



RESEARCH ARTICLE

Complete genus-level phylogenomics and new subtribal classification of the pantropical plant family Annonaceae

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DOI <https://doi.org/10.1002/tax.13260>

Abstract Annonaceae is a major tropical plant family particularly diverse in tropical rain forests of the world. Although the classification and systematics of the family has significantly improved over the past decade, the most recent classification was based on a reduced set of plastid markers and incomplete genus-level taxon sampling. This classification recognised 4 subfamilies and 20 tribes. Yet, several important problems persisted, especially the phylogenetic placement of the African genus *Meiocarpidium*, resolution of intertribal relationships within subfamily Malmeoideae, resolution and classification within the diverse tribe Miliuseae with 23 genera, and the contrasting placement of the liana genus *Artabotrys* when using nuclear versus plastid data. Here, using a previously published Annonaceae-specific nuclear bait kit, we generated for the first time a complete genus-level (108 taxa) phylogenomic tree of the family based on 373 loci. We show that *Meiocarpidium* is sister to Ambavioideae and should be considered as a tribe and not a separate subfamily. *Artabotrys* is recovered as belonging to tribe Duguetieae, and not Xylopieae as previously inferred based on plastid data, and is sister to two other African liana genera, *Letestudoxa* and *Pseudartabotrys*. Finally, we were able to resolve intertribal relationships within subfamily Malmeoideae and most of the relationships within tribe Miliuseae. Nevertheless, we recovered strong gene conflict mainly at the backbone of the tribe, probably linked to a rapid diversification at its origin, leading to substantial

Article history: Received: 16 Jan 2024 | returned for (first) revision: 19 Mar 2024 | (last) revision received: 15 Aug 2024 | accepted: 16 Aug 2024

Associate Editor: Michael D. Pirie | © 2024 The Author(s). *TAXON* published by John Wiley & Sons Ltd on behalf of International Association for Plant Taxonomy.

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incomplete lineage sorting. We suggest that this conflict will be hard to resolve. Using this novel phylogenomic framework we recognize 25 subtribes, 21 as new, to improve the infrafamilial classification of Annonaceae.

Keywords Annonaceae; high-throughput sequencing; incongruence; phylogenomics; rain forests; systematics

Supporting Information may be found online in the Supporting Information section at the end of the article.

■ INTRODUCTION

Annonaceae Juss. is a diverse flowering plant family of trees and lianas with 108 genera (but see Bangkomnate & al., 2021; Schatz & al., 2023) and c. 2500 species (see Table 1) distributed across tropical regions. Annonaceae is particularly species rich in tropical lowland rain forests (Erkens & al., 2023) and has been used as a model group to study the evolution and diversification of this complex biome (e.g., Erkens & al., 2007; Couvreur & al., 2011; Thomas & al., 2015; Pirie & al., 2018; Brée & al., 2020; Xue & al., 2020a; Dagallier & al., 2024). A solid phylogenetic framework is required to have a more comprehensive understanding of the evolutionary history of Annonaceae and tropical rain forests more broadly (Eiserhardt & al., 2017).

Long considered a “natural family” (Hutchinson, 1923), the considerable diversity of Annonaceae has been the subject of various formal and informal subfamilial classifications. Such works were based on different morphological characters (flowers, fruits, pollen) and resulted in different groupings of genera (Bentham, 1862; Baillon, 1868; Engler & Diels, 1901; Hutchinson, 1923; Fries, 1959; Walker, 1971; Van Heusden, 1992; Van Setten & Koek-Noorman, 1992). A review of historical classification systems is presented in Chatrou & al. (2012a). Over the last 40 years, research on the systematics and taxonomy of Annonaceae has been bolstered by a strong international research program led from what became the National Herbarium of the Netherlands (Maas, 1983). This research led to numerous taxonomic revisions across major tropical regions (e.g., Maas & Westra, 1985, 2003; Su & Saunders, 2006; Maas & al., 2007; Johnson & Murray, 2018) including large and complex genera (e.g., Maas & al., 1992, 2015; Hoekstra & al., 2021), and Floras (e.g., Le Thomas, 1969; Couvreur & al., 2022; Johnson & Murray, 2022; Maas & al., 2023), making Annonaceae one of the most taxonomically well-known tropical plant families to date.

More recently, our understanding of relationships within Annonaceae has greatly improved owing to the advancement of molecular phylogenetics. The first family-wide phylogenetic hypothesis was based on 45 *rbcL* sequences (Doyle & al., 2000). Richardson & al. (2004) extended taxon sampling to 202 species, and published phylogenetic trees based on *rbcL* and *trnLF* sequences. Chatrou & al. (2012b) subsequently presented a family-wide phylogenetic analysis of Annonaceae using a supermatrix approach based on up to eight plastid markers for 193 taxa. They proposed a subfamilial classification with four subfamilies, three of which were

newly described: Anaxagoreoideae Chatrou & al., Ambavioideae Chatrou & al., Annonoideae Raf., and Malmeoideae Chatrou & al. The latter two included 96% of all species, and 14 tribes. An updated phylogenetic hypothesis using the same eight plastid markers but with a significant increase in taxon sampling (105 genera, 705 species) by Guo & al. (2017) confirmed previous results and led to a newly described tribe (Phoenicantheae X.Guo & R.M.K.Saunders). To date, a total of 20 tribes are currently recognised across the family based on phylogenetic analyses using different markers (Table 1; Couvreur & al., 2019; Chaowasku, 2020; Dagallier & al., 2023).

Despite this progress, several important issues remain to be resolved. First, the phylogenetic position of the monotypic central African genus *Meiocarpidium* Engl. & Diels remains uncertain. *Meiocarpidium* was recovered as sister to the remaining genera of Ambavioideae with moderate support based on plastid data (Couvreur & al., 2008; Surveswaran & al., 2010; Guo & al., 2017; Chatrou & al., 2018). However, Chaowasku (2020) recovered *Meiocarpidium* as sister to the rest of Annonaceae except *Anaxagorea* A.St.-Hil. (Anaxagoreoideae), with improved support values based on an expanded plastid dataset but low overall taxon sampling across Annonaceae. On this basis, he described a fifth subfamily: Meiocarpidioideae Chaowasku. Second, although relationships among genera are generally well resolved based on plastid data, this is not the case within the diverse tribe Miliuseae Hook.f. & Thomson (of the subfamily Malmeoideae) which comprises roughly a quarter (646/~2500 spp., Table 1) of the family species diversity and 25 genera distributed in Southeast Asia and Central America. The backbone of Miliuseae remained largely unresolved based on plastid data (Mols & al., 2004; Chaowasku & al., 2014; Ortiz-Rodriguez & al., 2016; Guo & al., 2017). In addition to being morphologically diverse, this tribe is taxonomically complicated. A first step towards sorting out the higher-level taxonomy of this tribe was achieved by Ortiz-Rodriguez & al. (2016) who described the phylogenetically well supported subtribe Sapranthinae Ortiz-Rodr., Ruiz-Sanchez & Ornelas. The subtribe included the four Central American genera of tribe Miliuseae (Table 1).

A recent major advancement for Annonaceae systematics was reached when Couvreur & al. (2019) developed a custom Annonaceae-specific bait kit that allowed for the recovery of up to 469 nuclear low-copy loci using a target capture high-throughput sequencing approach. This kit was used to sequence 65 Annonaceae genera, resulting in the first phylogenomic analysis of Annonaceae. In parallel, the

Table 1. Intrafamilial classification of Annonaceae including four currently recognised subfamilies and their respective tribes, subtribes, genera, and number of species. Intrafamilial ranks are arranged according to phylogenetic order based on the concatenated IQ-TREE topology (Fig. 1). Species diversity based on estimates made in January 2024.

Subfamily	Tribe	Subtribe	Genus	# Species per genus/clade
TOTAL				2503
Anaxagoreoideae			<i>Anaxagorea</i>	25
Ambavioideae				56
	Canangeae			36
			<i>Cananga</i>	2
			<i>Cyathocalyx</i>	7
			<i>Drepananthus</i>	26
			<i>Lettowianthus</i>	1
	Meiocarpidae		<i>Meiocarpidium</i>	1
	Tetramerantheae			19
			<i>Ambavia</i>	2
			<i>Cleistopholis</i>	4
			<i>Mezzettia</i>	5
			<i>Tetrameranthus</i>	8
Annonoideae				1526
	Bocageae			65
		Bocageinae		24
			<i>Bocagea</i>	4
			<i>Hornschuchia</i>	12
			<i>Trigynaea</i>	8
		Cardiopetalinae		40
			<i>Cardiopetalum</i>	3
			<i>Cymbopetalum</i>	27
			<i>Froesiodendron</i>	3
			<i>Porcelia</i>	7
		Mkiluinae	<i>Mkilua</i>	1
	Annoneae			342
		Annoninae		333
			<i>Annona</i>	172
			<i>Asimina</i>	11
			<i>Diclinanona</i>	3
			<i>Disepalum</i>	10
			<i>Goniothalamus</i>	137
		Anonidiinae		9
			<i>Anonidium</i>	4
			<i>Neostenanthera</i>	5
	Duguetieae			213
		Artabotrydinae		114
			<i>Artabotrys</i>	110
			<i>Letestudoxa</i>	3
			<i>Pseudartabotrys</i>	1
		Duguetiinae		99
			<i>Duckeanthus</i>	1
			<i>Duguetia</i>	96
			<i>Fusaea</i>	2
	Guatterieae		<i>Guatteria</i>	183
	Monodoreae			90
		Hexalobinae		12

(Continues)

Table 1. Continued.

Subfamily	Tribe	Subtribe	Genus	# Species per genus/clade
(Annonoideae cont.)	(Monodoreae cont.)	(Hexalobinae cont.)	<i>Asteranthe</i>	2
			<i>Hexalobus</i>	5
			<i>Uvariastrum</i>	5
		Monodorinae		34
			<i>Isolona</i>	20
			<i>Monodora</i>	14
		Uvariopsidinae		44
			<i>Dennettia</i>	1
			<i>Lukea</i>	2
			<i>Mischogyne</i>	5
			<i>Monocyclanthus</i>	1
			<i>Uvariodendron</i>	18
			<i>Uvariopsis</i>	17
	Ophrypetaleae			2
			<i>Ophrypetalum</i>	1
			<i>Sanrafaelia</i>	1
	Uvarieae			440
		Cleistochlamydinae		19
			<i>Afroguatteria</i>	3
			<i>Cleistochlamys</i>	1
			<i>Sphaerocoryne</i>	11
			<i>Toussaintia</i>	4
		Desminae		187
			<i>Dasymaschalon</i>	28
			<i>Desmos</i>	19
			<i>Friesodielsia</i>	47
			<i>Monanthotaxis</i>	93
		Fissistigmatinae		67
			<i>Fissistigma</i>	55
			<i>Mitrella</i> ¹	10
			<i>Pyramidanthe</i> ¹	2
		Uvariinae		167
			<i>Dielsiothamnus</i>	1
			<i>Uvaria</i>	166
	Xylopieae		<i>Xylopia</i>	191
Malmeoideae				896
	Annickieae		<i>Annickia</i>	8
	Piptostigmateae			32
			<i>Brieya</i>	2
			<i>Greenwayodendron</i>	6
			<i>Mwasumbia</i>	1
			<i>Piptostigma</i>	13
			<i>Polyceratocarpus</i>	9
			<i>Sirdavidia</i>	1
	Malmeeae			184
		Malmeinae		64
			<i>Crematosperma</i>	34
			<i>Malmea</i>	6
			<i>Pseudoxandra</i>	24
		Oxandrinae		67
			<i>Ephedranthus</i>	7

(Continues)

Table 1. Continued.

Subfamily	Tribe	Subtribe	Genus	# Species per genus/clade	
(Malmeoideae cont.)	(Malmeeae cont.)	(Oxandrinae cont.)	<i>Klarobelia</i>	13	
			<i>Mosannona</i>	14	
			<i>Oxandra</i>	26	
			<i>Pseudephedranthus</i>	2	
			<i>Pseudomalmea</i>	4	
			<i>Ruizodendron</i>	1	
			Unonopsidinae		53
				<i>Bocageopsis</i>	4
				<i>Onychopetalum</i>	2
				<i>Unonopsis</i>	47
			Maasieae	<i>Maasia</i>	6
			Fenerivieae	<i>Fenerivia</i>	10
			Phoencantheae	<i>Phoencanthus</i>	2
			Monocarpieae		5
				<i>Leoheo</i>	1
				<i>Monocarpia</i>	4
			Dendrokingstonieae	<i>Dendrokingstonia</i>	3
			Miliuseae		646
			Oropheinae		134
				<i>Marsypopetalum</i>	5
		<i>Orophea</i>	58		
		<i>Pseuduvaria</i>	59		
		<i>Trivalvaria</i>	12		
	Huberanthinae	<i>Huberantha</i>	34		
	Neo-uvariinae		83		
		<i>Monoon</i>	76		
		<i>Neo-uvaria</i>	7		
	Winitinae		14		
		<i>Sageraea</i>	9		
		<i>Stelechocarpus</i>	1		
		<i>Winitia</i>	4		
	Popowiinae		113		
		<i>Polyalthia</i>	89		
		<i>Popowia</i>	24		
	Polyalthiopsidinae	<i>Polyalthiopsis</i>	3		
	Phaeanthinae		162		
		<i>Alphonsea</i>	35		
		<i>Miliusa</i>	61		
		<i>Mitrephora</i>	53		
		<i>Phaeanthus</i>	8		
		<i>Platymitra</i>	3		
		<i>Wangia</i>	2		
	Sapranthinae		103		
		<i>Desmopsis</i> ²	30		
		<i>Meiogyne</i>	36		
		<i>Sapranthus</i>	10		
		<i>Stenanona</i> ²	16		
		<i>Tridimeris</i> ³	10		
		<i>Wuodendron</i>	1		

¹ *Mitrella* was sunken into synonymy with *Pyramidanthe* Bangkomnate & al. (2021);

² *Stenanona* was sunken into synonymy with *Desmopsis* (Schatz & al., 2023);

³ Species diversity based on a recent in preparation revision of *Tridimeris*.

Angiosperms353 probe set was developed for the Plant and Fungal Trees of Life (PAFTOL) project (Johnson & al., 2019; Baker & al., 2021). This kit was used to generate a genus-level phylogeny of Magnoliids (Helmstetter & al., 2024) which included 78 genera of Annonaceae, with relationships highly congruent with the phylogenetic trees of Couvreur & al. (2019), even though both kits target largely different nuclear markers (just 18 markers in common). These studies were also quite congruent with published plastid phylogenetic hypotheses in retrieving the major subfamilies and tribes. However, some important differences were revealed, the most striking of which was the different phylogenetic position of the Paleotropical liana genus *Artabotrys* R.Br., sister to the pantropical genus *Xylopi*a L. (tribe Xylopieae Endl.) in plastid phylogenetic trees but sister to *Letestudoxa* Pellegr. and *Pseudartabotrys* Pellegr. (tribe Duguetieae Chatrou & R.M.K.Saunders) in nuclear phylogenomic trees. In addition, the position of *Meiocarpidium* remained uncertain in phylogenomic studies, it being sister to the rest of Annonaceae (excluding *Anaxagorea*) in the concatenated analysis supporting Chaowasku (2020), but sister to the rest of the Ambavioideae in the gene tree analysis, with more genes supporting this latter configuration (Couvreur & al., 2019). This result was used as evidence to place the subfamily Meiocarpidioideae in synonymy, reclassifying the clade at tribal rank (Meiocarpidae Chatrou & al.; Helmstetter & al., 2024). Additionally, phylogenetic analyses using the Annonaceae kit showed promising results in terms of resolution in Miliuseae, although generic sampling was still low (Couvreur & al., 2019).

Within this context, the present study aims to generate the first fully sampled genus-level phylogenomic framework for Annonaceae based on hundreds of nuclear loci (Couvreur & al., 2019). First, we focused on resolving the backbone of the recalcitrant Miliuseae tribe by sampling multiple species for all known genera. Then using the results of this prior analysis, we reconstructed a fully sampled genus-level phylogenomic tree of Annonaceae, and used this novel framework and expert knowledge of morphology to further refine the nomenclature and taxonomic classification of Annonaceae by recognising 25 subtribes, 21 as new.

■ MATERIALS AND METHODS

Taxon sampling, DNA sequencing and data processing.

— We generated two datasets. First, to resolve the relationships in Miliuseae, we sampled 76 taxa representing all 25 known genera (including *Stenanona* Standl.) within the tribe along with 13 outgroups. Miliuseae are nested in a grade containing six tribes all sampled here: Malmeae Chatrou & R.M.K.Saunders, Maasiae Chatrou & R.M.K.Saunders, Fenerivieae Chatrou & R.M.K.Saunders, Phoenicantheae, Monocarpeae Chatrou & R.M.K.Saunders, and Dendrokingstonieae Chatrou & R.M.K.Saunders. Resulting trees were rooted with *Annickia* Setten & Maas (Appendix 1). Second,

for the genus-level dataset, we sampled one representative for all currently accepted 108 genera, 38 of which were newly sequenced in this study using nuclear baits (see Appendix 2). We also included one representative each of *Mitrella* Miq. and *Stenanona* even though they have been subsumed into other genera (*Pyramidanthe* Miq. and *Desmopsis* Saff., respectively), to assess for congruence between our topologies and those from others using different data sources (Bangkomnate & al., 2021; Schatz & al., 2023). The newly sequenced samples were sourced from both herbarium and silica-dried samples. Data for the remaining 70 genera were sourced from our previous studies, sequenced using the custom Annonaceae baits (Couvreur & al., 2019; Dagallier & al., 2023; Lopes & al., 2024). The type species for each genus was included where possible. All genera were represented by one species each except for the polyphyletic *Oxandra* A.Rich. (Pirie & al., 2006; Chatrou & al., 2012b; Guo & al., 2017), where three taxa representing each of the three clades were included. The genus *Stenanona* was also retained even though it was recently recombined in *Desmopsis* based on phylogenetic evidence (Schatz & al., 2023). We also included species for both *Pyramidanthe* and *Mitrella*, even though the latter name was recently reduced to a taxonomic synonym of the former (Bangkomnate & al., 2021). This was done because the phylogenetic relationships between these two genera are not resolved based on plastid data alone and their morphological distinctions are trivial (Bangkomnate & al., 2021). The phylogenetic trees were rooted with *Anaxagorea*, which was confirmed to be sister to all other Annonaceae, based on phylogenies of both plastid (Chatrou & al., 2012b) and nuclear datasets with extensive sampling across outgroup Magnoliids (Couvreur & al., 2019; Helmstetter & al., 2024).

All specimens were sequenced using the Annonaceae bait kit, which targets up to 469 nuclear loci (Couvreur & al., 2019). Laboratory and sequencing processing protocols follow those from our previous studies (Couvreur & al., 2019; Brée & al., 2020). In brief, raw sequences were demultiplexed using the demultadapt script (<https://github.com/Maillol/demultadapt>). The adapters were removed using cutadapt v.1.18 (Martin, 2011) with “-b” option and the following parameters: “-O 7 -m 35 -q 20 -e 0.1”. Sequences were trimmed for quality (trimmed reads with mean quality phred score below 30 and less than 35 bp long) using a custom script (https://github.com/SouthGreenPlatform/arcad-hts/blob/master/scripts/arcad_hts_2_Filter_Fastq_On_Mean_Quality.pl) and sorted into paired reads per sample (https://github.com/SouthGreenPlatform/arcad-hts/blob/master/scripts/arcad_hts_3_synchronized_paired_fastq.pl).

We used the HybPiper v.1.2 pipeline (Johnson & al., 2016) to process paired reads and retrieve cleaned alignments for phylogenetic analyses. We used BWA v.0.7.12 (Martin, 2011) to map reads onto targeted nuclear exons, and mapped reads were assembled into contigs using SPAdes v.3.11.1 (Bankevich & al., 2012). Prior to the alignment step, we extracted the supercontig outputs from the HybPiper pipeline, and excluded loci that were flagged as potential paralogs. A

conservative approach was implemented where all flagged loci were excluded from downstream analyses following the approach of Shee & al. (2020) and others (Kuhnhäuser & al., 2021), as paralogous loci from recent duplication events may not be detected from manual filtering by eye. We adopted the `max_overlap` script Shee & al. (2020) conceived to filter out sequences that had poor coverage across the targeted loci and to reduce noise by filtering (1) underrepresented (proportion of species/genes for which sequences were obtained), (2) incomplete (proportion of target sequence obtained for each species/gene), and (3) unevenly distributed sequences (how evenly the sequence lengths are distributed across species/genes). The overall coverage score for each sample was calculated by combining these three metrics via a cube root function computed in R. Sequences with an overall score of less than 0.5 were excluded from subsequent alignment and phylogenetic analyses. Sequences were aligned using MAFFT v.7.305 (Kato & Standley, 2013) for each loci using the `-auto` option. Alignments were trimmed to remove poorly aligned regions using Gblocks v.0.91 (Castresana, 2000) with the `“-b5 = a”` parameter to allow for gap positions in the alignments. The raw sequence filtering, HybPiper pipeline, alignment and trimming steps were completed on a local high-performance computing (HPC) cluster. Parsimony-informative sites for the alignments were determined using PhyKIT (Steenwyk & al., 2021).

Phylogenetic reconstruction. — We generated concatenated (CON) and multi-species coalescent (MSC) phylogenetic trees from both datasets: (1) Miliuseae with multiple accessions for all non-monotypic genera except *Stelecholepis* Hook.f. & Thomson, *Wangia* X.Guo & R.M.K.Saunders, and *Winitia* Chaowasku (hereafter, MIL-), and (2) an overall genus-level phylogeny with all genera included (hereafter, GEN-). For CON analyses, concatenated alignments of filtered supercontigs were created using the Phyx v.0.9 software package (Brown & al., 2017). Concatenated phylogenetic trees were generated using IQ-TREE v.2.1.3 (Minh & al., 2020a) with alignments partitioned across the different nuclear loci for each dataset. The optimum partition model was selected for each locus in IQ-TREE and clade support assessed with 1000 replicates of ultrafast bootstrap (-B), gene (-gCF) and site (-sCF) concordance factors (Minh & al., 2020b).

For coalescent phylogenetic analyses, we implemented weighted ASTRAL v.1 (wASTRAL; Zhang & Mirarab, 2022), which has been shown to improve species tree support as it reduces noise from both low support and long terminal branches. The hybrid function command in wASTRAL was utilised as it takes into account both node support and branch lengths. The input gene trees for wASTRAL were constructed individually with RAxML v.8.2.9 using the GTRGAMMA substitution model and 100 bootstrap (BS) replicates (Abadi & al., 2019). Nodes with very low bootstrap support (BS < 10) were collapsed using Newick utilities v.1.6 (Junier & Zdobnov, 2010) to further improve the accuracy of MSC inference in wASTRAL (Zhang & al., 2018). For the GEN-

dataset, we also included a sensitivity test by collapsing nodes that were not strongly supported (BS < 70) and assessed how this threshold would affect downstream analyses. The relative proportion of gene trees congruent with the species tree derived from wASTRAL (MSC) was assessed using Phyparts v.0.01 (Smith & al., 2015) and visualised using scripts developed by Matt Johnson (<https://bitbucket.org/blackrim/phyiparts>). For input into Phyparts, all gene trees were rooted with *Anaxagorea* using Phyx v.0.9 (Brown & al., 2017). Gene trees without *Anaxagorea* were rooted with the next early-diverging lineage (Ambavioid representative). Long branches indicative of potentially low-quality sequence data were removed using TreeShrink v.1.3.3 (Mai & Mirarab, 2018) after the alignment Gblocks trimming steps. In addition to Phyparts, alternative topologies of selected nodes that were in conflict across CON and MSC analyses were visualised using DiscoVista (Sayyari & al., 2018) after collapsing gene tree nodes with bootstrap support below 80% using Newick utilities. Conflicts between the coalescent (wASTRAL) and concatenated (IQTree) topologies were visualised as a tanglegram using “`cophylo`” function in the R package phytools v.1.2.0 (Revell, 2012) implemented in R v.4.0 (R Core Team, 2016). The phylogenies were then labelled and edited in Inkscape v.1.2 (<https://inkscape.org>).

■ RESULTS

Sequence recovery. — We recovered an overall average coverage depth of 2 million reads across all sequenced individuals across loci from our two sample datasets (suppl. Figs. S1, S2, suppl. Table S1). For Miliuseae (MIL-dataset), 374 loci were included, with 90 paralogs and 5 low-coverage loci removed. For the GEN-dataset, 307 loci were included, with 157 paralogous and 5 low-coverage loci removed. The MIL-CON alignment had 38.9% (182,676/458,396 bp) parsimony-informative sites, with a sample range of 5–77 sequenced taxa (6%–100%) per locus (suppl. Appendix S1). The GEN-CON alignment had 58.5% (238,216/407,240 bp) parsimony-informative sites, with a sample range of 3–112 sequenced taxa (3%–100%) per locus (suppl. Appendix S2).

Miliuseae. — We use the following terms to discuss support values in our phylogenetic trees: (1) nodes with local posterior probability (LPP) = 1, quartet support (QS) = 100, ultrafast bootstrap (UFB) = 100, are fully supported; (2) nodes with LPP > 0.85, QS > 50, UFB > 95 are strongly supported; (3) nodes with LPP 0.6–0.85, QS 30–50, UFB 95 are moderately supported; (4) nodes with LPP < 0.6, QS < 30, UFB < 95 are weakly supported, as per recommendations from the respective developers (Sayyari & Mirarab, 2016; Minh & al., 2020b). Miliuseae were shown to be monophyletic and well-resolved with full to strong support of the crown node in both MIL-MS and MIL-CON topologies (LPP = 1, QS = 95, UFB = 100) (Fig. 1). Within Miliuseae, the CON topology showed greater support in general across nodes than the MSC topology (Fig. 1). Nevertheless, besides the good

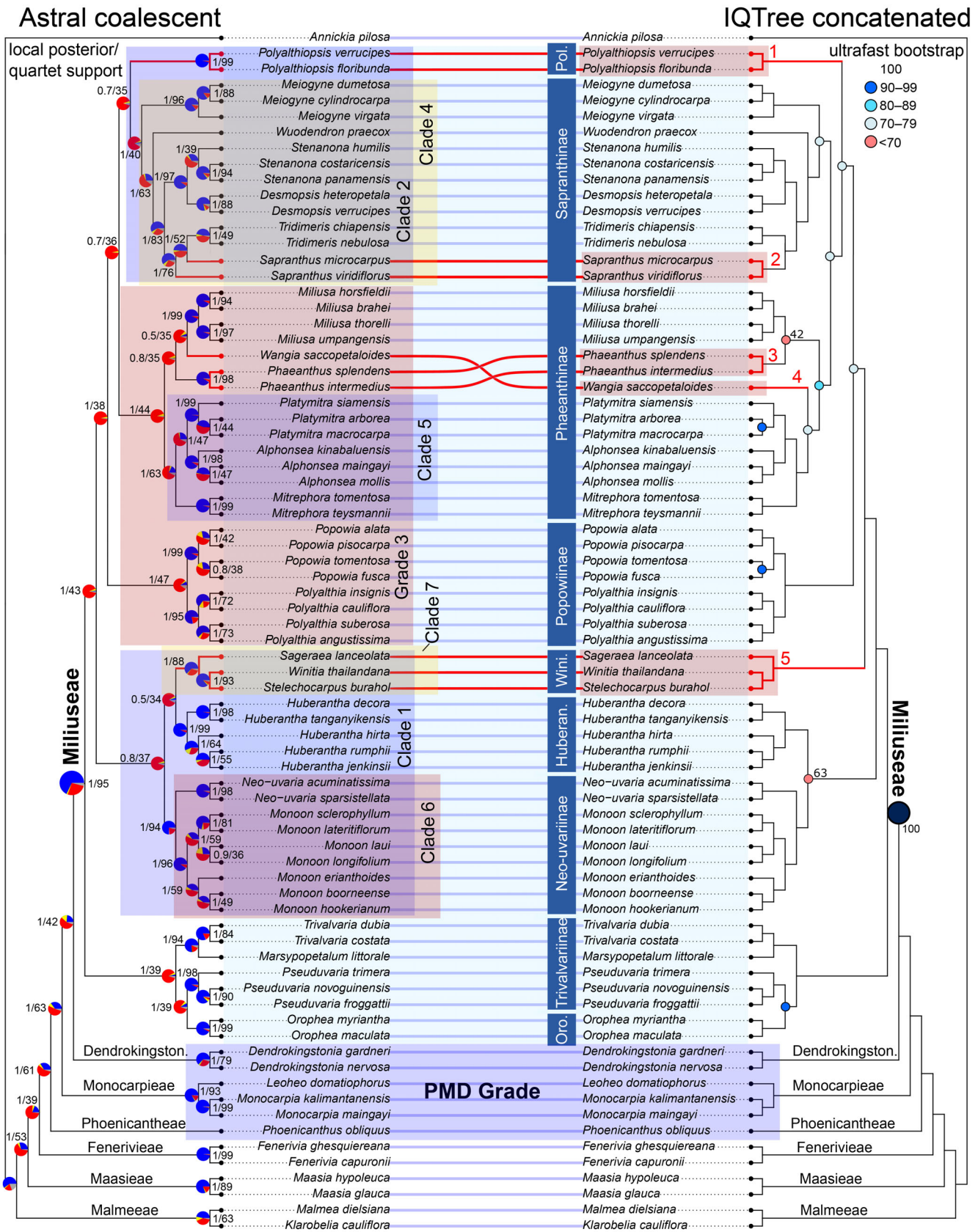


Fig. 1. Caption on next page.

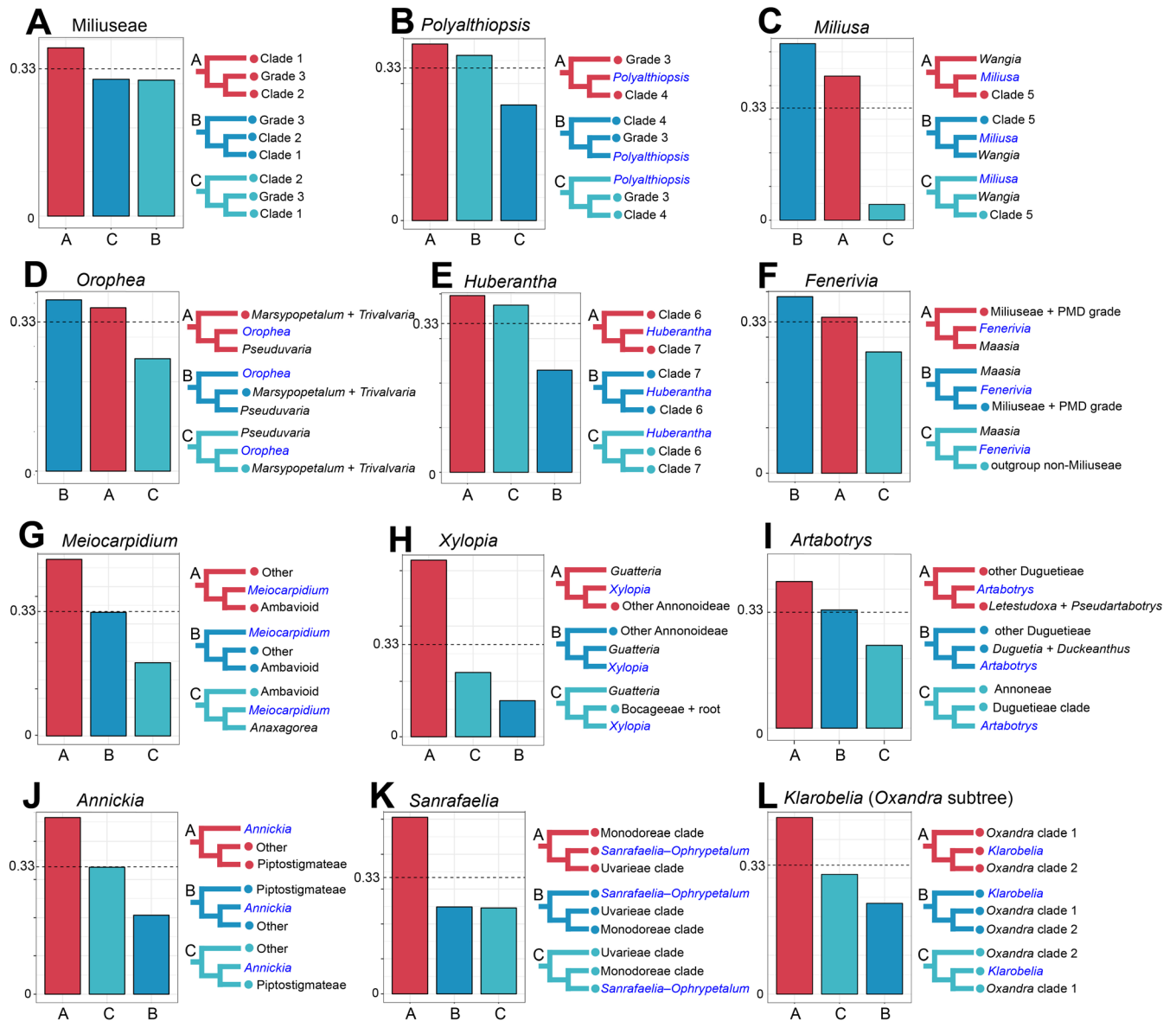


Fig. 2. Gene-tree conflict and alternative topologies of selected Annonaceae clades based on the genus-level phylogenetic tree. Gene tree quartet frequencies for alternative topologies were analysed using DiscoVista based on 307 unrooted nuclear gene trees. Dashed horizontal lines mark the equal frequency threshold (0.33) across three possible topologies. Lineage of interest for each plot is highlighted in blue font. Coloured circles mark clades containing more than one lineage/genus representative. The PMD grade includes three tribes of subfamily Malmeoideae – Phoeniciantheae, Monocarpeae, and Dendrokingstonieae. Other clades are highlighted in Fig. 1.

Fig. 1. Tanglegram showing phylogenetic trees of Miliuseae and sister tribes estimated with coalescent (wASTRAL, left) and concatenated (IQ-TREE, right) approaches. The Miliuseae tribe is highlighted in blue, and the crown node indicated with a larger circle. Red branches and connecting red lines indicate conflicting topologies between the two trees, with the five conflicting clades marked with red numbers. Pie charts at nodes on the wASTRAL tree show gene tree conflict for each node: proportion of gene trees in support (blue), in conflict (red) with the species tree, agreeing with the second alternative species-tree (yellow), and unsupported (grey). Local posterior probability and quartet support values are shown for each node for the Astral topology. For the IQ-TREE, only ultrafast bootstrap (UFB) support values of less than 100 are shown with coloured circles, and exact values of UFB < 70 are also annotated. Clades linked to the DiscoVista results are highlighted with coloured boxes. Subtribes are labelled with white text over blue boxes. Abbreviated subtribes: Huberan. = Huberanthinae, Oro. = Oropheinae, Pol. = Polyalthiopsidinae, Wini. = Winitinae.

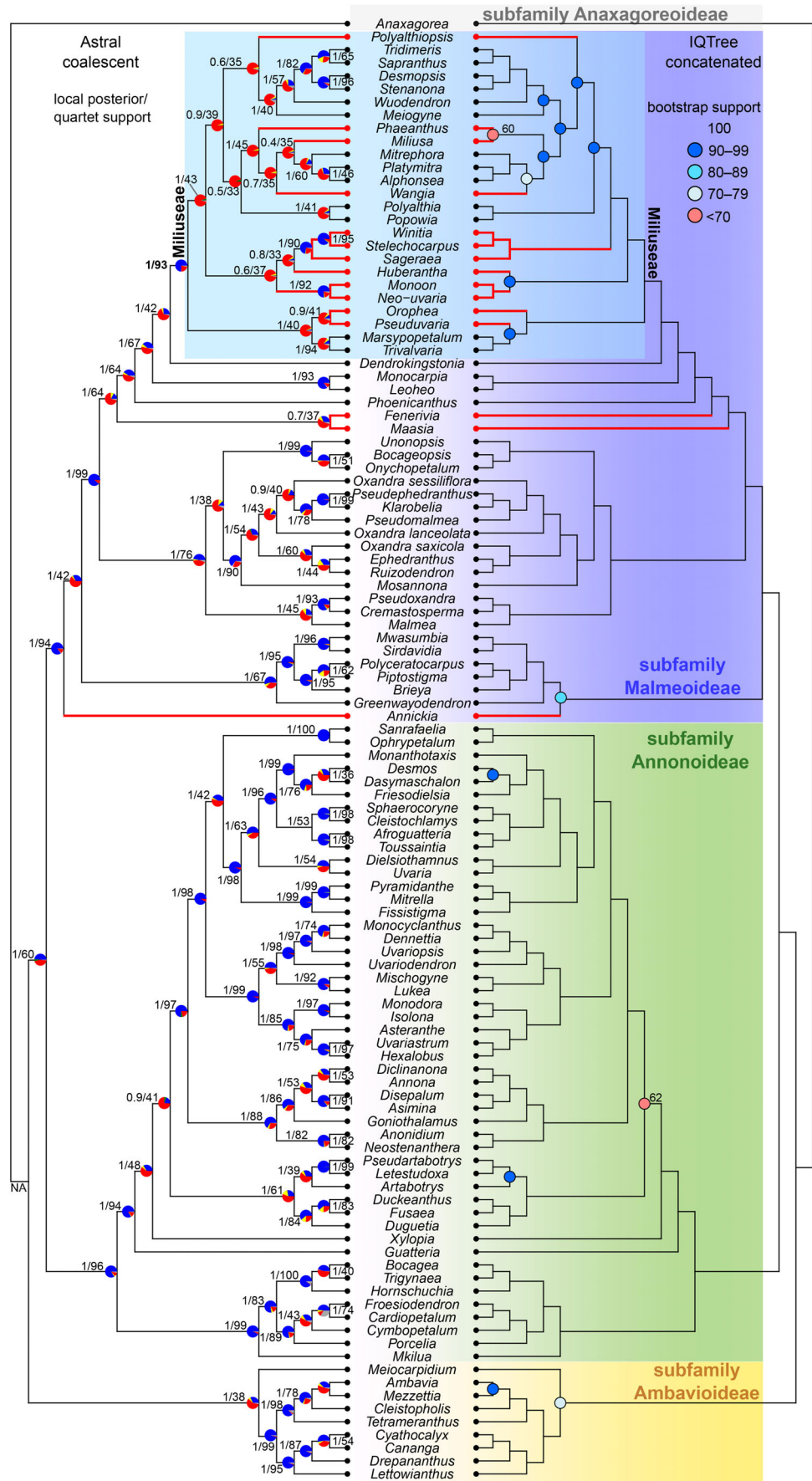


Fig. 3. Caption on next page.

overall support, significant conflict among gene-trees and the species-tree was recovered across the Miliuseae backbone and for intergeneric relationships within the tribe (Figs. 1, 2A–E). In contrast, shallower relationships within genera based on the species tree were generally well supported across most gene topologies (Fig. 1). All genera are monophyletic except for *Sapranthus* Seem. which is paraphyletic with respect to *Tridimeris* Baill. in the MIL-MSC tree (Fig. 1). Interestingly, substantial gene-tree conflict was also noted for a grade of six tribes successively sister to Miliuseae, despite strong support in both MIL-MSC and MIL-CON analyses. Our analyses result in the following topology: (Malmeae, (Maasieae, (Fenerivieae, (Phoenicantheae, (Monocarpieae, (Dendrokingstonieae, (Miliuseae)))))).

Within Miliuseae, five topological conflicts were noted between the MIL-MSC and MIL-CON trees. The most disparate of these included (1) *Polyalthiopsis* Chaowasku, which is sister to the *Meiogyne* Miq.–*Sapranthus* clade (Clade 4 with six genera) in MIL-MSC but sister to the *Meiogyne*–*Mitrephora* (Blume) Hook.f. & Thomson clade (12 genera) in MIL-CON (Fig. 1). Despite a moderate LPP support value of 0.7 in the MIL-MSC tree, significant gene tree conflict is present (Fig. 2B). Other conflicts include (2) a paraphyletic *Sapranthus* in MIL-MSC (with full support, LPP = 1) and a fully supported monophyly for this genus in MIL-CON (UFB = 100). Similarly, (3) *Phaeanthus* Hook.f. & Thomson was shown to have a different topological placement, with *Phaeanthus* and *Wangia* being successively sister to *Miliusa* in MIL-MSC. In MIL-CON, *Phaeanthus* is sister to *Miliusa* only. Conflicting phylogenetic placement of *Phaeanthus* has also affected the placement of (4) *Wangia*, with *Wangia* being sister to *Miliusa* in MIL-MSC (albeit weakly supported, LPP = 0.54) and sister to *Platymitra* Boerl., *Alphonsea* Hook.f. & Thomson, and *Mitrephora* in MIL-CON (UFB = 79). However, most nodes relevant to these genera are moderately or even poorly supported, alleviating the significance of this topological conflict. Lastly, (5) *Sageraea* Dalzell, *Winitia*, and *Stelechocarpus* (clade 7) is another conflicting clade, which is sister to *Huberantha* Chaowasku in MIL-MSC (LPP = 0.48) but sister to the *Polyalthiopsis*–*Polyalthia* Blume clade (15 genera) in MIL-CON (UFB = 100) (Fig. 1). These conflicting nodes generally are subject to poor support, particularly in MIL-MSC.

For *Miliusa*, the GEN-CON topology was the least supported (<10% gene trees) out of the different topological configurations (Fig. 2C). Significant gene-tree conflicts were also noted for *Huberantha* (clade 1; this clade includes *Stelechocarpus*, *Winitia*, *Sageraea*, *Neo-uvaria* Airy Shaw, *Monoon* Miq., and *Huberantha*), *Polyalthiopsis* (clade 2; this clade

includes *Meiogyne*, *Wuodendron* B.Xue & al., *Stenanona*, *Desmopsis* Saff., *Tridimeris*, and *Sapranthus*) and *Orophea* (including sister genera *Trivalvaria* (Miq.) Miq., *Marsypopetalum* Scheff., and *Pseuduvaria* Miq.) (Figs. 1, 2).

Generic relationships in Annonaceae. — Our analyses including all 108 Annonaceae genera confirmed the monophyly of its four subfamilies (Fig. 3). *Meiocarpidium* (Meiocarpidioideae sensu Chaowasku, 2020) was recovered as sister to Ambavioideae in both GEN-CON and GEN-MSC analyses with high to low support (LPP = 1, UFB = 76, respectively; Fig. 3). However, significant gene-tree conflict was present, as shown by our Phyparts and Disco-Vista analyses (Figs. 2, 3). Nevertheless, most genes support the placement of *Meiocarpidium* as sister to Ambavioideae (Fig. 2G).

Tribe Xylopieae was recovered as polyphyletic as currently circumscribed, with *Artabotrys* nested within Duguetieae. Indeed, an overwhelming majority of genes (>70%) support the placement of *Xylopia* as sister to all Annonoideae except *Guatteria* Ruiz & Pav. and tribe Bocageae Endl., while *Artabotrys* was recovered as sister to the genera *Pseudartabotrys* and *Letestudoxa* within Duguetieae (Fig. 2H,I). Most tribal and generic relationships were resolved as monophyletic with high support (LPP ≥ 0.85) in our GEN-MSC analysis, except for Xylopieae (see above) and genera within Miliuseae (Fig. 3). Strong support between genera was also obtained with the GEN-CON analysis with the exception of Duguetieae (including *Artabotrys*), which is weakly supported (UFB = 62) as sister to a clade containing the tribes Annoneae Endl., Monodoreae Baill., and Uvarieae Hook.f. & Thomson (Fig. 3).

Conflicts between ASTRAL and IQ-TREE topologies. — The backbone of Annonaceae was generally well supported across our gene-trees except for a few recalcitrant nodes, most of which are concentrated within Miliuseae (see above; Fig. 3). Our sensitivity test of a higher threshold for collapsing poorly supported nodes (BS < 70 compared with BS < 10) across gene trees did not result in fewer gene-tree conflicts from the species tree (red portions of pie charts from Phyparts). Instead, this higher threshold resulted in more unsupported nodes (grey portions of pie charts from Phyparts; suppl. Fig. S3).

Other nodes that were in conflict between the GEN-CON and GEN-MSC analyses include *Annickia* (tribe Piptostigmateteae Chatrou & R.M.K.Saunders), which is sister to other Piptostigmateteae genera in GEN-CON but sister to the rest of subfamily Malmeoideae in the GEN-MSC tree (Fig. 3). The GEN-MSC position of *Annickia* was supported by almost half (46%) of all nuclear loci, compared to 33% of the genes that

Fig. 3. Complete genus-level phylogenetic hypothesis of Annonaceae estimated with coalescent (wASTRAL, left) and concatenated (IQ-TREE2, right) approaches. The Miliuseae tribe is highlighted in blue. Red branches indicate conflicting topologies between the two trees. Pie charts at nodes on the wASTRAL tree show gene tree conflict for each node: proportion of gene trees in support (blue), in conflict (red) with the species tree, agreeing with the second alternative species-tree (yellow), and unsupported (grey). Local posterior probability (LPP) and quartet support values are included for the ASTRAL topology. For the IQ-TREE2, only ultrafast bootstrap (UFB) support values of less than 100 are shown with coloured circles, and exact values of UFB < 70 are also annotated.

support the GEN-CON topology (DiscoVista, Fig. 2J). Abundant gene-tree conflict was also noted for the placement of *Xylophia* (Phyparts; Fig. 3). However, the majority of gene-trees support the current phylogenetic placement of *Xylophia* as sister to the rest of Annonoideae with the exclusion of *Gutteria* and *Bocageae*, based on our DiscoVista analysis (Figs. 2, 3). This result and the strongly nested nature of *Artabotrys* within Duguetieae further confirms that the tribe Xylopieae as currently circumscribed (*Artabotrys* + *Xylophia*) is polyphyletic.

Fenerivia Diels and *Maasia* Mols & al. represent another conflicting placement between the two analyses, with the two monotypic tribes (Fenerivieae, Maasieae) shown to be sister in GEN-MSA but paraphyletic in GEN-CON. Interestingly, based on our DiscoVista analysis, the dominant topology supported by the greatest number of genes is congruent with the GEN-CON topology (Tree B, Fig. 2F). A similar result is shown for *Orophea* (Fig. 2D).

■ DISCUSSION

We present for the first time a completely sampled genus-level phylogenomic tree of the major tropical plant family Annonaceae based on 373 loci (108 genera). A total of 38 genera (35.2%, 38/108) were newly sequenced here when compared to Couvreur & al. (2019) and other previous studies using the Annonaceae bait kit (Dagallier & al., 2023; Lopes & al., 2024). Most relationships across the family are strongly supported independent of the phylogenetic reconstruction method used (Fig. 3), even within the recalcitrant Miliuseae tribe (but see below). Once again, this shows the huge potential of family-specific nuclear bait kits to resolve family-wide relationships of tropical plant families (e.g. Schneider & al., 2021; Fonseca & al., 2023; Haigh & al., 2023). We note that the Neotropical genus *Oxandra* is polyphyletic (Fig. 4C) and its phylogenetic characterisation will be dealt with in a subsequent article.

The phylogenetic framework presented here follows from the large efforts focusing on Annonaceae molecular phylogenetics that have been ongoing for more than two decades (Richardson & al., 2004; Chatrou & al., 2012b; Guo & al., 2017; Couvreur & al., 2019). The last genus-wide phylogenetic tree of the family based on plastid loci sampled all genera accepted at that time except two: *Froesiodendron* R.E.Fr. (Bocageae) and *Melodorum* Lour. (Guo & al., 2017). *Froesiodendron* is a west Amazonian genus with three species (Johnson & Murray, 1995), and sequencing was unsuccessful until recently (Lopes & al., 2024). *Melodorum* is no longer accepted as a distinct genus, as its names have been transferred to different genera, such as *Uvaria* L. or *Fissistigma* Griff. (Zhou & al., 2010; see Turner, 2018). Our results confirm the inclusion of *Froesiodendron* in tribe Bocageae (Fig. 3), which is nested in a clade with three other genera (*Cardiopetalum* Schldl., *Cymbopetalum* Benth., *Porcelia* Ruiz & Pav.). This tribal placement is also in agreement with the morphological cladistic analysis of Johnson & Murray

(1995) and the phylogenomic reconstruction of Lopes & al. (2024). When compared to Guo & al. (2017), our sampling also included all newly described genera since 2017. *Leoheo* Chaowasku is sister to *Monocarpia* Miq. in our analysis, confirming results obtained using plastid data (Chaowasku & al., 2018a). Both species of *Lukea* Cheek & Gosline were included in the species-level phylogeny of tribe Monodoreae from Dagallier & al. (2023) and are recovered as sister to *Mischogyne* Excell (Cheek & al., 2022; Dagallier & al., 2023), congruent with our findings here. *Polyalthiopsis* (Chaowasku & al., 2018b), a genus in tribe Miliuseae, is recovered here in two alternative positions (Figs. 1, 2). The DiscoVista analysis (Fig. 2B) suggested slightly more genes supporting its position as sister to Sapranthinae, *Wuodendron* and *Meiogyne* (*Tridimeris* clade in Fig. 3), which is congruent with morphology. Finally, *Wuodendron* is recovered with maximal support as sister to subtribe Sapranthinae, in agreement with plastid data (Ortiz-Rodriguez & al., 2016; Xue & al., 2020a). We also sequenced genera that were resurrected based on morphological or molecular data: *Brieya* De Wild., previously included in *Piptostigma* Oliv. (Ghogue & al., 2017) and *Dennettia* Baker f., previously included in *Uvariopsis* Engl. (Couvreur & al., 2022; Dagallier & al., 2024).

At the generic level, our nuclear phylogenomic hypothesis of Annonaceae is mostly congruent with those based on plastid data (Chatrou & al., 2012b; Guo & al., 2017). One major difference between plastid and nuclear data, besides increased resolution, concerns the placement of the Paleotropical liana genus *Artabotrys* within Duguetieae rather than in Xylopieae (Thomas & al., 2015). This was noted before when using different sets of nuclear genes (Couvreur & al., 2019; Helmstetter & al., 2024). Tribe Xylopieae, which contained just two genera *Artabotrys* and *Xylophia*, was broadly characterised morphologically but with no clear synapomorphies identified at the time (Chatrou & al., 2012b), despite some resemblance in the basally clawed petals with an elaborate rim (Chen & al., 2020) and wood anatomy (Koek-Noorman & Westra, 2012). The placement, however, of *Artabotrys* in Duguetieae remains puzzling. Indeed, genera in tribe Duguetieae are mostly (but not always) characterised by syncarpous fruits (carpels fusing only after fertilisation; referred to as pseudosyncarpy; Chatrou & He, 1999), while *Artabotrys* has clearly apocarpous fruits with stipitate or more rarely sessile monocarps (Couvreur & al., 2022). Interestingly, *Artabotrys* is here recovered as sister to two African genera, *Letestudoxa* and *Pseudartabotrys*, both of which are also lianas (Chatrou & al., 2000). Thus, this placement might not be so surprising, also given that *Pseudartabotrys* has petals resembling those of *Artabotrys* (Pellegrin, 1920).

The monotypic central African *Meiocarpidium* is recovered as sister to Ambavioideae with strong support in the GEN-MSA analysis and moderate support (UFB = 76) in the GEN-CON analysis (Fig. 3). There is nevertheless strong gene-tree conflict based on the Phyparts analysis, while the DiscoVista analysis suggests that most genes support the Ambavioideae sister relationship (Fig. 2). Thus, in contrast to the

results of Chaowasku (2020), the subfamily status is not supported, confirming once again the lowering to the rank of tribe within Ambavioideae (Helmstetter & al., 2024).

Relationships between clades in Miliuseae have generally been poorly resolved based on plastid data (Chaowasku & al., 2014; Guo & al., 2017). Here, we present an overall well-resolved phylogenetic tree of Miliuseae, based on both concatenated and coalescent approaches (Fig. 1). Intertribal relationships within Malmeoideae are clarified and Dendrokingstonieae is strongly supported as sister to Miliuseae, while previous phylogenetic studies either did not include Dendrokingstonieae samples (Chatrou & al., 2012b; Couvreur & al., 2019) or retrieved Monocarpieae, usually with poor support, as sister to Miliuseae (e.g., Chaowasku & al., 2014; Guo & al., 2017). Furthermore, the intertribal relationships of tribes Fenerivieae and Maasieae within subfamily Malmeoideae remained obscure in previous phylogenetic studies (e.g., Chatrou & al., 2012b; Guo & al., 2017). While our data show substantial gene-tree conflicts at the relevant nodes, it

also provides strong evidence with supported topologies and the majority of gene trees supporting Maasieae and Fenerivieae as subsequent sister clades to the rest of Malmeoideae, including tribes Phoenicantheae, Monocarpieae, Dendrokingstonieae, and Miliuseae (Figs. 1, 2F).

We identified substantial gene-tree conflict along the backbone of Miliuseae (indicated in red in pie charts of Fig. 1, left side) in the species tree, despite strong overall support. Interestingly, relationships between closely related genera are well resolved with negligible gene-tree conflict indicating that this conflict is limited to the backbone of the tribe. Gene-tree conflict is also visible in the DiscoVista analyses, in which two alternative topologies received a similar number of supporting loci (Fig. 2D–F). Although having high local posterior probability (also seen with quartet scores) in the presence of significant gene tree conflict might appear counter-intuitive, it is not unusual as they are computed differently (Sayyari & Mirarab, 2016). The LPP is recommended as the general measure of support for the species tree topology

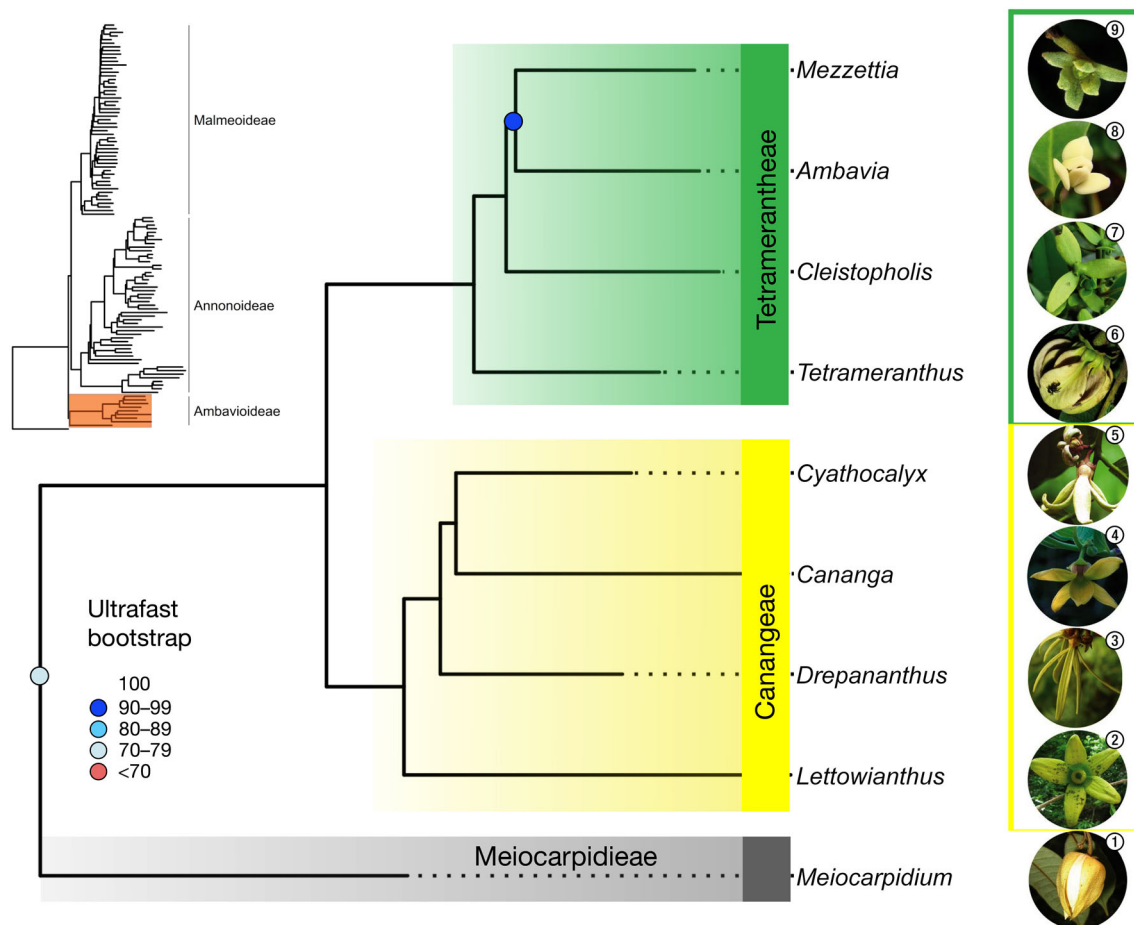


Fig. 4A. Phylogeny of Ambavioideae based on the concatenated IQ-TREE analysis. Insert in top left represents the Annonaceae phylogeny with the subfamily Ambavioideae highlighted. Different tribes are represented by coloured boxes. 1) *Meiocarpidium oliverianum* (Baill.) D.M.Johnson & N.A.Murray; 2) *Lettowianthus stellatus* Diels; 3) *Drepananthus ramuliflorus* Maingay ex Hook.f. & Thomson; 4) *Cananga brandisiana* (Pierre) Saff. (Photo: S. Gardner); 5) *Cyathocalyx martabanicus* Hook.f. & Thomson (Photo: P. Chalermglin); 6) *Tetrameranthus globulifer* Westra; 7) *Cleistopholis patens* (Benth.) Engl. & Diels; 8) *Ambavia gerrardi* (Baill.) Le Thomas (Photo: C. Davidson; <https://floraoftheworld.org/>); 9) *Mezzettia parviflora* Becc. (Photo: S. Gardner). Photos from Thomas L.P. Couvreur, unless stated otherwise.

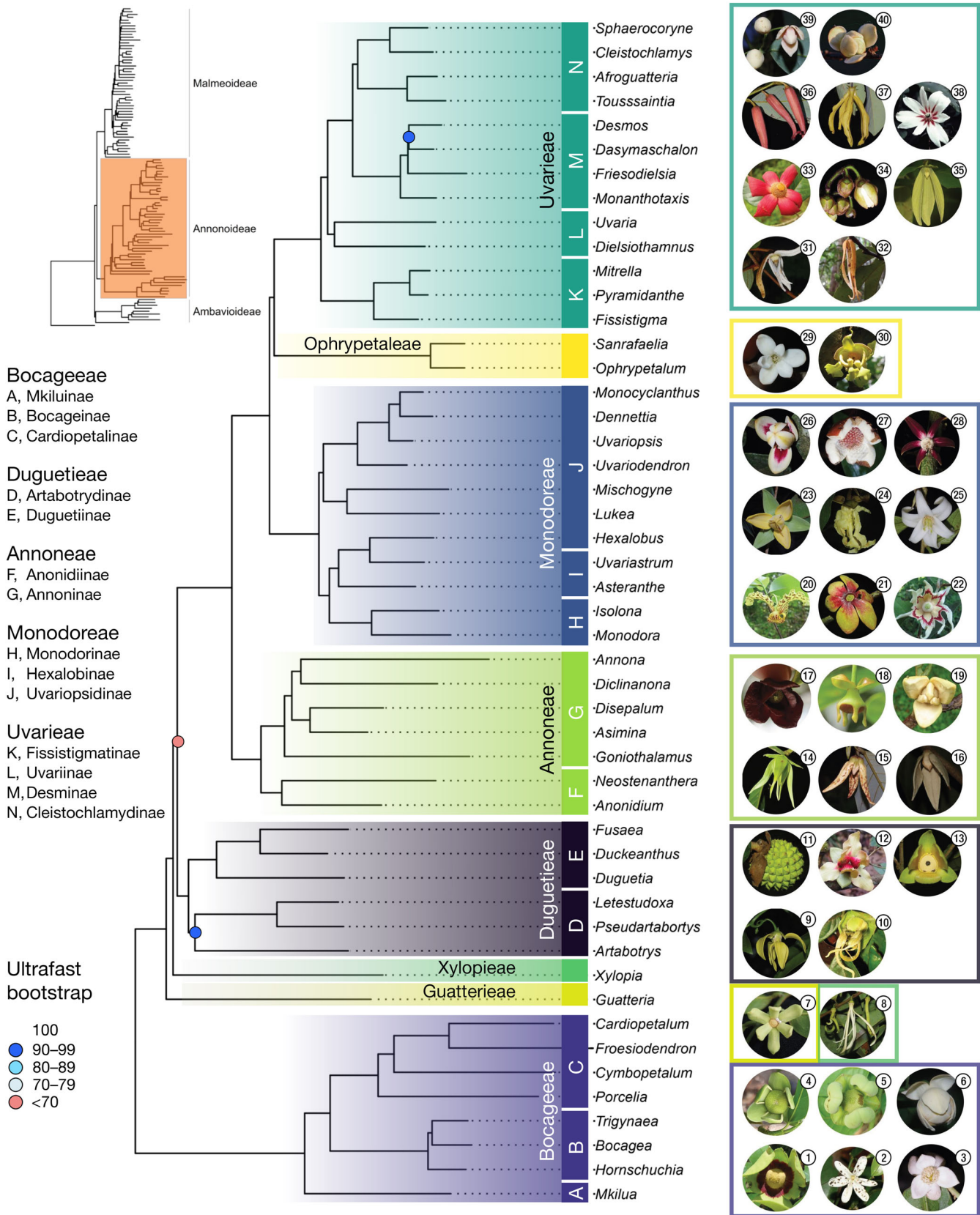


Fig. 4B. Caption on next page.

given that it indicates the probability of a selected node being the true node given the set of gene trees available, assuming the presence of incomplete lineage sorting (ILS) (Sayyari & Mirarab, 2016).

The presence of gene-tree conflict (Figs. 1, 2) along the backbone of Miliuseae even based on 373 nuclear loci indicates that clades within this tribe likely radiated rapidly, supporting a hypothesis advanced by Erkens & al. (2012) and also recovered in a recent family-wide diversification analysis based on plastid markers (Xue & al., 2020b). Alternatively, the nuclear loci included in this study are phylogenetically uninformative for this tribe. However, this appears as a less likely scenario given that the genes were selected specifically for Annonaceae (with a custom bait kit) and that other tribes within the family were resolved with high support across MSC and CON analyses (Couvreur & al., 2019; Brée & al., 2020; Dagallier & al., 2023; Martínez-Velarde & al., 2023). Deep coalescence (i.e., ILS) as a result of insufficient time for individual genes to sort in rapid radiations is not uncommon, and have been repeatedly documented across the Tree of Life (e.g., Koenen & al., 2020b; Nge & al., 2021; Strijk & al., 2022). These recalcitrant nodes are challenging and may never be resolved even with genomic datasets due to the persisting legacy of deep ILS (Koenen & al., 2020b). Our DiscoVista results showing selected clades within Miliuseae having alternate topologies with largely similar frequencies also suggest ILS as a dominant driver for gene-tree to species-tree conflicts, rather than from introgression. In contrast, non-Miliuseae lineages such as *Annickia*, *Xylopia*, and *Meiocarpidium* had highly discordant skews from our DiscoVista results, suggesting ancient hybridisation events in addition to ILS drove gene tree discordance for these lineages. Natural hybridisation events are relatively uncommon in Annonaceae but have been documented for sister genera *Dasydaschalon* (Hook.f. & Thomson) Dalla Toore & Harms, *Friesodielsia* Steenis in tribe Uvarieae (Guo & al., 2018) and *Oxandra* in tribe Malmeeae (Zwartsenberg, 2015). Other examples of hybrids in Annonaceae include *atemoia* (*Annona squamosa* L. × *A. cherimola* Mill, and *Cymbopetalum* (*C. costaricense* (Donn.Sm.) R.E.Fr. × *C. torulosum* G.E.

Schatz) (Schatz, 1985; Martin & al., 2019). Numerous approaches including simulation studies have been conducted to tease apart the effects of ILS and hybridisation, though untangling the two may be methodologically challenging (García & al., 2017; Nge & al., 2021; Joyce & al., 2024). Further studies on Miliuseae are required to investigate the dynamics and drivers of deep reticulate evolution across the tribe.

Our study adds to the growing literature demonstrating the promising utility of target capture high-throughput sequencing approaches in improving our understanding of phylogenomic relationships of tropical plant groups. Increased phylogenetic resolution has been demonstrated in broad-scale studies using the Angiosperms353 bait kit for Myrtales (Maurin & al., 2021), Sapindales (Joyce & al., 2023), Araceae (Haigh & al., 2023), Magnoliids (Helmstetter & al., 2024), and across all angiosperms (Zuntini & al., 2024). Similarly, studies on tropical groups using custom (family/order-specific) or a combination of custom and Angiosperms353 baits also recovered much improved phylogenetic resolution compared with Sanger sequence data: e.g., palms (Arecaceae; Loiseau & al., 2019; Kuhnhäuser & al., 2021), Bignoniaceae (Fonseca & al., 2023), Bromeliaceae (Yardeni & al., 2022; Bratzel & al., 2023), Caesalpinoideae (Fabaceae; Ringelberg & al., 2022) Mimosoid legumes (Fabaceae; Koenen & al., 2020a), Gesneriaceae (Ogutcen & al., 2021), Lecythidaceae (Vargas & al., 2019), Lowiaceae (Niissalo & al., 2022), Ochnaceae (Schneider & al., 2021; Shah & al., 2021), Orchidaceae (Eserman & al., 2021; Pérez-Escobar & al., 2021), Rubiaceae (Thureborn & al., 2022, 2024), Sapotaceae (Christe & al., 2021), and Zingiberales (Carlsen & al., 2018), just to name a few. Most of these studies were published in the last three years (since 2021), demonstrating the fast-evolving nature and increasing uptake of using target capture for future phylogenomic studies. In addition, all listed studies have used herbarium samples to increase taxonomic sampling and representation in their respective groups, highlighting the importance of herbaria and associated specimens as repositories for biodiversity research (Shee & al., 2020). These phylogenomic studies based on targeted nuclear loci often show incongruent topologies when compared with

Fig. 4B. Phylogeny of Annonoideae based on concatenated IQ-TREE analysis. Insert in top left represents the Annonaceae phylogeny with the subfamily Annonoideae highlighted. Different tribes are represented by coloured boxes. 1) *Mkilua fragrans* Verdc.; 2) *Hornsuchia myrtillus* Nees (Photo: J. Lopes); 3) *Trigynaea duckei* (R.E.Fr.) R.E.Fr.; 4) *Porcelia mediocris* N.A.Murray; 5) *Cymbopetalum baillonii* R.E.Fr.; 6) *Cardiopetalum surinamense* R.E.Fr. (Photo: Hervé Galliffet); 7) *Guatteria caribaea* (Photo: R.H.J. Erkens); 8) *Xylopia aethiopica* (Dunal) A.Rich.; 9) *Artabotrys hexapetalus* (L.f.) Bhandari (Photo: J. Chen); 10) *Pseudartabotrys letestui* Pellegr.; 11) *Letestudoxa glabrifolia* Chatrou & Repetur; 12) *Duguetia surinamensis* R.E.Fr.; 13) *Fusaea longifolia* (Aubl.) Saff.; 14) *Anonidium floribundum* Pellegr.; 15) *Neostenanthera myristicifolia* (Oliv.) Exell; 16) *Goniothalamus tapis* Miq. (Photo: J. Chen); 17) *Asimina triloba* (L.) Dunal; 18) *Disepalum anomalum* Hook.f. (Photo from: doi:10.1371/journal.pone.0143481.g001); 19) *Annona senegalensis* Pers.; 20) *Monodora carolinae* Couvreur; 21) *Isolona hexaloba* (Pierre) Engl. & Diels; 22) *Asteranthe asterias* (S.Moore) Engl. & Diels; 23) *Uvariastrum zenkeri* Engl. & Diels; 24) *Hexalobus crispiflorus* A.Rich.; 25) *Mischogyne gabonensis* (Pellegr. ex Le Thomas) Gosline; 26) *Uvariadendron molundense* (Diels) R.E.Fr.; 27) *Uvariopsis pedunculosa* (Diels) Robyns & Ghesq.; 28) *Monocyclanthus vignei* Keay; 29) *Sanrafaelia ruffonammari* Verdc.; 30) *Ophrypetalum odoratum* Diels; 31) *Fissistigma kingii* (Boerl.) Burkill; 32) *Pyramidanthe prismatica* (Hook.f. & Thomson) Merr. (Photo: Abdulromea Baka); 33) *Uvaria grandiflora* Roxb. ex Hornem.; 34) *Monanthotaxis filamentosa* (Diels) Verdc.; 35) *Friesodielsia discolor* (Craib) D.Das (Photo: C. Leeratiwong); 36) *Dasydaschalon* sp. (Photo: K. Armstrong); 37) *Desmos chinensis* Lour.; 38) *Toussaintia patriciae* Q.Luke & Deroin (Photo: Q. Luke); 39) *Sphaerocoryne gracilipes* (Benth.) X.Guo & R.M.K. Saunders; 40) *Cleisto-chlamys kirkii* (Benth.) Oliv. (Photo: B. Wursten). All photos from Thomas L.P. Couvreur, unless stated otherwise.

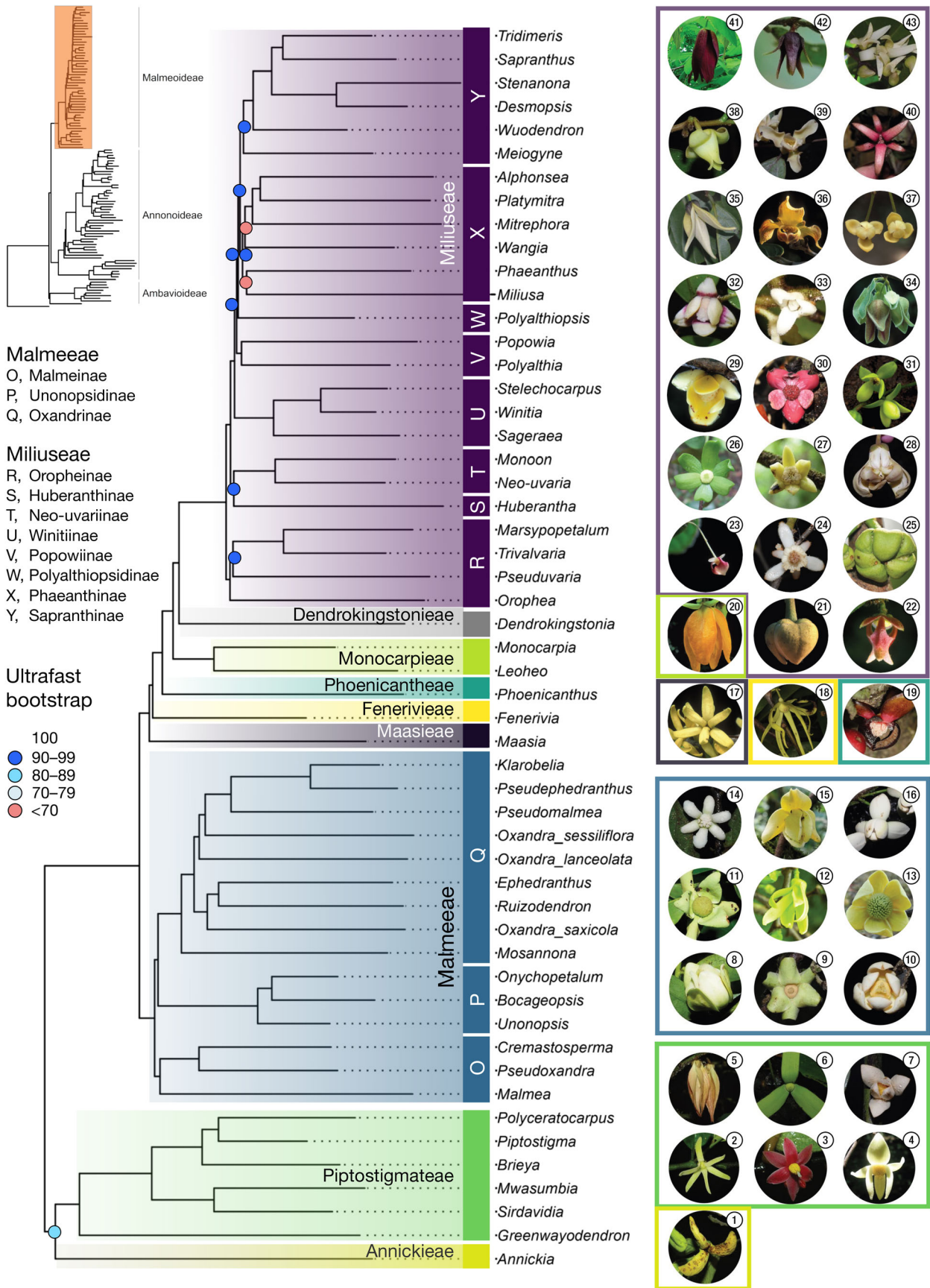


Fig. 4C. Caption on next page.

older works based on plastid sequence data. Some of these incongruences reflect lower resolution of previous studies that only included few plastid loci (i.e., soft conflict), as is the case for Annonaceae. But others show strongly supported conflicts, which may be attributed to hybridisation, incomplete lineage sorting, or a combination of both. Many of these conflicts are deep reticulation events that coincide with whole genome duplication events and high gene tree conflict (Stull & al., 2023; Zuntini & al., 2024). While most studies on deep reticulate evolution have focused on non-tropical plant groups (see examples in Stull & al., 2023), it is clear that this phenomenon is also present in tropical lineages. Further studies on these tropical groups are highly recommended to fill this gap in knowledge.

For Annonaceae, Chatrou & al. (2012b) provided a family-level classification defining subfamilies and tribes. Here, based on the novel robust phylogenomic framework we further refined the classification of Annonaceae by describing and redefining subtribes (Fig. 4A–C). The concept of subtribes in Annonaceae is useful as it is a taxonomically diverse family with many distinct clades based on both morphology and sequence divergence. This is especially important within Miliuseae, which with 25 genera is the most diverse tribe in the family. Describing subtribes was already started based on plastid data, such as Sapranthinae (Ortiz-Rodríguez & al., 2016). Providing subtribes for other larger tribes will also allow for better descriptions of clades and avoid referring to them with informal names (e.g., Uvariopsis clade, Cheek & al., 2022; Dagallier & al., 2023; Lopes & al., 2024). Finally, the phylogenomic work presented here and from previous phylogenetic studies have relied on foundational taxonomic work on this diverse pantropical plant family (Fries, 1959; Maas, 1983; Chatrou & al., 2012a). A dynamic systematic community focusing on Annonaceae have increased our understanding on the morphological diversity within the family (Le Thomas, 1980, 1981; Van Setten & Koek-Noorman, 1986, 1992; Van Heusden, 1992), allow-

ing for the identification of key characters in delimiting infrafamilial ranks congruent with phylogenomic molecular data. Encouragingly, this community is active and collaborative, with new species continuously being described even in recent times, reflecting ongoing taxonomic work (2022 onwards, e.g., Couvreur & al., 2022; Gosline & al., 2022; Jai-khamseub & al., 2022; Ortiz-Rodríguez, 2022; Bazante & al., 2023; Dagallier & al., 2023; Damthongdee & al., 2023a,b; Leeratiwong & al., 2023; Martínez-Velarde & al., 2023; Ortiz-Rodríguez & Linares, 2023; Page, 2023; Yang & al., 2023; Ferreira & al., 2024; Sathaphorn & al., 2024; Damthongdee & al., in press). Integrating morphological trait information with a phylogenomic framework could provide promising insights into the diversification of Annonaceae (Saunders, 2020; Xue & al., 2020b). We hope the phylogenomic framework presented here will help guide further research and promote interest in this pantropical plant family.

■ TAXONOMY

Below we provide an updated classification of Annonaceae including the description of 21 new subtribes (out of 25 total), arranged in phylogenetic linear sequence. For details of subfamilies and tribes, see Chatrou & al. (2012b), Guo & al. (2017), Couvreur & al. (2019), Chaowasku (2020), Dagallier & al. (2023). In addition, we amend the descriptions of tribes Duguetieae and Xylopieae given the transfer of the genus *Artabotrys* from Xylopieae to Duguetieae. Morphological descriptions are provided for all subtribes.

Fam. **Annonaceae** Juss.

Subfam. **Anaxagoreoideae** Chatrou, Pirie, Erkens & Couvreur – Type: *Anaxagorea* A.St.-Hil.

Included genus. – *Anaxagorea* A.St.-Hil.

Distribution. – Neotropics, Southeast Asia.

Fig. 4C. Phylogeny of Malmeoideae based on concatenated IQ-TREE analysis. Insert in top left represents the Annonaceae phylogeny with the subfamily Malmeoideae highlighted. Different tribes are represented by coloured boxes. 1) *Annickia affinis* (Exell) Versteegh & Sosef; 2) *Greenwayodendron suaveolens* (Engl. & Diels) Verdc.; 3) *Sirdavidia solanona* Couvreur & Sauquet; 4) *Mwasumbia alba* Couvreur & D.M.Johnson; 5) *Piptostigma fugax* A.Chev. ex Hutch. & Dalziel; 6) *Brieya fasciculata* De Wild.; 7) *Polyceratocarpus parviflorus* (Baker f.) Ghesq.; 8) *Pseudoxandra* sp.; 9) *Crematosperma cauliflorum* R.E.Fr.; 10) *Unonopsis* cf. *stipitata* Diels; 11) *Pseudomalmea declina* (R.E.Fr.) Chatrou; 12) *Ruizodendron ovale* (Ruiz & Pav.) R.E.Fr. (Photo: A. Monteagudo); 13) *Ephedranthus amazonicus* R.E.Fr. (Photo: N.C. Bigio); 14) *Oxandra euneura* Diels; 15) *Mosannonna pacifica* Chatrou; 16) *Klarobelia napoensis* Chatrou; 17) *Maasia glauca* (Hassk.) Mols, Kessler & Rogstad (Photo: S. Gardner); 18) *Fenerivia capuronii* (Cavaco & Keraudren) R.M.K.Saunders (Photo: L. Chatrou); 19) *Phoenicanthus coriacea* (Thwaites) H.Huber (Photo: Himesh Dilruwan Jayasinghe©); 20) *Monocarpia maingayi* (Hook.f. & Thomson) I.M.Turner (Photo: S. Gardner); 21) *Dendrokingstonia gardneri* Chaowasku (Photo: S. Gardner); 22) *Orophea* sp. (Photo: S. Gardner); 23) *Pseuduvaria* sp. (Photo: S. Gardner); 24) *Trivalvaria* sp. (Photo: K. Armstrong); 25) *Marsyopetalum crassum* (R. Parker) B.Xue & R.M.K.Saunders (Photo: V. Ramana); 26) *Huberantha tanganyikensis* (Vollesen) Chaowasku; 27) *Neo-uvaria acuminatissima* (Miq.) Airy Shaw (Photo: H. Sauquet); 28) *Monoon coriaceum* (Ridl.) B.Xue & R.M.K.Saunders; 29) *Sageraea elliptica* (A.DC.) Hook.f. & Thomson (Photo: S. Gardner); 30) *Winitia thailandana* Chaowasku & Aongyong (Photo: S. Gardner); 31) *Stelechocarpus burahol* (Blume) Hook.f. & Thomson (Photo: Wendy A. Mustaqim©); 32) *Polyalthia parviflora* Ridl. (Photo: C. Leeratiwong); 33) *Popowia alata* S.K.Ganesan; 34) *Miliusa horsfieldii* (Benn.) Baill. ex Pierre (Photo: S. Gardner); 35) *Phaeanthus ophthalmicus* (Roxb. ex G.Don) J.Sinclair (Photo: P. Bangcaya); 36) *Mitrephora vulpina* C.E.C.Fisch. (Photo: S. Gardner); 37) *Platymitra macrocarpa* Boerl. (Photo: S. Gardner); 38) *Alphonsea kinabaluensis* J.Sinclair; 39) *Meiogyne virgata* (Blume) Miq.; 40) *Desmopsis terriflora* G.E.Schatz, T.Wendt, Ortiz-Rodr. & Mart.-Vel.; 41) *Sapranthus foetidus* (Rose) Saff. (Photo: R. Otero); 42) *Stenanona wendtii* G.E.Schatz & Maas; 43) *Tridimeris huatuscoana* Marinero-Sobal & Ortiz-Rodr. (Photo: E. Marinero Sobal). All photos from Thomas L.P. Couvreur, unless stated otherwise.

Subfam. **Ambavioideae** Chatrou, Pirie, Erkens & Couvreur –
Type: *Ambavia* Le Thomas

Tr. **Canangeae** Chaowasku – Type: *Cananga* (Dunal) Hook.f. & Thomson, nom. cons.

Included genera. – *Cananga* (DC.) Hook.f. & Thomson, *Cyathocalyx* Champ. ex Hook.f. & Thomson, *Drepananthus* Maingay ex Hook.f. & Thomson, *Lettowianthus* Diels.

Distribution. – Southeast Asia, East Africa.

Tr. **Meiocarpidieae** Chatrou, Couvreur & Erkens – Type: *Meiocarpidium* Engl. & Diels.

Included genus. – *Meiocarpidium* Engl. & Diels.

Distribution. – Central Africa.

Tr. **Tetramerantheae** R.E.Fr. ex Reveal – Type: *Tetrameranthus* R.E.Fr.

Included genera. – *Ambavia* Le Thomas, *Cleistopholis* Pierre ex Engl., *Mezzettia* Becc., *Tetrameranthus* R.E.Fr.

Distribution. – Neotropics, central Africa, Madagascar, Southeast Asia.

Subfam. **Annonoideae** Raf. – Type: *Annona* L.

Tr. **Bocageae** Endl. – Type: *Bocagea* A.St.-Hil.

Subtr. **Mkiluinae** D.M.Johnson, N.A.Murray, J.C.Lopes & Couvreur, **subtr. nov.** – Type: *Mkilua* Verdc.

Description. – Trees; indument of simple hairs; inflorescences internodal, terminal; flowers bisexual; sepals three, abscising after anthesis; petals six, in two whorls, free; stamens numerous, connective apex truncate; carpels numerous, free, ovules several per carpel, lateral, stigma articulated; fruits apocarpous, monocarps dehiscent, sessile; seeds several with caruncle. Pollen units compound, tetrads.

Included genus. – *Mkilua* Verdc.

Distribution. – Tropical East Africa.

Subtr. **Cardiopetalinae** D.M.Johnson, N.A.Murray, J.C.Lopes & Couvreur, **subtr. nov.** – Type: *Cardiopetalum* Schldl.

Description. – Trees; indument of simple hairs; inflorescences internodal, terminal; flowers bisexual; sepals three, abscising after anthesis; specialised beetle-feeding tissue at margin of petals; petals six, in two whorls, free or more rarely fused; stamens numerous, connective apex truncate; carpels numerous, stigma articulated, ovules numerous per carpel, lateral; fruit apocarpous, monocarps indehiscent or dehiscent; stipitate or sessile; seeds several, with aril, caruncle, or hairy seed coat. Pollen units compound, polyads of 8, 16, or 32.

Included genera. – *Cardiopetalum* Schldl., *Cymbopetalum* Benth., *Froesiodendron* R.E.Fr., *Porcelia* Ruiz & Pav.

Distribution. – Neotropics.

Subtr. **Bocageinae** D.M.Johnson, N.A.Murray, J.C.Lopes & Couvreur, **subtr. nov.** – Type: *Bocagea* A.St.-Hil.

Description. – Trees; indument of simple hairs; inflorescences internodal, terminal; flowers bisexual; sepals three; petals six, in two whorls, free; stamens few, rarely numerous; connective apex elongate, pointed; carpels several, free, stigma unarticulated, ovules numerous per carpel, lateral; fruit apocarpous, monocarps indehiscent, stipitate or sessile; seeds one to several, carunculate. Pollen units compound, polyads of 4, 8, or 16.

Included genera. – *Bocagea* A.St.-Hil., *Hornschuchia* Nees, *Trigynaea* Schldl.

Distribution. – Neotropics.

Tr. **Xylopieae** Endl., **emend.** D.M.Johnson & N.A.Murray – Type: *Xylopia* L., nom. cons.

Description. – Trees and shrubs, rarely scandent; indument of simple hairs; inflorescences axillary; flowers bisexual; sepals three; petals six, in two whorls, free; stamens numerous; carpels one to numerous, ovules several per carpel, lateral; fruit apocarpous, monocarps abaxially dehiscent, stipitate or rarely sessile; seeds several, aril present or absent, sarcotesta present or absent. Pollen units compound.

Included genus. – *Xylopia*.

Distribution. – Pantropical.

Tr. **Duguetieae** Chatrou & R.M.K.Saunders, **descr. emend.** Chatrou & Couvreur – Type: *Duguetia* A.St.-Hil., nom. cons.

Description. – Trees, shrubs or lianas; indument of lepidote, stellate and/or simple hairs; inflorescences axillary or terminal; flowers bisexual; sepals three, sometimes fused into a single unit, tearing at anthesis; petals six, in two whorls, free or more rarely fused; stamens numerous, staminodes sometimes present; carpels numerous, free, ovule(s) one or two per carpel, basal; fruit apocarpous or syncarpous, monocarps indehiscent, sessile; seed(s) one or two. Pollen units simple or compound.

Included genera. – *Artabotrys* R.Br., *Duckeanthus* R.E.Fr., *Duguetia* A.St.-Hil., *Fusaea* (Baill.) Saff., *Letestudoxa* Pellegr., *Pseudartabotrys* Pellegr.

Distribution. – Pantropical.

Subtr. **Duguetiinae** Chatrou & Couvreur, **subtr. nov.** – Type: *Duguetia* A.St.-Hil.

Description. – Trees; indument of lepidote, stellate and/or simple hairs; inflorescences axillary or terminal; flowers bisexual; sepals three; petals six, in two whorls, free or rarely fused; stamens numerous, staminodes sometimes present; carpels numerous, free, ovule one per carpel, basal; fruit apocarpous or syncarpous, monocarps indehiscent, sessile; seed one. Pollen units simple or compound.

Included genera. – *Duckeanthus* R.E.Fr., *Duguetia* A.St.-Hil., *Fusaea* (Baill.) Saff.

Distribution. – Neotropics and Central Africa.

Subtr. **Artabotrydinae** Chatrou & Couvreur, **subtr. nov.** – Type: *Artabotrys* R.Br.

Description. – Lianas; indument of simple hairs; inflorescences terminal; flowers bisexual; sepals three, sometimes fused into a single unit, tearing at anthesis; petals six, in two whorls, free; stamens numerous; carpels numerous, free, ovule(s) one or two per carpel, basal; fruit apocarpous or syncarpous, monocarps indehiscent, stipitate or sessile; seed(s) one or two. Pollen units simple.

Included genera. – *Artabotrys* R.Br., *Letestudoxa* Pellegr., *Pseudartabotrys* Pellegr.

Distribution. – Tropical Africa, Madagascar, tropical Asia and Australia.

Tr. **Guatterieae** Hook.f. & Thomson – Type: *Guatteria* Ruiz & Pav., nom. cons.

Included genus. – *Guatteria* Ruiz & Pav.

Distribution. – Neotropics.

Tr. **Annoneae** Endl. – Type: *Annona* L.

Subtr. **Anonidiinae** Couvreur, **subtr. nov.** – Type: *Anonidium* Engl. & Diels.

Description. – Trees to scandent shrubs; indument of simple hairs; inflorescences terminal; flowers bisexual or plants (andro)dioecious; sepals three; petals six, in two whorls, free; stamens numerous; carpels numerous, free, ovule one per carpel, basal; fruits apocarpous or syncarpous, monocarps indehiscent, sessile or stipitate; seed one. Pollen units compound.

Included genera. – *Anonidium* Engl. & Diels, *Neostenanthera* Exell.

Distribution. – Tropical west and central Africa.

Subtr. **Annoninae** Hutch., **emend.** Couvreur – Type: *Annona* L.

Description. – Trees, rarely lianas; indument of simple hairs; inflorescences terminal or axillary; flowers bisexual or plants (andro)dioecious; sepals three, rarely two, petal number and whorls variable, from two whorls of three, one whorl of three, or petals fused with several lobes; stamens numerous, lateral; carpels numerous, free; ovule(s) one to several per carpel, basal, to numerous and lateral; fruits apocarpous or syncarpous, monocarps indehiscent; sessile or stipitate; seed one. Pollen units simple or compound.

Included genera. – *Annona* L., *Asimina* Adans., *Diclinanona* Diels, *Disepalum* Hook.f., *Goniothalamus* (Blume) Hook.f. & Thomson, nom. cons.

Distribution. – Neotropics, tropical Africa, east North America, tropical Asia and Australia.

Tr. **Monodoreae** Baill. – Type: *Monodora* Dunal.

Subtr. **Uvariopsidinae** Couvreur & Dagallier, **subtr. nov.** – Type: *Uvariopsis* Engl.

Description. – Trees; indument of simple hairs; leaves generally with conspicuous fine quaternary reticulate venation; inflorescences axillary, rarely terminal; flowers bisexual or unisexual (plants monoecious); sepals two or three; petals

in two whorls of six, free, or one whorl of four or three petals, free or fused; stamens numerous; carpels numerous, free, ovules several per carpel, lateral; fruit apocarpous, monocarps indehiscent, sessile; seeds several. Pollen units compound.

Included genera. – *Dennettia* Baker f., *Lukea* Cheek & Gosline, *Mischogyne* Exell, *Monocyclanthus* Keay, *Uvarioidendron* (Engl. & Diels) R.E.Fr., *Uvariopsis* Engl.

Distribution. – Tropical Africa.

Subtr. **Monodorinae** Couvreur & Dagallier, **subtr. nov.** – Type: *Monodora* Dunal.

Description. – Trees, rarely lianas; indument of simple hairs; leaves without conspicuous fine quaternary reticulate venation; inflorescences axillary or terminal; flowers bisexual; sepals three; petals six, in one whorl, fused; stamens numerous; carpels numerous, fused (true syncarpy), ovules several per carpel, lateral; fruit syncarpous, indehiscent; seeds several. Pollen units simple or compound.

Included genera. – *Isolona* Engl., *Monodora* Dunal.

Distribution. – Tropical Africa and Madagascar.

Subtr. **Hexalobinae** Couvreur & Dagallier, **subtr. nov.** – Type: *Hexalobus* A.DC.

Description. – Trees; indument of simple hairs; leaves without conspicuous fine quaternary reticulate venation; inflorescences axillary or terminal; flowers bisexual; sepals three; petals in one whorl of six, fused or two whorls of three, free; stamens numerous; carpels one to numerous, ovules several per carpel, lateral; fruit apocarpous, monocarps indehiscent, sessile; seeds numerous. Pollen units compound.

Included genera. – *Asteranthe* Engl. & Diels, *Hexalobus* A.DC., *Uvariastrum* Engl. & Diels.

Distribution. – Tropical Africa.

Tr. **Ophrypetaleae** Dagallier & Couvreur – Type: *Ophrypetalum* Diels.

Included genera. – *Ophrypetalum* Diels, *Sanrafaelia* Verdc.

Distribution. – Tropical East Africa.

Tr. **Uvarieae** Hook.f. & Thomson – Type: *Uvaria* L.

Subtr. **Uvariinae** Baill., **descr. emend.** Couvreur – Type: *Uvaria* L.

Description. – Lianas, scandent shrubs or rarely trees; leaves concolorous; indument of stellate, fasciculate or rarely simple hairs; inflorescences terminal rarely axillary; flowers bisexual; sepals three, sometimes fused into a single unit, tearing at anthesis; petals six, in two whorls, free; stamens numerous, connective apex truncate, elongate, or conical; carpels one to numerous, free, ovules several per carpel, lateral; fruit apocarpous, monocarps indehiscent, stipitate or sessile; seeds one to several. Pollen units simple.

Included genera. – *Dielsiothammus* R.E.Fr., *Uvaria* L.

Distribution. – Tropical Africa, Madagascar, tropical Asia, Australia.

Subtr. **Cleistochlamydinae** Couvreur, **subtr. nov.** – Type: *Cleistochlamys* Oliv.

Description. – Lianas, rarely trees; indument of simple hairs; leaves discolorous, ± glaucous on lower surface or not, inflorescences axillary or terminal; flowers bisexual; sepals three; petals six, in two whorls of three petals, or more rarely in three whorls with 6 to 12 petals, free; stamens numerous; carpels numerous, free, ovules one to several per carpel, basal to lateral; fruit apocarpous, monocarps indehiscent, stipitate or sessile; seeds one to several. Pollen units simple.

Included genera. – *Afroguatteria* Boutique, *Cleistochlamys* Oliv., *Sphaerocoryne* (Boerl.) Scheff. ex Ridl., *Toussaintia* Boutique.

Distribution. – Tropical Africa, Madagascar, tropical Asia.

Subtr. **Fissistigmatinae** Chaowasku & Damth., **subtr. nov.** – Type: *Fissistigma* Griff.

Description. – Lianas; indument of simple hairs; leaves somewhat discolorous, ± glaucous on lower surface, inflorescences axillary or terminal; flowers bisexual; sepals three; petals six, in two whorls, free; stamens numerous; carpels several to numerous, free, ovules several to numerous per carpel, lateral; fruit apocarpous, monocarps indehiscent, stipitate; seeds few to numerous. Pollen units simple.

Included genera. – *Fissistigma* Griff., *Pyramidanthe* Miq. (including *Mitrella* Miq.).

Distribution. – Tropical Asia, Australia.

Subtr. **Desminae** Chaowasku & Damth., **subtr. nov.** – Type: *Desmos* Lour.

Description. – Lianas, sometimes trees or shrubs; indument of simple hairs; leaves discolorous, glaucous on lower surface, often with a pair of gland-like structures at base of leaf blade; inflorescences axillary or terminal; flowers bisexual, rarely unisexual (plants monoecious or dioecious); sepals three, sometimes two; petals six, in two whorls, rarely three to six in one whorl; stamens few to numerous, staminodes sometimes present; carpels one to numerous, free, ovule(s) one to numerous per carpel, basal to lateral; fruit apocarpous, monocarps indehiscent, stipitate, rarely sessile; seeds one to numerous. Pollen units simple.

Included genera. – *Dasymaschalon* (Hook.f. & Thomson) Dalla Torre & Harms, nom. cons., *Desmos* Lour., *Friesodielsia* Steenis, nom. cons., *Monanthotaxis* Baill.

Distribution. – Tropical Africa, Madagascar, tropical Asia and Australia.

Subfam. **Malmeoideae** Chatrou, Pirie, Erkens & Couvreur – Type: *Malmea* R.E.Fr.

Tr. **Annickieae** Couvreur – Type: *Annickia* Setten & Maas.

Included genus. – *Annickia* Setten & Maas.

Distribution. – Tropical Africa.

Tr. **Piptostigmatae** Chatrou & R.M.K.Saunders – Type: *Piptostigma* Oliv.

Included genera. – *Brieya* De Wild., *Greenwayodendron* Verdc., *Mwasumbia* Couvreur & D.M.Johnson, *Piptostigma* Oliv., *Polyceratocarpus* Engl. & Diels, *Sirdavidia* Couvreur & Sauquet.

Distribution. – Tropical Africa.

Tr. **Dendrokingstonieae** Chatrou & R.M.K.Saunders – Type: *Dendrokingstonia* Rauschert.

Included genus. – *Dendrokingstonia* Rauschert.

Distribution. – Tropical East Asia.

Tr. **Fenerivieae** Chatrou & R.M.K.Saunders – Type: *Fenerivia* Diels.

Included genus. – *Fenerivia* Diels.

Distribution. – Madagascar.

Tr. **Maasiae** Chatrou & R.M.K.Saunders – Type: *Maasia* Mols, Kessler & Rogstad.

Included genus. – *Maasia* Mols, Kessler & Rogstad.

Distribution. – Southeast Asia.

Tr. **Malmecae** Chatrou & R.M.K.Saunders – Type: *Malmea* R.E.Fr.

Subtr. **Malmeinae** Chatrou & Couvreur, **subtr. nov.** – Type: *Malmea* R.E.Fr.

Description. – Trees; indument of simple hairs; primary vein raised on the upper side of leaves; inflorescences axillary or terminal; flowers bisexual, or plants androdioecious; sepals three; petals six, in two whorls, free; stamens numerous; carpels numerous, free; ovule one per carpel, basal; fruit apocarpous, monocarps indehiscent, stipitate or sessile; seed one. Pollen units simple or compound.

Included genera. – *Crematosperma* R.E.Fr., *Malmea* R.E.Fr., *Pseudoxandra* R.E.Fr.

Distribution. – Central and South America.

Subtr. **Unonopsidinae** Chatrou & Couvreur, **subtr. nov.** – Type: *Unonopsis* R.E.Fr.

Description. – Trees; indument of simple hairs; primary vein raised on the upper side of leaves; inflorescences axillary, rarely terminal; flowers bisexual; sepals three; petals six, in two whorls, free; stamens numerous; carpels numerous, free, ovule one per carpel, basal; fruit apocarpous, monocarps indehiscent, stipitate or sessile; seed one. Pollen units simple.

Included genera. – *Bocageopsis* R.E.Fr., *Onychopetalum* R.E.Fr., *Unonopsis* R.E.Fr.

Distribution. – South America.

Subtr. **Oxandrinae** Chatrou & Couvreur, **subtr. nov.** – Type: *Oxandra* A.Rich.

Description. – Trees; indument of simple hairs; primary vein sunken, or raised on the upper side of leaves; inflorescences axillary, rarely terminal; flowers bisexual or plants

androdioecious; sepals three; petals six, in two whorls, free; stamens numerous; carpels numerous, free, ovule one per carpel, basal; fruit apocarpous, monocarps indehiscent, stipitate or sessile; seed one. Pollen units simple.

Included genera. – *Ephedranthus* S.Moore, *Klarobelia* Chatrou, *Mosannonna* Chatrou, *Oxandra* A.Rich., *Pseudephedranthus* Aristeg., *Pseudomalmea* Chatrou, *Ruizodendron* R.E.Fr.

Distribution. – Central and South America.

Note. – The genus *Oxandra* as currently accepted is not monophyletic.

Tr. **Miliuseae** Hook.f. & Thomson – Type: *Miliusa* Lesch. ex A.DC.

Subtr. **Sapranthinae** Ortiz-Rodr., Ruiz-Sanchez & Ornelas, **descr. emend.** Ortiz-Rodr. – Type: *Sapranthus* Seem.

Description. – Trees; indument of simple hairs; inflorescences axillary or terminal; flowers bisexual; sepals two, three or four, free or fused; petals four, six or eight, in two whorls, free or fused; stamens numerous, connective apex \pm truncate and covering thecae, rarely much reduced and not covering thecae; carpels one to several, free; ovule(s) one to several per carpel, sub-basal or lateral; fruit apocarpous, monocarps indehiscent, sessile to stipitate; seeds one to several. Pollen units simple.

Included genera. – *Desmopsis* Saff. (including *Stenanona* Standl.), *Meiogyne* Miq., nom. cons., *Sapranthus* Seem., *Tridimeris* Baill., *Wuodendron* B.Xue, Y.H.Tan & Chaowasku.

Distribution. – Tropical Asia, Oceania, Central and South America.

Subtr. **Polyalthiopsidinae** Chaowasku & D.C.Thomas, **subtr. nov.** – Type: *Polyalthiopsis* Chaowasku.

Description. – Trees; indument of simple hairs; inflorescences axillary; flowers bisexual; sepals three; petals six, in two whorls, free; stamens numerous, connective apex \pm truncate and covering thecae; carpels several to numerous, free; ovule(s) one or two per carpel, sub-basal or lateral; fruit apocarpous, monocarps indehiscent, stipitate; seeds one or two. Pollen units simple.

Included genus. – *Polyalthiopsis* Chaowasku.

Distribution. – Tropical Asia.

Subtr. **Phaeanthinae** Benth. & Hook.f., **descr. emend.** Chaowasku & D.C.Thomas – Type: *Phaeanthus* Hook.f. & Thomson.

Description. – Treelets or trees; indument of simple hairs; inflorescences axillary or terminal; flowers bisexual, rarely polygamous (plants androdioecious); sepals three; petals six, in two whorls, free; stamens few to numerous, connective apex \pm truncate and covering thecae or much reduced (sometimes seemingly absent) and not covering thecae; carpels one to numerous, free, ovule(s) one to numerous per carpel, basal to lateral; fruit apocarpous, monocarps indehiscent, sessile to stipitate; seeds one to numerous. Pollen units simple or compound.

Included genera. – *Alphonsea* Hook.f. & Thomson, *Miliusa* Lesch. ex A.DC., *Mitrephora* Hook.f. & Thomson, *Phaeanthus* Hook.f., *Platymitra* Boerl., *Wangia* X.Guo & R.M.K.Saunders.

Distribution. – Tropical Asia and Australia.

Subtr. **Popowiinae** Chaowasku & D.C.Thomas, **subtr. nov.** – Type: *Popowia* Endl.

Description. – Shrubs, treelets or trees; indument of simple hairs; inflorescences axillary or terminal; flowers bisexual; sepals three; petals six, in two whorls, free or basally fused; stamens numerous, connective apex \pm truncate and covering thecae; carpels one to numerous, free, ovule(s) one to several per carpel, basal to lateral; fruit apocarpous, monocarps indehiscent, sessile to stipitate; seeds one to several. Pollen units simple.

Included genera. – *Polyalthia* Blume, *Popowia* Endl.

Distribution. – Tropical Asia and Oceania.

Subtr. **Winitinae** Wiya & Chaowasku, **subtr. nov.** – Type: *Winitia* Chaowasku.

Description. – Trees; indument of simple hairs; inflorescences axillary, but often appearing as cauliflorous; flowers bisexual or unisexual (plants monoecious); sepals three; petals six, in two whorls, free, \pm carnosose; stamens numerous, connective apex \pm truncate, \pm rounded or \pm reduced, not or (partially) covering thecae; carpels numerous, free; ovules several to numerous per carpel, lateral; fruit apocarpous, monocarps indehiscent, (sub)sessile; seeds few to numerous. Pollen units simple.

Included genera. – *Sageraea* Dalzell, *Stelechocarpus* Hook.f. & Thomson, *Winitia* Chaowasku.

Distribution. – Tropical Asia.

Subtr. **Huberanthinae** Chaowasku & D.C.Thomas, **subtr. nov.** – Type: *Huberantha* Chaowasku.

Description. – Treelets or trees; indument of simple hairs; frequent presence of hairy domatia in the axils of primary and secondary veins; inflorescences axillary; flowers bisexual; sepals three; petals six, in two whorls, free; stamens numerous, connective apex \pm truncate and covering thecae; carpels numerous, free; ovule one per carpel, sub-basal; fruit apocarpous, monocarps indehiscent, stipitate, rarely (sub)sessile; seed one. Pollen units simple.

Included genus. – *Huberantha* Chaowasku.

Distribution. – Tropical Asia, Oceania, Madagascar and tropical Africa.

Subtr. **Neo-uvariinae** Chaowasku & D.C.Thomas, **subtr. nov.** – Type: *Neo-uvaria* Airy Shaw.

Description. – Trees, rarely treelets; indument of simple hairs or simple hairs intermixed with stellate hairs; inflorescences axillary; flowers bisexual; sepals three; petals six, in two whorls, free or more rarely fused, sometimes carnosose; stamens numerous, connective apex \pm truncate and (partially) covering thecae; carpels several to numerous, free; ovule(s)

one or more rarely two per carpel, basal; fruit apocarpous, monocarps indehiscent, sessile to stipitate; seed one. Pollen units simple.

Included genera. – *Monoon* Miq., *Neo-uvaria* Airy Shaw.

Distribution. – Tropical Asia and Oceania.

Subtr. **Oropheinae** Chaowasku & D.C.Thomas, **subtr. nov.** –

Type: *Orophea* Blume.

Description. – Treelets or trees; indument of simple hairs; inflorescences axillary or terminal; flowers bisexual, unisexual (plants monoecious or dioecious) or polygamous (plants andromonoecious or androdioecious); sepals three; petals six, in two whorls, free, sometimes carnosely; stamens few to numerous, connective apex \pm truncate and covering thecae or much reduced (sometimes seemingly absent) and not covering thecae, sometimes staminodes present; carpels few to numerous, free; ovule(s) one to numerous per carpel, basal to lateral; fruit apocarpous, monocarps indehiscent, sessile to stipitate; seeds one to numerous. Pollen units simple or compound.

Included genera. – *Marsypopetalum* Scheff., *Orophea* Blume, *Pseuduvaria* Miq., *Trivalvaria* (Miq.) Miq.

Distribution. – Tropical Asia and Australia.

Tr. **Monocarpieae** Chatrou & R.M.K.Saunders – Type: *Monocarpia* Miq.

Included genera. – *Monocarpia* Miq., *Leoheo* Chaowasku.

Distribution. – Southeast Asia.

Tr. **Phoenicantheae** X.Guo & R.M.K.Saunders – Type: *Phoenicanthus* Alston.

Included genus. – *Phoenicanthus* Alston.

Distribution. – Southeast Asia.

■ AUTHOR CONTRIBUTIONS

FJN and TLPC conceptualised the ideas and designed the study. All co-authors contributed samples. VRCS, CRV and FJN gathered and analysed the data, FJN and TLPC wrote the manuscript with contributions from all co-authors. All authors reviewed the results and approved the final version of the manuscript.

■ ACKNOWLEDGEMENTS

This project has received funding from the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation program (GLOBAL project; grant agreement No. 865787) to TLPC. The National Parks Board Singapore supported sequencing of Annonaceae subfamily Malmeoideae samples provided by DCT at the Singapore Botanic Gardens. The Jason Swallen Herbarium fund of Ohio Wesleyan University supported DMJ and NAM. JCL was supported by a Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP) postdoctoral fellowship (2018/11272-5; 2022/08659-0). We acknowledge the ISO 9001 certified IRD i-Trop HPC (South Green Platform) at IRD Montpellier for providing HPC resources that have contributed to the phylogenetic results reported within this paper. Finally, we

thank Paul Maas, Mike Pirie and two anonymous reviewers for helpful comments on a previous version of this article.

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Appendix 1. The list of accessions used for the MIL-dataset in this study is presented as follows: Species name and authority, unique sample identifier (TC-S number), collection locality (country), collector and collection number, herbarium code for where the sampled specimens are stored, and sequence ID corresponding with sequences uploaded onto SRA. Newly generated sequences for this study are marked with an asterisk (*). A dash (–) indicates information that was unavailable. The paired fastq sequences included in this study are available in Genbank SRA under Bioproject number PRJNA508895 (<https://www.ncbi.nlm.nih.gov/bioproject/508895>).

Alphonsea kinabaluensis J.Sinclair, TC-S1203, Malaysia, *Couvreur, T.L.P. 820* (P), RUN62_I10_T61; *Alphonsea maingayi** Hook.f. & Thomson, –, Singapore, *Thomas, D. 3475* (SING), D558; *Alphonsea mollis** Dunn, –, cultivated at XTBG China, *Xue 173* (IBSC), D537; *Annickia pilosa* (Exell) Setten & Maas, TC-S0582, Gabon, *Couvreur, T.L.P. 866* (WAG), RUN62_I6_T30; *Dendrokingstonia gardneri** Chaowasku, –, Thailand, *Gandne Sidisumthom ST2214* (L), D535; *Dendrokingstonia nervosa** (Hook.f. & Thomson) Rauschert, –, cultivated at SBG Singapore, *Chen Koh 73* (SING), D505; *Desmopsis heteropetala* R.E.Fr., TC-S1109, Costa Rica, *Chatrou, L.W. 45* (U), RUN62_I10_T29; *Desmopsis verrucipes** Chatrou, G.E.Schatz & N.Zamora, –, Costa Rica, *Chatrou, L.W. 102* (IBSC), D550; *Fenerivia capuronii** (Cavaco & Keraudren) R.M.K.Saunders, –, Madagascar, *Chatrou, L.W. 667* (WAG), D533; *Fenerivia ghesquiereana** (Cavaco & Keraudren) R.M.K.Saunders, –, Madagascar, *Schatz & al. 3611* (MO), D534; *Huberantha decora** (Diels) Chaowasku, TC-S3634, Madagascar, *Razanatsima, A. 1453* (P), RUN101AN_I6_T79; *Huberantha hirta** (Miq.) Chaowasku, –, Papua New Guinea, *Thomas 2117* (SING), D584; *Huberantha jenkinsii** (Hook.f. & Thomson) Chaowasku, –, Thailand, *Chaowasku 60* (L), D538; *Huberantha rumphii** (Blume ex Hensch.) Chaowasku, –, Singapore, SING2022_233 (SING), D595; *Huberantha tanganyikensis** (Vollesen) Chaowasku, TC-S1211, Tanzania, *Couvreur, T.L.P. 66* (WAG), RUN101AN_I1_T9; *Klarobelia cauliflora** Chatrou, –, Peru, *Chatrou, L.W. 161* (U), D559; *Leoheo domatiophorus** Chaowasku, D.T.Ngo & Hung T.Le, –,

Appendix 1. Continued.

Vietnam, *Chaowasku 16* (CMUB), D549; *Maasia glauca** (Hassk.) Mols, Kessler & Rogstad, –, Singapore, *Thomas, D. 3435* (SING), D510; *Maasia hypoleuca** (Hook.f. & Thomson) Mols, Kessler & Rogstad, –, Singapore, BTJFS_T29T33 (SING), D511; *Malmia dielsiana** R.E.Fr., –, Peru, *Chatrou, L.W. 122* (U), D582; *Marsypopetalum littorale** (Blume) B.Xue & R.M.K.Saunders, –, cultivated at XTBG China, *Thomas, D. 12666* (SING), D518; *Meiogyne cylindrocarpa** (Burck) Heusden, –, cultivated at SBG Singapore, *Thomas, D. 3418* (SING), D501; *Meiogyne dumetosa** (Vieill. ex Guillaumin) Heusden, –, New Caledonia, *Mackee 196* (L), D542; *Meiogyne virgata** (Blume) Miq., –, Singapore, *Thomas, D. 3456* (SING), D513; *Miliusa brahei** (F.Muell.) Jessup, –, Australia, *Sankowsky Arb. 150* (CNS), D540; *Miliusa horsfieldii** (Benn.) Baill. ex Pierre, –, cultivated at XTBG China, *Xue 165* (IBSC), D574; *Miliusa thorelli** Fin. & Gagnep., –, cultivated at XTBG China, *Xue 180* (IBSC), D573; *Miliusa umpangensis** Chaowasku & Kessler, –, Thailand, *Chaowasku 89* (L), D539; *Mitrephora teysmannii** Scheff., –, Singapore, *Thomas, D. 3406* (SING), D507; *Mitrephora tomentosa** Hook.f. & Thomson, –, cultivated at XTBG, *Xue 182* (IBSC), D541; *Monocarpia kalimantanensis* Kessler, TC-S1168, Malaysia, *Couvreur, T.L.P. 831* (P), RUN62_110_T50; *Monocarpia maingayi** (Hook.f. & Thomson) I.M.Turner, –, Singapore, *Thomas, D. 3445* (SING), D506; *Monoon borneense** (H.Okada) B.Xue & R.M.K.Saunders, –, Singapore, *Thomas, D. 3431* (SING), D515; *Monoon erianthoides* (Airy Shaw) B.Xue & R.M.K.Saunders, TC-S1170, Malaysia, *Couvreur, T.L.P. 835* (L), RUN62_110_T51; *Monoon hookerianum** (King) B.Xue & R.M.K.Saunders, –, cultivated at SBG Singapore, *Thomas, D. 3409* (SING), D502; *Monoon lateriflorum** (Blume) Miq., –, Singapore, *Thomas, D. 3433* (SING), D514; *Monoon laui** (Merr.) B.Xue & R.M.K.Saunders, –, cultivated at SCBG China, *Xue, s.n.* (SING), D578; *Monoon longifolium** (Sonn.) B.Xue & R.M.K.Saunders, –, cultivated at SBG Singapore, *Thomas, D. 3434* (SING), D503; *Monoon sclerophyllum** (Hook.f. & Thomson) B.Xue & R.M.K.Saunders, –, cultivated at SBG Singapore, *Thomas, D. 1011* (SING), D520; *Neo-uvaria acuminatissima* (Miq.) Airy Shaw, TC-S1198, Malaysia, *Sauquet, H. 186* (P), RUN62_110_T58; *Neo-uvaria sparsistellata** Chaowasku, –, Thailand, *Chaowasku 99* (CMUB), D543; *Orophea maculata** (Merr.) Y.C.F.Su & R.M.K.Saunders, –, cultivated at SBG Singapore, *Thomas, D. 3417* (SING), D504; *Orophea myriantha* Merr., TC-S1163, Malaysia, *Onstein, R.E. 48* (P), RUN62_110_T48; *Phaeanthus intermedius** (P.Parm.) I.M.Turner & Veldkamp, –, Singapore, *Thomas, D. 3419* (SING), D508; *Phaeanthus splendens* Miq., TC-S1195, Malaysia, *Onstein, R.E. 73* (P), RUN62_110_T57; *Phoenicanthus obliquus** (Hook.f. & Thomson) Alston, –, Sri Lanka, *Huber 577* (WAG), D604; *Platymitra arborea** (Blanco) Kessler, TC-S4756, Philippines, *Merill, E.D. 2062* (NY), RUN104_I9_T28; *Platymitra macrocarpa** Boerl., –, Thailand, *Chaowasku 100* (CMUB), D569; *Platymitra siamensis** Craib, TC-S6752, Thailand, *Chaowasku 202* (CMUB), RUN107_I5_T39; *Polyalthia angustissima** Ridl., –, Singapore, *Thomas, D. 3407* (SING), D516; *Polyalthia cauliflora** Hook.f. & Thomson, –, Singapore, *Thomas, D. 3473* (SING), D557; *Polyalthia insignis* (Hook.f.) Airy Shaw, TC-S1162, Malaysia, *Onstein, R.E. 47* (P), RUN62_110_T47; *Polyalthia suberosa** (Roxb.) Thwaites, –, cultivated at XTBG China, *Thomas, D. 12651* (SING), D521; *Polyalthiopsis floribunda** (Jovet-Ast) Chaowasku, –, *Chaowasku s.n.*, Vietnam (CMUB), D536; *Polyalthiopsis verrucipes** (C.Y.Wu ex P.T.Li) B.Xue & Y.H.Tan, –, China, *Xue 1P7* (IBSC), D572; *Popowia alata* S.K.Ganesan, TC-S1189, Malaysia, *Sauquet, H. 180* (P), RUN62_110_T55; *Popowia fusca** King, –, Singapore, *Thomas, D. 3426* (SING), D522; *Popowia piscocarpa** (Blume) Endl. ex Walp., –, Singapore, *Thomas, D. 3427* (SING), D523; *Popowia tomentosa** Maingay ex Hook.f. & Thomson, –, Singapore, *Thomas, D. 3477* (SING), D598; *Pseuduvaria froggattii** (F.Muell.) Jessup, –, cultivated at SBG Singapore, *Thomas, D. 3414* (SING), D524; *Pseuduvaria novaguineensis** J.Sinclair, –, Papua New Guinea, *Thomas, D. 2153b* (SING), D591; *Pseuduvaria trimera** (Craib) Y.C.F.Su & R.M.K.Saunders, –, China, *Thomas 12_652* (HKU), D526; *Sageraea lanceolata* Miq., TC-S1192, Malaysia, *Onstein, R.E. 63* (P), RUN62_110_T56; *Sapranthus microcarpus** (Donn.Sm.) R.E. Fr., –, Honduras, *Maas & al. 8457* (U), D544; *Sapranthus viridiflorus* G.E.Schatz, TC-S1099, Costa Rica, *Maas, P.J.M. 9402* (U), RUN62_110_T24; *Stelecho-carpus burahol** (Blume) Hook.f. & Thomson, –, cultivated at SBG Singapore, *Thomas, D. 3446* (SING), D527; *Stenanona costaricensis** R.E.Fr., –, Costa Rica, *Chatrou, L.W. & al. 67* (U), D552; *Stenanona humilis* (Miranda) G.E.Schatz ex Maas, E.A.Mennega & Westra, TC-S1101, Mexico, *Ishiki Ishihara, M. 2233* (U), RUN62_110_T26; *Stenanona panamensis** Standl., –, Costa Rica, *Chatrou, L.W. 100* (U), D551; *Tridimeris chiapensis* M.A.Escobar & Ortiz-Rodr., TC-S2734, Mexico, *Gómez Dominguez, H. 3862* (MEXU), RUN89_I3_T15; *Tridimeris nebulosa* (Baillon) Ortiz-Rodr. & Hurtado-Reveles, TC-S2203, Mexico, *Schatz, G.E. 1198* (MO), RUN88_I9_T91; *Trivalvaria costata** (Hook.f. & Thomson) I.M.Turner, –, cultivated at XTBG China, *Wong 805* (HKU), D545; *Trivalvaria dubia** (Kurz) J.Sinclair, –, Thailand, *Chaowasku 35* (L), D570; *Wangia saccopetaloides** (W.T.Wang) X.Guo & R.M.K.Saunders, –, China, *Tan, D. 422* (HKU), D546; *Winitia thailandana** Chaowasku & Aongyong, –, Thailand, *Chaowasku 51* (CMUB), D571; *Wuodendron praecox** (Hook.f. & Thomson) B.Xue, Y.H.Tan & X.L.Hou, –, Thailand, *Chaowasku 108* (CMUB), D547.

Appendix 2. The list of accessions used for the GEN-dataset (genus-level) in this study is presented as follows: Species name and authority, unique sample identifier (TC-S number), collection locality (country), collector and collection number, herbarium code for where the sampled specimens are stored, and sequence ID corresponding with sequences uploaded onto SRA. Newly generated sequences for this study are marked with an asterisk (*). Genera with type species sampled for this study are marked with “^”. The paired fastq sequences included in this study are available in Genbank SRA under Bioproject number PRJNA508895 (<https://www.ncbi.nlm.nih.gov/bioproject/508895>).

*Afroguatteria globosa**^ C.N.Paiva, TC-S2027, Gabon, *Sosef, M.S.M. 2091* (WAG), RUN89_I7_T25; *Alphonsea gaudichaudiana* (Baill.) Finet & Gagnep., TC-S4026, Lao People's Democratic Republic, *Newman, M.F. 344* (L), RUN102_I9_T20; *Ambavia capuronii**^ (Cavaco & Keraudren) Le Thomas, TC-S3619, Madagascar, *Trigui, S.M. 519* (P), RUN100b_I12_T47; *Anaxagorea prinooides** (Dunal) A.St.-Hil. ex A.DC., TC-S3908, Brazil, *Sperling, C.R. 6078* (U), RUN102_I8_T84; *Annickia chlorantha** (Oliv.) Setten & Maas, TC-S0007, Cameroon, *Couvreur, T.L.P. 414* (MPU), RUN62_I6_T7; *Annona muricata** L., TC-S1913, The Netherlands, *Chatrou, L.W. 468* (U), RUN89_I2_T87; *Anonidium lesteui* Pellegr., TC-S2039, Gabon, *Sosef, M.S.M. 1899* (WAG), RUN100b_I06_T59; *Artobotrys stolzii* Diels, TC-S2011, Tanzania, *Couvreur, T.L.P. 72* (WAG), RUN89_I7_T17; *Asimina triloba**^ (L.) Dunal, TC-S3108, United States of America, *Mercier, K.D. 154* (NY), RUN100b_I06_T74; *Asteranthus asterias** (S.Moore) Engl. & Diels, TC-S1585, Tanzania, *Dagallier, L.-P.M.J. 53* (MPU), RUN79_I2_T61; *Bocagea longepedunculata** Mart., TC-S3431, Brazil, *Demuner, V. 4181* (U), RUN100b_I08_T33; *Bocageopsis multiflora**^ (Mart.) R.E.Fr., TC-S2548, Bolivia, *Chatrou, L.W. 357* (L), RUN100b_I05_T50; *Brieya fasciculata** De Wild., TC-S0298, Gabon, *Couvreur, T.L.P. 578* (WAG), RUN62_I6_T11; *Cananga odorata**^ (Lam.) Hook.f. & Thomson, TC-S3171, Ecuador, *Zapata, N. 820* (P), RUN100b_I06_T78; *Cardiopatulum calophyllum** Schltdl., TC-S2454, Brazil, *Santos, A.A. 1429* (U), RUN100b_I12_T42; *Cleistochlamys kirkii**^ (Benth.) Oliv., TC-S0363, Tanzania, *Couvreur, T.L.P. 58* (WAG), RUN88_I12_T85; *Cleistopholis patens** (Benth.) Engl. & Diels, TC-S1438, Cameroon, *Couvreur, T.L.P. 1202* (MPU), RUN88_I09_T76; *Crematosperma pedunculatum* (Diels) R.E.Fr., TC-S1931, Ecuador, *Homeier, J. 4056* (WAG), RUN89_I2_T95; *Cyathocalyx martabanicus** Hook.f. & Thomson, TC-S2650, Indonesia, *Mols, J.B. 11* (L), RUN101AN_I3_T16; *Cymbopetalum brasiliense** (Vell.) Benth. ex Baill., TC-S1825, Brazil, *Lopes, J.C. 20* (SPF), RUN87_T18; *Dasydaschalum dasydaschalum* (Blume) I.M.Turner, TC-S2086, Singapore, *Thomas, D.C. 3410* (SING), RUN101AN_I3_T30; *Dendrokingstonia nervosa**^ (Hook.f. & Thomson) Rauscher, D505, cultivated at SBG Singapore, *Chen Koh 73* (SING), D505; *Dennettia tripetala** Baker f., TC-S1632, Cameroon, *Thomas, D.W. 5661* (WAG), RUN79_I10_T65; *Desmopsis panamensis** (B.L.Rob.) Saff., TC-S1978, Costa Rica, *Lopez, M. 3* (MEXU), RUN100b_I05_T11; *Desmos dunalii* (Wall. ex Hook.f. & Thomson) Saff., TC-S2046, Singapore, *Niisalo, M. SING2020-207* (SING), RUN89_I7_T37; *Dielsianona tessmannii* Diels, TC-S1726, Peru, *Maas, P.J.M. 8198* (U), RUN88_I09_T57; *Dielsiothamnus divaricatus**^ (Diels) R.E.Fr., TC-S3225, Tanzania, *Bidgood, S. 1547* (K), RUN101AN_I4_T92; *Disepalum platypetalum** Merr., TC-S2666, Indonesia, *Takeuchi, W.N. 18201* (L), RUN102_I10_T76; *Drepananthus ramuliflorus* Maingay ex Hook.f. & Thomson, TC-S1155, Malaysia, *Sauquet, H. 167* (P), RUN62_I10_T45; *Duckeanthus grandiflorus** R.E.Fr., TC-S4684, Brazil, *Pieris, J.M. 444* (NY), RUN104_I10_T59; *Duguertia lanceolata** A.St.-Hil., TC-S2306, Brazil, *Passos, F.C. 21453* (U), RUN88_I06_T18; *Ephedranthus parviflorus** S.Moore, TC-S1121, Peru, *Prance, G.T. 19246* (U), RUN62_I10_T33; *Fenerivia ghesquiereana** (Cavaco & Keraudren) R.M.K.Saunders, D534, Madagascar, *Schatz & al. 3611* (MO), D534; *Fissistigma manubriatum* (Hook.f. & Thomson) Merr., TC-S2099, Singapore, *Thomas,*

Appendix 2. Continued.

D.C. SING2020-0038 (SING), RUN100b_I12_T11; *Friesodielsia kingii* (J.Sinclair) Steenis, TC-S4555, Malaysia, *Gardette, E. 2086* (L), RUN102_I12_T94; *Froesiodendron amazonicum*[^] R.E.Fr., TC-S3441, Brazil, *Maas, P.J.M. P12734* (U), RUN100b_I12_T38; *Fusaea longifolia*[^] (Aubl.) Saff., TC-S1095, Suriname, *Jansen-Jacobs, M.J. 6391* (U), RUN88_I09_T65; *Goniothalamus macrophyllus*[^] (Blume) Zoll., TC-S1176, Malaysia, *Sauquet, H. 174* (P), RUN89_I1_T44; *Greenwayodendron suaveolens*[^] (Engl. & Diels) Verdc., TC-S1292, Gabon, *Couvreur, T.L.P. 746* (WAG), RUN62_I6_T70; *Gutteria novogranatensis* R.E.Fr., TC-S3295, Colombia, *Lawrence, A.E. 552* (U), RUN100b_I06_T95; *Hexalobus monopetalus*[^] (A.Rich.) Engl. & Diels, TC-S1603, Mozambique, *Lotter, N.C. 1671* (K), RUN79_I9_T18; *Hornschuchia bryotrophe*[^] Nees, TC-S1826, Brazil, *Mello-Silva, R. 3141* (SPF), RUN87_T19; *Huberantha verdcourtii* (Vollesen) Chaowasku, TC-S3252, Tanzania, *Luke, W.R.Q. 9523* (K), RUN101AN_I4_T93; *Isolona madagascariensis*[^] (A.DC.) Engl., TC-S2181, Madagascar, *Rakotonirina, C.Z. 550* (MO), RUN88_I03_T25; *Klarobelia megalocarpa* Chatrou, TC-S1766, Ecuador, *Maas, P.J.M. 8521* (U), RUN89_I1_T27; *Leoheo domatiophorus*^{*} Chaowasku, D.T.Ngo & Hung, D549, Vietnam, *Chaowasku 16* (CMUB), D549; *Letestudoxa bella*[^] Pellegr., TC-S0316, Gabon, *Couvreur, T.L.P. 600* (WAG), RUN62_I10_T10; *Lettowianthus stellatus*^{*} Diels, TC-S5506, Kenya, *Robertson, S.A. 7505* (WAG), RUN105_I3_T101; *Lukea triciae*[^] Cheek & Gosline, TC-S1693, Tanzania, *Luke, W.R.Q. 11205* (MO), RUN79_I2_T15; *Maasia glauca*^{*} (Hassk.) Mols, Kessler & Rogstad, TC-S2070, Singapore, *Thomas, D.C. 3448* (SING), RUN101AN_I1_T26; *Malmea dielsiana*^{*} R.E.Fr., D582, Peru, *Chatrou, L.W. 122* (U), D582; *Marsypopetalum littorale* (Blume) B.Xue & R.M.K.Saunders, TC-S1144, Austria (cultivated), ANN120494 / ANN 128 (W), RUN62_I6_T57; *Meiocarpidium oliverianum* (Baill.) D.M.Johnson & N.A.Murray, TC-S0619, Gabon, *Couvreur, T.L.P. 920* (WAG), RUN62_I10_T13; *Meiogyne virgata*[^] (Blume) Miq., TC-S1159, Malaysia, *Onstein, R.E. 43* (P), RUN62_I10_T46; *Mezzettia parviflora*^{*} Becc., TC-S2078, Singapore, *Thomas, D.C. 3411* (SING), RUN101AN_I1_T33; *Miliusa horsfieldii*^{*} (Benn.) Baill. ex Pierre, D574, cultivated at XTBG China, *Xue 165* (IBSC), D574; *Mischogyne michelioides*^{*} Exell, TC-S1664, Angola, *Bamps, P. 4459* (WAG), RUN79_I9_T7; *Mitrella kentii*[^] (Blume) Miq., TC-S2048, Singapore, *Thomas, D.C. 3440* (SING), RUN89_I7_T39; *Mitrephora tomentosa*^{*} Hook.f. & Thomson, D541, cultivated at XTBG China, *Xue 182* (IBSC), D541; *Mkilua fragrans*^{*} Verdc., TC-S1149, Tanzania, *Couvreur, T.L.P. 25* (WAG), RUN62_I10_T43; *Monanthotaxis congoensis*^{*} Baill., TC-S0715, Cameroon, *Couvreur, T.L.P. 1018* (MPU), RUN62_I12_T98; *Monoecarpia kalimantanensis* Kessler, TC-S1168, Malaysia, *Couvreur, T.L.P. 831* (P), RUN62_I10_T50; *Monocyclanthus vignei*[^] Keay, TC-S1685, Ghana, *Enti, A.A. 1831* (MO), RUN79_I2_T38; *Monodora myristica*[^] (Gaertn.) Dunal, TC-S1067, Ghana, *Hawthorne, W.D. 93* (WAG), RUN79_I2_T51; *Monoon lateriflorum*[^] (Blume) Miq., TC-S2058, Singapore, *Thomas, D.C. 3433* (SING), RUN89_I7_T45; *Mosannona xanthochlora* (Diels) Chatrou, TC-S2284, Ecuador, *Couvreur, T.L.P. 1325* (QCA), RUN100b_I05_T40; *Mwasumbia alba*[^] Couvreur & D.M.Johnson, TC-S1146, Tanzania, *Couvreur, T.L.P. 76* (WAG), RUN62_I6_T58; *Neo-uvaria acuminatissima* (Miq.) Airy Shaw, TC-S1198, Malaysia, *Sauquet, H. 186* (P), RUN62_I10_T58; *Neostenanthera hamata*[^] (Benth.) Exell, TC-S2023, Liberia, *Jongkind, C.C.H. 11002* (WAG), RUN89_I7_T23; *Onychopetalum periquino* (Rusby) D.M.Johnson & N.A.Murray, TC-S1130, Bolivia, *Chatrou, L.W. 439* (U), RUN62_I10_T35; *Ophrypetalum odoratum* Diels, TC-S1586, Tanzania, *Dagallier, L.-P.M.J. 54* (MPU), RUN79_I11_T47; *Orophea maculata* Scort. ex King, TC-S2050, Singapore, *Thomas, D.C. 3417* (L), RUN89_I7_T40; *Oxandra lanceolata* (Sw.) Baill., TC-S1961, Mexico, *JRA18 930* (MO), RUN101AN_I1_T17; *Oxandra saxicola* Maas & Junikka, TC-S4162, Bolivia, *Parada, G.A. 944* (WAG), RUN102_I9_T49; *Oxandra sessiliflora* R.E.Fr., TC-S4166, Brazil, *Pereira-Silva, G. 8942* (U), RUN102_I9_T50; *Phaeanthus splendens* Miq., TC-S1195, Malaysia, *Onstein, R.E. 73* (P), RUN62_I10_T57; *Phoenicanthus obliquus*^{*} (Hook.f. & Thomson) Alston, -, Sri Lanka, *Huber 577* (WAG), D604; *Piptostigma pilosum*[^] Oliv., TC-S0802, Gabon, *Couvreur, T.L.P. 1103* (WAG), RUN62_I6_T43; *Platymitra macrocarpa* Boerl., -, Thailand, *Chaowasku 100* (CMUB), D569; *Polyalthia kinabaluensis* I.M.Turner, TC-S1177, Malaysia, *Sauquet, H. 175* (P), RUN89_I1_T45; *Polyalthiosis floribunda*[^] (Jovet-Ast) Chaowasku, -, Vietnam, *Chaowasku s.n.* (CMUB), D536; *Polyecarpaceus scheffleri*[^] Engl. & Diels, TC-S2240, Tanzania, *Reisen, A.P. 20024* (P), RUN88_I03_T35; *Popowia pisocarpa* (Blume) Endl. ex Walp., TC-S2059, Singapore, *Thomas, D.C. 3427* (SING), RUN89_I7_T46; *Porcelia nitidifolia*[^] Ruiz & Pav., TC-S2158, Peru, *Ruiz, H. s.n.* (P), RUN88_I12_T100; *Pseudartabotrys letestui*[^] Pellegr., TC-S2223, Gabon, *Lachenaud, O. 1989* (P), RUN100b_I05_T34; *Pseudephranthus fragrans*[^] (R.E.Fr.) Aristeg., TC-S3716, Venezuela, *Maas, P.J.M. 6878* (U), RUN100b_I12_T51; *Pseudomalmea declina*[^] (R.E.Fr.) Chatrou, TC-S1128, Ecuador, *Chatrou, L.W. 264* (U), RUN89_I1_T10; *Pseudoxandra angustifolia* Maas, TC-S1088, Peru, *Pirie, M.D. 139* (U), RUN62_I10_T19; *Pseuduvaria macrocarpa*^{*} (Burck) Y.C.F.Su & R.M.K.Saunders, TC-S1721, Papua New Guinea, *Munzinger, J. 6994* (MPU), RUN89_I1_T52; *Pyramidanthe prismatica*^{*} (Hook.f. & Thomson) Merr., TC-S2090, Singapore, *Thomas, D.C. 3421* (SING), RUN100b_I12_T8; *Ruizodendron ovale*[^] (Ruiz & Pav.) R.E.Fr., TC-S1108, Bolivia, *Chatrou, L.W. 453* (U), RUN62_I10_T28; *Sageraea lanceolata* Miq., TC-S1192, Malaysia, *Onstein, R.E. 63* (P), RUN62_I10_T56; *Sanrafaelia ruffonammari*[^] Verdc., TC-S1563, Tanzania, *Dagallier, L.-P.M.J. 31* (MPU), RUN79_I9_T32; *Sapranthus foetidus* (Rose) Saff., TC-S3730, Mexico, *Noriega Acosta 114* (FCME), RUN100b_I11_T100; *Sirdavidia solannona*[^] Couvreur & Sauquet, TC-S0826, Gabon, *Couvreur, T.L.P. 1127* (WAG), RUN62_I6_T44; *Sphaerocoryne affinis*^{*} (Teijsm. & Binn.) Ridl., TC-S2054, Singapore, *Thomas, D.C. 3415* (SING), RUN89_I7_T43; *Stelechocarpus burahol*[^] (Blume) Hook.f. & Thomson, TC-S2061, Singapore, *Thomas, D.C. 3446* (P), RUN89_I7_T48; *Stenanona panamensis*[^] Standl., TC-S2586, Costa Rica, *Chatrou, L.W. 100* (U), RUN89_I3_T25; *Tetrameranthus duckei*[^] R.E.Fr., TC-S2539, Brazil, *Stevenson, D.W. 1002* (U), RUN89_I7_T51; *Toussaintia congolensis*[^] Boutique, TC-S3238, Democratic Republic of the Congo, *Wagemans, J. 260* (K), RUN101AN_I5_T45; *Tridimeris hahniana*[^] Baill., TC-S2203, Mexico, *Schatz, G.E. 1198* (MO), RUN88_I09_T91; *Trigynaea caudata* (R.E.Fr.) R.E.Fr., TC-S2639, Republic of Guyana, *Raes, N. 44* (U), RUN88_I09_T95; *Trivalvaria nervosa*^{*} (Hook.f. & Thomson) J.Sinclair, TC-S4863, Thailand, *Larsen, K. 32676* (MO), RUN105_I7_T36; *Unonopsis spectabilis* Diels, TC-S1087, Peru, *Pirie, M.D. 121* (U), RUN62_I10_T18; *Uvaria comperei* Le Thomas, TC-S0291, Gabon, *Couvreur, T.L.P. 569* (WAG), RUN88_I12_T60; *Uvariastrum pierreanum*[^] Engl., TC-S0461, Cameroon, *Couvreur, T.L.P. 680* (MPU), RUN79_I2_T48; *Uvariadendron angustifolium* (Engl. & Diels) R.E.Fr., TC-S1680, Ivory Coast, *Staudt, A. 642* (G), RUN79_I2_T22; *Uvariopsis zenkeri* Engl., TC-S0723, Cameroon, *Couvreur, T.L.P. 1027* (WAG), RUN79_I9_T37; *Wangia saccopetaloides*[^] (W.T.Wang) X.Guo & R.M.K.Saunders, -, China, *Tan, D. 422* (HKU), D546; *Winitia thailandana*^{*} Chaowasku & Aongyong, -, Thailand, *Chaowasku 51* (CMUB), D571; *Wuodendron praecox*[^] (Hook.f. & Thomson) B.Xue, Y.H.Tan & X.L.Hou, -, Thailand, *Chaowasku 108* (CMUB), D547; *Xylopia villosa* Chipp., TC-S1463, Cameroon, *Couvreur, T.L.P. 1227* (MPU), RUN89_I1_T13.