Morphological Evolution in the Mulberry Family (Moraceae)

Wendy L. Clement and George D. Weiblen[1]

Bell Museum and Department of Plant Biology, University of Minnesota, 250 Biological Sciences,
1445 Gortner Avenue, St. Paul, Minnesota 55108 U. S. A.
[1]Author for correspondence (gweiblen@umn.edu)

Abstract—The mulberry family Moraceae comprises 37 genera and approximately 1,100 species distributed throughout tropical and temperate regions worldwide. Moraceae exhibit a complex array of inflorescence architectures, breeding systems, and pollination syndromes, which forms the basis of traditional taxonomic classification. However, morphologically based classification conflicts with evolutionary relationships proposed by molecular phylogenetics. In this study we assembled a morphological character matrix for analysis separately and in combination with existing molecular data. We evaluated 81 vegetative, reproductive, and wood anatomical characters for 94 species representing nearly all Moraceae genera. Using parsimony and Bayesian methods, these characters were evaluated with respect to *ndhF* chloroplast and 26S nuclear DNA sequences. Topological comparisons tested whether opposing classification schemes are more or less supported by the data. Results did not support any classification of Moraceae based on morphology. We present a revised tribal classification and describe a new tribe, **Maclureae**, revise the membership of tribe Castilleae and describe two subtribes, **Castillineae** and **Antiaropsineae**, and reinstate the genera *Malaisia* (including *Malaisia scandens*) and *Sloetia* (including *Sloetia elongata*). Lastly we discuss the evolution of inflorescence architecture in relation to other floral features.

Keywords—Antiaropsineae, Bayesian inference, Maclureae, *Malaisia*, parsimony ratchet, *Sloetia*.

"… yet the pieces of the puzzle are so strange, so splendidly different from the banalities of many other families, that the monography of the Moraceae is one of the most exciting chapters in angiosperm taxonomy. To relate a mulberry and a bread-fruit … calls for a working hypothesis of flowering tree evolution" (Corner 1962).

Corner (1962) suggested that the floral complexity of Moraceae (Fig. 1) had hindered the formulation of a well-supported hypothesis of morphological evolution in the family. Moraceae exhibit an amazing diversity of morphological and life history traits, particularly inflorescence architectures, breeding systems, and pollination syndromes (Berg 1990; Berg et al. 1990; Berg 1998; Sakai et al. 2000; Sakai 2001; Zerega et al. 2004). With 37 genera and approximately 1,100 species distributed across tropical and temperate regions (Corner 1962; Berg and Dewolf 1975; Berg 2005b), Moraceae diversity makes possible comparative studies of character evolution, plant-insect mutualisms, and breeding system evolution. Since 2006, more than 80 studies of Moraceae have been published including ecology and conservation biology (Fredriksson and Wich 2006; Harrison 2006; Kokou et al. 2006; Ssegawa and Nkuutu 2006; Mucunguzi 2007; Tobler et al. 2007), plant-insect interactions (Castellanos et al. 2006; Kojima 2006; Ufkes and Grams 2007), coevolution (Weiblen 2004; Marussich and Machado 2007), taxonomy (Palhares et al. 2007; Rønsted et al. 2007; Zhao et al. 2007), and phytochemistry (Moretti et al. 2006; Namdaung et al. 2006; Ngameni et al. 2006; Rastogi et al. 2006). Diverse lines of research on Moraceae require a well-supported evolutionary history to guide future work on this ecologically and economically important family.

The monophyly of Moraceae is strongly supported by molecular evidence, but only the combination of a few morphological characters is diagnostic, including milky latex, anatropous ovules, and apical placentation (Sytsma et al. 2002). Moraceae have been divided into five tribes: Moreae, Artocarpeae, Dorstenieae, Castilleae, and Ficeae (Berg 1977b; Berg 2001). The Moreae are characterized by simple inflorescences, such as racemes or spikes, with flower parts in fours. Many Moreae have inflexed stamens, which are structurally supported by pistillodes. The stamens spring back and eject

pollen into the air at anthesis. Moreae extend into temperate regions with some widely distributed species such as *Morus alba* L. (mulberry) and *Maclura pomifera* (Raf.) C. K. Schneid. (Osage orange). The Artocarpeae, or the breadfruit tribe, represent a "cross-section" of Moraceae (Berg et al. 2006) as inflorescence architecture varies from simple spikes to complex globose heads with numerous interfloral bracts, and partial to complete fusion of perianth. The Dorstenieae are also quite variable although most genera have bisexual inflorescences. This group exhibits a range of growth habits including trees, succulent shrubs, and herbs (Berg 2001), and is also known for highly variable pollen morphology, with the grains having ornate exine sculpturing and numerous pores (Hoen and Punt 1989). Castilleae are characterized by unisexual involucrate inflorescences with discoid to cup-shaped receptacles, self-pruning branches, septate wood fibers, and Cook's model of tree architecture (Berg 1977a). Castilleae are centered in the Neotropics but also include two genera endemic to the Paleotropics. Ficeae (figs) comprise a single genus, *Ficus* L., which is the largest in the family with over 800 species distributed throughout the tropics worldwide. Figs are defined by the syconium, an enclosed inflorescence in which internal flowers are accessible only to specialized fig wasp pollinators and parasites. Ranging from shrubs and trees to hemiepiphytes and stranglers, the diverse habits and vegetative morphologies of figs include exceptions to most general features of Moraceae, such as opposite rather than alternate leaves and the lack of latex.

Recent studies of Moraceae using DNA sequences have reconstructed the evolutionary history of the family to clarify relationships among genera, to identify the closest relatives of the figs (Datwyler and Weiblen 2004), and to examine biogeography (Zerega et al. 2005). Phylogeny based on chloroplast and nuclear DNA sequences largely supports the five-tribe system, and a minor reorganization allows four monophyletic tribes to be recognized (Datwyler and Weiblen 2004; Zerega et al. 2005). Moreae is paraphyletic with two species of the paraphyletic genera *Streblus* Lour. and *Trophis* P. Browne and three other genera being more closely related to Dorstenieae. Datwyler and Weiblen (2004) reduced Artocarpeae by
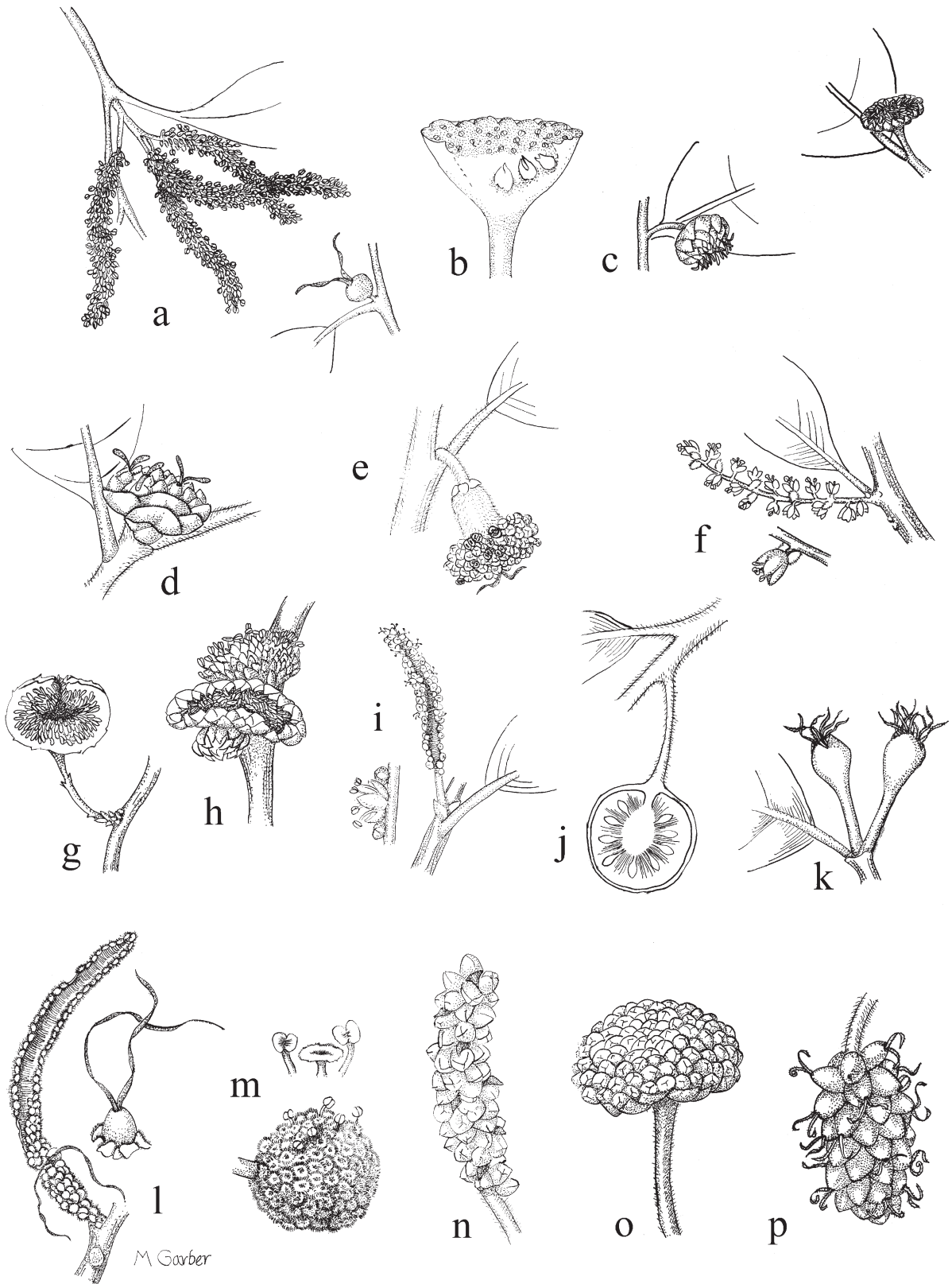
FIG. 1.   Illustrations of Moraceae inflorescence character states. Magnification shown in parentheses. a-c: Generalized arrangement of Moraceae flowers. a. *Clarisia biflora* staminate (left; × 0.75) and pistillate (right; × 0.75) inflorescences, dioecious species with dissimilar staminate and pistillate inflorescences. b. *Dorstenia choconiana* (× 2), monoecious species with a bisexual inflorescence. c. *Antiaropsis decipiens* pistillate (left; × 1) and staminate (right; × 1) inflorescences, dioecious species with similar male and female inflorescences. d-k: Inflorescence architectures of Moraceae. d. Pistillate *Naucleopsis guianensis* (× 3), disc shaped receptacle. e. Bisexual *Trymatococcus amazonicus* (× 2.5), turbinate receptacle. f. Staminate *Sorocea affinis* (× 1.5), raceme. g. Bisexual *Ficus wassa* (× 1), syconium. h. Staminate *Castilla elastica* (× 2), bivalvate receptacle. i. Staminate *Trophis racemosa* (× 2), spike. j. Pistillate *Artocarpus vrieseanus* (× 0.5), globose receptacle. k. Pistillate *Sparattosyce dioica* (× 1), urceolate receptacle. l-p: Interfloral bract character states. l. *Streblus elongatus* (× 0.75), interfloral bracts peltate on a spike. m. *Brosimum rubescens* (× 2.5), interfloral bracts peltate on a globose inflorescence. n. *Trophis scandens* (× 1.5), interfloral bracts not peltate. o. *Helicostylis tomentosa* (× 3.5), interfloral bracts absent on a disc shaped receptacle. p. *Morus alba* (× 4), interfloral bracts absent on spike.

transferring some genera to Castilleae and Moreae in a step toward a phylogenetic classification.

Recent floristic treatments, however, disagree with the phylogenetic classification of Moraceae tribes. Berg (2005a) presented a seven-tribe classification scheme focusing on morphologically heterogeneous Artocarpeae. He removed some Artocarpeae from the tribe and designated Antiaropsideae and Soroceae (Fig. 2). Antiaropsideae (Berg 2005a), including *Antiaropsis* K. Schum. and *Sparattosyce* Bur., is strictly paleotropical in distribution and differs from Artocarpeae in having involucrate inflorescences and dehiscent drupes. Soroceae (Berg 2005a) comprises five neotropical genera that show little morphological similarity but generally have flowers similar to Moreae but with straight rather than inflexed stamens. Artocarpeae was reduced to five genera that are strictly paleotropical in distribution and have indehiscent, many-seeded infructescences.

The seven-tribe system is problematic when compared to the molecular phylogeny. Artocarpeae and Antiaropsideae are monophyletic whereas Soroceae are not. There has been no

study of Moraceae incorporating recent advances in models of morphological evolution (Lewis 2001) to address whether a phylogenetic analysis of morphology can distinguish between competing classifications. Indeed, although morphology is the foundation of systematic botany, recent studies have questioned the utility of morphological characters in phylogenetic analyses. Scotland et al. (2003) suggested that inclusion of morphology may improve clade support but decrease phylogenetic accuracy by adding homoplasious characters. Other authors favor the analysis of morphology (Jenner 2004; Wiens 2004) even if only to increase clade support (Wortley and Scotland 2006). Although one can find both persuasive and dissuasive examples on the use of morphology in phylogenetic systematics, morphological characters provide opportunities to test alternative hypotheses (Lockhart and Cameron 2001). Just as genetic information from various parts of the genome (i.e. chloroplast versus nuclear DNA sequences) may present conflicting views on evolutionary history, the same can be said of morphology and molecules. Given the wealth of morphological information in floras and taxonomic treatments,

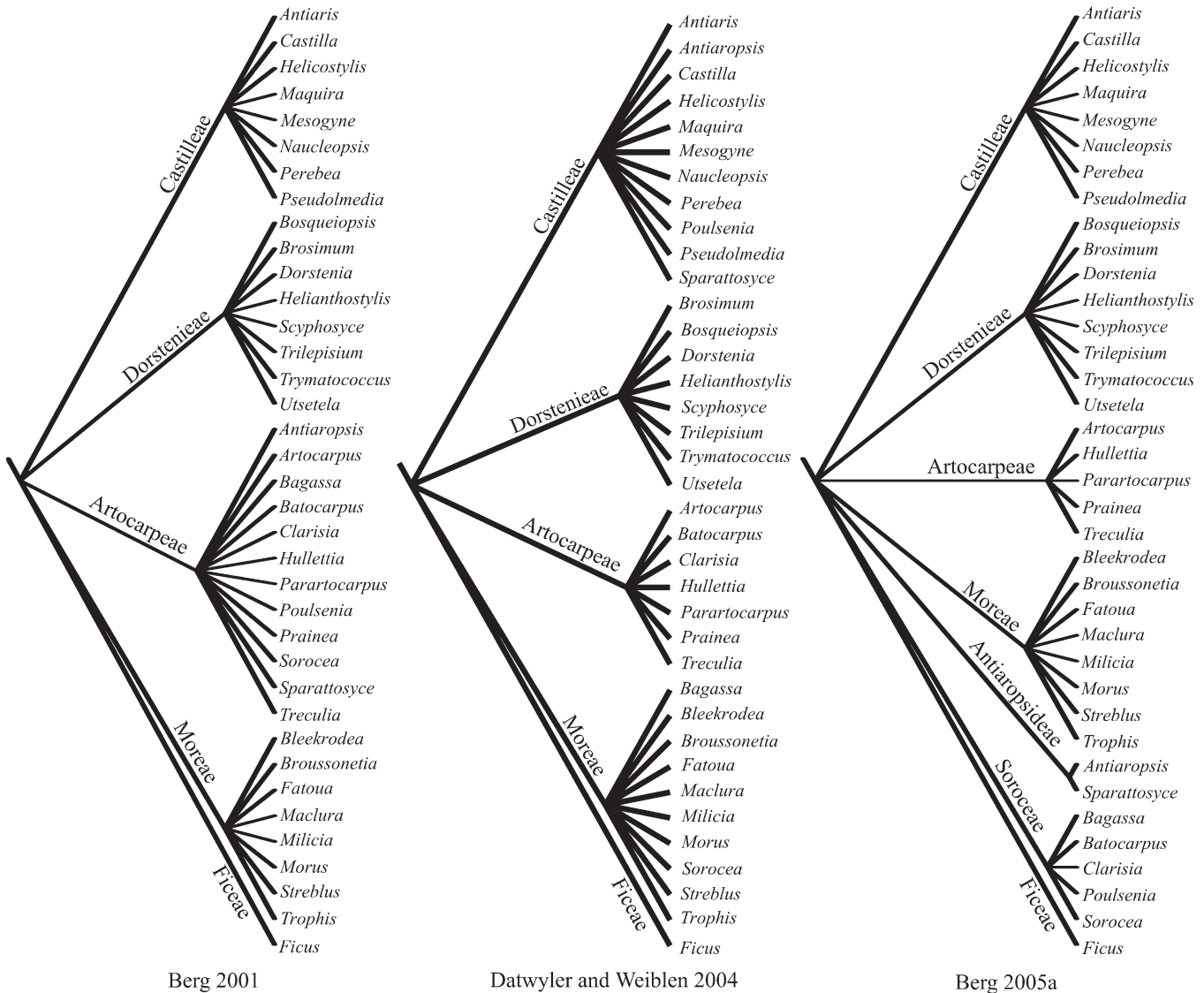Berg 2001   Datwyler and Weiblen 2004   Berg 2005a

Fig. 2.   Tree topologies representing the three most recent classifications of Moraceae genera. The tribe name is printed along the stem of the clade, and the reference for each classification scheme is noted below the tree.

we wish to know what can be learned from molecules and morphology when analyzed and evaluated separately and together using the same methods and criteria.

One of the few attempts at a phylogenetic analysis of Moraceae using morphology came at a time when a complete review of the family was lacking. The five tribes of Moracecae and members of Cannabaceae, Ulmaceae, and Urticaceae were scored for 15 morphological and anatomical characters (Humphries and Blackmore 1989). Not only were the results inconclusive but the analysis failed to establish the monophyly of Moraceae because of the exclusion of Artocarpeae from the clade containing all other Moraceae. The authors argued that too few characters and the use of overly broad groupings (tribes were terminals) accounted for the ambiguous results. The study suggested the paraphyly of Moreae and Artocarpeae and the problems these tribes posed for phylogenetic classification of the family.

Re-evaluation of Moraceae classification based on phylogenetic analysis of morphology alone and in combination with molecular data may offer insights on evolutionary relationships, and provide opportunities to study adaptive evolution of complex features such as inflorescences. With solitary flowers, simple spikes, dichasial cymes, capitula, and urceolate syconia, it is difficult to identify the ancestral condition of inflorescence architecture. Datwyler and Weiblen (2004) reconstructed the evolution of breeding systems, pollination syndromes, and involucral bracts using a molecular phylogeny. Dioecy was found to be the ancestral condition of the family, and repeated shifts to monoecy suggested that the shift from unisexual to bisexual inflorescences occurred more than once. (Monoecious species can have bisexual inflorescences or unisexual inflorescences of both kinds on the same individual). Additionally, entomophily was significantly correlated with the presence of involucral bracts; these enclose the inflorescence and are thought to protect seeds and breeding pollinators from parasitism (Berg 1990). Berg (1989, 1990) considered the basic form of the Urticalean inflorescence to be a bisexual cyme and hypothesized that floral evolution in the Urticales shows trends toward condensation and reduction of internodes and floral parts to achieve a capitulate inflorescence, with the proliferated inflorescence bracts assuming the protective role of a perianth. Phylogeny provides an opportunity to evaluate these hypothesized trends. Berg (1990) suggested that the evolutionary significance of floral reduction (i.e. loss of perianth, fusion of flowers, and condensed inflorescence branching) was either the promotion or the prevention of insect visitation in the cases of pollination and phytophagy, respectively (Berg 1990). The loss of perianth was thought to be associated with the appearance of "accessory protective structures" such as interfloral bracts, an involucre, or peltate bracts. The prediction of correlated evolutionary change in inflorescence architecture and floral features such as perianth merosity or perianth fusion can be tested. Not only might morphology contribute to the phylogenetic classification, it is essential for testing hypotheses on the diversification of Moraceae.

Our goal is to clarify phylogenetic relationships using all available data and modern phylogenetic methods. We compiled a morphological character matrix with vegetative, reproductive, and wood anatomical traits for phylogenetic analysis separately and in combination with DNA sequences. We used Templeton tests (Templeton 1983; Larson 1994) and searched among the 95% credible interval of trees from the posterior distribution of the Bayesian analyses (Buckley 2002; Brandley et al. 2005) to assess support for conflicting classification schemes based on molecules and morphology. We use our phylogenetic consensus to revise the tribal classification of Moraceae. Lastly, we used ancestral character state reconstruction to assess current hypotheses of Moraceae floral evolution.

Materials and Methods

Taxon Sampling—We sampled 76 species representing the 32 Moraceae genera studied by Datwyler and Weiblen (2004). Outgroups included 18 species representing Cannabaceae and Urticaceae (Stevens 2001 onwards). Five specimens misidentified by Zerega et al. (2005) were redetermined and corrected in Genbank: *Dorstenia arifolia* Lam. = *Dorstenia bahiensis* Klotzsch, *Maclura cochinchinensis* (Lour.) Corner = *Maclura amboinensis* Blume, *Perebea guianensis* Aubl. = *Perebea longepedunculata* C. C. Berg, *Perebea mollis* (Poepp. & Endl.) J. E. Huber = *Perebea rubra* (Trécul) C. C. Berg, and *Poulsenia armata* (Miq.) Standl. = *Castilla elastica* Sessé.

Morphology—We included characters that varied at or below the family level or were emphasized in the taxonomic literature by E. J. H. Corner and C. C. Berg. The extensive literature on the morphology and taxonomy of Moraceae contains descriptive information that has not been examined phylogenetically; thus, in addition to consulting herbarium specimens from A, F, MIN, MO, and P (Holmgren et al. 1990; Appendix 1), we collected data from the literature (Jarrett 1959a-d,1960a,b; Burger 1962; Burger et al. 1962; Corner 1962, 1967, 1970a, b, 1975; Nair and Sharma 1965; Berg 1972,1973, 1977a, b, 1978a, b, 1982, 1983, 1986, 1988, 1990, 1992, 1998, 2001, 2005a; Berg and Dewolf 1975; Niezgoda and Nowaczyk 1976; Mennega and Lanzing-Vinkenborg 1977; Punt and Eetgerink 1982; Bonsen and Ter Welle 1983,1984; Koek-Noorman et al. 1984a-c; Punt and Malotaux 1984; Berg and Akkermans 1985; Ter Welle et al. 1986a, b, 1992; Chew 1989a, b; Friis 1989; Hoen and Punt 1989; Humphries and Blackmore 1989; Oginuma et al. 1990; Rohwer 1993; Zomlefer 1994; Oginuma and Tobe 1995; Barker 1997; Boufford 1997; Small 1997; Wunderlin 1997; Berg and Hijman 1999; Berg and Simonis 2000; Kochummen and Go 2000; Fu et al. 2003; Jiarui et al. 2003a, b; Jiarui and Wilmot-Dear 2003; Zerega 2003; Zhekun and Gilbert 2003; Berg and Rosselli 2005). Taxa were scored at the species level unless the specimen had not been identified beyond the genus. Characters were coded as missing if the state was unknown, inconclusive upon examination of herbarium specimens, or inapplicable (i.e. a wood character for an herbaceous taxon). Characters and taxa were included in the analysis in spite of missing data (Wilkinson 1995; Wiens 1998; Kearney 2002; Wiens 2006). Unless otherwise noted, polymorphisms were limited to taxa for which only generic descriptions were available (Appendix 2). These "polymorphisms" need not necessarily represent variation at the species level, but were coded as such to maximize phylogenetic information. Alternatively, if characters are coded as missing, then information is lost from multistate characters with at least one state not present.

Phylogenetic Analysis of Morphology—Characters were analyzed using parsimony and Bayesian optimality criteria. All analyses treated binary and multistate characters as unweighted and unordered with the exception of five ordered characters (25, 46, 50, 56, 63; Appendix 2). Preliminary parsimony analyses were consistently attracted to a single local optimum with >1,000,000 equally parsimonious trees suggesting that the analysis was not effectively searching tree space. We used the parsimony ratchet (Nixon 1999) to improve our search strategy. The parsimony ratchet improves efficiency and decreases search time for analyses of extremely large data sets where tree space is very large (Nixon 1999; Quicke et al. 2001; Tehler et al. 2003; Bailey et al. 2006; Dentinger and McLaughlin 2006). The ratchet randomly varies taxon order, holds fewer trees per replicate, and samples many tree islands holding fewer trees per island to estimate phylogeny more efficiently (Nixon 1999). PAUPRat (Sikes and Lewis 2001) was used to generate a block file for execution in PAUP version 4.0b10 (Swofford 2002). We generated 10 blocks to facilitate 10 independent ratchet searches. Each ratchet was iterated 1,000 times with 30% of the characters weighted. Each PAUPRat analysis performs two searches, one in which all characters are equally weighted, and another in which a percentage of characters (determined by the user) chosen at random are up-weighted. The weighted search is designed to "perturb" the analysis from local optima and to better traverse tree space by favoring a random subset of characters in each iteration (Nixon 1999). Trees from the independent searches were combined and filtered to extract the most parsimonious trees under equal weighting. Clade

support was assessed with a bootstrap analysis of 1,000 bootstrap replicates and 100 addition sequence replicates saving a maximum of 100 trees per replicate, and with TBR branch swapping as implemented in PAUP version 4.0b10.

Although few morphological characters support the monophyly of Moraceae, molecular evidence provides strong support (Sytsma et al. 2002). We conducted additional analyses in which the monophyly of Moraceae was enforced by modifying the PAUPRat setup file to include a topological constraint. First, we added "Loadconstr File = filename" as a "startcmd" to load constraint trees, and second we added "enforce = yes" and "constraint = constraintname" to the "startcmd" that defines the heuristic search parameters. All other parameters were identical to the unconstrained analysis.

Bayesian analysis was conducted with default priors and the Markov k model with a gamma distribution (Lewis 2001) using MrBayes v3.1 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003). Ordered characters were defined using the "cytpe orderd" command. Two analyses ran in parallel each with six chains of five million generations and the posterior distribution was sampled every 100 generations. We concluded that the analysis had reached stationarity when the average standard deviation of split frequencies was less than 0.05, evidence of chain swapping was sufficient, and the potential scale reduction factors (PSRF) were near one. An appropriate burn-in was assessed by a plot of log likelihoods viewed in the program Tracer v1.4 (Rambaut and Drummond 2007) and was discarded before summarizing model parameters and tree statistics using the sump and sumt commands in MrBayes.

As in the case of parsimony, we repeated the Bayesian analysis enforcing the monophyly of Moraceae as a topological constraint. In the MrBayes block, we defined the constraint with the commands "constraint constraint_name -1 = taxon_1 taxon_2" and then specified the constraint as a prior in the analysis with the command "prset topologypr = constraints(constraint_name)." Implementing the Markov k model with gamma, two analyses were conducted in parallel each with six chains of five million generations.

Morphology and Molecules—We assembled a combined data set including morphology and DNA sequences from the chloroplast gene *ndhF* (AY289249-AY289287, AY289289-AY289300, AY289302-AY289332, AY289334-AY289335, AY289337-AY289344, AY289346-AY289349; Datwyler and Weiblen 2004) and the nuclear ribosomal 26S subunit (AY686766-AY686837, AY686839-AY686860; Zerega et al. 2005). Since the monotypic genus, *Poulsenia* Eggers, had not been included in earlier molecular phylogenetic studies (*Poulsenia armata* = *Castilla elastica* in Datwyler and Weiblen 2004 and Zerega et al. 2005), we sequenced *Poulsenia armata* (voucher: *G. D. Weiblen 1428*, Panama, MIN) for both 26S and *ndhF* using the methods described in Datwyler and Weiblen (2004) and Zerega et al. (2005). Maximum parsimony and Bayesian analyses were performed to reanalyze the 26S and *ndhF* data separately and combined in light of the new *P. armata* sequences.

After excluding uninformative characters, an incongruence length difference test (Farris et al. 1994) was performed to assess the compatibility

of the morphological data with either molecular data set. Templeton tests (Templeton 1983; Larson 1994) compared the topologies from separate analyses of the three data sets, as outlined in Zerega et al. (2005).

The combined data set (excluding uninformative characters) was analyzed under parsimony using a heuristic search with TBR branch swapping and 10,000 addition sequence replicates. Clade support was assessed with analyses of 1,000 bootstrap replicates each with 100 addition sequence replicates while saving a maximum of 100 trees per replicate as implemented in PAUP v. 4.0b10 (Swofford 2002). A partitioned Bremer support analysis, implemented using TreeRot v.3 (Sorenson and Franzosa 2007), was conducted to determine the contribution of the molecular and the morphological data to the decay index. Clades not supported by both data partitions are indicated by a negative partitioned Bremer support value, providing an additional assessment of the congruence of data partitions.

In addition, we conducted a partitioned Bayesian analysis in MrBayes, wherein each data set (*26S*, *ndhF*, and morphology) was assigned its own model (Ronquist and Huelsenbeck 2003) and all parameters were unlinked and estimated independently for each data partition. We used MrModeltest (Nylander 2004) and the Akaike Information Criterion (Posada and Buckley 2004) to select models and independent parameter estimates for each molecular partition. A Markov k model with gamma distribution was used for the morphology partition (Lewis 2001). Two analyses were conducted in parallel, each with 12 chains of 10 million generations with the temperature set to 0.01, and the posterior distribution was sampled every 100 generations. Stationarity was assessed as explained above, and Tracer v1.4 (Rambaut and Drummond 2007) was used to determine an appropriate burnin. Model parameters and tree statistics were summarized in MrBayes.

Hypothesis Testing—Three classifications of Moraceae have been published in less than a decade (Berg 2001; Datwyler and Weiblen 2004; Berg 2005a). Berg (2001) and Datwyler and Weiblen (2004) recognized five tribes, whereas Berg (2005a) recognized seven. The three schemes differ with regard to the placement of several genera (Fig. 2). A series of hypothesis tests compared these classification schemes to evaluate whether they are supported by morphology or by morphology and molecules. Under parsimony, we used nonparametric Templeton tests (Templeton 1983; Larson 1994) to compare trees resulting from constrained searches to trees from unconstrained searches and to address whether phylogenetic evidence rejects the monophyly of groups recognized by particular classifications. We tested the same hypotheses in a Bayesian framework using the 95% credible interval of trees sampled from the posterior distribution from Bayesian analyses of morphology and total evidence (Buckley 2002; Brandley et al. 2005). We tested 14 hypotheses of monophyly individually (Table 1) including the tribal membership of each of three Moraceae classification schemes. By testing each tribe individually, we identified those tribes whose membership is not supported by morphology or total evidence.

Under parsimony, we first conducted analyses enforcing each of the 14 topological constraints listed in Table 1. Constrained searches of morphology were performed using the parsimony ratchet as described previ

TABLE 1.   Topological incongruence test results for Moraceae classification evaluated against morphology and total evidence. The length difference between most parsimonious trees from constrained and unconstrained searches and p values of Wilcoxon sum of signed ranks tests are reported. Additionally, the number of trees containing the clade(s) of interest from the 95% credible interval (CI) of trees from the posterior distribution of Bayesian analyses is reported. If the clade of interest is recovered from among the 85,450 trees from the morphology analysis or the 93,310 trees from the total evidence analysis, the hypothesis of monophyly cannot be rejected. Asterisks indicate tests that rejected particular hypotheses of monophyly.

	Morphology			Total evidence		
Hypothesis of monophyly	Length difference	p value	# of trees in 95% CI	Length difference	p value	# of trees in 95% CI
Berg (2001)	11	0.1362	0*	118	<0.0001*	0*
Datwyler and Weiblen (2004)	4	0.5000	0*	44	0.0001*	0*
Berg (2005a)	10	0.2000	0*	156	<0.0001*	0*
Antiaropsideae sensu Berg (2005a)	0	0.7055	64,810	0	1.0000	93,221
Artocarpeae sensu Berg (2001)	9	0.1604	0*	84	<0.0001*	0*
Artocarpeae sensu Datwyler and Weiblen (2004)	2	0.7236	2,721	0	0.9827	93,310
Artocarpeae sensu Berg (2005a)	2	0.7104	5,392	0	0.9827	93,310
Castilleae sensu Berg (2001, 2005a)	0	0.6309	84,512	0	0.9827	90,605
Castilleae sensu Datwyler and Weiblen (2004)	0	0.7361	14,553	0	0.9827	93,310
Dorstenieae	0	0.7791	21,158	0	1.0000	93,306
Ficeae	0	1.0000	85,367	0	1.0000	93,310
Moreae sensu Berg (2001, 2005a)	0	0.5276	0*	65	<0.0001*	0*
Moreae sensu Datwyler and Weiblen (2004)	0	0.8396	0*	44	0.0001*	0*
Soroceae sensu Berg (2005a)	5	0.2876	0*	113	<0.0001*	0*

ously with a modified PAUPRat block to consider only trees compatible with a hypothesis of monophyly. Ratchet conditions included 10 independent analyses, each with 1,000 ratchets in which 30% of the characters were weighted. Constrained analyses of the combined data were conducted heuristically with TBR branch swapping, and 10,000 addition sequence replicates in PAUP version 4.0b10. Nonparametric Wilcoxon sum of signed rank tests (Templeton 1983; Larson 1994) as implemented in PAUP (Swofford 2002) compared most parsimonious trees from constrained and unconstrained searches. Significance ($p \leq 0.05$) indicates that the evidence rejects a hypothesis of monophyly (H_0) in favor of nonmonophyly (H_1).

Using the posterior tree distribution from the Bayesian analyses, we compiled the 95% credible interval of trees from the Bayesian analysis of morphology alone and morphology and molecules. We searched among these tree sets for topologies congruent with the hypothesis of monophyly. If any number of trees from the 95% credible interval was congruent with a constraint tree reflecting the hypothesis of monophyly, then the hypothesis cannot be rejected.

Morphological Evolution—MacClade version 4.08 (Maddison and Maddison 2005) was used to identify synapomorphies useful in supporting phylogenetic classification and to reconstruct ancestral states on topologies resulting from phylogenetic analyses. ACCTRAN and DELTRAN resolving options for equivocal character states were compared. Our analysis focused on characters of the inflorescence such as architecture, perianth merosity, and perianth connation that are pertinent to hypothesized trends in the morphological evolution of Moraceae (Berg 1990). Additionally, we reconstructed ancestral character states using maximum likelihood as implemented in the MultiState (Pagel 1999; Pagel et al. 2004) module of BayesTraits (available from www.evolution.rdg.ac.uk). For each character analyzed, we prepared a file with the character state data and a tree file with 200 trees sampled from the posterior distribution of the combined Bayesian analysis. We reported the average probability of each character state across all trees for major nodes in the Moraceae phylogeny.

Results

Morphology—We assembled 81 wood, vegetative, and reproductive characters. Appendix 2 includes an annotated list of characters, states and percentages of data missing from the morphological matrix (Supplemental Appendix 1). Analyses included 16 vegetative, 21 wood, 29 floral, 3 pollen, and 12 fruit or seed characters.

A thorough description of Moraceae wood anatomy was published in a series of papers (Mennega and Lanzing-Vinkenborg 1977; Bonsen and Ter Welle 1983, 1984; Koek-Noorman et al. 1984a-c; Ter Welle et al. 1986a, b, 1992). We selected variable wood characters from these papers, and defined character states following the International Association of Wood Anatomists (IAWA) and Herendeen and Miller (2000) who developed guidelines for the interpretation and phylogenetic utility of wood characters. Moraceae is predominantly woody but *Fatoua* and some members of *Dorstenia* L. are herbaceous. *Cannabis* L. and *Humulus* L. (Cannabaceae) were also coded as herbaceous as "wood" produced by these plants is due to diffuse secondary thickening. Wood characters for these taxa were coded as missing data. Only generic descriptions of wood anatomy were available.

Moraceae have unisexual flowers arranged in either unisexual or bisexual inflorescences (Fig. 1), and the structure of unisexual staminate and pistillate inflorescences within a species can vary (Fig. 1a-c). Characters that are present in both staminate and pistillate inflorescences, such as perianth merosity and perianth connation, were coded independently for each sex (Appendix 2). However, bisexual inflorescences (e.g. *Trymatococcus* Poepp. & Endl.; Fig. 1e) were effectively coded twice for characters common to both staminate and pistillate inflorescences such as inflorescence architecture and once for characters specific to staminate and pistillate flowers such as number of anthers or stigma shape (Appendix 2).

Morphological Phylogeny—Ratchet analysis resulted in 1,929 most parsimonious (MP) trees of 632 steps with a consistency index (CI) of 0.23, retention index (RI) of 0.73, and a rescaled consistency index (RC) of 0.17 (Fig. 3). Bayesian analysis of morphology with an Mk + G model recovered a tree with a score of $-lnL = 2,513.418$ and $G = 1.49$ (Fig. 4). Although morphology provided little resolution of relationships among genera, the monophyly of many genera in which more than one species was sampled was recovered with strong bootstrap support and posterior probability (Figs. 3, 4).

Neither the parsimony strict consensus nor Bayesian consensus resolved a monophyletic Moraceae yet trees compatible with the monophyly of Moraceae were of the same length (1,616 MP trees, CI = 0.22, RI = 0.73, RC = 0.16; Fig. 3). The constrained Bayesian analysis identified a tree with a score of $-lnL = 2,513.824$ (Fig. 4), which was not significantly less likely than the unconstrained tree.

Total Evidence Phylogeny—Before testing for conflict between molecules and morphology, we analyzed 26S and *ndhF* sequences including new *Poulsenia* sequences (EU422992 and EU422993 respectively). These sequences provided a total of 815 parsimony informative characters out of 3,106 characters analyzed (184 of 1,014 26S characters; 631 of 2,092 *ndhF* characters). Parsimony analysis with maxtrees set at 50,000 recovered as many trees of 933 steps (CI = 0.31, RI = 0.64, RC = 0.20; not shown) for 26S alone, as many trees of 2,182 steps (CI = 0.46, RI = 0.80, RC = 0.36; not shown) for *ndhF* alone, and 11,550 MP trees with 2,749 steps (CI = 0.47, RI = 0.81, RC = 0.38; Fig. 5) for 26S and *ndhF* combined (Fig. 5). The results of 26S and *ndhF* analysis both separately and in combination recovered *Poulsenia* as a well-supported member of Castilleae as found by Datwyler and Weiblen (2004) who transferred the genus from Artocarpeae.

The incongruence length difference test (ILD) indicated that there was significant conflict between morphology and molecules ($p = 0.01$). The utility of this test has been debated in the literature (Yoder et al. 2001; Barker and Lutzoni 2002; Hipp et al. 2004) but some such studies have shown that this test often identifies significant conflict among data sets when there is none. We used additional tests of congruence to investigate potential conflict among the morphology and molecular data partitions. A nonparametric test comparing 26S trees to trees from an analysis of 26S data constrained by the morphology strict consensus tree indicated significant topological conflict ($p = 0.0001$). Conflict was significant between *ndhF* and morphology as well ($p < 0.0001$). The main difference between morphological and molecular results was the failure of morphology to recover a monophyletic Moraceae (Figs. 3, 4). When we repeated the comparison with an added constraint enforcing the monophyly of Moraceae, there was no significant conflict between 26S and morphology ($p = 0.38$), or *ndhF* and morphology ($p = 0.56$). These results demonstrate the sensitivity of character congruence tests to simple topological differences. When morphology trees were compared to trees from searches constrained by molecular strict consensus trees, conflict was significant ($p \leq 0.0001$), a comparison essentially forcing a dataset with little phylogenetic signal (morphology) to fit a highly resolved phylogeny (molecules). The morphological tree had poor resolution, only 24 out of 75 possible nodes recovered (excluding the outgroup), compared to 67 and 72 nodes for 26S and *ndhF* topologies, respectively. When morphology data was compared to *ndhF*, four clades were in conflict, and one of these was supported by a high bootstrap percentage: morphology

Unconstrained   Constrained
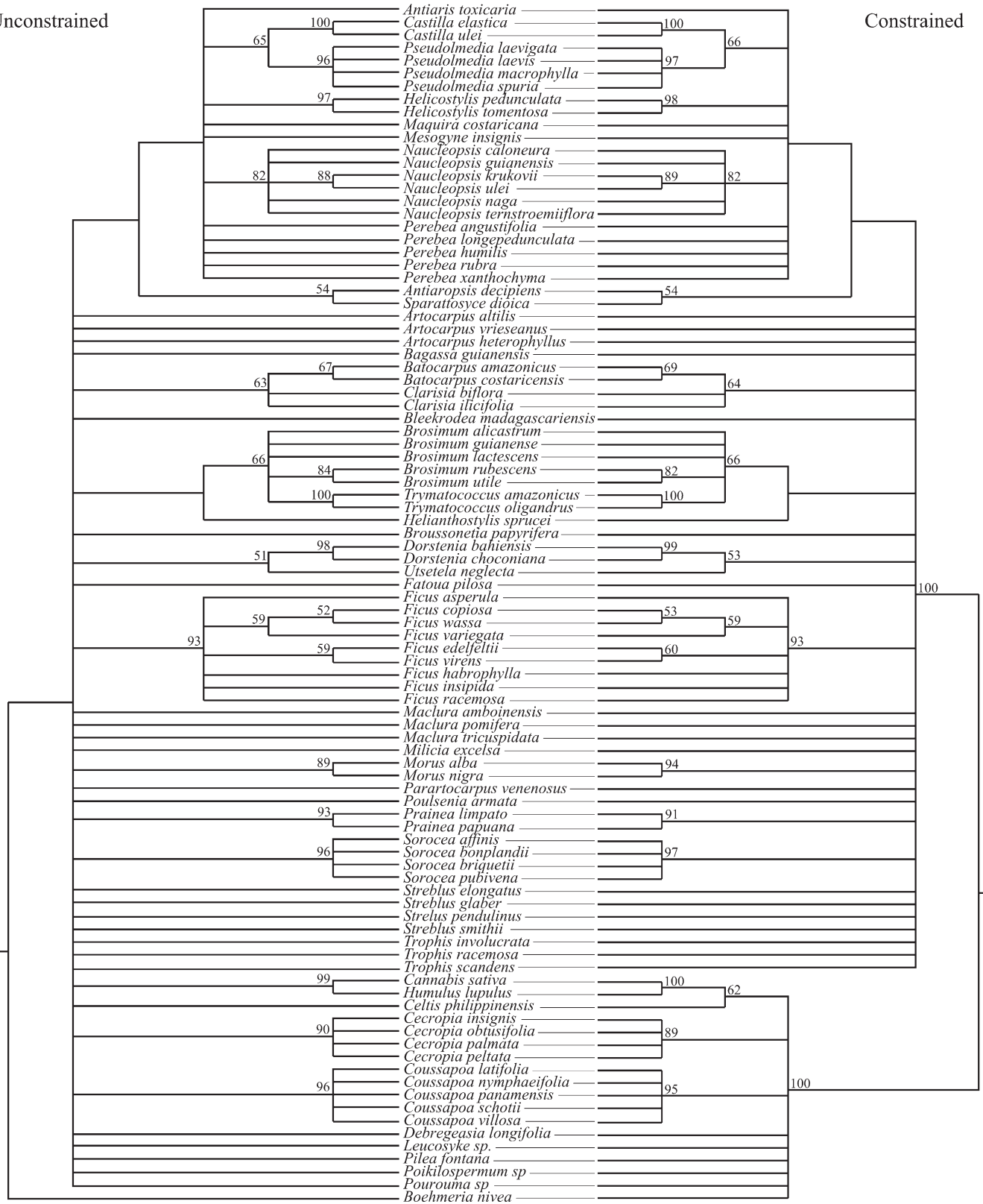
FIG. 3.   Strict consensus trees of the most parsimonious (MP) trees resulting from the parsimony ratchet searches of morphological data with (1,616 MP trees; right) and without (1,929 MP trees; left) the monophyly of Moraceae enforced as a topological constraint. Bootstrap percentages greater than or equal to 50% are indicated above the branches.

recovered the monophyly of *Prainea* (with 93% bootstrap support), whereas *ndhF* found *Parartocarpus* nested within *Prainea* (Zerega et al. 2005). Compared to *26S*, two clades were in conflict, but neither was highly supported.

Combining molecular and morphological data resulted in a total of 894 parsimony informative characters out of 3,186 in total. The complete dataset was deposited in TreeBASE (study number S2239). Parsimony recovered 288 trees of 3,452 steps

Unconstrained   Constrained
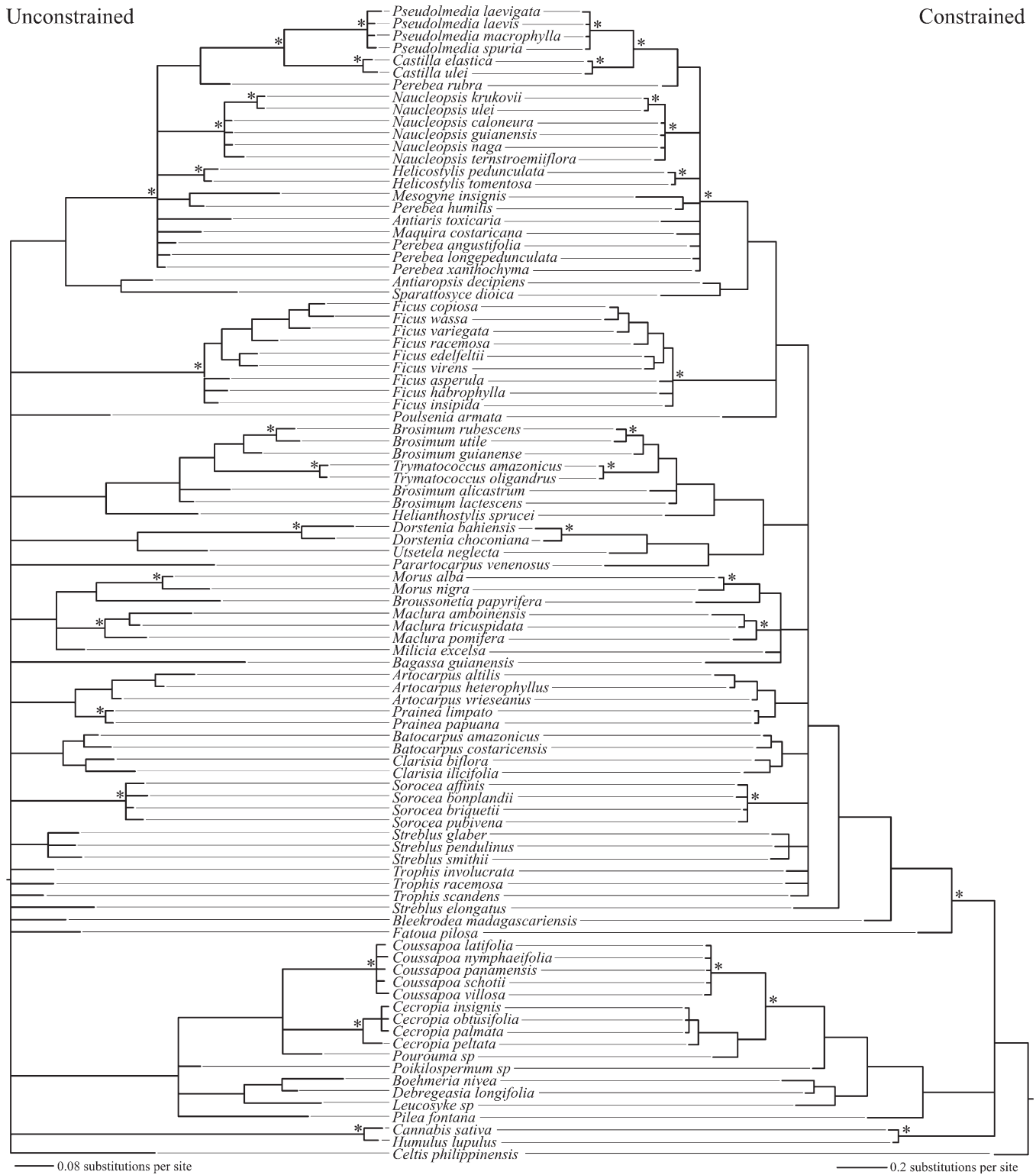

Fig. 4. Bayesian phylograms based on the analysis of morphological data with (right) and without (left) the monophyly of Moraceae enforced as a topological constraint. Posterior probability values ≥ 0.95 are indicated by an asterisk above the branches.

(CI = 0.42, RI = 0.78, RC = 0.32; Fig. 5). MrModeltest identified a general time reversible model with a gamma distribution and proportion of invariable sites (Rodriguez et al. 1990) as the best-fitting model of sequence evolution for both *ndhF* and 26S data partitions. After the burn-in was removed, the summary statistics for each partition and tree statistics were estimated based on the remaining 7,500,000 generations. The

likelihood of the tree identified by the Bayesian analysis was –lnL = 27,562.45 (Fig. 6).

The inclusion of morphology with molecular data in the phylogenetic analysis improved resolution and support, increasing the bootstrap support for 17 clades (3 of which increased to ≥90%), had no effect on the support for 18 clades, and decreased the support for 14 clades (Fig. 5). The

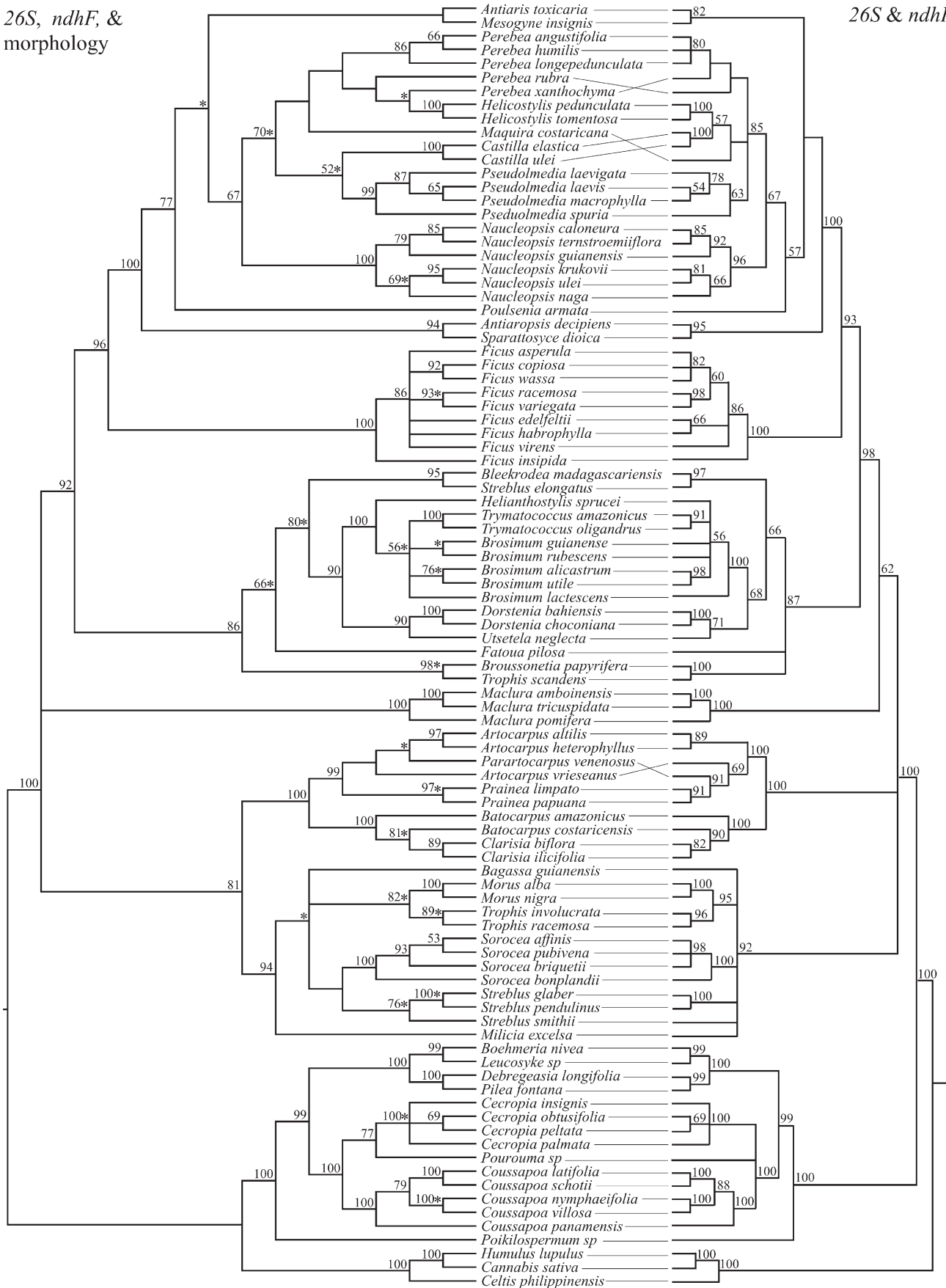FIG. 5. Strict consensus of 288 most parsimonious trees from the total evidence analysis (left) as compared to the strict consensus of 11,550 most parsimonious trees from the combined 26S and *ndhF* data analysis (right). Bootstrap percentages greater than or equal to 50% are shown on the branches. Clades for which Bremer support conflicted among molecular and morphological data sets are indicated by an asterisk above the branches.
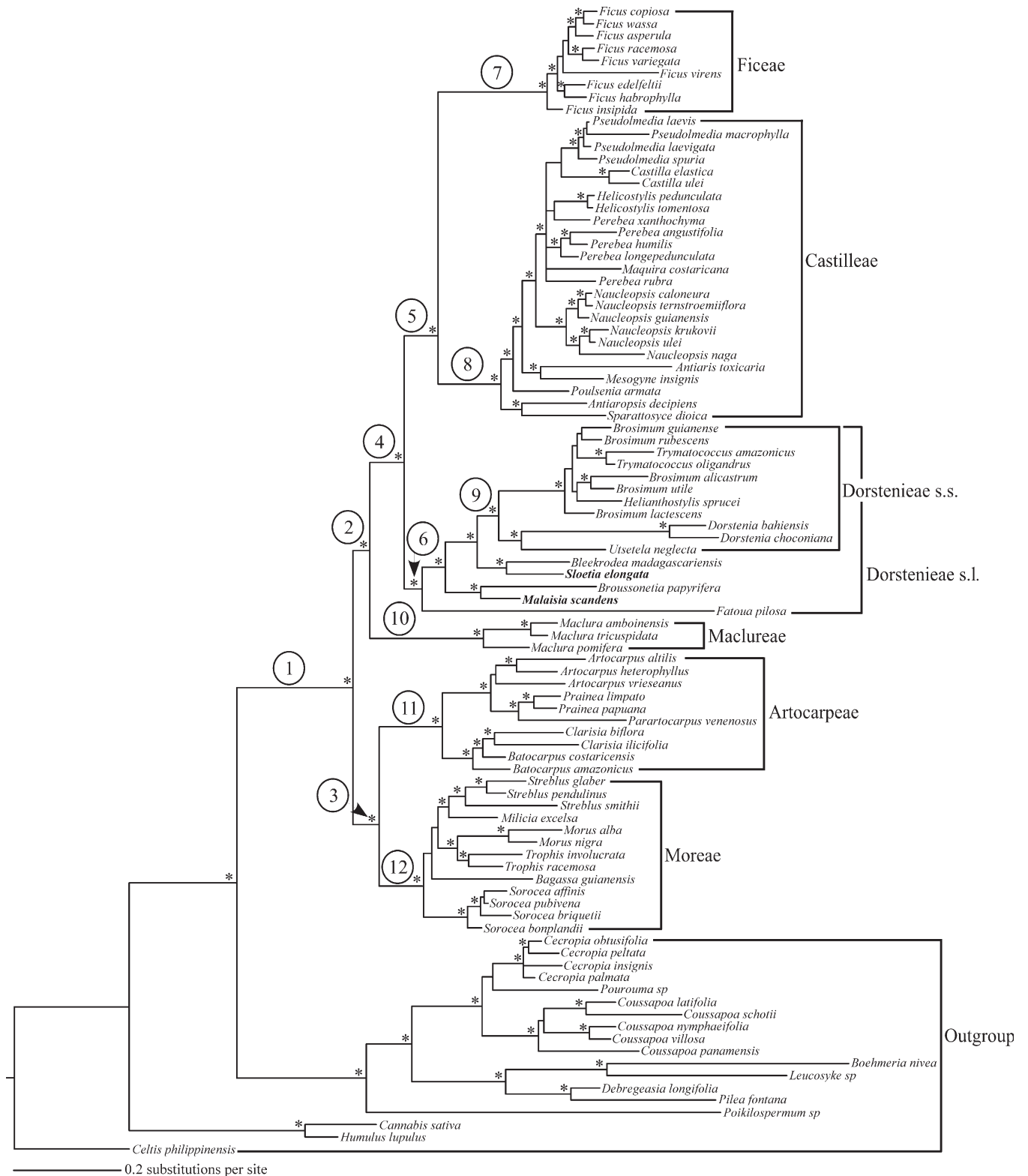
FIG. 6.   Bayesian phylogram based on the combined analysis of molecular and morphological data indicating the revised classification of the Moraceae genera and tribes (-lnL = 27,562.45). Posterior probability values ≥ 0.95 are indicated by an asterisk above the branches. Newly reinstated genera are in boldface. Circled numbers (1–12) refer to nodes in Table 2. Parameters are as follows: 26S partition: rate matrix - AC = 0.070, AG = 0.140, AT = 0.118, CG = 0.038, CT = 0.578, GT = 0.056, base pair frequencies - A = 0.214, C = 0.254, G = 0.335, T = 0.197, G = 0.564 and I = 0.448; *ndhF* partition: rate matrix - AC = 0.203, AG = 0.246, AT = 0.045, CG = 0.141 CT = 0.246, GT = 0.119, base pair frequencies - A = 0.303, C = 0.141, G = 0.160, T = 0.397, Γ = 1.004 and I = 0.141. Gamma for morphology was Γ = 0.198.

partitioned Bremer support analysis identified 22 out of 75 clades for which support from molecular or morphological data conflicted (Fig. 5). Taxonomic changes are limited to clades supported by both types of evidence.

Parsimony and Bayesian methods recovered the monophyly of Moraceae with 100% bootstrap support and a posterior probability of 1.0 (Figs. 5, 6). The topologies were largely congruent, and the only supported conflict was the position of *Fatoua pilosa* Gaudich relative to *Broussonetia papyrifera* (L.) Vent. and *Trophis scandens* (Lour.) Hook. & Arn. *Fatoua* is a particularly difficult genus to place due to its herbaceous habit and cymose inflorescences. Both methods recovered the three taxa as part of a well-supported clade that is closely related to Dorstenieae. Consistency and retention indices of each morphological character on the Bayesian total evidence phylogeny are listed in Appendix 2.

Additionally, both parsimony and Bayesian methods recovered the sister relationship of Moreae sensu stricto and Artocarpeae sensu Datwyler and Weiblen (2004). This relationship lacked support in the Bayesian analyses of Zerega et al. (2005), but here was supported by 81% bootstrap and posterior probability of 1.0 (Figs. 5, 6). Moreae sensu stricto plus Artocarpeae were sister to the rest of Moraceae according to Bayesian analysis.

Hypothesis Testing—Nonparametric and Bayesian test results fitting morphology to various phylogenetic hypotheses are reported in Table 1. Nonparametric tests of morphology failed to reject any tribal classifications of Moraceae (Berg 2001; Datwyler and Weiblen 2004; Berg 2005a) or the monophyly of individual tribes. However, results from the Bayesian analysis of morphology and total evidence and nonparametric tests using the total evidence were in agreement. Artocarpeae sensu Berg (2001), Moreae sensu Berg (2001), Moreae sensu Datwyler and Weiblen (2004), and Soroceae sensu Berg (2005a) were rejected whereas Antiaropsideae sensu Berg (2005a), Artocarpeae sensu Berg (2005a) and Castilleae sensu Berg (2001, 2005a) were not and also represent clades identified by Datwyler and Weiblen (2004). Monophyly was not rejected for either Dorstenieae or Ficeae, but the monophyly of each of these tribes has never been doubted.

Morphological Evolution—Ancestral state reconstructions for major Moraceae clades are listed in Table 2. Dioecy appeared to be the ancestral breeding system of Moraceae, as is often the case in angiosperm clades with unisexual flowers (Weiblen et al. 2000). However this inference is influenced by outgroup breeding systems and further sampling of Urticaceae is needed to confirm this finding. Bisexual inflorescences were derived from unisexual inflorescences with between one and five changes from unisexual to bisexual inflorescences in contrast to previous speculation that bisexuality was ancestral (Berg 1990).

Ancestral states of male and female inflorescences differed in perianth connation and inflorescence architecture (Table 2). According to phylogeny, the ancestral condition of the staminate inflorescence was a spike having many free flowers with four free tepals and four stamens. More derived staminate inflorescences, such as those of figs and breadfruit, have reduced numbers of stamens, and rarely fused staminate flowers as in *Parartocarpus*. The ancestral pistillate inflorescence was globose-capitate having many free flowers and a four-merous connate perianth. The gynoecium showed no trend toward reduction, as two equally long stigmas are present throughout the family. However, we inferred between

five and six changes from multiflorous to uniflorous inflorescences, with reduced flower numbers being derived in relatively small clades. Flowers embedded in the receptacle, as in *Naucleopsis* Miq. or *Trymatococcus*, also appear to be derived. Moreae and Artocarpeae generally possess the symplesiomorphic condition of staminate spikes whereas Ficeae, Castilleae, and Dorstenieae have more condensed inflorescences.

Secondary protective structures may play important functional roles, such as the peltate bracts (Fig. 1m) covering *Brosimum* Sw. inflorescences protecting immature flowers. This character had a high level of homoplasy (CI = 0.52) and the ancestral condition of staminate inflorescence bracts was equivocal. The ancestral condition of interfloral bracts in the pistillate inflorescence was equivocal under DELTRAN, but peltate under ACCTRAN. Using maximum likelihood, peltate bracts were reconstructed as the ancestral condition of staminate inflorescences (probability = 1.00; Fig. 7) and strongly suggested as ancestral in pistillate inflorescences (probability = 0.93; Fig. 7). Among staminate inflorescences, there was a loss of peltate bracts in Ficeae, Castilleae, and *Maclura* lineages. Among pistillate flowers, peltate bracts were lost independently, persisting mostly among Artocarpeae and Dorstenieae (Fig. 7).

DISCUSSION

Morphology and Molecules—We found little phylogenetic signal in morphology such that this information alone does not provide a clear picture of evolutionary relationships in Moraceae. Morphology may clarify, confuse, or have no effect on our understanding of phylogeny (Scotland et al. 2003). In the case of Moraceae, inclusion of homoplasious morphology in phylogenetic analysis of DNA sequences improves resolution and clade support but morphology alone suggests poorly resolved, and in some cases, erroneous historical relationships. Few morphological characters showed no homoplasy. However, the increased power of total evidence to resolve and support clades favors the inclusion of homoplasious morphology in phylogenetic analysis at the risk of decreasing phylogenetic accuracy (Jousselin et al. 2003; Scotland et al. 2003).

Traditional Moraceae taxonomy has relied on morphology but phylogenetic analysis of morphology failed to recover the monophyly of the family or any tribes with the exception of Ficeae. Indeed, preliminary analysis of morphology by Judd et al. (1994) also identified these problems. High levels of homoplasy and a paucity of characters not only contribute to a lack of phylogenetic signal, but also point to the ambiguity of morphology in phylogenetic classification. We argue that an analytically based classification is preferred over subjective classification especially given that phylogenetic analysis of morphology alone is often equivocal or disagrees with prior hypotheses of classification.

Molecular phylogeny did not completely resolve the early divergence of Moraceae with confidence, and the paraphyly of *Streblus* and *Trophis* were especially difficult to explain because of the uncertain position of Moreae relative to the rest of the family (Datwyler and Weiblen 2004). The addition of morphology in parsimony and Bayesian analysis (Figs. 5, 6) indicated that Moreae sensu stricto is sister to Artocarpeae. We base our taxonomic revision and our discussion of the evolution of inflorescence architecture on molecular phylogenetic findings that were not sensitive to the inclusion of morphology.

TABLE 2. Ancestral state reconstruction under ACCTRAN according to the total evidence phylogeny (Fig. 6). Nodes are numbered as in Fig. 6 and character states are defined in Appendix 2. The number of steps, consistency index (CI), and the number of most parsimonious reconstructions (MPR) are shown. Ancestral states that differed under DELTRAN are indicated with superscripts as follows: 1 = unisexual, 2 = spike, 3 = equivocal, 4 = four-merous, 5 = three-merous, 6 = globose, 7 = free, 8 = not peltate, 9 = connate, and 10 = two and equal.

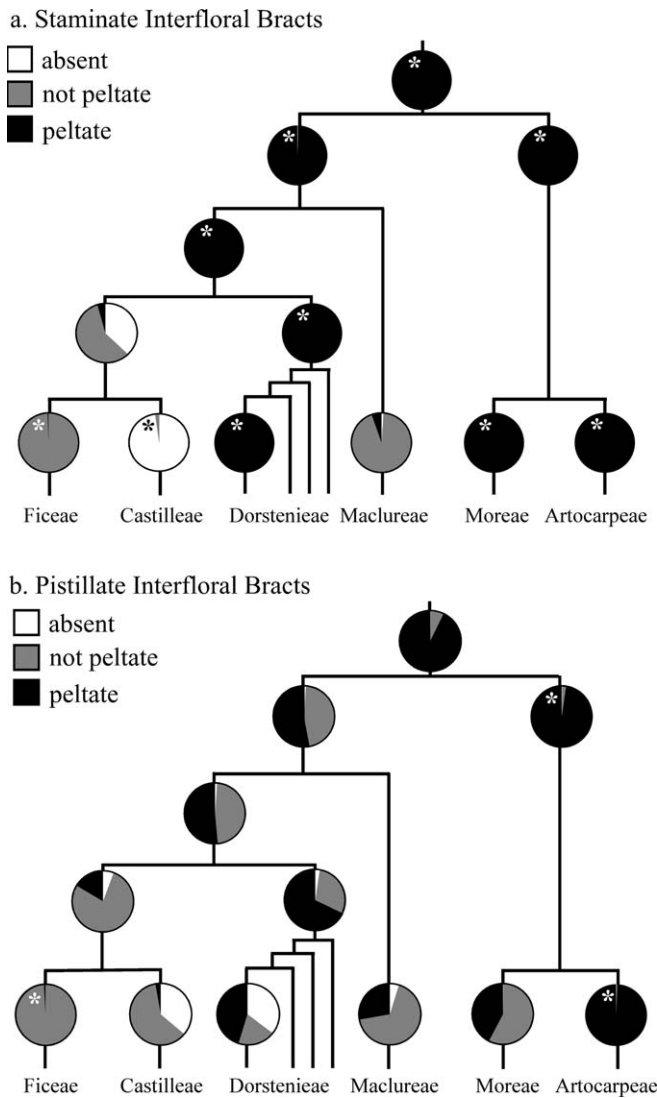| Character	# of steps	CI	MPR	Ancestral state by node											
				1	2	3	4	5	6	7	8	9	10	11	12
43. Inflorescence	12	0.17	14	unisexual	unisexual	unisexual	bisexual[1]	bisexual[1]	bisexual[1]	bisexual	unisexual	bisexual[1]	unisexual	unisexual	unisexual
Staminate flowers															
47. Inflorescence architecture	32	0.53	2,592	spike	spike	spike	spike	equivocal[2]	spike	syconium	disc	globose	spike	spike	spike
49. Interfloral bracts	25	0.62	132	equivocal	not peltate[3]	peltate	not peltate[3]	not peltate[3]	peltate[3]	not peltate	absent	peltate[3]	not peltate	peltate	peltate
50. Perianth merosity	108	0.87	90	4-merous	4-merous	4-merous	4-merous	4-merous	4-merous	3-merous	4-merous	3-merous[4]	4-merous	2-merous[4]	4-merous
51. Perianth connation	39	0.53	6	free	free	free	free	free	partially connate	free	free	connate	free	free	free
52. Adjacent flowers	7	0.57	3	free	free	free	free	free	free	free	free	free	free	free	free
53. Filaments	9	0.11	11	straight[3]	straight[3]	straight	straight[3]	straight	inflexed[3]	straight	straight	straight	straight[3]	straight	straight
56. Stamens per flower	74	0.67	864	four	four	four	four	four	four	two	four	two[5]	four	one	four
Pistillate flowers															
57. Inflorescence architecture	29	0.66	270	globose	globose	globose	globose	equivocal[6]	globose	syconium	disc[6]	globose	globose	globose	globose
59. Number of flowers	7	0.29	5	many	many	many	many	many	many	many	many	many	many	many	many
60. Adjacent flowers	40	0.87	12	free	free	free	free	free	free	free	free	adnate[7]	free	free	free
61. Interfloral bracts	21	0.33	1764	peltate[3]	not peltate	peltate	not peltate	not peltate	not peltate	not peltate	not peltate	peltate[8]	not peltate	peltate	peltate
62. Pistillate flower position	5	0.20	1	not embedded	not embedded	not embedded	not embedded	not embedded	not embedded	not embedded	embedded	embedded	not embedded	not embedded	not embedded
63. Perianth merosity	81	0.83	300	4-merous	4-merous	4-merous	4-merous	4-merous	4-merous	3-merous	4-merous	2-merous[4]	4-merous	4-merous	4-merous
64. Perianth connation	27	0.44	24	connate	connate	connate	connate	free	connate	free	free[9]	connate	connate	connate	connate
65. Stigma	33	0.72	60	two, equal	two, equal	two, equal	two, equal	two, equal	two, equal	equivocal[10]	two, equal	two, equal	two, equal	two, equal	two, equal

FIG. 7.   Maximum likelihood ancestral character reconstructions using the Multistate package of BayesTraits. Ancestral reconstructions of staminate (a) and pistillate (b) interfloral bracts are shown on a simplified Moraceae phylogeny. The probability of each character state as the ancestral character for each node is represented in a pie chart. Character states significant at the 0.05 level are indicated by asterisks.

Classification of Moraceae—Morphology alone did not unilaterally support any prior classification of Moraceae according to tests of monophyly (Table 1). The available evidence taken together rejects the traditional classification, and renders some newly proposed tribes unnecessary. We discuss a new classification of Moraceae building upon Datwyler and Weiblen (2004) with the addition of morphology. We describe taxonomic changes (Fig. 6; Appendix 3) and identify potential diagnostic characters for the revised tribes.

The monotypic Ficeae was the only tribe supported by morphology alone (Fig. 3), and total evidence added strength to this assertion. However, the monophyly of figs has never been doubted owing to the distinctive inflorescence and pollination syndrome. All Ficeae have syconia (Fig. 1g), waxy glands associated with the leaves, small seeds, and are insect pollinated. Additionally, most figs have cystoliths, endosperm, $n = 13$ chromosomes, banded apotracheal parenchyma, vasicentric paratracheal parenchyma, and the absence of square cells in uniseriate rays. Fig inflorescences are among the most

derivative in Moraceae and the tribe further exhibits the most diversity in vegetative features and growth habits.

The phylogeny based on cpDNA sequences, and later corroborated by nuclear DNA, showed that Castilleae is the sister group to the figs. Datwyler and Weiblen (2004) expanded Castilleae to include three additional genera previously placed in Artocarpeae: *Antiaropsis, Poulsenia,* and *Sparattosyce.* Berg (2005a) placed these genera outside of Castilleae in two new tribes: Antiaropsideae, including *Antiaropsis* and *Sparattosyce,* and Soroceae, including *Poulsenia* and other former Artocarpeae. Given the sister relationship of Castilleae and Antiaropsideae sensu Berg (2005a), in the context of this phylogenetic classification we designate these lineages as subtribes of Castilleae sensu Datwyler and Weiblen (2004). Antiaropsineae differs from Castillineae in having dehiscent fruits and folded cotyledons, and in lacking abscising branches whereas both subtribes Antiaropsineae and Castillineae share an involucre, septate wood fibers, large seeds, and the absence of cystoliths. In contrast to the rest of Castilleae, *Poulsenia* lacks self-pruning branches and septate wood fibers, but morphologically, the genus fits no better with any other tribe of Moraceae. Berg (2005a) placed *Poulsenia* in a heterogeneous Soroceae united only by neotropical distribution, but there is no phylogenetic basis for the tribe (Figs. 1, 6) and it must be dissolved.

Morphology and molecules together fail to reject the narrowly circumscribed Castilleae of Berg (2001, 2005a) as this group is a subclade of the expanded Castilleae of Datwyler and Weiblen (2004). Molecular data from two genes at the family level (Datwyler and Weiblen 2004; Zerega et al. 2005) and three more genes at the tribal level (Clement unpubl. data) strongly support Castilleae sensu Datwyler and Weiblen (2004). Additionally, both phylogenetic analysis of morphology alone and of molecular data support a close relationship of figs and Castilleae (Figs. 4, 5), adding weight to the assertion of Corner (1978) that Castilleae, and *Antiaropsis* and *Sparattosyce* in particular, share features indicative of a close relationship to the figs.

Traditionally, Artocarpeae has been considered heterogeneous and Datwyler and Weiblen (2004) reduced it to seven genera. Instead, Berg (2005a) transferred *Batocarpus* H. Karst. and *Clarisia* Ruiz & Pav. (as well as other Artocarpeae genera) to Soroceae. Phylogenetic analyses of the combined data rejected Soroceae and there are no morphological features unifying the tribe. Phylogenetic analyses of both molecular and combined data showed that *Batocarpus* and *Clarisia* are most closely related to Artocarpeae (Figs. 5, 6). Total evidence strongly rejects Artocarpeae sensu Berg (2001) but supports the circumscriptions of Berg (2005a) and Datwyler and Weiblen (2004). *Batocarpus* and *Clarisia* form a clade and possess a few unique traits such as yellow glands in the inflorescences, but also share features with Artocarpeae including one stamen per flower, peltate interfloral bracts, vitreous silica, and straight filaments.

With the exception of nonparametric tests of morphology, all other evidence (Table 1) rejected both Moreae sensu Berg (2001, 2005a) and sensu Datwyler and Weiblen (2004) due to the polyphyly of *Streblus* and *Trophis* (Fig. 5, 6). The combined analysis (Fig. 6) supports the sister relationship of Moreae sensu stricto and Artocarpeae sensu Datwyler and Weiblen (2004). However, the polyphyly of *Streblus* and *Trophis* requires taxonomic changes to achieve a monophyletic Moreae. *Streblus* is a heterogeneous group of 5 sections

(Berg et al. 2006) defined by plesiomorphic characters including explosive stamens associated with wind pollination. The outlying *Streblus elongatus* (Miq.) Corner was assigned to monotypic section *Sloetia* (Teijsm. & Binn. ex Kurz) Corner, which is strongly supported as sister to *Bleekrodea*. *Bleekrodea* was originally *Streblus* sect. *Bleekrodea* (including *S. insignis* and *S. madagascariensis;* Corner 1962) and Berg (1988) later elevated section *Bleekrodea* to genus status. *Sloetia* and *Bleekrodea* share morphological traits including uncinate hairs, filiform stigmas, bisexual inflorescences, conical pistillodes, inflexed stamens, dehiscent fruits, thick cotyledons, and short radicles, none of which is shared with the rest of *Streblus*. However, *S. elongatus* shares some features with *Streblus* alone, including extrorse anthers, peltate bracts, the lack of endosperm, and $n = 13$ chromosomes. We resurrect the genus *Sloetia* Teijsm. & Binn. ex Kurz and transfer it to Dorstenieae based on phylogeny (Fig. 6) and the great genetic distance and morphological discontinuity between *S. elongatus* and the rest of *Streblus*.

As in *Streblus*, morphological heterogeneity and monotypic sections characterize *Trophis*. Berg (1988) reduced *Malaisia scandens* (Lour.) Planch. to monotypic *Trophis* P. Browne section *Malaisia* (Blanco) C. C. Berg on account of superficial similarities between *Malaisia* and *Trophis*. However, combined phylogenetic analyses (Figs. 5, 6) show a close relationship between *Trophis scandens* and *Broussonetia*. They share spicate staminate inflorescences and similar geographic distributions. Here we reinstate the monotypic genus *Malaisia* Blanco (see Zhekun and Gilbert 2003) and transfer it to Dorstenieae based on phylogenetic evidence (Fig. 6).

Contrary to Berg (2005a), we exclude *Bleekrodea*, *Broussonetia*, *Fatoua*, *Maclura* Nutt., *Malaisia,* and *Sloetia* from Moreae but include *Bagassa* Aubl. and *Sorocea* A. St.-Hil. from his dissolved Soroceae. Moreae remains a diverse tribe and lacks morphological synapomorphies. The staminate inflorescences appear plesiomorphic in typically being loosely spicate or racemose and the flowers are four-merous.

Maclura does not belong in Moreae but represents a distinct lineage on morphological and genetic grounds. The genus possesses a unique combination of features including axillary thorns and glands with yellow dye in the inflorescences, as well as a distribution extending to temperate regions. Possibly due to a range expansion into the temperate zone, *Maclura* species tend to have growth rings, ring porous vessels, and distinct heartwood and sapwood. *Maclura* is also quite diverse; it is one of three genera with both inflexed and straight stamens in addition to variable inflorescence architecture. We transfer *Maclura* to the monotypic tribe, Maclureae, based on its morphological distinctiveness and phylogenetic position.

Dorstenieae and Ficeae are the two tribes on whose membership Berg (2001, 2005a) and Datwyler and Weiblen (2004) agree. These groups have never been controversial on account of their highly derivative morphologies that reflect major reorganizations of life history as with fig pollination and succulence in *Dorstenia*, and they are marked by long branches in the morphological phylogeny (Fig. 3).

Dorstenieae s. s. is well-supported (Fig. 6) but not monophyletic unless the closely related lineages (*Bleekrodea* and *Sloetia*, *Malaisia* and *Broussonetia*, and *Fatoua*) are also recognized as tribes. Instead, we transfer *Bleekrodea*, *Broussonetia*, *Fatoua*, *Sloetia,* and *Malaisia* to Dorstenieae on account of the strongly supported grade that these genera form with respect to Dorstenieae sensu stricto (Fig. 6). Given that the species and sections have yet to be completely sampled, it is possible that Dorstenieae s. l. could continue to expand. For instance, preliminary molecular phylogenetic analyses including *Treculia* Decne. ex Trécul suggest it is more closely related to Dorstenieae than to Artocarpeae (Zerega unpubl. data). Further sampling is warranted to identify the limits of the morphologically diverse Dorstenieae sensu lato.

Previous phylogenetic studies have focused on the identity of the figs' closest relatives in an effort to understand the origin of the fig-fig wasp mutualism, to reclassify Moraceae according to phylogeny (Datwyler and Weiblen 2004), and to infer biogeography (Zerega et al. 2005). With molecular and morphological data in hand, we can now attempt to understand the evolutionary relationships among all tribes of the family, not only for the purpose of taxonomic revision (Fig. 6), but also to study the complex morphological evolution for which Moraceae is known (Corner 1962). We recognize six tribes and confirm the sister relationship of Castilleae and Ficeae according to morphological and molecular evidence. Dorstenieae and Maclureae are close relatives to Castilleae and Ficeae, and the sister relationship of Moreae and Artocarpeae is strongly supported.

Morphological Evolution of Moraceae—Taxonomists (Trécul 1847; Corner 1962; Berg 1973, 2005b; Humphries and Blackmore 1989) have long appreciated how high levels of homoplasy and convergent evolution have hindered the development of phylogenetic hypotheses in which to study the morphological evolution of Moraceae as a whole. The results of this study open the door to comparative studies that can elucidate major shifts in morphological features, such as inflorescence architecture, and their possible effects on the diversification of lineages. Here we briefly outline some major morphological changes in the history of Moraceae and advance hypotheses as to their functional significances.

Although ancestors to Moraceae, Urticaceae, and Cannabaceae are hypothesized to have bisexual cymes, the ancestor of Moraceae appears to have been dioecious, wind-pollinated, and lacking an involucre (Datwyler and Weiblen 2004). The evolution of floral features within Moraceae is thought to have occurred in concert with shifts in pollination biology (Berg 1990). For example, Datwyler and Weiblen (2004) established a correlation between the presence of an involucre and the shift from wind to insect pollination. These findings agree with Berg's (1990) hypothesis that reduced numbers of floral parts and accrual of secondary protective structures, such as the involucre, may promote visitation by specialized insect pollinators while preventing phytophagy. On the contrary, some protective structures, such as peltate floral bracts, appear to be ancestral. Interestingly, peltate bracts were lost in lineages with other types of protective structures, such as the involucral bracts of Ficeae and Castilleae. However, the loss of peltate bracts is not correlated with a transition from wind to insect pollination. While some derived features of Moraceae have associations with phytophagy and pollination syndrome, the hypothesized trend may not explain all gains and losses of such "protective" features.

Ancestral state reconstruction suggested that early forms of staminate and pistillate inflorescences were indeterminate spikes or globose heads. The staminate inflorescence was reconstructed as a spike with flowers having four free tepals and four stamens, whereas the pistillate inflorescence was globose with a connate perianth. Although these characters may have evolved independently of pollination mode, these features evolved in a wind-pollinated ancestor prior to

the diversification of Moraceae, and though the staminate characteristics are indicative of wind pollination, the pistillate features are less so. In fact, the compact inflorescence architecture and fusion of perianth is more indicative of a reduced or condensed inflorescence considered by Berg (1990) to be a derived feature of the family. Extant Moreae, Artocarpeae, and Maclureae exhibit some plesiomorphic traits including spicate staminate inflorescences, globose pistillate inflorescences, and four-merous flower parts. Yet extant Dorstenieae, Castilleae, and Ficeae show greater derivation from simple spikes and globose inflorescence to disc-shaped receptacles, syconia, and other globose receptacles of turbinate or ellipsoidal form with either unisexual or bisexual conditions.

Our results suggest a major reorganization of floral morphology along the lineage leading to Dorstenieae, Ficeae, and Castilleae. It is noteworthy that the two most species-rich genera of Moraceae, *Ficus* (ca. 800 spp.) and *Dorstenia* (105 spp.), occur in this lineage. The origin of these three tribes is marked by shifts from unisexual to bisexual inflorescences, dioecious to monoecious breeding systems, a reduction in base chromosome number from 14–13, the presence of conical pistillodes, and the presence of radial latex tubes. All except the last of these states were reversed or lost in Castilleae. However, none of these changes is associated with the shift to insect pollination that preceded the diversification of Castilleae and Ficeae. This sequence of character change clarifies the morphological features that had evolved prior to the diversification of figs and Castilleae and their highly specialized pollination syndromes.

The total evidence phylogeny of Moraceae can facilitate further study of morphological evolution of the family. Although some genera, especially *Streblus* and *Trophis*, warrant more intensive sampling to determine their phylogenetic relationships, this framework provides a foundation for future work on the morphological evolution of Moraceae. Research in light of the revised phylogeny focused on the function and developmental genetics of morphological shifts, such as changes in stamen structure or shifts from unisexual to bisexual inflorescences, is a logical next step in understanding the diversification of Moraceae.

TAXONOMIC REVISIONS

The evolutionary relationships of Moraceae cannot be accurately understood by morphology alone as inferred in previous taxonomic treatments (Berg 1972, 1973, 1977a, b, 2001, 2005a; Berg and Dewolf 1975; Berg et al. 2006). Our taxonomic revisions are based on all currently available chloroplast and nuclear DNA sequences, and are not sensitive to the inclusion of vegetative, reproductive and wood anatomical information. There are few synapomorphies with which to recognize each tribe due to the low phylogenetic signal, high homoplasy, and ambiguity of morphology, but careful investigation in the light of phylogeny may reveal more.

We dissolve two newly created tribes, Antiaropsideae and Soroceae. While the former is a subtribe of Castilleae, the latter is a polyphyletic group and so members are assigned to tribes to which they show phylogenetic relationship: *Poulsenia* to Castilleae, *Batocarpus* and *Clarisia* to Artocarpeae, and *Bagassa* and *Sorocea* to Moreae (Appendix 3). *Maclura* is transferred from Moreae to Maclureae. The monotypic genera *Sloetia* and *Malaisia* are reinstated and transferred to

Dorstenieae along with *Bleekrodea, Broussonetia,* and *Fatoua* (Appendix 3).

MALAISIA Blanco, Fl. Filip. P. 789. 1837. *Trophis* P. Browne sect. *Malaisia* (Blanco) C. C. Berg, Proc. Kon. Ned. Akad. Wetensch. C, 91: 354. 1988.

MALAISIA SCANDENS (Lour.) Planch, Ann. Sci. Nat., Bot. sér 4, 3: 293. 1855. *Caturus scandens* Lour., Fl. Cochinch. P. 612. 1790. *Trophis scandens* (Lour.) Hook. & Arn., Bot. Beechey Voy. P. 214. 1837. *Alchornea scandens* (Lour.) Müll. Arg., Linnaea 34: 170. 1865. *Malaisia tortuosa* Blanco var. *scandens* (Lour.) Bureau in A. DC., Prodr. 17: 222. 1873.

Morus javanica Blume, Bijdr. P. 488. 1825. *Cephalotrophis javanica* (Blume) Blume, Ann. Mus. Bot. Lugduno-Batavi 2: 76, t. 27. 1856.

Malaisia tortuosa Blanco, Fl. Filip. P. 789. 1837.

Dumartroya fagifolia Gaudich., Voy. Bonite, Bot. P. 165, t. 97. 1844.

Malaisia viridescens Planch., Ann. Sci. Nat., Bot. sér 4, 3: 293. 1855. *Malaisia tortuosa* Blanco var. *viridescens* (Planch.) Bureau in A. DC., Prodr. 17: 222. 1873.

Malaisia acuminata Planch., Ann. Sci. Nat., Bot. sér 4, 3: 294. 1855. *Malaisia tortuosa* Blanco var. *acuminata* (Planch.) Bureau in A. DC., Prodr. 17: 222. 1873.

Malaisia cunninghamii Planch., Ann. Sci. Nat., Bot. sér 4, 3: 294. 1855.

Cephalotrophis ? puberula Miq., Fl. Ned. Ind., Eerste Bijv. P. 416. 1861. *Malaisia puberula* (Miq.) Bureau in A. DC., Prodr. 17: 222. 1873.

Caturus torulosus Seem., Fl. Vit. P. 254. 1868.

Malaisia tortuosa Blanco var. *racemosa* Bureau in A. DC., Prodr. 17: 222. 1873.

Malaisia scandens (Lour.) Planch. var. *rolfei* K. Schum., Bot Jahrb. Syst. 9: 199. 1888.

Malaisia blancoi Elmer, Leafl. Philipp. Bot. 5: 1812. 1913.

SLOETIA Teijsm. & Binn. ex Kurz, J. Linn. Soc., Bot. 8: 168. 1864. *Streblus* Lour. sect. *Sloetia* (Teijsm. & Binn. ex Kurz) Corner, Gard. Bull. Singapore 19: 218. 1962.

SLOETIA ELONGATA (Miq.) Koord., Exkurs.-Fl. Java 2: 90. 1912. *Artocarpus elongatus* Miq., Fl. Ned. Ind., Eerste Bijv. P. 419. 1861. *Streblus elongatus* (Miq.) Corner, Gard. Bull. Singapore 19: 227. 1962.

Sloetia sideroxylon Teijsm. & Binn. ex Kurz, J. Linn. Soc., Bot. 8: 168, t. 13. 1864.

Sloetia sideroxylon Teijsm. & Binn. ex Kurz var. *brevipes* Bureau in A. DC., Prodr. 17: 258. 1873.

Sloetia penangiana Oliv., Hooker's Icon. Pl. t. 1531. 1886.

Sloetia wallichii King ex Hook. f., Fl. Brit. India 5: 493. 1888.

MORACEAE tribe CASTILLEAE C. C. Berg, Acta Bot. Neerl. 26: 78. 1977.— TYPE. *Castilla* V. Cervantes.

Castilleae includes trees and shrubs with septate wood fibers and lacking cystoliths. Breeding systems include monoecy, dioecy, and androdioecy. Inflorescences are unisexual and involucrate with discoid to urceolate shaped receptacles, and staminate inflorescences lack a pistillode. Fruits are either dehiscent or indehiscent with large seeds.

Includes *Antiaris* (1 sp.), *Antiaropsis* (2 spp.), *Castilla* (3 spp.), *Helicostylis* (7 spp.), *Maquira* (4 spp.), *Mesogyne* (1 sp.), *Naucleopsis* (22 spp.), *Perebea* (9 spp.), *Poulsenia* (1 sp.), *Pseudolmedia* (9 spp.), and *Sparattosyce* (2 spp.).

MORACEAE subtribe **Antiaropsineae** (C. C. Berg) Clement & Weiblen, status nov. *Moraceae* tribe *Antiaropsineae* C. C. Berg, Blumea 50: 535–550. 2005.—TYPE. *Antiaropsis* K. Schum.

Antiaropsineae is comprised of dioecious small trees and shrubs that lack self-pruning branches. The group has axillary involucrate inflorescences with discoid to urceolate shaped receptacles. Adjacent flowers within the inflorescence are free, and flowers have four-merous free tepals. Fruits are dehiscent with large seeds and folded cotyledons.

Includes *Antiaropsis* (2 spp.) and *Sparattosyce* (2 spp.).

MORACEAE subtribe **Castillineae** Clement & Weiblen, subtrib. nov.—TYPE. *Castilla* V. Cervantes.

Arbores et frutices ramis dispositis spiratim perpendicularis ad truncum. Rami ipsi amputans et foliis sine cystolithis. Inflorescentiae involucratae aliqua genera unisexualibus inflorescentiis pistillatis.

Castillineae includes trees and shrubs with spirally arranged braches perpendicular to the main trunk (Cook's model). The group has self-pruning branches, and leaves lack cystoliths. Breeding systems include monoecy, dioecy, and androdioecy. Inflorescences are involucrate with some genera having uniflorous pistillate inflorescences.

Includes *Antiaris* (1 sp.), *Castilla* (3 spp.), *Helicostylis* (7 spp.), *Maquira* (4 spp.), *Mesogyne* (1 sp.), *Naucleopsis* (22 spp.), *Perebea* (9 spp.), *Poulsenia* (1 sp.), and *Pseudolmedia* (9 spp.).

MORACEAE tribe **Maclureae** Clement & Weiblen, trib. nov.—TYPE. *Maclura* Nutt.

Lianae, arbores vel frutices spinis axillaris armatis. Dioecious et saepe glandes lutum continentes in inflorescentias. Inflorescentiae staminatae, spicata vel racemosa usque ad globosum capitatum. Inflorescentiae globosae pistillata stigmate duobus saepe in longitudino inequalis.

Maclureae includes climbers, trees, or shrubs armed with axillary thorns. All species are dioecious and often have glands containing yellow dye in the inflorescence. Staminate inflorescences vary from spicate or racemose to globose-capitate, and have both inflexed and straight stamens. Pistillate inflorescences are globose typically with two stigmas that are often unequal in length. Fruits are mostly fleshy.

Includes *Maclura* (11 spp.).

LITERATURE CITED

Bailey, C. D., M. A. Koch, M. Mayer, K. Mummenhoff, S. L. O'Kane, S. I. Warwick, M. D. Windham, and I. A. Al-Shehbaz. 2006. Toward a global phylogeny of the Brassicaceae. *Molecular Biology and Evolution* 23: 2142–2160.

Barker, F. K. and F. M. Lutzoni. 2002. The utility of the incongruence length difference test. *Systematic Biology* 51: 625–637.

Barker, W. T. 1997. *Celtis*. pp. 616–616 in *Flora of North America north of Mexico* vol. 3, ed. Flora of North America Editorial Committee. New York: Oxford University Press.

Berg, C. C. 1972. *Olmedieae Brosimeae (Moraceae)*. Flora Neotropica. New York: Hafner Publishing Company.

Berg, C. C. 1973. Some remarks on the classification and differentiation of Moraceae. *Mededelingen van het Botanisch Museum en Herbarium van de Rijksuniversiteit te Utrecht* 386: 1–10.

Berg, C. C. 1977a. The Castilleae, a tribe of the Moraceae, renamed and redefined due to the exclusion of the type genus *Olmedia* from the "Olmedieae". *Acta Botanica Neerlandica* 26: 73–82.

Berg, C. C. 1977b. Revisions of African Moraceae (excluding *Dorstenia, Ficus, Musanga* and *Myrianthus*). *Bulletin du Jardin Botanique National de Belgique* 47: 267–407.

Berg, C. C. 1978a. Cecropiaceae a new family of the Urticales. *Taxon* 27: 39–44.

Berg, C. C. 1978b. Revisions of African Moraceae (excl. *Dorstenia, Ficus, Musanga* and *Myrianthus*); corrections and additions. *Bulletin du Jardin Botanique National de Belgique* 48: 466–468.

Berg, C. C. 1982. The reinstatement of the genus *Milicia* Sim (Moraceae). *Bulletin du Jardin Botanique National de Belgique* 52: 225–229.

Berg, C. C. 1983. *Dispersal and distribution in the Urticales - an outline*. pp. 219–229 in *Dispersal and distribution: An international symposium* vol. 7, ed. K. Kubitzki. Hamburg: Sonderbande des Naturwissenschaftlichen Vereins.

Berg, C. C. 1986. The delimitation and subdivision of the genus Maclura (Moraceae). *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappan, Amsterdam, the Netherlands* 89: 241–247.

Berg, C. C. 1988. The genera Trophis and Streblus (Moraceae) remodeled. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappan, Amsterdam, the Netherlands* 91: 345–362.

Berg, C. C. 1989. Systematics and phylogeny of the Urticales. Pp. 193–220 in *Evolution, systematics and fossil history of the Hamamelidae*. eds. P. R. Crane and S. Blackmore. Oxford: Clarendon Press.

Berg, C. C. 1990. Differentiation of flowers and inflorescences of Urticales in relation to their protection against breeding insects and to pollination. *Sommerfeltia* 11: 13–34.

Berg, C. C. 1992. *20–23 Urticales. 26. Casuarinales*. pp. 1–224 in *Flora of the Guianas* vol. A-11, ed. Rijn A. R. A. G.-v. Rijn. Koenigstein: Koeltz Scientific Books.

Berg, C. C. 1998. *27B. Moraceae*. pp. 1–128 in *Flora of Ecuador* vol. 60, eds. B. Harling and L. Andersson. Arlov, Sweden: Elanders Berlings.

Berg, C. C. 2001. *Moreae, Artocarpeae, and Dorstenia (Moraceae) with introductions to the family and* Ficus *and with additions and corrections to Flora Neotropica Monograph 7*. Flora *Neotropica*, vol. 83. New York: New York Botanical Garden.

Berg, C. C. 2005a. Flora Malesiana precursor for the treatment of Moraceae 8: Other genera than *Ficus*. *Blumea* 50: 535–550.

Berg, C. C. 2005b. Moraceae diversity in a global perspective. *Biologiska Skrifter* 55: 423–440.

Berg, C. C. and R. W. A. P. Akkermans. 1985. Studies on the flora of the Guianas 14: New taxa and combination in Sorocea (Moraceae) and a key to its species. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappan, Amsterdam, the Netherlands* 88: 381–394.

Berg, C. C. and G. P. Dewolf. 1975. *Moraceae*. The Netherlands: E. J. Brill.

Berg, C. C. and M. E. E. Hijman. 1999. The genus *Dorstenia* (Moraceae). *Ilicifolia* 2: 1–211.

Berg, C. C. and P. F. Rosselli. 2005. *Cecropia*. Flora Neotropica Monograph, vol. 94. New York: New York Botanical Garden.

Berg, C. C. and J. E. Simonis. 2000. *Moraceae - Cecropiaceae. in Flora de Venezuela* ed. R. Riina. Caracas: Fundacion Instituto Botanico de Venezuela.

Berg, C. C., R. W. A. P. Akkermans, and E. C. H. V. Heusden. 1990. *Cecropiaceae: Coussapoa and Pourouma with an introduction to the family*. New York: New York Botanical Garden.

Berg, C. C., E. J. H. Corner, and F. M. Jarrett. 2006. *Genera other than Ficus (Moraceae)*. Pp. 152 in *Flora Malesiana Series I - Seed Plants* vol. 17 Part 1, ed. H. P. Nooteboom. Leiden: National Herbarium Nederland.

Bonsen, K. and B. J. H. ter Welle. 1983. Comparative wood and leaf anatomy of the Cecropiaceae (Urticales). *Bulletin du Museum National d Histoire Naturelle, Paris, 4 series-section B Adansonia* 5: 151–177.

Bonsen, K. J. and B. J. H. ter Welle. 1984. Systematic wood anatomy and affinities of the Urticaceae. *Botanische Jahrbucher fur Systematik* 105: 49–71.

Boufford, D. E. 1997. *Urticaceae*. Pp. 400–411 in *Flora of North America north of Mexico* vol. 3, ed. Flora of North America Editorial Committee. New York: Oxford University Press.

Brandley, M. C., A. Schmitz, and T. W. Reeder. 2005. Partitioned Bayesian analyses, partition choice, and the phylogenetic relationships of Scincid lizards. *Systematic Biology* 54: 373–390.

Buckley, T. R. 2002. Model misspecification and probabilistic tests of topology: evidence from empirical data sets. *Systematic Biology* 51: 509–523.

Burger, W. C. 1962. Studies in New World Moraceae: *Trophis, Clarisia, Acanthinophyllum*. *Annals of the Missouri Botanical Garden* 49: 1–34.

Burger, W. C., J. Lanjouw, and J. G. W. Boer. 1962. The genus *Sorocea* St. Hil. (Morac.). *Mededelingen van het Botanisch Museum en Herbarium van de Rijksuniversiteit te Utrecht* 193: 428–474.

Castellanos, I., P. Cuevas-Reyes, L. Rios-Casanova, K. Oyama, and M.Quesada. 2006. Abundance of gall midges on *Poulsenia armata* (Moraceae): Importance of host plant size and light environment in tropical rain forests. *Biotropica* 38: 569–573.

Chew, W.-L. 1989a. *Urticaceae*. Pp. 68–92 in *Flora of Australia*. Vol. 3, Hamamelidales to Casuarinales, ed. A. S. George. Canberra: Australian Government Publishing Service.

Chew, W.-L. 1989b. *Moraceae*. Pp. 15–68 in *Flora of Australia*. Vol. 3, Hamamelidales to Casuarinales, ed. A. S. George. Canberra: Australian Government Publishing Service.

Corner, E. J. H. 1962. The classification of Moraceae. *The Gardens' bulletin, Singapore* 19: 187–252.

Corner, E. J. H. 1967. Ficus in the Solomon Islands and its bearing on the post-Jurassic history of Melanesia. *Philosophical Transactions of the Royal Society of London Series B* 253: 23–159.

Corner, E. J. H. 1970a. New species of *Streblus* and *Ficus* (Moraceae). *Blumea* 18: 393–411.

Corner, E. J. H. 1970b. Ficus subgen. Pharmacosycea with reference to the species of New Caledonia. *Philosophical Transactions of the Royal Society of London Series B* 259: 383–433.

Corner, E. J. H. 1975. The evolution of *Streblus* Lour. (Moraceae): with a new species of sect. *Bleekrodea*. *Phytomorphology* 25: 1–12.

Corner, E. J. H. 1978. Ficus dammaropsis and the multibracteate species of Ficus sect. Sycocarpus. *Philosophical Transactions of the Royal Society of London Series B* 281: 373–406.

Datwyler, S. L. and G. D. Weiblen. 2004. On the origin of the fig: phylogenetic relationships of Moraceae from *ndhF* sequences. *American Journal of Botany* 91: 767–777.

Dentinger, B. T. M. and D. J. McLaughlin. 2006. Reconstructing the Clavariaceae using nuclear large subunit rDNA sequences and a new genus segregated from *Clavaria*. *Mycologia* 98: 746–762.

Farris, J. S., M. Källersjö, A. G. Kluge, and C. Bult. 1994. Testing significance of incongruence. *Cladistics* 10: 315–319.

Fredriksson, G. M. and S. A. Wich. 2006. Frugivory in sun bears (*Helarctos malayanus*) is linked to El Niño related fluctuations in fruiting phenology, East Kalimantan, Indonesia. *Biological Journal of the Linnean Society* 89: 489–508.

Friis, I. B. 1989. 16. *The Urticaceae: a systematic review*. Pp. 285–308 in *Evolution, systematics, and fossil history of the Hamamelidae*, Volume 2:'higher' Hamamelidae. eds. P. R. Crane and S. Blackmore. Oxford: Clarendon Press.

Fu, L., Y. Xin, and A. Whittemore. 2003. *Celtis*. in *Flora of China* vol. 5, ed. Flora of China Editorial Committee. St. Louis: Missouri Botanical Garden Press.

Harrison, R. D. 2006. Mortality and recruitment of hemi-epiphytic figs in the canopy of a Bornean rain forest. *Journal of Tropical Ecology* 22: 477–480.

Herendeen, P. S. and R. B. Miller. 2000. Utility of wood anatomical characters in cladistic analysis. *IAWA Journal* 21: 247–276.

Hipp, A. L., J. C. Hall, and K. J. Sytsma. 2004. Congruence versus phylogenetic accuracy: revisiting the incongruence length difference test. *Systematic Biology* 53: 81–89.

Hoen, P. P. and W. Punt. 1989. Pollen morphology of the tribe Dorstenieae (Moraceae). *Review of Palaeobotany and Palynology* 57: 187–220.

Holmgren, P. K., N. H. Holmgren, and L. C. Barnett. 1990. *Index Herbariorum 1: the herbaria of the world*. Bronx: New York Botanical Garden.

Huelsenbeck, J. P. and F. R. Ronquist. 2001. MRBAYES: Bayesian inference of phylogeny. *Biometrics* 17: 754–755.

Humphries, C. J. and S. Blackmore. 1989. *A review of the classification of the Moraceae*. Pp. 267–277 in *Evolution, systematics, and fossil history of the Hamamelidae* vol. 2, eds. P. R. Crane and S. Blackmore. Oxford: Clarendon Press.

Jarrett, F. M. 1959a. Studies in *Artocarpus* and allied genera, II. A revision of *Prainea*. *Journal of the Arnold Arboretum* 40: 30–37.

Jarrett, F. M. 1959b. Studies in *Artocarpus* and allied genera, III. A revision of *Artocarpus* subgenus *Artocarpus*. *Journal of the Arnold Arboretum* 40: 114–155, 327–368.

Jarrett, F. M. 1959c. Studies in *Artocarpus* and allied genera, III. A revision of *Artocarpus* subgenus *Artocarpus*. *Journal of the Arnold Arboretum* 40: 298–326.

Jarrett, F. M. 1959d. Studies in *Artocarpus* and allied genera, I. General considerations. *Journal of the Arnold Arboretum* 40: 1–29.

Jarrett, F. M. 1960a. Studies in *Artocarpus* and allied genera, V. A revision of *Parartocarpus* and *Hullettia*. *Journal of the Arnold Arboretum* 41: 320–340.

Jarrett, F. M. 1960b. Studies in *Artocarpus* and allied genera, IV. A revision of *Artocarpus* subgenus *Pseudojaca*. *Journal of the Arnold Arboretum* 41: 73–140.

Jenner, R. A. 2004. Accepting partnership by submission? Morphological phylogenetics in a molecular millennium. *Systematic Biology* 53: 333–342.

Jiarui, C. and C. M. Wilmot-Dear. 2003. *Boehmeria*. in *Flora of China* vol. 5, ed. Flora of China Editorial Committee. St. Louis: Missouri Botanical Garden Press.

Jiarui, C., I. Friis, and C. M. Wilmot-Dear. 2003a. *Leucosyke*. in *Flora of China* vol. 5, ed. Flora of China Editorial Committee. St. Louis: Missouri Botanical Garden Press.

Jiarui, C., I. Friis, and C. M. Wilmot-Dear. 2003b. *Debregeasia*. in *Flora of China* vol. 5, ed. Flora of China Editorial Committee. St. Louis: Missouri Botanical Garden Press.

Jousselin, E., J.-Y. Rasplus, and F. Kjellberg. 2003. Convergence and coevolution in a mutualism: evidence from a molecular phylogeny of *Ficus*. *Evolution* 57: 1255–1269.

Judd, W. S., R. W. Sanders, and M. J. Donoghue. 1994. Angiosperm family pairs: preliminary phylogenetic analyses. *Harvard Papers in Botany* 5: 1–51.

Kearney, M. 2002. Fragmentary taxa, missing data, and ambiguity: mistaken assumptions and conclusions. *Systematic Biology* 51: 369–381.

Kochummen, K. M. and R. Go. 2000. *Moraceae*. Pp. 181–334 in *Tree Flora of Sabah and Sarawak* vol. 3, eds. E. Soepadmo and L. G. Saw. Kuala Lumpur: Ampang Press Sdn. Bhd.

Koek-Noorman, J., S. M. C. Topper, and B. J. H. ter Welle. 1984a. The systematic wood anatomy of the Moraceae (Urticales) I. Tribe Castilleae. *IAWA Bulletin* 5: 183–195.

Koek-Noorman, J., S. M. C. Topper, and B. J. H. ter Welle. 1984b. The systematic wood anatomy of the Moraceae (Urticales) II. Tribe Dorstenieae. *IAWA Bulletin* 5: 317–329.

Koek-Noorman, J., S. M. C. Topper, and B. J. H. ter Welle. 1984c. The systematic wood anatomy of the Moraceae (Urticales) III. Tribe Ficeae. *IAWA Bulletin* 5: 330–334.

Kojima, H. 2006. Association of viticiini (Coleoptera: Curculionidae: Cyclominae) with *Ficus* (Moraceae). *Coleopterists Bulletin* 60: 42–42.

Kokou, K., A. Atato, R. Bellefontaine, A. D. Kokutse, and G.Caballe. 2006. Diversity of dense dry forests in Togo (West Africa). *Revue D Ecologie-LA Terre et la Vie* 61: 225–246.

Larson, A. 1994. The comparison of morphological and molecular data in phylogenetic systematics. Pp. 371–390 in *Molecular ecology and evolution: Approaches and applications* eds., B. Schierwater, B. Streit, G. P. Wagner, and R. DeSalle. Basel, Switzerland: Birkhauser.

Lewis, P. O. 2001. A likelihood approach to estimating phylogeny from discrete morphological character data. *Systematic Biology* 50: 913–925.

Lockhart, P. J. and S. A. Cameron. 2001. Trees for bees. *Trends in Ecology & Evolution* 16: 84–88.

Maddison, D. R. and W. P. Maddison. 2005. MacClade version 4.08 for OS X. Sunderland: Sinauer Associates.

Marussich, W. A. and C. A. Machado. 2007. Host-specificity and coevolution among pollinating and nonpollinating New World fig wasps. *Molecular Ecology* 16: 1925–1946.

Mennega, A. M. W. and M. Lanzing-Vinkenborg. 1977. On the wood anatomy of the tribe "Olmedieae" (Moraceae) and the position of the genus *Olmedia* R. & P. *Acta Botanica Neerlandica* 26: 1–27.

Moretti, C., Y. Gaillard, P. Grenand, F. Bevalot, and J. M.Prevosto. 2006. Identification of 5-hydroxy-tryptamine (bufotenine) in takini (*Brosimum acutifolium* Huber subsp. *acutifolium* C. C. Berg, Moraceae), a shamanic potion used in the Guiana Plateau. *Journal of Ethnopharmacology* 106: 198–202.

Mucunguzi, P. 2007. Diversity and distribution of hemi-epiphytes and facultative herbaceous epiphytes in Kibale National Park, Uganda. *African Journal of Ecology* 45: 57–64 Suppl. 51.

Nair, P. K. K. and M. Sharma. 1965. Pollen morphological studies in Indian Urticales. *Botaniska Notiser* 118: 177–186.

Namdaung, U., N. Aroonrerk, S. Suksamrarn, K. Danwisetkanjana, J.Saenboonrueng, W.Arjchomphu, and A.Suksamrarn. 2006. Bioactive constituents of the root bark of *Artocarpus rigidus* subsp. *rigidus*. *Chemical & Pharmaceutical Bulletin* 54: 1433–1436.

Ngameni, B., M. Touaibia, R. Patnam, A. Belkaid, B. T. Ngadjui, B. Annabi, and R.Roy. 2006. Inhibition of MMP-2 secretion from brain tumor cells suggests chemopreventive properties of a furanocoumarin glycoside and of chalcones isolated from the twigs of *Dorstenia turbinata*. *Phytochemistry* 67: 2573–2579.

Niezgoda, C. J. and J. Nowaczyk. 1976. Palynological studies in *Acanthinophyllum, Clarisia, Sorocea*, and *Trophis* (Moraceae). *Pollen et Spores* 18: 513–522.

Nixon, K. C. 1999. The parsimony ratchet, a new method for rapid parsimony analysis. *Cladistics* 15: 407–414.

Nylander, J. A. A. 2004. MrModeltest v2. Uppsala University: Distributed by the author. Evolutionary Biology Centre.

Oginuma, K. and H. Tobe. 1995. Karyomorphology of some Moraceae and Cecropiaceae (Urticales). *Journal of Plant Research* 108: 313–326.

Oginuma, K., P. H. Raven, and H. Tobe. 1990. Karyomorphology and relationships of Celtidaceae and Ulmaceae (Urticales). *Botanical Magazine-Tokyo* 103: 113–131.

Pagel, M. 1999. The maximum likelihood approach to reconstructing ancestral character states of discrete characters on phylogenies. *Systematic Biology* 48: 612–622.

Pagel, M., A. Meade, and D. Barker. 2004. Bayesian estimation of ancestral character states on phylogenies. *Systematic Biology* 53: 673–684.

Palhares, D., J. E. D. Paula, L. A. R. Pereira, and C. E. D. Silveira. 2007. Comparative wood anatomy of stem, root and sylopodium of *Brosimum gaudichaudii* (Moraceae). *IAWA Journal* 28: 83–94.

Posada, D. and T. R. Buckley. 2004. Model selection and model averaging in phylogenetics: advantages of Akaike Information Criterion and Bayesian approaches over likelihood ratio tests. *Systematic Biology* 53: 793–808.

Punt, W. and E. Eetgerink. 1982. On the pollen morphology of some genera of the tribe Moreae (Moraceae). *Grana* 21: 15–19.

Punt, W. and M. Malotaux. 1984. Cannabaceae, Moraceae, and Urticaceae. *Review of Palaeobotany and Palynology* 42: 23–44.

Quicke, D. L. J., J. Taylor, and A. Purvis. 2001. Changing the landscape: a new strategy for estimating large phylogenies. *Systematic Biology* 50: 60–66.

Rambaut, A. and A. J. Drummond. 2007. Tracer v1.4, Available from http://beast.bio.ed.ac.uk/Tracer.

Rastogi, S., D. K. Kulshreshtha, and A. K. S. Rawat. 2006. *Streblus asper* Lour. (Shakhotaka): a review of its chemical, pharmacological and ethnomedicinal properties. *Evidence-Based Complementary and Alternative Medicine* 3: 217–222.

Rodriguez, F., J. F. Oliver, A. Marin, and J. R. Medina. 1990. The general stochastic model of nucleotide substitution. *Journal of Theoretical Biology* 142: 485–501.

Rohwer, J. G. 1993. *Moraceae.* Pp. 438–453 in *The families and genera of vascular plants* vol. 2, ed. K. Kubitzki. Heidelberg: Springer-Verlag.

Ronquist, F. and J. P. Huelsenbeck. 2003. MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics (Oxford, England)* 19: 1572–1574.

Rønsted, N., G. Salvo, and V. Savolainen. 2007. Biogeographical and phylogenetic origins of African fig species (*Ficus* section *Galoglychia*). *Molecular Phylogenetics and Evolution* 43: 190–201.

Sakai, S. 2001. Thrips pollination of androdioecious *Castilla elastica* (Moraceae) in a seasonal tropical rainforest. *American Journal of Botany* 88: 1527–1534.

Sakai, S., M. Kato, and H. Nagamasu. 2000. *Artocarpus (Moraceae)* - gall midge pollination mutualism mediated by a male-flower parasitic fungus. *American Journal of Botany* 87: 440–445.

Scotland, R. W., R. G. Olmstead, and J. R. Bennett. 2003. Phylogeny reconstruction: the role of morphology. *Systematic Biology* 52: 539–548.

Sikes, D. S. and P. O. Lewis. 2001. beta software, version 1. PAUPRat: PAUP* implementation of the parsimony ratchet. Storrs, Connecticut: Department of Ecology and Evolutionary Biology, University of Connecticut, distributed by the authors.

Small, E. 1997. *Cannabaceae.* Pp. 616 in *Flora of North America north of Mexico* vol. 3, ed. Flora of North America Editorial Committee. New York: Oxford University Press.

Sorenson, M. D. and E. A. Franzosa. 2007. TreeRot, version 3. Boston: Boston University.

Ssegawa, P. and D. N. Nkuutu. 2006. Diversity of vascular plants on Ssese islands in Lake Victoria, central Uganda. *African Journal of Ecology* 44: 22–29.

Stevens, P. F. 2001 onwards. Angiosperm Phylogeny Website. *Version 7* May 2007.

Swofford, D. L. 2002. PAUP* Phylogenetic Analysis Using Parsimony (*and other methods) version 4. Sunderland: Sinauer Associates.

Sytsma, K. J., J. Morawetz, J. C. Pires, M. Nepokroeff, E. Conti, M. Zjhra, J. C. Hall, and M. W. Chase. 2002. Urticalean rosids: circumscription, rosid ancestry, and phylogenetics based on *rbcL, trnL-F,* and *ndhF* sequences. *American Journal of Botany* 89: 1531–1546.

Tehler, A., D. P. Little, and J. S. Farris. 2003. The full-length phylogenetic tree from 1551 ribosomal sequences of chitinous fungi, Fungi*. *Mycological Research* 107: 901–916.

Templeton, A. R. 1983. Phylogenetic inference from restriction endonuclease cleavage site maps with particular reference to the evolution of humans and the apes. *Evolution* 37: 221–244.

Ter Welle, B. J. H., J. Koek-Noorman, and S. M. C. Topper. 1986a. The systematic wood anatomy of the Moraceae (Urticales) IV. Genera of the tribe Moreae with Urticaceous stamens. *IAWA Bulletin* 7: 91–128.

Ter Welle, B. J. H., J. Koek-Noorman, and S. M. C. Topper. 1986b. The systematic wood anatomy of the Moraceae (Urticales) V. Genera of the tribe Moreae without urticaceous stamens. *IAWA Bulletin* 7: 175–193.

Ter Welle, B. J. H., K. Bonsen, and P. Detienne. 1992. *20. Ulmaceae 21. Moraceae 22. Cecropiaceae 23. Urticaceae.* Pp. 141–191 in *Flora of the Guianas* vol. 20–23. 26., ed. A. R. A. G.-v. Rijn. Koenigstein: Koeltz Scientific Books.

Tobler, M., E. Honorio, J. Janovec, and C. Reynel. 2007. Implications of collection patterns of botanical specimens on their usefulness for conservation planning: an example of two neotropical plant families (Moraceae and Myristicaceae) in Peru. *Biodiversity and Conservation* 16: 659–677.

Trécul, A. 1847. Memoire sur la famille des Artocarpees. *Annales des Sciences Naturelles* 3: 38–157.

Ufkes, L. L., and G. W. Grams. 2007. The isolation and identification of volatile insect repellents from the fruit of the Osage orange (*Maclura pomifera*). *Journal of Essential Oil Research* 19: 167–170.

Weiblen, G. D. 2004. Correlated evolution in fig pollination. *Systematic Biology* 53: 128–139.

Weiblen, G. D., R. K. Oyama, and M. J. Donoghue. 2000. Phylogenetic analysis of dioecy in monocotyledons. *American Naturalist* 155: 46–58.

Wiens, J. J. 1998. Does adding characters with missing data increase or decrease phylogenetic accuracy? *Systematic Biology* 47: 625–640.

Wiens, J. J. 2004. The role of morphological data in phylogeny reconstruction. *Systematic Biology* 53: 653–661.

Wiens, J. J. 2006. Missing data and the design of phylogenetic analyses. *Journal of Biomedical Informatics* 29: 34–42.

Wilkinson, M. 1995. Coping with abundant missing entries in phylogenetic inference using parsimony. *Systematic Biology* 44: 501–514.

Wortley, A. H., and R. W. Scotland. 2006. The effect of combining molecular and morphological data in published phylogenetic analyses. *Systematic Biology* 55: 677–685.

Wunderlin, R. P. 1997. *Moraceae.* Pp. 616 in *Flora of North America north of Mexico* vol. 3, ed. Flora of North America Editorial Committee. New York: Oxford University Press.

Yoder, A. D., J. A. Irwin, and B. A. Payseur. 2001. Failure of the ILD to determine data combinability for slow loris phylogeny. *Systematic Biology* 50: 408–424.

Zerega, N. J. C. 2003. *Molecular phylogenetic and genome-wide analyses of Artocarpus (Moraceae): Implications for the systematics, origins, human-mediated dispersal, and conservation of breadfruit. Ph.D. dissertation*, New York University, New York.

Zerega, N. J. C., L. A. Mound, and G. D. Weiblen. 2004. Pollination in the New Guinea endemic *Antiaropsis decipiens* (Moraceae) is mediated by a new species of thrips, *Thrips antiaropsidis* spec. nov. (Thysanoptera: Thripidae). *International Journal of Plant Sciences* 165: 1017–1026.

Zerega, N. J. C., W. L. Clement, S. L. Datwyler, and G. D. Weiblen. 2005. Biogeography and divergence times in the mulberry family (Moraceae). *Molecular Phylogenetics and Evolution* 37: 402–416.

Zhao, W. G., Z. H. Zhou, X. X. Miao, Y. Zhang, S. B.Wang, J. H.Huang, H.Xiang, Y. L.Pan, and Y. P.Huang. 2007. A comparison of genetic variation among wild and cultivated *Morus* species (Moraceae: *Morus*) as revealed by ISSR and SSR markers. *Biodiversity and Conservation* 16: 275–290.

Zhekun, Z. and M. G. Gilbert. 2003. *Moraceae.* in *Flora of China* vol. 5, ed. Flora of China Editorial Committee. St. Louis: Missouri Botanical Garden Press.

Zomlefer, W. B. 1994. *Guide to flowering plant families*. Chapel Hill: University of North Carolina Press.

APPENDIX 1. Specimens examined for the morphological study of Moraceae. Herbarium abbreviations follow *Index Herbariorum* (Holmgren et al. 1990). For those species not listed, data was collected exclusively from the literature.

MORACEAE: *Antiaris toxicaria* Lesch-*G. D. Weiblen 1115*, Papua New Guinea (MIN); *G. D. Weiblen et al. 2690*, Papua New Guinea (MIN); *G. D. Weiblen et al. 2695*, Papua New Guinea (MIN); *McDonald 3758*, New Guinea (A); *C. C. H. Jongkind, C. M. J. Nieuwenuiss 1347*, Ghana (MO), *F. A. McClure*, China (MO); *Hall & Lock 46755*, Ghana (MO); *L. Gautier et al. LG4222*, Madagascar (MO); *G. J. Steck 203*, Togo (MO); *S. Kisseadoo 359*, Ghana (MO); *R. E. Gereau et al. 6487*, Tanzania (MO). **Antiaropsis decipiens** K. Schum-*G. D. Weiblen, B. Andreas 949*, Papua New Guinea (MIN); *N. Zerega 274*, Papua New Guinea (MIN); *G. D. Weiblen 1707*, Papua New

Guinea (MIN); *B. Andreas 1233,* Papua New Guinea (MIN); *G. D. Weiblen 1706,* Papua New Guinea (MIN); *N. Zerega 278,* Papua New Guinea (MIN), *G. D. Weiblen et al. 1865,* Papua New Guinea (MIN). **Artocarpus altilis** (Parkinson) Fosberg-*G. D. Weiblen 1104,* cult., Australia (MIN). **Artocarpus heterophyllus** Lam.-*G. D. Weiblen 1105,* cult., Australia (MIN). **Artocarpus vrieseanus** Miq.-*M. Janda Y058,* Papua New Guinea (MIN); *M. Janda Y060,* Papua New Guinea (MIN); *G. D. Weiblen 1229,* Papua New Guinea (MIN); *G. D. Weiblen 1845,* Papua New Guinea (MIN); *G. D. Weiblen 1116,* Papua New Guinea (MIN); *G. D. Weiblen 1843,* Papua New Guinea (MIN). **Bagassa guianensis** Aubl.-*G. D. Weiblen 1677,* French Guiana (MIN); *G. D. Weiblen 1663,* French Guiana (MIN); *Jansen-Jacobs 1200,* Guyana (F); *Zarucchi 2667,* Brazil (A); *Berg P19846,* Brazil (F); *Capucho 510,* Brazil (F); *Oldeman B-642,* French Guiana (P); *Oldeman B-628,* French Guiana (P); *J. Petrov 100,* French Guiana (P). **Batocarpus amazonicus** (Ducke) Fosberg-*G. D. Weiblen 1682,* French Guiana (MIN); *Vasquez 10667,* Peru (A). **Batocarpus costaricensis** Standl. & L. O. Williams-*G. D. Weiblen 1463,* Peru (MIN); *Herrera 4313,* Costa Rica (F); *Kernan 608,* Costa Rica (F); *Poveda 1092,* Costa Rica (F). **Bleekrodea madagascariensis** Blume-*Boivin 2228,* Madagascar (P); *A. J. M. Leeuwenberg 13945,* Madagascar (P). **Brosimum alicastrum** Sw.-*W. Robleto, D. Garcia 26A,* Nicaragua (MIN); *W. Robleto 435,* Nicaragua (MIN); *S. W. Brewer 809,* Belize (MIN); *W. D. Stevens, M. Araquistain 13250,* Nicaragua (MIN); *G. Davidse et al. 30524,* Nicaragua (MIN); *P. P. Moreno 23545,* Nicaragua (MIN); *P. Moreno 839,* Nicaragua (MIN); *G. D. Weiblen 1432,* Panama (MIN); *W. D. Stevens, M. Araquistain 13239,* Nicaragua (MIN); *Liesner 2260,* South America (F). **Brosimum guianense** (Aubl.) Huber-*C. Kernan, P. Phillips 964,* Costa Rica (MIN); *G. D. Weiblen 1476,* Peru (MIN); *E. T. Neto 891,* South America (F); *Smith, Shuhler 410,* South America (F); *G. D. Weiblen 1445,* Panama (MIN). **Brosimum lactescens** (S. Moore) C. C. Berg-*N. Zamora et al. 1826,* Costa Rica (MIN); *G. D. Weiblen 1458,* Peru (MIN); *G. D. Weiblen 1513,* Brazil (MIN); *R. Vasquez, N. Jaramillo 20258,* Peru (MIN); *G. D. Weiblen 1473,* Peru (MIN); *G. D. Weiblen 1467,* Peru (MIN). **Brosimum rubescens** Taub.-*G. D. Weiblen 1516,* Brazil (MIN); *G. D. Weiblen 1665,* French Guiana (MIN). **Brosimum utile** (H. B. & K.) Pittier-*G. D. Weiblen 1440,* Panama (MIN). **Broussonetia papyrifera** Vent.-*E. L. Morris,* USA (MIN); *H.L. Fisher* USA (MIN); *O. Lakela 18334,* USA (MIN); *J. A. Harris 1862,* USA (MIN); *B. C. Tharp 51-105,* USA (MIN); *R. F. Britt 3108,* USA (MIN); *W. T. Gillis 4683,* Japan (MIN). **Castilla elastica** Sessé-*R. B. Harvey,* USA, (MIN), *W. Robleto 355,* Nicaragua (MIN); *M. Nee 28351,* Nicaragua (MIN); *G. D. Weiblen 1406,* Costa Rica (MIN); *M. Rejmánek 1116,* Belize (MIN); *G. D. Weiblen 1415,* Costa Rica (MIN); *G. D. Weiblen 1433,* Panama (MIN); *J. A. Stevenson 2490,* Puerto Rico (F); *Estrada 519,* Costa Rica (F); *Bente,* Costa Rica (F); *Gentry 9661,* Ecuador (A); *R. L. Wilbur 34905,* Costa Rica (MO); *E. Martínez 18412,* Mexico (MO); *E. Martínez 11833,* Mexico (MO); *G. W. Frankie 128a,* Costa Rica (MO); *E. Martínez 17657,* Mexico (MO); *P. Gentle 2436,* Honduras (MO); *E. Martínez S., D. Alvarez, C. Galindo 30729,* Mexico (MO); *T. B. Croat 5420,* Panama (MO). **Castilla ulei** Warb-*G. D. Weiblen 1456,* Peru (MIN); *G. D. Weiblen 1499,* Peru (MIN); *C. C. Berg et al. BG603,* Brazil (MO); *P. Nuñez 5864,* Peru (MO); *P. Nuñez et al. 9998,* Peru (MO); *T. Killeen 8218,* Bolivia (MO); *A. Ducke 555,* Brazil (MO); *Flores and Tello 1896,* Peru (MO). **Clarisia biflora** Ruiz & Pav.- *P. Harmon 163,* Costa Rica (MIN); *G. D. Weiblen 1416,* Costa Rica (MIN); *W. D. Stevens, R. Riviere 20940,* Nicaragua (MIN); *M. Nee, S. Vega 27848,* Nicaragua (MIN); *G. D. Weiblen 1465,* Peru (MIN); *G. D. Weiblen 1460,* Peru (MIN); *Huber 11753,* Costa Rica (F); *Hernandez 241,* Costa Rica (F). **Clarisia ilicifolia** (Spreng.) Lanj. & Rossberg-*K562,* Brazil (SP); *Lowrie 487,* Brazil (A). **Dorstenia bahiensis** Klotzsch-*G. D. Weiblen 1101,* cult., Australia (MIN). **Dorstenia choconiana** S.Watson-*G. D. Weiblen 1417,* Costa Rica (MIN); *G. Davidse et al. 34415,* Honduras (MIN); *W. D. Stevens 23412,* Nicaragua (MIN); *J. C. Sandino 3319,* Nicaragua (MIN). **Fatoua pilosa** Gandich.-*UPNG6112,* Papua New Guinea (L.); *Vincent and Hickey 8333,* USA (MIN). **Ficus asperula** Bur.-*G. D. Weiblen 1217,* New Caledonia (MIN). **Ficus copiosa** Steud.-*G. D. Weiblen 2139,* Papua New Guinea (MIN); *M. Janda Y038,* Papua New Guinea (MIN); *B. Isua 1779,* Papua New Guinea (MIN); *G. D. Weiblen 1720,* Papua New Guinea (MIN); *G. D. Weiblen 2085,* Papua New Guinea (MIN); *G. D. Weiblen 1164,* Papua New Guinea (MIN); *G. D. Weiblen G057,* Papua New Guinea (MIN). **Ficus edelfeltii** King-*G. D. Weiblen, B. Isua B206,* Papua New Guinea (MIN); *G. D. Weiblen 821,* Papua New Guinea (MIN); *G. D. Weiblen, B. Isua 951,* Papua New Guinea (MIN); *D. Wright T5657,* Papua New Guinea (MIN). **Ficus habrophylla** G. Bennett & Seem.-*G. D. Weiblen 1226,* New Caledonia (MIN); *G. D. Weiblen 1224,* New Caledonia (MIN); *G. D. Weiblen 1225,* New Caledonia (MIN). **Ficus insipida** Willd.-*J. Ruiz et al.* Peru (MIN); *R. Vasquez, R. Apanu 19064,* Peru (MIN); *G. D. Weiblen V08,* Venezuela (MIN); *G. D. Weiblen 1455,* Peru (MIN); *G. D. Weiblen 1675,* French Guiana (MIN); *G. D. Weiblen 1423,* Costa Rica (MIN); *G. D. Weiblen 1434,* Panama (MIN); *S. W. Brewer 396,* Belize (MIN). **Ficus racemosa** L.-*G. D. Weiblen 940,* Australia (MIN); *K. R. Miller 125,* Java (MIN); *Purnomo,* Java (MIN). **Ficus** *variegata* Blume-*G. D. Weiblen et al. 1850,* Papua New Guinea (MIN); *G. D. Weiblen, B. Dumont 1784,* Papua New Guinea (MIN); *G. D. Weiblen 1730,* Papua New Guinea (MIN); *G. D. Weiblen 2069,* Papua New Guinea (MIN); *G. D. Weiblen et al. 892,* Borneo, Indonesia (MIN); *Purnomo,* Java (MIN); *Purnomo 75,* Java (MIN); *G. D. Weiblen 457,* Papua New Guinea (MIN); *G. D. Weiblen, J. Lai 1081,* Singapore (MIN). *G. D. Weiblen, B. Isua B165,* Papua New Guinea (MIN); *R. D. Harrison, L. Co RDH622,* Philippines (MIN); *R. D. Harrison, L. Co RDH592,* Philippines (MIN); *G. D. Weiblen 680,* Australia (MIN). **Ficus virens** Aiton-*G. D. Weiblen, J. Lai 1079,* Singapore (MIN); *D. Wright 5093,* Papua New Guinea (MIN); *G. D. Weiblen 2030,* Papua New Guinea (MIN); *G. D. Weiblen 1162,* Papua New Guinea (MIN); *Purnomo,* Java (MIN); *C. Abair,* USA (MIN); *G. D. Weiblen 555,* Papua New Guinea (MIN). **Ficus wassa** Roxb.-*G. D. Weiblen 1802,* Papua New Guinea (MIN); *G. D. Weiblen et al. 992,* Papua New Guinea (MIN); *G. D. Weiblen, B. Isua B155,* Papua New Guinea (MIN); *G. D. Weiblen TP088,* Papua New Guinea (MIN); *G. D. Weiblen 523,* Papua New Guinea (MIN); *G. D. Weiblen, R. Devo B68,* Papua New Guinea (MIN); *G. D. Weiblen 2067,* Papua New Guinea (MIN); *G. D. Weiblen 1151,* Papua New Guinea (MIN); *G. D. Weiblen 2009,* Papua New Guinea (MIN); *G. D. Weiblen 565,* Papua New Guinea (MIN); *G. D. Weiblen, U. Koil G044,* Papua New Guinea (MIN); *G. D. Weiblen G055,* Papua New Guinea (MIN); *G. D. Weiblen G051,* New Guinea (A). **Helianthostylis sprucei** Baill.-*G. D. Weiblen 1523,* Brazil (MIN). **Helicostylis pedunculata** Benoist-*G. D. Weiblen 1680,* French Guiana (MIN); *G. T. Prance, T. D. Pennington 1950,* Brazil (MO); *G. T. Prance et al. 25723,* Brazil (MO); *A. Gentry 49046,* Brazil (MO). **Helicostylis tomentosa** (Poepp. & Endl.) Rusby-*G. D. Weiblen 1475,* Peru (MIN); *Kileen 4383,* Bolivia (F); *P51834,* Brazil (SP); *Daly 4295,* Brazil (A); *Boom 4313,* Brazil (A); *Gentry 70409,* Bolivia (F); *I. Goldstein, L. Salas 290,* Venezuela (MO); *M. Aulestia 312,* Ecuador (MO); *S. Mori and B. Boom 15322,* French Guiana (MO); *N. A. Rosa and H. Vilar 2751,* Brazil (MO); *W. Palacios 3199,* Ecuador (MO); *G. Aymard et al. 4158,* Venezuela (MO). **Maclura amboinensis** Blume-*G. D. Weiblen 1109,* New Guinea (MIN); *R. Geesink et al. 8247,* Thailand (P); *C. F. van Beusekom, C. Phenklai 2354,* Thailand (P). **Maclura pomifera** (Raf.) C. K. Schneid.-*J. A. Harris 20540,* USA (MIN); *L. M. Umbach,* USA (MIN); *H. E. Hasse,* USA (MIN); *Hellersleat 3371,* USA (MIN); *J. K. Small,* USA (MIN); *R. L. McGregor E377,* USA (MIN); *S. Cotter 3199B,* USA (MIN); *B. Windler FC189,* USA (MIN); *E. L. Newcomb,* USA (MIN); *W. H. Evans,* USA (MIN). **Maclura tricuspidata** Carrière-*A. Chevalier 32231,* Vietnam (P); *M. de Montignt,* China (P); *Y.Z. Sun 97,* China (P); *M. de Montignt,* China (P). **Maquira costaricana** (Standl.) C. C. Berg-*P. P. Moreno 15123,* Nicaragua (MIN); *P. P. Moreno 15068,* Nicaragua (MIN); *C. Kernam, P. Phillips 1094,* Costa Rica (MIN); *P. P. Moreno 15035,* Nicaragua (MIN); *G. D. Weiblen 1402,* Costa Rica (MIN); *G. D. Weiblen 1408,* Costa Rica (MIN); *W. Stevens 9028,* Nicaragua (MIN); *P. P. Moreno 15043,* Nicaragua (MIN); *T. B. Croat 15248,* Panama (MO); *W. Palacios, M. Tirado 11146,* Ecuador (MO); *D. Smith 191,* Costa Rica (MO); *G. McPherson 8712,* Panama (MO); *J. Espina 1787,* Colombia (MO). **Mesogyne insignis** Engl.-*Schlieben 3133,* Tanzania (A); *A. Ntemi Sallu 474,* Tanzania (MO); *M. A. Mwangoka 161,* Tanzania (MO); *I. Rajabu Hizza 201,* Tanzania (MO); *M. A. Mwangoka 971,* Tanzania (MO); *J. & J. Lovett 574,* Tanzania (MO). **Milicia excelsa** (Welw.) C. C. Berg.-*Madoux 90,* Congo (A); *Lebrun 1452,* Congo (A); *A. Chevalier 23169,* Benin (P); *R. P. Tisserant,* Central African Republic (P); *A. Chevalier 7583,* Chad (P); *J. Lebrum 152,* Africa (P); *J. Louis 13803,* Congo (P); *J. Leonard 1049,* Congo (P); *M. Reekmans 6434,* Burundi (P); *H. de Foresia 1063,* Congo (P). **Morus alba** L.-*W. R. Smith 29281,* USA (MIN); *S. D. Swanson 785,* USA (MIN); *S. Galatowitsch 735,* USA (MIN); *J. W. Moore 20503,* USA (MIN); *H. W. Moore, E. Hsi,* USA (MIN); *J. B. Moyle,* USA (MIN); *R. D. Dorn 31,* USA (MIN); *J. W. Moore 22509,* USA (MIN); *J. W. Moore 20569,* USA (MIN); *J. W. Moore 26697,* USA (MIN); *J. W. Moore 26648,* USA (MIN); *J. W. Moore 25979,* USA (MIN); *J. W. Moore et al. 15704,* USA (MIN); *J. W. Moore 24343,* USA (MIN); *T. S. Cooperrider 1006,* USA (MIN); *D. N. Vixie 699,* USA (MIN); *S. W. Leonard, A. E. Radford 1131,* USA (MIN); *M. Eyhorn 16,* USA (MIN); *J. E. Bodin,* USA (MIN); *A. Harrison 18,* USA (MIN); *J. McCaskill 343,* USA (MIN); *J. K. Small,* USA (MIN); *R. C. Bright 60-197,* USA (MIN); *B. Shimek,* USA (MIN); *G. D. Weiblen 1173,* USA (MIN). **Morus nigra** L.-*L. M. Umbach,* USA (MIN); *G. W. Stevens 1896,* USA (MIN); *G. W. Stevens 2389,* USA (MIN); *J. E. Tilden,* USA (MIN). **Naucleopsis caloneura** (Huber) Ducke-*G. D. Weiblen 1517,* Brazil (MIN); *Daly 1411,* Brazil (A); *C. A. Cid, B. W. Nelson 2872,* Amazon (MO); *C. A. Cid Ferreira 9506,* Amazon (MO); *D. C. Daly et al. 1179,* Brazil (MO); *A. Rudas et al. 5195,* Colombia (MO); *G. T. Prance et al. 25386,* Brazil (MO); *L. Painter 62,* Bolivia (MO); *D. C. Daly et al. 1411,* Brazil (MO). **Naucleopsis guianensis** (Mildbr.) C. C. Berg-*G. D. Weiblen 1683,* French Guiana (MIN); *S. Mori et al.14901,* French Guiana (MO); *B. Boswezen 6299,* Surinam (MO); *S. Mori, A. Bolten 8405,* Surinam (MO); *B. Maguire, D. B. Fanshawe 22947,* Surinam (MO). **Naucleopsis krukovii** (Standl.) C. C. Berg-*G. D. Weiblen 1484,* Peru (MIN); *G. D. Weiblen 1498,* Peru (MIN); *C. Cid et al. 8362,* Amazon (MO); *B. A. Krukoff 8341,* Brazil (MO); *D. Neill*

et al. 7296, Ecuador (MO); *A. Rudas et al. 3324*, Colombia (MO); *M. Aulestia 2590*, Ecuador (MO); *B. W. de Albuquerque et al. 1292*, Brazil (MO); *R. Vásquez, N. Jaramillo 13090*, Peru (MO). **Naucleopsis naga** Pittier-*INBio 176*, Costa Rica (MIN); *G. D. Weiblen 1414*, Costa Rica (MIN); *G. D. Weiblen 1404*, Costa Rica (MIN); *Aguillar 5025*, Costa Rica (F); *Boyle 1248*, Costa Rica (F); *C. Davidson, J. Donahue 8859*, Costa Rica (MO); *R. Callejas et al. 6645*, Colombia (MO); *G. Herrera, A. Chacón 2674*, Costa Rica (MO); *R. Aguillar 5025*, Costa Rica (MO). **Naucleopsis ternstroemiiflora** (Mildbr.) C. C. Berg-*G. D. Weiblen 1518*, Brazil (MIN); *G. T. Prance et al. P26406*, Brazil (MO); *G. Vieira et al. 273*, Amazon (MO); *W. Thomas et al. 4119*, Brazil (MO); *G. Vieira et al. 311*, Amazon (MO); *C. C. Berg et al. P17624*, Brazil (MO). **Naucleopsis ulei** (Warb.) Ducke-*T. B. Croat 20753*, Peru (MIN); *G. D. Weiblen 1509*, Brazil (MIN); *D. N. Smith 12946*, Bolivia (MO); *M. Tirado et al. 450*, Ecuador (MO); *N. Pitman, G. Romero 342*, Ecuador (MO); *W. Palacios 2839*, Ecuador (MO); *M. Aulestia, T. Ahue 2939*, Ecuador (MO); *E. Ancuash Atsut 1161*, Peru (MO); *D. Cárdenas 1032*, Colombia (MO). **Perebea angustifolia** (Poepp. & Endl.) C. C. Berg-*G. D. Weiblen 1403*, Costa Rica (MIN); *R. H. Warner 305*, Colombia (MO); *O. Phillips et al. 316*, Peru (MO); *M. Grayum et al. 8015*, Costa Rica (MO); *J. A. Duke, T. S. Elias 13766*, Panama (MO); *S. Mori, J. Kallunki 5522*, Panama (MO); *G. S. Hartshorn 821*, Costa Rica (MO). **Perebea longepedunculata** C. C. Berg-*G. D. Weiblen 1477*, Peru (MIN); *R. Vásquez, N. Jaramillo 10097*, Peru (MO); *J. Revilla 2371*, Peru (MO); *R. Vásquez, N. Jaramillo 1112a*, Peru (MO); *L. Encarnación 26236*, Peru (MO). **Perebea humilis** C. C. Berg-*G. D. Weiblen 1468*, Peru (MIN); *R. Vásquez, N. Jaramillo 12880*, Peru (MO); *W. Palacios, D. Neill 617*, Ecuador (MO); *A. Gentry et al. 22174*, Peru (MO). **Perebea rubra** (Trécul) C. C. Berg-*G. D. Weiblen 1685*, French Guiana (MIN); *D. C. Daly et al. 4146*, Brazil (MO); *F. Forero, B. L. Wrigley 7038*, Brazil (MO); *S. Mori, J. Pipoly 15546*, French Guiana (MO); *J. Pipoly et al. 13372*, Peru (MO). **Perebea xanthochyma** Karst.-*G. D. Weiblen 1444*, Panama (MIN); *G. McPherson 12179*, Panama (MO); *V. Huashikat 1901*, Peru (MO), *D. Neill et al. 8357*, Ecuador (MO); *C. E. Cerón, N. Gallo 5123*, Ecuador (MO). **Poulsenia armata** (Miq.) Standl.-*G. D. Weiblen 1428*, Panama (MIN); *G. D. Weiblen 1441*, Panama (MIN); *D. N. Smith, V. García 13831*, Bolivia (MIN); *G. D. Weiblen 1487*, Peru (MIN); *D. N. Smith et al. 13716*, Bolivia (MIN); *Calderon 3007*, Mexico (A); *Kernam 375*, Costa Rica (F); *Rivera 1903*, Costa Rica (F); *M. Nee 37250*, Bolivia (MO); *J. Schunke V. 6232*, Peru (MO); *D. N. Smith et al. 13567*, Bolivia (MO); *T. Killeen et al. 3471*, Bolivia (MO); *G. Davidse et al. 20356*, Mexico (MO); *G. R. Proctor 35958*, Belize (MO); *H. Hernández G. 266*, Mexico (MO); *S .S. Colín, F. C. Seba 618*, Mexico (MO). **Prainea papuana** Becc.-*G. D. Weiblen 1809*, Papua New Guinea (MIN); *G. D. Weiblen 1117*, Papua New Guinea (MIN). **Pseudolmedia laevigata** Trécul-*C. Reynel et al. 5270*, Peru (MIN); *G. D. Weiblen 1461*, Peru (MIN); *Croat 20368*, Peru (A); *R. Rudea 924*, Bolivia (MO); *S. Defler 326*, Colombia (MO); *A. Gentry 9379*, Colombia (MO); *C. Aulestia et al. 298*, Ecuador (MO); *W. Palacios et al. 7775*, Ecuador (MO); *S. Defler 331*, Colombia (MO); *S. McDaniel, M. Rimachi Y. 16949*, Peru (MO); *M. Rimachi Y. 8574*, Peru (MO); *W. Palacios et al. 8092*, Ecuador (MO). **Pseudolmedia laevis** (Ruiz & Pav.) J. F. Macbr.-*D. Neill, R. Quevedo 9445*, Bolivia (MIN); *G. D. Weiblen 1459*, Peru (MIN); *G. D. Weiblen 1502*, Brazil (MIN); *D. Neill, R. Quevedo 9382*, Bolivia (MO); *W. Palacios 3285*, Ecuador (MO); *G. T. Prance et al. P26438*, Brazil (MO); *A. Rodrigues, J. Surubí 567*, Bolivia (MO); *A. Rodrigues, J. Surubí 564*, Bolivia (MO); *J. C. Solomon 6367*, Bolivia (MO); *W. Palacios et al. 3437*, Ecuador (MO); *V. Huashikat 881*, Peru (MO); *M. Grayum et al. 4990*, Costa Rica (MO). **Pseudolmedia macrophylla** Trécul-*C. Reynel et al. 5271*, Peru (MIN)*; G. D. Weiblen 1472*, Peru (MIN); *A. Dik 1254*, Ecuador (MO); *L. Arroyo et al. 283*, Bolivia (MO); *T. Killeen 4433*, Bolivia (MO); *M. G. Silva, C. Rosário 4782*, Amazon (MO); *W. W. Thomas et al. 6493, Brazil (MO)*; *V. Huashicat 516*, Peru (MO)*; V. Huashikat 1373*, Peru (MO). **Pseudolmedia spuria** (Sw.) Griseb.-*C. Kernan, P. Phillips 974*, Costa Rica (MIN); *P. P. Moreno 23662*, Nicaragua (MIN); *P. P. Moreno 23741*, Nicaragua (MIN); *P. P. Moreno 23987*, Nicaragua (MIN); *G. D. Weiblen 1427*, Costa Rica (MIN); *Bohlke 53*, Costa Rica (F); *Gentry 78535*, Costa Rica (F); *H. Hernández G. 1087*, Mexico (MO); *J. C. Sandino 4925*, Nicaragua (MO); *B. K. Holst 5786*, Belize (MO); *K. Thomsen 958*, Costa Rica (MO); *P. Gentle 5213*, Honduras (MO); *G. Herrera 1744*, Costa Rica (MO); *C. Whitefoord 10203*, Belize (MO). **Sorocea affinis** Hemsl.-*R. J. Seibert 464*, Panama (MIN); *Salick 7933*, Nicaragua (MIN); *R. J. Seibert 566*, Panama (MIN); *G. D. Weiblen 1437*, Panama (MIN); *R. Fonnegra et al.* Colombia (MIN). **Sorocea bonplandii** (Baill.) W. Burger, Lanj. & Boer-*G. D. Weiblen 1186*, Brazil (MIN); *G. D. Weiblen 1187*, Brazil (MIN); *C. Reynel et al. 5216*, Peru (MIN). **Sorocea briquetii** J. F. Macbr.-*G. D. Weiblen 1457*, Peru (MIN). **Sorocea pubivena** Hemsl.-*W. D. Stevens et al. 24898*, Costa Rica (MIN); *P. P. Moreno 26667*, Nicaragua (MIN); *Salick 7817*, Nicaragua (MIN); *W. D. Stevens 23444*, Nicaragua (MIN); *W. D. Stevens et al. 24991*, Costa Rica (MIN); *G. D. Weiblen 1409*, Costa Rica (MIN); *C. Kernan, P. Phillips 1093*, Costa Rica (MIN); *N. Jaramillo, D. Chamik 805*, Peru (MIN); *Wilbur 70044*, Costa Rica (F). **Sparattosyce dioica** Bur.-*G. D. Weiblen 1223*, New Caledonia (MIN); *McKee 3914*, New Caledonia (A); *Stauffer 5714*, New Caledonia (A); *G. McPherson 4190*, New Caledonia (MO); *G. McPherson 3153*, New Caledonia (MO); *G. McPherson 5826*, New Caledonia (MO); *A. Gentry et al. 34582*, New Caledonia (MO); *G. McPherson 2445*, New Caledonia (MO); *G. McPherson 3232*, New Caledonia (MO). **Streblus elongatus** (Miq.) Corner-*G. D. Weiblen 2002*, Singapore (MIN). **Streblus glaber** (Merr.) Corner-*G. D. Weiblen 2130*, Papua New Guinea (MIN); *G. D. Weiblen 1169*, Australia (MIN); *G. D. Weiblen 1235*, Papua New Guinea (MIN). **Streblus smithii** (Cheeseman) Corner-*G. D. Weiblen 1172*, cult., Sydney, Australia (MIN). **Trophis involucrata** W. C. Burger-*G. D. Weiblen 1405*, Costa Rica (MIN). **Trophis racemosa** (L.) Urb.-*M. Nee, S. Vega 28752*, Nicaragua (MIN); *P. P. Moreno 15797*, Nicaragua (MIN); *W. Robleto 1657*, Nicaragua (MIN); *A. Gentry et al. 43994*, Nicaragua (MIN); *P. P. Moreno 21136*, Nicaragua (MIN); *W. D. Stevens 9945*, Nicaragua (MIN); *J. C. Sandino, N. Reyes 3598*, Nicaragua (MIN); *W. D. Stevens, A. Grijalva 14752*, Nicaragua (MIN); *E. Puleston 6823*, Guatemala (MIN); *J. G. Ortega 7493*, Mexico (MIN); *W. Nee et al. 27961*, Nicaragua (MIN); *G. D. Weiblen 1400*, Costa Rica (MIN); *G. D. Weiblen 1401*, Costa Rica (MIN); *P. P. Moreno 24840*, Nicaragua (MIN); *P. P. Moreno 17195*, Nicaragua (MIN); *Lepiz 518*, Costa Rica (F); *Arrigo 762*, Belize (A); *Foster 988*, Panama (A); *Schatz 1036*, Costa Rica (F). **Trophis scandens** (Lour.) Hook. & Arn.-*J. H. Camfield*, Australia (MIN); *G. D. Weiblen 1221*, New Caledonia (MIN); *Harman 8006* (MIN); *B. Balansa 742*, Vietnam (P); *5845*, Vietnam (P); *R. Geesink et al. 8147*, Thailand (P). **Trymatococcus amazonicus** Poepp. & Endl.-*G. D. Weiblen 1522*, Brazil (MIN); *T. B. Croat 20125*, Peru (MIN); *Ferreira 7122*, Amazon (F); *Leisner 17394*, Venezuela (F); *T. Croat 19737*, Peru (A); *G. D. Weiblen 1519*, Brazil (MIN). **Trymatococcus oligandrus** (Benoist) Lanj.-*G. D. Weiblen 1684*, French Guiana (MIN); *R. Benoist 1573*, French Guiana (P); *S. A. Mori, T. D. Pennington 18079*, French Guiana (P). **Utsetela neglecta** Jongkind-*M. G. le Testu 7007*, Gabon (P); *M .G. le Testu 8012*, Gabon (P); *v. d. Maesen, Louis, de Bruijn 5764*, Gabon (P).

CANNABACEAE: Cannabis sativa L.-*N. H. Russell 815239*, USA (MIN); *L. M. Umbach*, USA (MIN); *C. C. Deam 53065*, USA (MIN); *E. S. Steele*, USA (MIN); *H. Jackson 2058*, USA (MIN); *G. D. Fuller 1107*, USA (MIN); *W. H. Horr E229*, USA (MIN); *V. H. Chase 3405*, USA (MIN); *W. Smith 10729*, USA (MIN). **Celtis philippinensis** Blanco-*G. D. Weiblen 1113*, Papua New Guinea (MIN). **Humulus lupulus** L.-*J. W. Moore, N. L. Huff 17993*, USA (MIN); *J. W. Moore 21304*, USA (MIN); *O. Lakela 19395*, USA (MIN); *J. W. Moore, N. L. Huff 18120*, USA (MIN); *G. A. Wheeler 4634*, USA (MIN); *G. D. H. L. Lyon, L. R. Moyer 1261*, USA (MIN); *J. W. Moore 22149*, USA (MIN).

URTICACEAE: Boehmeria nivea (L.) Gaudich-*J. W. Moore 666*, Society Islands (MIN); *O. Degener 2472*, USA (MIN). **Cecropia insignis** Liebm.-*G. D. Weiblen 1424*, Costa Rica (MIN). **Cecropia obtusifolia** Bertol.-*G. D. Weiblen 1435*, Panama (MIN). **Cecropia peltata** L.-*G. D. Weiblen 1436*, Panama (MIN); *C. Lane, R. Gieschen 191*, Puerto Rico (MIN); *S. F. Glassman 1694*, Honduras (MIN); *A. E. Ricksecker 449*, West Indies (MIN); *P. Sintenis 4803*, Puerto Rico (MIN); *H. H. Rusby, R. W. Squires 99*, Lower Orinoco (MIN). **Coussapoa latifolia** Aubl.-*G. D. Weiblen 1503*, Brazil (MIN). **Coussapoa nymphaeifolia** Standl.-*G. D. Weiblen 1412*, Costa Rica (MIN). **Coussapoa panamensis** Pitt.-*G. D. Weiblen 1447*, Panama (MIN); *G. D. Weiblen 1449*, Panama (MIN). **Coussapoa schottii** Miq.-*G. D. Weiblen 1188*, Brazil (MIN). **Coussapoa villosa** Poepp. & Endl.-*G. D. Weiblen 1418*, Costa Rica (MIN); *G. D. Weiblen 1486*, Peru (MIN); *G. D. Weiblen 1452*, Peru (MIN); *G. D. Weiblen 1492*, Peru (MIN). **Debregeasia longifolia** Wedd.-*K. Iwatauki et al. 618*, Sumatra (P); *B. H. Danser*, Java (P). **Pilea fontana** (Lunell) Rydb.-*C. C. Deam 53201*, USA (MIN); *J. Lunell*, USA (MIN); *C. C Deam 23830*, USA (MIN); *S. C. Wadmond 7741*, USA (MIN); *S. C. Wadmond 8741*, USA (MIN); *S. C. Wadmond 8141*, USA (MIN); *A. Hayden, L. W. Toldstead 352*, USA (MIN).

APPENDIX 2.   List of morphological characters and character states coded for Moraceae. The percentage of data missing, consistency index (CI), and retention index (RI) on the Bayesian total evidence phylogeny (Fig. 6) for each character is listed in parentheses. Characters were treated as unordered in phylogenetic analysis unless otherwise noted.

Growth form and habit. **1. Growth habit** (0%, 0.57, 0.28): (0) hemiepiphyte, (1) herb, (2) woody climber, (3) shrub, (4) tree. If a plant is erect it was scored as a shrub (woody, perennial, smaller than a tree, often with several stems), tree (woody, perennial, one main stem), or herb (without a woody stem).

Latex. **2. Latex** (0%, 0.50, 0.89): (0) absent, (1) milky, (2) clear. Latex of Moraceae species is milky while latex of Cecropiaceae is clear. **3. Radial latex tubes** (7.4%, 0.71, 0.70): (0) absent, (1) present. Lacticifers are located in the ray cells (those cells organized horizontally to the stem).

Wood anatomy. **4. Porosity** (7.4%, 0.75, 0.75): (0) diffuse porous, (1) ring porous. **5. Vessel arrangement** (7.4%, 0.33, 0.86): (0) vessels not in diagonal arrangement, (1) diagonal pattern present. **6. Heartwood color** (13.8%, 0.65, 0.40): (0) brown, (1) yellowish, (2) whitish to grey. **7. Distinction between heartwood and sapwood** (21.3%, 0.10, 0.63): (0) not defined, (1) defined. Because we could not quantitatively measure the difference between "weakly defined" and "strongly defined," we combined these descriptions and interpreted them as "defined." **8. Wood grain** (19.1%, 0.88, 0.55): (0) interlocked, (1) straight. **9. Growth ring boundaries** (7.4%, 0.88, 0.50): (0) boundaries indistinct or absent, (1) boundaries distinct. **10. Wood fibers** (6.4%, 0.25, 0.89): (0) not septate, (1) septate. **11. Diffuse apotracheal parenchyma** (7.4%, 0.50, 0,00): (0) absent, (1) present. **12. Banded apotracheal parenchyma** (10.6%, 0.20, 0.76): (0) absent, (1) present. **13. Paratracheal parenchyma** (9.6%, 0.95, 0.79): (0) aliform, (1) vasicentric (including scanty), (2) confluent. **14. Paratracheal parenchyma unilateral** (9.6%, 1.00, 1.00): (0) absent, (1) present. This morphological feature is characteristic of Dorstenieae and is present in *Brosimum*, woody *Dorstenia*, *Helianthostylis*, and *Trymatococcus*. **15. Vitreous silica** (8.5%, 0.22, 0.80): (0) absent, (1) present. **16. Rhombic crystals in ray cells** (7.4%, 0.33, 0.60): (0) absent, (1) present. The presence of rhombic crystals is often reported as "occasionally present" or "scarce" in the literature. We scored reports of any instance of this character as "present" since they indicated that members of the genus are capable of producing rhombic crystals. **17. Rhombic crystals in axial parenchyma** (7.4%, 0.07, 0.52): (0) absent, (1) present. **18. Uniseriate ray cell composition – procumbent cells** (9.6%, 0.17, 0.72): (0) absent, (1) present. With the exception of *Poikilospermum* (Urticaceae), all Moraceae, Urticaceae, and Cannabaceae are reported to have uniseriate rays. Cell types of uniseriate rays are not consistently reported as absent or present in the literature, but often are described as being "few," "some," "occasionally," or "rarely present." Any time a cell type was reported as occurring in a species, it was scored as present even if only rarely present; see also characters 19-23. **19. Uniseriate ray cell composition – upright cells** (11.7%, 1.00, 0.00): (0) absent, (1) present. **20. Uniseriate ray cell composition – square cells** (11.7%, 0.08, 0.71): (0) absent, (1) present. **21. Multiseriate ray cell composition – procumbent cells** (9.6%, 0.33, 0.71): (0) absent, (1) present. We scored the most common cell type excluding the upper and lower margin of the ray. **22. Multiseriate ray cell composition – upright cells** (9.6%, 0.50, 0.93): (0) absent, (1) present. **23. Multiseriate ray cell composition – square cells** (9.6%, 0.33, 0.78): (0) absent, (1) present. **24. Uniseriate margins of multiseriate rays** (9.6%, 0.17, 0.50): (0) absent, (1) present. Multiseriate rays often have uniseriate rows of cells at the upper and lower boundaries of the rays. Any mention of uniseriate margins was coded as present.

Pollen morphology. **25. Pore number** (51.1%; ordered, 0.26, 0.39): (0) two, (1) three, (2) four, (3) greater than 4. **26. Annulus** (57.4%, 0.14, 0.25): (0) absent, (1) present. **27. Operculum** (64.9%, 0.25, 0.50): (0) absent, (1) present.

Branch architecture. **28. Branches** (10.6%, 1.00, 1.00): (0) abscising, (1) persistent. Some members of Moraceae possess self-pruning branches, a phenomenon known as cladoptosis. This characteristic is considered diagnostic of the woody tribe Castilleae, as defined by (Berg 1977a). Herbaceous taxa were scored as missing. **29. Armature** (0%, 0.33, 0.50): (0) unarmed, (1) armed. **30. Shoot apex** (0%, 0.33, 0.33): (0) deciduous, (1) persistent.

Leaf and stipule architecture. **31. Stipules** (0%, 0.22, 0.65): (0) free, (1) partially connate, (2) fused. The partially connate condition (where only part of the length of the stipule is fused) is uncommon in Moraceae; among taxa examined this character state is present only in *Ficus edelfeltii* and *Ficus copiosa*. **32. Stipules** (0%, 0.40, 0.40): (0) caducous, (1) persistent. **33. Stipules** (0%, 0.10, 0.78): (0) not fully amplexicaul, (2) amplexicaul. **34. Phyllotaxis** (1.1%, 0.50, 0.75): (0) distichous, (1) spiral, (2) opposite. **35. Venation** (0%, 0.38, 0.56): (0) pinnate, (1) palmate, (2) triplinerved. **36. Lamina** (3.2%, 0.22, 0.42): (0) simple leaves, (1) with some lobed leaves. Often, species with lobed leaves have simple juvenile leaves, or display a gradient in lamina shape from simple or slightly lobed to lobed. The character state "simple leaves" implies all leaves on the plant were entire, while having lobed leaves implies that at least some of the leaves of the plant were lobed. Many *Artocarpus* (breadfruit) have simple juvenile leaves and incised mature leaves, while *Morus* (mulberries) shows considerable variation in lamina shape within a mature plant. **37. Leaf margin** (1.1%, 0.74, 0.29): (0) entire, (1) dentate/denticulate, (2) serrate, (3) crenate, (4) spinulose.

Leaf anatomy. **38. Uncinate hairs** (7.4%, 0.28, 0.83): (0) absent, (1) present. Hooked hairs on the surface of the leaf. **39. Cystoliths** (4.3%, 0.10, 0.80): (0) absent, (1) present. Cystoliths were scored as present when observed under a dissecting microscope on either the abaxial or adaxial leaf surface. **40. Waxy glands** (0%, 1.00, 1.00): (0) absent, (1) present. Glandular waxy

spots located on the lower surface of the midrib of the lamina or in the axils of the veins.

Reproductive characters. **41. Breeding system** (0%, 0.20, 0.57): (0) monoecious, (1) dioecious, (2) monoecious and dioecious, (3) androdioecious, (3) gynodioecious. **42. Pollination syndrome** (26.6%, 0.25, 0.90): (0) anemophily, (1) entomophily. Since comprehensive pollination studies were unavailable, character state determination was based on inflorescence morphology (Datwyler and Weiblen 2004). For instance, taxa with urticaceous stamens were considered wind pollinated. **43. Inflorescence** (0%, 0.17, 0.52): (0) unisexual, (1) bisexual, (2) unisexual and bisexual. Within Moraceae, monoecious, androdioecious and gynodioecious taxa vary in the combination of unisexual and bisexual inflorescences. For example, androdioecious *Castilla* have individuals with staminate inflorescences and individuals with separate pistillate and staminate inflorescences, while androdioecious *Helianthostylis* have unisexual staminate inflorescences on some individuals and bisexual inflorescences on other individuals. **44. Involucral bracts** (0%, 0.50, 0.97): (0) absent, (1) present. Involucral bracts refer to a series of imbricate bracts in multiple rows that subtend and enclose the immature inflorescence. **45. Glandular structures with yellow dye in the inflorescences** (0%, 0.50, 0.83): (0) absent, (1) present. Some Moraceae genera, such as *Maclura*, have pockets of yellow dye associated with the tepals or interfloral bracts. These structures are considered to be defense compounds to deter potential florivores (Berg 2001).

Chromosomes. **46. Base chromosome number** (38.3%, 0.33, 0.67; ordered): (0) less than 13, (1) 13, (2) 14, (3) greater than 14. The common base chromosome number for Moraceae is 13 or 14 (Oginuma et al. 1990; Oginuma and Tobe 1995).

Staminate inflorescences. **47. Inflorescence architecture** (0%, 0.53, 0.75): (0) raceme, (1) spike, (2) cyme, (3) syconium, (4) globose to ellipsoid capitulum, (5) disc, (6) urceolate disc, (7) cylindrical to turbinate, (8) bivalvate. Raceme: pedicellate flowers arranged along a single axis. Spike: sessile flowers arranged along the sides of an axis. Cyme: branched, determinate inflorescence. Syconium: enclosed inflorescence with a single bract-lined opening and flowers densely arranged on the interior surface of the inflorescence. Globose to ellipsoid capitulum: flowers attached to a spherical receptacle. Disc: flowers attached to a flattened receptacle. Urceolate disc: flowers attached to an urn shaped receptacle. Turbinate: flowers attached to a cylindrical shaped receptacle. **48. Inflorescences** (7.4%, 0.64, 0.66): (0) solitary, (1) paired, (2) clustered. **49. Interfloral bracts** (8.5%, 0.62, 0.76): (0) absent, (1) not peltate, (2) peltate. Peltate bracts are shaped like a tack with a stalk attached to the center of the bract. Many Moraceae have peltate bracts that completely surround the inflorescence to protect the floral primordia. Although peltate bracts are common in Moraceae, other forms of interfloral bracts occur, but due to their shape do not play a protective role. Bracts range from clavate to straight or tepaloid and with varying degrees of indumentum and for the purposes of this study were characterized as "not peltate." Taxa were coded as polymorphic (1&2) if interfloral bracts were present but the form was unknown. **50. Staminate perianth merosity** (0%, 0.87, 0.83; ordered): (0) absent, (1) 2-merous, (2) 3-merous, (3) 4-merous, (4) 5-merous. There is a wide range of perianth number throughout the Moraceae, and many species are polymorphic. For example, perianth number in *Naucleopsis* (Moraceae) is extremely variable within a species and ranges from 3-7-merous within an individual inflorescence. State 5 separated those species that were polymorphic for perianth number from those that had a more consistent number of perianth parts. For species in which only generic descriptions were available, each state present was coded. For instance, *Pourouma* has 3-4 perianth parts and was coded for states 2 and 3 rather than state 5. **51. Staminate perianth connation** (1.1%, 0.53, 0.50): (0) absent, (1) free, (2) partially connate, (3) connate. Fusion among perianth parts within a flower varies from none, to partially connate (less than half the length of the perianth was fused, often the perianth is apically or basally fused), to connate (more than half of the length of the perianth is fused). **52. Adjacent flowers** (25.5%, 0.57, 0.50): (0) free, (1) partially adnate, (2) completely adnate. Fusion between the perianths of adjacent flowers can range from partially adnate (basally or the apically), to fully adnate. **53. Filaments** (0%, 0.11, 0.53): (0) straight in bud, (1) inflexed in bud. Urticaceae and many Moraceae have urticaceous stamens with inflexed filaments that explosively straighten at anthesis and throw pollen away from the flower. **54. Anthers** (23.4%, 0.71, 0.71): (0) introrse, (1) extrorse, (2) latrorse. **55. Pistillode** (5.3%, 0.85, 0.73): (0) absent, (1) filiform, (2) conical, (3) quadrangular, (4) flat. Filiform: thread-like. Conical: cone shaped. Quadrangular: columnar with four corners. Taxa were coded as polymorphic (1&2&3&4) if a pistillode is present but the form was unknown. **56. Number of stamens per flower** (0%, 0.67, 0.73; ordered): (0) one, (1) two, (2) three, (3) four, (4) five, (5) six. Variation in stamen number is common throughout the Moraceae. We reported the most common number of stamens found in a given species as the actual number of stamens. In some cases, stamen number was consistently variable within a species and was reported as polymorphic. The

following taxa are polymorphic at the species level: *Antiaropsis decipiens*, *Batocarpus amazonicus*, *Brosimum lactescens*, *B. rubescens*, *B. utile*, *Ficus asperula*, *F. copiosa*, *F. wassa*, *Naucleopsis caloneura*, *N. guianensis*, *N. ternstroemiiflora*, *N. ulei*, and *Perebea rubra*.

Pistillate Inflorescences. **57. Inflorescence architecture** (9.6%, 0.66, 0.77): (0) raceme, (1) spike, (2) cyme, (3) syconium, (4) globose to ellipsoid capitulum, (5) disc, (6) urceolate disc, (7) cylindrical to turbinate. Refer to description of Inflorescence architecture in the "Staminate inflorescences" section. Uniflorous inflorescences were coded as "missing" as this state was inapplicable. **58. Inflorescences** (6.4%, 0.57, 0.51): (0) solitary, (1) paired, (2) clustered. Some species that are either androdioecious with unisexual flowers or monoecious/dioecious have a single pistillate inflorescence clustered with many staminate inflorescences and were coded as clustered. **59. Number of flowers in the inflorescence** (9.6%, 0.29, 0.55): (0) strictly uniflorous, (1) multiflorous. **60. Adjacent flowers** (9.6, 0.87, 0.67): (0) free, (1) partially adnate, (2) adnate. **61. Interfloral bracts** (13.8%, 0.33, 0.71): (0) absent, (1) not peltate (2) peltate. Refer to the description of Interfloral bracts in the "Staminate inflorescences" section. Taxa were coded as polymorphic (1&2) if interfloral bracts were present but the form was unknown. **62. Pistillate flowers** (9.6%, 0.20, 0.79): (0) embedded in the receptacle, (1) not embedded in the receptacle. **63. Pistillate perianth merosity** (1.1%, 0.83, 0.56; ordered): (0) absent, (1) 2-merous, (2) 3-merous, (3) 4-merous. Refer to character 50 description. **64. Pistillate perianth connation** (1.1%, 0.44, 0.56): (0) absent, (1) free, (2) partially connate, (3) connate. Refer to character 51 description. **65. Stigma** (6.4%, 0.72, 0.67): (0) one, (1) two, equal in length, (2) two, unequal in length. Taxa were coded as polymorphic (1&2) if two stigmas were present but the length of lobes was unknown. **66. Stigma shape** (8.5%, 0.53, 0.61): (0) filiform,

(1) pencillate, (2) semidiscoid, (3) linguiform, (4) vittiform (5) peltate. Filiform: thread-like. Pencillate: like a small brush. Semi-discoid: top of the stigma in the shape of a disc. Linguiform: tongue-shaped. Vittiform: strapshaped. Peltate: tack shaped. **67. Ovary** (9.6%, 0.14, 0.81): (0) free, (1) adnate to perianth. **68. Placentation** (0%, 1.00, 1.00): (0) apical, (1) basal. **69. Ovule** (0%, 0.50, 0.92): (0) anatropous or campylotropous, (1) orthotropous.

Fruit and seed characters. **70. Fruit** (6.4%, 0.20, 0.69): (0) dehiscent, (1) indehiscent. **71. Fruit** (21.3%, 0.13, 0.61): (0) dry, (1) fleshy. In Moraceae, various parts of the flower can become fleshy in fruit including the perianth, receptacle, and in some cases the exocarp. In the absence of detailed information on fruit development, we regarded any part of the flower becoming fleshy as evidence of fleshy fruit. **72. Adnation of seed** (28.7%, 0.33, 0.83): (0) free, (1) fused. Moraceae seeds can be fused to the perianth or the receptacle. Without detailed developmental studies, it could not be clearly determined which tissues were fused to the seed. If the seed showed indications of fusion with surrounding tissues, it was coded as "fused." **73. Endosperm** (2.1%, 0.08, 0.69): (0) absent, (1) present. **74. Seeds** (4.3%, 0.14, 0.82): (0) small (less than 5 mm long), (1) large (greater than 10 mm long). **75. Cotyledons** (22.3%, 0.33, 0.67): (0) thin, (1) thick. **76. Cotyledons** (6.4%, 0.27, 0.62): (0) unequal, (1) equal. Although coding binary characters as polymorphic is effectively the same as coding the state as missing, variation at the species level was coded as polymorphic to show that the length of the cotyledons did vary within a species. This criterion was also applied to character 76. **77. Cotyledons** (15.9%, 0.25, 0.44): (0) straight, (1) folded. **78. Radicle** (18.1%, 0.11, 0.58): (0) short, (1) long. **79. Radicle** (56.4%, 0.33, 0.88): (0) straight, (1) curved. **80. Testa** (32.9%, 0.50, 0.50): (0) not vascularized, (1) vascularized. **81. Embryo** (0%, 0.20, 0.83): (0) straight, (1) curved.

APPENDIX 3. Comparison of the classification of Moraceae according to the past three publications and findings from this research. The reference, tribes, and genera of the tribe are listed. *Bosqueiopsis*, *Hullettia*, *Scyphosyce*, *Treculia*, and *Trilepisium* were not included in phylogenetic analyses but are retained in their traditional position until evidence suggests otherwise.

Tribe	Berg 2001	Datwyler and Weiblen 2004	Berg 2005a	Clement and Weiblen 2009
Antiaropsideae	-	-	*Antiaropsis Sparattosyce*	-
Artocarpeae	*Antiaropsis*	*Artocarpus*	*Artocarpus*	*Artocarpus*
	Artocarpus	*Batocarpus*	*Hullettia*	*Batocarpus*
	Bagassa	*Clarisia*	*Parartocarpus*	*Clarisia*
	Batocarpus	*Hullettia*	*Prainea*	*Hullettia*
	Clarisia	*Parartocarpus*	*Treculia*	*Parartocarpus*
	Hullettia	*Prainea*		*Prainea*
	Parartocarpus	*Treculia*		*Treculia*
	Poulsenia			
	Prainea			
	Sorocea			
	Sparattosyce			
	Treculia			
Castilleae	*Antiaris*	*Antiaris*	*Antiaris*	*Antiaris*
	Castilla	*Antiaropsis*	*Mesogyne*	*Antiaropsis*
	Helicostylis	*Castilla*	*Castilla*	*Castilla*
	Maquira	*Helicostylis*	*Helicostylis*	*Helicostylis*
	Mesogyne	*Maquira*	*Maquira*	*Maquira*
	Naucleopsis	*Mesogyne*	*Naucleopsis*	*Mesogyne*
	Perebea	*Naucleopsis*	*Perebea*	*Naucleopsis*
	Pseudolmedia	*Perebea*	*Pseudolmedia*	*Perebea*
		Poulsenia		*Poulsenia*
		Pseudolmedia		*Pseudolmedia*
		Sparattosyce		*Sparattosyce*
Dorstenieae	*Bosqueiopsis*	*Bosqueiopsis*	*Bosqueiopsis*	*Bleekrodea*
	Brosimum	*Brosimum*	*Brosimum*	*Bosqueiopsis*
	Dorstenia	*Dorstenia*	*Dorstenia*	*Broussonetia*
	Helianthostylis	*Helianthostylis*	*Helianthostylis*	*Brosimum*
	Scyphosyce	*Scyphosyce*	*Scyphosyce*	*Dorstenia*
	Trilepisium	*Trilepisium*	*Trilepisium*	*Fatoua*
	Trymatococcus	*Trymatococcus*	*Trymatococcus*	*Helianthostylis*
	Utsetela	*Utsetela*	*Utsetela*	*Malaisia*
				Scyphosyce
				Sloetia
				Trilepisium
				Trymatococcus
				Utsetela

APPENDIX 3.   Continued.

Tribe	Berg 2001	Datwyler and Weiblen 2004	Berg 2005a	Clement and Weiblen 2009
Antiaropsideae				
	-	-	*Antiaropsis*	-
	-	-	*Sparattosyce*	-
Ficeae	*Ficus*	*Ficus*	*Ficus*	*Ficus*
Maclureae	-	-	-	*Maclura*
Moreae	*Bleekrodea*	*Bagassa*	*Bleekrodea*	*Bagassa*
	Broussonetia	*Bleekrodea*	*Broussonetia*	*Maclura*
	Fatoua	*Broussonetia*	*Fatoua*	*Milicia*
	Maclura	*Fatoua*	*Maclura*	*Morus*
	Milicia	*Maclura*	*Milicia*	*Sorocea*
	Morus	*Milicia*	*Morus*	*Streblus*
	Streblus	*Morus*	*Streblus*	*Trophis*
	Trophis	*Sorocea*	*Trophis*	
		Streblus		
		Trophis		
Soroceae	-	-	*Bagassa*	-
			Batocarpus	
			Clarisia	
			Poulsenia	
			Sorocea	