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Title: Time calibrated tree of *Dioscorea* (Dioscoreaceae) indicate four origins of yams in the Neotropics since the Eocene

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ABSTRACT

The yam genus *Dioscorea* comprises circa 650 species of tropical vines with starch rich tubers, usefull as an energy source and often containing secondary metabolites. The Neotropical Region holds the highest diversity of species and morphology of yams. We generated a time-calibrated tree for *Dioscorea* using, for the first time, a dense sampling of Neotropical species (64 sp., 20% of all Neotropical sp. and 22 sections) to trace the biogeography of these plants in this region. Four origins of *Dioscorea* in the neotropics were estimated since the Eocene. The two most diverse lineages originated between the Eocene and Oligocene, respectively in the Southern Andes and eastern South America. Both lineages occupied the South American 'Dry Diagonal' after the Miocene, but New World II clade remained associated with forest habitats. Several exchanges between Dry Diagonal and adjacent forested biomes occurred, corroborating the interchange between these vegetation types. Dispersals to Central America occurred before the closure of the Panama Isthmus. We highlight two important events of long distance dispersal, the colonization of Central American before the closure of Isthmus of Panama and the dispersal of *D. antaly* lineage to Madagascar. In addition, our phylogenetic tree evidenced the unnatural nature of the classical infrageneric classification of *Dioscorea*. The taxonomic implications of our results are also discussed.

Keywords: Biogeography – Dioscoreaceae – *Helmia* - molecular dating – monocots - South America

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INTRODUCTION

Dioscorea L. comprises approximately 95% of the known species of Dioscoreaceae (Govaerts, Wilkin, & Saunders, 2007) , as a reflection of this larger number of species the genus possess a tremendous morphological diversity, as several critical traits to distinguish from the other genus of the family (eg.: hermaphroditism in the other genera and dioecism in *Dioscorea*), and a considerable richness of chemical and genetic characters. Most species of *Dioscorea* are known as yam (and variations in different languages: inhame, ñame, igname, niam, enyame, nyami, etc.). They are mostly dioecious vines, usually with small flowers and starch-rich tubers as the underground organ. Due to the great nutritional value of its underground system, they are an important source of energy for human populations worldwide (Wilkin *et al.*, 2005). *Dioscorea* species have their history linked to humans for thousands of years by a slow and gradual process of domestication (Ayensu & Coursey, 1972). In addition, *Dioscorea* is economically important due to secondary metabolites present in the tubers; *diosgenin*, for example, has a molecular structure similar to steroidal hormones and has been used to synthesize steroids for the production of birth control pills, among other uses (Coursey, 1967). Yams have been studied by its secondary metabolites, however studies related on prospection of useful substances in tubers of Neotropical species are restricted to only a few species (eg.: *D. composita*, *D. floribunda* and *D. mexicana*) even with the great diversity of neotropical species (Mignouna, Abang, & Geeta, 2009; Coursey, 1967).

The family Dioscoreaceae currently includes 653 accepted species, distributed in four genera: *Dioscorea* (633 species), *Stenomeris* Planch. (2 species), *Tacca* J.R. Forst. & G. Forst. (17 species), and *Trichopus* Gaertn. (1 species) (Govaerts, Wilkin, & Saunders, 2007). A total of 1600 names are attributed to *Dioscorea*, among species, varieties and subspecies, mostly considered as synonyms (The Plant List, 2013). *Dioscorea* species occur mostly in tropical areas with some representatives in subtropical and temperate regions of the planet, but are

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especially diverse in the Neotropics, where about 50% of the species occur (e-Monocot team, 2017).

According to Viruel *et al.* (2016) in its study with 135 taxa and four plastid DNA markers, *Dioscorea* originated in the Laurasian Palearctic region between the late Cretaceous (57.7 – 85.9 mya) and the Mid Eocene (47.6 – 49.1 mya), with subsequent radiations to the Southern regions by long-distance dispersal or migration by land bridges in the Oligocene-Miocene (33.9 to 5.332 Mya) (Viruel *et al.*, 2016). They occur in several Neotropical environments, from dry *restinga* at sea level to the Andean paramos, including edges and interior of humid forests, natural grassland ecosystems, rupicolous areas, and even semi-desertic environments (Dorr & Stergios, 2003; Couto *et al.*, 2014). As a consequence of the great variety of environmental conditions in which they occur, *Dioscorea* species exhibit a wide range of ecological responses, evidenced by the large morphological variability found in the family, both in vegetative and reproductive organs. They range from large climbing vines (40m high) to dwarf species, monoecious or dioecious plants, and they can present impressively colored leaves and flowers, among other distinctive characters (Fig. 1).

Knuth (1924) proposed 58 sections and four subgenera for *Dioscorea*: *D.* subgenus *Helmia* (Kunth) Uline (seeds winged basally), *D.* subgenus *Dioscorea* (Pax) Uline (seeds winged all around), *D.* subgenus *Stenophora* (Uline) Knuth (seeds winged apically) and *D.* subgenus *Testudinaria* (Salisb.) Uline (seeds winged apically). This classification has undergone subsequent changes and additions (Burkill, 1960; Barroso *et al.*, 1974), although these were not based on phylogenetic studies. With great morphological variation and scarce knowledge on anatomy, ecology, chemistry and palynology of *Dioscorea* (Ayensu, 1972; Caddick *et al.*, 1998; Schols *et al.*, 2001, 2003; Wilkin *et al.*, 2009), external morphology was the base for the delimitation of taxonomic groups. Recent phylogenetic studies based on molecular data suggest eight main lineages distributed in the tropical and subtropical regions of the globe: ‘*Enantiophyllum*’, ‘Compound Leaved’, ‘Malagasy’, ‘Birmanica’, ‘Africa’, ‘European’, ‘New World’ and ‘*Stenophora*’ (Wilkin *et al.*, 2005; Viruel *et al.*, 2016). Viruel *et*

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al. (2016) obtained some clades not found in previous analyses: *Dioscorea* section *Rajania* (L.) Raz, a group of species endemic to the Caribbean islands (Raz, 2016), the clade *Epipetrum*, proposed by Philippi (1864) as genus for dwarf-sized species endemic to Chile (Viruel *et al*., 2010), and the clade *Nanarepenta*, for non-winged seeds species exclusive to Mexico, also previously proposed as a separate genus (Téllez-Valdés & Dávila-Aranda, 1998). Those clades fund by (Viruel *et al*., 2016) were sampled by previus studies (Caddick *et al*., 2002a,b; Wilkin *et al*., 2005)(), but (Viruel *et al*., 2016)presented a expanded the number of species and more a robustly supported results.

Full understanding of relationships among species of *Dioscorea* and a natural infrageneric classification will only be possible with strongly supported phylogenetic studies. However, the phylogenetic results to date do not allow a new formal and complete classification, especially for the Neotropical region, which is still poorly sampled in most recent published works (five neotropical taxa in Caddick *et al*., 2002a); three in Caddick *et al*., 2002b; 43 in Viruel *et al*., 2016). It should also be noted that the genera mentioned above — which are now known to be part of *Dioscorea* — still require a change of status regarding their positioning in an infrageneric taxonomic category within *Dioscorea*, with exception of *Rajania* that has been reduced to a section by Raz (2016).

Previous phylogenetic studies points to three events of radiation of *Dioscorea* into the Neotropics (Wilkin *et al*., 2005; Viruel *et al*., 2016), however their sampling did not completely reflect the diversity of Neotropical region. Species of *Dioscorea* arrived at least thrice in the Neotropics since the Oligocene and greatly diversified there, occupying various habitats in this region (Viruel *et al*., 2016). Since previous phylogenies did not include a dense sampling of Neotropical species, much of the taxonomic, morphological and geographical variation of Neotropical *Dioscorea* has not been covered, hampering inferences regarding its origin and diversification in this biogeographical region.

The present study increases by 45% the sampling of Neotropical species compared to previous phylogenetic studies in *Dioscorea*, including wider taxonomic and morphological

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diversity, and summed with sequences available in GenBank (mostly from Wilkin *et al*. (2005) and Viruel *et al*. (2016)), it represents the most densely sampled phylogeny of *Dioscorea* to date. This neotropical sampling (64 species in total) represents around 20% of all neotropical species. In terms of possible neotropical lineages, Knuth (1924) presented 56 sections for *D.* sect. *Helmia* and *D.* sect. *Dioscorea* (17 for *Helmia* and 39 for *Dioscorea*), 38 of these feature neotropical distribution (67%, 13 for *Helmia* and 23 for *Dioscorea*). In our study, we cover 22 of those sections (almost 40% of all sections, 7 for *Helmia* and 15 for *Dioscorea*) and four more species *Incertae sedis*, on which 14 of these lineages (10 sections and four *Incertae sedis*) had not been sampled in previous studies.

By reconstructing the phylogeny of *Dioscorea*, with special addition of Neotropical samples, we aimed to infer phylogenetic relationships among Neotropical taxa, as well as their arrival and divergence times in this region. As the richest lineages of the genus, we seek to test the infrageneric classification proposed Knuth (1924) (reestablishing any of the sections if supported by phylogeny) and to obtain a clear view of the lineages existing now at the Neotropical region, especially in cases where the Knuth, (1924) classification does not present clear delimitations between sections. Also, the understanding of how they occur in past, up to the present environments can provide tools for a better comprehension of the evolution of this group so rich morphologically. We also offer a more robust scenario of phylogenetic relationships in the genus, facilitating future proposals of an updated classification of *Dioscorea*.

MATERIALS AND METHODS

TAXON SAMPLING, DNA SEQUENCING AND ALIGNMENT

Species sampling aimed to cover a wide geographic and morphological range within *Dioscorea*. We produced new sequences for 34 species of *Dioscorea*: 12 spp. representatives of

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D. subg. *Helmia*, 18 spp. of *D.* subg. *Dioscorea*, and four spp. *incertae sedis*, plus *Tacca artocarpifolia* Seem as an outgroup representative of Dioscoreaceae (Table S1). The taxon sampling aimed to cover a great part of the lineages proposed as sections by classic authors (sensus the revisionmade by Knuth, 1924), covering 22 of the 38 sections proposed to the neotropical region, attending the sections with great number of species with more than one taxa (eg.: *D.* section *Dematostemon* Griseb., five species sampled in diferent morphological strata).

Most new sequences were generated from specimens collected in the field by R. S. Couto, prioritizing taxonomically well-delimited species from well-known populations. Vouchers were deposited in the Herbarium of National Museum (R), with duplicates at the Herbarium of the Botanical Garden of Rio de Janeiro, Brazil (RB).

Additionally, we included 143 sequences from GenBank: 129 from Dioscoreaceae (119 species of *Dioscorea*, two species *Trichopus*, seven of *Tacca* and one *Stenomeris*), and five from other families (three species of Burmanniaceae, one Stemonaceae and one Thismiaceae), totaliing 177 species sampled. All sampled species with geographic origin, herbarium vouchers and GenBank accession numbers are listed in Table S2.

Total genomic DNA was extracted from leaf samples, fresh or silica-dried following the 2x CTAB protocol (Doyle & Doyle, 1987), without the addition of RNase A and scaled to 2 ml tubes. The extracted DNA was measured in 1% agarose gel with a DNA mass ladder and deposited at the DNA collection of Laboratory of Systematics and Molecular Ecology of Plants, Federal University of Paraná (UFPR), Brazil, associated to the reference vouchers deposited in K, R, RB, RFA and UPCB (Herbarium acronyms follow *Index Herbariorum* (Thiers, continuously updated)). The plastid genome regions mat*K* and rbc*L* were amplified and sequenced using the following primer pairs, respectively: 3F_KIM-f (cgtacagtacttttgtgtttacgag) and 1R_KIM-r (acccagtccatctggaaatcttggttc) (Ki-Joong Kim, pers. com.), rbcLa_f (atgtcaccacaaacagagactaaagc) (Levin *et al.*, 2003) and rbcLa_r (gtaaaatcaagtccaccaccrcg) (Kress & Erickson, 2007). Additionally, the primers ITS92 and ITS75 or ITS18F and ITS26R, which is widely used in angiosperms (Bolson *et al.*, 2015), was used to amplify the nuclear ITS region,

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however without sucesss in sequencing. This negative result and the scarcity of ITS sequences for *Dioscorea* in GenBank lead us to use only plastidial genome markers. PCR amplifications were performed using initial 94°C pre-melt for 1 min followed by 40 cycles of (i) 94°C denaturation for 30s, (ii) 53°C annealing for 40s, and (iii) 72°C extension for 40s, followed by 72°C a final extension for 5 min. Following PCR, the samples were purified with 20% PEG and sequenced with Big Dye Terminator version 3.1 (Applied Biosystems, California, USA) by the company Macrogen Inc. (South Korea). Forward and reverse sequences were assembled using the Staden package v.2.0.0b11 (Staden, Judge, & Bonfield, 2003). Sequences were aligned with Clustal W using default parameters (Thompson *et al.*, 1997) implemented in the software MEGA6 (Tamura *et al.*, 2013).

GEOGRAPHICAL AND MORPHOLOGICAL DATA

We examined over 4,000 specimens deposited in 79 herbaria, in addition to field observations, with special effort on the Neotropics, for the selection of taxons sequenced, to obtain morphological comparisons between the analyzed species (detailed in the discussion of the clades) and especially for coding the geographic distributions used in biogeography. Specimens from the following herbaria were examined: B, BAA, BAFC, BR, C, CAY, CEPEC, CESJ, COAH, COL, CR, CTES, CUVC, CVRD, ESA, F, FAA, FCAB, FURB, GUA, HAL, HAS, HB, HCF, HMUC, HRCB, HST, HUCP, HUEFS, HUPG, HVASF, HXBH, IAC, ICN, INPA, IPA, IRBR, JE, JVR, K, L, LPS, M, MBM, MEXU, MG, MNHN, MO, MVFA, MVFQ, MVM, NY, OPUR, P, PACA, PEL, PH, R, RB, RBR, RFA, RFFP, S, SI, SMDB, SP, SSUC, U, UFP, UFPR, ULS, UNR, UPCB, US, UV, WU, XAL, Z, and ZT. Herbarium acronyms follow Index Herbariorum (Thiers, continuously updated).

PHYLOGENETIC ANALYSIS

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Maximum Likelihood, Parsimony and Bayesian inference were used to estimate tree topologies on the concatenated matrix of 177 taxa and 1658 nucleotides from rbc*L* and mat*K* genes. Maximum-likelihood tree searches were performed using raxmlGUI v.1.0 (Silvestro & Michalak, 2012) under the model GTR+I+G and statistical support for nodes were assessed with 1,000 bootstrap replicates, consistent with that used by Viruel *et al.* (2016). Parsimony analyses were conducted in PAUP 4.0b10a (Swofford, 2002) using heuristic tree searches with tree bisection-reconnection (TBR), 2,000 random-taxon-addition replicates holding 20 trees per replicate. Branch support was estimated with 2,000 bootstrap pseudo-replicates (Felsenstein, 1985). Bayesian phylogenetic inference with the Metropolis-coupled Markov Chain Monte Carlo (MCMC) was used to estimate tree topology and posterior probability distribution as implemented in MrBayes v.3.3.4 (Ronquist *et al.*, 2012), using two parallel runs, each with four chains and 10 million generations, with parameters sampled every 1,000 generations. Each gene was considered as one partition and the best-fitting models under the Akaike Information Criterion in the software Mega 6 (Tamura *et al.*, 2013) were GTR+G (mat*K*) and K2+G (rbc*L*). Convergence of runs was assessed in Tracer 1.6 (Rambaut, Suchard, & Drummond, 2014). A 25% burnin was applied to eliminate trees prior to convergence of chains and a 50% majority rule consensus tree was constructed from the remaining trees.

MOLECULAR DATING

The *Dioscorea* tree molecular clock was estimated using fossil and secondary calibrations and the full matrix of 177 taxa including 162 representatives of *Dioscorea* and 15 outgroups. The fossil record of Dioscoreaceae was recently reviewed by Raz (2017), who analyzed twenty fossils attributed to this family from different time periods and geographical origins, mostly leaves. Only three can be attributed to sections within *Dioscorea* and therefore are more suitable for molecular dating: *Dioscoroides lyelli* (Eocene), *Dioscorea wilkinii* (Oligocene) and *Dioscorea* sp. from Kenya (Sect. Asterotricha) (Miocene). Other fossils are attributed only to

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genus level or would require further information to confirm their position, and eight of them are not Dioscoreaceae (Raz, 2017). Three Dioscoreaceae fossils used to calibrate the tree were chosen by stratigraphic reliability and confidence of taxonomic assignment (Raz, 2017). We follow the fossil calibration described by Viruel et al. (2016): A. The fossilized leaf of *Dioscoroides lyelli* from the Eocene at the Paris basin, France (Potonié, 1921), dated from the Ypresian age, was assigned to the *Stenophora* stem due to similarities with the extant *Stenophora* species; B. The fossil seed attributed to *Tacca buzekii* from the Upper Eocene from Putschirn, Czech Republic (Gregor, 1983), was assigned to the crown node of *Tacca*; C. The fossilized leaflet attributed to *Dioscorea wilkinii*, from the Middle Oligoceneof Ethiopia (Pan, Jacobs, & Currano, 2014), was assigned to the crown node of section *D.* Section *Lasiophytum* A lognormal distribution prior was applied to all fossil calibrations nodes, with values also following Viruel *et al*. (2016), as follows: *Dioscoroides lyelli* (mean= 48.2, sd= 0.008); *Tacca* (mean: 35.85, sd= 0.028); *Dioscorea wilkinni* (mean: 27.23, sd= 0.002). Calibration points are depicted in Fig. S3.

Divergence times were inferred under a relaxed uncorrelated lognormal clock model in BEAST 1.8.3 (Drummond *et al.*, 2012) implemented in the CIPRES server (Miller, Pfeiffer, & Schwartz, 2010), using a Yule tree model of speciation, and HKY+I+G substitution model with empirical base frequencies. The MCMC chains ran for 50 million generations, sampled every 10,000 generations. Convergence was assessed using effective sample size (ESS) values ≥ 200 in Tracer 1.6 (Rambaut *et al.*, 2014). Two separated runs were performed and their results were combined in LogCombiner, totalizing 100 million generations. The maximum clade credibility tree was generated in TreeAnnotator (BEAST package), and visualized and edited in FigTree v 1.4 (Rambaut, 2009).

BIOGEOGRAPHIC ANALYSIS

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In order to estimate ancestral distribution areas of Neotropical *Dioscorea* we defined six major geographic areas: A= Central America, B= Northern Andes, C= Southern Andes, D= Amazonia, E= Dry Diagonal and F= Atlantic Forest. Definitions were based on the current distribution of Neotropical species of *Dioscorea*, considering areas with more than 10 endemic species, seeking to exclude areas that present only occasional endemisms. The delimited areas were also based on the Neotropical regional classification proposed by Morrone (2014) and a study on Rubiaceae by Antonelli *et. al*. (2009). Although another six species that also occur in the Neotropics were included in our analysis, we focused our biogeographical analysis on the most diverse clades, New World I and New World II (hereafter NWI and NWII).

We estimated ancestral range probabilities on the multimodel approach performed by the R package BioGeoBEARS (Matzke, 2013; R Core Team, 2016) using the three available models: DEC, BAYAREALIKE and DIVALIKE. The dispersal-extinction-cladogenesis model (DEC) considered cladogenetic processes as the evolution of range at speciation events and allows the estimation of free parameters *d* (dispersal) or range extension and *e* (extinction) or range loss by maximum likelihood (Ree & Smith, 2008). Dispersal-vicariance-analysis (DIVA) is a parsimony-based method that allows dispersal and extinction in anagenetic processes and vicariance in cladogenetic processes (Ronquist, 1997). The model is called DIVALIKE in BioGeoBEARS because it is a maximum likelihood implementation of DIVA. The BayArea method is a Bayesian approach specifically designed to analyze a large number of areas efficiently (in reasonable computer time) (Landis *et al.*, 2013). BAYAREALIKE implemented in BioGeoBEARS is a maximum likelihood interpretation of BayArea. The founder speciation event parameter *j* was also added to all analyses, creating the models DEC+*j*, DIVALIKE+*j*, BAYAREALIKE+*j*. The parameter *j* adds the possibility of a new cladogenesis event, where an individual ‘jumps’ to an area completely outside the ancestral range, founding a new genetically isolated lineage (Matzke, 2013, 2014). For selection of best-fit model, we relied on the best likelihood value as well as the Akaike Information Criterion (ΔAICc).

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RESULTS

PHYLOGENETIC ANALYSIS

Dioscorea species form a strongly supported clade (bootstrap support value (BS) ML and MP 100%, Posterior Probability (PP) 1) (Fig. 2, Fig. S1 and S2). Among the internal clades, *Dioscorea* section *Stenophora* has strong support (BS-ML and BS-MP 100%, PP 1) and represents a sister lineage to the remaining *Dioscorea*. Traditional classification systems and phylogenetic analysis results are compared in Table S4.

Most Neotropical species grouped into two clades, here indicated as 'New World I' and 'New World II'. New World I groups the species corresponding to *D.* subg. *Dioscorea,* restricted to the Neotropics. Within this clade it is possible to recognize another three small clades: *Epipetrum,* with high support (BS ML and MP 100%, PP 1), *Microdioscorea,* and *Nanarepenta,* with low support. New World II has strong support (BS-ML 99%, BS-MP 95%, PP 1) and groups species corresponding to *D.* subg. *Helmia* restricted to the Neotropics. The *Monadelpha* clade can be recognized in the New World II clade, as a strongly supported clade (BS-ML 98%, BS-MP 90%, PP 1) with sister species. Neotropical species that were external to NWI and NWII, *D. dodecaneura* Vell., *D. stegelmanniana* R.Knuth, and species representatives of *D.* section *Rajania* (L.) Raz form the clade 'New World III', appearing associated with clades of African and Asian species (Africa and Compound Leaved). The species of *D.* section *Rajania,* however, form a well supported clade (BS-ML 90%, BS-MP 75%, PP 1) within New World III. Only one species with Neotropical occurrence appears in this analysis outside the clades mentioned above, *D. mollis,* which is sister to *D. antaly*, and related to Asian species.

The clade *Shannicorea* appears for the first time and brings together the seven species from Southeast Asia, with moderate support (BS ML and MP 81%, PP 1). The remaining Old World species are organized in a large clade, where the inner clades 'Mediterranean', 'Africa', 'Compound Leaved', 'Birmanica', 'Malagasy' and *Enantiophyllum* can be highlighted, following Viruel *et al.* (2016) nomenclature. The results obtained in this analysis are congruent

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with Viruel *et al.* (2016), just with some differences in the support values of the clades, those values can be retrieved in Figure 1 and others in supplementary material (Fig. S1, S2, S3).

Bayesian and Maximum Likelihood analysis results did not differ considerably, except for small differences in the most recent clades in 'Birmanica', *D.* section *Shannicorea* and 'Malagasy'. Maximum Parsimony analysis also resulted in high support for most of the clades that were well-supported in other analyses (Fig S2).

DIVERGENCE TIMES AND BIOGEOGRAPHY

According to our divergence time analysis in BEAST, the most recent common ancestor of Dioscoreaceae (including *Tacca*) originated in the Cretaceous around 99 Mya (95% Highest posterior density interval (HPD): 72.7–132.4 Mya) (Fig. 3). All divergences in the genus level occurred in the Paleocene. The most diverse genus in the family, *Dioscorea*, is estimated to have originated in the Cretaceous-Paleocene boundary, around 66 Mya (54.8 –84.6 Mya) (stem age). The two main Neotropical clades originated between the Eocene and Oligocene: the crown age for New World I is 37.2 Mya (28–44.3 Mya) and around 28 Mya (20.8–37.8 Mya) for New World II. The third Neotropical clade comprises only four species and originated in the Oligocene, around 30 Mya (20.3 –37.5 Mya). The clade that includes Neotropical *Dioscorea mollis* plus the Malagasy *D. antaly* originated in the Miocene at 18.5 Mya (6–31.5 Mya).

Biogeographic analyses performed separately on clades New World I and New World II yielded the same model as the best scored model (i.e. with lowest likelihood): BAYAREALIKE+j (See Table S3 for all parameter results). The ancestral distribution of the MRCA for New World I clade in *Dioscorea* is predicted to be the "Southern Andes" biogeographic region (Fig. 3), a region that nowadays comprises Northern Argentina and Chile and corresponds to the southern part of the mountain range, not present at the time of origin of NWI clade. Some clades remain endemic to this area (for example, the *D. fastigiata* – *D. humilis* clade). *Dioscorea* expanded its distribution eastward during the Oligocene, diversifying

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in today's Atlantic Forest. Expansions to Central America probably occurred in the Miocene at least twice. Further occupations of Dry Diagonal plus Amazonia and/or Atlantic Forest occurred in the Middle Miocene (around 10 Mya).

In contrast, New World II is estimated to have originated in the eastern part of South America, i.e. in a region comprising the Dry Diagonal and Atlantic Forest (Fig. 3). Most of the extant species in this clade still inhabit these regions. In the Miocene, two independent occupations of Northern Andes occurred, corresponding to the *D. coriacea* and *D. larecajensis* stems. Approximately at the same time, around 15 Mya, the *D. convolvulacea – D. galeottiana* lineage dispersed into Central America, with *D. convolvulacea* still being distribuited in Northern South America.

Two species of very restricted distribution in completely distinct regions appear in a small recent clade in the phylogenetic analysis of *Dioscorea*, *D. mollis* and *D. antaly*, which are endemic species of Southeastern South America (Atlantic Forest) and Madagascar (Tropophylles Forest = Deciduous Dry Forest), respectively. *Dioscorea antaly* is the only endemic species of Madagascar to appear outside the Malagasy clade, and *D. mollis* is the only endemic species of the Neotropics to emerge outside the New World clades (NWI, NWII and NWIII).

DISCUSSION

PHYLOGENETIC ANALYSIS AND CLASSIFICATION OF *DIOSCOREA* AND POSITION OF NEOTROPICAL CLADES

Eleven major clades were obtained for the monophyletic genus *Dioscorea*, which was consistent with the clades observed in other recent studies. The nine clades and sections of *Dioscorea* already established in other studies (Wilkin *et al.*, 2005; Viruel *et al.*, 2016) were also recovered in this analysis, with the emergence of internal clades such as *D.* section

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Shannicorea (even though weakly supported) and the position of Neotropical species external to the clades New World I and II (Fig. 2).

The taxa of unique occurrence in the Neotropics form basically two clades, as also stated by Wilkin *et al*. (2005) and Viruel *et al*. (2016). The New World I clade (NWI) groups (although, with low support) the species with circular or semicircular winged seeds that occur in the tropical region of the Americas, once placed by Knuth (1924) in *D*. subgenus *Dioscorea* along with other *Dioscorea* of circular or semicircular winged seeds with wider, pantropical distribution. The seed morphology is part of the *Dioscorea* taxonomy since the the first classifications proposed, Kunth (1850) proposed the *Helmia* genus using (beside others) this character, as other follow in theirs infrageneric classification. Although Knuth (1924) knew that the use of this character to split the *Dioscorea* genus almost at half was not completely adequate, nor reflected a systematic relationship, it was used, at least for practical reasons, for many years as the base of the infrageneric classification of *Dioscorea*. Wilkin *et al.* (2005) had already shown that this character and subgenus classification were not a reflection of the evolutionary relations of the group, however, they obtained several clades where one of the states of this character were fixed in all specis sampled in their analisys. The autors used this condition to help to explain and separate the especies in the two internal clades of Madagascar and as a plesiomorfic condition of all species of their clade “Compund-leafed”, yet they didn’t discussed this character in the scope of the “New World” clade (probably by the lack of knowledge of the fruit morphology of neotropical species at the time).

Allthough, this clade does not include all the species placed by Knuth (1924) in this subgenus of pantropical distribution, it contemplates species from different regions and habitats of the Neotropics, as well as great morphological diversity (Fig. 1). This could mean that this character, had only a few changes between the the two states, at least in the Neotropics, where almost half of all species of the genus are distributed, and could point to a probable sinapomorphy to the NW I and II clades.

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The Chilean species in the NWI clade are basically arranged in three smaller clades (*Epipetrum*, *Microdioscorea* and *Nanarepenta*, with exception of *D. brachybotrya*), with poor internal resolution. In spite of the evidence for the relationship between the taxa endemic to Chile, the *Epipetrum* clade groups dwarf species that present non-winged seeds, characteristic to the dry regions of Chile, as seen in Viruel *et al*. (2016). Besides these species, we have six taxa placed by Knuth (1924) in the *D.* section *Microdioscorea*, a section composed mostly of Chilean species (only two taxa for Peru and Brazil) with stems of reduced length and six stamens. *Dioscorea* section *Microdioscorea* appears as monophyletic with low support in this analysis and also in Viruel *et al*. (2016).

Another clade within the NWI group is the group endemic to Mexico, previously designated by Matuda (1961) as the genus *Nanarepenta*, which also has non-winged seeds. In Viruel *et al*. (2016), *D. minima* appeared along with the other three species of *Nanarepenta*, but in the present analysis this species is distantly related. This lack of resolution could be a reflection of the increased number of taxon and the lower amount of markers used in this study. Due to the great diversity found in the Neotropics is desirable that a greater number of species, as well as the DNA regions, could be analysed to solve the internal relations of the largest Neotropical clade.

Whithin the species of NWI clade is possible to highlight *D. perdicum* Taub., one of the dwarf species endemic from Brazil that does not fit any specific infrageneric classification devotaded to this issue. *Dioscorea perdicum* is mistakenly placed by Knuth (1924) into the section *Cycladenium* Uline (*D.* subg. *Helmia*), as the autor didn't know the species fruits or seeds, that place *D. perdicum* in *D.* subg. *Dioscorea* by its all-round winged seeds. Burkill (1960) pointed out the mistake made in the allocation in the *Cycladenium* section suggesting to be placed in *D.* sect. *Pedicellatae* R. Knuth, but most importante he proposed this species as a possible link between the Neotropical and Paleotropical species, with relation to *D.* sect. *Stenophora*, specifically by the presence of what he called a rhizome. As a matter of fact, the underground organ of *D. perdicum* is a tuber of rhizomatous aspect (Fig. 2), as have all

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anatomical features of a tuber (Tenorio, pers. comm.) but the aspect is similar to a rhizome, as doesn't have cataphylls but it branches and produces roots and shoots from more than one point. This unique morphology leaded Burkill (1960) to assume the close relation to the Paleotropical species of *Dioscorea*, aspect not confirmed in our analisys, as *D. perdicum* appears without any special relation to the *Stenophora* clade.

The other species that are endemic to the Neotropics appear here as the strongly supported clade NWII (BS-ML 99%, BS-MP 95%, PP 1), which contains part of the formerly designated *D.* subg. *Helmia* (sensu Knuth, 1924), unlike the NWI clade, this group has been retrieved in all phylogenetic studys that have sampled the neotropical species (Wilkin *et al.*, 2005; Viruel *et al.*, 2016) and also strog support, demonstrating the likely single origin of the elongated seed wings in the Neotropical region. Even though the sections sampled here have been increased only by one, the number of species within key sections (*D.* sect. *Dematostemon* Griseb. and *Monadelpha* Uline) has been increased in order to contemplate more comprehensively the diversity of this group. *Dioscorea* sect. *Dematostemon* is one of the biggest sections of the Neotropical region, comprising 45 taxons of great morphological diversity and high distribution range, going from dwarf species (eg.: *D. anomala* (Kunth) Griseb. and *D. maianthemoides* Uline ex R. Knuth) endemic to the brazilian "Cerrado" to typical Atlantic Forest species (*D. campanulata* Uline ex R. Knuth and *D. cinnamomifolia* Hook.). Knuth (1924) also placed in this section species (*D. moyobambensis* R. Knuth, *D. galiiflora* R. Knuth and *D. triangularis* (Griseb.) R. Knuth) closely related to others in *D.* sect. *Centrostemon* Griseb., showing that the boundaries of this group are not well defined. With our increased sampled analisys, this section is shown to be polyphyletic.

In addition, we have a small clade with strong support, formed by *D.* section *Monadelpha* species, which present unusual characteristics, such large staminate flowers, three fertile stamens forming a fleshy column, free and entire stylus in pistillate flowers. Besides those characteristics, this section possess an almost unique feature related to sexuality in the genus, the monoecy, all species from this section present staminated inflorescences in the lower part of the plant and pistillated on the higher part. This character is only shared with a few species from *D.* section *Cycladenium* (probably misplaced) and *D. margarethia* G.M. Barroso, E.F. Guim. & Sucre (poorly know compoud-leafed species with six stamens on a column instead of three), and besides some unstable dioecy in *D.* sect. *Stenophora* and *D. convovulacea* Schltdl. & Cham. (Wilkin *et al.*, 2005). The monoecious species from *D.* section *Cycladenium* aro not well know and the boundaries of the section are not clear, as is a section with great diversity (i.e. monoecious and dioecious species). In our analisys, the only species from *D.* section *Cycladenium, D. coriacea* Humb. & Bonpl. ex Wild., (dioecious), doesn't appear to be closely related to this clade. Addition of more taxa from this group could clarify relationships the two sections and reinforce the monophyly of *D.* section *Monadelpha*.

The *Monadelpha* clade also appear as monophyletic in other studies with less dense taxon sampling for the Neotropic (Wilkin *et al.*, 2005; Viruel *et al.*, 2016), however, with no mention of the section, due in part to the smaller sample of the *Monadelpha* clade and due to a misidentification of one of the species used in Viruel *et al*. (2016) (*D. monandra* Hauman was iderntified as *D. calderillensis*, from *D.* section *Cycladenium*). Therefore, we understand that monoecy probably originated only once in the in the family, with origin in the Neotropical region. The position of *D. margarethia* should be tested to reinforce this organization, but the species is only know from its type specimens and a second gathering (that could not be sequenced), and even the fact that it has six stamens doesn't seem to be a problem as this character is volatile in the NW clades.

Even with the increased number of taxa sampled to the NWI clade from 23 to 64 species and 15 Knuth's sections for *D.* subg. *Dioscorea* and seven for *D.* subg. *Helmia*, plus four *incertae sedis* species the resolution in the Neotropical clades is not yet close to be solved. It has been increased the number of internal clades monophyletic (*Monadelpha, Nanarepenta, Epipetrum, Microdioscorea*) and species of most sections of Knuth (1924) are shown not to be phylogenetically related (e.g.: *Dematostemon*, *Apodostemon* Uline, *Cryptantha* Uline).

A small group of Neotropical species emerged outside the main Neotropical clades (NWI and NWII), being composed of three species from *D.* section *Rajania*, plus two South-American species, *D. dodecaneura* and *D. stegelmanniana*. Wilkin *et al*. (2005) already presented *Dioscorea cordata* (L.) Raz as a distinct lineage, separate from the NWI and NWII clades, which can also be observed in Viruel *et al*. (2016), also associated to the neotropical edible species *D. trifida* L. f.. Those species have very different morphological characteristics when compared to other Neotropical species, some of these characteristics being shared with those found in species from Asia and Africa. The common ground to this species is the presence of annualy renewed tubers, those are the only neotropical species sampled so far that have this character (absent in the NW clades and rather rare in the neotropical species). The matter of annual tubers has been addressed by Wilkin *et al.* (2005), showing that is a paleotropical characteristic (only present in their B clade), being these clades the ones related here to NWIII.

Dioscorea dodecaneura and *D. stegelmanniana* are morphologically very similar to each other, but they present marked differences in one key aspect of Knuth's classification, the fruit (transversely oblong and oblong, respectively) and seeds shape (circular and oblong, respectively). This indicates that besides the NWI and NWII clades the seed wing shape is not stable character, having closely related species on the NWIII clade with both of the states of this characteristic. Additionally, these two species present a particular pattern of organization of the vascular bundles of the aerial stem (Tenorio *et al.*, 2017), similar to that described by Ayensu (1972) as the typical Old World pattern. It is noteworthy that *D. trifida* and *D. stagelmanniana* have been sorted by Knuth (1924) to *D.* sect. *Macrogynodium* Uline, reflecting in his view the close relationship of this species.

Dioscorea section *Rajania* is composed of 18 species, besides one non-described species, with occurrence restricted to the West Indies (Raz, 2016; Raz & Pérez-Camacho, 2016)(Raz, 2016). The species belonging to *D.* section *Rajania* are distinguished by the samaroid fruits, although this is not an exclusive feature of this section, as pointed out by Raz

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(2016) in the most recent taxonomic treatment on this group. The morphological characteristics exhibited by this section exemplify the diversity found in the Neotropical region, even though it is a clade with lower morphological diversity, it presents great differences for the rest of the neotropical species and with a more recent arrival when compared to the other two Neotropical clades (NWI and NWII), with the maintenance of characteristics typical of species of the Asian and African region.

Dioscorea mollis shares several characteristics with paleotropical species, such as phyllotaxis ranging from alternate to subopposite or even opposite, a characteristic found in less than 2% of the species of the American continent, where most species presents alternate leaves. The species also present an underground system composed of several fibrous nodules from which numerous aerial stems appear (similar to a rhizomatous system), stems of woody aspect and prickles in the basal stem, which are also unusual characteristics for Neotropical species. These characteristics are shared with one closely related species of *D.* section *Chondrocarpa* Uline, *D. chondrocarpa* Griseb., not sampled here by the unsuccessful amplification of *matK* gene. *Dioscorea chondrocarpa* was also sampled by Viruel et al. (2016) but did not reached the final publication by lack of genes amplified successfully, however its position in their inicial analisys topology is congruent to the one fund here to *D. mollis* (Raz, pers comm.). Anatomically these species also presents similarities to the Old World species, as verified by Tenorio *et al*. (2017). All these evidences strongly indicate a fourth lineage of *Dioscorea* in the Neotropical region, more related to paleotropical species.

The Paleotropical clades obtained in our analysis were similar as those recovered in previous studies (Wilkin *et al.*, 2005; Maurin *et al.*, 2016; Viruel *et al.*, 2016), consisting in the Africa clade with the inner clade *Testudinaria* (composed of species occurring in the mountainous regions of eastern and southern Africa), the Malagasy clade (with all endemic species from the island of Madagascar, except for *D. antaly*), and the clade *Enantiophyllum* (composed by several species proposed to the *D.* section *Enantiophyllum* Uline). Previous and

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the present phylogenetic results contradict the main infrageneric classifications of *Dioscorea* (Uline, 1897; Knuth, 1924; Burkill, 1960), which grouped the species in various sections. Some aspects of those clade of these clades are interesting to emphasize, such as the Malagasy clade is internally organized into two small clades, one presenting circular winged seeds, and the second grouping the remainder species with elongated winged seeds, and that *Enantiophyllum* (with its enormous diversity and imprecise delimitation) has some polytomies in the present and previous phylogenetic analyses, indicating the need of more data to elucidate the internal relationships

Dioscorea section *Shannicorea* was proposed to group six species of occurrence restricted to Asia, mostly China. The taxa share the left twining stem, the staminate inflorescences composed of small scorpioid cymes, stamens inserted at the base of the tube segments and the elongated seed wings. Knuth (1924) treats the same species, with the addition of two taxa, as *D.* section *Shannicorea*, but subordinated to *D.* subg. *Stenophora*. In contrast to the initial position proposed by Uline (1897) for the *Stenophora* section, Knuth (1924) elevated *Stenophora* to subgenus and further organized it internally into two sections, *Eustenophora* R.Knuth and *Shannicorea* Prain & Burkill.

In our analyses, the six species listed by Prain & Burkill (1914) in *D.* section *Shannicorea* (*D. hemsleyi*, *D. martini*, *D. nitens*, *D. subcalva*, *D. velutipes* and *D. yunnanensis*) are grouped in a single clade, presenting similar internal relationships in all analyses, but positioned differently in the *Dioscorea* tree. It is the first time that this clade is supported in a widely sampled *Dioscorea* tree. Hsu *et al*. (2013) also recovered this clade, but their sampling included only species from East and Southeast Asia. Viruel *et al.* (2016) also analysed some of these species (*D. nitens* and *D. subcalva*), retrieving them inside the Birmanica clade, as they are related. In our analysis, *D.* section *Shannicorea* is distantly related to *D.* section *Stenophora*, demonstrating that Knuth's (1924) proposal to treat *D.* section *Shannicorea* as part of the subgenus *Stenophora* has no phylogenetic support and Prain & Burkill's (1914) proposal could be more accurate. This indicates that the section as proposed by Prain & Burkill (1914) could be monophyletic, but more DNA markers in a phylogeny that includes species from both clade that

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is closely related (*Shannicorea* and Birmanica) are needed to solve uncertainties in this part of the topology.

The placement of *D. sansibarensis* at the base of the Malagasy clade raises some questions regarding the evolution of this group in an insular environment. According to Viruel *et al*. (2016), Madagascar was colonized by *Dioscorea* species from Asia, and not from Africa as many angiosperms. On the other hand, the sister species *D. sansibarensis* occurs in several areas of Africa, besides Madagascar, presenting a high vegetative dispersal ability: they massively produce small aerial tubers in the leaf axils, which possibly facilitated their invasive behavior in several countries (Raz, 2002; Choo, 2009; Hsu & Wang, 2012). The presence of *D. sansibarensis* in Madagascar could be product of a recent natural dispersal event or human introduction, since this species has been used for food and for the production of venom (Wilkin *et al*., 2005).

We have new evidence suggesting that within both the biggest New World clades, some of the sections proposed by Uline (1897) may be supported and can fit in a phylogenetic sound revised classification of *Dioscorea* to come. The position and monophyletism of *D.* section *Microdioscorea* and *D.* section *Monadelpha* within a widely-sampled phylogenetic analysis of *Dioscorea* shows that the proposed infrageneric classification by classical works (Kunth 1924; Uline 1897) mostly do not represent natural lineages, but some of them still may be used in modern systematics of the genus. Increasing the Neotropical species sampling evidenced the role of this group of species as key to provide a complete and accurate infrageneric classification of *Dioscorea*, as it is the most diverse and taxonomically complex region, and at the same time, the most underrepresented in phylogenetic studies until the present study. Nevertheless, the Neotropical species still lack a wider sampling to reach a better resolution of these clades, 16 sections of the Knuth (1924) classification still don't have been used in any phylogeny up to the present (22 of 38 were coverd here), and this should be goal to persue to better undertand the infrageneric classification of Neotropical *Dioscorea*.

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DIOSCOREA LINEAGES ORIGINATED FOUR TIMES INDEPENDENTLY IN THE NEOTROPICS SINCE THE EOCENE

The phylogenetic analysis presented here, focused on the Neotropical clades of *Dioscorea*, provides a new perspective on the biogeographical history of this genus in South and Central America. The biogeographic analysis has shown that four independent lineages of *Dioscorea* diversified into the Neotropical Region, two of them becoming highly diverse and wide spread. The Neotropical species of *Dioscorea* present at least four different origins. The New World I and II clades are more diversified and widely distributed (Fig. 2), while another two species are grouped in the predominantly Caribbean group *Rajania*, and *D. mollis* is sister to the Malagasy *D. antaly*. With the exception of *D. mollis*, which has an independent origin, all the other hypotheses on origins of Neotropical clades of *Dioscorea* had been described before (Viruel *et al.*, 2016). For the first time, however, we presented a more detailed view on the biogeographic history of the group after the colonization of the Neotropics.

The pantropical genus *Dioscorea* putatively originated in Laurasia during the Late Cretaceous – Early Eocene, later dispersing into South America, Africa and Madagascar (Viruel *et al.*, 2016). The colonization of America could have been facilitated by the existence of land bridges during the Palaeocene-Eocene thermal maximum (Zachos, Dickens, & Zeebe, 2008), such as the North Atlantic Land Bridge (NALB) and Beringean Land Bridge (BLB), presumably during early Oligocene (Viruel *et al.*, 2016), further reaching South America by occasional island chains such as the proto-Greater Antilles (Antonelli *et al.*, 2009). Nevertheless, ancestral area reconstruction suggests a South American origin for the Neotropical *Dioscorea* with further dispersals towards Central America (Fig. 3), a result that was also found in the global analysis by Viruel *et al.*, (2016). Exchanges between Laurasia and South America are reported for other plant groups, such as Malpighiaceae, which is similarly

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pantropical, greatly diverse in South America, and possibly migrated through Laurasia after having originated in South America (Davis *et al.*, 2002).

At least three different origins are estimated for the Neotropical clades. The NWI clade originated in the Eocene-Oligocene boundary, in what is now the Southern Andes Region, and dispersed to eastern South America and Central America. At this time most of the Andes were not formed yet, which could allow eastwards expansions of range; however, the South American continent was partially occupied by marine incursions from the Caribbean and from the Pacific seas, which could be barriers to expansions (Antonelli *et al.*, 2009). Expansions towards the East in South America occurred only after the Oligocene, around 30 Mya. Since the end of Cretaceous, the South American humid forests dominated the terrestrial habitats and no evidence of dry vegetation exists for this period until the decrease in temperatures that took place after the Miocene Medium Climatic Optimum (Davis *et al.*, 2005; Hoorn *et al.*, 2010).

Occupation of dry vegetation biomes occurred in both clades, but only sparsely in NW II, which remained almost exclusive to rainforests. The MRCA of the clade that occurs in Dry Diagonal is ambiguous and could have been Amazonian or from the Dry Diagonal. It is known that the origin of the South American Dry Diagonal must have taken place only after 10 Mya, with climate gradual cooling and drying in the Miocene, and before the establishment of rainforests (Simon *et al.*, 2009). Some species of *Dioscorea* occur in both open vegetation formations (Dry Diagonal) and forested biomes, i.e. Amazonia (*D. acanthogene*, *D. pohlii* and *D. amaranthoides*) and Atlantic Forest (*D. sinuata*, *D. leptostachya* and *D. trisecta*). The most generalist species can occur in the Dry Diagonal and the two forested biomes (*D. multiflora*, *D. marginata* and *D. laxiflora*). Species with occurrence in forested habitats usually will appear in arboreous vegetation patches in the Cerrado, like the “Cerradão” and Gallery forests or Caatinga forest, and not in open vegetation. Connections between Amazonia and Cerrado occurred many times in history, not only because of the geographic proximity of the regions occupied by the two vegetation types, but also because during episodes of climatic fluctuations, forests are known to have expanded or retracted (Costa, 2003). Quaternary cooling and drying episodes

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during the glacial times favored the expansions of savanna-type vegetation (Cerrado), decreasing the extent of tropical forests (Werneck *et al.*, 2012). Only NWII presents species with distribution restricted to the open field formations (*D. maianthemoides*) and rocky savannas (*D. campos-portoi*) within the Cerrado biome.

Dispersals towards Central America occurred in Middle Miocene in both NW I and II, much earlier the estimated closure of the Ishtmus of Panama (3 Mya), which linked the still "isolated" biota of South America to North America (for a review of the long process of formation of Isthmus of Panama see O'Dea *et al.*, 2016). Flora exchange before the Isthmus formation is best explained by long distance dispersals (Antonelli & Sanmartín, 2011; Freitas *et al.*, 2016) and this seems to be the case of *Dioscorea*. Transoceanic dispersals explained much of plant biogeographic patterns and is hypothetically more explanatory than plate tectonics (Renner, 2004; Christenhusz & Chase, 2013). Besides the plant's dispersal capability, which in the case of *Dioscorea* is facilitated by seed and fruit morphology and production of aerial tubers, wind and sea currents also facilitate the dispersal across oceans, generating a "dispersal pattern" (Renner, 2004). Many plant and animal groups dispersed from South to North America (or the opposite direction) starting in the Eocene, such as Malpighiaceae (Davis *et al.*, 2002), *Hedyosmum* (Antonelli & Sanmartín, 2011) and Rubiaceae (Antonelli *et al.*, 2009).

The sister group relationship between the Neotropical *D. mollis* and Malagasy *D. antaly* is quite unusual, however there are a few examples of sister clades occurring in Neotropical region and Africa or Madagascar in ferns, such as *Leucotrichum* (Polypodiaceae) (for more examples see Rouhan *et al.*, 2012). Fern spores are efficient dispersal agents and greatly facilitated trans-atlantic dispersals and colonization (Rouhan *et al.*, 2012). In Solanaceae, the genus *Tsoala* also dispersed from South America to Madagascar, probably by long distance dispersal facilitated by sea currents (Olmstead, 2013). In this family, most fruits are fleshy, animal dispersed, but many are dry and could have been dispersed by wind and sea currents, and dispersal occurred in both cases, but more frequently in the fleshy fruited lineages (Olmstead, 2013; Dupin *et al.*, 2017). *Dioscorea antaly* could have dispersed from South America to

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Madagascar (or in the opposite direction) facilitated by its anemocoric dispersion syndrome, and specially by the shape of the seed, that is winged towards the base of the capsule, being more effective in high speed winds (Maurin *et al.*, 2016). In gramitid ferns and *Tsoala* the long distance dispersal event occurred from the Neotropics towards Madagascar. Stem anatomy results indicated the proximity between *D. mollis* and other Neotropical species (Tenorio *et al.*, 2017), possibly indicating that the direction of dispersal could have been from the Neotropical Region to Madagascar. Further phylogenetic analysis including more Neotropical species morphologically similar to *D. mollis* could further test this relationship hypothesis and clarify a scenario of dispersal between Neotropical Region and Madagascar.

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Figure legends

Fig. 1. Neotropical *Dioscorea* morphological diversity. **a** tuber of *D. therezopolensis*. **b** tuber of *D. perdicum*. **c** underground organ of *D. multiflora*. **d** dwarf plant of *D. perdicum*. **e** habit of *D. campos-portoi*. **f** spines of *D. mollis*. **g-h** colorful leaves of *D. dodecaneura*. **i** leaves of *D. pseudomacrocapsa*. **j** lobeded leaves of *D. sinuata*. **k**. lobaded and variegated leaves of *D. hassleriana*. **l** staminate flower of *D. asperula*. **m** staminate flower of *D. laxiflora*. **n** staminate

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flower of *D. demourae*. **o** staminate flower of *D. subhastata*. **p** staminate flower of *D. sinuata*. **q** pistilate flower of *D. monadelpha*. **r** pistilate flower of *D. laxiflora*. **s** fruit of *D. subhastata*. **t** fruit of *D. olfersiana*.

Fig. 2. Maximum likelihood tree derived from the analysis of 177 taxa and 1658 nucleotides of *Dioscorea* and outgroups. Thickened lines represent highly supported branches in at least one of the three analysis (ML, BI, and MP). Values on nodes represent supports obtained in the three analyses, respectively: BI, ML, MP. Branches with bootstrap values □70% and BPPs □95% were considered weakly supported.

Fig. 3. Combined time-calibrated tree and ancestral area reconstruction analyses for the groups New World I and II of *Dioscorea*. The tree is the maximum clade credibility tree based on the BEAST analysis of the molecular matrix with 177 taxa and 1658 nucleotides for *Dioscorea* and outgroups calibrated using fossils. Grey bars on nodes indicate the 95% confidence interval. Diagrams on nodes show the single most-probable ancestral range using the best model BAYAREALIKE+j in BioGeoBEARS (See Table S3 for the summary statistics). Squares on the tips represents the present range of each terminal. Areas used in the biogeographic analysis: A= Central America, B= Northern Andes, C= Southern Andes, D= Amazonia, E= Dry Diagonal and F= Atlantic Forest.

Supporting information

Figures

Fig. S1. Bayesian consensus tree resulting from the analysis of the complete data set (177 taxa and 1658 nucleotides), rooted in Burmmaniaceae. The main clades of *Dioscorea* are highlighted. Posterior probability values >95 are shown on nodes.

Fig. S2. Maximum Parsimony tree resulting from the analysis of the complete data set (177 taxa and 1658 nucleotides), rooted in Burmmaniaceae. The main clades of *Dioscorea* are highlighted. Bootstrap values >70 are show on nodes.

Fig. S3. Bayesian maximum clade credibility time tree for *Dioscorea* and outgroups obtained under a relaxed clock model in BEAST and fossil calibration points. For all significantly supported nodes, bars show the 95% Highest Posterior Density intervals around the estimated ages. Fossil calibration points are: A. *Dioscorea lyelli* (Potonié, 1921); B. *Tacca* seed (Gregor, 1983); C. *Dioscorea wilkinii* (Pan *et al*., 2014).

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Tables

Table S1. Sequences newly produced for this study, with information on voucher, country of origin and GenBank Accession Numbers. Herbarium acronyms follows the *Index Hebariorum* (Thiers, continuously updated).

Table S2. Species for which **s**equences were downloaded from GenBank with voucher information, GenBank accession numbers and references for the original publication. (Wilkin *et al.*, 2005; Gao *et al.*, 2008; China Plant BOL, 2011; Hsu *et al.*, 2013; Viruel *et al.*, 2016) (for complete reference, see References). Herbarium acronyms follows the *Index Hebariorum* (Thiers, continuously updated).

Table S3. Biogeographic models tested in this study using BioGeoBEARS package, and estimated parameters *d* (dispersion), *e* (extinction) and *j* (founder speciation event), log-likelihood and AIC values. Analysis performed on the clade New World I (a) and New World II (b).

Table S4. Species sampled and their position in two different infrageneric traditional classification systems for *Dioscorea* and in current phylogenetic molecular-based phylogenetic results. Complete references are given at the end.

Table S5. Species and their operational areas assigned in the biogeographic analysis.

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Supporting information

Table S1. Sequences newly produced for this study, with information on voucher, country of origin and GenBank Accession Numbers. Herbarium acronyms follows the *Index Hebariorum* (Thiers, continuously updated).

Species	**Voucher (Herbarium)**	**Country of origin**	**mat*K***	**rbc*L***
Dioscorea amaranthoides Presl.	Couto, R.S. et al. 204 (RFA)	Brazil	KU308788	KU308743
Dioscorea amazonum Griseb.	Couto, R.S. 10 (RB)	Brazil	KU308789	KU308744
Dioscorea asperula Pedralli	Couto, R.S. et al. 203 (RFA)	Brazil	KU308790	KU308746
Dioscorea bradei R.Knuth	Couto, R.S. 381 (RFA)	Brazil	KU308791	KU308747
Dioscorea campestris Griseb.	Couto, R.S. et al. 232 (RFA)	Brazil	KU308792	KU308748
Dioscorea campos-portoi R.Knuth	Couto, R.S. et al. 539 (R)	Brazil	KU308793	KU308749
Dioscorea coronata Hauman	Couto, R.S. et al. 352 (RFA)	Brazil	KU308797	KU308751
Dioscorea cynanchiolia Griseb.	Couto, R.S. s.n. (RFA)	Brazil	KU308798	KU308752
Dioscorea delicata R.Knuth	Couto, R.S. 499 (R)	Brazil	KU308799	KU308753
Dioscorea dodecaneura Vell.	Couto, R.S. et al. 377 (RFA)	Brazil	KU308800	KU308755
Dioscorea fastigiata Gay	Arancio, G. 15.438 (ULS)	Chile	KU308801	KU308756
Dioscorea hassleriana Chodat	Couto, R.S. et al. 324 (RFA)	Brazil	KU308804	KU308759
Dioscorea itatiaiensis R.Knuth	Couto, R.S. et al. 893 (R, RB)	Brazil	KU308805	KU308760
Dioscorea larecajensis Uline ex R.Knuth	Wood 9960 (K)	Bolivia	-	KU308787
Dioscorea laxiflora Mart. ex Griseb.	Couto, R.S. et al. 211 (R)	Brazil	KU308806	KU308761
Dioscorea leptostachya Gardner	Couto, R.S. 532 (R)	Brazil	KU308807	KU308762
Dioscorea maianthemoides Uline ex R.Knuth	Couto, R.S. et al. 190 (RB)	Brazil	KU308808	KU308763
Dioscorea marginata Griseb.	Couto, R.S. et al. 373 (R)	Brazil	KU308809	KU308764
Dioscorea mollis Kunth	Couto, R.S. et al. 90 (RFA)	Brazil	KU308810	KU308765
Dioscorea monadelpha (Kunth) Griseb.	Couto, R.S. et al. 145 (R, RFA)	Brazil	KU308811	KU308766
Dioscorea multiflora Mart. ex Griseb.	Couto, R.S. et al. 120 (R, RFA)	Brazil	KU308812	KU308767
Dioscorea olfersiana Klotzsch ex Griseb.	Couto, R.S. et al. 102 (RFA)	Brazil	KU308813	KU308768
Dioscorea pedalis (R.Knuth) R. S. Couto et J.M.A. Braga	Couto, R.S. et al. 587 (R, RB)	Brazil	KU308814	KU308770
Dioscorea perdicum Taubert	Couto, R.S. et al. 595 (R, RB)	Brazil	KU308815	KU308771
Dioscorea piperifolia Humb. et Bonpl. ex Wild.	Couto, R.S. et al. 176 (RFA)	Brazil	KU308816	KU308772
Dioscorea pseudomacrocapsa Barroso *et al.*	Couto, R.S. 495 (RFA)	Brazil	KU308817	KU308774
Dioscorea sinuata Vell.	Couto et al. 169 (RFA)	Brazil	KU308818	KU308777
Dioscorea cienegensis R.Knuth	Couto, R.S. 839 (RFA)	Brazil	KU308794	KU308775
Dioscorea sp.	Couto, R.S. et al. 895 (RFA)	Brazil	KU308819	KU308786
Dioscorea widgrenii R.Knuth	Couto, R.S. et al. 219 (R)	Brazil	KU308826	KU308784
Dioscorea sphaeroidae R. S. Couto et J.M.A. Braga	Couto, R.S. 316 (RB)	Brazil	KU308820	KU308778
Dioscorea stegelmanniana R.Knuth	Couto, R.S. et al. 107 (RFA)	Brazil	KU308821	KU308779

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Dioscorea subhastata Vell.	Couto, R.S. et al. 221 (RFA)	Brazil	KU308822	KU308780
Dioscorea therezopolensis Uline ex R.Knuth	Couto, R.S. et al. 301 (RFA)	Brazil	KU308823	KU308781
Dioscorea trisecta Griseb.	Couto, R. S. 352 (RFA)	Brazil	KU308825	KU308783
Tacca artocarpifolia Seem.	Roan 8 (K)	Madagascar	KU308827	KU308785

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Species	Voucher (Herbarium)	Reference	matk	rbcl
Burmannia biflora L.	Chase 157 (NCU)	1	AY956483	AF206742
Burmannia longifolia Becc.	Johns et al. 9157 (K)	1	AY956484	AF307484
Burmannia madagascariensis Mart. & Zucc.	Caddick et al. 312 (K)	1	AY956485	AF307486
Dioscorea acanthogene Rusby	Lewis 3210 (LOJA)	1	AY956477	AY667101
Dioscorea alata L.	Wilkin et al. 1090 (K)	5	AB040208	AY667098
Dioscorea alatipes Burkill & H. Perrier	Caddick et al. 334 (K)	1	AY950687	AY667099
Dioscorea althaeoides R.Knuth	Zhu & Zhao 0648572 (NAS)	2	EU407548	EU407550
Dioscorea antaly Jum. & H.Perrier	Wilkin et al. 1104 (K)	1	AY956476	AY667100
Dioscorea arachidna Prain & Burkill	Wilkin et al. 862 (K)	1	AY956478	AF307468
Dioscorea arcuatinervis Hochr.	Caddick et al. 310 (K)	1	AY956479	AY667102
Dioscorea aristolochiifolia Poepp.	Villar & Viruel 20 (JACA)	5	KM877834	KM877874
Dioscorea aspersa Prain & Burkill	No data	2	EF614211	EF614213
Dioscorea banzhuana S.J. Pei & C.T.Ting	Huang & Guo 0648582 (NAS)	2	DQ974182	DQ408174
Dioscorea bemarivensis Jum. & H. Perrier	Wilkin et al. 1124 (K) e Caddick 340 (K)	1	AY956480	AY667103
Dioscorea benthamii Prain & Burkill	Venus 101 (TCB)	4	JQ733666	JQ733743
Dioscorea besseriana Kunth	Villar & Viruel 14 (JACA)	5	KM877835	KM877875
Dioscorea biformifolia S.J. Pei & C. T. Ting	Zhu & Zhao 0648576 (NAS)	2	EU407549	EU301740
Dioscorea biloba (Phil.) Caddick & Wilkin subsp. *biloba*	Viruel & Villar Eb09 (JACA)	5	KM877836	KM877876
Dioscorea biloba subsp. *coquimbana* Viruel, Segarra-Moragues & Villar	Segarra-Moragues & Pérez-Collazos Eb01 (JACA)	5	KM877837	KM877877
Dioscorea birmanica Prain & Burkill	Thapyai et al. 409 (BKF)	1	AY956481	AY667104
Dioscorea brachybotrya Poepp.	Rudall 1/97 (K)	1	AY956482	AF307469
Dioscorea brevipetiolata Prain & Burkill	Wilkin et al. 964 (K)	1	AY956486	AY667105
Dioscorea buchananii Benth.	Bingham et al. 10290 (K)	1	AY956487	AY904790
Dioscorea bulbifera L.	Foster et al. 12 (K) e NASHYY065 (200911007 KUN)	1	AY956488	AY904791
Dioscorea burchellii Baker	Wilkin s.n. SANBI DNA Bank MWC 33240	5	KM877853	KM877905
Dioscorea calcicola Prain & Burkill	Wilkin et al. 814 (K)	4	AY956489	JQ733799.1
Dioscorea monandra Hauman	Wood et al. 22679 (K)	5	KM877849	KM877891
Dioscorea caucasica Lipsky	Zhou & Wu 0648584 (NAS)	2	DQ974188	DQ408182

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Dioscorea chouardii Gaussen	Segarra-Moragues & Catalán s.n. (Silica specimen)	5	KM877855	KM877907
Dioscorea cirrhosa Lour.	Chen 51 (TCB) andThapyai 375 (BKF)	1	JQ733663	AY904792
Dioscorea cirrhosa var. *cylindrica* C. T. Ting & M. C. Chang	No data	5	HQ637689	DQ408184
Dioscorea cochleariapiculata De Wild.	Chase 21046 (K)	5	KM877862	KM877921
Dioscorea colletii Hook.f.	Hsu 76 (TCB)	4	JQ733728	JQ733805
Dioscorea colletii var. *hypoglauca* (Palib.) S. J. Pei & C. T. Ting	No data	3	HQ637622	HQ637771
Dioscorea communis (L.) Caddick & Wilkin	Sánchez de la Campa & Sánchez Civila s.n. (Silica specimen)	5	KM877854	KM877906
Dioscorea composita Hemsl.	No data	2	DQ974180	DQ408172
Dioscorea convovulacea Schltdl. & Cham.	Chase 197 (NCU)	1	AY956491	AJ235805
Dioscorea cordata L.	Axelrod 8407 (UPR)	1	AY973835	AF307472
Dioscorea coriacea Humb. & Bonpl. ex Willd.	Lewis 3220 (LOJA)	5	AY956492	KM877893
Dioscorea cotinifolia Kunt	No data	2	DQ974185	EF614219
Dioscorea daunea Prain & Burkill	Thapyai et al. 518 (BKF)	1	AY956493	AY904793
Dioscorea decipiens Hook.f.	Wilkin et al. 861 (K) e Wilkin 860 (K)	1	AY956494	AF307454
Dioscorea deltoidea Wall. ex Griseb.	Huang & Guo 0648575 (NAS)	2	EF614207	EF614218
Dioscorea doryphora Hance	Hsu 56 (TCB)	4	JQ733669	JQ733746
Dioscorea dregeana (Kunth) T. Durand & Schinz	No data	5	KM877863	KM877922
Dioscorea dumetorum (Kunth) Pax	Wilkin 761 (K)	1	AY956495	AF307464
Dioscorea edulis Lowe	Catalán s.n. (Silica specimen)	5	KM877856	KM877908
Dioscorea elegans Ridl. ex Prain & Burkill	Rudall 113 (K)	5	KM877867	KM877931
Dioscorea elephantipes (L'Hér.) Engl.	UCI Arb. 6773 (NCU)	1	AY956496	AF307461
Dioscorea esculenta (Lour.) Burkill	Wilkin et al. 995 (K)	1	AY956497	AY904794
Dioscorea esquirolii Prain & Burkill	No data	2	DQ974177	DQ408168
Dioscorea exalata C.T. Ting & M.C. Chang	Y.S. Liang 1037 (TCB)	4	JQ733681	JQ733758
Dioscorea fandra H. Perrier	Caddick et al. 324 (K)	1	AY956498	AY904795
Dioscorea fordii Prain & Burkill	Shui 3526 (TNM)	4	JQ733706	JQ733783
Dioscorea formosana R.Knuth	Chen 42 (TCB)	4	JQ733691	JQ733768
Dioscorea futschauensis Uline ex R.Knuth	Hsu 32 (TCB)	4	JQ733671	JQ733748
Dioscorea galeottiana Kunth	Tellez 13090 (MEXU)	1	AY956499	AY904796
Dioscorea gilletii Milne-Redh.	Vollesen 61 (K)	1	AY956500	AY904797
Dioscorea glabra Roxb.	Wilkin et al. 874 (K)	1	AY956501	AF307456
Dioscorea glomerulata Hauman	Wood *et al.* 19466 (K) and Wood 8065 (K)	5	AY957586	KM877894
Dioscorea gracilis Hook. ex Poepp.	Villar & Viruel 18 (JACA)	5	KM877838	KM877878
Dioscorea gracillima Miq.	Tan 95288 (TNM)	4	JQ733709	JQ733786

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Dioscorea grandiflora Mart. Ex Griseb.	Pereira 378 (K)	5	KM877850	KM877895
Dioscorea hamiltonii Hook.f.	Wilkin et al. 886 (K)	1	AY957587	AF307465
Dioscorea hastifolia Nees	Chase 2231 (K)	5	KM877868	KM877932
Dioscorea hemsleyi Prain & Burkill	Yang 18467 (TNM)	4	JQ733701	JQ733778
Dioscorea hexagona Baker	Wilkin et al. 960 (K)	1	AY957588	AY904798
Dioscorea hispida Dennst.	Wilkin et al. 855 (K)	1	AY957589	AF307463
Dioscorea humifusa Poepp.	Villar & Viruel 01 (JACA)	5	KM877839	KM877879
Dioscorea humilis subsp. *humilis*	Segarra-Moragues & Pérez-Collazos Eh01 (JACA)	5	KM877840	KM877880
Dioscorea humilis subsp. *polyanthes* (F.Phil.) Viruel, Segarra & Villar	Segarra-Moragues & Pérez-Collazos Ep01 (JACA)	5	KM877841	KM877881
Dioscorea hyalinomarginata Raz	Livshultz 1012 (BH)	5	KM877865	KM877927
Dioscorea inopinata Prain & Burkill	Thapyai et al. 513 (BKF)	1	AY957590	AY904799
Dioscorea japonica Thunb.	Hsu 94 (TCB)	4	JQ733665	JQ733742
Dioscorea juxtlahuacensis (O. Téllez & Dávila) Caddick & Wilkin	Calzada 21129 (MEXU)	5	KM877842	KM877882
Dioscorea kamoonensis Kunth	CHC 7539 (TCB)	4	JQ733684	JQ733761
Dioscorea karatana Wilkin	Wilkin 950 (K) e Wilkin M947 (K)	5	AY957591	KM877916
Dioscorea kituiensis Wilkin & Muasya	Mwachala et al. 949A (EA)	5	KM877857	KM877910
Dioscorea lanata Bail	Miller 10423 (E)	1	AY957593	AF307458
Dioscorea larecajensis Uline ex R.Knuth	Wood 9960 (K)	1	AY957594	newly produced
Dioscorea lepcharum Prain & Burkill	Lu 16156 (TCB)	4	JQ733675	JQ733752
Dioscorea longirhiza Caddick & Wilkin	Téllez 13081 (MEXU)	5	AY957595	AF307473
Dioscorea maciba Jum. & H. Perrier	Caddick et al. 318 (K)	1	AY957596	AY904800
Dioscorea martini Prain & Burkill	Yang 14136 (TNM)	4	JQ733710	JQ733787
Dioscorea mayottensis Wilkin	Hladik 8507 (P)	5	KM877861	KM877917
Dioscorea mcvaughii B.G. Schub.	Tellez 13080 (MEXU)	1	AY957597	AF307460
Dioscorea melanophyma Prain & Burkill	CHC 9203 (TCB)	4	JQ733688	JQ733765
Dioscorea membranacea Pierre ex Prain & Burkill	Wilkin et al. 878 (K)	1	AY957598	AF307467
Dioscorea minima C. B. Rob. & Seaton	Téllez 13086 (K)	5	KM877843	KM877883
Dioscorea minutiflora Engl.	Hladik 6235 (P)	5	KJ629250	KM877933
Dioscorea modesta Phill.	Villar & Viruel 06 (JACA)	5	KM877844	KM877884
Dioscorea namorokensis Wilkin	Wilkin *et al*. 1123 (K) e Wilkin 1126 (K)	5	AY957599	KM877918
Dioscorea nipponica Makino	Chase 6225 (K)	1	AY957600	AF307455
Dioscorea *nipponica* subsp. *rosthornii* (Diels) C. T. Ting	No data	3	HQ637585	HQ637734
Dioscorea nitens Prain & Burkill	Liang 2628 (TCB)	4	JQ733733	JQ733810
Dioscorea nummularia Lam.	Lu 20549 (TCB)	4	JQ733723	JQ733800
Dioscorea orientalis (J. Thiébaut) Caddick & Wilkin	Danin A (Silica specimen)	5	KM877858	KM877911

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Dioscorea oryzetorum Prain & Burkill	Thapyai 464 (BKF)	1	AY972482	AY904801
Dioscorea ovata Vell.	Wood & Goyder 17012 (K) and Wood 9178 (K)	5	AY950686	KM877900
Dioscorea pedicellata Phil.	No data.	5	KM877845	KM877886
Dioscorea pentaphylla L.	Wilkin et al. 888 (K)	1	AY972483	AF307470
Dioscorea petelotii Prain & Burkill	Wilkin et al. 1023 (K)	1	AY973484	AY904802
Dioscorea pohlii Griseb.	Assis & Ladeira 67 (K)	5	KM877846	KM877887
Dioscorea polystachya Turcz.	Hsu 31 (TCB)	4	JQ733673	JQ733750
Dioscorea prazeri Prain & Burkill	Wilkin et al. 1075 (K)	1	AY973485	AY904803
Dioscorea preussii Pax	Davis 3019 (K) e Davi 2179 (K)	5	AY972486	KM877920
Dioscorea pyrenaica Bubani & Bordère ex Gren.	Segarra-Moragues & Catalán (Silica specimen)	5	KM877907	KM877912
Dioscorea quinquelobata Thunb.	Yonekura 6186 (TNM)	4	JQ733705	JQ733782
Dioscorea rockii Prain & Burkill	Wilkin et al. 1036 (K)	1	AY972488	AY939882
Dioscorea sansibarensis Pax	Wilkin et al. 973 (K)	1	AY972489	AY939883
Dioscorea saxatilis Poepp.	Villar & Viruel 11 (JACA)	5	KM877847	KM877889
Dioscorea schimperiana Hochst. ex Kunth	Wilkin et al. 762 (K)	1	AY972490	AF307466
Dioscorea scorpioidea C. Wright	Raz 339 (NY)	5	KM877866	KM877928
Dioscorea scortechinii Prain & Burkill	Lu 19238 (TCB)	4	JQ733714	JQ733791
Dioscorea simulans Prain & Burkill	Huang & Guo 0648583 (NAS)	2	EF614206	EF614217
Dioscorea sinoparviflora C. T. Ting, M. G. Gilbert & Turland	Huang & Guo 0648574 (NAS)	2	DQ974179	DQ408171
Dioscorea soso Jum. & H. Perrier	Wilkin et al. 1102 (K) and Wilkin et al. 1106 (K)	1	AY972491	AY939884
Dioscorea spongiosa J.Q. Xi, M. Mizuno & W.L.Zhao	Huang & Guo 0648581 (NAS)	2	DQ974191	DQ974194
Dioscorea strydomiana Wilkin	Lotter & Turpin 10627 (K)	5	KM877860	KM877913
Dioscorea subcalva Prain & Burkill	Liang 1045 (TCB)	4	JQ733682	JQ733759
Dioscorea sylvatica Eckl.	Chase 6184 (K)	1	AY972826	AF307462
Dioscorea tentaculigera Prain & Burkill	Thapyai 436 (BKF)	1	AY972828	AY939886
Dioscorea tokoro Makino ex Miyabe	Chen 5805 (TNM)	4	JQ733708	JQ733785
Dioscorea tomentosa J. König ex Spreng.	Chase 16311 (K)	5	KJ922833	KM877925
Dioscorea trichantha Baker	Wilkin et al. 1153 (K)	1	AY972829	AY939887
Dioscorea variifolia Betero	Villar & Viruel 03 (JACA)	5	KM877848	KM877890
Dioscorea velutipes Prain & Burkill	Liang 2609 (TCB)	4	JQ733732	JQ733809
Dioscorea wallichii Hook.f.	Wilkin et al. 1072 (K)	1	AY973830	AY939888
Dioscorea yunnanensis Prain & Burkill	Ma 7140 (TNM)	4	JQ733703	JQ733780
Dioscorea zingiberensis C.H. Wright	TCMK 244 (K)	1	AY973831	AY939889
Dioscorea seriflora Jum. & H. Perrier	Caddick et al. 302	1	AY973827	AY939885
Stemona tuberosa Lour.	Hsu 401 (TCB)	4	JQ733738	JQ733815
Stenomeris borneensis Oliv.	Brun 19174 (K) and Lu 20601 (TCB)	4	AY973836	JQ733811

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Tacca artocarpifolia Seem.	Caddick 305 (K)	1	newly produced	AF307481
Tacca chantrieri André	Chase 175 (NCU)	1	AY973837	AJ286561
Tacca integrifolia Ker Gawl.	Boyce 1074 (K)	1	AY973838	AF307478
Tacca leontopetaloides (L.) O. Kuntze	Wilkin et al. 817 (K)	1	AY973839	AF307480
Tacca palmata Blume	Boyce 1082 (K)	1	AY973840	AF307479
Tacca palmatifida Baker	Chase 1377 (K)	1	AY973841	AY939890
Tacca plantaginea (Hance) Drenth	Leiden 920520 (L)	1	AY973842	AF307483
Thismia rodwayi F. Muell.	Garnock-Jones 2218 (WELTU)	1	newly produced	AY939892
Trichopus sempervivens (H. Perrier) Caddick & Wilkin	Caddick 304 (K) and Wilkin 948 (K)	1	AF973844	AF307476
Trichopus zeylanicus Gaertn.	Caddick 346 (K) and Chase 16354 (K)	1	AY973845	AF307477

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Table S3. Biogeographic models tested in this study using BioGeoBEARS package, and estimated parameters *d* (dispersion), *e* (extinction) and *j* (founder speciation event), log-likelihood and AIC values. Analysis performed on the clade New World I (a) and New World II (b).

a) New World I

Model	**LnL**	**d**	**e**	**j**	**ΔAICc**	**AICc weight**
DEC	-93.36	0.005779	1E-12	0	191.037	0.142
DEC + J	-91.72	0.005095	1E-12	0.0150	190.094	0.228
DIVALIKE	-97.93	0.007399	1E-12	0	200.176	0.0014
DIVALIKE + J	-97.87	0.007373	1E-12	0.0001	200.072	0.0015
BAYAREALIKE	-96.94	0.001960	4.30E-2	0	198.196	0.0039
BAYAREALIKE + J	**-90.72**	**0.003768**	**1.00E-2**	**0.0333**	**188.093**	**0.6217**

b) New World II

Model	**LnL**	**d**	**e**	**j**	**ΔAICc**	**AICc weight**
DEC	-46.53	0.007106	0.0025	0	97.875	0.0818
DEC + J	-91.72	0.005095	1E-12	0.0150	191.160	4.531
DIVALIKE	-45.94	0.008520	1.8E-9	0	96.698	0.147
DIVALIKE + J	-49.11	0.008510	1E-12	1e-04	96.683	0.148
BAYAREALIKE	-43.06	0.005526	0.0462	0.0462	103.022	0.0062
BAYAREALIKE + J	**-43.06**	**0.003116**	**1E-07**	**1e-07**	**93.837**	**0.6160**

Table S4. Species sampled and their position in two different infrageneric traditional classification systems for *Dioscorea* and in current phylogenetic molecular-based phylogenetic results. Complete references are given at the end.

Species	Knuth (1924)	Burkill (1960)	Viruel et al. (2016)	Present study
Dioscorea acanthogene Rusby	*Incertis sedis*	—	New Word I	New Word I
Dioscorea alata L.	*Enantiophyllum* Uline	*Enantiophyllum* Uline	*Enantiophyllum* Uline	*Enantiophyllum* Uline
Dioscorea alatipes Burkill & H. Perrier	—	*Brachyandra* Uline	Malagasy	Malagasy
Dioscorea althaeoides R.Knuth	*Macropoda* Uline	—	*Stenophora* Uline	*Stenophora* Uline
Dioscorea amaranthoides Presl.	*Strutantha* Uline	*Strutantha* Uline	New Word I	New Word I
Dioscorea amazonum Griseb.	*Sarcantha* Uline	—	—	New Word I
Dioscorea antaly Jum. & H. Perrier	*Opsphyton* Uline (Subsection *Macrourae* R.Knuth)	*Xylinocapsa* Burkill & H. Perr.	Compound leaved	*"Incertis sedis"*
Dioscorea arachidna Prain & Burkill	*Trieuphorostemon* Uline	*Lasiophyton* Uline	Compound leaved (*Botryosicyos*)	Compound leaved (*Botryosicyos*)
Dioscorea arcuatinervis Hochr.	*Madagascariensis* R.Knuth	*Madagascariensis* R.Knuth	Malagasy	Malagasy
Dioscorea aristolochiifolia Poepp.	*Microdioscorea* Uline	—	New Word I	New Word I
Dioscorea aspersa Prain & Burkill	*Enantiophyllum* Uline	—	*Enantiophyllum* Uline	*Enantiophyllum* Uline
Dioscorea asperula Pedralli	—	—	—	New Word I
Dioscorea banzhuana S.J. Pei & C.T. Ting	—	—	*Stenophora* Uline	*Stenophora* Uline
Dioscorea bemarivensis Jum. & H. Perrier	*Cardiocarpa* Uline	*Cardiocarpa* Uline	Malagasy	Malagasy
Dioscorea benthamii Prain & Burkill	*Enantiophyllum* Uline	—	—	*Enantiophyllum* Uline
Dioscorea besseriana Kunth	*Microdioscorea* Uline	—	New Word I	New Word I ("*Microdioscorea*")
Dioscorea biformifolia S.J. Pei & C. T. Ting	—	—	*Stenophora* Uline	*Stenophora* Uline
Dioscorea biloba (Phil.) Caddick & Wilkin subsp. *biloba*	Genus *Epipetrum* Phil.	—	New Word I ("*Epipetrum*")	New Word I ("*Epipetrum*")
Dioscorea biloba subsp. *coquimbana* Viruel, Segarra-Moragues & Villar	Genus *Epipetrum* Phil.	—	New Word I ("*Epipetrum*")	New Word I ("*Epipetrum*")
Dioscorea birmanica Prain & Burkill	*Combilium* Prain & Burkill	*Stenophora* Uline	Birmanica	Birmanica

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Dioscorea brachybotrya Poepp.	*Chirophyllum* Uline	—	New Word I	New Word I
Dioscorea bradei R.Knuth	*Hemidematostemon* Griseb.	—	—	New Word I
Dioscorea brevipetiolata Prain & Burkill	*Enantiophyllum* Uline	*Enantiophyllum* Uline	*Enantiophyllum* Uline	*Enantiophyllum* Uline
Dioscorea buchananii Benth.	*Rhacodophyllum* Uline	*Rhacodophyllum* Uline	Africa	Africa
Dioscorea bulbifera L.	*Opsphyton* Uline (Subsection *Euopsophyton* R.Knuth)	*Opsphyton* Uline	Compound leaved	*"Incertis sedis"*
Dioscorea burchellii Baker	*Opsphyton* Uline (Subsection *Isocantha* (Uline) R.Knuth)	—	Africa	Africa
Dioscorea calcicola Prain & Burkill	—	*Enantiophyllum* Uline	*Enantiophyllum* Uline	*Enantiophyllum* Uline
Dioscorea monandra Hauma	*Cycladenium* Uline	—	New Word II	New Word II
Dioscorea campestris Griseb.	*Dematostemon* Griseb.	*Dematostemon* Griseb.	—	New Word II
Dioscorea campos-portoi R.Knuth	*Dematostemon* Griseb.	—	—	New Word II
Dioscorea caucasica Lipsky	*Macropoda* Uline	*Stenophora* Uline	*Stenophora* Uline	*Stenophora* Uline
Dioscorea chouardii Gaussen	—	*Borderea* Miégev. Prain & Burkill*	Mediterranean ("*Borderea*")	Mediterranean ("*Borderea*")
Dioscorea cienegensis R.Knuth	*Monadelpha* Uline	—	—	New Word II ("*Monadelpha*")
Dioscorea cirrhosa Lour.	*Enantiophyllum* Uline	*Enantiophyllum* Uline	*Enantiophyllum* Uline	*Enantiophyllum* Uline
Dioscorea cirrhosa var. *cylindrica* C. T. Ting & M. C. Chang	*Enantiophyllum* Uline	*Enantiophyllum* Uline	*Enantiophyllum* Uline	*Enantiophyllum* Uline
Dioscorea cochleariapiculata De Wild.	*Botryosicyos* (Hochst.) Uline	*Lasiophyton* Uline	Compound leaved (*Lasiophyton*)	Compound leaved (*Lasiophyton*)
Dioscorea collettii Hook.f.	*Orientali-asiatiae* R.Knuth	*Stenophora* Uline	*Stenophora* Uline	*Stenophora* Uline
Dioscorea collettii var. *hypoglauca* (Palib.) S. J. Pei & C. T. Ting	*Orientali-asiatiae* R.Knuth	*Stenophora* Uline	*Stenophora* Uline	*Stenophora* Uline
Dioscorea communis (L.) Caddick & Wilkin	Genus *Tamus* L.	Genus *Tamus* L.	Mediterranean ("*Tamus*")	Mediterranean ("*Tamus*")
Dioscorea composita Hemsl.	*Apodostemon* Uline	—	New Word I	New Word I
Dioscorea convovulaceae Schltdl. & Cham.	*Trigonobasis* Uline	*Trigonobasis* Uline	New Word II	New Word II

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Dioscorea cordata (L.) Raz	Genus *Rajania* L.	Genus *Rajania* L.	"*Rajania*"	New World III (*Rajania*)
Dioscorea coriacea Humb. & Bonpl. ex Willd.	*Cycladenium* Uline	—	New Word II	New Word II
Dioscorea coronata Hauman	*Monadelpha* Uline	*Monadelpha* Uline	—	New Word II ("*Monadelpha*")
Dioscorea cotinifolia Kunt	*Opsphyton* Uline (Subsection *Isocantha* (Uline) R.Knuth)	—	*Enantiophyllum* Uline	*Enantiophyllum* Uline
Dioscorea cynanchiolia Griseb.	*Apodostemon* Uline	—	—	New Word I
Dioscorea daunea Prain & Burkill	*Combilium* Prain & Burkill	*Stenocorea* Prain & Burkill	Birmanica	Birmanica
Dioscorea decipiens Hook.f.	*Enantiophyllum* Uline	*Enantiophyllum* Uline	*Enantiophyllum* Uline	*Enantiophyllum* Uline
Dioscorea delicata R.Knuth	*Dematostemon* Griseb.	—	—	New Word II
Dioscorea deltoidea Wall. ex Griseb.	*Macropoda* Uline	*Stenophora* Uline	*Stenophora* Uline	*Stenophora* Uline
Dioscorea dodecaneura Vell.	*Lasiogyne* Uline	*Lasiogyne* Uline	—	New World III
Dioscorea doryphora Hance	*Enantiophyllum* Uline	—	—	*Enantiophyllum* Uline
Dioscorea dregeana (Kunth) T. Durand & Schinz	*Lasiophyton* Uline	*Lasiophyton* Uline	Compound leaved (*Lasiophyton*)	Compound leaved (*Lasiophyton*)
Dioscorea dumetorum (Kunth) Pax	*Lasiophyton* Uline	*Lasiophyton* Uline	Compound leaved (*Lasiophyton*)	Compound leaved (*Lasiophyton*)
Dioscorea edulis Lowe	Genus *Tamus* L.	Genus *Tamus* L.	Mediterranean ("*Tamus*")	Mediterranean ("*Tamus*")
Dioscorea elegans Ridl. ex Prain & Burkill	—	*Enantiophyllum* Uline	*Enantiophyllum* Uline	*Enantiophyllum* Uline
Dioscorea elephantipes (L'Hér.) Engl.	Subg. *Testudinaria* (Salisb.) Uline	*Testudinaria* (Salisb.) Prain & Burkill	Africa ("*Testudinaria*")	Africa ("*Testudinaria*")
Dioscorea esculenta (Lour.) Burkill	*Combilium* Prain & Burkill	*Combilium* Prain & Burkill	Birmanica	*"Incertis sedis"*
Dioscorea esquirolii Prain & Burkill	—	*Lasiophyton* Uline	Compound leaved (*Botryosicyos*)	Compound leaved (*Botryosicyos*)
Dioscorea exalata C.T. Ting & M.C. Chang	—	—	*Enantiophyllum* Uline	*Enantiophyllum* Uline
Dioscorea fandra H. Perrier	—	*Brachyandra* Uline	Malagasy	Malagasy
Dioscorea fastigiata Gay	*Pygmaeophyton* Uline	—	—	New Word I
Dioscorea fordii Prain & Burkill	*Enantiophyllum* Uline	—	*Enantiophyllum* Uline	*Enantiophyllum* Uline

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Dioscorea formosana R.Knuth	*Enantiophyllum* Uline	—	—	*Enantiophyllum* Uline
Dioscorea futschauensis Uline ex R.Knuth	*Enantiophyllum* Uline	—	*Stenophora* Uline	*Stenophora* Uline
Dioscorea galeottiana Kunth	*Trigonobasis* Uline	*Trigonobasis* Uline	New Word II	New Word II
Dioscorea gillettii Milne-Redh.	—	*Borderea* Miégev. Prain & Burkill*	Africa	Africa
Dioscorea glabra Roxb.	*Enantiophyllum* Uline	*Enantiophyllum* Uline	*Enantiophyllum* Uline	*Enantiophyllum* Uline
Dioscorea glomerulata Hauman	*Dematostemon* Griseb.	—	New Word II	New Word II
Dioscorea gracilis Hook. ex Poepp.	*Microdioscorea* Uline	*Microdioscorea* Uline	New Word I	New Word I ("*Microdioscorea*")
Dioscorea gracillima Miq.	*Orientali-asiatiae* R.Knuth	*Stenophora* Uline	*Stenophora* Uline	*Stenophora* Uline
Dioscorea grandiflora Mart. ex Griseb.	*Centrostemon* Griseb.	—	New Word II	New Word II
Dioscorea hamiltonii Hook.f.	*Enantiophyllum* Uline	*Enantiophyllum* Uline	*Enantiophyllum* Uline	*Enantiophyllum* Uline
Dioscorea hassleriana Chodat	*Cryptantha* Uline	—	—	New Word I
Dioscorea hastifolia Nees	*Stenophyllidium* Uline	*Enantiophyllum* Uline	—	*Enantiophyllum* Uline
Dioscorea hemsleyi Prain & Burkill	Genus *Stenophora* (Uline) R.Knuth *Shannicorea* Prain & Burkill	—	—	*Shannicorea* Prain & Burkill
Dioscorea hexagona Baker	*Brachyandra* Uline	*Brachyandra* Uline	Malagasy	Malagasy
Dioscorea hispida Dennst.	*Lasiophyton* Uline	*Lasiophyton* Uline	Compound leaved (*Lasiophyton*)	Compound leaved (*Lasiophyton*)
Dioscorea humifusa Poepp.	*Microdioscorea* Uline	*Microdioscorea* Uline	New Word I	New Word I ("*Microdioscorea*")
Dioscorea humilis Bertero ex Colla subsp. *humilis*	—	*Epipetrum* (Phil.) Prain & Burkill*	New Word I ("*Epipetrum*")	New Word I ("*Epipetrum*")
Dioscorea humilis subsp. *polyanthes* (F.Phil.) Viruel, Segarra & Villar	—	*Epipetrum* (Phil.) Prain & Burkill*	New Word I ("*Epipetrum*")	New Word I ("*Epipetrum*")
Dioscorea hyalinomarginata Raz	—	—	"*Rajania*"	New World III (*Rajania*)
Dioscorea inopinata Prain & Burkill	—	*Opsphyton* Uline	*Enantiophyllum* Uline	*Enantiophyllum* Uline
Dioscorea itatiaiensis R.Knuth	*Disciferae* R.Knuth	—	—	New Word I
Dioscorea japonica Thunb.	*Enantiophyllum* Uline	*Enantiophyllum* Uline	*Enantiophyllum* Uline	*Enantiophyllum* Uline
Dioscorea juxtlahuacensis (O. Téllez & Dávila) Caddick & Wilkin	—	—	New Word I ("*Nanarepenta*")	New Word I ("*Nanarepenta*")

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Dioscorea kamoonensis Kunth	*Trieuphorostemon* Uline	*Lasiophyton* Uline	Compound leaved (*Botryosicyos*)	Compound leaved (*Botryosicyos*)
Dioscorea karatana Wilkin	—	*Campanuliflorae* Burkill & Perrier	Malagasy	Malagasy
Dioscorea kituiensis Wilkin & Muasya	—	—	Africa	Africa
Dioscorea lanata Bail	*Asterotricha* Uline	*Asterotricha* Uline	*Enantiophyllum* Uline	*Enantiophyllum* Uline
Dioscorea larecajensis Uline ex R.Knuth	*Centrostemon* Griseb.	—	New Word II	New Word II
Dioscorea laxiflora Mart. ex Griseb.	*Cryptantha* Uline	*Cryptantha* Uline	—	New Word I
Dioscorea lepcharum Prain & Burkill	*Enantiophyllum* Uline	—	—	*Enantiophyllum* Uline
Dioscorea leptostachya Gardner	*Periandrium* Uline	—	—	New Word I
Dioscorea longirhiza Caddick & Wilkin	—	—	New Word I ("*Nanarepenta*")	New Word I ("*Nanarepenta*")
Dioscorea maciba Jum. & H. Perrier	*Opsphyton* Uline (Subsection *Isocantha* (Uline) R.Knuth)	*Campanuliflorae* Burkill & Perrier	Malagasy	Malagasy
Dioscorea maianthemoides Uline ex R.Knuth	*Dematostemon* Griseb.	—	New Word II	New Word II
Dioscorea marginata Griseb.	*Apodostemon* Uline	—	—	New Word I
Dioscorea martini Prain & Burkill	Genus *Stenophora* (Uline) R.Knuth *Shannicorea* Prain & Burkill	—	—	*Shannicorea* Prain & Burkill
Dioscorea mayottensis Wilkin	—	—	Malagasy	Malagasy
Dioscorea mcvaughii B.G. Schub.	—	—	New Word I ("*Nanarepenta*")	New Word I ("*Nanarepenta*")
Dioscorea melanophyma Prain & Burkill	*Trieuphorostemon* Uline	*Lasiophyton* Uline	Compound leaved (*Botryosicyos*)	Compound leaved (*Botryosicyos*)
Dioscorea membranacea Pierre ex Prain & Burkill	Genus *Stenophora* (Uline) R.Knuth *Eustenophora* R.Knuth	*Stenophora* Uline	*Stenophora* Uline	*Stenophora* Uline
Dioscorea minima C. B. Rob. & Seaton	*Polyneuron* Uline	*Polyneuron* Uline	New Word I ("*Nanarepenta*")	New Word I
Dioscorea minutiflora Engl.	*Enantiophyllum* Uline	*Enantiophyllum* Uline	*Enantiophyllum* Uline	*Enantiophyllum* Uline
Dioscorea modesta Phill.	*Microdioscorea* Uline	—	New Word I	New Word I ("*Microdioscorea*")
Dioscorea mollis Kunth	*Chondrocarpa* Uline	—	—	*"Incertis sedis"*
Dioscorea monadelpha (Kunth) Griseb.	*Monadelpha* Uline	*Monadelpha* Uline	New Word II	New Word II

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				("*Monadelpha*")
Dioscorea multiflora Mart. ex Griseb.	*Sphaerantha* Uline	*Sphaerantha* Uline	—	New Word I
Dioscorea namorokensis Wilkin	—	—	Malagasy	Malagasy
Dioscorea nipponica Makino	Genus *Stenophora* (Uline) R.Knuth *Eustenophora* R.Knuth	*Stenophora* Uline	*Stenophora* Uline	*Stenophora* Uline
Dioscorea nipponica subsp. *rosthornii* (Diels) C. T. Ting	Genus *Stenophora* (Uline) R.Knuth *Eustenophora* R.Knuth	*Stenophora* Uline	*Stenophora* Uline	*Stenophora* Uline
Dioscorea nitens Prain & Burkill	Genus *Stenophora* (Uline) R.Knuth *Shannicorea* Prain & Burkill	*Shannicorea* Prain & Burkill	Birmanica	*Shannicorea* Prain & Burkill
Dioscorea nummularia Lam.	*Enantiophyllum* Uline	*Enantiophyllum* Uline	*Enantiophyllum* Uline	*Enantiophyllum* Uline
Dioscorea olfersiana Klotzsch ex Griseb.	*Cryptantha* Uline	—	—	New Word I
Dioscorea orientalis (J. Thiébaut) Caddick & Wilkin	—	—	Mediterranean ("*Tamus*")	Mediterranean ("*Tamus*")
Dioscorea oryzetorum Prain & Burkill	—	*Enantiophyllum* Uline	*Enantiophyllum* Uline	*Enantiophyllum* Uline
Dioscorea ovata Vell.	*Chondrocarpa* Uline	*Dematostemon* Griseb.	New Word II	New Word II
Dioscorea pedalis (R.Knuth) R. S. Couto & J.M.A. Braga	*Dematostemon* Griseb.	*Dematostemon* Griseb.	—	New Word II
Dioscorea pedicellata Phil.	*Parallelostemon* Uline	—	New Word I	New Word I
Dioscorea pentaphylla L.	*Trieuphorostemon* Uline	*Lasiophyton* Uline	Compound leaved (*Botryosicyos*)	Compound leaved (*Botryosicyos*)
Dioscorea perdicum Taubert	*Cycladenium* Uline	*Pedicellatae* Prain & Burkill	—	New Word I
Dioscorea petelotii Prain & Burkill	—	*Paramecocarpa* Prain & Burkill	Birmanica	Birmanica
Dioscorea piperifolia Humb. & Bonpl. ex Wild.	*Centrostemon* Griseb.	*Centrostemon* Griseb.	New Word II	New Word II
Dioscorea pohlii Griseb.	*Cryptantha* Uline	—	New Word I	New Word I
Dioscorea polystachya Turcz.	*Enantiophyllum* Uline	*Enantiophyllum* Uline	*Enantiophyllum* Uline	*Enantiophyllum* Uline
Dioscorea prazeri Prain & Burkill	*Macropoda* Uline	*Stenophora* Uline	*Stenophora* Uline	*Stenophora* Uline
Dioscorea preussii Pax	*Macrocarpaea* Uline	*Macrocarpaea* Uline	*Enantiophyllum* Uline	Birmanica
Dioscorea pseudomacrocapsa Barroso *et al.*	—	—	—	New Word I

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Dioscorea pyrenaica Bubani & Bordère ex Gren.	Genus *Borderea* Miégev.	*Borderea* Miégev. Prain & Burkill*	Mediterranean ("*Borderea*")	Mediterranean ("*Borderea*")
Dioscorea quinquelobata Thunb.	*Macropoda* Uline	*Stenophora* Uline	—	*Stenophora* Uline
Dioscorea rockii Prain & Burkill	—	*Stenophora* Uline	*Stenophora* Uline	*Stenophora* Uline
Dioscorea sansibarensis Pax	*Opsphyton* Uline (Subsection *Macrourae* R.Knuth)	*Macroura* Burkill	Malagasy	Malagasy
Dioscorea saxatilis Poepp.	*Microdioscorea* Uline	—	New Word I	New Word I ("*Microdioscorea*")
Dioscorea schimperiana Hochst. ex Kunth	*Asterotricha* Uline	*Asterotricha* Uline	*Enantiophyllum* Uline	*Enantiophyllum* Uline
Dioscorea scorpioidea C. Wright	Genus *Rajania* L.	Genus *Rajania* L.	"*Rajania*"	New World III (*Rajania*)
Dioscorea scortechinii Prain & Burkill	*Trieuphorostemon* Uline	*Lasiophyton* Uline	Compound leaved (*Botryosicyos*)	Compound leaved (*Botryosicyos*)
Dioscorea seriflora Jum. & H. Perrier	*Opsphyton* Uline (Subsection *Isocantha* (Uline) R.Knuth)	*Seriflorae* Burkill & Perrier	—	Malagasy
Dioscorea simulans Prain & Burkill	—	*Illigerastrum* Prain & Burkill	*Stenophora* Uline	*Stenophora* Uline
Dioscorea sinoparviflora C. T. Ting, M. G. Gilbert & Turland	—	—	*Stenophora* Uline	*Stenophora* Uline
Dioscorea sinuata Vell.	*Brachystigma* Uline	*Brachystigma* Uline	—	New Word I
Dioscorea soso Jum. & H. Perrier	*Brachyandra* Uline	*Brachyandra* Uline	Malagasy	Malagasy
Dioscorea sp.	—	—	—	New Word I
Dioscorea sphaeroidae R. S. Couto & J.M.A. Braga	—	—	—	New Word I
Dioscorea spongiosa J.Q. Xi, M. Mizuno & W.L. Zhao	—	—	*Stenophora* Uline	*Stenophora* Uline
Dioscorea stegelmanniana R.Knuth	*Macrogynodium* Uline	—	—	New World III
Dioscorea strydomiana Wilkin	—	—	Africa ("*Testudinaria*")	Africa ("*Testudinaria*")
Dioscorea subcalva Prain & Burkill	Genus *Stenophora* (Uline) R.Knuth *Shannicorea* Prain & Burkill	—	Birmanica	*Shannicorea* Prain & Burkill
Dioscorea subhastata Vell.	*Monadelpha* Uline	*Monadelpha* Uline	New Word II	New Word II ("*Monadelpha*")

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Dioscorea sylvatica Eckl.	—	*Testudinaria* (Salisb.) Prain & Burkill	Africa ("*Testudinaria*")	Africa ("*Testudinaria*")
Dioscorea tentaculigera Prain & Burkill	*Macropoda* Uline	—	*"Incertis sedis"*	*"Incertis sedis"*
Dioscorea therezopolensis Uline ex R.Knuth	*Triapodandra* Uline	—	—	New Word I
Dioscorea tokoro Makino ex Miyabe	Genus *Stenophora* (Uline) R.Knuth *Eustenophora* R.Knuth	*Stenophora* Uline	*Stenophora* Uline	*Stenophora* Uline
Dioscorea tomentosa J. König ex Spreng.	*Trieuphorostemon* Uline	—	Compound leaved (*Botryosicyos*)	Compound leaved (*Botryosicyos*)
Dioscorea trichantha Baker	*Opsphyton* Uline (Subsection *Isocantha* (Uline) R.Knuth)	*Brachyandra* Uline	Malagasy	Malagasy
Dioscorea trisecta Griseb.	*Apodostemon* Uline	—	—	New Word I
Dioscorea wallichii Hook.f.	*Enantiophyllum* Uline	—	*Enantiophyllum* Uline	*Enantiophyllum* Uline
Dioscorea variifolia Betero	*Microdioscorea* Uline	—	New Word I	New Word I ("*Microdioscorea*")
Dioscorea velutipes Prain & Burkill	Genus *Stenophora* (Uline) R.Knuth *Shannicorea* Prain & Burkill	—	—	*Shannicorea* Prain & Burkill
Dioscorea widgrenii R.Knuth	*Cryptantha* Uline	—	—	New Word I
Dioscorea yunnanensis Prain & Burkill	Genus *Stenophora* (Uline) R.Knuth *Shannicorea* Prain & Burkill	—	—	*Shannicorea* Prain & Burkill
Dioscorea zingiberensis C.H. Wright	*Macropoda* Uline	—	*Stenophora* Uline	*Stenophora* Uline

Knuth R. 1924. Dioscoreaceae. In: Engler A, ed. *Das Pflanzenreich*. Leipzig: Wilhelm Engelmann, 1–386; Burkill IH. 1960. The organography and the evolution of the Dioscoreaceae, the family of the yams. *Botanical Journal of the Linnean So* 56: 319–412; Viruel J, Segarra-Moragues JG, Raz L, Forest F, Wilkin P, Sanmartín I, Catalán P. 2016. Late Cretaceous-Early Eocene origin of yams (*Dioscorea*, Dioscoreaceae) in the Laurasian Palaearctic and their subsequent Oligocene-Miocene diversification. *Journal of Biogeography* 43: 750–762.

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Table S5. Species and their operational areas assigned in the biogeographic analysis.

Species	Operational Areas
Dioscorea amaranthoides Presl.	D+E
Dioscorea amazonum Griseb.	D+E
Dioscorea acanthogene Rusby	D+E
Dioscorea aristolochiifolia Poepp.	C
Dioscorea asperula Pedralli	E
Dioscorea besseriana Kunth	C
Dioscorea biloba (Phil.) Caddick & Wilkin subsp. *biloba*	C
Dioscorea biloba subsp. *coquimbana* Viruel, Segarra-Moragues & Villar	C
Dioscorea brachybotrya Poepp.	C
Dioscorea bradei R.Knuth	F
Dioscorea monandra Hauman	F
Dioscorea campestris Griseb.	E+F
Dioscorea campos-portoi R.Knuth	E+F
Dioscorea composita Hemsl.	A
Dioscorea convovulaceae Schltdl. & Cham.	A
Dioscorea coriacea Humb. & Bonpl. ex Willd.	B
Dioscorea coronata Hauman	F
Dioscorea cynanchiolia Griseb.	F
Dioscorea delicata R.Knuth	F
Dioscorea fastigiata Gay	C
Dioscorea galeottiana Kunth	A
Dioscorea glomerulata Hauman	C+F
Dioscorea gracilis Hook. ex Poepp.	C
Dioscorea grandiflora Mart. ex Griseb.	E+F
Dioscorea hassleriana Chodat	E+F

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Dioscorea humifusa Poepp.	C
Dioscorea humilis Bertero ex Colla subsp. *humilis*	C
Dioscorea humilis subsp. *polyanthes* (F.Phil.) Viruel, Segarra & Villar	C
Dioscorea sp.	F
Dioscorea itatiaiensis R.Knuth	F
Dioscorea juxtlahuacensis (O. Téllez & Dávila) Caddick & Wilkin	A
Dioscorea larecajensis Uline ex R.Knuth	B
Dioscorea laxiflora Mart. ex Griseb.	D+E+F
Dioscorea leptostachya Gardner	E+F
Dioscorea longirhiza Caddick & Wilkin	A
Dioscorea maianthemoides Uline ex R.Knuth	E
Dioscorea marginata Griseb.	D+E+F
Dioscorea mcvaughii B.G. Schub.	A
Dioscorea minima C. B. Rob. & Seaton	A
Dioscorea modesta Phill.	C
Dioscorea monadelpha (Kunth) Griseb.	B+F
Dioscorea multiflora Mart. ex Griseb.	D+E+F
Dioscorea olfersiana Klotzsch ex Griseb.	F
Dioscorea ovata Vell.	F
Dioscorea pedalis (R.Knuth) R. S. Couto & J.M.A. Braga	F
Dioscorea pedicellata Phil.	C
Dioscorea perdicum Taubert	F
Dioscorea piperifolia Humb. & Bonpl. ex Wild.	D+E+F
Dioscorea pohlii Griseb.	D+E
Dioscorea pseudomacrocapsa Barroso *et al.*	F
Dioscorea saxatilis Poepp.	C
Dioscorea cienegensis R.Knuth	F
Dioscorea sinuata Vell.	F

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Dioscorea sphaeroidae R. S. Couto & J.M.A. Braga	F
Dioscorea subhastata Vell.	F
Dioscorea therezopolensis Uline ex R.Knuth	F
Dioscorea trisecta Griseb.	E+F
Dioscorea variifolia Betero	C
Dioscorea widgrenii R.Knuth	F

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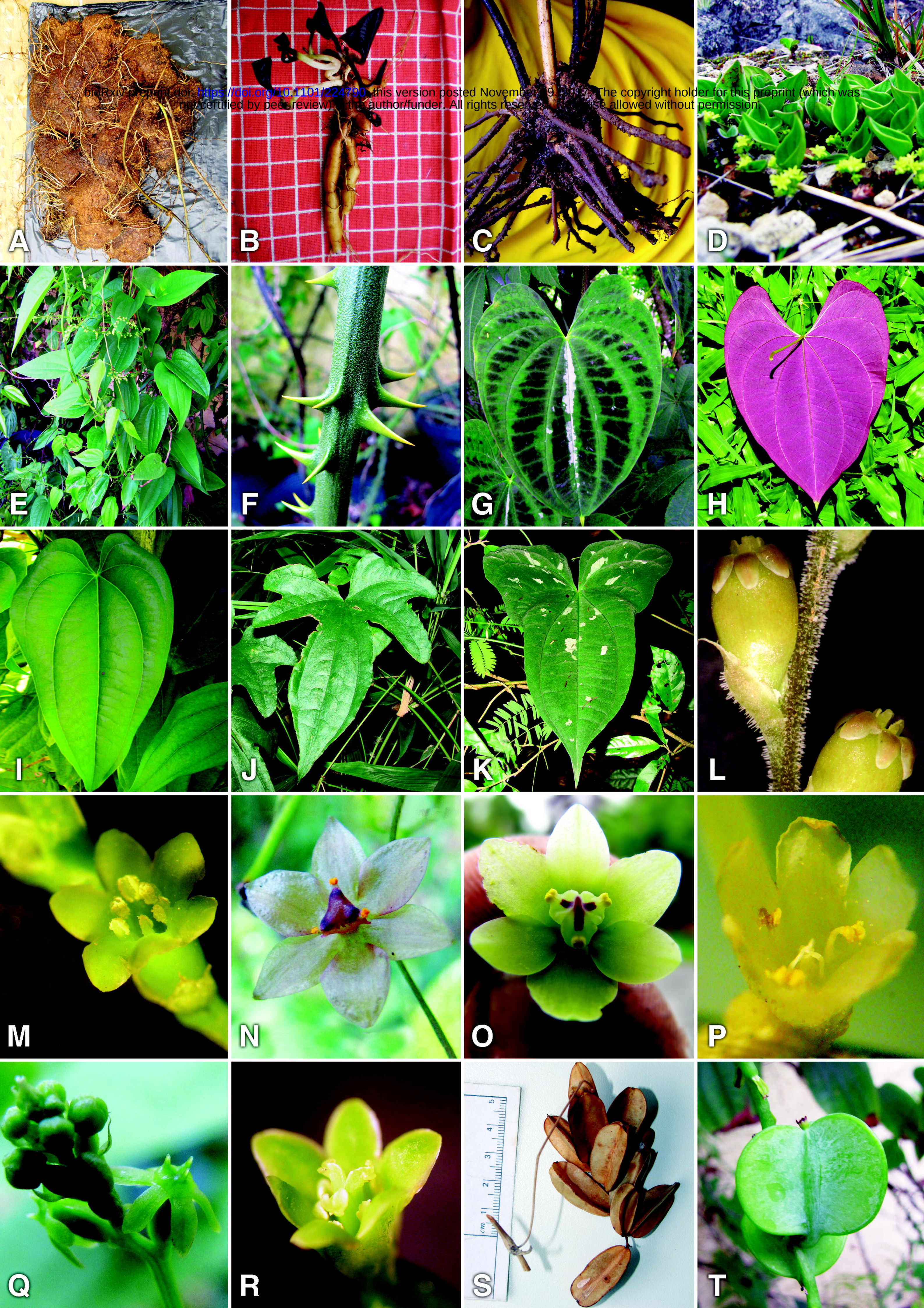
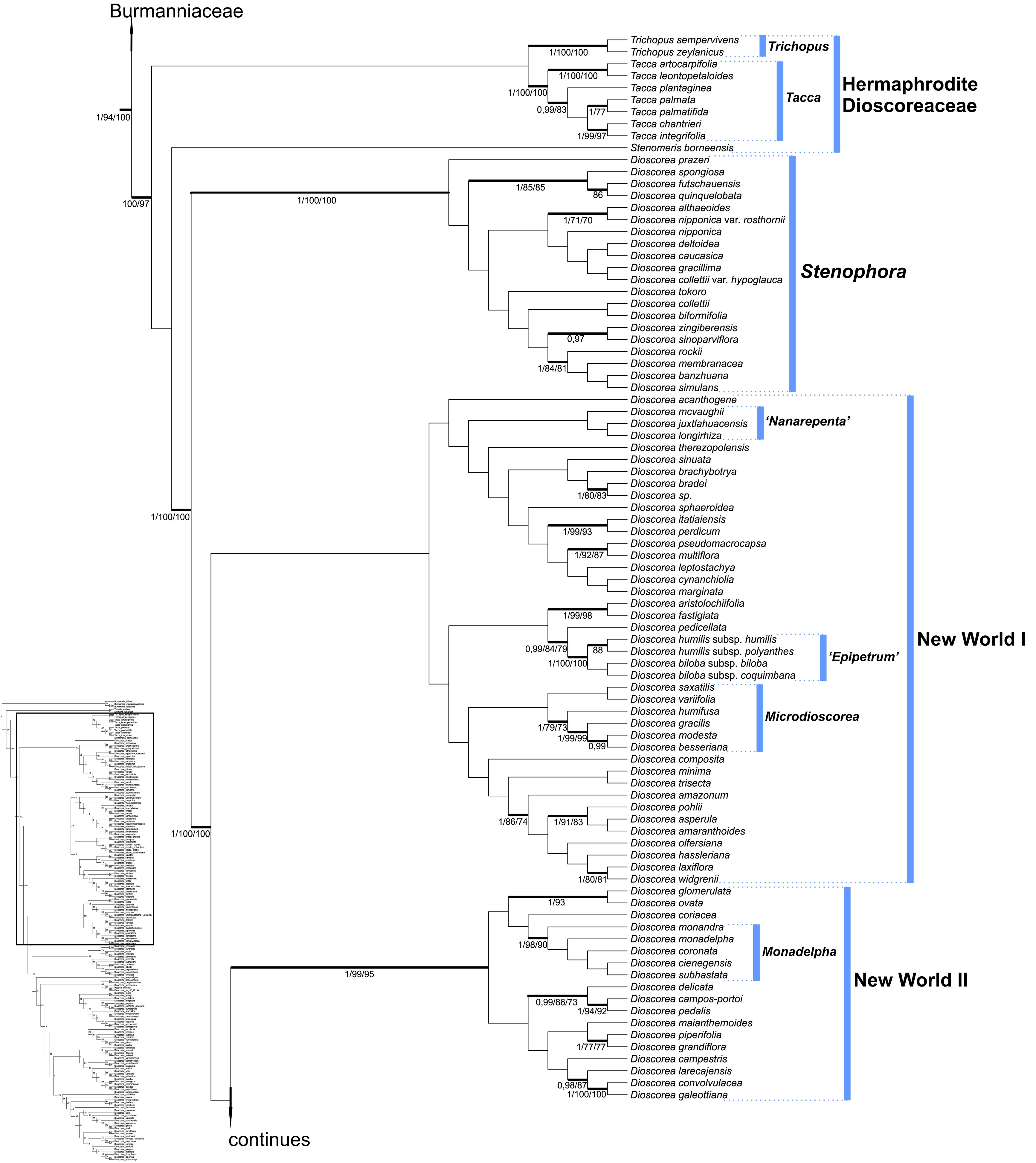
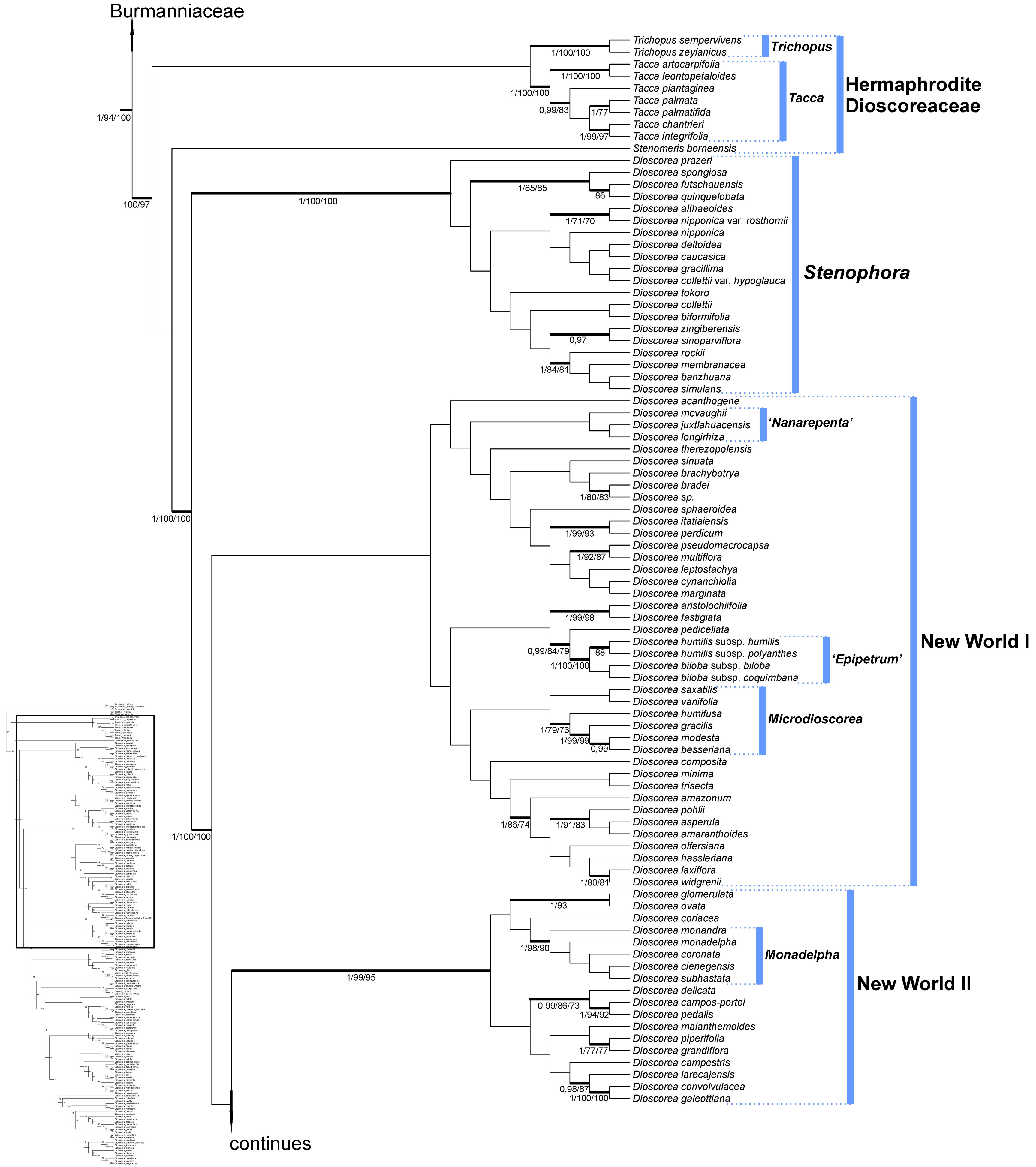



Burmanniaceae
1/94/100
100/97
Trichopus sempervivens
Trichopus zeylanicus
1/100/100
Trichopus
Tacca artocarpifolia
Tacca leontopetaloides
1/100/100
1/100/100
Tacca plantaginea
Tacca palmata
Tacca palmatifida
0,99/83
1/77
Tacca chantrieri
Tacca integrifolia
1/99/97
Tacca
Hermaphrodite Dioscoreaceae
Stenomeris borneensis
Dioscorea prazeri
Dioscorea spongiosa
Dioscorea futschauensis
Dioscorea quinquelobata
1/85/85
86
1/100/100
Dioscorea althaeoides
Dioscorea nipponica var. rosthornii
1/71/70
Dioscorea nipponica
Dioscorea deltoidea
Dioscorea caucasica
Dioscorea gracillima
Dioscorea collettii var. hypoglauca
Stenophora
Dioscorea tokoro
Dioscorea collettii
Dioscorea biformifolia
Dioscorea zingiberensis
Dioscorea sinoparviflora
0,97
Dioscorea rockii
Dioscorea membranacea
1/84/81
Dioscorea banzhuana
Dioscorea simulans
Dioscorea acanthogene
Dioscorea mcvaughii
Dioscorea juxtlahuacensis
Dioscorea longirhiza
'Nanarepenta'
Dioscorea therezopolensis
Dioscorea sinuata
Dioscorea brachybotrya
Dioscorea bradei
Dioscorea sp.
1/80/83
Dioscorea sphaeroidea
Dioscorea itatiaiensis
Dioscorea perdicum
1/99/93
1/100/100
Dioscorea pseudomacrocapsa
Dioscorea multiflora
1/92/87
Dioscorea leptostachya
Dioscorea cynanchiolia
Dioscorea marginata
Dioscorea aristolochiifolia
Dioscorea fastigiata
1/99/98
Dioscorea pedicellata
Dioscorea humilis subsp. humilis
Dioscorea humilis subsp. polyanthes
0,99/84/79
88
1/100/100
Dioscorea biloba subsp. biloba
Dioscorea biloba subsp. coquimbana
'Epipetrum'
New World I
Dioscorea saxatilis
Dioscorea variifolia
Dioscorea humifusa
Dioscorea gracilis
1/79/73
Dioscorea modesta
1/99/99
Dioscorea besseriana
0,99
Microdioscorea
Dioscorea composita
Dioscorea minima
Dioscorea trisecta
Dioscorea amazonum
Dioscorea pohlii
1/86/74
1/91/83
1/100/100
Dioscorea asperula
Dioscorea amaranthoides
Dioscorea olfersiana
Dioscorea hassleriana
Dioscorea laxiflora
Dioscorea widgrenii
1/80/81
Dioscorea glomerulata
Dioscorea ovata
1/93
Dioscorea coriacea
Dioscorea monandra
Dioscorea monadelpha
1/98/90
Dioscorea coronata
Monadelpha
Dioscorea cienegensis
1/99/95
Dioscorea subhastata
New World II
Dioscorea delicata
Dioscorea campos-portoi
0,99/86/73
Dioscorea pedalis
1/94/92
Dioscorea maianthemoides
Dioscorea piperifolia
Dioscorea grandiflora
1/77/77
Dioscorea campestris
Dioscorea larecajensis
Dioscorea convolvulacea
0,98/87
Dioscorea galeottiana
1/100/100
continues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Trichopus zeylanicus
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Trichopus
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Tacca leontopetaloides
1/100/100
1/100/100
Tacca plantaginea
Tacca palmata
Tacca palmatifida
0,99/83
1/77
Tacca chantrieri
Tacca integrifolia
1/99/97
Tacca
Hermaphrodite Dioscoreaceae
Stenomeris borneensis
Dioscorea prazeri
Dioscorea spongiosa
Dioscorea futschauensis
Dioscorea quinquelobata
1/85/85
86
1/100/100
Dioscorea althaeoides
Dioscorea nipponica var. rosthornii
1/71/70
Dioscorea nipponica
Dioscorea deltoidea
Dioscorea caucasica
Dioscorea gracillima
Dioscorea collettii var. hypoglauca
Stenophora
Dioscorea tokoro
Dioscorea collettii
Dioscorea biformifolia
Dioscorea zingiberensis
Dioscorea sinoparviflora
0,97
Dioscorea rockii
Dioscorea membranacea
1/84/81
Dioscorea banzhuana
Dioscorea simulans
1/100/100
Dioscorea acanthogene
Dioscorea mcvaughii
Dioscorea juxtlahuacensis
Dioscorea longirhiza
'Nanarepenta'
Dioscorea therezopolensis
Dioscorea sinuata
Dioscorea brachybotrya
Dioscorea bradei
Dioscorea sp.
1/80/83
Dioscorea sphaeroidea
Dioscorea itatiaiensis
Dioscorea perdicum
1/99/93
Dioscorea pseudomacrocapsa
Dioscorea multiflora
1/92/87
Dioscorea leptostachya
Dioscorea cynanchiolia
Dioscorea marginata
Dioscorea aristolochiifolia
Dioscorea fastigiata
1/99/98
Dioscorea pedicellata
Dioscorea humilis subsp. humilis
Dioscorea humilis subsp. polyanthes
0,99/84/79
88
1/100/100
Dioscorea biloba subsp. biloba
Dioscorea biloba subsp. coquimbana
'Epipetrum'
New World I
Dioscorea saxatilis
Dioscorea variifolia
Dioscorea humifusa
1/79/73
Dioscorea gracilis
Dioscorea modesta
1/99/99
0,99
Dioscorea besseriana
Microdioscorea
Dioscorea composita
Dioscorea minima
Dioscorea trisecta
Dioscorea amazonum
Dioscorea pohlii
1/86/74
1/91/83
Dioscorea asperula
Dioscorea amaranthoides
Dioscorea olfersiana
Dioscorea hassleriana
Dioscorea laxiflora
1/80/81
Dioscorea widgrenii
1/100/100
Dioscorea glomerulata
Dioscorea ovata
1/93
Dioscorea coriacea
Dioscorea monandra
1/98/90
Dioscorea monadelpha
Dioscorea coronata
Dioscorea cienegensis
Dioscorea subhastata
Monadelpha
1/99/95
New World II
Dioscorea delicata
Dioscorea campos-portoi
0,99/86/73
1/94/92
Dioscorea pedalis
Dioscorea maianthemoides
Dioscorea piperifolia
1/77/77
Dioscorea grandiflora
Dioscorea campestris
Dioscorea larecajensis
0,98/87
Dioscorea convolvulacea
1/100/100
Dioscorea galeottiana
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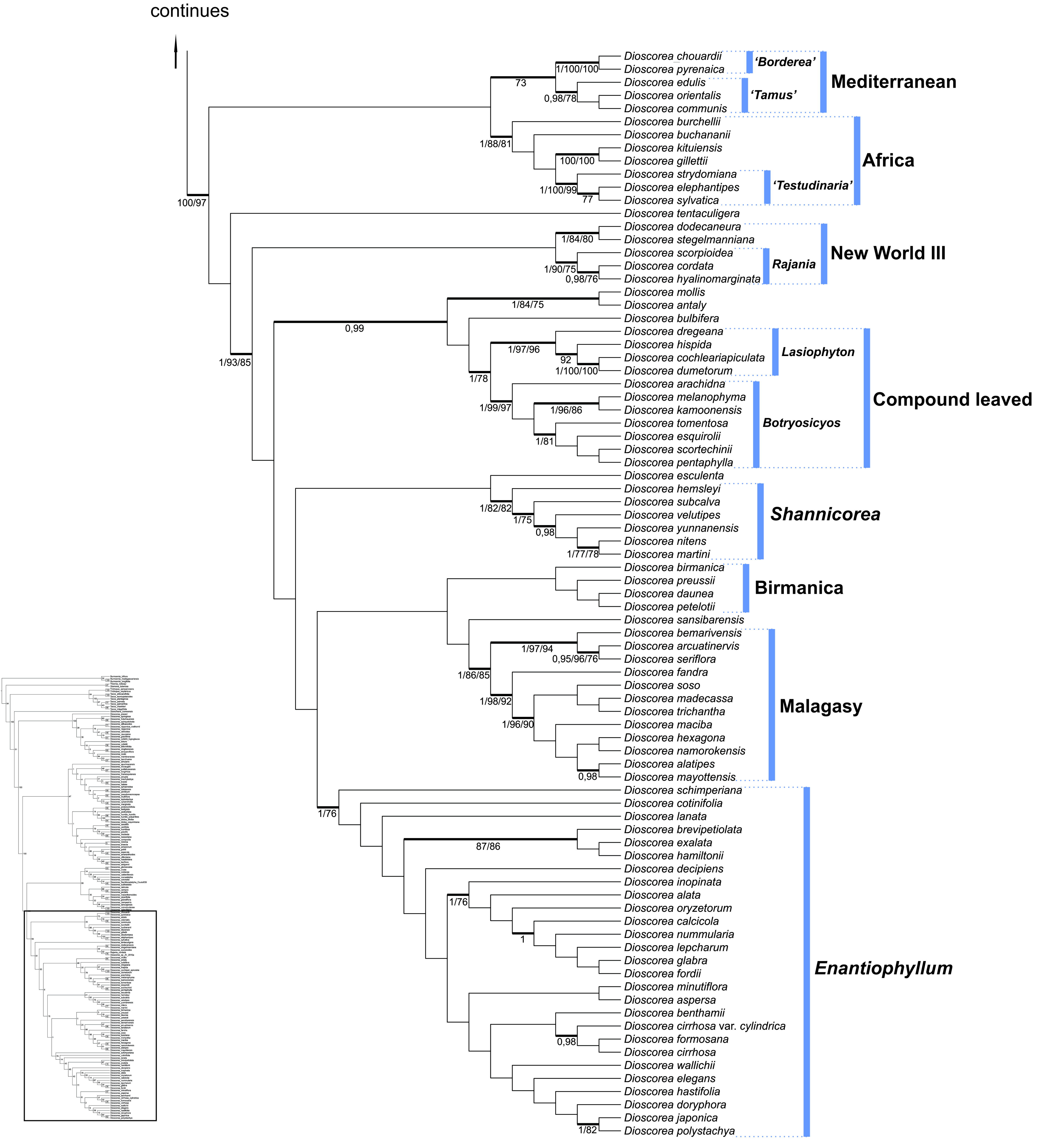
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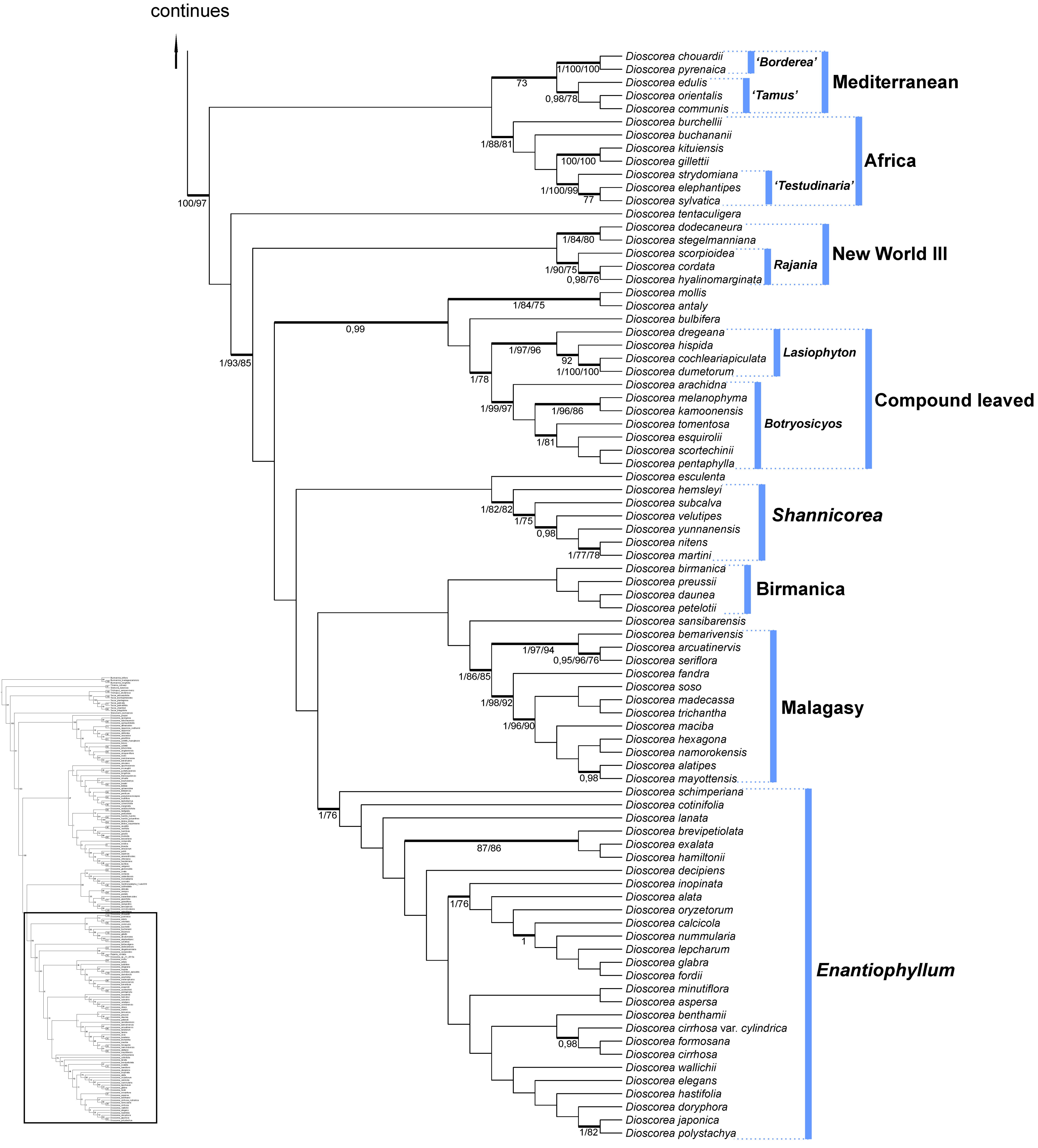
Dioscorea chouardii
Dioscorea pyrenaica
Dioscorea edulis
Dioscorea orientalis
Dioscorea communis
'Borderea'
'Tamus'
Mediterranean
1/100/100
73
0,98/78
Dioscorea burchellii
Dioscorea buchananii
Dioscorea kituiensis
Dioscorea gillettii
Dioscorea strydomiana
Dioscorea elephantipes
Dioscorea sylvatica
Africa
'Testudinaria'
1/88/81
100/100
1/100/99
77
100/97
Dioscorea tentaculigera
Dioscorea dodecaneura
Dioscorea stegelmanniana
Dioscorea scorpioidea
Dioscorea cordata
Dioscorea hyalinomarginata
New World III
Rajania
1/84/80
1/90/75
0,98/76
Dioscorea mollis
Dioscorea antaly
Dioscorea bulbifera
Dioscorea dregeana
Dioscorea hispida
Dioscorea cochleariapiculata
Dioscorea dumetorum
Dioscorea arachidna
Dioscorea melanophyma
Dioscorea kamoonensis
Dioscorea tomentosa
Dioscorea esquirolii
Dioscorea scortechinii
Dioscorea pentaphylla
Lasiophyton
Botryosicyos
Compound leaved
1/84/75
0,99
1/93/85
1/97/96
92
1/100/100
1/78
1/99/97
1/96/86
1/81
Dioscorea esculenta
Dioscorea hemsleyi
Dioscorea subcalva
Dioscorea velutipes
Dioscorea yunnanensis
Dioscorea nitens
Dioscorea martini
Shannicorea
1/82/82
1/75
0,98
1/77/78
Dioscorea birmanica
Dioscorea preussii
Dioscorea daunea
Dioscorea petelotii
Birmanica
Dioscorea sansibarensis
Dioscorea bemarivensis
Dioscorea arcuatinervis
Dioscorea seriflora
Dioscorea fandra
Dioscorea soso
Dioscorea madecassa
Dioscorea trichantha
Dioscorea maciba
Dioscorea hexagona
Dioscorea namorokensis
Dioscorea alatipes
Dioscorea mayottensis
Malagasy
1/97/94
0,95/96/76
1/86/85
1/98/92
1/96/90
0,98
Dioscorea schimperiana
Dioscorea cotinifolia
Dioscorea lanata
Dioscorea brevipetiolata
Dioscorea exalata
Dioscorea hamiltonii
Dioscorea decipiens
Dioscorea inopinata
Dioscorea alata
Dioscorea oryzetorum
Dioscorea calcicola
Dioscorea nummularia
Dioscorea lepcharum
Dioscorea glabra
Dioscorea fordii
Dioscorea minutiflora
Dioscorea aspersa
Dioscorea benthamii
Dioscorea cirrhosa var. cylindrica
Dioscorea formosana
Dioscorea cirrhosa
Dioscorea wallichii
Dioscorea elegans
Dioscorea hastifolia
Dioscorea doryphora
Dioscorea japonica
Dioscorea polystachya
Enantiophyllum
1/76
87/86
1/76
1
0,98
1/82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Dioscorea chouardii
Dioscorea pyrenaica
'Borderea'
Dioscorea edulis
Dioscorea orientalis
Dioscorea communis
'Tamus'
Mediterranean
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Dioscorea burchellii
Dioscorea buchananii
Dioscorea kituiensis
Dioscorea gillettii
Dioscorea strydomiana
Dioscorea elephantipes
Dioscorea sylvatica
'Testudinaria'
Africa
Dioscorea tentaculigera
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Dioscorea dodecaneura
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Dioscorea scorpioidea
Dioscorea cordata
Dioscorea hyalinomarginata
Rajania
New World III
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1/84/75
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Dioscorea antaly
Dioscorea bulbifera
1/78
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92
1/100/100
Dioscorea dregeana
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Dioscorea cochleariapiculata
Dioscorea dumetorum
Lasiophyton
1/99/97
1/96/86
1/81
Dioscorea arachidna
Dioscorea melanophyma
Dioscorea kamoonensis
Dioscorea tomentosa
Dioscorea esquirolii
Dioscorea scortechinii
Dioscorea pentaphylla
Botryosicyos
Compound leaved
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0,98
1/77/78
Dioscorea esculenta
Dioscorea hemsleyi
Dioscorea subcalva
Dioscorea velutipes
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Dioscorea nitens
Dioscorea martini
Shannicorea
Dioscorea birmanica
Dioscorea preussii
Dioscorea daunea
Dioscorea petelotii
Birmanica
Dioscorea sansibarensis
1/86/85
1/97/94
0,95/96/76
1/98/92
1/96/90
0,98
Dioscorea bemarivensis
Dioscorea arcuatinervis
Dioscorea seriflora
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Dioscorea soso
Dioscorea madecassa
Dioscorea trichantha
Dioscorea maciba
Dioscorea hexagona
Dioscorea namorokensis
Dioscorea alatipes
Dioscorea mayottensis
Malagasy
1/76
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1/82
Dioscorea schimperiana
Dioscorea cotinifolia
Dioscorea lanata
Dioscorea brevipetiolata
Dioscorea exalata
Dioscorea hamiltonii
Dioscorea decipiens
Dioscorea inopinata
Dioscorea alata
Dioscorea oryzetorum
Dioscorea calcicola
Dioscorea nummularia
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Dioscorea glabra
Dioscorea fordii
Dioscorea minutiflora
Dioscorea aspersa
Dioscorea benthamii
Dioscorea cirrhosa var. cylindrica
Dioscorea formosana
Dioscorea cirrhosa
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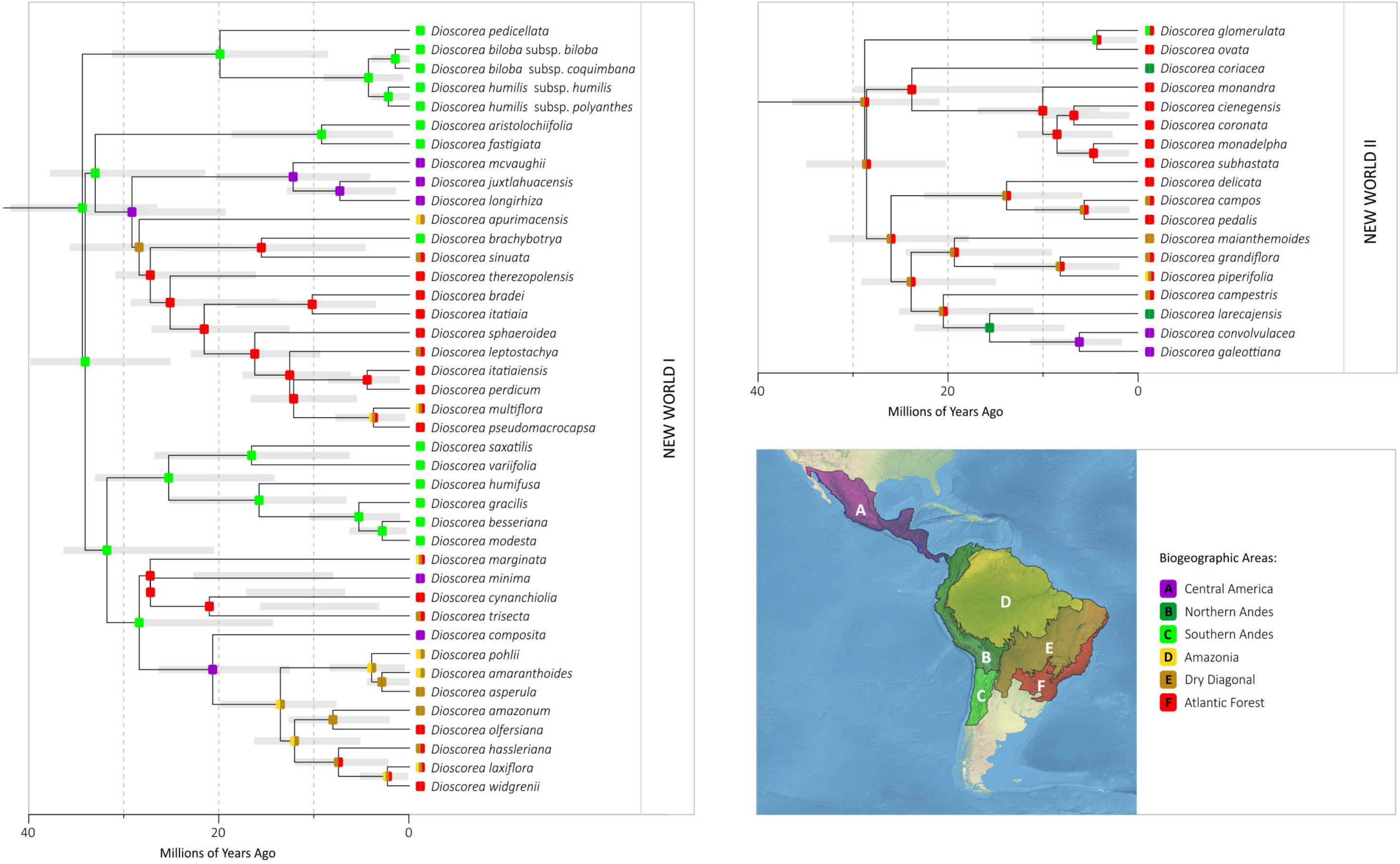
Dioscorea elegans
Dioscorea hastifolia
Dioscorea doryphora
Dioscorea japonica
Dioscorea polystachya
Enantiophyllum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Dioscorea biloba subsp. coquimbana
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Dioscorea aristolochiifolia
Dioscorea fastigiata
Dioscorea mcvaughii
Dioscorea juxtlahuacensis
Dioscorea longirhiza
Dioscorea apurimacensis
Dioscorea brachybotrya
Dioscorea sinuata
Dioscorea therezopolensis
Dioscorea bradei
Dioscorea itatiaia
Dioscorea sphaeroidea
Dioscorea leptostachya
Dioscorea itatiaiensis
Dioscorea perdicum
Dioscorea multiflora
Dioscorea pseudomacrocapsa
Dioscorea saxatilis
Dioscorea variifolia
Dioscorea humifusa
Dioscorea gracilis
Dioscorea besseriana
Dioscorea modesta
Dioscorea marginata
Dioscorea minima
Dioscorea cynanchiolia
Dioscorea trisecta
Dioscorea composita
Dioscorea pohlii
Dioscorea amaranthoides
Dioscorea asperula
Dioscorea amazonum
Dioscorea olfersiana
Dioscorea hassleriana
Dioscorea laxiflora
Dioscorea widgrenii
NEW WORLD I
40
20
0
Millions of Years Ago
Dioscorea glomerulata
Dioscorea ovata
Dioscorea coriacea
Dioscorea monandra
Dioscorea cienegensis
Dioscorea coronata
Dioscorea monadelpha
Dioscorea subhastata
Dioscorea delicata
Dioscorea campos
Dioscorea pedalis
Dioscorea maianthemoides
Dioscorea grandiflora
Dioscorea piperifolia
Dioscorea campestris
Dioscorea larecajensis
Dioscorea convolvulacea
Dioscorea galeottiana
NEW WORLD II
40
20
0
Millions of Years Ago
A
B
C
D
E
F
Biogeographic Areas:
A Central America
B Northern Andes
C Southern Andes
D Amazonia
E Dry Diagonal
F Atlantic Forest