitat: Climbing on tree trunks and branches in humid tropical forest, disturbed or primary.

Distribution: Brazil: Acre, Bahia, Ceará, Espírito Santo, Goiás, Minas Gerais, Paraná, Pernambuco, Rio de Janeiro, São Paulo states (Andrade & Mayo 2013). Altitude: 100–300 m.

Phenology: fertile material collected in March and October

Preliminary conservation status assessment within Bahia: Extent of Occurrence: Least Concern (LC); Area of Occupancy: Least Concern (LC). Based on 8 specimens from 8 localities.

Etymology: The authors allude to the fact that the species had not been previously recognized as new; "praetermissa" means "unnoticed".

#### Commentary:

Monstera praetermissa is easily distinguished from M. adansonii in vegetative material. The mature plant is generally smaller and the leaves turn dark brown to blackish on drying. The internodes are more slender, dark green and lack the numerous tiny pale dots characteristic of *M. adansonii*. Instead, the internode epidermis in M. praetermissa is verrucate but inconspicuously so because the verrucae are the same dark green colour as the rest of the surface. The petiole sheath is rapidly marcescent, turning into dark membranaceous fragments which are eventually deciduous. The leaf blade perforations are relatively larger and fewer, nearly always reaching the margin and rupturing it to make the leaf usually partially pinnatifid, at least on the wider side of the highly asymmetric and usually falcate blade. The mature berries are yellow-orange.

#### Material examined:

Brazil. Bahia. Ilhéus: Rodovia Ilhéus-Itabuna, a 1 km da entrada do CEPLAC, 6 Mar 2001, st., *E.G. Gonçalves et al.* 785 (CEPEC 87193). Itanhém: Fazenda Pedra Grande, 16.2 km west of Itanhém on road to Batinga, 18 Mar 2001, prefl., *W.W. Thomas et al.* 12343 (CEPEC 88065). Jussari: RPPN Serra do Teimoso, 2 May 2004, st., *J.L. Paixão et al.* 348 (CEPEC 99343). Porto Seguro: RPPN Estação Veracel, 5 Mar 2010, immfr., *G.M. Carvalho & P.M.C. Gouvêa* 250 (CEPEC 127699). Una: km 8 na rodovia São José da Vitória-Una, 14 May 1991, st., *S.J. Mayo et al.* 823 (K 000303021); Una: km 6–7 na rodovia São José da Vitória-Una, 14 May 1991, st., *S.J. Mayo et al.* 835 (K); 8.8 km east of BR-101 on road to São José and Una, 28 Oct 1993, prefl. fl., *W.W. Thomas et al.* 10179 (CEPEC not seen, K 000400560). Wences-

lau Guimarães: Condomínio União, na rodovia Teolândia-Jaguaquara entre Cocão e Nova Esperança, 1 Jun 1991, st., *S.J. Mayo & F.A. Carvalho 878* (K 000303019).

# 4.2.3 Nomenclatural note on *M. adansonii* subsp.

In order to provide a uniform proposal for the infraspecific nomenclature of *M. adansonii*, we feel it necessary to change the varietal status of this taxon to subspecies rank, even though we have not studied it in detail; Madison's (1977) taxon concept is fundamentally morphogeographical, making subspecies status appropriate under our current, albeit very imperfect, understanding of the taxon

# Monstera adansonii Schott subsp. laniata (Schott) Mayo & I.M. Andrade, stat.nov.

≡ Tornelia Ianiata Schott, Oesterr. Bot. Z. 8: 179 (1858).
 ≡ Monstera pertusa var. Ianiata (Schott) Engl. in C.F.P. von Martius & auct. suc. (eds.), Fl. Bras. 3(2): 113 (1878).
 ≡ Monstera adansonii var. Ianiata (Schott) Madison, Contr. Gray Herb. 207: 38 (1977). Type: Costa Rica, Candelaria, Oersted 15795 (holotype C, not seen).

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# 6 Supplementary Material

The following files are avaliable as supplementary material at the *CATE Araceae* website (Haigh 2013): –

 a. discrim\_R.txt: a text file containing the discriminant function coefficients from the linear discriminant analysis of untransformed vegtatove variables, together with the corresponding data from the two

- leaves of the type specimen of *M. adansonii* subsp. *blanchetii*.
- B. R script for calculating discriminant function values of blanchetii type specimen leaves.txt: a text file with the R code to calculate the d.f. values using file "a" as input.
- Monstera characters defined.pdf: an illustrated glossary for the definition of the characters used in the morphometric analyses.
- d. Raw\_Data\_Matrix\_Final.xlsx: the basic data matrix from which the observed and derivative variables were extracted.
- e. Maximum\_Characters\_Final.xlsx: the data for the 15 combined vegetative and reproductive variables.
- Vegetative\_Final.xlsx: the data for the 8 vegetative variables.
- g. Reproductive\_Final.xlsx: the data for the 7 reproductive variables.