

ON THE MONOPHYLY OF *MACROLOBIUM* SCHREB., AN ECOLOGICALLY DIVERSE NEOTROPICAL TREE GENUS (FABACEAE-DETARIOIDEAE)

Bruce Murphy,¹*†‡ Manuel de la Estrella,* Rowan Schley,*‡ Félix Forest,* and Bente Klitgård*

*Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AE, United Kingdom; †School of Biological and Chemical Sciences, Queen Mary University of London, Mile End Road, London E1 4NS, United Kingdom; and ‡Department of Life Sciences, Imperial College London, South Kensington, London SW7 2AZ, United Kingdom

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Premise of research. The Neotropical endemic *Macrobium* is one of the most species-rich genera (ca. 75 species) within subfamily Detarioideae (Fabaceae, alternatively Leguminosae). Two sections distinguished by floral morphology have been recognized in the past. Although morphologically diverse, species within the genus share several characters, including a single well-developed petal in adaxial position. However, previous analyses based on plastid markers have suggested that the genus is not monophyletic. We produce the most densely sampled molecular phylogeny of *Macrobium* and test the monophyly of the genus and the two sections.

Methodology. We analyzed nucleotide sequence data from the nuclear ribosomal internal transcribed spacer (ITS) and plastid (*matK*, *trnG*) genomes using Bayesian and maximum likelihood analyses.

Pivotal results. The combined analysis retains *Macrobium* as a monophyletic genus, with two well-supported subclades corresponding to the two recognized sections. *Macrobium pendulum* is the only species placed in a section different from its taxonomic treatment. The relationships recovered with the plastid markers differ slightly from the combined and ITS analyses, but without significant support.

Conclusions. *Macrobium* is shown to be a monophyletic genus and to contain two well-supported and morphologically defined sections with differing Amazonian and Andean/Central American distributions corresponding to the Gentry pattern. Species are also found to group partly according to habitat preferences and leaf morphology. Both sections contain groups of multijugate and unijugate species, and there appear to have been multiple shifts of this character.

Keywords: Amazon, Andes, biogeography, Brownea clade, Leguminosae, phylogenetics.

Online enhancements: appendix table and figures.

Introduction

Macrobium Schreb is a Neotropical genus of ca. 75 species of trees and shrubs within the Leguminosae. The latter has repeatedly been found to be the most abundant and species-rich Neotropical plant family (Valencia 1994; Burnham and Johnson 2004; ter Steege et al. 2013, 2016). Within the new six-subfamily arrangement of the family (LPWG 2017), *Macrobium* is the most species-rich genus within the Detarioideae, after the apparently paraphyletic *Cynometra* (de la Estrella et al. 2017; Radosavljevic et al., forthcoming).

Macrobium was described by von Schreber in 1789 (in von Linnaeus and von Schreber's *Genera Plantarum*) to merge two genera, *Vouapa* and *Outea*, described by Aublet (1775). This

circumscription was followed by Bentham (1870) in his treatment of the legume family for Martius's *Flora Brasiliensis*. In order to preserve nomenclatural stability, *Macrobium* was proposed and approved as a nomina conservanda (Rendle 1935). Initially, *Macrobium* included South American and African species, but Léonard (1952, 1954, 1955) considered South American and African taxa to be distinct. To accommodate the African species, he reinstated the genus *Anthonothea* P. Beauv. and published three new genera: *Paramacrobium* J. Léonard, *Pellegriniodendron* J. Léonard, and *Gilbertiodendron* J. Léonard (see de la Estrella and Devesa 2014 for a brief taxonomic history of this group). Cowan (1953) agreed with Léonard's Neotropical circumscription of *Macrobium* but considered it most closely related to the African genus *Berlinia* Sol. ex Hook. f. (Cowan 1953). Later, Cowan and Polhill (1981) described a *Macrobium* group that placed the genus *Macrobium* with the four morphologically similar African genera described or revived by Leonard (1952, 1954, 1955). Many new species of *Macrobium* have been described since

¹ Author for correspondence; e-mail: bruce.murphy@kew.org.

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Cowan's (1953) monograph, increasing the total species number by more than 50% (e.g., Cowan 1955, 1957, 1964, 1973, 1977, 1985; Burger 1968; Little 1969; Simpson 1975; Zarucchi 1990; Barneby 1992; see app. B for a list of *Macrolobium* species). Many of these new taxa were described from Central America and the Guianas.

Previous molecular studies have shown *Macrolobium* to be part of the tribe Detarieae, which, in response to the long-known paraphyly of the former Caesalpinioideae, has now been stabilized as a subfamily (Detarioideae) and revealed as one of the early branching lineages within the Leguminosae (Bruneau et al. 2001, 2008; LPWG 2017). The Detarioideae (or Detarieae) has been the focus of several studies in recent years (e.g., Bruneau et al. 2001, 2008, 2014; Fougère-Danezan et al. 2007, 2010; Redden et al. 2010; de la Estrella et al. 2014, 2017). Contrary to Cowan's (1953) and Cowan and Polhill's (1981) *Macrolobium* group hypothesis, Bruneau et al. (2001) found *Macrolobium* not closely related to African genera but part of a *Brownea* clade with five other endemic Neotropical genera (*Brownea* Jacq., *Browneopsis* Huber, *Paloue* Aubl., *Elizabetha* Schomb. ex Benth., and *Ecuadendron* Neill). Subsequent analyses with increased sampling and additional markers confirmed the monophyly of the *Brownea* clade (Herendeen et al. 2003; Bruneau et al. 2008, 2014), with the addition of *Heterostemon* Desf. by Bruneau et al. (2008) and *Paloveopsis* R.S. Cowan and *Brachycylix* (Harms) R.S. Cowan by Redden et al. (2010). Although the *Brownea* clade was strongly supported (Bruneau et al. 2008; de la Estrella et al. 2017), some of the constituent genera, including *Macrolobium*, were not monophyletic or appeared poorly resolved in these studies (e.g., Bruneau et al. 2008; de la Estrella et al. 2017).

Macrolobium is morphologically and ecologically diverse (Cowan 1953) but is well delimited by its grooved leaf rachis, single petal with auriculate claw, lack of vasculature in occasional vestigial petals, narrowly alate petiole and rachis, absence of staminodia, smooth fruit, and densely striate pollen exine (Cowan 1953; Redden et al. 2010). Despite these defining characters, recent molecular studies have questioned the monophyly of the genus (Bruneau et al. 2001, 2008; but see also Redden et al. 2010). However, these studies were focused on generic level relationships, and sampling within *Macrolobium* was limited.

Two subgeneric sections have been distinguished within *Macrolobium*: *Vouapa* (Aubl.) Benth., correctly named section *Macrolobium* (according to article 22.1 of the International Code of Nomenclature; McNeill et al. 2012), and *Stenosolen* Harms (fig. 1). Species belonging to section *Macrolobium* have fully opening bracteoles, a cuplike hypanthium, four or five sepals (when five, the adaxial pair is often partially fused), and an obvious petal claw, while species belonging to section *Stenosolen* have bracteoles that only partially separate along the adaxial seam, a cylindrical hypanthium, four sepals, and a more or less sessile petal.

Species belonging to section *Stenosolen* (sensu Cowan 1953) are distributed in the foothills on either side of the northern and central Andes, in the western Amazon, and in Central America (plus Trinidad), while species in section *Macrolobium* have a predominantly central and eastern Amazonian distribution, with an outlier group extending to coastal Brazil. This distribution appears to correspond to the Gentry pattern, a term coined

by Antonelli and Sanmartin (2011) in recognition of Gentry's (1982) observations concerning Amazonian-centered and Andean-centered plant groups. The rest of the *Brownea* clade displays a similar distribution pattern, with *Brachycylix*, *Brownea*, *Browneopsis*, and *Ecuadendron* (Cowan 1975; Klitgård 1991; Neill 1998) having a center of diversity in northwestern South America and *Elizabetha*, *Heterostemon*, *Paloue*, and *Paloveopsis* centered in the Guiana Shield region in the east (Cowan 1976a, 1976b; Redden et al. 2010). The occurrence of the same distribution pattern within *Macrolobium* that occurs between other genera of the *Brownea* clade further raises the question of whether the two sections of *Macrolobium* are separately derived.

Given the clear morphological differences and contrasting distributional patterns between sections *Macrolobium* and *Stenosolen*, our objective is to test whether they are monophyletic and also to investigate the monophyletic nature of the genus. To address these questions, we sequenced the plastid *matK* gene (including the flanking *trnK* intron) and *trnG* regions, as well as the nrDNA ITS region, producing the first densely sampled molecular phylogeny for *Macrolobium*.

Material and Methods

Taxon Sampling

Sequences were obtained for 39 *Macrolobium* species, together broadly representing all of Cowan's (1953, 1964) major groupings (fig. 1), along with a number of unidentified or new *Macrolobium* species. Sixty-three Detarioideae outgroup species were also included, 33 from within the *Brownea* clade. Samples were acquired from dried herbarium specimens from AAU, BOL, E, K, MT, NY, US, and WAG (acronyms following *Index Herbariorum*; Thiers 2016) and/or silica-collected field samples, and were complemented with sequences downloaded from GenBank. A total of 43 *Macrolobium* accessions were newly sequenced for at least one marker by the authors, amounting to 25 previously unsequenced *Macrolobium* species and a further seven *Macrolobium* accessions unidentified to species. Outgroup sequences were all from previous or forthcoming studies and available through GenBank. Details of voucher material and GenBank accession numbers are provided in appendix A.

Molecular Methods

DNA extractions were performed using an adapted cetyltrimethylammonium bromide method (Doyle and Doyle 1987). For the most recalcitrant samples, the Qiagen DNeasy Plant Mini Kit (Qiagen, Manchester, UK) was used according to the manufacturer's instructions. PCR amplifications and cycle sequencing were performed as described by de la Estrella et al. (2017), with nested amplifications used for difficult samples as described in that study and references therein, but also using the internal ITS primers ITS2 and ITS3 (White et al. 1990). Cloning was not performed, as double peaks were not common in the resulting chromatograms and polyploidy has not been reported in the genus. Sequencing reactions were run on an ABI 3730 au-

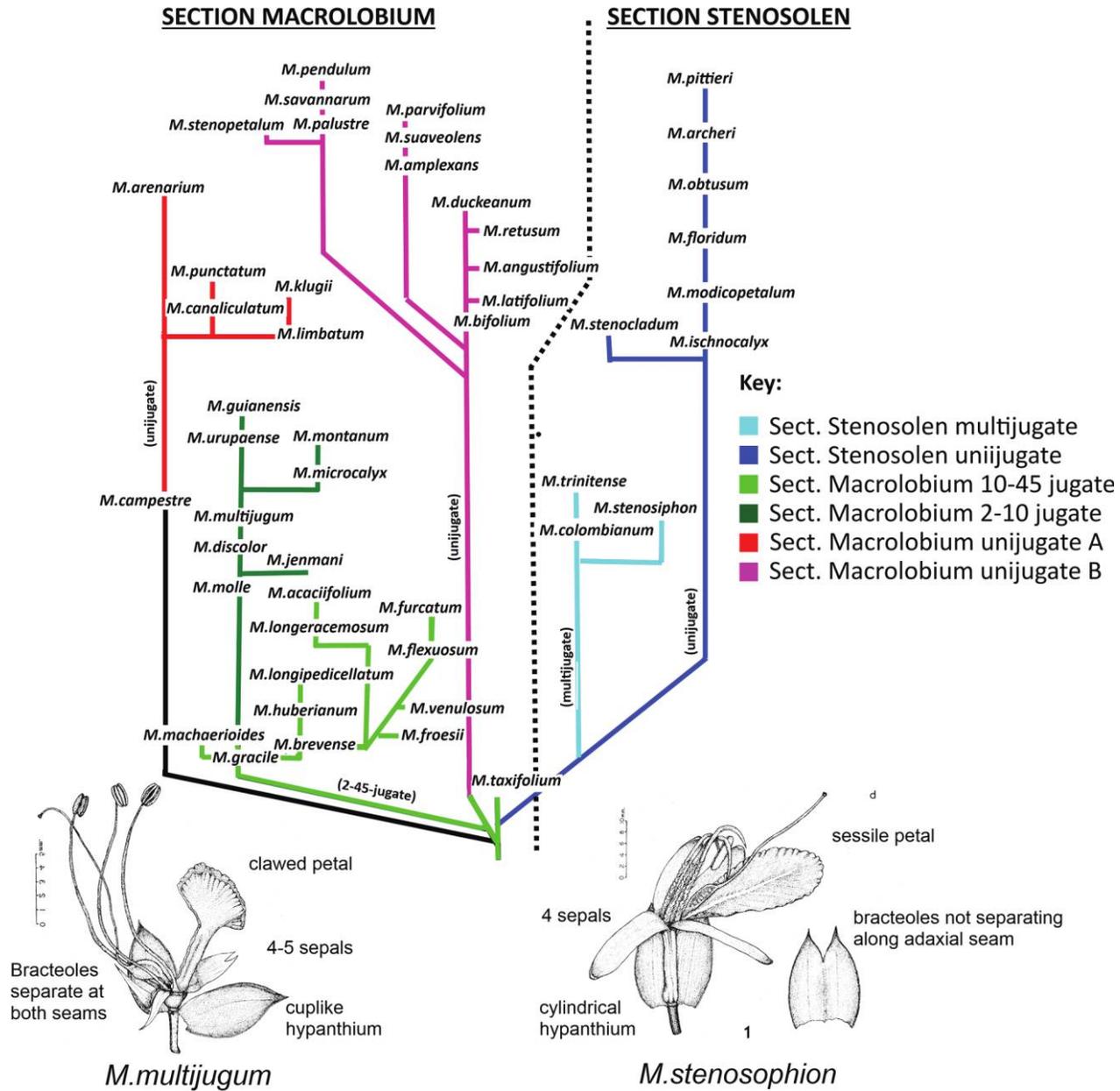


Fig. 1 Cowan's (1953) diagram of putative relationships in *Macrolobium*, adapted with permission of New York Botanical Garden. Colors indicating different groups have been added and correspond to the same colors in figs. 2, 3, and B1–B5, available online. Note that while the original author probably intended distance from the root to indicate evolutionary distance, he warned that “a line in the diagram from one species to another does not necessarily imply that . . . the one species has given rise to the other” (Cowan 1953, pp. 263, 266.). Illustrations show floral morphology typical of each section, also reproduced from Cowan (1953) with permission of New York Botanical Garden.

tomated sequencer (Applied Biosystems, Foster City, CA) following the manufacturer's protocols.

Phylogenetic Analyses

Forward and reverse sequences were inspected, aligned, and manually edited using default parameters in Geneious, version 8.0 (Biomatters, <http://www.geneious.com>). Where occasionally two conflicting peaks were present, bases were called

using International Union of Pure and Applied Chemistry ambiguity codes (Cornish-Bowen 1985). All sequences were verified using the BLAST approach (Altschul et al. 1990) and eliminated if they did not correspond to Leguminosae sequences in GenBank. Sequences were aligned using MAFFT v.7 (Katoh and Standley 2013). Maximum likelihood (ML) and Bayesian phylogenetic analyses were performed on ITS and combined *matK*+*trnG* matrices and subsequently on a combined ITS and plastid data set. The analyses were run on the CIPRES Science

Gateway (Miller et al. 2010). For the ML analysis, RaxML-HPC2 v8.2.8 (Stamatakis 2014) was used with the GTRCAT model and the default settings with 1000 rapid bootstrap replicates followed by the search of the best ML tree. The Bayesian analysis was conducted with MrBayes 3.2.3 (Ronquist and Huelsenbeck 2003). The Akaike information criterion (AIC; Akaike 1974), as implemented in Jmodeltest 2.1.6 (Darriba et al. 2012), was used to estimate the best evolutionary model for each DNA locus separately. Based on the AIC (Akaike 1974), the best models were GTR+I+G for ITS, TVM+G for *matK*, and TIMG1+G for *trnG*. Nevertheless, for all markers GTR+I+G was the model with the best likelihood, and it was implemented in subsequent MrBayes analyses.

Two independent runs of 50×10^6 generations were used, with two Markov chain Monte Carlo chains and four swaps per generation, sampling parameters and trees every 1000 generations. Tracer v 1.6 (Rambaut et al. 2014) was used to compare density plots of estimated parameters and likelihoods to ensure that effective sample sizes were sufficient and that chains had mixed appropriately. All estimated sample sizes were greater than 200. The first 5000 samples (10%) were discarded as burn-in, to ensure all retained samples were subsequent to reaching stationarity.

Mapping

Macrolobium distribution data were downloaded from the Global Biodiversity Information Facility and records sorted into sections *Macrolobium* and *Stenosolen*, according to Cowan's (1953, 1964) infrageneric classification and subsequent publications (Cowan 1957, 1973, 1976b, 1977, 1985; Burger 1968; Simpson 1975; Zarucchi 1990; Barneby 1992). The data set was manually reviewed and records not identified to species were removed, along with any obviously erroneous records such as those placed off the coast of South America. Georeferenced records for those sections were plotted using Simplemapp (http://www.simplemapp.net).

Results

The ITS matrix included 115 accessions, with a total aligned length of 1029 nucleotides; the plastid matrix was 2519 nucleotides long and contained 115 accessions; the combined ITS + plastid matrix had an aligned length of 3548 nucleotides and contained 127 accessions (table B1, available online). Although the plastid and ITS matrices contained the same number of accessions, there were several differences in the accessions they included, while for some accessions in the plastid matrix, *trnG* and *matK* markers were not both successfully sequenced (see app A). There were only 17.6% missing sequences in the combined matrix, although 37% of taxa were missing at least one of the three markers (table B1).

Combined Analyses

Analyses of the combined ITS + plastid matrix resolve a monophyletic *Macrolobium* with strong support (posterior probability [PP]: 1.0, bootstrap [BS]: 94%; figs. 2, B1; figs. B1–B5 available online). *Macrolobium* is returned as sister to a clade containing *Heterostemon* (except for *H. ingifolius*), *Elizabetha*,

and *Paloue* with strong PP (0.97) but weaker BS support (71%; figs. 2, B1). Within *Macrolobium* both Bayesian and ML trees retrieve two clades corresponding to Cowan's (1953) sections *Macrolobium* and *Stenosolen*, except for the position of *M. pendulum* Willd. ex Vogel (figs. 3, B1), which is resolved with section *Stenosolen*. Support for these clades is again weaker in the ML analysis (PP: 0.97, 0.97; BS: 66%, 68%). The Bayesian analysis (fig. 3) resolves a separate multijugate clade within section *Stenosolen* (PP: 0.97), as suggested by Cowan (1953) but without the multijugate *M. stenosphon*, which appears with unijugate species. These clades are not resolved in the ML analysis (fig. B1). Relationships within the sections are otherwise poorly resolved in both Bayesian and ML analyses.

ITS Analyses

The ITS analyses produced much the same topology as the combined analysis (figs. B2, B3). However, within *Macrolobium* support is higher for the two sections (PP: 1.0, BS: 98%, 99%). The unijugate and multijugate clades within section *Stenosolen* are also strongly resolved (PP: 0.99, 1; BS: 97%, 81%). Within section *Macrolobium* a main subclade (PP: 0.99; BS: 73%) is resolved, with a polytomy of mainly 10–45 jugate species unresolved outside it and clades partially corresponding to jugacy also resolved within it. The positions of species and clades within section *Macrolobium* have few similarities with those in the poorly resolved combined analysis.

Plastid Analyses

In the Bayesian analysis of the plastid matrix (*matK-trnK* and *trnG*; fig. B4) a *Brownea* clade is also strongly supported (PP: 0.99), although the outlying species *H. ellipticus* is oddly placed elsewhere in this tree. Support is much weaker in the ML analysis (BS: 64%; fig. B5). Within the *Brownea* clade, two main clades plus the single species *H. ingifolius* are returned with moderate support in the Bayesian analysis (PP: 0.89, 0.9). Unlike for the nuclear marker, the two large clades both combine *Macrolobium* with other species, although most of section *Macrolobium* is placed within a single clade, sister to species from *Elizabetha* and *Heterostemon*. Resolution is poor within these clades. Section *Stenosolen* is contained within two separate clades without other species. In the ML analysis, the *Brownea* clade is largely a polytomy (fig. B5).

Discussion

The Monophyly of Macrolobium

Our study achieves in-depth sampling across all groupings of *Macrolobium* species suggested by Cowan (1953, 1964), and our combined and ITS analyses (figs. 2, 3, B1–B3) resolve a monophyletic *Macrolobium*, in contrast with all previous studies based on plastid markers and more limited sampling (Bruneau et al. 2001, 2008). However, our plastid tree (figs. S4, S5), which is poorly resolved, fails to return a monophyletic *Macrolobium*. The sequenced plastid regions are known not to be the most variable at the species level (Shaw et al. 2005, 2007) but were used to allow the placement of *Macrolobium* in the context of the *Brownea* clade using previously published sequences. Other systematic and biogeographic studies using



Fig. 2 Bayesian maximum credibility tree based on the combined ITS and plastid partitions. Posterior probability support values are indicated at nodes; for values lower than 0.5, nodes have been collapsed. Colors correspond to groups suggested by Cowan (1953) as indicated on fig. 1. Species published after Cowan (1953) have been allocated to color groups based on published descriptions (Cowan 1957, 1964, 1973, 1985; Burger 1968; Zarucchi 1990; Barneby 1992). Undescribed species are black.

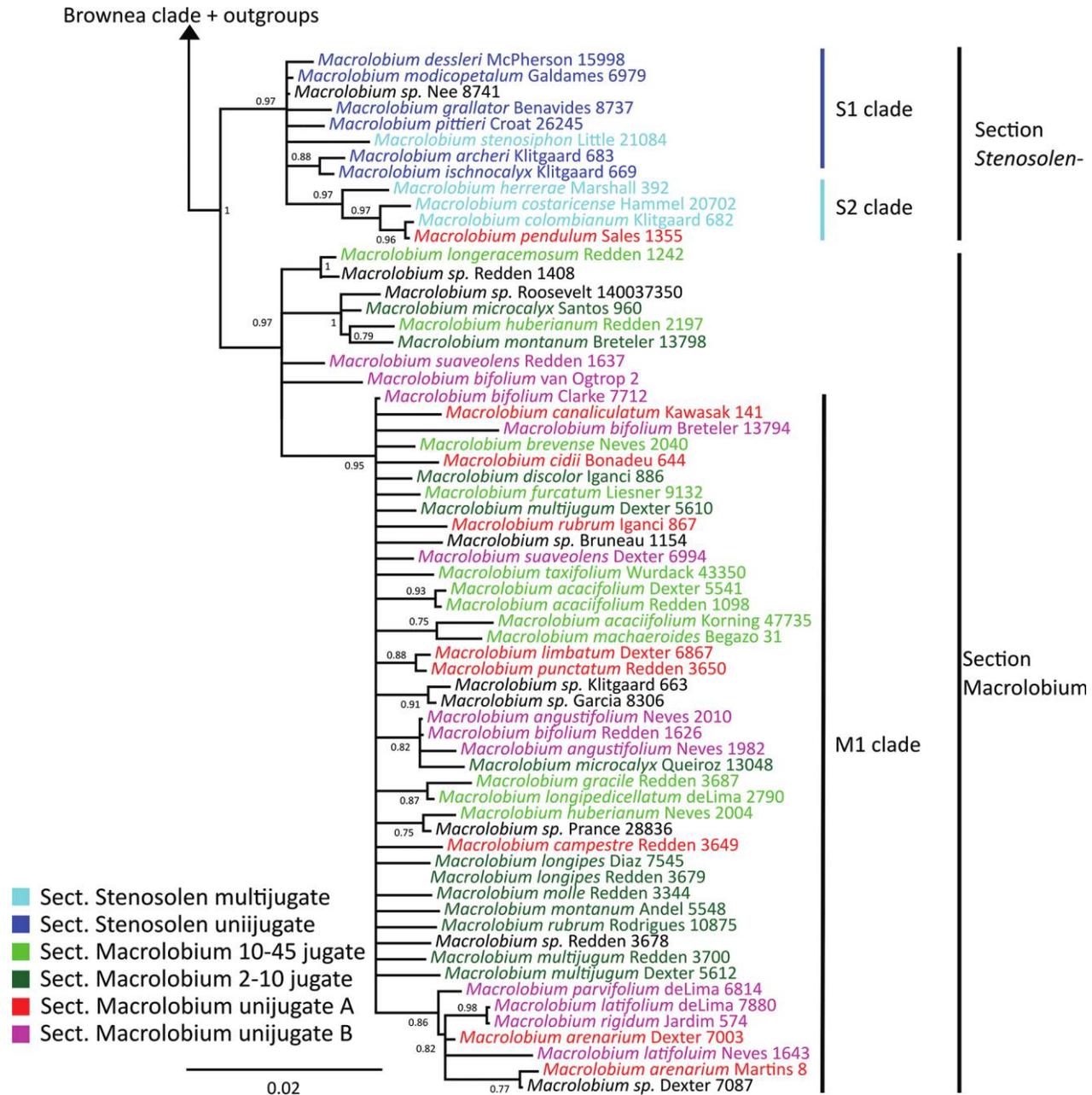


Fig. 3 Enlarged portion of fig. 2 showing the genus *Macrolobium*. Major clades discussed in the text are marked on the right of the tree.

the ITS marker (although with limited species-level sampling) also found *Macrolobium* to be monophyletic (Redden et al. 2010; de la Estrella et al. 2017). The monophyly of *Macrolobium* is an important finding because it is the most species-rich genus in subfamily Detarioideae after *Cynometra*, which has been revealed as paraphyletic (de la Estrella et al. 2017; Radosavljevic et al., forthcoming). The degree of morphological and ecological variation within *Macrolobium* also makes monophyly noteworthy (Cowan 1953; Berry et al. 1995; Mackinder et al. 2005).

At a lower taxonomic level, several species are resolved as nonmonophyletic in our combined analysis, notably, *Macrolo-*

bium huberianum, *M. suaveolens*, and *M. bifolium*. However, resolution is poor in this part of the combined tree, and these species are monophyletic in the ITS tree. In the ITS tree, other species are nonmonophyletic, including the widespread and abundant *M. acacifolium*. These findings merit further investigation with greater within-species sampling.

Distribution Patterns and Sectional Divisions

The Brownea clade has two centers of diversity that correspond to the Gentry pattern observed by Gentry (1982) and further discussed by Antonelli and Sanmartin (2011). The Ecu-

dendron clade (fig. 2) containing *Brachycylix*, *Brownea*, *Browneopsis*, and *Ecuadendron* is centered in the northwestern part of South America, while the Elizabetha clade comprising *Elizabetha*, *Paloue*, *Paloveopsis*, and *Heterostemon* is centered in the northeast and eastern parts of South America (Cowan 1975, 1976a, 1976b; Klitgård 1991; Neill 1998; Redden et al. 2010). Our mapping of *Macrolobium* shows that the geographical ranges of the two sections within the genus follow this same pattern (fig. 4). These two sections are well supported by our molecular analysis, with only *M. pendulum* not placed according to the taxonomic scheme of Cowan (1953). Given the distributional differences of these sections, the monophyly of *Macrolobium* is an interesting outcome, as previously the two sections could have been considered to have evolved from separate ancestors with different distributions.

Andean uplift has been linked with species diversity in the Neotropics (Antonelli et al. 2009; Hoorn et al. 2010; Antonelli and Sanmartin 2011; Luebert and Weigend 2014), but it is notable that section *Stenosolen* accounts for only one-quarter (19 out of 75) of the accepted species in the genus *Macrolobium* despite occurring in species-rich areas in the foothills of the

Andes. In fact, section *Macrolobium* contains approximately half of the entire *Brownea* clade's species (Mackinder 2005). Diversification has been found to have little to do with Andean orogeny in the Chrysobalanaceae (Bardon et al. 2013) despite its importance for many other Neotropical lineages, and this may also be the case for *Macrolobium*.

Phylogenetic and Morphological Correspondence

In each section of *Macrolobium*, Cowan (1953, 1964) grouped species based largely on leaf jugacy (fig. 1). Cowan (1953) suggested that multijugate leaves are plesiomorphic for *Macrolobium* and that in both sections a gradual reduction in leaflet number is correlated with advancement in floral morphology. Within the *Brownea* clade Redden and Herendeen (2006) found multijugacy to be ancestral, with a reduction to unijugate leaves in *Heterostemon* and simple or unifoliolate leaves in *Paloue*. However, their analysis excluded *Macrolobium* from the *Brownea* clade, while Cowan (1953) considered *Macrolobium* most closely related to the African genus *Berlinia*. Our combined analysis generally has insufficient resolution to test these hypotheses

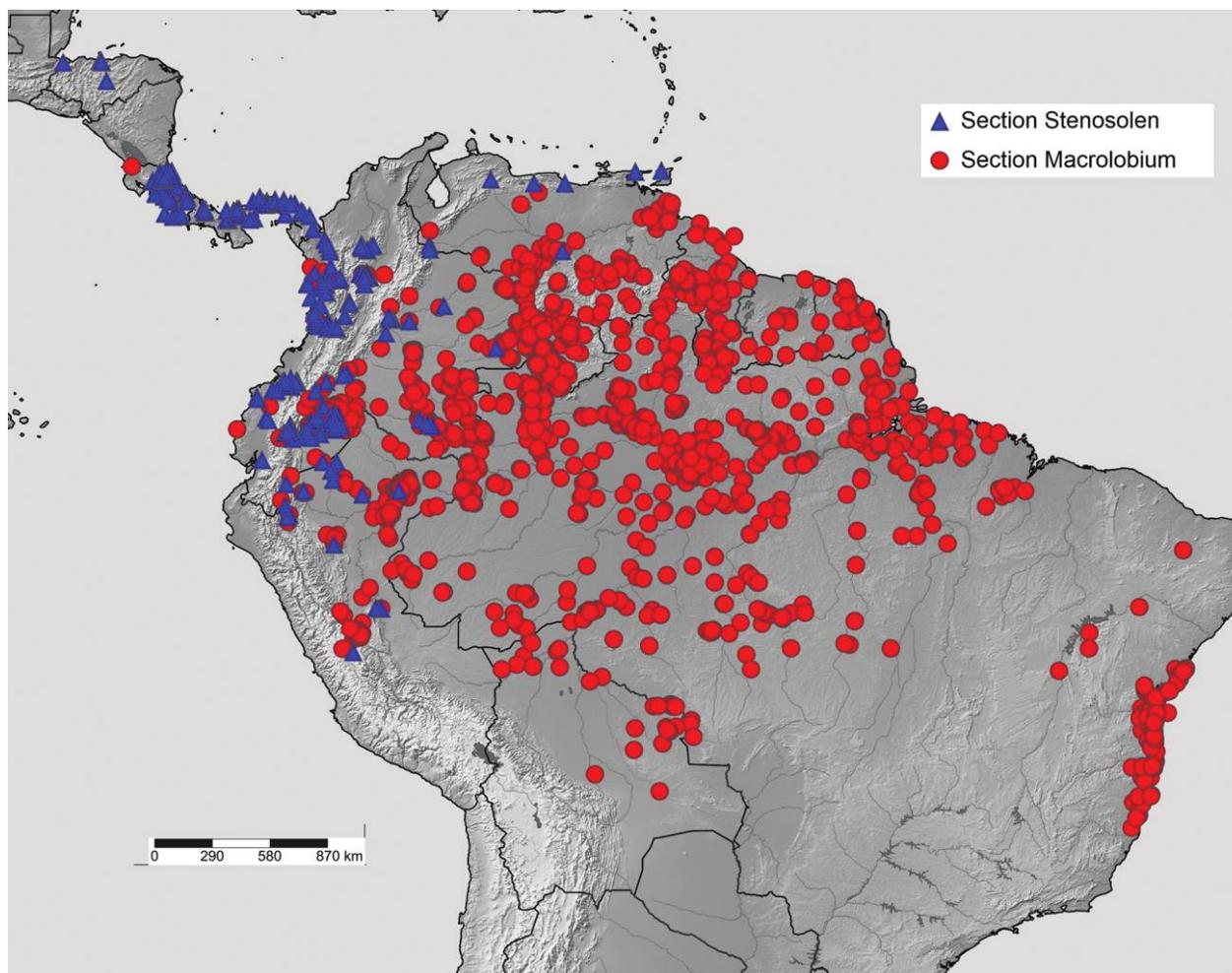


Fig. 4 Distribution of *Macrolobium* occurrence divided into sections *Macrolobium* (red circles) and *Stenosolen* (blue triangles).

properly, but some grouping of species by jugacy can be observed. Within section *Stenosolen*, Cowan (1953) suggested that multijugate and unijugate groups were evolutionarily separated. Our analyses appear to support this, particularly our ITS analysis (fig. B2), in which clades S1 and S2 are well supported and in agreement with Cowan's taxonomy, except for the position of *M. stenosphon*, which appears to indicate a separate origin of multijugacy.

Within section *Macrolobium*, Cowan (1953) suggested two separate origins of unijugacy (red and pink lines in fig. 1) and indicated a separation of many-jugate (light green) from few-jugate (dark green) species. These groups are not resolved in our combined analysis, but there is some support for them on our ITS tree (fig. B2). On this tree, many-jugate (light green) species are found mainly in a polytomy outside of the main M1 clade. Several (dark green) 2- to 10-jugate species (*M. longipes*, *M. molle*, *M. montanum*) are found in a well-supported clade along with *M. campestre*. This latter species is also multijugate and therefore fits well with this clade, but Cowan (1953) considered it to be allied with one of the unijugate groups. The unijugate species *M. angustifolium*, *M. bifolium*, and *M. suaveolens* are also resolved together as Cowan (1953) suggested. *Macrolobium latifolium* and *M. rigidum*, both unijugate species from the coastal restinga of Bahia and Espírito Santo in Brazil (Lewis 1987), are grouped together with *M. parvifolium*, also placed by Cowan (1953) in a closely related group. Unijugate *M. arenarium* is also included in this clade, rather than in the separate (red) unijugate group of figure 1. The latter group is scattered in our analysis, suggesting more transitions between multijugacy and unijugacy than envisioned by Cowan (1953).

Overall, it is evident that there have been at least two changes between unijugacy and multijugacy (or vice versa) within *Macrolobium* because both sections contain well-supported unijugate and multijugate or mixed clades (fig. 3). Our analysis finds *Macrolobium* to be sister to the group containing many-jugate *Elizabetha* as well as simple/unifoliolate *Paloue* and mixed-jugate *Heterostemon*, rather than the group containing bijugate *Ecuadendron* and few- to many-jugate *Brownea* and *Browneopsis*. However, it is not possible to speculate further on Cowan's (1953) hypothesis that multijugacy was plesiomorphic for *Macrolobium* without a full reconstruction based on a better-resolved tree.

Cowan's (1953) interpretation of floral evolution in *Macrolobium* is also affected by the analysis presented. Three floral characters suggested by Cowan (1953) to indicate the more derived status of section *Stenosolen* relative to section *Macrolobium* are better seen as plesiomorphic when the genus is considered as part of the *Brownea* clade. First, Cowan (1953) suggested that a reduction from five to four sepals took place in several lineages within *Macrolobium*, including the whole of section *Stenosolen* (fig. 1). However, while Leguminosae generally have five sepals, fusion of the adaxial sepals to form a tetramerous calyx is common in the Detarioideae and the norm for other genera within the *Brownea* clade (Klitgård 1991; Redden et al. 2010; Bruneau et al. 2014). Similarly, Cowan (1953)

considered the failure of the bracteoles to open completely along the adaxial seam in section *Stenosolen* to be a derived character state. However, although bracteoles are free in most of the Detarioideae (Bruneau et al. 2014), they are fused within the *Brownea* clade, again suggesting that section *Macrolobium*, not section *Stenosolen*, may feature the derived character state. Finally, the cylindrical hypanthium found in section *Stenosolen* is also more common to other *Brownea* clade genera than the cuplike hypanthium of section *Macrolobium* (Redden and Herendeen 2006, table 2). Floral morphology therefore does not appear to support Cowan's theory that section *Macrolobium* is closer to the ancestral *Macrolobium* flower.

Conclusions

While effort was made to sample across the genus, some groups and species are not well represented in our phylogeny and further sampling of *Macrolobium pendulum* is required to confirm its anomalous position. Other species of interest not sequenced here include those from the branch containing *M. furcatum* Ducke (fig. 1); *M. conjunctum* R.S. Cowan, an unusual species with a staminal tube; and *M. trinitense* Urban, the only nonmainland species. Dating the phylogeny produced here could help to test the theory that Neotropical diversity is recent and rapid. It could also enable comparison of speciation patterns within different areas and habitats of South America, and within the Detarioideae between the Neotropical *Brownea* clade and related groups from Africa, such as the *Berlinia* clade (de la Estrella et al. 2014, 2017; Schley et al., forthcoming). A monophyletic *Macrolobium* and the two well-delimited sections represent promising groups for further work examining speciation, adaptive radiation, and evolution of Neotropical diversity.

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Appendix A

Voucher Specimens

Voucher Information with GenBank Accession Numbers for Phylogenetic Analyses

Herbaria codes are indicated in parentheses. Sequences appearing in previously published work are indicated by an asterisk following the GenBank accession number. Data are ordered by *matK-trnK* intron, *trnG* intron, and ITS. Missing data are indicated with a dash.

Macrolobium Accessions

Macrolobium acaciifolium, Dexter 5541 (E), MF946625, MF987572, MF987606; *Macrolobium acaciifolium*, Korning 47735 (AAU), KX162225*, KY313050*, KY306616*; *Macrolobium acaciifolium*, Redden 1098, (US), MF946644, MF987573, MF987607; *Macrolobium angustifolium*, Neves 2010 (K), MF946641, MF987583, MF987609; *Macrolobium angustifolium*, Neves 1982 (K), MF946640, MF987577, MF987608; *Macrolobium archeri*, Klitgaard 683 (K), KX162227*, KY313051*, KY306617*; *Macrolobium arenarium*, Martins 8 (K), -, -, MF987611; *Macrolobium arenarium*, Dexter 7003 (E), MF946627, MF987591, MF987610; *Macrolobium bifolium*, van Ogtrop 2 (WAG), KX162229*, MF987574, MF987613; *Macrolobium bifolium*, Clarke 7712 (US), KX162228*, KY313052*, KY306618*; *Macrolobium bifolium*, Redden 1626 (US), -, -, MF987612; *Macrolobium bifolium*, Breteler 13794 (WAG), MF946643, -, -; *Macrolobium brevense*, Neves 2040 (K), MF946637, MF987594, MF987614; *Macrolobium campestre*, Redden 3649 (US), KX162230*, KY313053*, FJ817499*; *Macrolobium canaliculatum*, Kawasaki 141 (K), MF946632, MF987569, MF987615; *Macrolobium cidii*, Bonadeu 644 (E), MF946626, -, MF987616; *Macrolobium colombianum*, Klitgaard 682 (K), MF946624, MF987575, MF987617; *Macrolobium costaricense*, Hammel 20702 (K), -, -, MF987618; *Macrolobium discolor*, Iganci 886(E), MF946633, MF987582, MF987619; *Macrolobium dressleri*, McPherson 15998 (US), KX162231*,-,KY306619*; *Macrolobium sp.*, Garcia 140037350 (E), -, -, MF987620; *Macrolobium furcatum*, Liesner 9132 (US), -, MF987590, -; *Macrolobium gracile*, Redden 3687 (US), KX162232*, KY313054*, FJ817500*; *Macrolobium grallator*, de Benavides 8737 (NY), -, MF987596, MF987621; *Macrolobium herrerae*, Marshall 392 (K), -, MF987568, MF987622; *Macrolobium huberianum*, Neves 2004 (K), MF946650, -, -; *Macrolobium huberianum*, Redden 2197 (US), KX162233*, KY313055*, KY306620*; *Macrolobium sp.*, Dexter 7087 (E), MF946628, MF987593, MF987640; *Macrolobium ischnocalyx*, Klitgaard 669 (K), EU361997*, KY313056*, KY306621*; *Macrolobium latifolium*, de Lima 7880 (K), MF946631, MF987578, MF987623; *Macrolobium latifolium*, Neves 1643 (K), MF946649, -, -; *Macrolobium limbatum*, Dexter 6867 (E), MF946629, MF987592, MF987624; *Macrolobium longeracemosum*, Redden 1242 (K), -, MF987563, MF987625; *Macrolobium longipedicellatum*, de Lima 2790 (K), MF946634, MF987581, MF987626; *Macrolobium longipes*, Diaz 7545 (NY), -, -, MF987627; *Macrolobium longipes*, Redden 3679 (US), -, -, MF987628; *Macrolobium machaeroides*, Begazo 31 (US), -, MF987587, MF987629; *Macrolobium microcalyx*, Santos 960 (K), -, -, MF987630; *Macrolobium microcalyx*, Queiroz 13048 (E), MF946642, -, -; *Macrolobium modicopetalum*, Galdames 6979 (US), MF946652, MF987566, MF987631; *Macrolobium molle*, Redden 3344 (US), KX162234*, KY313057*, KY306622*; *Macrolobium montanum*, Andel 5548 (K), MF946645, MF987589, MF987632; *Macrolobium montanum*, Breteler 13798 (WAG), KX162235*, -, KY306623*; *Macrolobium multijugum*, Dexter 5612 (E), MF946635, -, MF987633; *Macrolobium multijugum*, Dexter 5612 (E), MF946636, MF987588, MF987634; *Macrolobium multijugum*, Redden 3700 (US), KX162236*, KY313058*, FJ817502*; *Macrolobium parvifolium*, de Lima 6814 (US), MF946648, MF987584, MF987635; *Macrolobium pendulum*, Sales 1355 (NY), -, -, MF987636; *Macrolobium pittieri*, Croat 26245 (US), MF946653, MF987567, MF987637; *Macrolobium punctatum*, Redden 3650 (US), KX162237*, KY313059*, KY306624*; *Macrolobium rigidum*, Jardim 574 (NY), -, MF987579, MF987638; *Macrolobium rubrum*, Iganci 867 (E), MF946646, -, -; *Macrolobium longipes*, Rodriguez 10875 (K), MF946639, MF987585, MF987639; *Macrolobium sp.*, Redden 1408 (E), KX162239, MF987564, MF987644; *Macrolobium sp.*, Bruneau 1154 (MT), -, 1154, -; *Macrolobium sp.*, Klitgaard 663 (K), KX162238, MF987586, MF987641; *Macrolobium sp.*, Redden 3678 (US), -, -, MF987645; *Macrolobium sp. nov.*, Nee 8741 (US), -, -, MF987642; *Macrolobium sp. nov.*, Prance 28836 (US), MF946647, -, MF987643; *Macrolobium sp.*, Garcia 8306 (E), MF946630, -, MF987646; *Macrolobium stenosphon*, Little 21084 (NY), -, -, MF987647; *Macrolobium suaveolens*, Dexter 6994 (E), MF946638, MF987595, MF987648; *Macrolobium suaveolens*, Redden, 1637 (US), KX162240*, KY313060*, KY306625*; *Macrolobium taxifolium*, Wurdack 43350 (US), -, MF987580, MF987649.

Brownea Clade Accessions

Brownea ariza, Fougere AA04210 (MT), KX161984*, KY312906*, KY306520*; *Brownea ariza*, Wieringa 4167 (WAG), KX161985*, MF987562, MF987598; *Brownea capitella*, Fougere 5419 (MT), KX161986*, KY312907*, KY306521*; *Brownea coccinea*, Baker 600 (K), KX161987*, -, MF987599*; *Brownea coccinea*, Clarke 4139 (US), EU361891*, MF987565, MF987600*; *Brownea coccinea*, Fougere 33 (MT), KX161988*, KY312908*, KY306522*; *Brownea grandiceps*, Klitgaard

67040 (K), KX161989*, -, MF987601; *Brownea grandiceps*, Fougere D10364 (MT), KX161990*, KY312909*, KY306523*; *Brownea latifolia*, Steyermark 88845 (NY), KX161991*, -, KY306524*; *Brownea leucantha*, Klitgaard 666 (K), KX161992*, KY312910*, KY306525*; *Brownea sp.*, Fougere 11 (MT), KX161993*, MF987561*, MF987602; *Brownea sp.*, Pitman 5721 (K), KX161994*, MF987570, MF987603; *Browneopsis disepala*, Klitgaard 67032 (US), KX161995*, KY312911*, KY306526*; *Browneopsis ucayalina*, Neill 6376 (K), KX161996*, -, KY306527*; *Ecuadendron acostasolisianum*, Clark 6220 (US), -, MF987571, MF987604; *Ecuadendron acostasolisianum*, Lewis 2876 (K), KX162067*, KY312951*, KY306561*; *Ecuadendron acostasolisianum*, Neill 10437 (K), EU361938*, KY312952*, KY306562*; *Elizabetha coccinea*, Redden 1181 (US), KX162068*, -, KY306563*; *Elizabetha fanshawei*, Redden 1733 (US), KX162069*, -, KY306564*; *Elizabetha grahamiae*, Redden 3090 (US), KX162070*, KY312953*, KY306565*; *Elizabetha grahamii*, Redden 3307 (US), KX162071*, KY312954*, KY306566*; *Elizabetha macrostachya*, Redden 3714 (US), KX162072*, KY312955*, FJ817516*; *Elizabetha paraensis*, Redden 13791 (US), EU361941*, KY312956*, KY306567*; *Elizabetha princeps*, Redden 3692 (US), KX162073*, KY312957*, FJ817519*; *Heterostemon ellipticus*, Cid 8361 (K), -, KY313007*, KY306581*; *Heterostemon ingifolius*, Redden 3194 (US), KX162178*, KY313008*, FJ817525*; *Heterostemon mimosoides*, Cowan 10415 (NY), -, -, MF987605; *Heterostemon mimosoides*, Redden 3727 (US), KX162179*, KY313009*, FJ817528*; *Paloue guianensis*, Lindeman 874 (U), KX162250*, -, KY306633*; *Paloue induata*, Clarke 7587 (US), EU362015*, KY313069*, KY306634*; *Paloue riparia*, Redden 1161A (US), EU362016*, KY313070*, FJ817546*; *Paloue riparia*, Redden 3314 (US), -, -, MF987650.

Other Outgroup Accessions

Azelia africana, Jongkind 2440 (WAG), KX161926*, KY312862*, KY306485*; *Anthonotha macrophylla*, Breteler 1435 (WAG), EU361852*, -, MF987597; *Anthonotha stipulacea*, Walters 591 (WAG), KX161940*, KY312871*, KY306496*; *Aphanocalyx djumaensis*, Breteler 13056 (WAG), EU361856*, KY312874*, AF513655*; *Aphanocalyx ledermannii*, Wieringa 131 (WAG), KX161942*, KY312875*, AF513660*; *Berlinia brunelii*, Sosef, 2248 (WAG), KX161961*, KY312887*, KY306505*; *Berlinia confusa*, Breteler 15455 (WAG), EU361879*, KY312888*, KY306506*; *Copaifera officinalis*, Fougere 27 (MT), EU361918*, KY312915*, AY955816*; *Crudia gabonensis*, Breteler 13770 (WAG), KX162004*, KY312922*, KY306534*; *Crudia klainei*, Wieringa 2104 (WAG), KX162006*, -, KY306535*; *Daniellia pilosa*, Wieringa 1462 (WAG), KX162042*, KY312940*, KY306552*; *Englerodendron conchyliophorum*, Sosef 1151 (WAG), KX162074*, KY312959*, KY306569*; *Gilbertiodendron aylmeri*, Jongkind 7003 (WAG), KX162087*, KY312969*, KJ777191*; *Gilbertiodendron dewevrei*, Anel 4045 (WAG), KX162100*, KY312974*, KJ777205*; *Gilbertiodendron diphyllum*, Anel 3502 (WAG), KX162106*, KY312976*, KJ777211*; *Gilbertiodendron jongkindii*, Jongkind 4502 (WAG), KX162123*, KY312981*, KJ777227*; *Hymenostegia elegans*, Wieringa 6066 (WAG), KX162188*, KY313021*, KY306589*; *Julbernardia hochreutineri*, Breteler 13009 (WAG), KX162211*, KY313040*, AF513693*; *Kingiodendron platycarpum*, Smith 7549 (K), KX162280*, KY313089*, -, *Lysodice rhodostegia*, Manos (K), EU361995*, -, KY306614*; *Oddoniodendron micranthum*, Wieringa 6165 (WAG), KX162247, KY313068, KY306632; *Prioria oxyphylla*, Breteler 14768 (WAG), KX162279, KY313088, KY306642; *Prioria platycarpa*, Smith 7549 (K), KX162280, KY313089, AY955784; *Schotia afra*, Hodgkiss 1 (BOL), EU362037, KY313095, AY955774; *Schotia brachypetala*, Bruneau sn (K), KX162288, KY313096, KY306646; *Sindora klaineana*, Breteler 14415 (WAG), -, KY313101, AY955819; *Tamarindus indica*, Herendeen 29.IV.99.5 (US), KX162297, KY313111, KY306654; *Tamarindus indica*, Steeves sn (MT), KX162298, -, KY306655; *Tetraberlinia bifoliata*, Breteler 13081 (WAG), KX162310, KY313119, KY306662; *Tetraberlinia morelina*, Breteler 13097 (WAG), KX162313, KY313120, AF513702; *Tetraberlinia polyphylla*, Wieringa 3151 (WAG), EU362061, KY313121, AF513705.

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