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**Rapid diversification rates in Amazonian Chrysobalanaceae
inferred from plastid genome phylogenetics**

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3 1 **Rapid diversification rates in Amazonian Chrysobalanaceae inferred from plastid**
4 **genome phylogenetics**
5 2
6 3

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34 19

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2
3 **20 Abstract**
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5 21 We studied the evolutionary history of Chrysobalanaceae with phylogenetic analyses of
6
7 22 complete plastid genomes from 156 species to assess the tempo of diversification in the
8
9 23 Neotropics and help to unravel the causes of Amazonian plant diversification. These plastid
10
11 24 genomes had a mean length of 162,204 base pairs, and the nearly complete DNA sequence
12
13 25 matrix, with reliable fossils, was used to estimate a phylogenetic tree. Chrysobalanaceae
14
15 26 diversified from 38.9 Mya (95% highest posterior density, 95%HPD: 34.2-43.9 Mya). A
16
17 27 single clade containing almost all Neotropical species arose after a single dispersal event from
18
19 28 the Palaeotropics into the Amazonian biome *c.* 29.1 Mya (95%HPD: 25.5-32.6 Mya), with
20
21 29 subsequent dispersals into other Neotropical biomes. All Neotropical genera diversified from
22
23 30 10 to 14 Mya, lending clear support to the role of Andean orogeny as a major cause of
24
25 31 diversification in Chrysobalanaceae. In particular, the understory genus *Hirtella* diversified
26
27 32 extremely rapidly, producing > 100 species in the last 6 My (95% HPD: 4.9-7.4 My). Our
28
29 33 study suggests that a large fraction of the Amazonian tree flora has been assembled *in situ*
30
31 34 within the last 15 My.
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39 36 ADDITIONAL KEYWORDS: Amazonia, molecular dating, Malpighiales, phylogenetic
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41 37 inference, tropical forest.
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INTRODUCTION

How the Neotropical rainforest biome has been assembled is a fascinating question for biogeography and evolutionary biology (Gentry, 1982). The Neotropics harbour no fewer than 90,000 species of plants, more than the rest of the tropics combined (Antonelli & Sanmartín, 2011), and this outstanding diversity appears to be the result of a confluence of factors, including large areas with stable, favourable environmental conditions for clade persistence (Wallace, 1878), and long periods of continental isolation (Raven & Axelrod, 1974). Also, major geological events, especially the uplift of the Andes (Gregory-Wodzicki, 2000; Hoorn *et al.*, 2010) are thought to have contributed to the hydrological remodelling of the region now covered by Amazon forest (Hughes *et al.*, 2012; Hoorn *et al.*, 2017; Jaramillo *et al.*, 2017). In the late Miocene, the demise of the Pebas wetland in western Amazonia (Figueiredo *et al.*, 2009; Sacek, 2014) created new habitats such as white sand forests that may have promoted edaphic specialization (Fine *et al.*, 2010) and contributed to allopatric speciation by creating dispersal barriers (Coyne & Orr, 2004; Smith *et al.*, 2014). Pliocene Pleistocene climatic fluctuations could also explain some recent rates of increased diversification (Prance, 1982; Haffer, 2008). These repeated drier and cooler episodes (Wang *et al.*, 2017) could have spurred diversification as they would have caused geographical isolation of wet-forest clades.

Dated molecular phylogenetic trees have proven essential to advance our understanding on the diversification of plants in the tropical rainforest biome, and they shed light on episodes of intercontinental migration and pace of *in situ* diversification (Eiserhardt *et al.*, 2017). A common feature in the history of Neotropical lowland plant clades is that they cannot be understood without accounting for inter-continental dispersal during the Neogene (Pennington & Dick, 2004). Combined with reliable fossil constraints, studies have identified key migrations across biomes (Donoghue & Edwards, 2014; Donoghue & Sanderson, 2015; Fine *et al.*, 2014), and a large number of Neotropical forest clades turn out to have originated outside the lowland Neotropical forests, as is the case, for the palms in Arecoideae (Arecaceae), which results from a single dispersal event into the Neotropics (Baker & Couvreur, 2013). The complex environmental history of South America has left an imprint on *in situ* diversification for many woody plant clades that today characterize the Amazonian forest (Antonelli & Sanmartín, 2011). Miocene onsets of diversification have been detected in Arecaceae (Roncal *et al.*, 2013; Bacon *et al.*, 2018), Burseraceae (Fine *et al.*, 2014), Annonaceae (Pirie *et al.*, 2018), Fabaceae (Schley *et al.*, 2018), Orchidaceae (Pérez-Escobar

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2
3 73 *et al.*, 2017) and Meliaceae (Koenen *et al.*, 2015). However, a complete picture of
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5 74 diversification for Amazonia should ideally be based on a comprehensive sampling of its tree
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7 75 flora, and here we provide insights from a floristically important plant family in lowland
8
9 76 Amazonian habitats.

10 77 Chrysobalanaceae, the coco plum family, with 545 species, are a mid-sized
11
12 78 pantropical family and a notable component of the Neotropical tree flora (Prance, 1972), with
13
14 79 *c.* 80% of its species found only in the Neotropics (Prance & Sothers, 2003). All
15
16 80 Chrysobalanaceae are woody plants, ranging in height from 10 cm to > 40 m, with a uniform
17
18 81 vegetative architecture (Prance & White, 1988). Across Amazonian rainforests, an analysis of
19
20 82 1,170 tree inventory plots (≥ 10 cm in trunk diameter) reveals that Chrysobalanaceae rank
21
22 83 seventh in tree dominance behind Fabaceae, Lecythidaceae, Sapotaceae, Malvaceae,
23
24 84 Moraceae and Burseraceae (ter Steege *et al.*, 2013). Their centre of diversity is Amazonia,
25
26 85 with 251 species restricted to lowland Amazonian forests, but the family is found in virtually
27
28 86 all Neotropical biomes, notably the Brazilian Atlantic forest (47 species), forests of Central
29
30 87 America, Colombian Chocó and the Caribbean (47 species), dry habitats (29 species: 15 in
31
32 88 the Brazilian cerrado, 11 in South American savannas, and three in seasonally dry forests),
33
34 89 and at high elevation (29 species: 18 in the Andes, 11 restricted to the Guyana highlands;
35
36 90 Prance & Sothers, 2003).

37 91 Generic delimitation has been challenging in Chrysobalanaceae (for a historical
38
39 92 account, see Prance & White, 1988). There are currently 27 genera recognized, 11
40
41 93 Palaeotropical, 12 Neotropical, and three amphi-Atlantic (*Chrysobalanus* L., *Parinari* Aubl.,
42
43 94 and *Maranthes* Blume). The two non-Neotropical species of *Hirtella* L. from eastern Africa
44
45 95 and Madagascar should be reassigned to the old genus name from Madagascar, *Thelira*
46
47 96 Thouars. Eight genera are found in Oceania and Southeast Asia, and ten occur in Africa and
48
49 97 Madagascar. Recent changes to generic delimitations in Chrysobalanaceae include the
50
51 98 resurrection of *Angelesia* Korth. for three Southeast Asian species previously included in
52
53 99 *Licania* Aubl. (Sothers & Prance, 2014), a revision of *Couepia* Aubl., with four species
54
55 100 transferred to other genera, and a new genus, *Gaulettia* Sothers & Prance, created to
56
57 101 accommodate species of the former *parillo* clade of *Couepia* (Sothers *et al.*, 2014), and
58
59 102 splitting of the large polyphyletic Neotropical genus *Licania* into eight genera (Sothers *et al.*,
60
103 2016). With clarified generic delimitation, an improved interpretation of the diversification
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105 and biogeography is now possible for the family.

106 105 In this contribution, we provide a phylogenetic reconstruction based on an expanded
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108 106 taxon sampling, aimed at all major clades of Chrysobalanaceae, and with a focus on the

1
2
3 107 Neotropical clades. In a previous study, Bardon *et al.* (2016) sequenced plastid genomes for
4 108 51 species of Chrysobalanaceae, complemented with limited DNA sequences of 88 additional
5 109 species, and concluded that the family diversified in the Palaeotropics in the early Oligocene
6 110 (33 Mya) and subsequently dispersed once to the Neotropics. The hypothesis of a
7 111 Palaeotropical origin for the family was motivated by the postulated position of the Southeast
8 112 Asian genus *Kostermanthus* Prance as sister to the rest of the family, followed by the
9 113 *Parinari-Neocarya* (DC.) Prance clade, which is pantropical. However, limited taxon
10 114 sampling was a major issue, with the risk that ‘rogue’ taxa, widely divergent taxa with a
11 115 poorly supported placement, reduced the overall phylogenetic signal. To minimize this risk,
12 116 we built an improved dataset, with a threefold increase in species sampling, including all
13 117 currently recognized genera, and sequencing of the full plastid genome for each of the
14 118 sampled species.

15 119 Here, we ask when and how Chrysobalanaceae arose to become an important
16 120 component of Amazonian tree communities. To this end, we use a novel approach to date the
17 121 major events of diversification, including the crown age of the family. We then build a
18 122 revised biogeographic scenario for this family both pantropically and in the Neotropics.
19 123 Finally, based on an analysis of changes in diversification rates across the phylogenetic tree,
20 124 we discuss shifts in diversification rates in Chrysobalanaceae.

21 125

22 126 MATERIAL AND METHODS

23 127

24 128 DE-NOVO PLASTID GENOME SEQUENCING

25 129

26 130 We sequenced full plastid genomes for 163 specimens of Chrysobalanaceae, which represent
27 131 156 species, and all 27 currently recognized genera (Table S1). Two accessions of the
28 132 following species were sampled: *Bafodeya benna* (Scott-Elliot) Prance, *Chrysobalanus*
29 133 *cuspidatus* Griseb. ex Duss, *Couepia bracteosa* Benth., *Hymenopus heteromorphus* (Benth.)
30 134 Sothers & Prance, *Leptobalanus octandrus* (Hoffmanns. ex Roem. & Schult.) Sothers &
31 135 Prance, *Maranthes robusta* (Oliv.) Prance, and *Parinari excelsa* Sabine. Tissue was taken
32 136 from herbarium collections or leaf samples dried in silica. Total DNA was extracted using
33 137 standard methods. A separate Illumina library was prepared for each sample, and the libraries
34 138 were then multiplexed in groups of 24 or 48. The pools were sequenced on HiSeq 2000-2500
35 139 high-throughput sequencers, yielding 101-nucleotide pair-ended DNA reads, or the more
36 60

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2
3 140 recent HiSeq 3000 sequencer, yielding 150 pair-ended reads. Each run produces *c.* 700 giga
4
5 141 bases in total. Runs generated for Bardon *et al.* (2016) were treated as new accessions and
6
7 142 reassembled *de-novo* using the bioinformatic pipeline described below.

8 143 Plastome assembly was performed on a local cluster running Linux CentOS version
9
10 144 6.7. We used the NOVOplasty organelle genome assembler version 2.7.2 (Dierckxsens *et al.*,
11
12 145 2016). We assumed a genome size range of 140–180 kbp, K-mer size of 39 and disabled the
13
14 146 ‘variant detection’ option. We obtained unique circularized plastid genomes for 54 specimens.
15
16 147 For another 58 specimens, we set a reference sequence to guide the assembly (using *Licania*
17
18 148 *canescens* Benoist available in NCBI NC300566). In some cases, NOVOplasty returns two or
19
20 149 more optional genomes, corresponding to large inversions, and we manually selected the
21
22 150 option matching gene order. Points of reference of the circularized plastid genomes were
23
24 151 aligned using the CSA software (Fernandes *et al.*, 2009). For the remaining 51 specimens
25
26 152 (30% of our final dataset), we mapped the reads directly against a reference plastid genome
27
28 153 using the ‘map to reference’ option in Geneious version 9.0.5.

29 154 Plastomes were then rotated to a common starting point, and aligned using MAFFT
30
31 155 version 7.222 (Katoch *et al.*, 2017). The first raw alignment of 163 plastomes was initially of
32
33 156 207,248 nucleotides. It was manually edited to remove ambiguous characters produced at the
34
35 157 assembly stage. We annotated the alignment for Chrysobalanaceae by using that previously
36
37 158 published for *Hirtella physophora* Mart. & Zucc. by Malé *et al.* (2014; accession NC 024066
38
39 159 on NCBI). The alignment was realigned with this plastome, and annotations were transferred
40
41 160 to all sequences in Geneious using the ‘transfer annotations’ option. Within the alignment, we
42
43 161 also carefully checked the reading frames of the coding DNA sequences (CDS).

44 162

45 163 RECONSTRUCTION AND DATING OF THE CROWN AGE OF CHRYSOBALANACEAE

46 164

47 165 To reconstruct a dated phylogenetic tree of the family, we used a two-step approach. We
48
49 166 estimated divergence times for the crown node of Chrysobalanaceae and the deeper
50
51 167 divergences in the family. For this first analysis, we selected high-quality plastid genomes
52
53 168 spanning Malpighiales, together with representatives of the main clades of the family. We
54
55 169 included only CDSs, which resulted in a high-quality global alignment, with 20 taxa, 19
56
57 170 members of Malpighiales (including five Chrysobalanaceae), and one outgroup from
58
59 171 Oxalidales [*Sloanea latifolia* (Rich.) K.Schum., Elaeocarpaceae]. We used this first analysis
60
172 to infer the crown age of Chrysobalanaceae. We conducted a second analysis using the full

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2
3 173 163-plastome dataset, in which the crown age inferred from the first analysis was set as a
4
5 174 constraint.

6 175 The 20-taxon sequence matrix was used to reconstruct phylogenetic relationships
7
8 176 using maximum likelihood in RAxML version 8.2.10 (Stamatakis, 2014). The best model was
9
10 177 found to be the general time reversible model for site substitution, with a gamma site model
11
12 178 (GTR+ Γ) for all partitions, as identified using the JmodelTest2 software (Darriba *et al.*,
13
14 179 2012). We considered two scenarios: all CDSs as a single partition; and two partitions,
15
16 180 first/second codons and third codons. All analyses gave the same results, so we subsequently
17
18 181 analysed only the single partition. We ran the analysis on the CIPRES supercomputing portal
19
20 182 (Miller *et al.*, 2010) using rapid bootstrapping with an automatic halting option and searching
21
22 183 for the best-scoring tree.

23 184 To generate a time-calibrated tree, we relied on Bayesian relaxed molecular clock
24
25 185 models as implemented in BEAST version 2.5.1 (Bouckaert *et al.*, 2019) using the DNA
26
27 186 matrix together with fossil constraints (also available on CIPRES). The input file was
28
29 187 generated using the BEAUTi software. We imported the same alignment as used in the
30
31 188 RAxML analysis. We also used the GTR+ Γ model for each partition and assumed a relaxed
32
33 189 clock log-normal model (Drummond *et al.*, 2006). We expected a Cenozoic age for the
34
35 190 Chrysobalanaceae clade, and because our tree dating only used few internal priors, we set the
36
37 191 branching process prior to be the Yule process (or pure birth process; Condamine *et al.*,
38
39 192 2015).

40 193 For the age priors, the split between Malpighiales and Oxalidales was constrained by
41
42 194 imposing a uniform prior between 103 and 112 My (constraint 1; Xi *et al.*, 2012). The dating
43
44 195 of the flowering plant tree has recently been revisited using an extensive plastome dataset (Li
45
46 196 *et al.*, 2019), and although Celastrales were proposed as a new sister group to Malpighiales,
47
48 197 the split between Malpighiales+Celastrales and Oxalidales was inferred at 106.2 Mya (range:
49
50 198 93.2-125.0 Mya), close to the date proposed by Magallón *et al.* (2015), and our prior is
51
52 199 consistent with both analyses.

53 200 We also used internal dating constraints, each modelled as uniform priors in the
54
55 201 BEAST analysis as recommended by Condamine *et al.* (2015): the minimal age was that of
56
57 202 the fossil and the maximum age was set at 110 My, the stem age of Malpighiales. Fossils
58
59 203 based on reproductive structures were selected over other fossils and obtained from carefully
60
204 documented studies (Parham *et al.*, 2011). The stem age of Clusiaceae was constrained with
205 *Paleoclusia chevalieri* Crepet & Nixon as the oldest fossil assigned to this order, dated at 89
206 Mya (Crepet & Nixon, 1998; constraint 2). We constrained the stem age of genus *Parinari* to

1
2
3 207 be > 19 My based on endocarp fossils recently found in Panama and reliably assigned to this
4
5 208 genus (Jud *et al.*, 2016; constraint 3). We also constrained the crown age of the Neotropical
6
7 209 Chrysobalanaceae clade based on the fossil flower found in Dominican amber and reliably
8
9 210 assigned to *Licania* section *Hymenopus* Benth. (Chambers & Poinar, 2010; constraint 4),
10
11 211 which is likely to be > 16 My (see below). The stem age of the Euphorbiaceae clade was
12
13 212 constrained at > 61 My (*Acalypha* pollen type found in China, reported by Xi *et al.*, 2012;
14
15 213 constraint 5). The stem age of Salicaceae was constrained to be more than 48 Mya (fossil
16
17 214 flower of *Pseudosalix handleyi* Boucher, Manchester & Judd; Boucher *et al.*, 2003, constraint
18
19 215 6), the stem age of Caryocaraceae > 55 My (pollen of *Retisyncolporites angularis* González-
20
21 216 Guzmán; Germeraad *et al.*, 1968, constraint 7), and the stem age of Humiriaceae > 37 My
22
23 217 (fossil endocarp of *Lacunofructus cuatrecasana* Herrera, Manchester & Jaramillo; Herrera *et*
24
25 218 *al.*, 2012, constraint 8).

26
27 219 The default starting tree for BEAST is incompatible with the imposed age constraints,
28
29 220 so we started the MCMC search using an ultrametric starting tree modified from the RAxML
30
31 221 output tree. We used the `chronos()` function of the *ape* package (Paradis *et al.*, 2004) in the R
32
33 222 software to generate an dated initial tree within age constraints consistent with the constraints
34
35 223 described above. In the BEAST input file, we fixed the topology, i.e. we assumed that the
36
37 224 input tree had the correct topology, and optimized only the parameters for evolutionary rates
38
39 225 and branch lengths. This was achieved by manually removing the ‘narrow exchange’, ‘wide
40
41 226 exchange’, ‘Wilson Balding’ and ‘subtree slide’ operators from the xml input file. MCMC
42
43 227 was run for 200 million generations, sampling parameters and trees every 10000 generations.
44
45 228 Convergence was evaluated using Tracer version 1.7.1 (Rambaut *et al.*, 2018). The effective
46
47 229 sampling sizes (ESS) of each parameter were checked at the end of each analysis and
48
49 230 considered to be of good quality when > 200. Divergence times were computed using
50
51 231 TreeAnnotator version 2.5.1 after the removal of the 25% burn-in part of the MCMC
52
53 232 (Bouckaert *et al.*, 2019).

54 233

55 234 DATED PHYLOGENETIC RECONSTRUCTION FOR CHRYSOBALANACEAE

56 235

57 236 To construct a dated phylogenetic hypothesis for 163 specimens of Chrysobalanaceae, we
58
59 237 followed the same strategy described above for reconstruction of the dated phylogenetic tree
60
61 238 of Chrysobalanaceae. We used a two-partition model. All CDS were treated as a first
62
63 239 partition. All other regions, including intergenic regions, intronic regions, rRNA and tRNA,
64
65 240 were a second partition. Prior to partitioning the aligned matrix, we removed the second copy

1
2
3 241 of the inverted repeat, to avoid double weighting the phylogenetic signal of the inverted
4
5 242 repeat.

6 243 Considerable age uncertainty has surrounded the biogeographical history of
7
8 244 Chrysobalanaceae, which in part traces back to the attribution of Eocene leaf and pollen
9
10 245 fossils from North America to Chrysobalanaceae (Berry, 1916; Wodehouse, 1932),
11
12 246 constraining the crown age of Chrysobalanaceae to being > 50 My (Davis *et al.*, 2005; Xi *et*
13
14 247 *al.*, 2012; Bardon *et al.*, 2012). However, Jud *et al.* (2016) found no solid evidence for fossils
15
16 248 of Chrysobalanaceae prior to the Miocene. In the Neotropics, the first undisputed evidence of
17
18 249 fossils of Chrysobalanaceae is demonstrated with flowers and fruits, possibly of *Licania*
19
20 250 section *Hymenopus* (Chambers & Poinar, 2010), preserved in amber from the northern
21
22 251 mountain range of the Dominican Republic, dated to 15–20 Mya (Iturralde-Vinent & McPhee
23
24 252 1996; Iturralde-Vinent, 2001), here assumed to be > 16 Mya. We also used three independent
25
26 253 fossils of *Parinari*, including wood and fruits from 21 Mya in Panama (Jud *et al.*, 2016),
27
28 254 fruits from 19 Mya in Ethiopia (Tiffney *et al.*, 1994) and wood from the mid-Miocene in
29
30 255 India (Srivastava & Awasthi, 1996).

31 256 The dated tree was produced using BEAST v.2.5.1 using the same DNA matrix as for
32
33 257 the RAxML analysis, linking the relaxed clock, log-normal models between the two
34
35 258 partitions. The crown of Chrysobalanaceae was constrained with a Gaussian prior of mean 36
36
37 259 My with variance +/- 2 My, consistent with the first analysis. We also used constraints 3 and
38
39 260 4 of the first analysis: the stem age of *Parinari* was set to be > 19 My, and the Neotropical
40
41 261 Chrysobalanaceae clade was set to be older than 16 My. MCMC was run for 100 million
42
43 262 generations, sampling parameters and trees every 10,000 generations. Divergence times were
44
45 263 computed using TreeAnnotator after the first 25% of the trees was discarded.

46 264

47 265 DIVERSIFICATION AND BIOGEOGRAPHIC ANALYSES

48 266

49 267 We first tested whether the dated phylogenetic tree was consistent with phases of accelerated
50
51 268 or decelerated diversification. One prediction is that the major orogenic changes during the
52
53 269 Miocene spurred plant diversification (Lagomarsino *et al.*, 2016; Pérez-Escobar *et al.*, 2017).
54
55 270 We estimated rates of diversification and shifts in these rates using the Bayesian analysis of
56
57 271 macroevolutionary mixture (BAMM, Rabosky *et al.*, 2013; Rabosky 2014). BAMM tests the
58
59 272 hypothesis that diversification has occurred homogeneously across the phylogenetic tree, the
60
273 alternative being that shifts in diversification rate have occurred on specific branches of the
274 tree. We used the initial control file with priors on rate parameters inferred by the function

1
2
3 275 setBAMMpriors() of the BAMMtools package in R (Rabosky *et al.*, 2014). BAMM also
4
5 276 provides an analytical correction for incompletely sampled trees, and here we assigned a
6
7 277 sampling weight to each genus. The species sampling rates within the genera ranged from
8
9 278 13% (*Moquilea* Aubl.), to 57% (*Couepia*), for a 29% mean across the family. For *Hymenopus*
10
11 279 (*Benth.*) Sothers & Prance, which appears in two separate clades in our analysis, we assumed
12
13 280 an equal sampling of both clades (set at 36%). BAMM can also be used to compute
14
15 281 diversification rates within subclades of the tree. We ran the reverse-jump MCMC simulation
16
17 282 for ten million iterations to ensure convergence, which was assessed with the EffectiveSize()
18
19 283 function of BAMMtools. For each of the four well-sampled Neotropical genera (*Couepia*,
20
21 284 *Hirtella*, *Licania*, *Moquilea*), plus *Parinari*, we inferred the speciation rates from the BAMM
22
23 285 run. This was done by selecting the subclade using the ape R package (Paradis *et al.*, 2004),
24
25 286 and analysing the inferred diversification parameters on it.
26
27 287

28
29 288 We also reconstructed the biogeographic history of Chrysobalanaceae by inferring the
30
31 289 most likely ancestral area(s). To this end, we attributed each species to a region. Because of
32
33 290 the Neotropical focus of this study, we defined two broad regions outside the Neotropics:
34
35 291 Africa and Southeast Asia (including Oceania). In the Neotropics, we defined five regions:
36
37 292 Caribbean and Central America (including the Chocó region of Colombia, and southeast
38
39 293 USA), savannas and seasonally dry tropical forests (including the Llanos of Colombia and
40
41 294 Venezuela, cerrado in Brazil and dry forests such as the Chiquitania in Bolivia and caatinga in
42
43 295 Brazil), Atlantic rainforest, the Andes and Amazonia. To reconstruct the ancestral area(s), we
44
45 296 used an unconstrained dispersal-extinction-cladogenesis (DEC) model (Ree & Smith, 2008)
46
47 297 as implemented in the R-package BioGeoBEARS version 1.1.2 (Matzke, 2014). We did not
48
49 298 perform a model comparison approach including the founder-event speciation option of
50
51 299 BioGeoBEARS because taxon sampling in our dataset remains too incomplete and because
52
53 300 this approach has limits (Ree & Sanmartín, 2018).
54
55 301

56 302 RESULTS

57 303
58 304 The 163 plastomes had a mean length of 162,204 +/-1195 bp and were fully assembled,
59 305 except for *Licania densiflora* Kleinhoonte (151,268 bp), *Parinari curatellifolia* Planch. ex
60 306 *Benth.* (157,972 bp) and *Licania micrantha* Miq. (158,098 bp). Average sequencing depth
307 was 369 +/- 233 (range: 30–1,110). Manual editing of the DNA sequences focused on just 42

1
2
3 308 bp or less than 0.03% of the plastome, except for four species: *Kostermanthus heteropetalus*
4 (Scort. ex King) Prance (2,479 edits, close to *K. robustus* Prance, which had only 43 edits),
5 309 *Bafodeya benna2* (Scott-Elliot) Prance (1,726 edits, close to *Bafodeya benna1* with 286 edits),
6 310 *Parinariopsis licaniiflora* (Sagot) Sothers & Prance (1,075 edits) and *Cordillera platycalyx*
7 311 (Cuatrec.) Sothers & Prance (1,040 edits). The full DNA alignment and dated tree is available
8 312 on Dryad (<https://doi.org/10.5061/dryad.ghx3ffbkp>).
9 313

10 314 The 20-taxon reconstruction was based on an alignment of coding DNA sequences of
11 315 61,953 sites and 7,292 patterns (Supplementary Information, Fig. S1). The crown age of
12 316 Chrysobalanaceae was inferred in the late-Eocene, at *c.* 38.9 Mya (95% highest posterior
13 317 density, 95% HPD: 34.2–43.9 Mya). *Kostermanthus* Prance and *Bafodeya* Prance ex. F. White
14 318 were sister to the rest of Chrysobalanaceae.

15 319 The phylogenetic reconstruction of Chrysobalanaceae was based on 67,317 CDS sites
16 320 with 3,335 patterns and 82,566 non-CDS sites with 13,935 patterns (Figs 1–3). Of the 162
17 321 internal nodes, 114 (70%) had bootstrap percentages > 90, and 133 (82%) had bootstrap
18 322 percentages > 70. Most poorly resolved nodes correspond to within-genus splits and/or recent
19 323 events. The tree inferred from RAxML with branch lengths showed no heterogeneity in
20 324 substitution rates across the family (Supplementary Information, Fig. S2).

21 325 Excluding *Kostermanthus-Bafodeya*, three clades are mainly African (A–C, Fig 1).
22 326 Pantropical *Parinari* was inferred to have diversified 7.6 Mya (95% HPD: 5.7–9.3 Mya),
23 327 although its stem age was 28 My (95% HPD: 23–33.2 My).

24 328 Clade D is predominantly Neotropical and displays a secondary dispersal from the
25 329 Neotropics into Oceania and Southeast Asia (*Hunga* Pancher ex Prance and *Angelesia*), which
26 330 diverged from Neotropical *Exellodendron* Prance 15.9 Mya (95% HPD: 11.4–19.8 Mya). The
27 331 Neotropical clade and clade D diversified in the early Oligocene, 33.6 Mya (95% HPD: 30.6–
28 332 36.9 Mya).

29 333 The crown age of the Neotropical clade was inferred at 29.1 My (95% HPD: 25.5–
30 334 32.6 My, Fig 2). *Moquilea*, *Couepia*, *Leptobalanus* (Benth.) Sothers & Prance and *Licania*
31 335 *sensu* Sothers *et al.* (2016) were monophyletic. Species-rich genera of the Neotropical clade
32 336 diversified in the mid to late Miocene: *Moquilea* 15.1 Mya (95% HPD: 11.9–18.5 Mya),
33 337 *Couepia* 10.3 Mya (8.4–12.3 Mya), *Leptobalanus* 10.3 Mya (7.6–13.0 Mya) and *Licania* 16.8
34 338 Mya (13.6–20 Mya).

35 339 *Gaulettia* (Sothers *et al.*, 2014) and Neotropical *Hirtella* are monophyletic (Fig. 3).
36 340 The myrmecophilous species of *Hirtella* (*Hirtella* section *Myrmecophila* Prance; seven
37 341 species), did not form a clade. The sister of *Gaulettia* (23.4 Mya) included *Hirtella* plus a

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2
3 342 complex of seven groups with low bootstrap support: *Hymenopus* cf. *occultans* (Prance)
4 343 Sothers & Prance, *Microdesmia* (Benth.) Sothers & Prance, *Hymenopus*1, *Afrolicania*
5 344 Mildbr., *Cordillera* Sothers & Prance, *Parinariopsis* (Huber) Sothers & Prance and
6 345 *Hymenopus*2. Except for *Hymenopus*, each genus was monophyletic. However, based on
7
8 346 bootstrap support in this analysis, we cannot exclude the possibility that the clades of
9
10 347 *Hymenopus* (Fig. 3) form a single group. The Neotropical genera in Figure 3 also diversified
11
12 348 in the mid to late Miocene: *Gaulettia* 10.8 Mya (7.8–13.8 Mya), *Hirtella* 10.4 Mya (8.1–13.1
13
14 349 Mya), *Hymenopus*1 12.6 Mya (9.3–16 Mya) and *Hymenopus*2 12.4 Mya (9.5–15.8 Mya). The
15
16 350 position of *Afrolicania*, the only non-Neotropical species of the core Neotropical clade,
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18 351 suggests a single dispersal event from the Neotropics to Africa 24 Mya (95% HPD: 22.4–25.6
19
20 352 Mya).

21
22 353 The BioGeoBEARS analysis detected that the combined Neotropical clade and clade
23
24 354 D were unambiguously assigned to Amazonia, with secondary dispersal events into Central
25
26 355 America, the Atlantic forest and savannas/dry tropical forests (Fig. 4). Migration events to the
27
28 356 cerrado were mainly in the Pliocene, confirming Simon *et al.* (2009).

29 357 The BAMM analysis converged (effect size for number of shifts was $> 1,000$ with a
30
31 358 log-likelihood > 400). It identified four shifts in diversification rates as the most likely (Fig.
32
33 359 5). A rate-through time analysis for Chrysobalanaceae demonstrated a clear increase in
34
35 360 speciation rates after 10 Mya (Fig. 5). The four outlying clades correspond to *Parinari*,
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37 361 *Moquilea*+*Couepia*, *Licania*+*Leptobalanus* and *Hirtella* [excluding *H. recurva* (Spruce ex
38
39 362 Prance) Sothers & Prance and *H. punctillata* Ducke]. The most rapid diversification was in
40
41 363 *Hirtella* minus *H. punctillata* and *H. recurva*, for which BAMM inferred a speciation rate of
42
43 364 $\lambda=0.60$ (in lineages per My, 90% confidence interval: 0.42–0.85), compared with a family
44
45 365 mean-speciation rate of $\lambda=0.23$ (0.19–0.27), and family mean-speciation rate excluding
46
47 366 *Hirtella* of $\lambda=0.20$ (0.17–0.25). A rate-through time analysis for *Hirtella* demonstrates a
48
49 367 decline in rate through time (Fig. 5, right panels). *Parinari* was the other clade that exhibited
50
51 368 a significantly higher speciation rate compared to the average but with much greater
52
53 369 confidence intervals, $\lambda=0.49$ (0.14–0.96).

54 370

55 371 DISCUSSION

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58 373 In this study, we provide a comprehensive analysis of the evolutionary history of
59
60 374 Chrysobalanaceae based on the analysis of 163 fully sequenced plastid genomes, including

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2
3 375 about a third of the species currently recognized in the family. As discussed below, our results
4
5 376 provide new support for the Miocene origin of the Neotropical flora, and to our knowledge it
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7 377 is the first to be built on a fully sampled matrix of plastid genome data for a Neotropical tree
8
9 378 family. Our study was based on an aligned length of 162,204 bp, far more than recently
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11 379 published studies on Neotropical plant diversification.

12 380 In contrast, virtually all existing evolutionary papers of Neotropical plant families
13
14 381 have been based on selected plastid markers combined with sequences from the ribosomal
15
16 382 cluster (internal transcribed spacer). Important recent studies on the Miocene diversification
17
18 383 of Amazonian clades have focused on Annonaceae based on an aligned length of 7,960 bp
19
20 384 (Pirie *et al.*, 2018), Meliaceae with 5,207 bp (Koenen *et al.*, 2015) and in clade Detarioideae
21
22 385 in Fabaceae with 2,463 bp (Schley *et al.*, 2018). In our study, the most poorly sampled species
23
24 386 had a 93% plastome coverage. Generally, coverage is in excess of 99%, and the matrix was
25
26 387 almost complete. We also included 156 species, 131 of which are Neotropical, with much
27
28 388 increased taxon and character sampling compared to previous efforts. The results include
29
30 389 important new biogeographic and systematic results about Chrysobalanaceae and confirm
31
32 390 results for the Neotropical flora, but with much greater confidence than the other studies due
33
34 391 to the greater amounts of data included.

392 393 EARLY DIVERSIFICATION OF CHRYSOBALANACEAE

394
395 *Bafodeya* plus *Kostermanthus* were found to be sister to the rest of the family. Both results
396
397 were unexpected based on floral morphology and previous molecular results. *Bafodeya* was
398
399 placed in the *Parinari-Neocarya* clade, whereas *Kostermanthus* was proposed to have a
400
401 relationship to *Atuna* Raf. or Neotropical *Acioa* Aubl. and African *Dactyladenia* Welw.,
402
403 although none of these relationships was well supported (Yakandawala *et al.*, 2010).
404
405 *Kostermanthus* occurs in Southeast Asian rainforests in mixed dipterocarp and heath
406
407 associations. Monospecific *Bafodeya* is endemic to mid-elevation sandstone plateaus of West
408
409 Africa. *Euphronia* Mart & Zucc., the sole genus of Euphroniaceae (sister family to
410
411 Chrysobalanaceae; Xi *et al.*, 2012), is endemic to the Guiana Shield and restricted to white
412
413 sand or rocky areas. Thus, *Kostermanthus* and *Bafodeya* share ecological affinities with
414
415 *Euphronia*. If the phylogenetic structure proposed here is confirmed, this suggests that the
416
417 ancestral habitat of Chrysobalanaceae was nutrient-poor and sandier than modern tropical
418
419 rainforests. It would be important to reassess the position of both genera, and this is a good
420
421 example where nuclear gene data would be helpful.

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2
3 409 The crown age of the *Parinari* clade was inferred at 9 My (95% HPD: 8.2–9.8 My).
4
5 410 *Parinari* possesses the most reliable fossil record of the family, due to the diagnostic features
6
7 411 of its endocarp (Jud *et al.*, 2016). The early Miocene *Parinari* fossils in Africa (Tiffney *et al.*,
8
9 412 1994) and South America (Jud *et al.*, 2016) predate by *c.* 10 My the crown age of *Parinari*,
10
11 413 consistent with their high rates of speciation and extinction. Bardon *et al.* (2016) supported an
12
13 414 African origin for *Parinari* due to the native African distribution of *Neocarya*, but the
14
15 415 increased sampling of our study leads to a less clear-cut result. The two earliest-diverging
16
17 416 clades in *Parinari* contain all five Neotropical accessions. One clade with a crown age 7.4 My
18
19 417 contains all Palaeotropical accessions. Noteworthy is the position of *P. nonda* F.Muell. ex
20
21 418 Benth., from tropical Australia and Papua New Guinea, close to African *P. capensis* Harv.
22
23 419 (inferred age of 0.37 My for the *P. capensis*/*P. nonda* split), which suggests a recent long-
24
25 420 distance dispersal event from Africa to Australasia. Overall, if more research on *Parinari*
26
27 421 confirms the crown age of < 10 My, it would be a striking case of a pantropically distributed
28
29 422 genus of long-lived tropical trees with a trans-oceanic dispersal (Renner, 2004). On the
30
31 423 whole, our species sampling is currently insufficient to confidently resolve the
32
33 424 biogeographical history of *Parinari* because our results are based on sampling of only 11
34
35 425 species of the 39 currently described *Parinari* spp.

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37 426 Clade B has a strong African component. Increased sampling for *Maranthes* (five of
38
39 427 the 12 species now included) produced a date of 14.4 Mya (95%HPD: 10.9–18.1 Mya).
40
41 428 *Maranthes* is present on all three continents, including the Neotropical species: *M.*
42
43 429 *panamensis* (Standl.) Prance & F.White, which our analysis places as sister to *M. gabunensis*
44
45 430 (Engl.) Prance. This suggests that *M. panamensis* is the product of a recent dispersal from
46
47 431 Africa. We also emphasize that *Magnistipula* Engl. remains an unresolved puzzle in
48
49 432 Chrysobalanaceae and further research should include more comprehensive taxon coverage
50
51 433 including all three subgenera. Clade C also contains only African species: *Dactyladenia* plus
52
53 434 the African *Hirtella* spp. (Prance & White, 1988; p. 149), which need to be revised and
54
55 435 segregated from *Hirtella* based on our results.

56
57 436 Clade D contains 28 species (14 Neotropical) and five genera. *Hunga* (endemic to
58
59 437 New Caledonia) and *Angelesia* (more broadly Australasian) are sister to Neotropical
60
438 *Exellodendron* (one species out of five sampled here). Thus, the *Angelesia-Hunga* clade
439 probably results from a long-distance dispersal event from the Neotropics to Australasia
440 between 9.3 and 15.9 Mya. Cases of dispersal from South America to Australasia via
441 Antarctica probably occurred before the cooling event of the mid-Oligocene, *c.* 30 Mya

1
2
3 442 (Siegert, 2008), but our dating seems to reject this scenario, pointing instead to a much more
4
5 443 recent dispersal.

6 444 In clade D, *Chrysobalanus icaco* L. also has a well-documented amphi-Atlantic
7
8 445 distribution. We include for the first time all three species of *Chrysobalanus*, *C. icaco*, *C.*
9
10 446 *cuspidatus* Griseb. and *C. prancei* I.M. Turner (formerly *C. venezuelanus* Prance), which were
11
12 447 divergent based on plastid genome information, with an early divergence in the mid Miocene
13
14 448 at *c.* 12.4 Mya (95% HPD: 9.1–15.7 Mya). It would be important to further explore the
15
16 449 divergence of the African populations of *C. icaco*, which includes two subspecies. The
17
18 450 placement of *Acioa* sister to *Chrysobalanus* differs from that in Bardon *et al.* (2016), and
19
20 451 increased taxon sampling proved important to further resolve this clade.

21 452 We emphasize that our dated phylogenetic tree is based on limited fossil material and
22
23 453 discovery of new fossils could alter these dates. The crown of Chrysobalanaceae was dated at
24
25 454 *c.* 38.9 Mya (95% HPD: 34.2–43.9 Mya), slightly older than a previous estimate of 33 Mya
26
27 455 (Bardon *et al.*, 2016). This discrepancy is easily explained because this analysis is based on a
28
29 456 better sampling of the early-diverging clade in Chrysobalanaceae, and we used flat priors
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31 457 rather than log-normal ones (Condamine *et al.*, 2015).

32 458 33 459 STRUCTURE OF THE CORE NEOTROPICAL CLADE

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36 461 The main focus of this study was to better resolve the evolutionary history of
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38 462 Chrysobalanaceae in the Neotropics. Prior to 2014, the ‘core Neotropical clade’ (> 99%
39
40 463 Neotropical), included only three genera, but no fewer than 395 species (Prance, 1972; Prance
41
42 464 & Sothers, 2003). After redefinition of *Couepia* (Sothers *et al.*, 2014) and *Licania* (Sothers *et*
43
44 465 *al.*, 2016), the structure of the core Neotropical clade has been considerably clarified.

45 466 Here we recognize 12 genera of Chrysobalanaceae as members of the core Neotropical
46
47 467 clade: Neotropical *Hirtella* (105 species), *Geobalanus* Small (three species), *Microdesmia*
48
49 468 (two species), *Cordillera* (one species), *Parinariopsis* (one species), *Moquilea* (54 species),
50
51 469 *Couepia* (62 species), *Leptobalanus* (31 species), *Licania* (100 species), *Gaulettia* (nine
52
53 470 species), *Hymenopus* (28 species), and *Afrolicania* (1 species) the only non-Neotropical genus
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55 471 in this clade. In addition, *Exellodendron* (five species) and *Acioa* (six species) are exclusively
56
57 472 Neotropical but outside the core clade.

58 473 The stem age of the core Neotropical clade is estimated in the mid-Eocene, and the
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60 474 crown age is in the early Oligocene *c.* 29.1 Mya (25.5–32.6 Mya). According to the
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62 475 biogeographical analysis, this core Neotropical clade diversified in Amazonia. The various

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3 476 non-Amazonian clades (notably *Couepia* in the Atlantic rainforest and beyond the Andes into
4 the Chocó and Central America) are interpreted as dispersal events. This scenario confirms
5 477 the more general analysis of Antonelli *et al.* (2018), but also shows that it is difficult to
6 478 attribute extant diversity to a single biome: in the case of Chrysobalanaceae, diversification in
7 479 Amazonia was preceded by a long extra-Neotropical evolutionary history, even potentially
8 480 outside the forest biome.
9 481

10 482 We now turn to the sister clade of *Gaulettia*, which contains some of the unresolved
11 483 taxonomic issues in Chrysobalanaceae. This clade, dated at 26.3 My (95% HPD: 24.7–27.9
12 484 My), includes *Hirtella* plus seven clades with low bootstrap support for their inter-
13 485 relationships: *Microdesmia*, *Hymenopus*1, *Afrolicania*, *Cordillera*, *Parinariopsis*,
14 486 *Hymenopus*2 and *Hymenopus cf. occultans*. Our analysis suggests that *Hymenopus* may
15 487 include two genera (designated as 1 and 2), but further research is needed to confirm this
16 488 proposal, especially in the light of the weak support for their separation. One hypothesis for
17 489 the lack of support in this clade is that it may have resulted from a single diversification event
18 490 giving rise to a variety of new forms associated with the end of the Oligocene. Global
19 491 warming at this time was associated with a loss of palynofloral diversity in the foothills of the
20 492 Andes (Jaramillo *et al.*, 2006), which could be due to the rapid Andean uplift around this time
21 493 (Hoorn *et al.*, 2010). The current distribution of these genera sheds little light on a possible
22 494 allopatric diversification scenario, in part because the extant distribution due to cultivation of
23 495 *Microdesmia* species may not reflect their historical distribution (Sothers *et al.*, 2016), and
24 496 also because extant species of both *Hymenopus* and *Hirtella* have large modern distributions.
25 497 Bardon *et al.* (2016) was published before the generic realignments illustrated here. This tree
26 498 also differs from that in Sothers *et al.* (2016) based on plastid and nuclear (*Xdh*, ITS) DNA
27 499 sequences.
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501 EVOLUTIONARY HISTORY OF NEOTROPICAL CHRYSOBALANACEAE GENERA

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49 503 According to our results, onset of diversification for seven genera spanned the mid Miocene:
50 504 *Moquilea* (15.1 Mya), *Couepia* (10.3 Mya), *Leptobalanus* (10.3 Mya), *Licania* (16.8 Mya),
51 505 *Hirtella ss.* (10.4 Mya), *Gaulettia* (10.8 Mya), *Hymenopus*1 (12.4 Mya) and *Hymenopus*2
52 506 (12.6 Mya). This precedes the initiation of the modern Amazon River and demise of the Pebas
53 507 wetland (Figueiredo *et al.*, 2009).
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58 508 Against the backdrop of this geological and climatic setting, the evolutionary history
59 509 of *Couepia* is informative. The genus clearly split into two groups, one with an affinity for

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3 510 dry forests (*paraensis* clade) with a recent (early Pliocene) unique dispersal to the Atlantic
4 511 rainforest. In the other (*guianensis* clade) there was an early-diverging clade of Central
5 512 American/Chocó species sister to the rest, which are predominantly Amazonian. From the
6 513 ancestral area reconstruction analysis, we were unable to assign this clade to a specific region,
7 514 although the most likely area is Amazonia+Central America/Chocó. Finally, *Couepia* spp.
8 515 currently found in the Atlantic rainforest of Brazil seem to have resulted from two
9 516 independent dispersals, both post-Miocene. *Moquilea*, *Licania*, and *Hymenopus* have species
10 517 in both Amazonia and Central America. However, for these, it would be important to better
11 518 sample the populations on both sides of the Andes to ensure that these are not divergent
12 519 “cryptic” species. If our result is confirmed, cross-Andean dispersals have occurred frequently
13 520 since the Pleistocene.

21
22 521 Sister to the rest of *Hirtella* is a clade of two species including *H. recurva* (Spruce ex
23 522 Prance) Sothers & Prance (Sothers *et al.*, 2014), found at >2,000 m in the Ecuadorian Andes,
24 523 and *H. punctillata* Ducke, collected at >1,000 m in the Serra do Aracá tepui (Prance &
25 524 Johnson, 1992). The fact that these two species cluster together, although distant and
26 525 morphologically distinct, is unexpected. Aside from these two species, the remaining large
27 526 clade of *Hirtella* did not diversify before the end of the Miocene at *c.* 6 Mya. Thus, *Hirtella* is
28 527 an example of explosive diversification, with a speciation rate inferred *c.* 0.60 lineages per
29 528 My (90% confidence interval: 0.42–0.85). Diversification in *Hirtella* thus has a comparable
30 529 magnitude to that in *Inga* Miller, which is thought to have diversified around 10 Mya,
31 530 producing *c.* 300 species (Dexter *et al.*, 2017), and two genera of Meliaceae, *Trichilia*
32 531 P.Browne and *Guarea* F.Allemão, as reported by Koenen *et al.* (2015). All four genera have
33 532 their centre of diversity in Amazonia, and it is thus tempting to speculate that the timing of
34 533 these events is consistent with a westward expansion of Amazonian forests after drainage of
35 534 the Pebas wetland (Figueiredo *et al.*, 2009). However, it is also possible that ecological
36 535 attributes of these groups may have played a role: these genera are predominantly understory
37 536 plants, and their seeds are dispersed by animals (Baker *et al.*, 2014). Remarkably, like *Inga*,
38 537 *Hirtella* has a well-documented association with ants, and this could be a major factor in their
39 538 diversification (Kursar *et al.*, 2009).

40
41 539 We failed to find support for a single myrmecophilous group in *Hirtella*, meaning that
42 540 the myrmecophilous association has been repeatedly derived in the genus. However, an
43 541 alternative interpretation is that incomplete lineage sorting is prevalent in this recent clade,
44 542 and that plastid genomes are unable to uncover such shallow phylogenetic relationships.

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3 543 Greater species and regional sampling would be necessary to confirm relationships in this
4
5 544 intriguing group.

6 545 This analysis included only a few species with multiple accessions, and some of these
7
8 546 revealed surprises. Two accessions of *Parinari excelsa* Sabine (Parque Estadual Cristalino,
9
10 547 Brazil, and Saint Laurent du Maroni, French Guiana) fell into separate clades, and so did the
11
12 548 accessions of *Couepia bracteosa* (Sinnamary, French Guiana, and Manaus, Brazil),
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14 549 *Leptobalanus octandrus* (Manaus and São Paulo, Brazil) and *Hymenopus heteromorphus*
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16 550 (Benth.) Sothers & Prance (Régina, French Guiana and Manaus). In all these cases, the
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18 551 accessions were from distant localities. One explanation may be that there are actually several
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20 552 cryptic, or previously unreported, species within the currently large ranges of these species.
21
22 553 With more comprehensive sequencing of targeted species across their distribution, it will be
23
24 554 possible to assess the prevalence of such entities in Chrysobalanaceae. This situation probably
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26 555 holds more generally across Amazonian plant families (Misiewicz & Fine, 2014; Loiseau *et*
27
28 556 *al.*, 2019).

29 557
30 558 ON THE USE OF PLASTID GENOMES TO INFER THE EVOLUTIONARY HISTORY OF TROPICAL
31 559 FLOWERING PLANTS

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33 561 High-throughput technologies have greatly facilitated the sequencing of plastid genomes and
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35 562 these have been used in plant phylogenomics for well over a decade (Jansen *et al.*, 2007;
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37 563 Moore *et al.*, 2007; Straub *et al.*, 2012). About 500 complete flowering plant plastomes had
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39 564 been sequenced by 2014 (Wicke & Schneeweiss, 2015), and there were close to 5,000 fully
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41 565 sequenced plastomes representing > 1,300 genera available on the NCBI website just five
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43 566 years later (July 2019).

44 567 Plastomes have been used to infer phylogenetic relationships in Poales (Givnish *et al.*,
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46 568 2010), Malpighiales (Xi *et al.*, 2012), Zingiberales (Barrett *et al.*, 2013), all angiosperms
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48 569 (Ruhfel *et al.*, 2014), Apocynaceae (Straub *et al.*, 2014), Rosaceae (Zhang *et al.*, 2017) and
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50 570 Caryophyllales (Yao *et al.*, 2019). In such analyses, proper curation of data (Philippe *et al.*,
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52 571 2011) and appropriate phylogenetic reconstruction methods (Gonçalves *et al.*, 2019) have
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54 572 been crucial to ensure reliable results. Heterogeneity in evolutionary rates should be carefully
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56 573 considered, as it provides insights into modes of evolution (Ruhfel *et al.*, 2014).

57 574 Several mechanisms are known to impact the rate of evolution of plastomes. Groups
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59 575 with known symbiotic associations, such as mycoheterotrophy, show different evolutionary
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576 rates, due to gene silencing and loss (Wilke *et al.*, 2011). Also, plastid genomes turn out to be

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3 577 biparentally inherited in at least 20% of the land plants (Zhang, 2010), suggesting the
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5 578 potential for recombination and therefore a more complex picture than often assumed for
6
7 579 evolution of this compartment.

8 580 It is not known how often cytonuclear incongruence occurs in the tree of flowering
9
10 581 plants, and previously found contradictions between plastid genome data and morphology
11
12 582 may be solved using large nuclear gene datasets. For example, because of incomplete lineage
13
14 583 sorting, recent and rapidly diversifying clades can be resolved only based on nuclear gene
15
16 584 data, such as Andean *Espeletia* Mutis ex Humb. & Bompl. (Asteraceae; Pouchon *et al.*, 2018)
17
18 585 and Australian *Nicotiana* L. (Solanaceae; Dodsworth *et al.*, 2020).

19 586 Targeted capture of hundreds of nuclear genes could bring even further insight into the
20
21 587 question of plant diversification, as has been shown for the Neotropical palm clade
22
23 588 Geonomateae (>3 million bp; Loiseau *et al.*, 2019), Fabaceae (*c.* 1 million bp; Koenen *et al.*,
24
25 589 2020) or land plants (Leebens-Mack *et al.*, 2019). However, it is noteworthy that nuclear gene
26
27 590 information did not radically transform the phylogenetic tree of Geonomateae (Roncal *et al.*,
28
29 591 2012), and that plastid genome data were found to be consistent with nuclear gene data in
30
31 592 Fabaceae except at the root node, the latter probably caused by incomplete lineage sorting
32
33 593 (Koenen *et al.*, 2020). Also, assembling such large nuclear gene datasets represents specific
34
35 594 challenges, and phylogenetic reconstruction methods using these data are still in development
36
37 595 (Zhang *et al.*, 2018). Although nuclear genes are necessary to resolve parts of the plant tree of
38
39 596 life where plastid genomes are insufficiently informative, many Amazonian plant families
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41 597 have not been included in such phylogenetic work, and plastome analyses are a natural step to
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43 598 document systematic relationships and study Amazonian plant diversification.
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45 599

600 CONCLUSIONS

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47 602 Chrysobalanaceae have long been promoted as a model for the study of Neotropical
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49 603 diversification, but unravelling their systematics has represented a major challenge (Prance
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51 604 1972; Prance & White, 1988; Yakandawala *et al.*, 2010). Previously, we have proposed a
52
53 605 phylogenetic analysis of the family based on 51 species with fully sequenced plastid genomes
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55 606 and an additional 88 species sequenced for only a few markers (Bardon *et al.*, 2016). With a
56
57 607 total of 163 sequenced plastomes in Chrysobalanaceae, and 156 species, the present study is a
58
59 608 major update of this previous work and demonstrates that a more comprehensive strategy
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609 helps gain greater confidence on the monophyly of several genera, even if a few issues

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3 610 remain. In the future, it would be important to: explore whether the *Hymenopus* complex can
4
5 611 be clarified, determine if nuclear DNA confirms the position of *Bafodeya* and *Kostermanthus*
6
7 612 as sister to the rest of the family, examine the evolutionary history of Neotropical *Hirtella* and
8
9 613 of *Parinari* with better species coverage, and add more *Magnistipula* spp. to include all three
10
11 614 subgenera. For six lowland Amazonian genera of Chrysobalanaceae, we document
12
13 615 accelerated diversification in the wake of the Andean uplift. This study thus provides support
14
15 616 for the view that much of the extant Neotropical plant diversity has arisen within the past 15
16
17 617 My, Amazonian diversification has played a key role in this diversification process and the
18
19 618 majority of diversification events have taken place *in situ*, rather than being the product of
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21 619 intercontinental dispersal.
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3 969 **Figure captions**
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5 970
6 971 Figure 1. Phylogenetic tree for the basal clades of Chrysobalanaceae, obtained from the
7 software RAxML 8.2.10, with dating from the software BEAST 2.5.1. The arrows illustrate
8 the internal calibration points used for tree dating (n=3). Clade support < 95% was colour-
9 coded with circles; all other clades had support percentages > 95%. The numbers next to each
10 node are the inferred ages in millions of years. Grey bars represent the 95% confidence
11 intervals. Asterisks indicate plastid genomes published in Bardon *et al.* (2016).
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18 977
19 978 Figure 2. Phylogenetic tree of Chrysobalanaceae, continuation of Figure 1. The biome map is
20 modified from Olson *et al.* (2001). Dark red: Amazonia; orange: savannas and seasonally dry
21 tropical forests; green: Atlantic tropical forests; blue: forests of Central America, the
22 Caribbean and Chocó; black: high-elevation ecosystems (>1,000 m asl).
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26 982
27 983 Figure 3. Phylogenetic tree of Chrysobalanaceae, continuation of Figure 2. In the *Hirtella*
28 clade, the ant symbols indicate myrmecophilous species.
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32 985
33 986 Figure 4. Ancestral area reconstruction of Chrysobalanaceae using the dispersal, extinction,
34 and cladogenesis (DEC) algorithm as implemented in the BioGeoBears software. Pie charts
35 indicate relative support for the dominant ancestral area; all other ancestral area probabilities
36 are lumped and represented in white.
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40 990
41 991 Figure 5. Plot with branches coloured by speciation rate (lineages/My), representing a
42 summary of BAMM analysis. Grey circles indicate the positions of regime shifts in the best
43 configuration. Side plots represent the speciation rate-through-time (RTT) plots for each of
44 the four clades with regime shifts, whereas the bottom plot represents the RTT plot for the
45 entire tree. Finally, the bottom-right histograms indicate the distribution of speciation rates for
46 the four regime-shift clades and the entire family.
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3 1 **Supplementary Information for: Rapid diversification rates in Amazonian**
4 **Chrysobalanaceae inferred from plastid genome phylogenetics**
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8 4 Jerome Chave^{1*}, Cynthia Sothers², Amaia Iribar¹, Uxue Suescun¹, Mark W Chase^{2,3}, Ghilleen
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PDF Proof

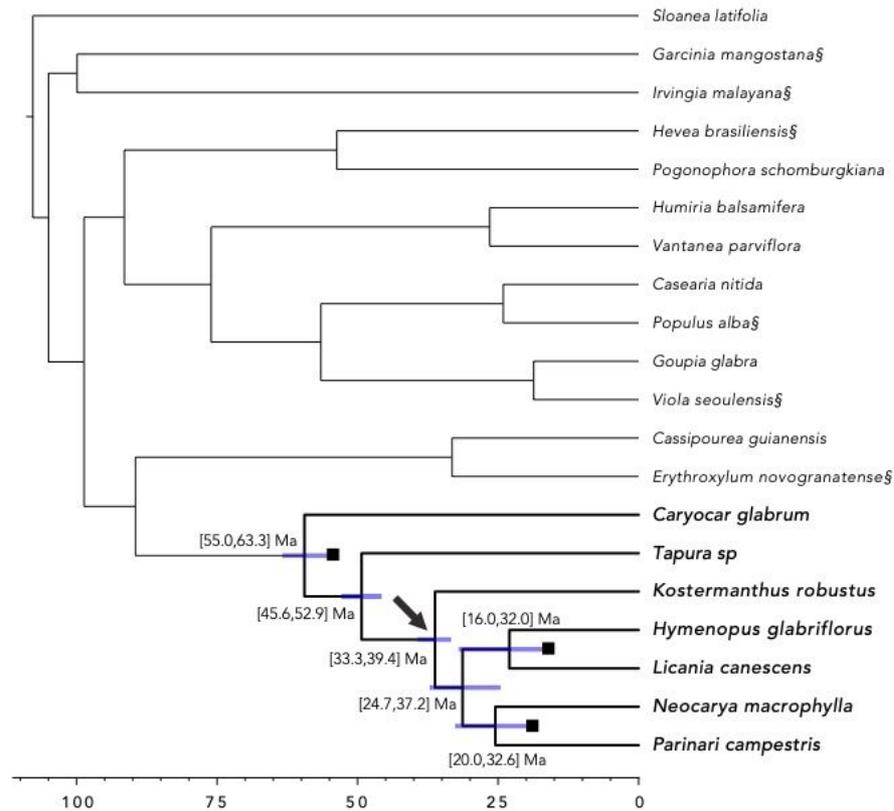


Figure S1. Phylogenetic tree for the 20-taxon dataset, including Chrysobalanaceae, obtained from the software BEAST2. The arrow points to the crown age of Chrysobalanaceae, inferred at ca. 38.9 Ma. Squares indicate fossil constraints.

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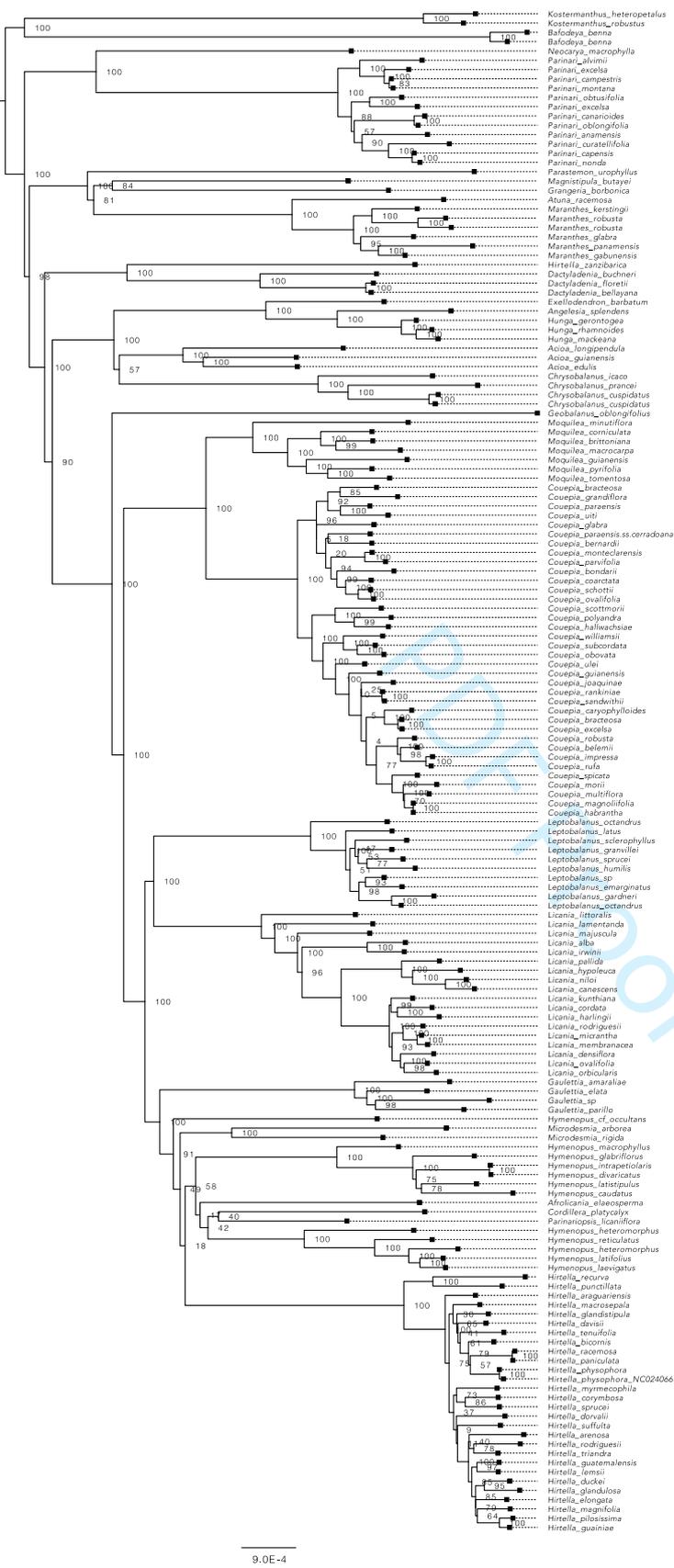


Figure S2. Phylogenetic tree for Chrysobalanaceae, obtained from the software RAxML 8.2.10. Branch support was reported along the branches.

19 Table S1. Description of the accessions included in this study, with plastid genome length and
 20 area coding. Codes for biogeographical areas are as follows: AM: Amazonia, AF: Atlantic
 21 rainforest, DRY: dry corridor and savannas of South America (llanos, cerrado and caatinga),
 22 CA: Central America, the Caribbean, and the Chocó province, AUST: Australia and Oceania;
 23 AFRICA: Africa, SEASIA: Southeast Asia. The column 'Voucher information' includes
 24 details about the voucher are provided, including the sequence laboratory code (in bold),
 25 collector and/or geographical location, and country of collection.
 26

Species	plastome length (bp)	Ecology (from Sothers & Prance, 2003)	Area coding	VOUCHER INFORMATION
<i>Acioa edulis</i>	162850	Known only from a small area of Amazonas, Brazil, where it is locally abundant. Forest of non-flooded ground (terra firme). Also cultivated outside its natural range, especially along the Rio Solimões in Amazonas.	AM	49 ; Sothers1512; BR-174, Reserva de Fruticultura do INPA, Amazonas, KEW11547; Brazil
<i>Acioa guianensis</i>	162332	French Guiana and Amazonian Brazil (AM, AP). Terra firme forest.	AM	108 ; Prance30841; KEW11593; Brazil
<i>Acioa longipendula</i>	162648	Brazil (lower Rio Negro region) (AM, PA). Non-flooded forest.	AM	109 ; Sothers1600; Manaus, grounds of INPA; KEW11571; Brazil
<i>Afrolicania elaeosperma</i>	162176	Scattered distribution from Sierra Leone to Gabon. Coastal forest and fringing forest inside the Guineo-Congolian rainforest region.	AFRICA	Aela ; ADN:GiD1563, voucherGD1606; Gilles Dauby 2012; Gabon
<i>Angelesia splendens</i>	162201	Thailand and Sumatera, Malay Peninsula to Philippines and Sulawesi. Lowland rainforest and in peat swamp, fresh water swamp forest, on seashores and in rocky places.	AUST	Lsplen ; Ambriansyah & Arifin 411; East Kalimantan, Wanariset research station, at MNHN P05562869; Indonesia
<i>Atuna racemosa</i>	162717	Thailand to the Pacific, including Malay Peninsula, Sumatera, Borneo, Sulawesi, Philippines, Maluku, New Guinea, New Britain, Solomon Is., Caroline Is., Fiji, Samoa, Tonga. Well-drained lowland or hill forest up to 600 m, above riverbeds, freshwater or brackish swamp.	AUST	Aracemosa ; Ridsale, Baquiran et al. ISU420 Digallorin, Divinisa camp site; at MNHN; Philippines
<i>Bafodeya benna l</i>	161468	Only known for certain from Fouta Djallon in Guinea, adjacent upland areas in Sierra Leone and in Mali. Derived savanna on well-drained hill soil, and in arborescent savanna, at about 900-1000 m.	AFRICA	110 ; Couch916; Guinea Conakry

					111 ; Mamaden Saiden (M Saiden); Mamou, Fouta Djallon, forest border
<i>Bafodeya benna 2</i>	161360	Idem		AFRICA	'Foret de Quehuel' ENATEF; Guinea
<i>Chrysobalanus cuspidatus 1</i>	162892	Islands	Only known from St. Kitts and Guadeloupe in the Leeward Islands, and Dominica, Martinique and St. Lucia in the Windward Islands	CA	50 ; Hill28129; Kew KEW11520
<i>Chrysobalanus cuspidatus 2</i>	162572	Idem		CA	51 ; Barrier3068; Kew KEW11521. Forêt domaniale de la Basse-Terre, trace des Crêtes, forêt dense humide; Guadeloupe
<i>Chrysobalanus icaco</i>	162845		Widespread in tropical America and tropical Africa. Mainly coastal distribution	AFR,AM, AF,CA	Ci ; KD5286 Kyle Dexter; beachfront Cayenne; French Guiana
<i>Chrysobalanus prancei</i>	162736		Venezuela (Bolívar State) and recently collected in Brazil (near Manaus). Submontane and lowland forests	AM	52 ; Cardozo2536; Kew KEW11522
<i>Cordillera platycalyx</i>	162459		Costa Rica, Venezuela, Colombia and Ecuador. High altitude Andean and Central American forests	AND	57 ; Clark4639; Kew: KEW11542; Bilsa Biological Station. Reserva Ecologica Mache-Chindu, 35 km. W of Quininde. Cube River (NE corner of Station); Ecuador
<i>Couepia belemii</i>	162079		E and SE Brazil. Common in the remnants of the southern Bahia wet forest and in coastal forest.	AF	A ; Sothers1531, Espírito Santo, Linhares, Res. Natural da CVRD; Brazil
<i>Couepia bernardii</i>	162952		Western Amazonia. Growing in terra firme forest	AM	B ; JH6/5 Jenaro Herrero; Roosevelt Garcia; Peru
<i>Couepia bondarii</i>	162065		Brazil, state of Bahia, Forest.	AF	53 ; Sothers1517; EMARC Gregório Bondar, Mun. Ilhéus, Bahia KEW11546; Brazil
<i>Couepia bracteosa 1</i>	162194		Guianas and Amazonia. In primary and secondary forest on non-flooded ground.	AM	C ; P00610245; Paracou Station; French Guiana
<i>Couepia bracteosa 2</i>	162106	Idem		AM	113 ; Sothers1550; Manaus, Reserva Florestal Ducke; Brazil
<i>Couepia caryophylloides</i>	162014		Guianas and Brazil. Primary forest on terra firme.	AM	A110372 ; Acarouany plot; French Guiana
<i>Couepia coarctata</i>	161806		Brazil (Bahia, Mun. de Maraú). Restinga.	AF	54 ; Sothers1519; Bahia, KEW11545; Brazil

1			Eastern Amazonian Brazil and in French		E ; JC 152; Juliette Chamagne;
2					
3					
4	<i>Couepia excelsa</i>	162057	Guiana. Non-flooded forest.	AM	French Guiana
5					
6			Brazil (lower Rio Negro region). Forest on		F ; Sothers1516, Amazonas, ZF-2,
7	<i>Couepia glabra</i>	161977	terra firme.	AM	Reservas do PDBFF; Brazil
8					
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10					
11			Brazil, Bolivia and Paraguay. Cerrados and		Sothers1507 ; Brasília, Distrito
12	<i>Couepia grandiflora</i>	162092	savannas.	CER	Federal, Jardim Botânico; Brazil
13					
14			Guianas and Brazil. Growing on terra firme		Cg ; B421045; BAFOG plot near St
15	<i>Couepia guianensis</i>	162127	or flooded river bank.	AM	Laurent; French Guiana
16					
17			Guyana, Colombia, Venezuela and C		
18			Brazilian Amazonia. In riverine and non-		G ; LV109174; Saut Lavilette; French
19	<i>Couepia habrantha</i>	162148	flooded forest.	AM	Guiana
20					
21					
22					55 ; Aguilar8227; Reinaldo Aguilar,
23	<i>Couepia</i>				San Ramon, camino a el P.N. Braulio
24	<i>hallwachsiae</i>	162082	Endemic to Costa Rica.	CA	Carrillo, KEW11523; Costa Rica
25					
26					H ; Sothers1529; Pernambuco,
27	<i>Couepia impressa</i>	162019	NE Brazil. Primary forest.	AM	Restinga de Ariquindá; Brazil
28					
29			French Guiana and Brazil (Amapá). Forest on		I ; NH200492; Nouragues Station;
30	<i>Couepia joaquinae</i>	162089	terra firme on a table-top hill on clay oxisol	AM	French Guiana
31					
32	<i>Couepia</i>		French Guiana and Brazil. In non-flooded		J ; P01860371; Paracou brown sand;
33	<i>magnoliifolia</i>	162147	forest.	AM	French Guiana
34					
35					K ; Maas9807; Reserva Natural Vale
36	<i>Couepia</i>		NE and SE Brazil. Growing in Atlantic		(CVRD) Joao Neiva; Atlantic Rain
37	<i>monteclarensis</i>	161890	coastal forest.	AF	Forest; Brazil
38					
39			Central Amazonia, Brazil. Forest on terra		L ; Sothers1470; Amazonas, ZF-2,
40	<i>Couepia morii</i>	162131	firmé.	AM	Reservas do PDBFF; Brazil
41					
42			Guyana and Brazil (Roraima). Savannas and		56 ; Dexter5603; KEW11528;
43	<i>Couepia multiflora</i>	162027	savanna scrublands.	CER	Guyana
44					
45			Guianas, Venezuela and central, Colombian,		115 ; Sothers sn; Amazonas, Manaus,
46			Peruvian and Ecuadorean Amazonia. Non-		Reserva Florestal Ducke;
47	<i>Couepia obovata</i>	162030	flooded forest.	AM	KEW11601; Brazil
48					
49			On the coast of Brazil from Pernambuco to		
50			Rio de Janeiro. Restingas, littoral forest, sand		Sothers1509 ; R.J., Rio de Janeiro,
51	<i>Couepia ovalifolia</i>	161928	plains, and sand bars.	AF	Barra da Tijuca, Lote 2; Brazil
52					
53			Eastern and central Amazonian Brazil. Sandy		Sothers1510 ; Amazonas, Manaus,
54	<i>Couepia paraensis</i>	161930	river banks and beaches, and open riverine	AM	Praia Dourada; Brazil
55			forest.		
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<i>Couepia paraensis</i>		In the north of the Planalto of central Brazil.		DUARTE47 ; Mato Grosso, Mun.
<i>cerradonana</i>	162067	Growing in cerrado.	CER	Novo Santo Antônio; Brazil
<i>Couepia parvifolia</i>	161902	Brazil; known only from Rio de Janeiro. Forests.	AF	N; Oliveira1713; C. A. L. de Oliveira Alto da Boa Vista, Estr. da Vista Chinesa; Brazil
<i>Couepia polyandra</i>	162048	Central America from Sinaloa in Mexico to Panama. Riverine forest and low woodland.	CA	JASMITH1530 ; J.Amith 1530; Mexico
<i>Couepia rankinae</i>	162048	Central Amazonia (N of Manaus) and recently collected in central French Guiana. Forest on terra firme.	AM	Sothers1454 ; Manaus, Amazonas, ZF-2, Reservas do PDBFF; Brazil
<i>Couepia robusta</i>	162085	Brazilian Amazonia. Non-flooded forest.	AM	O ; Sothers167; Reserva Florestal Ducke, Manaus - Itacoatiara, km 26; Brazil
<i>Couepia rufa</i>	161992	NE and SE Brazil. Primary forests.	AF	116 ; Sothers1528; Pernambuco; Brazil
<i>Couepia sandwithii</i>	162068	Guyana and Venezuela. Primary forest.	AM	Sothers1465 ; Amazonas, ZF-2, Reservas do PDBFF; Brazil
<i>Couepia schottii</i>	161850	Brazil (Bahia to Rio de Janeiro). Coastal restingas.	AF	Q ; Sothers1532; Espírito Santo, Linhares, Res. Natural da CVRD; Brazil
<i>Couepia scottmorii</i>	162166	Panama; known only from Cerro Jefe. In cloud forest dominated by <i>Clusia</i> and <i>Colpotherinax cookii</i> at 1000m.	CA	58 ; McPherson12340, Cerro Jefe; Panama
<i>Couepia spicata</i>	161955	Brazil (Amazonas). Growing in terra firme forest	AM	R ; Sothers1556, Amazonas, rio Urucu, Área de Exploração da Petrobrás; Brazil
<i>Couepia subcordata</i>	162081	Amazonia. Forest.	AM	Sothers1511 ; Amazonas, Manaus, Campus da UFAM; Brazil
<i>Couepia uiti</i>	162824	Bolivia, Brazil and Paraguay. Savannas, cerrados, and rocky places beside streams and sandy riverbanks.	CER	S ; Parada26; Parada-Gutierrez 26; Laguna la Gaiba, MO; Bolivia
<i>Couepia ulei</i>	162088	Western Amazonia. Riverine forest and non- flooded forest.	AM	T ; Sothers992; Reserva Florestal Ducke, Manaus-Itacoatiara, Km 26; Brazil
<i>Couepia williamsii</i>	161516	Western Amazonia. Forest on non-flooded and periodically flooded ground.	AM	U ; PA10/55; Roosevelt Garcia, Puerto Almendras; Peru
<i>Dactyladenia bellayana</i>	162309	Cameroon, Gabon and perhaps Democratic Republic of Congo. Lowland forests	AFRICA	GiD1956 ; Gilles Dauby; Gabon

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3	<i>Dactyladenia</i>	Central African Republic, Congo, DRC and			V101849 ; Pierre Fabre collection;
4	<i>buchneri</i>	162156 Angola. Riverine forests	AFRICA		Democratic Republic of the Congo
5					
6		Gabon. Rainforest, forest edge next to			
7		savanna, coastal thicket and secondary			
8	<i>Dactyladenia floretii</i>	162312 vegetation.	AFRICA		GiD1939 ; ADN:GiD1939, voucher
9					GD2766, Gilles Dauby 2012; Gabon
10					
11	<i>Exellodendron</i>	Venezuela, Guianas and Amazonian Brazil.			A110225 ; Acarouany plot; French
12	<i>barbatum</i>	162325 Riverine and non-flooded forest	AM		Guiana
13					
14		Restricted to one locality in northern Brazil,			
15		in the foothills and surroundings of Serra do			
16		Aracá, a sandstone mountain of the Guayana			
17	<i>Gaulettia amaraliae</i>	163538 Highlands	TEP		117 ; Stevenson1011 South of Serra
18					do Aracá, KEW11590; Brazil
19					
20		French Guiana, Guyana, western and central			
21		Amazonian Brazil (Acre, Amazonas) and			
22		Colombia. Found in non-flooded forests; also			
23		occurs infrequently in sandy campinarana			
24	<i>Gaulettia elata</i>	162251 vegetation.	AM		Sothers1450 ; Reserva Florestal
25					Ducke, Manaus, Amazonas; Brazil
26					
27		Guyana, French Guiana, Suriname,			
28		Venezuela, Amazonian Brazil (Acre,			
29		Amazonas, Amapá, Roraima), Peru, Ecuador			
30		and Colombia. Savannas, primary and			
31	<i>Gaulettia parillo</i>	162440 secondary forests	AM		118 ; Pereira67; KEW11580; Brazil
32					
33					
34	<i>Gaulettia sp</i>	162059	AM		GEM ; described as <i>L. discolor</i> ;
35					Soesdyke-Linden Highway SL
36					Roosevelt Garcia; Guyana
37					
38					
39					20553S2 ; collected JB Nelson(1999)
40	<i>Geobalanus</i>	SE United States. Pine barrens, sand dunes			ten Mile Creek, Georgia; sampled in
41	<i>oblongifolius</i>	162547 and oak scrubland.	CA		Paris Herbarium (P05562808);
42					Georgia; United States of America
43					
44		Mauritius and Réunion. Forest at low and			
45		medium altitudes on the east and southern			
46		sides of the islands which are exposed to the			
47	<i>Grangeria</i>	SE monsoon and receive more than 3000 mm			Gbor ; Colorado, plot1; Dominique
48	<i>borbonica</i>	162797 of rainfall a year.	AFRICA		Strasberg; La Réunion
49					
50	<i>Hirtella</i>	Brazil, from north of Manaus eastward to			LBD ; NL110214; Nouragues; French
51	<i>araguariensis</i>	163072 Amapá and French Guiana. Upland forest.	AM		Guiana
52					
53		Brazil (C to W Amazonia). White sand			GDP ; MHT410; São Gabriel da
54	<i>Hirtella arenosa</i>	162144 campina.	AM		Cachoeira Morro dos Seis Lagos
55					Lago do Jacaré; Brazil
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		Colombia to the Guianas, Brazil and		
<i>Hirtella bicornis</i>	162909	Amazonian Peru.	AM	GCA ; P01110528; French Guiana
				120 ; Sothers1533; Espírito Santo, Linhares, Reserva Natural da CVRD;
<i>Hirtella corymbosa</i>	164173	Eastern Brazil. Open restinga with savannas	AF	Brazil
		Nicaragua and Costa Rica, Eastern		
		Venezuela, Guianas, and eastern Amazonian		
<i>Hirtella davisii</i>	160638	Brazil. Primary forest on high ground.	AM, CA	GBT ; JC 111; French Guiana
				GEA ; Myrmecophila; VIC2428
		Northern Brazil. Low caatinga forest on		Vicentini, North of Manaus (tbc);
<i>Hirtella dorvalii</i>	162872	sandy soils.	AM	Brazil
		Guyana and C and W Amazonia. Non-		GEI ; Myrmecophila; JH6/515A
<i>Hirtella duckei</i>	162922	flooded forest.	AM	Jenaro JH Roosevelt Garcia; Peru
		Venezuela and W Amazonia. River banks		GEE ; JH1/60 Jenaro JH Roosevelt
<i>Hirtella elongata</i>	162685	and riverine forest.	AM	Garcia; Peru
<i>Hirtella glandistipula</i>	163798	French Guiana and Brazil. Primary and secondary forest on non-flooded ground.	AM	GBI ; P00610010; Paracou; French Guiana
		Commonest in the planalto of C Brazil, but extending into the savannas of Amazonia and the Guianas. Damp forest in open places, mainly gallery forest, river banks and		GBF ; NH200142; Nouragues;
<i>Hirtella glandulosa</i>	162929	savanna margins.	AM, CER	French Guiana
				61 ; Myrmecophila;
				Duivenvoorden2352; Araracuara, bosque alto, suelo arcilloso rojizo de tierra firme; Colombia
<i>Hirtella guainiae</i>	162560	Western Amazonia. Non-flooded forest.	AM	
<i>Hirtella guatemalensis</i>	162922	Central America. Forest on well-drained soil.	CA	121 ; Peterson6824; Panama
<i>Hirtella lemsii</i>	164050	Endemic to Costa Rica. Primary rainforest.	CA	62 ; Aguilar9823; Costa Rica
<i>Hirtella macrosepala</i>	162958	Eastern Venezuela and the Guianas. Primary forest.	AM	B445070 ; BAFOG near Saint Laurent du Maroni; French Guiana
<i>Hirtella magnifolia</i>	162386	Peru and Brazil. Upland forest on terra firme; understorey in open clearings.	AM	LCS ; Jenaro Herrero JH; Roosevelt Garcia et al.; JH6/95A; Peru
<i>Hirtella myrmecophila</i>	162880	Brazil (Central Amazonia). Non-flooded forest	AM	63 ; Myrmecophila; Sothers 1503; Reserva Florestal Ducke, Manaus, Amazonas; Brazil

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4			St. Vincent, Trinidad, Venezuela, Guianas,		
5			Colombia and N Brazil. Open sandy places,		
6			savannas, savanna margins, sandy river banks		GDS ; V200031; Herbar Pierre
7	<i>Hirtella paniculata</i>	163046	and islands.	AM,CA	Fabre, cf French Guiana
8					
9					
10	<i>Hirtella physophora</i>	162984	Guianas and Amazonia. Non-flooded forest.	AM	Hp ; Myrmecophila; French Guiana
11					
12					
13	<i>Hirtella pilosissima</i>	162381	Western Amazonia. Non-flooded forest.	AM	GEN ; TS55rg 169; Tamshiyacu TS; Roosevelt Garcia et al.; Peru
14					
15					
16			Venezuela, Guianas, Colombia and E		
17			Amazonian Brazil. Common species of the		
18			Guayana Highland and the Upper Rio Negro		GDM ; Barcelos Serra do Araca
19			in sandy savannas, open and low forest in		Arredores da serra FMC0386; FM
20	<i>Hirtella punctillata</i>	163084	sandstone areas, and open river margins.	TEP	Costa, sent by Vicentini; Brazil
21					
22					
23					
24			Central America and Trinidad to Bolivia and		
25			E Brazil Primary forest especially beside		
26			rivers and streams, but also in understorey of		Hr ; Pierre-Jean Malé, Nouragues ;
27	<i>Hirtella racemosa</i>	162890	forest on non-flooded ground	AM	French Guiana
28					
29					
30					122 ; Ecuador, Homeier2190; Reserva
31			Ecuador and Peru. Andean primary forest, to		San Francisco, ca 2000m asl,
32	<i>Hirtella recurva</i>	163411	1700 m.	MONT	Zamora-Chinchipe; Ecuador
33					
34					
35	<i>Hirtella rodriguesii</i>	162164	Peru and C Amazonian Brazil. Non-flooded		GEH ; JH6/123 Jenaro JH; Roosevelt
36			forest. Flowering June–Sept.	AM	Garcia et al.; Peru
37					
38					123 ; Sothers 1530; Brazil, Espírito
39					Santo, Linhares, Res. Natural da
40	<i>Hirtella sprucei</i>	164140	Northeastern and E-C Brazil. Forests.	AF	CVRD; Brazil
41					
42			French Guiana and N Brazil. Non-flooded		NH200131 ; Nouragues Station;
43	<i>Hirtella suffulta</i>	162646	forest.	AM	French Guiana
44					
45			French Guiana and N Brazil. Primary and		GBS ; JC 084; noted as <i>Emmotum</i> in
46	<i>Hirtella tenuifolia</i>	162715	secondary forest.	AM	previous analysis; French Guiana
47					
48			Central Mexico through Central America and		KTT ; BOLLC391; La Chonta J. C.
49			the Antilles to northern South America and		Liconia; Bolivia
50	<i>Hirtella triandra</i>	163055	SE Brazil	CA, AM	
51					
52			Endemic to NW New Caledonia. Frequent		H-gerontogea ; Hequet 4104;
53			beside creeks and in riverine woodland in		Vanessa Hequet; Nouméa; Nouvelle
54	<i>Hunga gerontogea</i>	162404	serpentine terrain and on serpentine alluvia	AUST	Calédonie
55					
56					
57			Known only from New Caledonia (northern		37 ; Vardrot938; Vanessa Hequet;
58	<i>Hunga mackeeana</i>	162414	part). Maquis.	AUST	Nouméa; Nouvelle Calédonie
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3			S New Caledonia (including Île des Pins),		
4			and Lifou, in the Loyalty Islands. Forests on		38 ; Hequet1; Vanessa Hequet;
5	<i>Hunga rhamnoides</i>	162377	serpentine	AUST	Noumea; Nouvelle Calédonie
6					
7					
8	<i>Hymenopus</i>		Widespread in Amazonia (Guianas,		67 ; Sothers sin#; Reserva Florestal
9	<i>caudatus</i>	162527	Colombia, Ecuador, Peru, Brazil). Flooded as	AM	Ducke, Manaus, Amazonas; Brazil
10			well as non-flooded forest.		
11					125 ; Gillespie725; Linden Highway,
12	<i>Hymenopus</i>		Guianas and northern Brazil. Forest on terra		near turnoff to St. Cuthbert's
13	<i>divaricatus</i>	162843	firme and savanna margins.	AM	Mission; Guyana
14					
15					
16	<i>Hymenopus</i>		Costa Rica, Colombia, Venezuela, Guianas	CA, CHOCO,	A110093 ; Acarouany plot; French
17	<i>glabriflorus</i>	163010	and Brazil (Amapá, Pará). Terra firme forest.	AM	Guiana
18					
19	<i>Hymenopus</i>		Central and South America.	AM, CA	Lh ; LV109473; French Guiana
20	<i>heteromorphus 1</i>	162910			
21	<i>Hymenopus</i>		Idem	AM, CA	126: Sothers1547; Porto Urucu,
22	<i>heteromorphus 2</i>	162580			Amazonas; Brazil
23					
24	<i>Hymenopus</i>		Guianas, N Brazil and Amazonian Colombia,		GEK ; MH-046; Mabura-Hill MH;
25	<i>intrapetiolaris</i>	162838	Peru and Venezuela. Lowland forest in open	AM	Roosevelt Garcia; Guyana
26			places.		
27	<i>Hymenopus</i>		Venezuela, Guianas, Brazil and Peru. Terra		GBD ; M17116512; Montagne
28	<i>laevigatus</i>	160126	firme forest	AM	Tortue; French Guiana
29					
30	<i>Hymenopus</i>		Guianas, Venezuela and Amazonian Ecuador,		LCD ; PE5397; French Guiana
31	<i>latifolius</i>	160446	Peru and Brazil. Non-flooded forest	AM	
32					
33	<i>Hymenopus</i>		French Guiana and Venezuela. Forest on high		GBB ; M17116079; Montagne
34	<i>latistipulus</i>	162994	ground.	AM	Tortue; French Guiana
35					
36	<i>Hymenopus</i>		Guianas, Venezuela, Peru and Amazonian		KD5284 ; Kyle Dexter, French
37	<i>macrophyllus</i>	162677	Brazil. Periodically flooded forest	AM	Guiana
38					
39	<i>Hymenopus</i>		French Guiana, western (Colombia, Ecuador,		68 ; Sothers, Ducke tree#499; Brazil
40	<i>reticulatus</i>	162555	Peru) and Brazilian Amazonia. Non-flooded	AM	
41			and periodically flooded forest.		
42					
43	<i>Kostermanthus</i>		Malay Peninsula, Borneo and Sumatera to		69 ; Ahmad7485; near Sungai Liang
44	<i>heteropetalus</i>	161914	Sulawesi and S Philippines. Lowland	SEASIA	Arboretum Forest Reserve; Brunei
45			rainforest from sea level to 500 m.		
46					
47	<i>Kostermanthus</i>		Borneo (Sarawak). Hill slope in mixed		Kostermanthus ; Sarawak,
48	<i>robustus</i>	161788	dipterocarp forest to 200 m., and in kerangas	SEASIA	Semengoh Arboretum, 1st Division;
49			(heath) forest to 600 m.		Paie; Lee, B. 38000; Malaysia
50					
51	<i>Hymenopus cf.</i>		Widespread in Amazonia. Gallery forest,		130 ; D daSilvaCosta396 ; previously
52	<i>occultans</i>	162471	periodically flooded forest, river margins,	AM,SAV	identified as <i>Leptobalanus apetalus</i> ,
53			savanna margins, and open river beaches on		identification modified in Feb. 2020;
54			sandy soil.		Brazil
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4	<i>Leptobalanus</i>		Venezuelan Guayana and Amazonian Brazil	
5	<i>emarginatus</i>	162196	and Peru. Non-flooded forest, especially on granitic outcrops.	AM,TEP GEF ; JH1/168; Jenaro Herrero, R Garcia; Peru
6				
7				
8	<i>Leptobalanus</i>		Bolivia, and in C, NE, SE and N Brazil.	
9	<i>gardneri</i>	162289	Riverine forest bordering cerrado, and in cerrado itself.	CER 131 ; Queiroz11012; Brazil
10				
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12	<i>Leptobalanus</i>		From Panama, Ecuador and Colombia to	
13	<i>granvillei</i>	162207	French Guiana, Guyana, Venezuela and Brazil (Amazonas). Upland forest on terra firme and along riverbanks.	AM,CA GDV ; V200639; Herbar Pierre Fabre; French Guiana
14				
15	<i>Leptobalanus</i>			KVF ; Estação Ecologica de Assis
16	<i>humilis</i>	162057	Bolivia and Brazil. In cerrados.	PEEA; Renato Lima, São Paulo ; Brazil
17				
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19	<i>Leptobalanus</i>		Guianas, Venezuela, C & W Amazonia	
20	<i>latus</i>	162060	(Colombia, Ecuador, Peru and Brazil). Non- flooded forest and secondary scrub on sandy soil	AM GED ; Allpahuayo AM; AM59 rg- 059; Roosevelt Garcia; Peru
21				
22				
23	<i>Leptobalanus</i>		Widely distributed from N Venezuela	
24	<i>octandrus 1</i>	162298	through the Guianas, Peru, Colombia, Bolivia and E & C Amazonia to Northeast, East- central & Southeast Brazil. Forest	AM 132 ; Castro165; Brazil
25				
26	<i>Leptobalanus</i>			GAL ; Brazil LIC OCT 10447 (PECB
27	<i>octandrus 2</i>	162340	Idem	119) Parque Estadual Carlos Botelho, São Paulo, Renato Lima; Brazil
28				
29	<i>Leptobalanus</i>		Bolivia, Colombia, Peru, eastern and	
30	<i>sclerophyllus</i>	162377	southern Amazonia and the planalto of central Brazil. Non-flooded forest, riverine forest or cerrado	AM,CER 133 ; Pereira3558; Brazil
31				
32				
33	<i>Leptobalanus</i>			KTQ ; JH6/325 Jenaro Herrero,
34	<i>sp</i>	159487		Roosevelt Garcia, misdet as <i>L. blackii</i> (perhaps <i>L. longistylus?</i>); Peru
35				
36	<i>Leptobalanus</i>		Guianas, Venezuela and in the Amazon	
37	<i>sprucei</i>	162234	region of Brazil. Primary forest on non- flooded ground and secondary forest	AM Ls ; P01860159; Paracou Station; French Guiana
38				
39	<i>Licania</i>		Guianas and adjacent Venezuela and Brazil	
40	<i>alba</i>	162489	(Amapá, Amazonas, Pará). Primary forest.	AM La ; P00610185; Paracou Station; French Guiana
41				
42	<i>Licania</i>		Guianas, Venezuela, Bolivia, Peru and	
43	<i>canescens</i>	162624	widespread in Amazonian Brazil. Riverine and periodically flooded forest	AM Lc ; NH200019; Nouragues Station; French Guiana
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		Venezuela (Cerro Yapacana, where it is reported to be abundant) and in Amazonian		
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6	<i>Licania cordata</i>	160064 Brazil (Amazonas). Savannas	SAV	GDQ ; MHTA486; Brazil
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8				
9	<i>Licania densiflora</i>	151268 Guianas and adjacent Venezuela and Brazil. Primary forest on high ground and slopes.	AM	GBV ; JC 136; Juliette Chamagne; French Guiana
10				
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12				
13	<i>Licania harlingii</i>	163427 Western Amazonia: Bolivia, Colombia, Ecuador, Peru and Brazil (Acre). Terra firme forest.	AM	136 ; Homeier31755; Ecuador
14				
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20	<i>Licania hypoleuca</i>	162444 A wide-ranging variety from Southern Mexico to Bolivia, the Guianas, Venezuela, Colombia, Peru and scattered localities in NE and Amazonian Brazil. Sandy soils in forest and savannas	AM,CA	LCB ; NH22023; Nouragues Station; French Guiana
21				
22				
23	<i>Licania irwinii</i>	162686 Guianas, Venezuela and Brazil (Amazonas). Forested slopes.	AM	LCE ; KD5287; Kyle Dexter; French Guiana
24				
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29	<i>Licania kunthiana</i>	162255 A wide-ranging species from Costa Rica to Bolivia, the Guianas, Venezuela, Peru and throughout Brazil. Non-flooded forest, riverine forest, cerrados, or secondary forest	AM,CER, CA	GAV ; LV113008; Saut Lavilette; French Guiana
30				
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32				
33	<i>Licania lamentanda</i>	162683 Brazil (Bahia). Restinga on sandy soil, 25 m altitude, growing with many individuals of piaçaba palm	AF	137 ; Sothers tree1870; Bahia; KEW11607; Brazil
34				
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36				
37	<i>Licania littoralis</i>	162242 E Brazil, from Paraíba to Rio de Janeiro. Confined to coastal restingas and coastal forests.	AF	138 ; Sothers tree2850; Bahia; KEW11608; Brazil
38				
39				
40	<i>Licania majuscula</i>	162436 Guianas and Amazonian Brazil. Upland forest and high riverine forest.	AM	A110139 ; Acarouany Plot; French Guiana
41				
42	<i>Licania membranacea</i>	162204 Trinidad, the Guianas, Venezuela and Brazil. Forested slopes and non-flooded forest.	AM	M17116059 ; Montagne Tortue; French Guiana
43				
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53	<i>Licania micrantha</i>	158098 Widespread from Costa Rica to the Guianas, Venezuela, Colombia, Peru, Amazonian Brazil and Bolivia. Its known range has been recently extended west of the Andes in Colombia (Chocó and Valle) and in Brazil (Bahia). Non-flooded forests and Atlantic coastal forests.	AM,CA	NH200679 ; Nouragues Station; French Guiana
54				
55				
56	<i>Licania niloi</i>	162518 Bolivia and N Brazil (Amazonas, Rondônia). Primary forest.	AM	140 ; Sothers tree219-02; KEW11600; Brazil
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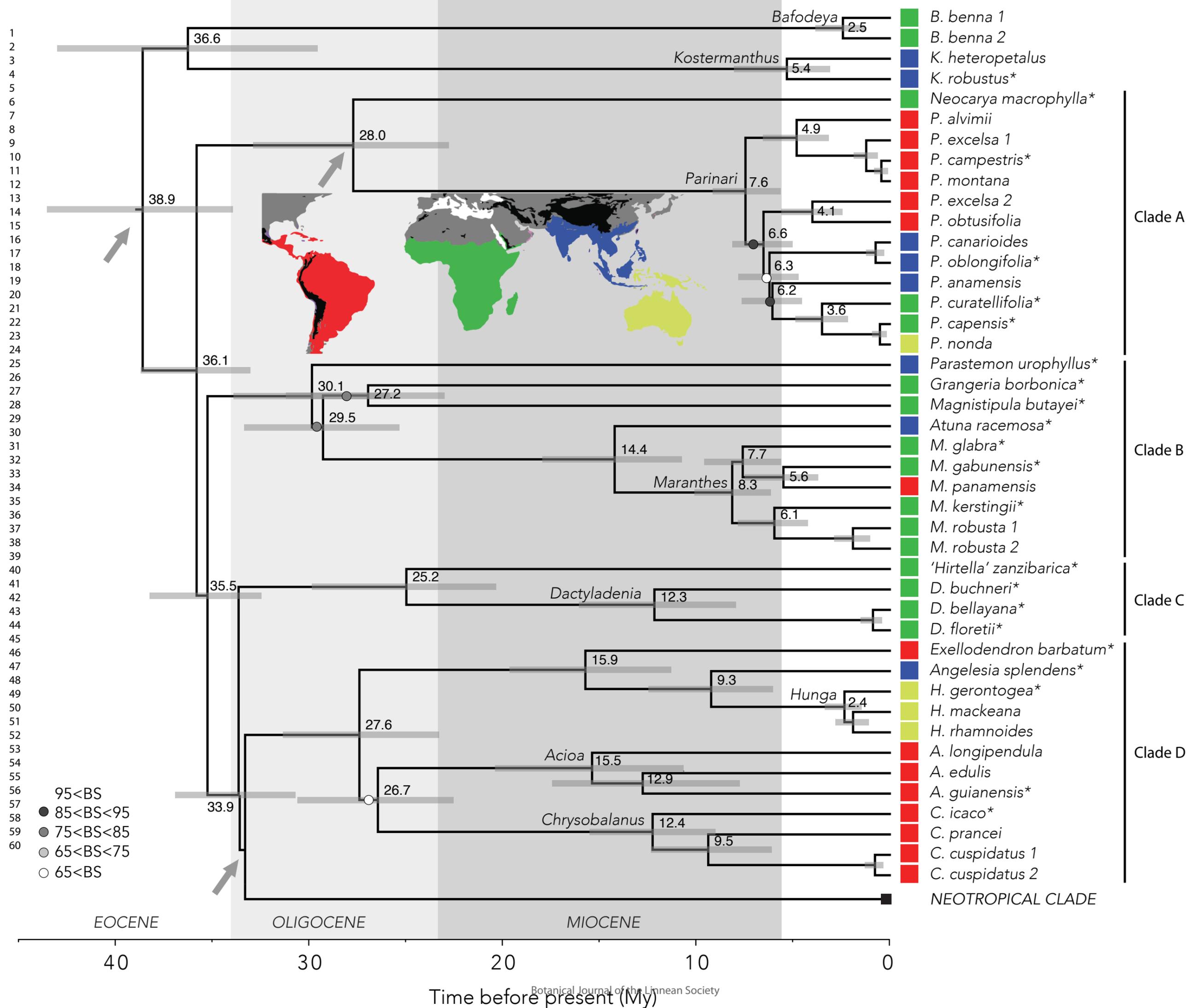
		Amazonian Venezuela and adjacent Brazil (Amazonas). Riverine forest and savanna margins.	AM	LCT ; SL-07; Soesdyke-Linden Road, Guyana; Roosevelt Garcia
<i>Licania orbicularis</i>	162259			P610256 ; Paracou Station; French Guiana
<i>Licania ovalifolia</i>	162320	Guianas and Brazil (Amapá). Primary forest.	AM	
<i>Licania pallida</i>	162406	Guianas and Venezuela to Brazilian Amazonia, Peru and Ecuador. Non-flooded forest	AM	GDR ; P009 Prance14070; rio Ituxi, vicinity of Boca do Curuquete, varzea forest, 1971; at MNHN; Brazil
<i>Licania rodriguesii</i>	162314	French Guiana and Brazilian Amazonia (Amazonas, Pará). Non-flooded forest.	AM	141 ; Sothers tree245-02; KEW11599 ; Brazil
<i>Magnistipula butayei</i>	162546	Throughout the Congo River basin and some of its tributaries to the south. River banks and sometimes also in forest on dry land in valley bottoms, in lowlands up to 450 m.	AFRICA	NONB ; F2P2C2603; M'Baiki Plot; collected M Réjou-Méchain; Central African Republic
<i>Maranthes gabunensis</i>	162774	West Africa in a narrow coastal belt from SE Nigeria to the extreme SW corner of DRC, just N of the River Congo. Evergreen rainforest.	AFRICA	GD1917 ; ADN:GiD1917, voucher GD2800; Gilles Dauby; Gabon
<i>Maranthes glabra</i>	162290	Widely distributed throughout the greater part of the Guineo-Congolian region from Sierra Leone to Ituri in E DRC and in Cabinda and Angola. Evergreen and semi-evergreen rainforest; absent only from the drier types.	AFRICA	GD1845 ; ADN:GiD1845, voucher:GD2848; Gilles Dauby; Gabon
<i>Maranthes kerstingii</i>	162400	Sudanian Region from Togo to the Central African Republic. Fringing forest in the wetter parts of the Sudanian region. In West Africa occurs mainly in upland areas.	AFRICA	F1P1C4988 ; M'Baiki Forest Station; Maxime Réjou Méchain; Central African Republic
<i>Maranthes panamensis</i>	162462	Panama (Isthmus), and recently collected in Nicaragua and Costa Rica. Dense rainforest.	CA	143 ; Hammel16653; Parque Nacional Corcovado. Sirena station; lower Olla trail; Costa Rica
<i>Maranthes robusta 1</i>	162417	West Africa from the Ivory Coast to Nigeria. Swamp forest and semi-evergreen rainforest	AFRICA	26 ; MH2306; Myriam Heuertz; Benin
<i>Maranthes robusta 2</i>	162130	Idem	AFRICA	27 ; MH2285; Myriam Heuertz; Benin
<i>Microdesmia arborea</i>	162521	From Mexico through Central America to Bolivia, Colombia, Peru, Ecuador, Venezuela and northern Brazil. Dry plains, slopes and scrub forest.	CA,AM	72 ; Ibarra-Manriquez6065; Nueva Italia; Mexico

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4	<i>Microdesmia rigida</i>	162617	Native to northeastern Brazil. Dry forest and gallery forest	AF	144 ; Cardoso1052; Brazil
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6	<i>Moquilea</i>		W Amazonia in Bolivia, Colombia, Ecuador,		
7			Peru and Brazil. Non-flooded and		GEG ; JH2/286 jen2/286; Roosevelt
8	<i>brittoniana</i>	162443	periodically flooded forest	AM	Garcia; Peru
9					
10					73 ; Aguilar9846; Rincon, margen
11	<i>Moquilea</i>		Costa Rica (Puntarenas and Osa Peninsula).		derecha de Quebrada Aparicio; Costa
12	<i>corniculata</i>	162438	Lowland rainforest.	CA	Rica
13					
14			Guianas, Venezuela, the Amazon delta, W		
15			Amazonia, Ecuador, Peru and in Brazil.		
16	<i>Moquilea guianensis</i>	161828	Riverine, terra firme and premontane forests	AM	LCC ; PE1075; French Guiana
17					
18					139 ; Homeier38001; Province of
19	<i>Moquilea</i>		Panama, Colombia, Ecuador and Peru.		Napo, Parque Nacional Sumaco-
20			Lowland forests to 600 m and in premontane		Galeras, Rio Hollin watershed;
21	<i>macrocarpa</i>	162389	rain forest in Panama.	CA,AM	Ecuador
22					
23	<i>Moquilea</i>		Guianas, Venezuela, Bolivia and Amazonian		
24			Brazil. Non-flooded forests and gallery		NH200162 ; Nouragues Station;
25	<i>minutiflora</i>	162438	forests.	AM	French Guiana
26					
27			Martinique to Trinidad, adjacent Venezuela		39 ; Licania pyrifolia; Hato Pinero;
28	<i>Moquilea pyrifolia</i>	162493	and Colombia. Lowland forest and riverine		AF28517 Angel Fernandez & J
29			forest in open places.	AM	Chave; Venezuela
30					
31			Northeastern, southeastern and southern		Ltom ; Olivier Maurin NA cultivated
32	<i>Moquilea tomentosa</i>	162555	Brazil. Native to the coastal restinga forest	AF	in South Africa; South Africa
33					
34			Common in West Africa in a coastal strip, in		
35	<i>Neocarya</i>		places up to 300 km wide, from Senegal to		
36			Liberia, and with a scattered east-west		
37			distribution in the much drier and more		
38			continental northern half of the Sudanian		
39	<i>macrophylla</i>	162410	region 700.1000 km inland. Cultivated in		Nmac ; Association France-Sahel,
40			Panama. Apparently confined to sandy soils.	AFRICA	Sénégal
41					
42			Widely distributed species from the Nicobar		
43	<i>Parastemon</i>		Islands and Thailand through the Malay		
44			Peninsula to Borneo and Sumatra. Lowland		SARAWAK100485 ;
45	<i>urophyllus</i>	162681	and coastal forest; commonest in swamp and		Niyomdham1083; Thailand
46			secondary forest	SEASIA	
47					
48			Brazil (coastal Bahia). Littoral forest. Some		74 ; Barbosa-Silva sin#; Bahia;
49	<i>Parinari alvimii</i>	162320	collections of this species have ants nests		KEW11534 ; Brazil
50			formed by the curvature of the leaves	AF	
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3			Thailand, Cambodia, Laos, Vietnam. 41:		
4			CBD, LAO, THA, VIE. Open deciduous		
5			forest, forest beside streams, hill forest to		
6					
7	<i>Parinari anamensis</i>	161810	1000 m altitude.	SEASIA	LCL ; V105002; Herbar Pierre Fabre
8					
9					
10			Trinidad, the Guianas, and adjacent		
11			Venezuela, Colombia and Brazil. River		
12					
13	<i>Parinari campestris</i>	162638	margins, savanna margins, and open forests.	AM	Pca ; Paracou Station ; French Guiana
14					
15			Sumatera, Borneo (Kalimantan, Brunei,		
16			Sarawak, Sabah) and Philippines (Palawan).		LCI ; SAN152336; Sandakan
17	<i>Parinari canarioides</i>	159646	Rainforest up to 800 m	SEASIA	Herbarium; Malaysia
18					
19			Throughout the greater part of the Zambezi		
20			region and southwards to Natal and		
21			northwards into the Congo Republic and		Pcap ; OM3613 subspecies incohata;
22					Olivier Maurin; South Africa
23	<i>Parinari capensis</i>	162529	DRC.	AFRICA	
24					
25			Widespread in woodland on the African		
26			mainland from Senegal to Kenya and		
27			southwards to Namibia and the Transvaal, but		
28			absent from the forests of the Guineo-		
29			Congolian region; also in coastal forest on the		
30			east side of Madagascar and in the		
31					
32			Seychelles. Woodland, wooded grassland and		Pcura ; OM2621; Olivier Maurin;
33	<i>Parinari</i>				South Africa
34	<i>curatellifolia</i>	157972	coastal forests	AFRICA	
35					
36			From Amazonian Colombia, Peru, Bolivia		
37			and E Venezuela through the Guianas and		GAS ; B445017; BAFOG; French
38					Guiana
39	<i>Parinari excelsa 1</i>	160789	Amazonian Brazil to E-C and S Brazil	AM, AF	
40					75 : Brazil(Sasaki1493); Parque
41					Estadual Cristalino, Vegetação aberta
42			From Amazonian Colombia, Peru, Bolivia		marginal do Rio Cristalino;
43			and E Venezuela through the Guianas and		
44					KEW11533 ; Brazil
45	<i>Parinari excelsa 2</i>	162412	Amazonian Brazil to E-C and S Brazil	AM, AF	
46					
47			French Guiana, Colombia and N Brazilian		LAK ; LV109130; Saut Lavilette;
48	<i>Parinari montana</i>	160283	Amazonia. Non-flooded forest.	AM	French Guiana
49					
50			New Guinea and northern Australia. Savanna,		
51			open forest, forest on rocky areas in lowlands	AUST	76 ; Crawford434; KEW11531
52	<i>Parinari nonda</i>	162368			
53			Malesian Peninsula (S Kelantan to Johore),		
54			Sumatera, Borneo (Sabah, Kalimantan).		SAN152336 ; is not the correct code:
55					SAN152716; Sandakan Herbarium;
56	<i>Parinari</i>		Lowland rainforest and beside rivers or in		
57	<i>oblongifolia</i>	162515	valleys and extending to 450 m altitude	SEASIA	Malaysia
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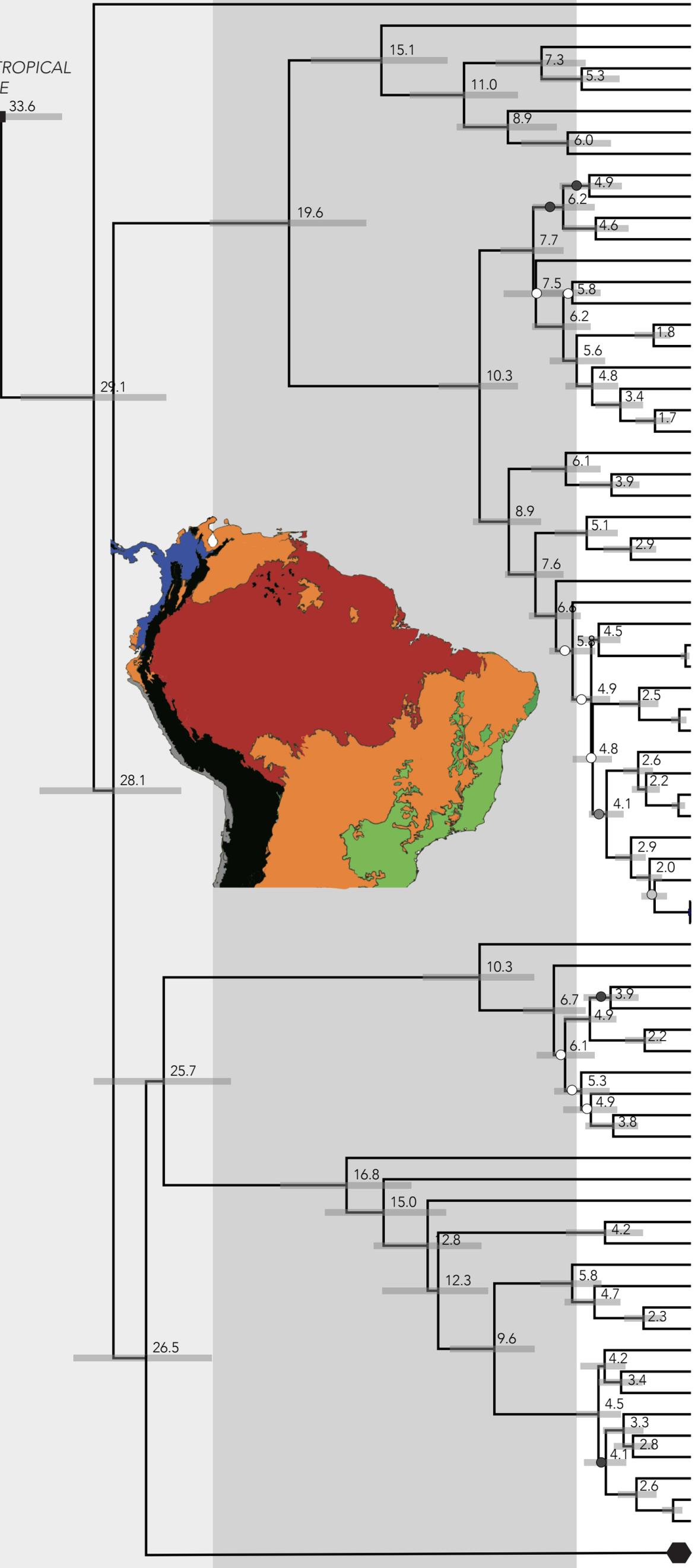
				77; Queiroz15137; Queiroz, L.P.de; Rodovia Go - 118 (São João d'Aliança para Alto Paraiso)
		Planalto of Central Brazil, SE Brazil, Paraguay and Bolivia. Cerrado and open disturbed areas	CER	KEW11532; Brazil
<i>Parinari obtusifolia</i>	162518			
		Guianas, Venezuela and Amazonia. Open forest at river margins, savanna margins and in secondary forest.	AM	GBK ; P00610743; Paracou Station ; French Guiana
<i>Parinariopsis licaniiflora</i>	160393			
		Eastern Africa in Tanzania, Kenya, Malawi, Mozambique and Zambia. Widespread in fringing forest, coastal forest, forest in lower slopes of mountains to about 900 m.	AFRICA	OM2649 ; Olivier Maurin; South Africa
<i>'Hirtella' zanzibarica</i>	162362			

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NEOTROPICAL
CLADE



- Geobalanus oblongifolius*
- M. minutiflora*
- M. corniculata
- M. brittoniana
- M. macrocarpa
- M. guianensis
- M. pyrifolia
- M. tomentosa*
- C. bracteosa 2
- C. grandiflora
- C. paraensis*
- C. uiti
- C. glabra
- C. bernardii
- C. paraensis.cerradoana*
- C. monteclarensis
- C. parvifolia
- C. bondarii
- C. coarctata
- C. ovalifolia*
- C. schottii
- C. scottmorii
- C. hallwachsiae
- C. polyandra*
- C. williamsii
- C. obovata
- C. subcordata*
- C. ulei
- C. guianensis*
- C. joaquinae
- C. rankinae*
- C. sandwithii*
- C. caryophylloides*
- C. bracteosa 1
- C. excelsa
- C. robusta
- C. belemii
- C. impressa
- C. rufa
- C. spicata
- C. morii
- C. multiflora
- C. habrantha
- C. magnoliifolia
- L. octandrus 2
- L. latus
- L. emarginatus
- L. sp
- L. gardneri
- L. octandrus 1
- L. sclerophyllus
- L. granvillei
- L. humilis
- L. sprucei*
- L. littoralis
- L. lamentanda
- L. majuscula*
- L. alba*
- L. irwinii
- L. pallida
- L. hypoleuca
- L. canescens*
- L. niloi
- L. kunthiana
- L. cordata
- L. harlingii
- L. densiflora
- L. orbicularis
- L. ovalifolia*
- L. rodriguesii
- L. membranacea*
- L. micrantha*
- REST OF NEOTROPICAL CLADE

Moquilea

Couepia

Leptobalanus

Licania

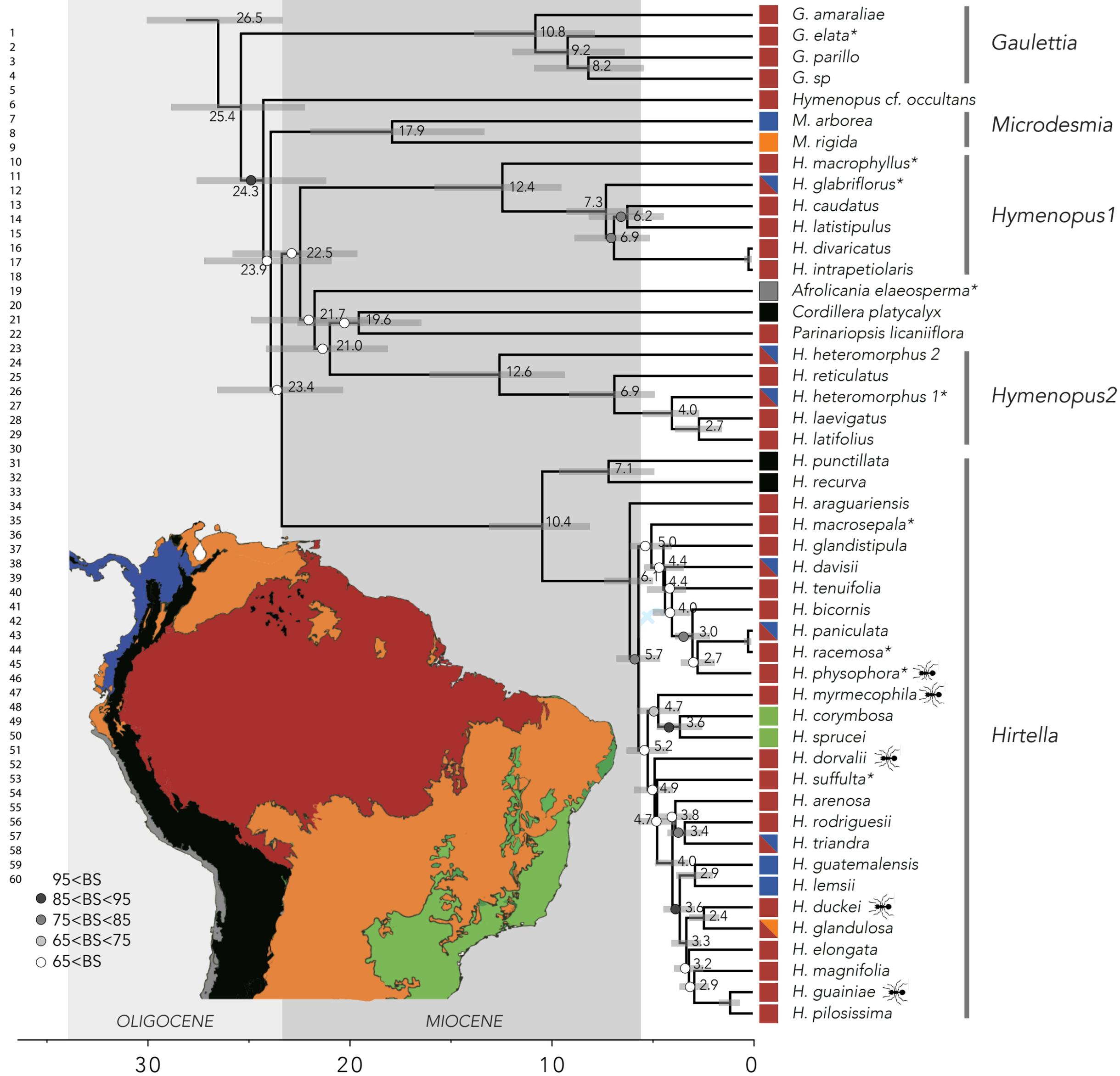
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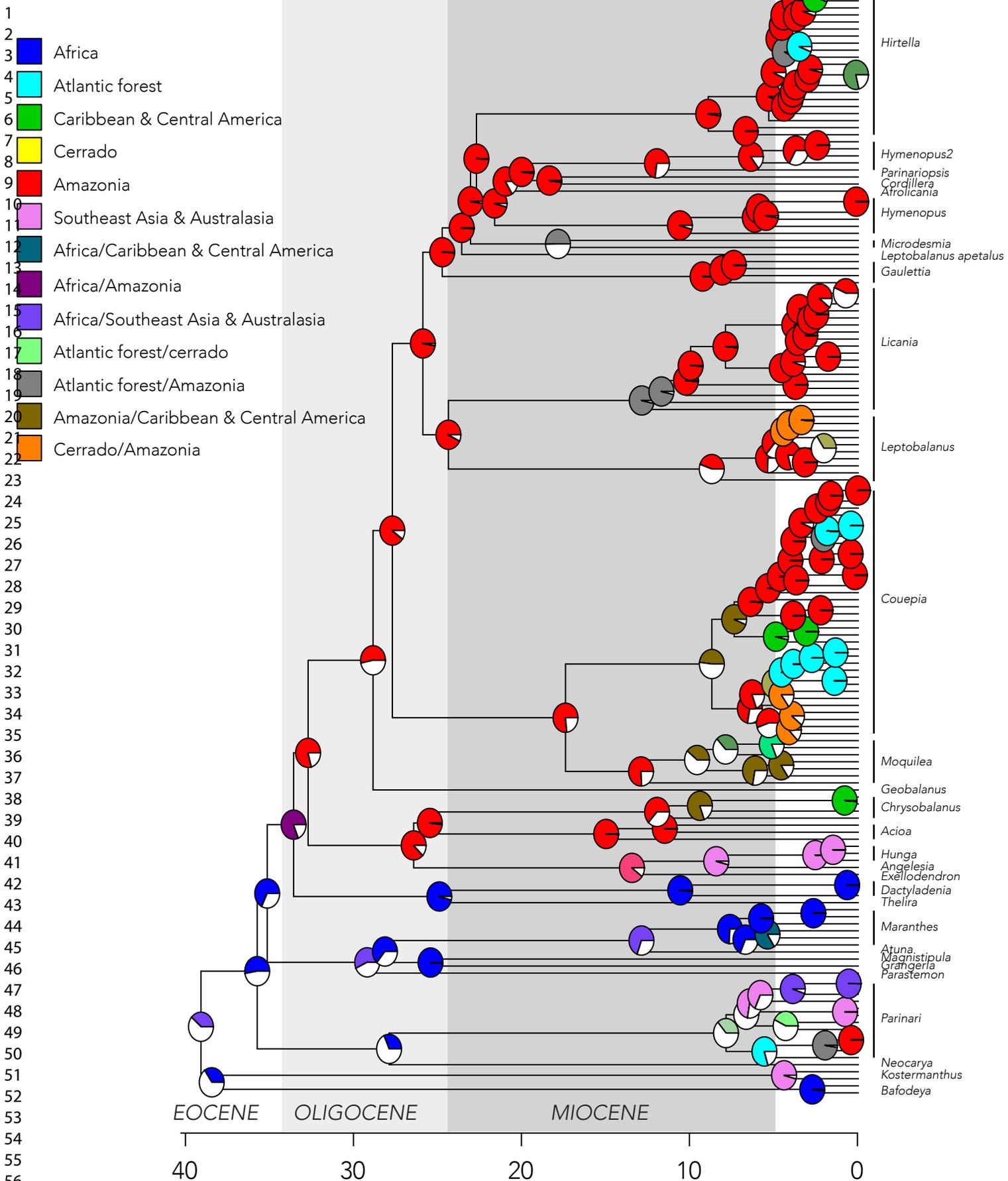
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MIOCENE

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Time before present (My)





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