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

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Running head: Origins of yams in the Neotropics

28 ABSTRACT

29

30 The yam genus *Dioscorea* comprises circa 650 species of tropical vines with starch rich tubers,
 31 usefull as an energy source and often containing secondary metabolites. The Neotropical Region
 32 holds the highest diversity of species and morphology of yams. We generated a time-calibrated
 33 tree for *Dioscorea* using, for the first time, a dense sampling of Neotropical species (64 sp.,
 34 20% of all Neotropical sp. and 22 sections) to trace the biogeography of these plants in this
 35 region. Four origins of *Dioscorea* in the neotropics were estimated since the Eocene. The two
 36 most diverse lineages originated between the Eocene and Oligocene, respectively in the
 37 Southern Andes and eastern South America. Both lineages occupied the South American ‘Dry
 38 Diagonal’ after the Miocene, but New World II clade remained associated with forest habitats.
 39 Several exchanges between Dry Diagonal and adjacent forested biomes occurred, corroborating
 40 the interchange between these vegetation types. Dispersals to Central America occurred before
 41 the closure of the Panama Isthmus. We highlight two important events of long distance
 42 dispersal, the colonization of Central American before the closure of Isthmus of Panama and the
 43 dispersal of *D. antaly* lineage to Madagascar. In addition, our phylogenetic tree evidenced the
 44 unnatural nature of the classical infrageneric classification of *Dioscorea*. The taxonomic
 45 implications of our results are also discussed.

46

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

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53 INTRODUCTION

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

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

79 especially diverse in the Neotropics, where about 50% of the species occur (e-Monocot team,
80 2017).

81 According to Viruel *et al.* (2016) in its study with 135 taxa and four plastid DNA
82 markers, *Dioscorea* originated in the Laurasian Palearctic region between the late Cretaceous
83 (57.7 – 85.9 mya) and the Mid Eocene (47.6 – 49.1 mya), with subsequent radiations to the
84 Southern regions by long-distance dispersal or migration by land bridges in the Oligocene-
85 Miocene (33.9 to 5.332 Mya) (Viruel *et al.*, 2016). They occur in several Neotropical
86 environments, from dry *restinga* at sea level to the Andean paramos, including edges and
87 interior of humid forests, natural grassland ecosystems, rupicolous areas, and even semi-desertic
88 environments (Dorr & Stergios, 2003; Couto *et al.*, 2014). As a consequence of the great variety
89 of environmental conditions in which they occur, *Dioscorea* species exhibit a wide range of
90 ecological responses, evidenced by the large morphological variability found in the family, both
91 in vegetative and reproductive organs. They range from large climbing vines (40m high) to
92 dwarf species, monoecious or dioecious plants, and they can present impressively colored
93 leaves and flowers, among other distinctive characters (Fig. 1).

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

106 *al.* (2016) obtained some clades not found in previous analyses: *Dioscorea* section *Rajania* (L.)
 107 Raz, a group of species endemic to the Caribbean islands (Raz, 2016), the clade *Epipetrum*,
 108 proposed by Philippi (1864) as genus for dwarf-sized species endemic to Chile (Viruel *et al.*,
 109 2010), and the clade *Nanarepenta*, for non-winged seeds species exclusive to Mexico, also
 110 previously proposed as a separate genus (Téllez-Valdés & Dávila-Aranda, 1998). Those clades
 111 fund by (Viruel *et al.*, 2016) were sampled by previus studies (Caddick *et al.*, 2002a,b; Wilkin
 112 *et al.*, 2005)(), but (Viruel *et al.*, 2016)presented a expanded the number of species and more a
 113 robustly supported results.

114 Full understanding of relationships among species of *Dioscorea* and a natural
 115 infrageneric classification will only be possible with strongly supported phylogenetic studies.
 116 However, the phylogenetic results to date do not allow a new formal and complete
 117 classification, especially for the Neotropical region, which is still poorly sampled in most recent
 118 published works (five neotropical taxa in Caddick *et al.*, 2002a); three in Caddick *et al.*, 2002b;
 119 43 in Viruel *et al.*, 2016). It should also be noted that the genera mentioned above — which are
 120 now known to be part of *Dioscorea* — still require a change of status regarding their positioning
 121 in an infrageneric taxonomic category within *Dioscorea*, with exception of *Rajania* that has
 122 been reduced to a section by Raz (2016).

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

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

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

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

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

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

175 Total genomic DNA was extracted from leaf samples, fresh or silica-dried following the
 176 2x CTAB protocol (Doyle & Doyle, 1987), without the addition of RNase A and scaled to 2 ml
 177 tubes. The extracted DNA was measured in 1% agarose gel with a DNA mass ladder and
 178 deposited at the DNA collection of Laboratory of Systematics and Molecular Ecology of Plants,
 179 Federal University of Paraná (UFPR), Brazil, associated to the reference vouchers deposited in
 180 K, R, RB, RFA and UPCB (Herbarium acronyms follow *Index Herbariorum* (Thiers,
 181 continuously updated)). The plastid genome regions *matK* and *rbcL* were amplified and
 182 sequenced using the following primer pairs, respectively: 3F_KIM-f (cgtacagtactttgtgtttacgag)
 183 and 1R_KIM-r (accagtcctcttggaatcttggttc) (Ki-Joong Kim, pers. com.), *rbcLa_f*
 184 (atgtcaccacaaacagactaaagc) (Levin *et al.*, 2003) and *rbcLa_r* (gtaaaatcaagtccaccaccrcg) (Kress
 185 & Erickson, 2007). Additionally, the primers ITS92 and ITS75 or ITS18F and ITS26R, which is
 186 widely used in angiosperms (Bolton *et al.*, 2015), was used to amplify the nuclear ITS region,

187 however without success in sequencing. This negative result and the scarcity of ITS sequences
188 for *Dioscorea* in GenBank lead us to use only plastidial genome markers. PCR amplifications
189 were performed using initial 94°C pre-melt for 1 min followed by 40 cycles of (i) 94°C
190 denaturation for 30s, (ii) 53°C annealing for 40s, and (iii) 72°C extension for 40s, followed by
191 72°C a final extension for 5 min. Following PCR, the samples were purified with 20% PEG and
192 sequenced with Big Dye Terminator version 3.1 (Applied Biosystems, California, USA) by the
193 company Macrogen Inc. (South Korea). Forward and reverse sequences were assembled using
194 the Staden package v.2.0.0b11 (Staden, Judge, & Bonfield, 2003). Sequences were aligned with
195 Clustal W using default parameters (Thompson *et al.*, 1997) implemented in the software
196 MEGA6 (Tamura *et al.*, 2013).

197

198 GEOGRAPHICAL AND MORPHOLOGICAL DATA

199

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

211

212 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 *rbcL* and *matK* 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 (*matK*) and K2+G (*rbcL*). 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.

231

232 MOLECULAR DATING

233

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

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 Oligocene of 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 wilkinii* (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

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

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

293

294 RESULTS

295

296 PHYLOGENETIC ANALYSIS

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

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

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

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

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

327

DIVERGENCE TIMES AND BIOGEOGRAPHY

329

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

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

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

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

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

365

366 **DISCUSSION**

367

368 PHYLOGENETIC ANALYSIS AND CLASSIFICATION OF *DIOSCOREA* AND POSITION OF 369 NEOTROPICAL CLADES

370

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

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

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

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

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

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

418 Whithin the species of NWI clade is possible to highlight *D. perdicum* Taub., one of
 419 the dwarf species endemic from Brazil that does not fit any specific infrageneric classification
 420 devotaded to this issue. *Dioscorea perdicum* is mistakenly placed by Knuth (1924) into the
 421 section *Cycladenium* Uline (*D.* subg. *Helmia*), as the autor didn't know the species fruits or
 422 seeds, that place *D. perdicum* in *D.* subg. *Dioscorea* by its all-round winged seeds. Burkill
 423 (1960) pointed out the mistake made in the allocation in the *Cycladenium* section suggesting to
 424 be placed in *D.* sect. *Pedicellatae* R. Knuth, but most importante he proposed this species as a
 425 possible link between the Neotropical and Paleotropical species, with relation to *D.* sect.
 426 *Stenophora*, specifically by the presence of what he called a rhizome. As a matter of fact, the
 427 underground organ of *D. perdicum* is a tuber of rhizomatous aspect (Fig. 2), as have all

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 analisis, 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 analisis, 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

454 genus, the monoecy, all species from this section present staminate inflorescences in the lower
455 part of the plant and pistillate on the higher part. This character is only shared with a few
456 species from *D.* section *Cycladenium* (probably misplaced) and *D. margarethia* G.M. Barroso,
457 E.F. Guim. & Sucre (poorly known compound-leaved species with six stamens on a column
458 instead of three), and besides some unstable dioecy in *D.* sect. *Stenophora* and *D. convolvulacea*
459 Schltdl. & Cham. (Wilkin *et al.*, 2005). The monoecious species from *D.* section *Cycladenium*
460 are not well known and the boundaries of the section are not clear, as is a section with great
461 diversity (i.e. monoecious and dioecious species). In our analysis, the only species from *D.*
462 section *Cycladenium*, *D. coriacea* Humb. & Bonpl. ex Wild., (dioecious), doesn't appear to be
463 closely related to this clade. Addition of more taxa from this group could clarify relationships
464 the two sections and reinforce the monophyly of *D.* section *Monadelpha*.

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

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

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

493 *Dioscorea dodecaneura* and *D. stegelmanniana* are morphologically very similar to
 494 each other, but they present marked differences in one key aspect of Knuth's classification, the
 495 fruit (transversely oblong and oblong, respectively) and seeds shape (circular and oblong,
 496 respectively). This indicates that besides the NWI and NWII clades the seed wing shape is not
 497 stable character, having closely related species on the NWIII clade with both of the states of this
 498 characteristic. Additionally, these two species present a particular pattern of organization of the
 499 vascular bundles of the aerial stem (Tenorio *et al.*, 2017), similar to that described by Ayensu
 500 (1972) as the typical Old World pattern. It is noteworthy that *D. trifida* and *D. stegelmanniana*
 501 have been sorted by Knuth (1924) to *D.* sect. *Macrogynodium* Uline, reflecting in his view the
 502 close relationship of this species.

503 *Dioscorea* section *Rajania* is composed of 18 species, besides one non-described
 504 species, with occurrence restricted to the West Indies (Raz, 2016; Raz & Pérez-Camacho,
 505 2016)(Raz, 2016). The species belonging to *D.* section *Rajania* are distinguished by the
 506 samaroid fruits, although this is not an exclusive feature of this section, as pointed out by Raz

(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 initial analysis topology is congruent to the one found 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

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

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

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

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

586

587 *DIOSCOREA* LINEAGES ORIGINATED FOUR TIMES INDEPENDENTLY IN THE NEOTROPICS SINCE
588 THE EOCENE

589

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

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

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

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

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

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 Isthmus 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

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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890 Figure legends

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

896 flower of *D. demourae*. **o** staminate flower of *D. subhastata*. **p** staminate flower of *D. sinuata*. **q**
897 pistillate flower of *D. monadelphica*. **r** pistillate flower of *D. laxiflora*. **s** fruit of *D. subhastata*. **t**
898 fruit of *D. olfersiana*.

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

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

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914 **Supporting information**

915 **Figures**

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

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

922 **Fig. S3.** Bayesian maximum clade credibility time tree for *Dioscorea* and outgroups obtained
923 under a relaxed clock model in BEAST and fossil calibration points. For all significantly
924 supported nodes, bars show the 95% Highest Posterior Density intervals around the estimated
925 ages. Fossil calibration points are: A. *Dioscorea lyelli* (Potonié, 1921); B. *Tacca* seed (Gregor,
926 1983); C. *Dioscorea wilkinii* (Pan *et al.*, 2014).

927 **Tables**

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

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

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

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

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

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948 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 Herbariorum* (Thiers, continuously updated).

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

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

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Table S2. Species for which sequences were downloaded from GenBank with voucher information, GenBank accession numbers and references for the original publication. (¹Wilkin *et al.*, 2005; ²Gao *et al.*, 2008; ³China Plant BOL, 2011; ⁴Hsu *et al.*, 2013; ⁵Viruel *et al.*, 2016) (for complete reference, see References). Herbarium acronyms follows the *Index Herbariorum* (Thiers, continuously updated).

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

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

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

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

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

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955 **Table S3.** Biogeographic models tested in this study using BioGeoBEARS package, and estimated
956 parameters *d* (dispersion), *e* (extinction) and *j* (founder speciation event), log-likelihood and AIC values.
957 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

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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

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

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

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

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

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

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

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

<i>Dioscorea sylvatica</i> Eckl.	—	<i>Testudinaria</i> (Salisb.) Prain & Burkill	Africa (" <i>Testudinaria</i> ")	Africa (" <i>Testudinaria</i> ")
<i>Dioscorea tentaculigera</i> Prain & Burkill	<i>Macropoda</i> Uline	—	" <i>Incertis sedis</i> "	" <i>Incertis sedis</i> "
<i>Dioscorea therezopolensis</i> Uline ex R.Knuth	<i>Triapodandra</i> Uline	—	—	New Word I
<i>Dioscorea tokoro</i> Makino ex Miyabe	Genus <i>Stenophora</i> (Uline) R.Knuth <i>Eustenophora</i> R.Knuth	<i>Stenophora</i> Uline	<i>Stenophora</i> Uline	<i>Stenophora</i> Uline
<i>Dioscorea tomentosa</i> J. König ex Spreng.	<i>Trieuphorostemon</i> Uline	—	Compound leaved (<i>Botrysicyos</i>)	Compound leaved (<i>Botrysicyos</i>)
<i>Dioscorea trichantha</i> Baker	<i>Opsphyton</i> Uline (Subsection <i>Isocantha</i> (Uline) R.Knuth)	<i>Brachyandra</i> Uline	Malagasy	Malagasy
<i>Dioscorea trisecta</i> Griseb.	<i>Apodostemon</i> Uline	—	—	New Word I
<i>Dioscorea wallichii</i> Hook.f.	<i>Enantiophyllum</i> Uline	—	<i>Enantiophyllum</i> Uline	<i>Enantiophyllum</i> Uline
<i>Dioscorea variifolia</i> Betero	<i>Microdioscorea</i> Uline	—	New Word I	New Word I (" <i>Microdioscorea</i> ")
<i>Dioscorea velutipes</i> Prain & Burkill	Genus <i>Stenophora</i> (Uline) R.Knuth <i>Shannicorea</i> Prain & Burkill	—	—	<i>Shannicorea</i> Prain & Burkill
<i>Dioscorea widgrenii</i> R.Knuth	<i>Cryptantha</i> Uline	—	—	New Word I
<i>Dioscorea yunnanensis</i> Prain & Burkill	Genus <i>Stenophora</i> (Uline) R.Knuth <i>Shannicorea</i> Prain & Burkill	—	—	<i>Shannicorea</i> Prain & Burkill
<i>Dioscorea zingiberensis</i> C.H. Wright	<i>Macropoda</i> Uline	—	<i>Stenophora</i> Uline	<i>Stenophora</i> 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 Palaeartic and their subsequent Oligocene-Miocene diversification. *Journal of Biogeography* 43: 750–762.

963

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

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

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

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

967

1/94/100

Burmanniaceae

Hermaphrodite
Dioscoreaceae

Trichopus

Tacca

Stenophora

'Nanarepenta'

New World I

'Epipetrum'

Microdioscorea

Monadelpha

New World II

continues

continues

continues