Evolution of the family Araceae in the tropics:

Diversification rates, biogeography, and morphological evolution at different taxonomic and geographic scales

By

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TABLE OF CONTENT

ABSTRACT

This research analyzes several aspects of the systematics and evolutionary biology of the family Araceae at different taxonomic and geographic scales. First, we investigated the patterns in the diversification rates for major clades in the family in the context of the order Alismatales. We found evidence for a complex pattern including several different rate regimes within the Araceae decoupled from the background rate. Main shifts towards higher in speciation rates are located in the subfamilies Aroideae, Pothoideae, and Monsteroideae. These rates may be associated with floral characters, pollination interactions, and epiphytism. Second, we studied the subfamily Monsteroideae, and produced a robust phylogenetic hypothesis including all genera and ca. 100 taxa to test the current infrafamilial classification. We found support for the monophyly of three major clades and only seven of twelve genera within Monsteroideae. We investigated the historical biogeography of this group and estimated a Laurasian origin for the subfamily. The continental disjunction between *Monstera* and *Amydrium* + *Epipremnum* is product of a Boreotropical flora, while the other disjunctions (species of *Spathiphyllum* between South America and South East Asia; and *Rhaphidophora* South East Asia and Africa) are most probable product of long distance dispersal. Third, we studied the Neotropical genus *Monstera*. Due to the lack of genomic tools for phylogenetics in tropical aroids, we used a genome skimming approach to recover molecular data from three different DNA regions, the plastid, mitochondrial and nuclear ribosomal DNA. Despite low variation (ca. 1%) in plastome sequences, we recovered a strongly supported phylogenetic hypothesis for *Monstera,* which does not support the current infrageneric classification.

Finally, we focused in the taxonomical aspects of the genus *Monstera*. We used 108 morphological, anatomical and geographical traits from about 4200 herbarium specimens and living plants to produce a web-based interactive tool for the identification of species in the genus. In the process we discovered and described two new species of *Monstera* from Panama and Costa Rica.

Chapter 1

Rates of diversification and patterns of morphological evolution of the tropical family Araceae and ther order Alismatales at a global scale

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ABSTRACT

The family Araceae (order Alismatales) is one of the most diverse monocot families with about 3500 described species, in contrast with the rest of the order, which includes twelve other families and ca. 500 species. The family is especially abundant in the tropics, and exhibits remarkable morphological, anatomical, ecological, and geographical variation. The highest diversity of the subfamily Aroideae (ca. 2000 species) has been hypothesized to be product of an increase in the speciation rates associated with a set of morphological characters (e.g., unisexual flowers, inaperturated and exineless pollen, chemical defense). Despite several recent phylogenetic studies, we still know rather little about the dynamics of lineage and species diversification across the family, or about the underlying drivers of diversification. We explored diversification rates of the major clades in Araceae compared to the rest of the order Alismatales using two datasets: 1) a fossil calibrated phylogeny using Bayesian relaxed molecular clock methods (two genes, ca. 230 taxa); and a supermatrix (ten genes, ca. 950 taxa). We used a Bayesian approach (BAMM), to evaluate the dynamics of the diversification rates in Alismatales. The two-gen dataset showed evidence for a different rate regime located in "True Araceae" clade. The ten-gen dataset revealed a more complex dynamics in rates of diversification with several clades presenting decoupled regimes from the background process. Finally, we analyzed the evolution of the potential characters associated with the evolutionary rates in Araceae. Although high rates in the subfamily Aroideae seems to be associated with traits previously hypothesized, other traits like epiphytism but also geography have play an important role in the diversification of the family.

Keywords

Araceae, Alismatales, BAMM, character evolution, diversification rates, speciation rates

INTRODUCTION

The angiosperm order Alismatales is a monocot clade composed of 13 families and ca. 4000 species (Stevens 2001; Iles et al., 2013) that is sister to the rest of the monocots, excluding Acoraceae (Graham et al., 2006; Iles et al., 2013; Ruhfel et al., 2014; Zeng et al., 2014). Earlier molecular phylogenetic evidence has confirmed the inclusion of Araceae and Tofieldiaceae in the traditional concept of Alismatales (Les et al., 1997; Chase 2004; Graham et al., 2006), and yet the phylogenetic relationships within Alismatales are still controversial (Iles et al., 2013; Les & Tippery 2013; Petersen et al., 2015). Three main clades are usually recovered: Araceae, Tofieldiaceae, and the rest of the Alismatales ("alismatids"), but strong support is lacking for the relationships among these clades. The most common and robust topologies among different studies show Tofieldiaceae as sister to all remaining Alismatales, including Araceae (Iles et al., 2013; Les & Tippery 2013).

Most families of Alismatales are mostly aquatic plants distributed worldwide. Tofieldiaceae with four genera and ca. 20 species is a terrestrial family distributed mainly in the northern hemisphere, though it has also reached high elevations in the Andes, and the Guyana Highlands (Campbell 2008; Azuma & Tobe 2010; Remizowa et al., 2011). The remaining eleven families of Alismatales (exluding aroids) collectively contain 56 genera and about 500 species (Les & Tippery, 2013). These have diversified in both freshwater (e.g. Hydrocharitaceae, Les et al., 1997) and marine environments (e.g. Potamogetonaceae, Zosteraceae, Posidoniaceae; Les et al., 1997) through the entire world.

One family of Alistmatales, the Araceae, is significantly more diverse than all the others combined, with around 3,500 described species (or perhaps as many as 4,000; according to Boyce & Croat [2014]). Aroids contain approximately 85% of the diversity in the order, and their diversification has occurred especially in terrestrial, rather than aquatic, environments (Croat, 1988; Mayo et al., 1997). The family is currently divided into eight subfamilies. One of these, subfamily Aroideae, contains ca. 50 genera and 2000 species, more than all the other subfamilies combined. Outside the Aroideae, most of the remaining Araceae diversity is concentrated in one megadiverse genus of ca. 1,000 species, *Anthurium*, which is a member of the subfamily Pothoideae (Croat 1983; 1986; Boyce & Croat; 2014; Carlsen et al., 2014).

The family Araceae is one of the most morphological and ecologically diverse monocot families, especially diverse in the tropics (Mayo et al., 2007). Araceae includes geophytic, terrestrial, hemiepiphytic, epiphytic, rheophytic and also a few aquatic plants, including free-floating species (Croat, 1988; Grayum, 1990; Mayo et al., 2007). Despite several recent molecular phylogenetic studies (Cabrera et al., 2008; Cusimano et al., 2011; Chartier et al. 2014; Henriquez et al., 2014) there are still many problems in generic delimitation and relationships within Araceae. The most recent classification recognizes eight subfamilies, including the former family Lemnaceae, now considered to be Araceae subfamily Lemnoideae (Cusimano et al., 2011). All subfamilies have been shown convincingly to be monophyletic except Aroideae (Cusimano et al., 2011; Chartier et al., 2014; Henriquez et al., 2014). Nevertheless, Aroideae seems to be a

morphologically consistent group defined mainly by the presence of unisexual aperigonated flowers, and inaperturate pollen with reduced exine (ektexines). The main issues concerning phylogenetic reconstruction in Aroideae relate to the backbone of the clade, and exact the position of certain problematic genera such as *Montrichardia*, *Callopsis*, *Anubias Zantedeschia,* and *Calla* (the latter of which curiously has bisexual flowers), (Cusimano et al., 2011; Chartier et al., 2014; Henríquez et al., 2014). The monotypic genus *Calla* is distributed in the temperate zone of United States and has been consistently include in the subfamily Aroideae in all molecular analysis using plastid data, despite the fact that morphologically it does not resembles any members of this subfamily. Chartier et al. (2014) using the nuclear gene PHYC, recovered *Calla* as sister to the rest of the Aroideae, so the position of this genus should still be considered ambiguous.

Perhaps the most distinguishable feature of Araceae is its inflorescence organization. Unlike many other groups in Alismatales, Araceae have very reduced flowers, organized in compact inflorescences, that are specialized for a variety of pollination strategies, including food rewards, mating mutualism, ovipositing mutualism, and deception (Gibernau et al., 2010; Bröderbauer et al., 2012; Chartier, 2011). Trapping inflorescences, which usually involve deceptive pollination, have evolved multiple times in at least 27 genera, mainly in the subfamily Aroideae (Bröderbauer et al., 2012). Several patterns have been described regarding the evolution of aroid flowers, and pollination evolution (e.g. Chartier et al., 2014; Cusimano et al., 2011). Two main types of inflorescences have been described, hermaphroditic inflorescences with bisexual

flowers, present in most of the subfamilies (Orontioideae, Lemnaceae, Pothoideae, Monsteroideae and Lasiodeae); and monoecious inflorescences with unisexual flowers, which are present in the *Stylochaeton* clade and Aroideae (Mayo et al., 1997; Cusimano et al., 2011). The role of inflorescence and flower structure, together with plant-pollinator relationships, as a driver of species diversification in the family has not been explored quantitatively, but hypotheses have been proposed for how inflorescence structure and pollination might have played a role in affecting diversification rates.

Hesse (2006a; 2006b) hypothesized that the evolution of the monoecious inflorescence type, together with other traits are responsible for an increased rate of speciation in Aroideae. The other characters Hesse argued are part of the key innovation model are: 1) switch from perigonated to aperigonated flowers; 2) from physical (calcium crystals, sclereids) to chemical defense (laticiferous, biforines) against herbivory (Hay & Mabberley, 1991); 3) from aperturated to omniaperturated (inaperturated) pollen; and 4) from developed to reduced exines with a polysaccharide outer exine layer instead of sporopollenin. Pollen with reduced exine (exineless pollen) has been described from other monocot groups like Zingiberales (Kress et al., 1978), and other Alismatales like Cymodoceaceae or Hydrocharitaceae (Chanda et al. 1988; Tanaka et al., 2004; Furness & Banks, 2010). This particular feature seems to be associated to pollination in humid and wet environments, and at least for Alismatales the presence of exineless pollen is always correlated with the presence of omniaperturate pollen (Furness & Banks, 2010).

Hesse (2006a; 2006b) further argued that all these traits are "connected by causal relationships", and may followed on from the loss of bisexual flowers in Aroideae by the early Tertiary. His hypothesis was based on the idea that that these changes are associated (as a pre-requisite or a result) with the pollination behavior observed in most of the species of the clade. Species of the Aroideae (as for most of Araceae) live in humid and wet environments (Mayo et al., 1997), and have a short time span in which to achieve successful pollination, thereby leading to: 1) pollen with short viability, 2) rapid germination of pollen tubes; and 3) brief periods of stigma receptivity (Hesse, 2006a; 2006b; Barabe et al., 2008). Other authors, in contrast, have proposed that traits like epiphytism and pollinator interactions could have contributed to some of the diversity found in Aracaceae, especially outside of subfamily Aroideae. For example, Madison (1978) suggested that the large number of species in *Anthurium* might be the result of two adaptive radiations, the first one related to the diversification of pollination interactions with bees and flies, and the second related to the epiphytism. That paper, like so many others, was written without the presence of a robust and objective phylogenetic reconstruction for the family.

The objective of this study is to investigate the patterns in the diversification rates within the entire order Alismatales, particularly in the family Araceae. We are also interested in evaluating the effect of taxon sampling in documenting rate shifts by using data sets of differing size. Additionally, we investigated the evolution of some morphological characters that may be associated with increases or decreases in rates of diversification rates.

METHODS

DNA sampling and data matrix assembly. We built two molecular datasets in order to perform analyses for this study. The first one included 229 species representing all families and 56 genera in the order Alismatales, and seven outgroups representing Petrosaviales, Acoraceae, Amborellales, Ceratophyllales, Chloranthales and Austrobailetyales. This matrix is composed of two molecular markers, *matK* and *rbcL*, mostly based on data from Cabrera et al., (2008) for Araceae, and Les et al. (1997) for Alismataceae (but see Supplementary **Table S1**, for a complete list of GENBANK accession numbers). The second dataset is a supermatrix that includes 946 species sampled across Alismatales and 10 sparsely sampled molecular markers obtained from GenBank (**Table S1**), but also from our extensive studies in the Araceae subfamily Monsteroideae (CHAPTER 2).

Sequences were downloaded and organized using Geneious 8.0 (Biomatters, http://www.geneious.com, Kearse et al., 2012). Each gene was aligned individually using an initial alignment was performed in MAFFT v7 (Katoh et al., 2002, Katoh, 2013) followed by two subsequent refinements using Muscle v3.8.31 (Edgar 2004). All alignments were visually inspected and manually adjusted in Geneious 8.0 using protein translation for the coding regions. For the two-gene dataset we used PartitionFinder (Lanfear et al., 2012) to select the best-fit partitioning schemes and models. However, because not all the models are available in RaxML (Statamakis, 2006) or BEAST v1.8 (Drummond & Rambaut, 2007, Drummond et al., 2012) we performed a second run

restricting PartitionFinder to only the models RaxML and BEAST could apply. For the initial data blocks in PartitionFinder we allocated nucleotides in protein-coding genes (*rbcL, matK*) according to whether they belonged to the first, second or third codon position, and all the other markers as independent data blocks. The PartitionFinder analysis resulted in five partitions for the two-gene dataset; the models and partition schemes are shown in **Table 1**. Since RaxML does not allow for different models, and because our 11-gene dataset has a great amount of missing data, we assigned every molecular marker as a different partition.

We performed two maximum likelihood (ML) searches for each dataset using RAxMLv8.4.2 (Stamatakis, 2014) as implemented in CIPRES (Millet et al., 2010). The first ML search was performed with all data unpartitioned, and the second one was performed using the data partitioning schemes from PartitionFinder. We inferred the maximum likelihood trees using 100 independent searches for the two-gen and 20 for the ten-gene datasets. Bootstrap support values were obtained by 1000 independent throughout searches instead of using the fast bootstrap option in RaxML. For our 10-gene supermatrix analysis we also ran a constrained analysis using clades recovered and strongly supported in previously published studies (Cusimano et al. 2011; Les & Tippery, 2103; and Henriquez et al., 2014; Ross et al., Unpublished) to reflect the most currently understood phylogenetic relationships in Alismatales. Briefly, we defined our “major” clades in Alismatales and constrained the tree so these clades are monophyletic. The clades are and constraints are: Tofieldiaceae as sister to the rest of Alismatales; the eight aroid subfamilies (Gysmonstachyoideae, Orontioideae, Lemnoideae, Pothoideae,

Monsteroideae, Lasiodieae, Zamioculcoideae and Aroideae); and two clades in alismatids (tepaloid and petaloid clades).

Molecular dating. To estimate ages of nodes, we used the two-gene dataset for Bayesian molecular dating using BEAST 1.8 (Drummond et al., 2012), and employed eight calibrations points following recommendations of Sytsma *et al.,* (2013) for the priors on the calibrations points. The two genes were partitioned as suggested by PartitionFinder. We performed a preliminary analysis using different prior combinations to define the best parameters for our dataset. Evaluation of the ucld.stdev and coefficient of variations under uncorrelated lognormal relaxed clock showed that our data do not fit a strict molecular clock. We also evaluated the differences between choosing a pure birth (Yule) prior versus a Birth-Death prior for the tree. We performed three analyses; in the first analysis the topology was not constrained (except by the fossil calibrations); secondly, we constrained the position of Tofieldiaceae as sister to the rest of Alismatales; and finally we constrained the entire tree to reflect the most updated phylogenetic relationships in Alismatales. In all analysis we used a pure birth (Yule) prior for the tree, and rate variation across branches (clock prior) as uncorrelated and log-normally distributed. For all analysis we used lognormal priors in the calibrations points with mean=1 and SD 0.75, except for the root where we used a conservative uniform prior (see fossil calibrations section). For every analysis we ran two independent chains of 75 000 000 generations, sampling every 10 000 generations in BEAST v1.8 as implemented in CIPRES, or more until they reached an effective sample sizes (ESSs) >200. Results from BEAST were checked for convergence and ESSs on Tracer, version

1.6 (http://beast.bio.ed.ac.uk/Tracer). We concatenated the trees using LogCombiner version 1.7.2 (http://beast.bio.ed.ac.uk/LogCombiner) using a 20% burn-in fraction, and we resampled the posterior distribution to obtain a final sample of 10000 trees. The final chronogram was constructed using the maximum clade credibility tree with mean node heights in TreeAnnotator version 1.7.2 (http://beast.bio.ed.ac.uk/TreeAnnotator).

Fossil Calibrations. We evaluated all the reliable fossils available for Alismatales based on previous studies (Nauheimer et al., 2012, Iles et al., 2015), and chose nine that covered a wide range of clades and were assignable with some certainty to a clade in Alismatales (**Table 2**). For the root we used a uniform prior (120-160 Ma) comprising some of the youngest and oldest ages estimates for Angiosperm (e.g. Bell et al., 2010; Magallón & Castillo, 2009;). For the crown node of monocots we used a constraint similar to Nauheimer et al. (2012) but a lognormal distribution so the median agrees with the age of the fossil pollen *Liliacidites* sp. A (Doyle & Hickey, 1976). Within the Alismatids we chose the oldest known *Stratiotes* fossil from the top of the Paleocene (56.0 Ma) (Sille et al., 2006) to constrain the minimum age of the crown clade of Hydrocharitaceae. The fossil of *Aponogeton harryi* from the Late Cretaceous (Lower Campanian, 82-81Ma) in United States (Hicks, 1993) was used to calibrate the stem node of Aponogetonaceae (= crown node alismatids).

For Araceae, we assigned the fossil of *Spixiarum kipea* (Coiffard et al., 2013) from the upper Cretaceous (113 Ma) in Brazil to the stem node of Orontiodeae (Proto-Araceae). Friis et al., (2010) presented two fossils named “Araceae fossil sp. A” and

"Araceae fossil sp. B", from the early Cretaceous (110 Ma) in Portugal. They argued that it represents a taxon with bisexual and unisexual flowers respectively. As a conservative approach we assigned both of these fossils to the crown node of a clade comprising Lemnoideae and the rest of Araceae (sensu Cusimano *et al.,* 2011). We assigned *Petrocardium cerrejoense* from the Mid to Late Paleocene (56-61.6 Ma) in Colombia (Herrera et al., 2008) for the crown node of Pothoideae. The fossil pollen *Lasioideaecidites* from the Late Cretaceous (70-75 Ma) in Siberia (Hofmann & Zetter, 2010) represents the subfamily Lasioideae. We used this fossil to calibrate the stem node of Lasiodeae (Podolasia clade [*sensu* Cusimano *et al.,* 2011]). For the stem node of the *Heteropsis* + *Rhaphidophora* clades (in the subfamily Monsteroideae) we assigned fossil *Rhodospathodendron tomlinsonii*, from the Late Cretaceous (66 Ma) (Bonde, 2000). For the stem node of the *Typhonodorum* clade (sensu Cusimano et al., [2011]) we used *Nitophyllites zaisanicus* from the Palaeocene (55.8 Ma) in Kazakhstan (Iljinskaja, 1986; Wilde *et al.,* 2005).

Molecular dating of the supermatix. Due to the size of the supermatrix a Bayesian molecular dating approach was not possible. Instead we used penalized likelihood (PL, Sanderson, 2002) as implemented in the function 'chronos' from the package APE (Paradis et al., 2003) in R (R Development Core Team, 2008). Because our topology differences between two and ten-gene, and constrained and unconstrained analysis are not at the major clades but at the generic level -were not strong support has been found in any study-, we constrained the ten-gene dataset to our two-gene topology from BEAST in all subsequent analyses. As an input tree for PL we used the maximum likelihood tree derived from the constrained analysis described above. As calibration

points we used the age estimates from our two-gene BEAST analysis for each subfamily in Araceae, and each family in the rest of Alismatales. For lambda we tested values of 0.1, 0.25, and 0.5 to see which values will give us the closest result to our BEAST analysis.

Diversification Analysis. To investigate shifts in diversification rate through time and among lineages we performed analyses using the software BAMM v2.1 (Rabosky, 2014). When taxon sampling is incomplete and non-random BAMM requires a file in which every tip is assigned to a clade and the number of species that it represents is given. Numbers of described and currently accepted species for each genus of Araceae were obtained from Boyce & Croat (2014), and we used numbers from Les & Tippery (2013) for Alismataceae. Additional information was obtained from the *World Checklist of Selected Plant Families* (WCSP, Royal Botanic Gardens, Kew). Because of some issues concerning taxonomic uncertainty and higher-level classification within the family Araceae we assigned ambiguous genera to unambiguous clades strongly supported in our molecular analysis or in previous studies. We used two different clade schemes, the first scheme (Clades1) used recognized subfamilies within Araceae, but only considered families for the rest of Alismatales; the second scheme (Clades2) used all of the highly supported clades from Cusimano et al. (2011) for Araceae, but again only families for the rest of Alismatales. We performed two different analyses in BAMM for each of the two datasets and the two sets of clade designations. The first analysis used a MEDUSA-like approach implemented in BAMM, the second analysis used the complete BAMM model. We performed preliminary runs with poissonRatePrior of 1, 0.5 and 0.1 respectively, and

allowing shifts to occur on all branches (minCladeSizeForShift = 1). For each analysis we completed 50 million generations of Markov Chain Monte Carlo (MCMC) runs with poissonRatePrior of 1 for the two-gene dataset, and 100 million and poissonRatePrior of 0.5 for the ten-gene dataset, sampling parameters every 10000 generations. Results were summarized using the packages Coda (Plummer et al., 2006) and BammTools (Rabosky et al., 2014) in R. We assessed convergence of BAMM runs by computing effective sample sizes of log-likelihoods, numbers of processes, and evolutionary rate parameters using CODA. For every analysis we evaluated the 95% credibility set of shifts configurations, the best shift configuration and used Bayes Factors to evaluate rate heterogeneity and significant shifts in our dataset.

Evolution of characters potentially associated with diversification. Flower characters. We recorded data associated with flower traits proposed by others as potential key innovations and possible drivers of diversification in the subfamily Aroideae. The traits considered were: flower sexuality, presence of perianth, pollen aperture, exine presence, pollen size and shape, and pollen starch content. Data from aroid pollen was obtained mainly from Grayum (1990) for Araceae, but from many other sources for Alismatales (e.g. Chanda et al. 1988; Kubitzki, 1998; Tanaka et al., 2004; Furness & Banks, 2010). For pollen size we used the longest and shortest distances in polar view, and the diameter for spherical pollen shapes. Because there are many factors affecting pollen size (e.g. hydration, folding, angle of the photograph) we used mean value reported in the literature or calculated mean values per genera after recording as many species has possible. Finally, the flower traits associated with Aroideae were tested

for correlated evolution using the discrete module from BayesTraits (Pagel, 1994; Pagel & Maede, 2006). We tested flower sexuality against, perianth presence, pollen aperture, and exine reduction. We used the MCMC method with 50 million generations, and likelihood ratio for model testing. We also tested contigent evolution in these traits as described in (Pagel, 1994).

Ecology and Life form. Some superficial traits describing ecological and habitat preferences were also coded for each genus. Climatic region was coded as either tropical or temperate; seasonality was coded as evergreen or seasonally dormant (we included annual plants from Alismatales in this category); life form was coded in several ways based on categories defined by Croat (1988) and Mayo et al. (1997). First we coded the habitat as aquatic free-floating, aquatic rooted (including helophytes and submersed aquatics), terrestrial (including geophytes and lithophytes), or epiphytes (including hemiepiphytes). Secondly, we coded the growth form (shoot architecture) as either acaulescent, caulescent (and terrestrial), rhizomatous, tuberous, or climbing stems. Discrete characters were reconstructed using a stochastic mapping Bollback (2006) and the rerooting method as implemented in the R package phytools (Revell, 2012). Continuous characters (size) were reconstructed using ML approach as implemented in the function contMap from R package phytools (Revell, 2012).

RESULTS

Maximum likelihood analyses. The two-gene and ten-gene alignments contained 3150 bp (19% missing data) and 10343 bp (76% missing data) respectively, and the

maximum likelihood analyses from partitioned and unpartitioned datasets recovered the same topology with only slight differences in branch support (**Figures 1 & 2**). Topologies from the two different datasets did not differ for the major clades in Alismatales (**Figures 1 & 2**), but did show differences in the generic relationships within certain clades. The main differences among our ML topologies and Cusimano et al. (2011) were the position of the aroid genus *Montrichardia,* the aroid tribe Spathiphylleae, and the exact intergeneric relationships within the clades Lasioideae, Spathicarpeae, Schismattoglotideae and Caladieae, although no strong support was found for these alternative relationships in the previously published trees or in our new analyses. We recovered Tofieldiaceae as sister to the rest of the Alismatales in the two-gene ML but bootstrap support was low. Within the alismatids, all families as proposed by Les & Tippery (2013) and Iles et al. 2013 were recovered as monophyletic, but family relationships did not agree completely with those of Iles et al. (2013), particularly with regards to the positions of Aponogetonaceae, Scheuzeriaceae, Posidoniaceae, Cymodoceaceae, and Ruppiaceae.

Molecular dating. We based our results on the BEAST analysis with the Tofieldiaceae constraint, but ages for major clades from the three analyses and the PL chronogram are shown in **Table 3.** Molecular clock analysis showed our data does not fit a strict molecular clock, so we used the lognormal relaxed clock. The BEAST analysis without any topology constraint (except by fossil calibrations) did not recover Tofieldiaceae sister to the rest of the Alismatales; however age estimation from the major clades did not differ greatly from the constrained analyses (**Table 3**). The age for the

crown of Alismatales is 129.6 Ma (CI 122.8-136.5) with a stem node age of 134.3 Ma (CI 127.6-141.7). Tofieldiaceae, alismatids and Araceae crown ages are 73.7, 113.6, and 121.2 Ma respectively. All stem nodes for the aroid subfamilies are dated well into the Cretaceous, whereas crown nodes for these clades are closer to the K/T boundary except for Orontioideae (52 Ma), and Lasioideae (24.1 Ma) (**Table 3**). Our penalized likelihood approach agreed with ages of the BEAST analysis for major clades and subfamilies in Araceae, but it was less accurate for clades far from the root of the tree (e.g., clades Thomsonieae and Caladieae, **Table 3**).

Diversification. *Two-gene dataset.* All the BAMM analyses using the two-gene dataset produced very similar results regarding the speciation, extinction and diversification rates, and the best shift configuration, so we will focus our discussion on the BAMM model with the clade set 1 (**Table 4 & 5, Figure 3**). The different models and clade sets produced different number of shift configurations in the 95 % credibility interval; however, one shift configuration with a single shift in diversification rates within Alismatales was recovered consistently through all the analyses (**Figure 3**). This shift in diversification rates is located along the stem of the "True Araceae" clade with probabilities between 0.45-0.8 and Bayes factors >17000. The crown Araceae showed mean speciation rates between 0.46-0.577, whereas the crowns of alismatids and Tofieldiaceae showed rates of 0.053-0.055 and 0.054-0.056 respectively (**Tables 4 & 5**).

Ten-gene dataset. As expected BAMM analyses from our ten-gene analysis produced a high number (454-677) of shift configurations in the 95 % credibility set, and

there is not a best shift configuration with significant highest probability (**Table 4**). Overall, mean speciation, extinction, and diversification rates are similar among all analyses with the ten-gene dataset so we will focus our discussion in the BAMM model with the clade set 1 (**Table 4**). The two clade sets analyses found slightly different number and location of core shifts (**Figures 5 & 6**). Different clade sets share the same shift configuration regardless of the model used (MEDUSA-like or BAMM). Taking into account the results from the two different clade sets we observed a total of ten shifts (named a, b, and 1-8, **Figures 5 & 6**). Shifts a and b are not discussed since they reflect a shift in diversification rates between outgroup (Acoraceae) and the ingroup. The other eight shifts are associated with the following clades: 1) Pothoideae + Monsteroideae (Bisexual climbers clade); 2) Aroideae (excluding *Callopsis*); 3) *Pistia* clade + *Protarum*; 4) and 5) *Anthurium*; 6) Lasioideae; 7) and 8) *Philodendron* clade. The *Philodendron* clade showed the highest net diversification rate (0.242-0.291) followed by Pothoideae (0-196-0.198) and Monsteroideae (0.139) (**Table 6 & Figure 7**).

Character evolution. Analyses using the rerooting method and stochastic mapping produced very similar ancestral state reconstructions. All characters associated with the subfamily Aroideae have evolved more than once in Alismatales (**Figures 8, 9 & 12**). Unisexual flowers, absence of perianth, omniaperturated pollen, and reduced outer exine layer have evolved together in Aroideae and a clade of Alismatales comprising the families Cymodoceaceae and Posidoniaceae (**Figure 8 & 9**). The ancestral states estimated for these characters are: outer exine layer present, pollen monosulcate, and hermaphroditic flowers with perianth. Analysis of correlated evolution showed that

pollen aperture and exine reduction show patterns of correlated evolution with flower sexuality, whereas perianth evolves indepdendently in Alismatales (**Table 7**). Pollen size did not show a lot of variation except for the long and narrow filamentous pollen from the families Zosteraceae and Cymodoceaceae (**Figure 12**). All characters associated with ecology and life form showed a complex pattern of evolution with homoplasy (**Figure 10 & 11**). As a general pattern, we found that habit, growth form, and seasonality have evolved multiple times in Aroideae, whereas in all the other subfamilies they have evolved only once (with some exceptions, such as growth form in Lasioideae). The ancestral estimated states for these characters are: tropical regions, evergreen plants, terrestrial and rhizomatous.

DISCUSSION

Phylogenetic analyses and molecular dating. The recent generation of expanded genomic tools for the Araceae has opened the possibility of developing larger molecular datasets for generating better supported hypotheses about genera and species relationships among aroids. Accurate phylogenetic reconstructions are critical for investigating historical biogeography and character evolution, and we feel confident that the current state of phylogenetic reconstruction in the order Alismatales presented here is sufficient for investigating questions about diversification in major clades in this group. The only obvious differences among previously published phylogenetic reconstructions (e.g. Cusimano et al. 2011, Iles et al. 2013) and our two and ten-gene datasets involved nodes that are only weakly resolved, mainly involving relationships of Alismatales families and among genera of Araceae. There are no examples of conflict or hard

incongruence detected with previous analyses. All genera that included more than one species were recovered monophyletic for alismatids, and again, main taxa with uncertainty in Araceae are *Montrichardia, Calla, Callopsis,* and *Anubias*.

Our age estimates for Alismatales (129.56 Ma) agree with recent studies using different methods and fossil calibrations (Magallón & Castillo, 2009; Anderson & Janssen, 2009; Hertweck et al., 2015; Magallon et al., 2015,). Despite using older and different fossil calibrations, our estimates for subfamilies in Araceae are very similar to Nauheimer et al. (2012). The main differences for the major clades are ages estimated for Monsteroideae (56.3 Ma vs. 68.8 in our analysis), and clades within this subfamily, which are older than previously estimated. This is mainly due to differences in the relationships among clades of Monsterodieae and the inclusion of an older fossil to calibrate the stem of Monsterodieae. Recent fossil evidence has shown that at least some groups of Araceae were widespread by the early Cretaceous (Coiffard et al., 2013, Gallego et al., 2014), and that all the subfamilies were present by the late Cretaceous. However, some of the older fossils resembling Pothoideae or Monsteroideae are difficult to interpret or have not been studied in detailed (Friis et al. 2010a; Friis et al., 2010b). The main factor affecting the dating of our ten-gene phylogeny was the number of calibrations points and not the smoothing parameter (lambda) used during the penalized likelihood calculation. We obtained ages similar to our BEAST tree for the major clades, but differences increased with the distance from a particular node to a calibration point.

Diversification and character evolution in Alismatales. Recent studies of diversification rates among monocots did not find any increase in the order Alismatales, but some evidence for a decrease was found in the alismatid family Butomaceae (Hertweck et al., 2015). In contrast, our findings reveal a complex pattern of ecological and morphological evolution, and changes in diversification rates throughout the order Alismatales, particularly in the family Araceae. The reason for these differences is that diversification analysis methods such as BAMM or MEDUSA will depend on the scale of the phylogenetic tree, as we showed with the different results when comparing our two vs. ten-gene dataset. In our study the Tofieldiaceae and alismatids showed both low rates of diversification and decrease in rates through time. The aquatic subfamily Lemnoideae, the Proto-Araceae, and the *Stylochaeton* clade showed the same pattern. The first two contain aquatic plants or helophytes, which suggest that adaptation to aquatic environments could have a direct negative effect on diversification rates in this order. The *Stylochaeton* clade is an interesting group, it has flower traits intermediate between the subfamily Aroideae and the rest of Araceae (having unisexual flowers with a reduced perianth), and it is the only clade restricted to Tropical Africa with only 32 species. Hesse (2006a) suggested that this group represents a "dead end" in the evolution of Araceae, because it has acquired the unisexual flowers but none of the other traits that have made Aroideae "successful". The slowing and decreasing speciation rate in the group supports his idea.

Taxon sampling and different clade sets. As expected analyses of two vs. ten-gene datasets produce very different shift configurations due to the differences in taxon

sampling (229 vs. 946 taxa). We tested impact of allocating species numbers to different set of clades when using BAMM for incomplete sample phylogenies. We found that different clade sets produced different core shifts configurations; however in our case the shifts were located in the same major clades. Despite that clade allocation had an impact in the distribution of shifts this was not an issue for our discussion of the rates diversification in Alismatales.

Shifts in diversification. Diversification analysis of the two-gene dataset showed strong evidence for a shift in the "true Araceae" clade. We did not find evidence of an increase in rates in the subfamily Arodieae, in fact, when looking at the rates of individual clades, Aroideae and 'Bisexual Climbers' shared similar rates. Initially, this increase seems be associated with an adaption to terrestrial environments in the family Araceae as we see that the two sister clades to the True Araceae (Orontioideae and Lemnoideae), which have low rates of diversification, are helophytes or free-floating aquatics. However, analysis of the ten-gene dataset allowed to dissect the pattern of diversification within Araceae further, and showed that at least six clades have undergone shifts in rates of diversification.

Lasioideae (shift 6). This aroid subfamily is a small clade with only nine genera and ca. 60 species with a pantropical distribution (Mayo et al., 1997; Boyce & Croat, 2014). Members of this group are terrestrial plants or helophytes, with tuberous or rhizomatous growth form, and it is the only clade with bisexual flowers that has evolved insect trap inflorescences (Bröderbauer et al., 2012). Despite an overall increase in the net

diversification of this clade, we also detected a high rate of extinction (also reflected in the long stem branch leading to the crown of the group). The fossil record and molecular dating analyses have supported the hypothesis of a boreotropical origin for the current distribution of this clade. This may help explain the pattern on diversification rates with high extinction during the dispersal from the northern hemisphere to the tropics, and recent increase in the diversification rates. However, this seemingly contradictory pattern is intriguing and suggests that Lasioideae may be an ideal clade for future, focused investigation into the evolutionary process within Araceae.

Pothoideae + Monsteroideae (shifts 1, 4 and 5). At least two shifts showing increases in diversification rates were found in this clade of sister subfamilies, one in the stem of the clade, and the second one in the genus *Anthurium* of Pothoideae, with different locations in the clade set 1 vs. clade set 2 analysis (shifts 4 and 5 in **figures 5 & 6**). With ca. 1200 species, this clade represents most of the diversity of Araceae in the Neotropics, while only ca. 300 species from the group are present in the Paleotropics. Additionally, ca. 80% of the species are epiphytes or hemiepiphytes, whereas other non-epiphytic growth forms are restricted to the genera *Spathiphyllum*, *Stenospermation*, and *Anthurium*. Madison (1978) hypothesized that the high species diversity in *Anthurium* is a product of two adaptive radiations (related to epiphytism, and bee and fly pollination, respectively). Our analyses show that, in fact, there is an increase in speciation and net diversification in *Anthurium*, but we do not have evidence to support the idea of an adaptive radiation. Givnish (1997; 2015 In Press) has discussed the problems in the misuse of the terms adaptive radiation and explosive speciation. Based on his definition

and our observations we believe that Madison was suggesting not a true radiation following adaptation, but rather an explosive speciation event instead. Although epiphytism and pollination relationships may be factors contributing significantly to the high speciation rate in *Anthurium*, we do not consider that there is a wide range of ecological diversity that will indicate the presence of an adaptive radiation in this genus; however, we did not explore these questions directly in this study. It is worthy of further consideration.

Aroideae (shifts 2,3,7,and 8). At least three shifts were found in this subfamily, the first one at the stem node of the clade (excluding *Callopsis*); the second one in the *Philodendron* clade (represent by shifts 7 and 8 in the different clade set analyses); and the third one in the *Pistia* clade + *Protarum*. Despite the lack of support and the uncertainty in the position of some taxa, Aroideae seems to be a clearly defined group by morphological characters (e.g., bisexual flowers lacking perianth, omniapeturate pollen, absence of sporopollenin in the exine) (Cusimano et al., 2011). At least the unisexual flowers, omniaperturate pollen and exine reduction showed a pattern of contigent evolution in Alismatales (**Table 7**). All these characters together have evolved independently at least one other time in Alismatales, but their combination, along with other vegetative characters (e.g., presence of biforines and laticifers), and specialized pollination strategy (spathe behavior and short pollination window) are unique in the order. Although it is difficult to determine the causal relationships between these characters and the pollination strategy (Hesse 2006a; 2006b), we agree with the hypothesis that these represent key innovations that led to an adaptive radiation in

Aroideae, and that in this particular case the radiation is also associated with an increase in net diversification rate. Aroideae with ca. 2000 species shows remarkable morphological and ecological diversity. It is the only subfamily with an almost cosmopolitan distribution (Boyce & Croat 2014), growing in very diverse habitats. Pollination interactions are strikingly diverse, including many types of deception and insect-trap inflorescences (Diaz & Kite, 2006; Bröderbauer et al., 2012, Chartier et al., 2014). All the growth forms and habits, including submersed and free-floating aquatic plants, are represented, and have evolved in a complex manner (i.e., independent origins for the same character, **Figure 11**). Previously, Cusimano et al. (2011a) reconstructed 81 morphological characters for Araceae and found a large amount of homoplasy, suggesting repeated adaptive shifts.

Potential divers of diversification in Araceae. Although we did not test for any character to be directly associated with increases in speciation rates we can describe some patterns in Araceae based on our diversification and character evolution analyses. Epiphytism (especially hemiepiphytism) is the most common habit in the three most diverse clades of Araceae (*Anthurium* [ca. 80%], *Philodendron* [ca. 80%], and *Monsteroidieae* [ca. 90%]), which also showed increases in diversification rates. Epiphytism has found to be related to increases in diversification in other monocot families like Bromeliaceae and Orchidaceae (Gravendeel et al., 2004; Givnish 2010; Givnish et al., 2014; Givnish et al. Unpublished). However, outside the Neotropics epiphytism is not the prevalent habit, and sister clades to these epiphytic groups present complete different patterns except by Monsteroideae. *Pothos* (plus *Pedicellarum* and

Pothoidium), the sister clade to *Anthurium* has only ca. 60 species of scandent hemiepiphytes distributed across South East Asia. *Homalomena* and *Adelonema* (sister to *Philodendron*) are neither epiphityc (rheophytic is the most common habitat) or as diverse (ca. 75 species). This implies that Araceae inhabiting different tropical areas seem to be affected by different abiotic (e.g., geographical and topographical complexity) and biotic factors (e.g., pollination interactions [Chartier et al., 2014]). Further research should be focus on improving the phylogenetic hypothesis for Araceae and disentangling the factors affecting the complex pattern of speciation and diversification rates in the family.

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TABLES and FIGURES

Table 1. DNA substitutions models, partitioning scheme and partition subsets resulting from analyses conducted in PartitionFinder using the BIC criterion for RAXML and BEAST analyses.

	Partition no.	Best Model	Partition subsets
RaxML	1	GTR+G	matK_pos1, matk_pos2
	2	GTR+I+G	matk_pos3
	3	GTR+I+G	rbcL_pos1
	4	GTR+I+G	rbcL_pos2
	5	GTR+I+G	rbcL_pos3
BEAST	1	GTR+G	matK_pos1, matk_pos2
	2	GTR+I+G	matk_pos3
	3	GTR+I+G	rbcL_pos1
	4	SYM+I+G	rbcL_pos2
	5	GTR+I+G	rbcL_pos3

Table 2. Fossil calibrations used in the BEAST analyses. The name of the fossil and estimated ages, node constraint by the fossil, and the source are shown. The prior distribution for the calibration is represented by U (Uniform) or L (lognormal). St.Dev represents the log(St.Dev.) value use for the lognormal distribution in Beauti. A range is shown for the root node.

Name of fossil	Age	Node	Prior	St.Dev. or range	Source
Nitophyllites zaisanicus	55.8	Stem node of *Typhonodorum* clade, sensu Cusimano et al (2011)	L	0.75	Iljinskaja, 1986; Wilde *et al.,* 2005
Rhodospathodendron tomlinsonii	66	Stem node of *Heteropsis* + *Rhaphidophora* clades	L	0.75	Bonde, 2000
Lasioideaecidites	70-75	Stem node of subfamily Lasiodeae	L	0.75	Hofmann & Zetter, 2010
Petrocardium cerrejoense	56-61.6	Crown node of Pothoideae	L	0.75	Herrera et al., 2008
“Araceae fossil sp. A” and “Araceae fossil sp. B”,	110	Crown node of Lemnoideae + "True Araceae"	L	0.75	Friis et al., 2010
Spixiarum kipea	113	Stem node of Orontiodeae (crown of Proto-Araceae)	L	0.75	Coiffard et al., 2013
Stratiotes sp.	56	Crown of Hydrocharitaceae	L	0.75	Sille et al., 2006
Aponogeton harryi	82-81	Stem node of Aponogetonaceae (Crown of alismatids	L	0.75	Hicks, 1993
Liliacidites sp	113-124	Crown node of monocots	L	0.75	Doyle & Hickey, 1976
Root			U	120-160	

Table 3. Calculated ages and confidence intervals (CI) for the main clades in Alismatales from the BEAST analyses with the Tofieldiaceae constraint, the complete constraint constrained topologies and the penalized likelihood. Clade names in Araceae follow Cusimano et al. (2011).

	Tofieldiaceae constraint		**Tree constraint**		**Penalized likelihood**
CLADE	**Age**	**CI(5-95%)**	**Age**	**CI(5-95%)**	**Age**
ROOT	158.35	(153.37-160)	158.23	(153.09-160)	NA
Monocots	139.94	(132.35-146.9)	138.59	(131.19-146.12)	139
Tofieldiaceae	73.67	(42.93-106.72)	73.66	(44.76-107.04)	73.7
Alismatids	113.61	(102.92-123.59)	112.69	(100.54-124.04)	113.5
Alismatids clade 2	101.08	(88.39-113.1)	100.21	(84.73-114.45)	101.8
Alismatids clade 1	103.49	(90.89-116.23)	102.44	(87.18-115.94)	103.5
Alismatales	129.56	(122.76-136.5)	128.78	(122.15-135.93)	132.1
Alsimatids+Araceae	128.52	(122.32-135.88)	127.73	(121.33-134.96)	125.2
Araceae	121.24	(116.28-127.47)	121.04	(116.13-127.08)	118.3
Proto-Araceae	115	(110.92-120.62)	114.97	(110.95-120.2)	115
Orontioideae	51.97	(22.42-86.71)	52.08	(24.91-87.89)	76.67
Lemanceae + True Araceae	111.09	(108.65-114.81)	112.11	(109.72-115.8)	111.4
Lemnaceae	74.73	(51.73-102.07)	74.14	(52.73-97.6)	74.7
True Araceae	101.68	(88.33-111.35)	103.32	(90.16-113.14)	104.5
Pothoideae + Monsteroideae	85.44	(73.44-100.11)	85.51	(72.91-100.45)	84.32
Monsteroideae	68.14	(63.97-75.15)	68.35	(63.98-75.64)	64.15
Pothoideae	64.41	(56.47-77.24)	64.73	(56.54-77.72)	55.71
Podolasia clade	87.72	(74.82-101.68)	89.21	(76.98-102.95)	97.6
Zamioculcoideae	63.6	(32.88-87.99)	64.92	(32.74-87.46)	60.47
Lasiodeae	24.09	(12.65-39.9)	26.87	(14.27-45.46)	24.1
Unisexual Clade	83.01	(71.58-96.27)	84.49	(73.14-97.6)	90.7
Aroideae	76.82	(66.7-87.93)	78.6	(68.86-90.37)	83.8
Schismatoglottideae	19.8	(9.09-34.63)	20.63	(9.09-35.97)	38.4
Cryptpcoryneae	14.89	(6.59-26.64)	15.18	(6.18-26.96)	35.3
Zantedeschia	51.83	(36.39-68.25)	65.89	(49.04-79.09)	44.6
Spathicarpeae	36.58	(23.95-52.13)	62.32	(45.6-76.04)	41.2
Nephthytideae	14.23	(4.81-27.87)	14.36	(5.02-27.98)	15.4
Aglaonemateae	14.62	(5.25-27.07)	15.44	(5.12-30.23)	17.29
Philodendron clade	19.24	(9.92-32.13)	20.86	(10.62-34.38)	19.2
Culcasieae	24.77	(7.46-44.7)	26.35	(7.72-48.57)	19.21
Calla	68.64	(61.52-78.23)	67.34	(60.56-75.66)	63.1
Dracunculus	62.96	(57.48-70.14)	62.23	(57.19-69.14)	56.2
Ambrosina	59.83	(55.33-65.73)	59.52	(55.4-65.22)	49.3
Protarum Clade	42.43	(30.22-54.04)	42.74	(31.27-54.66)	42.4
Pistia Clade	38.76	(27.88-50.33)	NA	NA	40.7
Thyphonodorum clade	56.43	(53.8-60.51)	56.44	(53.72-60.37)	39.44
Caladieae	34.33	(22.33-48.27)	36.56	(23.92-50.53)	48.42

Thomsonieae	18.52	(7.25-35.92)	19.02	(6.86-36.34)	48.9

Table 4. Information from the diversification analyses using BAMM. Mean speciation (Lambda), extinction (Mu) and net diversification are shown. For the two-gene dataset a single shift was recovered; probability and Bayes factors are given.

Model, Dataset	Clade set	Distinct shift configurations in credible set	Number of core shifts	Bayes Factor	Probability	Mean Lambda	Mean Mu	Mean net diversification
BAMM, two-gene	1	34	1	179132.5	0.449	0.249 (0.183,0.328)	0.204 (0.132,0.284)	0.046(0.037-0.055)
BAMM, two-gene	2	4	1	359657.7	0.695	0.311 (0.219,0.425)	0.265 (0.167,0.384)	0.046(0.037-0.055)
MEDUSA-like, two-gene	1	16	1	Inf	0.59	0.279 (0.219,0.345)	0.236 (0.173,0.305)	0.043(0.036-0.051)
MEDUSA-like, two-gene	2	2	1	358543.8	0.799	0.343 (0.270,0.420)	0.3 (0.225,0.381)	0.043(0.036-0.051)
BAMM, ten-gene	1	585	NA	NA	NA	0.098 (0.09,0.108)	0.02 (0.01,0.033)	0.078(0.073-0.082)
BAMM, ten-gene	2	677	NA	NA	NA	0.102 (0.093,0.111)	0.024 (0.013,0.037)	0.078(0.073-0.082)
MEDUSA-like, ten-gene	1	454	NA	NA	NA	0.098 (0.09,0.108)	0.019 (0.009,0.032)	0.079(0.074-0.083)
MEDUSA-like, ten-gene	2	636	NA	NA	NA	0.1 (0.092,0.111)	0.021 (0.011,0.033)	0.079(0.074-0.084)

Table 5. Speciation (Lambda) and extinction rates (Mu) with confidence intervals (CI) for the major clades in Alismatales from BAMM analyses using the two-gene dataset. Values for the MEDUSA-like model and the complete BAMM model, for both of the alternative clade sets are provided.

Analysis	Clade set	Clade	Lambda	CI	Mu	CI
BAMM, two-gene	1	Tofieldiaceae	0.055	(0.041-0.079)	0.019	(0.002-0.048)
BAMM, two-gene	2	Tofieldiaceae	0.053	(0.04-0.074)	0.017	(0.001-0.043)
MEDUSA-like, two-gene	1	Tofieldiaceae	0.055	(0.041-0.078)	0.019	(0.002-0.047)
MEDUSA-like, two-gene	2	Tofieldiaceae	0.055	(0.041-0.077)	0.019	(0.002-0.046)
BAMM, two-gene	1	Alismatids	0.055	(0.041-0.077)	0.019	(0.002-0.048)
BAMM, two-gene	2	Alismatids	0.054	(0.041-0.075)	0.017	(0.001-0.043)
MEDUSA-like, two-gene	1	Alismatids	0.055	(0.041-0.077)	0.019	(0.002-0.045)
MEDUSA-like, two-gene	2	Alismatids	0.056	(0.041-0.078)	0.019	(0.002-0.045)
BAMM, two-gene	1	Araceae	0.407	(0.287-0.544)	0.353	(0.222-0.502)
BAMM, two-gene	2	Araceae	0.519	(0.355-0.727)	0.465	(0.292-0.681)
MEDUSA-like, two-gene	1	Araceae	0.46	(0.355-0.577)	0.411	(0.297-0.535)
MEDUSA-like, two-gene	2	Araceae	0.577	(0.447-0.712)	0.527	(0.389-0.669)
BAMM, two-gene	1	True Araceae	0.472	(0.331-0.633)	0.415	(0.262-0.59)
BAMM, two-gene	2	True Araceae	0.605	(0.41-0.848)	0.548	(0.344-0.801)
MEDUSA-like, two-gene	1	True Araceae	0.535	(0.41-0.673)	0.484	(0.349-0.631)
MEDUSA-like, two-gene	2	True Araceae	0.673	(0.517-0.832)	0.621	(0.46-0.791)
BAMM, two-gene	1	Aroideae	0.472	(0.33-0.634)	0.414	(0.26-0.591)
BAMM, two-gene	2	Aroideae	0.607	(0.413-0.852)	0.549	(0.341-0.804)
MEDUSA-like, two-gene	1	Aroideae	0.533	(0.407-0.674)	0.482	(0.345-0.631)
MEDUSA-like, two-gene	2	Aroideae	0.674	(0.519-0.834)	0.622	(0.462-0.795)
BAMM, two-gene	1	Pothoideae + Monsteroideae	0.478	(0.338-0.653)	0.419	(0.267-0.603)
BAMM, two-gene	2	Pothoideae + Monsteroideae	0.607	(0.413-0.849)	0.550	(0.345-0.8)
MEDUSA-like, two-gene	1	Pothoideae + Monsteroideae	0.541	(0.413-0.687)	0.489	(0.35-0.643)
MEDUSA-like, two-gene	2	Pothoideae + Monsteroideae	0.675	(0.521-0.835)	0.623	(0.464-0.796)

Table 6. Values and confidence intervals (CI) for clades with shifts in diversification from the BAMM analyses using the ten-gene dataset. Caluclations are provided for speciation (Lambda), extinction rate (Mu), and net diversification (NetDiv) within for major clades of Alismatales, and subfamilies of Araceae.All values are for the complete BAMM model analysis but with the two clade sets of different size (1 & 2) also showed.

Clade Name	Clade set	lambda	CI	mu	CI	NetDiv	CI
Tofieldiaceae	1	0.039	(0.035-0.044)	0.003	(<0.001-0.009)	0.036	(0.032-0.04)
Alismatids	1	0.038	(0.035-0.043)	0.003	(<0.001-0.009)	0.035	(0.031-0.038)
Alismatids tepaloid	1	0.039	(0.035-0.046)	0.004	(<0.001-0.01)	0.035	(0.032-0.039)
Alismatids petaloid	1	0.037	(0.034-0.042)	0.003	(<0.001-0.008)	0.034	(0.03-0.038)
Araceae	1	0.144	(0.131-0.163)	0.032	(0.016-0.056)	0.111	(0.104-0.118)
Proto-Araceae	1	0.046	(0.038-0.054)	0.004	(<0.001-0.019)	0.041	(0.03-0.048)
Lemnoideae	1	0.037	(0.033-0.041)	0.003	(<0.001-0.008)	0.034	(0.029-0.038)
Bisexual climbers clade	1	0.264	(0.21-0.345)	0.098	(0.027-0.197)	0.166	(0.138-0.191)
Pothoideae	1	0.338	(0.248-0.504)	0.14	(0.032-0.331)	0.198	(0.159-0.234)
Monsteroideae	1	0.2	(0.156-0.256)	0.061	(0.008-0.133)	0.139	(0.107-0.167)
Lasioideae	1	0.194	(0.098-0.342)	0.108	(0.004-0.271)	0.086	(0.036-0.134)
Stylochaeton clade	1	0.048	(0.036-0.102)	0.004	(<0.001-0.016)	0.043	(0.033-0.091)
Aroideae	1	0.128	(0.117-0.141)	0.016	(0.005-0.033)	0.112	(0.104-0.12)
Philodendron clade	1	0.397	(0.323-0.508)	0.106	(0.02-0.255)	0.291	(0.238-0.34)
Pistia clade + *Protarum*	1	0.106	(0.097-0.117)	0.008	(<0.001-0.023)	0.098	(0.09-0.105)
Tofieldiaceae	2	0.04	(0.035-0.045)	0.003	(<0.001-0.009)	0.036	(0.032-0.04)
Alismatids	2	0.039	(0.035-0.044)	0.004	(<0.001-0.009)	0.035	(0.031-0.039)
Alismatids tepaloid	2	0.039	(0.035-0.048)	0.004	(<0.001-0.011)	0.036	(0.032-0.04)
Alismatids petaloid	2	0.038	(0.034-0.043)	0.003	(<0.001-0.009)	0.035	(0.03-0.038)
Araceae	2	0.15	(0.135-0.167)	0.039	(0.02-0.062)	0.111	(0.103-0.118)
Proto-Araceae	2	0.047	(0.04-0.056)	0.006	(<0.001-0.021)	0.042	(0.03-0.049)
Lemnoideae	2	0.037	(0.033-0.041)	0.003	(<0.001-0.009)	0.034	(0.029-0.038)
Bisexual climbers clade	2	0.263	(0.21-0.337)	0.098	(0.03-0.19)	0.165	(0.139-0.188)
Pothoideae	2	0.336	(0.246-0.482)	0.141	(0.033-0.31)	0.196	(0.157-0.229)

Monsteroideae	2	0.199	(0.156-0.255)	0.06	(0.01-0.134)	0.139	(0.112-0.166)
Lasioideae	2	0.163	(0.091-0.314)	0.08	(0.008-0.244)	0.083	(0.043-0.129)
Stylochaeton clade	2	0.072	(0.037-0.124)	0.016	(<0.001-0.054)	0.056	(0.034-0.087)
Aroideae	2	0.138	(0.123-0.156)	0.027	(0.009-0.052)	0.111	(0.101-0.12)
Philodendron clade	2	0.31	(0.25-0.386)	0.068	(0.01-0.168)	0.242	(0.2-0.285)
Pistia clade + *Protarum*	2	0.146	(0.121-0.181)	0.026	(0.003-0.071)	0.119	(0.102-0.135)

Table 7. Tests for correlated and contigent evolution of the characters associated with subfamily Aroideae. Flower sexuality vs. perianth presence, pollen aperture, and exine reduction. P-values from likelihood ratio test comparing the likelihood of the models produced by BayesTraits are shown. Significance for correlated test is 0.05 and for contigent evolution test is 0.05/4=0.0125

Character	States	Dependent vs. Independent	State 1 evolves more often in unisexual flowers	Unisexual flowers evolved more often in clades with state 1	Bisexual flowers evolved more often in clades with state 0	State 0 evolves more often in bisexual flowers
Perianth	absent(0), present(1)	1	NA	NA	NA	NA
Pollen Aperture	other(0), omniaperturate (1)	5.34E-27	1.60E-20	8.21E-21	3.55E-21	2.44E-20
Exine	complete(0), reduced (1)	1.82E-25	2.89E-02	4.12E-05	7.09E-05	1

Figure 1. Phylogram from maximum likelihood analysis in RaxMLtree using the two-gene dataset and 229 taxa with no constraints. Major clades in Alismatales are labeled and bootstrap support values are shown above the branches.


Tofieldiaceae
Alismatids tepaloids
Alismatids tepaloids
Gymnostacgyoideae
Orontioideae
Lemnoideae
Pothoideae
Monsteroideae
Lasioideae
Zamioculcoideae
Montrichardia arborescens
Cryptocoryneae
Schismattoglotideae
Calla palustris
Thomsonieae
Caladieae
Typhonodorum
Pistia clade
Aroideae
0.05

Figure 2. Phylogram from Maximum likelihood analysis in RaxMLtree using the ten-gene dataset and 946 taxa with no constraints. Major clades in Alismatales are labeled and bootstrap support values are shown above the branches.

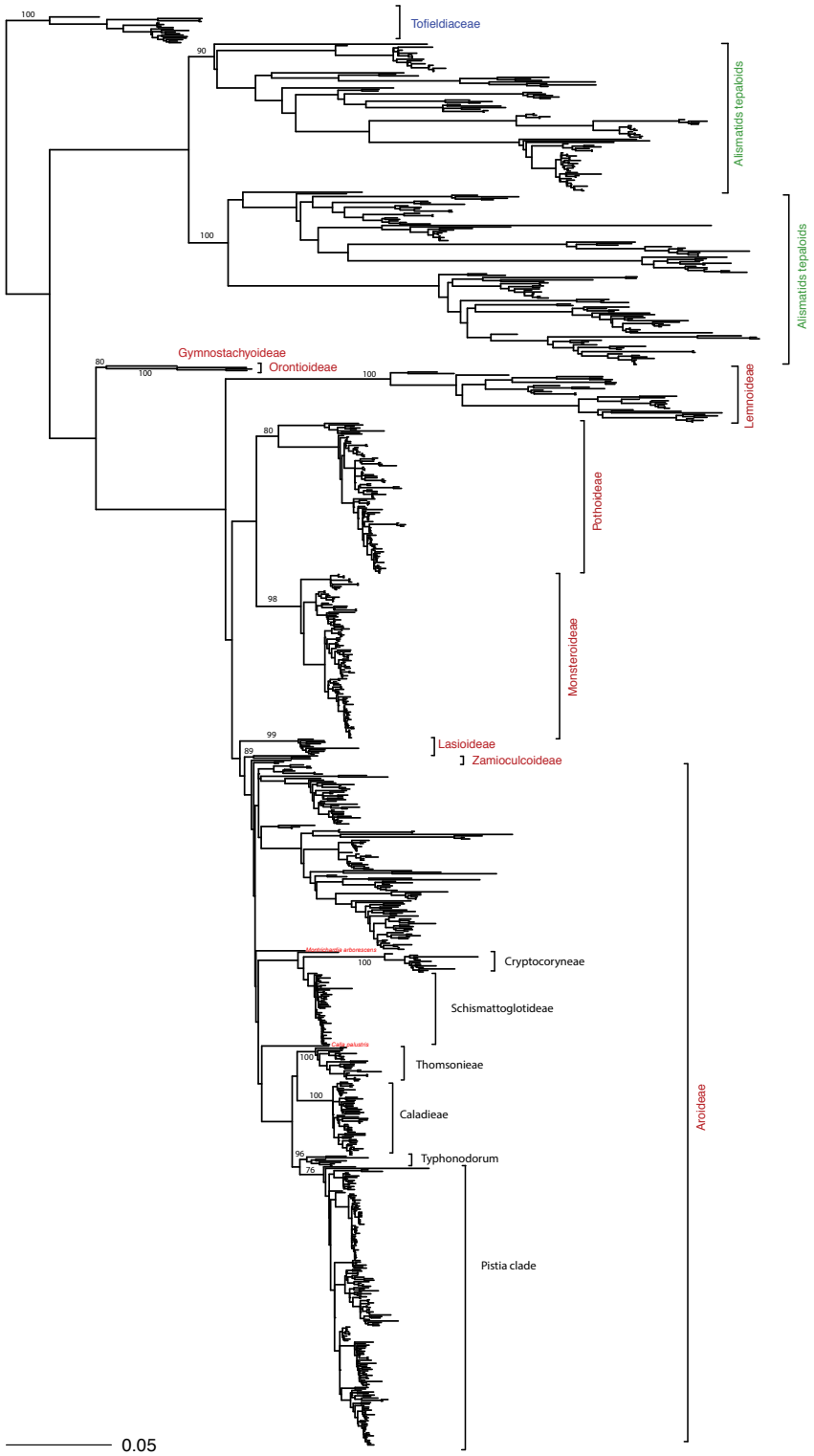
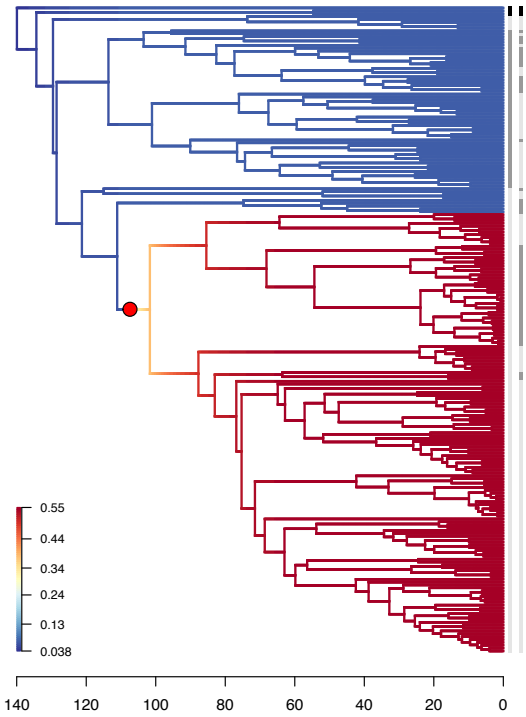
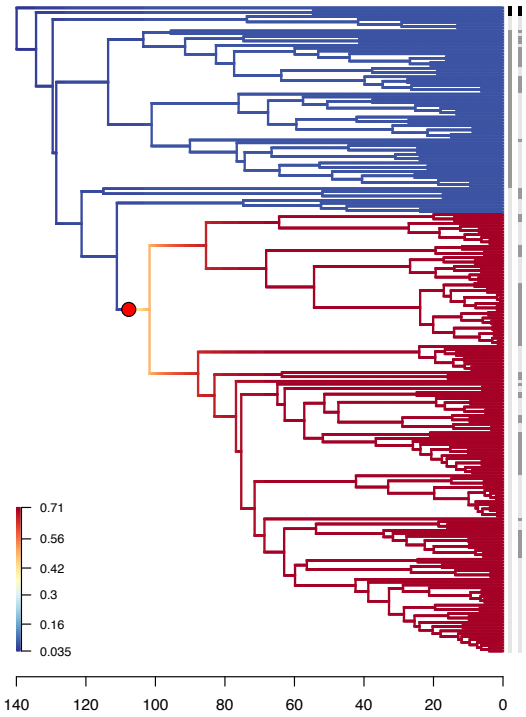

Tofieldiaceae
Alismatids tepaloids
Alismatids tepaloids
Gymnostachyoideae
Orontioideae
Lemnoideae
Pothoideae
Monsteroideae
Lasioideae
Zamioculcoideae
Cryptocoryneae
Schismattoglotideae
Thomsonieae
Caladieae
Typhonodorum
Pistia clade
Aroideae
0.05

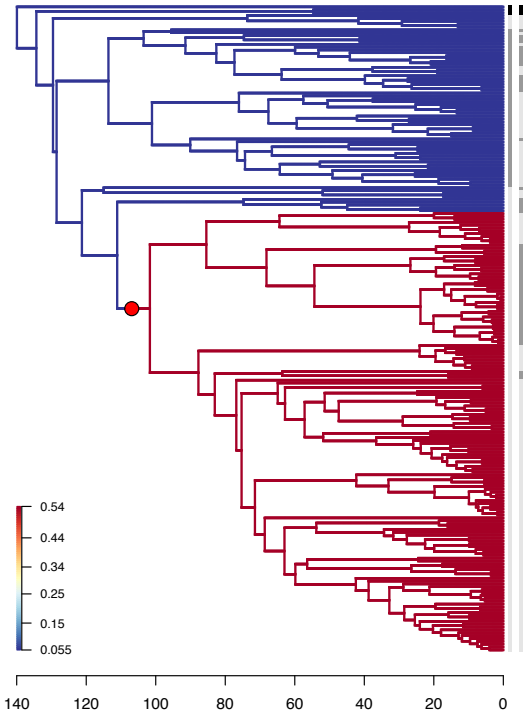
Figure 3. Chronograms depicting rates of net diversification obtained with BAMM. Rates are indicated on the branches, with warmer colors representing higher rates, and cooler colors representing lower rates; shifts are indicated by red colors. The top figures correspond to analyses using the complete BAMM model with clade set 1 (left) and clade set 2 (right). The bottom figures correspond to analyses using a MEDUSA-like model with clade set 1 (left) and clade set 2 (right). Bars next to the trees indicate the size of the clades; left bar indicates outgroups (black), Tofieldiaceae, alismatids, Araceae (grey shades); bars to the right indicate clade sets 1 and 2.



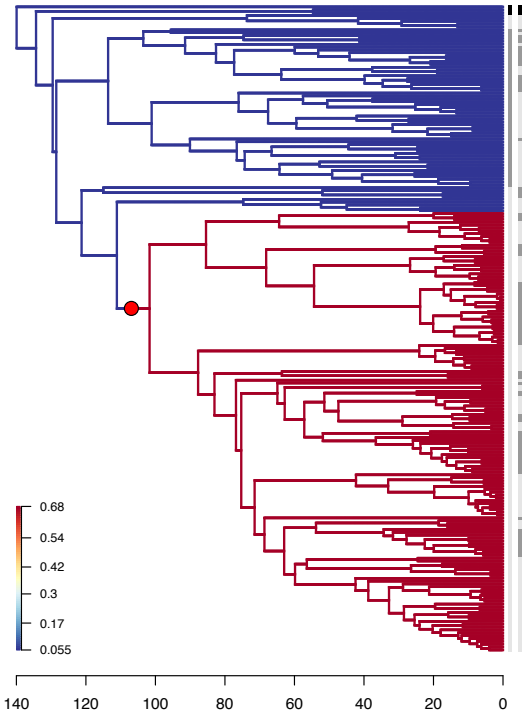
Best Configuration BAMM Model, 2 Genes−Clades set 1



Best Configuration BAMM Model, 2 Genes−Clades set 2



Best Configuration Medusa−like Model, 2 Genes−Clades set 1



Best Configuration Medusa−like Model, 2 Genes−Clades set 2

Figure 4. Rates through time plots from the two-gene diversification analyses. Figure a shows the rate through time plot for speciation (left), extinction (center), and net diversification (right) for Alismatales; **b** represents a comparison of the speciation (solid line), extinction (dot line), and net diversification (dashed line) for all of the four different two-gene analyses; **c** shows the speciation rate through time plot for All Alismatales (left), the True Araceae (center), and background (Alismatales without "True Araceae" [right]).

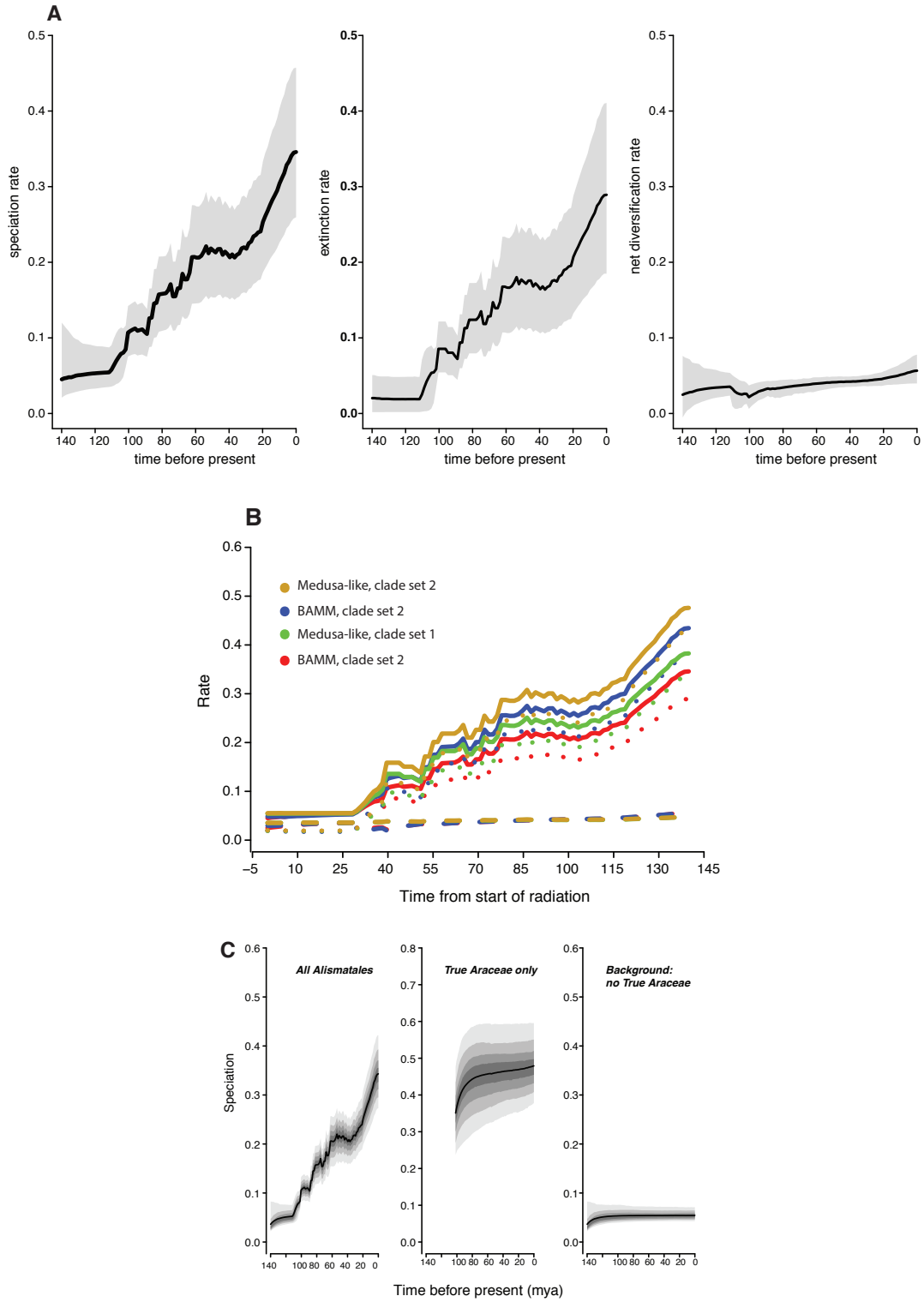
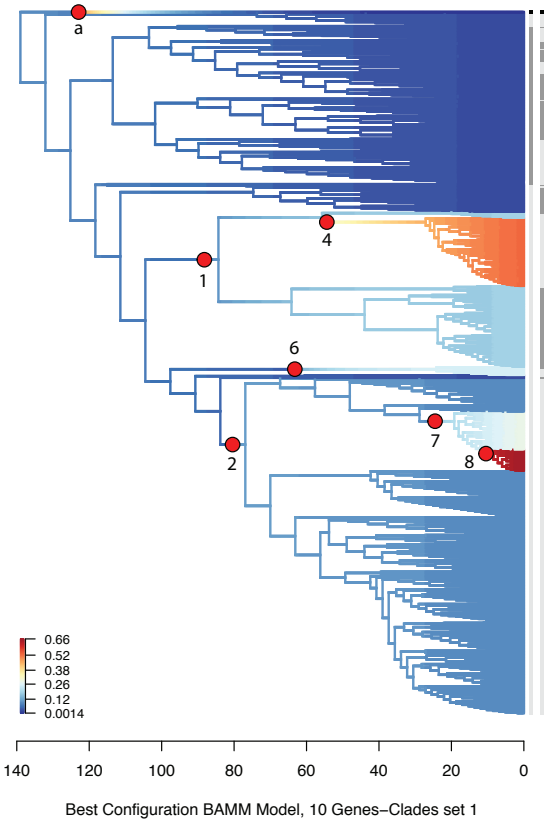
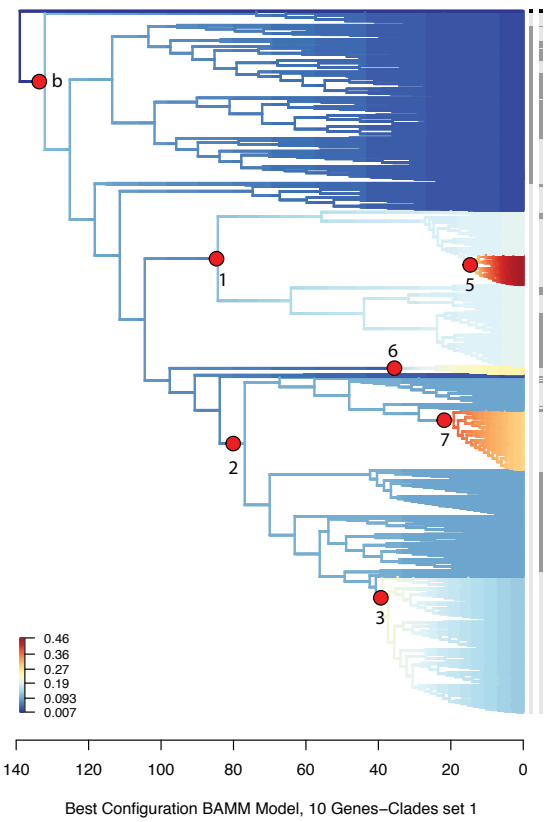
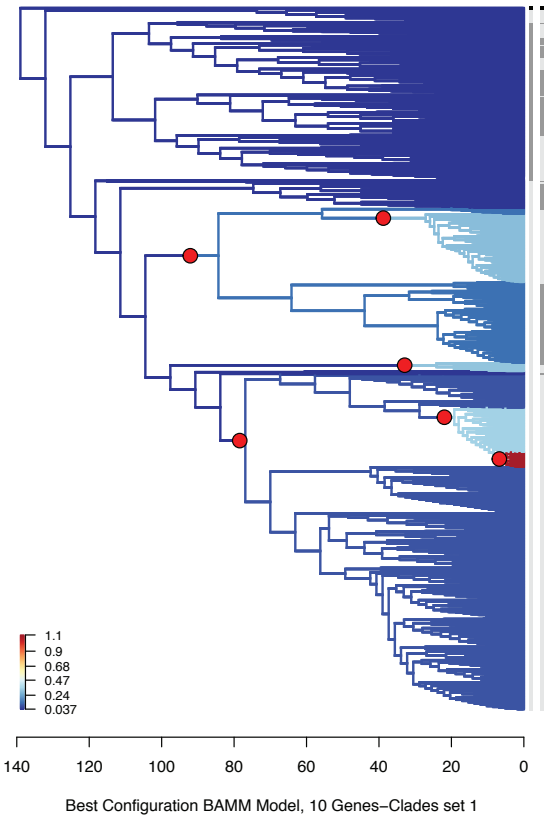

A
speciation rate
extinction rate
net diversification rate
time before present
B
Medusa-like, clade set 2
BAMM, clade set 2
Medusa-like, clade set 1
BAMM, clade set 2
Rate
Time from start of radiation
C
All Alismatales
True Araceae only
Background:
no True Araceae
Speciation
Time before present (mya)

Figure 5. Chronograms depicting rates of net diversification obtained with BAMM for the ten-gene dataset with 946 taxa. Rates are indicated on the branches;h warmer colors represent higher rates, cooler color low rates, and shifts are numbered and indicated by red colors. The top figures correspond to analyses using a complete BAMM model with clade set 1(left) and clade set 2 (right). Bottom figures correspond to analyses using a MEDUSA-like model with clade set 1(left) and clade set 2 (right). Bars next to the trees indicate the size of the clades; left bar indicates outgroups (black), Tofieldiaceae, alismatids, Araceae (grey shades); bars to the right indicate clade set 1 and 2.


a
4
1
6
7
2
8
0.66
0.52
0.38
0.26
0.12
0.0014
140
120
100
80
60
40
20
0
Best Configuration BAMM Model, 10 Genes−Clades set 1


b
1
5
6
7
2
3
0.46
0.36
0.27
0.19
0.093
0.007
140
120
100
80
60
40
20
0
Best Configuration BAMM Model, 10 Genes−Clades set 1


1.1
0.9
0.68
0.47
0.24
0.037
140
120
100
80
60
40
20
0
Best Configuration BAMM Model, 10 Genes−Clades set 1

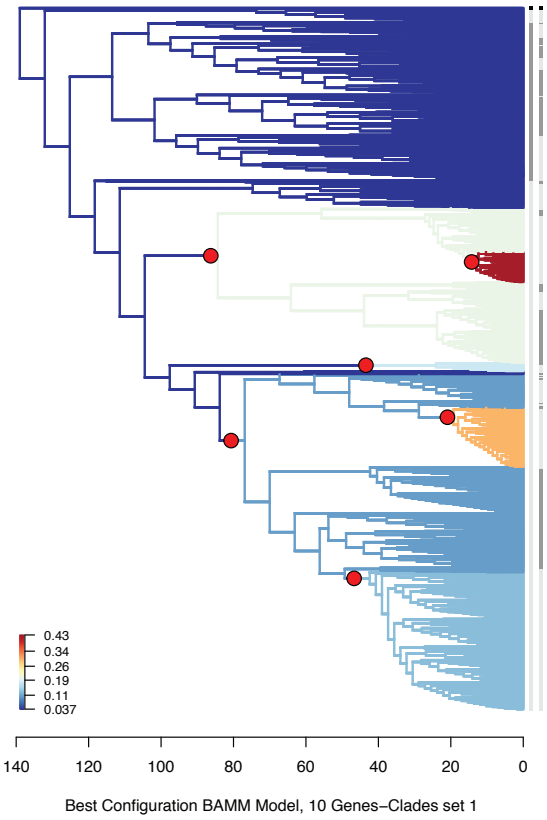
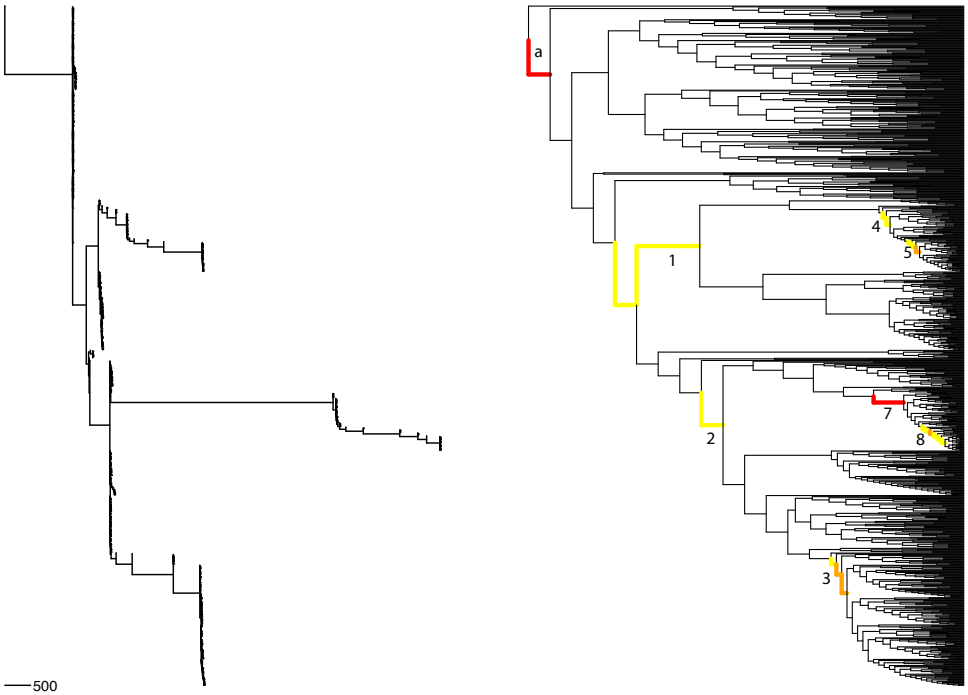

0.43
0.34
0.26
0.19
0.11
0.037
140
120
100
80
60
40
20
0
Best Configuration BAMM Model, 10 Genes−Clades set 1

Figure 6. Bayes factor values associated with the different shifts from the BAMM analysis for the ten-gene dataset using the complete BAMM model and clade set 1 (top figures) and clade set 2 (bottom figures). Figures to the right show branches of the phylogram proportional to the Bayes factor values for the probability of a shift occurring on a particular branch. Figures to the left show branches color code by Bayes factors, yellow >100, orange >500, and red >1000.

Bayes Factors BAMM Model, 10 Genes–Clades set 1



Best Configuration BAMM Model, 10 Genes–Clades set 2

Figure 7. Rate through time plots for the different BAMM analyses with the ten-gene dataset (**A**), and for the different clades in Alismatales (**B**) and Araceae (**C**). **A**, rate throught time plots for the BAMM analyses using the complete BAMM and the MEDUSA-like models, and the two different clade sets. Speciation is represented by the solid line and extinction by the dot line. **B**, rate through time plots from the BAMM analysis using the complete BAMM model and the clade set 1. Gray dot lines represent the rates for entire Alismatales (speciation, net diversification and extinction from top to bottom); solid lines represent the net diversification rates of the major clades in Alismatales. **C**, rate through time plots rate through time plots from the BAMM analysis using the complete BAMM model and the clade set 1. Gray dot lines represent the rates for entire Alismatales, speciation (dot line), net diversification (solid line), and extinction (dashed line); solid lines represent the the net diversification rates for the subfamilies in Araceae.

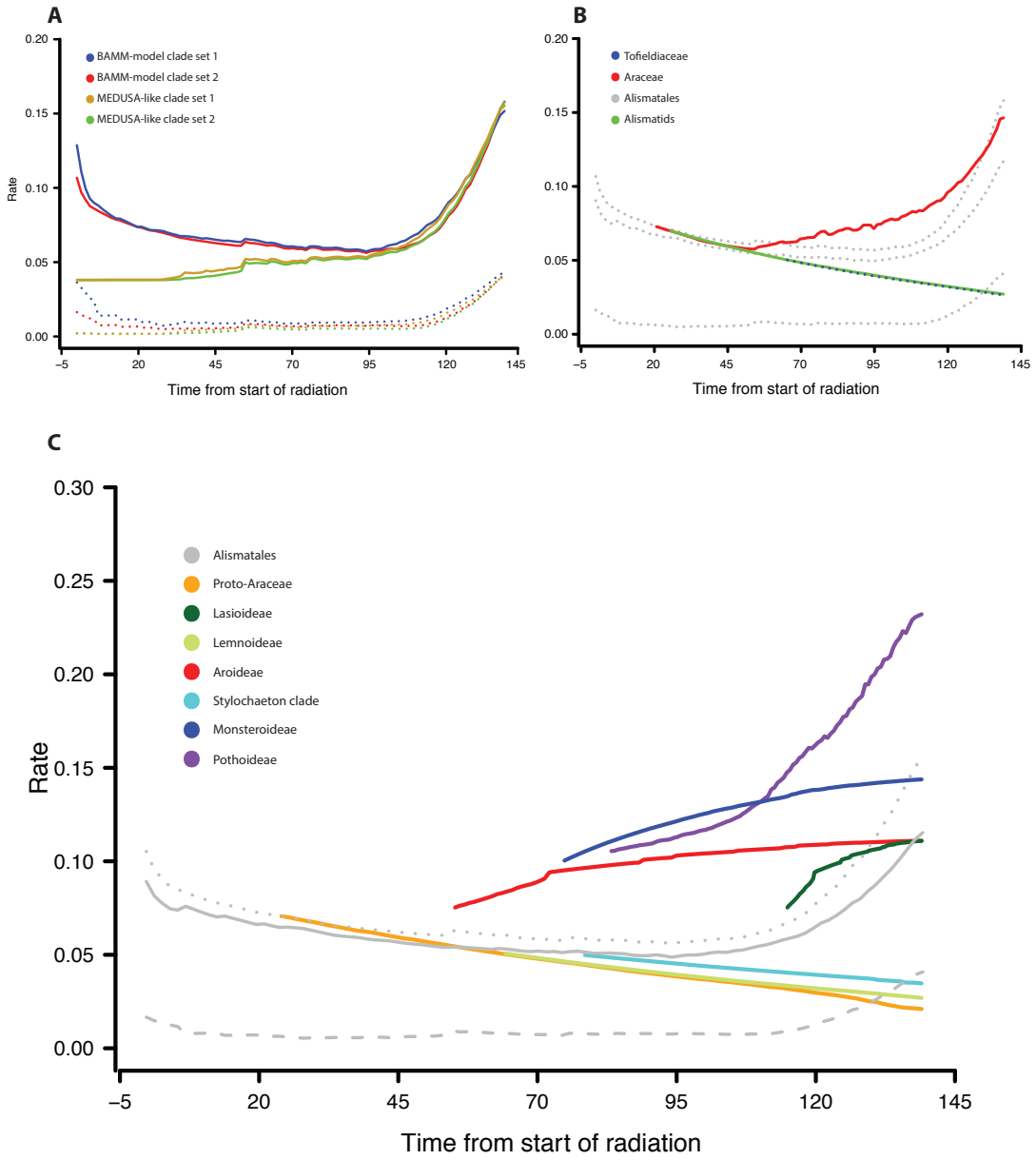

A
BAMM-model clade set 1
BAMM-model clade set 2
MEDUSA-like clade set 1
MEDUSA-like clade set 2
Rate
0.20
0.15
0.10
0.05
0.00
–5
20
45
70
95
120
145
Time from start of radiation
B
Tofieldiaceae
Araceae
Alismatales
Alismatids
0.20
0.15
0.10
0.05
0.00
–5
20
45
70
95
120
145
Time from start of radiation
C
Alismatales
Proto-Araceae
Lasioideae
Lemnoideae
Aroideae
Stylochaeton clade
Monsteroideae
Pothoideae
Rate
0.30
0.25
0.20
0.15
0.10
0.05
0.00
–5
20
45
70
95
120
145
Time from start of radiation

Figure 8. Ancestral state reconstruction for the characters exine reduction (top) and pollen aperture (bottom) in Alismatales. Figures to the left show reconstructions using the rerooting method (ML); figures to the right show reconstruction using 1000 stochastic mappings. States and color codes for each character are shown in the legend.

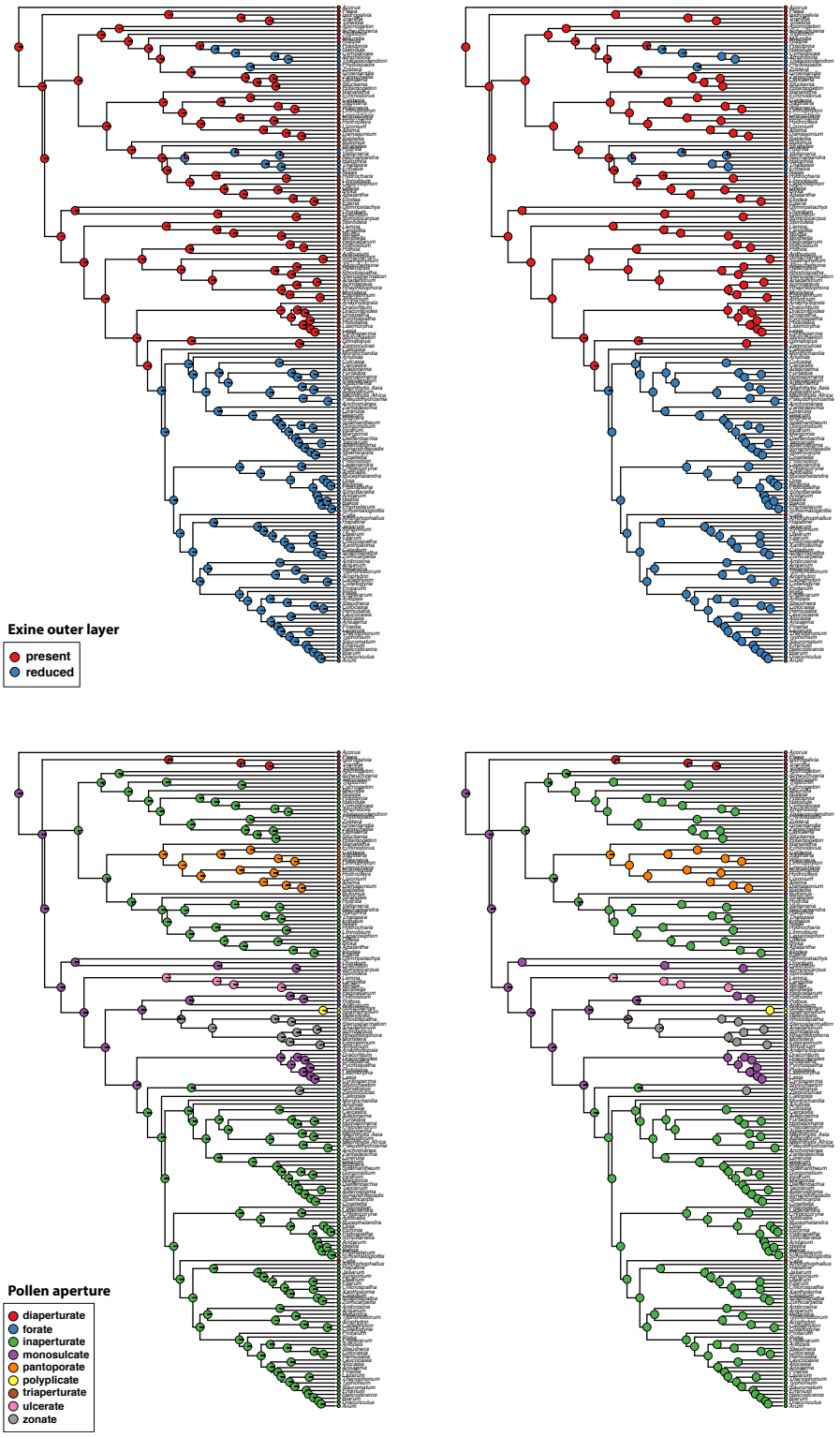

Exine outer layer
present
reduced
Pollen aperture
diaperturate
forate
inaperturate
monosulcate
pantoporate
polyplicate
triaperturate
ulcerate
zonate

Figure 9. Ancestral state reconstruction for the characters flower sexuality (top) and perianth (bottom) in Alismatales. Figures to the left show reconstructions using the rerooting method (ML); figures to the right show reconstruction using 1000 stochastic mappings. States and color codes for each character are shown in the legend.

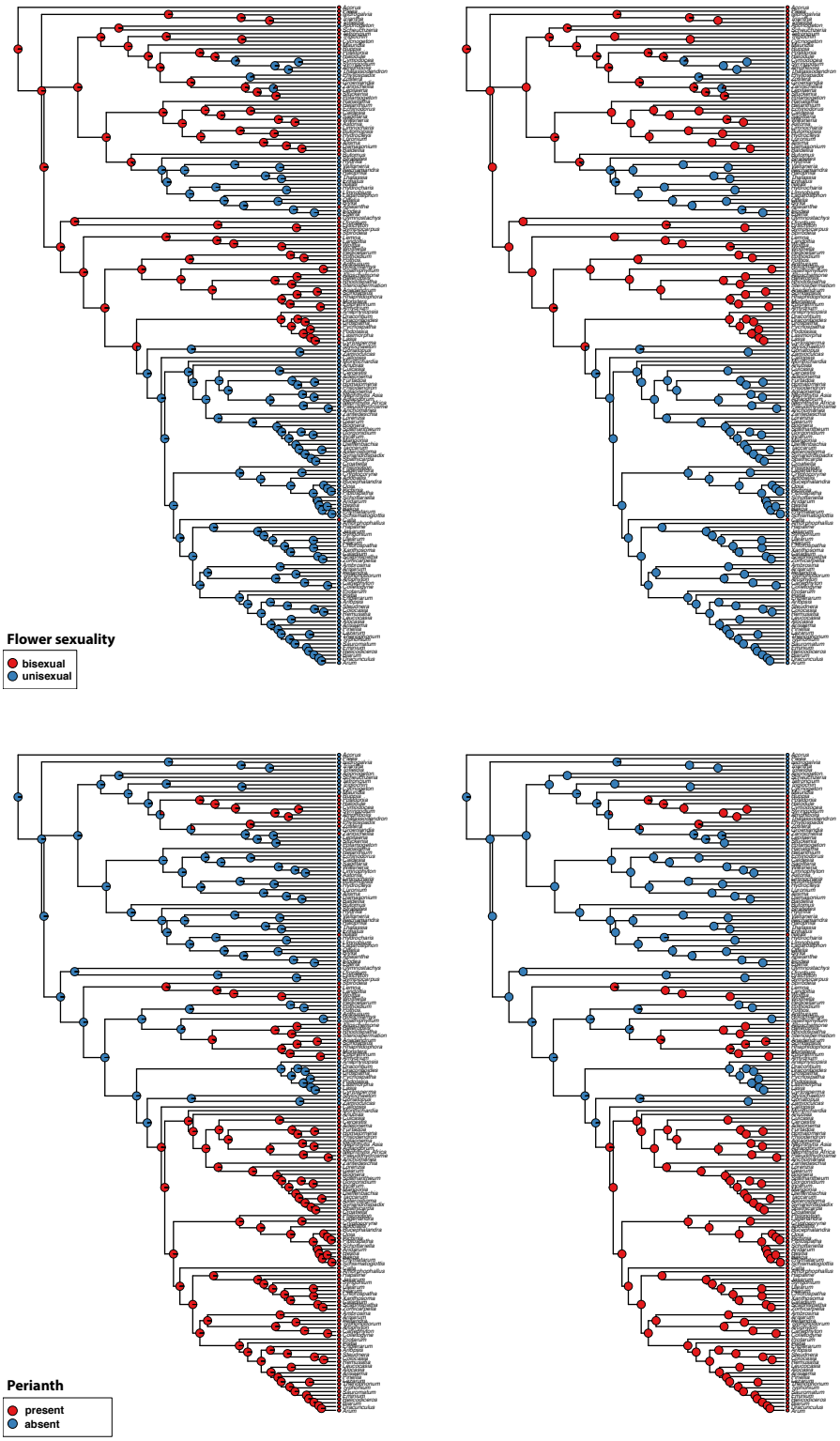

Flower sexuality
bisexual
unisexual
Perianth
present
absent

Figure 10. Ancestral state reconstruction for the characters distribution (top) and seasonality (bottom) in Alismatales. Figures to the left show reconstructions using the rerooting method (ML); figures to the right show reconstruction using 1000 stochastic mappings. States and color codes for each character are shown in the legend.

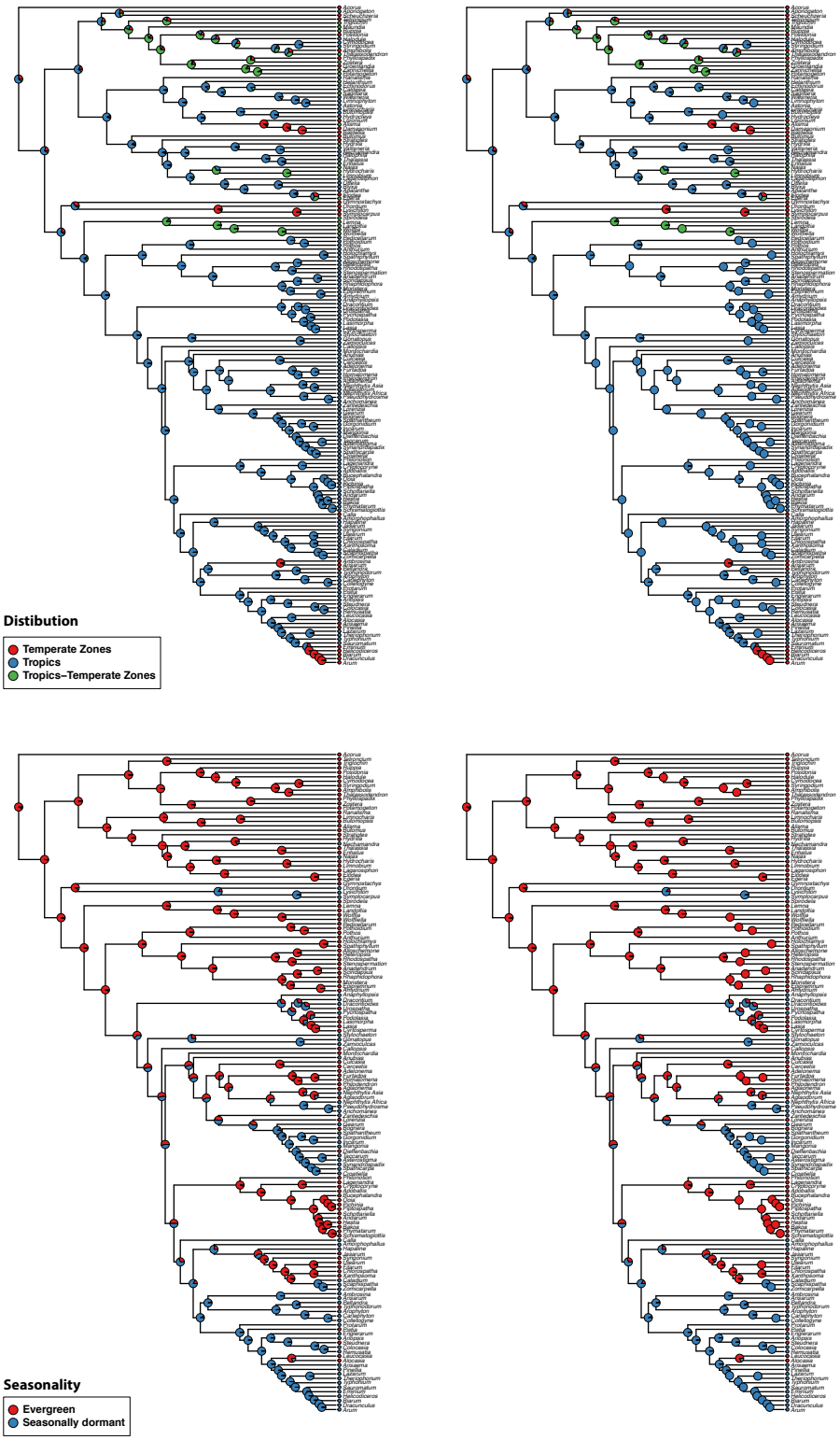

Distibution
Temperate Zones
Tropics
Tropics–Temperate Zones
Seasonality
Evergreen
Seasonally dormant

Figure 11. Ancestral state reconstruction for the characters habitat (top) and growth form (bottom) in Alismatales. Figures to the left show reconstructions using the rerooting method (ML); figures to the right show reconstruction using 1000 stochastic mappings. States and color codes for each character are shown in the legend.

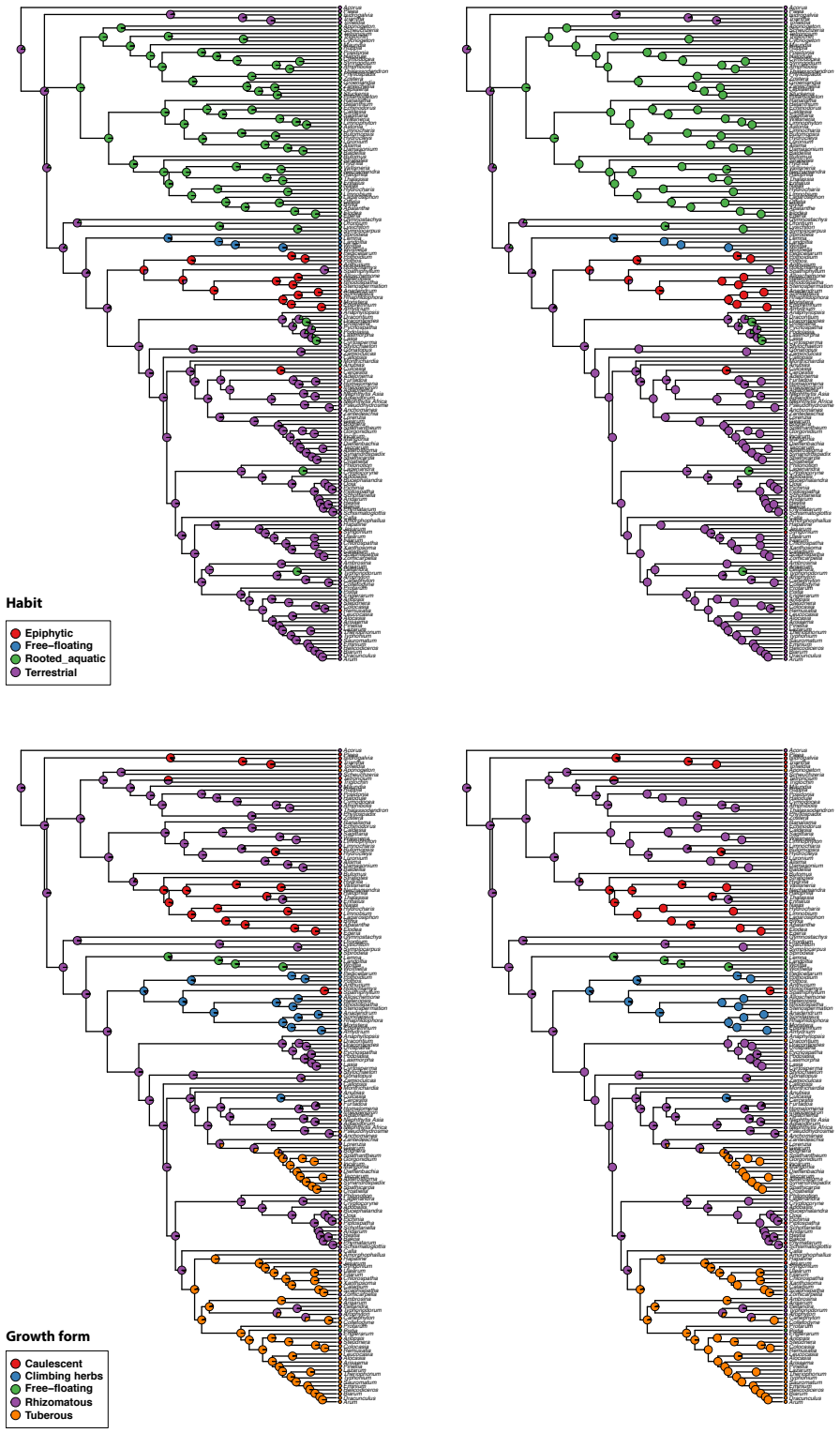
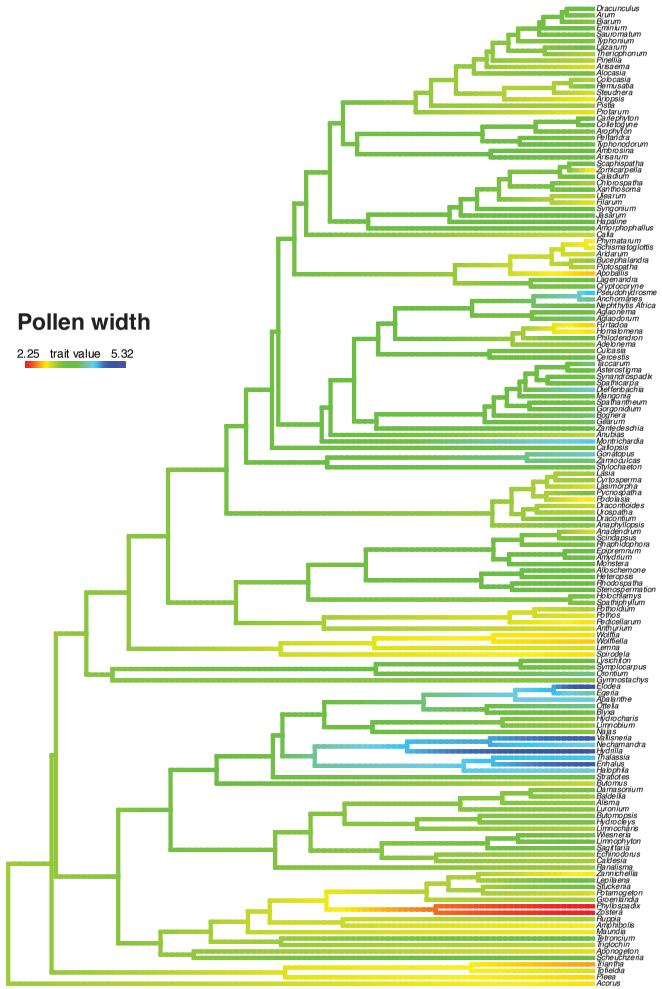
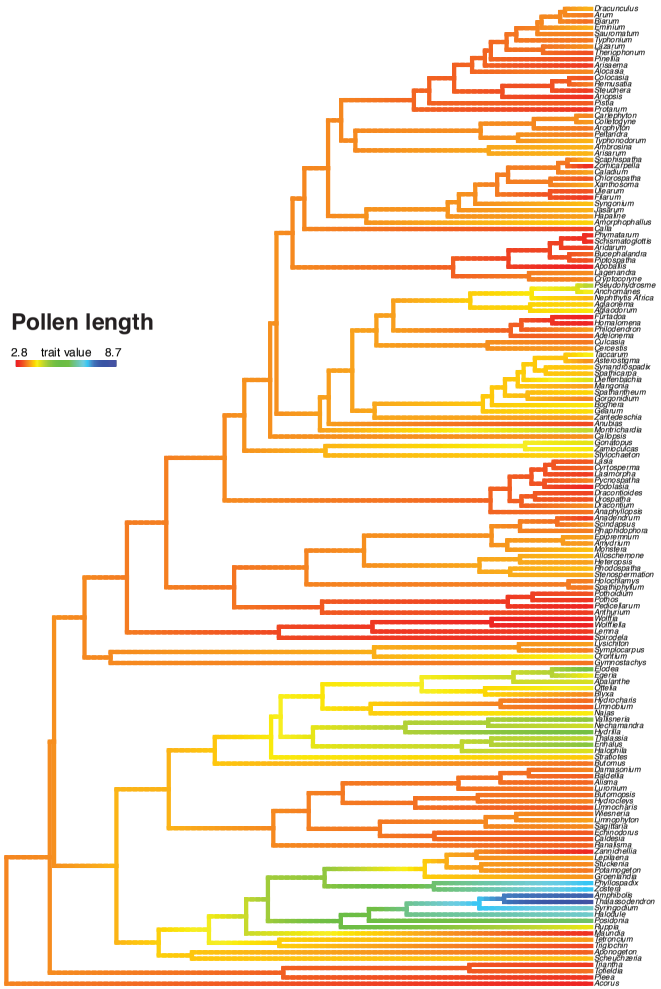

Habit
Epiphytic
Free–floating
Rooted_aquatic
Terrestrial
Growth form
Caulescent
Climbing herbs
Free–floating
Rhizomatous
Tuberous

Figure 12. Ancestral state reconstruction for the characters seed length (top) and seed width (bottom) in Alismatales. Figures to the left show reconstructions using the rerooting method (ML); figures to the right show reconstruction using 1000 stochastic mappings. States and color codes for each character are shown in the legend.


Pollen width
2.25 trait value 5.32


Pollen length
2.8 trait value 8.7

SUPPLEMENTARY TABLES AND FIGURES

TABLE S1. GenBank accesion numbers for the taxa used in the BAMM analyses**. NOTE: This table corresponds to all the sequences gathered for Alismatales from GENBANK and our own data. Some were excluded from the analysis because several reasons (length of the sequence, identification issues, repeat sequences). Additionally, GENBANk accessions numbers from chapter two are missing.**

Species	CHS	ETS	ITS	matK	rbcL	rpl20-rps12	trnC-ycf6	trnG	trnH-psbA	trnLF
Aglaodorum_griffithii				AM920580	AM905758					
Aglaonema_crispum				EF173528						EF173563
Aglaonema_modestum				AM920579	AM905757					
Aglaonema_modestum										AY054700
Aglaonema_nitidum										GQ220953
Aglaonema_rotundum										AY290843
Alloschemone_occidentalis				AM920566	AM905744					AY398567
Alocasia_acuminata				JQ238813		JQ238900				
Alocasia_alba				JQ238814		JQ238901				
Alocasia_argyrea				JQ238815		JQ238902				
Alocasia_argyrea										
Alocasia_atropurpurea				JQ238816		JQ238903				
Alocasia_beccarii				JQ238817		JQ238904				
Alocasia_boa				JQ238818		JQ238905				
Alocasia_boyceana				JQ238819		JQ238906				
Alocasia_brancifolia				JQ238820		JQ238907				
Alocasia_brisbanensis				JQ238821	KF496352, JN105555					
Alocasia_chaii				JQ238822		JQ238908				
Alocasia_clypeolata				JQ238823		JQ238909				
Alocasia_cucullata			AB429332	EU886579	JQ237188	JQ238910				
Alocasia_cucullata										JQ237218
Alocasia_culionensis				JQ238825		JQ238911				

Alocasia_cuprea		JQ238826		JQ238912	
Alocasia_denudata		JQ238827		JQ238913	
Alocasia_gageana		EU886580		AY248909	
Alocasia_grandis		JQ238828			JQ238743
Alocasia_heterophylla		JQ238829		JQ238914	
Alocasia_hollrungii		JQ238830		JQ238915	JQ238745
Alocasia_infernalis		JQ238832		JQ238917	
Alocasia_inornata		JQ238833			
Alocasia_korthalsii		JQ238834		JQ238918	
Alocasia_lauterbachiana		JQ238835		JQ238919	
Alocasia_longiloba		JQ238836		JQ238922	JQ238751
Alocasia_lowii		JQ238840		JQ238924	
Alocasia_macrorrhizos		JQ238841	JN407238	JQ238925	
Alocasia_maquilingensis		JQ238842		JQ238926	
Alocasia_melo		JQ238843		JQ238927	
Alocasia_micholitziana		JQ238844			
Alocasia_monticola		JQ238845		JQ238928	
Alocasia_navicularis		EU886581		AY248925	
Alocasia_nebula		JQ238846		JQ238929	
Alocasia_nycteris		JQ238847		JQ238930	
Alocasia_odora	AB429312	JQ238848	KC466582	JQ238931	
Alocasia_odora					AF469028
Alocasia_pangeran		JQ238849		JQ238932	
Alocasia_peltata		JQ238850		JQ238933	
Alocasia_perakensis		JQ238851			JQ238767
Alocasia_plumbea		JQ238852		JQ238934	
Alocasia_portei		JQ238853		JQ238935	
Alocasia_princeps		JQ238854		JQ238936	
Alocasia_principiculus		JQ238855		JQ238937	
Alocasia_ramosii		JQ238856		JQ238938	
Alocasia_reginae		JQ238857		JQ238939	
Alocasia_reginula		JQ238858		JQ238940	
Alocasia_reversa		JQ238859		JQ238941	
Alocasia_ridleyi		JQ238860		JQ238942	
Alocasia_robusta		JQ238862		JQ238945	
Alocasia_sanderiana		JQ238864	EU193192	JQ238946	

Alocasia_sarawakensis	JQ238865		JQ238947	
Alocasia_scabriuscula	JQ238866		JQ238948	
Alocasia_scalprum	JQ238867		JQ238949	
Alocasia_sinuata	JQ238868		JQ238950	
Alocasia_sp._Bo011	JQ238869		JQ238951	
Alocasia_sp._Bo07	JQ238870		JQ238952	
Alocasia_sp._Gomantong	JQ238871		JQ238953	
Alocasia_sp._inopinata	JQ238879		JQ238961	
Alocasia_sp._kelamensis	JQ238880		JQ238962	
Alocasia_sp._Kerby	JQ238872		JQ238954	
Alocasia_sp._kulat	JQ238881		JQ238963	
Alocasia_sp._MPM1	JQ238873		JQ238955	
Alocasia_sp._MPM2	JQ238874		JQ238956	
Alocasia_sp._MPM3	JQ238875		JQ238957	
Alocasia_sp._MPM4	JQ238876		JQ238958	
Alocasia_sp._ridleythai	JQ238882		JQ238964	
Alocasia_sp._Septier	JQ238877		JQ238959	
Alocasia_sp._Setiam	JQ238878		JQ238960	
Alocasia_suhirmaniana	JQ238883		JQ238965	
Alocasia_warburgii	JQ238884		JQ238966	
Alocasia_watsoniana	JQ238886		JQ238967	
Alocasia_wongii	JQ238887		JQ238969	
Alocasia_zebrina	JQ238888		JQ238970	
Ambrosina_bassii	AM920620	AM905798		AY555185
Amorphophallus_abyssinicus	AF387379	AF497060		
Amorphophallus_abyssinicus				AF387433
Amorphophallus_albus	EU193570	EU193179		
Amorphophallus_amygdaloides		DQ012482		
Amorphophallus_angolensis	AF387404	AF497061		AF387458
Amorphophallus_angolensis				
Amorphophallus_angustispathus		DQ012483		
Amorphophallus_ankarana	AF387380	AF497062		AF387434
Amorphophallus_baumannii	AF387382	AF497063		AF387436
Amorphophallus_beccarii	AF387383	AF497064		AF387437
Amorphophallus_bhandarensis		KM093849		

Amorphophallus_bonaccordensis		KM093850		
Amorphophallus_borneensis		DQ012484		
Amorphophallus_brevispathus	AF387384	AF497065		AF387438
Amorphophallus_bulbifer	EU542582	KM093839		
Amorphophallus_canaliculatus	AF387385	AF497066		AF387439
Amorphophallus_cirrifer	AF387386	AF497067		AF387440
Amorphophallus_coaetaneus	AF387381	AF497068		AF387435
Amorphophallus_commutatus		AF387392	KM093835, KM093836, KM093837, KM093838, AF497069	AF387441
Amorphophallus_corrugatus	AF387387	AF497070		AF387442
Amorphophallus_dactylifer		DQ012485		
Amorphophallus_declinatus		DQ012486		
Amorphophallus_decus-silvae	AF387388	AF497071		AF387443
Amorphophallus_discophorus		DQ012487		
Amorphophallus_dracontioides	AF387389	AF497072		AF387444
Amorphophallus_eburneus	AF387390	AF497073		AF387445
Amorphophallus_eichleri	AF387391	AF497074		AF387446
Amorphophallus_galbra	AF387393	AF497075		AF387447
Amorphophallus_glossophyllus		DQ012489		
Amorphophallus_henryi	AF387394	AF497076		AF387448
Amorphophallus_hewitii		DQ012490		
Amorphophallus_hirsutus	AF387395	KM093840, AF497077		AF387449
Amorphophallus_hirtus	AF387396	AF497078		AF387450
Amorphophallus_hohenackeri		KM093843, DQ012491		
Amorphophallus_hottae	AF387397	AF497079		AF387451
Amorphophallus_impressus		DQ012493		
Amorphophallus_interruptus		DQ012492		
Amorphophallus_johnsonii		DQ012494		
Amorphophallus_konjac	AF387398	AF497080		AF387452
Amorphophallus_konkanensis		KM093842, DQ012495		

Amorphophallus_krausei	AF387399	AF497081		AF387453
Amorphophallus_lambii	AF387400	AF497082		AF387454
Amorphophallus_lanuginosus		DQ012496		
Amorphophallus_laoticus		DQ012497		
Amorphophallus_lewallei	AF387401	AF497083		AF387455
Amorphophallus_longiconnectivus			KM093851, DQ012498	
Amorphophallus_longituberosus	AF387402	AF497084		AF387456
Amorphophallus_margaritifer	AF387403		KM093844, AF497085	AF387457
Amorphophallus_maxwellii	AF387405	AF497086		AF387459
Amorphophallus_mossambicensis		DQ012499		
Amorphophallus_muelleri	AF387406		KM093841, AF497087	AF387460
Amorphophallus_mysorensis		KM093852		
Amorphophallus_napalensis	AF387408	AF497088		AF387462
Amorphophallus_napiger	AF387407	AF497089		AF387461
Amorphophallus_nicolsonianus		KM093853		
Amorphophallus_ochroleucus	AF387409	AF497090		AF387463
Amorphophallus_paeoniifolius	AF387410		KM093846, KM093847, AF497091	AY054703
Amorphophallus_palawanensis	AF387411	AF497092		AF387465
Amorphophallus_pendulus		DQ012501		
Amorphophallus_pingbianensis	AF387412	AF497093		AF387466
Amorphophallus_pusillus	AF387413	AF497094		AF387467
Amorphophallus_pygmaeus	AF387414	AF497095		AF387468
Amorphophallus_rhizomatosus	AF387415	AF497096		AF387469
Amorphophallus_sagittarius	AF387416	AF497097		AF387470
Amorphophallus_salmoneus		DQ012502		
Amorphophallus_scutatus		DQ012503		
Amorphophallus_smithsonianus	AF387417		KM093854, AF497098	AF440738
Amorphophallus_sp._KP-2014		KM093845		
Amorphophallus_sumawongii	AF387418	AF497099		AF387471
Amorphophallus_sylvaticus		KM093855		

Amorphophallus_symonianus			AF387419	AF497100				AF387472
Amorphophallus_taurostigma			AF387420	AF497101				AF387473
Amorphophallus_thaiensis				DQ012504				
Amorphophallus_tinekeae				DQ012505				
Amorphophallus_titanum			AF387421	AF497102				AY555180
Amorphophallus_variabilis			AF387422	AF497103				AF387475
Amorphophallus_yunnanensis			AF387423	AF497104				AF387476
Amorphophallus_zenkeri			AF387424	AF497105				AF387477
Amydrium_hainanense								AY398552
Amydrium_humile			AM920567	AM905745				AY398550
Amydrium_magnificum								AY054735
Amydrium_medium								AY555161
Anadendrum_microstachyum								AY398559
Anadendrum_sp._Boyce_1173								AY398560
Anadendrum_sp._Chase_9985			AM920547	AM905740				
Anaphyllopsis_americana			AM920575	AM905753				AY054726
Anaphyllum_wightii			HQ687766					
Anchomanes_difformis			AF387427	AF497108				AY555186
Anthurium_acaule	JX894473		AM920557	AM905735	JX894684	JX894576	JX894791	
Anthurium_andicola	JX894474				JX894685	JX894577	JX894792	
Anthurium_andraeanum		JN602206	FN668824					
Anthurium_antioquiense	JX894475				JX894686	JX894578	JX894793	
Anthurium_bakeri	JX894476		JQ586582	JQ590265	JX894687	JX894579	JX894794	
Anthurium_balaoanum	JX894477				JX894688	JX894580	JX894795	
Anthurium_bellum	JX894478				JX894689	JX894581	JX894796	
Anthurium_berriozabalense	JX894479				JX894690	JX894582	JX894797	
Anthurium_besseae	JX894480				JX894691	JX894583	JX894798	
Anthurium_bradeanum	JX894482				JX894693	JX894585	JX894800	
Anthurium_brenesii			JQ589934	JQ594929				
Anthurium_brevipedunculatum	JX894483				JX894694	JX894586	JX894801	
Anthurium_bromelicola_subsp._bahiense	JX894484				JX894695	JX894587	JX894802	
Anthurium_brownii	JX894485				JX894696	JX894588	JX894803	
Anthurium_carchiense	JX894486				JX894697	JX894589	JX894804	
Anthurium_chiapasense_subsp._tlaxiacense	JX894489				JX894700	JX894592	JX894807	

Anthurium_citrifolium	JX894490			JX894701	JX894593	JX894808	
Anthurium_clarinervium	JX894491			JX894702	JX894594	JX894809	
Anthurium_clavigerum	JX894492			JX894703	JX894595	JX894810	
Anthurium_clidemioides	JX894471			JX894704	JX894596	JX894811	
Anthurium_consobrinum		JQ586585	JQ590267				AY555155
Anthurium_cordatum	JX894493			JX894705	JX894597	JX894812	
Anthurium_cordifolium	JX894494			JX894706	JX894598	JX894813	
Anthurium_coriaceum	JX894495			JX894707	JX894599	JX894814	
Anthurium_crenatum	JX894496			JX894708	JX894600	JX894815	
Anthurium_croatii	JX894497			JX894709	JX894601	JX894816	
Anthurium_crystallinum	JX894498			JX894710	JX894602	JX894817	
Anthurium_curvispadix	JX894499			JX894711	JX894603	JX894818	
Anthurium_cuspidatum	JX894500			JX894712	JX894604	JX894819	
Anthurium_digitatum	JX894501			JX894713	JX894605	JX894820	
Anthurium_dolichostachyum	JX894502			JX894714	JX894606	JX894821	
Anthurium_dominicense	JX894503			JX894715	JX894607	JX894822	
Anthurium_dressleri	JX894504			JX894716	JX894608	JX894823	
Anthurium_durandii	JX894481			JX894692	JX894584	JX894799	
Anthurium_eminens	JX894505			JX894717	JX894609	JX894824	
Anthurium_flexile_subsp._flexile	JX894472			JX894718	JX894610	JX894825	
Anthurium_formosum	JX894506			JX894719	JX894611	JX894826	
Anthurium_fornicifolium	JX894507			JX894720	JX894612	JX894827	
Anthurium_friedrichsthalii	JX894508			JX894721	JX894613	JX894828	
Anthurium_furcatum	JX894509			JX894722	JX894614	JX894829	
Anthurium_gracile	JX894510			JX894723	JX894615	JX894830	
Anthurium_graciliacuminatum	JX894511			JX894724	JX894616	JX894831	
Anthurium_grandifolium	JX894512			JX894725	JX894617	JX894832	
Anthurium_halmoorei	JX894513			JX894726	JX894618	JX894833	
Anthurium_harrisii	JX894514			JX894727	JX894619	JX894834	
Anthurium_hoffmannii	JX894515			JX894728	JX894620	JX894835	
Anthurium_huixtlense	JX894516			JX894729	JX894621	JX894836	
Anthurium_interruptum		JQ586589	JQ590272				
Anthurium_kunthii	JX894517			JX894730	JX894622	JX894837	
Anthurium_laciniosum	JX894518			JX894731	JX894623	JX894838	
Anthurium_lancea	JX894519			JX894732	JX894624	JX894839	

Anthurium_lancetillense	JX894520			JX894733	JX894625	JX894840		
Anthurium_lancifolium	JX894521			JX894734	JX894626	JX894841		
Anthurium_leuconeurum	JX894522			JX894735	JX894627	JX894842		
Anthurium_longicaudatum				JX894737	JX894629	JX894844		
Anthurium_longipes	JX894524			JX894738	JX894630	JX894845		
Anthurium_longissimum	JX894525			JX894739	JX894631	JX894846		
Anthurium_lucens	JX894526			JX894740	JX894632	JX894847		
Anthurium_lucidum	JX894527			JX894741	JX894633	JX894848		
Anthurium_macleanii	JX894529			JX894743	JX894635	JX894850		
Anthurium_maculosum	JX894530			JX894744	JX894636	JX894851		
Anthurium_margaricarpum	JX894531			JX894745	JX894637	JX894852		
Anthurium_michelii	JX894532, JX894487			JX894746, JX894698	JX894638, JX894590	JX894853, JX894805		
Anthurium_microspadix	JX894533			JX894747	JX894639	JX894854		
Anthurium_mindense	JX894534			JX894748	JX894640	JX894855		
Anthurium_morae	JX894535			JX894749	JX894641	JX894856		
Anthurium_muyunense	JX894536			JX894750	JX894642	JX894857		
Anthurium_napaeum				JX894751	JX894643	JX894858		
Anthurium_obtusilobum	JX894537			JX894752	JX894644	JX894859		
Anthurium_obtusum	JX894488, JX894538			JX894753, JX894699	JX894591, JX894645	JX894806, JX894860		
Anthurium_ochranthum		JQ586590	JQ590274					AY290833
Anthurium_ovatifolium	JX894540			JX894755	JX894647	JX894862		
Anthurium_oxyphyllum	JX894541			JX894756	JX894648	JX894863		
Anthurium_palenquense				JX894757	JX894649	JX894864		
Anthurium_parasiticum	JX894539			JX894754	JX894646	JX894861		
Anthurium_parvispathum	JX894542			JX894758	JX894650	JX894865		
Anthurium_parvum	JX894543			JX894759	JX894651	JX894866		
Anthurium_pedatoradiatum	JX894544			JX894760	JX894652	JX894867		
Anthurium_pedatum	JX894545							
Anthurium_peltigerum	JX894546			JX894762	JX894654	JX894869		
Anthurium_polydactylum	JX894547			JX894763	JX894655	JX894870		
Anthurium_protensum	JX894548			JX894764	JX894656	JX894871		
Anthurium_punctatum	JX894549			JX894765	JX894657	JX894872		
Anthurium_radicans	JX894550			JX894766	JX894658	JX894873		
Anthurium_ravenii		JQ589978	JQ590282					AY290835

Anthurium_sagittatum	JX894551						JX894659	JX894874	
Anthurium_scandens	JX894552		JQ586592	JQ590277		JX894767	JX894660	JX894875	
Anthurium_scherzerianum				AJ005627					
Anthurium_schottianum	JX894553					JX894768	JX894661	JX894876	
Anthurium_sinuatum	JX894554					JX894769	JX894662	JX894877	
Anthurium_sp._1_Croat_et_al._99678	JX894523					JX894736	JX894628	JX894843	
Anthurium_sp._2_Croat_et_al._99766	JX894528					JX894742	JX894634	JX894849	
Anthurium_spathiphyllum	JX894555					JX894770	JX894663	JX894878	
Anthurium_spectabile	JX894556		JQ586593	JQ590279		JX894771	JX894664	JX894879	
Anthurium_subsignatum	JX894557					JX894772	JX894665	JX894880	
Anthurium_thrinax	JX894558					JX894773	JX894666	JX894881	
Anthurium_tremulum	JX894559					JX894774	JX894667	JX894882	
Anthurium_trilobum	JX894560					JX894775	JX894668	JX894883	
Anthurium_umbrosum	JX894561					JX894776	JX894669	JX894884	
Anthurium_urbanii	JX894562					JX894777	JX894670	JX894885	
Anthurium_veitchii	JX894563					JX894778	JX894671	JX894886	
Anthurium_venosum	JX894564					JX894779	JX894672	JX894887	
Anthurium_verapazense	JX894565					JX894780	JX894673	JX894888	
Anthurium_vittariifolium	JX894566					JX894781	JX894674	JX894889	
Anthurium_wendlingeri	JX894567					JX894782	JX894675	JX894890	
Anthurium_willdenowii	JX894568					JX894783	JX894676	JX894891	
Anthurium_willifordii	JX894569					JX894784	JX894677	JX894892	
Anubias_barteri			AM920578	AM905756					AY054710
Apoballis_acuminatissima			GQ220907						GQ220977
Apoballis_mutata									AY290846
Aridarum_borneense		JN544438	GQ220886					KC454019	GQ220954
Aridarum_caulescens		JN544440, JN544428	KC454002					KC454011	KC454027
Aridarum_crassum		JN544426	GQ220889					KC454009	GQ220957
Aridarum_nicolsonii		JN544427, JN544437	AM920606	AM905784				KC454018	JN177481
Aridarum_purseglovei		JN544435, JN544444	GQ220891					KC454025	GQ220960
Ariopsis_peltata			AM920626	AM905804					JQ237222
Ariopsis_protanthera			EU886587		AY248910				

Arisaema_album				AY279138		
Arisaema_amurense		KC466571	DQ859161			
Arisaema_amurense_var._serratum	FJ980445, GQ434867					
Arisaema_angustatum	AF291914					
Arisaema_aridum				AY248912		
Arisaema_auriculatum				AY376845		
Arisaema_balansae				AY279139		AY275568
Arisaema_bonatianum			JQ237193			JQ237223
Arisaema_candidissimum				AY279140		
Arisaema_ciliatum				AY248913		
Arisaema_clavatum				AY279142		AY275595
Arisaema_concinnum				AY279143		AY275591
Arisaema_consanguineum	KF913386	KF913421				AY275587
Arisaema_costatum		KC466572	KC466584	AY279144		
Arisaema_costatum						
Arisaema_dracontium		KC466573	KC466585	AY248914		AY248951, AY248989
Arisaema_elephas			JQ237194	AY279145		
Arisaema_erubescens	JF975895, JF975892	GQ434310	GQ436779	AY279146	JN043993	AY275592
Arisaema_fargesii				AY279148		
Arisaema_flavum	JF975899, JF975900	JF953250	JF940894	AY248915	JN043994	
Arisaema_formosanum				AY279151		
Arisaema_franchetianum		AM920628	AM905806	AY279152		
Arisaema_harmandii				AY279153		
Arisaema_heterocephalum				AY279154		
Arisaema_heterophyllum	FJ980446	KC466574	GQ436775	AY248916	JN043996	
Arisaema_ilanense				AY279155		
Arisaema_jacquemontii				AY279156		
Arisaema_macrospathum		KC466575	KC466587	AY248917		
Arisaema_matsudae				AY279158		
Arisaema_microspadix				AY279159		
Arisaema_mildbraedii						AY275604
Arisaema_negishii				AY279161		
Arisaema_nepenthoides				AY279162		AY275584

Arisaema_polyphyllum						AY248918			
Arisaema_rhizomatum				JF953255	JF940900	AY248919		JN043999	
Arisaema_ringens			AF274295						
Arisaema_schimperianum				KC466576	KC466588	AY279166			
Arisaema_serratum			AB605025, EF017383	EU193586	EU193195	AB494543			
Arisaema_sikokianum			AB513178						
Arisaema_sikokianum_var._serratum		GQ434307	GQ436776						
Arisaema_speciosum				EU886502	EU193196	AY279168			EU193411
Arisaema_thunbergii_subsp._urashima	AB894250								
Arisaema_tortuosum				AF387428	AF497109	AY248920			AF387481
Arisaema_tosaense			AB513179						
Arisaema_triphyllum			KF977433, AF203678	KC466577	AY298817	AY248921		HQ596605	
Arisaema_undulatifolium_subsp._uwajimense	AB611695								
Arisaema_wattii			AF469031		JQ237195				
Arisarum_vulgare				EU886582	HM849791	EU886630			AY555181
Arophyton_buchetii				AM920642	AM905820				
Arum_alpinum				EU193636	EU193245				
Arum_apulum			GU067541	GU067591	GU067566				
Arum_balansanum			GU067542	EU886512	GU067567	EU886624			GU067617
Arum_besserianum									
Arum_byzantinum			GU067543	GU067593	GU067568				GU067618
Arum_concinnatum			GU067544	EU886516	GU067569	GU255991			
Arum_creticum			GU067545	EU886504	GU067570	EU886595			
Arum_cylindraceum			GU067540	EU886514	EU193244	EU886626			
Arum_cyrenaicum			GU067546	EU886515	GU067581	EU886623			
Arum_dioscoridis			GU067547	EU886505	GU067572				
Arum_dioscoridis_var._cypricum									
Arum_dioscoridis_var._dioscor									

idis							
Arum_elongatum		GU067549	GU067598	GU067573			
Arum_elongatum_subsp._elongatum							
Arum_euxinum		GU067548	GU067599	GU067574			GU067624
Arum_gratum		GU067552	GU067600	GU067575			
Arum_hygrophilum		GU067550	GU067601	GU067576	EU886620		AM932296
Arum_idaeum		GU067553	GU067602	GU067577			
Arum_italicum		GU067554	EU886517	GU067578			
Arum_italicum_subsp._albispathum	EU193627	EU193236					
Arum_italicum_subsp._canariense							
Arum_jacquemontii		GU067555	GU067604	GU067579			GU067630
Arum_korolkowii		GU067556	EU886589	GU067580	EU886598		GU067631
Arum_lucanum							
Arum_maculatum		GU067558	EU886506	GU067582	EU886593		
Arum_megobrebi			EU886513		EU886625		
Arum_nigrum		GU067559	EU886507	GU067583	EU886597		
Arum_orientale			EU886510	EU193240	EU886621		
Arum_orientale_subsp._longispathum	EU193639	EU193248					
Arum_orientale_subsp._orientale							
Arum_palaestinum		GU067551	GU067607	GU067584			GU067629
Arum_pictum		GU067560	EU886518	GU067585	EU886596		AY555182
Arum_purpureospathum		GU067561	EU886508	GU067586	EU886594		
Arum_rupicola		GU067562	EU886519	GU067587	EU886592		
Arum_rupicola_subsp._rupicola							
Arum_rupicola_subsp._virescens							
Arum_sintenisii		GU067563	GU067613	GU067588			
Arum_sp._Lobin_26940					EU886622		
Asterostigma_cryptostylum			EF173530				EF173565

Asterostigma_cubense			EF173531				EF173566
Asterostigma_lividum			EF173532				EF173567
Asterostigma_lombardii			EF173533				EF173568
Asterostigma_reticulatum			EF173534, EF173535				EF173569
Asterostigma_tweedianum			EF173536				EF173571
Bakoa_lucens			GQ220894				GQ220962
Biarum_arundanum			EU193608	EU193217			
Biarum_bovei			EU886529				
Biarum_carduchorum			EU886521				
Biarum_davisii			EU886525				
Biarum_davisii_subsp._davisii				EU193220			
Biarum_davisi i_subsp._mar marisense		EU193221					
Biarum_dispar			EU886522	EU193222			
Biarum_ditschianum			EU886526				
Biarum_kotschyi			EU886527				
Biarum_pyrami			EU886523				
Biarum_straussii			EU886524				
Biarum_tenuifolium			EU886528	AM905810			
Biarum_tenuif olium_subsp._ abbreviatum	EU193603	EU193212					
Biarum_tenuif olium_subsp._i domenaeum	EU193605	EU193214					
Biarum_tenuif olium_subsp._ zeleborii	EU193602	EU193211					
Bognera_recondita			EF173537	AM905765			EF173572
Bucephalandra_motleyana		JN544425	AM920644	AM905822		KC454008	GQ220963
Caladium_bicolor			EU886501	EU193181	AY248943		AY054708
Caladium_lindenii			AM920610	AM905788			AF521871
Calla_palustris		AF168829	HQ687764	AM905819			AY555174
Callopsis_volkensii			AM920595	AM905773			AM932330
Carlephyton_glaucophyllum			AM920643	AM905821			

Cercestis_mirabilis			AM920639	AM905817				EF173564
Cercestis_stigmaticus								AY555170
Chlorospatha_atropurpurea			EU542584					
Chlorospatha_longipoda								AF521872
Chlorospatha_sp._Chase_11912			AM920613, AM920613	AM905791, AM905791				
Colletogyne_perrieri			AM920645	AM905823				
Colocasia_affinis_var._jenningsii			JQ238889	JN105544	JQ238971			
Colocasia_antiquorum		AH001599, AF469032	JF828113	JQ237199			JF828132	AF469018
Colocasia_esculenta		AY081000	JQ238890	AM905800	JQ238972	AB494616	GU135448	AY555184
Colocasia_esculenta_var._fontanesii	JQ238892			JQ238974				
Colocasia_fallax			JQ238891	JN105548	JQ238973			
Colocasia_formosana			JN105375	JN105547				
Colocasia_heterochroma			JF828117	JF828099			JF828138	
Colocasia_lihengiae			JF828118	JF828094, JF828098				
Colocasia_menglaensis			JQ238894		JQ238976			
Colocasia_sp._Boyce_s.n.			JQ238895		JQ238977			
Colocasia_yunnanensis			JF828112	JF828092			JF828131	
Croatiella_integrifolia			EF173538					EF173573
Cryptocoryne_auriculata			JX218026	JX258151				
Cryptocoryne_balansae								AY555173
Cryptocoryne_bullosa			JX258137	JX196335				
Cryptocoryne_ciliata		L41594, JN695007						
Cryptocoryne_ciliata_var._latifolia			JX258138	JX196336				
Cryptocoryne_cordata_var._zonata			JX258139	JX196337				
Cryptocoryne_ferruginea			JX258141	JX196339				GQ220965
Cryptocoryne_fusca			JX258142	JX196340				
Cryptocoryne_keei			JX258143	JX196341				
Cryptocoryne_lingua			AM920601	AM905779				AM933329
Cryptocoryne_longicauda			JX258145	JX196343				

Cryptocoryne_pallidinervia		JX258146	JX196344		
Cryptocoryne_sp._FL09-16		JX258150	JX196349		
Cryptocoryne_spiralis	JQ436581				
Cryptocoryne_striolata		JX258148	JX196347		
Cryptocoryne_uenoi		JX258140	JX196338		GQ220966
Cryptocoryne_yujii		GQ220897			
Cryptocoryne_zaidiana		JX258149	JX196348		
Culcasia_liberica		AM920638	AM905816		
Culcasia_mannii					AY555169
Culcasia_saxatilis					AY054713
Culcasia_striolata					AY290844
Cyrtosperma_cuspidispathum					AY290836
Cyrtosperma_macrotum		AM920572	AM905750		
Dieffenbachia_aglaonematifolia		AM920586	AM905764		EF173574
Dieffenbachia_humilis		EF173540			EF173575
Dieffenbachia_oerstedii		EF173541	JQ590304		EF173576
Dieffenbachia_parlatorei		EF173542			
Dieffenbachia_seguine		FN668814			
Dieffenbachia_sp._A.Guadamuz			JQ590299		
Dieffenbachia_sp._Goncalves_164		EF173543			
Dieffenbachia_sp._KRJ-2009		GQ429082			
Dieffenbachia_sp._Qiu_96007			AJ005631		
Dieffenbachia_spruceana		GQ220898			
Dieffenbachia_tonduzii		JQ586623	JQ590319		
Dracontioides_desciscens		AM920576	AM905754		AM932316
Dracontium_gigas		JQ586629	JQ590325		
Dracontium_polyphyllum		AM920569	AM905747		AY054727
Dracunculus_canariensis		EU886531	EU193230		
Dracunculus_vulgaris	GU067564	EU886532	GU067589		
Eminium_jaegeri		EU886520			
Eminium_spiculatum		EU886530	AM905813		
Englerarum_hypnosum		JQ238831		JQ238916	
Epipremnum_aureum		GQ434255	AJ005625		

Epipremnum_falcifolium							AY398558
Epipremnum_papuanum							LC000733, AY398557
Epipremnum_pinnatum			AM920568	KF496862, AM905746		GU135365	AY398551
Filarum_manserichense			AF387429	AF497110			
Furtadoa_mixta			FR832766	FN870821			
Furtadoa_sumatrensis			HQ687767				
Gearum_brasiliense			AM920585	AM905763			EF173579
Gonatopus_angustus			AF387430	AF497111			AY555167
Gorgonidium_intermedium			AM920591	AM905769			EF173580
Gorgonidium_striatum			EF173546				EF173581
Gorgonidium_vermicidum			EF173547				
Gymnostachys_anceps		AF069200	AM920548	M91629			AY398579
Hapaline_benthamiana			EU542586	AM905787			AM933336
Hapaline_ellipticifolium							AY081004
Hapaline_sp._HAR_056			AF387431	AF497112			AF387483
Helicodiceros_muscivorus			EU886533	AM905811			AY249004
Hestia_longifolia			GQ220928				GQ220996
Heteropsis_oblongifolia			AM920560	AM905737			AY398561
Heteropsis_sp._Barabe_147							AY054739
Holochlamys_beccarii			AM920558	AM905736			AY398505
Homalomena_asmae		JQ413317, JX076771	JX024970				
Homalomena_atrox		JQ955571					
Homalomena_borneensis		JX076772, JQ955578, JQ955573, JQ413327	JX024982				
Homalomena_clandestina		JQ413328, JX076775, JX076774, JQ413329	JX024983				
Homalomena_cochinchinensis	DQ870560	DQ866877	KF981856				
Homalomena_crinipes	DQ870561	DQ866878					
Homalomena_curvata		JX076777, JX076776, JQ413314,	JX024967				

		JQ413313				
Homalomena_debilicrista		JQ955574				
Homalomena_erythropus	DQ870562	DQ866879				
Homalomena_expedita		JQ413312, JX076778	JX024965			
Homalomena_giamensis		JQ929129	JX024996			
Homalomena_hanneae		JQ413339, JX076779, JX076804, JX076803, JX076802, JX076801, JX076780, JQ413318	JX024974			
Homalomena_havilandii		JX076781, JQ413332	JX024985			
Homalomena_humilis		JQ413316, JX076806, JX076805	JX024969			
Homalomena_insignis		JX076783, JX076782, JQ413331, JQ413330	JX024987			GQ220968
Homalomena_josefii		JX076784, JQ413325	JX024980			
Homalomena_magna			AM920596	AM905774		
Homalomena_matangae		JQ955577				
Homalomena_occulta			GQ434258	GQ436695	GQ435386	
Homalomena_panamensis	DQ870563	DQ866880				
Homalomena_philippinensis	DQ870564	DQ866881				
Homalomena_picturata	DQ870565	DQ866882				
Homalomena_punctulata		JX076785, JQ413337	JX024989			
Homalomena_rostrata		JX076786, JX024998	JX024995			
Homalomena_rubescens	DQ870566					AY054723
Homalomena_sengkenyang		JX076790, JX076789, JX076788,	JX024977			

Homalomena_sp._Ar3065		JX076787, JQ413321, JQ413319, JX076794			
Homalomena_sp._Barabe_151					AY054724
Homalomena_sp._Batang_Ai		JX076791, JQ413334	JX024991		
Homalomena_sp._Croat_90162	DQ870559				
Homalomena_sp._HYC-2012a		JQ955572			
Homalomena_sp._HYC-2012b		JQ955575			
Homalomena_sp._HYC-2012c		JQ955576			
Homalomena_sp._KKN-2012		JX076795, JQ413338	JX024988		
Homalomena_sp._Melaka		JQ413315, JX076792	JX024968		
Homalomena_sp._Pahang		JX076793, JQ413326	JX024981		
Homalomena_sp._SYW-2013		JX076773			
Homalomena_speariae			KC466578	KC466589	
Homalomena_symplocarpifolia		JQ413322, JX076808, JX076807	JX024984		
Homalomena_vagans		JX076809, JQ413333	JX024990		
Homalomena_vivens		JX076796, JX076797, JQ413324, JQ413323	JX024978		
Homalomena_wallisii		JX076798, JQ413335	JX024992		
Homalomena_wendlandii	DQ870567	DQ866883			
Incarum_pavonii			AM920590	AM905768	EF173583
Jasarum_steyermarkii			AM920614	AM905792	
Lagenandra_ovata			AM920602	AM905780	AM933330
Landoltia_punctata			AY034185	HM850382	
Lasia_spinosa			AM920571	AM905749	AM932312
Lasimorpha_senegalensis			AM920577	AM905755	AM932317
Lemna_aequinoctialis			AY034190	AY034228	
Lemna_disperma			AY034198	AY034236	

Lemna_ecuadoriensis		AY034193	AY034231					
Lemna_gibba		AY034197	AY034235					AY290848
Lemna_japonica		AY034195	AY034233					
Lemna_minor	S67398	AM920552	AM905730					
Lemna_minuta		AY034186	AY034224					
Lemna_obscura		AY034194	AY034232					
Lemna_perpusilla		AY034191	AY034229					
Lemna_tenera		AY034189	AY034227					
Lemna_trisulca		AY034199	AY034237					
Lemna_turionifera		AY034192	AY034230					
Lemna_valdiviana		AY034187	AY034225					
Lemna_yungensis		AY034188	AY034226					
Leucocasia_gigantea		JQ238893	EU193194	JQ238975				JQ237227
Lorenzia_umbrosa		JF803495						
Lysichiton_americanus		AM920549	AM905728		KC241917	KC241908	KC241913	DQ400863
Lysichiton_camtschatcensis						AB206655		AY054740
Mangonia_tweedieana		AM920588	AM905766					EF173584
Monstera_adansonii		AM920565						
Monstera_ada nsonii_var._kl otzschiana								AY555162
Monstera_deliciosa		FN668812						
Monstera_falcifolia								AY398547
Monstera_obliqua								AY398548
Monstera_tenuis		JQ586635						
Montrichardia_arborescens		AM920640						
Nephthytis_afzelii		AM920581						
Nephthytis_bintuluensis		KC466579						
Nephthytis_poissonii								AY290842
Ooia_grabowskii		GQ220903						
Orontium aquaticum		AM920550						
Orontium_aquaticum	AF293753							
Pedicellarum_paiei		AM920555						
Peltandra_virginica		EU886583						
Philodendron bipinnatifidum		JX024993						
Philodendron corcovadense		KF981850						

Philodendron fragrantissimum			JQ586638
Philodendron lundii			KF971332
Philodendron lundii			KF981857
Philodendron pedatum			KF981852
Philodendron petraeum			KF981853
Philodendron radiatum			JX024994
Philodendron saxicola			KF971327
Philodendron saxicola			KF981854
Philodendron solimoesense			KF981858
Philodendron stenolobum			KF971334
Philodendron stenolobum			KF981859
Philodendron undulatum			KF971328
Philodendron undulatum			KF981855
Philodendron venezuelense			KF971329
Philodendron williamsii			KF971330
Philodendron_acutatum	DQ870570		
Philodendron_adamantinum	KF895425		
Philodendron_angustisectum	DQ870576		
Philodendron_anisotomum		DQ866885	
Philodendron_barrosoanum	DQ870577		
Philodendron_billietiae	DQ870578		
Philodendron_bipinnatifidum	DQ870614		
Philodendron_brasiliense	KF895413		
Philodendron_brevispathum	DQ870579		
Philodendron_callosum	DQ870580		
Philodendron_cannifolium	DQ870581		
Philodendron_corcovadense	KF895417		
Philodendron_crassinervium	DQ870582		
Philodendron_dardanianum	KF895411		
Philodendron_davidsonii	DQ870583		
Philodendron_deltoideum			AM920597
Philodendron_distantilobum	DQ870584		
Philodendron_duckei			
Philodendron_ecordatum		DQ866890	
Philodendron_erubescens	DQ870585		
Philodendron_findens	DQ870586		

Philodendron_fragrantissimum	DQ870587		
Philodendron_glaziovii	DQ870588		
Philodendron_gloriosum	DQ870589		
Philodendron_goeldii	DQ870571		
Philodendron_grandifolium	DQ870590		
Philodendron_grandipes	DQ870591		
Philodendron_grazielae			
Philodendron_hederaceum	DQ870613		
Philodendron_ hederaceum_v ar._oxycardiu m	DQ401355		
Philodendron_heleniae	DQ870592		
Philodendron_hylaeae	DQ870593		
Philodendron_ilsemanii	DQ870594		
Philodendron_imbe	DQ870595		
Philodendron_insigne	DQ870596		
Philodendron_lazorii	DQ870597		
Philodendron_leal-costae	KF895427		
Philodendron_lindenii	DQ870598		
Philodendron_linnaei	DQ870599		
Philodendron_loefgrenii	DQ870600		
Philodendron_longistilum	DQ870601		
Philodendron_lundii	KF895420		
Philodendron_malesevichiae	DQ870602		
Philodendron_mamei		DQ866904	
Philodendron_megalophyllum			
Philodendron_melinonii	DQ870603		
Philodendron_mello-barretoanum	KF895423		
Philodendron_oblongum			KF981851
Philodendron_ornatum	DQ870604		
Philodendron_paludicola	KF895412		
Philodendron_panamense	DQ870605		
Philodendron_panduriforme	DQ870606		
Philodendron_pedatum	DQ870607		

Philodendron_petraeum	KF895422				
Philodendron_pinnatifidum	DQ870608				
Philodendron_placidum	DQ870609				
Philodendron_platypetiolatum				JQ590343	
Philodendron_pterotum		DQ866907			
Philodendron_radiatum	DQ870610				
Philodendron_rhodoaxis			JQ586644		
Philodendron_rudgeanum	DQ870568				
Philodendron_ruizii	DQ870611				
Philodendron_sagittifolium	DQ870612				
Philodendron_saxicola	KF895426				
Philodendron_ schottii_subsp. _talamancae	*DQ870619*				
Philodendron_serpens		DQ866911			
Philodendron_simsii	DQ870615				
Philodendron_smithii	DQ870616				
Philodendron_sodiroi		DQ866913			
Philodendron_solimoesense	DQ870572				
Philodendron_ sp._Barabe_an d_Archambaul t_184					AY555166
Philodendron_sp._Croat_8491 4	DQ870573				
Philodendron_speciosum	KF895414				
Philodendron_squamiferum	DQ870617				
Philodendron_stenolobum	KF895424				
Philodendron_stenophyllum	DQ870618				
Philodendron_sulcatum			JQ589932		
Philodendron_surinamense		DQ866918			
Philodendron_tenue			JQ586647		
Philodendron_tripartitum	DQ870620				
Philodendron_tweedieanum	KF895421				
Philodendron_uliginosum	KF895419				
Philodendron_undulatum	DQ870574				
Philodendron_venezuelense	KF895415				

Philodendron_verrucosum	DQ870621		
Philodendron_wendlandii	DQ870622		
Philodendron_williamsii	KF895416		
Philodendron_xanadu	DQ870575		
Philonotion americanum			GQ220908
Philonotion_americanum		JN544445	
Phymatarum borneense			AM920605
Phymatarum_borneense		JN544433	
Pichinia_disticha			GQ220917
Pinellia cordata			JF828130
Pinellia pedatisecta			AM920629
Pinellia peltata			JF828126
Pinellia polyphylla			JF828125
Pinellia ternata			EU886503
Pinellia tripartita			AB494681
Pinellia_cordata		AF469039	
Pinellia_fujianensis			JF828129
Pinellia_integrifolia		AF469033	
Pinellia_pedatisecta		AF469040	
Pinellia_peltata		AF469034	
Pinellia_polyphylla		AF469035	
Pinellia_ternata		AF469036	
Pinellia_tripartita		AF469037	
Pinellia_yaoluopingensis		AF469038	
Piptospatha truncata			JN177493
Piptospatha_burbidgei			GQ220901
Piptospatha_elongata			GQ220902
Piptospatha_impolita			GQ220905
Piptospatha_perakensis			JN177495
Piptospatha_ridleyi			AM920603
Piptospatha_truncata		JN544443	
Piptospatha_viridistigma			GQ220906
Pistia stratiotes			EU886585
Pistia_stratiotes		AF168869	
Podolasia_stipitata			AM920574
Pothoidium_lobbianum			AM920556

Pothos_chinensis						JX894678		
Pothos_junghuhnii						JX894679		
Pothos_longipes			KF496718					
Pothos_ovatifolius						JX894680		
Pothos_scandens		AM920554						
Pothos_tener						JX894681		
Protarum_sechellarum		EU886588						
Pseudodracontium_harmandii		AF387425						
Pseudodracontium_lacourii		AM920608						
Pseudodracontium_lanceolatum		AF387426						
Pseudohydrosme_gabunensis		AM920582						
Pycnospatha_arietina		AM920573						
Remusatia_hookeriana	AF469041	JF828124	JQ237206				JF828134	AF469027
Remusatia_pumila	AY081001	JQ238896	JQ237209	JQ238978				AY081006
Remusatia_vivipara	AY081002	EU886584	KC466593	JQ238979, AY248934				AY081005
Remusatia_yunnanensis	AY081003	JF828114	JQ237214				JF828135	AY081007
Rhaphidophora_africana								AY054736
Rhaphidophora_angulata								AY398512
Rhaphidophora_angustata								AY398514
Rhaphidophora_apiculata								AY398543
Rhaphidophora_australasica			KF496472					AY398519
Rhaphidophora_beccarii								AY398526
Rhaphidophora_bognerii		KC466581	KC466594					
Rhaphidophora_bonii								AY398517
Rhaphidophora_crassicaulis								AY398529
Rhaphidophora_crassifolia		AM920563	AM905741					AY398511
Rhaphidophora_decursiva								AY398523
Rhaphidophora_elliptifolia								AY398509
Rhaphidophora_foraminifera								AY398542
Rhaphidophora_geniculata								AY398546
Rhaphidophora_glauca								AY398524
Rhaphidophora_hayi								AY398537
Rhaphidophora_hongkongensis								AY398507
Rhaphidophora_hookeri								AY398531

Rhaphidophora_korthalsii					AY398534
Rhaphidophora_latevaginata					AY398532
Rhaphidophora_lobbii					AY398508
Rhaphidophora_luchunensis					AY398533
Rhaphidophora_maingayi					AY398520
Rhaphidophora_megaphylla					AY398527
Rhaphidophora_megasperma					AY398513
Rhaphidophora_montana					AY398506
Rhaphidophora_nicolsonii					AY398541
Rhaphidophora_novo-guineensis					AY398535
Rhaphidophora_pachyphylla					AY398540
Rhaphidophora_peepla					AY398518
Rhaphidophora_pertusa					AY398539
Rhaphidophora_petrieana					AY398515
Rhaphidophora_puberula					AY398545
Rhaphidophora_schlechteri					AY398536
Rhaphidophora_schottii					AY398516
Rhaphidophora_spathacea					AY398525
Rhaphidophora_spuria					AY398530
Rhaphidophora_subfalcata					AY398538
Rhaphidophora_sylvestris					AY398510
Rhaphidophora_tetrasperma					AY398528
Rhaphidophora_waria					AY398544
Rhodospatha_falconensis					AY398563
Rhodospatha_guanchensis					AY398562
Rhodospatha_oblongata		AM920562	AM905739		AY398564
Sauromatum_gaoligongense				KC460384	
Scaphispatha_gracilis		EU542587	AM905793		
Schismatoglottis_adoceta	JN544432	JN570739			
Schismatoglottis_asperata		GQ220909			GQ220979
Schismatoglottis_bauensis		GQ220910			GQ220980
Schismatoglottis_brevicuspis		GQ220911			GQ220981
Schismatoglottis_calyptrata					AY555172
Schismatoglottis_ciliata		GQ220913			GQ220982
Schismatoglottis_clausula		GQ220949			GQ221014

Schismatoglottis_confinis				GQ220914		GQ220983
Schismatoglottis_corneri				GQ220915		GQ220985
Schismatoglottis_dulosa				GQ220918		
Schismatoglottis_elegans				JN570747		
Schismatoglottis_erecta				GQ220919		GQ220990
Schismatoglottis_jepomii				GQ220925		GQ220993
Schismatoglottis_jitinae				GQ220927		GQ220994
Schismatoglottis_josefii			JN544431	GQ220947	KC454013	GQ221012
Schismatoglottis_linae				JN570743		
Schismatoglottis_matangensis				JN570741		
Schismatoglottis_mayoana				GQ220929		GQ220997
Schismatoglottis_monoplacenta				GQ220931		GQ220999
Schismatoglottis_motleyana				GQ220933		GQ221001
Schismatoglottis_multiflora				GQ220934		
Schismatoglottis_multinervia				GQ220940		GQ221005
Schismatoglottis_nervosa			JX076800	JN570742		
Schismatoglottis_nicolsonii				GQ220941		GQ221006
Schismatoglottis_patentinervia				GQ220942		GQ221007
Schismatoglottis_pyrrhias				GQ220944		GQ221008
Schismatoglottis_sarikeensis			JN544434		KC454015	JN177488
Schismatoglottis_simonii				JN570740		
Schismatoglottis_sp._A_SLL-2011		GQ220946				
Schismatoglottis_sp._AR-1930				JN570744		
Schismatoglottis_sp._AR-2078				JN570749		
Schismatoglottis_sp._AR-2482				JN570745		
Schismatoglottis_sp._AR108				GQ220945		
Schismatoglottis_sp._AR134				GQ220948		
Schismatoglottis_sp._B_SLL-2011	JN544424	KC454001				
Schismatoglottis_sp._SLL-2011c			JN544429			
Schismatoglottis_sp._SYW-2010f			JN544430			
Schismatoglottis_tecturata				GQ220950		GQ221015

Schismatoglottis_tessellata		JN570748						
Schismatoglottis_trifasciata		AM920604	AM905782					
Schismatoglottis_turbata		JN570750						
Schismatoglottis_ulusarikeiensis		JN570746						
Schismatoglottis_viridissima		GQ220952						GQ221017
Schottariella_mirifica		GQ220912						GQ221009
Scindapsus_hederaceus		AM920564	AM905742					AY398556
Scindapsus_longistipitatus								AY398555
Scindapsus_pictus								AY398554
Spathantheum_orbignyanum		EF173550						EF173585
Spathicarpa_gardneri		EF173552						
Spathicarpa_hastifolia		AM920594	AM905772					EF173589
Spathicarpa_lanceolata		EF173556						
Spathicarpa_sagittifolia		EF173558						
Spathiphyllum_cannifolium								AY398570
Spathiphyllum_cochlearispathum								AY398569
Spathiphyllum_floribundum		AF542575						AY555159
Spathiphyllum_patinii								AY555158
Spathiphyllum_phryniifolium			JQ590355		KC241920	KC241911	KC241916	
Spathiphyllum_wallisii	AF207023	AM920559	AJ235807				FN675813	AY054738
Spirodela_intermedia		AY034183	U68092					
Spirodela_polyrhiza	KC573839	AM920553	AM905731					
Stenospermation_multiovulatum					KC241919, KC241919	KC241910	KC241915	AY398566
Stenospermation_popayanense								AY054737
Stenospermation_ulei		AM920561	AM905738					AY398565
Steudnera_assamica		JQ238898		EF517224				
Steudnera_colocasiifolia		AM920623	AM905801				JF828140	JQ237247
Steudnera_discolor		EU886586		EF517221				
Steudnera_henryana	AF469042							AF469029
Steudnera_kerrii		JQ238899	KC466595	EF517223				
Stylochaeton_bogneri		AM920598	AM905776					
Symplocarpus_foetidus	FJ874946	AM920551	L10247			AB206656	KC241912	AY054741
Symplocarpus_nabekuraensis						AB206658		

Symplocarpus_nipponicus						AB206657		DQ400870
Symplocarpus_renifolius								DQ400867
Synandrospadix_vermitoxicus		AM920593	AM905771					EF173594
Syngonium_angustatum		EU542588	JQ590362					
Syngonium_auritum		AM920611	AM905789					AY555177
Syngonium_podophyllum	GQ434866	GU135034	JQ734528, GQ436773				GU135363, AB331278, GU135446	AY555178
Syngonium_wendlandii			JQ590364					
Taccarum_crassispathum		EF173560						
Taccarum_warmingii		EF173561						
Taccarum_weddellianum		AM920592	AM905770					EF173597
Theriophonum_dalzellii		EU886534		AY248936		AB494603		
Theriophonum_infaustum		EU886535		EU886602				
Typhonium_adnatum		EU886547						
Typhonium_albidinervum		EU886548		AY248937		AB494584		
Typhonium_alismifolium		GU255975						
Typhonium_angustilobum		EU886576		EU886609				
Typhonium_bachmaense		EU886549		KC460350				
Typhonium_baoshanense		EU886591		EU886629				
Typhonium_blumei		EU886553	AM905808	AB494518		AB494586		
Typhonium_brevipes		EU886539		EU886608				
Typhonium_brownii		EU886538		EU886607				
Typhonium_bulbiferum		AB494653		AB494517		AB494585		AB494483
Typhonium_calcicola		AB494663		AB494527		AB494595		AB494493
Typhonium_circinnatum		EU886551						
Typhonium_cordifolium		EU886560		AB494519		AB494587		AB494485
Typhonium_digitatum		EU886552		KC460354				
Typhonium_divaricatum	AY863058		JX011628					
Typhonium_diversifolium		EU886540		AB494526		AB494593		
Typhonium_echinulatum		EU886554		KC460355				
Typhonium_eliosurum		EU886537		EU886606				
Typhonium_filiforme		EU886555		KC460356				
Typhonium_flagelliforme	AM777883	EU886556	JN090013	AB494520		AB494588		AB494486
Typhonium_gallowayi		EU886558		KC460358				
Typhonium_gaoligongense		EU886590		EU886628				

Typhonium_giganteum		AY334502	EU886536	EU193201	AB494533		GQ435382	
Typhonium_glaucum			EU886559		KC460359			
Typhonium_gracile			EU886563		AY279174	AB494589		AY275632
Typhonium_griseum			EU886561		KC460361			
Typhonium_hirsutum			EU886542		AY248939	AB494600		
Typhonium_horsfieldii			EU886541	EU193202	AY248940	AB494596		
Typhonium_huense			EU886557		KC460362			
Typhonium_jinpingense			EU886564		EU886614			
Typhonium_kungmingense			AB494665		AB494529	AB494597		AB494495
Typhonium_laoticum			KC434093					
Typhonium_larsenii			AB494666		AB494530	AB494598		AB494496
Typhonium_lineare			EU886565		KC460365			
Typhonium_nudibaccatum			GU255981		GU255990			
Typhonium_omeiense			AB494667		AB494531	AB494599		AB494497
Typhonium_orbifolium			EU886566		KC460366			
Typhonium_pedunculatum			EU886567		KC460367			
Typhonium_peltandroides			GU255973		GU255986			
Typhonium_praecox			AB494660		AB494524	AB494592		AB494490
Typhonium_praetermissum			GU255982					
Typhonium_reflexum			EU886568		KC460368			
Typhonium_roxburghii			EU886569		AB494522	AB494590		
Typhonium_russell-smithii			GU255985					
Typhonium_saraburiense			EU886570		KC460370			
Typhonium_sp._'corrugatum'			GU255984					
Typhonium_sp._4_Hettersche id_532	EU886572							
Typhonium_sp._5_Hettersche id_543	EU886573							
Typhonium_sp._6_Hettersche id_555	EU886550							
Typhonium_sp._Kununurra			GU255979					
Typhonium_sp._Morgan_River			GU255980					
Typhonium_sp._Prince_Regent			GU255978					
Typhonium_subglobosum			EU886546		KC460380			

Typhonium_tentaculatum		EU886543		EU886612		
Typhonium_trilobatum	KC478077	EU886571		AY248941	AB494591	
Typhonium_tubispathum		EU886574		KC460382		
Typhonium_varians		EU886575		KC460383		
Typhonium_venosum		EU886544	KM093848, AF497113	AB494534	AB494602	
Typhonium_violifolium		EU886562		EU886611		
Typhonium_wilbertii		GU255976	KF496356	EU886610		
Typhonodorum_lindleyanum		EU886578	AM905814	EU886627		
Ulearum_sagittatum		EU542590	AM905794			
Urospatha_sagittifolia		AM920570	AM905748			AM932311
Wolffia_angusta		AY034215	AY034253			
Wolffia_arrhiza		AY034216	AY034254			
Wolffia_australiana		AY034213	AY034251			
Wolffia_borealis		AY034212	AY034250			
Wolffia_brasiliensis		AY034210	AY034248			
Wolffia_columbiana		AY034217	AY034255			
Wolffia_cylindracea		AY034218	AY034256			
Wolffia_elongata		AY034220	AY034258			
Wolffia_globosa		AY034219	AY034257			
Wolffia_microscopica		AY034211	AY034249			
Wolffia_neglecta		AY034214	AY034252			
Wolffiella_caudata		AY034206	AY034244			
Wolffiella_denticulata		AY034209	AY034247			
Wolffiella_gladiata		AY034205	AY034243			AY290851
Wolffiella_hyalina		AY034202	AY034240			
Wolffiella_lingulata		AY034203	AY034241			
Wolffiella_neotropica		AY034208	AY034246			
Wolffiella_oblonga		AY034204	AY034242			
Wolffiella_repanda			AY034239			
Wolffiella_rotunda		AY034200	AY034238			
Wolffiella_welwitschii		AY034207	AY034245			
Xanthosoma_brasiliense		EU542591				
Xanthosoma_helleborifolium		AM920612	AM905790			
Xanthosoma_mafaffa		DQ401357	AJ007543			

Xanthosoma_mexicanum	JQ586654	JQ590366			
Xanthosoma_sagittifolium	EU886500	L10246	AY248944		AY555175
Xanthosoma_violaceum	EU193571	EU193180			
Xanthosoma_wendlandii	JQ586659	JQ590370			
Zamioculcas_zamiifolia	AM920600	AM905778			AY054725
Zantedeschia_aethiopica	JQ412304	AF065474		JQ279761	
Zantedeschia_albomaculata	AM920584	AM905762			
Zomicarpa_steigeriana	EU542592				
Zomicarpella_amazonica	EU542593	AM905796			AM932346

TABLE S2. Clade set and species numbers used in the BAMM analyses.

Clade set 1	Code	Species number
Alismataceae	Ali	111
Aponogetonaceae	Apo	50
Aroideae	Aro	1889
Butomaceae	But	1
Cymodoceaceae	Cym	20
Gymnostachioideae	Gym	1
Hydrocharitaceae	Hyd	126
Juncaginaceae	Jun	17
Lasioideae	Las	58
Lemnoideae	Lem	38
Maundiaceae	Mau	1
Monsteroideae	Mon	358
Orontiodeae	Oro	8
Posidoniaceae	Pos	5
Potamogetonaceae	Pot	115
Pothoideae	Poh	1010
Scheuchzeriaceae	Sch	1
Tofieldiaceae	Tof	28
Zamioculcoideae	Zam	32
Zosteraceae	Zos	14

Clade set 2	Code	Species number
Aglaonemateae	Agl	24
Alismataceae	Ali	111
Anthurium	Ant	950
Anubias	Anu	8
Aponogetonaceae	Apo	50
Butomaceae	But	1
Caladieae	Cal	169
Calla	Caa	1
Callopsis	Cll	1
Culcasieae	Cul	38
Cymodoceaceae	Cym	20
Heteropsis clade	Het	97
Hydrocharitaceae	Hyd	126
Juncaginaceae	Jun	17
Lasioideae	Las	58
Lemnoideae	Lem	38
Maundiaceae	Mau	1
Rhaphidophora clade	Mon	211
Montrichardia	Mot	2
Nephthytideae	Nep	13
Philodendron clade	Phi	572
Philonotion clade	Phi	272
Posidoniaceae	Pos	5
Potamogetonaceae	Pot	115
Pothos clade	Poh	60
Protarum clade	Pro	472
Protoaraceae	Pra	9
Scheuchzeriaceae	Sch	1
Spathicarpeae	Spa	92
Spathiphylleae	Spt	50
Thomsonieae	Tho	197
Thyphonodorum clade	Thy	20
Tofieldiaceae	Tof	28
Zamioculcoideae	Zam	32
Zantedeschia clade	Zan	8
Zosteraceae	Zos	14

TABLE S3. Clade set allocation for each taxon in the two-gene dataset, with the species fraction from the total number of species in the clade that they represent. Ten-gene dataset follows the same allocation for each genus.

Species	Clade set 1	Sp fraction	Clade set 2	Sp fraction
Acorus calamus	Aco	0.5	Aco	0.5
Aglaodorum griffithii	Aro	0.050291159	Agl	0.125
Aglaonema modestum	Aro	0.050291159	Agl	0.125
Nephthytis bintuluensis	Aro	0.050291159	Agl	0.125
Luronium natans	Ali	0.14159292	Ali	0.14159292
Damasonium alisma	Ali	0.14159292	Ali	0.14159292
Baldellia ranunculoides	Ali	0.14159292	Ali	0.14159292
Alisma canaliculatum	Ali	0.14159292	Ali	0.14159292
Alisma plantagoaquatica	Ali	0.14159292	Ali	0.14159292
Limnophyton LYC2011	Ali	0.14159292	Ali	0.14159292
Hydrocleys nymphoides	Ali	0.14159292	Ali	0.14159292
Butomopsis latifolia	Ali	0.14159292	Ali	0.14159292
Limnocharis flava	Ali	0.14159292	Ali	0.14159292
Ranalisma rostratum	Ali	0.14159292	Ali	0.14159292
Caldesia parnassifolia	Ali	0.14159292	Ali	0.14159292
Echinodorus cordifolius	Ali	0.14159292	Ali	0.14159292
Helanthium parvulum	Ali	0.14159292	Ali	0.14159292
Sagittaria latifolia	Ali	0.14159292	Ali	0.14159292
Wiesneria triandra	Ali	0.14159292	Ali	0.14159292
Astonia australiensis	Ali	0.14159292	Ali	0.14159292
Anthurium acaule	Poh	0.010891089	Ant	0.008421053
Anthurium andreanum	Poh	0.010891089	Ant	0.008421053
Anthurium bakeri	Poh	0.010891089	Ant	0.008421053
Anthurium brenesii	Poh	0.010891089	Ant	0.008421053
Anthurium interruptum	Poh	0.010891089	Ant	0.008421053
Anthurium ravenii	Poh	0.010891089	Ant	0.008421053
Anthurium scandens	Poh	0.010891089	Ant	0.008421053
Anthurium spectabile	Poh	0.010891089	Ant	0.008421053
Anubias barteri	Aro	0.050291159	Anu	0.25
Anubias heterophylla	Aro	0.050291159	Anu	0.25
Aponogeton fenestralis	Apo	0.02	Apo	0.02
Butomus umbellatus	But	1	But	1
Caladium bicolor	Aro	0.050291159	Cal	0.059171598
Chlorospatha Chase1821912	Aro	0.050291159	Cal	0.059171598
Filarum manserichense	Aro	0.050291159	Cal	0.059171598
Hapaline benthamiana	Aro	0.050291159	Cal	0.059171598

Jasarum steyermarkii	Aro	0.050291159	Cal	0.059171598
Scaphispatha gracilis	Aro	0.050291159	Cal	0.059171598
Syngonium AZ128	Aro	0.050291159	Cal	0.059171598
Ulearum sagittatum	Aro	0.050291159	Cal	0.059171598
Xanthosoma sagittifolium	Aro	0.050291159	Cal	0.059171598
Zomicarpella amazonica	Aro	0.050291159	Cal	0.059171598
Calla palustris	Aro	0.050291159	Caa	1
Callopsis volkensii	Aro	0.050291159	Cll	1
Cercestis mirabilis	Aro	0.050291159	Cul	0.052631579
Culcasia liberica	Aro	0.050291159	Cul	0.052631579
Ruppia megacarpa	Cym	0.285714286	Cym	0.285714286
Halodule uninervis	Cym	0.285714286	Cym	0.285714286
Cymodocea serrulata	Cym	0.285714286	Cym	0.285714286
Syringodium filiforme	Cym	0.285714286	Cym	0.285714286
Thalassodendron ciliatum	Cym	0.285714286	Cym	0.285714286
Amphibolis antarctica	Cym	0.285714286	Cym	0.285714286
Alloschemone occidentalis	Mon	0.097765363	Het	0.092783505
Heteropsis oblongifolia	Mon	0.097765363	Het	0.092783505
Heteropsis spruceana	Mon	0.097765363	Het	0.092783505
Rhodospatha AZ125	Mon	0.097765363	Het	0.092783505
Rhodospatha AZ82	Mon	0.097765363	Het	0.092783505
Rhodospatha wendlandii	Mon	0.097765363	Het	0.092783505
Stenospermation AZ129	Mon	0.097765363	Het	0.092783505
Stenospermation AZ80	Mon	0.097765363	Het	0.092783505
Stenospermation escobariae	Mon	0.097765363	Het	0.092783505
Stratiotes aloides	Hyd	0.129032258	Hyd	0.129032258
Lagarosiphon muscoides	Hyd	0.129032258	Hyd	0.129032258
Ottelia acuminata	Hyd	0.129032258	Hyd	0.129032258
Blyxa echinosperma	Hyd	0.129032258	Hyd	0.129032258
Apalanthe granatensis	Hyd	0.129032258	Hyd	0.129032258
Elodea nuttallii	Hyd	0.129032258	Hyd	0.129032258
Egeria densa	Hyd	0.129032258	Hyd	0.129032258
Hydrilla verticillata	Hyd	0.129032258	Hyd	0.129032258
Hydrocharis dubia	Hyd	0.129032258	Hyd	0.129032258
Limnobium laevigatum	Hyd	0.129032258	Hyd	0.129032258
Najas flexilis	Hyd	0.129032258	Hyd	0.129032258
Vallisneria asiatica	Hyd	0.129032258	Hyd	0.129032258
Nechamandra alternifolia	Hyd	0.129032258	Hyd	0.129032258
Halophila ovalis	Hyd	0.129032258	Hyd	0.129032258
Enhalus acoroides	Hyd	0.129032258	Hyd	0.129032258
Thalassia hemprichii	Hyd	0.129032258	Hyd	0.129032258
Tetroncium magellanicum	Jun	0.235294118	Jun	0.235294118
Cycnogeton rheophilum	Jun	0.235294118	Jun	0.235294118

Triglochin maritima	Jun	0.235294118	Jun	0.235294118
Anaphyllopsis americana	Las	0.101694915	Las	0.101694915
Cyrtosperma macrotum	Las	0.101694915	Las	0.101694915
Dracontioides desciscens	Las	0.101694915	Las	0.101694915
Dracontium polyphyllum	Las	0.101694915	Las	0.101694915
Lasia spinosa	Las	0.101694915	Las	0.101694915
Lasimorpha senegalensis	Las	0.101694915	Las	0.101694915
Podolasia stipitata	Las	0.101694915	Las	0.101694915
Pycnospatha arietina	Las	0.101694915	Las	0.101694915
Urospatha sagittifolia	Las	0.101694915	Las	0.101694915
Landoltia punctata	Lem	0.131578947	Lem	0.131578947
Lemna minor	Lem	0.131578947	Lem	0.131578947
Spirodela polyrhiza	Lem	0.131578947	Lem	0.131578947
Wolffia columbiana	Lem	0.131578947	Lem	0.131578947
Wolffiella gladiata	Lem	0.131578947	Lem	0.131578947
Maundia triglochinoides	Mau	1	Mau	1
Amydrium hainanense	Mon	0.097765363	Mon	0.104265403
Amydrium humile	Mon	0.097765363	Mon	0.104265403
Amydrium medium	Mon	0.097765363	Mon	0.104265403
Anadendrum microstachyum	Mon	0.097765363	Mon	0.104265403
Epipremnum aureum	Mon	0.097765363	Mon	0.104265403
Epipremnum falcifolium	Mon	0.097765363	Mon	0.104265403
Epipremnum papuanum	Mon	0.097765363	Mon	0.104265403
Epipremnum pinnatum	Mon	0.097765363	Mon	0.104265403
Monstera adansonii	Mon	0.097765363	Mon	0.104265403
Monstera deliciosa	Mon	0.097765363	Mon	0.104265403
Monstera dubia	Mon	0.097765363	Mon	0.104265403
Monstera tuberculata	Mon	0.097765363	Mon	0.104265403
Monstera xanthospatha	Mon	0.097765363	Mon	0.104265403
Rhaphidophora bognerii	Mon	0.097765363	Mon	0.104265403
Rhaphidophora crassifolia	Mon	0.097765363	Mon	0.104265403
Rhaphidophora decursiva	Mon	0.097765363	Mon	0.104265403
Rhaphidophora hongkongensis	Mon	0.097765363	Mon	0.104265403
Rhaphidophora lobbii	Mon	0.097765363	Mon	0.104265403
Rhaphidophora megaphylla	Mon	0.097765363	Mon	0.104265403
Rhaphidophora spuria	Mon	0.097765363	Mon	0.104265403
Rhaphidophora sylvestris	Mon	0.097765363	Mon	0.104265403
Scindapsus hederaceus	Mon	0.097765363	Mon	0.104265403
Montrichardia arborescens	Aro	0.050291159	Mot	0.5
Anchomanes difformis	Aro	0.050291159	Nep	0.230769231
Nephthytis afzelii	Aro	0.050291159	Nep	0.230769231
Pseudohydrosme gabunensis	Aro	0.050291159	Nep	0.230769231
Japonolirion osense	Pet	0.5	Pet	0.5

Petrosavia sakuraii	Pet	0.5	Pet	0.5
Furtadoa mixta	Aro	0.050291159	Phi	0.01048951
Homalomena magna	Aro	0.050291159	Phi	0.01048951
Homalomena speariae	Aro	0.050291159	Phi	0.01048951
Philodendron bipinnatifidum	Aro	0.050291159	Phi	0.01048951
Philodendron deltoideum	Aro	0.050291159	Phi	0.01048951
Philodendron fragrantissimum	Aro	0.050291159	Phi	0.01048951
Apoballis acuminatissima	Aro	0.050291159	Phl	0.055147059
Aridarum nicolsonii	Aro	0.050291159	Phl	0.055147059
Bakoa lucens	Aro	0.050291159	Phl	0.055147059
Bucephalandra motleyana	Aro	0.050291159	Phl	0.055147059
Cryptocoryne ferruginea	Aro	0.050291159	Phl	0.055147059
Cryptocoryne uenoi	Aro	0.050291159	Phl	0.055147059
Hestia longifolia	Aro	0.050291159	Phl	0.055147059
Lagenandra ovata	Aro	0.050291159	Phl	0.055147059
Ooia grabowskii	Aro	0.050291159	Phl	0.055147059
Philonotion americanum	Aro	0.050291159	Phl	0.055147059
Phymatarum borneense	Aro	0.050291159	Phl	0.055147059
Pichinia disticha	Aro	0.050291159	Phl	0.055147059
Piptospatha ridleyi	Aro	0.050291159	Phl	0.055147059
Schismatoglottis trifasciata	Aro	0.050291159	Phl	0.055147059
Schottariella mirifica	Aro	0.050291159	Phl	0.055147059
Posidonia oceanica	Pos	0.2	Pos	0.2
Stuckenia pectinata	Pot	0.051282051	Pot	0.051282051
Potamogeton distinctus	Pot	0.051282051	Pot	0.051282051
Potamogeton perfoliatus	Pot	0.051282051	Pot	0.051282051
Groenlandia densa	Pot	0.051282051	Pot	0.051282051
Lepilaena australis	Pot	0.051282051	Pot	0.051282051
Zannichellia palustris	Pot	0.051282051	Pot	0.051282051
Pedicellarum paiei	Poh	0.010891089	Poh	0.05
Pothoidium lobbianum	Poh	0.010891089	Poh	0.05
Pothos scandens	Poh	0.010891089	Poh	0.05
Alocasia macrorrhizos	Aro	0.050291159	Pro	0.05720339
Alocasia odora	Aro	0.050291159	Pro	0.05720339
Ariopsis peltata	Aro	0.050291159	Pro	0.05720339
Arisaema dracontium	Aro	0.050291159	Pro	0.05720339
Arisaema speciosum	Aro	0.050291159	Pro	0.05720339
Arisaema tortuosum	Aro	0.050291159	Pro	0.05720339
Arum cylindraceum	Aro	0.050291159	Pro	0.05720339
Arum pictum	Aro	0.050291159	Pro	0.05720339
Biarum tenuifolium	Aro	0.050291159	Pro	0.05720339
Colocasia esculenta	Aro	0.050291159	Pro	0.05720339
Colocasia fallax	Aro	0.050291159	Pro	0.05720339

Dracunculus vulgaris	Aro	0.050291159	Pro	0.05720339
Eminium spiculatum	Aro	0.050291159	Pro	0.05720339
Englerarum hypnosum	Aro	0.050291159	Pro	0.05720339
Helicodiceros muscivorus	Aro	0.050291159	Pro	0.05720339
Lazarum brownii	Aro	0.050291159	Pro	0.05720339
Leucocasia gigantea	Aro	0.050291159	Pro	0.05720339
Lorenzia umbrosa	Aro	0.050291159	Pro	0.05720339
Pinellia pedatisecta	Aro	0.050291159	Pro	0.05720339
Pistia stratiotes	Aro	0.050291159	Pro	0.05720339
Protarum sechellarum	Aro	0.050291159	Pro	0.05720339
Remusatia pumila	Aro	0.050291159	Pro	0.05720339
Remusatia vivipara	Aro	0.050291159	Pro	0.05720339
Sauromatum venosum	Aro	0.050291159	Pro	0.05720339
Steudnera kerrii	Aro	0.050291159	Pro	0.05720339
Theriophonum dalzellii	Aro	0.050291159	Pro	0.05720339
Typhonium blumei	Aro	0.050291159	Pro	0.05720339
Gymnostachys anceps	Gym	1	Pra	0.444444444
Lysichiton americanus	Oro	0.375	Pra	0.444444444
Orontium aquaticum	Oro	0.375	Pra	0.444444444
Symplocarpus foetidus	Oro	0.375	Pra	0.444444444
Scheuchzeria palustris	Sch	1	Sch	1
Asterostigma lividum	Aro	0.050291159	Spa	0.130434783
Bognera recondita	Aro	0.050291159	Spa	0.130434783
Croatiella integrifolia	Aro	0.050291159	Spa	0.130434783
Dieffenbachia aglaonematifolia	Aro	0.050291159	Spa	0.130434783
Gearum brasiliense	Aro	0.050291159	Spa	0.130434783
Gorgonidium intermedium	Aro	0.050291159	Spa	0.130434783
Incarum pavonii	Aro	0.050291159	Spa	0.130434783
Mangonia tweedieana	Aro	0.050291159	Spa	0.130434783
Spathantheum orbignyanum	Aro	0.050291159	Spa	0.130434783
Spathicarpa hastifolia	Aro	0.050291159	Spa	0.130434783
Synandrospadix vermitoxicus	Aro	0.050291159	Spa	0.130434783
Taccarum weddellianum	Aro	0.050291159	Spa	0.130434783
Holochlamys beccarii	Mon	0.097765363	Spt	0.08
Spathiphyllum cannifolium	Mon	0.097765363	Spt	0.08
Spathiphyllum commutatum	Mon	0.097765363	Spt	0.08
Spathiphyllum wallisii	Mon	0.097765363	Spt	0.08
Amorphophallus angolensis	Aro	0.050291159	Tho	0.015228426
Amorphophallus paeoniifolius	Aro	0.050291159	Tho	0.015228426
Pseudodracontium lanceolatum	Aro	0.050291159	Tho	0.015228426
Ambrosina bassii	Aro	0.050291159	Thy	0.35
Arisarum vulgare	Aro	0.050291159	Thy	0.35
Arophyton buchetii	Aro	0.050291159	Thy	0.35

Carlephyton glaucophyllum	Aro	0.050291159	Thy	0.35
Colletogyne perrieri	Aro	0.050291159	Thy	0.35
Peltandra virginica	Aro	0.050291159	Thy	0.35
Typhonodorum lindleyanum	Aro	0.050291159	Thy	0.35
Isidrogalvia sessiliflora	Tof	0.178571429	Tof	0.178571429
Pleea tenuifolia	Tof	0.178571429	Tof	0.178571429
Tofieldia coccinea	Tof	0.178571429	Tof	0.178571429
Tofieldia pusilla	Tof	0.178571429	Tof	0.178571429
Triantha glutinosa	Tof	0.178571429	Tof	0.178571429
Gonatopus angustus	Zam	0.09375	Zam	0.09375
Stylochaeton bogneri	Zam	0.09375	Zam	0.09375
Zamioculcas zamiifolia	Zam	0.09375	Zam	0.09375
Zantedeschia aethiopica	Aro	0.050291159	Zan	0.25
Zantedeschia albomaculata	Aro	0.050291159	Zan	0.25
Phyllospadix iwatensis	Zos	0.136363636	Zos	0.136363636
Zostera marina	Zos	0.136363636	Zos	0.136363636
Zostera tasmanica	Zos	0.136363636	Zos	0.136363636

TABLE S3. Morphological and ecological traits used in the ancestral state reconstructions. NA represents missing information.

Genus	Life form1	Life form2	Life_Form3	Distribution	Life cycle	Flower sexuality	Perianth	Pollen_exine	Pollen_type
Acorus	Terrestrial	Rhizomatous	Terrestrial	Temperate Zones	Evergreen	bisexual	present	present	monosulcate
Alisma	Rooted_aquatic	Rhizomatous	Aquatic	Tropics-Temperate Zones	Evergreen	bisexual	present	present	pantoporate
Astonia	Rooted_aquatic	?	Aquatic	Tropics	NA	bisexual	present	NA	NA
Baldellia	Rooted_aquatic	Rhizomatous	Aquatic	Temperate Zones	NA	bisexual	present	present	pantoporate
Butomopsis	Rooted_aquatic	Caulescent	Aquatic	Tropics	Evergreen	bisexual	present	present	pantoporate
Caldesia	Rooted_aquatic	Rhizomatous	Aquatic	Tropics-Temperate Zones	NA	bisexual	present	present	pantoporate
Damasonium	Rooted_aquatic	Rhizomatous	Aquatic	Temperate Zones	NA	bisexual	present	present	pantoporate
Echinodorus	Rooted_aquatic	Rhizomatous	Aquatic	Tropics	NA	bisexual	present	present	pantoporate
Helanthium	Rooted_aquatic		Aquatic	Tropics-Temperate Zones	NA	bisexual	present	NA	NA
Hydrocleys	Rooted_aquatic	Caulescent	Aquatic	Tropics	NA	bisexual	present	present	pantoporate
Limnocharis	Rooted_aquatic	Rhizomatous	Aquatic	Tropics	Evergreen	bisexual	present	present	pantoporate
Limnophyton	Rooted_aquatic	Rhizomatous	Aquatic	Tropics	NA	NA	present	present	pantoporate
Luronium	Rooted_aquatic	Rhizomatous	Aquatic	Temperate Zones	NA	bisexual	present	present	pantoporate
Ranalisma	Rooted_aquatic	Rhizomatous	Aquatic	Tropics	Evergreen	bisexual	present	present	pantoporate
Sagittaria	Rooted_aqu	Rhizomato	Aquatic	Tropics-	NA	unisexual	present	present	pantoporate

	atic	us		Temperate Zones					
Wiesneria	Rooted_aquatic	Rhizomatous	Aquatic	Tropics	NA	bisexual	present	present	pantoporate
Aponogeton	Rooted_aquatic	Tuberous	Aquatic	Tropics	NA	unisexual	present	present	monosulcate
Adelonema	Terrestrial	?	Terrestrial	Tropics	Evergreen	unisexual	absent	reduced	inaperturate
Aglaodorum	Rooted_aquatic	Rhizomatous	Aquatic	Tropics	Evergreen	unisexual	absent	reduced	inaperturate
Aglaonema	Terrestrial	Caulescent	Terrestrial	Tropics	Evergreen	unisexual	absent	reduced	inaperturate
Alocasia	Terrestrial	Rhizomatous	Terrestrial	Tropics	Evergreen	unisexual	absent	reduced	inaperturate
Ambrosina	Terrestrial	Tuberous	Terrestrial	Temperate Zones	Seasonally dormant	unisexual	absent	reduced	inaperturate
Amorphophallus	Terrestrial	Tuberous	Terrestrial	Tropics	Seasonally dormant	unisexual	absent	reduced	inaperturate
Anchomanes	Terrestrial	Rhizomatous	Terrestrial	Tropics	Seasonally dormant	unisexual	absent	reduced	inaperturate
Anubias	Rooted_aquatic	Rhizomatous	Aquatic	Tropics	Seasonally dormant	unisexual	absent	reduced	inaperturate
Apoballis	Terrestrial	Rhizomatous	Terrestrial	Tropics	Evergreen	unisexual	absent	reduced	inaperturate
Aridarum	Terrestrial	Caulescent	Terrestrial	Tropics	Evergreen	unisexual	absent	reduced	inaperturate
Ariopsis	Terrestrial	Tuberous	Terrestrial	Tropics	Seasonally dormant	unisexual	absent	reduced	inaperturate
Arisaema	Terrestrial	Tuberous	Terrestrial	Temperate Zones	Seasonally dormant	unisexual	absent	reduced	inaperturate
Arisarum	Terrestrial	Tuberous	Terrestrial	Temperate Zones	Seasonally dormant	unisexual	absent	reduced	inaperturate
Arophyton	Terrestrial	Rhizomatous	Terrestrial	Tropics	Seasonally dormant	unisexual	absent	reduced	inaperturate
Arum	Terrestrial	Tuberous	Terrestrial	Temperate Zones	Seasonally dormant	unisexual	absent	reduced	inaperturate
Asterostigma	Terrestrial	Tuberous	Terrestrial	Tropics	Seasonally dormant	unisexual	absent	reduced	inaperturate
Bakoa	Terrestrial	Rhizomato	Terrestrial	Tropics	Evergreen	unisexual	absent	reduced	inaperturate

		us							
Biarum	Terrestrial	Tuberous	Terrestrial	Temperate Zones	Seasonally dormant	unisexual	absent	reduced	inaperturate
Bognera	Terrestrial	Rhizomatous	Terrestrial	Tropics	Evergreen	unisexual	absent	reduced	inaperturate
Bucephalandra	Terrestrial	Caulescent	Terrestrial	Tropics	Evergreen	unisexual	absent	reduced	inaperturate
Caladium	Terrestrial	Tuberous	Terrestrial	Tropics	Seasonally dormant	unisexual	absent	reduced	inaperturate
Calla	Rooted_aquatic	Rhizomatous	Aquatic	Temperate Zones	Seasonally dormant	bisexual	absent	present	diaperturate
Callopsis	Terrestrial	Rhizomatous	Terrestrial	Tropics	Evergreen	unisexual	absent	reduced	inaperturate
Carlephyton	Terrestrial	Tuberous	Terrestrial	Tropics	Seasonally dormant	unisexual	absent	reduced	inaperturate
Cercestis	Epiphytic	Climbing herbs	Terrestrial	Tropics	Evergreen	unisexual	absent	reduced	inaperturate
Chlorospatha	Terrestrial	Caulescent	Terrestrial	Tropics	Evergreen	unisexual	absent	reduced	inaperturate
Colletogyne	Terrestrial	Tuberous	Terrestrial	Tropics	Seasonally dormant	unisexual	absent	reduced	inaperturate
Colocasia	Terrestrial	Tuberous	Terrestrial	Tropics	Seasonally dormant	unisexual	absent	reduced	inaperturate
Croatiella	Terrestrial	Tuberous	Terrestrial	Tropics	Seasonally dormant	unisexual	absent	reduced	inaperturate
Cryptocoryne	Rooted_aquatic	Rhizomatous	Aquatic	Tropics	Evergreen	unisexual	absent	reduced	inaperturate
Culcasia	Epiphytic	Climbing herbs	Terrestrial	Tropics	Evergreen	unisexual	absent	reduced	inaperturate
Dieffenbachia	Terrestrial	Caulescent	Terrestrial	Tropics	Evergreen	unisexual	absent	reduced	inaperturate
Dracunculus	Terrestrial	Tuberous	Terrestrial	Temperate Zones	Seasonally dormant	unisexual	absent	reduced	inaperturate
Eminium	Terrestrial	Tuberous	Terrestrial	Temperate Zones	Seasonally dormant	unisexual	absent	reduced	inaperturate
Englerarum	Terrestrial	Rhizomatous	Terrestrial	Tropics	Seasonally dormant	unisexual	absent	reduced	inaperturate
Filarum	Terrestrial	Tuberous	Terrestrial	Tropics	Evergreen	unisexual	absent	reduced	inaperturate

Furtadoa	Terrestrial	Caulescent	Terrestrial	Tropics	Evergreen	unisexual	absent	reduced	inaperturate
Gearum	Terrestrial	Tuberous	Terrestrial	Tropics	Seasonally dormant	unisexual	absent	reduced	inaperturate
Gorgonidium	Terrestrial	Tuberous	Terrestrial	Tropics	Seasonally dormant	unisexual	absent	reduced	inaperturate
Hapaline	Terrestrial	Tuberous	Terrestrial	Tropics	Seasonally dormant	unisexual	absent	reduced	inaperturate
Helicodiceros	Terrestrial	Tuberous	Terrestrial	Temperate Zones	Seasonally dormant	unisexual	absent	reduced	inaperturate
Hestia	Terrestrial	Rhizomatous	Terrestrial	Tropics	Evergreen	unisexual	absent	reduced	inaperturate
Homalomena	Terrestrial	Rhizomatous	Terrestrial	Tropics	Evergreen	unisexual	absent	reduced	inaperturate
Hottarum	Terrestrial	Caulescent	Terrestrial	Tropics	Evergreen	unisexual	absent	reduced	inaperturate
Incarum	Terrestrial	Tuberous	Terrestrial	Tropics	Seasonally dormant	unisexual	absent	reduced	inaperturate
Jasarum	Rooted_aquatic	Caulescent	Aquatic	Tropics	Evergreen	unisexual	absent	reduced	inaperturate
Lagenandra	Rooted_aquatic	Rhizomatous	Aquatic	Tropics	Evergreen	unisexual	absent	reduced	inaperturate
Lazarum	Terrestrial	Tuberous	Terrestrial	Tropics	Seasonally dormant	unisexual	absent	reduced	inaperturate
Leucocasia	Terrestrial	Tuberous	Terrestrial	Tropics	Evergreen	unisexual	absent	reduced	inaperturate
Lorenzia	Terrestrial	Rhizomatous	Terrestrial	Tropics	Evergreen	unisexual	absent	reduced	inaperturate
Mangonia	Terrestrial	Tuberous	Terrestrial	Tropics	Seasonally dormant	unisexual	absent	reduced	inaperturate
Montrichardia	Rooted_aquatic	Caulescent	Aquatic	Tropics	Evergreen	unisexual	absent	reduced	inaperturate
Nephthytis_Africa	Terrestrial	Rhizomatous	Terrestrial	Tropics	Seasonally dormant	unisexual	absent	reduced	inaperturate
Nephthytis_Asia	Terrestrial	Tuberous	Terrestrial	Tropics	Seasonally dormant	unisexual	absent	reduced	inaperturate
Ooia	Terrestrial	Rhizomatous	Terrestrial	Tropics	Evergreen	unisexual	absent	reduced	inaperturate
Peltandra	Rooted_aqu	Rhizomato	Aquatic	Temperate	Seasonall	unisexual	absent	reduced	inaperturate

	atic	us		Zones	y dormant				
Philodendron	Epiphytic	Climbing herbs	Terrestrial	Tropics	Evergreen	unisexual	absent	reduced	inaperturate
Philonotion	Terrestrial	Rhizomatous	Terrestrial	Tropics	Evergreen	unisexual	absent	reduced	inaperturate
Phymatarum	Terrestrial	Caulescent	Terrestrial	Tropics	Evergreen	unisexual	absent	reduced	inaperturate
Pichinia	Terrestrial	Rhizomatous	Terrestrial	Tropics	Evergreen	unisexual	absent	reduced	inaperturate
Pinellia	Terrestrial	Tuberous	Terrestrial	Temperate Zones	Seasonally dormant	unisexual	absent	reduced	inaperturate
Piptospatha	Terrestrial	Caulescent	Terrestrial	Tropics	Evergreen	unisexual	absent	reduced	inaperturate
Pistia	Free-floating	Free-floating	Aquatic	Tropics	Evergreen	unisexual	absent	reduced	inaperturate
Protarum	Terrestrial	Tuberous	Terrestrial	Tropics	Seasonally dormant	unisexual	absent	reduced	inaperturate
Pseudohydrosme	Terrestrial	Tuberous	Terrestrial	Tropics	Seasonally dormant	unisexual	absent	reduced	inaperturate
Remusatia	Epiphytic	Tuberous	Terrestrial	Tropics	Seasonally dormant	unisexual	absent	reduced	inaperturate
Sauromatum	Terrestrial	Tuberous	Terrestrial	Tropics	Seasonally dormant	unisexual	absent	reduced	inaperturate
Scaphispatha	Terrestrial	Tuberous	Terrestrial	Tropics	Seasonally dormant	unisexual	absent	reduced	inaperturate
Schismatoglottis	Terrestrial	Rhizomatous	Terrestrial	Tropics	Evergreen	unisexual	absent	reduced	inaperturate
Schottariella	Terrestrial	Rhizomatous	Terrestrial	Tropics	Evergreen	unisexual	absent	reduced	inaperturate
Schottarum	Terrestrial	Rhizomatous	Terrestrial	Tropics	Evergreen	unisexual	absent	reduced	inaperturate
Spathantheum	Terrestrial	Tuberous	Terrestrial	Tropics	Seasonally dormant	unisexual	absent	reduced	inaperturate
Spathicarpa	Terrestrial	Tuberous	Terrestrial	Tropics	Seasonally dormant	unisexual	absent	reduced	inaperturate
Steudnera	Terrestrial	Caulescent	Terrestrial	Tropics	Evergreen	unisexual	absent	reduced	inaperturate
Synandrospadix	Terrestrial	Tuberous	Terrestrial	Tropics	Seasonally dormant	unisexual	absent	reduced	inaperturate

Syngonium	Epiphytic	Climbing herbs	Terrestrial	Tropics	Evergreen	unisexual	absent	reduced	inaperturate
Taccarum	Terrestrial	Tuberous	Terrestrial	Tropics	Seasonally dormant	unisexual	absent	reduced	inaperturate
Theriophonum	Terrestrial	Tuberous	Terrestrial	Tropics	Seasonally dormant	unisexual	absent	reduced	inaperturate
Typhonium	Terrestrial	Tuberous	Terrestrial	Tropics	Seasonally dormant	unisexual	absent	reduced	inaperturate
Typhonodorum	Rooted_aquatic	Rhizomatous	Aquatic	Tropics	Evergreen	unisexual	absent	reduced	inaperturate
Ulearum	Terrestrial	Rhizomatous	Terrestrial	Tropics	Evergreen	unisexual	absent	reduced	inaperturate
Xanthosoma	Terrestrial	Tuberous	Terrestrial	Tropics	Evergreen	unisexual	absent	reduced	inaperturate
Zantedeschia	Terrestrial	Tuberous	Terrestrial	Tropics	Seasonally dormant	unisexual	absent	reduced	inaperturate
Zomicarpa	Terrestrial	Rhizomatous	Terrestrial	Tropics	Seasonally dormant	unisexual	absent	reduced	inaperturate
Zomicarpella	Terrestrial	Rhizomatous	Terrestrial	Tropics	Seasonally dormant	unisexual	absent	reduced	inaperturate
Butomus	Rooted_aquatic	Rhizomatous	Aquatic	Temperate Zones	Evergreen	bisexual	present	present	monosulcate
Amphibolis	Rooted_aquatic	Rhizomatous	Aquatic	Temperate Zones	Evergreen	unisexual	absent	reduced	inaperturate
Cymodocea	Rooted_aquatic	Rhizomatous	Aquatic	Tropics	Evergreen	unisexual	absent	reduced	inaperturate
Halodule	Rooted_aquatic	Rhizomatous	Aquatic	Tropics	Evergreen	unisexual	absent	reduced	inaperturate
Ruppia	Rooted_aquatic	Rhizomatous	Aquatic	Tropics-Temperate Zones	Evergreen	bisexual	absent	present	triaperturate
Syringodium	Rooted_aquatic	?	Aquatic	Tropics	Evergreen	unisexual	absent	NA	NA
Thalassodendron	Rooted_aquatic	Rhizomatous	Aquatic	Tropics-Temperate Zones	Evergreen	unisexual	absent	reduced	inaperturate
Gymnostachys	Terrestrial	Rhizomatous	Terrestrial	Temperate Zones	Evergreen	bisexual	present	present	monosulcate

Apalanthe	Rooted_aquatic	Caulescent	Aquatic	Tropics	NA	bisexual	present	present	inaperturate
Blyxa	Rooted_aquatic	Caulescent	Aquatic	Tropics	NA	unisexual	present	present	inaperturate
Egeria	Rooted_aquatic	Caulescent	Aquatic	Tropics-Temperate Zones	Evergreen	unisexual	present	present	inaperturate
Elodea	Rooted_aquatic	Caulescent	Aquatic	Temperate Zones	Evergreen	unisexual	present	present	inaperturate
Enhalus	Rooted_aquatic	Rhizomatous	Aquatic	Tropics-Temperate Zones	Evergreen	unisexual	present	reduced	inaperturate
Halophila	Rooted_aquatic	Caulescent	Aquatic	Tropics	NA	unisexual	present	reduced	inaperturate
Hydrilla	Rooted_aquatic	Caulescent	Aquatic	Tropics-Temperate Zones	Evergreen	unisexual	present	reduced	inaperturate
Hydrocharis	Rooted_aquatic	Caulescent	Aquatic	Tropics-Temperate Zones	Evergreen	unisexual	present	present	inaperturate
Lagarosiphon	Rooted_aquatic	Caulescent	Aquatic	Tropics	Evergreen	unisexual	present	present	inaperturate
Limnobium	Rooted_aquatic	Caulescent	Aquatic	Tropics-Temperate Zones	Evergreen	unisexual	present	present	inaperturate
Najas	Rooted_aquatic	Caulescent	Aquatic	Tropics-Temperate Zones	Seasonally dormant	unisexual	absent	reduced	inaperturate
Nechamandra	Rooted_aquatic	Caulescent	Aquatic	Tropics	Seasonally dormant	unisexual	present	present	inaperturate
Ottelia	Rooted_aquatic	?	Aquatic	Tropics	NA	unisexual	present	present	inaperturate
Stratiotes	Rooted_aquatic	Caulescent	Aquatic	Temperate Zones	Evergreen	unisexual	present	present	inaperturate
Thalassia	Rooted_aquatic	Rhizomatous	Aquatic	Tropics	Evergreen	unisexual	present	reduced	inaperturate
Vallisneria	Rooted_aqu	Caulescent	Aquatic	Tropics	NA	unisexual	present	reduced	inaperturate

	atic								
Cycnogeton	Rooted_aquatic	?	Aquatic	NA	NA	bisexual	present	NA	inaperturate
Tetroncium	Rooted_aquatic	Caulescent	Aquatic	Temperate Zones	Evergreen	bisexual	present	NA	inaperturate
Triglochin	Rooted_aquatic	Caulescent	Aquatic	Tropics-Temperate Zones	Evergreen	bisexual	present	present	inaperturate
Anaphyllopsis	Terrestrial	Rhizomatous	Terrestrial	Tropics	Seasonally dormant	bisexual	present	present	monosulcate
Anaphyllum	Terrestrial	Rhizomatous	Terrestrial	Tropics	Evergreen	bisexual	present	present	monosulcate
Cyrtosperma	Rooted_aquatic	Rhizomatous	Aquatic	Tropics	Evergreen	bisexual	present	present	monosulcate
Dracontioides	Rooted_aquatic	Rhizomatous	Aquatic	Tropics	Seasonally dormant	bisexual	present	present	monosulcate
Dracontium	Terrestrial	Tuberous	Terrestrial	Tropics	Seasonally dormant	bisexual	present	present	monosulcate
Lasia	Rooted_aquatic	Rhizomatous	Aquatic	Tropics	Evergreen	bisexual	present	present	monosulcate
Lasimorpha	Terrestrial	Rhizomatous	Terrestrial	Tropics	Evergreen	bisexual	present	present	monosulcate
Podolasia	Rooted_aquatic	Rhizomatous	Aquatic	Tropics	Evergreen	bisexual	present	present	monosulcate
Pycnospatha	Terrestrial	Tuberous	Terrestrial	Tropics	Seasonally dormant	bisexual	present	present	monosulcate
Urospatha	Rooted_aquatic	Rhizomatous	Aquatic	Tropics	Evergreen	bisexual	present	present	monosulcate
Landoltia	Free-floating	Free-floating	Aquatic	Tropics-Temperate Zones	Evergreen	bisexual	absent	present	ulcerate
Lemna	Free-floating	Free-floating	Aquatic	Tropics-Temperate Zones	Evergreen	bisexual	absent	present	ulcerate
Spirodela	Free-floating	Free-floating	Aquatic	Tropics-Temperate Zones	Evergreen	bisexual	absent	present	ulcerate

Wolffia	Free-floating	Free-floating	Aquatic	Tropics-Temperate Zones	Evergreen	bisexual	absent	present	ulcerate
Wolffiella	Free-floating	Free-floating	Aquatic	Tropics-Temperate Zones	Evergreen	bisexual	absent	present	ulcerate
Maundia	Rooted_aquatic	Rhizomatous	Aquatic	Tropics-Temperate Zones	NA	bisexual	present	present	inaperturate
Alloschemone	Epiphytic	Climbing herbs	Terrestrial	Tropics	Evergreen	bisexual	absent	present	
Amydrium	Epiphytic	Climbing herbs	Terrestrial	Tropics	Evergreen	bisexual	absent	present	zonate
Anadendrum	Epiphytic	Climbing herbs	Terrestrial	Tropics	Evergreen	bisexual	present	present	inaperturate
Epipremnum	Epiphytic	Climbing herbs	Terrestrial	Tropics	Evergreen	bisexual	absent	present	zonate
Heteropsis	Epiphytic	Climbing herbs	Terrestrial	Tropics	Evergreen	bisexual	absent	present	zonate
Holochlamys	Terrestrial	Caulescent	Terrestrial	Tropics	Evergreen	bisexual	present	present	polyplicate
Monstera	Epiphytic	Climbing herbs	Terrestrial	Tropics	Evergreen	bisexual	absent	present	zonate
Rhaphidophora	Epiphytic	Climbing herbs	Terrestrial	Tropics	Evergreen	bisexual	absent	present	zonate
Rhodospatha	Epiphytic	Climbing herbs	Terrestrial	Tropics	Evergreen	bisexual	absent	present	zonate
Scindapsus	Epiphytic	Climbing herbs	Terrestrial	Tropics	Evergreen	bisexual	absent	present	zonate
Spathiphyllum	Terrestrial	Caulescent	Terrestrial	Tropics	Evergreen	bisexual	present	present	polyplicate
Stenospermation	Epiphytic	Climbing herbs	Terrestrial	Tropics	Evergreen	bisexual	absent	present	zonate
Lysichiton	Rooted_aquatic	Rhizomatous	Aquatic	Temperate Zones	Seasonally dormant	bisexual	present	present	monosulcate
Orontium	Rooted_aquatic	Rhizomatous	Aquatic	Temperate Zones	Seasonally dormant	bisexual	present	present	monosulcate
Symplocarpus	Rooted_aqu	Rhizomato	Aquatic	Temperate	Seasonall	bisexual	present	present	monosulcate

	atic	us		Zones	y dormant				
Posidonia	Rooted_aquatic	Rhizomatous	Aquatic	Temperate Zones	Evergreen	bisexual	absent	reduced	inaperturate
Groenlandia	Rooted_aquatic	?	Aquatic	Temperate Zones	NA	bisexual	present	present	inaperturate
Lepilaena	Rooted_aquatic	?	Aquatic	NA	NA	unisexual	present	present	inaperturate
Potamogeton	Rooted_aquatic	?	Aquatic	Tropics-Temperate Zones	Evergreen	bisexual	present	present	inaperturate
Stuckenia	Rooted_aquatic	?	Aquatic	NA	NA	bisexual	present	present	inaperturate
Zannichellia	Rooted_aquatic	?	Aquatic	Tropics-Temperate Zones	NA	unisexual	absent	present	inaperturate
Anthurium	Epiphytic	Climbing herbs	Terrestrial	Tropics	Evergreen	bisexual	present	present	forate
Pedicellarum	Epiphytic	Climbing herbs	Terrestrial	Tropics	Evergreen	bisexual	present	present	monosulcate
Pothoidium	Epiphytic	Climbing herbs	Terrestrial	Tropics	Evergreen	bisexual	present	present	monosulcate
Pothos	Epiphytic	Climbing herbs	Terrestrial	Tropics	Evergreen	bisexual	present	present	monosulcate
Scheuchzeria	Rooted_aquatic	Rhizomatous	Aquatic	Temperate Zones	NA	bisexual	present	present	inaperturate
Isidrogalvia	Rooted_aquatic	Caulescent	Aquatic	NA	NA	bisexual	present	present	monosulcate
Pleea	Terrestrial	Caulescent	Terrestrial	NA	NA	bisexual	present	present	diaperturate
Tofieldia	Terrestrial	Caulescent	Terrestrial	NA	NA	bisexual	present	present	diaperturate
Triantha	Terrestrial	Caulescent	Terrestrial	NA	NA	bisexual	present	present	diaperturate
Gonatopus	Terrestrial	Tuberous	Terrestrial	Tropics	Seasonally dormant	unisexual	present	present	zonate
Stylochaeton	Terrestrial	Rhizomatous	Terrestrial	Tropics	Seasonally dormant	unisexual	present	present	inaperturate
Zamioculcas	Terrestrial	Rhizomatous	Terrestrial	Tropics	Seasonally dormant	unisexual	present	present	zonate

Phyllospadix	Rooted_aquatic	Rhizomatous	Aquatic	Temperate Zones	Evergreen	unisexual	absent	reduced	inaperturate
Zostera	Rooted_aquatic	Rhizomatous	Aquatic	Tropics-Temperate Zones	Evergreen	unisexual	absent	reduced	inaperturate

Chapter 2

Systematics, biogeography and morphological character evolution of the hemi-epiphytic subfamily Monsteroideae (Araceae)

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ABSTRACT

The subfamily Monsteroideae (Araceae) is the third richest clade in the family with about 500 species. It comprises mostly hemi-epiphytic or epiphytic species restricted to the tropics, with three continental tropical disjunctions. Using a dataset representing all twelve genera in Monsteroideae (ca. 100 taxa), and five plastid and two nuclear markers, we studied the systematics and historical biogeography. We found high support for the monophyly of the three major clades (Spathiphylleae, *Heteropsis* clade and *Rhaphidophora* clade), and for seven of the genera within Monsteroideae. However, we found low rates of DNA variation, and the lack of molecular markers suitable for species level phylogenies in the group. Seed shape, size, number of seeds, and presence of endosperm showed utility in the classification of genera in Monsteroideae. We estimated ancestral ranges using a dispersal-extinction-cladogenesis model as implemented in the R package BioGeoBEARS and found evidence for a Laurasian origin of the clade. One tropical disjunction (*Monstera* sister to *Amydrium* + *Epipremnum*) was found to be the product of a previous Boreotropical distribution. Two other disjunctions are more recent and probably due to long distance dispersal. *Spathiphyllum* (with *Holochlamys* nested within) represents dispersal from South America to the islands in the Pacific of South East Asia; and *Rhaphidophora* represents dispersal from Asia to Tropical Africa.

Keywords

Araceae, BioGeoBEARS, biogeography, character evolution, tropical disjunction, Monsteroideae

INTRODUCTION

The family Araceae belongs to the early diverging monocot order Alismatales and comprises ca. 122 genera and ca. 3500 species —although ca. 4000 are estimated by Boyce & Croat (2014); they are distributed worldwide (Mayo *et al.* 1997; Cusimano et al., 2011a). Approximately 90% of the genera and 95% of the species of Araceae are found in the tropics, with approximately half of the species believed to be exclusively Neotropical (Croat, 1979; Nauheimer et al., 2012). Araceae is considered one of the dominant tropical families of angiosperms, and one of the most important components of humid forests, where aroids are characterized for both high species diversity and local endemism (Croat 1983, 1988, 1992). Despite extensive work by many fine taxonomists (see Croat, 1998 for a detailed taxonomic history of the family), systematics of tropical Araceae remains a field of active research with about 280 new species described in the last four years alone. In addition, several molecular phylogenetic studies in Araceae have been published recently. Although these have focused mostly on the family level, species level studies of Old World and temperate taxa have been conducted as well (e.g., Grob et al., 2004; Renner et al., 2004; Mansion et al., 2008; Wong et al., 2010). In spite of the fact that tropical America holds ca. 2000 species of aroids, only six species-level phylogenetic studies focused on Neotropical taxa have been published to date (*Anthurium* [Carlsen et al., 2013]; *Philodendron* [De Oliveirra et al., 2014; Gauthier et al., 2008], Spathicarpeae [Gonçalves et al., 2007], and Caladieae [Loh et al., 2000]).

The most recent classification of Araceae divides the family into eight clear subfamilies, although some issues of delimitation remain, especially in the largest

subfamily Aroideae (Cabrera et al., 2008; Cusimano et al., 2011a, Chartier et al., 2014; Henriquez et al., 2014). The subfamilies Monsteroideae and Pothoideae form a clade that is sister to the rest of 'true Araceae' (Cabrera et al., 2008; Cusimano et al., 2011a; Henriquez et al., 2014). The Monsteroideae is one of the most taxonomically challenging clades within Araceae (Tam et al., 2004; Zuluaga et al., 2015 **See Appendix 1**), and is the third richest subfamily with some 400 described species (and many still undescribed). As part of one of the earliest diverging lineages in the family, Monsteroideae may help to provide a clearer picture of the evolution within the ecologically important family Araceae. It comprises mostly hemiepiphytic and epiphytic climbers (Croat, 1988; Madison, 1977; Croat & Boyce, 2014) restricted to tropical America and Asia, except for one or two species that are native to tropical Africa (this intercontinental disjunction is interesting in its own right). The subfamily has a long taxonomic history, with *Monstera* being one of the first genera described in Araceae by Adanson in 1763. Schott (1860) first grouped together various genera from Monsteroideae based on floral morphology. Engler (1876) and Engler & Krause (1908) carried out two early taxonomic revisions of the group in which they circumscribed Monsteroideae to have two tribes and 12 genera based on leaf and inflorescence morpho-anatomical characters. Since then, many studies using different approaches and datasets have attempted to propose a robust classification of Araceae, including a classification for Monsteroideae (e.g., Bunting, 1962; Madison, 1977; Grayum, 1990; Bogner & Nicholson, 1991; Hay & Mabberley, 1991; French et al., 1995; Mayo et al., 1997; Carvell, 1989; Keating, 2003, 2004a, 2004b). However, a review of the historical systematic treatments of Monsteroideae has revealed the lack of consistent morphological characters used to delimit the genera and species (Tam et al.

2004). For instance, different authors have recognized 2-12 genera using the same set of characters (e.g., Bunting, 1962; Madison, 1977; Carvell, 1989; Grayum, 1990). Vegetative characters, in particular, (e.g., leaf shape) have been shown to be polymorphic within species, and convergent among genera (Madison, 1977). For this reason, currently, non-vegetative characters such as placentation, seed shape and size, septation of the ovary, and geography are regularly in use to define the genera (Bunting, 1962; Madison, 1977; Madison & Tiffany, 1976; Mayo et al., 1997). The current circumscription of Monsteroideae was not established until French et al. (1995) and Mayo et al. (1997) initiated phylogenetic work at the family level using AFLPs and morphology respectively. They found evidence to include *Heteropsis, Anadendrum,* and the tribe Spathiphylleae (*Spathiphyllum* + *Holochlamys*) within Monsteroideae. Tam et al. (2004) proposed the first molecular phylogenetic hypothesis for Monsteroideae using the plastid *trnL-trnF* spacer, and found strong support for the subfamily, but not much support for clades within the subfamily. Family-level molecular phylogenetic studies by Cabrera et al. (2008) and Cusimano et al. (2011a), based also exclusively on plastid DNA (*trnL-trnF* spacer, *rbcL* and *matK*), found the same clades as Tam et al. (2004) with slightly better support, but the monophyly of the genera was not tested. As a result, considerable debate has persisted around the circumscription of several genera of Monsteroideae such as *Amydrium, Epipremnum*, *Monstera*, *Rhaphidophora* and *Scindapsus*.

The current classification of Monsteroideae by Cusimano et al. (2011a) recognizes 12 genera grouped into three clades: 1) a Tropical America clade formed by *Alloschemone*, *Heteropsis*, *Rhodospatha* and *Stenospermation,* sister to the rest of the

subfamily; 2) the tribe Spathiphylleae comprising *Holochlamys* and *Spathiphyllum*; and 3) a mostly Old world clade comprising *Amydrium*, *Anadendrum*, *Epipremnum*, *Monstera*, *Scindapsus*, and *Rhaphidophora*. The first and third of these clades have been informally named the '*Heteropsis'* and '*Rhaphidophora'* Clades, respectively, by the same authors, and we will follow these names for simplicity. More recent studies using nuclear, chloroplast, and even plastome datasets have instead found Spathiphylleae to be sister to the rest of the Monsteroideae (Chartier et al., 2014, Henriquez et al., 2014; Zuluaga et al., 2015), as opposed to the *Heteropsis* Clade being sister to the rest.

Monsteroideae exhibits three unusual intercontinental geographic disjunctions: 1) *Spathiphyllum*, found primarily in Tropical America, also contains three species in Southeast Asia; these are in a clade with *Holochlamys becarii* from New Guinea; 2) *Monstera,* an exclusively Tropical American genus, is nested in a clade of otherwise Old World genera; and 3) *Rhaphidophora*, mostly from Asia, has one (or two) species in Africa. This pattern of sister groups being disjunct between tropical regions of the New and Old Worlds is shared with several angiosperm groups (e.g., Malphigiaceae, Rubiaceae (Nie et al., 2013), Magnoliaceae (Azuma et al., 2001), Leguminosae and Lauraceae (Renner, 2004)). The pattern has been explained by several competing hypotheses: 1) vicariance involving the break up of the Gondwanan supercontinent (Raven and Axelrod, 1974; Conti et al., 2002); 2) existence of a Boreotropical flora with subsequent extinction/migration across land bridges during Eocene/Oligocene (Davis et al., 2002); and 3) long-distance dispersal (LDD) (Renner et al., 2001; Givnish et al., 2004; Renner, 2004; Clayton et al., 2009; Christenhusz & Chase, 2013). Disjunction

between the tropics of Africa and Asia include two additional hypothesis: 1) an overland dispersal from eastern or south west Asia to Africa during the Miocene (Kappelman et al., 2003); and 2) dispersal from India to Madagascar through the 'Lemurian stepping stones' across the western Indian Ocean, and then to Africa during the Eocene-Oligocene (Schatz, 1996). Nauhmeier et al. (2012) investigated the history of geographic distribution in Araceae and suggested that many of the actual tropical disjunctions are products of extinction in Eurasia and North America, and migration to the tropics during the Oligocene (Boreotropical hypothesis) or the Quaternary. A trans-Laurasian range expansion has been suggested for the current distribution of *Spathiphyllum*. Madison (1977) and van Steenis (1962) mentioned that the Boreotropical flora hypothesis might explain the current distribution of *Monstera* and *Epipremnum*. Until now, however, there has been no objective attempt to explain disjunctions in Araceae using dated phylogenetic reconstructions.

Unlike most angiosperm families, the fossil record of Araceae is extensive, and represents (along with some other members of Alismatales) the oldest fossil records in the monocots (Stockey et al., 1997, 2007; Friis et al., 2004, 2006, 2010a; Bogner et al., 2005, 2007; Wilde et al., 2005). However, it is often difficult to assign fossils to particular subfamilies or extant genera within Araceae (Friis et al., 2010a; 2010b). Fossils that with certainty can be attributed to Monsteroideae come from the Cretaceous in India (Bonde 2000), and from the Pleistocene in southwestern Europe (Madison & Tiffney, 1976).

Here we expand previously published taxon and gene sampling across the subfamily Monsteroideae in order to test alternative phylogenetic and historical biogeographic hypotheses. One objective is to assess the utility of different molecular markers in reconstructing phylogenetic hypothesis down to the species level in Araceae, and we compare our results to previous classification systems. We also estimate ancestral ranges, and investigate the origin of the three unusual tropical geographic disjunctions in Monsteroideae. Finally, we evaluate the evolution of several key morphological characters traditionally used in taxonomic revisions of the subfamily.

METHODS

Sampling. A total of 126 accessions from subfamily Monsteroideae and members of the other seven subfamilies were sampled for this study. We included all 12 genera of the subfamily Monsteroideae, and available sequences in GenBank for 14 species of genera in the subfamily Pothoideae (*Anthurium*, *Pothos, Pedicellarum* and *Pothoideum*), and ten species representing the other six aroid subfamilies as outgroups **(Table 1).** Monsteroideae sampling included: one accession of the genus *Alloschemone*, five of *Amydrium*, three of *Anadendrum*, seven of *Epipremnum*, the monotypic genus *Holochalmys*, 28 of *Monstera*, 24 of *Rhaphidophora*, eight of *Rhodospatha*, four of *Scindapsus*, nine of *Spathiphyllum* (both Old and New World spp.), and nine of *Stenospermation* **(Table 1).** DNA samples from Neotropical genera were obtained from fieldwork (especially in Colombia, Ecuador and Panama), herbarium specimens, and/or the Araceae Greenhouse at the Missouri Botanical Garden in St. Louis, Missouri. Most of the DNA samples for species from Tropical Asia (e.g., *Rhaphidophora*, *Epipremnum*)

were obtained from the Royal Botanical Gardens Kew DNA Bank, and from the Jardin Botanique de Lyon.

DNA extraction, amplification and sequencing. DNA was extracted from silica-dried plant material, herbarium specimens, and/or living collections using the DNeasy Plant Mini Kit (Qiagen, Valencia, CA, USA) according to the manufacturer's specifications. Some recalcitrant samples were extracted using a CTAB method adapted from Doyle and Doyle (1987), or using the Promega, Maxwell® 16 platform.

Three plastid markers (*matK*, *rbcL* and *trnL-trnF* spacer) used in previous aroid studies were amplified (Cabrera et al., 2008; Cusimano et al., 2011a). Primers for *rbcL* came from Kress & Erickson (2007), for *matK* from Cuénoud et al. (2002), and for the *trnL-trnF* spacer from Taberlet et al. (1991). Additionally, ten other plastid markers highlighted in Shaw et al. (2005) were screened in a subset of samples across Monsteroideae in order to determine their nucleotide variability. The plastid regions *psbB-psbH*, *petA-psbJ*, *psbE-petL*, *rps16-trnQ*, and *trnT-psbD* spacers, and *ndhA* gene were amplified and sequenced successfully, but showed little variation, and were not used further in this study. The plastid markers *trnC-petN* spacer and partial *ycf1* showed the highest variation, and were amplified for the rest of the samples. We sequenced about 1000 bp of the first exon of the nuclear Phytochrome C (*PHYC*) gene using primers from Chartier et al. (2014) and new primers designed based on our sequences. PHYC sequences for several of the species in the *Rhaphidophora* clade presented many ambiguous nucleotides in the same positions among all the samples, suggesting the

presence of multiple copies in this clade. We performed BLAST searches of the *PHYC* gene sequences in the transcriptomes of *Anthurium andreanum* and *Landoltia punctata*, and in the *Spirodela polyrhiza* genome available in GenBank, and found a single match to the *PHYC* gene. Although previous studies in Araceae do not report the detection of multiple copies for the *PHYC* gene (Chartier et al. 2014), and our limited BLAST searches support this fact, we excluded all *PHYC* sequences from samples of the *Rhaphidophora* clade in our analysis since allele homology could not be verified. Finally, we developed primers for a region of about 700 bp in the second intron of the nuclear gene Chalcone Synthase (CHS), based on sequences from Carlsen & Croat (2013) and other monocots available in GenBank. We performed the same blast searches as in *PHYC*, and did not find multiple matches for these *CHS* sequences. Specific primers developed for *ycf1*, PHYC, and CHS are shown in **Table 2.**

PCR amplification was performed following the protocols from Cabrera et al. (2008). Nuclear marker amplification was enhanced by using 1-3 ul of betaine (10%) in a 25-ul reaction, and/or by adding up to 2 ul of DNA. The PCR products were purified using ExoSap-It (Cleveland, OH). Sequencing reactions used the BigDye Terminator Cycle Sequencing Kit (Applied Biosystems, Foster City, CA, USA), and were cleaned using Agencourt CleanSeq (Beverly, MA) magnetic beads. Samples were sequenced at the University of Wisconsin–Madison Biotechnology Center.

Molecular analysis. All sequences were assembled and manually edited in Geneious v8.0 (Biomatters, http://www.geneious.com/). Every gene was aligned using a

combination of MAFFT v7 (Katoh et al., 2002; Katoh & Standley, 2013) and MUSCLE v3.8. (Edgar, 2004). An initial alignment was performed in MAFFT with two subsequent refinements using MUSCLE. All alignments were checked manually in Geneious v8.0 using protein translation for the coding regions. We used PartitionFinder (Lanfear et al., 2012) to select the best-fit partitioning schemes and models. For the initial data blocks in PartitionFinder we allocated nucleotides from the protein-coding genes (*rbcL, matK, PHYC*, and *CHS*) according to whether they belonged to the first, second or third codon position, and all the other markers as independent data blocks, including the partial *trnK* intron flanking the *matK* gene, and the partial *ycf*1 gene. The *ycf1* sequences were not allocated into codon positions because of the difficulty in establishing the reading frame due to the presence of a 37bp inversion. We performed an initial PartitionFinder run allowing all models, and then a subsequent run allowing only models available in RAxML and MrBayes respectively. We used Bayesian information criteria (BIC) to choose the best-fit models. PartitionFinder suggested three partitions for the plastid dataset (**Table 3**): (1) the entire *matK* gene, the second codon position of *rbcL*, the *trnL-trnF* spacer and the partial *ycf1*; (2) the *trnK* intron, and the *trnc-petN* spacer; and (3) the first and third positions of *rbcL*. The nuclear PHYC data set had two partitions: (1) first and second codons positions; and (2) the third codon position. The nuclear CHS data set had three partitions, one for each codon position. Individual phylogenetic analyses for each marker were performed under Maximum Likelihood (ML) using RAxML v8.0 (Statamakis, 2006), and Bayesian Inference (BI) using MrBayes v3.2.3 (Ronquist et al., 2012) as implemented in the CIPRES portal (Miller et al., 2010). For RAxML, we used the best scheme for PartitionFinder, and GTRGAMMA model in all cases. We performed

100 independent tree searches and 1000 independent bootstraps analyses. For MrBayes we used the best scheme and models suggested by PartitionFinder. Bayesian analyses were performed using two independent MCMC runs with four chains and 20 million generations. A combined plastid analysis and also a "total evidence" analysis were performed in the same way. Additional unpartitioned analyses were performed for every individual and variously combined dataset.

Molecular dating. We employed the five-plastid markers dataset for Bayesian molecular dating using BEAST 1.8 (Drummond et al., 2012), and three calibrations points as used in Zuluaga et al. (**Chapter 1)** following recommendations of Sytsma et al. (2014). We used a set of fossils from the early Cretaceous (110 Ma) in Portugal described by Friis et al. (2010a) and Friis et al. (2010b) to constrain the crown node of a clade comprising Lemnoideae and the rest of Araceae (sensu Cusimano et al., 2011a). These fossils correspond to bisexual and unisexual inflorescences that can be assigned with certainty to the family, but their precise affinities within Araceae need more study. Secondly, we assigned *Petrocardium cerrejoense* from the Mid to Late Paleocene (56-61.6 Ma) in Colombia (Herrera et al., 2008) for the crown node of Pothoideae. Finally, for the stem node of the tribe Monstereae (subfamily Monsteroideae) we assigned *Rhodospathodendron tomlinsonii*, from the Late Cretaceous (66 Ma) from India (Bonde, 2000). We used lognormal priors with a mean=10 and SD=0.75 on the fossil calibrations. For the root of the tree we used a Uniform prior (110-135 Ma), based on previous dates calculated for the family Araceae (Nauheimer et al. 2012; Zuluaga et al. unpublished data)

Ancestral range estimation. We used the chronogram from our BEAST analysis as an input for the biogeography analysis. The chronogram was pruned to contain one sample per operational taxonomical unit (OTU). We chose the package BioGeoBEARS (Matkze, 2013) in R (R Development Core Team, 2008) for ancestral geographic area reconstruction because it allows us to compare several models and include parameters such as unequal rates of dispersal between areas and different dispersal rates through time. However, we focused on the comparison between the DEC model (Ree et al., 2005; Ree and Smith, 2008) and the DEC+j model, which incorporates founder-event speciation and allows for dispersal without range expansion (Matzke, 2012).

Initially we defined eight geographic areas modified from Kissling et al. (2012) to accommodate the distribution of the genera in Monsteroideae and outgroups. Nearctic (A), representing North America; Central America (B) including Southern Mexico, and the Caribbean islands; South America (C); Palearctic (D), including Europe and Temperate Asia; Africa (E); Southeast Asia (F); Australasia (G) including, Australia, New Zealand, New Guinea and the Pacific islands; and India (H). An additional set of analyses were performed merging Neotropical areas B and C. Areas occupied for each OTU were defined based on data provided by the Monocot CheckList (WCSP, 2014), herbarium specimens, and taxonomic monographs. *Rhodospatha* and *Stenospermation* were coded as present in Central and South America, since our sampling did not allow for finer separation. *Heteropsis* has only one species extending north into Central America, which is absent from our phylogenetic analysis, so this genus was coded as South

America only. Finally, *Monstera* species were coded according to their current distributions, either Central or South America or both.

We used a time-slice model, and different dispersal multipliers among areas, to try to represent connectivity among different areas at different periods of time. We performed a second analysis giving all areas equal dispersal probability through time to evaluate the effect of the time-slice model. The time slices used were 0-10, 10-50, 50-90 and 90-140 Ma. For the 0-10 Ma slice all main landmasses were in their current position. Palearctic and Nearctic were connected by the Beringian land bridge, and the connection between the Nearctic and Tropical America was completed. From 10 to 50 Ma main landmasses were close to their current position. India connected with Southeast Asia and the Paleartic. From 50-90 Ma (the Late Cretaceous to the Eocene and across the K-T boundary), India was moving towards Asia and the Paleartic, and Australasia separated from Antarctica. Finally, from 90-140 Ma (Early to Late Cretaceous), West Gondwana (South America + Africa) began to separate, as well as India and Madagascar, as both masses started to drift away from East Gondwana (including Australasia).

Since models used are nested, we compared them using a Likelihood ratio test (LRT) as implemented in BioGeoBEARS. To account for uncertainty in the phylogenetic reconstructions we used 100 randomly selected trees from the posterior distribution from the BEAST analysis after burn-in. We ran the DEC model (the preferred model according to LRT) on these 100 trees and counted the ancestral area estimation with highest frequency in nodes of particular interest. The nodes evaluated were the most common

recent ancestors (MRCA) of: *Rhaphidophora africana*, the genus *Monstera*, *Rhaphidophora* + *Anadendrum,* the *Rhaphidophora* clade, the *Heteropsis* clade, the Spathiphylleae, a clade comprising the so-called *Heteropsis* and *Rhaphidophora* clades, Monsteroideae, and a clade comprising Pothoideae plus Monsteroideae.

Character evolution. From the literature, herbarium specimens, spirit collections, and fieldwork observations we coded a set of characters traditionally used by aroid systematists in the delimitation of genera in Monsteroideae. The characters coded were: number of ovules, number of locules, presence of endosperm, seed length in lateral view, and seed width in lateral view (**Table 8**). The same species as the ones in our phylogenetic tree were used when possible, however the reduced number of collections and the lack of taxonomic clarity in genera like *Rhodospatha* and *Rhaphidophora* made it impossible to match our molecular and morphological sampling. In addition to discrete characters, images of seeds in lateral view for several species of each genus were obtained. These 2D-images were processed using the software Gimp v.2.8 to obtain outlines of the shape, and measurements of length and width in lateral view for each seed. Shapes were quantified using elliptic Fourier analysis in the R package Momocs v1.0 (Bonhomme et al., 2014), and principal component analysis (PCA) was performed on the harmonics produced by the outline analysis. Discrete characters were reconstructed using stochastic mapping (Bollback, 2006), and the rerooting method in the R package phytools (Revell, 2012). Because of the issues matching our phylogenetic tree with our seed data, continuous characters (seed size and PC components from pollen shape) were not evaluated in a phylogenetic framework.

RESULTS

Phylogenetic reconstructions. The concatenated alignment of the five plastid markers represents 6192 bp, and contains 38% gaps or missing data (**Table 4**). Variable sites vary between 8.3% (*rbcL*) and 51.7% (*matK*) for the ingroup. However, most of this variation is among genera, whereas variation within genera is low, ranging from only 1-10%. The partial *ycf1* has an indel of about 200 bp in the genus *Stenospermation*, and presents an inversion of 37 bp in several species across the subfamily; this region was excluded of the analyses. *trnL-trnF* spacer contains several indels, and a region of ca. 250 bp with high TA content and repeats was also excluded from the analyses. Finally, the *trnC-petN* spacer is considerably reduced in some species of the genus *Rhaphidophora* (only 300-340 bp) relative to the other taxa. CHS and PHYC alignments contain 692 bp and 1093 bp with 0.3 and 16.8 % missing data respectively (**Table 4**).

In general, Maximum Likelihood and Bayesian analyses of the individual plastid and nuclear datasets produced topologies largely lacking in resolution within the genera of Monsteroideae. ML bootstrap (BS) values > 75% and posterior probabilities from Bayesian inference (PP) > 0.95 are considered as "strong" support for the following results and discussion. The three major clades within Monsteroideae discussed earlier are recovered with strong support in all individual and combined analyses with plastid and nuclear markers, except with the nuclear marker CHS (**Table 5, Figures. 1-2**). There are no significant topology differences among ML partitioned and "unpartitioned" analyses, but support values varied, especially for the CHS marker **(Table 5, Fig 1-2)**. ML and BI

topologies vary slightly for some species relationships in nodes with low support. Concatenated analyses resemble the CHS gene tree for the relationships among genera.

Intergeneric relationships within Monsteroideae. The tribe Spathiphylleae is sister to the rest of Monsteroideae in all cases, but the support for this position is low (BS < 75; PP<0.95) for CHS analysis (**Figure 1-5**). Hypotheses for the generic relationships from different analyses are summarized in **Figure 5**. The plastid analyses recovered eight genera as monophyletic, seven of them with strong support (**Table 5**, **Figure 5**). However, only the genera *Anadendrum*, *Monstera*, *Rhodospatha*, *Scindapsus,* and *Stenospermation* are recovered as monophyletic consistently through all the analyses with high support (**Table 5, Figures 1-5**). The genera *Amydrium, Epipremnum, Heteropsis, Rhaphidophora, Spathiphyllum* and *Holochlamys*, appeared as not monophyletic in at least one analysis (**Table 5**). *Epipremnum* comprises at least two clades, the first one sister to the genus *Scindapsus*, and the second one to the genus *Amydrium*. *Rhaphidopora* is recovered as monophyletic in the combined plastid analyses (with no support), but not in the nuclear and total evidence analyses, where some species are sister to *Anadendrum*. Finally, the monotypic genus *Holochlamys* is nested within the genus *Spathiphyllum* with the plastid datasets. Nuclear dataset did not include enough samples to test *Spathiphyllum* vs. *Holochlamys* monophyly.

Molecular dating. Divergence time estimation analysis found an age of 68.83 Ma (95% confidence interval (CI) 64.20-76.73) for the crown age of Monsteroideae corresponding to the Late Cretaceous **(Figure 6)**. The ages for the crown of the three

main Monsteroideae clades are considerably younger than the crown of the subfamily, all falling into the Oligocene, but with the 95% confidence intervals extending into the Miocene and Eocene. The crown age for Spathiphylleae is 26.97 Ma (95% CI 14.64-42.9), 38.44 Ma (95% CI 27.68-50.88) for the *Rhaphidophora* clade, and 38.56 Ma (95% CI 26.92-51.60) for the *Heteropsis* clade **(Table 6, Figure 6)**.

Ancestral range estimation. The models with the addition of the time period slices conferred better likelihoods to the data (DEC+time periods LnL=-196.8 vs DEC LnL=-189, p=7.6e-05). Addition of the founder event (DEC + J) did not increase significantly the likelihood in any of the analyses (p=0.55-0.66), so we chose the simpler model to estimate the historical ranges within Monsteroideae. We will focus on the results of the seven-area analyses with time periods (DEC ln L=-190.81, DECj ln L=-190.91, p=0.66) for the results and discussion. The ancestor of Monsteroideae and the *Heteropsis* clade were estimated to range from Tropical America (BC) with higher probability (P=0.64 and P=0.99 respectively), and our analysis taking into account uncertainty recovered the range BC as the most probable (P>0.5) over the 100 trees (**Table 7, Figures 7 & 8**). The ancestral range of the *Rhaphidophora* clade was estimated to be in South East Asia (F) (P=0.54); however, this range was only recovered in 24 trees with P>0.50 (P=0.31, SD=0.22). Alternatively a range comprising areas BC (Tropical America) and F (South East Asia) has P=0.09 in the single chronogram, but its average probability over 100 trees is 0.23. The ancestral range of the Spathiphylleae was estimated to include Tropical America and Australasia (BC+G) (P=0.77) and the same range was recovered in 93 trees in the uncertainty analyses (P=0.24, SD=0.19).

Character evolution. ML and Bayesian estimations of the ancestral states for the discrete characters produced very similar results (**Figures 9 & 10**). The characters traditionally used for taxonomic purposes have evolved several times in Monsteroideae. Perianth was lost in *Rhaphidophora* + *Heteropsis* clades and regained in the genus *Anadendrum.* Endosperm is absent or very reduced in *Monstera*, *Heteropsis* and *Anadendrum.* Ancestral seed number is >10 with reductions to smaller numbers in several genera. PC1 of the seed shape analysis explain 69.2% of the variation, whereas PC2 and PC3 explained 13 % and 9.1 % respectively (**Figure 11**). There is not a clear separation among clades (p=0.1503) or genera (p=0.78) in Monsteroideae regarding seed shape, only the genus *Monstera* seems to have a distinctive in shape (**Figure 11**).

DISCUSSION

Monsteroideae classification and character evolution. Species level molecular studies of tropical aroids have been limited mainly because of the difficultly in obtaining samples, the lack of genomic tools, and the low variation of the molecular markers available. Taxonomic identification is another issue that remains problematic when working within the family Araceae. Our study explored the utility of several plastid and nuclear genes, and confirmed the lack of genetic informative regions for phylogenetic reconstruction at the species level in Tropical Araceae. The three main clades within Monsteroideae have been supported since the early molecular work (Tam et al., 2004; Cabrera et al., 2008). However, the position of Spathiphyllleae as sister to rest of

Monsteroideae is only recovered in the most recent studies with nuclear (Chartier et al., 2014), and plastome datasets (Henriquez et al., 2014). Our results strongly support the position of Spathiphylleae as sister to the rest of the Monsteroideae, in contrast to the topology used for the most recent aroid classification (Cusimano et al., 2011a); highlighting the importance of dense sampling for more accurate phylogenetic reconstructions when few molecular markers are available. The authors of that study proposed a set of synapomorphies to define the entire subfamily Monsteroideae that are, in fact, more appropriate for diagnosing the clade containing all Monsteroideae except Spathiphylleae (Zuluaga et al., 2015). These synapomorphies and the alternative characters present in Spathiphylleae are: 1) pollen zonate (i.e., ring-like or hamburger shape) (vs. pollen multiaperturate with exine surface striate/polyplicate in Spathiphylleae); 2) spathe soon deciduous with a distinct basal abscission (vs. spathe marcescent in Spathiphylleae); 3) large trichosclereids not in bundles (vs. smaller trichosclereids in bundles in Spathiphylleae). Additionally, another character that could be added is the hemiepiphytic or epiphytic habit (vs. terrestrial plants growing in shaded, wet places for Spathiphylleae). The only synapomorphy remaining for the entire Monsteroideae is the presence of trichosclereids, as proposed by Nicolson (1960). However, it is important to mention that detailed anatomical studies have found that trichosclereids are absent in the genera *Heteropsis* and *Anadendrum* (Carvell, 1989; Seubert, 1997; Keating, 2002, 2004a); they might be considered secondarily lost in these genera. Furthermore, trichosclerids are very occasionally present in at least four other species outside of Monsteroideae, for example in the genera *Pothos* (Nicolson, 1960), *Anthurium* (Keating, 2002), and *Montrichardia* (Solerder & Meyer, 1928). The last one is

a dubious report, and has never been confirmed with modern studies of *Montrichardia* tissues (Keating, 2002). Flower and seed characters investigated showed different levels of homoplasy. The clade Spathiphylleae is defined by having ovary trilocular. There seems to be convergence between *Heteropsis*, *Monstera* and *Anadendrum*, all having 1-2 large seeds, lacking endosperm; and between *Stenospermation* and *Rhaphidophora* with >10 small seeds with very similar shapes. However, a more dense morphological sampling is needed to test this hypothesis.

Spathiphylleae Clade. The support for the position of *Holochlamys becarii* within *Spathiphyllum* is low and therefore not conclusive, but the molecular analyses indicate that this species may in fact belong to the genus *Spathiphyllum*. *Holochlamys becarri* and the Asian species of *Spathiphyllum* form a monophyletic group (along with one accession of a South American species, *S. cannifolium,* that is nested in this clade as well). Species of this group are more closely related to the species of *Spathiphyllum* section *Massowia* than to the rest of *Spathiphyllum* (Zuluaga et al. 2015). *Holochlamys* and *Spathiphyllum* are very similar in habit and morphology (Bunting, 1960), stem vasculature (French & Tomlinson, 1981), palynological features (Grayum, 1992), and floral anatomy (Carvell, 1989). Moreover, *Holochlamys* shares with *Spathiphyllum* section *Massowia* the presence of fused perianth parts forming a cup around the pistil (Bunting, 1960; Carvell, 1989). Zuluaga et al. (2015) listed in detail the morpho-anatomical similarities between these two genera, but pointed out the need for wider sampling and well supported molecular data before drawing any conclusion about the taxonomic status of *Holochlamys*. At this point in time, all lines of evidence suggest that the two genera should be synonymized.

Heteropsis clade. Despite the fact that genera in this group form a clade, the relationships among them remain unclear. Only *Heteropsis* and *Alloschemone,* the most morphologically unique genera in Monsteroideae regarding morphology, form a consistent clade through all the analyses. There are no apparent similarities between these two groups, besides their geographic distribution (restricted to the Amazon Basin), and so their shared ancestry was unexpected. *Alloschemone* is an enigmatic taxon; only two species with very few collections are known, and they grow far apart in the Amazon (Madison, 1976; Bogner et al., 2001). *Alloschemone* was previously considered to be part of the old world genus *Scindapsus* (Madison, 1976) based on the presence of unilocular ovaries. However, its combination of morphological and anatomical characters does not resemble that or any other Monsteroideae. There are some superficial similarities shared with the flower anatomy of *Rhodospatha*, *Stenospermation* and *Monstera* (Carvell, 1989; see Bogner et al., 2001 for a throughout revision of *Alloschemone* morpho-anatomical characters), but our molecular data do not support a close relationship to any of these other genera. Fruits of *Alloschemone* have never been seen, and their pollen grains have been described as problematic to interpret, with a very inconspicuous sulcus, whereas all other Monsteroideae have fully zonate aperturate pollen. Most interestingly, Monsterodieae has a particular chromosome number evolution. The haploid number for the subfamily seems to be 15, with a genome duplication in the *Rhaphidophora* clade, n=30 (Cusimano et al., 2011b). Additionally, there are counts of n=56 in *Rhodospatha*, and n=56 and 84 in *Alloschemone*. Bogner et al. (2001) commented on the possibility of *Alloschemone* being a hexaploid. This polyploid origin, probably through hybridization,

could explain the unusual morphology, pollen anomalies, and the absence of fruit in *Alloschemone*, although better field collections and more molecular data are needed to support this hypothesis. Based on our results, future researchers are encouraged to more thoroughly compare *Alloschemone* with *Heteropsis*, and to consider the latter as putative parent for this unusual aroid genus.

Rhaphidophora clade. This group represents the most taxonomically challenging within Monsteroideae (Boyce, 2001), and the status of several genera within it has been challenged as a result of our study. *Rhaphidophora* is monophyletic in the plastid dataset, but there is no support for this hypothesis. Additional data will be needed to confirm it. Only the genera *Monstera* and *Anadendrum* are clearly monophyletic, and morphological characters and geographical distribution support their status as well. *Monstera* presents with flowers with one locule, producing generally one seed, with a distinctive shape and lacking endosperm; whereas *Anadendrum*, present flowers with perianth and fruits with one seed, lacking endosperm. In contrast, the genus *Epipremnum* is polyphyletic, with some species related to *Scindapsus* and others to *Amydrium*. Seubert (1997) studied trichosclereids in the vegetative tissues of Monsteroideae and found that *Amydrium* species and *E. pinnatum* do not have trichosclereids in the aerial roots and lamina. Additionally, *Amydrium* species and *E. pinnatum* share adult pinnatifid leaves, although we concede that vegetative characters shown high plasticity in the *Rhaphidophora* clade (Bogner et al., 2001). Nevertheless, these features support the results of the gene tree topologies, and the taxonomy of *Epipremnum* may need to be revisited.

Molecular dating and ancestral range estimation. Our time divergence estimation agrees with that of Zuluaga et al. (unpublished data, **Chapter 1**), which included greater taxon sampling for Araceae, Alismatales, and more fossil calibrations. Because of the already mentioned disagreements in tree topology with Nauheimer et al. (2012), and the use of a different set of fossils, our date estimates differ significantly for the crown age of Monsteroideae and the major clades within the subfamily. Nauheimer et al. (2012) estimated an age of 56.3 Ma (vs. 68.8 in our analysis) for Monsterodieae; 34.16 Ma (vs 21.3) for Spathiphylleae; 21.6 Ma (vs. 38.5) for the *Heteropsis* clade; and 29.7 (vs. 38.4) for the *Rhaphidophora* clade. We considered our estimates reflect closer the current knowledge of fossil record of Araceae and in particular of Monsteroideae. Recently described and other undescribed fossils (Friis et al., 2004; Friis et al., 2010a; 2010b; Coiffard et al., 2013; Kvaček & Smith, 2015) show that the Araceae, and very clearly the subfamily Orontiodeae, was widespread by the end of the Early Cretaceous (ca. 110 Ma). Most of the other subfamilies are already in the fossil record by the beginning of the Cenozoic (Friis et al., 2004), but it is probable they were already present by the late Cretaceous as indicated by previous studies and our molecular dating analysis. (Nauheimer et al., 2012; Zuluaga Unpublished data, **Chapter 1**). The affinity of some of the older fossils to Monsteroideae is inconclusive. *Mayoa portugallica* (110-120 Ma) resembles pollen from *Spathiphyllum* and *Holochlamys* (Friis et al., 2004; Friis et al., 2010), but these affinities have been challenged recently (Nauheimer et al., 2012a). Accurate fossil remains unquestionably assigned to Monsteroideae are from the Late Cretaceous (Bonde, 2000) in India, and from the Oligocene in Europe (Zetter et al., 2001; Madison & Tiffney, 1976). Other fossils from the Late Cretaceous in Europe resemble

Monsteroideae but they remain unpublished and were not used in our analyses (Friis et al. 2004).

Our biogeographic analyses estimated a Gondwanan ancestral range for the subfamily Monsteroideae, particularly in Tropical America. However, the fossil record and current distributions of extant taxa are difficult to explain completely with our biogeographic model. Additionally, the estimation for range the crown node of Pothoideae + Monsteroideae is ambiguous in our analyses (**Table 7**). The fossil record (albeit incomplete and poorly sampled from tropical areas of the world today) suggests that many members of Monsterodieae were part of the Boreotropical Flora, being widespread in the northern hemisphere from the late Cretaceous at least until the Oligocene (Madison & Tiffney, 1976), and then migrated to their current distributions in the tropics. This is not in conflict with a Gondwanan origin, but the inclusion of fossil distribution into the ancestral range estimation could change estimation drastically. Independently if the subfamily originated or arrived early to Tropical America during the late Cretaceous, we found evidence for independent dispersals events between tropical continental landmasses in the Monsteroideae. There are several cases of tropical disjunctions between sister groups in Araceae at the suprageneric level. For example, the Neotropical genera *Anthurium, Philodendron,* and *Jasarum* are sister to the Paleotropical Asian taxa *Pothos* (plus *Pothoidium* and *Pedicellarum*), *Homalomena*, and *Hapaline* respectively (Mayo et al., 1997; Grayum, 1992; Nauheimer et al., 2012). Many of these disjunctions have been explained by an early widespread distribution of Araceae in the Northern Hemisphere (Boreotropical Flora hypothesis) with migration southward to the

tropics of Central and South America, Asia, and Africa, and subsequent extinction in North America and Europe (Nauheimer et al., 2012). In our case only the disjunction between *Monstera* and the rest of the *Rhaphidophora* clade can be explained by this hypothesis. Madison (1977) and van Steenis (1962) already proposed this based solely on fossils and morphology affinities. The sister taxa of *Monstera* (*Amydrium* +some *Epipremnum*) are represented by several Oligocene and Pleistocene fossils from Europe (Madison & Tiffney, 1976). Additionally, our ancestral range estimation using Central and South America as independent areas showed that *Monstera* most probably migrated from North and Central to South America in the last 25 Ma (**Figure 6**).

In contrast, at the infrageneric level, tropical disjunctions are less common is Araceae. Species in the genera *Homalomena*, *Schismatoglottis* and *Spathiphyllum* were believed to be present in both the Neotropics and Asian Paleotropics (van Steenis, 1962; Grayum, 1990; Mayo et al., 1997). However, recent studies (Barabé et al., 2002, Gauthier et al., 2008, Wong et al., 2013; Zuluaga et al., 2015) have challenged the monophyly of both *Homalomena* and *Schismatoglottis* indicating that they do not contain disjunct species at all. This leaves *Spathiphyllum* as the only genus of Aracaeae exhibiting a New and Old World tropical disjunction. A second monsteroid genus, *Rhaphidophora*, exhibits a less dramatic tropical disjunction between Asia and Africa. In any event, our ancestral range estimation and molecular dating suggests that both of these generic tropical disjunctions (*Spathiphyllum* and *Rhaphidophhora*) correspond to more recent events. The divergence time estimates for the crown of Spathiphylleae (29.9 Ma) and current species distribution suggest long distance dispersal (LDD) between Tropical

America and Asia probably through the Pacific. Transoceanic dispersal in Tropical Araceae is uncommon (Nauheimer et al. 2012); however, one species of *Spathiphyllum*, (*S. leavae* -- which is morphologically very similar to *S. cannifolium* and the other Asian species) is present on Cocos Island, 342 mi from the Pacific shore of Costa Rica. Moreover, all the Asian species in the Spathiphylleae are distributed on islands in Australasia with only one species, *S. commutatum,* actually reaching continental Asia. Alternatively, if fossils like *Mayoa* (100-110 Ma) were confirmed to belong to Spathiphylleae, it will place this clade as distributed in the northern hemisphere, and a completely different hypothesis for the origin and dispersal of Monsteroideae (and even Araceae) may be needed.

Divergence times for *Rhaphidphora africana* (14 Ma) also suggest LDD from South East Asia to Africa. LDD between Tropical Asia and Africa is more common, and has been described to the genus level in several angiosperm groups (e.g. Nie et al., 2012; Nie et al. 2013), and so is less remarkable than the case of *Spathiphyllum*. However, dispersal from Asia to Africa seems to be less common than the opposite direction (Nie et. al, 2012). Since sampling among the Asian species of the *Rhaphidophora* clade is small and resolution within genera is poor and weakly supported in our tress, we cannot speculate further in terms of the patterns of historical biogeography within this diverse clade in Asia. We described a complex pattern of geographical distribution and morphological evolution in Monsteroideae. Future research based on stronger phylogenetic reconstructions and complete morphological datasets is needed to explore

the details of speciation and migration within and among areas of Asia, and movements between islands and continental landmasses.

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TABLES AND FIGURES

Table 1. Voucher information and Genbank accession numbers. NOTE: **This table would be completed with GENBANK accession numbers for publication.**

Species	Voucher	*matK*	*rbcl*	*trnC-petN* spacer	*trnL-trnF* spacer	*ycf1*	*PHYC*	*CHS*
Alloschemone occidentalis	Chase, M. 9996							
Amydrium sp	Hahn 3295							
Amydrium hainanense	Chase, M. 9975							
Amydrium humile	Chase, M. 9974							
Amydrium medium	Chase, M. 9976							
Amydrium zippelianum	Zuluaga, A. s.n.							
Anadendrum affine	Scherberich, D. 50950							
Anadendrum angustifolium	Chase, M. 9985							
Anadendrum microstachyum	Chase, M. 9983							
Anthurium_acaule	GENBANK							
Anthurium_andraeanum	GENBANK							
Anthurium_bakeri	GENBANK							
Anthurium_brenesii	GENBANK							
Anthurium_interruptum	GENBANK							
Anthurium ravenii	GENBANK							
Anthurium_scandens	GENBANK							
Anthurium_scherzerianum	GENBANK							
Anthurium_spectabile	GENBANK							
Dracontioides_desciscens	GENBANK							
Epipremnum aureum	Zuluaga, A s.n							
Epipremnum carolinense	Scherberich, D. 010363A							

Epipremnum falcifolium	Chase, M. 9979
Epipremnum papuanum	Chase, M. 9978
Epipremnum pinnatum	Chase, M. 9977
Epipremnum pinnatum	Zuluaga, A. s.n.
Epipremnum amplissimum	GENBANK
Gymnostachys_ anceps	GENBANK
Heteropsis flexuosa	Croat, T. 103206
Heteropsis robusta	Betancur, J. 13955
Heteropsis spruceana	Betancur, J. 13851
Heteropsis steyermarkii	Croat, T. 103150
Holochlamys beccarii	Chase, M. 9992
Lasia_spinosa	GENBANK
Lemna_minor	GENBANK
Lysichiton_ americanus	Zuluaga, A. 919
Monstera acacoyaguensis	Croat, T. 71913
Monstera acuminata	Zuluaga, A s.n.
Monstera adansonii	Betancur, J. 13211
Monstera adansonii	Betancur, J. 16021
Monstera aureopinnata	Betancur, J. 13979
Monstera buseyi	Zuluaga, A. 901
Monstera sp nov integrifolia	Zuluaga, A. 916
Monstera deliciosa	Zuluaga, A. 902
Monstera dissecta	Zuluaga, A. 911
Monstera dubia	Zuluaga, A. s.n.
Monstera egregia	Croat, T. 100357a
Monstera epipremnoides	Croat, T. 69750
Monstera filamentosa	Zuluaga, A. 893
Monstera florescanoana	Zuluaga, A. s.n.
Monstera gracilis	Zuluaga, A. 463
Monstera	Zuluaga, A. 311

lechleriana	
Monstera obliqua	Clavijo, L 1565
Monstera oreophila	Zuluaga, A. 886
Monstera_pichinchensis	Croat, T. 96437
Monstera pinnatipartita	Zuluaga, A. 874
Monstera pittieri	Zuluaga, A. 894
Monstera planadensis	Zuluaga, A. 351
Monstera punctulata	Zuluaga, A. 887
Monstera siltepecana	Croat, T. 90214
Monstera spruceana	Zuluaga, A. 899
Monstera subpinnata	Zuluaga, A. 417
Monstera tuberculata	Zuluaga, A s.n.
Monstera xanthospatha	Zuluaga, A. 884
Orontium_aquaticum	GENBANK
Pedicellarum_paiei	GENBANK
Pothoidium_lobbianum	GENBANK
Pothos_chinensis	GENBANK
Pothos_scandens	GENBANK
Pothos_tener	GENBANK
Rhaphidophora africana	Chase, M. 8595
Rhaphidophora sp	Chase, M. 8597
Rhaphidophora angustata	Chase, M. 8628
Rhaphidophora beccarii	Chase, M. 8626
Rhaphidophora crassicaulis	Chase, M. 8630
Rhaphidophora decursiva	Chase, M. 8601
Rhaphidophora guamensis	Chase, M. 8625
Rhaphidophora hongkongensis	Chase, M. 8002
Rhaphidophora hookeri	Chase, M. 8632
Rhaphidophora	Chase, M. 8604

lobbii	
Rhaphidophora luchunensis	Chase, M. 8634
Rhaphidophora maingayi	Chase, M. 8599
Rhaphidophora megaphylla	Chase, M. 8627
Rhaphidophora montana	Croat, T. 59140b
Rhaphidophora peepla	Chase, M. 7382
Rhaphidophora schlechteri	Chase, M. 8637
Rhaphidophora spathacea	Chase, M. 8624
Rhaphidophora spuria	Chase, M. 8608
Rhaphidophora sylvestris	Chase, M. 7398
Rhaphidophora tetrasperma	Chase, M. 8629
Rhaphidophora korthalsii	Chase, M. 8635
Rhaphidophora latevaginata	Chase, M. 8633
Rhaphidophora neoguineensis	Chase, M. 8636
Rhodospatha	Betancur, J. 15319
Rhodospatha moritziana	Zuluaga, A. 565
Rhodospatha	Betancur, J. 14578
Rhodospatha	Zuluaga, A. 567
Rhodospatha	Zuluaga, A. 567
Rhodospatha latifolia	Zuluaga, A. 460
Rhodospatha venosa	Croat, T. 104784
Rhodospatha wendlandii	Zuluaga, A. 551
Scindapsus hederaceus	Chase, M. 9986
Scindapsus rupestris	Chase, M. 8623
Spathiphyllum cannifolium	Zuluaga, A. 532
Spathiphyllum cochlearispathum	Croat, T. 73887
Spathiphyllum minor	Betancur, J. 14022
Spathiphyllum solomonense	Lavarack 31268
Spathiphyllum	Croat, T. 78313

wallisii	
Spathiphyllum cannifolium	Betancur, J. 14976
Spathiphyllum commutatum	Medecilo, M. 498
Spathiphyllum patulinervum	GENBANK
Spathiphyllum pygmaeum	GENBANK
Spirodela_polyrhiza	GENBANK
Stenospermation	Zuluaga, A. 371
Stenospermation	Zuluaga, A. 756
Stenospermation angustifolium	Zuluaga, A. 553
Stenospermation	Zuluaga, A. 900
Stenospermation andreanum	Zuluaga, A. 321
Stenospermation ellipticum	Zuluaga, A. 379
Stenospermation	Zuluaga, A. 518
Stenospermation escobariae	Zuluaga, A. 496
Stenospermation multiovulatum	GENBANK

Table 2. Primers design for *ycf1,* PHYC and CHS.

Region	Primer sequence
***ycf1* Forward**	TCCRYGATATGGTCCATTCAA
***ycf1* Reverse**	TYMTGGATACGGCAAAATCA
phyC Forward	GCCTGTGAATTTTTGATGCA
phyC Reverse	AAGAACGTGGATGCATCTTC
CHS Forward	GCCCAMTAAAAATAACAATGCG
CHS Reverse	CCTGCTGGTACATCATGAG

Table 3. DNA substitutions models and partitioning scheme and partition subsets resulting for RAXML and BEAST analyses from partition analyses conducted in PartitionFinder using the BIC criterion.

	Partition number	Best Model	Partition subsets
RAxML	1	GTR+I+G	matK_pos1, matk_pos2, matK_pos3, rbcl_pos2, trnL-F, ycf1
	2	GTR+G	matk-trnK intron, trnC-petN
	3	GTR+G	rbcL_pos1, rbcL_pos3
MrBayes	1	GTR+I+G	matK_pos1, matk_pos2, matK_pos3, rbcl_pos2, trnL-F, ycf1
	2	GTR+G	matk-trnK intron, trnC-petN
	3	K80+I+G	rbcL_pos1, rbcL_pos3

Table 4. Information about the different plastid, nuclear, and combined datasets and alignments. Number of taxa, the length of the aligment, the number of characters excluded, and percentage of missing data and variable sites (for all taxa and the ingroup) are shown.

	Plastid						Nuclear		
	rbcL	***matK***	***trnC-petN* spacer**	***trnL-trnF* spacer**	**partial *ycf1***	**Concatenated plastid**	**PHYC**	**CHS**	**Concatenated**
Number of taxa	98	99	107	106	90	125	79	72	133
Alignment length (bp)	1376	1810	1071	1198	878	6192	1093	692	7977
Excluded characters	0	0	0	101	40	141	0	54	NA
% gaps and missing data	8	14.8	30.1	32	10.2	38	16.8	0.3	49
% variable sites (ingroup)	8.3	51.7	48.7	32.5	47	90.7	34.5	35.8	89.9
% variable sites (all)	20.7	68.2	92.8	74.6	55.6	96.6	54.2	40.8	92.6

Table 5. Support information for the genera and clades within Monsteroideae with different datasets from different phylogenetic analyses. Supports higher than 70 for Maximum likelihood (ML) partition and unpartition analysis, and higher than 0.9 posterior probabilities for Bayesian inference (BI) are shown. Clades represented by one species are considered no tested unless they are nested in another clade.

Genus	**Combined plastid**	***CHS***	***PHYC***	**Concatenated**
Alloschemone	not tested	not tested	not tested	not tested
Amydrium	ML: 89, 90; BI; 0.99	not monophyletic	not monophyletic	ML:79, 61
Anadendrum	ML: 100, 99; BI; 1	ML: 100, 100; BI; 1	ML: 100, 100; BI; 1	ML: 100, 100
Epipremnum	not monophyletic	not monophyletic	ML: 91, 91; BI; 1	not monophyletic
Heteropsis	not supported	ML: 98, 100; BI; 1	not monophyletic	not supported
Holochlamys	Nested in Spathiphyllum	no tested	no tested	Nested in Spathiphyllum
Monstera	ML: 94, 96; BI; 1	not supported	no tested	ML:97, 94
Rhaphidophora	ML: no supported; BI; 0.99	not monophyletic	not monophyletic	not monophyletic
Rhodospatha	ML: 82, 79; BI; 1	ML: no supported, 92; BI; 0.99	not supported	ML:94, 94
Scindapsus	ML: 96, 94; BI; 0.99	no tested	ML: 100, 100; BI; 1	ML:96, 96
Spathiphyllum	not monophyletic	no tested	ML: 100, 100; BI; 1	not monophyletic
Stenospermation	ML: 100, 100; BI; 1	ML: 77, 86; BI; 0.99	ML: 95, 94; BI; 1	not supported
Spathiphylleae	ML: 100, 100; BI; 1	ML: 100, 100; BI; 1	ML: 100, 100; BI; 1	ML: 100, 100
Heteropsis clade	ML: 100, 100; BI; 1	ML: no supported, 88; BI; 0.99	ML: 100, 100; BI; 1	ML: 99, 100
Rhaphidophora clade	ML: 100, 100; BI; 1	ML: no supported, 72; BI; 0.99	ML: 100, 100; BI; 1	ML: 100, 100
Rhaphidophora clade* + *Heteropsis clade	ML: 99, 100; BI; 1	not supported	ML: 99, 100; BI; 1	ML: 100, 100
Monsteroideae	ML: 100, 100; BI; 1	not supported	ML: 100, 100; BI; 1	ML: 100, 100; BI; 1

Table 6. Information about BEAST analysis. Node number according to **Figure 4**, age in Ma, and 5-95 % Highest Posterior Density (HPD) intervals are shown.

Node	Age	CI (5-95%)	Node	Age	CI (5-95%)
126	125.44	(114.85-134.99)	170	28.92	(13.78-48.95)
127	115.24	(109.2-125.83)	189	21.99	(8.77-39.33)
128	108.84	(94.67-121.62)	190	59.79	(28.55-87.76)
129	90.77	(78.26-104.08)	169	125.44	(114.85-134.99)
130	68.83	(64.2-76.73)	192	115.24	(109.2-125.83)
131	59.08	(45.75-70.5)	132	59.08	(45.75-70.5)
132	38.45	(27.68-50.89)	194	38.45	(27.68-50.89)
133	36.75	(26.02-48.07)	195	36.75	(26.02-48.07)
134	28.01	(18.71-38.85)	196	28.01	(18.71-38.85)
135	18.67	(11.63-27.07)	194	6.3	(3.51-9.99)
136	15.69	(9.76-22.92)	131	0.85	(0.1-2.23)
137	9.8	(5.78-14.71)	199	0.5	(0-1.63)
138	7.79	(4.61-11.85)	200	0.23	(0-1.13)
139	6.3	(3.51-9.99)	201	0.47	(0-1.84)
140	4.72	(2.16-8.03)	202	4.25	(1.59-7.46)
141	1.74	(0.45-3.71)	203	1.55	(0.19-3.8)
142	0.85	(0.1-2.23)	204	5.18	(2.29-8.57)
143	0.5	(0-1.63)	203	8.19	(4.4-12.9)
141	5.18	(2.29-8.57)	201	2.14	(0.56-4.51)
139	8.19	(4.4-12.9)	207	2.2	(0.06-6.72)
146	6.26	(2.86-10.39)	200	3.98	(1.07-8.16)
138	2.2	(0.06-6.72)	209	17.13	(9.54-26.27)
148	14.57	(8.26-21.81)	210	12.48	(6.33-20.16)
149	8.35	(3.92-14.07)	211	10	(4.67-16.73)
148	12.48	(6.33-20.16)	212	7.06	(2.75-12.67)
137	2.67	(0.32-6.48)	211	32.29	(23.06-43.58)
152	8.53	(2.99-16.05)	209	19.9	(13.19-28.61)
153	1.72	(0.15-4.94)	199	9.84	(5.48-15.44)
154	32.29	(23.06-43.58)	216	7.02	(3.5-11.66)
155	29.05	(20.49-39.42)	217	5.5	(2.16-10.1)
153	13.15	(7.32-20.02)	218	3.26	(0.78-6.86)
135	0.86	(0-3.55)	130	12.4	(6.47-20.19)
158	3.23	(0-9.3)	220	9.13	(4.17-16.39)
159	13.96	(6.69-21.91)	221	7.01	(2.91-12.62)
160	3.15	(0.57-7.64)	222	3.11	(0.69-7.02)
134	11.66	(4.93-20.87)	222	5.72	(1.66-11.95)
162	8.01	(3.04-15.48)	221	17.03	(8.05-29.26)
163	5.72	(1.66-11.95)	225	5.57	(1.8-11.45)
164	7.73	(2.48-16.03)	226	2.33	(0.48-5.52)
165	5.09	(1.26-11.25)	220	21.17	(13.53-30.62)
162	38.56	(26.93-51.61)	129	11.5	(6.13-18.32)
167	34.86	(24.06-47.71)	229	7	(2.65-12.74)
133	11.5	(6.13-18.32)	230	3.65	(0.43-9.63)
169	7	(2.65-12.74)	231	12.67	(5.52-21.82)
170	3.65	(0.43-9.63)	232	5.85	(1.62-12.26)

171	12.67	(5.52-21.82)	233	23.68	(12.38-36.67)
172	5.85	(1.62-12.26)	231	5.95	(1.65-12.16)
173	23.68	(12.38-36.67)	235	0.89	(0.01-3.66)
174	18.11	(8.99-29.81)	230	0.38	(0-2.04)
175	10.11	(4.3-18.29)	229	11.14	(4.66-19.79)
176	1.56	(0.14-4.51)	238	6.06	(0.69-13.5)
177	0.34	(0-1.62)	239	4.59	(1.2-9.83)
178	5.95	(1.65-12.16)	239	2.22	(0-8.43)
179	0.89	(0.01-3.66)	128	19.53	(10.39-30.64)
176	21.36	(11.75-34.36)	242	14.76	(6.74-24.7)
173	7.66	(2.43-15.16)	243	9.33	(2.89-17.74)
182	2.22	(0-8.43)	242	10.2	(3.01-20.24)
171	14.76	(6.74-24.7)	127	17.18	(7.13-29.04)
184	9.33	(2.89-17.74)	246	11.65	(3.47-22.46)
185	3.34	(0-10.34)	126	59.79	(28.55-87.76)
186	12.5	(4.08-23.44)	248	73.42	(53.71-90.98)
187	5.71	(0.8-14.25)	249	34.09	(16.42-57.14)

Table 7. Information from selected nodes about ancestral range estimation over 100 trees from BEAST posterior distribution using seven areas and DEC model in BioGeoBears. Columns show the most probable range using the chronogram from BEAST; the probability of that range; the frequency of the range as the most probable (P>50) over 100 trees chosen from posterior distribution from BEAST; and the average and standard deviation (SD) for the probability of that range over 100 trees. Clades in bold were constrained in the BEAST analysis.

Node	Clade	Most probable range	Probability on chronogram	Frecuency over 100 trees P>50	Average and SD over 100 trees
126	**Monsteroideae + Pothoideae**	BC or BCGH	0.19	0	0.19(0.09)
127	**Monsteroideae**	BC	0.64	100	0.61(0.09)
128	*Rhaphidophora* + *Heteropsis* clades	BC	0.57	58	0.51(0.13)
129	*Rhaphidophora* clade	F	0.54	24	0.31(0.22)
132	*Monstera*	BC	1	100	1(0.001)
177	*Rhaphidophora africana*	ED	0.68	87	0.64(0.09)
194	Heteropsis clade	BC	0.99	100	0.99(0.002)
215	Spathiphylleae	BCG	0.77	93	0.74(0.19)
164	*Rhaphidophora* + *Anadendrum*	F	0.96	100	0.9(0.08)

Table 8. Morphological characters used in the ancestral state reconstruction. Pearianth and endosperm are coded as absent-present; locule number as 1, 2, 3; and seed number as 1, 2, 3 (representing 3-8 seeds) and 4 (representing >8 seeds).

Species	Perianth	SEED endosperm	# Locules	SEED_Number
Alloschemone_occidentalis	Absent	NA	1	NA
Amydrium_sp	Absent	NA	NA	NA
Amydrium_hainanense	Absent	Present	1	2
Amydrium_humile	Absent	Present	1	2
Amydrium_medium	Absent	Present	1	2
Amydrium_zippelianum	Absent	Present	1	2
Anadendrum_affine	Present	Absent	1	1
Anadendrum_angustifolium	Present	Absent	1	1
Anadendrum_microstachyum	Present	Absent	1	1
Anthurium_acaule	Present	Present	2	4
Anthurium_andraeanum	Present	Present	2	4
Anthurium_bakeri	Present	Present	2	4
Anthurium_brenesii	Present	Present	2	4
Anthurium_interruptum	Present	Present	2	4
Anthurium_ravenii	Present	Present	2	4
Anthurium_scandens	Present	Present	2	4
Anthurium_scherzerianum	Present	Present	2	4
Anthurium_spectabile	Present	Present	2	4
Dracontioides_desciscens	Present	Present	2	2
Epipremnum_aureum	Absent	Present	1	2
Epipremnum_carolinense	Absent	Present	1	4
Epipremnum_falcifolium	Absent	Present	1	2
Epipremnum_papuanum	Absent	Present	1	4
Epipremnum_pinnatum	Absent	Present	1	4
Epipremnum_pinnatum2	Absent	Present	1	4
Epipremnum_amplissimum	Absent	Present	1	4
Gymnostachys_anceps	Present	Present	1	1
Heteropsis_flexuosa	Absent	Absent	2	2
Heteropsis_robusta	Absent	Absent	2	4
Heteropsis_spruceana	Absent	Absent	2	2
Heteropsis_steyermarkii	Absent	Absent	2	2
Holochlamys_beccarii	Present	Present	1	4
Lasia_spinosa	Present	Present	1	1
Lemna_minor	Absent	Present	1	4

Lysichiton_americanus	Present	Absent	2	4
Monstera_acacoyaguensis	Absent	Absent	2	1
Monstera_acuminata	Absent	Absent	2	1
Monstera_adansonii	Absent	Absent	2	1
Monstera_adansonii2	Absent	Absent	2	1
Monstera_aureopinnata	Absent	Absent	2	1
Monstera_buseyi	Absent	Absent	2	1
Monstera_sp_nov1	Absent	Absent	2	1
Monstera_deliciosa	Absent	Absent	2	1
Monstera_dissecta	Absent	Absent	2	1
Monstera_dubia	Absent	Absent	2	1
Monstera_egregia	Absent	Absent	2	1
Monstera_epipremnoides	Absent	Absent	2	1
Monstera_filamentosa	Absent	Absent	2	1
Monstera_florescanoana	Absent	Absent	2	1
Monstera_gracilis	Absent	Absent	2	1
Monstera_lechleriana	Absent	Absent	2	1
Monstera_obliqua	Absent	Absent	2	1
Monstera_oreophila	Absent	Absent	2	1
Monstera_spnov2	Absent	Absent	2	1
Monstera_pinnatipartita	Absent	Absent	2	1
Monstera_pittieri	Absent	Absent	2	1
Monstera_planadensis	Absent	Absent	2	1
Monstera_punctulata	Absent	Absent	2	1
Monstera_siltepecana	Absent	Absent	2	1
Monstera_spruceana	Absent	Absent	2	1
Monstera_subpinnata	Absent	Absent	2	1
Monstera_tuberculata	Absent	Absent	2	1
Monstera_xanthospatha	Absent	Absent	2	1
Orontium_aquaticum	Present	Absent	1	1
Pedicellarum_paiei	Present	Absent	3	NA
Pothoidium_lobbianum	Present	Absent	1	NA
Pothos_chinensis	Present	Absent	3	NA
Pothos_scandens	Present	Absent	3	NA
Pothos_tener	Present	Absent	3	NA
Rhaphidophora_africana	Absent	Present	1	10
Rhaphidophora_sp	Absent	Present	1	10
Rhaphidophora_angustata	Absent	Present	1	10
Rhaphidophora_beccarii	Absent	Present	1	10
Rhaphidophora_crassicaulis	Absent	Present	1	10
Rhaphidophora_decursiva	Absent	Present	1	10
Rhaphidophora_guamensis	Absent	Present	1	10
Rhaphidophora_hongkongensis	Absent	Present	1	10

Rhaphidophora_hookeri	Absent	Present	1	10
Rhaphidophora_lobbii	Absent	Present	1	10
Rhaphidophora_luchunensis	Absent	Present	1	10
Rhaphidophora_maingayi	Absent	Present	1	10
Rhaphidophora_megaphylla	Absent	Present	1	10
Rhaphidophora_montana	Absent	Present	1	10
Rhaphidophora_peepla	Absent	Present	1	10
Rhaphidophora_schlechteri	Absent	Present	1	10
Rhaphidophora_spathacea	Absent	Present	1	10
Rhaphidophora_spuria	Absent	Present	1	10
Rhaphidophora_sylvestris	Absent	Present	1	10
Rhaphidophora_tetrasperma	Absent	Present	1	10
Rhaphidophora_korthalsii	Absent	Present	1	10
Rhaphidophora_latevaginata	Absent	Present	1	10
Rhaphidophora_neoguineensis	Absent	Present	1	10
Rhodospatha_sp1	Absent	Present	2	10
Rhodospatha_moritziana	Absent	Present	2	10
Rhodospatha_sp2	Absent	Present	2	10
Rhodospatha_sp3	Absent	Present	2	10
Rhodospatha_sp4	Absent	Present	2	10
Rhodospatha_latifolia	Absent	Present	2	10
Rhodospatha_venosa	Absent	Present	2	10
Rhodospatha_wendlandii	Absent	Present	2	10
Scindapsus_hederaceus	Absent	Present	1	1
Scindapsus_rupestris	Absent	Present	1	1
Spathiphyllum_cannifolium	Present	Present	3	10
Spathiphyllum_cochlearispathum	Present	Present	3	10
Spathiphyllum_minor	Present	Present	3	10
Spathiphyllum_solomonense	Present	Present	3	10
Spathiphyllum_wallisii	Present	Present	3	10
Spathiphyllum_cannifolium2	Present	Present	3	10
Spathiphyllum_commutatum	Present	Present	3	10
Spathiphyllum_patulinervum	Present	Present	3	10
Spathiphyllum_pygmaeum	Present	Present	3	10
Spirodela_polyrhiza	Absent	Present	1	4
Stenospermation_sp1	Absent	Present	2	10
Stenospermation_sp2	Absent	Present	2	10
Stenospermation_angustifolium	Absent	Present	2	10
Stenospermation_sp3	Absent	Present	2	10
Stenospermation_andreanum	Absent	Present	2	10
Stenospermation_ellipticum	Absent	Present	2	10
Stenospermation_sp4	Absent	Present	2	10

Stenospermation_escobariae	Absent	Present	2	10
Stenospermation_multiovulatum	Absent	Present	2	10

Figure 1. Cladogram depicting the topology obtained from Maximum Likelihood analyses using RAxML for a dataset including five palstid regions (*matK, rbcl, trnC-petN* spacer*, trnL-trnF* spacer*,* and partial *ycf1*). Bootstrap support values from partitioned analysis are show above the branches, and from unpartitioned below. Inset phylogram indicates branch lengths.

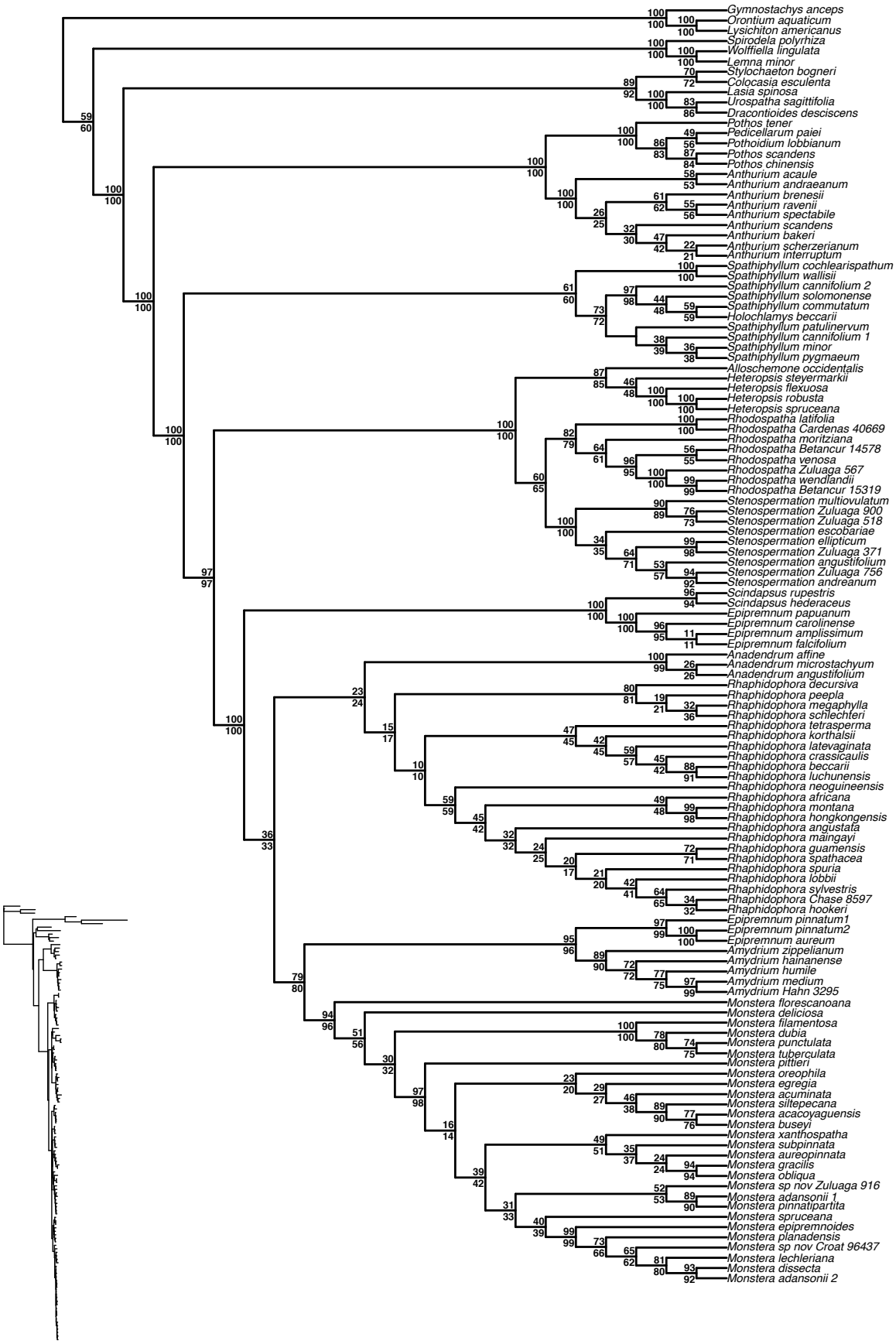

Gymnostachys anceps
Orontium aquaticum
Lysichiton americanus
Spirodela polyrhiza
Wolffiella lingulata
Lemna minor
Stylochaeton bogneri
Colocasia esculenta
Lasia spinosa
Urospatha sagittifolia
Dracontioides desciscens
Pothos tener
Pedicellarum paiei
Pothoidium lobbianum
Pothos scandens
Pothos chinensis
Anthurium acaule
Anthurium andraeanum
Anthurium brenesii
Anthurium ravenii
Anthurium spectabile
Anthurium scandens
Anthurium bakeri
Anthurium scherzerianum
Anthurium interruptum
Spathiphyllum cochlearispathum
Spathiphyllum wallisii
Spathiphyllum cannifolium 2
Spathiphyllum solomonense
Spathiphyllum commutatum
Holochlamys beccarii
Spathiphyllum patulinervum
Spathiphyllum cannifolium 1
Spathiphyllum minor
Spathiphyllum pygmaeum
Alloschemone occidentalis
Heteropsis steyermarkii
Heteropsis flexuosa
Heteropsis robusta
Heteropsis spruceana
Rhodospatha latifolia
Rhodospatha Cardenas 40669
Rhodospatha moritziana
Rhodospatha Betancur 14578
Rhodospatha venosa
Rhodospatha Zuluaga 567
Rhodospatha wendlandii
Rhodospatha Betancur 15319
Stenospermation multiovulatum
Stenospermation Zuluaga 900
Stenospermation Zuluaga 518
Stenospermation escobariae
Stenospermation ellipticum
Stenospermation Zuluaga 371
Stenospermation angustifolium
Stenospermation Zuluaga 756
Stenospermation andreanum
Scindapsus rupestris
Scindapsus hederaceus
Epipremnum papuanum
Epipremnum carolinense
Epipremnum amplissimum
Epipremnum falcifolium
Anadendrum affine
Anadendrum microstachyum
Anadendrum angustifolium
Rhaphidophora decursiva
Rhaphidophora peepla
Rhaphidophora megaphylla
Rhaphidophora schlechteri
Rhaphidophora tetrasperma
Rhaphidophora korthalsii
Rhaphidophora latevaginata
Rhaphidophora crassicaulis
Rhaphidophora beccarii
Rhaphidophora luchunensis
Rhaphidophora neoguineensis
Rhaphidophora africana
Rhaphidophora montana
Rhaphidophora hongkongensis
Rhaphidophora angustata
Rhaphidophora maingayi
Rhaphidophora guamensis
Rhaphidophora spathacea
Rhaphidophora spuria
Rhaphidophora lobbii
Rhaphidophora sylvestris
Rhaphidophora Chase 8597
Rhaphidophora hookeri
Epipremnum pinnatum1
Epipremnum pinnatum2
Epipremnum aureum
Amydrium zippelianum
Amydrium hainanense
Amydrium humile
Amydrium medium
Amydrium Hahn 3295
Monstera florescanoana
Monstera deliciosa
Monstera filamentosa
Monstera dubia
Monstera punctulata
Monstera tuberculata
Monstera pittieri
Monstera oreophila
Monstera egregia
Monstera acuminata
Monstera siltepecana
Monstera acacoyaguensis
Monstera buseyi
Monstera xanthospatha
Monstera subpinnata
Monstera aureopinnata
Monstera gracilis
Monstera obliqua
Monstera sp nov Zuluaga 916
Monstera adansonii 1
Monstera pinnatipartita
Monstera spruceana
Monstera epipremnoides
Monstera planadensis
Monstera sp nov Croat 96437
Monstera lechleriana
Monstera dissecta
Monstera adansonii 2

Figure 2. Cladogram depicting the topology obtained from Maximum Likelihood analyses using RAxML for a dataset including the nuclear gene Chalcone synthase (CHS). Bootstrap support values from partitioned analysis are show above the branches, and from unpartitioned below. Inset phylogram indicates branch lengths.

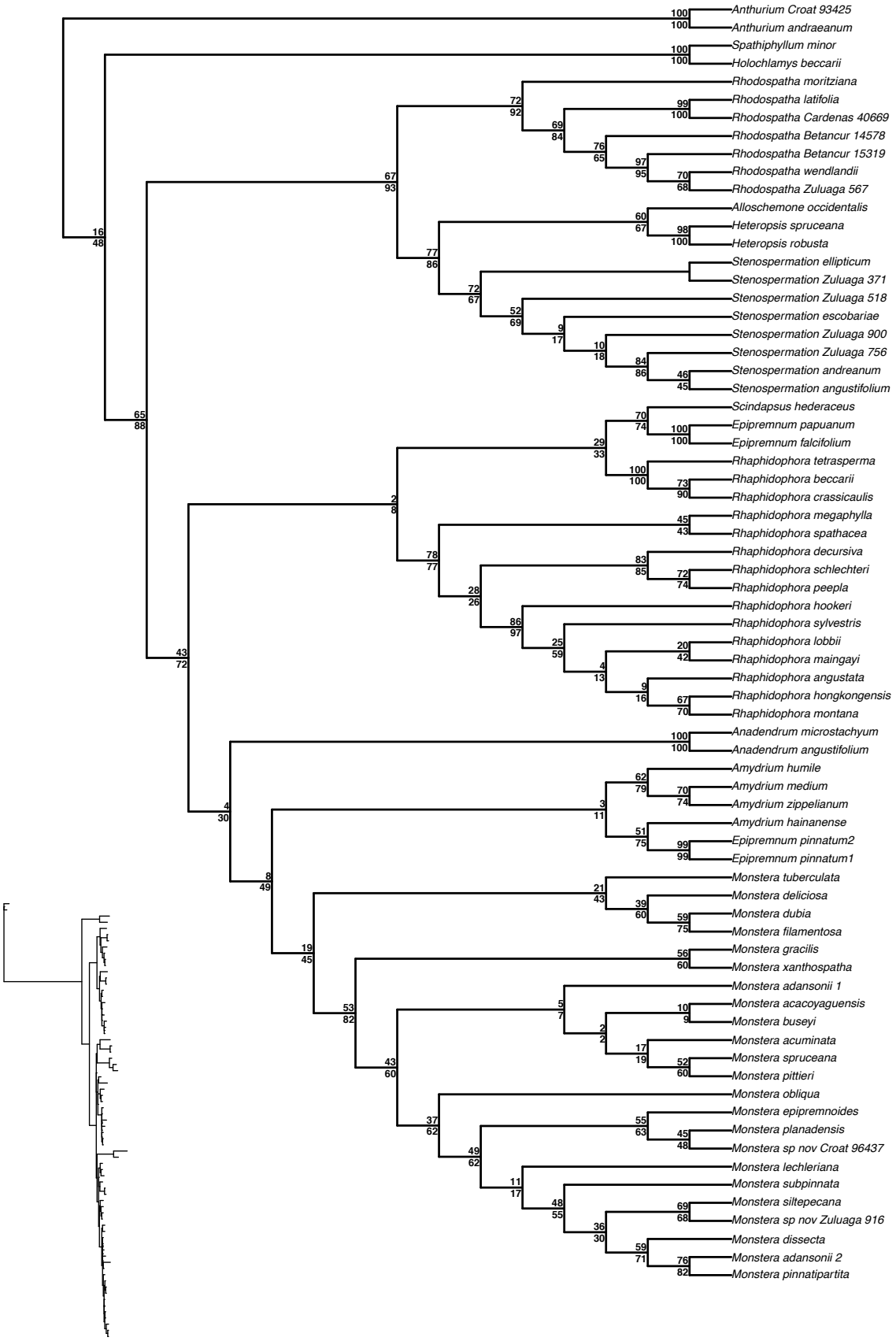

Anthurium Croat 93425
Anthurium andraeanum
Spathiphyllum minor
Holochlamys beccarii
Rhodospatha moritziana
Rhodospatha latifolia
Rhodospatha Cardenas 40669
Rhodospatha Betancur 14578
Rhodospatha Betancur 15319
Rhodospatha wendlandii
Rhodospatha Zuluaga 567
Alloschemone occidentalis
Heteropsis spruceana
Heteropsis robusta
Stenospermation ellipticum
Stenospermation Zuluaga 371
Stenospermation Zuluaga 518
Stenospermation escobariae
Stenospermation Zuluaga 900
Stenospermation Zuluaga 756
Stenospermation andreanum
Stenospermation angustifolium
Scindapsus hederaceus
Epipremnum papuanum
Epipremnum falcifolium
Rhaphidophora tetrasperma
Rhaphidophora beccarii
Rhaphidophora crassicaulis
Rhaphidophora megaphylla
Rhaphidophora spathacea
Rhaphidophora decursiva
Rhaphidophora schlechteri
Rhaphidophora peepla
Rhaphidophora hookeri
Rhaphidophora sylvestris
Rhaphidophora lobbii
Rhaphidophora maingayi
Rhaphidophora angustata
Rhaphidophora hongkongensis
Rhaphidophora montana
Anadendrum microstachyum
Anadendrum angustifolium
Amydrium humile
Amydrium medium
Amydrium zippelianum
Amydrium hainanense
Epipremnum pinnatum2
Epipremnum pinnatum1
Monstera tuberculata
Monstera deliciosa
Monstera dubia
Monstera filamentosa
Monstera gracilis
Monstera xanthospatha
Monstera adansonii 1
Monstera acacoyaguensis
Monstera buseyi
Monstera acuminata
Monstera spruceana
Monstera pittieri
Monstera obliqua
Monstera epipremnoides
Monstera planadensis
Monstera sp nov Croat 96437
Monstera lechleriana
Monstera subpinnata
Monstera siltepecana
Monstera sp nov Zuluaga 916
Monstera dissecta
Monstera adansonii 2
Monstera pinnatipartita

Figure 3. Cladogram depicting the topology obtained from Maximum Likelihood analyses using RAxML for a dataset including the nuclear gen phytochrome C (PHYC). Bootstrap support values from partitioned analysis are show above the branches, and from unpartitioned below. Inset phylogram indicates branch lengths.

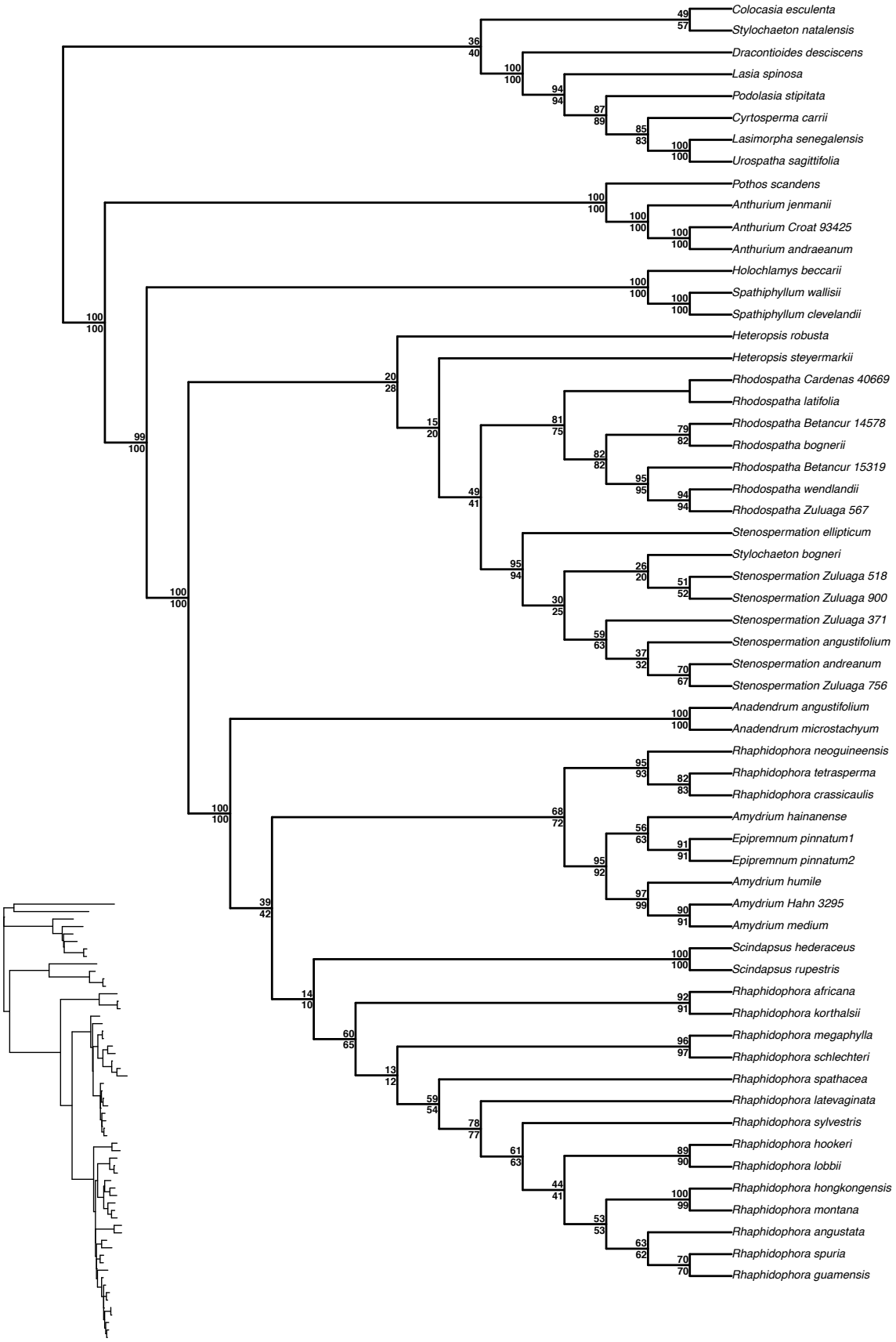
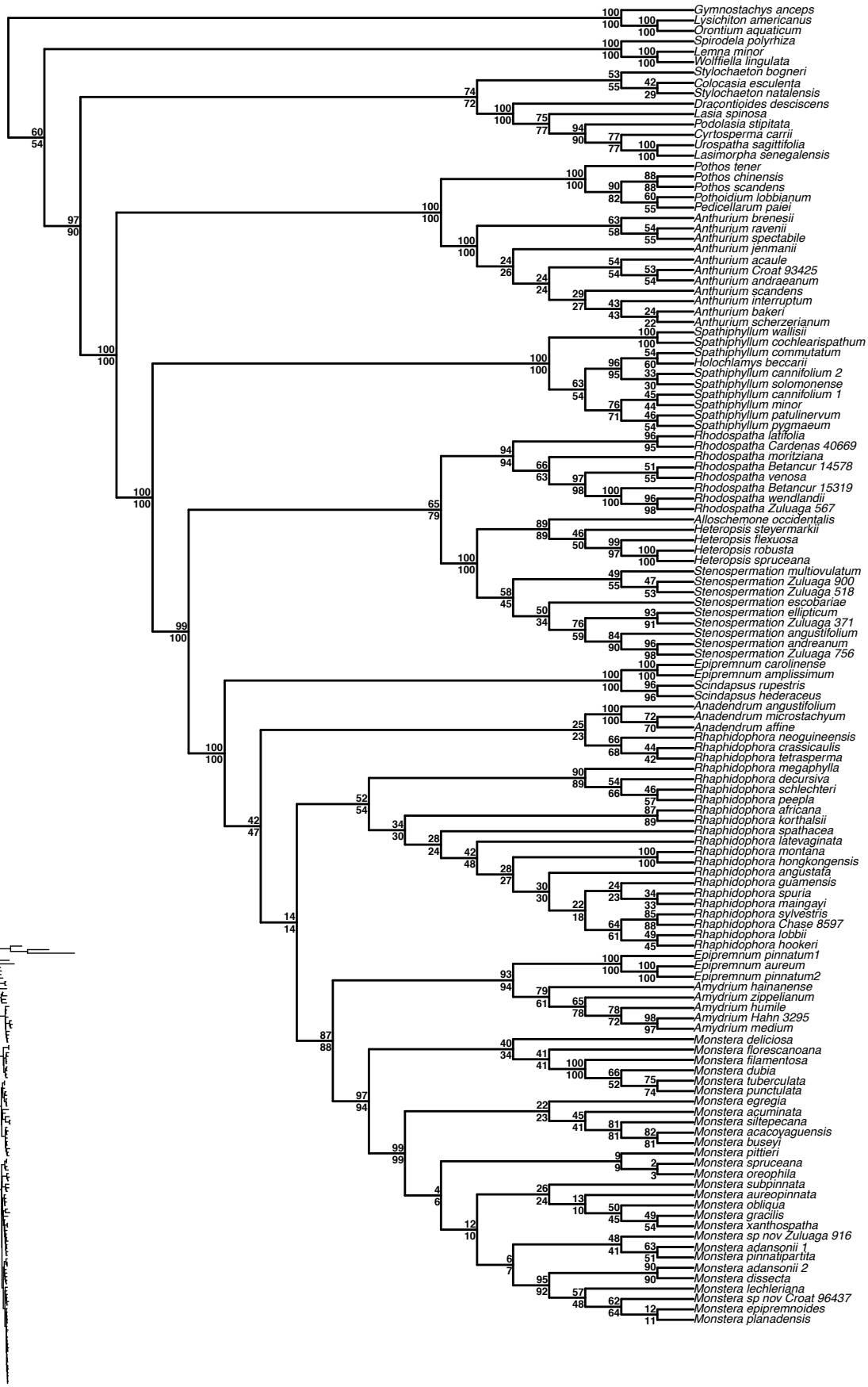

Colocasia esculenta
Stylochaeton natalensis
Dracontioides desciscens
Lasia spinosa
Podolasia stipitata
Cyrtosperma carrii
Lasimorpha senegalensis
Urospatha sagittifolia
Pothos scandens
Anthurium jenmanii
Anthurium Croat 93425
Anthurium andraeanum
Holochlamys beccarii
Spathiphyllum wallisii
Spathiphyllum clevelandii
Heteropsis robusta
Heteropsis steyermarkii
Rhodospatha Cardenas 40669
Rhodospatha latifolia
Rhodospatha Betancur 14578
Rhodospatha bognerii
Rhodospatha Betancur 15319
Rhodospatha wendlandii
Rhodospatha Zuluaga 567
Stenospermation ellipticum
Stylochaeton bogneri
Stenospermation Zuluaga 518
Stenospermation Zuluaga 900
Stenospermation Zuluaga 371
Stenospermation angustifolium
Stenospermation andreanum
Stenospermation Zuluaga 756
Anadendrum angustifolium
Anadendrum microstachyum
Rhaphidophora neoguineensis
Rhaphidophora tetrasperma
Rhaphidophora crassicaulis
Amydrium hainanense
Epipremnum pinnatum1
Epipremnum pinnatum2
Amydrium humile
Amydrium Hahn 3295
Amydrium medium
Scindapsus hederaceus
Scindapsus rupestris
Rhaphidophora africana
Rhaphidophora korthalsii
Rhaphidophora megaphylla
Rhaphidophora schlechteri
Rhaphidophora spathacea
Rhaphidophora latevaginata
Rhaphidophora sylvestris
Rhaphidophora hookeri
Rhaphidophora lobbii
Rhaphidophora hongkongensis
Rhaphidophora montana
Rhaphidophora angustata
Rhaphidophora spuria
Rhaphidophora guamensis

Figure 4. Cladogram depicting the topology obtained from Maximum Likelihood analyses using RAxML for a concatenated dataset (plastid and nuclear regions). Bootstrap support values from partitioned analysis are show above the branches, and from unpartitioned below. Inset phylogram indicates branch lengths.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Lysichiton americanus
Orontium aquaticum
Spirodela polyrhiza
Lemna minor
Wolffiella lingulata
Stylochaeton bogneri
Colocasia esculenta
Stylochaeton natalensis
Dracontioides desciscens
Lasia spinosa
Podolasia stipitata
Cyrtosperma carrii
Urospatha sagittifolia
Lasimorpha senegalensis
Pothos tener
Pothos chinensis
Pothos scandens
Pothoidium lobbianum
Pedicellarum paiei
Anthurium brenesii
Anthurium ravenii
Anthurium spectabile
Anthurium jenmanii
Anthurium acaule
Anthurium Croat 93425
Anthurium andraeanum
Anthurium scandens
Anthurium interruptum
Anthurium bakeri
Anthurium scherzerianum
Spathiphyllum wallisii
Spathiphyllum cochlearispathum
Spathiphyllum commutatum
Holochlamys beccarii
Spathiphyllum cannifolium 2
Spathiphyllum solomonense
Spathiphyllum cannifolium 1
Spathiphyllum minor
Spathiphyllum patulinervum
Spathiphyllum pygmaeum
Rhodospatha latifolia
Rhodospatha Cardenas 40669
Rhodospatha moritziana
Rhodospatha Betancur 14578
Rhodospatha venosa
Rhodospatha Betancur 15319
Rhodospatha wendlandii
Rhodospatha Zuluaga 567
Alloschemone occidentalis
Heteropsis steyermarkii
Heteropsis flexuosa
Heteropsis robusta
Heteropsis spruceana
Stenospermation multiovulatum
Stenospermation Zuluaga 900
Stenospermation Zuluaga 518
Stenospermation escobariae
Stenospermation ellipticum
Stenospermation Zuluaga 371
Stenospermation angustifolium
Stenospermation andreanum
Stenospermation Zuluaga 756
Epipremnum carolinense
Epipremnum amplissimum
Scindapsus rupestris
Scindapsus hederaceus
Anadendrum angustifolium
Anadendrum microstachyum
Anadendrum affine
Rhaphidophora neoguineensis
Rhaphidophora crassicaulis
Rhaphidophora tetrasperma
Rhaphidophora megaphylla
Rhaphidophora decursiva
Rhaphidophora schlechteri
Rhaphidophora peepla
Rhaphidophora africana
Rhaphidophora korthalsii
Rhaphidophora spathacea
Rhaphidophora latevaginata
Rhaphidophora montana
Rhaphidophora hongkongensis
Rhaphidophora angustata
Rhaphidophora guamensis
Rhaphidophora spuria
Rhaphidophora maingayi
Rhaphidophora sylvestris
Rhaphidophora Chase 8597
Rhaphidophora lobbii
Rhaphidophora hookeri
Epipremnum pinnatum1
Epipremnum aureum
Epipremnum pinnatum2
Amydrium hainanense
Amydrium zippelianum
Amydrium humile
Amydrium Hahn 3295
Amydrium medium
Monstera deliciosa
Monstera florescanoana
Monstera filamentosa
Monstera dubia
Monstera tuberculata
Monstera punctulata
Monstera egregia
Monstera acuminata
Monstera siltepecana
Monstera acacoyaguensis
Monstera buseyi
Monstera pittieri
Monstera spruceana
Monstera oreophila
Monstera subpinnata
Monstera aureopinnata
Monstera obliqua
Monstera gracilis
Monstera xanthospatha
Monstera sp nov Zuluaga 916
Monstera adansonii 1
Monstera pinnatipartita
Monstera adansonii 2
Monstera dissecta
Monstera lechleriana
Monstera sp nov Croat 96437
Monstera epipremnoides
Monstera planadensis

Figure 5. Phylogenetic relationships among clades and genera within Monsteroideae resulted from plastid and nuclear regions datasets. **A,** Phylogram depicting the topology obtained from Maximum Likelihood analyses using RAxML for a dataset including five palstid regions (*matK, rbcl, trnC-petN* spacer*, trnL-trnF* spacer*,* and partial *ycf1*); Clades and genera within Monsterodieae are indicated with bars. **B-C**, reduced phylograms showing the topologies resulted from the nuclear regions CHS and PHYC respectively. Bootstrap support values are indicated by circles; white < 75, grey <=75<95, black >=95. Posterior probabilities from Bayesian inference >= 95 are indicated in grey triangles.

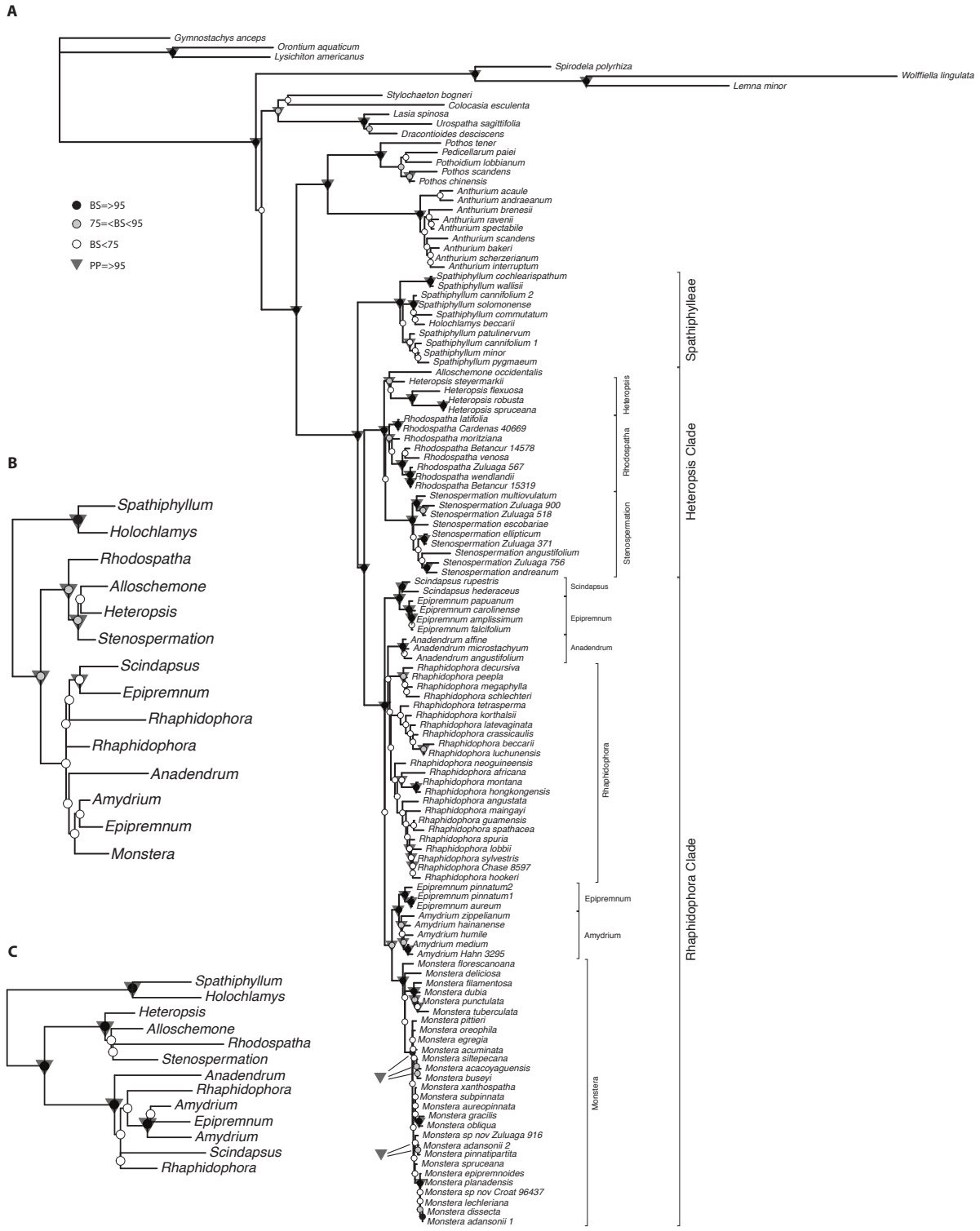

A
Gymnostachys anceps
Orontium aquaticum
Lysichiton americanus
Spirodela polyrhiza
Wolffiella lingulata
Lemna minor
Stylochaeton bogneri
Colocasia esculenta
Lasia spinosa
Urospatha sagittifolia
Dracontioides desciscens
Pothos tener
Pedicellarum paiei
Pothoidium lobbianum
Pothos scandens
Pothos chinensis
Anthurium acaule
Anthurium andraeanum
Anthurium brenesii
Anthurium ravenii
Anthurium spectabile
Anthurium scandens
Anthurium bakeri
Anthurium scherzerianum
Anthurium interruptum
BS=>95
75=<BS<95
BS<75
PP=>95
Spathiphyllum cochlearispathum
Spathiphyllum wallisii
Spathiphyllum cannifolium 2
Spathiphyllum solomonense
Spathiphyllum commutatum
Holochlamys beccarii
Spathiphyllum patulinervum
Spathiphyllum cannifolium 1
Spathiphyllum minor
Spathiphyllum pygmaeum
Alloschemone occidentalis
Heteropsis steyermarkii
Heteropsis flexuosa
Heteropsis robusta
Heteropsis spruceana
Rhodospatha latifolia
Rhodospatha Cardenas 40669
Rhodospatha moritziana
Rhodospatha Betancur 14578
Rhodospatha venosa
Rhodospatha Zuluaga 567
Rhodospatha wendlandii
Rhodospatha Betancur 15319
Stenospermation multiovulatum
Stenospermation Zuluaga 900
Stenospermation Zuluaga 518
Stenospermation escobariae
Stenospermation ellipticum
Stenospermation Zuluaga 371
Stenospermation angustifolium
Stenospermation Zuluaga 756
Stenospermation andreanum
Scindapsus rupestris
Scindapsus hederaceus
Epipremnum papuanum
Epipremnum carolinense
Epipremnum amplissimum
Epipremnum falcifolium
Anadendrum affine
Anadendrum microstachyum
Anadendrum angustifolium
Rhaphidophora decursiva
Rhaphidophora peepla
Rhaphidophora megaphylla
Rhaphidophora schlechteri
Rhaphidophora tetrasperma
Rhaphidophora korthalsii
Rhaphidophora latevaginata
Rhaphidophora crassicaulis
Rhaphidophora beccarii
Rhaphidophora luchunensis
Rhaphidophora neoguineensis
Rhaphidophora africana
Rhaphidophora montana
Rhaphidophora hongkongensis
Rhaphidophora angustata
Rhaphidophora maingayi
Rhaphidophora guamensis
Rhaphidophora spathacea
Rhaphidophora spuria
Rhaphidophora lobbii
Rhaphidophora sylvestris
Rhaphidophora Chase 8597
Rhaphidophora hookeri
Epipremnum pinnatum2
Epipremnum pinnatum1
Epipremnum aureum
Amydrium zippelianum
Amydrium hainanense
Amydrium humile
Amydrium medium
Amydrium Hahn 3295
Monstera florescanoana
Monstera deliciosa
Monstera filamentosa
Monstera dubia
Monstera punctulata
Monstera tuberculata
Monstera pittieri
Monstera oreophila
Monstera egregia
Monstera acuminata
Monstera siltepecana
Monstera acacoyaguensis
Monstera buseyi
Monstera xanthospatha
Monstera subpinnata
Monstera aureopinnata
Monstera gracilis
Monstera obliqua
Monstera sp nov Zuluaga 916
Monstera adansonii 2
Monstera pinnatipartita
Monstera spruceana
Monstera epipremnoides
Monstera planadensis
Monstera sp nov Croat 96437
Monstera lechleriana
Monstera dissecta
Monstera adansonii 1
Heteropsis
Rhodospatha
Stenospermation
Scindapsus
Epipremnum
Anadendrum
Rhaphidophora
Amydrium
Monstera
Spathiphylleae
Heteropsis Clade
Rhaphidophora Clade
B
Spathiphyllum
Holochlamys
Rhodospatha
Alloschemone
Heteropsis
Stenospermation
Scindapsus
Epipremnum
Rhaphidophora
Rhaphidophora
Anadendrum
Amydrium
Epipremnum
Monstera
C
Spathiphyllum
Holochlamys
Heteropsis
Alloschemone
Rhodospatha
Stenospermation
Anadendrum
Rhaphidophora
Amydrium
Epipremnum
Amydrium
Scindapsus
Rhaphidophora

Figure 6. Chronogram from BEAST, indicating node numbers. 95% HPD are indicated with blue bars over the nodes.

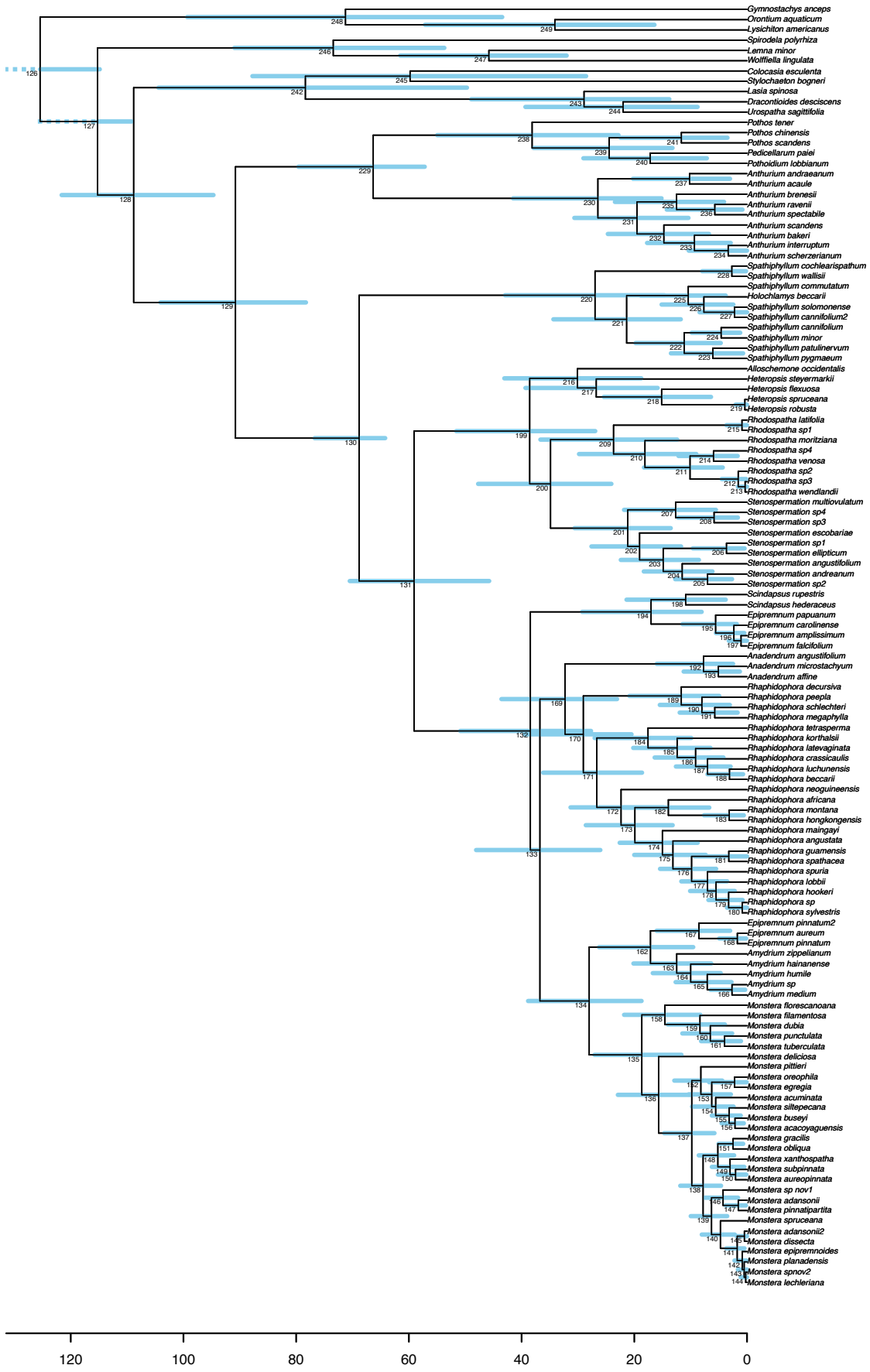
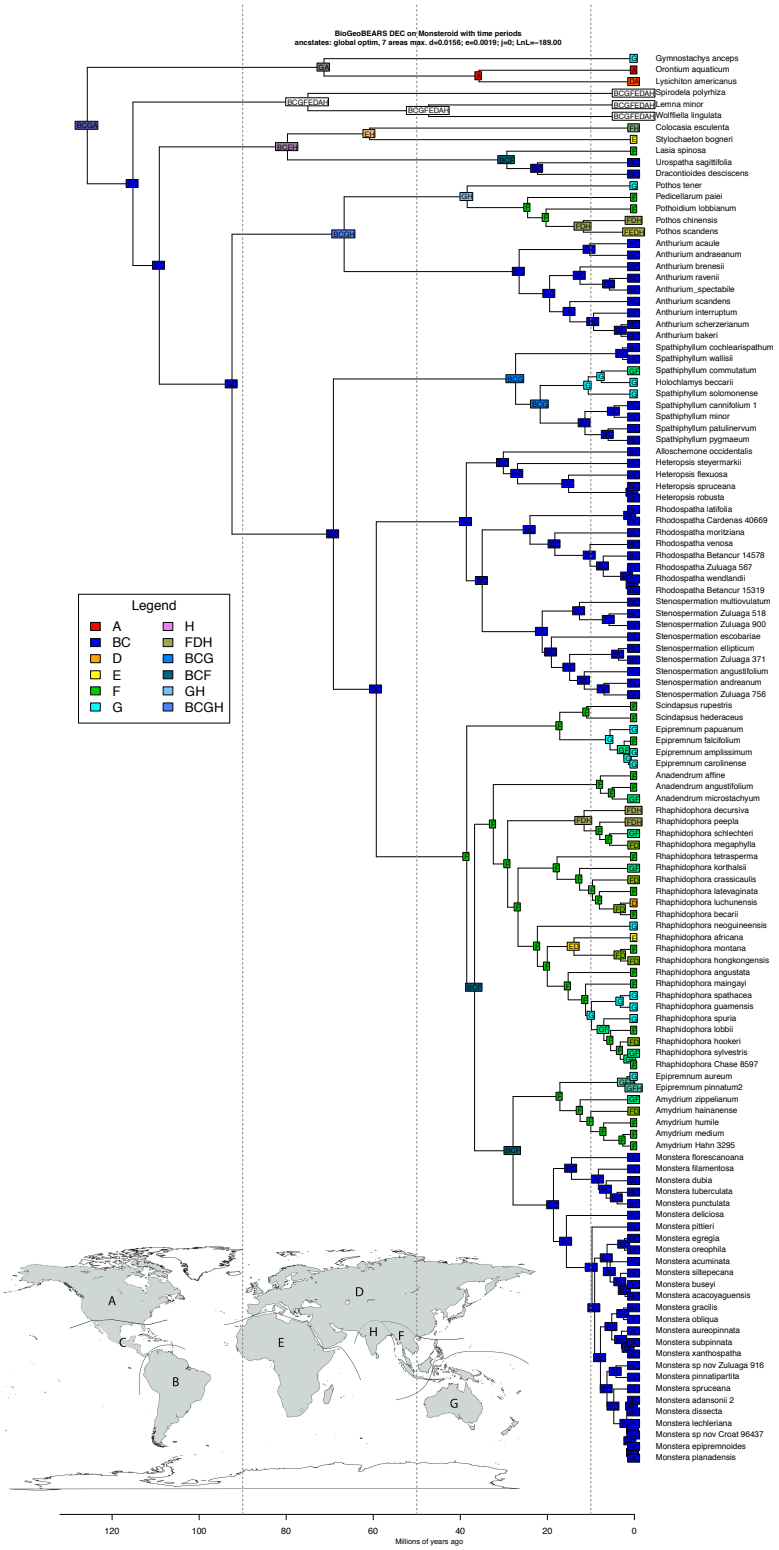

Gymnostachys anceps
Orontium aquaticum
Lysichiton americanus
Spirodela polyrhiza
Lemna minor
Wolffiella lingulata
Colocasia esculenta
Stylochaeton bogneri
Lasia spinosa
Dracontioides desciscens
Urospatha sagittifolia
Pothos tener
Pothos chinensis
Pothos scandens
Pedicellarum paiei
Pothoidium lobbianum
Anthurium andraeanum
Anthurium acaule
Anthurium brenesii
Anthurium ravenii
Anthurium spectabile
Anthurium scandens
Anthurium bakeri
Anthurium interruptum
Anthurium scherzerianum
Spathiphyllum cochlearispathum
Spathiphyllum wallisii
Spathiphyllum commutatum
Holochlamys beccarii
Spathiphyllum solomonense
Spathiphyllum cannifolium2
Spathiphyllum cannifolium
Spathiphyllum minor
Spathiphyllum patulinervum
Spathiphyllum pygmaeum
Alloschemone occidentalis
Heteropsis steyermarkii
Heteropsis flexuosa
Heteropsis spruceana
Heteropsis robusta
Rhodospatha latifolia
Rhodospatha sp1
Rhodospatha moritziana
Rhodospatha sp4
Rhodospatha venosa
Rhodospatha sp2
Rhodospatha sp3
Rhodospatha wendlandii
Stenospermation multiovulatum
Stenospermation sp4
Stenospermation sp3
Stenospermation escobariae
Stenospermation sp1
Stenospermation ellipticum
Stenospermation angustifolium
Stenospermation andreanum
Stenospermation sp2
Scindapsus rupestris
Scindapsus hederaceus
Epipremnum papuanum
Epipremnum carolinense
Epipremnum amplissimum
Epipremnum falcifolium
Anadendrum angustifolium
Anadendrum microstachyum
Anadendrum affine
Rhaphidophora decursiva
Rhaphidophora peepla
Rhaphidophora schlechteri
Rhaphidophora megaphylla
Rhaphidophora tetrasperma
Rhaphidophora korthalsii
Rhaphidophora latevaginata
Rhaphidophora crassicaulis
Rhaphidophora luchunensis
Rhaphidophora beccarii
Rhaphidophora neoguineensis
Rhaphidophora africana
Rhaphidophora montana
Rhaphidophora hongkongensis
Rhaphidophora maingayi
Rhaphidophora angustata
Rhaphidophora guamensis
Rhaphidophora spathacea
Rhaphidophora spuria
Rhaphidophora lobbii
Rhaphidophora hookeri
Rhaphidophora sp
Rhaphidophora sylvestris
Epipremnum pinnatum2
Epipremnum aureum
Epipremnum pinnatum
Amydrium zippelianum
Amydrium hainanense
Amydrium humile
Amydrium sp
Amydrium medium
Monstera florescanoana
Monstera filamentosa
Monstera dubia
Monstera punctulata
Monstera tuberculata
Monstera deliciosa
Monstera pittieri
Monstera oreophila
Monstera egregia
Monstera acuminata
Monstera siltepecana
Monstera buseyi
Monstera acacoyaguensis
Monstera gracilis
Monstera obliqua
Monstera xanthospatha
Monstera subpinnata
Monstera aureopinnata
Monstera sp nov1
Monstera adansonii
Monstera pinnatipartita
Monstera spruceana
Monstera adansonii2
Monstera dissecta
Monstera epipremnoides
Monstera planadensis
Monstera spnov2
Monstera lechleriana
120
100
80
60
40
20
0

Figure 7. Ancestral range estimation using the DEC model, four time periods, and seven areas as implemented in BioGeoBears. **A,** squares represent the most probable range at nodes and corners**. B,** pies represents all probable ranges at nodes and corners. Inset map show the different areas: Neartic (A), Tropical America (BC; C-B-Central America, C South America in the eight area analysis), Paleartic (D), Africa (E), SouthEast Asia (F), Australasia (G), India (H).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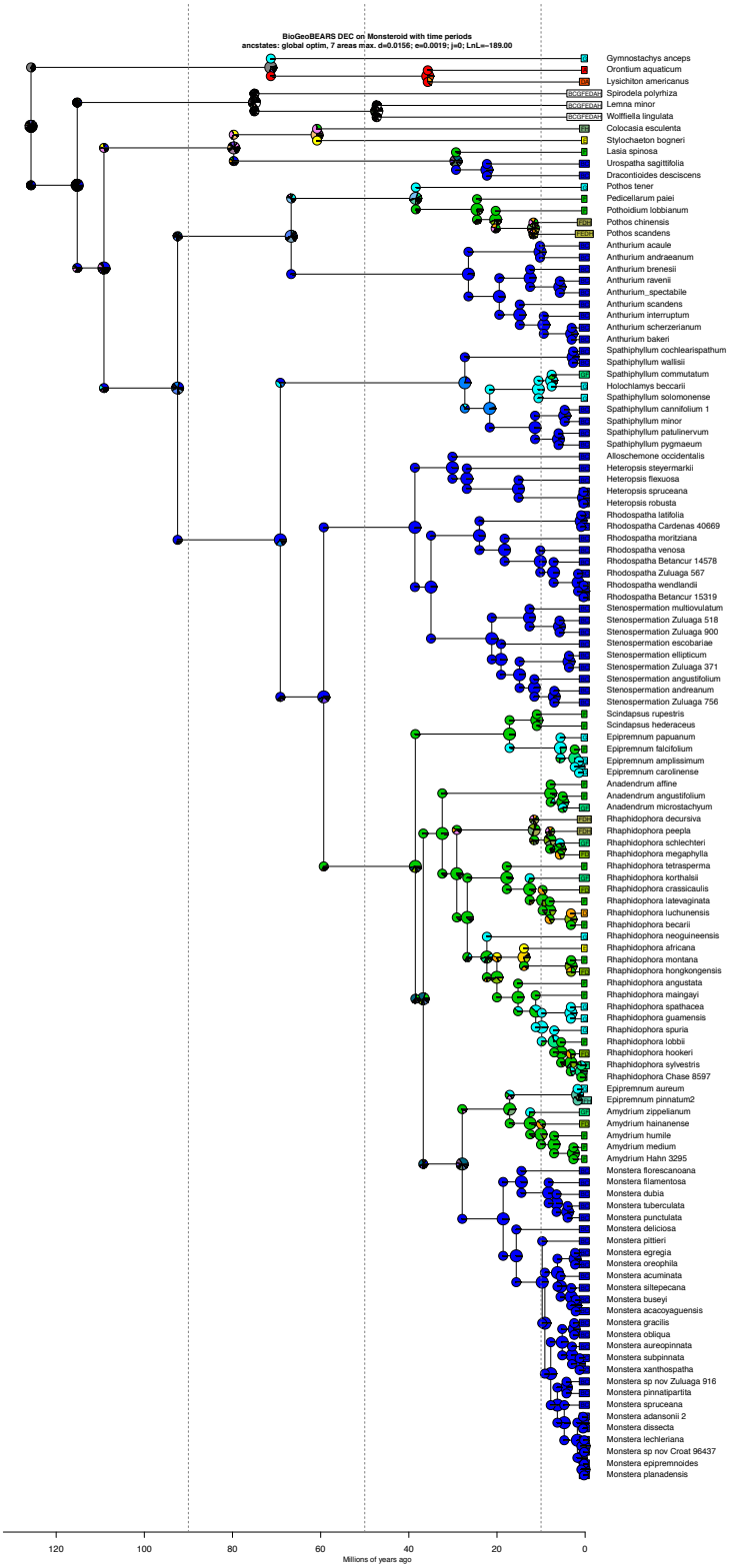
Orontium aquaticum
Lysichiton americanus
Spirodela polyrhiza
Lemna minor
Wolffiella lingulata
Colocasia esculenta
Stylochaeton bogneri
Lasia spinosa
Urospatha sagittifolia
Dracontioides descriscens
Pothos tener
Pedicellarum paiei
Pothoidium lobbianum
Pothos chinensis
Pothos scandens
Anthurium acaule
Anthurium andraeanum
Anthurium brenesii
Anthurium ravenii
Anthurium_spectabile
Anthurium scandens
Anthurium interruptum
Anthurium scherzerianum
Anthurium bakeri
Spathiphyllum cochlearispathum
Spathiphyllum wallisii
Spathiphyllum commutatum
Holochlamys beccarii
Spathiphyllum solomonense
Spathiphyllum cannifolium 1
Spathiphyllum minor
Spathiphyllum patulinervum
Spathiphyllum pygmaeum
Alloschemone occidentalis
Heteropsis steyermarkii
Heteropsis flexuosa
Heteropsis spruceana
Heteropsis robusta
Rhodospatha latifolia
Rhodospatha Cardenas 40669
Rhodospatha moritziana
Rhodospatha venosa
Rhodospatha Betancur 14578
Rhodospatha Zuluaga 567
Rhodospatha wendlandii
Rhodospatha Betancur 15319
Stenospermation multiovulatum
Stenospermation Zuluaga 518
Stenospermation Zuluaga 900
Stenospermation escobariae
Stenospermation ellipticum
Stenospermation Zuluaga 371
Stenospermation angustifolium
Stenospermation andreanum
Stenospermation Zuluaga 756
Scindapsus rupestris
Scindapsus hederaceus
Epipremnum papuanum
Epipremnum falcifolium
Epipremnum amplissimum
Epipremnum carolinense
Anadendrum affine
Anadendrum angustifolium
Anadendrum microstachyum
Rhaphidophora decursiva
Rhaphidophora peepla
Rhaphidophora schlechteri
Rhaphidophora megaphylla
Rhaphidophora tetrasperma
Rhaphidophora korthalsii
Rhaphidophora crassicaulis
Rhaphidophora latevaginata
Rhaphidophora luchunensis
Rhaphidophora becarii
Rhaphidophora neoguineensis
Rhaphidophora africana
Rhaphidophora montana
Rhaphidophora hongkongensis
Rhaphidophora angustata
Rhaphidophora maingayi
Rhaphidophora spathacea
Rhaphidophora guamensis
Rhaphidophora spuria
Rhaphidophora lobbii
Rhaphidophora hookeri
Rhaphidophora sylvestris
Rhaphidophora Chase 8597
Epipremnum aureum
Epipremnum pinnatum2
Amydrium zippelianum
Amydrium hainanense
Amydrium humile
Amydrium medium
Amydrium Hahn 3295
Monstera florescencoana
Monstera filamentosa
Monstera dubia
Monstera tuberculata
Monstera punctulata
Monstera deliciosa
Monstera pittieri
Monstera egregia
Monstera oreophila
Monstera acuminata
Monstera siltepecana
Monstera buseyi
Monstera acacoyaguensis
Monstera gracilis
Monstera obliqua
Monstera aureopinnata
Monstera subpinnata
Monstera xanthospatha
Monstera sp nov Zuluaga 916
Monstera pinnatipartita
Monstera spruceana
Monstera adansonii 2
Monstera dissecta
Monstera lechleriana
Monstera sp nov Croat 96437
Monstera epipremnoides
Monstera planadensis
Legend
A
BC
D
E
F
G
H
FDH
BCG
BCF
GH
BCGH
A
B
C
D
E
F
G
H
120
100
80
60
40
20
0
Millions of years ago


BioGeoBEARS DEC on Monsteroid with time periods
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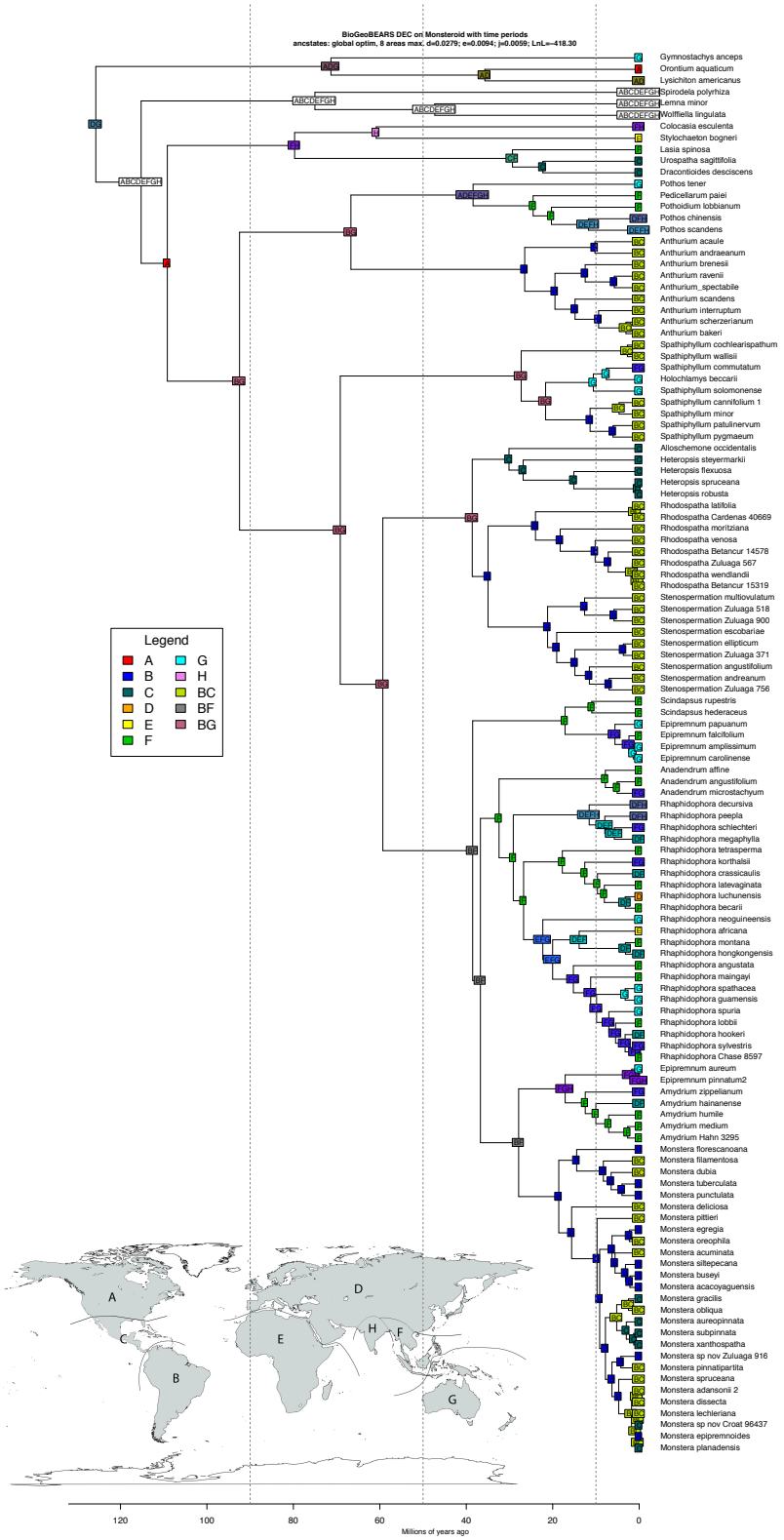
Gymnostachys anceps
Orontium aquaticum
Lysichiton americanus
Spirodela polyrhiza
Lemna minor
Wolffiella lingulata
Colocasia esculenta
Stylochaeton bogneri
Lasia spinosa
Urospatha sagittifolia
Dracontioides desciscens
Pothos tener
Pedicellarum paiei
Pothoidium lobbianum
Pothos chinensis
Pothos scandens
Anthurium acaule
Anthurium andraeanum
Anthurium brenesii
Anthurium ravenii
Anthurium_spectabile
Anthurium scandens
Anthurium interruptum
Anthurium scherzerianum
Anthurium bakeri
Spathiphyllum cochlearispathum
Spathiphyllum wallisii
Spathiphyllum commutatum
Holochlamys beccarii
Spathiphyllum solomonense
Spathiphyllum cannifolium 1
Spathiphyllum minor
Spathiphyllum patulinervum
Spathiphyllum pygmaeum
Alloschemone occidentalis
Heteropsis steyermarkii
Heteropsis flexuosa
Heteropsis spruceana
Heteropsis robusta
Rhodospatha latifolia
Rhodospatha Cardenas 40669
Rhodospatha moritziana
Rhodospatha venosa
Rhodospatha Betancur 14578
Rhodospatha Zuluaga 567
Rhodospatha wendlandii
Rhodospatha Betancur 15319
Stenospermation multiovulatum
Stenospermation Zuluaga 518
Stenospermation Zuluaga 900
Stenospermation escobariae
Stenospermation ellipticum
Stenospermation Zuluaga 371
Stenospermation angustifolium
Stenospermation andreanum
Stenospermation Zuluaga 756
Scindapsus rupestris
Scindapsus hederaceus
Epipremnum papuanum
Epipremnum falcifolium
Epipremnum amplissimum
Epipremnum carolinense
Anadendrum affine
Anadendrum angustifolium
Anadendrum microstachyum
Rhaphidophora decursiva
Rhaphidophora peepla
Rhaphidophora schlechteri
Rhaphidophora megaphylla
Rhaphidophora tetrasperma
Rhaphidophora korthalsii
Rhaphidophora crassicaulis
Rhaphidophora latevaginata
Rhaphidophora luchunensis
Rhaphidophora becarii
Rhaphidophora neoguineensis
Rhaphidophora africana
Rhaphidophora montana
Rhaphidophora hongkongensis
Rhaphidophora angustata
Rhaphidophora maingayi
Rhaphidophora spathacea
Rhaphidophora guamensis
Rhaphidophora spuria
Rhaphidophora lobbii
Rhaphidophora hookeri
Rhaphidophora sylvestris
Rhaphidophora Chase 8597
Epipremnum aureum
Epipremnum pinnatum2
Amydrium zippelianum
Amydrium hainanense
Amydrium humile
Amydrium medium
Amydrium Hahn 3295
Monstera florescanoana
Monstera filamentosa
Monstera dubia
Monstera tuberculata
Monstera punctulata
Monstera deliciosa
Monstera pittieri
Monstera egregia
Monstera oreophila
Monstera acuminata
Monstera siltepecana
Monstera buseyi
Monstera acacoyaguensis
Monstera gracilis
Monstera obliqua
Monstera aureopinnata
Monstera subpinnata
Monstera xanthospatha
Monstera sp nov Zuluaga 916
Monstera pinnatipartita
Monstera spruceana
Monstera adansonii 2
Monstera dissecta
Monstera lechleriana
Monstera sp nov Croat 96437
Monstera epipremnoides
Monstera planadensis
120
100
80
60
40
20
0
Millions of years ago

Figure 8. Ancestral range estimation using the DEC model, four time periods, and eight areas as implemented in BioGeoBears. **A,** squares represent the most probable range at nodes and corners**. B,** pies represents all probable ranges at nodes and corners. Inset map show the different areas: Neartic (A), Tropical America (BC; C-B-Central America, C South America in the eight area analysis), Paleartic (D), Africa (E), SouthEast Asia (F), Australasia (G), India (H).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Orontium aquaticum
Lysichiton americanus
Spirodela polyrhiza
Lemna minor
Wolffiella lingulata
Colocasia esculenta
Stylochaeton bogneri
Lasia spinosa
Urospatha sagittifolia
Dracontioides desciscens
Pothos tener
Pedicellarum paiei
Pothoidium lobbianum
Pothos chinensis
Pothos scandens
Anthurium acaule
Anthurium andraeanum
Anthurium brenesii
Anthurium ravenii
Anthurium_spectabile
Anthurium scandens
Anthurium interruptum
Anthurium scherzerianum
Anthurium bakeri
Spathiphyllum cochlearispathum
Spathiphyllum wallisii
Spathiphyllum commutatum
Holochlamys beccarii
Spathiphyllum solomonense
Spathiphyllum cannifolium 1
Spathiphyllum minor
Spathiphyllum patulinervum
Spathiphyllum pygmaeum
Alloschemone occidentalis
Heteropsis steyermarkii
Heteropsis flexuosa
Heteropsis spruceana
Heteropsis robusta
Rhodospatha latifolia
Rhodospatha Cardenas 40669
Rhodospatha moritziana
Rhodospatha venosa
Rhodospatha Betancur 14578
Rhodospatha Zuluaga 567
Rhodospatha wendlandii
Rhodospatha Betancur 15319
Stenospermation multiovulatum
Stenospermation Zuluaga 518
Stenospermation Zuluaga 900
Stenospermation escobariae
Stenospermation ellipticum
Stenospermation Zuluaga 371
Stenospermation angustifolium
Stenospermation andreanum
Stenospermation Zuluaga 756
Scindapsus rupestris
Scindapsus hederaceus
Epipremnum papuanum
Epipremnum falcifolium
Epipremnum amplissimum
Epipremnum carolinense
Anadendrum affine
Anadendrum angustifolium
Anadendrum microstachyum
Rhaphidophora decursiva
Rhaphidophora peepla
Rhaphidophora schlechteri
Rhaphidophora megaphylla
Rhaphidophora tetrasperma
Rhaphidophora korthalsii
Rhaphidophora crassicaulis
Rhaphidophora latevaginata
Rhaphidophora luchunensis
Rhaphidophora becarii
Rhaphidophora neoguineensis
Rhaphidophora africana
Rhaphidophora montana
Rhaphidophora hongkongensis
Rhaphidophora angustata
Rhaphidophora maingayi
Rhaphidophora spathacea
Rhaphidophora guamensis
Rhaphidophora spuria
Rhaphidophora lobbii
Rhaphidophora hookeri
Rhaphidophora sylvestris
Rhaphidophora Chase 8597
Epipremnum aureum
Epipremnum pinnatum2
Amydrium zippelianum
Amydrium hainanense
Amydrium humile
Amydrium medium
Amydrium Hahn 3295
Monstera florescanoana
Monstera filamentosa
Monstera dubia
Monstera tuberculata
Monstera punctulata
Monstera deliciosa
Monstera pittieri
Monstera egregia
Monstera oreophila
Monstera acuminata
Monstera siltepecana
Monstera buseyi
Monstera acacoyaguensis
Monstera gracilis
Monstera obliqua
Monstera aureopinnata
Monstera subpinnata
Monstera xanthospatha
Monstera sp nov Zuluaga 916
Monstera pinnatipartita
Monstera spruceana
Monstera adansonii 2
Monstera dissecta
Monstera lechleriana
Monstera sp nov Croat 96437
Monstera epipremnoides
Monstera planadensis
Legend
A
B
C
D
E
F
G
H
BC
BF
BG
120
100
80
60
40
20
0
Millions of years ago

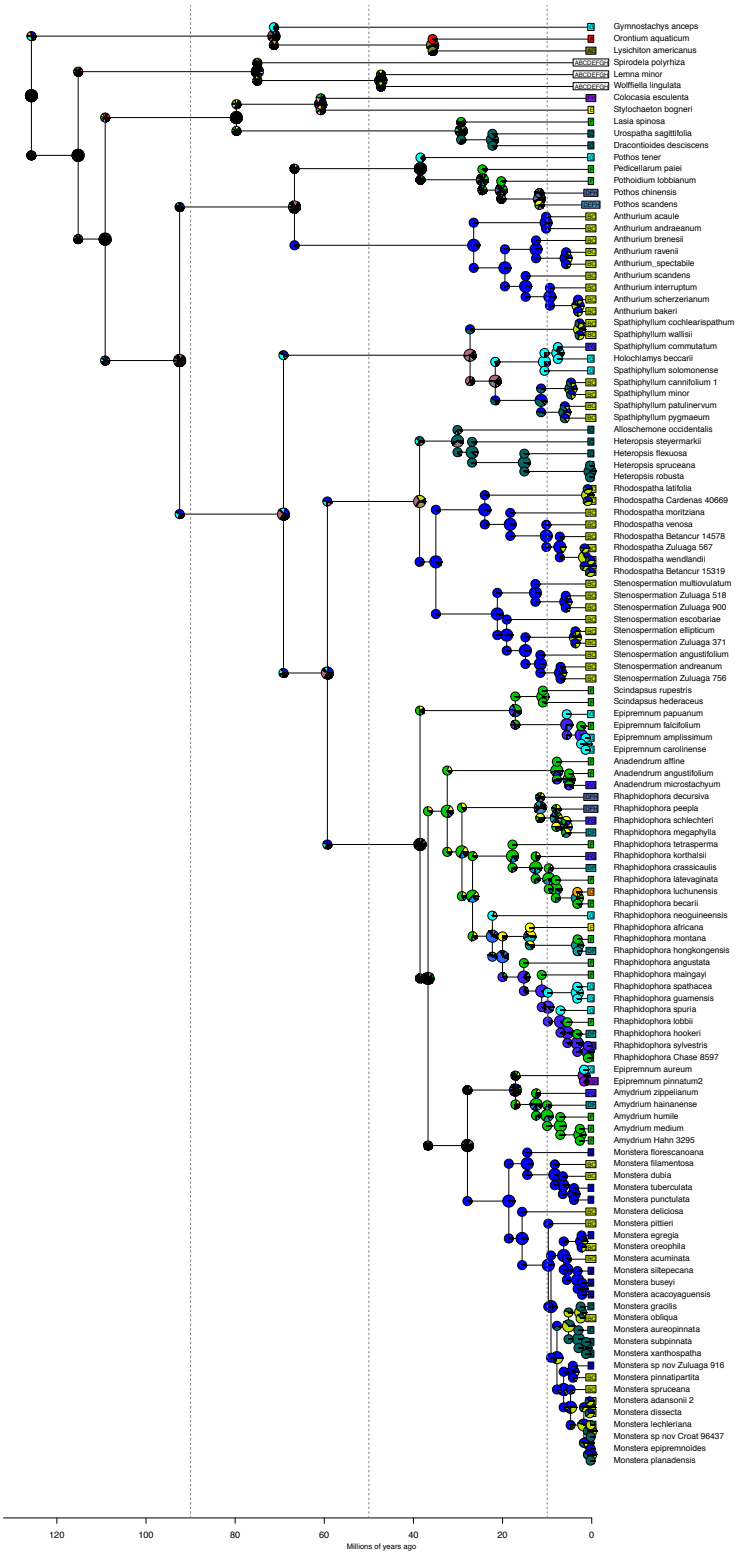

Gymnostachys anceps
Orontium aquaticum
Lysichiton americanus
Spirodela polyrhiza
Lemna minor
Wolffiella lingulata
Colocasia esculenta
Stylochaeton bogneri
Lasia spinosa
Urospatha sagittifolia
Dracontioides descriscens
Pothos tener
Pediciellarum paiei
Pothoidium lobbianum
Pothos chinensis
Pothos scandens
Anthurium acaule
Anthurium andraeanum
Anthurium brenesii
Anthurium ravenii
Anthurium_spectabile
Anthurium scandens
Anthurium interruptum
Anthurium scherzerianum
Anthurium bakeri
Spathiphyllum cochlearispathum
Spathiphyllum wallisii
Spathiphyllum commutatum
Holochlamys beccarii
Spathiphyllum solomonense
Spathiphyllum cannifolium 1
Spathiphyllum minor
Spathiphyllum patulinervum
Spathiphyllum pygmaeum
Alloschemone occidentalis
Heteropsis steyermarkii
Heteropsis flexuosa
Heteropsis spruceana
Heteropsis robusta
Rhodospatha latifolia
Rhodospatha Cardenas 40669
Rhodospatha moritziana
Rhodospatha venosa
Rhodospatha Betancur 14578
Rhodospatha Zuluaga 567
Rhodospatha wendlandii
Rhodospatha Betancur 15319
Stenospermation multiovulatum
Stenospermation Zuluaga 518
Stenospermation Zuluaga 900
Stenospermation escobariae
Stenospermation ellipticum
Stenospermation Zuluaga 371
Stenospermation angustifolium
Stenospermation andreanum
Stenospermation Zuluaga 756
Scindapsus rupestris
Scindapsus hederaceus
Epipremnum papuanum
Epipremnum falcifolium
Epipremnum amplissimum
Epipremnum carolinense
Anadendrum affine
Anadendrum angustifolium
Anadendrum microstachyum
Rhaphidophora decursiva
Rhaphidophora peepla
Rhaphidophora schlechteri
Rhaphidophora megaphylla
Rhaphidophora tetrasperma
Rhaphidophora korthalsii
Rhaphidophora crassicaulis
Rhaphidophora latevaginata
Rhaphidophora luchuensis
Rhaphidophora becarii
Rhaphidophora neoguineensis
Rhaphidophora africana
Rhaphidophora montana
Rhaphidophora hongkongensis
Rhaphidophora angustata
Rhaphidophora maingayi
Rhaphidophora spathacea
Rhaphidophora guamensis
Rhaphidophora spuria
Rhaphidophora lobbii
Rhaphidophora hookeri
Rhaphidophora sylvestris
Rhaphidophora Chase 8597
Epipremnum aureum
Epipremnum pinnatum2
Amydrium zippelianum
Amydrium hainanense
Amydrium humile
Amydrium medium
Amydrium Hahn 3295
Monstera florescanoana
Monstera filamentosa
Monstera dubia
Monstera tuberculata
Monstera punctulata
Monstera deliciosa
Monstera pittieri
Monstera egregia
Monstera oreophila
Monstera acuminata
Monstera siltepecana
Monstera buseyi
Monstera acacoyaguensis
Monstera gracilis
Monstera obliqua
Monstera aureopinnata
Monstera subpinnata
Monstera xanthospatha
Monstera sp nov Zuluaga 916
Monstera pinnatipartita
Monstera spruceana
Monstera adansonii 2
Monstera dissecta
Monstera lechleriana
Monstera sp nov Croat 96437
Monstera epipremnoides
Monstera planadensis
120
100
80
60
40
20
0
Millions of years ago

Figure 9. Ancestral state reconstruction for the characters number of locules (top) and number of seeds (bottom) in the subfamily Monsteroideae. Figures to the left show reconstructions using the rerooting method (ML); figures to the right show reconstruction using 1000 stochastic mappings.

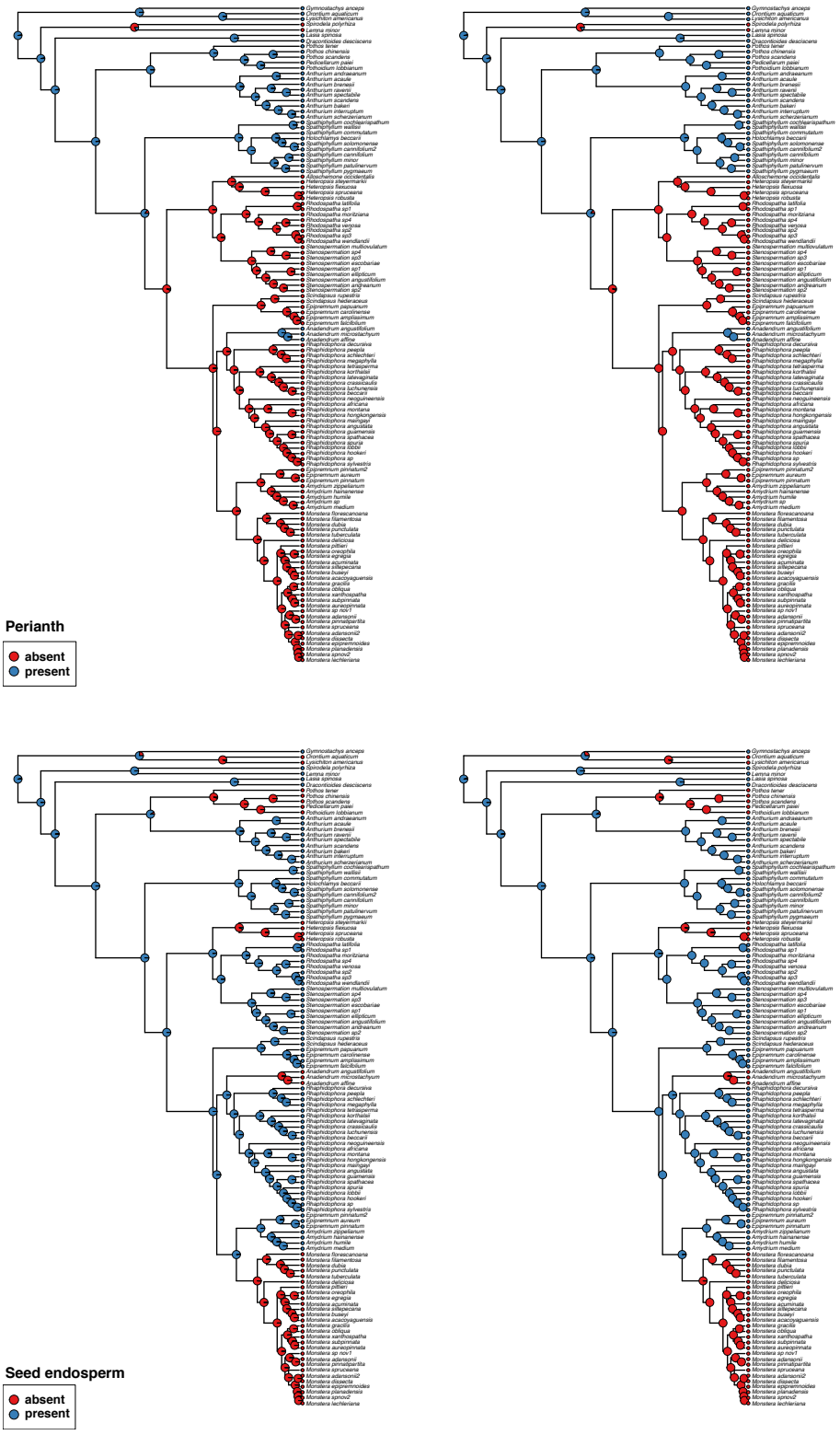

Perianth
absent
present
Seed endosperm
absent
present

Figure 10. Ancestral state reconstruction for the characters presence of perianth (top) and the presence of endosperm (bottom) in the subfamily Monsteroideae. Figures to the left show reconstructions using the rerooting method (ML); figures to the right show reconstruction using 1000 stochastic mappings.

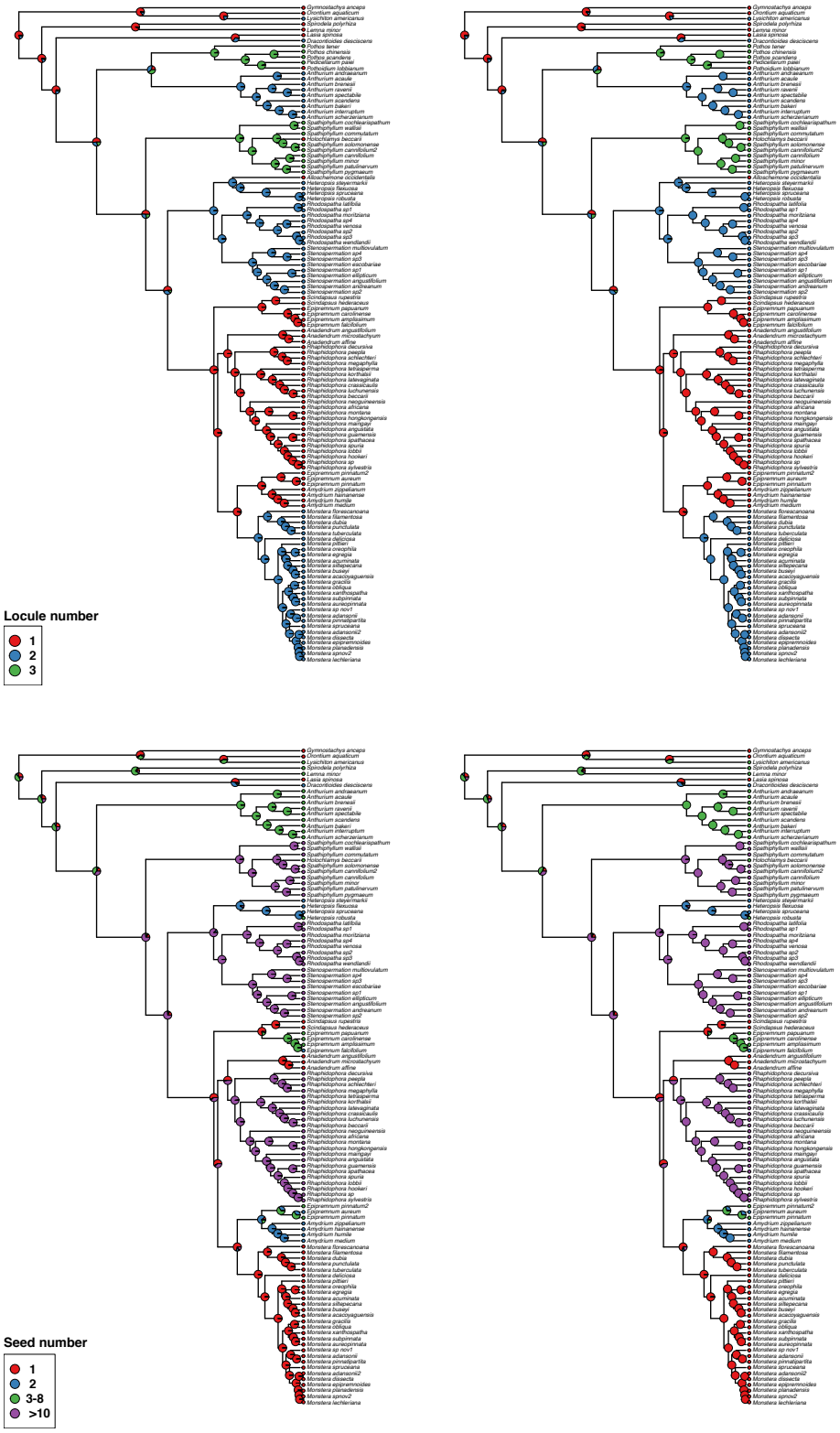
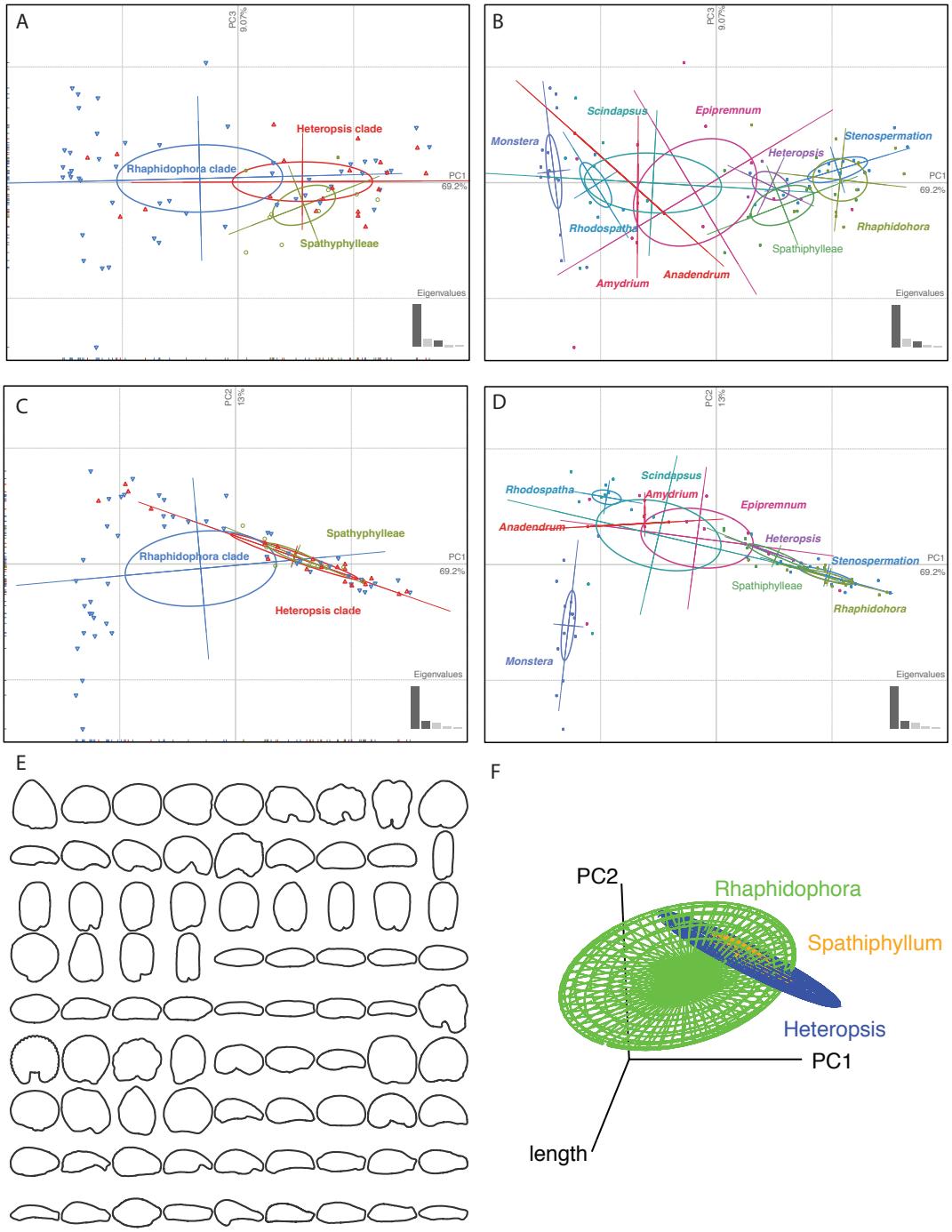

Locule number
1
2
3
Seed number
1
2
3-8
>10

Figure 11. Morphometric analyses from seed shape and size in Monsteroideae. **A-B**, scatter plots showing the PC1 and PC3 of the resulting form a principal component analysis on the harmonics produce from the outline analysis (elliptical fourier analysis). **A** is color code by clade in Monsteroideae and **B** is color code by genus. **C-D**, scatter plots showing the PC1 and PC2 from the same analysis; points are color code in the same way. **E**, panel showing outlines for the species of Monsteroideae used in the outline analysis. **F**, 3D-scatter plot using PC1, PC2 and length of the seed (in lateral view) with ellipsoids and color code by clade.


A
PC3
9.07%
Heteropsis clade
Rhaphidophora clade
PC1
69.2%
Spathyphylleae
Eigenvalues
B
PC3
9.07%
Scindapsus
Epipremnum
Monstera
Stenospermation
Heteropsis
PC1
69.2%
Rhodospatha
Rhaphidohora
Spathiphylleae
Anadendrum
Amydrium
Eigenvalues
C
PC2
13%
Spathyphylleae
Rhaphidophora clade
PC1
69.2%
Heteropsis clade
Eigenvalues
D
PC2
13%
Scindapsus
Rhodospatha
Amydrium
Epipremnum
Anadendrum
Heteropsis
Stenospermation
PC1
69.2%
Spathiphylleae
Rhaphidohora
Monstera
Eigenvalues
E
F
PC2
Rhaphidophora
Spathiphyllum
Heteropsis
PC1
length

SUPLEMENTARY TABLES AND FIGURES

TABLE S1. Area coding for each taxa used in the BioGeoBears analyses. Areas are coded as: Neartic (A), Tropical America (BC; C-B-Central America, C South America in the eight area analysis), Paleartic (D), Africa (E), SouthEast Asia (F), Australasia (G), India (H).

Species Name	A	BC	D	E	F	G	H
Alloschemone_occidentalis	0	1	0	0	0	0	0
Amydrium_sp	0	0	0	0	1	0	0
Amydrium_hainanense	0	0	1	0	1	0	0
Amydrium_humile	0	0	0	0	1	0	0
Amydrium_medium	0	0	0	0	1	0	0
Amydrium_zippelianum	0	0	0	0	1	1	0
Anadendrum_affine	0	0	0	0	1	0	0
Anadendrum_angustifolium	0	0	0	0	1	0	0
Anadendrum_microstachyum	0	0	0	0	1	1	0
Anthurium_acaule	0	1	0	0	0	0	0
Anthurium_andraeanum	0	1	0	0	0	0	0
Anthurium_bakeri	0	1	0	0	0	0	0
Anthurium_brenesii	0	1	0	0	0	0	0
Anthurium_interruptum	0	1	0	0	0	0	0
Anthurium_ravenii	0	1	0	0	0	0	0
Anthurium_scandens	0	1	0	0	0	0	0
Anthurium_scherzerianum	0	1	0	0	0	0	0
Anthurium_spectabile	0	1	0	0	0	0	0
Dracontioides_desciscens	0	1	0	0	0	0	0
Epipremnum_aureum	0	0	0	0	0	1	0
Epipremnum_carolinense	0	0	0	0	0	1	0
Epipremnum_falcifolium	0	0	0	0	1	0	0
Epipremnum_papuanum	0	0	0	0	0	1	0
Epipremnum_pinnatum	0	0	0	0	1	1	1
Epipremnum_amplissimum	0	0	0	0	0	1	0
Gymnostachys_anceps	0	0	0	0	0	1	0
Heteropsis_flexuosa	0	1	0	0	0	0	0
Heteropsis_robusta	0	1	0	0	0	0	0
Heteropsis_spruceana	0	1	0	0	0	0	0
Heteropsis_steyermarkii	0	1	0	0	0	0	0
Holochlamys_beccarii	0	0	0	0	0	1	0
Lasia_spinosa	0	0	0	0	1	0	0

Lemna_minor	1	1	1	1	1	1	1
Lysichiton_americanus	1	0	1	0	0	0	0
Monstera_acacoyaguensis	0	1	0	0	0	0	0
Monstera_acuminata	0	1	0	0	0	0	0
Monstera_adansonii2	0	1	0	0	0	0	0
Monstera_aureopinnata	0	1	0	0	0	0	0
Monstera_buseyi	0	1	0	0	0	0	0
Monstera_sp_nov1	0	1	0	0	0	0	0
Monstera_deliciosa	0	1	0	0	0	0	0
Monstera_dissecta	0	1	0	0	0	0	0
Monstera_dubia	0	1	0	0	0	0	0
Monstera_egregia	0	1	0	0	0	0	0
Monstera_epipremnoides	0	1	0	0	0	0	0
Monstera_filamentosa	0	1	0	0	0	0	0
Monstera_florescanoana	0	1	0	0	0	0	0
Monstera_gracilis	0	1	0	0	0	0	0
Monstera_lechleriana	0	1	0	0	0	0	0
Monstera_obliqua	0	1	0	0	0	0	0
Monstera_oreophila	0	1	0	0	0	0	0
Monstera_spnov2	0	1	0	0	0	0	0
Monstera_pinnatipartita	0	1	0	0	0	0	0
Monstera_pittieri	0	1	0	0	0	0	0
Monstera_planadensis	0	1	0	0	0	0	0
Monstera_punctulata	0	1	0	0	0	0	0
Monstera_siltepecana	0	1	0	0	0	0	0
Monstera_spruceana	0	1	0	0	0	0	0
Monstera_subpinnata	0	1	0	0	0	0	0
Monstera_tuberculata	0	1	0	0	0	0	0
Monstera_xanthospatha	0	1	0	0	0	0	0
Orontium_aquaticum	1	0	0	0	0	0	0
Pedicellarum_paiei	0	0	0	0	1	0	0
Pothoidium_lobbianum	0	0	0	0	1	0	0
Pothos_chinensis	0	0	1	0	1	0	1
Pothos_scandens	0	0	1	1	1	0	1
Pothos_tener	0	0	0	0	0	1	0
Rhaphidophora_africana	0	0	0	1	0	0	0
Rhaphidophora_sp	0	0	0	0	1	0	0
Rhaphidophora_angustata	0	0	0	0	1	0	0
Rhaphidophora_beccarii	0	0	0	0	1	0	0
Rhaphidophora_crassicaulis	0	0	1	0	1	0	0
Rhaphidophora_decursiva	0	0	1	0	1	0	1
Rhaphidophora_guamensis	0	0	0	0	0	1	0
Rhaphidophora_hongkongensis	0	0	1	0	1	0	0

Rhaphidophora_hookeri	0	0	1	0	1	0	0
Rhaphidophora_lobbii	0	0	0	0	1	0	0
Rhaphidophora_luchunensis	0	0	1	0	0	0	0
Rhaphidophora_maingayi	0	0	0	0	1	0	0
Rhaphidophora_megaphylla	0	0	1	0	1	0	0
Rhaphidophora_montana	0	0	0	0	1	0	0
Rhaphidophora_peepla	0	0	1	0	1	0	1
Rhaphidophora_schlechteri	0	0	0	0	1	1	0
Rhaphidophora_spathacea	0	0	0	0	0	1	0
Rhaphidophora_spuria	0	0	0	0	0	1	0
Rhaphidophora_sylvestris	0	0	0	0	1	1	0
Rhaphidophora_tetrasperma	0	0	0	0	1	0	0
Rhodospatha_sp1	0	0	0	0	1	1	0
Rhodospatha_moritziana	0	0	0	0	1	0	0
Rhodospatha_sp2	0	0	0	0	0	1	0
Rhodospatha_sp3	0	1	0	0	0	0	0
Rhodospatha_sp4	0	1	0	0	0	0	0
Rhodospatha_latifolia	0	1	0	0	0	0	0
Rhodospatha_venosa	0	1	0	0	0	0	0
Rhodospatha_wendlandii	0	1	0	0	0	0	0
Rhaphidophora_korthalsii	0	1	0	0	0	0	0
Rhaphidophora_latevaginata	0	1	0	0	0	0	0
Rhaphidophora_neoguineensis	0	1	0	0	0	0	0
Scindapsus_hederaceus	0	0	0	0	1	0	0
Scindapsus_rupestris	0	0	0	0	1	0	0
Spathiphyllum_cannifolium	0	1	0	0	0	0	0
Spathiphyllum_cochlearispathum	0	1	0	0	0	0	0
Spathiphyllum_minor	0	1	0	0	0	0	0
Spathiphyllum_solomonense	0	0	0	0	0	1	0
Spathiphyllum_wallisii	0	1	0	0	0	0	0
Spathiphyllum_commutatum	0	0	0	0	1	1	0
Spathiphyllum_patulinervum	0	1	0	0	0	0	0
Spathiphyllum_pygmaeum	0	1	0	0	0	0	0
Spirodela_polyrhiza	1	1	1	1	1	1	1
Stenospermation_sp1	0	1	0	0	0	0	0
Stenospermation_sp2	0	1	0	0	0	0	0
Stenospermation_angustifolium	0	1	0	0	0	0	0
Stenospermation_sp3	0	1	0	0	0	0	0
Stenospermation_andreanum	0	1	0	0	0	0	0
Stenospermation_ellipticum	0	1	0	0	0	0	0
Stenospermation_sp4	0	1	0	0	0	0	0
Stenospermation_escobariae	0	1	0	0	0	0	0
Stenospermation_multiovulatum	0	1	0	0	0	0	0

Stylochaeton_bogneri	0	0	0	1	0	0	0
Urospatha_sagittifolia	0	1	0	0	0	0	0
Wolffiella_lingulata	1	1	1	1	1	1	1
Colocasia_esculenta	0	0	0	0	1	0	1

TABLE S2. Dispersal multipliers matrices used in the time period analyses with BioGeoBEARS. Areas are coded as: Neartic (A), Tropical America (BC; C-B-Central America, C South America in the eight area analysis), Paleartic (D), Africa (E), South East Asia (F), Australasia (G), India (H). The matrices correspond to the following time periods from top to bottom: 10, 50 90, and 150 Ma.

BC	**G**	**F**	**E**	**D**	**A**	**H**
1	0.001	0.001	0.001	0.001	1	0.001
0.001	1	1	0.001	0.1	0.001	0.1
0.001	1	1	0.1	1	0.1	1
0.001	0.001	0.1	1	0.5	0.001	0.1
0.001	0.1	1	0.5	1	0.5	1
1	0.001	0.1	0.001	0.5	1	0.001
0.001	0.1	1	0.1	1	0.001	1

BC	**G**	**F**	**E**	**D**	**A**	**H**
1	0.1	0.001	0.001	0.5	0.5	0.001
0.1	1	0.001	0.001	0.001	0.001	0.001
0.001	0.001	1	0.001	1	0.01	1
0.001	0.001	0.001	1	0.5	0.001	0.001
0.5	0.001	1	0.5	1	0.5	0.5
0.5	0.001	0.01	0.001	0.5	1	0.001
0.001	0.001	1	0.001	0.5	0.001	1

BC	**G**	**F**	**E**	**D**	**A**	**H**
1	0.1	0.001	0.5	0.001	0.5	0.1
0.1	1	0.001	0.01	0.001	0.001	0.1
0.001	0.001	1	0.001	1	0.001	0.001
0.5	0.01	0.001	1	0.5	0.001	0.5
0.001	0.001	1	0.5	1	0.5	0.001
0.5	0.001	0.001	0.001	0.5	1	0.001
0.1	0.1	0.001	0.5	0.001	0.001	1

BC	**G**	**F**	**E**	**D**	**A**	**H**
1	0.5	0.001	1	0.01	0.5	0.5
0.5	1	0.001	0.5	0.001	0.001	1
0.001	0.001	1	0.001	1	0.001	0.001

1	0.5	0.001	1	0.5	0.01	1
0.01	0.001	1	0.5	1	0.5	0.001
0.5	0.001	0.001	0.01	0.5	1	0.001
0.5	1	0.001	1	0.001	0.001	1

Chapter 3

Using genome skimming to resolve the phylogenetic relationships of the Neotropical genus *Monstera* (Araceae)

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ABSTRACT

The reconstruction of phylogenetic hypotheses for tropical aroids has been restricted to the use of traditional PCR amplification and Sanger sequencing of few individual genes. We used Next-Generation Sequencing (NGS) data from a genome skimming approach to recover plastid, mitochondrial, and nuclear ribosomal DNA for 22 samples comprising 18 species in the Neotropical genus *Monstera* and two other close related genera. We recovered complete plastomes for 15 samples, and plastid coding regions for the remaining four samples; 15 mitochondrial coding regions; and the 18S, 5.8S and 26S nrRNA. Plastomes in *Monstera* are collinear with no differences in arrangement or number of genes. Genetic variation among *Monstera* species plastid DNA was low, with only 1% of the complete plastome providing parsimony informative characters for phylogenetic analysis. However, phylogenetic reconstructions showed resolution and high support for the majority of the nodes. Previous infrageneric classifications of *Monstera* are not supported suggesting high levels of homoplasy in vegetative and reproductive structures used for classification. Our phylogenetic hypothesis represents a robust framework for the future studies systematics and evolution in the genus.

Keywords

Araceae, genome skimming, *Monstera*, next-generation sequencing, plastomes

INTRODUCTION

The reconstruction of molecular phylogenetic hypotheses for non-model taxa has been restricted primarily to the use of traditional PCR amplification and Sanger sequencing of individual genes (Cronn et al., 2012; Godden et al., 2012). This approach is both expensive and time consuming, and has been limited to a few plastid markers, nuclear ribosomal loci, or rarely low copy nuclear markers, depending on the availability of genomic tools for the group of interest. Additionally, for many groups, phylogenetic hypotheses of relationships based on few markers lack resolution and support due to the presence of relatively few variable and informative sites (Davis et al. 2005; Whitfield & Lockhart, 2007; Davis & Anderson, 2010). Other limitations for non-model taxa regard the difficulty of obtaining adequate tissue samples and extracting high-quality DNA. Historical herbarium specimens have been useful in some cases, but they often yield degraded DNA, and are usually only applicable for short segments of high copy number DNA regions (Varma et al., 2007), such as nuclear ribosomal and plastid markers.

High throughput DNA sequencing or 'Next Generation Sequencing' (NGS) approaches are rapidly improving our ability to produce phylogenetic hypotheses for non-model organisms (Atherton et al. 2010; Egan et al., 2012; Malé et al. 2014; Ripma et al., 2014). Most of the approaches developed so far involve some method of genome reduction by physical means (e.g., Restriction site associated DNA markers), or by targeting selected parts of the genome (e.g., transcriptomes [Wen et al., 2013; Yang et al., 2015], plastomes [e.g., Stull et al., 2013], or pre-determined single copy nuclear loci [e.g., Mandel et al., 2014; Weitemier et al., 2014; Zeng et al., 2014]). Reduction

techniques capturing large numbers of nuclear loci are ideal, but require some basic genomic knowledge (Cronn et al., 2012) or at least initial investment to achieve this goal. Reduction approaches using Restriction site associated DNA markers (RAD) are less expensive, viable for non-model organisms, and particularly useful for population genetics studies (e.g. Hohenlohe et al., 2010; Hohenlohe et al., 2011), but have been used with success for phylogenetic reconstruction at the species level as well (e.g., Eaton & Ree, 2013; Escudero et al., 2014).

On the other hand, high throughput DNA sequencing of total genomic DNA (gDNA) without genome reduction during library preparation, and with shallow depth of coverage (genome skimming method [Straub et al., 2012]), allows for assembly of the high-copy fraction of gDNA. For plants, this method has been successful in recovering the complete plastomes (cpDNA), the nuclear ribosomal cistron (nrDNA), and several regions of the mitochondria (mtDNA) (Ripma et al., 2014). The genome skimming method has been used to produce family-level phylogenies (Malé et al., 2014), species level phylogenies (Parks et al., 2009; Straub et al., 2012), and infra-species phylogenies (Whittall et al., 2010; Kane et al., 2012). Moreover, while directly recovering complete nuclear DNA sequences suitable for phylogenetic reconstruction is not an immediate outcome of these methods, the data from genome skimming studies may help to provide information to later identify low-copy nuclear genes (LCNG) of known identity that could be used for targeted sequencing studies in the absence of genomic tools for the group of interest (Straub et al., 2012; Ripma et al., 2014).

In this study we used genome skimming as a tool to generate a phylogenetic hypothesis in a poorly known genus of the tropical plant family Araceae. Molecular studies at the species and even the genus level in the family Araceae are particularly well known for their lack of resolution (e.g. *Anthurium*, [Carlsen et al., 2013]; *Amorphophallus* [Grob et al., 2004]), and only a handful of commonly used molecular markers have been traditionally employed in these studies (e.g., Grob et al., 2004; Cabrera et al., 2008). Only recently have genomic tools been developed that may help to identify new markers or to design targeted gene sequencing studies across the family. Henriquez et al. (2014), using genome skimming, sequenced gDNA for 32 taxa across Araceae and assembled complete plastid genomes and some mitochondrial coding regions. Additionally, several aroid transcriptomes have been sequenced (e.g., *Arum, Anthurium, Amorphophallus*), but although raw data are available in public databases the assembled sequences for the transcripts are not. Moreover, a disproportionate amount of work has been focused on the subfamily Lemnoideae (duckweeds) relative to other aroids, due to its bioenergy application potential. Mardanov et al. (2008) and Wang & Messing (2011) sequenced complete plastomes for four genera in the Lemnoideae; and Wang et al. (2014) sequenced and assembled the complete genome of *Spirodela polyrhiza*. These tools combined with the increasing popularity of NGS techniques need to be explored in order to improve our understanding of the relationships and evolution in Araceae.

The genus *Monstera* is a Neotropical member of the aroid subfamily Monsterodieae, and has evolved within a clade of otherwise Old World genera (Tam et

al., 2004; Cusimano et al., 2011; Zuluaga et al., **CHAPTER 2**). Members of the Monsteroideae are mostly hemiepiphytic plants inhabiting wet and moist forests across the tropics (Madison, 1977). The genus *Monstera* ranges from southern Mexico to Brazil and Bolivia, from rain forest at sea level up to cloud forest at 2300 m (Madison et al., 1977). Among other characteristics, *Monstera* is recognized by its remarkable heteroblastic development and the adult leaves with fenestrations (resulting in the common name of 'Swiss cheese plant'). *Monstera* has a convoluted taxonomic history, and currently comprises 42 described species –significantly more than 23 species that were known at the time of the last taxonomic revision by Madison (1977)– and about 15 new taxa are awaiting description (Croat, 2005; Zuluaga et al., unpublished). No previous molecular studies have focused on the genus itself; only Tam et al. (2004) sequenced the plastid *trnL-trnF* spacer for four species of *Monstera* in a phylogenetic analysis of the subfamily Monsterodieae. Additionally, AFLP analysis was used to investigate taxonomic subtleties in the *Monstera adansonii* species complex in Brazil (Andrade et al., 2007). Our phylogenetic studies (Zuluaga et al., **CHAPTER 2**) have shown a striking lack of molecular variation within the genus despite the fact that it seems to be a relatively old lineage (crown age 20 Ma) with many morphologically unique taxa.

METHODS

Taxonomic sampling. 19 samples of the genus *Monstera* were used for the genome skimming approach, including species from the four sections proposed by Madison (1977). One *Epipremnum* and one *Rhodospatha* species were included to be used as outgroups. One sample of *Spathiphyllum* and one of *Monstera* from Henriquez et

al. (2014) were also included in the phylogenetic analysis. Leaf tissue samples were obtained from fieldwork carried out in Panama, Colombia and Ecuador, and the Araceae Greenhouse at the Missouri Botanical Garden in St. Louis, Missouri. The list of species, vouchers, and GENBANK accession numbers are shown in (**TABLE S1**).

Library preparation and sequencing. 10-30 mg of silica dried leaf tissue was used to extract total genomic DNA using Qiagen DNeasy Minikit (Qiagen, Germantown, Maryland, USA) following the manufacturer's protocol. CTAB method using the protocol from Doyle & Doyle (1987) was used for some recalcitrant samples. The tissue was ground using TissueLyser II (Qiagen, Courtaboeuf, France), and final DNA was eluted using 80 ul of Qiagen elution buffer. 2 ul of each extraction were run in agarose gel electrophoresis to confirm the presence of high molecular weight DNA. DNA concentrations were calculated using a fluorescence method via a Qubit fluorometer and the dsDNA HS Assay (Life Technologies, Invitrogen division, Darmstadt, Germany). 20 ng of DNA for each sample were sheared using a Covaris device (Covaris Inc.) to average size of 300-400 bp at the University of Missouri DNA Core Facility. Library preparation was performed in the lab of E. Kellog at the University of Missouri, Columbia, using the NEBNext DNA Library Prep kit for Illumina (New England Biolabs, MA). Briefly, purified fragments were A-tailed and ligated to sequencing indexed adapters. Fragments with an insert size of approximately 200 bp were size selected using AMPure® XP Beads (Beckman Coulter, Inc. #A63881). Libraries were enriched using five cycles of PCR and clean using AMPure® XP Beads (Beckman Coulter, Inc. #A63881) before library quantification and validation. Real time-PCR (qPCR) was

performed on each sample to quantify the relative amount of plastid fragments in each sample. Twenty-two samples were pooled together using the concentrations obtained after qPCR quantification. Sequencing was performed using 100 bp single-end read in one lane of Illumina HiSeq 2000 (Illumina, Inc., San Diego, California) at the University of Missouri DNA Core Facility.

Demultiplexing and quality trimming. Raw fastq reads were demultiplexed, barcodes and adapters were removed, and an initial quality trim was performed using Cutadapat v. 1.7 (Martin, 2011). Subsequent quality trimming was performed using the fastq_quality_trimmer function from the FASTX-Toolkit v. 0.0.13 (Gordon, 2010)

Plastid, mitochondria and ribosomal DNA assembly. Demultiplexed reads for each sample were assembled using a hybrid approach combining de novo and reference guided assemblies, similar to the one used by Henriquez et al. (2014) or the one proposed by Wysocki et al. (2014). *De novo* assembly was performed using the software SPAdes v 3.1.1 (Bankevich et al., 2012) and Velvet (Zerbino & Birney, 2008). We used k-mer lengths of 19 for velvet and 19, 21, 33, 55 for SPAdes. SPAdes and Velvet analyses were performed via server clusters at the Center for High Throughput Sequencing (CHTC) at the University of Wisconsin- Madison. An initial reference guide assembly was performed using YASRA v. 2.33 (Ratan, 2009) using an *Anthurium* sample as reference (Carlsen et al., unpublished data), and 85% similarity threshold. One initial *Monstera* plastome (*M. adansonii*-Brazil) was completely assembled and used as the reference for

the rest of the samples in the YASRA runs. This reference only included one copy of the plastome inverted repeat to avoid double matches during the assembly.

Post assembly analysis was performed almost entirely using Geneious 8.0 (Biomatters, http://www.geneious.com, Kearse et al., 2012) in a similar way as described by Ripma et al. (2014). Final contigs from both the reference guided and the *de novo* assemblies where transferred to Geneious. Contigs with average coverage <5 were discarded. Two subsequent assemblies runs using the Geneious assembler were performed to create longer contigs. These "final" contigs were mapped back to the initial *Monstera* plastome using the Geneious map reference tool to obtain a plastome draft. Each plastome draft was preliminary annotated based on the *Spirodela polyrhiza* plastid genome using the transfer annotations tool in Geneious. We checked each draft manually looking for regions of no coverage or regions of incongruence among different contigs (i.e., regions with long repeats). To solve these incongruences the 100 bp ends of the contigs were deleted and subsequently extended manually by looking back into the original reads using command line. Extended contigs were assembled back in Geneious. When no unambiguous assembly was found Ns were added to the consensus sequence to represent unknowns. We confirmed start and stop codons of each coding region, and evaluated reading frames using protein translation in Geneious. Finally, a consensus sequence was generated and this complete plastome sequence was exported into a FASTA for final annotation using DOGMA (Wyman et al., 2004).

We mapped *Monstera adansonii*-Brazil contigs from the de novo assembly to the ribosomal DNA of *Wolffia* (Lemnoideae) using the Geneious Map to reference tool, and extracted contigs with high similarity and high coverage. These contigs were used as reference for a new YASRA run, to finally assemble one complete ribosomal DNA repeat region containing 26S, 18S, 5.8S and portions of the internal and external transcribed spacers. This complete nrDNA was used as a reference for the rest of the samples. Similarly, *M. adansonii*-Brazil contigs from the *de novo* assembly were mapped to the *Spirodela polyrhiza* mitochondrial genome. The contigs that mapped protein-coding regions were extracted, and used as our reference for all the subsequent mitochondrial assemblies using YASRA and de novo contigs. Only 15 protein coding mitochondrial genes were identified, and we included up to 500 bases flanking each side of the regions for our alignments.

Alignment and phylogenetic reconstruction. For the plastomes, individual protein-coding regions, rRNA and tRNA, introns and spacers were aligned independently using one initial MAFFT v7 (Katoh et al., 2002, Katoh & Standley, 2013) run, and two subsequent MUSCLE v3.8.31 (Edgar 2004) runs. We concatenated: 1) all regions, and also 2) only coding regions (exons, rRNA, tRNA), and 3) only non-coding regions (introns and spacers). nrDNA and mtDNA consensus sequences were aligned the same way, and then concatenated. Phylogenetic reconstructions were performed under maximum parsimony (MP) and maximum likelihood (ML). MP analyses were conducted in PAUP* v. d104 (Swofford 2003), with 1000 bootstrap replicates to assess the relative degree of support for individual nodes. ML analyses were conducted in RAxML v. 8.0.9

(Stamatakis 2014), as implemented in the CIPRES Science Gateway (Miller et al. 2010). For each case during the ML analyses we used the GTRCAT model of substitution and performed 20 independent tree searches, and 1000 subsequent bootstraps replicates. To calculate average coverage of each genomic region we averaged the coverage of all the contigs that were mapped to the reference plastome. In that sense, measurements of the mitochondrial and nrDNA are relative only to the regions recovered.

RESULTS

Sequencing and assembly of plastid, mitochondrial and nrDNA. We found large variation in the amount of raw and filtered reads for each sample. *Monstera adansonii* -Colombia produced 1,240,022 raw reads (1,154,270 filtered reads) whereas *Rhodospatha* produce 35,887,362 raw reads (3,3288,989 filtered reads) (**TABLE 2**). The average coverage for the plastid varied between 7.5-157.6. Due to low coverage many contigs from *M. tuberculata*, *M. dubia*, *M. acacoyaguensis*, and *M. adansonii*-Colombia were discarded, and not all plastid regions were recovered, especially the spacer regions (**TABLE 3**). In general, assemblies and coverage of plastid DNA were more homogeneous through the length of the genome, whereas assemblies of mitochondrial DNA were sporadic and variable among species. Using *S. polyrhiza* as a reference for the mitochondrial DNA we were able to assemble up to 15 protein-coding regions including some of the flanking regions (between 50 and 500 bp). Assemblies for nrDNA were more problematic. Although the 18S, 5.8S and 26S nrRNA matched few contigs with high coverage producing consensus sequences without or with very ambiguities, assemblies from external and internal transcribed regions (ETS, ITS) matched hundreds of contigs

producing consensus sequences with many ambiguities that made it nearly impossible to obtain reliable sequences. Despite discarding all contigs with low coverage (<5), sequences for the ETS and ITS remained ambiguous, thus only 18S, 5.8S and 26S were considered for the alignments. The average coverage for the 15 mitochondrial coding regions varied between 6.3 and 76.4, and for the nrDNA between 15.6 and 396.5.

Structure of the plastid genome in *Monstera*. For the species where complete or almost complete plastomes were assembled the sequences were collinear with no differences in arrangement or number of genes. We used data for the species with better coverage in the genus (*M. adansonii*-Brazil) for the purposes of describing plastome structure. The plastid of *M. adansonii*-Brazil is 163,244 nucleotides long including the two inverted repeat regions (IRs) with a GC content of 38 %; whereas the range in *Monstera* species was approximately 163,000-166,000 nucleotides long. The IRs contain 25,721 nucleotides. The boundary between the large single copy region (LSC) and the inverted repeat (IRa) was between *rpl2* and *rpl19*. The boundary between the IRa and the small single copy region (SSC) was between *tRNA-Asn (GUU)* and *ndhF* in all species. The SSC-IRb boundary was between *ycf1* and *tRNA-Asn (GUU)*. Finally, the IRb-LSC boundary was between *tRNA-His (GUG)* and *rpl2* in all species (**Figure 1**).

We identified a total of 77 protein-coding regions (plus seven duplicated in the IR), four rRNA regions, and 30 tRNA regions. Additionally, we identified three regions with high similarity to the protein coding genes *cemA* (*ycf10*), *infA*, and *ycf68*, but we did not find a reading frame for protein translation of them.

DNA alignments and phylogenetic reconstruction. Complete plastid alignments, excluding the IRb were 129,162 bp long with 2.3% representing variable sites and just 1% of the total being parsimony informative characters (PIC) (**TABLE 3**). Alignment of the protein coding regions comprised 79,062 bp (2.2% variable sites), whereas the alignment of the non-coding regions was 50,100 bp (2.4% variable sites). Fifteen spacer regions were excluded from the alignment since they did not contain any variable sites. In general, missing data varied between 1.2 and 9.7 %, with only one sample, *M. tuberculata* falling outside this range and reaching 36 % (**TABLE 2**). Final alignment of mitochondrial regions and nrDNA comprised 21768 bp (0.7 % variable sites), and 5386 bp (2.2 % variable sites) respectively. In general, alignments of mitochondrial coding regions and nrDNA lacked variability within *Monstera*, even when flanking regions were considered for the mitochondria. Phylogenetic reconstructions from these regions do not have any resolution besides supporting the monophyly of the genus *Monstera* so they are no presented or discussed. ML and MP analyses of the plastid matrices produced identical topologies (**Figures 2 & 3)**. Analyses from non-coding vs. coding regions produced different topologies (**Figures 2 & 3)**, particularly regarding the position of *M deliciosa* and *M. florescanoana*. However, nodes with incongruence have low bootstrap support (< 75). Three species in section *Marcgraviopsis* from Central America are grouped in a clade, with the monotypic section *Echinospadix* (*M. tuberculata*) nested within (clade 1, **figure 3**). This clade is sister to the rest of *Monstera* in the non-coding and complete plastid datasets, but not in the coding regions analysis. *Monstera deliciosa* and/or *M. florescanoana,* also from Central America appear sister to

the remaining *Monstera* (excluding the clade 1). The remaining species form four well-supported clades (BS >=95 but relationships among them remaining unkown, **figure 3**).

DISCUSSION

Sequencing and assembly of plastid, mitochondrial, and nrDNA. Large differences in read coverage restricted us from recovering complete plastomes for all species (**TABLE 2**); however, we showed that even very shallow sequencing allowed us to recover large amounts of information (e.g., ca. 104,000 nucleotides with 36% missing data for the plastid genome in the sample with less success). The three plastid coding regions that seem not to be functional (*cemA*, *infA*, and *ycf68*) were also reported as problematic by Henriquez et al., (2015) across Araceae. Additionally these genes have been reported as losses or pseudogenes in many other groups of angiosperms (Millen et al., 2001). A study of the plastid evolution within the family Araceae including plastomes from this study is underway (Carlsen et al. Unpublished data) so we will not discuss differences among the three clades in the subfamily Monsteroideae. Briefly, *Spathiphyllum*, *Rhodospatha* and *Monstera* plastid sequences are collinear, without any major rearrangements, the main differences are in the length of spacer regions. For the mitochondrial genome we recovered few coding regions, which had low variation among *Monstera* species (0.06 % PICs). The low amount of coding regions recovered in the mtDNA may be due to size and structure of the *Monstera* mitochondrial genome in comparison with the reference used (*S. polyrhiza*). *Spirodela* represents the most compact monocot mitochondrial genome known so far, with 228,493 bases, containing 35 proteins-coding regions, 3 ribosomal RNAs and 19 transfer RNAs (Wang et al., 2012).

Studies in the chloroplast of Lemnoideae have shown high rates of mutation in comparison with other aroids, so it is probable the same is true for the mitochondria. The closest available mitochondrial genome to Araceae is for the palm *Phoenix dactylifera*, which comprises 715,001 bp and contains 38 proteins, 30 tRNAs, and 3 ribosomal RNAs. Using other mitochondrial genomes as references may yield more and longer regions for our data; but due to the lack of variability found so far we did not pursue this. Similarly, nrDNA lacked variation for *Monstera* (0.4% PICs). ITS and ETS regions have been used once in Araceae for phylogenetic reconstruction (Gauthier et al., 2008), but other studies have failed to use this DNA region and the presence of pseudogenes has been suggested (Carlsen, 2011). Many biological processes like allopolyploidy or incomplete lineage sorting can cause polymorphism and/or pseudogenic sequences in the ITS region (Alvarez & Wendel, 2003; Won & Renner, 2005); however it is difficult to establish which may be causing the problems with the assembly of the nrDNA in *Monstera*.

The amount of variable sites and PICs observed in our plastid DNA dataset (2.3 % and 1 %, **TABLE 3**) are similar to what has been found in other species level studies using complete plastid genomes, (e.g., 3% PIC in *Ipomoea* [Eserman et al., 2014]; 0.48% in *Oreocarya* [Ripma et al., 2014]). However, if we considered only the *Monstera* species (ingroup) the amount of PIC is only 0.5%, again similar to Ripma et al., (2014) for *Oreocarya* (0.32%). In the absence of genomic tools the discovery of molecular markers of phylogenetic utility in tropical Aroids has been evasive. Few chloroplast markers, and even less from nuclear DNA have been used that are suitable for species level phylogenies. In this context, NGS approaches like Genome Skimming offer an alternative

to produce large amounts of data from high copy regions of the DNA in a very efficient and inexpensive manner. Moreover, in a preliminary approach we performed blast searches (E-value < 1e-5) of *Monstera* contigs from the de novo assembly against the 959 single copy genes that are shared in the genomes of *Arabidopsis thaliana, Populus trichocarpa, Vitis vinifera* and *Oryza sativa* (Duarte et al., 2010). We recovered ca. 100 matches to exons of these genes. The utility of these data to develop nuclear markers either for individual sequencing of for NGS target approaches seems to have great potential.

Phylogenetic reconstruction and implications for the systematics of *Monstera*. Despite the low variation in the plastid DNA, we were able to recovered highly supported phylogenetic reconstructions for the genus *Monstera*. Some incongruence was found among coding and non-coding regions of the plastid genome, but they corresponded to nodes of low support (BS<75), particularly regarding the positions of *M. deliciosa* and *M. florescanoana*. Several studies have shown that the mechanisms of molecular evolution present in non-coding regions of the chloroplast may produce homoplasious patterns that could obscure the actual relationships amount taxa (Kelchner, 2000). Despite we tried to exclude regions with ambiguous alignment, inversions, and regions with repeats, other contradictory sequences may persist.

The sectional classification proposed by Madison (1977) was not supported completely in any of our analyses. Phylogenetic relationships of *Monstera* do not reflect the morphological patterns described by Madison (1977), and morphological characters

that are important for taxonomic purposes appear to be homoplasious in *Monstera*. The one that is especially interesting is the presence of shingled leaves, which has been the defining characteristic for the section *Marcgraviopsis* (Madison, 1977). Species from this group appeared in three unrelated high supported clades, implying that the extreme heteroblastic development (i.e., development of a stolon-like seedling, follow by shingled-leave juveniles, and large adult leaves) has evolved more than once in *Monstera*. Although an unexpected result, this type of development has evolved several times in Araceae, especially in the family Monsteroideae (e.g., *Rhaphidophora* and *Scindapsus*), but also in other groups (e.g., *Philodendron*). However the homology of the process resulting in the shingles leaves has not been tested. A group of species from Central America, all having shingled leaves, but very different adult leaf morphologies form a clade (clade 1, **Figure 3)**. The neotenic species *M. tuberculata* placed by Madison in a monotypic section (*Echinospadix*) is nested in this clade. Neoteny has evolved several times in Monsteroideae as well, one in *Scindapsus* and at least one other time in *Rhaphidophora* (Boyce & Bogner, 2000). Other species of *Monstera* (e.g., *M. pittieri*, *M minima*) not included in this study exhibit reduction of the adult leaves, but they are not considered neotenic since adult leaf shapes are slightly different. Evolution of leaf shape in *Monstera* (and in general in Monsteroideae) is an interesting topic for future research. The other defining character of *M. tuberculata*, the echinate spadix has been found in other unrelated species in these analyses (*M. lentii*).

The position of *M. deliciosa* (section *Tornelia*) and *M. florescanoana* varies in the different reconstructions. They appear as sister to the rest of the genus (excluding clade 1,

Figure 3), and they are very distinctive species morphologically. *Monstera florescanoana* is endemic from Veracruz in Mexico, the northern most extreme range for the genus (Croat et al., 2010). This species was assigned to the section *Monstera*, and is the only species in the genus with glaucous leaves in the lower surface. *Monstera deliciosa* also has a unique set of morphological and anatomical characters. Among these unique features we can mention: 1) wide flowers (0.7-1 cm, whereas in all the other species flower width range between 0.2-6 mm); 2) flowers with trichosclereids distributed across the entire flower, whereas in the rest of the species studied the trichosclereids are concentrated in rings around the ovary; and 3) vascular bundles in the flower are distributed in two concentric rings vs. only one a ring of vascular bundles in other species (Zuluaga et al. Unpublished data). Clade 2 comprises four species from Central and South America without extreme heteroblastic development (section *Monstera*); all having lobulated leaves. Clade 3 comprises five species of Central America with a wide morphological variation, including one species with shingled leaves (*M. acuminata*). Clade 4 is composed by two Central American species with the distinctive characters of section *Marcgraviopsis.* These two species are robust plants (with leaves reaching 1.5 m long.) that flower high in the canopy (10-20 m). Finally, clade 5 comprises three species with a wide distribution range. *Monstera adansonii* is the most wide spread species in the genus, from Costa Rica to Brazil and Bolivia, reaching the Caribbean islands.

The phylogenetic reconstructions from plastid genomes in the genus *Monstera* suggest a striking pattern of parallel evolution of morphological characters in vegetative

and reproductive structures. However, the lack of nuclear markers with informative characters prevented us of investigating other hypotheses like the presence of hybridization, and subsequent chloroplast capture. DNA sequences from three nuclear regions (Chalcone synthase, Phytochrome C, and at103 putative protein) showed low or no variation for the species in the genus (Unpublished data). Nauheimer et al. (2012) found incongruences between chloroplast and nuclear markers in the genus *Alocasia*, suggesting hybridization and chloroplast capture in this group. Hybridization has been hypothesized to be common in *Monstera* (Madison, 1977); however there is not evidence supporting this hypothesis. The use of approaches that allow us to recover information from several variable nuclear regions is critical to advance in the understanding of the evolution of the genus *Monstera*, and data generated from this study may help to achieve this goal.

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TABLES AND FIGURES

Table 1. Species names and voucher information for the samples use in this study. **Note: Some voucher numbers still need to be assigned.**

Species	Voucher	GenBank accesion numbers
Monstera lechleriana	Zuluaga A. s.n. (COL)	
Monstera egregia	Zuluaga A. s.n. (WIS)	
Montera sp nov anomala	Zuluaga A. 888 (WIS, PMA, MO)	
Monstera oreophila	Zuluaga A. 886 (WIS, PMA, MO)	
Monstera punctulata	Zuluaga A. 887 (WIS, PMA, MO)	
Monstera pinnatiparita	Zuluaga A. 892 (WIS)	
Monstera acuminata	Zuluaga A. s.n. (WIS)	
Monstera florescanoana	Zuluaga A. s.n. (WIS)	
Monstera tuberculata	Zuluaga A. s.n (WIS)	
Monstera dubia	Zuluaga A. s.n. (WIS)	
Monstera acacoyaguensis	Zuluaga A. s.n. (WIS)	
Epipremnum pinnatum	Zuluaga A. s.n (WIS)	
Monstera adansonii-Colombia	Zuluaga A. 400 (COL)	
Monstera adansonii-Brazil	Monsteiro 465	
Monstera gracilis	Zuluaga A. 421 (COL)	
Rhodospatha venosa	Croat, T. 104784 (MO)	
Monstera deliciosa	Zuluaga A. 902 (WIS, PMA, MO)	
Monstera filamentosa	Zuluaga A. 893 (WIS, PMA)	
Monstera sp nov integrigolia	Zuluaga A. 916 (WIS, PMA, MO)	
Monstera lentii	Zuluaga A. 911 (WIS, PMA, MO)	
Monstera spruceana	Zuluaga A. 899 (WIS)	

Table 2. Information from the Illumina sequencing of genomic DNA for 21 samples used in this study. Number of raw reads and number of reads after quality filter are shown. mtDNA and nrDNA were calculated only for the length of the regions we recovered.

Species	**Raw reads**	**Filter reads**	**Plastid mean coverage**	**mtDNA mean coverage**	**nrDNA mean coverage**
Monstera lechleriana	7974607	7303098	94.9	26.3	126.4
Monstera egregia	5059727	4775714	86.0	35.8	99.7
Monstera sp nov anomala	2522940	2340270	20.6	11.5	50.7
Monstera oreophila	3750804	3540264	15.6	11.9	250
Monstera punctulata	2838671	2679330	15.0	8.9	44.6
Monstera pinnatiparita	2078598	1903568	15.1	7	34.5
Monstera acuminata	3320896	3041257	21.0	16.4	48.7
Monstera florescanoana	2847041	2650159	16.0	13.9	55.6
Monstera tuberculata	1845985	1690542	7.5	7.1	18.5
Monstera dubia	1829675	1697200	9.9	6.3	43.5
Monstera acacoyaguensis	1804758	1674087	11.0	6.8	15.6
Epipremnum pinnatum	3824160	3502143	27.3	13.8	66.7
Monstera adansonii	1240022	1154270	8.9	7.5	25.4
Monstera adansonii	23834154	21827177	103.5	45.7	271
Monstera gracilis	15780683	14689397	37.5	15.6	156.4
Rhodospatha venosa	35887362	33288989	157.6	76.4	396.5
Monstera deliciosa	14556713	13502755	46.3	25	234.6
Monstera filamentosa	11103196	10168241	78.3	28.1	125.7
Monstera coloradense	11198974	10570352	49.7	26.4	176.5
Monstera lentii	10060891	9332447	110.7	36.5	101.6
Monstera spruceana	9816048	9137236	75.6	33.2	102.4

Table 3. Alignment information for the different genomic regions; coding and non- coding regions of the plastid, complete plastid, mtDNA, and nr DNA. The length of the alignment, the percentage of missing data, the variable sites and the Parsimony informative characters (PICs) are shown.

Alignment	**Length**	**Missing Data**	**Variable sites**	**PICs**	**PICs(*Monstera*)**
Non-coding regions	50100	8.8%	1236 (2.4%)	543(1.1%)	291(0.6%)
Coding regions	79062	3.2%	1719 (2.2%)	699 (0.88%)	363(0.45%)
Plastids (excluding IR)	129162	5.9%	2955 (2.3%)	1242(1%)	666(0.5%)
nrDNA	5386	1.8 %	123(2.2%)	34(0.63%)	21(0.4%)
mtDNA	21768	29.9 %	153(0.7%)	22(0.1%)	15(0.06%)

Figure 1. Complete annotated chloroplast of *Monstera adansonii.* Genes (including introns) are coded in green, coding regions in yellow, rRNA in red, tRNA in pink, and inverted repeats in light blue.

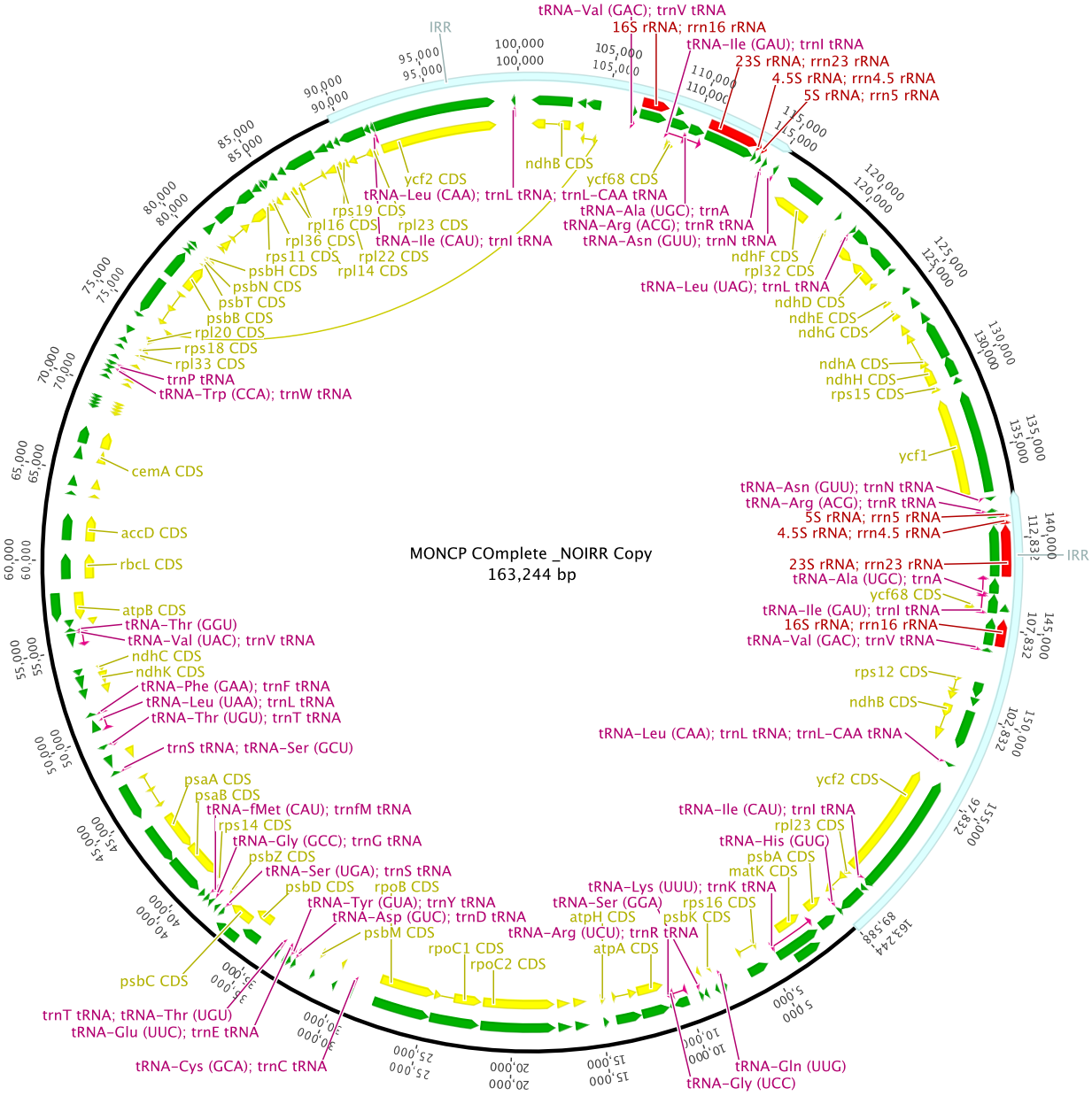

MONCP COmplete _NOIRR Copy
163,244 bp
IRR
IRR
tRNA-Val (GAC); trnV tRNA
16S rRNA; rrn16 rRNA
tRNA-Ile (GAU); trnI tRNA
23S rRNA; rrn23 rRNA
4.5S rRNA; rrn4.5 rRNA
5S rRNA; rrn5 rRNA
ndhB CDS
ycf68 CDS
ycf2 CDS
tRNA-Leu (CAA); trnL tRNA; trnL-CAA tRNA
rps19 CDS
tRNA-Ala (UGC); trnA
rpl16 CDS
rpl23 CDS
tRNA-Arg (ACG); trnR tRNA
rpl36 CDS
tRNA-Ile (CAU); trnI tRNA
tRNA-Asn (GUU); trnN tRNA
rps11 CDS
rpl22 CDS
ndhF CDS
psbH CDS
rpl14 CDS
rpl32 CDS
psbN CDS
tRNA-Leu (UAG); trnL tRNA
psbT CDS
ndhD CDS
psbB CDS
ndhE CDS
rpl20 CDS
ndhG CDS
rps18 CDS
rpl33 CDS
ndhA CDS
trnP tRNA
ndhH CDS
tRNA-Trp (CCA); trnW tRNA
rps15 CDS
ycf1
cemA CDS
tRNA-Asn (GUU); trnN tRNA
tRNA-Arg (ACG); trnR tRNA
5S rRNA; rrn5 rRNA
accD CDS
4.5S rRNA; rrn4.5 rRNA
rbcL CDS
23S rRNA; rrn23 rRNA
tRNA-Ala (UGC); trnA
ycf68 CDS
atpB CDS
tRNA-Ile (GAU); trnI tRNA
tRNA-Thr (GGU)
16S rRNA; rrn16 rRNA
tRNA-Val (UAC); trnV tRNA
tRNA-Val (GAC); trnV tRNA
ndhC CDS
ndhK CDS
rps12 CDS
tRNA-Phe (GAA); trnF tRNA
ndhB CDS
tRNA-Leu (UAA); trnL tRNA
tRNA-Thr (UGU); trnT tRNA
tRNA-Leu (CAA); trnL tRNA; trnL-CAA tRNA
trnS tRNA; tRNA-Ser (GCU)
ycf2 CDS
psaA CDS
psaB CDS
tRNA-fMet (CAU); trnfM tRNA
tRNA-Ile (CAU); trnI tRNA
rps14 CDS
rpl23 CDS
tRNA-Gly (GCC); trnG tRNA
tRNA-His (GUG)
psbZ CDS
psbA CDS
tRNA-Ser (UGA); trnS tRNA
matK CDS
psbD CDS
rpoB CDS
tRNA-Lys (UUU); trnK tRNA
tRNA-Tyr (GUA); trnY tRNA
tRNA-Ser (GGA)
rps16 CDS
tRNA-Asp (GUC); trnD tRNA
atpH CDS
psbK CDS
psbM CDS
tRNA-Arg (UCU); trnR tRNA
rpoC1 CDS
atpA CDS
rpoC2 CDS
psbC CDS
trnT tRNA; tRNA-Thr (UGU)
tRNA-Glu (UUC); trnE tRNA
tRNA-Cys (GCA); trnC tRNA
tRNA-Gln (UUG)
tRNA-Gly (UCC)

Figure 2. Phylograms from Maximum Likelihood (RAxML) analysis of coding (left) and non-coding regions (right) from the plastid genome of species in the genus *Monstera*. Bootstrap support values are shown. Grey bars indicate species with positions supported in both trees, black bars indicate species with incoungruences.

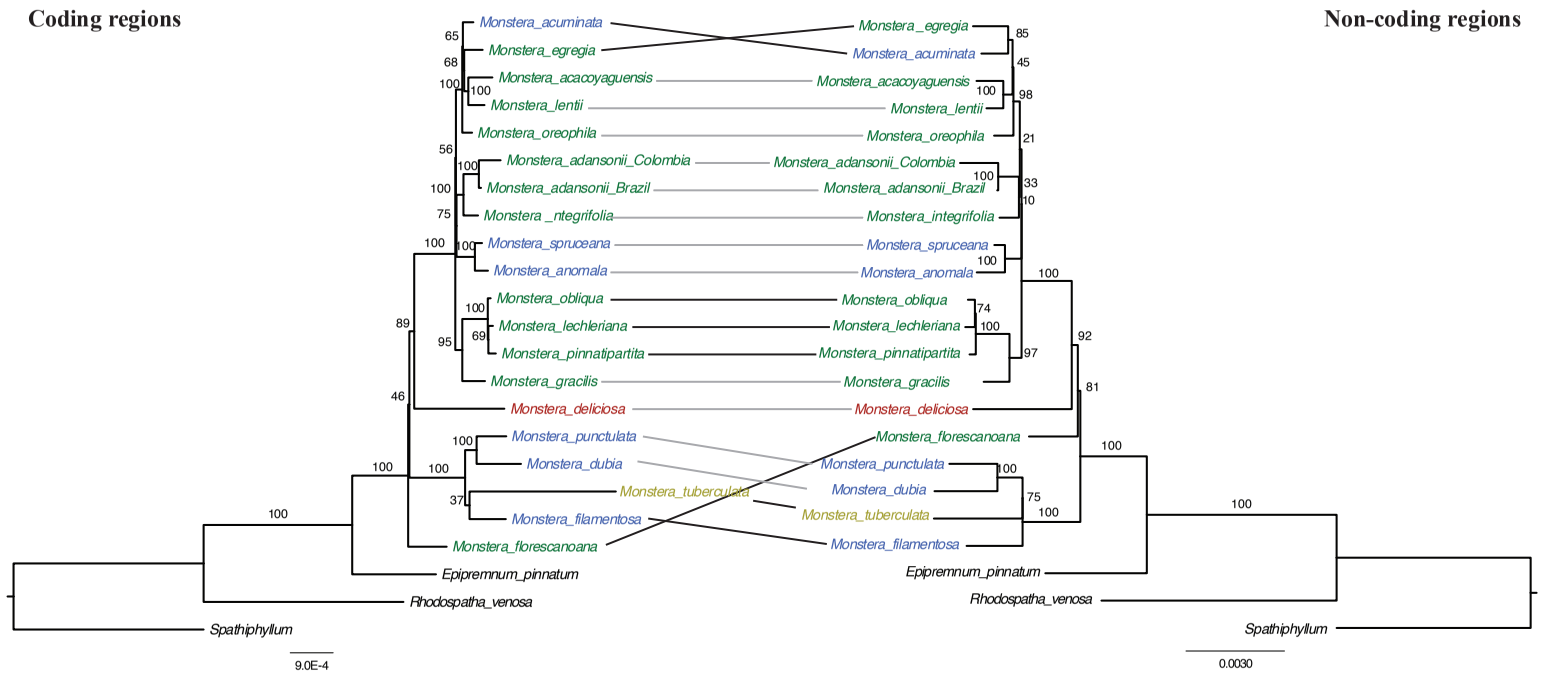
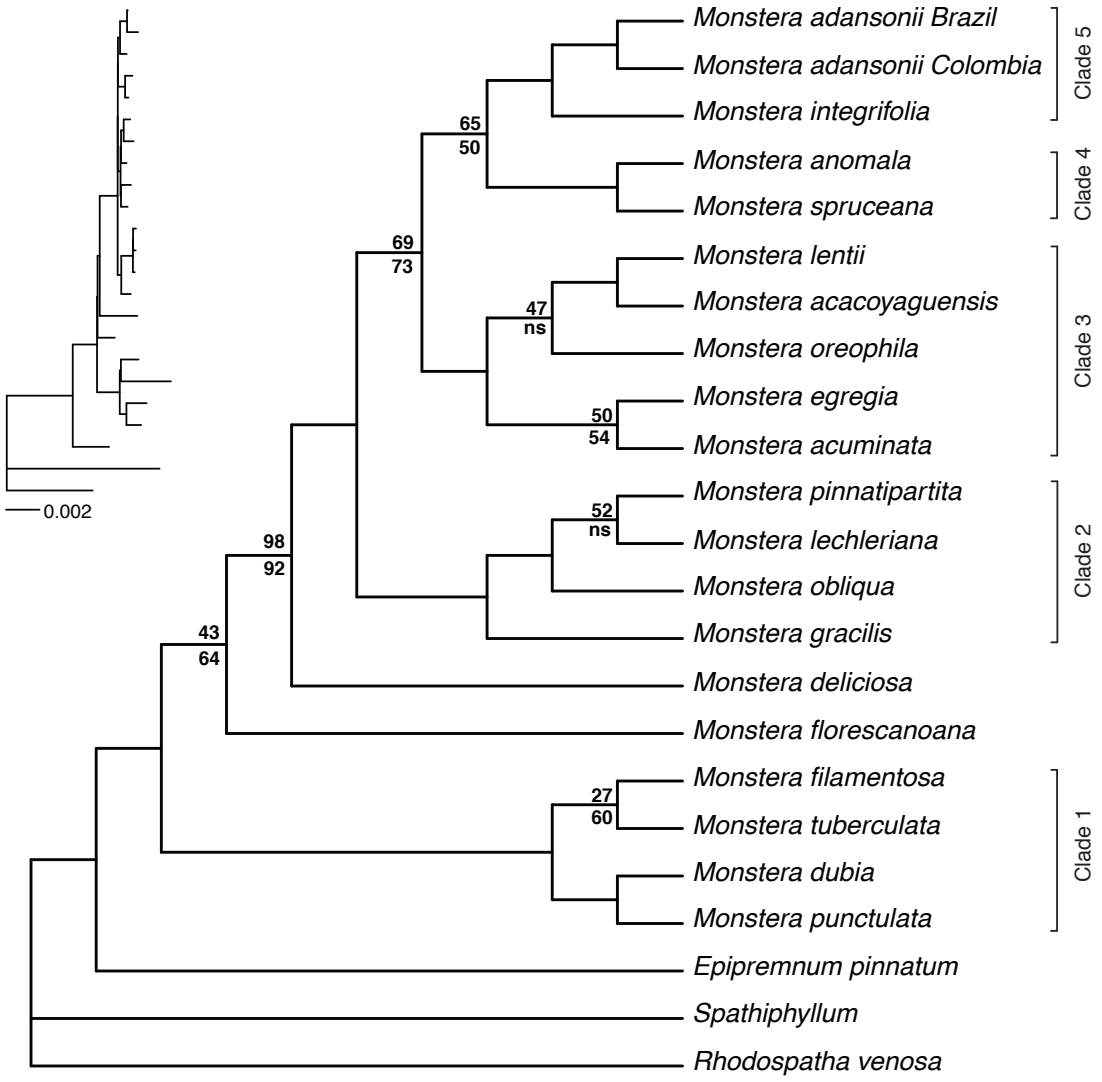

Coding regions
Non-coding regions
Monstera_acuminata
Monstera_egregia
Monstera_acacoyaguensis
Monstera_lentii
Monstera_oreophila
Monstera_adansonii_Colombia
Monstera_adansonii_Brazil
Monstera _ntegrifolia
Monstera_spruceana
Monstera_anomala
Monstera_obliqua
Monstera_lechleriana
Monstera_pinnatipartita
Monstera_gracilis
Monstera_deliciosa
Monstera_punctulata
Monstera_dubia
Monstera_tuberculata
Monstera_filamentosa
Monstera_florescanoana
Epipremnum_pinnatum
Rhodospatha_venosa
Spathiphyllum
9.0E-4
Monstera_egregia
Monstera_acuminata
Monstera_acacoyaguensis
Monstera_lentii
Monstera_oreophila
Monstera_adansonii_Colombia
Monstera_adansonii_Brazil
Monstera_integrifolia
Monstera_spruceana
Monstera_anomala
Monstera_obliqua
Monstera_lechleriana
Monstera_pinnatipartita
Monstera_gracilis
Monstera_deliciosa
Monstera_florescanoana
Monstera_punctulata
Monstera_dubia
Monstera_tuberculata
Monstera_filamentosa
Epipremnum_pinnatum
Rhodospatha_venosa
Spathiphyllum
0.0030

Figure 3. Cladogram depicting the topology from Maximum Likelihood (ML) analysis of complete plastomes of species in the genus *Monstera* using RAxML. Bootstrap support values less than 100 are shown above the brances for ML, and below for Maximum Parsimony (MP); unsupported node in MP are indicated by n.s. Inset tree indicates branch lengths.


Monstera adansonii Brazil
Monstera adansonii Colombia
Monstera integrifolia
Monstera anomala
Monstera spruceana
Monstera lentii
Monstera acacoyaguensis
Monstera oreophila
Monstera egregia
Monstera acuminata
Monstera pinnatipartita
Monstera lechleriana
Monstera obliqua
Monstera gracilis
Monstera deliciosa
Monstera florescanoana
Monstera filamentosa
Monstera tuberculata
Monstera dubia
Monstera punctulata
Epipremnum pinnatum
Spathiphyllum
Rhodospatha venosa
Clade 5
Clade 4
Clade 3
Clade 2
Clade 1
65
50
69
73
47
ns
50
54
52
ns
98
92
43
64
27
60
0.002

Chapter 4

Taxonomic studies in the Neotropical genus *Monstera* (Araceae)

Part 1. Two new species of *Monstera* (Araceae) with entire leaves from Panama and Costa Rica

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ABSTRACT

The genus *Monstera* (Araceae) is a poorly known genus in terms of its systematics and ecology, and historically its taxonomy has been problematic due to the large number of existing names, incorrect use of them, and existence of few complete herbarium specimens. The last taxonomic revision of the genus included 22 species, but now is very much out of date, and there are more species than this recognized today in Panama or Costa Rica alone. Today, among ca. 130 names, only 42 species are recognized, and as many as 10-15 new taxa remain undescribed. A product of field explorations and study of herbarium specimens, in the first part of this chapter we described two new species of *Monstera* from Panama and Costa Rica. In the second part, we developed a web based interactive tool for the identification of the species in the genus using the software Lucid. For this purpose we created a geographic database with ca. 4200 herbarium specimens; and an identification database including 108 ecological, morphological and anatomical characters. So far we have included 42 recognized species plus the two new species described in this study.

Keywords

Araceae, Costa Rica, interactive key, Lucid, *Monstera*, new species, Panama,

INTRODUCTION

Species of the genus *Monstera* (Araceae) are an abundant and important hemiepiphytic component of montane and lowland tropical rainforests (Madison, 1977). The genus is exclusively Neotropical and has two principal centers of diversity: Costa Rica–Panamá and the Colombian Andes. *Monstera* is a poorly known genus in terms of its ecology, and historically its taxonomy has been problematic due to the large number of existing names, incorrect use of them, and prevalence of incomplete herbarium specimens (Madison, 1977). The last taxonomic revision of the genus (Madison, 1977) included 22 species, but now is very much out of data, and there are more species than this recognized today in Panama or Costa Rica alone (Andrade & Mayo, 1998; Grayum, 2003; Croat *et al*., 2005). Today, among ca. 130 names, only 42 species are recognized, and as many as 10–15 new taxa remain undescribed. Based on morphological characters Madison (1977) proposed four sections within *Monstera*, changing considerably previous classifications (e.g., Engler, 1908). The species of sections *Marcgraviopsis*, *Tornelia*, and *Echinospadix* (ca. 10 species collectively) are easily recognized based on their morphology, growth habits, and habitat preferences. Section *Marcgraviopsis* is characterized by a heteroblastic development with three clear stages: a stolon-like seedling lacking leaves; an early juvenile phase with adpressed leaves (shingled) similar to those of the eudicot genus *Marcgarvia*; and pre-adult and/or adult plants with exserted leaves that are otherwise different in shape from shingled leaves (Madison, 1977; Ray, 1987; Oberbauer & Noudali, 1998). *Monstera* section *Tornelia* (= *M. deliciosa* Liebmann [1849:19]) and section *Echinospadix* (= *M. tuberculata* Lundell [1939:78]) are both monotypic, and recognized by its large pistils and seeds, and for the neotenic adult leaves with a ligule

respectively (Madison, 1977). In contrast, delimitation of species in the fourth section, *Monstera*, is notoriously difficult because of the presence of numerous intermediates connecting them (Madison, 1977). Recent molecular phylogenetic studies (Zuluaga et al., unpublished data) do not support the monophyly of the *Monstera* sections, showing that morphological used in classifications are homoplasic. However, most of the species in section *Marcgraviopsis* do form a clade (albeit with monotypic sections *Echinospadix* and *Tornelia* nested within).

MATERIALS AND METHODS

Field explorations in Panama and study of herbarium collections, especially at the Missouri Botanical Garden (MO), have revealed several undescribed taxa in the genus *Monstera*. Many of these new taxa are being described for the treatment of the forthcoming Flora Mesoamericana (Croat personal communication), and here we describe two new species of *Monstera* bearing entire leaves and lacking fenestrations.

TAXONOMIC TREATMENT

***Monstera anomala* Zuluaga & Croat *sp. nov*. (Figs 1 & 2)**

Diagnosis:—*Monstera anomala* is easy to distinguish from other species in the genus with shingled leaves because of its flowers with a long and constricted stylar region, 4–6 mm long, which is narrower than the ovary. It is most similar to *M. acuminata* K.Koch (1855[App]: 4), but adult plants are more robust, with entire leaves lacking fenestrations, and with secondary and tertiary veins inconspicuous on the upper surface.

Type: —PANAMA. Veraguas: Distrito Santa Fe, corregimiento El Pantano, Parque Nacional Santa Fe, alto Los Gonzales to alto El Viro, 800–1000 m. 8°33.162'N–8°33.625'N, 81°4.586'–81°4.767'W, 16 Jan 2013, *A. Zuluaga, A. Doucette, E. Brantner & E. González 888* (Holotype: WIS!; Isotypes: PMA!, MO!).

Seedling stolon-like, on the ground of the forest, green, 1–3 mm diameter. *Juvenile plants* completely adpressed to the host (i.e., with shingled leaves); petioles less than 6 mm long; blades oblate to circular, 0.5–10 cm in diameter, size increasing gradually with the height on the host, asymmetrical, apex with a short acumen, suddenly switching to the adult shape. *Pre-adult and adult* stems adpressed to the host, circular in cross section, 1.5–2.8 cm across, internodes 3–7 cm long. Pre-adult and adult leaves exserted from the host, alternate, most of the leaves distichous, except for the ones close to the apex of the plant; petioles 20–50 cm long, 0.4–1.2 cm diameter, circular in cross section, departing 45–90 degrees from the host, petiole sheathed for the almost entire petiole (excluding the geniculum); sheath marcescent, the base persistent as fibers; geniculum 1.8–3.8 cm long, 0.4–1.2 diameter; blades entire, very rarely with fenestrations or lobate, perpendicular to the host to slightly pendent, elliptical to oblong, 0.9–1.5 times longer than the petiole, 27–60 cm long, 9–20 cm width, 2.1–4.2 times longer than wider, symmetrical to asymmetrical, apex turning towards one side, discolor, upper surface bright green and glossy, lower surface paler looking whitish, and mate, base obtuse, apex acuminate; main vein flat in the upper surface, raised in the lower surface, primary lateral veins sunken in the upper surface, raised in the lower surface, 10–15 per side, secondary lateral veins

inconspicuous on the upper surface, visible in the lower surface; tertiary veins reticulate, inconspicuous. Plants flowering (6–)10–20 m above the ground, inflorescence axillary, solitary; peduncle 6–14 cm long, 0.6–1.4 cm diameter, circular in cross section, green; spathe white in anthesis, 10–13 cm long, 1–3 cm longer than the spadix; spadix terete in cross section, slightly narrower at the apex, 12–22 cm long, 2.7–5 cm diameter, 1.7–2.8 times longer than the peduncle. Flowers white, 15–22 in the primary spiral, 17–25 in the secondary spiral, 8–18 mm long, cross section at the ovary circular, 3–4 mm diameter, style 3–5 mm long, cross section at the style narrower than the ovary, 2–4 mm diameter, apex of the flower as wide as the ovary, hexagonal viewed from the top, trichosclereids abundant in the stylar region and reaching the ovary; stigma linear, 2–3 mm long; stamens four, filaments laminar, 3–4 mm long; anthers 2–3 mm long; ovary 3–4 mm long, 2-locular, two ovules per locule. Fruiting spadix first green, yellow at maturity, 15–27 cm long, 5–8 cm diameter; stylar cap falling off the fruits exposing the white aril. Seeds one per fruit, green–blue, 4–6 mm long, 3–4 cm wide, 1–2 mm thick; embryo green.

Etymology:— The epithet *anomala* (meaning anomalous or strange), was chosen because of the species unique combination of foliar and flower characters not common in other *Monstera* species.

Distribution and habitat:— *Monstera anomala* ranges from North Central Panama to South Central Costa Rica, at elevations between 100–1200 m. This species grows high (10-20 m) into the canopy of humid premontane and montane forests (**Figure 3**).

Observations:— *Monstera anomala* has all the general characteristics of the species in the section *Marcgraviopsis* sensu Madison (1977). From among this group of species *M. anomala* it is most similar to *M. acuminata* K. Koch, a widespread species from Mexico to Panama. However, *M. anomala* differs from *M. acuminata* in having more coriaceous leaves, larger length/width leaf ratio, inconspicuous secondary lateral veins on the lower surface (vs. conspicuous), and flowers with a long and narrow style (vs. style as wide as the ovary) (**Table 1**). Some specimens of *M. spruceana* (Schott) Engler (1878: 115) with leaves lacking fenestrations could be confused with *M. anomala;* however, *M. spruceana* is a more robust plant with deeply lobate leaves. Grayum and Croat first recognized several specimens of *M. anomala* as a different taxon, and assigned the name *M. skuctchii* to several collections from Costa Rica. However, all these specimens were later identified as *M. spruceana* for the Araceae treatment of the Costa Rican Flora (Grayum, 2003). Morphologically *M. spruceana* is a species distinctive from *M. anomala*, and its distribution throughout Central America is not clear.

Additional specimens examined:—COSTA RICA. Cartago: Turrialba, along camino Raíz de Hule, south east of Platanillo (Tsipirí), 9°49'12"N, 83°24'W, 1200–1400 m, 1 Jul 1976, *T.B. Croat 36788* (MO); Turrialba, along Quebrada Platanillo near confluence of Quebrada Sipiri, Platanillo de Chirripó, 9°48'36"N, 83°24'W, 1135 m, 2 Mar 1990, *M.H. Grayum* 9727 (MO). **Heredia:** Sarapiquí, finca El Bejuco, S base of Cerros Sardinal, Chilamate de Sarapiquí. 10°27'N, 84°3'36"W, 70–100 m, 2 Jun 1985, *M.H. Grayum* 5327 (MO); Sarapiquí, finca La Selva, Puerto Viejo de Sarapiquí, ridge near end of Pasos

Perdidos, 10º25'N, 84º2'W, 120 m, 3 Jun 1985, *M.H. Grayum 5356* (DUKE, MO). **Limón:** Talamanca, Cantón de Talamanca, Alto Urén, subiendo a Cerro Chun, siguiendo un antiguo camino de Quebrada Chaho a Alto Lari, 9°24'N, 83°19'48"W, 800 m, 24 Jul 1989, *G. Herrera–Chacón 3330* (MO); along road between Puerto Viejo de Talamanca and Manzanillo, stretch from Quebrado Ernesto to Manzanillo, 9°37'48"–09°38'N, 82°40'48"–82°42'W, 5 m, 3 Nov 1984, *M.H. Grayum 4352* (AAU, CR, MO); hills 3.5 airline km S of Islas Buena Vista in the Río Colorado, 16 airline km SW of Barra del Colorado, premontane wet forest on low hills, 10°39'N, 83°40'12"W, 10–120 m, 15 Sep 1986, *G. Davidse 31269* (MO); Refugio Barra del Colorado, forests and pastures between Río Chirripocito and Río Sardina (Sardinal on Chirripó Atlántico quadrangle), 10°37'48"N, 83°45'W, 12 m, 21 Apr 1990, *M.H. Grayum 9809* (MO). **Puntarenas:** Osa, hills north of Palmar Norte, along trail to Jalisco, 8°58'48"N, 83°25'12"W, 50–700 m, 21 May 1976, *T.B. Croat 35187* (MO); along highway to Golfito from Panamerican highway at Río Claro, 2.5 mi SE of Golfito, 8°36'N, 83°3'36"W, 60 m, 14 Sep 1987, *T.B. Croat 67585* (HNMN, MO); along road between Palmar Norte and Panamerican border, 3 km N of turn–off to Rincón, 8°48'39"N, 83°16'18"W, 110 m, 10 Sep 1996, *T.B. Croat 79200* (INB, MO); along road between Rincón de Osa and Rancho Quemado, ca. 10 km W of main Rincón–Pto. Jimenez Road, 8°41'N, 83°32'W, 150–260 m, 3 Mar 1985, *T.B. Croat 59755* (CAS, GB, HNMN, MO); Rincón de Osa, along ridge between quebrada Aparicio and quebrada Aguabuena, 8°42'N, 83°30'36"W, 200–400 m, 7 Oct 1984, *M.H. Grayum 4015* (MO, NY). **San José:** Perez Zeledon, about 1 mile beyond divide between San Isidro del General and coastal town of Dominical, 9°16'12"N, 83°51'36"W, 900 m, 22 May 1976, *T.B. Croat 35304* (MO). **PANAMA. Chiriquí:** San Bartolo Limite, 18 km

W of Puerto Armuelles, rainforest, 8°17'24"N, 82°58'36"W, 450 m, 24 Feb 1973, *P. Busey 604* (MO). **Colón:** Teck Cominco Petaquilla mining concession, forested slopes along ridge road, 8°49'28"N, 80°39'29"W, 110 m, 10 Mar 2008, *G.D. Mcpherson 20496* (MO, PMA). **Panamá:** Capira, cloud forest on Cerro Campana above Su Lin Motel, 8°43'N, 79°54'W, 209 m, 25 May 1971, *T.B. Croat 14767* (MO); middle slopes of Cerro Campana, ca. 1 mi from Interamerican Highway, 8°43'9"N, 79°53'25"W, 150 m, 15 Jun 1976, *T.B. Croat 35989* (MO); Panamá, vicinity of Cerro Jefe, 4.6 km beyond peak on road to Altos de Pacora, 26.3 km from the Inter–American Highway, 9°14'20"N, 79°20'25"W, 600 m, 12 Jun 1976, *T.B. Croat 35914* (MO); Cerro Campana, 6.1 miles above Pan–American highway, 3.2 miles beyond park entrance and Guarda Bosque Station, 8°41'N, 79°56'W, 800 m, 23 Mar 1993, *T.B. Croat 74767* (CM, MO). **Veraguas:** Santa Fé, along 1st branch of Río Santa María, roadside and forest a short way S of river, road from Santa Fé, 8°31'26"N, 81°7'46"W, 600 m, 26 Oct 1975, *J.T. Witherspoon 8903* (MO); NW of Santa Fé, ca. 1km from Escuela Agrícola Alto de Piedra, Pacific slope, 8°31'22"N, 81°7'35"W, 800 m, 21 Dec 1974, *S.A. Mori 4024* (MO); vicinity of Santa Fé, along dirt road from Santa Fé to Río San Luis, past Escuela Circlo Alto de Piedra, at Río Segundo Brazo (2nd stream below school on Atlantic Coast), 8°33'N, 81°8'W, 480 m, 28 Jun 1987, *T.B. Croat 66902* (MEXU, MO).

***Monstera integrifolia* Zuluaga & Croat *sp. nov*.** (**Figures 4 & 5**).

Diagnosis:—*Monstera integrifolia* has erect and small entire leaf blades (16–31cm long) lacking fenestrations. It is most similar in appearance to *M. xanthospataha* Madison

(1977: 65–67) but differs in the shorter peduncles (9–14 vs. 13–25 cm), longer spadix (8–10 vs. 5–7 cm), and raised stylar region (vs. flat).

Type: PANAMA. Chiriqui: Distrito Gualaca, corregimiento Hornito, Reserva Forestal Fortuna, trails near to research center Jorge L. Arauz. 1200–1500 m elevation, 8°47'W, 82°12.8'N, 31 Jan 2013, *A. Zuluaga 916* (Holotype: WIS!, Isotypes: PMA!, MO!).

Seedling not seen. *Juvenile* plants with stems adpressed to the host; leaves exserted from the host in an angle less than 45 degrees, leaf blade shape the same as adults leaves but increasing gradually in size. *Pre-adult and adult* plants growing on vertical stems and lateral branches; stem depressed, D shape in cross section, flat side facing the host, 1–3 cm diameter, internodes 4–6 cm long. Leaves erect or almost erect, spreading from an angle less than 45 degrees on a vertical host, or 45–90 degrees when host is horizontal; petioles 5–10 cm long, 1–2 cm diameter, D shape in cross section, petiole sheathed almost its entire length, sheath marcescent, not persistent; geniculum 2–3 cm long; blades ovate to lanceolate, assymetrical, 16–31 cm long, 7–10 cm width, blade 1.2–1.6 times longer than petiole, coriaceous, dark green on both surfaces, paler in the lower surface, base obtuse, apex acuminate; main vein flat in the upper surface, raised in the lower surface, primary lateral veins sunken in the upper surface, raised in the lower surface, 4–8 per side, secondary lateral veins sunken on the upper surface, slightly raised in the lower surface; tertiary veins reticulate, inconspicuous. Plants flowering 3–5 m above the ground, inflorescence solitary; peduncle 9–14 cm long, 0.6–1.2 cm diameter, circular in cross section, green; spathe white in anthesis, 15–18 cm long, 8–9 cm width, 5–8 cm

longer than the spadix; spadix terete, slightly narrower at the apex, 8–10 cm long, 1.7–2 cm diameter, 0.6–0.9 times longer than the peduncle. Flowers white, 12-14 in the primary spiral, 14–17 in the secondary spiral, 4–5 mm long, cross section at the ovary circular, 3–4 mm diameter, apex of style narrower than the ovary, raised, 1–2 mm long; stigma capitated, 1–2–mm long; stamens four; filaments laminar, 3–4 mm long; anthers 2–3 mm long. Infructescence, fruits, and seeds not seen.

Etymology:—The specific epithet *integrifolia* refers to the entire leaves lacking fenestrations, a character not common in *Monstera*.

Distribution and habitat:— *Monstera integrifolia* is only known from four collections from North Panama and the Panama–Costa Rica border. It grows in wet and humid forests at 1000–2000 m above sea level (**Figure 6**).

Observations:—*Monstera integrifolia* is most similar to *M. xanthospatha*, a species endemic to the West and Central Cordilleras of Colombia at elevations between 1500–2300 m. Both species are small plants, flowering when they are less than 10 m high in the host, and inhabit montane cloud forests. *Monstera integrifolia* differs from *M. xanthospatha* in having shorter petioles and peduncules, a longer spadix, and flowers with raised stylar regions (vs. flat) (see **Table 2**.)

Additional specimens examined:—COSTA RICA. Puntarenas: Corredores, along road between San Vito de Java and Villa Neily, 8.8 miles north of Villa Neily,

8°42'28"N, 82°56'16"W, 1010 m, 14 Jun 1987, *T.B. Croat 66170* (MO). **PANAMA. Bocas del Toro:** Cerro Colorado, 9.2 mi W of Chamé, along trail E of road which leads down to stream, 8°35'N, 81°50'W, 1450–1480 m, 6 Jul 1988, T.*B. Croat 69067* (MO, PMA); Changuinola, about 1 mile S of Changuinola on the Changuinola River, forest edge of banana grove, 9°24'06"N, 82°30'W, 19 Apr 1969, *R.L. Lazor 2658* (MO). **Chiriquí:** Fortuna Dam site, forest area, 8°44'N, 82°15'W, 1400 1600 m, 15 Sep 1977, *J.P. Folsom 5598* (MO).

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TABLES AND FIGURES

Table 1. Morphological differences between *Monstera anomala* and *M. acuminata*

Species	Leaf fenestrations	Blade space orientation	Secondary veins	Length/width leaf ratio	Style shape
M. anomala	absent	Perpendicular to slightly pendent	Inconspicuous on the lower surface	1.7–2.8	Constricted, narrower than ovary
M. acuminata	present or absent	Pendent	Visible on the lower surface	1.3–2.0	Straight, as wide as ovary

Table 2. Morphological differences between *Monstera integrifolia* and *M. xanthospatha*

Species	Leaf fenestrations	Peduncule length	Spadix length	Flower stylar region
M. integrifolia	absent	9–14 cm	8–10 cm	Raised
M. xanthospatha	present or absent	13–25 cm	5–7 cm	Flat

Figure 1. Comparison between *Monstera anomala* sp. nov. (**A–C, E–F**), and *M. acuminata* (**D, G–I**). *Monstera anomala*: **A**, Adult plant showing leaves lacking fenestrations and infrustescence; **B–C**, mature infrustescence showing stylar caps falling off; **E**, Juvenile shingled–leaf plant; **F**, individual fruits showing narrow stylar region of the flower. *Monstera acuminata:* **D,** inflorescence; **G–I**, adult leaves of with and without fenestrations.

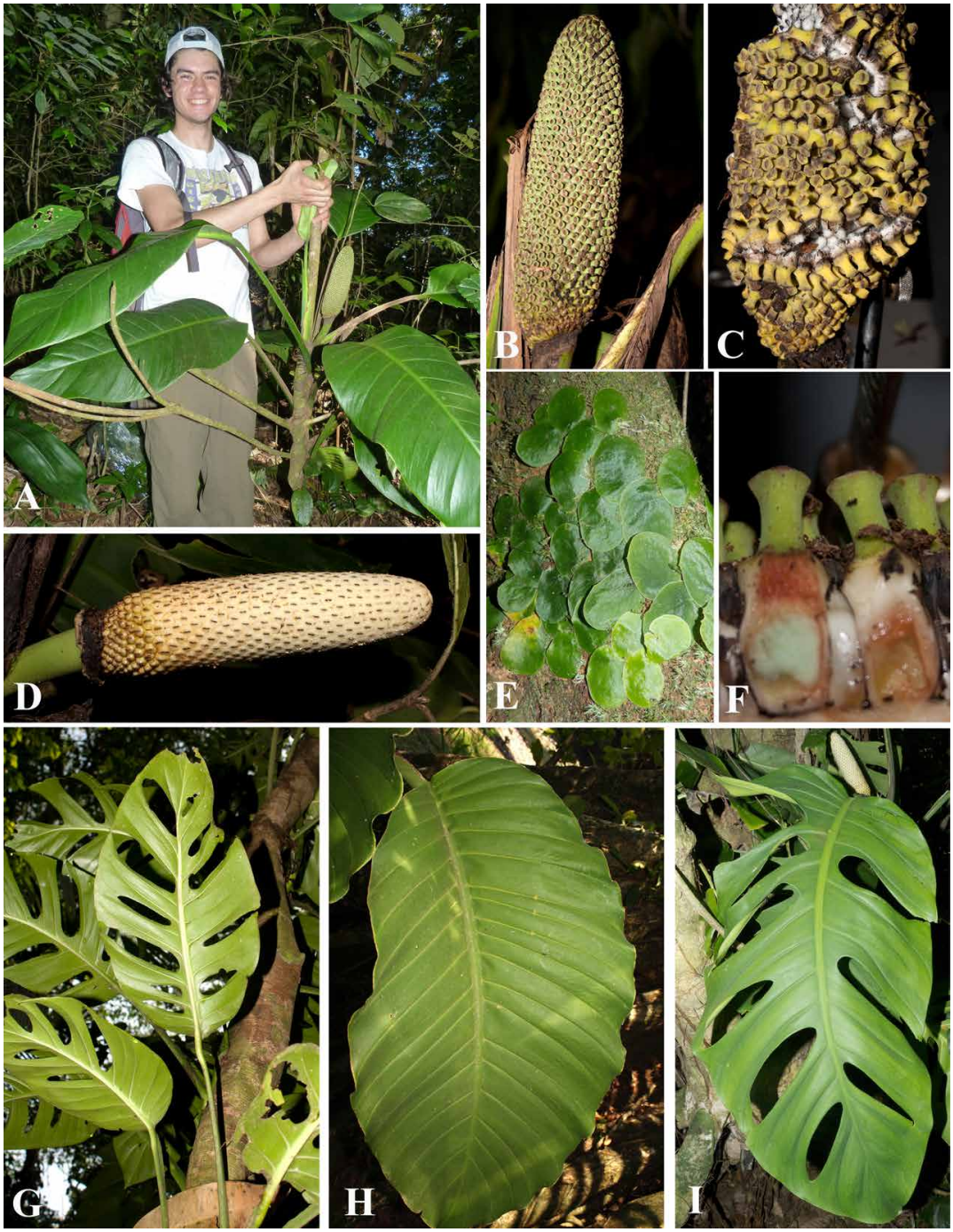

A
B
C
D
E
F
G
H
I

Figure 2. Illustration of *Monstera anomala* sp. nov.


10 cm
1 cm
A
10 cm
5 cm
B
C
D

Figure 3. Distribution map of *Monstera anomala.*

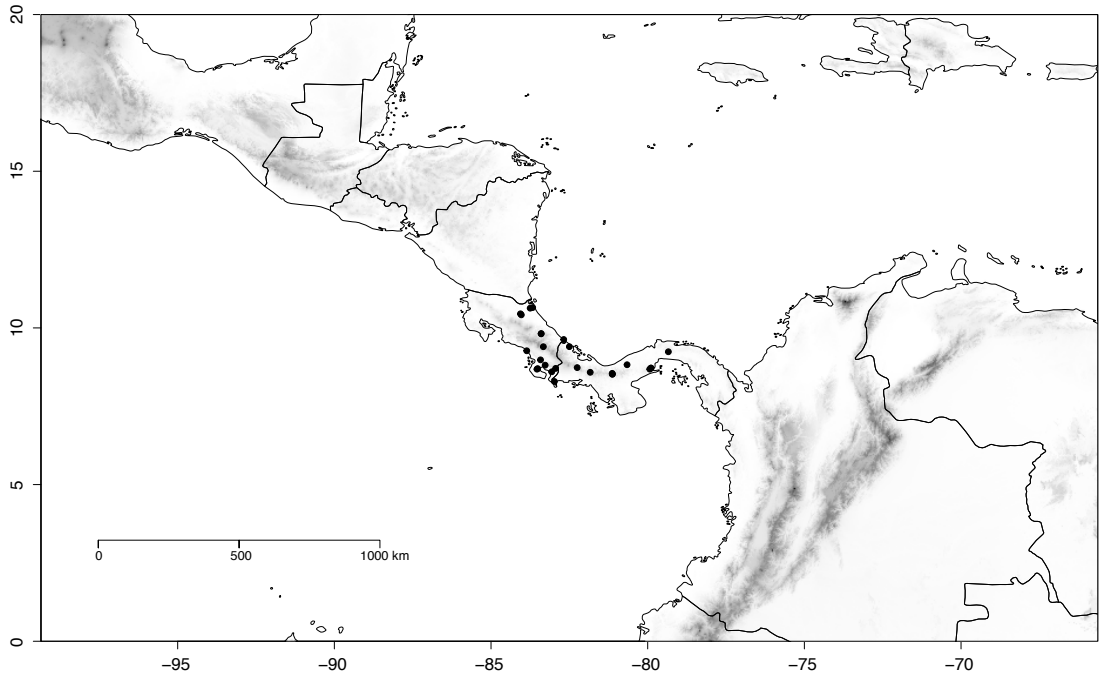


Figure 4. Comparison between *Monstera integrifolia* sp. nov. (**A–C**) and *M. xanthospatha* (**D–G**). *Monstera integrifolia*: **A**, adult leaf lacking fenestrations; **B**, detail of the periole showing the punctuated pattern; **C**, young spadix showing blunt flowers. *Monstera xanthospatha:* **D–E,** Adult leaves of with and without fenestrations; **F**, young spadix enclosed by the spathe; **G**, infrutescence.

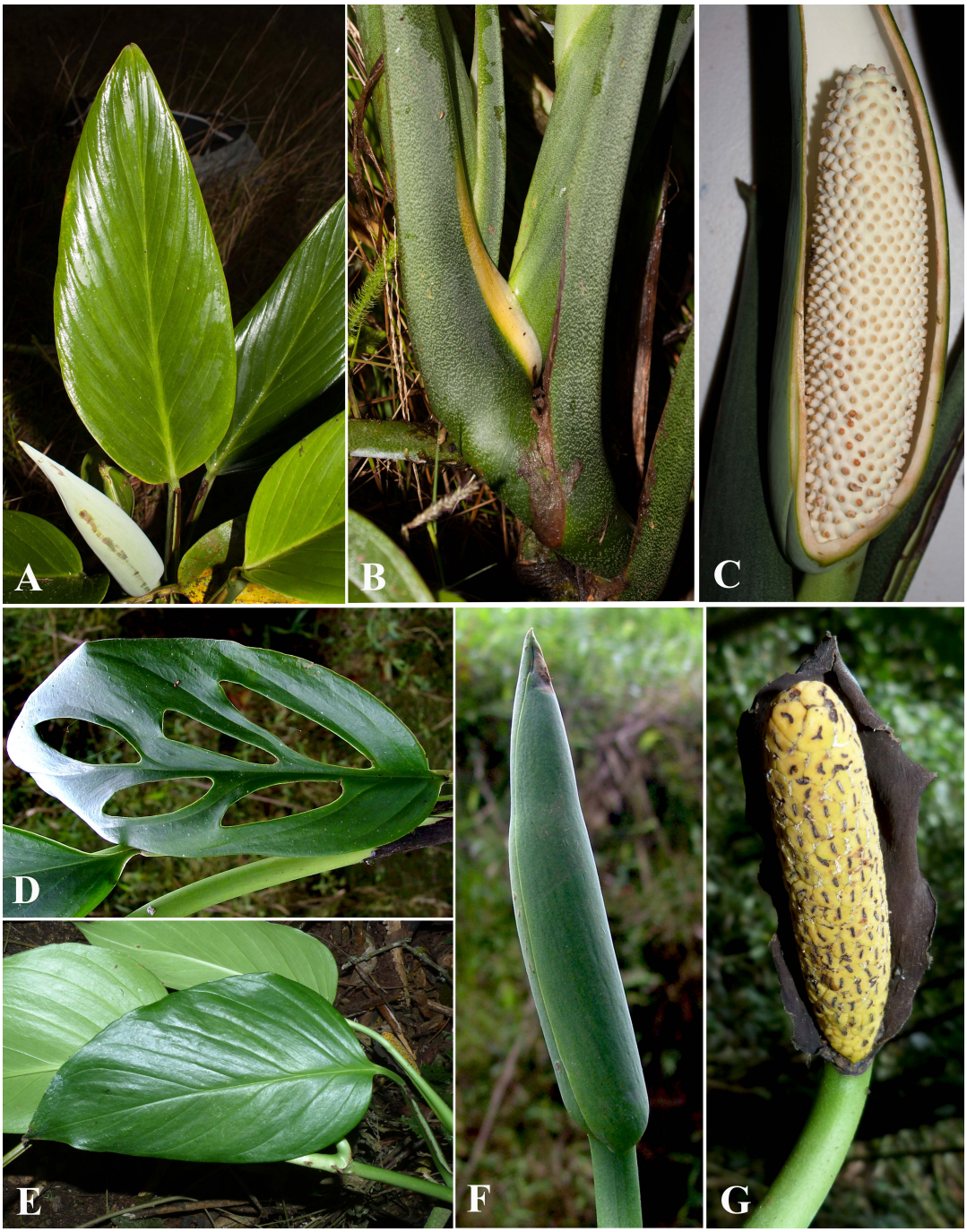

A
B
C
D
E
F
G

Figure 5. Illustration of *Monstera integrifolia* sp. nov.

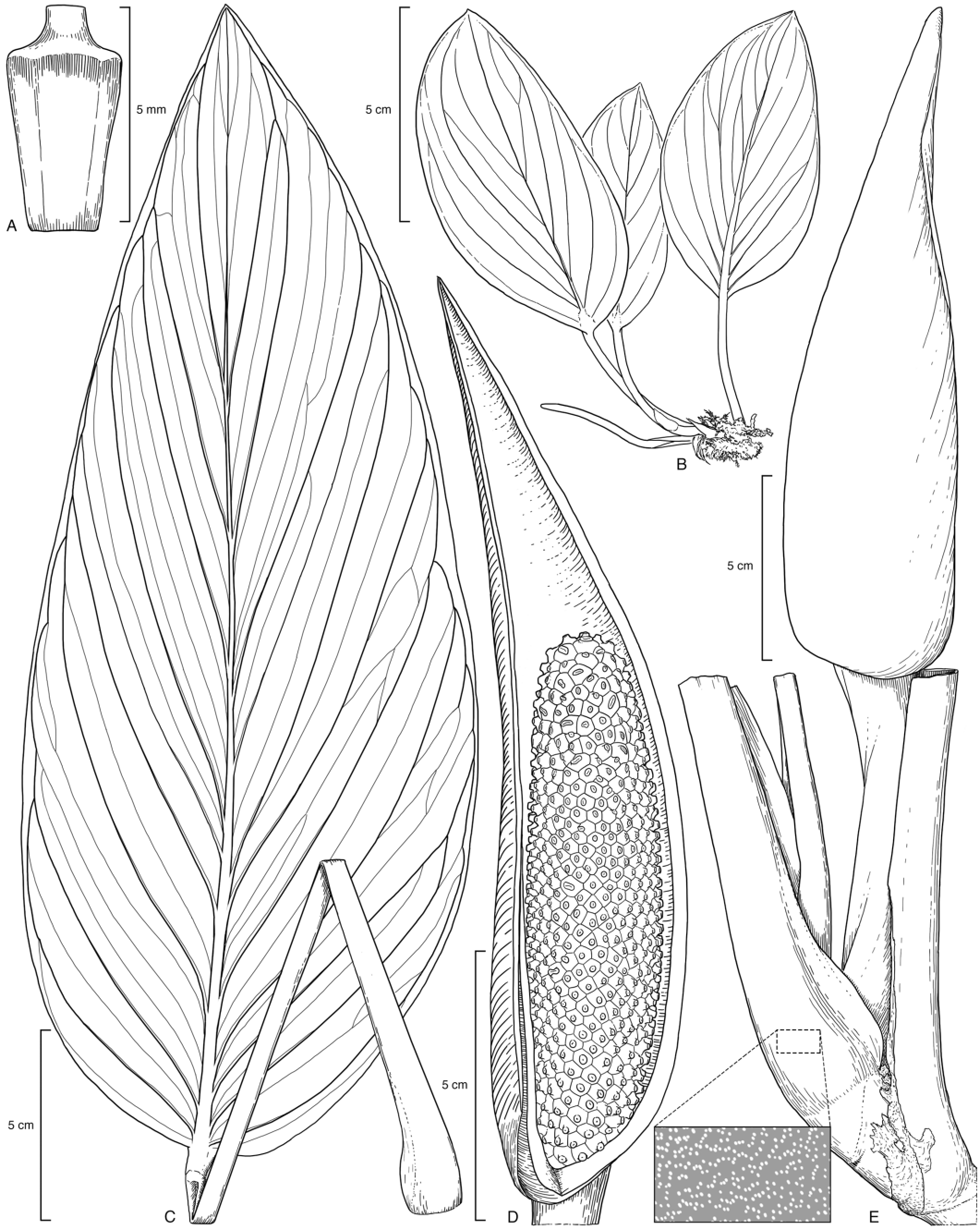
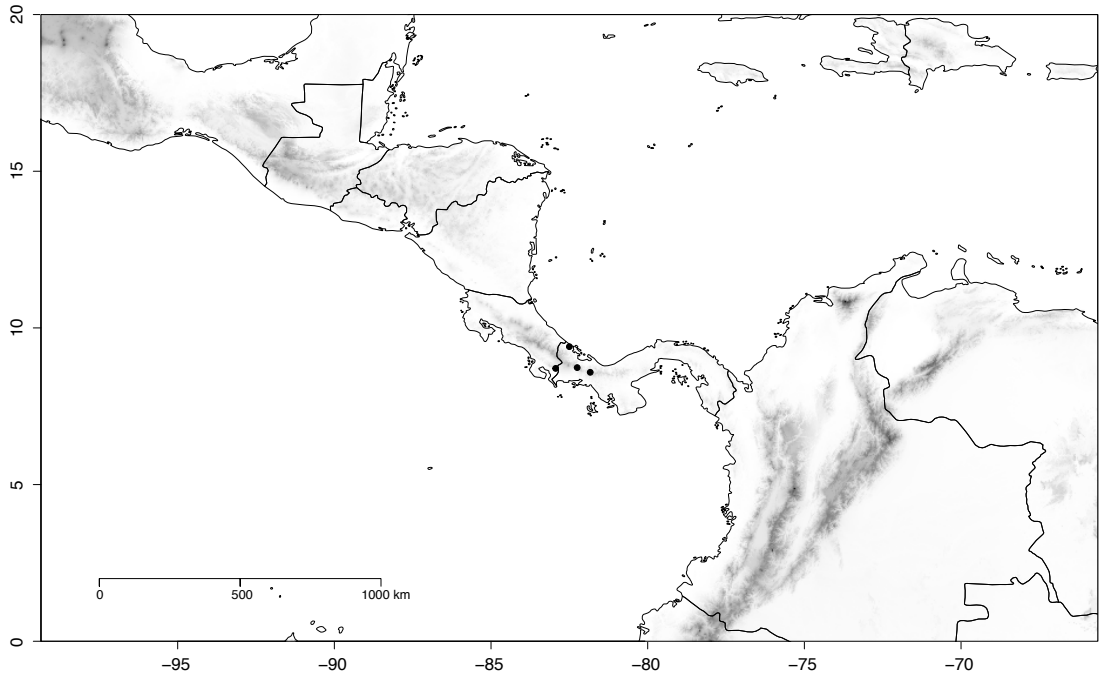

5 mm
A
5 cm
B
5 cm
C
5 cm
D
5 cm
E

Figure 6. Distribution map of *Monstera integrifolia.*



Part 2. A preliminary interactive web tool for the identification of the species in the genus *Monstera* (Araceae)

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INTRODUCTION

New web-based tools are being used to facilitate the gathering, storage, and access of taxonomical, geographical, and ecological information about particular taxonomical groups or for complete inventories from particular regions (Brach et al., 2005; Brach & Song, 2006; Clark et al., 2009). Web-based tools used to document taxonomical groups have many advantages: 1) they can be constantly updated and modified, allowing the inclusion/deletion new taxa, or any information about morphology, geography or ecology; 2) there is not limitation to the amount visual material that can be added for a particular taxon; and 3) they generally free and easily access for anyone with an Internet connection. Many flexible and multifunctional tools have been developed to facilitate this task. The Scratchpad Virtual Research Environment (http://scratchpads.eu/) (Smith et al., 2009; Smith et al., 2011) is one of the most flexible and easy to use resources of this kind, with about ca. 680 web-based sites using it to date (http://scratchpads.eu/).

The family Araceae was used as a model group for the Creating a Taxonomic e-Science (CATE) project, which goal was to create an E-Taxonomy of the family, including a full taxonomic revision for all genera and species (Haigh et al., 2009). This information was later transferred to the Scratchpad environment, and it is now available at eMonocot Team Araceae (*CATE Araceae* Monocot Portal, http://araceae.e-monocot.org/). One of the tools available through the *CATE Araceae*-eMonocot portal is a series of interactive keys for identification of genera in Araceae, Araceae from Africa, *Anthurium* species, among others; all of them built using the software Lucid (www.lucidcentral.com). These

tools are from great utility not only for scientist but also for enthusiasts and growers. Interactive keys and other digital identification tools have become very popular in recent years and several options are available (e.g., Linnaeus II [www.eti.uva.nl/products/linnaeus.php]; Lucid Key Server [www.lucidcentral.com]; Xper2 [http://lis-upmc.snv.jussieu.fr/lis/?q=en/resources/software/xper2]. but see Dallwitz et al., and 2013; Farnsworth et al., 2013, for a list and comparison of interactive key tools). The Lucid software offers a series of tools to build interactive and dichotomous keys as well as fact sheets for taxa, and is one of the most used interactive key tools with more than 250 keys available from a variety of organisms and regions around the world (lucidcentral.org). One of the downsides of this software is that the most up to date version is not freely available to the public, although older versions are.

Traditional taxonomy for many groups of Araceae is complex, especially for those from the tropics, and current taxonomic revisions and dichotomous keys are very much out of date, and/or are insufficient for species identification. In some cases like for the genera *Anthurium* and *Philodendron* the main limitation to build efficient taxonomy databases and identification tools is the large number of species (ca.1000 and 500 respectively) and its constant growing; in other cases like the genus *Monstera* (ca. 50 species) the limitation is the deficient collections, the chaotic taxonomic history, and the general poor knowledge about the natural history of the group. Our goal is to create a complete web-based tool for the genus *Monstera* that includes not only taxonomical information, but also geographical and ecological information in a phylogenetic framework. This will help not only with taxonomic identification, but will build the basis

to answer evolutionary questions about this group and to develop comparative analysis combining several sources of information. Here we present the first step of this undertake, an interactive key for the genus including all species described so far plus some taxa in the process of being described.

METHODS

Sources of information. *Herbarium and fieldwork.* We visited the main aroid collections in the United States, including the herbarium at the Missouri Botanical Garden (MO), the Field Museum (F), Gray Herbarium at Harvard (GH), The New York Botanical Garden (NY), and the National Herbarium (US). We also visited collections in Colombia (COL, COAH, JAUM, MEDEL, HUA, CUVC), Ecuador (QCA, QCNE, QPLS), Panama (PMA, SCZ), and Mexico (MEXU, UJAT, and XAL). Additionally, we studied digital images of the specimens from other herbaria that could not be visited. Type specimens were studied when available or digital images were use instead. Fieldwork was conducted in Colombia, Ecuador, Mexico and Panama.

Floral morphological and anatomical work. Due to the limited amount of vegetative characters of utility for *Monstera* species identification we explored morphological and anatomical characters from reproductive structures, in particular flowers. Anatomical work was conducted in the Plant Anatomy Lab at the National Herbarium (US, Smithsonian Institution) through a short-term visitor grant. We used flowers collected in the field and other available in the spirit collection at the National Herbarium (US) built by Dr. Dan Nicolson and Dr. R Eyde. . In brief, tissues were fixed

in FAA, and then transferred to 70 % ETOH until paraffin infiltration and embedding. We placed individual flowers in 10% Ethylenediamine at 60 °C for 24h to soft the trichosclereids and facilitate the sectioning. Then we infiltrated and embedded the tissues in paraffin wax (POLYFIN) using tert-butyl alcohol (TBA) as the intermediate solvent. All infiltration and embedding procedures we done under vacuum. After paraffin embedding, tissues were sectioned using a rotary microtome. Sections were stained using Toluidine blue and mounted for microscopy observation. Additional slides containing floral anatomy sections were obtained from Dr R. Eyde collection at the National Herbarium (US), and others provide by Dr. W. Carvell (Benedictine University, Lisle, IL)

Geographical database. We built a geographical database comprises a record for each specimen, and it includes collector and collection number, geographic location, and geographic coordinates, and herbarium were the specimen is deposited. Other information that may be present in herbarium collection, and that was collected includes, collection date, phenology and uses. When available digital databases were obtained directly from the herbaria, and then complete manually by the revision of the physical specimen. GBIF database records were used but only collections for which taxonomical identification was confirmed were used. Distribution maps will be built using scripts developed in the software R and the packages maps, ggmap, maptools, and raster (**Figure 1**).

Interactive key. We built a database to record morpho-anatomical information for each taxonomical unit (**Table 1**). The morpho-anatomical database was built using the software Lucid v3.5 (lucidcentral.org). It contains 108 ecological, morphological and anatomical traits from vegetative and reproductive structures and it is divided in three phenological stages, seedling, juvenile and adult plants. Within each stage characters are subdivided in the following order: habit, stem, leaves, inflorescence/infrutescence. The database includes discrete and continuous characters. We included 44 taxonomical units representing the currently 42 described species in the genus and other two new described species (Zuluaga et al. **Chapter 4, part 1**). The traits and their states were introduced to the lucid software using the Lucid Builder tool. Each taxonomical unit was coded or measure for each trait using field observations, literature, living plants, and spirit and herbarium collections deposited in herbaria in previously mentioned.

PRELIMINARY RESULTS

Interactive key implementation. The information in the interactive key includes data from 25 species studied *in vivo* during fieldwork or at botanical gardens, and ca. 4208 herbarium collections, 80% of them with geographic coordinates (**Table 2**). See **Figure 2** for views of the interactive key).

Anatomical work. 16 species were been embedded, and six have been sectioned and mounted. Additionally, slides for other six species were obtained from Dr. W. Carvell. Microscopy work has revealed heretofore underappreciated differences in style

length, stigma surface, distribution of trichosclereids and vascular bundles (see **Figures 3** for examples of anatomical characters).

The taxonomic work in the genus *Monstera* is being actively being developed. We still need to analyze and include all our anatomical studies into the interactive key, as well as describe and include all the potential new taxa for the genus. Our ultimate goal is to develop a database of geographic and morpho-anatomical data that will allow us to answer questions about the evolution of this enigmatic group.

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TABLES AND FIGURES

Table 1. List of geographical, ecological and morpho-anatomical characters and states used for the lucid key. Characters are divided in four sections; ecology and distribution, seedling, juvenile and adult plants. Within morphological section characters are subdivided by structures in the following order: habit, internodes, leaves, inflorescence/infrutescence.

Ecology and distribution		
Geographic distribution		
Height on the tree (adult plant)		
Elevation		
Seedling		
Seedling habit		
stolon-like		
with foliage leaves		
Juvenile plants		
Growth habit		
terrestrial creepers		
scandent		
adpressed climbers		
Internodes		
Internodes length		
Internodes diameter		
Internodes surface		
	smooth	
	verrucose	
	papillate-papillose	
Leaves		
Juvenile leaf host attachment		
	adpressed (shingled)	
	spreading from host	
Juvenile/adult leaf shape differentiation		
	not differentiated	
	differentiated	
Petiole		
	Petiole length in proportion to the leaf blade	
		longer than leaf blade
		shorter than leaf blade
		about as long as leaf blade
	Petiole length	
	Petiole diameter	
	Sheating section	

	persistence	
		deciduos
		marcescent
		persistent
		fibers-like
	Sheating section lenght in proportion to the petiole	
		less than 1/2
		between 1/2 and 3/4
		all the petiole
	Sheating section lenght	
Blades		
	Symmetry	
		Equilateral
		Inaequilateral
	Shape	
		falcate
		lanceolate
		oblong
		rounded
		elliptic
		ovate
	Blade apex	
		acute
		gradually acuminate
		abrutly acuminate
	Blade base	
		attenuate
		oblique
		obtuse
		cuneate
		subcordate
		cordate
	Blade coloration	
		concolorous
		bicolorous
		variegated
	Blade texture	
		membranaceous
		chartaceous
		subcoriaceus
		coriaceus
	Perforations	
		present
		absent
	Blade overall length	
	Blade overall maximum width	
Adult plants		
Growth habit		
vine		
adpressed climber		
Stem		
Internodes length/width		

relation		
	longer than broad	
	broader than long	
Adult internode length		
Adult internode/Stem diameter		
Leaf scars wide		
Axillary buds		
Stem cross section		
	subcylindric	
	dorsiventrally flattened	
	flattened laterally	
Stem surface		
	smooth	
	papillate	
	verrucose	
	striate	
	speckled	
	lineated raised ridged	
	lenticellate	
Stem epidermis (when dry)		
	flaking	
	no flaking	
Cataphylls		
Cataphyll number		
Cataphyll length		
Leaves		
Spatial disposition		
	along of the stem	
	apex clustered	
Petiole		
	Petiole cross-sectional shape	
		subterete to terete
		C to D-shaped or broader than thick
		U-shaped or thicker than broad
	Petiole surface	
		smooth
		verrucose
		glaucous
		papillate
		white dotted or flecks
		green dotted
	Petiole length	
	Petiole diameter	
	Petiole length in proportion to the leaf blade	
		longer than leaf blade
		shorter than leaf blade
		about as long as leaf blade

	Petiole/Blade length ratio		
	Petiole upper (adaxial) surface		
		sulcate	
		flattened	
		with medial rib	
		convex	
	Petiole lower (abaxial) surface		
		rounded	
		angular	
		ribbed	
	Geniculum		
		Geniculum length	
	Sheating section		
		Sheating section lenght in proportion to the petiole	
			less than 1/2
			between 1/2 and 3/4
			more than 3/4
		Persistence	
			deciduos fibers-like
			deciduos intact
			fiber persistent
			marcescent
			persistent
		Sheat "vernation"	
			no margins
			acutely raised
			winged
			obtusely raised
		Sheating section lenght sheat extension (beyond geniculum)	
Blades			
	Shape		
		lanceolate	
		falcate	
		elliptic	
		ovate	
		oblong	
		rounded	
	Symmetry		
		equilateral	
		inaequilateral	
	Blade apex		
		obtuse to weakly emarginate	
		acute	
		mucronate	
		gradually acuminate	

	abruptly acuminate
Blade base	
	attenuate
	obtuse
	truncate
	cuneate
	subcordate
	oblique
	cordate
Blade margins	
	entire
	pinnatifid
	lacerate
	lobed
	one side pinnatifid
Blade overall length	
Blade overall maximum width	
Proportion Length/width	
Blade coloration	
	concolorous
	bicolorous
Blade glossiness on upper surface	
	matte
	semiglossy
	glossy
	velvety
Blade glossiness on lower surface	
	matte
	velvety
	semiglossy
	glossy
Blade texture	
	membranaceous
	chartaceous
	coriaceus
	subcoriaceus
Blade color when dried on upper surface	
	yellowish
	greenish to olive-green
	grayish
	brownish
	dark brown
	blackish
	reddish brown
Blade color when dried on lower surface	
	yellowish
	greenish to olive-green
	grayish
	brownish

	dark brown	
	blackish	
	reddish brown	
Midrib		
	Midrib shape above	
		acute
		convex or round
		raised
		flat
		sunken
	Midrib shape below	
		acute
		convex or round
		flat
		quadrangular (square to rectangular)
		multi-ribbed
Primary lateral veins		
	Number of pairs of primary lateral veins	
	Distance between primary lateral veins	
	Departing angle of primary lateral veins	
	Primary lateral veins appearance above	
		sunken
		acute
		convex
		flat or obscure
	Primary lateral veins appearance below	
		flat or obscure
		acute
		sunken
		convex
Secondary veins		
	reticulate	
	parallel (only reticulate close to the margin)	
Perforations (fenestrations)		
	Perforations spatial distribution	
		irregular
		absent
		in series
	Number of perforation series	
Number of segments (lobes) per side		
Distance between pinnae		
Difference between wider		

	and thinner side	
	Pinnae width	
Flowering shoots		
	erect	
	pendent	
Inflorescence		
Number per axile		
Spatial position		
	erect	
	spreading	
	pendent	
Length in proportion to leaves		
	shorter than leaves	
	longer than leaves	
	about as long as leaves	
Peduncle		
	Surface	
		smooth
		papillate
		verrucose
		whitish dotted
	Peduncle length	
	Peduncle diameter	
Spathe		
	Spathe shape (when flattened)	
		ovate
		elliptic
		oblong
		obovate
		subcircular
	Spathe color outside	
		white to cream
		greenish white
		green
		yellow to orange
		light yellow
		pinkish
	Spathe color inside	
		greenish white
		green
		white to cream
		light yellow
		yellow to orange
		pinkish
	Spathe length	
	Spathe width	
	Length in proportion to spadix	
		much longer than spadix
		slighty longer than the sapdix

Spadix			
	Spadix length in proportion to peduncle		
		shorter than peduncle	
		longer than peduncle	
		about as long as peduncle	
	Spadix shape		
		cylindroid	
		apex tapered	
		clavate	
		base tapered	
	Spadix color (Anthesis)		
		white to cream	
		yellow to yellowish	
		orange to orangish	
		pinkish	
	Portion of sterile flowers		
		absent	
		present	
	Spadix frontal length		
	Spadix posterior length		
	Spadix diameter		
	Length in proportion to peduncle (number)		
Flowers			
	Shape		
		prismatic	
		cilindrical	
		conical	
	Pistil		
		conical acuminate	
		style	
		trunctae style	
Infructescence			
Spatial disposition			
	erect		
	pendent		
Infrutescence color (before stylar cap fall off)			
	white to cream		
	greenish white		
	green		
	light yellow		
	orange		
Infrutescence peduncle length			
Infrutescence peduncle diameter			
Infrutescence length			
Infrutescence diameter			
Seeds			
	Seed number		
			1
			2
			3

Seed color	
	green
	brown
	gray/white
	black
Seed shape	
	oblong
	spheroidal
Seed length	
Seed diameter	

Table 2. Number of specimens studied per species. Excluded specimens included specimens with ambiguous identification or others that represent new taxa to be described.

Species Name	Number of specimens
Monstera acacoyaguensis	12
Monstera acuminata	147
Monstera adansonii	1013
Monstera amargalensis	3
Monstera anomala sp. nov.	20
Monstera aureopinnata	69
Monstera barrieri	6
Monstera buseyi	49
Monstera cenepensis	3
Monstera costaricensis	24
Monstera deliciosa	166
Monstera dilacerata	55
Monstera dissecta	82
Monstera dubia	279
Monstera egregia	12
Monstera epipremnoides	16
Monstera filamentosa	23
Monstera florescanoana	2
Monstera glaucescens	89
Monstera gracilis	41
Monstera kessleri	2
Monstera lechleriana	243
Monstera lentii	18
Monstera luteynii	4
Monstera maderaverde	2
Monstera membranacea	23
Monstera minima	3
Monstera molinae	19
Monstera obliqua	709
Monstera oreophila	103
Monstera pinnatipartita	161
Monstera pittieri	55
Monstera planadaensis	5
Monstera punctulata	39
Monstera puntarenense	2
Monstera siltepecana	158

Monstera spruceana	256
Monstera standleyana	44
Monstera subpinnata	107
Monstera tenuis	53
Monstera tuberculata	64
Monstera vasquezii	4
Monstera xanthospatha	19
Monstera integrifolia sp. nov.	4
Total	4208
Excluded specimens	791

Figure 1. An example of distribution maps for *Monstera* species to be included in the interactive key.

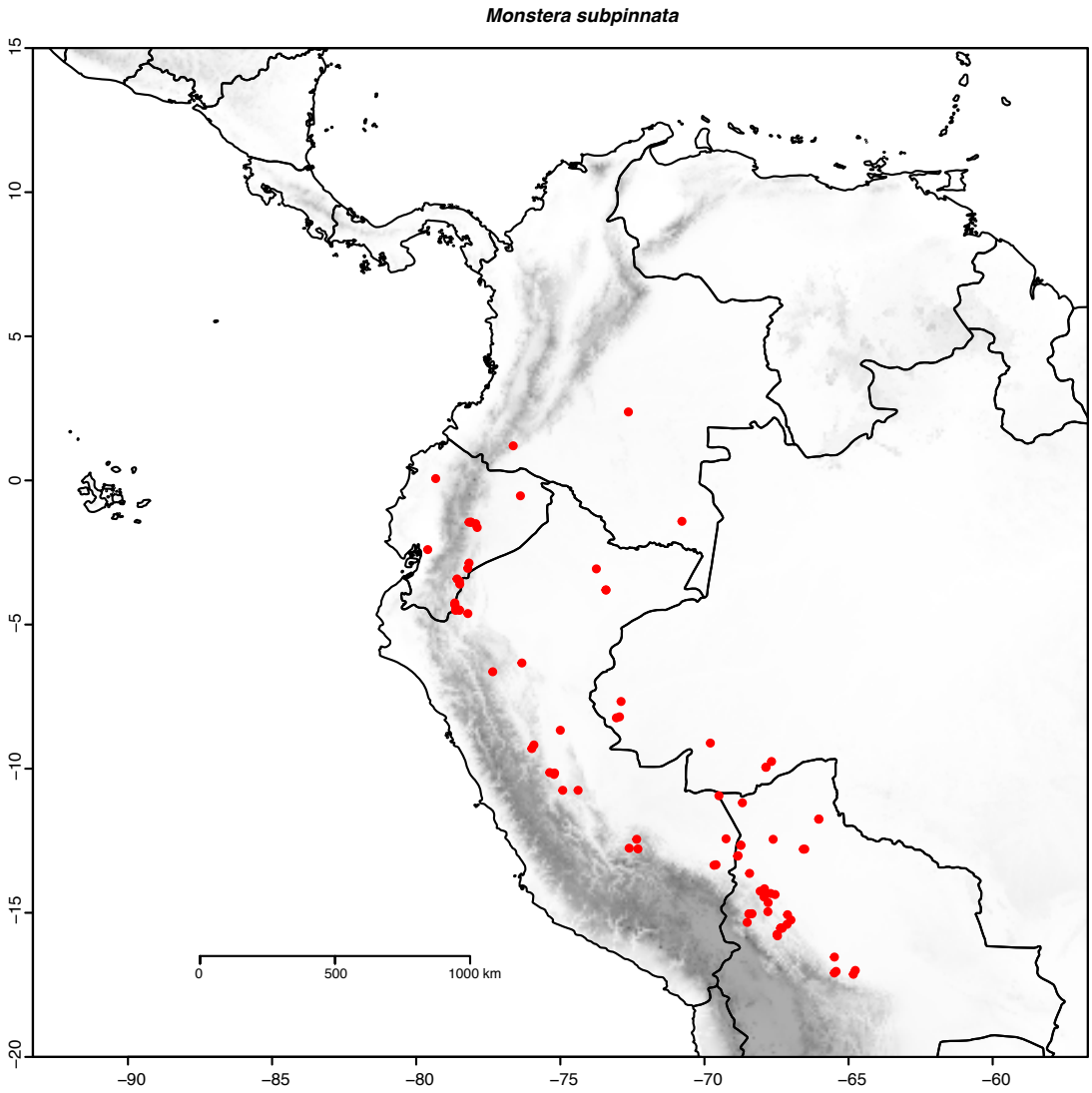


Figure 2. View of the Lucid Player tool. Four windows are available. Top left window contains the characters (features available); bottom left contain the characters chosen; top right contain the taxa remaining; and bottom left the taxa discarded.

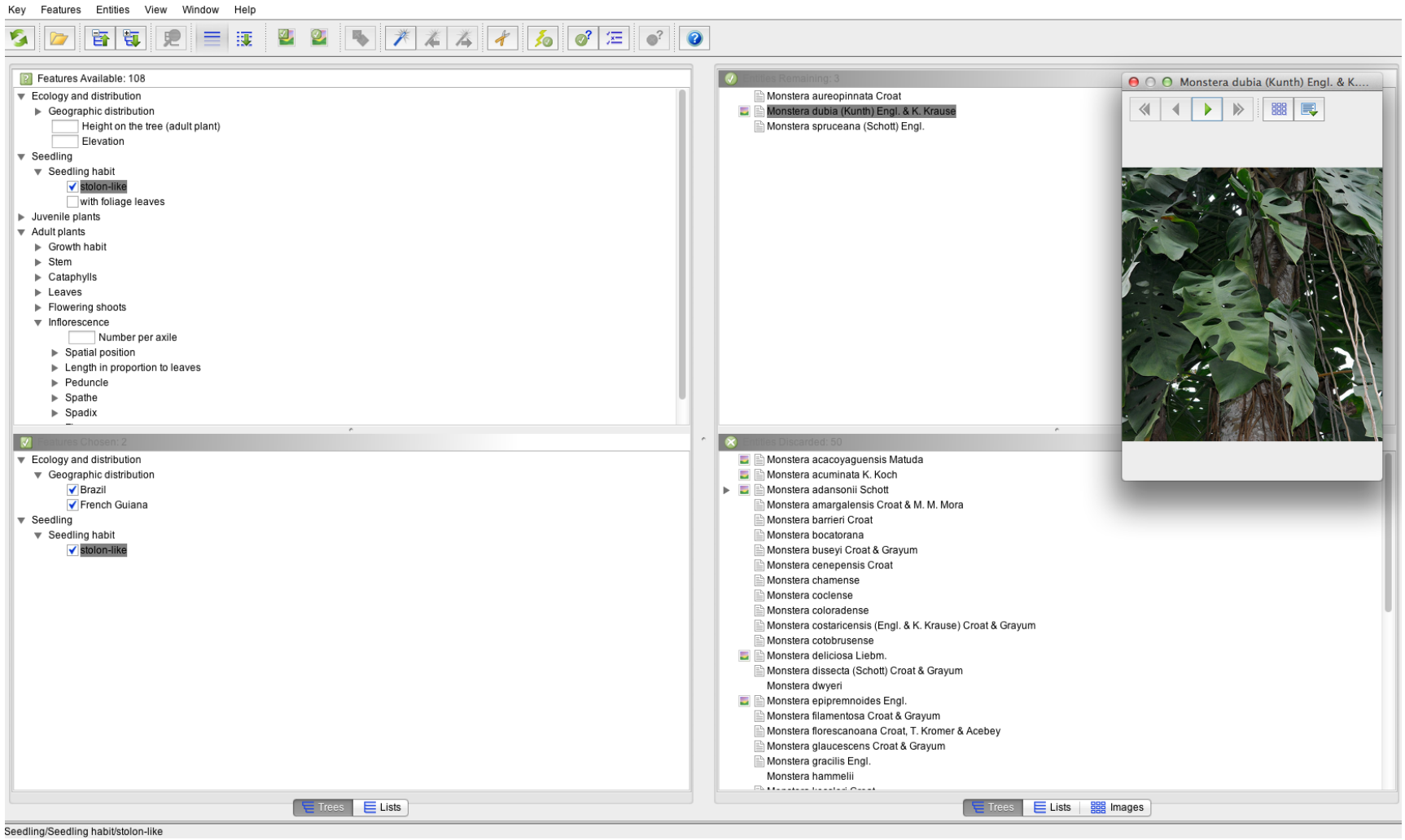
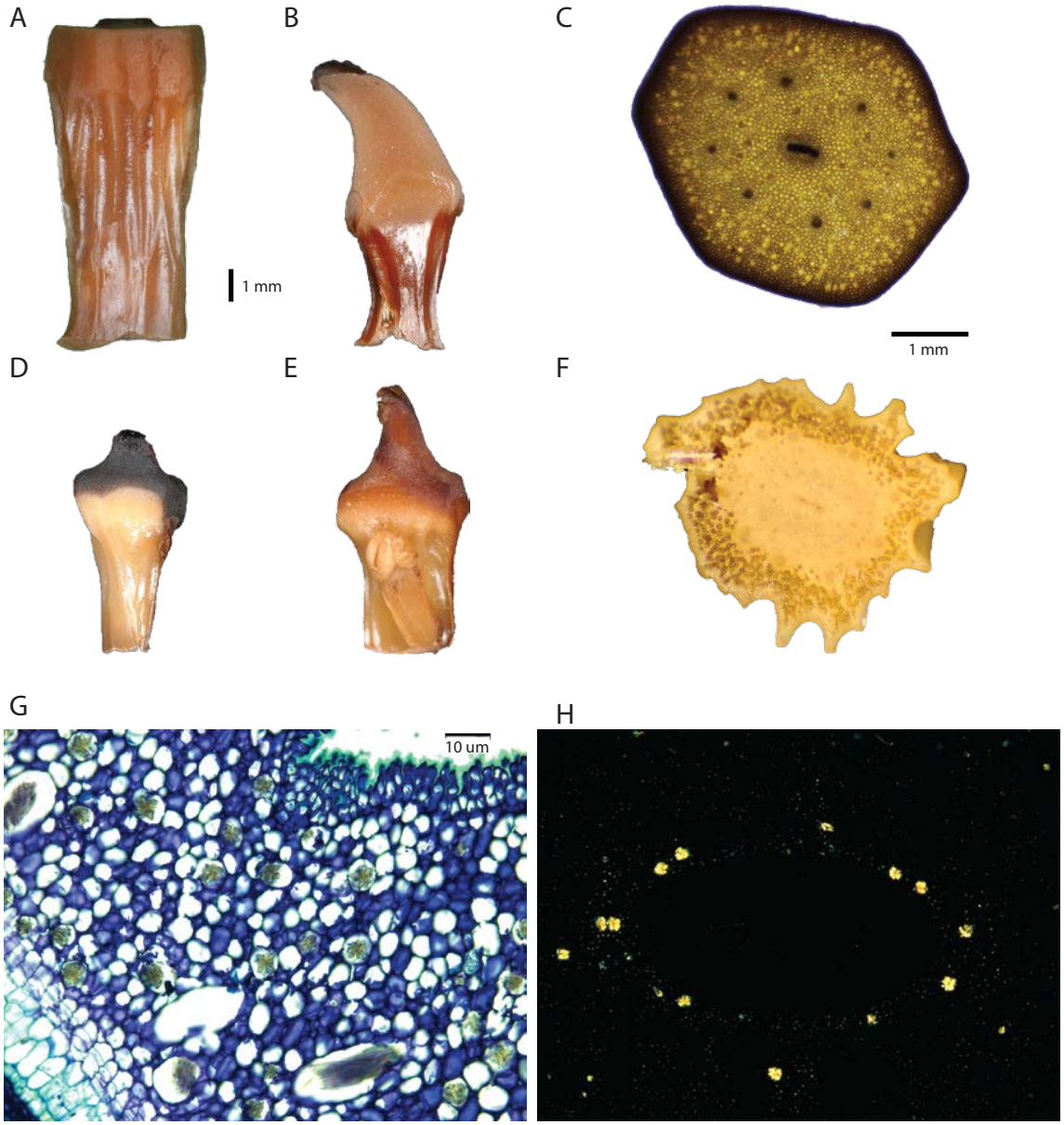

Key Features Entities View Window Help
Features Available: 108
Ecology and distribution
Geographic distribution
Height on the tree (adult plant)
Elevation
Seedling
Seedling habit
stolon-like
with foliage leaves
Juvenile plants
Adult plants
Growth habit
Stem
Cataphylls
Leaves
Flowering shoots
Inflorescence
Number per axile
Spatial position
Length in proportion to leaves
Peduncle
Spathe
Spadix
Features Chosen: 2
Ecology and distribution
Geographic distribution
Brazil
French Guiana
Seedling
Seedling habit
stolon-like
Trees
Lists
Entities Remaining: 3
Monstera aureopinnata Croat
Monstera dubia (Kunth) Engl. & K. Krause
Monstera spruceana (Schott) Engl.
Entities Discarded: 50
Monstera acacoyaguensis Matuda
Monstera acuminata K. Koch
Monstera adansonii Schott
Monstera amargalensis Croat & M. M. Mora
Monstera barrieri Croat
Monstera bocatorana
Monstera buseyi Croat & Grayum
Monstera cenepensis Croat
Monstera chamense
Monstera coclense
Monstera coloradense
Monstera costaricensis (Engl. & K. Krause) Croat & Grayum
Monstera cotobrusense
Monstera deliciosa Liebm.
Monstera dissecta (Schott) Croat & Grayum
Monstera dwyeri
Monstera epipremnoides Engl.
Monstera filamentosa Croat & Grayum
Monstera florescanoana Croat, T. Kromer & Acebey
Monstera glaucescens Croat & Grayum
Monstera gracilis Engl.
Monstera hammelii
Trees
Lists
Images
Monstera dubia (Kunth) Engl. & K....
Seedling/Seedling habit/stolon-like

Figure 3. Examples of morpho-anatomical traits from flowers in *Monstera*. **A, B, D, & E** show different flower shapes present in *Monstera*; **A**, *M. punctulata*; **B**, *M. tuberculata*; **D**, *M. integrifolia*; **E**, *M. lentii*. **C** & **G** show cross section from the stylar region (**C**), and the ovary (**D**) of *M. punctulata;* distribution of vascular bundles and trichosclereids are visible. **G,** cross section of the stylar region of *M. punctulata;* druses and rhapides are visible. **H,** cross section to the stigma level of *M. pittieri* using polarized light; druses are visible.


A
B
C
1 mm
1 mm
D
E
F
G
10 um
H

APPENDIX 1. Zuluaga, A., K. Cameron, T. Croat & M. Medecilo. 2015. Testing the monophyly of Spathiphyllum, and the relationship between Asian and tropical American species. *Aroideana* 38E(1):107-115.

Testing the monophyly of *Spathiphyllum*, and the relationship between Asian and tropical American species.

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ABSTRACT

As part of a broader phylogenetic study of the subfamily Monsteroideae we used three plastid and one nuclear markers to test the monophyly of the genus *Spathiphyllum*. Our results support the tribe Spathiphylleae as sister of the remaining Monsteroideae, and the monophyly of *Spathiphyllum*. The monotypic genus *Holochlamys* appears nested within *Spathiphyllum* in a clade with the Asian species and *S. cannifolium*. However, support for this clade is low. The section *Spathiphyllum* shows a high support and is sister to the remaining species in the genus. As a consequence *Spathiphyllum* remains as the only disjunct aroid genus between the Old and New World Tropics.

INTRODUCTION

With the increased application of molecular data for phylogenetic analysis, the understanding of relationships within Araceae has been improved considerably (Cabrera, 2008, Cusimano, 2011, Henríquez, 2014). Additionally, new fossils and biogeographical studies have helped to elucidate the historical and current geographic distribution patterns in the family (Nauheimer, 2012a). As a result, aroid classification has changed

dramatically; several genera have been resurrected; and new genera have been created (Cabrera, 2008, Cusimano, 2011). Nevertheless, many critical issues are still in need of more data.

Before this molecular era there were thought to be three geographically disjunct genera between the old world and new world tropics. Species in the genera *Homalomena*, *Schismatoglottis* and *Spathiphyllum* were found in both tropical America and tropical Asia, particularly within the Malay Archipelago and Melanesia (van Steenis, 1962, Grayum, 1990, Mayo et al., 1997). However, recent studies (Barabé, 2002, Gauthier, 2008, Wong et al., 2013) have shown evidence challenging the monophyly of disjunct *Schismatoglottis* and *Homalomena* (they are no longer disjunct in their revised circumscriptions), leaving *Spathiphyllum* as the only remaining aroid genus with a tropical disjunction.

The genus *Schismatoglottis*, with only three species in South America, and about 150 in tropical Asia, belongs to the tribe Schismatoglottidae that in its current circumscription comprises 11 genera. Several of these genera are small groups recognized thanks to molecular data (Wong et al., 2010a, 2010b, Low, 2014). The three Neotropical species previously recognized in *Schismattoglotis* are now in the resurrected genus *Philonotion* (Wong, 2010c) that belong to its own tribe Philonotieae. Equally, the genus *Homalomena* is considerable more diverse in Tropical Asia with about 500 species, versus only 10 species in Tropical America (Boyce & Croat, 2013). Unlike *Schismatoglottis*, molecular evidence for the separation of Neotropical *Homalomena* is not conclusive (Barabé, 2002, Gauthier, 2008, Wong et al., 2013). The most plausible options for the assignment of the Neotropical *Homalomena* would be the resurrection of the genus *Adelomena,* or the combination of these species of *Homalomena* with *Philodendron* subgenus *Pterosmischum* in the genus *Elopium* (Wong et al., 2013). Thus, more extensive sampling and more molecular data are necessary to fully understand the relationships among *Homalomena*, and the subgenera of *Philodendron*.

Finally, we have the genus *Spathiphyllum,* which has a different distribution pattern. The genus is more diverse in Tropical America with about 50 species (Cardona, 2004), and only three species in Southeast Asia. *Spathiphyllum commutatum* Schott is widespread in Malesia and reaches Micronesia; *S. solomonense* Nicolson is restricted to the Solomon Islands; and *S. schlechteri* (Engl. & K.Krause) Nicolson is restricted to New Guinea. Neotropical species are concentrated in the northern Andes, with only a few species reaching Central America and Mexico (Cardona, 2004), and one species, *S. leave* reaches Cocos Island in the Pacific Ocean west of Costa Rica. No comprehensive phylogenetic studies, until now, have included more than three *Spathiphyllum* from Tropical America, or any of the Asian species.

Spathiphyllum together with *Holochlamys becarii* form the tribe Spathiphylleae in the subfamily Monsteroideae (Cabrera, 2008, Cusimano, 2011). The relationships of the tribe Spathiphylleae within Monsteroideae have been controversial, but recent studies strongly support Spathiphylleae as sister to the remaining Monsteroideae (Chartier, 2014, Henriquez, 2014). These two genera are very similar morphologically and ecologically, differing mainly in a few characteristics of the flowers. Whereas *Spathiphyllum* species have two to three locules and ovules with axillar placentation, *Holochamys* has one locule and ovules with basal placentation (Bunting, 1960, Mayoet al.,1997). Nevertheless, anatomical studies suggest that the *Holochlamys* ovary could actually have two locules, and the placentation may not be basal (Eyde, 1967, Carvell,1989).

Currently, *Spathiphyllum* is divided into four sections based the fusion of the perianth segments, the form and length of the pistils relative to the perianth, and the attachment the spathe to the peduncle (Bunting, 1960). Asian species together with *S. cannifolium* and *S. leave* form the section *Massowia,* which is recognized by having the perianth segments completely connate forming a cup around the pistil. This trait led Bunting (1960) to propose the monophyly of this group. However, Williams & Dressler (1967) and Grayum (1984, 1990) suggested this could be an artificial group with *Holochlamys* nested within it. Sections *Amomophyllum, Dysspathiphyllum*, *and Spathiphyllum* have free perianth segments.

As part of a broader systematic study of the subfamily Monsteroideae (Zuluaga, unpublished data) we tested the monophyly of *Spathiphyllum* and *Holochlamys,* and investigated the relationships of the Asian and American species of *Spathiphyllum*.

METHODS

Taxon Sampling and DNA sequencing. During the sampling for the study of systematics of the subfamily Monsteroideae we sequenced a total of seven accessions of the genus *Spathiphyllum* from Tropical America, *S. commutatum* and *S. solomonense* from Tropical Asia, and one accession of *Holochlamys becarii*. Additional sequences for *S. phryniifolium* were obtained from GENBANK. For this study we used representatives from all ten additional Monsteroideae genera, plus six other aroids as outgroups.

DNA was extracted from silica-dried plant material using the DNeasy Plant Mini Kit (Qiagen, Valencia, CA, USA) according to the manufacturer's specifications. Some samples were extracted using a CTAB method adapted from Doyle & Doyle (1987). We sequenced four plastid markers, *matK*, *rbcL, trnC-petN* spacer, and partial *ycf1*. PCR products were purified using ExoSap-It (Cleveland, OH). Sequencing reactions used the BigDye Terminator Cycle Sequencing Kit, and cleaned using Agencourt CleanSeq (Beverly, MA) magnetic beads. BigDye Terminator Cycle Sequencing Ready Reaction Kit (Applied Biosystems, Foster City, CA, USA). Samples

were sequenced using PE-Biosystems version3.7 of Sequencing Analysis at the University Wisconsin–Madison Biotechnology Center.

Molecular analysis. All sequences were manually edited in Geneious6.0 (Biomatters, http://www.geneious.com). Sequences were aligned in Geneious6.0 using a combination of Muscle (Edgar 2004) and MAFFT (Katoh 2002). Finally, all alignments were checked manually. We performed individual and combined phylogenetic analyses. Analyses for each marker/dataset were performed under Maximum Likelihood using RaxML 7.0 (Statamakis, 2006), and MrBayes 3.1.2 on XSEDE, as implemented in the CIPRES portal. For RaxML, we used the GTRGAMMA model in all cases. For Bayesian analysis models were calculated using Jmodeltest2 (Darriba, 2012).

RESULTS.

So far at least one of the four molecular markers has been successfully sequenced for *S. cannifolium* (two accessions), *S cochlearispathum*, *S. commutatum*, *S. floribundum*, *S. minor*, *S. patulinervum, S. solomonense, S. wallisii*, and *Holochlamys becarii*. Only the *trnC-petN* spacer was sequenced for the Asian *Spathiphyllum*. The combined alignment length is 4970 bp with 36% missing data. Despite using four molecular markers the identical sites between pairs of species within *Spathiphyllum* is more than 97%. This low variation is common within the genera of the subfamily Monsteroideae (Unpublished data).

Trees derived from individual gene analyses are congruent, however the resolution is low except for a clade comprising the species of the section *Spathiphyllum*. Thus, a combined gene analysis is presented (**Figure 1)**. All individual and combined analyses show the tribe Spathiphylleae as monophyletic and sister to the remaining Monsteroideae, thus supporting the topology presented by Chartier (2014) and Henríquez (2014). Section *Spathiphyllum* represented by *S. cochlearispathum*, *S. phryniifolium*, and *S. wallisii* shows strong support, and is sister to the remaining Spathiphylleae. The genus *Holochlamys* appears nested within *Spathiphyllum* in a clade with the Asian species and one accession of *S. cannifolium* (section *Massonia*). Section *Amomophyllum* (*S. minor*, *S. floribundum*, *S. patulinervum*) and one accession of *S. cannifolium* are sister to the clade containing *Holochlamys*. However support for the last two clades is low (Figure1).

DISCUSSION.

A monophyletic tribe Spathiphylleae has been supported since the first molecular studies in Araceae, based on only a few genes, were published (Tam, 2004, Cabrera, 2008). However, the position of Spathiphyllleae as sister to rest of Monsteroideae is only recovered in the most recent studies with more data included

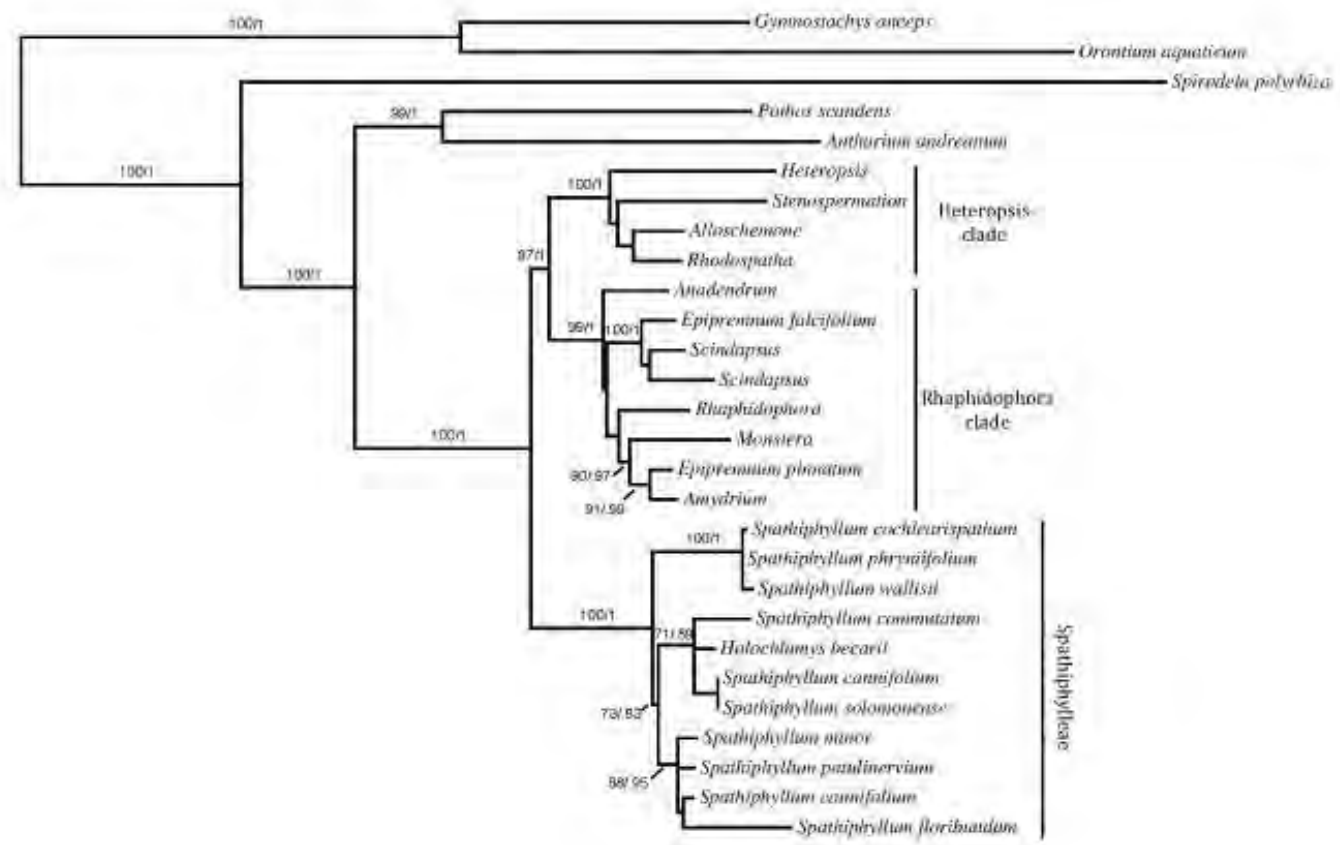

Figure 1. Maximum likelihood tree from RaxML using four plastid markers (*matK*, *rbcL, trnC-petN*spacer, and partial *ycf1*). Bootstrap supports >75 and Bayesian posterior probabilities >0.85 are shown on the branches.

(Chartier, 2014, Henriquez, 2014). Our results strongly support this topology (**Figure 1)**. Most of the synapomorphies defining Monsteroideae as presented in Cusimano (2011) seem to be more appropriate to be assigned to the clade containing all Monsteroideae but Spathiphylleae. These synapomorphies and the alternative characters in Spathiphylleae are: pollen zonate (ring-like) (vs. pollen multiaperturate with exine surface striate/polyplicate); spathe soon deciduous with a distinct basal abscission (vs. Spathe marcescent), large trichosclereids not in bundles (vs. smaller trichosclereids in bundles). The only synapomorphy remaining for Monsteroideae is the presence of trichosclereids.

Within the tribe Spathiphylleae, the support for the position of *H. becarii* is not conclusive, but some markers suggest this

species may belong to the genus *Spathiphyllum*. *Holochlamys* appears consistently embedded in a clade with section *Massowia*. These two genera are very similar in habit and morphology (Bunting,1960), stem vasculature (French & Tomlison, 1981), palynological features (Grayum,1992), and floral anatomy (Carvell, 1989). Moreover, *Holochlamys* shares with section *Massowia* the presence of fused perianth parts forming a cup around the pistil (Bunting, 1960, Carvell, 1989). The proposed differences between these two genera - a unilocular ovary, and ovules with basal placentation - have been challenged by more detailed anatomical studies (Eyde, 1967). Carvell (1989) undertook a very detailed anatomical study of Monsteroideae and Pothoideae, and reported unilocular ovaries, and basal ovules for *H. becarii*. However, he also reported the presence of an incomplete septum in several flowers, and the attachment of some the ovules to that septum. Additionally, Carvell (1989) found considerable intra- and interspecific variation in locule, ovules, tepals, and stamen numbers in *Spathiphyllum*. Despite the fact that we consider there to be no strong morphological evidence to separate *Holochlamys* from *Spathiphyllum* (especially from the section *Massowia*), our analysis currently lacks adequate resolution within this clade, and so we prefer to be cautious at this point in time, necessarily gathering more data before proposing any taxonomic changes for these species.

Our sampling did not allow a complete assessment of the sectional classification in *Spathiphyllum* as proposed by Bunting (1960). The only section with strong support through all our analysis is the section *Spathiphyllum*, which is also supported by the morphology of their flowers with a long and conical pistil exceeding the perianth (Bunting, 1960). Williams and Dressler (1967), and Grayum (1984, 1990), discussed hypotheses for the origin and biogeography of *Spathiphyllum* and *Holochlamys*. We are undertaking additional molecular and biogeographical analyses of the subfamily Monsteroideae, and more detailed discussion on this topic will be presented in subsequent papers.

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