Plant Ecology and Evolution 150 (1): 87–108, 2017
https://doi.org/10.5091/plecevo.2017.1193

REGULAR PAPER

Straddling the Mozambique Channel: molecular evidence for two major clades of Afro-Malagasy *Schefflera* (Araliaceae) co-occurring in Africa and Madagascar

Morgan R. Gostel[1,2,*], Gregory M. Plunkett[3] & Porter P. Lowry II[4,5]

[1]Department of Biology, Virginia Commonwealth University, Richmond, Virginia 23284-2012, U.S.A.
[2]Current address: Department of Botany, MRC 166, Smithsonian Institution, Washington, DC 20013-7012, U.S.A.
[3]Cullman Program for Molecular Systematics, New York Botanical Garden, Bronx, New York 10458-5126, U.S.A.
[4]Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166-0299 U.S.A.
[5]Institut de Systématique, Évolution et Biodiversité (ISYEB), Unité Mixte de Recherche 7205 (Centre National de la Recherche Scientifique/Muséum National d'Histoire Naturelle/École Pratique des Hautes Études/Université Pierre et Marie Curie), Muséum national d'Histoire naturelle, Sorbonne Universités, CP 39, 57 rue Cuvier, 75231, Paris CEDEX 05, France
*Author for correspondence: gostelm@gmail.com

Background and introduction – *Schefflera* is the largest genus in Araliaceae, with approximately 900 species. However, recent studies have shown that *Schefflera* is polyphyletic, representing no fewer than five distinct clades, each corresponding to a specific geographic region: Asia, continental Africa plus Madagascar, Melanesia, the Neotropics, and a small clade in several archipelagos of the Pacific Ocean. The Afro-Malagasy clade comprises 49 species distributed throughout tropical Africa, Madagascar, the Comoro Islands, and the Seychelles. Previous studies have suggested that this group is monophyletic, identifying two subclades (which largely correspond to informal morphogroups identified as 'Meiopanax' and 'Sciodaphyllum').
Methods – Using sequence data from nuclear rDNA and chloroplast spacers derived from 33 of the 49 currently circumscribed species of Afro-Malagasy *Schefflera*, this study tested the group's monophyly and that of its two informal subgroups. We utilized alternative partitioning schemes to explore the combinability of datasets from the distinct genomic regions sampled.
Key results – Our results support the monophyly of Afro-Malagasy *Schefflera* and its two informal subgroups, 'Meiopanax' and 'Sciodaphyllum'. Each of these subgroups include species from both continental Africa and Madagascar, although species diversity in 'Meiopanax' is heavily based in Madagascar. In 'Sciodaphyllum', species diversity is much greater in continental Africa, despite evidence for more widespread dispersal events that have led to subsequent speciation in both Madagascar and the Seychelles Islands. Among several species that appear to be non-monophyletic, *S. myriantha* stands out as particularly problematic. This species, which shows very little morphological variation across its wide distribution in Africa and Madagascar, forms two subclades, one restricted to Africa, and another from Madagascar that also includes two additional, morphologically distinctive species.
Conclusions – This study makes an important contribution towards the circumscription of one of the five clades currently treated as *Schefflera* s. lat. and is the most inclusive systematic study of Afro-Malagasy *Schefflera* to date. Our results support the monophyly of both informal groups 'Meiopanax' and 'Sciodaphyllum', which we propose to recognize as two separate genera, *Neocussonia* and *Astropanax*, respectively.

Key words – Africa, biogeography, chloroplast spacers, Madagascar, molecular systematics, nrITS, nrETS.

ISSN: 2032-3913 (print) – 2032-3921 (online)

INTRODUCTION

The genus *Schefflera* is the largest of the 37 genera currently recognized in the family Araliaceae (Frodin & Govaerts 2003). Recent estimates indicate that Araliaceae include more than 1,600 species, and *Schefflera* comprises at least half of these (Plunkett et al. 2005, Frodin et al. 2010). The taxonomic history of *Schefflera* dates back to its description by Forster & Forster (1776), who recognized a single species, *S. digitata* J.R.Forst. & G.Forst., endemic to New Zealand. Since then, the circumscription of the genus has been significantly modified several times as authors placed varying emphasis on particular morphological features, using either a narrow definition or broadening its limits by including several previously recognized genera (Frodin et al. 2010). Early efforts to expand *Schefflera* were undertaken by Baillon (1878, 1879), Harms (1894–1897) and Viguier (1906, 1909). More recently, an even broader approach was promoted by Frodin (1975), who went farther than his predecessors by including all woody araliads having palmately compound leaves, ligulate stipules, and valvate petal aestivation, while also lacking armaments and articulated pedicels. Since that time, the discovery and description of many new entities has increased the number of species, resulting largely from focused inventory work in areas with high diversity, such as Madagascar, South America and Southeast Asia.

Molecular phylogenetic studies have profoundly changed our understanding of this complex genus. Recent analyses of Araliaceae and more specifically of *Schefflera* have uncovered extensive polyphyly (Plunkett et al. 2004a, 2005), revealing five distinct clades of *Schefflera* distributed across the phylogenetic tree of the family. These five clades correspond closely to well delimited geographic areas and have been informally named Asian *Schefflera*, Neotropical *Schefflera*, Melanesian (or Pacific) *Schefflera*, Afro-Malagasy *Schefflera*, and *Schefflera* s. str. (Plunkett et al. 2005). Reconstruction of these relationships was based on a representative, albeit somewhat limited, sampling of species from throughout the genus designed to test the monophyly of *Schefflera*, identify its major subclades, and, once identified, initiate more extensive studies of relationships within each subclade. To that end, a series of research projects was initiated to clarify relationships, update the taxonomy, and refine the overall circumscription of each of these groups. Work on Melanesian *Schefflera* has largely resolved phylogenetic relationships among its 49 species (Plunkett & Lowry 2012, unpubl. data), including sixteen that remain to be described, all of which are now placed in the genus *Plerandra* A.Gray (Lowry et al. 2013). Work in the much larger Neotropical *Schefflera* clade has also been initiated (Fiaschi & Plunkett 2011). The goal of the present study is to clarify relationships in the Afro-Malagasy *Schefflera* clade, thereby providing a basis for placing its nearly fifty species in a new generic framework and enabling a comprehensive taxonomic revision of the group.

Evidence from the most recent comprehensive phylogenetic study of *Schefflera* (Plunkett et al. 2005) suggests that the Afro-Malagasy clade is part of a large basal polytomy in Araliaceae. Eight additional small lineages have also been placed in this basal polytomy: *Astrotricha*, *Cephalaralia*, *Cheirodendron* + *Raukaua*, *Cussonia* + *Seemannaralia*, *Harmsiopanax*, *Motherwellia*, *Osmoxylon*, and *Schefflera* s. str., along with three much larger clades, *Aralia-Panax*, the *Polyscias-Pseudopanax* clade (which includes *Plerandra*), and the Asian Palmate clade (which includes both the Asian and Neotropical clades of *Schefflera*).

The early taxonomic history of Afro-Malagasy *Schefflera* dates to Seemann's (1865) work, which initially described collections from Africa in the genera *Astropanax* and *Sciodaphyllum*. It was not until nearly three decades later that Harms (1894–1897) began placing palmately-leaved African araliads in *Schefflera* based on an expanded definition that encompassed these and other segregate genera. Much later, Bernardi (1969) and Bamps (1974) revisited the Malagasy and African species, respectively. Bernardi's work (1969), focusing primarily on endemics from Madagascar and the nearby Comoro islands, described three new species and two new varieties of *Schefflera*, while transferring ten species from *Cussonia* to *Schefflera*, where they joined two other species (*S. umbellifera* (Sond.) Baillon from Africa and *S. bojeri* (Seem.) R.Vig. from Madagascar) that had previously been placed there by Baillon (1878) and Viguier (1906), respectively. Bamps' (1974) study, which focused exclusively on representatives from continental Africa, led to the description of two additional new species of *Schefflera*, adding to those already recognized from the region (*S. barteri* (Seem.) Harms, *S. goetzenii* Harms, *S. mannii* (Hook.f.) Harms, and S. *umbellifera*). Together, these studies resulted in the recognition of a total of thirty species of *Schefflera* in the Africa-Madagascar region. Field and herbarium studies conducted over the last three decades have revealed an additional 19 taxa that appear to deserve recognition as new species (Lowry et al., unpubl. data), bringing the total to 49 species of Afro-Malagasy *Schefflera*. Elsewhere in the western Indian Ocean, *Schefflera* is absent from the Mascarene Islands but is represented by a single species in the Seychelles, *S. procumbens* (Helms.) F.Friedmann, which Frodin (in Plunkett et al. 2005) associated with several taxa occurring in Africa and Madagascar, namely *S. barteri*, *S. evrardii* Bamps, and *S. goetzenii*.

According to the infrageneric classification of *Schefflera* proposed by Bernardi (1969), the Malagasy members represent three series, namely *Anticipes*, *Myrianthae*, and *Racemosae*. The latter was based upon the presence of racemose or spicate ultimate inflorescence units and 2–3- or more rarely 4–5-carpellate ovaries, whereas *Anticipes* and *Myrianthae* had an umbellate inflorescence structure and either (4–)5- or 2(–3)-carpellate ovaries, respectively. These series were not, however, used by subsequent authors. Frodin (in Plunkett et al. 2005) used a different approach in which the species from Africa and Madagascar belong to two of the many subgeneric groups he recognized, namely 'Meiopanax' and 'Sciodaphyllum', which can be distinguished from one another on the basis of several morphological characteristics, but most readily by the presence of (often) compound-umbellate inflorescences and pseudo-ruminate endosperm in 'Meiopanax', as opposed to terminal paniculate inflorescences and non-ruminate endosperm in 'Sciodaphyllum'. In the broad study of *Schefflera* s. lat. by Plunkett et al. (2005), the nine species representing the Africa-Madagascar region formed two

subgroups, one of which corresponded closely with Frodin's 'Meiopanax' group, whereas the other fell among species comprising part of Frodin's large, pantropical 'Sciodaphyllum' group (now recognized as polyphyletic). Currently, 32 species (including both described and undescribed taxa) are recognized in the 'Meiopanax' group, while sixteen have been placed in 'Sciodaphyllum' (Lowry et al., unpubl. data).

Geography

The geographic structuring of the major clades of *Schefflera* s. lat. suggests that geography may have played a major role in the diversification of these groups (and Araliaceae as a whole). Within Afro-Malagasy *Schefflera*, however, both 'Meiopanax' and 'Sciodaphyllum' appear to be represented in both continental Africa and Madagascar, and this pattern raises intriguing questions regarding the origin and diversification of these groups. Madagascar, the fourth largest island in the world, is the primary center of diversity of Afro-Malagasy *Schefflera*, with 33 of the 49 currently recognized species (Lowry et al., unpubl. data). The island is separated from the African continent by the Mozambique Channel, lying approximately 400 km to the east of Mozambique and Tanzania. The Comoro Islands, a small archipelago of geologically recent volcanic islands situated between Africa and the northern tip of Madagascar, have a single species of *Schefflera* (the widespread *S. myriantha* (Baker) Drake, which is also found in both Madagascar and continental Africa). Another fifteen species occur only in tropical Africa. While both 'Meiopanax' and 'Sciodaphyllum' are represented on the continent and one or more of the islands in the Indian Ocean, 'Meiopanax' is more diverse in Madagascar and 'Sciodaphyllum' better represented in Africa. Clarifying the geographic origins of these groups remains a fundamental question for understanding diversification in the Afro-Malagasy clade.

Originally part of Gondwana, present-day Madagascar, India, and the Seychelles are estimated to have separated from Africa between 165 and 175 mya (Besse & Courtillot 1988, Schettinot & Scotese 2005, Ali & Aitchison 2008), with Madagascar reaching its present position approximately 125 mya (Rabinowitz et al. 1983). The subsequent separation of India and what now comprises the older granitic islands of the Seychelles from Madagascar has been dated to c. 88 mya (Storey et al. 1995). The ability to test hypotheses regarding biogeographic divergence among related plant groups in the Indian Ocean Basin (IOB) has been facilitated by an abundance of paleomagnetic and geophysical data and has contributed to a growing interest in the region's phytogeography (Schatz 1996, Yuan et al. 2005, Yoder & Nowak 2006). Recent molecular phylogenetic reconstructions have provided evidence for both vicariance and dispersal events in the floras endemic to landmasses that once comprised Gondwana and this has fuelled debate regarding patterns of biogeography (Donoghue & Smith 2004, McGlone 2005, Yoder & Nowak 2006, Crisp & Cook 2007, Agnarsson & Kuntner 2012). Historically, phylogenetic divergence in many elements of the southern hemisphere flora and fauna has been attributed to Gondwanan vicariance, but more recent studies have challenged these conclusions (Sanmartín et al. 2004). In particular, the application of molecular-dating techniques suggests long-distance dispersal or a combination of vicariance and dispersal events have been responsible for much of the diversity once attributed largely or exclusively to the appearance of geological barriers (Barker et al. 2007, Cook & Crisp 2005, Weeks et al. 2005, Zerega et al. 2005, Yoder & Nowak 2006, Gostel et al. 2016).

While phylogenetic connections between the Afro-Malagasy region, Malesia, and the Pacific have been suggested in some groups, this can be ruled out for *Schefflera* based on phylogenetic studies of the genus, which have shown that the taxa from each region are not sister groups (see Plunkett et al. 2005). A more useful point of comparison within Araliaceae for understanding the biogeography of Afro-Malagasy *Schefflera* can be found in the study of another araliaceous genus, *Polyscias*, and in particular the work that focused on phylogenetic relationships among the species belonging to the IOB clade (Plunkett et al. 2004b). This group is distributed across a region that includes continental Africa, Madagascar, the Comoros, and the Mascarene islands. Of particular note is one clade identified as the '*Polyscias fulva* group', representing ten species, three of which are endemic to Madagascar, one to the Comoros and six to Africa (Plunkett et al. 2004b, Plunkett & Lowry 2010). Within the *Polyscias fulva* clade, Plunkett & Lowry (2010) suggested that multiple dispersal events between Africa and Madagascar likely occurred.

Habit and morphology

Afro-Malagasy *Schefflera* includes trees (to 30 m), shrubs, and lianas, many of which are epiphytic (Tennant 1961, Bamps 1974, Bernardi 1980). Historically, species of Afro-Malagasy *Schefflera* have been distinguished using a combination of morphological features including inflorescence structure (in particular umbellate or racemose arrangement of the ultimate units), the number of carpels (which range from 2 to 9), and leaf structure (palmately compound or more rarely unifoliolate), as well as other leaf and inflorescence features (Bamps 1974, Bernardi 1980). However, these character states are present in many different combinations across the species in both informal groups. In several cases, morphological characters have failed to yield consistent species definitions. Bernardi (1969) noted problems with species delimitations in his treatment, which emphasized leaf shape. In particular, he described the great variation in the leaf shape of *S. longipedicellata* (Lecomte) Bernardi, not only among specimens but also in a single individual, and he suggested the possibility that hybridization between two Malagasy species, *S. longipedicellata* and *S. monophylla* (Baker) Bernardi, may have produced the character states exhibited by *S. staufferana* Bernardi. A careful review of morphological characters among the species of Afro-Malagasy *Schefflera*, particularly from a phylogenetic perspective, may help to identify the sources of confusion leading to these taxonomic problems and could assist in developing more robust, reliable species circumscriptions that reflect the full range of variation in each taxon.

Objectives and scope

The findings outlined in Plunkett et al. (2005) suggest that the species of *Schefflera* from Africa and Madagascar form a monophyletic group. The current study employs a greatly expanded sampling of the species from this region to test this hypothesis and to explore species-level phylogenetic relationships within Afro-Malagasy *Schefflera*. Previous studies have demonstrated the utility of molecular data in phylogenetic reconstruction among the species and genera of Araliaceae, using multiple molecular markers from both the nuclear (ITS and ETS) and plastid (notably, *trnL-trnF*) genomes (e.g. Eibl et al. 2001, Plunkett et al. 2004b, 2005, Tronchet et al. 2005, Nicolas & Plunkett 2009, Plunkett & Lowry 2010, 2012). A repeated problem in species-level molecular phylogenetics of plants has been the scarcity of informative plastid markers, resulting in poorly resolved trees at this level (Miller et al. 2009). In response to this deficit, recent studies have identified several plastid sequence regions that accumulate mutations rapidly enough to resolve relationships among taxa at the species level in many groups of angiosperms (Shaw et al. 2005, 2007, Miller et al. 2009). While several of these plastid markers were considered as candidates for this study, three chloroplast intergenic spacers (*trnK-rps16*, *ndhF-rpl32*, and *rpl32-trnL*) and two nuclear spacers (nrETS and nrITS) were ultimately chosen for sequencing across all sampled taxa because they amplified well in all samples. Sequences for all five of these markers were derived from representative material of 33 of the 49 currently recognized species of Afro-Malagasy *Schefflera*, more than three and a half times as many as were used by Plunkett et al. (2005). We aimed to (1) test the presumed monophyly of Afro-Malagasy *Schefflera*, (2) explore patterns of interspecific relationships within the group, (3) test biogeographic hypotheses regarding the origin and diversification of Afro-Malagasy *Schefflera*, and (4) identify morphological features that could be used in diagnosing subgeneric and interspecific groups of taxa.

MATERIALS AND METHODS

Sampling

Comprehensive sampling of all 49 currently recognized species of Afro-Malagasy *Schefflera* was initially attempted, but the material available from sixteen species proved to be inadequate. The resulting samples comprise a total of 162 accessions from the remaining 33 species, including nine putative undescribed species ('sp. ined. 1', etc) and seven collections left unidentified ('sp.') (see table 1). This sampling is nevertheless fully representative of the morphological and geographic diversity present within Afro-Malagasy *Schefflera*. Most of the material used was obtained from fresh field collections, dried on silica gel, but 25 of the 160 samples were derived from older herbarium specimens. Many taxa are represented by multiple accessions, making it possible to test their monophyly and to identify potential cases of hybrid origin. Outgroup taxa, selected on the basis of relationships suggested by previous studies (i.e. Plunkett et al. 2005), included species of *Astrotricha* DC., *Cussonia* Thunb., *Osmoxylon* Miq., *Schefflera* s. str., and the monotypic African genus *Seemannaralia* R.Vig.

Extraction, amplification and sequencing

For each accession, total DNA was extracted using the DNeasy Plant extraction kit (QIAGEN Inc.) or a modification of the protocol described by Alexander et al. (2007). Selected DNA regions were amplified using the polymerase chain reaction (PCR) for each accession with a combination of existing and newly developed primers for each spacer (see table 2 for list of primers). PCR reaction conditions included 0.5 µL of both forward and reverse primers (5 µ*M*), 0.5 µL spermidine (4 m*M*), 2 µL total DNA, and 5 µL of either the Jumpstart REDTaq ReadyMix (SigmaAldrich) or the GoTaq Green Master Mix (Promega Corp.) *Taq* polymerase mixes. With the exception of three modifications for *trnK-rps16* and *ndhF-rpl32*, all thermocycler protocols for PCR amplification included a pre-soak step of 4 min at 94°C, followed by 35 cycles of 30 sec at 94°C (denaturation), 1 min at 52°C (annealing), and 50 sec at 72°C (extension), and then a single post-soak of 72°C for 4 min. Due to lower primer melting temperatures, thermocycler protocols were slightly modified for both *ndhF-rpl32* and *trnK-rps16* by lowering the annealing temperature to 48°C (for *trnK-rps16*) or 50°C (for *ndhF-rpl32*) and by extending the annealing time to 90 sec (for both markers). In addition, the extension time was modified to 135 sec for *ndhF-rpl32* due to the increased length of this marker. PCR products were purified using 1.5 µL exonuclease I and 3 µL shrimp alkaline phosphatase per 5 µL of product (USB Corp.). Purified PCR products were sequenced directly using a thermocycler program of 20 sec at 94°C, 15 sec at 55°C, and 1 min at 60°C for 30 cycles. Sequencing reactions were carried out using DYEnamic ET Terminators (GE Healthcare, Inc.) or BigDye Terminator (vers. 3.1, Applied Biosystems Corp.) and then purified using the MultiScreen$_{384}$ SEQ filtration system (Millipore Corp.) or the BigDye XTerminator purification kit (Applied Biosystems Corp.). Capillary gel electrophoresis of cleaned products was performed on a MegaBACE 1000 DNA Sequencing System (GE Healthcare, Inc.) or an ABI 3730 DNA Analyzer (Applied Biosystems Corp.) and then assembled and edited using the Sequencher 4.7 software package (Gene Codes Corp.). Sequence alignment was adjusted manually following an initial alignment using ClustalX (Thompson et al. 1997). All sequences have been deposited in the GenBank database.

Phylogenetic analyses

Three complementary approaches to phylogenetic analysis were used in this study, maximum parsimony (MP), maximum likelihood (ML), and Bayesian inference (BI). Five separate datasets were used, (1) ITS, (2) ETS, (3) combined ITS + ETS, (4) the plastid markers (*trnK-rps16*, *ndhF-rpl32*, and *rpl32-trnL*, treated together), and (5) a set combining sequences from all five markers. To test for congruence among the separate datasets, the incongruence length difference (ILD) test of Farris et al. (1994) was performed using the partition homogeneity test in PAUP* 4.0b10 (Swofford 2002). Three partitions were established, representing the ITS, ETS, and combined plastid markers. An ILD test was

Table 1 – **Sampled species and voucher information.**
Species and DNA samples used in this study, including Genbank accession number, and specimen voucher information.

Taxon	**Genbank accession no. (ETS/ITS/*ndhF-rpl32*/*rpl32-trnL*/ *trnk-rps16*) *indicates missing sequence**	**Source and accession no.**
Outgroups		
Astrotricha pterocarpa Benth.	KY203609/AF229761/KY203616/ KY203623/KY203630	Queensland, Australia, *Plunkett* 1527 (NY)
Cussonia holstii Harms ex Engl.	KY203614/AY389031/ KY203621/ KY203628/ KY203635	Arusha, NP, Tanzania, *Lowry* 4986 (MO)
Cussonia paniculata Eckl. & Zeyh.	KY203615/AT389032/ KY203622/ KY203629/ KY203636	Amatole Mountains, South Africa, *Phillipson* 5263 (MO)
Cussonia thyrsiflora Thunb.	KY203613/KY203638/ KY203620/ KY203627/ KY203634	Kenton-on-sea, South Africa, *Phillipson* 5110 (MO)
Osmoxylon pectinatum (Merr.) Philipson	KY203610/AY389045/KY203617/ KY203624/KY203631	Green Is., Taiwan, *Huang* 756 (HAST)
Schefflera digitata J.R.Forst. & G.Forst.	KY203611/KY203637/KY203618/ KY203625/KY203632	North Island, New Zealand, *Plunkett* 2190 (NY)
Seemannaralia gerrardii (Seem.) R.Vig.	KY203612/AY389062/ KY203619/ KY203626/ KY203633	Tabankulu, South Africa, *Phillipson* 5471 (MO)
Ingroup, 'Meiopanax' clade		
Schefflera bojeri (Seem.) R.Vig.	KY088800/KY088684/KY088403/ KY088568/KY088453	Faliarivo, Madagascar, *Lowry* 5818 (MO)
	KY088798/KY088682/KY088329/ KY088566/KY088451	Col des Tapias, Madagascar, *Lowry* 7071 (MO)
	KY088799/KY088683/KY088346/ KY088567/KY088452	Antoetra, Madagascar, *Lowry* 7109 (MO)
Schefflera bracteolifera Frodin	KY088791/KY088675/KY088417/ KY088559/KY088444	Tsaratanana, Madagascar, *Lowry* 5327 (MO)
Schefflera capuroniana (Bernardi) Bernardi	KY088790/KY088674/KY088409/ KY088558/KY088443	Ambohitantely, Madagascar, *Bernardi* 11118 (P)
	KY088788/KY088672/KY088327/ KY088556/KY088441	Ankazobe, Madagascar, *Plunkett* 2328 (MO)
	KY088789/KY088673/KY088341/ KY088557/KY088442	Ambatovy, Madagascar, *Gostel* 28 (MO)
Schefflera favargeri Bernardi	KY088802/KY088686/KY088318/ KY088570/KY088455	Mangindrano, Madagascar, *Callmander 384* (MO)
	KY088805/KY088689/KY088332/ KY088573/KY088458	Ambohimirahavavy, Madagascar, *Callmander* 444 (MO)
	KY088803/KY088687/KY088347/ KY088571/KY088456	Tsaratanana, Madagascar, *Ratovoson* 476 (MO)
	KY088804/KY088688/KY088424/ KY088572/KY088457	Tsaratanana, Madagascar, *Lowry* 5344A (MO)
	KY088806/KY088690/KY088420/ KY088574/KY088459	Tsaratanana, Madagascar, *Lowry* 5386 (MO)
	KY088876/KY088760/KY088374/ KY088644/KY088528	Makirovana, Madagascar, *Ravelonarivo* 3332 (MO)
	KY088877/KY088761/KY088375/ KY088645/KY088529	Makirovana, Madagascar, *Ravelonarivo* 3333 (MO)
	KY088864/KY088748/KY088363/ KY088632/KY088516	Marojejy, Madagascar, *Ravelonarivo* 3339 (MO)
Schefflera fosbergiana (Bernardi) Bernardi	KY088801/KY088685/KY088404/ KY088569/KY088454	Marojejy, Madagascar, *Schmidt* 4322 (MO)
	KY088868/KY088752/KY088368/ KY088636/KY088520	Marojejy, Madagascar, *Ravelonarivo* 3350 (MO)
	KY088874/KY088758/KY088372/ KY088642/KY088526	Makirovana, Madagascar, *Ravelonarivo* 3337 (MO)

Table 1 (continued) – **Sampled species and voucher information.**
Species and DNA samples used in this study, including Genbank accession number, and specimen voucher information.

Taxon	Genbank accession no. (ETS/ITS/*ndhF-rpl32*/*rpl32-trnL*/*trnk-rps16*) **indicates missing sequence*	Source and accession no.
Ingroup, 'Meiopanax' clade		
Schefflera frodiniana Bernardi	KY088867/KY088751/KY088365/ KY088635/KY088519	Andohahela, Madagascar, *Bernard* 1486 (MO)
Schefflera halleana Bernardi	KY088807/KY088691/KY088406/ KY088575/KY088460	Marojejy, Madagascar, *Schmidt* 4261 (MO)
	KY088866/KY088750/KY088366/ KY088634/KY088518	Marojejy, Madagascar, *Ravelonarivo* 3340 (MO)
	KY088865/KY088749/KY088364/ KY088633/KY088517	Marojejy, Madagascar, *Ravelonarivo* 3343 (MO)
	KY088881/KY088765/KY088377/ KY088649/KY088533	Marojejy, Madagascar, *Ravelonarivo* 3342 (MO)
	KY088882/KY088766/KY088378/ KY088650/KY088534	Marojejy, Madagascar, *Ravelonarivo* 3344 (MO)
	KY088883/KY088767/KY088380/ KY088651/KY088535	Marojejy, Madagascar, *Ravelonarivo* 3345 (MO)
Schefflera longipedicellata (Lecomte) Bernardi	KY088781/KY088665/KY088392/ KY088549/KY088434	Masoala, Madagascar, *Lowry* 6153 (MO)
	KY088775/KY088659/KY088415/ KY088543/KY088428	Lakato, Madagascar, *Lowry* 6220 (MO)
	KY088776/KY088660/KY088418/ KY088544/KY088429	Ambohitantely, Madagascar, *Lowry* 6264 (MO)
	KY088779/KY088663/KY088335/ KY088547/KY088432	Antoetra, Madagascar, *Lowry* 7098 (MO)
	KY088780/KY088664/KY088336/ KY088548/KY088433	Antoetra, Madagascar, *Lowry* 7104 (MO)
	KY088777/KY088661/KY088333/ KY088545/KY088430	Ambatovy, Madagascar, *Gostel* 21 (MO)
	KY088778/KY088662/KY088334/ KY088546/KY088431	Ambatovy, Madagascar, *Gostel* 23 (MO)
	KY088782/KY088666/KY088337/ KY088550/KY088435	Ambatovy, Madagascar, *Gostel* 33 (MO)
	KY088887/KY088771/KY088381/ KY088655/KY088539	Marojejy, Madagascar, *Ravelonarivo* 3349 (MO)
Schefflera lukwangulensis (Tennant) Bernardi	KY088794/KY088678/KY088344/ KY088562/KY088447	Tanzania, *Mabberly* 1197 (MO)
Schefflera macerosa Bernardi	KY088869/KY088753/KY088367/ KY088637/KY088521	Andohahela, Madagascar, *Bernard* 1499 (MO)
	KY088871/KY088755/KY088369/ KY088639/KY088523	Andohahela, Madagascar, *Bernard* 1509 (MO)
Schefflera moratii Bernardi	KY088824/KY088708/KY088354/ KY088592/KY088476	Antsevabe, Madagascar, *Gostel* 31 (MO)
	KY088825/KY088709/KY088356/ KY088593/KY088477	Antsevabe, Madagascar, *Gostel* 34 (MO)
Schefflera rainaliana Bernardi	KY088796/KY088680/KY088325/ KY088564/KY088449	Mandena, Madagascar, *McPherson* 14791 (MO)
	KY088795/KY088679/KY088399/ KY088563/KY088448	Sainte Luce, Madagascar, *Rakotovao* 4444 (MO)
	KY088797/KY088681/KY088345/ KY088565/KY088450	Sainte Luce, Madagascar, *Lowry* 7151 (MO)

Table 1 (continued) – **Sampled species and voucher information.**
Species and DNA samples used in this study, including Genbank accession number, and specimen voucher information.

Taxon	Genbank accession no. (ETS/ITS/*ndhF-rpl32*/*rpl32-trnL*/*trnk-rps16*) **indicates missing sequence*	Source and accession no.
Ingroup, 'Meiopanax' clade		
Schefflera sp. ined. 1	KY088872/KY088756/KY088370/KY088640/KY088524	Andohahela, Madagascar, *Bernard* 1485 (MO)
	KY088873/KY088757/KY088371/KY088641/KY088525	Andohahela, Madagascar, *Bernard* 1487 (MO)
	KY088810/KY088694/KY088331/KY088578/KY088463	Ivorona, Madagascar, *Razakamalala* 4558 (MO)
	KY088812/KY088696/KY088386/KY088580/KY088465	Ivorona, Madagascar, *Razakamalala* 4941 (MO)
Schefflera sp. ined. 2	KY088808/KY088692/KY088319/KY088576/KY088461	Ivorona, Madagascar, *Plunkett* 2378 (MO)
	KY088809/KY088693/KY088384/KY088577/KY088462	Bemangidy, Madagascar, *Lowry* 7156 (MO)
Schefflera sp. ined. 3	KY088828/KY088712/KY088359/KY088596/KY088480	Bevoay, Madagascar, *Lowry* 7171 (MO)
Schefflera sp. ined. 4	KY088822/KY088706/KY088352/KY088590/KY088474	Ivorona, Madagascar, *Lowry* 7162 (MO)
	KY088823/KY088707/KY088353/KY088591/KY088475	Ivorona, Madagascar, *Lowry* 7172 (MO)
Schefflera sp. ined. 5	KY088821/KY088705/KY088351/KY088589/*	Ivorona, Madagascar, *Lowry* 7160 (MO)
Schefflera sp. ined. 6	KY088819/KY088703/KY088349/KY088587/KY088472	Antoetra, Madagascar, *Lowry* 7088 (MO)
	KY088820/KY088704/KY088350/KY088588/KY088473	Antoetra, Madagascar, *Lowry* 7091 (MO)
Schefflera sp. ined. 7	KY088783/KY088667/KY088338/KY088551/KY088436	Mangindrano, Madagascar, *Callmander* 432 (MO)
	KY088884/KY088768/KY088379/KY088652/KY088536	Marojejy, Madagascar, *Ravelonarivo* 3347 (MO)
	KY088885/KY088769/KY088320/KY088653/KY088537	Marojejy, Madagascar, *Ravelonarivo* 3352 (MO)
Schefflera sp. ined. 8	KY088863/KY088747/KY088362/KY088631/KY088515	Andohahela, Madagascar, *Bernard* 1505 (MO)
Schefflera sp.	KY088826/KY088710/KY088355/KY088594/KY088478	Ivorona, Madagascar, *Lowry* 7164 (MO)
	KY088827/KY088711/KY088357/KY088595/KY088479	Ivorona, Madagascar, *Lowry* 7169 (MO)
	KY088878/KY088762/KY088330/KY088646/KY088530	Makirovana, Madagascar, *Ravelonarivo* 3334 (MO)
	KY088879/KY088763/KY088376/KY088647/KY088531	Makirovana, Madagascar, *Ravelonarivo* 3335 (MO)
	KY088880/KY088764/KY088326/KY088648/KY088532	Makirovana, Madagascar, *Ravelonarivo* 3336 (MO)
	KY088886/KY088770/KY088383/KY088654/KY088538	Marojejy, Madagascar, *Ravelonarivo* 3351 (MO)
	KY088811/KY088695/KY088385/KY088579/KY088464	Ivorona, Madagascar, *Rakotovao* 4710 (MO)
Schefflera staufferana Bernardi	KY088813/KY088697/KY088414/KY088581/KY088466	Ambodisatrana, Madagascar, *McPherson* 17219 (MO)
	KY088814/KY088698/KY088321/KY088582/KY088467	Zahamena, Madagascar, *Ratovoson* 170 (MO)

Table 1 (continued) – **Sampled species and voucher information.**
Species and DNA samples used in this study, including Genbank accession number, and specimen voucher information.

Taxon	Genbank accession no. (ETS/ITS/*ndhF-rpl32*/*rpl32-trnL*/*trnk-rps16*) **indicates missing sequence*	Source and accession no.
Ingroup, 'Meiopanax' clade		
Schefflera staufferana Bernardi	KY088816/KY088700/KY088388/KY088584/KY088469	Ambatovy, Madagascar, *Gostel* 24 (MO)
	KY088815/KY088699/KY088387/KY088583/KY088468	Ambatovy, Madagascar, *Gostel* 25 (MO)
	KY088817/KY088701/KY088389/KY088585/KY088470	Ambatovy, Madagascar, *Gostel* 26 (MO)
	KY088818/KY088702/KY088348/KY088586/KY088471	Antoetra, Madagascar, *Lowry* 7082 (MO)
Schefflera umbellifera (Sond.) Baillon	KY088773/KY088657/KY088411/KY088541/KY088426	Soutpansberg, S. Africa, *Goldblatt* 11950 (MO)
	KY088774/KY088658/KY088416/KY088542/KY088427	Lusikisiki, Msikaba, Pondoland, South Africa, *Phillipson* 5494 (MO)
Schefflera vantsilana (Baker) Bernardi	KY088784/KY088668/KY088402/KY088552/KY088437	Lakato, Madagascar, *Lowry* 6225 (MO)
	KY088785/KY088669/KY088413/KY088553/KY088438	Zahamena, Madagascar, *A. Randrianasolo* 152 (MO)
	KY088786/KY088670/KY088339/KY088554/KY088439	Ambatovy, Madagascar, *Gostel* 32 (MO)
	KY088787/KY088671/KY088340/KY088555/KY088440	Antoetra, Madagascar, *Lowry* 7103 (MO)
Schefflera vantsilana var. *littoralis* Bernardi	KY088792/KY088676/KY088342/KY088560/KY088445	Sainte Luce, Madagascar, *Lowry* 7148 (MO)
	KY088793/KY088677/KY088343/KY088561/KY088446	Sainte Luce, Madagascar, *Lowry* 7149 (MO)
Ingroup, 'Sciodaphyllum' clade		
Schefflera barteri (Seem.) Harms	KY088858/KY088742/*/KY088626/KY088510	Cameroon, *Etuge* 5208 (P)
	KY088859/KY088743/*/KY088627/KY088511	Ogooue-Maritime, Gabon, *McPherson* 16998 (P)
	KY088860/KY088744/KY088397/KY088628/KY088512	Prov. Southwest, Vicinity of Mundemba, Cameroon, *Thomas* 6782 (NY)
Schefflera goetzenii Harms	KY088849/KY088733/KY088408/KY088617/KY088501	Bvumba Mountains, Zimbabwe, *Lowry* 4807 (MO)
	KY088851/KY088735/KY088396/KY088619/KY088503	Rwanda, *Auquier* 3503 (BR)
	KY088850/KY088734/KY088400/KY088618/KY088502	D.R. Congo, *Cephas* 358 (BR)
Schefflera humblotiana Drake	KY088861/KY088745/*/KY088629/KY088513	Toamasina, Madagascar, *Schatz* 3883 (P)
Schefflera kivuensis Bamps	KY088857/KY088741/KY088322/KY088625/KY088509	D.R. Congo, *Gutzwiller* 2145 (BR)
Schefflera mannii (Hook.f.) Harms	KY088855/KY088739/KY088419/KY088623/KY088507	Equatorial Guinea, *Cavalho* 4406 (BR)
	KY088854/KY088738/KY088315/KY088622/KY088506	South West Province, Cameroon, *Cable* 2947 (P)
Schefflera monophylla (Baker) Bernardi	KY088832/KY088716/KY088393/KY088600/KY088484	Ampitiliantsambo, Madagascar, *A. Randrianasolo* 409 (MO)
	KY088833/KY088717/KY088407/KY088601/KY088485	Zahamena, Madagascar, *S. Randrianasolo* 131 (MO)
	KY088829/KY088713/KY088358/KY088597/KY088481	Antoetra, Madagascar, *Lowry* 7087 (MO)

Table 1 (continued) – **Sampled species and voucher information.**
Species and DNA samples used in this study, including Genbank accession number, and specimen voucher information.

Taxon	**Genbank accession no. (ETS/ITS/*ndhF-rpl32*/*rpl32-trnL*/*trnk-rps16*)** **indicates missing sequence*	**Source and accession no.**
Ingroup, 'Sciodaphyllum' clade		
Schefflera monophylla (Baker) Bernardi	KY088830/KY088714/KY088328/ KY088598/KY088482	Antoetra, Madagascar, *Lowry* 7097 (MO)
	KY088831/KY088715/KY088360/ KY088599/KY088483	Ivorona, Madagascar, *Lowry* 7173 (MO)
	KY088870/KY088754/KY088373/ KY088638/KY088522	Andohahela, Madagascar, *Bernard* 1492 (MO)
	KY088888/KY088772/KY088382/ KY088656/KY088540	Marojejy, Madagascar, *Ravelonarivo* 3348 (MO)
Schefflera myriantha (Baker) Drake	KY088848/KY088732/KY088421/ KY088616/KY088500	Arusha NP, Tanzania, *Lowry* 4988 (MO)
	KY088845/KY088729/KY088423/ KY088613/KY088497	Angavokely, Madagascar, *Lowry* 5808 (MO)
	KY088844/KY088728/KY088412/ KY088612/KY088496	Angavokely, Madagascar, *Lowry* 5810 (MO)
	KY088846/KY088730/KY088425/ KY088614/KY088498	Angavokely, Madagascar, *Lowry* 5812 (MO)
	KY088844/KY088728/KY088412/ KY088612/KY088496	Analamanga, Madagascar, *Lowry* 5816 (MO)
	KY088835/KY088719/KY088405/ KY088603/KY088487	Tsaratanana, Madagascar, *Lowry* 5347 (MO)
	KY088836/KY088720/KY088410/ KY088604/KY088488	Tsaratanana, Madagascar, *Lowry* 5445 (MO)
	KY088839/KY088723/KY088391/ KY088607/KY088491	Anjavokely, Madagascar, *Lowry* 5796 (P)
	KY088843/KY088727/KY088390/ KY088611/KY088495	Anjavokely, Madagascar, *Lowry* 5798 (MO)
	KY088834/KY088718/KY088422/ KY088602/KY088486	Chome Forest Reserve, Tanzania, *Mwangulango* 501 (MO)
	KY088840/KY088724/KY088317/ KY088608/KY088492	Rwanda, *Bamps* 3050 (BR)
	KY088838/KY088722/KY088314/ KY088606/KY088490	Ethiopia, *Danish-Ethiopian Exp.* 1885 (BR)
	KY088847/KY088731/KY088316/ KY088615/KY088499	Malawi, *Van der Linden* L365 (BR)
	KY088837/KY088721/KY088401/ KY088605/KY088489	Zahamena, Madagascar, *Ratovoson* 470 (MO)
	KY088875/KY088759/KY088323/ KY088643/KY088527	Andohahela, Madagascar, *Bernard* 1498 (MO)
Schefflera procumbens (Hemsl.) F.Friedmann	KY688295/KY688293/KY688291/ KY688299/KY688297	Silhouette Isl., Seychelles, *Santerre* 5021 (SEY)
	KY688296/KY688294/KY688292/ KY688300/KY688298	Mahé Isl., Seychelles, *Santerre* 5642 (SEY)
Schefflera sp. ined. 9	KY088842/KY088726/KY088361/ KY088610/KY088494	Analanjirofo, Madagascar, *Lowry* 6117 (MO)
Schefflera stolzii Harms	KY088862/KY088746/*/KY088630/ KY088514	Ludewa, Tanzania, *Gereau* 3577 (P)
Schefflera tessmannii Harms	KY088856/KY088740/KY088398/ KY088624/KY088508	Gabon, *Reitsma* 2107 (P)
Schefflera volkensii (Engl.) Harms	KY088853/KY088737/KY088395/ KY088621/KY088505	Arusha NP, Tanzania, *Lowry* 4987 (MO)
	KY088852/KY088736/KY088324/ KY088620/KY088504	Shengena Peak, Tanzania, *Phillipson* 5129 (P)

Table 2 – **Marker statistics for the five markers used in this study**.

[a]Fiaschi & Plunkett (2011). [b]Linder et al. (2000). [c]White et al. (1990). [d]Wen & Zimmer (1996). [e]Plunkett (unpubl.). [f]Gostel (unpubl.). [g]Nicolas (unpubl.). Aligned lengths are provided in number of aligned base pairs (bp), average pairwise (PW) distances among are reported for ingroup taxa only for each marker as a percentage, total parsimony informative characters (PICs), consistency index (CI), and retention index (RI) were calculated in PAUP* (Swofford 2002), Substitution models were calculated using PartitionFinder (Lanfear et al. 2012) as reported in the text and tree lengths were calculated according to respective programs for MP and ML analyses reported in the methods, above.

DNA Region	Primer name [(ref)]	Primer Sequence (5'–3')	Aligned length (bp)	Average PW (%) distance	Total PICs (# / %)	Missing Data (%)	Substitution Model	Tree length (MP/ML)	CI/RI
ETS	ETS400F[a]	GTT GGT CGG ATC CCT GCT TGT	474	4.1%	103 / 21.7%	<1%	TVM+Γ	281 / -2294.07	0.765 / 0.955
	18S-2L[b]	TGA CTA CTG GCA GGA TCA ACC AG							
ITS	ITS5-F[c]	GGA AGT AAA AGT CGT AAC AAG G	675	2.5%	95 / 14.1%	<1%	GTR+I+Γ	271 / -2614.1	0.801 / 0.960
	C26A-R[d]	TTT CTT TTC CTC CGC T							
ndhF–rpl32	ndhF-rpl32-F[e]	GCA TAT TGA TAT GTC TGT TCC AT	1389	0.8%	55 / 5.1%	1.2%	GTR+I+Γ	N/A	N/A
	ndhF-rpl32-R[e]	AAG AGA TTT CCC TAA TGA CAA CGC							
	ndhF-rpl32-MF[f]	GAG TAC TTG ATT CTG ATA TGA ATC							
	ndhF-rpl32-MR[f]	AGA ATC CGC CGT TAT GCC ATA G							
rpl32–trnL	rpl32/trnL_F[g]	GCG TTG TCA TTA GGG AAA TCT CTT	944	0.6%	43 / 4.6%	5%	GTR+I+Γ	N/A	N/A
	rpl32/trnL_R[g]	GCT TCC TAA GAG CAG CGT GTC T							
	rpl32-trnL MF[f]	CTA TCT CTA TAT CTA TAG AAG GGC AAA							
	Rpl32-trnL MR[f]	TGA TTG GGT TGA AAG CAG GAG ATA TAT GGG AGA TTG AT							
trnK–rps16	trnK-(rps16)_ NF[g]	AGC CGA GTA CTC TAC CGT TGA	1188	0.5	30 / 2.1%	1.2%	GTR+I+Γ	N/A	N/A
	(trnK)-rps16_ NR[g]	GAG CCG TCT ATC GAA TCG TTG CAA							
	trnK-rps16-MF[e]	GCA CGG AAA TAA ATC GAT CCG C							
	trnK-rps16-MR[e]	CGT TGG AAC TTT ACT AAC ACG							
Nuclear, combined	N/A	N/A	1149	N/A	198 / 17.2%	<1%	N/A, partitioned as above	567 / -5063.82	0.762 / 0.952
Plastid, combined	N/A	N/A	3521	N/A	152 / 4.3%	3.6%	N/A, partitioned as above	599 / -8551.58	0.825 / 0.921
Nuclear + Plastid, combined	N/A	N/A	4670	N/A	350 / 7.5%	2.4%	N/A, partitioned as above	1199 / -14035	0.772 / 0.934

performed comparing all three partitions simultaneously, as well as separate, pairwise ILD tests. For the model based approaches (ML & BI), PartitionFinder (Lanfear et al. 2012) was used to select the most appropriate model of sequence evolution and to maximize computational accuracy.

Maximum parsimony analyses were performed using PAUP* and a two-step protocol modified from Plunkett et al. (2005). In the first step, a heuristic search of 1,000 replicates was generated by random, stepwise addition and TBR branch swapping, but saving no more than 100 trees per replicate. The strict consensus from this initial search was then loaded as a topological constraint for a second heuristic search that was performed following the same protocol as the first step (1,000 reps, saving 100 trees per replicate) but saving only shortest-length trees that did not agree with the topological constraint. If no additional shortest-length trees were recovered, the strict consensus from the first analysis was used as a conservative estimate of phylogenetic relationships. Bootstrap values were calculated from 1,000 replicates using PAUP*.

The model-based analyses were performed using GARLI (version 2.01; Zwickl 2006) for ML and MrBayes (version 3.2.6; Ronquist & Huelsenbeck 2003) for BI. ML analyses were performed by applying most of the default parameters in GARLI and MrBayes and the appropriate model of sequence evolution selected according to the corrected Akaike Information Criterion (AICc) using the program PartitionFinder (version 1.1.1; Lanfear et al. 2012). For the ML analyses, the maximum number of generations was set to 5 million, saving the ML tree with the best score. ML bootstrap values were also calculated using GARLI (with the same parameters) with 100 bootstrap replicates. Maximum Likelihood bootstrapping analyses and Bayesian inference (for four million generations, sampling every 1,000 generations) were both run using the CIPRES Science Gateway (Miller et al. 2010).

RESULTS

Sequence characteristics

A total of 162 accessions were sequenced for each of the five DNA spacer regions employed in this study, although four specimens did not amplify for the *ndhF-rpl32* marker and one specimen did not amplify for the *trnK-rps16* marker (table 2). After examining the sequences for redundancy, 37 samples were removed because they shared identical sequences with others in the dataset. The remaining 125 accessions representing 33 species were used for phylogenetic analyses. Uncorrected pairwise distances were calculated between all sequences for each molecular marker (treating the three plastid markers separately). Pairwise distances were also calculated for plastid markers. Sequence characteristics for each marker, including the primer name and sequence, are provided in table 2.

Significant incongruence among the three partitions established in this study could not be rejected based on results of the ILD test ($p = 0.01$), suggesting that the partitions may not be combinable. There is a wide body of literature weighing the merits of the ILD test (Yoder et al. 2001, Barker & Lutzoni 2002, Hipp et al. 2004) and suggesting that it be used in combination with the consideration of other factors. Although significant incongruence could not be rejected in this study, taken together, our analyses support the topologies produced by each partition and individual cases of incongruence do not reflect 'hard' incongruence between datasets (see Farris et al. 1994). Thus we conclude that the incongruence detected by the ILD test is likely an artifact of insufficient data and we chose to compare topologies resulting from the analysis of each nuclear marker independently and from three concatenated matrices comprising both nuclear markers, all three plastid markers, and the combined nuclear and plastid markers, respectively. What little incongruence exists does not appear to significantly alter conclusions regarding species relationships among Afro-Malagasy *Schefflera*. Rather, the concatenated dataset disrupts what appears to be a soft polytomy produced by limited variation in chloroplast markers, and our measure of incongruence may also be affected by missing data (table 2). To explore the effects of combining the datasets, all three partitions were concatenated and analysed simultaneously. We have provided results from the strict consensus of MP analyses from each of the three concatenated datasets (figs 1–3) as well as the results from the ML analysis for the combined nuclear (ETS+ITS) dataset because it shows branch lengths for groups resolved in this analysis (fig. 4). Results from all other analyses are provided as electronic appendices, including the strict consensus trees from the separate MP analyses of ETS and ITS (electronic appendix 1A & B), ML analyses for all remaining datasets (electronic appendix 2A–D), and majority-rule consensus topologies resulting from Bayesian Inference with all datasets (electronic appendix 3A–E).

Results from analysis of the combined plastid dataset produced topologies with the least resolution (fig. 3, electronic appendices 2C & 3D), but a clade comprising all species of African and Malagasy *Schefflera* is well supported. Two additional clades that are well supported in other analyses are likewise moderately supported in the strict consensus MP analysis of the combined plastid dataset ('Meiopanax' and 'Sciodaphyllum', fig. 2, BS = 75 and 76, respectively; see also electronic appendices 2C & 3D). The combined plastid analyses did not yield strong internal resolution of branching patterns within either the 'Meiopanax' or 'Sciodaphyllum' clades; only two moderately to well supported subclades were recognized, referred to as the 'Goetzenii' subclade (BS = 90, PP = 1.0, fig. 2) and the 'African myriantha' subclade (BS = 93, fig. 2). In the combined nuclear (ETS + ITS) analyses, all species of African and Malagasy *Schefflera* are strongly supported as a clade, within which the 'Meiopanax' and 'Sciodaphyllum' clades are likewise well supported (figs 1 & 4, electronic appendix 3C). Relationships suggested by the combined nuclear analyses provide support for five subclades. These included the two subclades in 'Sciodaphyllum' that are resolved in the combined plastid analyses along with a third subclade (viz. the 'Myriantha-monophylla' subclade, figs 1 & 4, electronic appendix 3C), and two additional subclades in the 'Meiopanax' clade, which we refer to as the 'Diversifolia' and 'Palmate-vantsilana' subclades (figs 1, 3 & 4, electronic appendix 3C). These seven clades/subclades are also well supported in our combined analysis of nuclear and chloroplast data (fig. 3, electronic appendices 2D & 3E).

Figure 1 – The strict consensus of 100,000 trees resulting from the maximum parsimony (MP) analysis of 125 sequences from the combined nuclear ITS + ETS rDNA spacers. Tree length = 567 steps, CI = 0.762, and RI = 0.952. Brackets to the right of taxon labels correspond to informal clade names discussed in the text. Parsimony bootstrap and Bayesian posterior probability values are provided above the branches (e.g. BS% / PP)s; bootstrap values less than 50% and Bayesian posterior probabilities less than 0.9 are recorded as '<', respectively.

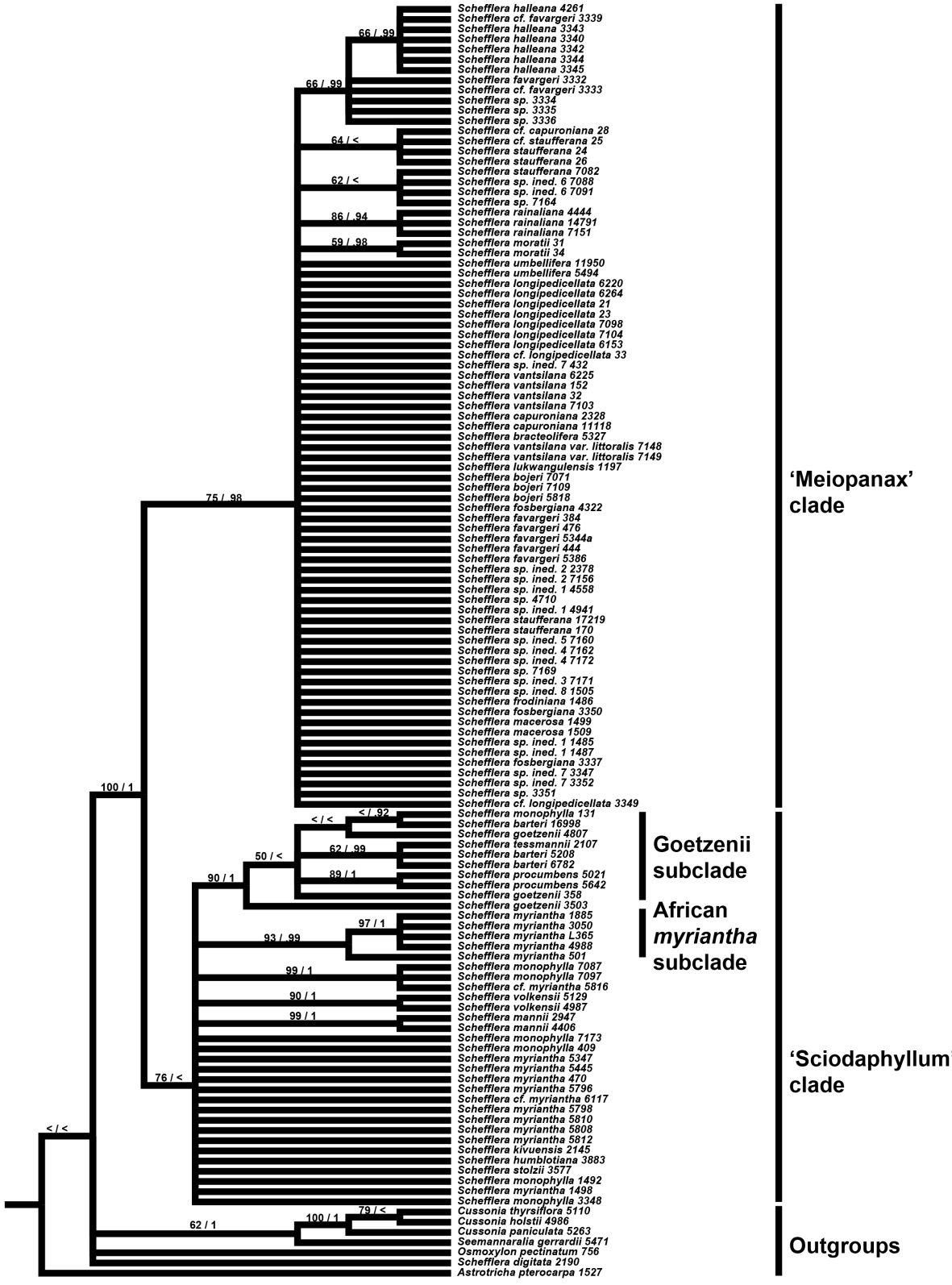

Figure 2 – The strict consensus of 100,000 trees resulting from the maximum parsimony (MP) analysis of 125 sequences from the combined plastid markers, *trnK-rps16*, *rpl32-trnL*, and *ndhF-rpl32*. Tree length = 599 steps, CI = 0.825, RI = 0.921. Brackets to the right of taxon labels correspond to informal clade names discussed in the text. Parsimony bootstrap and Bayesian posterior probability values are provided above the branches (e.g. BS% / PP)s; bootstrap values less than 50% and Bayesian posterior probabilities less than 0.9 are recorded as '<', respectively. Gray arrows indicate specimens whose placement has moved considerably from other analyses.

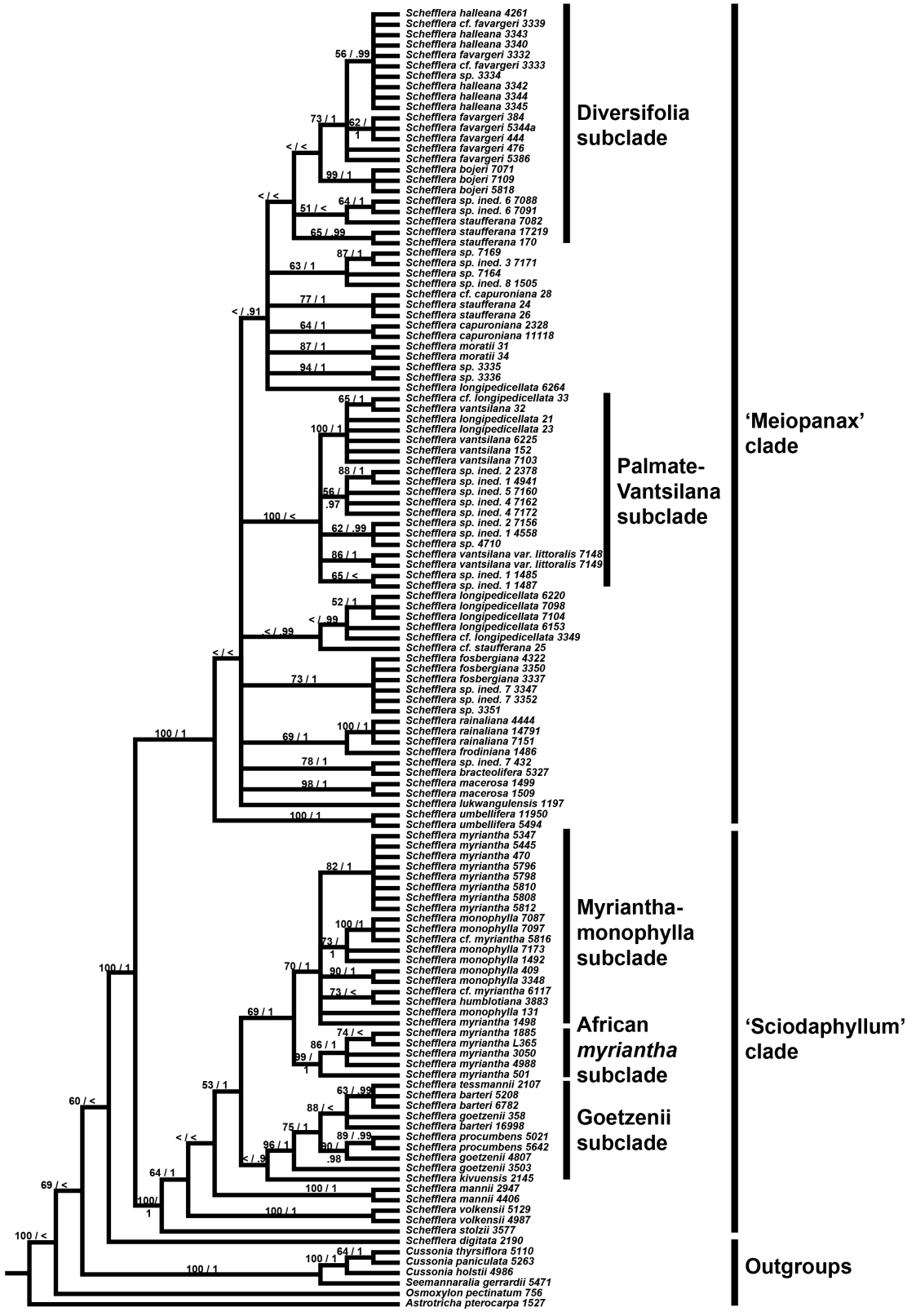

Figure 3 – The strict consensus of 100,000 trees resulting from the maximum parsimony (MP) analysis of 125 sequences from the combined nuclear and plastid spacers. Tree length = 1199, CI = 0.772, RI = 0.934. Brackets to the right of taxon labels correspond to informal clade names discussed in the text. Parsimony bootstrap and Bayesian posterior probability values are provided above the branches (e.g. BS% / PP) s; bootstrap values less than 50% and Bayesian posterior probabilities less than 0.9 are recorded as '<', respectively. Gray arrows indicate specimens whose placement has moved considerably from other analyses.

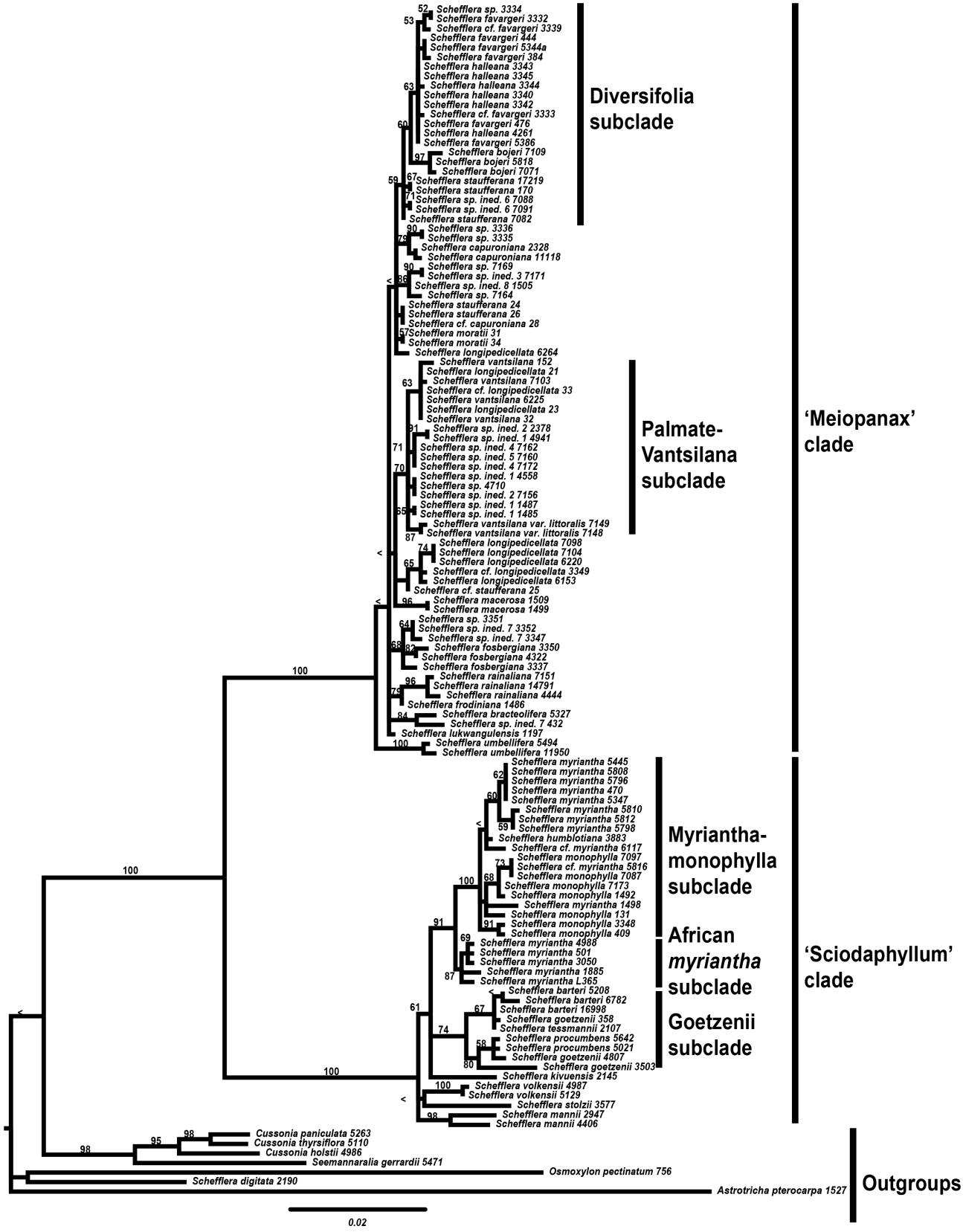

Figure 4 – The best tree (log likelihood = -5,075.1868) based on maximum likelihood (ML) analysis of 125 sequences from the combined nuclear ITS + ETS rDNA spacers. Brackets to the right of taxon labels correspond to informal clade names discussed in the text. ML bootstrap percentages are provided above the branches; bootstrap values less than 50% are recorded as '<'.

In each of our analyses, a total of 22 species are included in 'Meiopanax' and eleven in 'Sciodaphyllum'.

DISCUSSION

The Afro-Malagasy *Schefflera* clade

Plunkett et al. (2005) demonstrated extensive polyphyly in *Schefflera*, as currently circumscribed, and suggested that recircumscription of the genus should proceed by testing relationships in each of the five geographically distinct clades individually, beginning with in-depth studies of the smaller clades, including Pacific (Melanesian) *Schefflera* and Afro-Malagasy *Schefflera* (both with approx. fifty species), as well as *Schefflera* s. str. (eight species), in parallel with broad surveys of the larger Asian and Neotropical clades (c. 200–400 species each). The results presented here help to advance this strategy by exploring relationships among members of the Afro-Malagasy clade using significantly expanded sampling that represents nearly 70% of its species diversity. First of all, these results confirm the monophyly of this group with strong support (BS = 100, PP = 1.0). Since the publication of the most recent taxonomic treatments of *Schefflera* in Africa and Madagascar (Bamps 1974, Bernardi 1969, 1980), no fewer than seventeen new species have been proposed, but remain undescribed (Lowry et al., unpubl. data) and of these, seven were included in our sampling. The results presented here provide insight into the broad relationships among the accepted species of this clade as well as the placements for the species that have not yet been formally described. In the following sections, we discuss these relationships and reevaluate previous infrageneric classifications proposed for Afro-Malagasy *Schefflera*.

Anticipes, *Myrianthae*, and *Racemosae*

Bernardi's (1969) treatment of Afro-Malagasy *Schefflera* assigned fourteen species and three varieties to these three series. Our results indicate that none of these infrageneric groups appear to be monophyletic. Series *Anticipes* was defined to include three species (*S. bojeri*, *S. favargeri* Bernardi, and *S. halleana* Bernardi), and while our analyses place each of them in the 'Meiopanax' clade, they do not form a monophyletic group therein (figs 1–4), although they do fall within the broader 'Diversifolia' subclade, which also includes some species that Bernardi assigned to his series *Racemosae* (viz. *S. capuroniana* (Bernardi) Bernardi and *S. staufferana*). Series *Myrianthae* was circumscribed to include four species (*S. frodiniana* Bernardi, *S. humblotiana* Drake, *S. monophylla*, and *S. myriantha*, with two varieties). In our analyses, these species are consistently scattered among the two main clades we have identified, 'Meiopanax' and 'Sciodaphyllum' (figs 1–4), and therefore our trees fail to support the monophyly of this series. Similarly, Bernardi (1969) included seven species in his series *Racemosae* (*S. capuroniana*, with two varieties, *S. fosbergiana* (Bernardi) Bernardi, *S. longipedicellata*, *S. macerosa* Bernardi, *S. staufferana*, *S. vantsilana* (Baker) Bernardi, also with two varieties, and *S. weibeliana* Bernardi). While each of the five species sampled from series *Racemosae* falls within the 'Meiopanax' clade in our trees, they do not form a monophyletic group but rather are interspersed throughout 'Meiopanax', within both the 'Diversifolia' and 'Palmate-vantsilana' subclades (figs 1–4). Our results thus do not support the monophyly of any of Bernardi's (1969) series and point instead towards the need for an alternative infrageneric system to accommodate African and Malagasy *Schefflera*.

By contrast, Frodin's (see Plunkett et al. 2005) suggestion that species of Afro-Malagasy *Schefflera* represent two morphologically distinct groups is supported by our trees, in which two well supported clades (BS = 100, PP = 1.0) correspond to his 'Meiopanax' group and the Afro-Malagasy members of his 'Sciodaphyllum' group. Due to this close correspondence between Frodin's infrageneric system and our findings, his informal names will be used as a framework for discussing the results of the current study.

The 'Meiopanax' clade

The informal name 'Meiopanax' is used here to highlight this clade's correspondence to Frodin's morphogroup of the same name (see Plunkett et al. 2005). Our phylogenetic reconstruction placed 23 of the 33 species examined from the Afro-Malagasy *Schefflera* in this clade (figs 1–4, BS = 75–100, PP = 0.98–1.0). Of the species sampled, only two are African endemics (*S. lukwangulensis* (Tennant) Bernardi and *S. umbellifera*), while the remaining twenty species included in our study are all endemic to Madagascar. Resolution of relationships among the species in this clade varies depending on the markers used and, in some cases, the type of analysis performed. Within 'Meiopanax', two large subclades, accounting for eleven of the 23 species sampled in the group, are resolved in most of the trees, which we refer to as the 'Diversifolia' and 'Palmate-vantsilana' subclades (figs 1–4). These two subclades, as well as the remaining members of the group, form a large, weakly supported clade (whose subclades are polytomous) that is sister to *S. umbellifera* (fig. 1, BS = 65).

Morphologically, *Schefflera umbellifera* is distinct from other members of the group in having serrate (vs. entire or crenate) leaflet margins. Similarities exist between the umbellate inflorescence in *S. umbellifera*, which has a long, narrow primary axis, and those of three other species in the group (*S. frodiniana*, *S. lukwangulensis* and *S. rainaliana* Bernardi). Geographically, *S. umbellifera* has a fairly widespread distribution in tropical east Africa, from Zimbabwe and Malawi to South Africa, whereas the only other continental member of the group, *S. lukwangulensis*, is restricted to the Eastern Arc ranges in Tanzania. Results from both the ML and BI analyses of the combined plastid datasets place *S. umbellifera* among a large polytomy in the 'Meiopanax' clade, but branch support for this is low (electronic appendices 2C & 3D).

The 'Palmate-vantsilana' subclade is so named because of the shared tendency toward palmately compound leaves among its members together with the inclusion of *Schefflera vantsilana*, whose epithet is also the Malagasy vernacular name for most species of *Schefflera*. Within this subclade, several additional subclades are resolved containing accessions assigned to two species, identified as *S. longipedicellata* and *S. vantsilana*, as well as a smaller subclade that in-

cludes the samples of four undescribed species (referred to herein as *Schefflera* sp. ined. 1, 2, 4 and 5). Also placed in the 'Palmate-vantsilana' subclade is *S. vantsilana* var. *littoralis* Bernardi (1969), whose monophyly is well supported in most analyses (figs 1–2, BS = 86, PP = 1.0; fig. 4, BS = 87; electronic appendix 1B, BS = 87, PP = 1.0). While this variety resembles typical *S. vantsilana* in some respects, its leaves are quite distinct (with a long petiole and large, palmately compound leaflets with a retuse apex) and it has a restricted distribution in low-elevation east coast littoral forests (compared to other members of the 'Palmate-vantsilana' subclade, which are typically found at upland sites; Madagascar Catalogue 2015).

The 'Palmate-vantsilana' subclade provides evidence for the polyphyly of *Schefflera longipedicellata* and *S. vantsilana.* Accessions identified as these two species form a smaller subclade here (fig. 1, BS = 65, PP = 0.99, fig. 3, BS = 100...) however, other samples of both species are also found outside the 'Palmate-vantsilana' subclade. All of the *S. longipedicellata* specimens in this subclade come from individuals collected in forests located within a mining concession near Moramanga, Madagascar, whereas the accessions of *S. vantsilana* come from a much wider geographic range. The inclusion of material of both taxa in this subclade suggests the possibility of hybridization or that their circumscriptions may need to be refined. As currently delimited, *S. vantsilana* has distinctively larger leaflets than *S. longipedicellata*, as well as a strongly retuse apex and an overall obdeltoid leaflet shape, resembling those belonging to the unifoliolate *S. capuroniana* (see fig. 5).

The second subclade within the 'Meiopanax' group is referred to as 'Diversifolia', a reference to the diversity of leaf morphologies and leaflet numbers found among its members. Resolution is limited within this subclade in the MP analyses, but the BI analyses provide moderate to strong support for 'Diversifolia' as a whole (fig. 1, BS = 57, PP = 0.96; fig. 4 BS = 60; electronic appendix 3B & C, PP = 0.96–0.98). Within this subclade, only *Schefflera bojeri* forms a species-specific clade (electronic appendix 1A, BS = 94, PP = 1), whose distinctiveness is corroborated by several morphological characters (see Bernardi 1969, 1980). Two other species of 'Diversifolia', *S. favargeri* and *S. halleana*, are recovered in the majority of the trees, with moderate to strong support (fig. 1, BS = 60, PP = 0.96; fig. 2, BS = 69; fig. 3, BS = 65, PP = 0.99). In several trees, the 'Diversifolia' subclade also includes two additional taxa, *S. staufferana* and *Schefflera* sp. ined. 6 (figs 1 & 4, electronic appendix 3B & C). All of these taxa, except *S. bojeri*, have unifoliolate leaves.

The remaining nine species in the 'Meiopanax' group (*Schefflera capuroniana*, *S. frodiniana*, *S. longipedicellata*, *S. lukwangulensis*, *S. moratii* Bernardi, *S. rainaliana*, *Schefflera* sp. ined. 3, *Schefflera* sp. ined. 7, and *Schefflera* sp. ined. 8) are left unresolved, not falling within either the 'Diversifolia' or 'Palmate-vantsilana' subclade. *Schefflera frodiniana* and *S. rainaliana* form a clade in most analyses (fig. 1, BS = 69, PP = 1.0; fig. 2 BS = 79; fig. 3 BS = 69, PP = 1.0; electronic appendices 1B, 2B & D, 3B, C & E) and share an umbellate inflorescence with long, narrow axes, but the leaves of *S. rainaliana* are unifoliolate, whereas those of *S. frodiniana* have 3–5 leaflets. Similarly, *S. bracteolifera* and *Schefflera* sp. ined. 7 also form a clade in many trees (fig. 1 BS = 69, PP = 1.0; fig. 3, BS = 69, PP = 1.0; electronic appendices 1B, 2B & D, 3B, C & E). Like *S. frodiniana* and *S. rainaliana*, these two species differ considerably in their morphologies, most notably the fact that *S. bracteolifera* has unifoliolate leaves, while *Schefflera* sp. ined. 7 has 5–7 leaflets.

Three putatively new species in the 'Meiopanax' clade (*Schefflera* sp. ined. 3, *Schefflera* sp. ined. 6, and *Schefflera* sp. ined. 8) share distinctive unifoliolate leaves with obovate, coriaceous leaflets, but differ subtly along a continuum of leaf shape and texture. *Schefflera* sp. ined. 3 and *Schefflera* sp. ined. 6 both produce copious amounts of thick, milky latex in all organs, when cut or damaged. Of these two, *Schefflera* sp. ined. 3 is known only from a single population in the Vohimena mountains in far southeastern Madagascar, and has narrowly obovate and only weakly coriaceous leaves, the largest of which are c. 6–8 cm long and c. 2.5 cm wide. *Schefflera* sp. ined. 6, which is found c. 500 km to the north of *Schefflera* sp. ined. 3 and persists as a tiny remnant population near the village of Antoetra in central Madagascar, by contrast, has much larger obovate and extremely coriaceous leaves, the largest of which are 20–30 cm long and 7–8 cm wide. The third undescribed species, *Schefflera* sp. ined. 8, lacks milky latex and has broadly obovate to nearly obtriangular and only moderately coriaceous leaves of intermediate size, the largest of which are 7–10 cm long and 5–6 cm wide. *Schefflera* sp. ined. 8 is restricted to the summit of Trafanaomby, the highest peak in southern Madagascar (1957 m), located in the Anosy mountains, to the west of the Vohimena chain.

Several taxa were left unsampled in this study, but may be assignable to the 'Meiopanax' group based on a combination of characteristics (including, but not limited to carpel number, inflorescence arrangement, and number of leaflets), including *S. weibeliana* and 11 yet undescribed species.

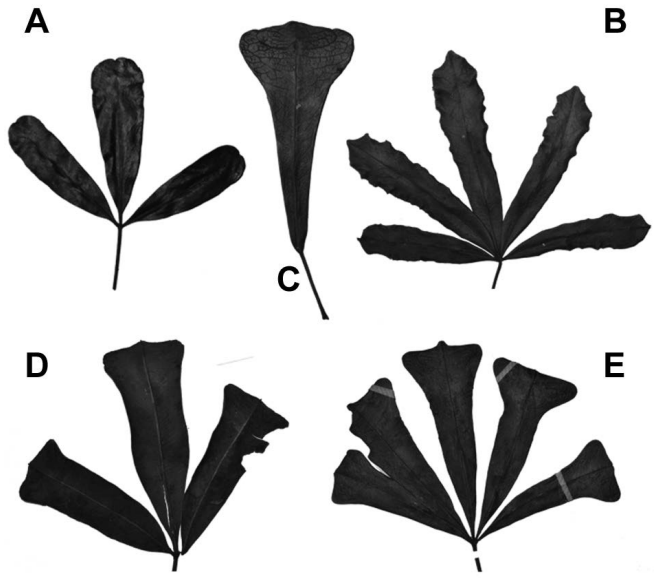

Figure 5 – Examples of leaf morphological variation: A & B, *Schefflera longipedicellata*; C, *S. capuroniana*; D & E, *S. vantsilana*.

The 'Sciodaphyllum' clade

Twelve species were placed in this clade (figs 1–4, BS = 78–100, PP = 1.0) and of these, all but three are endemic to continental Africa. Perhaps the most surprising relationship suggested from our results is the paraphyly of *Schefflera myriantha* with respect to two distinctive, well-delimited endemic Malagasy species, *S. humblotiana* and *S. monophylla*, and one yet undescribed new species, *Schefflera* sp. ined. 9. The first of these three species has a restricted distribution in central-eastern Madagascar, whereas the second is morphologically diverse and has a wide distribution, extending the full length of the island (Madagascar Catalogue 2015). By contrast, *S. myriantha* has a much broader geographic range, occurring throughout mountainous areas in tropical east Africa (Ethiopia to Malawi) as well as in the Comoros and Madagascar, but is morphologically highly coherent throughout its entire range, with specimens from Africa being nearly indistinguishable from those found on the Indian Ocean islands. Both the separate and combined analyses of the nuclear and plastid datasets indicate paraphyly in *S. myriantha* with strong branch support (fig. 1, BS = 97, PP = 1.0; fig. 3, BS = 69, PP = 1.0; fig. 4, BS = 91, electronic appendices 1–3). Lower branch support in the plastid and combined nuclear + plastid topologies appears to result from inconsistent placement of a single accession of *S. monophylla* (*Randrianasolo* 131). The morphological distinctions among *S. humblotiana*, *S. monophylla*, *S. myriantha*, as well as *Schefflera* sp. ined. 9, are quite strong. Despite its epithet, *S. monophylla* is typically not truly unifoliolate, but instead generally has a comparatively large central leaflet with two smaller lateral leaflets that are sometimes scarcely evident but only rarely absent. Morphologically, *S. humblotiana* is the most distinctive of these three species, possessing extremely long, narrow leaflets, whereas those of *S. myriantha* are elliptical (sometimes broadly so). On the other hand, the lack of any apparent morphological differences between *S. myriantha* from Africa and Madagascar suggests the need for further analysis in light of the relationships revealed in this study. Given the molecular divergence (in both the plastid and nuclear datasets) among the lineages belonging to the '*myriantha-monophylla*' and 'African *myriantha*' subclades, it seems that *S. myriantha*, as currently circumscribed, represents two distinct but cryptic species. The only alternative treatments would include the recognition of *S. myriantha* as a paraphyletic species or including the material of all three taxa in a single, highly variable and broadly defined species. The placement of *S. myriantha* from the Comoros cannot be inferred until samples for molecular analysis become available.

There is strong support for another subclade in the 'Sciodaphyllum' group, referred to as the 'Goetzenii' subclade, which includes four species, *Schefflera barteri*, *S.*, *goetzenii*, *S. procumbens*, and *S. tessmannii* Harms (fig. 1, BS = 73, PP = 1.0; fig. 2, BS = 90, PP = 1.0; fig. 3, BS = 96, PP = 1.0; fig. 4, BS = 79, electronic appendices 1–3). Resolution is poor within this clade, and while some phylogenetic structuring can be detected, the topology varies among the datasets. Only one member of this clade, *S. procumbens*, forms a species-specific subclade (figs 2–3, BS = 89, PP = 0.99–1.0; electronic appendices 2C & D, 3D & E). The placement of *S. procumbens*, which is endemic to Mahé and Silhouette islands in the Seychelles, strongly suggests a dispersal event from continental Africa. Notwithstanding these results, each of the species in the 'Goetzenii' subclade is highly distinct morphologically and geographically (Bamps 1974). *Schefflera goetzenii* has caducous subtending inflorescence bracts, flowers with 6-carpellate ovaries, palmately compound leaves with 6 or 7 narrowly obovate leaflets, and occurs in tropical east Africa. Both *S. barteri* (widespread from west to central Africa) and *S. tessmannii* (ranging from Equatorial Guinea (Rio Muni) and Gabon to northern Democratic Republic of Congo) have long, persistent subtending inflorescence bracts but differ in carpel number (*S. barteri* is 7–9-carpellate, *S. tessmannii* is 5–6-carpellate) and number of leaflets (5–8 in *S. barteri* vs. 6–8 in *S. tessmannii*), although *S. barteri* and *S. tessmannii* both share a paniculate-racemose inflorescence arrangement with *S. goetzenii*. Limited resolution in this clade is likely attributable to a combination of factors including, but not limited to, insufficient variation among the sequenced molecular markers and limited species sampling.

The remaining four species in the 'Sciodaphyllum' clade, *Schefflera kivuensis* Bamps, *S. mannii*, *S. stolzii* Harms, and *S. volkensii* (Engl.) Harms, form a basal polytomy with the *Schefflera myriantha-S. monophylla* complex and the 'Goetzenii' subclade. Differences in resolution among species belonging to the 'Sciodaphyllum' group may be due at least in part to incomplete *ndhF-rpl32* data for *S. humblotiana*, *S. stolzii*, and two samples of *S. barteri*.

Among the Afro-Malagasy taxa, we have sampled 62% of the species included Frodin's 'Sciodaphyllum' group, and our results differ only in the placement of a single species, *S. moratii*, which we suggest belongs instead to the 'Meiopanax' group. Like several other species in 'Meiopanax', *S. moratii* has paniculate inflorescences and large, unifoliolate leaves that dry dark and resemble species in the 'Diversifolia' subclade. Of the species that we were unable to sample, morphological (and to a certain degree geographical) characters suggest that species with flowers having long pedicels, 4–5 carpellate ovaries, and expanded umbellate inflorescences may also belong to the 'Sciodaphyllum' clade, including, *S. abyssinica* Harms, *S. evrardii*, *S. hierniana* Harms, *S. mannii*, *S. stuhlmannii* Harms, and *S. urostachya* Harms.

CONCLUSIONS

The phylogenic trees produced for this study are consistent with those resulting from previous work based on much more limited sampling, helping to confirm and strengthen the conclusion that Afro-Malagasy *Schefflera* comprise a well-supported, monophyletic group (Plunkett et al. 2005). The results presented here contribute to a broader, ongoing effort to clarify relationships within each of the five major clades that comprise the polyphyletic genus *Schefflera*. Ultimately, this effort will require the recognition of several separate genera since the generic type (*S. digitata*) belongs to a small Pacific clade comprising just eight species. Given this need for taxonomic change, the *Schefflera* species from Africa, Madagascar and the Seychelles could be treated as a single genus comprising all members of the Afro-Malagasy

clade. Alternatively, they could be recognized as two separate genera corresponding to the 'Meiopanax' and the Afro-Malagasy 'Sciodaphyllum' clades. Frodin (see Plunkett et al. 2005) recognized his pantropical 'Sciodaphyllum' group on the basis of an 'unspecialized' or 'generalized' morphology that includes terminal paniculate inflorescences, leaves crowded at the end of stems, limited branching, and non-ruminate endosperm, features shared among many geographically diverse species of *Schefflera* in Africa, Asia, and the Neotropics, as well as other genera of Araliaceae (see Plunkett et al. 2004a). Plunkett et al. (2005) demonstrated, however, that Frodin's 'Sciodaphyllum' group was polyphyletic. Moreover, the type species of *Sciodaphyllum* (*S. brownii* K.P.J.Sprengel = *Schefflera sciodaphyllum* (Sw.) Harms) belongs to the Neotropical *Schefflera* clade and therefore cannot be applied to any of the Afro-Malagasy taxa.

If the species from Africa and Madagascar were to be treated as a single genus, they would be placed in *Astropanax* Seem. (Seemann 1865), the oldest available name, which has nomenclatural priority over several other generic names whose types belong to this group. On the other hand, if the two clades are treated as separate genera, *Astropanax* would apply to the largely African 'Sciodaphyllum' clade, since Seemann's genus included the three taxa originally assigned to this group (*S. abyssinica*, *S. barteri* and *S. mannii*), although no lectotype has yet been designated. *Meiopanax* is available for the second subclade, but it does not have priority. Instead, the 'Meiopanax' clade would have to be recognized as *Neocussonia* (Harms) Hutch. (Hutchinson 1967), based on *Cussonia* sect. *Neocussonia* Harms (Harms 1897), typified by *N. umbellifera* (= *S. umbellifera*). This latter approach has been adopted in a synopsis (Lowry et al. in press) in which each of the currently accepted species is assigned either to *Astropanax* or to *Neocussonia*.

An important note should be made with regard to the taxonomic status of *Schefflera myriantha*, which our analyses suggest is paraphyletic with respect to *S. humblotiana* and *S. monophylla*. We have identified three taxonomic options. First, *S. myriantha* could be recognized as a single paraphyletic species, although this solution would contravene currently accepted practice (but see Hörandl & Stuessy 2010). Alternatively, to avoid a paraphyletic *S. myriantha*, its circumscription could be broadened to include the two morphologically distinct and well delimited species *S. humblotiana* and *S. monophylla*, but this option would result in the recognition of a species whose circumscription would be so broad as to be taxonomically impractical. Thirdly, *S. myriantha* could be divided into two morphologically cryptic species, one in Madagascar, which would include the type of *S. myriantha*, and another in Africa, for which the oldest available name is *S. polysciadia* Harms. This option could be problematic because we are not aware of any morphological character or combination of characters that can be used to distinguish these African and Malagasy segregates of *S. myriantha*. As such, assignment to species would be based solely on geographic origin and molecular sequence data. Based upon the evidence provided by results from this study, we prefer the third option, recognizing two distinct species, one in Madagascar corresponding to *S. myriantha* and another in continental Africa corresponding to *S. polysciadia*. Notwithstanding the morphological similarity between these two entities, the analyses based on each of the five molecular markers used in this study strongly suggest that African and Malagasy populations represent distinct lineages that have evolved in geographic isolation from one another, and that speciation within the lineage in Madagascar has led to the evolution of two additional, morphologically distinctive taxa long recognized as *S. humblotiana* and *S. monophylla*. Thus, while it may be impossible to assign specimens based on morphology, geographic origin provides a reliable and unambiguous basis for distinguishing between *S. myriantha* and *S. polysciadia*.

Our work clearly points toward further studies, which should aim to include the 16 as-yet unsampled species and to apply an expanded, rigorous morphometric approach to delimiting species in the Afro-Malagasy *Schefflera* clade, which has proven successful for other groups in the region (e.g. Hong-Wa 2008, Kenfack 2011, Simo-Droissart et al. 2013). Such an approach might be particularly helpful for clarifying species limits in difficult complexes, including several in the 'Sciodaphyllum' clade (e.g. *S. humblotiana*, *S. monophylla*, and *S. myriantha*), as well as the members of the 'Palmate-vantsilana' group within the 'Meiopanax' clade. The present study provides the foundation for such future work, while making a significant contribution toward the realignment of genera that will be required to accommodate the species from Africa and Madagascar historically included in *Schefflera* s. lat.

SUPPLEMENTARY DATA

Supplementary data are available in pdf at *Plant Ecology and Evolution*, Supplementary Data Site (http://www.ingentaconnect.com/content/botbel/plecevo/supp-data), and consist of the following: (1) strict consensus from Maximum Parsimony analyses; (2) best trees based on Maximum likelihood analyses; and (3) best trees based on Bayesian inference.

ACKNOWLEDGEMENTS

Support for field and laboratory work was provided by grants from the U.S. National Science Foundation (DEB 9981641, 0613728, 0614152 and 0743355). The authors wish to thank the Botanic Garden Meise in Belgium (BR) for access to their collections. We are grateful for field assistance provided by several colleagues in Madagascar, including P. Antilahimena, R. Bernard, J. Rabenantoandro, C. Rakotovao, O. Randriambololomamonjy, R. Randrianaivo, D. Ravelonarivo, and R. Razakamalala. MG also thanks A. Nicolas and P. Fiaschi for assistance in the laboratory, and B. De Villiers and C. Rodrigues for help with herbarium specimens. Fieldwork in Madagascar was carried out under collaborative agreements between the Missouri Botanical Garden and the Parc Botanique et Zoologique de Tsimbazaza and the Direction de la Recherche Forestière et Piscicole, FOFIFA. We are grateful for courtesies extended by the Government of Madagascar (Direction Générale de la Gestion des Ressources Forestières) and by Madagascar National Parks.

REFERENCES

Agnarsson I., Kuntner M. (2012) The generation of a biodiversity hotspot: biogeography and phylogeography of the western Indian Ocean islands. In: Kesara Anamthawat-Jonsson K. (ed.) Current topics in phylogenetics and phylogeography of terrestrial and aquatic systems: 33–82. Rijeka, In Tech Publishers.

Alexander P.J., Rajanikanth G., Bacon C.D., Bailey C.D. (2007) Recovery of plant DNA using a reciprocating saw and silica-based columns. Molecular Ecology Notes 7: 5–9. https://doi.org/10.1111/j.1471-8286.2006.01549.x

Ali J.R., Aitchison J.C. (2008) Gondwana to Asia: plate tectonics, paleogeography and the biological connectivity of the Indian sub-continent from the Middle Jurassic through latest Eocene (166–35 Ma). Earth-Science Reviews 88: 145–166. https://doi.org/10.1016/j.earscirev.2008.01.007

Baillon, H. (1878) Recherches nouvelles sur les Araliées et sur la famille des Ombellifères en général. Adansonia 12: 125–178.

Baillon H. (1879) Ombellifères. In: Baillon H. (ed.) Histoire des Plantes 7: 84–256. Paris, Hachette.

Bamps P. (1974) Contribution à l'étude des Araliacées africaines. Bulletin du Jardin botanique national de Belgique 44: 101–139. https://doi.org/10.2307/3667430

Barker F.K, Lutzoni F.M. (2002) The utility of the incongruence length difference test. Systematic Biology 51: 625–637. https://doi.org/10.1080/10635150290102302

Barker N.P., Weston P.H., Rutschmann F., Sauquet H. (2007) Molecular dating of the 'Gondwanan' plant family Proteaceae is only partially congruent with the timing of the break-up of Gondwana. Journal of Biogeography 34: 2012–2027. https://doi.org/10.1111/j.1365-2699.2007.01749.x

Besse J., Courtillot V. (1988) Paleogeographic maps of the continents bordering the Indian Ocean since the early Jurassic. Journal of Geophysical Research 93(B10): 11791–11808. https://doi.org/10.1029/JB093iB10p11791

Bernardi L. (1969) Araliacearum Madagascariae et Comores exordium. 1. Revisio et taxa nova Scheffl erarum. Candollea 24: 89–122.

Bernardi L. (1980) Synopsis Araliacearum Madagascariae et Comorarum Insularum (auxilio methodi 'Ferulago'). Candollea 35: 117–131.

Cook L.G., Crisp M.D. (2005) Not so ancient: the extant crown group of Nothofagus represents a post-Gondwanan radiation. Proceedings of the Royal Society B 272: 2535–2544. https://doi.org/10.1098/rspb.2005.3219

Crisp M.D., Cook L.G. (2007) A congruent molecular signature of vicariance across multiple plant lineages. Molecular Phylogenetics and Evolution 43: 1106–1117. https://doi.org/10.1016/j.ympev.2007.02.030

Donoghue M.J., Smith S.A. (2004) Patterns in the assembly of temperate forests around the Northern Hemisphere. Philosophical Transactions of the Royal Society in London 359: 1633–1644. https://doi.org/10.1098/rstb.2004.1538

Eibl J., Plunkett G.M., Lowry II P.P. (2001) Phylogenetic relationships in Polyscias sect. Tieghemopanax (Araliaceae) based on DNA sequence data. Adansonia, série 3: 23–48.

Farris J.S., Källersjö M., Kluge A.G., Bult C. (1994) Testing significance of incongruence. Cladistics 10: 315–319. https://doi.org/10.1111/j.1096-0031.1994.tb00181.x

Fiaschi P., Plunkett G.M. (2011) Monophyly and phylogenetic relationships of Neotropical Schefflera (Araliaceae) based on plastid and nuclear markers. Systematic Botany 36: 806–817. https://doi.org/10.1600/036364411X583754

Forster J.R., Forster G. (1776) Characteres Generum Plantarum. London, B. White, T. Cadell & P. Elmsly. https://doi.org/10.5962/bhl.title.4448

Frodin D.G. (1975) Studies in Schefflera (Araliaceae): The Cephaloschefflera complex. Journal of the Arnold Arboretum 56: 427–448.

Frodin D.G., Govaerts R. (2003) World Checklist and Bibliography of Araliaceae. London, Royal Botanic Gardens, Kew.

Frodin D.G., Lowry II P.P., Plunkett G.M. (2010) Schefflera (Araliaceae): taxonomic history, overview and progress. Plant Diversity and Evolution 128: 561–595. https://doi.org/10.1127/1869-6155/2010/0128-0028

Gostel M.R., Phillipson P.B., Weeks A. (2016) Phylogenetic reconstruction of the myrrh genus, Commiphora (Burseraceae) reveals multiple radiations in Madagascar and clarifies infrageneric relationships. Systematic Botany 41: 67–81. https://doi.org/10.1600/036364416X690598

Harms H. (1894–1897) Araliaceae. In: Engler A., Prantl K. (eds) Die natürlichen Pflanzenfamilien III, vol. 8: 1–62. Leipzig, Wilhelm Engelmann.

Hipp A.L., Hall J.C., Sytsma K.J., Lutzoni F. (2004) Convergence versus phylogenetic accuracy: revisiting the incongruence length difference test. Systematic Biology 53: 81–89. https://doi.org/10.1080/10635150490264752

Hong-Wa C. (2008) Multivariate analyses of morphological characters of Leptolaena Thouas s.l. subgenera Mediusella and Xerochlamys (Sarcolaenaceae). Botanical Journal of the Linnean Society. 157: 559–574. https://doi.org/10.1111/j.1095-8339.2008.00815.x

Hörandl E., Stuessy T.F. (2010) Paraphyletic groups as natural units of biological classification. Taxon 59: 1641–1653.

Hutchinson J. (1967) The Genera of Flowering Plants. Col. II. London, Oxford University Press.

Kenfack D. (2011) Resurrection in Carapa (Meliaceae): a reassessment of morphological variation and species boundaries using multivariate methods in a phylogenetic context. Botanical Journal of the Linnean Society 165: 186–221. https://doi.org/10.1111/j.1095-8339.2010.01104.x

Lanfear R., Calcott B., Ho S.Y.W., Guindon S. (2012) PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. Molecular Biology and Evolution 29: 1695–1701. https://doi.org/10.1093/molbev/mss020

Linder C.R., Goertzen L.R., Vanden Heuvel B., Francisco-Ortega J., Jansen R.K. (2000) The complete external transcribed spacer of 18S-26S rDNA: amplification and phylogenetic utility at low taxonomic levels in Asteraceae and closely allied families. Molecular Phylogenetics and Evolution 14: 285–303. https://doi.org/10.1006/mpev.1999.0706

Lowry II P.P., Plunkett G.M. (2010) Recircumscription of Polyscias (Araliaceae) to include six related genera, with a new infrageneric classification and a synopsis of species. Plant Diversity and Evolution 128: 55–84. https://doi.org/10.1127/1869-6155/2010/0128-0003

Lowry II P.P., Plunkett G.M., Frodin D.G. (2013) Revision of Plerandra (Araliaceae). I. A synopsis of the genus with an expanded circumscription and a new infrageneric classification. Brittonia 65: 42–61. https://doi.org/10.1007/s12228-012-9260-2

Lowry P.P., Plunkett G.M., Gostel M.R., Frodin D.G. (in press) A synopsis of the Afro-Malagasy species included in Schefflera J.R. Forst. & G. Forst. (Araliaceae): resurrection of the genera Astropanax Seem. and Neocussonia (Harms) Hutch. Candollea.

Madagascar Catalogue (2015) Catalogue of the Vascular Plants of Madagascar. St. Louis, U.S.A. & Antananarivo, Madagascar, Missouri Botanical Garden. Available from http://www.tropicos.org/project/mada [accessed: 1 Mar. 2015].

McGlone M.S. (2005) Goodbye Gondwana. Journal of Biogeography 32: 739–740. https://doi.org/10.1111/j.1365-2699.2005.01278.x

Miller J.S., Kamath A., Levin R.A. (2009) Do multiple tortoises equal a hare? The utility of nine noncoding plastid regions for species-level phylogenetics in tribe Lycieae (Solanaceae). Systematic Botany 34: 796–804. https://doi.org/10.1600/036364409790139709

Miller M.A., Pfeiffer W., Schwartz T. (2010) Creating the CIPRES Science Gateway for inference of phylogenetic trees. In: Proceedings of the Gateway Computing Environments Workshop (GCE), 14 Nov. 2010, New Orleans, LA: 1–8.

Nicolas A.N., Plunkett G.M. (2009) The demise of subfamily Hydrocotyloideae (Apiaceae) and the realignment of its genera across the entire order Apiales. Molecular Phylogenetics and Evolution 53: 134–151. https://doi.org/10.1016/j.ympev.2009.06.010

Plunkett G.M., Wen J., Lowry II P.P. (2004a) Infrafamilial classifications and characters in Araliaceae: insights from the phylogenetic analysis of nuclear (ITS) and plastid (trnL-trnF) sequence data. Plant Systematics and Evolution 245: 1–39. https://doi.org/10.1007/s00606-003-0101-3

Plunkett G.M., Lowry II P.P., Vu N.V. (2004b) Phylogenetic relationships among Polyscias (Araliaceae) and close relatives from the western Indian Ocean Basin. International Journal of Plant Sciences 165: 861–873. https://doi.org/10.1086/421855

Plunkett G.M., Lowry II P.P., Frodin D.G., Wen J. (2005) Phylogeny and geography of Schefflera: Pervasive polyphyly in the largest genus of Araliaceae. Annals of the Missouri Botanical Garden 92: 202–224.

Plunkett G.M., Lowry II P.P. (2010) Paraphyly and polyphyly in Polyscias sensu lato: molecular evidence and the case for recircumscribing the 'pinnate genera' of Araliaceae. Plant Diversity Evolution 128: 23–54. https://doi.org/10.1127/1869-6155/2010/0128-0002

Plunkett G.M., Lowry II P.P. (2012) Phylogeny and diversification in the Melanesian Schefflera clade (Araliaceae) based on evidence from nuclear rDNA spacers. Systematic Botany 37: 279–291. https://doi.org/10.1600/036364412X616837

Rabinowitz P.D., Coffin M.F., Falvey D. (1983) The separation of Madagascar and Africa. Science 220: 67–69. https://doi.org/10.1126/science.220.4592.67

Ronquist F., Huelsenbeck J.P. (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19: 1572–1574. https://doi.org/10.1093/bioinformatics/btg180

Sanmartín I., Ronquist F., Cunningham C. (2004) Southern hemisphere biogeography inferred by event-based models: plant versus animal patterns. Systematic Biology 53: 216–243. https://doi.org/10.1080/10635150490423430

Schatz G.E. (1996) Malagasy/Indo-Australo-Malesian phytogeographic connections. In: Lourenco W.R. (ed.) Biogeography of Madagascar: 73–83. Paris, ORSTOM editions.

Schettino A., Scotese C.R. (2005) Apparent polar wander paths for the major continents (200 Ma to the present day): a paleomagnetic reference frame for global plate tectonic reconstructions. Geophysical Journal International 163: 727–759. https://doi.org/10.1111/j.1365-246X.2005.02638.x

Seemann B. (1865) Revision of the natural order Hederaceae [continued]. Journal of Botany 3: 173–181.

Shaw J., Lickey E.B, Beck J.T., Farmer S.B., Liu W., Miller J., Siripun K.C., Winder C.T., Schilling E.E., Small R.L. (2005) The tortoise and the hare II: relative utility of 21 noncoding chloroplast DNA sequences for phylogenetic analysis. American Journal of Botany 92: 142–166. https://doi.org/10.3732/ajb.92.1.142

Shaw J., Lickey E.B., Schilling E.E., Small R.L. (2007) Comparison of whole chloroplast genome sequences to choose noncoding regions for phylogenetic studies in angiosperms: the tortoise and the hare III. American Journal of Botany 94: 275–288. https://doi.org/10.3732/ajb.94.3.275

Simo-Droissart M., Micheneau C., Sonké B., Droissart V., Plunkett G.M., Lowry II P.P., Hardy O.J., Stévart T. (2013) Morphometrics and molecular phylogenetics of the continental African species of Angraecum section Pectinaria (Orchidaceae). Plant Ecology and Evolution. 146: 295–309. https://doi.org/10.5091/plecevo.2013.900

Storey M., Mahoney J.J., Saunders A.D., Duncan R.A., Kelley S.P., Coffin M.F. (1995) Timing of hot spot-related volcanism and the breakup of Madagascar and India. Science 267: 852–855. https://doi.org/10.1126/science.267.5199.852

Swofford D.L. (2002) PAUP*: Phylogenetic Analysis Using Parsimony (*and other methods), Version 4.6b10. Sunderland, Massachusetts, Sinauer Associates.

Tennant J.R. (1961) Notes on African Araliaceae: III. Kew Bulletin 15: 331–335. https://doi.org/10.2307/4109379

Thompson J.D., Gibson T.J., Plewniak F., Jeanmougin F., Higgins D.G. (1997) The CLUSTAL_X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. Nucleic Acids Research 25: 4876–4882. https://doi.org/10.1093/nar/25.24.4876

Tronchet F., Plunkett G.M., Jérémie J., Lowry II P.P. (2005) Monophyly and major clades of Meryta (Araliaceae). Systematic Botany 30: 657–670. https://doi.org/10.1600/0363644054782279

Viguier R. (1906) Recherches anatomiques sur la classification des Araliacées. Annales des Sciences Naturelles, Botanique, série 9, 4: 1–210.

Viguier R. (1909) Nouvelles recherches sur les Araliacées. Annales des Sciences Naturelles, Botanique, série 9, 9: 305–405.

Weeks A., Daly D.C., Simpson B.B. (2005) The phylogenetic history and biography of the frankincense and myrrh family (Burseraceae) based on nuclear and chloroplast sequence data. Molecular Phylogenetics and Evolution 35: 85–101. https://doi.org/10.1016/j.ympev.2004.12.021

Wen J., Zimmer E.A. (1996) Phylogeny and biogeography of Panax L. (the ginseng genus, Araliaceae): inferences from ITS sequences of nuclear ribosomal DNA. Molecular Phylogenetics and Evolution 6: 167–177. https://doi.org/10.1006/mpev.1996.0069

White T.J., Bruns T., Lee S., Taylor J. (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis M.A., Gelfand D.H., Shinsky J.J., White T.J. (eds) PCR protocols: a guide to methods and applications: 315–322. San Diego, Academic Press.

Yoder A.D., Irwin J.A., Payseur B.A., Wiens J. (2001) Failure of the ILD to determine data combinability for slow loris phylogeny. Systematic Biology 50: 408–424. https://doi.org/10.1080/10635150116801

Yoder A.D., Nowak M.D. (2006) Has vicariance or dispersal been the predominant biogeographic force in Madagascar? Only time will tell. Annual Review of Ecology, Evolution and Systematics 37: 405–431. https://doi.org/10.1146/annurev.ecolsys.37.091305.110239

Yuan Y-M., Wohlhauser S., Möller M., Klackenberg J., Callmander M.W., Küpfer P., Mason-Gamer R. (2005) Phylogeny and biogeography of Exacum (Gentianaceae): a disjuntive distribution in the Indian Ocean basin resulted from long distance dispersal and extensive radiation. Systematic Biology 54: 21–34. https://doi.org/10.1080/10635150590905867

Zerega N.J.C., Clement W.L., Datwyler S.L., Weiblen G.D. (2005) Biogeography and divergence times in the mulberry family (Moraceae). Molecular Phylogenetics and Evolution 37: 402–416. https://doi.org/10.1016/j.ympev.2005.07.004

Zwickl D.J. (2006) GARLI. Genetic algorithm approaches for the phylogenetic analysis of large biological sequence datasets under the maximum likelihood criterion. Unpubl. PhD thesis, University of Texas, Austin, Texas, USA.

Manuscript received 25 Oct. 2015; accepted in revised version 13 Sep. 2016.

Communicating Editor: Elmar Robbrecht.