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Rapid diversification rates in Amazonian Chrysobalanaceae inferred from plastid genome phylogenetics

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Abstract

We studied the evolutionary history of Chrysobalanaceae with phylogenetic analyses of complete plastid genomes from 156 species to assess the tempo of diversification in the Neotropics and help to unravel the causes of Amazonian plant diversification. These plastid genomes had a mean length of 162,204 base pairs, and the nearly complete DNA sequence matrix, with reliable fossils, was used to estimate a phylogenetic tree. Chrysobalanaceae diversified from 38.9 Mya (95% highest posterior density, 95%HPD: 34.2-43.9 Mya). A single clade containing almost all Neotropical species arose after a single dispersal event from the Palaeotropics into the Amazonian biome *c.* 29.1 Mya (95%HPD: 25.5-32.6 Mya), with subsequent dispersals into other Neotropical biomes. All Neotropical genera diversified from 10 to 14 Mya, lending clear support to the role of Andean orogeny as a major cause of diversification in Chrysobalanaceae. In particular, the understory genus *Hirtella* diversified extremely rapidly, producing > 100 species in the last 6 My (95% HPD: 4.9-7.4 My). Our study suggests that a large fraction of the Amazonian tree flora has been assembled *in situ* within the last 15 My.

ADDITIONAL KEYWORDS: Amazonia, molecular dating, Malpighiales, phylogenetic inference, tropical forest.

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

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

Chrysobalanaceae, the coco plum family, with 545 species, are a mid-sized pantropical family and a notable component of the Neotropical tree flora (Prance, 1972), with *c.* 80% of its species found only in the Neotropics (Prance & Sothers, 2003). All Chrysobalanaceae are woody plants, ranging in height from 10 cm to > 40 m, with a uniform vegetative architecture (Prance & White, 1988). Across Amazonian rainforests, an analysis of 1,170 tree inventory plots (≥ 10 cm in trunk diameter) reveals that Chrysobalanaceae rank seventh in tree dominance behind Fabaceae, Lecythidaceae, Sapotaceae, Malvaceae, Moraceae and Burseraceae (ter Steege *et al.*, 2013). Their centre of diversity is Amazonia, with 251 species restricted to lowland Amazonian forests, but the family is found in virtually all Neotropical biomes, notably the Brazilian Atlantic forest (47 species), forests of Central America, Colombian Chocó and the Caribbean (47 species), dry habitats (29 species: 15 in the Brazilian cerrado, 11 in South American savannas, and three in seasonally dry forests), and at high elevation (29 species: 18 in the Andes, 11 restricted to the Guyana highlands; Prance & Sothers, 2003).

Generic delimitation has been challenging in Chrysobalanaceae (for a historical account, see Prance & White, 1988). There are currently 27 genera recognized, 11 Palaeotropical, 12 Neotropical, and three amphi-Atlantic (*Chrysobalanus* L., *Parinari* Aubl., and *Maranthes* Blume). The two non-Neotropical species of *Hirtella* L. from eastern Africa and Madagascar should be reassigned to the old genus name from Madagascar, *Thelira* Thouars. Eight genera are found in Oceania and Southeast Asia, and ten occur in Africa and Madagascar. Recent changes to generic delimitations in Chrysobalanaceae include the resurrection of *Angelesia* Korth. for three Southeast Asian species previously included in *Licania* Aubl. (Sothers & Prance, 2014), a revision of *Couepia* Aubl., with four species transferred to other genera, and a new genus, *Gaulettia* Sothers & Prance, created to accommodate species of the former *parillo* clade of *Couepia* (Sothers *et al.*, 2014), and splitting of the large polyphyletic Neotropical genus *Licania* into eight genera (Sothers *et al.*, 2016). With clarified generic delimitation, an improved interpretation of the diversification and biogeography is now possible for the family.

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

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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.

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24 126 MATERIAL AND METHODS

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27 128 DE-NOVO PLASTID GENOME SEQUENCING

28 129
29 130 We sequenced full plastid genomes for 163 specimens of Chrysobalanaceae, which represent
30 131 156 species, and all 27 currently recognized genera (Table S1). Two accessions of the
31 132 following species were sampled: *Bafodeya benna* (Scott-Elliot) Prance, *Chrysobalanus*
32 133 *cuspidatus* Griseb. ex Duss, *Couepia bracteosa* Benth., *Hymenopus heteromorphus* (Benth.)
33 134 Sothers & Prance, *Leptobalanus octandrus* (Hoffmanns. ex Roem. & Schult.) Sothers &
34 135 Prance, *Maranthes robusta* (Oliv.) Prance, and *Parinari excelsa* Sabine. Tissue was taken
35 136 from herbarium collections or leaf samples dried in silica. Total DNA was extracted using
36 137 standard methods. A separate Illumina library was prepared for each sample, and the libraries
37 138 were then multiplexed in groups of 24 or 48. The pools were sequenced on HiSeq 2000-2500
38 139 high-throughput sequencers, yielding 101-nucleotide pair-ended DNA reads, or the more
39 60

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

Plastome assembly was performed on a local cluster running Linux CentOS version 6.7. We used the NOVOplasty organelle genome assembler version 2.7.2 (Dierckxsens *et al.*, 2016). We assumed a genome size range of 140–180 kbp, K-mer size of 39 and disabled the ‘variant detection’ option. We obtained unique circularized plastid genomes for 54 specimens. For another 58 specimens, we set a reference sequence to guide the assembly (using *Licania canescens* Benoist available in NCBI NC300566). In some cases, NOVOplasty returns two or more optional genomes, corresponding to large inversions, and we manually selected the option matching gene order. Points of reference of the circularized plastid genomes were aligned using the CSA software (Fernandes *et al.*, 2009). For the remaining 51 specimens (30% of our final dataset), we mapped the reads directly against a reference plastid genome using the ‘map to reference’ option in Geneious version 9.0.5.

Plastomes were then rotated to a common starting point, and aligned using MAFFT version 7.222 (Kato *et al.*, 2017). The first raw alignment of 163 plastomes was initially of 207,248 nucleotides. It was manually edited to remove ambiguous characters produced at the assembly stage. We annotated the alignment for Chrysobalanaceae by using that previously published for *Hirtella physophora* Mart. & Zucc. by Malé *et al.* (2014; accession NC 024066 on NCBI). The alignment was realigned with this plastome, and annotations were transferred to all sequences in Geneious using the ‘transfer annotations’ option. Within the alignment, we also carefully checked the reading frames of the coding DNA sequences (CDS).

RECONSTRUCTION AND DATING OF THE CROWN AGE OF CHRYSOBALANACEAE

To reconstruct a dated phylogenetic tree of the family, we used a two-step approach. We estimated divergence times for the crown node of Chrysobalanaceae and the deeper divergences in the family. For this first analysis, we selected high-quality plastid genomes spanning Malpighiales, together with representatives of the main clades of the family. We included only CDSs, which resulted in a high-quality global alignment, with 20 taxa, 19 members of Malpighiales (including five Chrysobalanaceae), and one outgroup from Oxalidales [*Sloanea latifolia* (Rich.) K.Schum., Elaeocarpaceae]. We used this first analysis to infer the crown age of Chrysobalanaceae. We conducted a second analysis using the full

163-plastome dataset, in which the crown age inferred from the first analysis was set as a constraint.

The 20-taxon sequence matrix was used to reconstruct phylogenetic relationships using maximum likelihood in RAxML version 8.2.10 (Stamatakis, 2014). The best model was found to be the general time reversible model for site substitution, with a gamma site model (GTR+ Γ) for all partitions, as identified using the JmodelTest2 software (Darriba *et al.*, 2012). We considered two scenarios: all CDSs as a single partition; and two partitions, first/second codons and third codons. All analyses gave the same results, so we subsequently analysed only the single partition. We ran the analysis on the CIPRES supercomputing portal (Miller *et al.*, 2010) using rapid bootstrapping with an automatic halting option and searching for the best-scoring tree.

To generate a time-calibrated tree, we relied on Bayesian relaxed molecular clock models as implemented in BEAST version 2.5.1 (Bouckaert *et al.*, 2019) using the DNA matrix together with fossil constraints (also available on CIPRES). The input file was generated using the BEAUTi software. We imported the same alignment as used in the RAxML analysis. We also used the GTR+ Γ model for each partition and assumed a relaxed clock log-normal model (Drummond *et al.*, 2006). We expected a Cenozoic age for the Chrysobalanaceae clade, and because our tree dating only used few internal priors, we set the branching process prior to be the Yule process (or pure birth process; Condamine *et al.*, 2015).

For the age priors, the split between Malpighiales and Oxalidales was constrained by imposing a uniform prior between 103 and 112 My (constraint 1; Xi *et al.*, 2012). The dating of the flowering plant tree has recently been revisited using an extensive plastome dataset (Li *et al.*, 2019), and although Celastrales were proposed as a new sister group to Malpighiales, the split between Malpighiales+Celastrales and Oxalidales was inferred at 106.2 Mya (range: 93.2–125.0 Mya), close to the date proposed by Magallón *et al.* (2015), and our prior is consistent with both analyses.

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

be > 19 My based on endocarp fossils recently found in Panama and reliably assigned to this genus (Jud *et al.*, 2016; constraint 3). We also constrained the crown age of the Neotropical Chrysobalanaceae clade based on the fossil flower found in Dominican amber and reliably assigned to *Licania* section *Hymenopus* Benth. (Chambers & Poinar, 2010; constraint 4), which is likely to be > 16 My (see below). The stem age of the Euphorbiaceae clade was constrained at > 61 My (*Acalypha* pollen type found in China, reported by Xi *et al.*, 2012; constraint 5). The stem age of Salicaceae was constrained to be more than 48 Mya (fossil flower of *Pseudosalix handleyi* Boucher, Manchester & Judd; Boucher *et al.*, 2003, constraint 6), the stem age of Caryocaraceae > 55 My (pollen of *Retisyncolporites angularis* González-Guzmán; Germeraad *et al.*, 1968, constraint 7), and the stem age of Humiriaceae > 37 My (fossil endocarp of *Lacunofructus cuatrecasana* Herrera, Manchester & Jaramillo; Herrera *et al.*, 2012, constraint 8).

The default starting tree for BEAST is incompatible with the imposed age constraints, so we started the MCMC search using an ultrametric starting tree modified from the RAxML output tree. We used the *chronos()* function of the *ape* package (Paradis *et al.*, 2004) in the R software to generate an dated initial tree within age constraints consistent with the constraints described above. In the BEAST input file, we fixed the topology, i.e. we assumed that the input tree had the correct topology, and optimized only the parameters for evolutionary rates and branch lengths. This was achieved by manually removing the ‘narrow exchange’, ‘wide exchange’, ‘Wilson Balding’ and ‘subtree slide’ operators from the xml input file. MCMC was run for 200 million generations, sampling parameters and trees every 10000 generations. Convergence was evaluated using Tracer version 1.7.1 (Rambaut *et al.*, 2018). The effective sampling sizes (ESS) of each parameter were checked at the end of each analysis and considered to be of good quality when > 200. Divergence times were computed using TreeAnnotator version 2.5.1 after the removal of the 25% burn-in part of the MCMC (Bouckaert *et al.*, 2019).

DATED PHYLOGENETIC RECONSTRUCTION FOR CHRYSOBALANACEAE

To construct a dated phylogenetic hypothesis for 163 specimens of Chrysobalanaceae, we followed the same strategy described above for reconstruction of the dated phylogenetic tree of Chrysobalanaceae. We used a two-partition model. All CDS were treated as a first partition. All other regions, including intergenic regions, intronic regions, rRNA and tRNA, were a second partition. Prior to partitioning the aligned matrix, we removed the second copy

of the inverted repeat, to avoid double weighting the phylogenetic signal of the inverted repeat.

Considerable age uncertainty has surrounded the biogeographical history of Chrysobalanaceae, which in part traces back to the attribution of Eocene leaf and pollen fossils from North America to Chrysobalanaceae (Berry, 1916; Wodehouse, 1932), constraining the crown age of Chrysobalanaceae to being > 50 My (Davis *et al.*, 2005; Xi *et al.*, 2012; Bardon *et al.*, 2012). However, Jud *et al.* (2016) found no solid evidence for fossils of Chrysobalanaceae prior to the Miocene. In the Neotropics, the first undisputed evidence of fossils of Chrysobalanaceae is demonstrated with flowers and fruits, possibly of *Licania* section *Hymenopus* (Chambers & Poinar, 2010), preserved in amber from the northern mountain range of the Dominican Republic, dated to 15–20 Mya (Iturralde-Vinent & McPhee 1996; Iturralde-Vinent, 2001), here assumed to be > 16 Mya. We also used three independent fossils of *Parinari*, including wood and fruits from 21 Mya in Panama (Jud *et al.*, 2016), fruits from 19 Mya in Ethiopia (Tiffney *et al.*, 1994) and wood from the mid-Miocene in India (Srivastava & Awasthi, 1996).

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

DIVERSIFICATION AND BIOGEOGRAPHIC ANALYSES

We first tested whether the dated phylogenetic tree was consistent with phases of accelerated or decelerated diversification. One prediction is that the major orogenic changes during the Miocene spurred plant diversification (Lagomarsino *et al.*, 2016; Pérez-Escobar *et al.*, 2017). We estimated rates of diversification and shifts in these rates using the Bayesian analysis of macroevolutionary mixture (BAMM, Rabosky *et al.*, 2013; Rabosky 2014). BAMM tests the hypothesis that diversification has occurred homogeneously across the phylogenetic tree, the alternative being that shifts in diversification rate have occurred on specific branches of the tree. We used the initial control file with priors on rate parameters inferred by the function

setBAMMpriors() of the BAMMtools package in R (Rabosky *et al.*, 2014). BAMM also provides an analytical correction for incompletely sampled trees, and here we assigned a sampling weight to each genus. The species sampling rates within the genera ranged from 13% (*Moquilea* Aubl.), to 57% (*Couepia*), for a 29% mean across the family. For *Hymenopus* (Benth.) Sothers & Prance, which appears in two separate clades in our analysis, we assumed an equal sampling of both clades (set at 36%). BAMM can also be used to compute diversification rates within subclades of the tree. We ran the reverse-jump MCMC simulation for ten million iterations to ensure convergence, which was assessed with the EffectiveSize() function of BAMMtools. For each of the four well-sampled Neotropical genera (*Couepia*, *Hirtella*, *Licania*, *Moquilea*), plus *Parinari*, we inferred the speciation rates from the BAMM run. This was done by selecting the subclade using the ape R package (Paradis *et al.*, 2004), and analysing the inferred diversification parameters on it.

We also reconstructed the biogeographic history of Chrysobalanaceae by inferring the most likely ancestral area(s). To this end, we attributed each species to a region. Because of the Neotropical focus of this study, we defined two broad regions outside the Neotropics: Africa and Southeast Asia (including Oceania). In the Neotropics, we defined five regions: Caribbean and Central America (including the Chocó region of Colombia, and southeast USA), savannas and seasonally dry tropical forests (including the Llanos of Colombia and Venezuela, cerrado in Brazil and dry forests such as the Chiquitania in Bolivia and caatinga in Brazil), Atlantic rainforest, the Andes and Amazonia. To reconstruct the ancestral area(s), we used an unconstrained dispersal-extinction-cladogenesis (DEC) model (Ree & Smith, 2008) as implemented in the R-package BioGeoBEARS version 1.1.2 (Matzke, 2014). We did not perform a model comparison approach including the founder-event speciation option of BioGeoBEARS because taxon sampling in our dataset remains too incomplete and because this approach has limits (Ree & Sanmartín, 2018).

RESULTS

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

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

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

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

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

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

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

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

complex of seven groups with low bootstrap support: *Hymenopus* cf. *occultans* (Prance) Sothers & Prance, *Microdesmia* (Benth.) Sothers & Prance, *Hymenopus*1, *Afrolicania* Mildbr., *Cordillera* Sothers & Prance, *Parinariopsis* (Huber) Sothers & Prance and *Hymenopus*2. Except for *Hymenopus*, each genus was monophyletic. However, based on bootstrap support in this analysis, we cannot exclude the possibility that the clades of *Hymenopus* (Fig. 3) form a single group. The Neotropical genera in Figure 3 also diversified in the mid to late Miocene: *Gaulettia* 10.8 Mya (7.8–13.8 Mya), *Hirtella* 10.4 Mya (8.1–13.1 Mya), *Hymenopus*1 12.6 Mya (9.3–16 Mya) and *Hymenopus*2 12.4 Mya (9.5–15.8 Mya). The position of *Afrolicania*, the only non-Neotropical species of the core Neotropical clade, suggests a single dispersal event from the Neotropics to Africa 24 Mya (95% HPD: 22.4–25.6 Mya).

The BioGeoBEARS analysis detected that the combined Neotropical clade and clade D were unambiguously assigned to Amazonia, with secondary dispersal events into Central America, the Atlantic forest and savannas/dry tropical forests (Fig. 4). Migration events to the cerrado were mainly in the Pliocene, confirming Simon *et al.* (2009).

The BAMM analysis converged (effect size for number of shifts was $> 1,000$ with a log-likelihood > 400). It identified four shifts in diversification rates as the most likely (Fig. 5). A rate-through time analysis for Chrysobalanaceae demonstrated a clear increase in speciation rates after 10 Mya (Fig. 5). The four outlying clades correspond to *Parinari*, *Moquilea*+*Couepia*, *Licania*+*Leptobalanus* and *Hirtella* [excluding *H. recurva* (Spruce ex Prance) Sothers & Prance and *H. punctillata* Ducke]. The most rapid diversification was in *Hirtella* minus *H. punctillata* and *H. recurva*, for which BAMM inferred a speciation rate of $\lambda=0.60$ (in lineages per My, 90% confidence interval: 0.42–0.85), compared with a family mean-speciation rate of $\lambda=0.23$ (0.19–0.27), and family mean-speciation rate excluding *Hirtella* of $\lambda=0.20$ (0.17–0.25). A rate-through time analysis for *Hirtella* demonstrates a decline in rate through time (Fig. 5, right panels). *Parinari* was the other clade that exhibited a significantly higher speciation rate compared to the average but with much greater confidence intervals, $\lambda=0.49$ (0.14–0.96).

DISCUSSION

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

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

In contrast, virtually all existing evolutionary papers of Neotropical plant families have been based on selected plastid markers combined with sequences from the ribosomal cluster (internal transcribed spacer). Important recent studies on the Miocene diversification of Amazonian clades have focused on Annonaceae based on an aligned length of 7,960 bp (Pirie *et al.*, 2018), Meliaceae with 5,207 bp (Koenen *et al.*, 2015) and in clade Detarioideae in Fabaceae with 2,463 bp (Schley *et al.*, 2018). In our study, the most poorly sampled species had a 93% plastome coverage. Generally, coverage is in excess of 99%, and the matrix was almost complete. We also included 156 species, 131 of which are Neotropical, with much increased taxon and character sampling compared to previous efforts. The results include important new biogeographic and systematic results about Chrysobalanaceae and confirm results for the Neotropical flora, but with much greater confidence than the other studies due to the greater amounts of data included.

EARLY DIVERSIFICATION OF CHRYSOBALANACEAE

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

The crown age of the *Parinari* clade was inferred at 9 My (95% HPD: 8.2–9.8 My). *Parinari* possesses the most reliable fossil record of the family, due to the diagnostic features of its endocarp (Jud *et al.*, 2016). The early Miocene *Parinari* fossils in Africa (Tiffney *et al.*, 1994) and South America (Jud *et al.*, 2016) predate by *c.* 10 My the crown age of *Parinari*, consistent with their high rates of speciation and extinction. Bardon *et al.* (2016) supported an African origin for *Parinari* due to the native African distribution of *Neocarya*, but the increased sampling of our study leads to a less clear-cut result. The two earliest-diverging clades in *Parinari* contain all five Neotropical accessions. One clade with a crown age 7.4 My contains all Palaeotropical accessions. Noteworthy is the position of *P. nonda* F.Muell. ex Benth., from tropical Australia and Papua New Guinea, close to African *P. capensis* Harv. (inferred age of 0.37 My for the *P. capensis*/*P. nonda* split), which suggests a recent long-distance dispersal event from Africa to Australasia. Overall, if more research on *Parinari* confirms the crown age of < 10 My, it would be a striking case of a pantropically distributed genus of long-lived tropical trees with a trans-oceanic dispersal (Renner, 2004). On the whole, our species sampling is currently insufficient to confidently resolve the biogeographical history of *Parinari* because our results are based on sampling of only 11 species of the 39 currently described *Parinari* spp.

Clade B has a strong African component. Increased sampling for *Maranthes* (five of the 12 species now included) produced a date of 14.4 Mya (95%HPD: 10.9–18.1 Mya). *Maranthes* is present on all three continents, including the Neotropical species: *M. panamensis* (Standl.) Prance & F.White, which our analysis places as sister to *M. gabunensis* (Engl.) Prance. This suggests that *M. panamensis* is the product of a recent dispersal from Africa. We also emphasize that *Magnistipula* Engl. remains an unresolved puzzle in Chrysobalanaceae and further research should include more comprehensive taxon coverage including all three subgenera. Clade C also contains only African species: *Dactyladenia* plus the African *Hirtella* spp. (Prance & White, 1988; p. 149), which need to be revised and segregated from *Hirtella* based on our results.

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

(Siegert, 2008), but our dating seems to reject this scenario, pointing instead to a much more recent dispersal.

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

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

STRUCTURE OF THE CORE NEOTROPICAL CLADE

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

Here we recognize 12 genera of Chrysobalanaceae as members of the core Neotropical clade: Neotropical *Hirtella* (105 species), *Geobalanus* Small (three species), *Microdesmia* (two species), *Cordillera* (one species), *Parinariopsis* (one species), *Moquilea* (54 species), *Couepia* (62 species), *Leptobalanus* (31 species), *Licania* (100 species), *Gaulettia* (nine species), *Hymenopus* (28 species), and *Afrolicania* (1 species) the only non-Neotropical genus in this clade. In addition, *Exellodendron* (five species) and *Acioa* (six species) are exclusively Neotropical but outside the core clade.

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

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

We now turn to the sister clade of *Gaulettia*, which contains some of the unresolved taxonomic issues in Chrysobalanaceae. This clade, dated at 26.3 My (95% HPD: 24.7–27.9 My), includes *Hirtella* plus seven clades with low bootstrap support for their inter-relationships: *Microdesmia*, *Hymenopus*1, *Afrolicania*, *Cordillera*, *Parinariopsis*, *Hymenopus*2 and *Hymenopus* cf. *occultans*. Our analysis suggests that *Hymenopus* may include two genera (designated as 1 and 2), but further research is needed to confirm this proposal, especially in the light of the weak support for their separation. One hypothesis for the lack of support in this clade is that it may have resulted from a single diversification event giving rise to a variety of new forms associated with the end of the Oligocene. Global warming at this time was associated with a loss of palynofloral diversity in the foothills of the Andes (Jaramillo *et al.*, 2006), which could be due to the rapid Andean uplift around this time (Hoorn *et al.*, 2010). The current distribution of these genera sheds little light on a possible allopatric diversification scenario, in part because the extant distribution due to cultivation of *Microdesmia* species may not reflect their historical distribution (Sothers *et al.*, 2016), and also because extant species of both *Hymenopus* and *Hirtella* have large modern distributions. Bardon *et al.* (2016) was published before the generic realignments illustrated here. This tree also differs from that in Sothers *et al.* (2016) based on plastid and nuclear (*Xdh*, ITS) DNA sequences.

EVOLUTIONARY HISTORY OF NEOTROPICAL CHRYSOBALANACEAE GENERA

According to our results, onset of diversification for seven genera spanned the mid Miocene: *Moquilea* (15.1 Mya), *Couepia* (10.3 Mya), *Leptobalanus* (10.3 Mya), *Licania* (16.8 Mya), *Hirtella* ss. (10.4 Mya), *Gaulettia* (10.8 Mya), *Hymenopus*1 (12.4 Mya) and *Hymenopus*2 (12.6 Mya). This precedes the initiation of the modern Amazon River and demise of the Pebas wetland (Figueiredo *et al.*, 2009).

Against the backdrop of this geological and climatic setting, the evolutionary history of *Couepia* is informative. The genus clearly split into two groups, one with an affinity for

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

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

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

Greater species and regional sampling would be necessary to confirm relationships in this intriguing group.

This analysis included only a few species with multiple accessions, and some of these revealed surprises. Two accessions of *Parinari excelsa* Sabine (Parque Estadual Cristalino, Brazil, and Saint Laurent du Maroni, French Guiana) fell into separate clades, and so did the accessions of *Couepia bracteosa* (Sinnamary, French Guiana, and Manaus, Brazil), *Leptobalanus octandrus* (Manaus and São Paulo, Brazil) and *Hymenopus heteromorphus* (Benth.) Sothers & Prance (Régina, French Guiana and Manaus). In all these cases, the accessions were from distant localities. One explanation may be that there are actually several cryptic, or previously unreported, species within the currently large ranges of these species. With more comprehensive sequencing of targeted species across their distribution, it will be possible to assess the prevalence of such entities in Chrysobalanaceae. This situation probably holds more generally across Amazonian plant families (Misiewicz & Fine, 2014; Loiseau *et al.*, 2019).

ON THE USE OF PLASTID GENOMES TO INFER THE EVOLUTIONARY HISTORY OF TROPICAL FLOWERING PLANTS

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

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

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

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

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

Targeted capture of hundreds of nuclear genes could bring even further insight into the question of plant diversification, as has been shown for the Neotropical palm clade Geonomeae (>3 million bp; Loiseau *et al.*, 2019), Fabaceae (c. 1 million bp; Koenen *et al.*, 2020) or land plants (Leebens-Mack *et al.*, 2019). However, it is noteworthy that nuclear gene information did not radically transform the phylogenetic tree of Geonomeae (Roncal *et al.*, 2012), and that plastid genome data were found to be consistent with nuclear gene data in Fabaceae except at the root node, the latter probably caused by incomplete lineage sorting (Koenen *et al.*, 2020). Also, assembling such large nuclear gene datasets represents specific challenges, and phylogenetic reconstruction methods using these data are still in development (Zhang *et al.*, 2018). Although nuclear genes are necessary to resolve parts of the plant tree of life where plastid genomes are insufficiently informative, many Amazonian plant families have not been included in such phylogenetic work, and plastome analyses are a natural step to document systematic relationships and study Amazonian plant diversification.

CONCLUSIONS

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

remain. In the future, it would be important to: explore whether the *Hymenopus* complex can be clarified, determine if nuclear DNA confirms the position of *Bafodeya* and *Kostermanthus* as sister to the rest of the family, examine the evolutionary history of Neotropical *Hirtella* and of *Parinari* with better species coverage, and add more *Magnistipula* spp. to include all three subgenera. For six lowland Amazonian genera of Chrysobalanaceae, we document accelerated diversification in the wake of the Andean uplift. This study thus provides support for the view that much of the extant Neotropical plant diversity has arisen within the past 15 My, Amazonian diversification has played a key role in this diversification process and the majority of diversification events have taken place *in situ*, rather than being the product of intercontinental dispersal.

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Figure captions

Figure 1. Phylogenetic tree for the basal clades of Chrysobalanaceae, obtained from the software RAxML 8.2.10, with dating from the software BEAST 2.5.1. The arrows illustrate the internal calibration points used for tree dating (n=3). Clade support < 95% was colour-coded with circles; all other clades had support percentages > 95%. The numbers next to each node are the inferred ages in millions of years. Grey bars represent the 95% confidence intervals. Asterisks indicate plastid genomes published in Bardon *et al.* (2016).

Figure 2. Phylogenetic tree of Chrysobalanaceae, continuation of Figure 1. The biome map is modified from Olson *et al.* (2001). Dark red: Amazonia; orange: savannas and seasonally dry tropical forests; green: Atlantic tropical forests; blue: forests of Central America, the Caribbean and Chocó; black: high-elevation ecosystems (>1,000 m asl).

Figure 3. Phylogenetic tree of Chrysobalanaceae, continuation of Figure 2. In the *Hirtella* clade, the ant symbols indicate myrmecophilous species.

Figure 4. Ancestral area reconstruction of Chrysobalanaceae using the dispersal, extinction, and cladogenesis (DEC) algorithm as implemented in the BioGeoBears software. Pie charts indicate relative support for the dominant ancestral area; all other ancestral area probabilities are lumped and represented in white.

Figure 5. Plot with branches coloured by speciation rate (lineages/My), representing a summary of BAMM analysis. Grey circles indicate the positions of regime shifts in the best configuration. Side plots represent the speciation rate-through-time (RTT) plots for each of the four clades with regime shifts, whereas the bottom plot represents the RTT plot for the entire tree. Finally, the bottom-right histograms indicate the distribution of speciation rates for the four regime-shift clades and the entire family.

**Supplementary Information for: Rapid diversification rates in Amazonian
Chrysobalanaceae inferred from plastid genome phylogenetics**

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T Prance²

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 indicates fossil constraints.

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

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

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

<i>Bafodeya benna</i> 2	161360	Idem	AFRICA	111 ; Mamaden Saiden (M Saiden); Mamou, Fouta Djallon, forest border 'Foret de Quehuel' ENATEF; Guinea
<i>Chrysobalanus cuspidatus</i> 1	162892	Islands	CA	50 ; Hill28129; Kew KEW11520
<i>Chrysobalanus cuspidatus</i> 2	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</i> 1	162194	Guianas and Amazonia. In primary and secondary forest on non-flooded ground.	AM	C ; P00610245; Paracou Station; French Guiana
<i>Couepia bracteosa</i> 2	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

		Eastern Amazonian Brazil and in French		E ; JC 152; Juliette Chamagne;
<i>Couepia excelsa</i>	162057	Guiana. Non-flooded forest.	AM	French Guiana
<i>Couepia glabra</i>	161977	Brazil (lower Rio Negro region). Forest on terra firme.	AM	F ; Sothers1516, Amazonas, ZF-2, Reservas do PDBFF; Brazil
<i>Couepia grandiflora</i>	162092	Brazil, Bolivia and Paraguay. Cerrados and savannas.	CER	Sothers1507 ; Brasília, Distrito Federal, Jardim Botânico; Brazil
<i>Couepia guianensis</i>	162127	Guianas and Brazil. Growing on terra firme or flooded river bank.	AM	Cg ; B421045; BAFOG plot near St Laurent; French Guiana
<i>Couepia habrantha</i>	162148	Guyana, Colombia, Venezuela and C Brazilian Amazonia. In riverine and non-flooded forest.	AM	G ; LV109174; Saut Lavilette; French Guiana
<i>Couepia hallwachsiae</i>	162082	Endemic to Costa Rica.	CA	55 ; Aguilar8227; Reinaldo Aguilar, San Ramon, camino a el P.N. Braulio Carrillo, KEW11523; Costa Rica
<i>Couepia impressa</i>	162019	NE Brazil. Primary forest.	AM	H ; Sothers1529; Pernambuco, Restinga de Ariquindá; Brazil
<i>Couepia joaquinae</i>	162089	French Guiana and Brazil (Amapá). Forest on terra firme on a table-top hill on clay oxisol	AM	I ; NH200492; Nouragues Station; French Guiana
<i>Couepia magnoliifolia</i>	162147	French Guiana and Brazil. In non-flooded forest.	AM	J ; P01860371; Paracou brown sand; French Guiana
<i>Couepia monteclarensis</i>	161890	NE and SE Brazil. Growing in Atlantic coastal forest.	AF	K ; Maas9807; Reserva Natural Vale (CVRD) Joao Neiva; Atlantic Rain Forest; Brazil
<i>Couepia morii</i>	162131	Central Amazonia, Brazil. Forest on terra firme.	AM	L ; Sothers1470; Amazonas, ZF-2, Reservas do PDBFF; Brazil
<i>Couepia multiflora</i>	162027	Guyana and Brazil (Roraima). Savannas and savanna scrublands.	CER	56 ; Dexter5603; KEW11528; Guyana
<i>Couepia obovata</i>	162030	Guianas, Venezuela and central, Colombian, Peruvian and Ecuadorean Amazonia. Non-flooded forest.	AM	115 ; Sothers sn; Amazonas, Manaus, Reserva Florestal Ducke; KEW11601; Brazil
<i>Couepia ovalifolia</i>	161928	On the coast of Brazil from Pernambuco to Rio de Janeiro. Restingas, littoral forest, sand plains, and sand bars.	AF	Sothers1509 ; R.J., Rio de Janeiro, Barra da Tijuca, Lote 2; Brazil
<i>Couepia paraensis</i>	161930	Eastern and central Amazonian Brazil. Sandy river banks and beaches, and open riverine forest.	AM	Sothers1510 ; Amazonas, Manaus, Praia Dourada; Brazil

<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>Colpothrinax 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

<i>Dactyladenia buchneri</i>	162156	Central African Republic, Congo, DRC and Angola. Riverine forests	AFRICA	V101849 ; Pierre Fabre collection; Democratic Republic of the Congo
<i>Dactyladenia floretii</i>	162312	Gabon. Rainforest, forest edge next to savanna, coastal thicket and secondary vegetation.	AFRICA	GiD1939 ; ADN:GiD1939, voucher GD2766, Gilles Dauby 2012; Gabon
<i>Exellodendron barbatum</i>	162325	Venezuela, Guianas and Amazonian Brazil. Riverine and non-flooded forest	AM	A110225 ; Acarouany plot; French Guiana
<i>Gaulettia amaraliae</i>	163538	Restricted to one locality in northern Brazil, in the foothills and surroundings of Serra do Aracá, a sandstone mountain of the Guayana Highlands	TEP	117 ; Stevenson1011 South of Serra do Aracá, KEW11590; Brazil
<i>Gaulettia elata</i>	162251	French Guiana, Guyana, western and central Amazonian Brazil (Acre, Amazonas) and Colombia. Found in non-flooded forests; also occurs infrequently in sandy campinarana vegetation.	AM	Sothers1450 ; Reserva Florestal Ducke, Manaus, Amazonas; Brazil
<i>Gaulettia parillo</i>	162440	Guyana, French Guiana, Suriname, Venezuela, Amazonian Brazil (Acre, Amazonas, Amapá, Roraima), Peru, Ecuador and Colombia. Savannas, primary and secondary forests	AM	118 ; Pereira67; KEW11580; Brazil
<i>Gaulettia sp</i>	162059		AM	GEM ; described as <i>L. discolor</i> ; Soesdyke-Linden Highway SL Roosevelt Garcia; Guyana
<i>Geobalanus oblongifolius</i>	162547	SE United States. Pine barrens, sand dunes and oak scrubland.	CA	20553S2 ; collected JB Nelson(1999) ten Mile Creek, Georgia; sampled in Paris Herbarium (P05562808); Georgia; United States of America
<i>Grangeria borbonica</i>	162797	Mauritius and Réunion. Forest at low and medium altitudes on the east and southern sides of the islands which are exposed to the SE monsoon and receive more than 3000 mm of rainfall a year.	AFRICA	Gbor ; Colorado, plot1; Dominique Strasberg; La Réunion
<i>Hirtella araguariensis</i>	163072	Brazil, from north of Manaus eastward to Amapá and French Guiana. Upland forest.	AM	LBD ; NL110214; Nouragues; French Guiana
<i>Hirtella arenosa</i>	162144	Brazil (C to W Amazonia). White sand campina.	AM	GDP ; MHT410; São Gabriel da Cachoeira Morro dos Seis Lagos Lago do Jacaré; Brazil

		Colombia to the Guianas, Brazil and		
<i>Hirtella bicornis</i>	162909	Amazonian Peru.	AM	GCA ; P01110528; French Guiana
<i>Hirtella corymbosa</i>	164173	Eastern Brazil. Open restinga with savannas	AF	120 ; Sothers1533; Espírito Santo, Linhares, Reserva Natural da CVRD; Brazil
<i>Hirtella davisii</i>	160638	Nicaragua and Costa Rica, Eastern Venezuela, Guianas, and eastern Amazonian Brazil. Primary forest on high ground.	AM, CA	GBT ; JC 111; French Guiana
<i>Hirtella dorvalii</i>	162872	Northern Brazil. Low caatinga forest on sandy soils.	AM	GEA ; Myrmecophila; VIC2428 Vicentini, North of Manaus (tbc); Brazil
<i>Hirtella duckei</i>	162922	Guyana and C and W Amazonia. Non-flooded forest.	AM	GEI ; Myrmecophila; JH6/515A Jenaro JH Roosevelt Garcia; Peru
<i>Hirtella elongata</i>	162685	Venezuela and W Amazonia. River banks and riverine forest.	AM	GEE ; JH1/60 Jenaro JH Roosevelt 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
<i>Hirtella glandulosa</i>	162929	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 savanna margins.	AM, CER	GBF ; NH200142; Nouragues; French Guiana
<i>Hirtella guainiae</i>	162560	Western Amazonia. Non-flooded forest.	AM	61 ; Myrmecophila; Duivenvoorden2352; Araracuara, bosque alto, suelo arcilloso rojizo de tierra firme; Colombia
<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

<i>Hirtella paniculata</i>	163046	St. Vincent, Trinidad, Venezuela, Guianas, Colombia and N Brazil. Open sandy places, savannas, savanna margins, sandy river banks and islands.	AM,CA	GDS ; V200031; Herbar Pierre Fabre, cf French Guiana
<i>Hirtella physophora</i>	162984	Guianas and Amazonia. Non-flooded forest.	AM	Hp ; Myrmecophila; French Guiana
<i>Hirtella pilosissima</i>	162381	Western Amazonia. Non-flooded forest.	AM	GEN ; TS55rg 169; Tamshiyacu TS; Roosevelt Garcia et al.; Peru
<i>Hirtella punctillata</i>	163084	Venezuela, Guianas, Colombia and E Amazonian Brazil. Common species of the Guayana Highland and the Upper Rio Negro in sandy savannas, open and low forest in sandstone areas, and open river margins.	TEP	GDM ; Barcelos Serra do Araca Arredores da serra FMC0386; FM Costa, sent by Vicentini; Brazil
<i>Hirtella racemosa</i>	162890	Central America and Trinidad to Bolivia and E Brazil Primary forest especially beside rivers and streams, but also in understorey of forest on non-flooded ground	AM	Hr ; Pierre-Jean Malé, Nouragues ; French Guiana
<i>Hirtella recurva</i>	163411	Ecuador and Peru. Andean primary forest, to 1700 m.	MONT	122 ; Ecuador, Homeier2190; Reserva San Francisco, ca 2000m asl, Zamora-Chinchipe; Ecuador
<i>Hirtella rodriguesii</i>	162164	Peru and C Amazonian Brazil. Non-flooded forest. Flowering June–Sept.	AM	GEH ; JH6/123 Jenaro JH; Roosevelt Garcia et al.; Peru
<i>Hirtella sprucei</i>	164140	Northeastern and E-C Brazil. Forests.	AF	123 ; Sothers 1530; Brazil, Espírito Santo, Linhares, Res. Natural da CVRD; Brazil
<i>Hirtella suffulta</i>	162646	French Guiana and N Brazil. Non-flooded forest.	AM	NH200131 ; Nouragues Station; French Guiana
<i>Hirtella tenuifolia</i>	162715	French Guiana and N Brazil. Primary and secondary forest.	AM	GBS ; JC 084; noted as <i>Emmotum</i> in previous analysis; French Guiana
<i>Hirtella triandra</i>	163055	Central Mexico through Central America and the Antilles to northern South America and SE Brazil	CA, AM	KTT ; BOLL391; La Chonta J. C. Liconia; Bolivia
<i>Hunga gerontogea</i>	162404	Endemic to NW New Caledonia. Frequent beside creeks and in riverine woodland in serpentine terrain and on serpentine alluvia	AUST	H-gerontogea ; Hequet 4104; Vanessa Hequet; Nouméa; Nouvelle Calédonie
<i>Hunga mackeeana</i>	162414	Known only from New Caledonia (northern part). Maquis.	AUST	37 ; Vardrot938; Vanessa Hequet; Nouméa; Nouvelle Calédonie

<i>Hunga rhamnoides</i>	162377	S New Caledonia (including Île des Pins), and Lifou, in the Loyalty Islands. Forests on serpentine	AUST	38 ; Hequet1; Vanessa Hequet; Noumea; Nouvelle Calédonie
<i>Hymenopus caudatus</i>	162527	Widespread in Amazonia (Guianas, Colombia, Ecuador, Peru, Brazil). Flooded as well as non-flooded forest.	AM	67 ; Sothers sin#; Reserva Florestal Ducke, Manaus, Amazonas; Brazil
<i>Hymenopus divaricatus</i>	162843	Guianas and northern Brazil. Forest on terra firme and savanna margins.	AM	125 ; Gillespie725; Linden Highway, near turnoff to St. Cuthbert's Mission; Guyana
<i>Hymenopus glabriflorus</i>	163010	Costa Rica, Colombia, Venezuela, Guianas and Brazil (Amapá, Pará). Terra firme forest.	CA, CHOCO, AM	A110093 ; Acarouany plot; French Guiana
<i>Hymenopus heteromorphus 1</i>	162910	Central and South America.	AM, CA	Lh ; LV109473; French Guiana
<i>Hymenopus heteromorphus 2</i>	162580	Idem	AM, CA	126: Sothers1547; Porto Urucu, Amazonas; Brazil
<i>Hymenopus intrapetiolaris</i>	162838	Guianas, N Brazil and Amazonian Colombia, Peru and Venezuela. Lowland forest in open places.	AM	GEK ; MH-046; Mabura-Hill MH; Roosevelt Garcia; Guyana
<i>Hymenopus laevigatus</i>	160126	Venezuela, Guianas, Brazil and Peru. Terra firme forest	AM	GBD ; M17116512; Montagne Tortue; French Guiana
<i>Hymenopus latifolius</i>	160446	Guianas, Venezuela and Amazonian Ecuador, Peru and Brazil. Non-flooded forest	AM	LCD ; PE5397; French Guiana
<i>Hymenopus latistipulus</i>	162994	French Guiana and Venezuela. Forest on high ground.	AM	GBB ; M17116079; Montagne Tortue; French Guiana
<i>Hymenopus macrophyllus</i>	162677	Guianas, Venezuela, Peru and Amazonian Brazil. Periodically flooded forest	AM	KD5284 ; Kyle Dexter, French Guiana
<i>Hymenopus reticulatus</i>	162555	French Guiana, western (Colombia, Ecuador, Peru) and Brazilian Amazonia. Non-flooded and periodically flooded forest.	AM	68 ; Sothers, Ducke tree#499; Brazil
<i>Kostermanthus heteropetalus</i>	161914	Malay Peninsula, Borneo and Sumatera to Sulawesi and S Philippines. Lowland rainforest from sea level to 500 m.	SEASIA	69 ; Ahmad7485; near Sungai Liang Arboretum Forest Reserve; Brunei
<i>Kostermanthus robustus</i>	161788	Borneo (Sarawak). Hill slope in mixed dipterocarp forest to 200 m., and in kerangas (heath) forest to 600 m.	SEASIA	Kostermanthus ; Sarawak, Semengoh Arboretum, 1st Division; Paie; Lee, B. 38000; Malaysia
<i>Hymenopus cf. occultans</i>	162471	Widespread in Amazonia. Gallery forest, periodically flooded forest, river margins, savanna margins, and open river beaches on sandy soil.	AM, SAV	130 ; D daSilvaCosta396 ; previously identified as <i>Leptobalanus apetalus</i> , identification modified in Feb. 2020; Brazil

<i>Leptobalanus emarginatus</i>	162196	Venezuelan Guayana and Amazonian Brazil and Peru. Non-flooded forest, especially on granitic outcrops.	AM,TEP	GEF ; JH1/168; Jenaro Herrero, R Garcia; Peru
<i>Leptobalanus gardneri</i>	162289	Bolivia, and in C, NE, SE and N Brazil. Riverine forest bordering cerrado, and in cerrado itself.	CER	131 ; Queiroz11012; Brazil
<i>Leptobalanus granvillei</i>	162207	From Panama, Ecuador and Colombia to French Guiana, Guyana, Venezuela and Brazil (Amazonas). Upland forest on terra firme and along riverbanks.	AM,CA	GDV ; V200639; Herbiere Pierre Fabre; French Guiana
<i>Leptobalanus humilis</i>	162057	Bolivia and Brazil. In cerrados.	CER	KVF ; Estação Ecologica de Assis PEEA; Renato Lima, São Paulo ; Brazil
<i>Leptobalanus latus</i>	162060	Guianas, Venezuela, C & W Amazonia (Colombia, Ecuador, Peru and Brazil). Non-flooded forest and secondary scrub on sandy soil	AM	GED ; Allpahuayo AM; AM59 rg-059; Roosevelt Garcia; Peru
<i>Leptobalanus octandrus 1</i>	162298	Widely distributed from N Venezuela through the Guianas, Peru, Colombia, Bolivia and E & C Amazonia to Northeast, East-central & Southeast Brazil. Forest	AM	132 ; Castro165; Brazil
<i>Leptobalanus octandrus 2</i>	162340	Idem	AF	GAL ; Brazil LIC OCT 10447 (PECB 119) Parque Estadual Carlos Botelho, São Paulo, Renato Lima; Brazil
<i>Leptobalanus sclerophyllus</i>	162377	Bolivia, Colombia, Peru, eastern and southern Amazonia and the planalto of central Brazil. Non-flooded forest, riverine forest or cerrado	AM,CER	133 ; Pereira3558; Brazil
<i>Leptobalanus sp</i>	159487		AM	KTQ ; JH6/325 Jenaro Herrero, Roosevelt Garcia, misdet as <i>L. blackii</i> (perhaps <i>L. longistylus</i> ?); Peru
<i>Leptobalanus sprucei</i>	162234	Guianas, Venezuela and in the Amazon region of Brazil. Primary forest on non-flooded ground and secondary forest	AM	Ls ; P01860159; Paracou Station; French Guiana
<i>Licania alba</i>	162489	Guianas and adjacent Venezuela and Brazil (Amapá, Amazonas, Pará). Primary forest.	AM	La ; P00610185; Paracou Station; French Guiana
<i>Licania canescens</i>	162624	Guianas, Venezuela, Bolivia, Peru and widespread in Amazonian Brazil. Riverine and periodically flooded forest	AM	Lc ; NH200019; Nouragues Station; French Guiana

		Venezuela (Cerro Yapacana, where it is reported to be abundant) and in Amazonian		
<i>Licania cordata</i>	160064	Brazil (Amazonas). Savannas	SAV	GDQ ; MHTA486; Brazil
<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
<i>Licania harlingii</i>	163427	Western Amazonia: Bolivia, Colombia, Ecuador, Peru and Brazil (Acre). Terra firme forest.	AM	136 ; Homeier31755; Ecuador
<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
<i>Licania irwinii</i>	162686	Guianas, Venezuela and Brazil (Amazonas). Forested slopes.	AM	LCE ; KD5287; Kyle Dexter; French Guiana
<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
<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
<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
<i>Licania majuscula</i>	162436	Guianas and Amazonian Brazil. Upland forest and high riverine forest.	AM	A110139 ; Acarouany Plot; French Guiana
<i>Licania membranacea</i>	162204	Trinidad, the Guianas, Venezuela and Brazil. Forested slopes and non-flooded forest.	AM	M17116059 ; Montagne Tortue; French Guiana
<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
<i>Licania niloi</i>	162518	Bolivia and N Brazil (Amazonas, Rondônia). Primary forest.	AM	140 ; Sothers tree219-02; KEW11600; Brazil

		Amazonian Venezuela and adjacent Brazil		
		(Amazonas). Riverine forest and savanna		LCT ; SL-07; Soesdyke-Linden
6	<i>Licania orbicularis</i>	162259 margins.	AM	Road, Guyana; Roosevelt Garcia
8	<i>Licania ovalifolia</i>	162320 Guianas and Brazil (Amapá). Primary forest.	AM	P610256 ; Paracou Station; French
11		Guianas and Venezuela to Brazilian		GDR ; P009 Prance14070; rio Ituxi,
12		Amazonia, Peru and Ecuador. Non-flooded		vicinity of Boca do Curuquete,
13	<i>Licania pallida</i>	162406 forest	AM	varzea forest, 1971; at MNHN; Brazil
15		French Guiana and Brazilian Amazonia		141 ; Sothers tree245-02;
16	<i>Licania rodriguesii</i>	162314 (Amazonas, Pará). Non-flooded forest.	AM	KEW11599 ; Brazil
18		Throughout the Congo River basin and some		NONB ; F2P2C2603; M'Baiki Plot;
19		of its tributaries to the south. River banks and		collected M Réjou-Méchain; Central
20	<i>Magnistipula</i>	sometimes also in forest on dry land in valley		African Republic
21	<i>butayei</i>	162546 bottoms, in lowlands up to 450 m.	AFRICA	
24		West Africa in a narrow coastal belt from SE		GD1917 ; ADN:GiD1917, voucher
25		Nigeria to the extreme SW corner of DRC,		GD2800; Gilles Dauby; Gabon
26	<i>Maranthes</i>	just N of the River Congo. Evergreen		
27	<i>gabunensis</i>	162774 rainforest.	AFRICA	
30		Widely distributed throughout the greater part		GD1845 ; ADN:GiD1845,
31		of the Guineo-Congolian region from Sierra		voucher:GD2848; Gilles Dauby;
32		Leone to Ituri in E DRC and in Cabinda and		Gabon
33	<i>Maranthes glabra</i>	162290 rainforest; absent only from the drier types.	AFRICA	
37		Sudanian Region from Togo to the Central		F1P1C4988 ; M'Baiki Forest Station;
38		African Republic. Fringing forest in the		Maxime Réjou Méchain; Central
39		wetter parts of the Sudanian region. In West		African Republic
40	<i>Maranthes kerstingii</i>	162400 Africa occurs mainly in upland areas.	AFRICA	
43	<i>Maranthes</i>	Panama (Isthmus), and recently collected in		143 ; Hammel16653; Parque Nacional
44	<i>panamensis</i>	162462 Nicaragua and Costa Rica. Dense rainforest.	CA	Corcovado. Sirena station; lower Olla
47		West Africa from the Ivory Coast to Nigeria.		26 ; MH2306; Myriam Heuertz;
48	<i>Maranthes robusta 1</i>	162417 Swamp forest and semi-evergreen rainforest	AFRICA	Benin
51				27 ; MH2285; Myriam Heuertz;
52	<i>Maranthes robusta 2</i>	162130 Idem	AFRICA	Benin
54		From Mexico through Central America to		72 ; Ibarra-Manriquez6065; Nueva
55		Bolivia, Colombia, Peru, Ecuador, Venezuela		Italia; Mexico
56	<i>Microdesmia</i>	and northern Brazil. Dry plains, slopes and		
57	<i>arborea</i>	162521 scrub forest.	CA,AM	

<i>Microdesmia rigida</i>	162617	Native to northeastern Brazil. Dry forest and gallery forest	AF	144 ; Cardoso1052; Brazil
<i>Moquilea brittoniana</i>	162443	W Amazonia in Bolivia, Colombia, Ecuador, Peru and Brazil. Non-flooded and periodically flooded forest	AM	GEG ; JH2/286 jen2/286; Roosevelt Garcia; Peru
<i>Moquilea corniculata</i>	162438	Costa Rica (Puntarenas and Osa Peninsula). Lowland rainforest.	CA	73 ; Aguilar9846; Rincon, margen derecha de Quebrada Aparicio; Costa Rica
<i>Moquilea guianensis</i>	161828	Guianas, Venezuela, the Amazon delta, W Amazonia, Ecuador, Peru and in Brazil. Riverine, terra firme and premontane forests	AM	LCC ; PE1075; French Guiana
<i>Moquilea macrocarpa</i>	162389	Panama, Colombia, Ecuador and Peru. Lowland forests to 600 m and in premontane rain forest in Panama.	CA,AM	139 ; Homeier38001; Province of Napo, Parque Nacional Sumaco-Galeras, Rio Hollin watershed; Ecuador
<i>Moquilea minutiflora</i>	162438	Guianas, Venezuela, Bolivia and Amazonian Brazil. Non-flooded forests and gallery forests.	AM	NH200162 ; Nouragues Station; French Guiana
<i>Moquilea pyrifolia</i>	162493	Martinique to Trinidad, adjacent Venezuela and Colombia. Lowland forest and riverine forest in open places.	AM	39 ; Licania pyrifolia; Hato Pinero; AF28517 Angel Fernandez & J Chave; Venezuela
<i>Moquilea tomentosa</i>	162555	Northeastern, southeastern and southern Brazil. Native to the coastal restinga forest	AF	Ltom ; Olivier Maurin NA cultivated in South Africa; South Africa
<i>Neocarya macrophylla</i>	162410	Common in West Africa in a coastal strip, in places up to 300 km wide, from Senegal to Liberia, and with a scattered east-west distribution in the much drier and more continental northern half of the Sudanian region 700.1000 km inland. Cultivated in Panama. Apparently confined to sandy soils.	AFRICA	Nmac ; Association France-Sahel, Sénégal
<i>Parastemon urophyllus</i>	162681	Widely distributed species from the Nicobar Islands and Thailand through the Malay Peninsula to Borneo and Sumatra. Lowland and coastal forest; commonest in swamp and secondary forest	SEASIA	SARAWAK100485 ; Niyomdham1083; Thailand
<i>Parinari alvimii</i>	162320	Brazil (coastal Bahia). Littoral forest. Some collections of this species have ants nests formed by the curvature of the leaves	AF	74 ; Barbosa-Silva sin#; Bahia; KEW11534 ; Brazil

		Thailand, Cambodia, Laos, Vietnam. 41: CBD, LAO, THA, VIE. Open deciduous forest, forest beside streams, hill forest to		
<i>Parinari anamensis</i>	161810	1000 m altitude.	SEASIA	LCL ; V105002; Herbar Pierre Fabre
<i>Parinari campestris</i>	162638	Trinidad, the Guianas, and adjacent Venezuela, Colombia and Brazil. River margins, savanna margins, and open forests.	AM	Pca ; Paracou Station ; French Guiana
<i>Parinari canarioides</i>	159646	Sumatera, Borneo (Kalimantan, Brunei, Sarawak, Sabah) and Philippines (Palawan). Rainforest up to 800 m	SEASIA	LCI ; SAN152336; Sandakan Herbarium; Malaysia
<i>Parinari capensis</i>	162529	Throughout the greater part of the Zambezian region and southwards to Natal and northwards into the Congo Republic and DRC.	AFRICA	Pcap ; OM3613 subspecies incohata; Olivier Maurin; South Africa
<i>Parinari curatellifolia</i>	157972	Widespread in woodland on the African mainland from Senegal to Kenya and southwards to Namibia and the Transvaal, but absent from the forests of the Guineo- Congolian region; also in coastal forest on the east side of Madagascar and in the Seychelles. Woodland, wooded grassland and coastal forests	AFRICA	Pcura ; OM2621; Olivier Maurin; South Africa
<i>Parinari excelsa 1</i>	160789	From Amazonian Colombia, Peru, Bolivia and E Venezuela through the Guianas and Amazonian Brazil to E-C and S Brazil	AM, AF	GAS ; B445017; BAFOG; French Guiana
<i>Parinari excelsa 2</i>	162412	From Amazonian Colombia, Peru, Bolivia and E Venezuela through the Guianas and Amazonian Brazil to E-C and S Brazil	AM, AF	75 : Brazil(Sasaki1493); Parque Estadual Cristalino, Vegetação aberta marginal do Rio Cristalino; KEW11533; Brazil
<i>Parinari montana</i>	160283	French Guiana, Colombia and N Brazilian Amazonia. Non-flooded forest.	AM	LAK ; LV109130; Saut Lavilette; French Guiana
<i>Parinari nonda</i>	162368	New Guinea and northern Australia. Savanna, open forest, forest on rocky areas in lowlands	AUST	76 ; Crawford434; KEW11531
<i>Parinari oblongifolia</i>	162515	Malesian Peninsula (S Kelantan to Johore), Sumatera, Borneo (Sabah, Kalimantan). Lowland rainforest and beside rivers or in valleys and extending to 450 m altitude	SEASIA	SAN152336 ; is not the correct code: SAN152716; Sandakan Herbarium; Malaysia

<i>Parinari obtusifolia</i>	162518	disturbed areas	CER	77; Queiroz15137; Queiroz, L.P.de; Rodovia Go - 118 (São João d'Aliança para Alto Paraíso) KEW11532; Brazil
<i>Parinariopsis licaniiflora</i>	160393	Guianas, Venezuela and Amazonia. Open forest at river margins, savanna margins and in secondary forest.	AM	GBK; P00610743; Paracou Station ; French Guiana
<i>'Hirtella' zanzibarica</i>	162362	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