SYSTEMATICS AND PHYLOGENY

Repeated parallel losses of inflexed stamens in Moraceae: Phylogenomics and generic revision of the tribe Moreae and the reinstatement of the tribe Olmedieae (Moraceae)

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Abstract We present a densely sampled phylogenomic study of the mulberry tribe (Moreae, Moraceae), an economically important clade with a global distribution, revealing multiple losses of inflexed stamens, a character traditionally used to circumscribe Moreae. Inflexed stamens facilitate ballistic pollen release and are associated with wind pollination, and the results presented here suggest that losses of this character state may have evolved repeatedly in Moraceae. Neither Moreae nor several of its major genera (*Morus*, *Streblus*, *Trophis*) were found to be monophyletic. A revised system for a monophyletic Moreae is presented, including the reinstatement of the genera *Ampalis*, *Maillardia*, *Taxotrophis*, and *Paratrophis*, and the recognition of the new genus *Afromorus*. *Pseudostreblus* is reinstated and transferred to the Parartocarpeae, and *Sloetiopsis* is reinstated and transferred to the Dorstenieae. The tribe Olmedieae is reinstated, replacing the Castilleae, owing to the reinstatement of the type *Olmedia* and its exclusion from Moreae. *Streblus* s.str. is excluded from Moreae and transferred to the Olmedieae, which is characterized primarily by involucrate inflorescences without regard to stamen position. Nine new combinations are made.

Keywords *Afromorus*; *Ampalis*; Antiarideae; *Bagassa*; Castilleae; *Maillardia*; *Milicia*; Moraceae; Moreae; *Morus*; mulberry family; *Olmedia*; Olmedieae; Parartocarpeae; *Paratrophis*; *Pseudostreblus*; *Sloetiopsis*; *Sorocea*; *Streblus*; *Taxotrophis*; *Trophis*

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

■ INTRODUCTION

The preservation of plesiomorphic (ancestral) characters can result in species that are similar in appearance but distantly related, connected only by a remote common ancestor. The mulberry family (Moraceae Gaudich., 7 tribes, ca. 39 genera and 1200 species) illustrates this principle well. Inflexed stamens in bud—an adaptation to wind pollination that allows explosive pollen dispersal when flowers open (Taylor & al., 2006)—were traditionally used to define a tribe of the family, the Moreae Gaudich. (mulberries and their allies). Yet phylogenetic analyses have revealed that inflexed stamens, an ancestral feature of both Moraceae and their sister family Urticaceae Juss. (nettles), have been lost repeatedly (Clement & Weiblen, 2009). Thus, for example, Cecropiaceae C.C.Berg, traditionally distinguished from the nettle family by the absence of inflexed stamens, is in fact embedded within the Urticaceae (Berg, 1978; Clement & Weiblen, 2009). Likewise, while mulberries (*Morus* L.), paper mulberries (*Broussonetia* L'Hér. ex Vent.), and osage oranges (*Maclura* Nutt.) were once treated as tribe Moreae on account of their inflexed stamens, phylogenetic analyses have revealed them to belong to three distinct clades, each containing an assemblage of genera with and without inflexed

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stamens (Clement & Weiblen, 2009; Zerega & Gardner, 2019).

This study focuses on the tribe Moreae, a clade of 6 genera and an estimated 66 species (Clement & Weiblen, 2009). This widespread group of plants contains species of ecological and cultural importance, as well as the economically important white mulberry (*Morus alba* L.), whose leaves sustain *Bombyx mori* L. (Bombycidae), the invertebrate engine of the silk industry.

Morphological basis for higher classification in Moraceae. — By the end of the 19th century, Engler (1889) had circumscribed a Moraceae that is quite similar to the modern concept of the family, with two subfamilies. The first was the Moroideae, comprising tribes Broussonetieae Bureau, Dorstenieae Dumort., Fatoueae Engl., Moreae, and Strebleae Bureau, characterized by stamens inflexed in bud (broadly construed to include stamens in *Dorstenia* L., which straighten gradually rather than springing outward suddenly). The other was the Artocarpoideae, composed of the tribes Brosimeae Trécul, Euartocarpeae Trécul, Ficeae Dumort., and Olmedieae Trécul and characterized by stamens straight in bud. The two most influential scholars of Moraceae classification in the 20th century were E.J.H. Corner and C.C. Berg. Corner considered inflorescence architecture to be the most important character for higher-rank taxonomy within the family and inflexed stamens consequently of secondary importance (Corner, 1962). Berg by contrast questioned the utility of inflorescence architecture and took into account a variety of characters, especially the presence of inflexed stamens (Berg, 1977b, 2001).

The taxonomic history of the family has leaned heavily on this stamen character. Engler's (1889) Moreae, unchanged in substance from Bureau's (1873), contained six genera, *Ampalis* Bojer, *Pachytrophe* Bureau, *Paratrophis* Blume, *Pseudomorus* Bureau, *Morus*, and *Trophis* P.Browne (Table 1), all with inflexed stamens that spring out suddenly at anthesis. Corner's expanded Moreae consisted of eight genera with either straight or inflexed stamens, but with pistillate inflorescences never condensed into a head: *Ampalis*, *Clarisia* Ruiz & Pav., *Fatoua* Gaudich., *Morus*, *Pachytrophe*, *Sorocea* A.St.-Hil. (apparently including *Paraclarisia* Ducke), *Streblus* Lour. (including *Bleekrodea* Blume, *Neosloetiopsis* Engl., *Paratrophis*, *Pseudomorus*, *Pseudostreblus* Bureau, *Taxotrophis* Blume, *Sloetia* Teijsm. & Binn. and *Sloetiopsis* Engl.), and *Trophis* (including *Maillardia* Frapp. ex Duch.). Corner himself, however, found the diversity of his Moreae unsatisfactory, noting that "[t]oo many genera on insufficient and invalid grounds trouble this small tribe" (Corner, 1962). Perhaps in response, Berg's Moreae comprised all of the genera with inflexed stamens and none without, including *Broussonetia* and *Maclura* but excluding *Sorocea* and *Clarisia*, providing a simple character with which to delimit the tribe (Berg, 2001; Berg & al., 2006).

Recent phylogenetic work has supported a third approach, with the Moreae comprising six genera, including genera with both straight (*Bagassa* Aubl., *Sorocea*) and inflexed (*Broussonetia*, *Maclura*) stamens (Clement & Weiblen, 2009). These studies also suggest that the character state of inflexed stamens is plesiomorphic and is the ancestral state for both Moraceae and Urticaceae (Datwyler & Weiblen, 2004; Zerega & al., 2005; Clement & Weiblen, 2009). Inflexed stamens, which are precursors to ballistic pollen release, are associated with wind pollination (Bawa & Crisp, 1980; Berg, 2001; Pedersoli & al., 2019), while the loss of inflexed stamens is associated with animal pollination. Although dominant in the Moreae, inflexed stamens also occur in two other tribes: Chlorophoreae A.Juss. (= Maclureae W.L.Clement & Weiblen) and Dorstenieae. Genera lacking inflexed stamens occur in all seven tribes of Moraceae (Clement & Weiblen, 2009; Zerega & Gardner, 2019).

Taxonomic summary of Moreae. — Following Clement & Weiblen (2009), the Moreae comprises 6 genera and an estimated 66 species: *Bagassa* (1), *Milicia* Sim (2), *Morus* (16), *Sorocea* (19), *Streblus* (23), and *Trophis* P.Browne (8) (Berg, 1977a, 2001; Berg & al., 2006; Clement & Weiblen, 2009; Filho & al., 2009; Machado & al., 2013; Santos & Neto, 2015). Here, we present an overview of these genera.

Morus, the true mulberries, is characterized by leaves with crenate margins and trinerved bases, stamens inflexed in bud, and many-flowered pistillate spikes whose 4-parted perianths become fleshy in fruit, the aggregations superficially resembling a blackberry. *Morus* comprises approximately 16 species whose delimitation requires further research. There are three subgenera: *M.* subg. *Morus* (ca. 14 species), which is found in temperate to tropical Asia and from North America to Mexico; *M.* subg. *Gomphomorus* J.-F.Leroy, a single species restricted to tropical South America; and "*M.* subg. *Afromorus* Bureau ex J.-F.Leroy" (not validly published), a single species restricted to tropical Africa. Previous phylogenetic work has suggested that these three subgenera may not form a clade (Nepal, 2012). *Milicia* (2 spp., Africa) has inflorescences that somewhat resemble those of *Morus*, but the leaves of *Milicia*, with entire margins and pinnate venation, prevent any confusion of the two genera.

Streblus, with 23 species from India to Southeast Asia and Oceania, is morphologically heterogeneous, but its species are all characterized by stamens inflexed in bud and pistillate flowers with more or less free tepals that enclose the fruit loosely or not at all. Initially described by Loureiro based on the widespread *S. asper* Lour.—notable for its discoid-capitate staminate inflorescences with the rudiments of an involucre—*Streblus* was broadened by Corner (1962), bringing in as sections *Bleekrodea*, *Paratrophis* (including *Pseudomorus*), *Phyllochlamys* Bureau, *Pseudostreblus* Bureau, *Sloetia* Teijsm. & Binn., *Taxotrophis*, and apparently *Neosloetiopsis* and *Sloetiopsis* but without making any new combinations for these last two. None of these have discoid-capitate inflorescences; they mostly have spicate staminate inflorescences, and several (*Bleekrodea*, *Sloetia*, and *Sloetiopsis*) can have bisexual inflorescences. Corner viewed these sections as fragments of an ancient lineage preserving ancestral characters (Corner, 1975). Following additional work by Corner (1970, 1975), Berg included the genera *Ampalis* and *Pachytrophe* as *Streblus* sect. *Ampalis*

(Bojer) C.C.Berg, subsumed *Sloetiopsis* and *Streblus* sect. *Taxotrophis* (Blume) Corner into *S.* sect. *Streblus*, and excluded *S.* sect. *Bleekrodea* (Blume) Corner, reinstating it as a genus (Berg, 1988). Berg later reinstated *S.* sect. *Taxotrophis*, whose species are unique in bearing spines (Berg, 2005; Berg & al., 2006). In 2009, Clement and Weiblen reinstated *Sloetia* at generic rank and transferred it and *Bleekrodea* to Dorstenieae based on phylogenetic evidence (Clement & Weiblen, 2009).

Trophis is characterized by stamens inflexed in bud, spicate staminate inflorescences, and tubular pistillate perianths that become fleshy and enclose the fruit, except for the monotypic *T.* sect. *Olmedia* (Ruiz & Pav.) C.C.Berg (*T. caucana*), which has discoid-capitate staminate inflorescences with an involucre. *Trophis* as recognized by Berg (1988, 2001) has five sections: *Trophis* sect. *Trophis*, restricted to Latin America; sect. *Calpidochlamys* (Diels) Corner (previously included in *Paratrophis* and *Uromorus*), restricted to Southeast Asia (Corner, 1962); sect. *Maillardia* (Frapp. ex Duch.) C.C.Berg, restricted to Africa; sect. *Malaisia* (Blanco) C.C.Berg, from Southeast Asia to the western Pacific; and sect. *Olmedia*, restricted to Latin America. After sinking *Olmedia* into *Trophis*, Berg (1988) defined a new tribe Castilleae C.C.Berg based on *Castilla* Cerv., in order to maintain a tribe consisting of the remaining genera of the former Olmedieae (which had been typified by *Olmedia*). Recently, *Malaisia* Blanco was reinstated as a genus and transferred to Dorstenieae based on phylogenetic evidence (Clement & Weiblen, 2009), reducing the current number of sections to four.

Two Neotropical genera included in Moreae by Clement & Weiblen (2009) but not by Berg (2001) have straight stamens. While the monotypic *Bagassa*, with its long staminate catkins, is wind pollinated (Bawa & Crisp, 1980), evidence suggests that *Sorocea* (19 spp.), which produces racemose staminate inflorescences that do not have as many flowers as those of *Bagassa*, likely contains both wind- and insect-pollinated species (Zapata & Arroyo, 1978; Bawa & al., 1985; Lewis, 1986). The pistillate perianths are subtended by pluricellular hairs, believed to serve as a substrate for a fungus, which in turn attracts pollinators (Berg, 2001). The staminate flowers of *Sorocea affinis* Hemsl. are apparently fragrant (fide *S. Zona 778*, 21 Nov 1997, FTBG♂♀), suggesting insect pollination for that species. If insect pollination were confirmed in *Sorocea*, it would likely represent

Table 1. Overview of the taxonomic history of Moreae.

Engler (1889)	Corner (1962)	Berg (2001)	Clement & Weiblen (2009)	This study
				Afromorus[c]
Ampalis	*Ampalis*	(*Ampalis*)[a]	(*Ampalis*)[a]	*Ampalis*
			Bagassa	*Bagassa*
	(*Bleekrodea*)[a]	*Bleekrodea*		
		Broussonetia		
	Clarisia			
	Fatoua	*Fatoua*		
		Maclura		
	(*Maillardia*)[b]	(*Maillardia*)[b]	(*Maillardia*)[b]	*Maillardia*
		(*Malaisia*)[b]		
		Milicia	*Milicia*	*Milicia*
Morus	*Morus*	*Morus*	*Morus*	*Morus*
Pachytrophe	*Pachytrophe*	(*Pachytrophe*)[a]	(*Pachytrophe*)[a]	(*Pachytrophe*)[d]
Paratrophis	(*Paratrophis*)[a]	(*Paratrophis*)[a]	(*Paratrophis*)[a]	*Paratrophis*
Pseudomorus	(*Pseudomorus*)[a]	(*Pseudomorus*)[a]	(*Pseudomorus*)[a]	(*Pseudomorus*)[e]
	(*Pseudostreblus*)[a]	(*Pseudostreblus*)[a]	(*Pseudostreblus*)[a]	
	(*Sloetia*)	(*Sloetia*)[a]		
	(*Sloetiopsis*)[a]	(*Sloetiopsis*)[a]	(*Sloetiopsis*)[a]	
		(*Neosloetiopsis*)[a]	(*Neosloetiopsis*)[a]	
	Sorocea		*Sorocea*	*Sorocea*
	Streblus	*Streblus*	*Streblus*	
	(*Taxotrophis*)[a]	(*Taxotrophis*)[a]	(*Taxotrophis*)[a]	*Taxotrophis*
Trophis	*Trophis*	*Trophis*	*Trophis*	*Trophis*

[a]Included in *Streblus*. – [b]Included in *Trophis*. – [c]Newly separated from *Morus*. – [d]Included in *Ampalis*. – [e]Included in *Paratrophis*.

another transition from ancestral wind to derived insect pollination in Moraceae.

Disagreement between the two principal recent monographers of the Moraceae, Corner (1962) and Berg (2001, 2005; Berg & al., 2006), over the delimitation of the Moreae has been compounded by molecular phylogenetic studies that have redefined genera and their relationships. This has resulted in a poorly delimited tribe with respect to diagnostic morphological characters, the genera it comprises, and the rank of several taxa (see above). Ensuring that the tribe and its genera are monophyletic will result in a classification that better reflects evolutionary history, providing a framework for answering broader scientific questions. Our aim, therefore, was to generate a comprehensive phylogeny of the Moreae (Fig. 1) and its near allies by sampling all of the potential genera and species in the tribe sensu Berg, sensu Corner, and sensu Clement & Weiblen (2009) and use this to redelimit the tribe and its genera. We aimed to do so through increased taxon and genome sampling compared to previous studies, including a nearly comprehensive sample of the taxa in Moreae (56/66 species) and the allied tribes Artocarpeae (76/83 taxa) and Chlorophoreae (12/12). Our dataset combines phylogenomic data generated using two largely nonoverlapping sets of enrichment baits, one developed specifically for the Moraceae (Gardner & al., 2016), the other for the whole of the Angiosperms (Johnson & al., 2019), allowing us to explore the possibilities and challenges of combining samples based on largely nonoverlapping loci. The resulting generic revision lays the groundwork for species-level revisionary work and provides clarity to this economically important clade.

We also set out to reconstruct the evolutionary history of inflexed stamens within Moraceae using ancestral state reconstruction. The loss of inflexed stamens in Castilleae + Ficeae and Artocarpeae have been associated with transitions from wind to animal pollination (Momose & al., 1998; Sakai & al., 2000; Datwyler & Weiblen, 2004; Gardner & al., 2018). A more complete picture of evolutionary transitions between inflexed and straight stamens may help focus further research on transitions in pollination biology with Moraceae.

■ MATERIALS AND METHODS

We used target enrichment sequencing (Hyb-Seq) (Weitemier & al., 2014) to capture 333 genes previously developed for phylogenetic work in Moraceae ("Moraceae333")

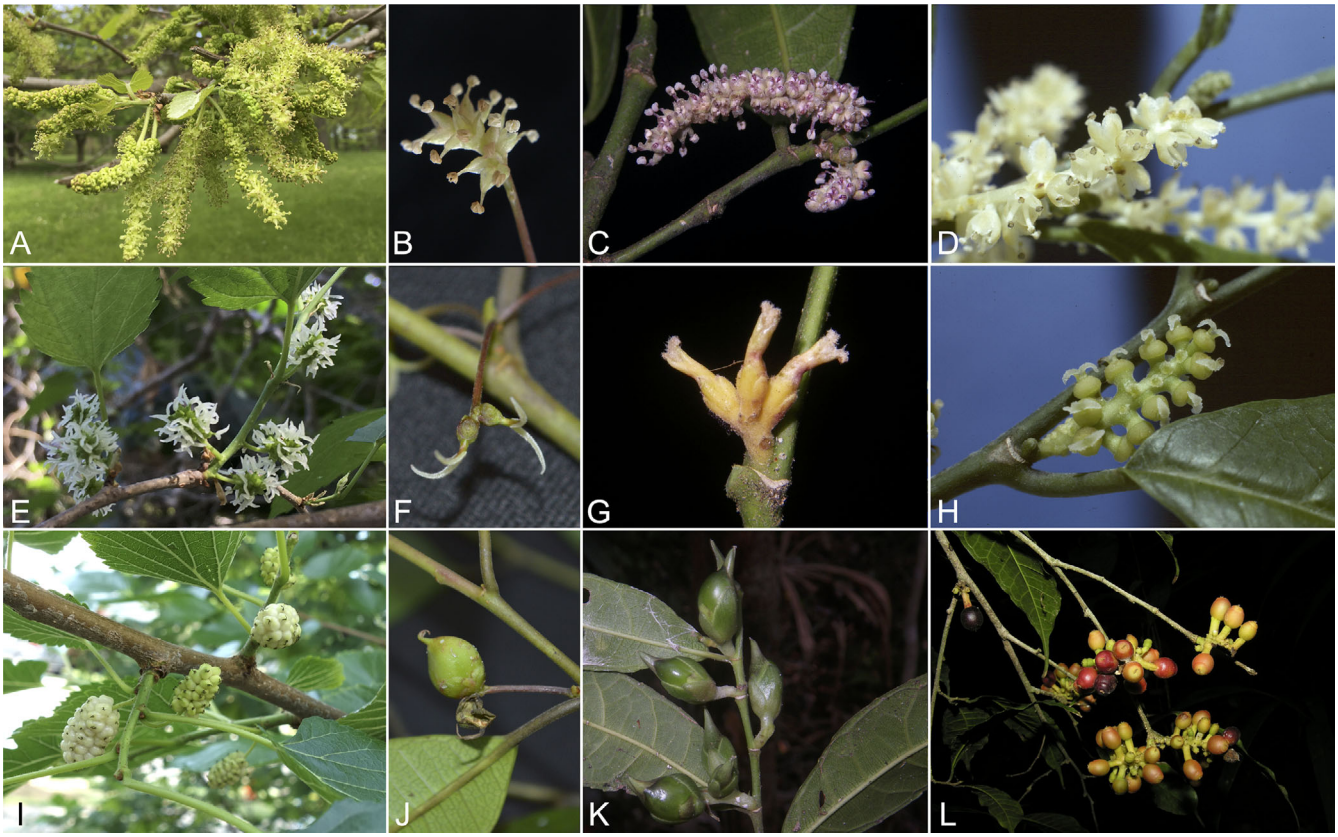


Fig. 1. Reproductive parts of Moreae. **A–D**, Staminate inflorescences of: **A**, *Morus alba* L.; **B**, *Paratrophis glabra* (Merr.) Steenis (= *Streblus glaber* (Merr.) Corner); **C**, *Taxotrophis macrophylla* (Blume) Boerl. (= *Streblus macrophyllus* Blume); **D**, *Sorocea affinis* Hemsl. **E–H**, Pistillate inflorescences of the same taxa; **I–L**, Infructescences. — Photo credits: E. Gardner (A, B, E, F, I, J); M. Nuraliyev (C, G, K); S. Zona (D, H); R. Aguilar (L); D, H, and L reproduced under a CC BY-NC-SA 2.0 license.

(Gardner & al., 2016; Johnson & al., 2016). This method allows for efficient capture of hundreds of loci and is suitable for both fresh material and degraded DNA from herbarium material (Villaverde & al., 2018; Brewer & al., 2019), which comprises much of the material employed in this study.

Taxon sampling. — We employed species-level sampling in Moreae (56 out of ca. 66 species), Artocarpeae (73/75), Chlorophoreae (12/12), and Parartocarpeae Zerega & E.M.Gardner (4/4), complemented by genus-level sampling in Dorstenieae (11/15 genera), Castilleae (9/11) and Ficeae (1/1). Outgroups included seven samples representing the major clades of Urticaceae and *Trema orientale* (L.) Blume.

Library preparation, and sequencing. — For new libraries, we sampled 56 out of 66 species (and all genera) in Moreae, all 12 species of Chlorophoreae, as well as select outgroup taxa from other tribes using DNA from leaf tissue preserved on silica gel or—in most cases—samples from herbarium specimens (Appendix 1). In either case, DNA was extracted using a modified CTAB method, usually with increased incubation times to maximize yield from herbarium tissue (Doyle & Doyle, 1987; Hale & al., 2020). Samples were quantified using a Qubit fluorometer (Invitrogen, Life Technologies, California, U.S.A.), and herbarium samples were run on a gel to test for degradation. For most samples 200 ng of DNA was used for library preparation; for some low-yield samples, as little as 50 ng was used, and for very degraded samples, as much input as possible was used, up to 400 ng. Undegraded DNA was fragmented either using NEB DNA Fragmentase (New England Biolabs, Ipswich, Massachusetts, U.S.A.) or on a Covaris M220 (Covaris, Wobum, Massachusetts, U.S.A.). DNA samples with an average fragment size less than 500 bp were not fragmented at all, but partially degraded samples with an average fragment size of over 500 bp were still fragmented on the Covaris M220. TruSeq-style library preparation was carried out using either the KAPA Hyper Prep kit (Kapa Biosystems, Wilmington, Massachusetts, U.S.A.) or the NEB DNA Ultra 2 kit following the manufacturer's protocols, except that end repair, A-tailing, and adapter ligation were carried out in reduced-volume reactions (0.25× for KAPA and 0.5× for NEB) to reduce costs. Final products were quantified on the Qubit and combined in equal molecular weights into pools of 16–20 samples. The pools totaled 1200 µg each if enough library preparation was available. Pools were hybridized for 16–24 hours to custom Moraceae probes (Gardner & al., 2016) using a myBaits kit (Arbor Biosciences, Ann Arbor, Michigan, U.S.A.) following the manufacturer's protocol, except that the probes were diluted 1 : 1 with nuclease-free water. Hybridization products were reamplified using KAPA Hot Start PCR reagents following the myBaits protocol, quantified on the Qubit, and quality-checked on an Agilent BioAnalyzer (Agilent Technologies, Palo Alto, California, U.S.A.). Samples with adapter dimer peaks were cleaned using 0.7× SPRI beads and re-run on the Qubit and BioAnalyzer. An initial sequencing run took place on a MiSeq 2 × 300 bp run (v.3) (Illumina, San Diego, California, U.S.A.) at the Field Museum of Natural History, and then additional samples were sequenced on a HiSeq 4000 2 × 150 bp run at the Northwestern University Genomics Core.

We also included 46 Moraceae and Urticaceae samples enriched for the Angiosperm353 probes and sequenced as part of the Plant and Fungal Trees of Life project (PAFTOL, RBG Kew; https://www.kew.org/science/our-science/projects/plant-and-fungal-trees-of-life; suppl. Table S1). Sample preparation and sequencing followed Johnson & al. (2019). The PAFTOL samples were enriched with a universal probe set developed for angiosperms (the "Angiosperms353").

Finally, we used samples sequenced for previous phylogenetics projects in *Artocarpus* J.R.Forst. & G.Forst. and Parartocarpeae to complete our sampling (Johnson & al., 2016; Kates & al., 2018; Zerega & Gardner, 2019; Gardner & al., 2021). The final dataset contained 246 samples.

Assembly of reads. — We trimmed reads using Trimmomatic v.0.36 (ILLUMINACLIP: TruSeq3-PE.fa:2:30:10 HEADCROP:3 LEADING:30 TRAILING:25 SLIDINGWINDOW:4:25 MINLEN:20) (Bolger & al., 2014) and assembled them with HybPiper, which produces gene-by-gene, reference-guided *de novo* assemblies (Johnson & al., 2016). For the samples enriched with the Angiosperms353 baits, we used the reference described by Johnson & al. (2019), and for the samples enriched with the Moraceae333 baits, we used the reference described in Zerega & Gardner (2019). To increase overlap between the two datasets beyond the 5 genes they inherently have in common, we used HybPiper to assemble the Angiosperms353-enriched reads using the Moraceae333 targets and vice-versa, in order to capture any additional genes found in off-target reads. The exception was the *Artocarpus* dataset, which was previously assembled for another study using only the Moraceae333 targets. We used the HybPiper script "intronerate.py" to build "supercontig" sequences for each gene, consisting of exons as well as any assembled flanking noncoding sequences (intronic or intergenic). To these new assemblies, we added 76 Moraceae333 assemblies from Gardner & al. (2021) to complete sampling for the Artocarpeae.

Summary of phylogenetic analyses. — We conducted four main phylogenetic analyses, labeled as follows, and detailed below. Main phylogenomic analyses: (1) *exon-supermatrix* – all taxa, 686 nuclear genes, coding sequences only, concatenated supermatrix; (2) *exon-species-tree* – all taxa, 686 nuclear genes, coding sequences only, species tree; (3) *supercontig-supermatrix* – Moreae only, 686 nuclear genes, coding and noncoding sequences, concatenated supermatrix; (4) *supercontig-species-tree* – Moreae only, 686 nuclear genes, coding and noncoding sequences, species tree. We also conducted the following supplemental analyses: (5) *plastome* – most taxa, all chloroplast genes, coding and noncoding sequences, concatenated supermatrix (to investigate cyto-nuclear discordance); (6) *network* – Paratrophis clade, 686 nuclear genes, coding and noncoding sequences, maximum-pseudolikelihood network based on individual gene trees (to investigate hybridization in the Paratrophis clade); (7) *Involucrata-supermatrix* and *Involucrata-species-tree* – The Involucrata clade, 686 nuclear genes, coding

and noncoding sequences, concatenated supermatrix and species tree; (8) *ITS-tree* and *rbcL-tree* – most taxa plus select GenBank sequences, ITS or *rbcL* only (to place *Streblus* taxa not included in our own sampling).

Main phylogenetic analyses. — The full dataset was analyzed using the "exon" sequences to ensure good alignment across the entire family. For non-*Artocarpus* samples, for each of the 686 genes assembled, we discarded sequences shorter than 25% of the average length for the gene and discarded genes containing sequences for less than 30 samples. We aligned each gene with MAFFT v.7.453 (Katoh & Standley, 2013) and used trimAl v.1.4 (Capella-Gutiérrez & al., 2009) to discard sequences with an average pairwise identity of less than 0.5 to all other sequences in the alignment (indicative of a poor quality sequence that could not be properly aligned) as well as columns containing more than 75% gaps. Subsets of similarly trimmed alignments from the previous *Artocarpus* study (Gardner, 2017; Gardner & al., 2021) were then added to these alignments using the –merge option in MAFFT. We used RAxML v.8.2.4 (Stamatakis, 2014) to estimate a maximum-likelihood tree for a partitioned supermatrix of all genes (*exon-supermatrix* analysis) as well as for each gene individually (GTRCAT model, 200 bootstrap replicates). We then used ASTRAL-III (C. Zhang & al., 2017), a summary-coalescent method, to estimate a species tree from all gene trees (*exon-species-tree* analysis), estimating node support using both bootstrap (160 replicates, resampling across and within genes) and quartet scores (representing gene tree concordance). Finally, we used ASTRAL-III to test whether, for each node, the null hypothesis of a polytomy could be rejected (Sayyari & Mirarab, 2018). Alignment, trimming, and estimation of gene trees were parallelized using GNU Parallel v.20191122 (Tange, 2018). To maximize phylogenetic resolution within Moreae, a smaller dataset consisting only of Moreae taxa and a single outgroup taxon (*Artocarpus heterophyllus*) was analyzed using the "supercontig" sequences but following the same methodology (*supercontig-supermatrix* and *supercontig-species-tree* analyses).

Whole-chloroplast phylogenetic tree. — We also built a whole-chloroplast phylogenetic tree (*plastome* analysis) as follows. Rather than assembling full-length genomes, which can be extremely slow to align, we assembled and aligned the genomes in sections, dramatically speeding up the process. We created HybPiper targets using the chloroplast genome of *Morus indica* L. (NCBI RefSeq accession no. NC_008359.1) and the associated gene annotations. Each target consisted of a gene feature concatenated with any internal or subsequent noncoding sequence, terminating one base before the start of the next gene feature. These intervals were generated by manually editing the NCBI gff3 file in Excel (Microsoft, Redmond, Washington, U.S.A.) and then extracted using BedTools v.2.29.2 (Quinlan & Hall, 2010). Assemblies for all Moraceae samples and *Boehmeria nivea* (L.) Gaudich. were carried out in HybPiper using a coverage cutoff of 2 and otherwise with default parameters. Within each target, sequences less than 25% of the average length were discarded, and after alignment with MAFFT, sequences with an average pairwise identity of less than 0.7 were discarded (the higher cutoff reflecting the conserved nature of chloroplast DNA). Alignments were then concatenated into a supermatrix, and samples with more than 50% undetermined characters were discarded. Alignments were then rebuilt, filtered, and concatenated, and columns in the final supermatrix with more than 75% missing characters were discarded. A maximum-likelihood tree was generated using RAxML v.8.2.4 under the GTRCAT model, with 200 rapid bootstrap replicates.

Phylogenetic network analysis. — To further investigate relationships within the Paratrophis clade, including the proper placement of *Morus insignis* Bureau and *Trophis philippinensis* (Bureau) Corner, we constructed phylogenetic networks (*network* analysis) based on two reduced 8-taxon datasets ("exon" and "supercontig") consisting of those taxa plus *Streblus anthropophagorum* (Seem.) Corner, *S. glaber* (Merr.) Corner, *S. glaber* subsp. *australianus* (C.T.White) C.C. Berg, and *S. heterophyllus* (Blume) Corner, with *S. mauritianus* (Jacq.) Blume as the outgroup. Alignment preparation followed the workflow outlined above except that only genes with sequences for all eight taxa were retained. Rooted gene trees were used to infer the network in PhyloNet v.3.8.0 using the "InferNetwork_MPL" command, allowing a maximum of four hybridization events and collapsing gene tree nodes with less than 30% bootstrap support (Yu & Nakhleh, 2015; Wen & al., 2018); the Akaike information criterion (AIC) was scored for the best five networks from 10 runs, using the number of branch lengths and hybridization events calculated as the number of parameters (Kamneva & al., 2017).

Involucrata supercontig analyses. — To improve resolution within the Involucrata (Ficeae and Castilleae) clade and further test the positions of *Streblus asper* and *Trophis caucana*, we conducted additional phylogenetic analyses using "supercontig" sequences for members of the Involucrata clade, with *Fatoua pilosa* Gaudich. as the outgroup. Methods followed those used for the *supercontig-supermatrix* and *supercontig-species-tree* analyses, except that genes with at least 4 taxa present were retained (*Involucrata-supermatrix* and *Involucrata-species-tree*).

ITS and *rbcL* phylogenetic trees. — While we did not have our own sequences for *Streblus ascendens* Corner, *S. banksii* (Cheeseman) C.J.Webb, *S. smithii* (Cheeseman) Corner, and *S. tonkinensis* (Eberh. & Dubard) Corner, either ITS or *rbcL* sequences existed in NCBI GenBank for these taxa. To investigate the phylogenetic affinities of these species, we therefore assembled ITS and *rbcL* datasets from off-target reads from our own samples using HybPiper, using *Streblus* sequences for these loci (obtained from GenBank) as targets and reducing the coverage cutoff to 2 to recover the loci from off-target reads. To these sequences, we added GenBank sequences of *Streblus* taxa as well as *Trophis caucana* (Pittier) C.C.Berg (*rbcL* only for the latter), to examine an alternative line of evidence regarding their placement. We were not able to examine the underlying specimens ourselves, but we considered the chances of misidentification low because those species are morphologically and/or geographically distinctive;

one of the *T. caucana* samples came from a vouchered tree in the Smithsonian Tropical Research Institute's plot on Barro Colorado Island. For each locus, we aligned sequences with MAFFT, discarded short sequences (<490 bp), trimmed alignments to remove columns with over 75% gaps, and built maximum-likelihood trees using RAxML (GTRGAMMA, 1000 rapid bootstrap replicates) (*ITS-tree* and *rbcL-tree* analyses).

Divergence time estimation. — The supermatrix maximum-likelihood tree was time calibrated using penalized likelihood as implemented in ape v.5.3 (Paradis & Schliep, 2019) in R v.3.5.1 (R Core Team, 2019). First, the tree was pruned of duplicate taxa and non-Moraceae outgroup taxa, and edge lengths (in substitutions per site) were multiplied by the number of sites in the alignment (to convert them to substitutions). The following stem nodes were constrained with minimum ages (in million years, Ma) based on fossil data, following Q. Zhang & al. (2019): *Ficus*, 56 Ma; *Broussonetia*, 33.9 Ma; *Morus* (subg. *Morus*, based on the U.S.S.R. locality of the fossil), 33.9 Ma; and *Artocarpus*, 64 Ma. The crown node of Moraceae was constrained to a minimum age of 73.2 Ma and a maximum age of 84.7 Ma based on Q. Zhang & al. (2019), which had a more extensive outgroup sampling than this study. The tree was then time-calibrated using the "chronos" function under three different models ("discrete", "correlated", "relaxed") (Kim & Sanderson, 2008; Paradis, 2013). The smoothing parameter (λ) was chosen using the cross-validation method implemented in the "chronopl" function (testing $\lambda = 0$ and 0^{-5} through 10^{15}), selecting the value of λ that minimized the cross-validation statistic (Sanderson, 2002). Models were compared using penalized log-likelihood and "Phylogenetic information criterion" (ΦIC) scores (Paradis, 2013). The resulting trees were also visualized using the "densiTree" function in phangorn v.2.4.0 (Schliep, 2011) to assess the sensitivity of the three models to changes in λ. As the penalized likelihood approach used does not integrate over model uncertainty or uncertainty in calibration placement and timing, confidence intervals on node ages are not provided in this study. A geologic timescale based on the strat2012 dataset was added to tree figures using PHYLOCH v.1.5-3 (Heibl, 2008).

Ancestral state reconstruction for inflexed stamens. — All taxa were coded for presence (1) or absence (0) of inflexed stamens in bud. Members of the Dorstenieae with stamens that are inflexed in bud but gradually straighten were coded as 0. We reconstructed ancestral character states on the entire phylogeny by stochastic mapping using the "make.simmap" function in phytools v.0.6-99 (Revell, 2012). We also tested for trait-associated shifts in diversification rates using BAMM v.2.5.0 (Rabosky & al., 2013, 2014a; Rabosky, 2014), specifying the amount of missing taxa per clade to account for the high proportion of missing taxa in Ficeae, Castilleae, and Dorstenieae. Parameters were optimized using BAMMtools v.2.1.7 (Rabosky & al., 2014b). We also tested for trait-dependent diversification using diversitree v.0.9-13 (FitzJohn, 2012). We evaluated BiSSE and trait-independent models on the entire tree and on a pruned tree consisting only of the densely sampled Chlorophoreae + Moreae + Artocarpeae clade.

Reads have been deposited in GenBank (Non-PAFTOL samples: BioProject PRJNA322184; PAFTOL samples: BioProject PRJEB35285, subprojects PRJEB37667 for Moraceae and PRJEB37665 for Urticaceae). Tree files and scripts outlining the phylogenetic analyses have been deposited in the Dryad Data Repository, https://doi.org/10.5061/dryad.v41ns1rrt).

■ RESULTS

Assembly results. — The final dataset contained 246 samples (46 enriched with the Angiosperms353 baits, 196 enriched with the Moraceae333 baits, and 4 extracted from whole genomes) and 619 genes (286 Angiosperms353 and all of the Moraceae333) (Appendix 1; suppl. Table S1). The *exon-supermatrix* alignment (all taxa) contained 613,126 characters, and the *supercontig-supermatrix* alignment (Moreae and select outgroup taxa only) contained 799,926 characters. The *chloroplast* alignment contained 113 loci.

Dataset combination. — On average, we assembled 39 Moraceae333 genes from the Angiosperms353-enriched samples and 20 Angiosperms353 genes from the Moraceae333-enriched samples, and the average pairwise overlap in assembled loci was 210 (suppl. Tables S1, S2; suppl. Fig. S1). Nineteen taxa were represented in both sets of samples, and 15 of these were always monophyletic in the main analyses (*exon-supermatrix*, *exon-species-tree*, *supercontig-supermatrix*, *supercontig-species-tree*) (Figs. 2, 3, suppl. Fig. S1). Twelve resolved as sister pairs: *Antiaropsis decipiens* (31 loci overlapping), *Bagassa guianensis* Aubl. (38), *Batocarpus amazonicus* (Ducke) Fosberg (22), *Batocarpus orinocensis* H.Karst. (34), *Brosimum alicastrum* Sw. (42), *Clarisia racemosa* Ruiz & Pav. (59), *Maclura africana* (Bureau) Corner (213), *Milicia excelsa* (Welw.) C.C.Berg (45), *Streblus asper* (Retz.) Lour. (75), *Streblus mauritianus* (Jacq.) Blume (40), *Streblus usambarensis* (Engl.) C.C. Berg (43), and *Trophis caucana* (32). Three more represented by more than two samples always resolved as a clade: *Sorocea bonplandii* (Baill.) W.C.Burger & al. (3 samples; 19–35 loci overlapping), *Maclura tinctoria* (L.) D.Don ex Steud. (4 samples; 37–43 loci overlapping), and *Malaisia scandens* (Lour.) Planch. (3 samples; 27–43 loci overlapping). Three additional taxa resolved as sister pairs in the ASTRAL analyses (*exon-species-tree* and when applicable, *supercontig-species-tree*) but as a grade in the supermatrix analysis: *Maclura cochinchinensis* (Lour.) Corner (28 loci overlapping), *Streblus heterophyllus* (Blume) Corner (50), and *Trophis montana* (Leandri) C.C.Berg (56). Only one species, *Utsetela gabonensis* Pellegr. (18 loci overlapping) was never monophyletic, always forming a grade with *U. neglecta* Jongkind. All genera (as revised below) with samples from both sets were monophyletic except for *Dorstenia* in the *exon-species-tree* analysis; the two *Dorstenia* samples both had a high proportion of missing data (with 203 + 4 and 7 + 88 M333 + A353 loci, respectively) and only 6 loci overlapping.

Phylogenetic relationships. — For the main phylogenomic analyses, supermatrix, species tree, exon, and supercontig

analyses were broadly concordant, with disagreements largely restricted to shallow phylogenetic depths, such as relationships within *Streblus* sect. *Paratrophis*. For the species-tree analyses sets, the polytomy hypothesis was rejected ($P < 0.05$) for Moraceae and all tribe and genus-level clades (following the revised classification presented below) (Figs. 2, 3).

(I) exon-supermatrix. – Of the genera in Moreae sensu Clement & Weiblen, only *Bagassa*, *Milicia*, and *Sorocea* were monophyletic; *Morus*, *Streblus*, and *Trophis* were not. The monotypic *Bagassa* resolved as sister to Sorocea, with which it shares straight stamens. Four Moreae species resolved with other tribes: *Trophis caucana* was nested within Castilleae, *Streblus asper* (Retz.) Lour. was sister to Castilleae, *Streblus indicus* (Bureau) Corner was sister to Parartocarpeae, and *Streblus usambarensis* was nested within Dorstenieae. Moreae was otherwise monophyletic, comprising the following subclades: (1) *Streblus* sect. *Taxotrophis*, sister to all other Moreae; (2) (a) *Trophis* sect. *Maillardia*, (b) *Milicia* + *Morus* subg. *Afromorus*, (c) *Streblus* sect. *Ampalis*, (d) *Streblus* sect. *Paratrophis* in part + *Morus* subg. *Gomphomorus*, (e) *Streblus* sect. *Paratrophis* in part + *Trophis* sect. *Calpidochlamys*; (3) *Bagassa* + *Sorocea*; and (4) *Morus* + *Trophis* sect. *Trophis* and sect. *Echinocarpa* C.C.Berg. These are roughly geographic clades: (1) Southeast Asia; (2) (a) Madagascar, (b) Southeast Africa, (c) Madagascar, (d) Pacific + South America, (e) Southeast Asia + Pacific; (3) South America; (4) South America.

(II) exon-species-tree. – This analysis was largely concordant with the supermatrix, with no differences at the tribe level. Within Moreae, only minor within-genus rearrangements were observed, including rearrangements within the white mulberry complex (*Morus alba* and allies) and a change in the position of *Morus insignis* within the Paratrophis clade. The polytomy hypothesis could not be rejected for the position of *M. insignis* as sister to *Streblus anthropophagorum* + *S. heterophyllus*. Outside of Moreae, disagreements included minor rearrangements within *Maclura* sect. *Cudrania* (Trécul) Corner, Dorstenieae (the position of *Dorstenia* in relation to *Utsetela* Pellegr.), and Castilleae (the positions of *Antiaris* and *Naucleopsis*).

(III and IV) supercontig-supermatrix and *supercontig-species-tree.* – The addition of noncoding sequences generally increased concordance between the supermatrix and species-tree analyses within some clades in Moreae. In both the *supercontig-supermatrix* and *supercontig-species-tree* analyses, *Morus insignis* was sister to *Streblus* sect. *Paratrophis*, and the polytomy test was rejected for that node (Fig. 3). However, within *Streblus* sect. *Taxotrophis*, in the *supercontig-supermatrix* analysis, *Streblus zeylanicus* (Thwaites) Kurz was sister to all other member of that section, whereas in the *supercontig-species-tree* analysis, *S. zeylanicus* was sister to *S. taxoides* (B.Heyne ex Roth) Kurz.

(V) plastome. – The whole-choloroplast analysis (suppl. Fig. S2) was generally in agreement with the nuclear phylogenetic trees, with three notable differences. *Streblus indicus* and the Parartocarpeae formed a grade paraphyletic to Dorstenieae, Castilleae, and Ficeae, rather than a clade. *Streblus zeylanicus* was sister to *S. taxoides* as in the *supercontig-species-tree* analysis instead of sister to all of *Streblus* sect. *Taxotrophis* as in the other nuclear analyses, although with low support (62%). In addition, *S. glaber* subsp. *australianus* was not sister to subsp. *glaber*, although its placement was not strongly supported (80%). Finally, *Morus insignis* was sister to *Paratrophis*, agreeing with the *supercontig* analyses but not the *exon* analyses.

(VI) network. – In the five best maximum-pseudolikelihood networks, *M. insignis* was within the Paratrophis clade in three, had a hybrid origin involving *Paratrophis* in one, and was unambiguously sister to *Paratrophis* in one (Fig. 4). AIC values for the five networks appear in supplementary Table S3.

(VII) Involucrata-supermatrix and *Involucrata-species-tree.* – In the analyses of the Involucrata clade (suppl. Fig. S3), *Streblus asper* was always sister to Castilleae, which always comprised the following three subclades: (1) *Antiaropsis* + *Sparattosyce*, (2) *Antiaris*, (3) the Neotropical genera +

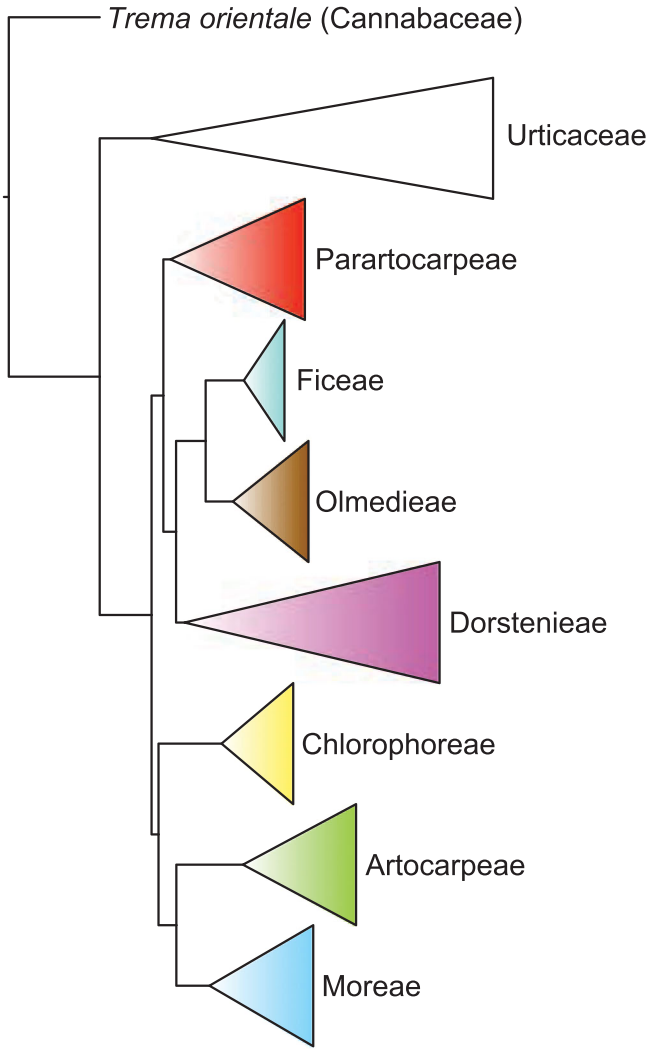


Fig. 2A. Summary of topology by tribe (revised classification) and color legend for Fig. 2B–D.

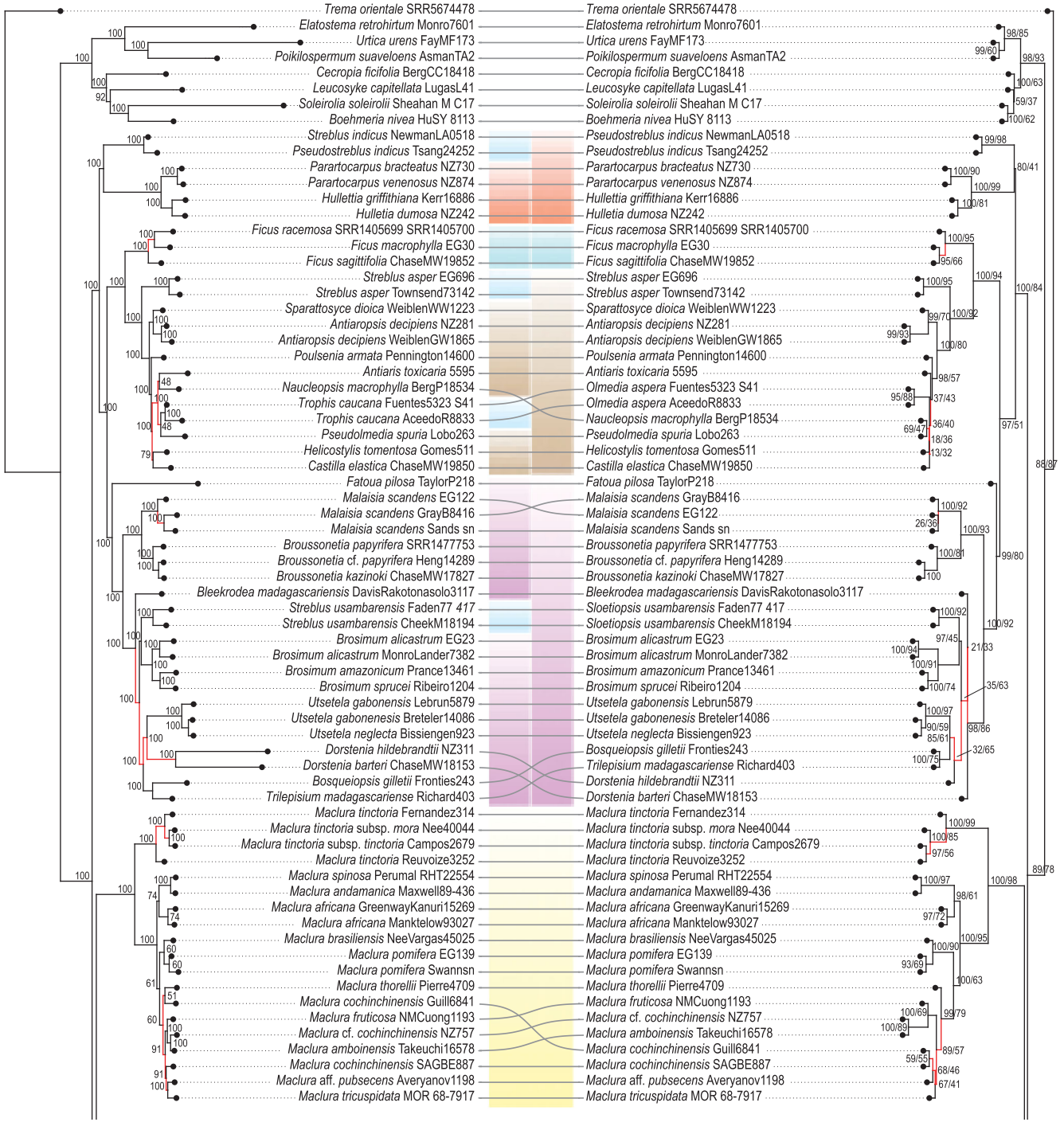
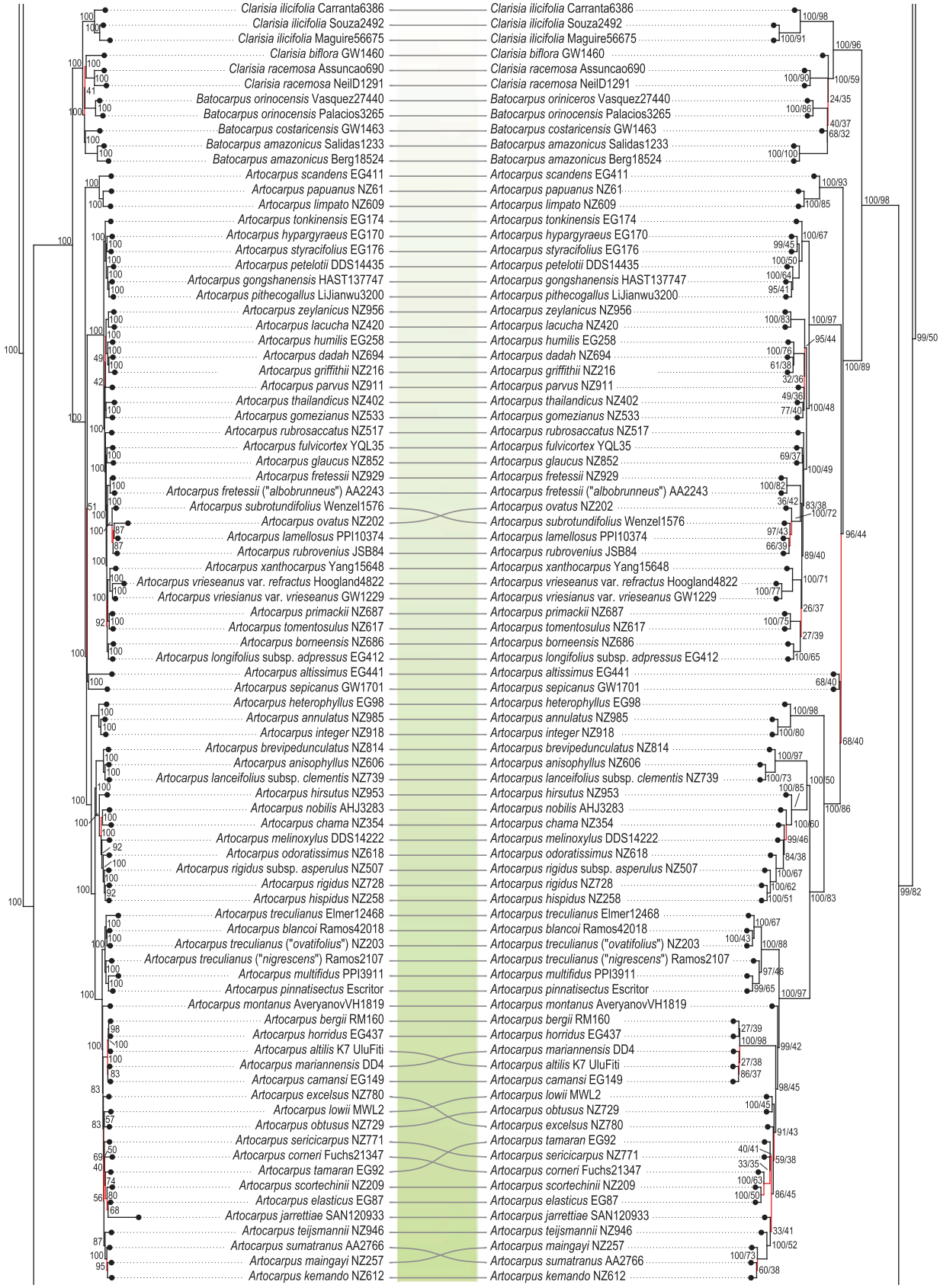


Fig. 2B–D. Phylogenetic trees from the "exon" dataset. Maximum-likelihood tree based on a supermatrix of all loci, with bootstrap support and previous nomenclature (**left**), and a species tree based on gene trees from all loci with bootstrap/quartet support and revised nomenclature (**right**). Discordant branches are colored in red, and tribal classifications are shaded with previous (**left**) and revised (**right**) classifications presented here. For summary topology and color legend, see Fig. 2A.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Clarisia ilicifolia Souza2492
Clarisia ilicifolia Maguire56675
Clarisia biflora GW1460
Clarisia racemosa Assuncao690
Clarisia racemosa NeilD1291
Batocarpus orinocensis Vasquez27440
Batocarpus orinocensis Palacios3265
Batocarpus costaricensis GW1463
Batocarpus amazonicus Salidas1233
Batocarpus amazonicus Berg18524
Artocarpus scandens EG411
Artocarpus papuanus NZ61
Artocarpus limpato NZ609
Artocarpus tonkinensis EG174
Artocarpus hypargyraeus EG170
Artocarpus styracifolius EG176
Artocarpus petelotii DDS14435
Artocarpus gongshanensis HAST137747
Artocarpus pithecogallus LiJianwu3200
Artocarpus zeylanicus NZ956
Artocarpus lacucha NZ420
Artocarpus humilis EG258
Artocarpus dadah NZ694
Artocarpus griffithii NZ216
Artocarpus parvus NZ911
Artocarpus thailandicus NZ402
Artocarpus gomezianus NZ533
Artocarpus rubrosaccatus NZ517
Artocarpus fulvicortex YQL35
Artocarpus glaucus NZ852
Artocarpus fretessii NZ929
Artocarpus fretessii ("albobrunneus") AA2243
Artocarpus subrotundifolius Wenzel1576
Artocarpus ovatus NZ202
Artocarpus lamellosus PPI10374
Artocarpus rubrovenius JSB84
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Artocarpus vrieseanus var. refractus Hoogland4822
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Artocarpus tomentosulus NZ617
Artocarpus borneensis NZ686
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Artocarpus altissimus EG441
Artocarpus sepicanus GW1701
Artocarpus heterophyllus EG98
Artocarpus annulatus NZ985
Artocarpus integer NZ918
Artocarpus brevipedunculatus NZ814
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Artocarpus lanceifolius subsp. clementis NZ739
Artocarpus hirsutus NZ953
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Artocarpus chama NZ354
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Artocarpus rigidus NZ728
Artocarpus hispidus NZ258
Artocarpus treculianus Elmer12468
Artocarpus blancoi Ramos42018
Artocarpus treculianus ("ovatifolius") NZ203
Artocarpus treculianus ("nigrescens") Ramos2107
Artocarpus multifidus PPI3911
Artocarpus pinnatisectus Escritor
Artocarpus montanus AveryanovVH1819
Artocarpus bergii RM160
Artocarpus horridus EG437
Artocarpus altilis K7 UluFiti
Artocarpus mariannensis DD4
Artocarpus camansi EG149
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Artocarpus lowii MWL2
Artocarpus obtusus NZ729
Artocarpus sericicarpus NZ771
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Artocarpus montanus AveryanovVH1819
Artocarpus bergii RM160
Artocarpus horridus EG437
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Artocarpus altilis K7 UluFiti
Artocarpus camansi EG149
Artocarpus lowii MWL2
Artocarpus obtusus NZ729
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Artocarpus tamaran EG92
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Artocarpus corneri Fuchs21347
Artocarpus scortechinii NZ209
Artocarpus elasticus EG87
Artocarpus jarrettiae SAN120933
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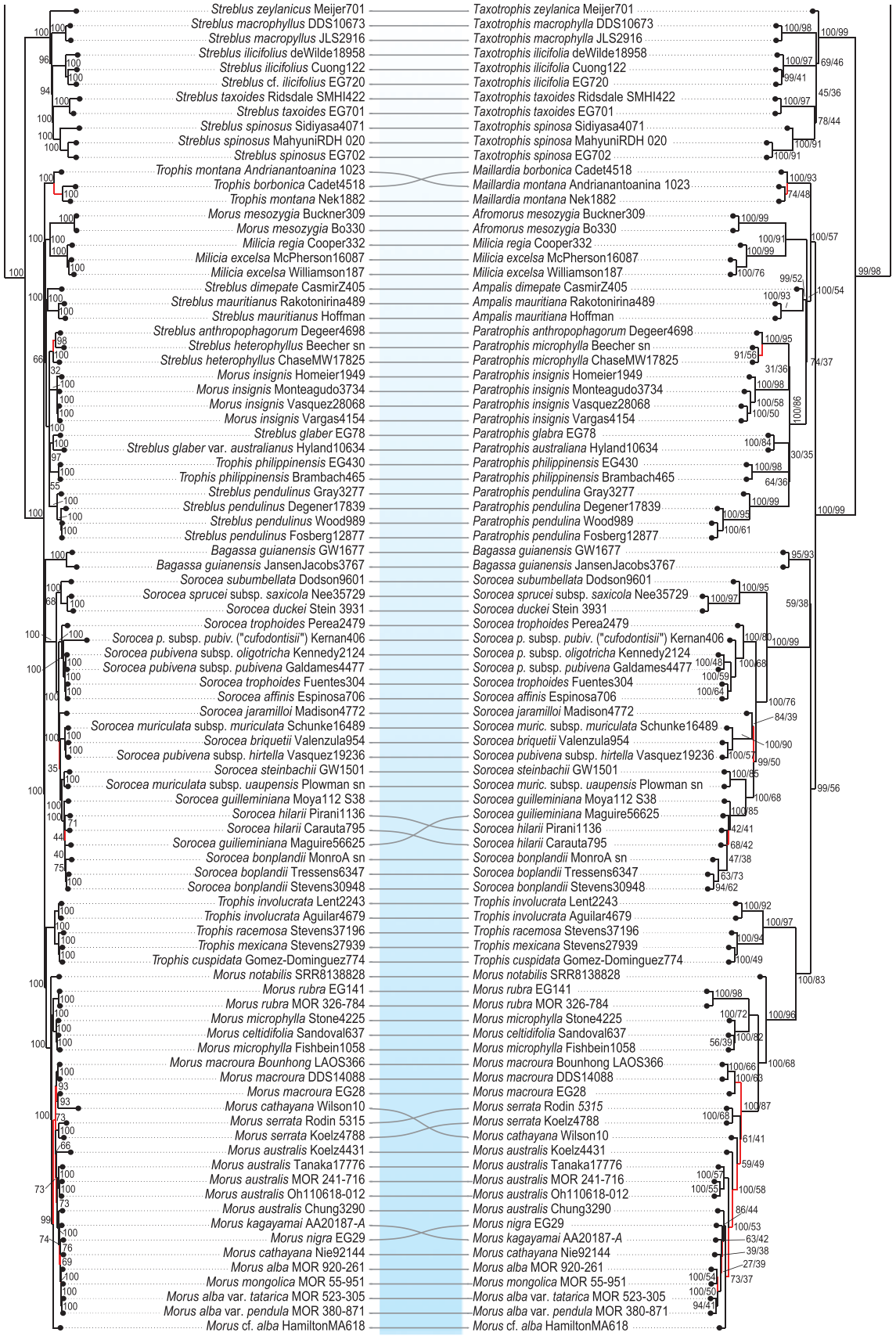
Artocarpus maingayi NZ257
Artocarpus sumatranus AA2766
Artocarpus kemando NZ612

Fig. 2C.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Streblus ilicifolius Cuong122
Streblus cf. ilicifolius EG720
Streblus taxoides Ridsdale SMHI422
Streblus taxoides EG701
Streblus spinosus Sidiyasa4071
Streblus spinosus MahyuniRDH 020
Streblus spinosus EG702
Trophis montana Andrianantoanina 1023
Trophis borbonica Cadet4518
Trophis montana Nek1882
Morus mesozygia Buckner309
Morus mesozygia Bo330
Milicia regia Cooper332
Milicia excelsa McPherson16087
Milicia excelsa Williamson187
Streblus dimepate CasmirZ405
Streblus mauritianus Rakotonirina489
Streblus mauritianus Hoffman
Streblus anthropophagorum Degeer4698
Streblus heterophyllus Beecher sn
Streblus heterophyllus ChaseMW17825
Morus insignis Homeier1949
Morus insignis Monteagudo3734
Morus insignis Vasquez28068
Morus insignis Vargas4154
Streblus glaber EG78
Streblus glaber var. australianus Hyland10634
Trophis philippinensis EG430
Trophis philippinensis Brambach465
Streblus pendulinus Gray3277
Streblus pendulinus Degener17839
Streblus pendulinus Wood989
Streblus pendulinus Fosberg12877
Bagassa guianensis GW1677
Bagassa guianensis JansenJacobs3767
Sorocea subumbellata Dodson9601
Sorocea sprucei subsp. saxicola Nee35729
Sorocea duckei Stein 3931
Sorocea trophoides Perea2479
Sorocea p. subsp. pubiv. ("cufodontisii") Kernan406
Sorocea pubivena subsp. oligotricha Kennedy2124
Sorocea pubivena subsp. pubivena Galdames4477
Sorocea trophoides Fuentes304
Sorocea affinis Espinosa706
Sorocea jaramilloi Madison4772
Sorocea muriculata subsp. muriculata Schunke16489
Sorocea briquetii Valenzula954
Sorocea pubivena subsp. hirtella Vasquez19236
Sorocea steinbachii GW1501
Sorocea muriculata subsp. uaupensis Plowman sn
Sorocea guilleminiana Moya112 S38
Sorocea hilarii Pirani1136
Sorocea hilarii Carauta795
Sorocea guilleminiana Maguire56625
Sorocea bonplandii MonroA sn
Sorocea boplandii Tressens6347
Sorocea bonplandii Stevens30948
Trophis involucrata Lent2243
Trophis involucrata Aguilar4679
Trophis racemosa Stevens37196
Trophis mexicana Stevens27939
Trophis cuspidata Gomez-Dominguez774
Morus notabilis SRR8138828
Morus rubra EG141
Morus rubra MOR 326-784
Morus microphylla Stone4225
Morus celtidifolia Sandoval637
Morus microphylla Fishbein1058
Morus macroura Bounhong LAOS366
Morus macroura DDS14088
Morus macroura EG28
Morus cathayana Wilson10
Morus serrata Rodin 5315
Morus serrata Koelz4788
Morus australis Koelz4431
Morus australis Tanaka17776
Morus australis MOR 241-716
Morus australis Oh110618-012
Morus australis Chung3290
Morus kagayamai AA20187-A
Morus nigra EG29
Morus cathayana Nie92144
Morus alba MOR 920-261
Morus mongolica MOR 55-951
Morus alba var. tatarica MOR 523-305
Morus alba var. pendula MOR 380-871
Morus cf. alba HamiltonMA618
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Taxotrophis macrophylla JLS2916
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Taxotrophis ilicifolia Cuong122
Taxotrophis ilicifolia EG720
Taxotrophis taxoides Ridsdale SMHI422
Taxotrophis taxoides EG701
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Taxotrophis spinosa MahyuniRDH 020
Taxotrophis spinosa EG702
Maillardia borbonica Cadet4518
Maillardia montana Andrianantoanina 1023
Maillardia montana Nek1882
Afromorus mesozygia Buckner309
Afromorus mesozygia Bo330
Milicia regia Cooper332
Milicia excelsa McPherson16087
Milicia excelsa Williamson187
Ampalis dimepate CasmirZ405
Ampalis mauritiana Rakotonirina489
Ampalis mauritiana Hoffman
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Sorocea duckei Stein 3931
Sorocea trophoides Perea2479
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Morus alba var. tatarica MOR 523-305
Morus alba var. pendula MOR 380-871
Morus cf. alba HamiltonMA618

Fig. 2D.

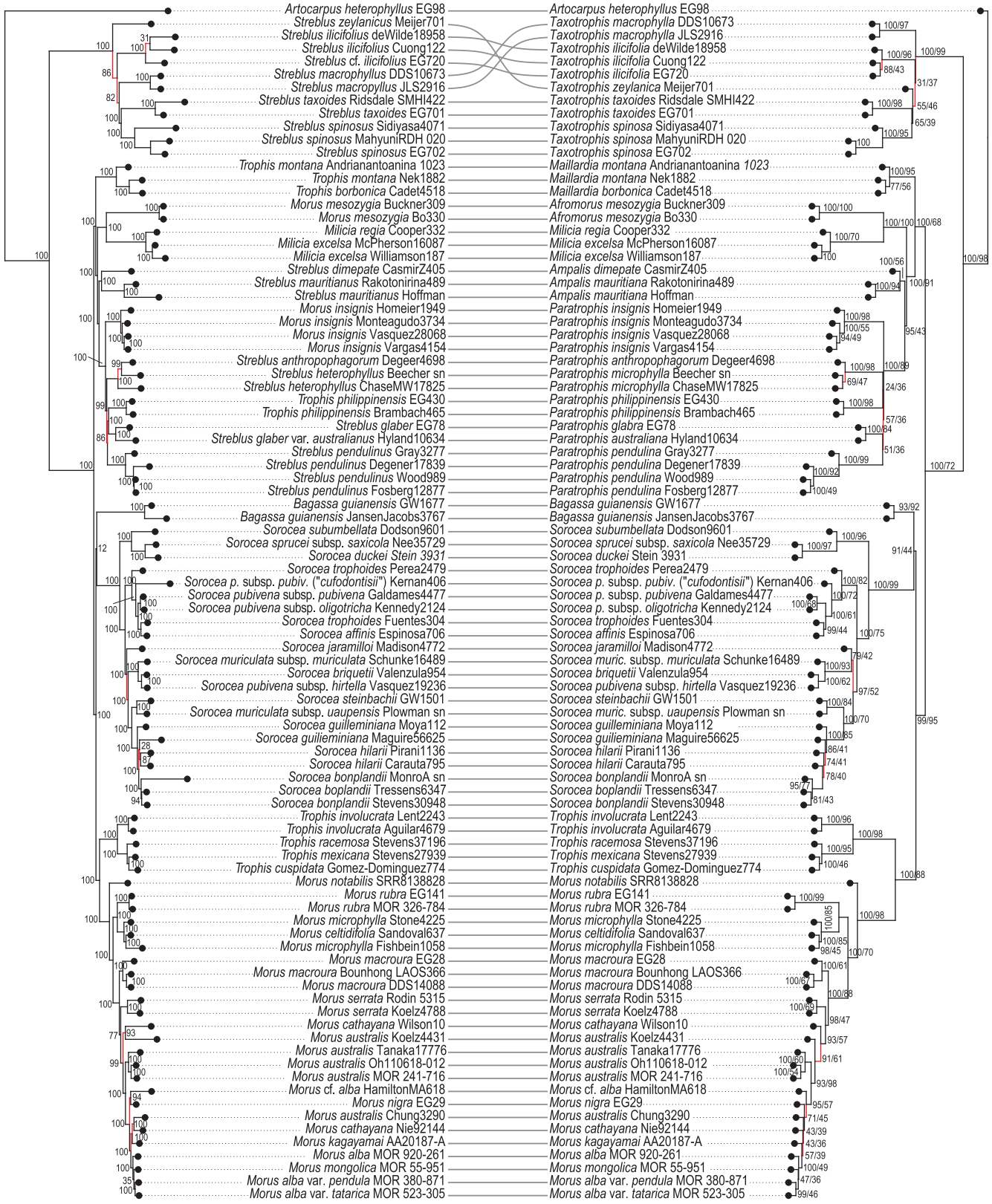

Fig. 3. Phylogenetic trees of the Moreae clade from the "supercontig" dataset. Maximum-likelihood tree based on a supermatrix of all loci, with bootstrap support and previous nomenclature (**left**), and a species tree based on gene trees from all loci with bootstrap/quartet support and revised nomenclature (**right**). Discordant branches are colored in red.

Trophis caucana. Within the Neotropical clade, *Trophis caucana* was sister to *Naucleopsis* + *Pseudolmedia* in the *Involucrata-supermatrix* analysis but was sister to all Neotropical genera except *Poulsenia* in the *Involucrata-species-tree* analysis. The polytomy hypothesis ($P < 0.05$) was rejected for all relationships except for the positions of *Poulsenia* and *Naucleopsis*.

(VIII) ITS-tree and rbcL-tree. – The ITS and *rbcL* phylogenetic trees, based on few characters, were not very well resolved, with only few nodes attaining 100% bootstrap support (suppl. Fig. S4). Nevertheless, with the exception of a few stray taxa (one *Dorstenia* sample in ITS and one *Streblus indicus* sample in *rbcL*), both phylogenetic trees reconstructed monophyletic tribes with at least moderate support. In the ITS phylogenetic tree, *Streblus smithii* and *S. banksii* were both in a well-supported clade comprising *S.* sect. *Paratrophis*. In the *rbcL* phylogenetic tree, the two *S. ascendens* samples, the four samples of the undetermined *Streblus* from Papua New Guinea, and *S. smithii* were part of a well-supported clade comprising *S.* sect. *Paratrophis*, and *S. tonkinensis*, *S. asper* and *Trophis caucana* were part of a well-supported Castilleae clade.

Time-calibration and ancestral state reconstruction. — The cross-validation criterion was minimized by a smoothing

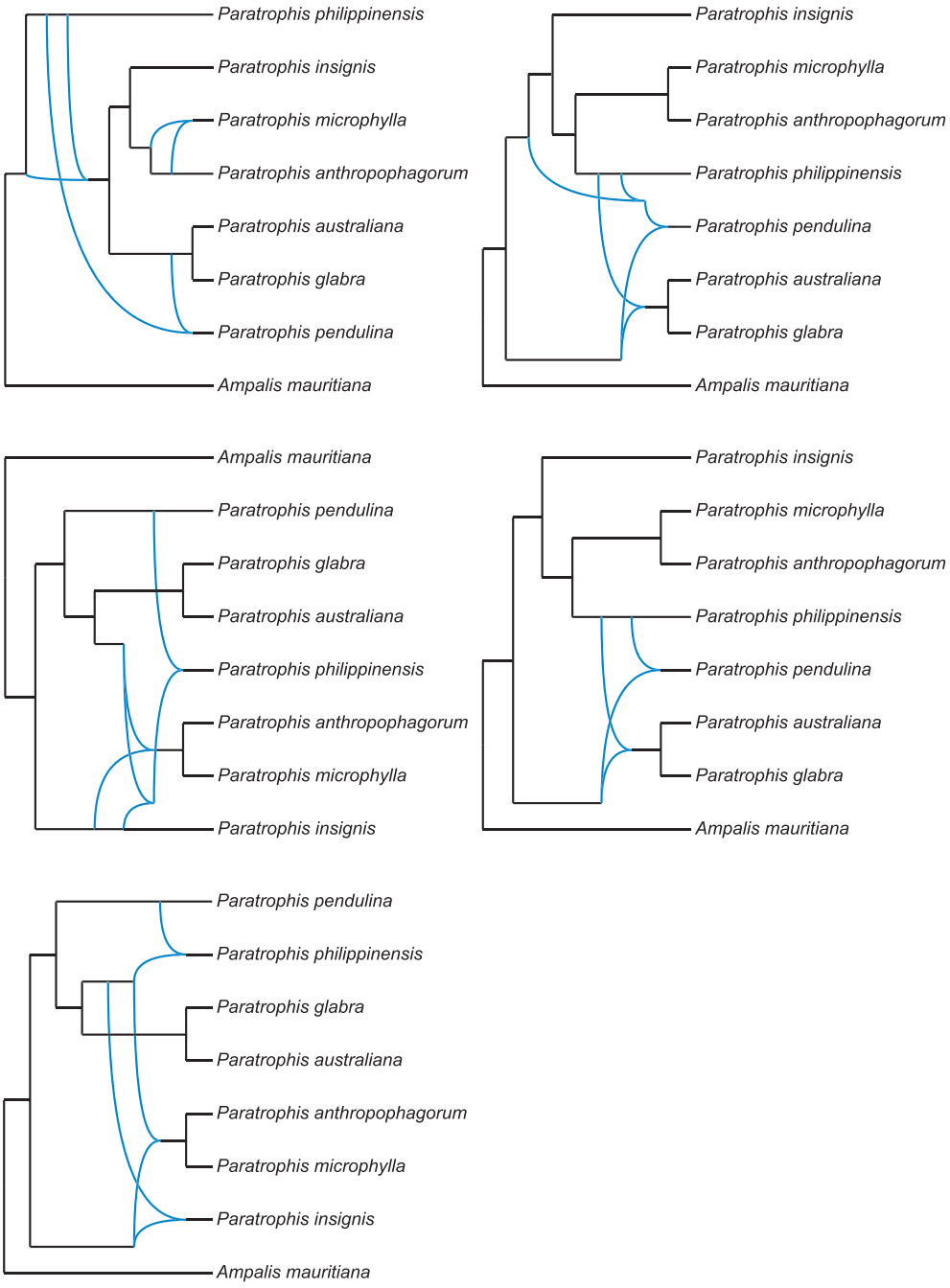

Fig. 4. The best five maximum-pseudolikelihood phylogenetic networks for the Paratrophis clade, with revised nomenclature. Blue lines represent hybridization events.

parameter (λ) value of 10. The tree with the highest likelihood score was that calibrated under the "correlated" model, closely followed by that calibrated under the "discrete" model (Table 2); we note however that scores for those two models may not be directly comparable (Paradis, 2013). The tree calibrated under the relaxed model was the poorest fit (Table 2), was much more sensitive to changes in λ than the other trees, and had perhaps implausibly long terminal branches (suppl. Fig. S5). The correlated and discrete trees had similar ages for Moreae (64.8 and 57.5 Ma, respectively) and were more consistent with past family-wide studies (Zerega & al., 2005; Q. Zhang & al., 2019).

The correlated tree was used for further analyses (Fig. 5). The BAMM analysis found a single credible rate shift, not surprisingly at the crown node of *Ficus* (suppl. Fig. S6); that rate shift was—also not surprisingly—associated with a loss of inflexed stamens, which are never found in *Ficus* ($P = 0.027$); no rate shifts were found within Moreae. Ancestral reconstruction on the entire tree found that ancestral Moraceae had stamens inflexed in bud; these were lost nine times (in Ficeae, Olmedieae [= Castilleae], Parartocarpeae, twice in Dorstenieae, *Maclura* sect. *Cudrania* (Trécul) Corner, Artocarpeae, *Bagassa*, *Sorocea*) and regained once (in *Trophis caucana*) (Fig. 6). Model testing on both the whole tree and on the Moreae + Artocarpeae + Chlorophoreae subtree indicated that a BiSSE model was not substantially better than a trait-independent model (Moreae only: AIC for BiSSE = 1110.4; trait-independent = 1112.8; ΔAIC = 2.4; whole family: AIC for BiSSE = 1552.1; trait-independent = 1555.0; ΔAIC = 2.9). In any event, the reconstructions were identical.

■ DISCUSSION

The analyses here comprise the most complete phylogenomic analysis within Moraceae to date, with species-level sampling in four out of seven tribes. Broad agreement and high statistical support across the analyses at the genus and tribe levels provide a well-supported framework for the revisions outlined below.

Sequencing and combination of datasets. — This study was materially improved by our ability to combine samples enriched with two largely nonoverlapping bait sets. Despite minimal by-design overlap, we were able to assemble many overlapping loci for samples with moderate to deep coverage (suppl. Table S2), adding taxa that would not otherwise have been included in the study and replicating taxa to confirm unexpected phylogenetic placement (e.g., *Streblus asper*). Species replicated across the two datasets performed well in phylogenetic analyses, with 15 out of 19 always resolving as monophyletic in supermatrix analyses and 18/19 monophyletic in ASTRAL analyses, with only *Utsetela gabonensis* always forming a grade instead (with a difficult-to-distinguish congener). We hope that our results embolden others to combine and repurpose datasets in similar ways.

Essential to successful combination appears to be sufficient sequence overlap and the employment of robust methodologies. In general, the species tree method (ASTRAL) appeared to be more robust to missing data overall than the supermatrix method. For example, three species with 28–56 overlapping loci were monophyletic in the *exon-species-tree* analysis but not in the *exon-supermatrix* analysis. The Castilleae topology in the *Involucrata-species-tree* analysis was also more consistent with a recent well-sampled study (Clement & al., 2020) than the *Involucrata-supermatrix* analysis. But there is a limit, evidenced perhaps by the nonmonophyly of *Dorstenia* in the *exon-species-tree* analysis, where the two samples had 6 loci overlapping. That genus was monophyletic in the *exon-supermatrix* analysis, perhaps because the six loci taken together had enough characters to unite the samples, but the six individual gene trees were not sufficiently informative. We thus recommend that both supermatrix and species-tree

Table 2. Divergence times (in Ma) estimated using penalized likelihood under the three tested models.

Clade	Discrete logLik = −22.3 p-logLik = −17 ΦIC = 437	Correlated logLik = −16.7 p-logLik = −16.7 ΦIC = 1095	Relaxed logLik = −28.7 p-logLik = −1059 ΦIC = 1193
Moraceae	84.7	84.7	84.7
Parartocarpeae	75.7	75.3	14.1
Ficeae	24.0	30.7	43.3
Olmedieae	36.5	39.1	46.1
Dorstenieae	73.6	67.6	82.5
Maclureae	44.3	54.8	24.8
Artocarpeae	64.0	64.0	78.5
Moreae	57.5	64.8	83.0

Taxonomy follows the revisions proposed in this study.
logLik, log-likelihood; p-logLik, penalized log-likelihood; ΦIC, Phylogenetic information criterion.

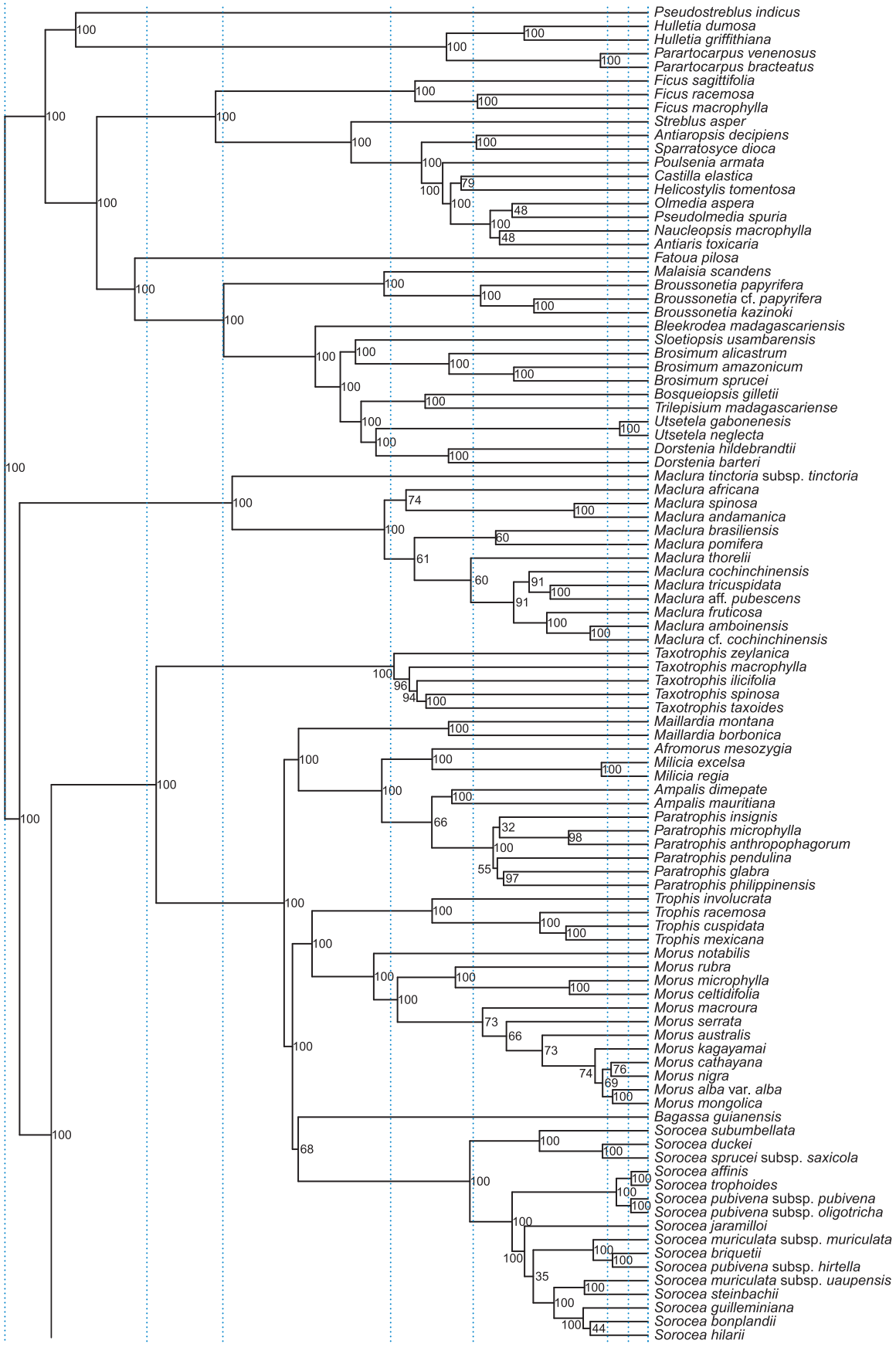

Fig. 5. Time-calibrated phylogenetic tree under the correlated model, with revised nomenclature.

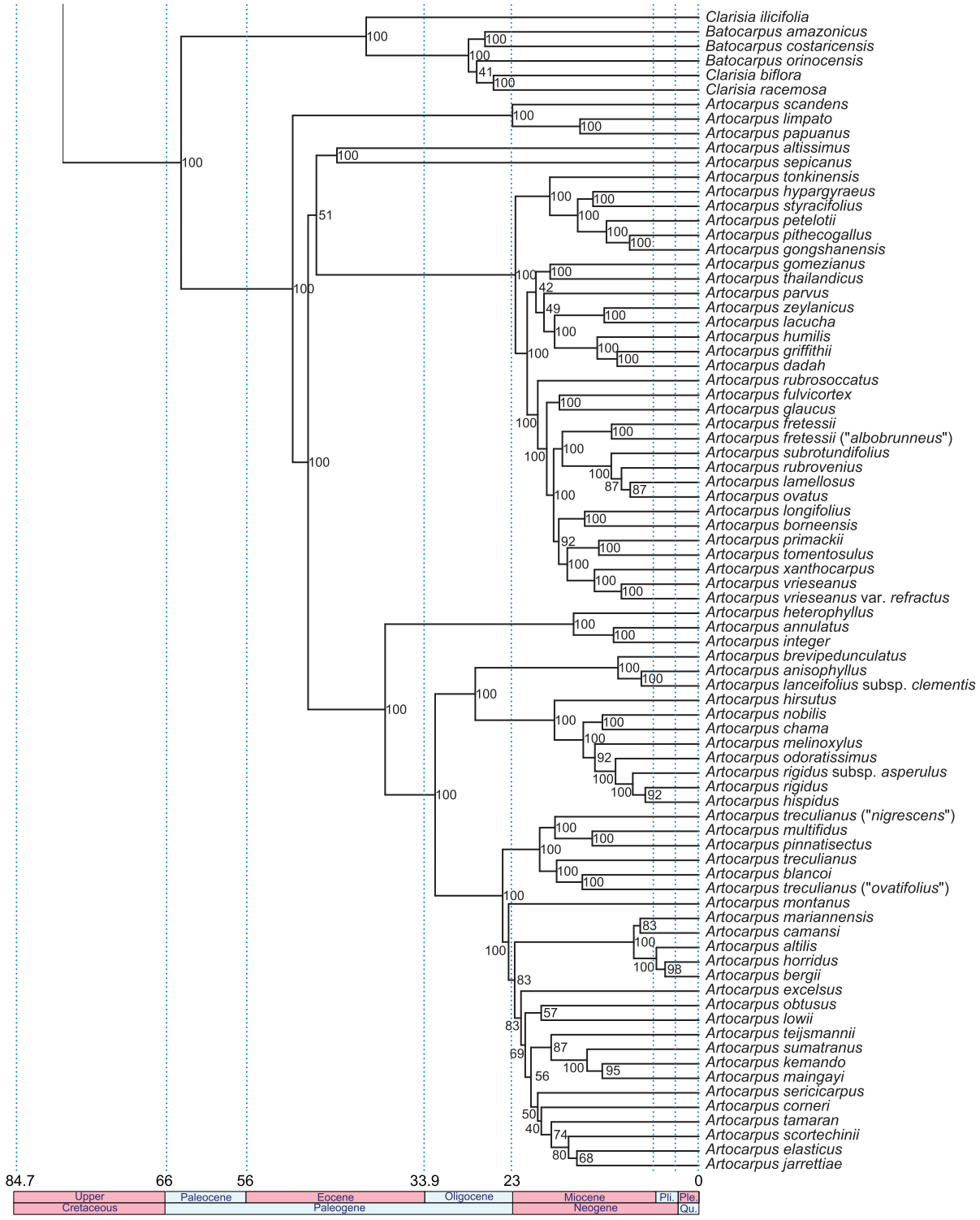

Fig. 5. Continued.

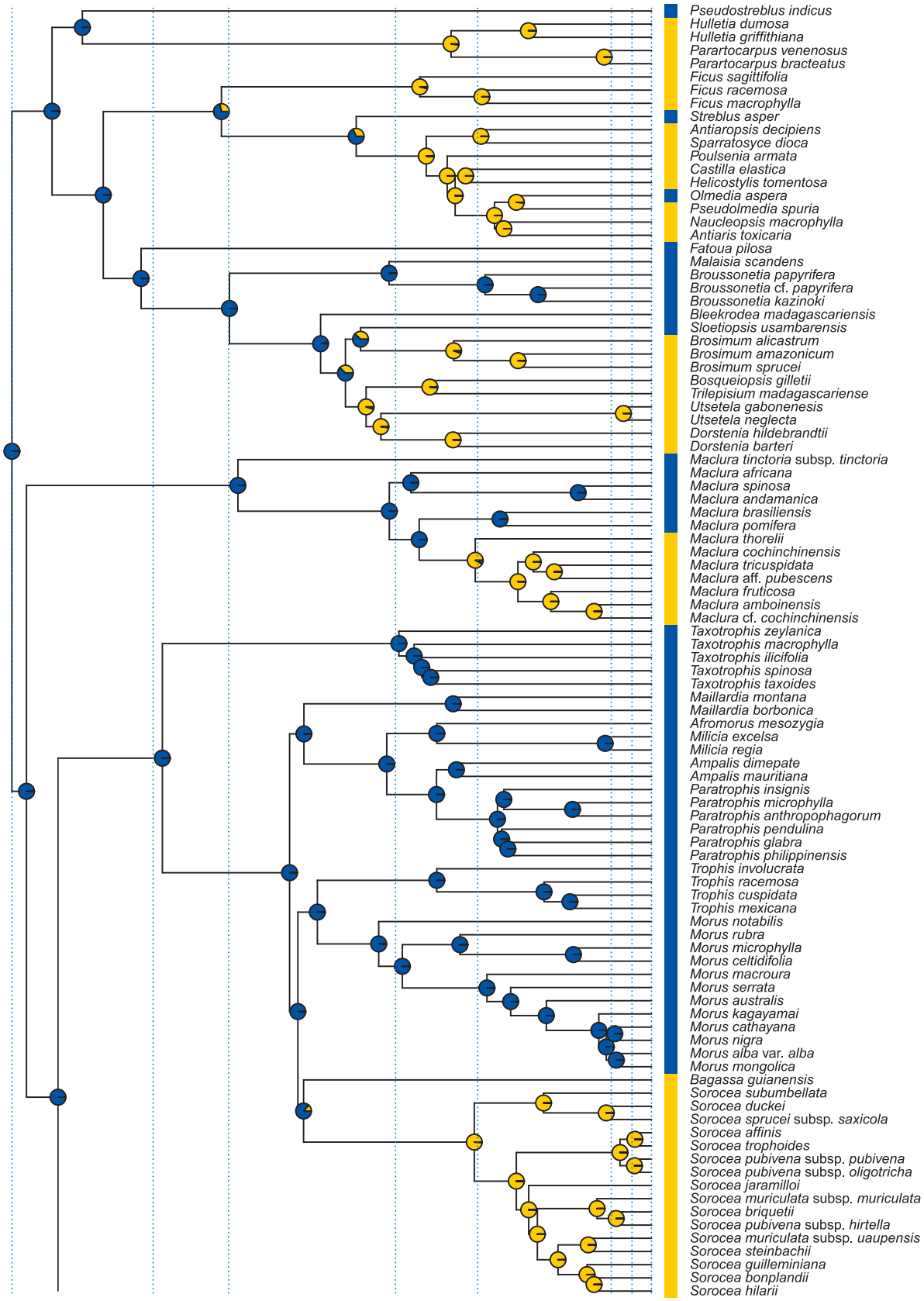

Fig. 6. Ancestral reconstruction of stamen position, with revised nomenclature. The reconstruction was identical under a trait-dependent (BiSSE) or a trait-independent model. Blue = inflexed in bud; yellow = straight in bud.

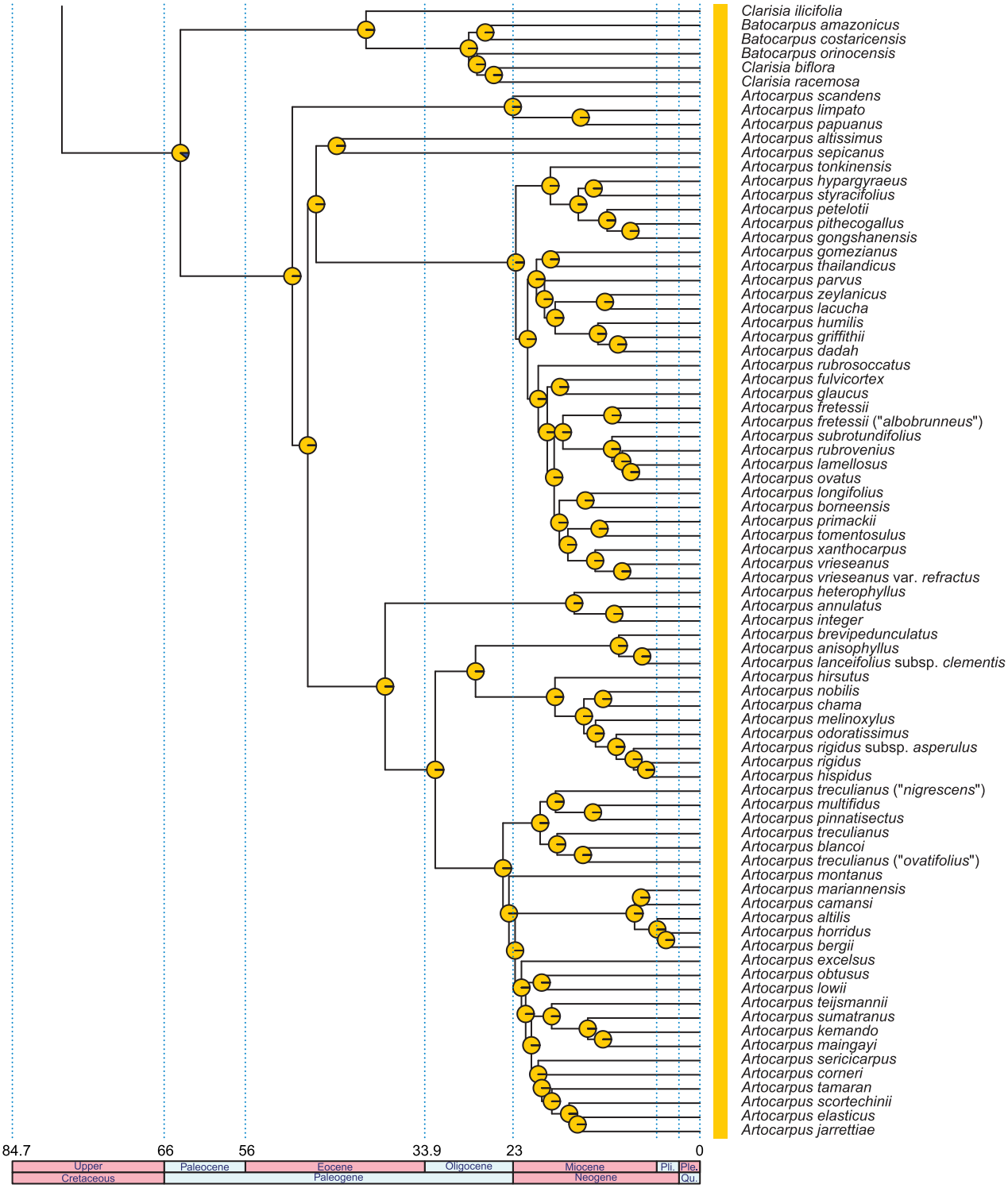

Fig. 6. Continued.

analyses be employed and compared when combining datasets in this manner.

Higher taxonomy in Moraceae and the delimitation of the tribe Moreae. — Our results support Corner's overall approach to the classification of Moraceae, if not all of its details, including the primacy of inflorescence architecture and the unreliability of inflexed stamens for higher taxonomy (Corner, 1962). Inflexed stamens are a plesiomorphy that was lost nine times in Moraceae (Fig. 6), a preserved ancestral character whose past taxonomic importance accounts for the rather extreme nonmonophyly of the Moreae. *Streblus* s.l. provides the best illustration of this principle, appearing in four out of seven tribe-level clades within Moraceae. We may justly call its disparate sections, as Corner did, "fragments of an ancestral *Streblus*" (Corner, 1975)—or in modern parlance, a paraphyletic remnant preserving plesiomorphic staminate flowers similar to those likely to have occurred in the ancestor of all Moraceae, with four free tepals and four inflexed stamens (Clement & Weiblen, 2009). If one of the goals of modern systematics is to establish taxonomic frameworks that reflect as far as possible real evolutionary relationships, our results may serve as a warning to carefully investigate whether characters used for taxonomy are derived (synapomorphic) or ancestral (symplesiomorphic).

Broadly speaking, a tribal delimitation based on inflorescence architecture (supplemented with other characters in some cases) agrees best with the phylogenetic trees presented here. Moreae (as revised below) have unisexual spicate or racemose inflorescences (the pistillate ones sometimes uniflorous), with the globose-capitate pistillate inflorescences of the monotypic *Bagassa* as the sole exception. Stamens may be either inflexed or straight. Elsewhere in the family, racemes and spikes are rare, with the former found in *Maclura* (in part) and the latter found in the related genera *Broussonetia*, *Allaeanthus* Thwaites, and *Malaisia* and arguably in *Batocarpus* H.Karst. and *Clarisia*; all of these have capitate pistillate inflorescences. The taxa of *Streblus* s.l. and *Trophis* s.l. that must be excluded from Moreae all have inflorescences that do not fit our general rule: discoid-capitate (*Streblus asper*, *Trophis caucana*), cymose (*Streblus indicus*), or (sometimes) bisexual (*Streblus usambarensis*). In these cases, perhaps Corner did not follow his own belief in the primacy of inflorescence architecture quite far enough, including too much variety in this one tribe. In critiquing the utility of inflorescence architecture for classification, Berg (1977b) noted the similarity in the inflorescence structure of *Bleekrodea* (then part of Moreae, and included in *Streblus* by Corner) to that of *Utsetela* and *Helianthostylis* Baill. (= *Brosimum* subg. *Helianthostylis* (Baill.) E.M.Gardner & Zerega) (Dorstenieae), an observation that proved prescient when *Bleekrodea* was found to belong to Dorstenieae (Clement & Weiblen, 2009).

Olmedieae (as revised below, including Castilleae) can be defined entirely based upon the presence of a discoid inflorescence subtended by an involucre of imbricate bracts. Two species with such involucres previously classified as Moreae, *Streblus asper* (rudimentary) and *Trophis caucana* (= *Olmedia aspera*) (well developed) always appeared in the Olmedieae (= Castilleae) clade in our analyses (Figs. 2, 3). *Olmedia aspera* (= *Trophis caucana*)—the nomenclatural type of the tribe Olmedieae—was transferred to Moreae because of its inflexed stamens and lack of self-pruning branches (Berg, 1977b). In inflorescence morphology, however, *T. caucana* closely resembles other Castilleae, always subtended by an involucre of imbricate bracts (Berg, 1977b, 2001). The staminate inflorescences of *Streblus asper* are strikingly similar to those of *T. caucana*, and it is remarkable that the affinity between *S. asper* and the Olmedieae has not been seriously considered until now. Previous barcoding or phylogenetic studies have placed *Trophis caucana* (Kress & al., 2009) and *Streblus tonkinensis* (Chen & al., 2016) (closely allied to *S. asper*) in the Castilleae clade, but those results went unremarked upon, perhaps because of the broad scale of the studies (respectively, forest community phylogenetics and the vascular plants of China).

The remaining five tribes can all be broadly defined based on inflorescence architecture as Corner argued, sometimes supplemented by other characters as Berg preferred, allowing of course for the exceptions made inevitable by the vicissitudes of evolution. Ficeae of course is defined by the syconium (essentially an urceolate disc that has been closed at the top) and together with Olmedieae comprises the Involucrata clade (Clement & al., 2020). Chlorophoreae have densely packed globose infructescences and can be distinguished from Artocarpeae by their four stamens (inflexed in most sections) and armature. Artocarpeae also have densely packed globose infructescences but only one straight stamen and no armature. Parartocarpeae have a few connate involucral bracts and (in large part) flowers embedded in fleshy receptacles. Dorstenieae are perhaps the most heterogeneous group, but in large part they have bisexual inflorescences, often capitate or discoid, and often with ballistically ejected endocarps.

The role of inflexed stamens in the evolution of Moraceae. — The repeated losses of inflexed stamens (Fig. 6), which are associated with wind pollination (Bawa & Crisp, 1980; Berg, 2001), raise the possibility that transitions from wind to animal pollination, which have already been documented in Moraceae (Momose & al., 1998; Sakai & al., 2000; Datwyler & Weiblen, 2004; Gardner & al., 2018), are even more common within the family. Generally considered rare (Culley & al., 2002), the shift from wind to animal pollination may be a repeated feature of Moraceae deserving of further investigation. Further investigation of *Sorocea*, with its straight stamens and sometimes-scented inflorescences, may reveal that, like *Artocarpus*, it contains both wind and animal pollination. And while little is known about pollination in the Dorstenieae, the presence of unisexual inflorescences and inflexed stamens (e.g., *Broussonetia*) as well as bisexual inflorescences with straight stamens (e.g., *Brosimum*, *Dorstenia*) raises the possibility of transitions within that clade as well; taxa with inflexed stamens but bisexual inflorescences such as *Bleekrodea* and *Sloetia* (the latter of which is visited by bees, E.M. Gardner, pers. obs.) may represent remnants of an intermediate state. *Pseudostreblus*, which has inflexed stamens but fragrant

flowers (fide *W. Tsang 24252*, F) and is sister to the straight-stamen *Parartocarpus* and *Hullettia* clade, also warrants investigation. Finally, the conclusion that a single transition to insect pollination preceded the split between the Ficeae and Olmedieae (Castilleae) should be re-evaluated in light of the position of *Streblus asper* as sister to the latter (Figs. 2, 3). The only shift in diversification rates our analyses recovered was on the branch leading to the very diverse *Ficus*, suggesting that the shift away from wind pollination may not by itself lead to increased diversification.

Explanation of taxonomic revisions. — We present a generic revision of Moreae (Fig. 7) based on the present phylogenetic study as well as morphological characters. Arranging monophyletic and morphologically coherent genera requires one new genus and nine new combinations, but no new epithets. Four taxa are transferred to other tribes, one of which (Castilleae) must revert to its previous name (Olmedieae). These revisions provide a framework for within-genus revisionary work, which will require more intensive sampling and review of specimens within the genera circumscribed here, as well as further exploration of the areas of disagreement between analyses (for example, within *Paratrophis* and *Taxotrophis*). We provide an explanation of the taxonomic changes, followed by a formal presentation of the affected tribes and genera, with complete species lists and synonymy.

Reinstatement of Olmedieae. — As detailed above, *Trophis caucana* fell within the Castilleae with high support in all analyses in which it was included here (*exon-supermatrix*, *exon-species-tree*, *plastome*, *rbcL*) as well as in a previous study (Kress & al., 2009), and we are unaware of any countervailing phylogenetic evidence. Moreover, its involucrate morphology is typical of Castilleae. We therefore exclude it from *Trophis*, reinstating its previous name *Olmedia aspera*, and transfer it to Castilleae. Because the tribe name Olmedieae, typified by *Olmedia*, has priority over Castilleae, that too must be reinstated. We note, however, that should a pending

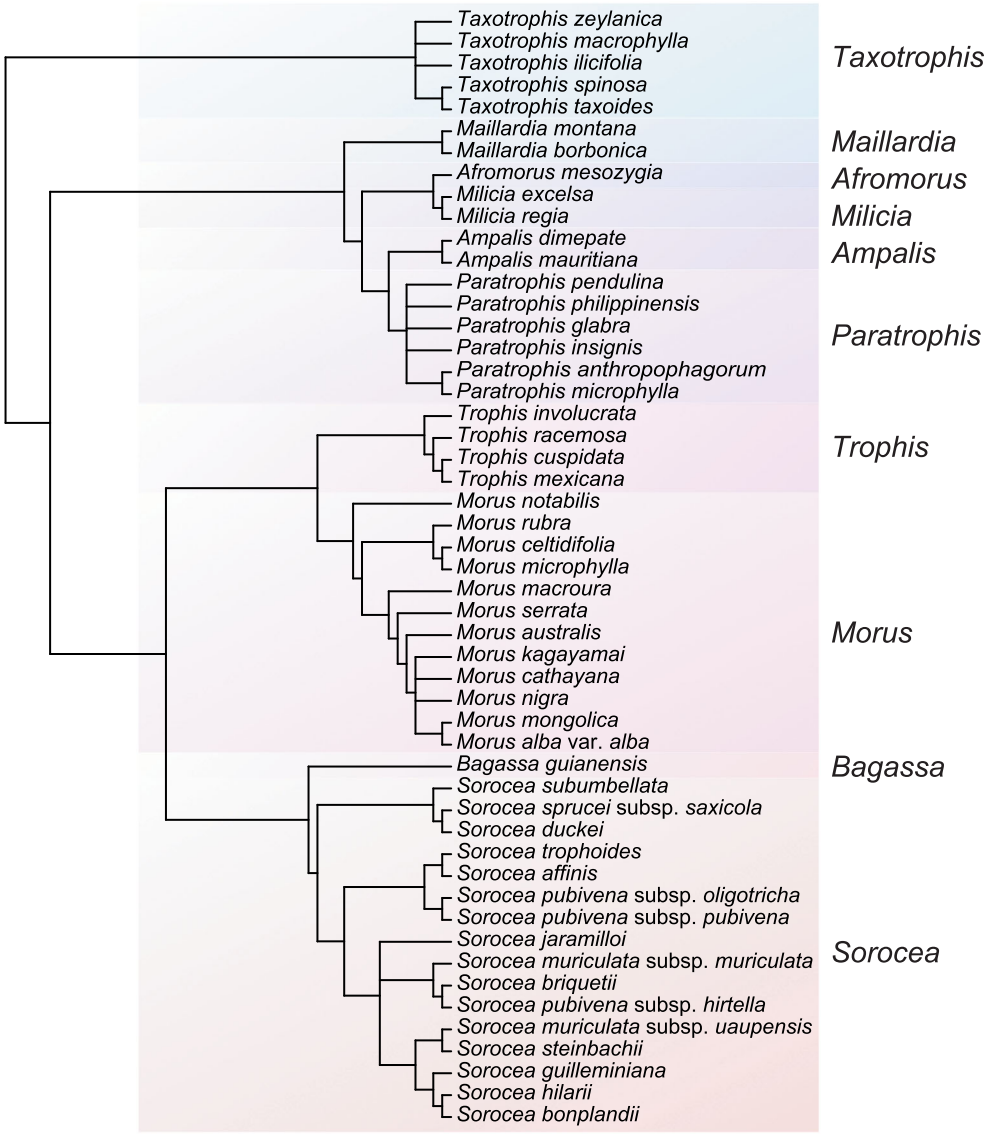

Fig. 7. Revised classification of Moreae on a strict consensus tree of all four main phylogenomic analyses (*exon-supermatrix*, *exon-species-tree*, *supercontig-supermatrix*, *supercontig-species-tree*).

nomenclatural proposal fail, the name must instead revert to Antiarideae Dumort. (nom. utique rej. prop.), which has ultimate priority (Gardner & al., 2020).

***Trophis*. —** To make *Trophis* monophyletic, we propose that it be applied strictly to the Neotropical clade that includes the type *Trophis americana* L. (= *Trophis racemosa* (L.) Urb.). To accomplish this, we reinstate the genus *Maillardia* and transfer *Trophis philippinensis* to *Paratrophis* (discussed below), reinstating its former name *Paratrophis philippinensis* (Bureau) Fern.-Vill. In addition, *Trophis caucana* must be excluded, as discussed above.

***Streblus*. —** We restrict the genus *Streblus* to three species comprising most of *Streblus* sect. *Streblus*—*S. asper*, *S. celebensis* C.C.Berg, and *S. tonkinensis*—and transfer the genus to Olmedieae. As detailed above, this placement is supported by inflorescence morphology, all analyses here, as well as a previous study (Chen & al., 2016), and we are unaware of any countervailing phylogenetic evidence. Although *S. celebensis* was not included in our phylogeny, the subinvolucrate inflorescences are similar to those of *S. asper*, with which *S. celebensis* differs primarily in vegetative characters, the latter having broadly toothed margins in the distal half of the leaf. Both occur in Sulawesi, where at least one specimen with intermediate leaf morphology has been collected (Sulawesi, Kendari: *Kjellberg 452*, 24 Feb 1929, L, det. *S. asper* by E.J.H. Corner). We therefore retain its taxonomic position in *Streblus*.

Streblus usambarensis fell within the Dorstenieae in all of our analyses, and we are unaware of any countervailing evidence. It is morphologically similar to *Sloetia* (Dorstenieae), with nearly amplexicaul stipules and a fleshy dehiscent exocarp that ejects the endocarp body at maturity—a distinctive character typical of many Dorstenieae. Berg (1977a) noted an alliance based on this character between *Sloetiopsis usambarensis*, *Sloetia*, *Fatoua*, and *Bleekrodea*, observing that Bureau had previously classified all four in Dorstenieae (Bureau, 1873). The latter three were restored to Dorstenieae by Clement & Weiblen (2009). We reinstate *Sloetiopsis usambarensis* Engl. and transfer it to Dorstenieae, reuniting the quartet.

Streblus indicus, remarkable in Moraceae for its 5-parted staminate flowers, was sister to Parartocarpeae in our nuclear phylogenomic analyses (*exon-supermatrix*, *exon-species-tree*); however, it formed a grade with Parartocarpeae in the *plastome* analysis. In a previously published whole-chloroplast study, its position—sister to Dorstenieae + Olmedieae + Ficeae—could be consistent with either result because no members of Parartocarpeae were included. What appears certain is that it does not belong in Moreae and that its closest allies are *Parartocarpus* and *Hullettia*, with which it shares a small involucre of a few connate bracts (not imbricate as in Olmedieae). We therefore reinstate its previous name *Pseudostreblus indicus* Bureau and transfer it to Parartocarpeae.

The remaining species of *Streblus* s.l. are properly placed in Moreae but are still paraphyletic. We therefore reinstate the genera *Ampalis*, *Paratrophis*, and *Taxotrophis*, largely corresponding to Berg's sections but requiring some new combinations. *Paratrophis* as understood here is united by spicate staminate and (usually) pistillate inflorescences with peltate or reniform bracts, mostly without fleshy enlarged tepals in fruit. Within *Paratrophis* we follow Corner (1975) and include *Paratrophis ascendens* (Corner) E.M.Gardner (= *Streblus ascendens* Corner) based on its inflorescence morphology and phylogenetic position in the *rbcL* tree (suppl. Fig. S4B). Corner (1970) and Berg (1988) included this species in the monotypic *Protostreblus* due to the type specimen's spiral phyllotaxy, but the latter may be atypical, as a more recent collection (*Womersley NGF 24791* [BO, K, L]) has distichous leaves.

Berg (1988), recognizing the close affinity between *Pachytrophe dimepate* Bureau and *Ampalis mauritiana*, included both in *Streblus* sect. *Ampalis*. Our phylogenetic results support this grouping, which we maintain in the reinstated genus *Ampalis*, requiring one new combination. We follow Baillon in maintaining *Pachytrophe* as a section of *Ampalis* in order to recognize the differences between them in phyllotaxy, stipule amplexicaulity, and embryo characters. Further intensive study of these species may ultimately warrant a different approach, including potentially reducing both to a section of *Paratrophis*.

Our species concepts within *Taxotrophis* and *Paratrophis* follow Berg's (1988; Berg & al., 2006) approach, with two exceptions. We provisionally recognize *Taxotrophis zeylanica* (Thwaites) Thwaites as distinct from *T. taxoides* (B.Heyne ex Roth) Chew ex E.M.Gardner (= *Streblus taxoides* (B.Heyne ex Roth) Kurz) following the *Flora of China*, which recognizes *Streblus zeylanicus* as distinct from *S. taxoides* based on its clustered pistillate inflorescences. This separation is consistent with our analyses, although maintaining a broad *T. taxoides* would not be inconsistent with the *supermatrix-species-tree* and *plastome* trees. In addition, we provisionally recognize *Paratrophis australiana* (= *S. glaber* subsp. *australianus*) as distinct from *Paratrophis glabra* based on its geographic and consistent morphological distinctiveness. *Taxotrophis* and *Paratrophis* warrant further investigation to refine species limits.

***Morus*. —** *Morus* is in need of revision. Species concepts within the genus are often based on minor morphological differences (Berg, 2001; Berg & al., 2006), and the paraphyly of several species in our analyses suggests that a broad *M. alba* similar to Bureau's (1873) may be worth a second look. *Morus mesozygia*, sole member of the not validly published "*M.* subg. *Afromorus*", was sister to *Milicia* in our analyses, but the leaf morphology is markedly different, instead resembling other *Morus* species in its trinerved based and crenate margins. We therefore describe the new genus *Afromorus* to accommodate this species. *Morus insignis*, from western Central and South America, bears a remarkable resemblance to *Paratrophis*, in particular *P. pendulina*, especially in leaf morphology, which in *M. insignis* is not consistently trinerved as in other mulberries. The infructescence appears superficially like a mulberry because of its basally fleshy tepals, although with more loosely packed flowers, but closer inspection places it firmly within *Paratrophis*, with drupes protruding from the persistent tepals, peltate bracts, and a sterile groove. Because

analyses differ as to whether *M. insignis* is sister to *Paratrophis* or part of it, it seems safest to treat it as a member of *Paratrophis* for the time being, rather than erecting a monotypic genus for it.

These changes result in 10 monophyletic genera of Moreae, providing a framework for revisionary work within the genera. Below, we present a complete genus and species list for Moreae with brief descriptions for all genera and synonymies for new combinations and reinstated or recircumscribed taxa. All cited protologues were reviewed, and dates for works published piecemeal were confirmed by reference to *TL-2* (Stafleu & Cowan, 1976–2009).

■ TAXONOMIC REVISIONS

Key to the tribes of Moraceae. — This key follows the tribal circumscription of Clement & Weiblen (2009), as subsequently modified by Zerega & al. (2010), Chung & al. (2017), Zerega & Gardner (2019), and this study.

1. Inflorescence a syconium (urceolate with the opening entirely closed by ostiolar bracts, flowers enclosed at all stages of development)……**Ficeae** (*Ficus*)
1. Inflorescence not a syconium (capitate, spicate, discoid, or urceolate, but flowers not entirely enclosed at all developmental stages)……2
2. Inflorescences (at least staminate) with an involucre of imbricate bracts; often with self-pruning horizontal branches (except *Olmedia*, *Poulsenia*, *Streblus*)……**Olmedieae** (*Antiaris*, *Antiaropsis*, *Castilla*, *Helicostylis*, *Maquira*, *Mesogyne*, *Naucleopsis*, *Olmedia*, *Perebea*, *Poulsenia*, *Pseudolmedia*, *Sparattosyce*, *Streblus*)
2. Inflorescences not involucrate or involucre with few non-overlapping bracts; plants without self-pruning branches……3
3. Plants woody; dioecious; pistillate inflorescences globose-capitate; spines axillary or terminating short shoots……**Chlorophoreae** (*Maclura*)
3. Plants woody, herbaceous, or succulent; dioecious or monoecious; pistillate inflorescences various; spines absent or if present, then pistillate inflorescences not globose capitate……4
4. Trees or shrubs; monoecious; inflorescences unisexual; staminate flowers with 1 stamen (rarely 2)……**Artocarpeae** (*Artocarpus*, *Batocarpus*, *Clarisia*)
4. Trees, shrubs, lianas, herbaceous, or succulent; monoecious or dioecious; inflorescences unisexual or bisexual; staminate flowers with more than 1 stamen (or if 1stamen then dioecious)……5
5. Trees or shrubs; monoecious; inflorescences unisexual; stamens straight in bud or staminate flowers 5-parted and inflexed in bud……**Parartocarpeae** (*Hullettia*, *Parartocarpus*, *Pseudostreblus*)
5. Trees, shrubs, lianas, herbaceous, or succulent; monoecious or dioecious; inflorescences bisexual or unisexual; stamens straight or inflexed in bud but staminate flowers never 5-parted……6
6. Trees, shrubs, lianas, herbaceous, or succulent; inflorescences bisexual (or if unisexual then a climber or herbaceous); endocarp body often ballistically ejected from infructescence……**Dorstenieae** in part (*Allaeanthus* in part, *Bleekrodea*, *Bosqueiopsis*, *Brosimum*, *Broussonetia* in part, *Dorstenia*, *Fatoua*, *Malaisia*, *Scyphosyce*, *Sloetia*, *Sloetiopsis*, *Treculia*, *Trilepsium*, *Utsetela*)
6. Trees or shrubs; inflorescences unisexual; endocarp body never ballistically ejected……7
7. Trees; stamens inflexed in bud; pistillate inflorescences globose-capitate……**Dorstenieae** in part (*Allaeanthus* in part, *Broussonetia* in part)
7. Trees or shrubs; stamens inflexed or straight in bud; pistillate inflorescences various, not globose-capitate if stamens are inflexed in bud……**Moreae** (*Afromorus*, *Ampalis*, *Bagassa*, *Maillardia*, *Milicia*, *Morus*, *Paratrophis*, *Taxotrophis*, *Sorocea*, *Trophis*)

Tribe MOREAE

Moreae Dumort., Anal. Fam. Pl.: 17. 1829 – Type: *Morus* L. = [Moreae] subtr. Soroceae Miq. in Martius, Fl. Bras. 4(1): 111. 1853 ≡ tr. Soroceae Bureau in Candolle, Prodr. 17: 283. 1873.

Monoecious or dioecious trees or shrubs. *Leaves* alternate or opposite, distichous or spirally arranged; stipules lateral to amplexicaul. *Inflorescences* unisexual, uniflorous or racemose, spicate, capitate, or globose; bracteate; tepals 4, free to connate; staminate flowers with 4 stamens, filaments straight or inflexed in bud, pistillode usually present; pistillate flowers with (mostly) free ovary, 2 stigmas. *Fruits* drupaceous or achene-like with a fleshy persistent perianth, dehiscent or not. *Seeds* with or without endosperm, testa usually with a thick vascularized part below the hilum, cotyledons equal or unequal, straight or folded.

Genera and distribution: 10 genera (*Afromorus*, *Ampalis*, *Bagassa*, *Maillardia*, *Milicia*, *Morus*, *Paratrophis*, *Sorocea*, *Taxotrophis*, *Trophis*) and 66 species with a worldwide distribution.

Afromorus

Afromorus E.M.Gardner, **gen. nov.** – Type: *Afromorus mesozygia* (Stapf) E.M.Gardner (≡ *Morus mesozygia* Stapf).

Dioecious trees, shoot apices deciduous. *Leaves* distichous, triplinerved or at least trinerved at the base. *Stipules* free, more or less lateral. *Inflorescences* solitary or paired, bracts of varying shapes. Staminate inflorescences spicate, to 2.5 mm long, flower 4-parted, tepals imbricate, ciliolate, pistillode small, apiculate. Pistillate inflorescences subglobose, ca. 5 mm across, flowers 4-parted, tepals ciliolate, stigma bifid, equal or unequal, arms filiform to 5 mm long. *Infructescences* subglobose or less often slightly elongate, ca. 1 mm

across, tepals fleshy, yellowish to greenish, drupes ca. 5 × 3–5 mm. *Seeds* ca. 4.5 × 2.5–4.5 mm.

Species and distribution: 1 species, in tropical Africa.

Note: The leaves of *Afromorus*—with crenate margins and trinerved bases—bear a striking resemblance to those of *Morus*, and it is thus not surprising that the former was heretofore included within the latter. However, leaves of *Afromorus* are distinct in being usually completely triplinerved, without an upper pinnately veined portion as in most species of *Morus*. The name of the new genus is based on "*Morus* subg. *Afromorus* A.Chev. ex J.-F.Leroy". However, the latter was not validly published as neither Chevalier's initial (Chevalier, 1949) publication nor Leroy's two subsequent papers (Leroy, 1949a,b) contained the necessary Latin description, and it is therefore not available for use as a formal basionym.

1. ***Afromorus mesozygia*** (Stapf) E.M.Gardner, **comb. nov.** ≡ *Morus mesozygia* Stapf in J. Bot. (Morot), ser. 2, 2: 99. Apr 1909.

= *Celtis lactea* Sim, Forest Fl. Port. E. Afr.: 97, t. 96. Sep 1909 ≡ *Morus lactea* (Sim) Mildbr. in Notizbl. Bot. Gart. Berlin 8: 243. 1922 ≡ *Morus mesozygia* var. *lactea* (Sim) A.Chev. in Rev. Bot. Appl. Agric. Trop. 29: 72. 1949. Figure 8.2.

Ampalis

Ampalis Bojer ex Bureau in Candolle, Prodr. 17: 250. 1873 ≡ *Streblus* sect. *Ampalis* (Bojer ex Bureau) C.C.Berg in Proc. Kon. Ned. Akad. Wetensch. C 91(4): 358. 1988 – Type: *Ampalis madagascariensis* Bojer (= *Ampalis mauritiana* (Jacq.) Urb.).

= *Streblus* subg. *Parastreblus* Blume, Mus. Bot. 2: 89. 1856 – Type: *Streblus mauritianus* (Jacq.) Blume (≡ *Ampalis mauritiana* (Jacq.) Urb.).

– "*Ampalis* Bojer", Hortus Maurit.: 291. 1837, not validly published.

Dioecious trees or shrubs. *Leaves* distichous to spirally arranged, pinnately veined. *Stipules* free, nearly lateral. *Inflorescences* solitary or paired in the leaf axils, spicate, with an abaxial sterile groove, flowers in longitudinal rows, bracts basally attached to subpeltate. Staminate inflorescences to 9 cm long, flowers 4-parted, decussate-imbricate, stamens 4, inflexed in bud, pistillode present. Pistillate inflorescences to 12 cm long, tepals 4, separate, decussate-imbricate, ovary free, stigmas 2, equal. *Infructescences* with enlarged fleshy perianths ca. 6–8 mm long, surrounding drupaceous fruits, the latter ca. 5–6 mm long. *Seeds* ca. 4 × 4 mm, testa thickened and not distinctly vascularized, cotyledons equal.

Species and distribution: 2 species, native to Madagascar and the Comoros.

Note: The two sections differ in their phyllotaxy (usually spiral in *Ampalis* and distichous in *Pachytrophe*) and stipules (free in *Ampalis*, connate in *Pachytrophe*). *Ampalis* sect. *Ampalis* usually has somewhat larger inflorescences.

Ampalis sect. ***Ampalis***

1. ***Ampalis mauritiana*** (Jacq.) Urb., Symb. Antill. 8: 165. 1920 ≡ *Morus mauritiana* Jacq., Collectanea 3: 206. 1791 ≡ *Streblus mauritianus* (Jacq.) Blume, Mus. Bot. 2: 80. 1856.

= *Morus nitida* P.Willemet in Ann. Bot. (Usteri) 18: 56. 1796.

= *Morus ampalis* Poir. in Lamarck, Encycl. 4: 380. 1797.

= *Trophis cylindrica* Roxb., Fl. Ind., ed. 1832, 3: 599. 1832, nom. illeg., pro syn.

= *Ampalis madagascariensis* Bojer, Hortus Maurit.: 291. 1837, nom. illeg.

= *Morus rigida* Hassk., Pl. Jav. Rar.: 198. 1848.

= *Streblus maritimus* Palacký, Catal. Pl. Madagasc. 2: 31. 1907.

= *Ampalis madagascariensis* var. *occidentalis* Leandri in Mém. Inst. Sci. Madagascar, Sér. B, Biol. Vég. 1: 12. 1948. Figure 9.1.

Ampalis sect. ***Pachytrophe*** (Bureau) Baill., Hist. Pl. 6: 191. 1875 ≡ *Pachytrophe* Bureau in Candolle, Prodr. 17: 234. 1873 – Type: *Pachytrophe dimepate* Bureau.

2. ***Ampalis dimepate*** (Bureau) E.M.Gardner, **comb. nov.** ≡ *Pachytrophe dimepate* Bureau in Candolle, Prodr. 17: 234. 1873 ≡ *Streblus dimepate* (Bureau) C.C.Berg in Proc. Kon. Ned. Akad. Wetensch. C 91(4): 358. 1988.

= *Pachytrophe obovata* Bureau in Candolle, Prodr. 17: 235. 1873.

= *Plecospermum (?) laurifolium* Baill. in Grandidier, Hist. Phys. Madagascar: t. 294A. 1895 ≡ *Pachytrophe obovata* var. *laurifolia* (Baill.) Leandri in Mém. Inst. Sci. Madagascar, Sér. B, Biol. Vég. 1: 16. 1948.

= *Pachytrophe obovata* var. *montana* Leandri in Mém. Inst. Sci. Madagascar, Sér. B, Biol. Vég. 1: 16. 1948.

Bagassa

Bagassa Aubl., Hist. Pl. Guiane 2, Suppl.: 15 & 4: t. 376. 1775 – Type: *Bagassa guianensis* Aubl.

Dioecious trees. *Leaves* opposite and decussate, lamina triplinerved, 3-lobed to entire. *Stipules* free, lateral. *Inflorescences* solitary or paired in the leaf axils, bracteate. Staminate inflorescences spicate with an abaxial sterile groove, to 12 cm long, flowers in longitudinal rows with, tepals 4, stamens 2, straight in bud, pistillode present. Pistillate inflorescences globose-capitate, ca. 1–1.5 cm across, flowers 4-lobed to 4-parted, stigmas 2, filiform. *Infructescences* globose, ca. 2.5–3.5 cm across, green, tepals fleshy, yellowish to greenish, drupes ca. 7–8 mm long. *Seeds* ca. 3 × 2 mm, testa thin and not vascularized, cotyledons equal.

Species and distribution: 1, in tropical South America.

1. ***Bagassa guianensis*** Aubl., Hist. Pl. Guiane 2, Suppl.: 15 & 4: t. 376. 1775.

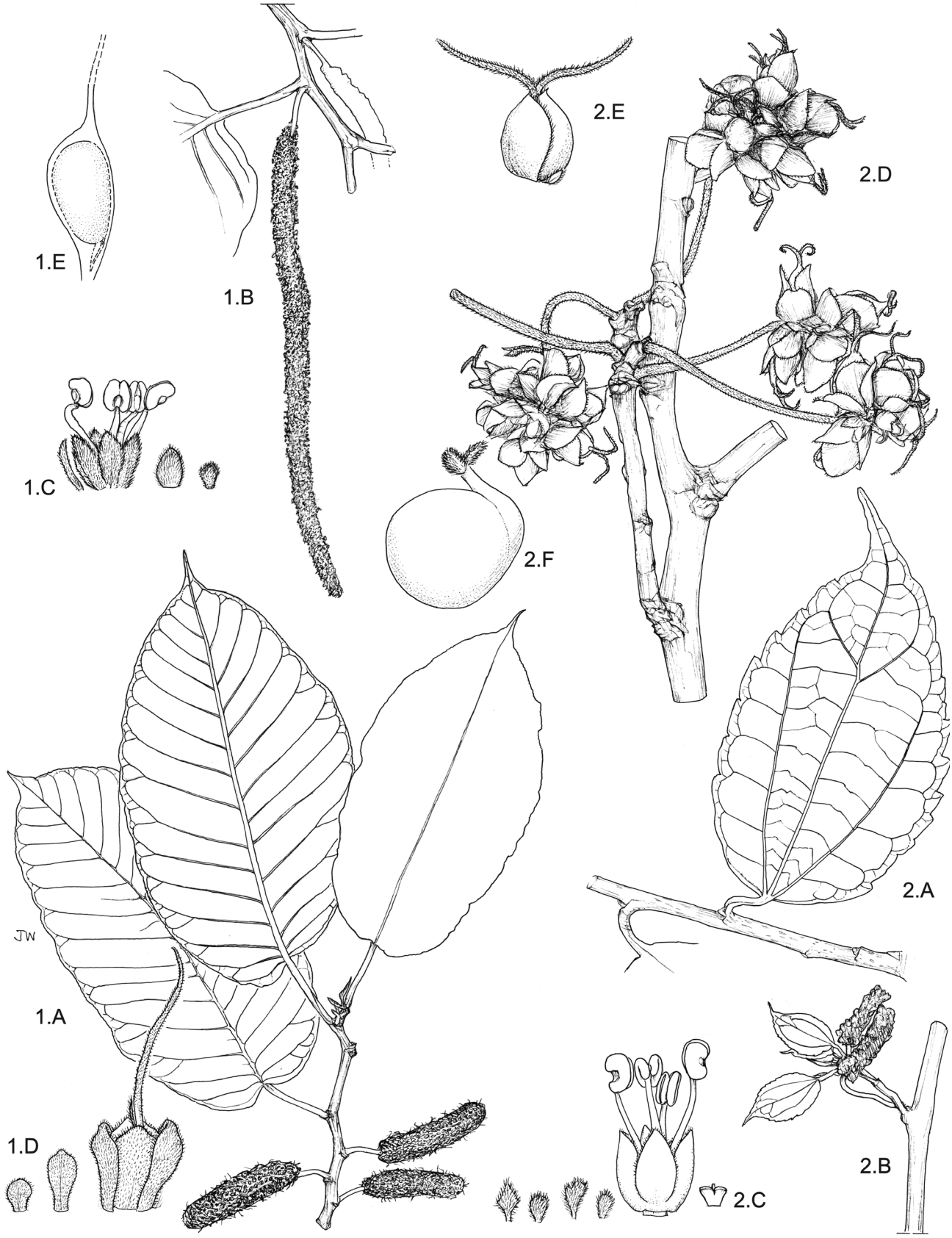

Fig. 8.1. *Milicia excelsa* (Welw.) C.C.Berg: **A**, Leafy shoot with pistillate inflorescences; **B**, Staminate inflorescence; **C**, Staminate flower and bracts; **D**, Pistillate flower and bracts; **E**, Fruit in section. **8.2.** *Afromorus mesozygia* (Stapf) E.M.Gardner: **A**, Leafy shoot; **B**, Staminate inflorescences; **C**, Staminate flowers; **D**, Pistillate inflorescences; **E**, Pistillate flower; **F**, Fruit. — Drawn by J. Williamson.

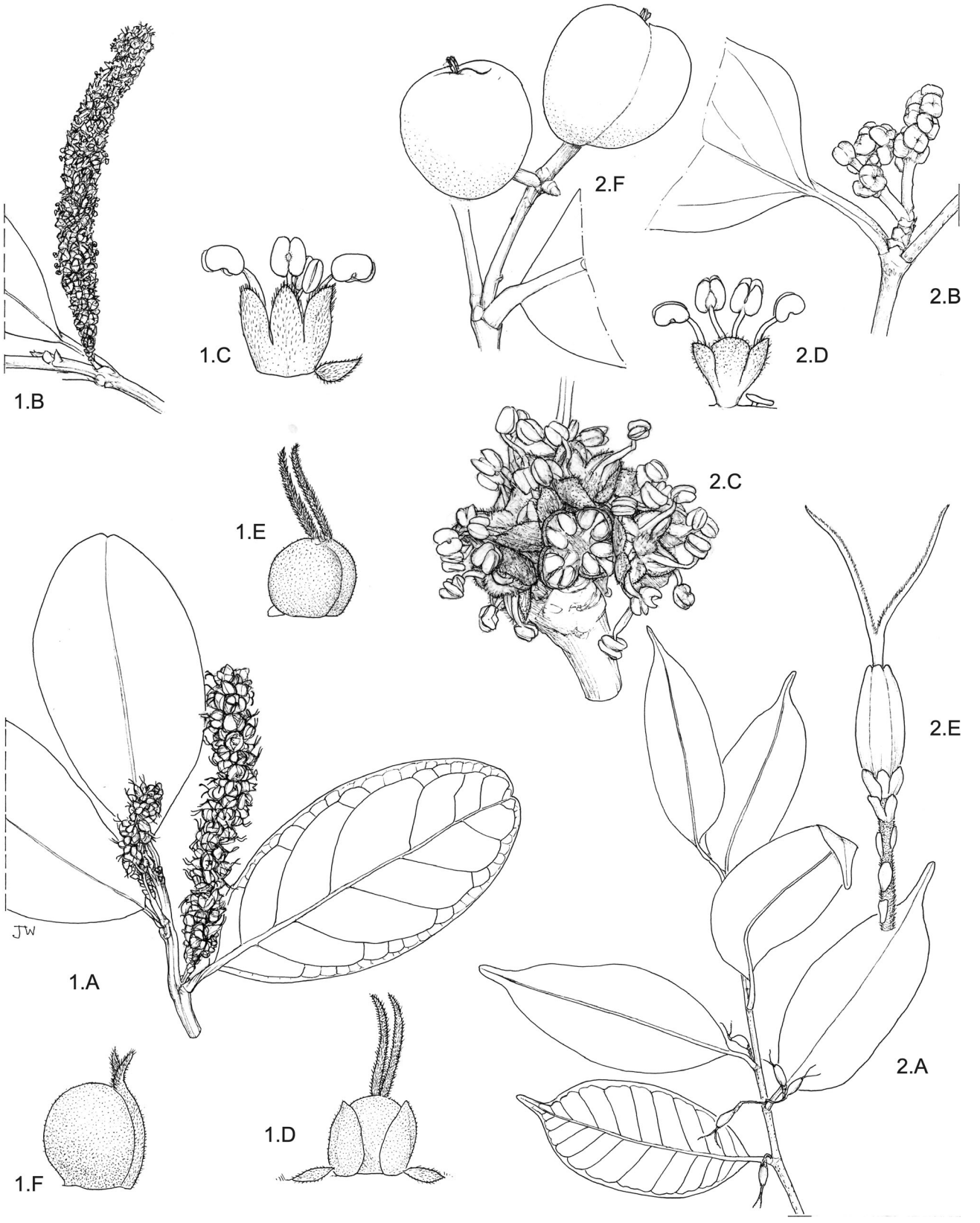

Fig. 9.1. *Ampalis mauritiana* Urb.: **A**, Leafy shoot with pistillate inflorescences; **B**, Staminate inflorescence; **C**, Staminate flower; **D**, Pistillate flower; **E**, Immature fruit; **F**, Mature fruit. **9.2.** *Maillardia montana* Leandri: **A**, Leafy shoot with pistillate inflorescences; **B**, Immature staminate inflorescences; **C**, Staminate inflorescence; **D**, Staminate flower and bract; **E**, Pistillate inflorescence; **F**, Fruiting perianths. — Drawn by J. Williamson.

= *Piper tiliifolium* Desv. ex Ham., Prodr. Pl. Ind. Occid.: 4. 1825 ('*tiliæfolium*').
= *Laurea tiliifolia* Gaudich., Voy. Uranie: 513. 1830 ('*tiliæfolia*') ≡ *Bagassa tiliifolia* (Desf.) Benoist in Arch. Bot. Mém. 5(1): 31. 1933.
= *Bagassa sagotiana* Burch. ex Benth. & Hook.f., Gen. Pl. 3: 362. 1880.
Figure 10.1.

Maillardia

Maillardia Frapp. ex Duch. in Maillard, Notes Ile Réunion 2, Annexe P.: 3. 1862 ≡ *Trophis* sect. *Maillardia* (Frapp. ex Duch.) Corner in Gard. Bull. Singapore 19: 230. 1962 – Type: *Maillardia borbonica* Duch.

Dioecious trees or shrubs. *Leaves* distichous, pinnately veined. *Stipules* free, semi-amplexicaul. *Inflorescences* solitary or paired in the leaf axils, bracts subpeltate. Staminate inflorescences spicate with an abaxial sterile groove, flowers 4-parted, decussate-imbricate, stamens 4, inflexed in bud, pistillode present. Pistillate inflorescences up to three together, uni- or bi-florous, perianth tubular 4-lobed, ovary adnate to the perianth, stigmas 2, equal. *Infructescences* with enlarged fleshy perianths surrounding drupaceous fruits, the latter to 18 mm long. *Seeds* to 13 mm long, testa thin, with a thickened vascularized part below the hilum, cotyledons unequal.

Species and distribution: 2 species, in Madagascar, the Comoros, and the Seychelles.

1. ***Maillardia borbonica*** Duch. in Maillard, Notes Ile Réunion, Annexe P.: 3. 1862 ≡ *Trophis borbonica* (Duch.) C.C.Berg in Proc. Kon. Ned. Akad. Wetensch. C 91(4): 355. 1988.

2. ***Maillardia montana*** Leandri in Mém. Inst. Sci. Madagascar, Sér. B, Biol. Vég. 1: 25. 1948 ≡ *Trophis montana* (Leandri) C.C.Berg in Proc. Kon. Ned. Akad. Wetensch. C 91(4): 355. 1988.
= *Maillardia occidentalis* Leandri in Mém. Inst. Sci. Madagascar, Sér. B, Biol. Vég. 1: 26. 1948.
= *Maillardia orientalis* Leandri in Mém. Inst. Sci. Madagascar, Sér. B, Biol. Vég. 1: 27. 1948.
= *Maillardia mandrarensis* Leandri in Mém. Inst. Sci. Madagascar, Sér. B, Biol. Vég. 1: 28. 1948.
= *Maillardia pendula* Fosberg in Kew Bull. 29: 266, t. 2. 1974.
Figure 9.2.

Milicia

Milicia Sim, Forest Fl. Port. E. Afr.: 97. 1909 – Type: *Milicia africana* Sim (= *M. excelsa* (Welw.) C.C.Berg).

Dioecious trees. *Leaves* distichous, lamina pinnately veined. *Stipules* free, not fully amplexicaul. *Inflorescences* spicate, usually solitary in the leaf axils or on leafless nodes, spicate, flowers in longitudinal rows alternating with rows of bracts, bracts mostly basally attached, abaxial sterile groove present. Staminate inflorescences to 20 cm long, flowers 4-parted, imbricate, stamens 4, inflexed in bud, pistillode present. Pistillate inflorescences to 4.5 cm long, flowers 4-parted, decussate-imbricate, ovary free, stigmas 2, unequal. *Infructescences* with enlarged fleshy perianths, surrounding slightly flattened drupaceous fruits, the latter to ca. 3 mm long. *Seeds* ca. 2 mm long, testa thin with a slightly thickened vascularized part below the hilum, cotyledons equal.

Species and distribution: 2 species, in tropical Africa.

1. ***Milicia excelsa*** (Welw.) C.C.Berg in Bull. Jard. Bot. Natl. Belg. 52(1–2): 227. 1982 ≡ *Morus excelsa* Welw. in Trans. Linn. Soc. London 27: 69, t. 23. 1869 ≡ *Maclura excelsa* (Welw.) Bureau in Candolle, Prodr. 17: 231. 1873 ≡ *Chlorophora excelsa* (Welw.) Benth. & Hook.f., Gen. Pl. 3(1): 363. 1880.
= *Chlorophora tenuifolia* Engl. in Bot. Jahrb. Syst. 20: 139. 1894.
= *Milicia africana* Sim, Forest Fl. Port. E. Afr.: 97, t. 122. 1909.
= *Chlorophora alba* A.Chev. in Bull. Soc. Bot. France 58 [Mém. Soc. Bot. France 2] (Mém. 8): 209. 1912.
Figure 8.1.

2. ***Milicia regia*** (A.Chev.) C.C.Berg in Bull. Jard. Bot. Natl. Belg. 52(1–2): 227. 1982 ≡ *Chlorophora regia* A.Chev. in Bull. Soc. Bot. France 58 [Mém. Soc. Bot. France 2] (Mém. 8d): 209. 1912 ≡ *Maclura regia* (A.Chev.) Corner in Gard. Bull. Singapore 19: 237. 1962.

Morus

Morus L., Sp. Pl. 2: 986. 1753 – Type: *Morus nigra* L.

Dioecious trees or shrubs. *Leaves* trinerved (to 5-nerved) at the base. *Stipules* free, nearly lateral. *Inflorescences* solitary or paired in the leaf axils, without an obvious sterile groove, interfloral bracts absent. Staminate inflorescences spicate or racemose, to 8 cm long, flowers 4-parted, imbricate, stamens 4, inflexed in bud, pistillode present. Pistillate inflorescences subcapitate to spicate, up to 16 cm long, flowers tepals 4, separate, decussate-imbricate, ovary free, stigmas 2, equal. *Infructescences* with enlarged fleshy perianths enclosing achene-like fruits, the latter ca. 1 mm long. *Seeds* less than 1 mm long, cotyledons equal.

Species and distribution: Perhaps 16 species, Asia and North to Central America; introduced worldwide.

1. ***Morus alba*** L. var. ***alba***, Sp. Pl. 2: 986. 1753. — Figure 11.2.

1.1 ***Morus alba*** var. ***multicaulis*** (Perr.) Loudon, Arbor. Frutic. Brit. 3: 1348, fig. 1223. 1838.

2. ***Morus australis*** Poir. in Lamarck, Encycl. 4: 380. 1797.

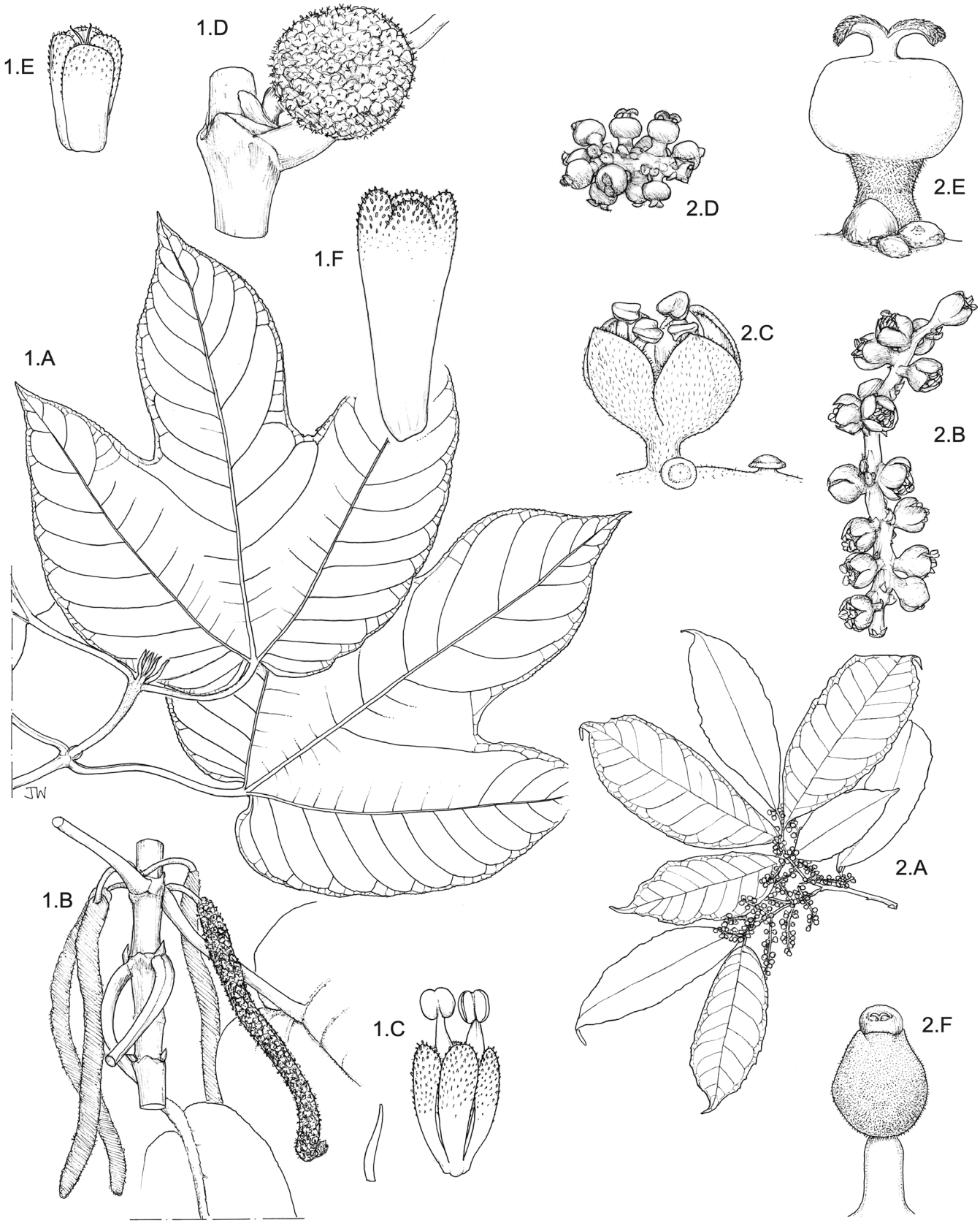

Fig. 10.1. *Bagassa guianensis* Aubl.: **A**, Leafy shoot; **B**, Staminate inflorescences; **C**, Staminate flower; **D**, Pistillate inflorescence; **E**, Pistillate flower; **F**, Fruiting perianth. **10.2.** *Sorocea affinis* Hemsl.: **A**, Leafy shoot with pistillate inflorescences; **B**, Staminate inflorescence; **C**, Staminate flower and bracts; **D**, Pistillate inflorescence; **E**, Pistillate flower and bracts; **F**, Fruiting perianth. — Drawn by J. Williamson.

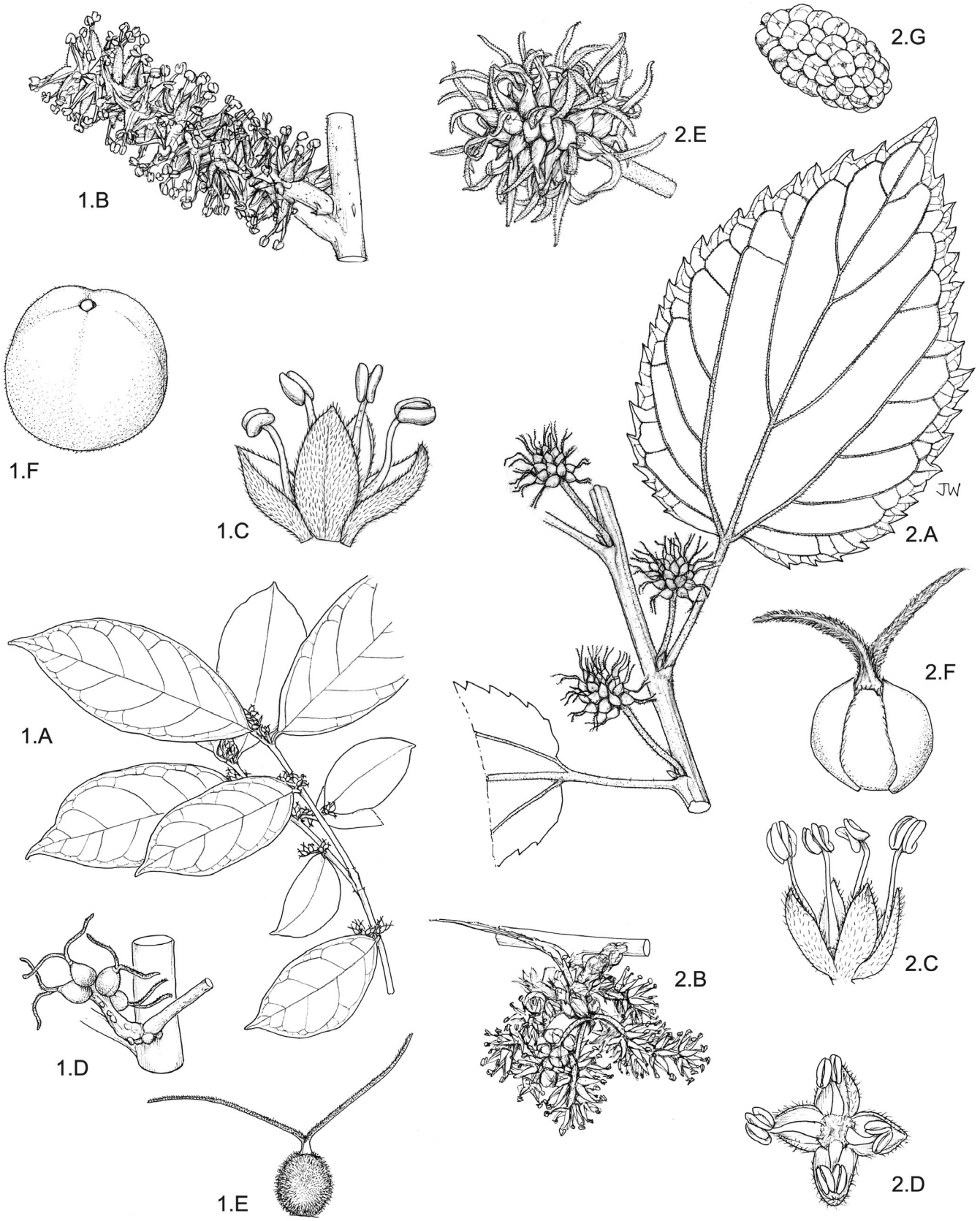

Fig. 11.1. *Trophis racemosa* (L.) Urb.: **A**, Leafy shoot with pistillate inflorescences; **B**, Staminate inflorescence; **C**, Staminate flower; **D**, Pistillate inflorescence; **E**, Pistillate flower; **F**, Fruiting perianth. **11.2.** *Morus alba* L.: **A**, Leafy shoot with pistillate inflorescences; **B**, Staminate inflorescences; **C** & **D**, Staminate flowers; **E**, Pistillate inflorescence; **F**, Pistillate flower; **G**, Infructescence. — Drawn by J. Williamson.

3. ***Morus boninensis*** Koidz. in Bot. Mag. (Tokyo) 31: 38. 1917.

4. ***Morus cathayana*** Hemsl. var. ***cathayana*** in J. Linn. Soc., Bot. 26: 456. 1894.

4.1 ***Morus cathayana*** var. ***gongshanensis*** (Z.Y.Cao) Z.Y.Cao in Acta Bot. Yunnan. 17: 154. 1995 ≡ *Morus gongshanensis* Z.Y.Cao in Acta Phytotax. Sin. 29(3): 264. 1991.

5. ***Morus celtidifolia*** Kunth in Humboldt & al., Nov. Gen. Sp. 2: 33. 1817.

6. ***Morus liboensis*** S.S.Chang in Acta Phytotax. Sin. 22: 66. 1984.

7. ***Morus macroura*** Miq. var. ***macroura***, Pl. Jungh. 1: 42. 1851.

7.1 ***Morus macroura*** var. ***laxiflora*** G.K.Upadhyay & A.A. Ansari in Rheedea 20: 44. 2010.

8. ***Morus koordersiana*** J.-F.Leroy in Bull. Mus. Natl. Hist. Nat., sér. 2, 21: 729. 1949.

Comment: Endemic to Sumatra and possibly synonymous with *M. macroura*. However, it was not cited by Berg & al. (2006) either as a good species or as a synonym of the latter.

9. ***Morus microphylla*** Buckley in Proc. Acad. Nat. Sci. Philadelphia 1862: 8. 1863.

Comment: Recognized in the *Flora of North America* (Wunderlin, 1997) but likely conspecific with *M. celtidifolia* and considered so by Berg (2001).

10. ***Morus mongolica*** (Bureau) C.K.Schneid. in Sargent, Pl. Wilson. 3: 296. 1916 ≡ *Morus alba* var. *mongolica* Bureau in Candolle, Prodr. 17: 241. 1873.

11. ***Morus nigra*** L., Sp. Pl. 2: 986. 1753.

12. ***Morus notabilis*** C.K.Schneid. in Sargent, Pl. Wilson. 3: 293. 1916.

13. ***Morus rubra*** L. var. ***rubra***, Sp. Pl. 2: 986. 1753.

13.1 ***Morus rubra*** var. ***murrayana*** (Saar & Galla) Saar & Galla in Phytologia 94(2): 246. 2012 ≡ *Morus murrayana* Saar & Galla in Phytologia 91(1): 106, t. 1–2. 2009.

14. ***Morus serrata*** Roxb., Fl. Ind., ed. 1832, 3: 596. 1832.

15. ***Morus trilobata*** (S.S.Chang) Z.Y.Cao in Acta Phytotax. Sin. 29: 265. 1991 ≡ *Morus australis* var. *trilobata* S.S. Chang in Acta Phytotax. Sin. 22(1): 66, pl. 5. 1984.

16. ***Morus wittiorum*** Hand.-Mazz. in Anz. Akad. Wiss. Wien, Math.-Naturwiss. Kl. 58: 88. 1921.

Paratrophis

Paratrophis Blume, Mus. Bot. 2: 81. 1856 ≡ *Streblus* sect. *Paratrophis* (Blume) Corner in Gard. Bull. Singapore 19: 216. 1962 – Type: *Paratrophis heterophylla* Blume (= *P. microphylla* (Raoul) Cockayne).

= *Pseudomorus* Bureau in Ann. Sci. Nat., Bot., sér. 5, 11: 371. 1869 – Type: *Pseudomorus brunoniana* (Endl.) Bureau (= *Paratrophis pendulina* (Endl.) E.M.Gardner).

= *Uromorus* Bureau in Candolle, Prodr. 17: 214, 236. 1873 – **Type (designated here):** *Uromorus anthropophagorum* (Seem.) Bureau (≡ *Paratrophis anthropophagorum* (Seem.) Benth. & Hook.f. ex Drake).

= *Calpidochlamys* Diels in Bot. Jahrb. Syst. 67: 172. 1935 ≡ *Trophis* sect. *Calpidochlamys* Corner in Gard. Bull. Singapore 19: 230. 1962 – Type: *Calpidochlamys drupacea* Diels (= *Paratrophis philippinensis* (Bureau) Fern.-Vill.).

= *Chevalierodendron* J.-F.Leroy in Compt. Rend. Hebd. Séances Acad. Sci. 227: 146. 1948 – **Type (designated here):** *Chevalierodendron glabrum* (Merr.) J.-F.Leroy (≡ *Paratrophis glabra* (Merr.) Steenis).

= *Morus* subg. *Gomphomorus* J.-F.Leroy in Bull. Mus. Hist. Nat. (Paris), ser. 2, 21: 732. 1949 – Type: *Morus insignis* Bureau (≡ *Paratrophis insignis* (Bureau) E.M.Gardner).

= *Streblus* sect. *Protostreblus* Corner in Blumea 18: 393. 1970 – Type: *Streblus ascendens* Corner (≡ *Paratrophis ascendens* (Corner) E.M.Gardner).

Dioecious trees or shrubs. *Leaves* distichous (or spiral in *P. ascendens*), pinnately veined, sometimes trinerved at the base. Stipules free, lateral. *Inflorescences* axillary, solitary or up to 5 together, spicate, with an abaxial sterile groove, interfloral bracts mostly peltate, flowers sessile in longitudinal rows, tepals 4, valvate, ciliolate. Staminate inflorescences up to at least 20 cm. long, flowers with filaments inflexed in bud, pistillode present. Pistillate inflorescences up to at least 10 cm long, flowers usually at least 2 (to many), tepals free (except in *P. philippinensis*), stigma bifid, arms equal. *Fruits* drupaceous, red to black, with tepals persistent but usually not enlarged or fleshy (except in *P. philippinensis* and *P. insignis*), up to ca. 1 cm long. *Seeds* up to ca. 8 × 6 mm, cotyledons equal.

Species and distribution: 12 species from the Malesian region to Australia, New Zealand, and Oceania, Central and western South America.

1. ***Paratrophis anthropophagorum*** (Seem.) Benth. & Hook.f. ex Drake, Ill. Fl. Ins. Pacif.: 296. 1892 ≡ *Trophis anthropophagorum* Seem., Fl. Vit.: 258, t. 68. 1868 ≡ *Uromorus anthropophagorum* (Seem.) Bureau in Candolle, Prodr. 17: 236. 1873 ≡ *Streblus anthropophagorum* (Seem.) Corner in Gard. Bull. Singapore 19: 221. 1962.

= *Caturus oblongatus* Seem., Fl. Vit.: 254. 1868.

= *Pseudomorus brunoniana* var. *tahitensis* J.Nadeaud, Énum. Pl. Tahiti: 43. 1873 ≡ *Uromorus tahitensis* (J.Nadeaud) Bureau in Candolle, Prodr. 17: 237. 1873 ≡ *Paratrophis tahitensis* (Bureau) Benth. & Hook.f. ex Drake, Ill. Fl. Ins. Pacif.: 296. 1892 ≡ *Streblus tahitensis* (J.Nadeaud) Corner

in Gard. Bull. Singapore 19: 225. 1962 = *Paratrophis ostermeyeri* Rech. in Repert. Spec. Nov. Regni Veg. 5: 130. 1908.
= *Paratrophis viridissima* Rech. in Repert. Spec. Nov. Regni Veg. 5: 130. 1908.
= *Paratrophis zahlbruckneri* Rech. in Repert. Spec. Nov. Regni Veg. 5: 130. 1908.
Figure 12.2.

2. ***Paratrophis ascendens*** (Corner) E.M.Gardner, **comb. nov.** ≡ *Streblus ascendens* Corner in Blumea 18: 395, t. 1. 1970.

3. ***Paratrophis australiana*** C.T.White in Contr. Arnold Arbor. 4: 15. 1933 ≡ *Streblus glaber* var. *australianus* (C.T.White) Corner in Gard. Bull. Singapore 19: 221. 1962 ≡ *Streblus glaber* subsp. *australianus* (C.T.White) C.C.Berg in Blumea 50: 548. 2005.

4. ***Paratrophis banksii*** Cheeseman, Man. New Zealand Fl.: 633. 1906 ≡ *Streblus banksii* (Cheeseman) C.J.Webb in New Zealand J. Bot. 25(1): 136. 1987.
= *Paratrophis heterophylla* var. *elliptica* Kirk in Trans. & Proc. New Zealand Inst. 29: 500, t. 46. 1897 ≡ *Streblus heterophyllus* var. *ellipticus* (Kirk) Corner in Gard. Bull. Singapore 19: 222. 1962.
Comment: Morphologically very close to and not always distinguishable from *P. microphylla*.

5. ***Paratrophis glabra*** (Merr.) Steenis in J. Bot. 72: 8. 1934 ≡ *Gironniera glabra* Merr. in Philipp. J. Sci. 1(Suppl.): 42. 1906 ≡ *Chevalierodendron glabrum* (Merr.) J.-F.Leroy in Compt. Rend. Hebd. Séances Acad. Sci. 227: 146. 1948 ≡ *Streblus glaber* (Merr.) Corner in Gard. Bull. Singapore 19: 221. 1962.
= *Aphananthe negrosensis* Elmer in Leafl. Philipp. Bot. 2: 575. 1909.
= *Pseudostreblus caudatus* Ridl. in J. Fed. Malay States Mus. 6: 54. 1915.
= *Streblus laevifolius* Diels in Bot. Jahrb. Syst. 67: 171. 1935.
= *Streblus urophyllus* Diels in Bot. Jahrb. Syst. 67: 172. 1935 ≡ *Streblus glaber* subsp. *urophyllus* (Diels) C.C.Berg in Blumea 50(3): 548. 2005.
= *Streblus urophyllus* var. *salicifolius* Corner in Gard. Bull. Singapore 19: 225. 1962.
Comments: Berg & al. (2006) treated *Paratrophis australiana* and *Streblus urophyllus* as subspecies of *S. glaber*. *Paratrophis australiana*, endemic to Australia, has crenate leaf margins and somewhat larger staminate inflorescences with more interfloral bracts than *P. glabra*; these morphological differences are consistent and geographically confined, and we therefore reinstate *P. australiana*. This stands in contrast to *S. urophyllus*, which we provisionally maintain in synonymy under *P. glabra*. Although collections from Mt. Wilhelm in New Guinea are remarkable for their thick coriaceous leaves and spinose margins, similar toothed margins can be found at higher elevations in Borneo and Sulawesi, suggesting that the striking leaf morphology of *S. urophyllus* is an alpine effect not indicative of speciation. We reserve judgement on the status of *S. urophyllus* var. *salicifolius*, applied by Corner (1962) to specimens with linear leaves, provisionally maintaining it in synonymy following Berg & al. (2006).

6. ***Paratrophis insignis*** (Bureau) E.M.Gardner, **comb. nov.** ≡ *Morus insignis* Bureau in Candolle, Prodr. 17: 247. 1873.
= *Morus peruviana* Planch. ex Koidz., Fl. Symb. Orient.-Asiat.: 88. 1930.
= *Morus trianae* J.-F.Leroy in Bull. Mus. Hist. Nat. (Paris), ser. 2, 21: 731. 1949.
= *Morus marmolii* Legname in Lilloa 33: 334. 1973.
Comment: The infructescences differ from most other *Paratrophis* in their fleshy free tepals and denser aggregation of flowers, but the staminate inflorescences are typical of the genus.

7. ***Paratrophis microphylla*** (Raoul) Cockayne, Bot. Notes Kennedy's Bush & Scenic Res. Port Hills, Lyttelton (Rep. Scenery Preserv.): 12. 1915 ≡ *Epicarpurus microphyllus* Raoul, Choix Pl. Nouv.-Zél.: 14. 1846 ≡ *Taxotrophis microphylla* (Raoul) F.Muell., Fragm. 6: 193. 1868 ≡ *Streblus microphyllus* (Raoul) Corner in Gard. Bull. Singapore 19: 221. 1962.
= *Trophis opaca* Banks & Sol. ex Hook.f., Bot. Antarct. Voy. II (Fl. Nov.-Zel.) 1: 224. 1853., nom. illeg ≡ *Paratrophis opaca* Druce, Rep. Bot. Soc. Exch. Club Brit. Isles 4 (Suppl. 2): 639. 1917.
= *Paratrophis heterophylla* Blume, Mus. Bot. 2: 81. 1856.

8. ***Paratrophis pendulina*** (Endl.) E.M.Gardner, **comb. nov.** ≡ *Morus pendulina* Endl., Prodr. Fl. Norfolk.: 40. 1833 ≡ *Pseudomorus pendulina* (Endl.) Stearn in J. Arnold Arbor. 28: 427. 1947 ≡ *Pseudomorus brunoniana* var. *pendulina* (Endl.) Bureau in Ann. Sci. Nat., Bot., ser. 5, 11: 372. 1869 ≡ *Streblus pendulinus* (Endl.) F.Muell., Fragm. 6: 192. 1868.
= *Morus brunoniana* Endl., Atakta Bot.: t. 32. 1835 ≡ *Streblus brunonianus* (Endl.) F.Muell., Fragm. 6: 192. 1868 ≡ *Pseudomorus brunoniana* (Endl.) Bureau in Ann. Sci. Nat., Bot., ser. 5, 11: 372. 1869.
= *Pseudomorus brunoniana* var. *australiana* Bureau in Ann. Sci. Nat., Bot., ser. 5, 11: 373. 1869 ≡ *Pseudomorus pendulina* var. *australiana* (Bureau) Stearn in J. Arnold Arbor. 28: 427. 1947.
= *Pseudomorus brunoniana* [var. *australiana*] subvar. *castaneaefolia* Bureau in Ann. Sci. Nat., Bot., ser. 5, 11: 372. 1869.
= *Pseudomorus brunoniana* var. *obtusa* Bureau in Ann. Sci. Nat., Bot., ser. 5, 11: 373. 1869 ≡ *Pseudomorus pendulina* var. *obtusa* (Bureau) Stearn in J. Arnold Arbor. 28: 428. 1947 ('*obtusata*').
= *Pseudomorus sandwicensis* O.Deg., Fl. Hawaiiensis: fam. 96. 21 Dec 1938 ≡ *Pseudomorus brunoniana* var. *sandwicensis* (O.Deg.) Skottsb. in Acta Horti Gothob. 15: 347. 1944 ≡ *Pseudomorus pendulina* var. *sandwicensis* (O.Deg.) Stearn in J. Arnold Arbor. 28: 428. 1947 ≡ *Streblus sandwicensis* (O.Deg.) H.St.John in Mem. Pacific Trop. Bot. Gard. 1: 374. 1973.

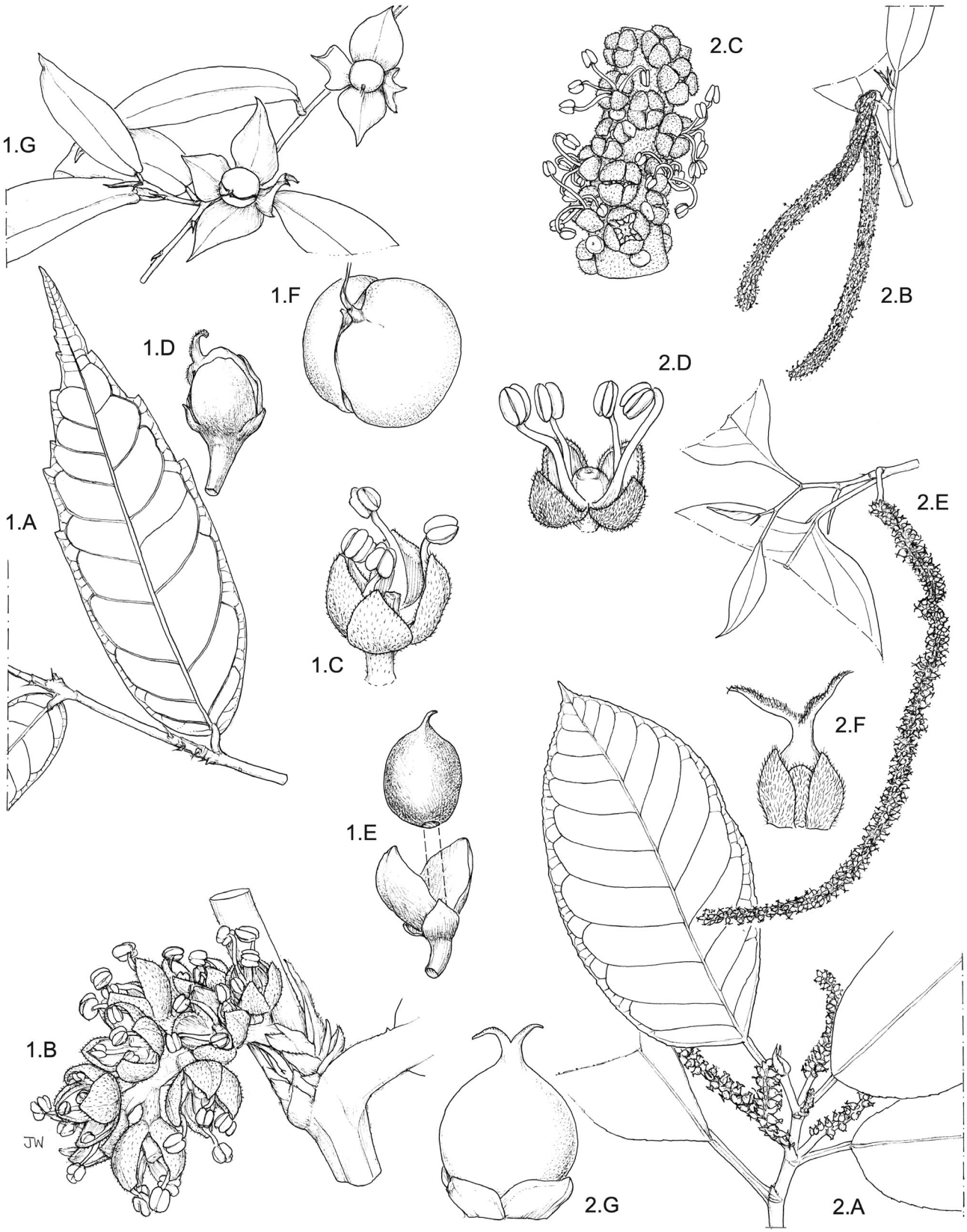

Fig. 12.1. *Taxotrophis taxoides* (B.Heyne ex Roth) Chew ex E.M.Gardner: **A**, Leafy shoot; **B**, Staminate inflorescence; **C**, Staminate flower; **D** & **E**, Pistillate flowers; **F**, Fruit; **G**, Leafy shoot with fruits. **12.2.** *Paratrophis anthropophagorum* (Seem.) Benth. & Hook.f. ex Drake: **A**, Leafy shoot with pistillate inflorescences; **B**, Staminate inflorescences; **C**, Detail of staminate flowers and bracts; **D**, Staminate flower; **E**, Pistillate inflorescence; **F**, Pistillate flower; **G**, Fruit. — Drawn by J. Williamson.

Comments: This complex requires further investigation. Although the types of *Morus pendulina*, *M. brunoniana*, *Pseudomorus sandwicensis*, and *P. brunoniana* var. *obtusa* differ from one another, it has so far been difficult to discern clear geographic patterns that warrant maintaining separate species. We therefore provisionally treat them all as one widespread and variable species, awaiting further study before making additional new combinations. Besides additional phylogenetic work, expanding on the careful morphological study by Conn (2015), who found consistent differences between material from Norfolk Island (there assigned to *Streblus pendulinus*) and mainland Australia (assigned to *S. brunonianus*), would be most welcome in that regard.

9. ***Paratrophis philippinensis*** (Bureau) Fern.-Vill. in Fernandez-Villar & Naves, Nov. App.: 98. 1880 ≡ *Uromorus philippinensis* Bureau in Candolle, Prodr. 17: 237. 1873 ≡ *Trophis philippinensis* (Bureau) Corner in Gard. Bull. Singapore 19: 231. 1962.

= *Sloetia minahassae* Koord. in Meded. Lands Plantentuin 19: 645. 1898.

= *Paratrophis grandifolia* Elmer in Leafl. Philipp. Bot. 5: 1814. 1913.

= *Calpidochlamys branderhorstii* Diels in Bot. Jahrb. Syst. 67: 173. 1935 ≡ *Trophis branderhorstii* (Diels) Corner in Gard. Bull. Singapore 19: 231. 1962.

= *Calpidochlamys drupacea* Diels in Bot. Jahrb. Syst. 67: 173. 1935 ≡ *Trophis drupacea* (Diels) Corner in Gard. Bull. Singapore 19: 231. 1962.

Comments: This species is the only *Paratrophis* with fused tepals and one of only two whose tepals develop into a fleshy accessory fruit. The staminate inflorescences, however, are typical of the genus.

10. ***Paratrophis sclerophylla*** (Corner) E.M.Gardner, **comb. nov.** ≡ *Streblus sclerophyllus* Corner in Blumea 18: 399. 1970.

11. ***Paratrophis smithii*** Cheeseman in Trans. & Proc. New Zealand Inst. 20: 148. 1888 ≡ *Streblus smithii* (Cheeseman) Corner in Gard. Bull. Singapore 19: 224. 1962.

Comment: Morphologically very close to *Paratrophis anthropophagorum*.

12. ***Paratrophis solomonensis*** (Corner) E.M.Gardner, **comb. nov.** ≡ *Streblus solomonensis* Corner in Gard. Bull. Singapore 19: 224. 1962.

Comment: Morphologically very close to *Paratrophis anthropophagorum*.

Sorocea

Sorocea A.St.-Hil. in Mém. Mus. Hist. Nat. 7: 473. 1821 – Type (designated by Burger & al. in Acta Bot. Neerl. 11: 430. 1962): *Sorocea bonplandii* (Baill.) W.C.Burger, Lanj. & Wess.Boer (≡ *Pseudosorocea bonplandii* Baill.).

= *Pseudosorocea* Baill., Hist. Pl. 6: 210. 1875 – Type: *Pseudosorocea bonplandii* Baill. (≡ *Sorocea bonplandii* (Baill.) W.C.Burger, Lanj. & Wess.Boer).

= *Trophisomia* Rojas Acosta in Bull. Géogr. Bot. 24: 211. 1914 – Type: *Trophisomia edulis* Rojas Acosta (= *Sorocea sprucei* subsp. *saxicola* (Hassler) C.C.Berg).

= *Paraclarisia* Ducke in Arq. Serv. Florest. 1(1): 2. 1939 – Type: *Paraclarisia amazonica* Ducke (= *Sorocea duckei* W.C.Burger).

Dioecious trees. *Leaves* alternate, distichous, lamina pinnately veined, 3-lobed to entire. *Stipules* free, lateral. *Inflorescences* solitary or paired in the leaf axils or below the leaves, racemose to spicate to subcapitate or uniflorous, bracts basally attached to peltate. Staminate flowers 4-lobed to 4-parted, tepals decussate-imbricate, stamens (3–)4, straight in bud, pistillode usually absent. Pistillate flowers tubular, 4-lobed to subentire, ovary basally adnate to the perianth, stigmas 2, short, usually tongue-shaped. *Infructescences* with drupaceous fruits enclosed by fleshy enlarged perianths, the latter red to orange, turning black at maturity. *Seeds* large, testa thin, embryo green, cotyledons very unequal, the smaller one minute and enclosed by the larger.

Species and distribution: 19 species in Central and South America from Mexico to Argentina.

Note: This species list follows the *Flora Neotropica* monograph (Berg, 2001) with the addition of four new species and one status change published later. Names synonymized by Berg (2001) but recognized by Burger & al. (1962) are noted in comments. Complete synonymies can be found in those treatments.

Sorocea subg. ***Sorocea***

1. ***Sorocea affinis*** Hemsl., Biol. Cent.-Amer., Bot. 3: 150. 1883. — Figure 10.2.

2. ***Sorocea angustifolia*** Al.Santos & Romaniuc in Novon 24(2): 199. 2015.

3. ***Sorocea bonplandii*** (Baill.) W.C.Burger, Lanj. & Wess. Boer in Acta Bot. Neerl. 11: 465, t. 12, fig. 1. 1962 ≡ *Pseudosorocea bonplandii* Baill. in Adansonia 11: 296. 1875.

4. ***Sorocea briquetii*** J.F.Macbr. in Publ. Field Columb. Mus., Bot. Ser. 11: 16. 1931.

Comment: Includes *Sorocea pileata* W.C.Burger.

5. ***Sorocea carautana*** M.D.M.Vianna, Carrijo & Romaniuc in Novon 19: 549, fig. 1. 2009.

6. ***Sorocea ganevii*** R.M.Castro in Neodiversity 1: 18. 2006.

7. ***Sorocea guilleminiana*** Gaudich., Voy. Bonite, Bot. 3: t. 74. 1843

Comment: Includes *Sorocea klotzschiana* Baill. and *S. macrogyna* Lanj. & Wess.Boer.

8. ***Sorocea hilarii*** Gaudich., Voy. Bonite, Bot. 3: t. 71. 1843.
Comment: Includes *Sorocea racemosa* Gaudich.

9. ***Sorocea jaramilloi*** C.C.Berg in Novon 6: 241, fig. 9. 1996.

10. ***Sorocea longipedicellata*** A.F.P.Machado, M.D.M. Vianna & Romaniuc in Syst. Bot. 38(3): 687. 2013.

11. ***Sorocea muriculata*** Miq. subsp. ***muriculata*** in Martius, Fl. Bras. 4(1): 113. 1853.
Comment: Includes *Sorocea amazonica* Miq.

11.1 ***Sorocea muriculata*** subsp. ***uaupensis*** (Baill.) C.C.Berg in Proc. Kon. Ned. Akad. Wetensch. C 88: 387. 1985 ≡ *Pseudosorocea uaupensis* Baill. in Adansonia 11: 297. 1875.
Comment: Includes *Sorocea guayanensis* W.C.Burger.

12. ***Sorocea pubivena*** Hemsl. subsp. ***pubivena***, Biol. Cent.-Amer., Bot. 3: 150. 1883.
Comment: Includes *Sorocea cufodontii* W.C.Burger.

12.1 ***Sorocea pubivena*** subsp. ***hirtella*** (Mildbr.) C.C.Berg in Novon 6(3): 243. 1996 ≡ *Sorocea hirtella* Mildbr. in Notizbl. Bot. Gart. Berlin-Dahlem 10: 183. 1927.
Comment: Includes *Sorocea opima* J.F.Macbr.

12.2 ***Sorocea pubivena*** subsp. ***oligotricha*** (Akkermans & C.C.Berg) C.C.Berg in Novon 6(3): 243. 1996 ≡ *Sorocea hirtella* subsp. *oligotricha* Akkermans & C.C.Berg in Proc. Kon. Ned. Akad. Wetensch. C 88: 383, t. 1. 1985.

13. ***Sorocea ruminata*** C.C.Berg in Novon 6(3): 244. 1996.

14. ***Sorocea sarcocarpa*** Lanj. & Wess.Boer in Acta Bot. Neerl. 11: 452. 1962.

15. ***Sorocea steinbachii*** C.C.Berg in Proc. Kon. Ned. Akad. Wetensch. C 88: 385. 1985.

16. ***Sorocea trophoides*** W.C.Burger in Acta Bot. Neerl. 11: 450. 1962.

Sorocea subg. ***Paraclarisia*** (Ducke) W.C.Burger, Lanj. & Wess. Boer in Acta Bot. Neerl. 11: 468. 1962 ≡ *Paraclarisia* Ducke in Arq. Serv. Florest. 1(1): 2. 1939 – Type: *Paraclarisia amazonica* Ducke (= *Sorocea duckei* W.C.Burger).

17. ***Sorocea duckei*** W.C.Burger in Acta Bot. Neerl. 11: 473. 1962.

18. ***Sorocea sprucei*** (Baill.) J.F.Macbr. subsp. ***sprucei*** in Publ. Field Mus. Nat. Hist., Bot. Ser. 11: 16. 1931 ≡ *Pseudosorocea sprucei* Baill. in Adansonia 11: 296. 1875.
Comment: Includes *Sorocea arnoldoi* Lanj. & Wess.Boer.

18.1 ***Sorocea sprucei*** subsp. ***saxicola*** (Hassl.) C.C.Berg in Proc. Kon. Ned. Akad. Wetensch. C. 88: 391. 1985 ≡ *Sorocea saxicola* Hassl. in Bull. Herb. Boissier, ser. 2, 7: 11. 1906.

19. ***Sorocea subumbellata*** (C.C.Berg) Cornejo in Novon 19(3): 297–299. 2009.

Taxotrophis

Taxotrophis Blume, Mus. Bot. 2: 77. 1856 ≡ *Streblus* sect. *Taxotrophis* (Blume) Corner in Gard. Bull. Singapore 19: 217–218. 1962 – Type: *Taxotrophis javanica* Blume (= *T. spinosa* (Blume) Boerl.).
= *Phyllochlamys* Bureau in Candolle, Prodr. 17: 217. 1873 ≡ *Streblus* sect. *Phyllochlamys* (Bureau) Corner in Gard. Bull. Singapore 19: 217. 1962 – **Type (designated here):** *Phyllochlamys spinosa* (Roxb.) Bureau (= *Taxotrophis taxoides* (B.Heyne ex Roth) E.M.Gardner).
= *Balanostreblus* Kurz in J. Asiat. Soc. Bengal., Pt. 2, Nat. Hist. 42: 247. 1874 – Type: *Balanostreblus ilicifolia* Kurz (= *Taxotrophis ilicifolia* (Kurz) S.Vidal).
= *Pseudotrophis* Warb. in Bot. Jahrb. Syst. 13(3–4): 294. 1891 ≡ *Streblus* sect. *Pseudotrophis* (Warb.) Corner in Gard. Bull. Singapore 19: 217. 1962 – Type: *Pseudotrophis laxiflora* Warb. (= *Taxotrophis ilicifolia* S.Vidal).
= *Dimerocarpus* Gagnep. in Bull. Mus. Natl. Hist. Nat. 27: 441. 1921 – **Type (designated here):** *Dimerocarpus brenieri* Gagnep. (= *Taxotrophis macrophylla* (Blume) Boerl.).

Monoecious or dioecious trees or shrubs, usually with lateral or terminal thorns. *Leaves* distichous, pinnately veined, petioles adaxially pubescent. Stipules free, lateral. *Inflorescences* axillary, solitary or paired, with an abaxial sterile groove, interfloral bracts basally attached, flowers with 4 free tepals, valvate. Staminate inflorescences spicate to subcapitate, flowers with filaments inflexed in bud, pistillode present. Pistillate inflorescences uniflorous or subspicate, flowers usually pedicellate, stigma bifid, arms equal. *Fruits* drupaceous, up to ca. 1 cm long, usually loosely enclosed by the enlarged persistent tepals. *Seeds* up to ca. 8 × 6 mm, cotyledons subequal to unequal.

Species and distribution: 6 species, ranging from Sri Lanka to New Guinea.

1. ***Taxotrophis ilicifolia*** (Kurz) S.Vidal, Revis. Pl. Vasc. Filip.: 249. 1886 ≡ *Balanostreblus ilicifolia* Kurz in J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 42(4): 248. 1874 ≡ *Streblus ilicifolius* (Kurz) Corner in Gard. Bull. Singapore 19: 227. 1962.
= *Pseudotrophis laxiflora* Warb. in Bot. Jahrb. Syst. 13: 294. 1891.
= *Taxotrophis obtusa* Elmer in Leafl. Philipp. Bot. 5: 1813. 1913.
= *Taxotrophis triapiculata* Gamble in Bull. Misc. Inform. Kew 1913: 188. 1913.
= *Taxotrophis eberhardtii* Gagnep. in Lecomte, Fl. Indo-Chine 5: 700. 1928.
= *Taxotrophis laxiflora* Hutch. in Bull. Misc. Inform. Kew 1918: 151. 1918 ≡ *Streblus laxiflorus* (Hutch.) Corner in Gard. Bull. Singapore 19: 229. 1962.

= *Taxotrophis aquifolioides* W.C.Ko in Acta Phytotax. Sin. 8(4): 353. 1963.

The correct basionym for this species under Art. 41.4 of the *Code* (cf. Ex. 10) is *Balanostreblus ilicifolia* Kurz. As detailed by Gardner (2021), the latter has been misapplied to *Sorocea guilleminiana* Gaudich. based on original material without type status, the extant syntypes being clearly identifiable as *Taxotrophis ilicifolia* (Hutchinson, 1918; Jarrett, 1958).

2. ***Taxotrophis macrophylla*** (Blume) Boerl., Handl. Fl. Ned. Ind. 3: 359. 1900 ≡ *Streblus macrophyllus* Blume, Mus. Bot. 2: 80. 1856 ≡ *Diplocos? macrophyllus* (Blume) Bureau in Candolle, Prodr. 17: 216. 1873.
= *Pseudotrophis mindanaensis* Warb. in Perkins & al., Fragm. Fl. Philipp. 1: 165. 1905 ≡ *Taxotrophis mindanaensis* (Warb.) Elmer in Leafl. Philipp. Bot. 5: 1815. 1913 ('*Taxatrophis*' in nota).
= *Paratrophis caudata* Merr. in Philipp. J. Sci. 1(Suppl.): 183. 1906.
= *Taxotrophis balansae* Hutch. in Bull. Misc. Inform. Kew 1918(4): 151. 1918.
= *Dimerocarpus brenieri* Gagnep. in Bull. Mus. Hist. Nat. (Paris) 27: 441. 1921.

3. ***Taxotrophis perakensis*** (Corner) E.M.Gardner, **comb. nov.** ≡ *Streblus perakensis* Corner in Gard. Bull. Singapore 19: 223. 1962.

Note: Although Corner (1962) considered *Streblus perakensis* part of *S.* sect. *Paratrophis*, albeit with some hesitation, Berg & al. (2006), whom we follow, placed it in *Taxotrophis* based on the spines that appear on some specimens. This is a rather variable species that requires further investigation to properly elucidate its limits and affinities.

4. ***Taxotrophis spinosa*** (Blume) Steenis in Backer & Bakhuizen van den Brink, Fl. Java 2: 16. 1965 ≡ *Urtica spinosa* Blume, Bijdr. Fl. Ned. Ind. 10: 507. 1825 ≡ *Streblus spinosus* (Blume) Corner in Gard. Bull. Singapore 19: 229. 1962.
= *Taxotrophis javanica* Blume, Mus. Bot. 2: 77, t. 26. 1856.

5. ***Taxotrophis taxoides*** (B.Heyne ex Roth) Chew ex E.M. Gardner, **comb. nov.** ≡ *Trophis taxoides* B.Heyne ex Roth, Nov. Pl. Sp.: 368. 1821 ≡ *Trophis taxiformis* Spreng., Syst. Veg. 3: 902. 1826, nom. illeg. ≡ *Streblus taxoides* (B.Heyne ex Roth) Kurz, Prelim. Rep. Forest Pegu, App. A: cxviii. 1875 ≡ *Phyllochlamys taxoides* (B.Heyne ex Roth) Koord., Exkurs.-Fl. Java 2: 89. 1912.
= *Trophis spinosa* Roxb., Fl. Ind., ed. 1832, 3: 762. 1832, nom. illeg., non Willd. 1806, nec Blume 1826 ≡ *Epicarpurus spinosus* (Roxb.) Wight, Icon. Pl. Ind. Orient. 6: 7, t. 1962. 1853, p.p ≡ *Albrandia spinosa* (Roxb.) D.Dietr., Syn. Pl. 5: 280. 1852 ≡ *Phyllochlamys spinosa* (Roxb.) Bureau in Candolle, Prodr. 17: 218. 1873.
= *Epicarpurus timorensis* Decne. in Nouv. Ann. Mus. Hist. Nat. 3: 499, t. 21. 1834 ≡ *Epicarpurus involucratus* Zipp. ex Span. in Linnaea 15(4): 344. 1841, pro syn., nom. illeg. ≡ *Albrandia timorensis* (Decne.) D.Dietr., Syn. Pl. 5: 280. 1852.
= *Taxotrophis roxburghii* Blume, Mus. Bot. 2: 78. 1856.
= *Streblus microphyllus* Kurz in Prelim. Rep. Forest Pegu App. A: cxviii; App. B: 86. 1875 ≡ *Streblus taxoides* var. *microphylla* (Kurz) Kurz, Forest Fl. Burma 2: 465. 1877.
= *Phyllochlamys wallichii* King ex Hook.f., Fl. Brit. India 5: 489. 1888.
= *Phyllochlamys taxoides* var. *parvifolia* Merr., Enum. Philipp. Fl. Pl. 2: 38. 1923.
= *Taxotrophis poilanei* Gagnep. in Lecomte, Fl. Indo-Chine 5: 701. 1928.
= *Taxotrophis crenata* Gagnep. in Lecomte, Fl. Indo-Chine 5: 702, t. 82. 1928 ≡ *Streblus crenatus* (Gagnep.) Corner in Gard. Bull. Singapore 19: 226. 1962.
= *Phyllochlamys tridentata* Gagnep. in Lecomte, Fl. Indo-Chine 5: 714. 1928.

Figure 12.1.

Comments: The species authority recognizes the contribution of Dr. Chew Wee Lek, who in the 1950s annotated quite a lot of specimens (including at K, L, and SING) with the new combination *Taxotrophis taxoides*, proposed in his doctoral dissertation (Chew, 1960). However, the combination was never published, probably because the need for the combination was obviated in 1962 when Corner, his doctoral supervisor, reduced *Taxotrophis* to a section of *Streblus*.

6. ***Taxotrophis zeylanica*** (Thwaites) Thwaites, Enum. Pl. Zeyl.: 264. 1861 ≡ *Epicarpurus zeylanicus* Thwaites in Hooker's J. Bot. Kew Gard. Misc. 4: 1. 1852 ≡ *Diplocos zeylanica* (Thwaites) Bureau in Candolle, Prodr. 17: 215. 1873 ≡ *Streblus zeylanicus* (Thwaites) Kurz, Forest Fl. Burma 2: 464. 1877.
= *Taxotrophis caudata* Hutch. in Bull. Misc. Inform. Kew 1918(4): 149. 1918.

Trophis

Trophis P.Browne, Civ. Nat. Hist. Jamaica: 357. 1756, nom. cons. – Type: *Trophis americana* L. (= *T. racemosa* (L.) Urb.).
= *Bucephalon* L., Sp. Pl. 2: 1190. 1753, nom. rej. – Type: *Bucephalon racemosum* L. (≡ *Trophis racemosa* (L.) Urb.).
= *Skutchia* Pax & K.Hoffm. ex C.V.Morton in J. Wash. Acad. Sci. 27: 306. 1937 – Type: *Skutchia caudata* Morton (= *Trophis mexicana* (Liebm.) Bureau).

Dioecious trees or shrubs. *Leaves* distichous, pinnately veined. Stipules free, lateral. *Inflorescences* axillary or just below the leaves, solitary or paired, interfloral bracts basally attached. Staminate inflorescences spicate to racemose with an abaxial sterile groove, tepals 4, basally connate, stamens 4, filaments inflexed in bud, pistillode present. Pistillate inflorescences spicate to racemose or subcapitate, tepals 4, connate,

forming a tubular perianth, ovary adnate to the perianth or not, stigma bifid, arms equal. *Fruits* drupaceous, up to ca. 1.5 cm long, adnate to the perianth or not, the perianth enlarged and fleshy or not. *Seeds* up to ca. 1 cm long, cotyledons equal.

Species and distribution: 5 species in the Neotropics.

Trophis sect. ***Trophis***

1. ***Trophis cuspidata*** Lundell in Amer. Midl. Naturalist 19: 427. 1938.

2. ***Trophis mexicana*** (Liebm.) Bureau in Candolle, Prodr. 17: 253. 1873 ≡ *Sorocea mexicana* Liebm., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Math. Afd., ser. 5, 2: 335. 1851.

3. ***Trophis noraminervae*** Cuevas & Carvajal in Acta Bot. Mex. 47: 2, fig. 1–7. 1999.

4. ***Trophis racemosa*** Urb., Symb. Antill. 4(2): 195. 1905. — Figure 11.1.

Trophis sect. ***Echinocarpa*** C.C.Berg in Proc. Kon. Ned. Akad. Wetensch. C 91: 353. 1988 – Type: *Trophis involucrata* W.C.Burger.

5. ***Trophis involucrata*** W.C.Burger in Phytologia 26: 432. 1973.

Tribe OLMEDIEAE

Olmedieae Trécul in Ann. Sci. Nat., Bot., ser. 3, 8: 126. 1847.
= Antiarideae Dumort., Anal. Fam. Pl.: 16. 1829 ('Anthiarideae'), nom. utique rej. prop. – Type: *Antiaris* Lesch.
= Strebleae Bureau in Candolle, Prodr. 17: 215. 1873 – Type: *Streblus* Lour.
= Castilleae C.C.Berg in Acta Bot. Neerl. 26: 78. 1977 – Type: *Castilla* Cerv.
= Antiaropsideae C.C.Berg in Blumea 50: 536. 2005 – Type: *Antiaropsis* K.Schum.

Tree or shrubs, monoecious or dioecious (or androdioecious), mostly with self-pruning branches. *Leaves* alternate or opposite, distichous or spirally arranged; stipules lateral to amplexicaul. *Inflorescences* mostly unisexual, capitate, mostly discoid to urceolate, involucrate, tepals mostly 4, connate or not. Staminate inflorescences usually many-flowered; stamens 4 or fewer, with filaments straight or less often inflexed in bud, pistillode mostly absent. Pistillate inflorescences one to many-flowered, ovary free or not, stigmas 2, filiform. *Fruits* mostly drupaceous, mostly enclosed by a fleshy perianth or embedded in a fleshy receptacle. *Seeds* with or without endosperm, testa thin, vascularized, cotyledons mostly equal.

Genera and distribution: 13 genera with 63 species. Eight Neotropical genera: *Castilla* Cerv. (3 spp.), *Helicostylis* Trécul (7), *Maquira* Aubl. (4), *Naucleopsis* Miq. (22), *Olmedia* Ruiz & Pav. (1), *Perebea* Aubl. (9), *Poulsenia* Eggers (1), and *Pseudolmedia* Trécul (9); and five Paleotropical genera: the widespread *Antiaris* Lesch. (1); *Antiaropsis* K.Schum. (2) in New Guinea; *Mesogyne* Engl. (1) in Africa; *Sparattosyce* Bureau (1) in New Caledonia; and *Streblus* Lour. (3) in South to Southeast Asia.

Note: During review of the manuscript, it became apparent that Antiarideae Dumort., a little-used name, has priority over both Olmedieae and Castilleae, neither of which had ever been conserved. A proposal has been made to reject that name, but should the proposal not be accepted, the legitimate name of this tribe must be Antiarideae.

Olmedia

Olmedia Ruiz & Pav., Fl. Peruv. Prodr.: 129, t. 28. 1794 ≡ *Trophis* sect. *Olmedia* (Ruiz & Pav.) Berg in Proc. Kon. Ned. Acad. Wetensch. C. 91: 354. 1988 – Type: *Olmedia aspera* Ruiz & Pav.

Dioecious trees or shrubs. *Leaves* distichous, lamina pinnately veined. *Stipules* free, not fully amplexicaul. *Inflorescences* unisexual, with a well-developed involucre of imbricate bracts. Staminate inflorescences discoid, multiflorous; tepals 4, valvate, stamens 4, inflexed in bud, pistillode absent. Pistillate inflorescences usually uniflorous, perianth tubular, 4-dentate, ovary free, stigmas 2, equal. *Fruits* drupaceous, surrounded by fleshy persistent perianth and subtended by spreading, fleshy involucral bracts. *Seeds* ca. 5 mm long, cotyledons equal.

Species and distribution: 1 species, in the Neotropics.

1. ***Olmedia aspera*** Ruiz & Pav., Syst. Veg. Fl. Peruv. Chil. 1: 257. 1798.
= *Olmedia caucana* Pittier in Contr. U.S. Natl. Herb. 13: 434. 1912 ≡ *Trophis caucana* (Pittier) C.C.Berg in Proc. Kon. Ned. Acad. Wetensch. C. 91: 354. 1988.
= *Olmedia aspera* Poepp. & Endl., Nov. Gen. Sp. Pl. 2: 31. 1838, nom. illeg., non Ruiz & Pav. 1798.
= *Olmedia poeppigiana* Klotzsch in Linnaea 20: 525. 1847, pro syn., nom. illeg., non Mart. 1841.
= *Trophis aurantiaca* Herzog in Repert. Spec. Nov. Regni Veg. 7: 51. 1909.
= *Olmedia falcifolia* Pittier in Contr. U.S. Natl. Herb. 13: 435. 1912.
Figure 13.2.

Streblus

Streblus Lour., Fl. Cochinch.: 615. 1790 ≡ *Achimus* Vahl ex Poir. in Lamarck, Encycl. 8: 123. 1808 – Type: *Streblus asper* (Retz.) Lour. (≡ *Trophis aspera* Retz.)
= *Epicarpurus* Blume, Bijdr. Fl. Ned. Ind. 10: 488. 1825 – **Type (designated here):** *Epicarpurus orientalis* Blume.
= *Albrandia* Gaudich., Voy. Uranie: 509. 1830 – **Type (designated here):** *Albrandia orientalis* (Blume) D.Dietr. (= *Streblus asper* (Retz.) Lour.).
= *Calius* Blanco, Fl. Filip.: 698. 1837 – **Type (designated here):** *Calius lactescens* Blanco (= *Streblus asper* (Retz.) Lour.).

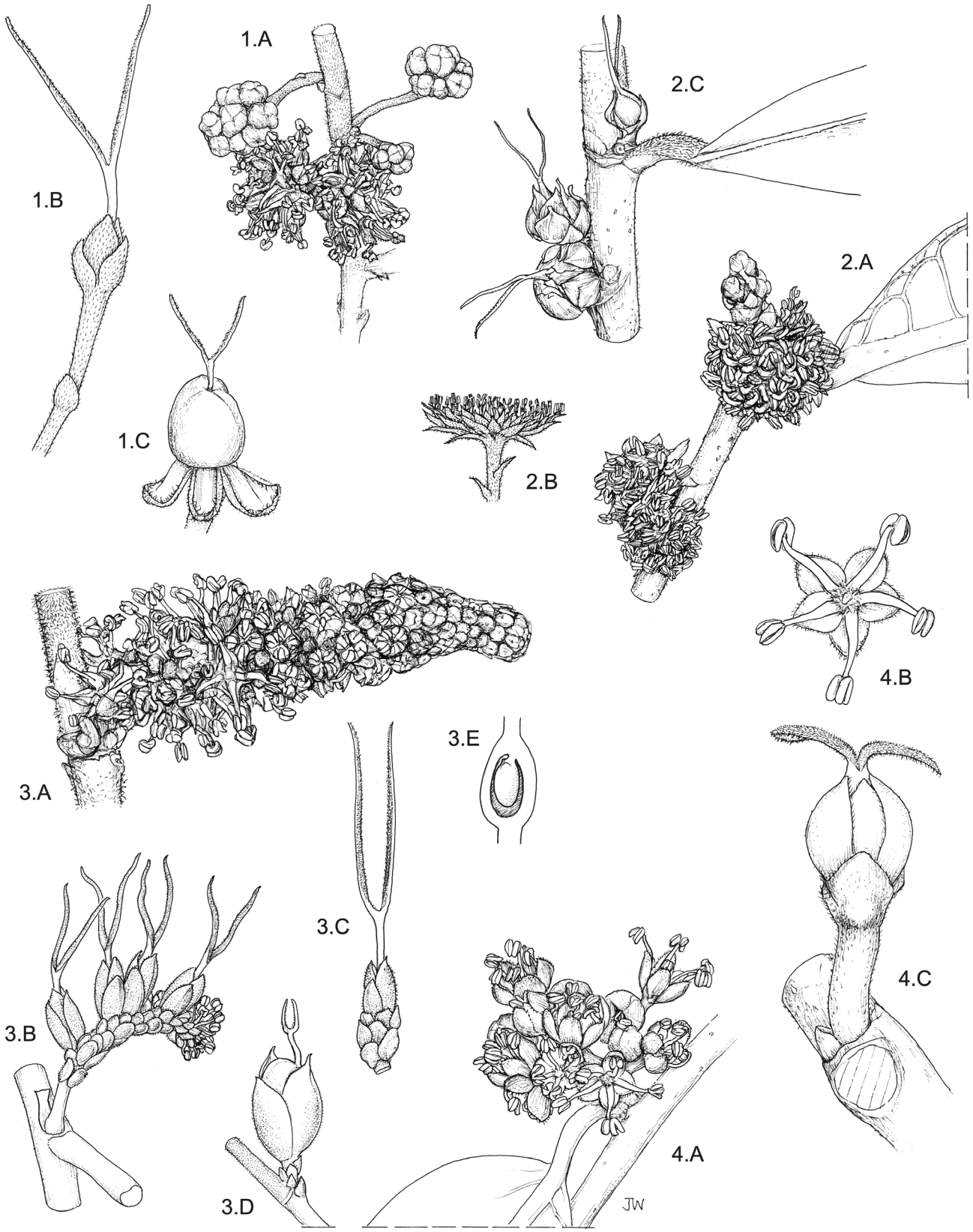

Fig. 13.1. *Streblus asper* (Retz.) Lour.: **A**, Staminate inflorescences; **B**, Pistillate inflorescence; **C**, Fruit. **10.2.** *Olmedia aspera* Ruiz & Pav.: **A** & **B**, Staminate inflorescences; **C**, Pistillate inflorescences. **10.3.** *Sloetiopsis usambarensis* Engl.: **A**, Staminate inflorescence; **B**, Bisexual inflorescence; **C**, Pistillate inflorescence; **D**, Fruiting perianth; **E**, Detail of ovule, showing subapical placentation typical of Moraceae. **10.4.** *Pseudostreblus indicus* Bureau: **A**, Staminate inflorescences; **B**, Pistillate inflorescence; **C**, Fruiting perianth. — Drawn by J. Williamson.

= *Teonongia* Stapf in Hooker's Icon. Pl. 30: t. 2947. 1911 – **Type (designated here):** *Teonongia tonkinensis* (Eberh. & Dubard) Stapf (≡ *Streblus tonkinensis* (Eberh. & Dubard) Corner).

= *Diplothorax* Gagnep. in Bull. Soc. Bot. France 75: 98. 1928 – **Type (designated here):** *Diplothorax tonkinensis* Gagnep. (= *Streblus asper* (Retz.) Lour.).

Trees or shrubs, dioecious or monoecious. *Leaves* distichous, lamina pinnately veined. *Stipules* free, lateral. *Inflorescences* bisexual or unisexual, capitate, with a rudimentary involucre, bracts basally attached. Staminate inflorescences discoid capitate, multiflorous; tepals 4, imbricate, stamens 4, inflexed in bud, pistillode present but small. Pistillate inflorescences usually uniflorous, tepals 4, ovary free, stigmas 2, equal. *Fruits* drupaceous, up to ca. 8 mm long, initially enclosed by enlarged but not fleshy tepals, which may open later. *Seeds* ca. 5 mm long, cotyledons equal or very unequal.

Species and distribution: 3 species from India to South China and from mainland Southeast Asia to the Philippines and the Moluccas.

1. ***Streblus asper*** (Retz.) Lour., Fl. Cochinch.: 615. 1790 ≡ *Trophis aspera* Retz., Observ. Bot. 5: 30. 1788 ≡ *Epicarpurus asper* (Retz.) Steud., Nomencl. Bot., ed. 2, 1: 556. 1840 ≡ *Trophis zeylanica* J.Koenig ex Blume, Mus. Bot. 2: 79. 1856, pro syn., nom. illeg ≡ *Achymus pallens* Sol. ex Blume, Mus. Bot. 2: 79. 1856, pro syn., nom. illeg.

= *Trophis cochinchinensis* Poir. in Lamarck, Encycl. 8: 123. 1808.

= *Epicarpurus orientalis* Blume, Bijdr. Fl. Ned. Ind. 10: 488. 1825 ≡ *Albrandia orientalis* (Blume) D.Dietr., Syn. Pl. 5: 280. 1852.

= *Calius lactescens* Blanco, Fl. Filip.: 698. 1837 ≡ *Streblus lactescens* (Blanco) Blume, Mus. Bot. 2: 80. 1856.

= *Epicarpurus gaudichaudii* Steud., Nomencl. Bot., ed. 2, 1: 556. 1840 ≡ *Albrandia gaudichaudii* (Steud.) D.Dietr., Syn. Pl. 5: 280. 1852.

= *Cudrania crenata* C.H.Wright in J. Linn. Soc., Bot. 26: 469. 1899 ≡ *Vanieria crenata* (C.H.Wright) Chun in J. Arnold Arbor. 8: 21. 1927.

= *Diplothorax tonkinensis* Gagnep. in Bull. Soc. Bot. France 75: 98. 1928.

Figure 13.1.

Note: Retzius's *Trophis aspera* predated Loureiro's *Streblus asper* by two years, and we therefore treat the latter a presumed new combination under Art. 41.4 of the *Code* (cf. Ex. 10). Synonymies of *S. asper* have sometimes erroneously included *T. aculeata* Roth, which is actually *Maclura spinosa* (Roxb. ex Willd.) C.C.Berg.

2. ***Streblus celebensis*** C.C.Berg in Blumea 50: 547. 2005.

3. ***Streblus tonkinensis*** (Eberh. & Dubard) Corner in Gard. Bull. Singapore 19: 228. 1962 ≡ *Bleekrodea tonkinensis* Eberh. & Dubard in Compt. Rend. Hebd. Séances Acad. Sci. 145: 632. 1907 ≡ *Teonongia tonkinensis* (Eberh. & Dubard) Stapf. in Hooker's Icon. Pl. 30: t. 2947. 1911.

Tribe DORSTENIEAE

Dorstenieae Dumort., Anal. Fam. Pl.: 16. 1829 – Type: *Dorstenia* L.

= Broussonetieae Gaudich., Voy. Uranie: 508. 1830 – Type: *Broussonetia* L'Hér. ex Vent.

= Brosimeae Trécul in Ann. Sci. Nat., Bot., ser. 3, 8: 146. 1847 – Type: *Brosimum* Sw.

= Fatoueae Engl. in Engler & Prantl, Nat. Pflanzenfam. 3(1): 71. 1888 – Type: *Fatoua* Gaudich.

Monoecious or less often dioecious trees, shrubs, lianas, and herbs. *Leaves* alternate or less commonly (sub)opposite, distichous or spirally arranged; stipules lateral to fully amplexicaul. *Inflorescences* unisexual or bisexual, cymose, spicate, globose, or discoid to turbinate or cup-shaped, multiflorous or uniflorous (the latter in pistillate inflorescences only), bracteate or not, interfloral bracts mostly peltate. Staminate flowers with tepals (1–)2–4 or absent, stamens 1–4 with filaments straight or inflexed in bud, pistillode present or (more often) absent. Pistillate flowers free or connate or embedded in the receptacle, tepals 2–4, ovary free or not, stigmas 1 or 1, equal or unequal. *Fruits* drupaceous or drupe-like due to a persistent fleshy perianth and/or receptacle, the whole endocarp unit often ballistically ejected from the infructescence. *Seeds* with or without endosperm, large or small; cotyledons equal or unequal.

Genera and distribution: 12 genera and 156 species with a worldwide distribution: *Bleekrodea* Blume (Africa, Southeast Asia), *Bosqueiopsis* De Wild. & T.Durand (Africa), *Brosimum* Sw. (Neotropics), *Broussonetia* L'Hér. ex Vent. (Asia to Oceania; introduced worldwide), *Dorstenia* Plum. ex L. (Africa and South America, with one species in India), *Fatoua* Gaudich. (Madagascar and Japan to New Caledonia; introduced worldwide), *Malaisia* Blanco (Southeast Asia to New Caledonia), *Scyphosyce* Baill. (Africa), *Sloetia* Teijsm. & Binn. ex Kurz (Southeast Asia), *Sloetiopsis* Engl. (Africa), *Trilepisium* Thouars (Africa), *Utsetela* Pellegr. (Africa).

Sloetiopsis

Sloetiopsis Engl. in Bot. Jahrb. Syst. 39: 573. 1907 – Type: *Sloetiopsis usambarensis* Engl.

= *Neosloetiopsis* Engl. in Bot. Jahrb. Syst. 51: 426. 1914 – Type: *Neosloetiopsis kamerunensis* Engl.

Dioecious (or monoecious) trees or shrubs. *Leaves* distichous, pinnately veined, cystoliths present; stipules free, nearly amplexicaul. *Inflorescences* unisexual (or bisexual); staminate inflorescences spicate with an abaxial sterile groove, bracts mostly peltate, tepals 4, free or basally connate filaments inflexed in bud, pistillode small; pistillate inflorescences uniflorous, bracts mostly basally attached, tepals 4, free, imbricate, 2 stigmas. *Fruits* drupaceous, fleshy endocarp dehiscent, tepals enlarged and persistent but not fleshy. *Seeds* globose, ca. 4 mm,

endocarp coriaceous with a hard disc against the hilum, testa vascularized with a thick apical cap, cotyledons equal.

1. ***Sloetiopsis usambarensis*** Engl. in Bot. Jahrb. Syst. 39: 573. 1907 ≡ *Streblus usambarensis* (Engl.) C.C. Berg in Proc. Kon. Ned. Acad. Wetensch. C. 91: 357. 1988.

= *Neosloetiopsis kamerunensis* Engl. in Bot. Jahrb. Syst. 51: 426. 1914.

Figure 13.3.

Comment: The nearly amplexicaul stipules, occasional bisexual inflorescences, and ballistic ejection of the endocarp body reflect an affinity with the Southeast Asian *Sloetia*, also a member of the Dorstenieae.

Tribe PARARTOCARPEAE

Parartocarpeae Zerega & E.M.Gardner in Phytotaxa 388(4): 260. 2019 – Type: *Parartocarpus* Baill.

Monoecious or dioecious shrubs to large trees; abundant white exudate. *Leaves* distichous or spirally arranged; simple; entire; pinnately veined; thin to thick coriaceous; glabrous, pubescent, scabrid, or hispid pubescent. *Stipules* axillary, simple or paired, lateral. *Inflorescences* solitary or paired in leaf axils, unisexual (or bisexual with a single apical pistillate flower), uniflorous, cymose, or capitate with stamens or ovaries sunken into the receptacle; pedunculate; involucre of 3–8 triangular bracts, basally connate. Staminate inflorescences with numerous flowers, tepals 4–5, stamens 5 and normally positioned or 1–3 in cavities in the receptacle with the anthers exerted through perforations in the upper surface of the receptacle, filaments free or united. Pistillate inflorescences uniflorous or (sub)globose with ovaries solitary in each cavity, unilocular, the style apical with a short exerted stigma. *Fruits* drupaceous, enclosed by persistent tepals, or aggregated into syncarps formed by the enlargement of the entire inflorescence.

Genera and distribution: 3 genera and 5 species, from southern China to the Solomon Islands: *Hullettia* King, *Parartocarpus* Baill., and *Pseudostreblus* Bureau.

Pseudostreblus

Pseudostreblus Bureau in Candolle, Prodr. 17: 220. 1873 ≡ *Streblus* sect. *Pseudostreblus* (Bureau) Corner in Gard. Bull. Singapore 19: 217. 1962 – Type: *Pseudostreblus indicus* Bureau.

Monoecious trees. *Leaves* distichous, pinnately veined. Stipules free, lateral. *Inflorescences* axillary. Staminate inflorescences cymose, tepals 5, imbricate, filaments inflexed in bud but apparently straightening gradually upon anthesis, pistillode minute, conical, pubescent, interfloral bracts few, basally attached. Pistillate inflorescences uniflorous, pedunculate, involucral bracts 3, ± connate, tepals 4, imbricate, stigma bifid, arms equal. *Fruits* drupaceous, ca. 1 cm long, with tepals enlarged and loosely enclosing the fruit. *Seeds* ellipsoid, ca. 6 × 8 mm, cotyledons unequal.

Species and distribution: 1, in South to Southeast Asia and southern China.

Note: *Pseudostreblus* is remarkable for its 5-parted staminate flowers.

1. ***Pseudostreblus indicus*** Bureau in Candolle, Prodr. 17: 220. 1873 ('*indica*') ≡ *Streblus indicus* (Bureau) Corner in Gard. Bull. Singapore 19: 226. 1962.

Figure 13.4.

■ CONCLUSION

The revisions presented here provide for seven monophyletic tribes of Moraceae and ten monophyletic genera within Moreae. We hope that the resulting taxonomic and phylogenetic framework will provide a solid foundation for further research into the systematics and evolution of Moraceae.

■ AUTHOR CONTRIBUTIONS

EMG led the writing of the manuscript, did field, lab, and herbarium work, conducted all phylogenetic analyses, and was responsible for the taxonomic treatment. MG performed lab work for the Moraceae333 samples. RC, SD, NE, and OM performed lab work for the PAFTOL samples, and OM curated the PAFTOL data. DA collaborated on all herbarium work at BO and contributed to the taxonomic treatment. Sahromi facilitated access and participated in field collections at the Bogor Botanical Gardens. NJCZ provided overall guidance on Moraceae and facilitated sequencing at Northwestern University. WJB and FF acquired funding for and supervised the PAFTOL project. AKM performed herbarium sampling at K and supervised the Moraceae portion of the PAFTOL project. EMG designed the overall study with input from ALH and NJCZ. ALH supervised the overall study. All authors commented on and contributed to the manuscript.

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Appendix 1. Accessions used for sequencing, showing taxon, geographic origin, voucher information, GenBank SRA accession number, and number of loci recovered (Moraceae333/Angiosperms353). Asterisks (*) denote samples newly sequenced for this study.

Afromorus mesozygia (Stapf) E.M.Gardner, Nigeria: *Daramola 330* (F), SRR12282929* (330/31); Central African Republic: *Buckner 309* (MO), SRR12282928* (330/29). ***Ampalis dimepate*** (Bureau) E.M.Gardner, Madagascar: *Rakotonirina & al. 405* (MO), SRR12282873* (331/30). ***Ampalis mauritiana*** (Jacq.) Urb., Madagascar: *Rakotonirina & Be 489* (MO), SRR12283062* (329/12); Comoros (the): *Hoffmann & al. 438* (K (K000618250)), ERS4414222* (39/302). ***Antiaris toxicaria*** Lesch., Indonesia: *Nooteboom 5995* (K (K000618256)), ERS4414194* (8/186). ***Antiaropsis decipiens*** K.Schum, Papua New Guinea: *Zerega & al. 281* (NY), SRR3907583 (298/7); Papua New Guinea: *Weiblen & al. 1865* (K (K000618255)), ERS4414199* (59/327). ***Artocarpus altilis*** (Parkinson) Fosberg, U.S.A. (cult. from Samoa): *Breadfruit Institute grid no. K7* (PTBG), SRR12282879 (331/NA). ***Artocarpus altissimus*** (Miq.) J.J.Sm., Java (cult.): *Gardner & al. 441* (F), SRR12283100 (322/NA). ***Artocarpus anisophyllus*** Miq., Borneo: *Zerega & al. 606* (CHIC), SRR3907106 (328/NA). ***Artocarpus annulatus*** F.M.Jarrett, Borneo: *Zerega & al. 985* (F), SRR12283099 (324/NA). ***Artocarpus bergii*** E.M.Gardner, Arifiani & Zerega, Moluccas: *Mahroji & al. 160* (BO, L, MO), SRR12283019 (331/NA). ***Artocarpus blancoi*** (Elmer) Merr., Philippines: *Ramos 42018* (L), SRR12282902 (331/NA). ***Artocarpus borneensis*** Merr., Borneo: *Zerega & al. 686* (F, SAN), SRR12283067 (331/NA). ***Artocarpus brevipedunculatus*** (F.M.Jarrett) C.C.Berg, Borneo: *Zerega & al. 814* (F, SAN), SRR3907332 (327/NA). ***Artocarpus camansi*** Blanco, U.S.A. (cult.): *Gardner 149* (PTBG), SRR12283098 (332/NA). ***Artocarpus chama*** Buch.-Ham., Bangladesh: *Zerega & al. 354* (F), SRR12283079 (331/NA). ***Artocarpus corneri*** Kochummen, Borneo: *Fuchs 21347* (K, SAR), SRR12283015 (318/NA). ***Artocarpus dadah*** Miq., Borneo: *Zerega & al. 694* (F, SAN), SRR3907210 (330/NA). ***Artocarpus elasticus*** Reinw. ex. Blume, Borneo: *Gardner & al. 87* (F, SAN), SRR3907457 (332/NA). ***Artocarpus excelsus*** F.M.Jarrett, Borneo: *Gardner & al. 222* (F, SAN, SNP), SRR3907331 (330/NA). ***Artocarpus fretessii*** Teijsm. & Binnend., Borneo: *Adriansyah AA2243* [type of *A. albobrunneus* C.C.Berg] (LE, MO, P), SRR12282906 (328/NA); *Zerega & al. 929* (F, SAN), SRR3907410 (330/NA). ***Artocarpus frutescens*** (Becc.) Renner, Borneo: *Gardner & al. 411* (F, SAN), SRR12283088 (263/NA). ***Artocarpus fulvicortex*** F.M.Jarrett, Singapore: *Lee YQ 35* (CHIC, SING), SRR12283075 (331/NA). ***Artocarpus glaucus*** Blume, Borneo: *Zerega & al. 852* (F, SAN), SRR12283074 (330/NA). ***Artocarpus gomezianus*** Wall. ex Trécul, Thailand: *Zerega & al. 533* (CHIC, KKU), SRR12283072 (329/NA). ***Artocarpus gongshanensis*** S.K.Wu ex. C.Y.Wu & S.S.Chang, China: *Gaoligong Shan Biodiversity Survey 24987* (HAST, MO), SRR12283006 (324/NA). ***Artocarpus griffithii*** (King) Merr., Malaysia (Peninsula): *Zerega & al. 216* (F), SRR12283066 (330/NA). ***Artocarpus heterophyllus*** Lam., Borneo: *Gardner & al. 98* (F, SAN), SRR3907497 (330/NA). ***Artocarpus hirsutus*** Lam., India: *Zerega & al. 953* (ATREE (photo voucher CHIC)), SRR12283116 (323/NA). ***Artocarpus hispidus*** F.M.Jarrett, Malaysia (Peninsula): *Zerega & al. 258* (F), SRR12283071 (322/NA). ***Artocarpus horridus*** F.M.Jarrett, Java (cult.): *Gardner & al. 437* (F), SRR12283095 (332/NA). ***Artocarpus humilis*** Becc., Borneo: *Gardner & al. 258* (F, SAN), SRR12283050 (329/NA). ***Artocarpus hypargyreus*** Hance ex. Benth., China (Hong Kong): *Gardner & al. 170* (F, HK), SRR12283054 (329/NA). ***Artocarpus integer*** (Thunb.) Merr. var. ***integer***, Borneo: *Zerega & al. 918* (F, SAN), SRR3907371 (329/NA). ***Artocarpus jarrettiae*** Kochummen, Borneo: *Amin & Francis SAN120933* (K, L, SAN), SRR12282898 (116/NA). ***Artocarpus kemando*** Miq., Borneo: *Zerega & al. 612* (F, SAN), SRR3907163 (331/NA). ***Artocarpus lacucha*** Roxb. ex Buch.-Ham., Thailand: *Zerega & al. 420* (CHIC, KKU), SRR3907082 (330/NA). ***Artocarpus lamellosus*** Blanco, Philippines: *Gaerlan & al. PPI10374* (L), SRR12282893 (327/NA). ***Artocarpus lanceifolius*** Roxb. subsp. ***clementis*** (Merr.) F.M.Jarrett, Borneo: *Zerega & al. 739* (F, SAN), SRR3907263 (328/NA). ***Artocarpus limpato*** Miq., Borneo: *Zerega & al. 609* (F, SAN), SRR3907129 (325/NA). ***Artocarpus longifolius*** Becc. subsp. ***adpressus*** C.C.Berg, Borneo: *Gardner & Zerega 412* (F, SAR), SRR12283094 (328/NA). ***Artocarpus lowii*** King, Malaysia (Peninsula): *Wang & al. MWL2* (CHIC), SRR3907544 (332/NA). ***Artocarpus maingayi*** King, Malaysia (Peninsula): *Zerega & al. 257* (F), SRR12283069 (324/NA). ***Artocarpus mariannensis*** Trécul, U.S.A. (cult. from Micronesia): *Breadfruit Institute grid no. DD4* (PTBG), SRR12283068 (332/NA). ***Artocarpus melinoxylus*** Gagnep., Vietnam: *Soejarto & al. 14222* (F), SRR12282896 (324/NA). ***Artocarpus montanus*** E.M.Gardner & Zerega, Vietnam: *Averyanov & al. VH1819* (LE, MO, P), SRR12283017 (322/NA). ***Artocarpus multifidus*** F.M.Jarrett, Philippines: *Stone & Fuentes PPI3911* (K), SRR12282895 (132/NA). ***Artocarpus nobilis*** Thwaites, Sri Lanka: *Jayasuriya 3283* (US), SRR12282892 (332/NA). ***Artocarpus obtusus*** F.M.Jarrett, Borneo: *Zerega & al. 729* (F, SAN), SRR12283064 (331/NA). ***Artocarpus odoratissimus*** Blanco, Borneo: *Zerega & al. 618* (F, SAN), SRR12283115 (329/NA). ***Artocarpus ovatus*** Blanco, U.S.A. (Hawaii): *Zerega & al. 202* (F), SRR12283063 (148/NA). ***Artocarpus papuanus*** (Becc.) Renner, Papua New Guinea: *Zerega & al. 61* (NY), SRR12283061 (323/NA). ***Artocarpus parvus*** Gagnep., Malaysia (cult.): *Zerega & al. 911* (F, SAN), SRR3907350 (330/NA). ***Artocarpus petelotii*** Gagnep., Vietnam: *Soejarto & al. 14435* (F), SRR12282891 (327/NA). ***Artocarpus pinnatisectus*** Merr., Philippines: *Escritor 20789* (K, US), SRR12282890 (305/NA). ***Artocarpus pithecogallus*** C.Y.Wu, China: *Li Jianwu 3200* (KUN), SRR12282992 (328/NA). ***Artocarpus primackii*** Kochummen, Malaysia (Borneo): *Zerega & al. 687* (F, SAN), SRR3907189 (329/NA). ***Artocarpus rigidus*** Blume subsp. ***asperulus*** (Gagnep.) F.M.Jarrett, Thailand: *Zerega & al. 507* (CHIC), SRR12283043 (333/NA). ***Artocarpus rigidus*** Blume subsp. ***rigidus***, Malaysia (Borneo): *Zerega & al. 728* (F, SAN), SRR3907233 (333/NA). ***Artocarpus rubrosoccatus*** E.M.Gardner, Chaveer. & Zerega, Thailand: *Zerega & al. 517* (CHIC, KKU), SRR12283080 (329/NA). ***Artocarpus rubrovenius*** Warb., Philippines: *Burley 84* (F), SRR12283021 (327/NA). ***Artocarpus scortechinii*** King, Malaysia (Peninsula): *Zerega & al. 209* (F), SRR12283022 (330/NA). ***Artocarpus sepicanus*** Diels, Papua New Guinea: *Weiblen & al. 1701* (MIN), SRR3907521 (322/NA). ***Artocarpus sericicarpus*** F.M.Jarrett, Malaysia (Borneo): *Zerega & al. 771* (F, SAN), SRR3907288 (332/NA). ***Artocarpus styracifolius*** Pierre, China (Hong Kong): *Gardner & al. 176* (F, HK), SRR12283038

Appendix 1. Continued.

(324/NA). ***Artocarpus subrotundifolius*** Elmer, Philippines: *Wenzel 1576* (F), SRR12282887 (328/NA). ***Artocarpus sumatranus*** F.M.Jarrett, Sumatra: *Ambriansyah AA2766* (L), SRR12282886 (330/NA). ***Artocarpus tamaran*** Becc., Malaysia (Borneo): *Gardner & al. 92* (F, SAN), SRR3907480 (332/NA). ***Artocarpus teijsmannii*** Miq., Malaysia (Borneo): *Zerega & al. 946* (F, SAN), SRR3907434 (331/NA). ***Artocarpus thailandicus*** C.C.Berg, Thailand: *Zerega & al. 402* (CHIC), SRR3907065 (326/NA). ***Artocarpus tomentosulus*** F.M.Jarrett, Malaysia (Borneo): *Zerega & al. 617* (F, SAN), SRR12283060 (330/NA). ***Artocarpus tonkinensis*** Chev. ex. Gagnep., China (Hong Kong): *Gardner & al. 174* (F, HK), SRR12283037 (325/NA). ***Artocarpus treculianus*** Elmer, Philippines: *Elmer 12468* (US), SRR12282985 (286/NA); [*A. nigrescens* Elmer] *Ramos BS-34736* (US), SRR12282995 (317/NA); U.S.A., Hawaii cultivated: [*A. ovatifolius* Merr.] *Zerega & al. 203* (F), SRR12283058 (330/NA). ***Artocarpus vriesianus*** Miq. var. ***refractus*** (Becc.) F.M.Jarrett, Papua New Guinea: *Hoogland 4822* (L), SRR12282981 (314/NA). ***Artocarpus vriesianus*** Miq. var. ***vriesianus***, Papua New Guinea: *Weiblen & al. 1229* (MIN), SRR12283057 (331/NA). ***Artocarpus xanthocarpus*** Merr., Taiwan (cult.): *Yang 15648* (MO), SRR12283033 (327/NA). ***Artocarpus zeylanicus*** (F.M.Jarrett) E.M.Gardner & Zerega, India: *Zerega & al. 956* (ATREE (photo voucher CHIC)), SRR12283117 (327/NA). ***Bagassa guianensis*** Aubl., Guyana: *Jansen-Jacobs & al. 3767* (K (K000618248)), ERS4414223* (60/324); French Guiana: *Weiblen & al. 1677* (MIN), SRR12283114 (333/NA). ***Batocarpus amazonicus*** (Ducke) Fosberg, Bolivia: *Salidas 1233* (F), SRR12283113 (329/NA); Brazil: *Berg & al. 18524* (K (K000946661)), ERS4414214* (36/310). ***Batocarpus costaricensis*** Standl. & L.O.Williams, Costa Rica: *Weiblen & al. 1463* (MIN), SRR12283111 (329/NA). ***Batocarpus orinocensis*** H.Karst., Peru: *Vasquez 27440* (F), SRR12283110 (330/NA); Ecuador: *Palacios 3265* (K (K001257751)), ERS4414228* (50/315). ***Bleekrodea madagascariensis*** Blume, Madagascar: *Davis & Rakotonasolo 3117* (K), ERS4414207* (37/297). ***Boehmeria nivea*** (L.) Gaudich.: *Hu S.Y. 8113* (K), ERS4414210* (11/297). ***Bosqueiopsis gilletii*** De Wild. & T.Durand, Tanzania: *Frontier Tanzania Coastal Forest Research Program 243* (K (K000618258)), ERS4414219* (30/209). ***Brosimum alicastrum*** Sw.: *Monro & Lander 7382* (K), ERS4414237* (54/209); U.S.A. (cult.): *Gardner 23* (CHIC), SRR12283030 (287/NA). ***Brosimum amazonicum*** (Poepp. & Endl.) E.M.Gardner & Zerega, Brazil: *Prance & al. 13461* (K (K000618261)), ERS4414195* (28/295). ***Brosimum sprucei*** (Baill.) E.M.Gardner & Zerega, Brazil: *Ribeiro & al. 1204* (K (K001257756)), ERS4414229* (34/305). ***Broussonetia kazinoki*** Siebold: *Chase 17827* (K), ERS4414202* (33/304). ***Broussonetia papyrifera*** (L.) L'Hér. ex Vent., China: *unknown*, SRR1477753 (268/343). ***Broussonetia* sp.**, China Yunnan: *Heng 14289* (F), SRR12283034* (309/22). ***Castilla elastica*** Cerv.: *Chase 19850* (K), ERS4414204* (26/257). ***Cecropia ficifolia*** Warb. ex Snethl., Brazil: *Berg & al. 18418* (K), ERS4414209* (24/305). ***Clarisia biflora*** Ruiz & Pav., NA: *Weiblen & al. 1460* (NA), SRR12283032 (314/NA). ***Clarisia ilicifolia*** (Spreng.) Lanj. & Rossbach, Brazil: *Maguire & al. 56675* (F), SRR12283023* (322/22); Brazil: *Souza 2492* (F), SRR12283012* (329/26); NA: *Carranta 6386* (F), SRR12282978 (290/NA). ***Clarisia racemosa*** Ruiz & Pav., Brazil: *Assuncaõ 690* (F), SRR12283109 (329/NA); Ecuador: *Palacios & Neill 1291* (K (K000618272)), ERS4414218* (83/318). ***Dorstenia barteri*** Bureau: *Chase 18153* (K), ERS4414203* (7/88). ***Dorstenia hildebrandtii*** Engl., U.S.A. (cult.): *Zerega & al. 311* (CHIC), SRR3907584 (203/4). ***Elatostema retrohirtum*** Dunn: *Monro & al. 7601* (K), ERS4414235* (9/208). ***Fatoua pilosa*** Gaudich., Indonesia: *Taylor 218* (K (K000618252)), ERS4414197* (41/306). ***Ficus macrophylla*** Roxb. & Buch.-Ham. ex Sm., U.S.A. (cult.): *Gardner 30* (CHIC), SRR3907044 (326/12). ***Ficus racemosa*** L., China: *unknown*, SRR1405699, SRR1405700 (188/101). ***Ficus sagittifolia*** Warb. ex Mildbr. & Burret: *Chase 19852* (K), ERS4414205* (45/309). ***Helicostylis tomentosa*** (Poepp. & Endl.) J.F.Macbr., Brazil: *Gomes & al. 511* (K (K001257758)), ERS4414220* (25/239). ***Hullettia dumosa*** King, Malaysia (Peninsula): *Zerega & al. 242* (CHIC), SRR12283106 (232/7). ***Hullettia griffithiana*** (Kurz) Hook.f., Thailand: *Kerr 16866* (US), SRR12282908 (275/NA). ***Leucosyke capitellata*** (Poir.) Wedd., *Lugas 41* (K), ERS4414208* (13/293). ***Maclura africana*** (Bureau) Corner, Tanzania: *Greenway & Kanuri 15269* (S), SRR12282990* (316/25); Tanzania: *Manktelow 93027* (K (K000618268)), ERS4414226* (6/217). ***Maclura amboinensis*** Blume, Papua New Guinea: *Takeuchi 16378* (US), SRR12282979* (319/24). ***Maclura andamanica*** (Hook.f.) Corner, Thailand: *Maxwell 89-436* (L), SRR12282968* (322/23). ***Maclura brasiliensis*** Endl., Bolivia: *Nee & Vargas 45025* (NY), SRR12282959* (322/23). ***Maclura cochinchinensis*** (Lour.) Corner, Malaysia (Borneo): *Zerega & al. 757* (F, SAN, SNP), SRR12283027* (232/NA); China Guizhou: *Sino-American Guizhou Botanical Expedition 887* (NY), SRR12282958* (324/24); New Caledonia: *Baumann 6841* (K (K000618267)), ERS4414221* (22/297). ***Maclura fruticosa*** (Roxb.) Corner, Vietnam: *Cuong & al. 1193* (F), SRR12282957* (323/27). ***Maclura pomifera*** (Raf.) C.K.Schneid., U.S.A. (Illinois): *Gardner 139* (CHIC), SRR3907028 (324/9); U.S.A.: *Swann s.n.* (K (K000618269)), ERS4414232* (20/288). ***Maclura* sp.**, Vietnam: *Averyanov & al. CBL1198* (MO), SRR12283001* (327/31). ***Maclura spinosa*** (Willd.) C.C.Berg, India: *Perumal RHT 22554* (L), SRR12282955* (326/21). ***Maclura tinctoria*** (L.) D.Don ex Steud., Costa Rica: *Fernàndez 314* (F), SRR12282953* (325/28); Argentina: *Renvoize & al. 3252* (K (K000618246)), ERS4414230* (21/311); subsp. ***tinctoria***, Peru: *Campos & Diaz 2679* (F), SRR12282951* (325/31); subsp. ***mora*** (Griseb.) Vázq.Avila, Bolivia: *Nee 40044* (NY), SRR12282952* (326/34). ***Maclura thorelii*** (Gagnep.) Corner, Cambodia: *Pierre 4709* (NY), SRR12282954* (323/22). ***Maclura tricuspidata*** Carrière, U.S.A. (Illinois): *Gardner MOR 68-7917* (MOR), SRR12282950* (301/20). ***Maillardia borbonica*** Duch., Réunion: *Cadet 4518* (K (K000618265)), ERS4414217* (49/319). ***Maillardia montana*** Leandri, Madagascar: *van Nek 1882* (K (K000618270)), ERS4414227* (81/326); *Andrianantoanina 1023* (F), SRR12283024 (328/NA). ***Malaisia scandens*** (Lour.) Planch., *Gray 8416* (K), ERS4414231* (70/265); Indonesia: *Sands 6590* (K (K000618264)), ERS4414236* (45/321); Borneo: *Gardner & al. 122* (F, SAN), SRR12283025 (304/NA). ***Milicia excelsa*** (Welw.) C.C.Berg, Gabon: *Williamson 187* (K (K000618247)), ERS4414198* (53/319); Gabon: *McPherson 16087* (US), SRR12283108 (332/NA). ***Milicia regia*** (A.Chev.) C.C.Berg, Liberia: *Cooper 332* (F), SRR12282949* (331/40). ***Morus alba*** L., U.S.A., Illinois, cultivated: *Gardner MOR 920-26*1* (MOR), SRR12282946* (325/17); *Gardner MOR 38087*1* (MOR), SRR12282944* (326/17); *Gardner MOR 523-30*5* (MOR), SRR12282943* (326/20). ***Morus australis*** Poir., India: *Koelz 4431* (F), SRR12282948* (261/9); Taiwan: *Tanaka 17776* (F), SRR12282947* (331/25); U.S.A., Illinois, cultivated: *Gardner MOR 241-71*6* (MOR), SRR12282942* (326/17); South Korea: *Chung In-Cho 3290* (F), SRR12282941* (332/23); *Oh & al. 110618-012* (MOR), SRR12282940* (332/30). ***Morus cathayana*** Hemsl., China, Jiangxi: *Nie Min-xiang 92144* (MOR), SRR12282939* (331/31); Western Hupeh: *Wilson 10* (F), SRR12282938* (164/5). ***Morus celtidifolia*** Kunth, Mexico: *Sandoval & Gutierrez 637* (MO), SRR12282937* (332/33). ***Morus*** cf. ***alba*** L., Bermuda: *Hamilton 618* (K (K000214340)), ERS4414211* (52/310). ***Morus kagayamae*** Koidz., U.S.A., cult from Algeria: *AA20187-A* (F), SRR12282931* (333/35). ***Morus macroura*** Miq., U.S.A., Florida: *Gardner 28* (CHIC), SRR12282930* (332/21); Laos: *Bounhong Southavony LAOS_366* (F), SRR12282918* (332/49); Vietnam: *Soejarto & al. 14088* (F), SRR12282917* (331/29). ***Morus microphylla*** Buckley, Mexico Sonora: *Fishbein & al. 1058* (F), SRR12282927* (332/33); U.S.A., Texas: *Stone & al. 4225* (MO), SRR12282926* (333/34). ***Morus mongolica*** (Bureau) C.K.Schned., U.S.A., Illinois, cultivated: *Gardner MOR 55-95*1* (MOR), SRR12282925* (325/14). ***Morus nigra*** L., U.S.A., Florida, cultivated: *Gardner 29* (CHIC), SRR12282924* (331/21). ***Morus notabilis*** C.K.Schneid., China: *unknown*, SRR8138828 (333/333). ***Morus rubra*** L., U.S.A., Florida: *Gardner 141* (CHIC), SRR12282922* (327/20); U.S.A., Illinois, cultivated: *Gardner MOR 326-78*4* (MOR), SRR12282921* (327/20). ***Morus serrata*** Roxb., India: *Koelz 4788* (F), SRR12282920* (296/14); Pakistan: *Rodin 5315* (F), SRR12282919* (274/12). ***Naucleopsis macrophylla*** Miq., Brazil: *Berg & al. 18534* (K (K000946832)), ERS4414215* (30/316). ***Olmedia aspera*** Ruiz & Pav., Bolivia: *Fuentes & al. 5323* (MO), SRR12282905* (258/8); Peru: *Acevedo & al. 8833* (K (K000618263)), ERS4414213* (57/316). ***Parartocarpus bracteatus*** (King) Becc., Malaysia (Borneo): *Zerega & al. 730* (F, SAN), SRR12283105 (189/NA). ***Parartocarpus venenosus*** (Zoll. ex Moritzi) Becc., Malaysia (Borneo): *Zerega & al. 874* (F, SAN), SRR3907334 (221/3). ***Paratrophis anthropophagorum*** (Seem.) Benth & Hook.f. ex Drake, Fiji: *Degener 4698* (F), SRR12282876* (331/31). ***Paratrophis australiana*** C.T.White, Australia: *Hyland 10634* (BO), SRR12282872* (324/14). ***Paratrophis glabra*** (Merr.) Steenis, Malaysia (Borneo): *Gardner & al. 78* (F, SAN), SRR3907307 (320/NA). ***Paratrophis insignis*** (Bureau) E.M.Gardner, Ecuador: *Homeier 1949* (MO), SRR12282936* (326/19); Peru: *Monteagudo & al. 3734* (F), SRR12282935* (332/30); Bolivia: *Vargas 4154* (F), SRR12282933* (332/36); Peru: *Vasquez & Francis 28068* (F), SRR12282932* (332/33). ***Paratrophis microphylla*** (Raoul) Cockayne, New Zealand: *Beecher s.n.* (F), SRR12282870* (314/16); New Zealand: *Chase 17825* (K), ERS4414201* (56/316). ***Paratrophis pendulina*** (Endl.) E.M.Gardner, U.S.A., Hawaii: *Degener 17839* (F), SRR12282863* (327/19); *Fosberg 12877* (F), SRR12282862* (331/27); Wood 989 (F), SRR12282859* (330/26); Australia: *Gray 3277* (SING), SRR12282861* (331/27). ***Paratrophis philippinensis*** (Bureau) Fern.-Vill., Indonesia (cult.): *Gardner & al. 430* (F), SRR12283026* (333/9); Sulawesi: *Brambach 465* (BO), SRR12283087* (331/30). ***Poikilospermum suaveolens*** (Blume) Merr., Indonesia: *Asman 2* (K (K000576177)), ERS4414136* (9/251). ***Poulsenia armata*** (Miq.) Standl., *Pennington & al. 14600* (K), ERS4414206* (29/295). ***Pseudolmedia spuria*** (Sw.) Griseb., Costa Rica: *Lobo & al. 263* (K (K001257760)), ERS4414224* (17/301). ***Pseudostreblus indicus*** Bureau, China,

Appendix 1. Continued.

Guangxi: *Tsang 24252* (F), SRR12282867* (201/NA); Laos: *Newman & al. LA0518* (SING), SRR12282866* (327/NA). ***Sloetiopsis usambarensis*** Engl., Kenya: *Faden & al. 77/417* (F), SRR12282916* (320/20); Guinea: *Cheek & al. 18194* (K (K000743352)), ERS4414216* (42/295). ***Soleirolia soleirolii*** (Req.) Dandy: *Sheahan 17* (K), ERS4414200* (12/175). ***Sorocea affinis*** Hemsl., Costa Rica: *Espinosa 706* (F), SRR12282915* (331/32). ***Sorocea bonplandii*** (Baill.) W.C.Burger, Paraguay: *Stevens & al. 30948* (MO), SRR12282914* (329/29); Argentina: *Tressens & al. 6347* (F), SRR12283086* (300/4); Brazil: *Cloclet & al. 21.236* (K (K000618271)), ERS4414212* (22/242). ***Sorocea briquetii*** J.F.Macbr., Peru: *Valenzula & Huamantupa 954* (F), SRR12283085* (322/9). ***Sorocea duckei*** W.C.Burger, Peru: *Stein & Kallunki 3931* (F), SRR12282911* (330/27). ***Sorocea guilleminiana*** Gaudich., Bolivia: *Moya & al. 112* (MO), SRR12283035* (307/5); Brazil: [*S. klotzschiana* Baill.] *Maguire & al. 56625* (F), SRR12282910* (325/28). ***Sorocea hilarii*** Gaudich., Brazil: *Carauta 795* (F), SRR12282956* (316/7); *Pirani & Zappi 1136* (F), SRR12282878* (319/6). ***Sorocea jaramilloi*** C.C.Berg, Ecuador: *Madison 4772* (F), SRR12282934* (318/8). ***Sorocea muriculata*** Miq. subsp. ***muriculata***, Peru: *Vigo & Graham 16489* (F), SRR12282923* (324/14). ***Sorocea muriculata*** Miq. subsp. ***uaupensis*** (Baill.) C.C.Berg, Venezuela: *Plowman s.n.* (F), SRR12282912* (324/13). ***Sorocea pubivena*** Hemsl. subsp. ***hirtella*** (Mildbr.) C.C.Berg, Peru: *Vasquez & al. 19236* (F), SRR12282880* (332/29). ***Sorocea pubivena*** Hemsl. subsp. ***oligotricha*** (Akkermans & C.C.Berg) C.C.Berg, Panama: *Kennedy 2124* (F), SRR12282945* (325/11). ***Sorocea pubivena*** Hemsl. subsp. ***pubivena***, Panama: *Galdames 4477* (F), SRR12282871* (322/12); Costa Rica: [*S. cufodontisii* W.C.Burger] *Kernan 406* (F), SRR12282913* (261/3). ***Sorocea sprucei*** (Baill.) J.F.Macbr. subsp. ***saxicola*** (Hassl.) C.C.Berg, Bolivia: *Nee 35729* (F), SRR12282860* (323/9). ***Sorocea steinbachii*** C.C.Berg, Brazil: *Weiblen & al. 1501* (MIN), SRR12283107 (332/NA). ***Sorocea subumbellata*** (C.C.Berg) Cornejo, Ecuador: *Dodson 9601* (F), SRR12283084* (304/4). ***Sorocea trophoides*** W.C.Burger, Costa Rica: *Fuentes 304* (F), SRR12282877* (330/30); Peru: *Perea 2479* (F), SRR12283073* (283/4). ***Sparattosyce dioica*** Bureau, New Caledonia: *Weiblen 1223* (K (K000618253)), ERS4414234* (21/262). ***Streblus asper*** (Retz.) Lour., Indonesia Java cultivated: *Gardner 696* (F), SRR12282875* (327/36); Sri Lanka: *Townsend 73/42* (K (K000618251)), ERS4414233* (95/329). ***Taxotrophis ilicifolia*** (Kurz) S.Vidal, Singapore, cultivated from Johor: *Gardner & al. 720* (SING), SRR12282874* (329/28); Vietnam: *Cuong 122* (F), SRR12282869* (326/NA); Sumatra: *de Wilde 18958* (BO), SRR12282868* (327/NA). ***Taxotrophis macrophylla*** (Blume) Boerl., Vietnam: *Soejarto & al. 10673* (F), SRR12282865* (329/NA); Vietnam: *Scornickova & al. JLS 2916* (SING), SRR12282857* (330/31). ***Taxotrophis spinosa*** (Blume) Steenis, Indonesia, Sumatra: *Mahyuni & al. 020* (BO), SRR12282864* (325/NA); Sulawesi: *Sidiyasa & Arifin 4071* (BO), SRR12282858* (317/18); Indonesia, Java, cult.: *Gardner & al. 702* (F), SRR12282856* (330/30). ***Taxotrophis taxoides*** (B.Heyne ex Roth) W.L.Chew ex E.M.Gardner, Indonesia, Java, cult.: *Gardner & al. 701* (F), SRR12282855* (331/26); Philippines Palawan: *Ridsdale SMHI 422* (BO), SRR12282854* (290/14). ***Taxotrophis zeylanica*** (Thwaites) Thwaites, Sri Lanka: *Meijer 701* (SING), SRR12282853* (230/4). ***Trema orientale*** (L.) Blume, Netherlands: *unknown*, SRR5674478 (236/245). ***Trilepisium madagascariense*** DC., Madagascar: *Richard 403* (K (K000618259)), ERS4414196* (19/199). ***Trophis cuspidata*** Lundell, Mexico: *Gomez-Dominguez 774* (MO), SRR12282852* (331/27). ***Trophis involucrata*** W.C.Burger, Costa Rica: *Aguilar 4679* (F), SRR12283089* (333/36); Costa Rica: *Lent 2243* (F), SRR12282894* (323/12). ***Trophis mexicana*** (Liebm.) Bureau, Nicaragua: *Stevens & Montiel 27939* (MO), SRR12282883* (327/12). ***Trophis racemosa*** (L.) Urb., Nicaragua: *Stevens 37196* (MO), SRR12283112* (327/NA). ***Urtica urens*** L., *Fay 173* (K), ERS4414127* (8/185). ***Utsetela gabonensis*** Pellegr., Gabon: *Breteler 14086* (MO), SRR12283083* (302/24); Congo (the Democratic Republic of the): *Lebrun 5879* (K (K000618257)), ERS4414225* (11/232). ***Utsetela neglecta*** Jongkind, Gabon: *Bissiengou 923* (MO), SRR12283082* (308/30).