American Journal of Botany 96(8): 1551–1570. 2009.

MALPIGHIALES PHYLOGENETICS: GAINING GROUND ON ONE OF THE MOST RECALCITRANT CLADES IN THE ANGIOSPERM TREE OF LIFE[1]

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The eudicot order Malpighiales contains ~16 000 species and is the most poorly resolved large rosid clade. To clarify phylogenetic relationships in the order, we used maximum likelihood, Bayesian, and parsimony analyses of DNA sequence data from 13 gene regions, totaling 15 604 bp, and representing all three genomic compartments (i.e., plastid: *atpB*, *matK*, *ndhF*, and *rbcL*; mitochondrial: *ccmB*, *cob*, *matR*, *nad1B-C*, *nad6*, and *rps3*; and nuclear: 18S rDNA, *PHYC,* and newly developed low-copy *EMB2765*). Our sampling of 190 taxa includes representatives from all families of Malpighiales. These data provide greatly increased support for the recent additions of *Aneulophus*, *Bhesa*, *Centroplacus*, *Ploiarium*, and Rafflesiaceae to Malpighiales; sister relations of Phyllanthaceae + Picrodendraceae, monophyly of Hypericaceae, and polyphyly of Clusiaceae. Oxalidales + Huaceae, followed by Celastrales are successive sisters to Malpighiales. Parasitic Rafflesiaceae, which produce the world's largest flowers, are confirmed as embedded within a paraphyletic Euphorbiaceae. Novel findings show a well-supported placement of Ctenolophonaceae with Erythroxylaceae + Rhizophoraceae, sister-group relationships of *Bhesa* + *Centroplacus*, and the exclusion of *Medusandra* from Malpighiales. New taxonomic circumscriptions include the addition of *Bhesa* to Centroplacaceae, *Medusandra* to Peridiscaceae (Saxifragales), Calophyllaceae applied to Clusiaceae subfamily Kielmeyeroideae, Peraceae applied to Euphorbiaceae subfamily Peroideae, and Huaceae included in Oxalidales.

Key words: Centroplacaceae; classification; low-copy nuclear gene; Malpighiales; multigene analyses; Peridiscaceae; Rafflesiaceae; rapid radiation.

Malpighiales are one of the most surprising angiosperm clades discovered in broad molecular phylogenetic studies (Chase et al., 1993; Savolainen et al., 2000a, b; Soltis et al., 2000). The order contains ~16 000 species, that span tremendous morphological and ecological diversity, and includes submerged thalloid aquatics (Podostemaceae), holoparasites (Rafflesiaceae), amentiferous wind-pollinated taxa (temperate Salicaceae), and leafless cactus-like succulents (Euphorbiaceae). Malpighiales include numerous economically important species such as cassava (*Manihot*, Euphorbiaceae), flax (*Linum*, Linaceae), poinsettia (*Euphorbia*, Euphorbiaceae), poplar (*Populus*, Salicaceae), and the rubber tree (*Hevea*, Euphorbiaceae). In addition, genomic resources for the order are growing rapidly and include whole genome sequencing projects completed or near completion for poplar (*Populus*, Salicaceae; Tuskan et al., 2006), castor bean (*Ricinus*, Euphorbiaceae; http://castorbean.tigr.org), and cassava (*Manihot*, Euphorbiaceae; http://www.jgi.doe.gov) and large expressed sequence tag (EST) libraries for several other taxa (e.g., Anderson and Horvath, 2001; Day et al., 2005; Miyama et al., 2006; C. C. Davis et al., unpublished data).

The clade was first identified by Chase et al. (1993), and its name, Malpighiales, was reappropriated from Hutchinson (1926, 1959) and applied to the group to break from previous classifications (APG, 1998). The composition of the order has enlarged considerably since 1993 and herein includes 42 families that have previously been assigned to 13 orders in morphology-based classifications (sensu Cronquist, 1981). Numerous molecular studies (Chase et al., 1993, 2002; Fay et al., 1997; Litt and Chase, 1999; Soltis et al., 1999, 2000, 2003, 2007b; Savolainen et al., 2000a, b; Cameron et al., 2001; Davis et al., 2001, 2005a, b, 2007; Kita and Kato, 2001;Wurdack, 2002; Hilu et al., 2003; Davis and Chase, 2004; Wurdack et al., 2004, 2005; Samuel et al., 2005; Kathriarachchi et al., 2005; Tokuoka and Tobe, 2006; Zhang and Simmons, 2006; Tokuoka, 2007, 2008; Zhu et al., 2007; Korotkova et al., in press) employing multiple gene regions have confirmed the monophyly of the order or many of its component families with a high degree of confidence, in addition to identifying a handful of well-supported interfamilial relationships. None of them, however, has resolved relationships along the spine of the tree with high statistical support, making this one of the least resolved large angiosperm clades (Fig. 1).

The difficulty in determining deep relationships within Malpighiales appears to be related to the ancient and rapid origin of the group during the mid-Cretaceous (Davis et al., 2005b). This phenomenon seems to be mirrored in early-diverging angio-

[1] Manuscript received 24 June 2008; revision accepted 26 March 2009.

The authors thank the following individuals and institutions for providing plant or DNA samples: M. Alford, P. Berry, M. Chase, D. Erickson, L. Gillespie, C. Parks, K. Redden, M. Simmons, Y.-L. Qiu, J. Wen, J. Wieringa, A, DUKE, FTG, K, L, MICH, MO, NY, US, and WAG. They have had valuable discussions with M. Alford, P. Endress, M. Matthews, M. Simmons, and P. Stevens. K. Han, M. Latvis, and Z. Xi are gratefully acknowledged for assisting with some of the labwork. Funding for this study came from National Science Foundation Assembling the Tree of Life grant DEB-0622764. Research by K.J.W. was also supported by the Smithsonian Institution and the Lewis B. and Dorothy Cullman Program for Molecular Systematic Studies at The New York Botanical Garden; and C.C.D. was also supported by the Michigan Society of Fellows, a Rackham Faculty grant from the University of Michigan, and by the Department of Organismic and Evolutionary Biology at Harvard University.

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doi:10.3732/ajb.0800207

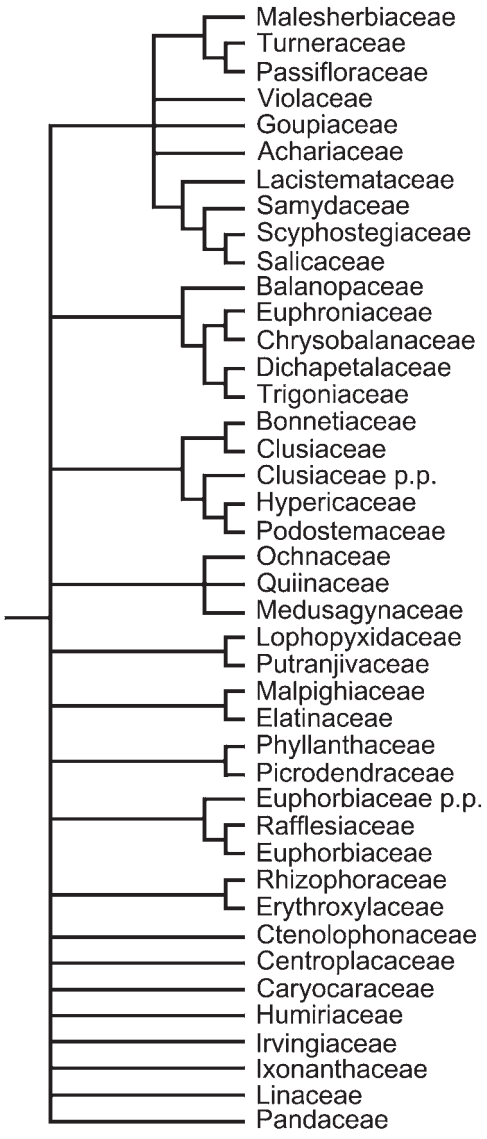


Fig. 1. Summary tree of strongly supported (>85 BP) Malpighiales family relationships reported prior to this study.

sperms (Moore et al., 2007) and Saxifragales (Fishbein et al., 2001; Jian et al., 2008). Further complicating our understanding of the evolution of Malpighiales is that their sister group is unclear. Celastrales, Oxalidales, and Huaceae are close relatives, but relationships among these clades are unresolved or conflicting (Soltis et al., 2000, 2007b; Davis et al., 2005b, 2007; Zhang and Simmons, 2006; Zhu et al., 2007; Wang et al., 2009).

Now that the monophyly and membership of this large and diverse clade is better established, we want to further resolve relationships among its major subclades. This will allow us to uncover broader evolutionary patterns within this fascinating group. In particular, Malpighiales have a combination of species-rich lineages (e.g., Euphorbiaceae with ~6300 species), as well as species-poor lineages (e.g., Ctenolophonaceae with only three species) whose closest phylogenetic relatives are not yet apparent. Resolving relationships among these unbalanced lineages will help to localize dramatic shifts in rates of cladogenesis, which will pave the way for more focused inquiries into adaptive speciation in the group (Magallón and Sanderson, 2001; Ricklefs, 2007). In addition, several of these unplaced species-poor lineages, and many of the earliest-diverging members of the species-rich clades, exhibit striking patterns of continental endemism. By clarifying extracontinental relatives of these unplaced lineages, we may uncover patterns of ancient angiosperm biogeography. Classic examples of temperate Gondwanan angiosperm biogeography include Proteaceae (Barker et al., 2007) and Nothofagaceae (Swenson et al., 2001; Knapp et al., 2005), but there are very few compelling instances of tropical angiosperm lineages that exhibit patterns consistent with vicariant Gondwanan biogeography (Davis et al., 2004). Malpighiales, and possibly Ericales, may provide the first insights into tropical vicariant Gondwanan angiosperm biogeography and patterns of tropical community assembly during the Cretaceous (Davis et al., 2005b).

The molecular data needed to resolve relationships involving radiations of ages similar to Malpighiales is considerable and perhaps upward of 25 000–50 000 bp (Jian et al., 2008). The use of multiple gene regions not only provides the characters to attain such sequence lengths but can also reveal emergent phylogenetic signal not evident in single-gene analyses (i.e., the sum of the whole is greater than its parts) and reduce the effects of single-gene or genome-specific processes (Gatesy and Baker, 2005; Burleigh and Mathews, 2007). We recognize that there is complexity in large multigene data sets and a total evidence approach (Kluge, 1989) must be considered cautiously (Gatesy and Baker, 2005; Qiu et al., 2005; Gatesy et al., 2007; Rodríguez-Ezpeleta et al., 2007), but increased phylogenetic resolution in Malpighiales has only been achieved through combined analyses, and many findings utilizing this philosophy have been corroborated on morphological grounds (Stevens, 2001 onward).

The goals of our study are to (1) identify the sister group to Malpighiales, (2) better clarify major subclades in the deepest parts of the Malpighiales phylogeny, (3) discuss nonmolecular characters that corroborate novel relationships we uncover, and (4) use this phylogenetic framework to propose an up-to-date family classification for the order. To accomplish these goals, we use 13 gene regions that represent all three plant genomes: plastid *atpB*, *matK*, *ndhF,* and *rbcL*; mitochondrial *ccmB*, *cob*, *matR, nad1B-C*, *nad6*, and *rps3*; and nuclear 18S rDNA, exon 9 of *EMB2765*, and *PHYC*. The phylogenetic utility of most of these markers has been previously demonstrated in Malpighiales (e.g., Chase et al., 2002; Wurdack, 2002; Davis and Chase, 2004; Davis and Wurdack, 2004; Davis et al., 2005b, 2007; Tokuoka and Tobe, 2006). We also present *EMB2765* as a new low-copy nuclear gene that we anticipate will have broad utility for inferring phylogenetic relationships in angiosperms.

MATERIALS AND METHODS

Sampling—Our taxon sampling contains 190 terminals, of which 144 represent Malpighiales. Voucher information and GenBank numbers for all sequences are provided in Appendix 1. All 42 families of Malpighiales recognized here were included. To adequately represent taxa of interest, composite terminals combining data from different species (Nixon and Davis, 1991) comprised 16% of the total sampling. Additional Malpighiales sampling is desirable for Ixonanthaceae (*Allantospermum*) and Podostemaceae (Tristichoideae and Weddellinoideae; Kita and Kato, 2001) in future analyses. We were also unable to include the poorly known taxa *Haptanthus* (Haptanthaceae; Goldberg and Nelson, 1989) and *Nicobariodendron* (doubtfully Celastraceae; Simmons, 2004a), which have been suggested to be affiliated with Malpighiales. On the basis of morphological grounds, however, it appears that *Haptanthus* may be better placed among the early-diverging eudicots (Doust and Stevens, 2005).

Extraordinal sampling was focused on resolving the sister group to the order and on determining the relationships of *Medusandra,* which has recently been placed in Malpighiales (Soltis et al., 2005; Haston et al., 2007). For the sampling related to resolving the sister group to Malpighiales, we included Huaceae, all families of Oxalidales and Celastrales (except the poorly known Pottingeriaceae; Zhang and Simmons, 2006) and representatives of seven more distant rosid orders. *Calycanthus* (magnoliid clade) was used to root our trees and did not create additional ambiguously aligned regions.

Our choice of genes was based in part on existing data sets (Soltis et al., 2000; Davis and Chase, 2004; Davis and Wurdack, 2004; Davis et al., 2005b, 2007). However, given the need to further corroborate the mostly mitochondrial placement of Rafflesiaceae (Davis et al., 2007), we sought additional low-copy nuclear data for our matrix. Despite the informativeness of low-copy nuclear loci, there are few that have been identified for higher-level utility in angiosperms (Small et al., 2004). We screened for low-copy loci with large, >800-bp exons using the *Populus* genome (http://genome.jgi-psf.org/Poptr1/Poptr1.home.html; Tuskan et al., 2006), and then searched GenBank for orthologs of each locus to aid in primer design. While Rafflesiaceae could be amplified and directly sequenced for several candidate genes, *EMB2765* (*EMBRYO DEFECTIVE 2765*, At2g38770), proved the most successful for amplification across a range of Malpighiales, plus more distant outgroups. Exons 9 and 12 are over 1000 bp in *EMB2765*, but exon 9 was easier to amplify and thus used for our study.

Laboratory methods—Our methods for DNA extraction, polymerase chain reaction (PCR) amplification, and automated fluorescent sequencing for the 964 newly generated sequences mostly followed those previously outlined (Wurdack, 2002; Davis and Chase, 2004; Davis and Wurdack, 2004; Wurdack et al., 2004; Davis et al., 2005b, 2007). All genes were not obtained for all taxa, especially for the low-copy nuclear genes *PHYC* and *EMB2765*. Most technical difficulties related to probable gene loss (e.g., plastid gene loss in holoparasitic Rafflesiaceae [Nickrent et al., 1997; Davis and Wurdack, 2004] and *PHYC* in members of Salicaceae Salicaceae [Howe et al., 1998]), primer mismatches, or to a lesser extent degraded templates. In addition to basic precautions to control for contamination in degraded samples (i.e., dedicated materials for preparing archival samples and negative controls to detect contamination), the very degraded *Medusandra* sample was extracted at the Smithsonian by K.J.W. using equipment and materials that had never been exposed to DNAs of their close phylogenetic relatives identified here (i.e., Saxifragales).

Amplification of *rbcL* used 1F and 1460R, and additionally 636F and 724R for sequencing (Lledó et al., 1998). Amplification of *atpB* used S2 (rarely RBCL1 or S20) and S1494R, and additionally S611 and S766R for sequencing (Hoot et al., 1995). Amplification of *matK* used matK-400F and trnK-2R and additionally 842F, 1390R (Cameron et al., 2001), 1053F (5′-GTCAATNTCATTTTKATGTGTGST-3′), and 1159R (5′-CTAGCATTTGACTYCGTACCACTRA-3′) for sequencing. Amplification and sequencing of *ndhF* used 5.5F, 5.5Fm, or 972F, and 10.2R or 2110R (Olmstead and Sweere, 1994; Davis et al., 2001); 5.5Fm (5′-GAAATTCTTAATRMTAGTTGGTTGTATTC-3′) is a variant of 5.5F that is newly modified for Malpighiales. Amplification and sequencing of *ccmB, cob*, and *nad6* followed Davis et al. (2007). Amplification and sequencing of *nad1B-C* followed Davis and Wurdack (2004). Extensive clone screening of *nad1B-C* PCR products from all three genera of Rafflesiaceae did not yield an obvious native sequence, but only horizontally transferred copies from their Vitaceae hosts. Amplification and sequencing of *matR* followed Davis and Wurdack (2004). Amplifications of *matR* that failed, suggesting the loss of this gene, were further tested with the *nad1* primer pair nad1x4F (5′-GTATGCTAATAYGATCTYAATGAG-3′) and nad1x5R (5′-ACTACCCGAGCTAATGATAGAGGCA-3′), which spans exons 4 and 5. Amplification and sequencing of *rps3* mostly followed Davis et al. (2007). It was most efficiently amplified as two overlapping fragments using F1 with R1.5 (5′-CTATTCCCTTTATCAATTCTCCTAT-3′) and F2 (5′-CCCGTCGTAGTTCTCAATCATTTYG-3′) with R1 or the nested primer R1n (5′-TGATACCTGAGATTCCGTAACGAG-3′). Amplification of 18S rDNA used NS1 and C18L, and additionally C18H, N18O, and 626R for sequencing (Bult et al., 1992; Nickrent and Starr, 1994). For *PHYC*, primers CDO and DLE were used initially (Mathews and Donoghue, 1999), but we subsequently designed additional sets of primers to target a ~600-bp internal fragment that could be more easily amplified. Primers PHYC-INT1F (5′-CCAGCTACTGATATACCWCARGCTTC-3′) and PHYC-INTR (5′-CCAGCTTCCATAAGGCTATCAGTRCT-3′) are based on the priming sites in Samuel et al. (2005); a slightly downstream primer pair used for some taxa was PHYC-INT5F (5′-GGTTMGRATGATATGYGAYTG-3′) and PHYC-INT3R (5′-GTTTTGCACCACCCCACTTGATCTC-3′). Difficult taxa and complex multibanded initial amplifications using primers CDO + DLE yielded single bands after reamplification with nested primers. New *PHYC* data were directly sequenced and rarely yielded polymorphic sites. Amplification of exon 9 of *EMB2765* used EMB2765ex9F (5′-TGATACCTGAGATTCCGTAACGAG-3′) or EMB2765ex9F2 (5′-TATCCAAATGAGCAGATTATGTGGGA-3′) and EMB2765ex9R (5′- TTGGTCCAYTGTGCWGCAGAAGGRT-3′). For degraded samples, EMB2765ex9F was paired with the internal reverse primer EMB2765ex9R2 (5′-CCGYACATAYTGGAGGCCAAG-3′) to obtain partial sequences. The amplification of *EMB2765* was robust and nearly always yielded single bands, although sequencing sometimes indicated discrete polymorphic sites, which we treated as ambiguous. *Cratoxylum* (Hypericaceae) and *Podocalyx* (Picrodendraceae) had multiple copies (i.e., full length and shorter pseudogenes) that were directly sequenced after gel isolation.

Sequence assembly—Sequences were assembled and edited in the program Sequencher 3.1–4.5 (Gene Codes, Ann Arbor, Michigan, USA) and trimmed of primer regions. Relative branch lengths were generally comparable across data partitions and exceptionally divergent sequences were further examined for sequencing errors and orthology assignment. Previously used divergent data that we excluded here were *PHYC* for *Podostemum* and *Quiina* (Davis and Chase, 2004), an aberrant 18S sequence for *Hugonia*, and an *atpB* pseudogene for *Vismia* (Davis et al., 2005b). We also made numerous sequence substitutions relative to our previous studies to improve data quality and to reduce the number of composite terminals.

No indels were present in *ccmB*, *cob*, *EMB2765*, and *rbcL*, but among the remaining loci, indel content and the degree of alignment ambiguity varied greatly. Most alignments were performed manually using the program Se-Al version 2.0a11 (Rambaut, 1996–2002) and a similarity criterion (Simmons, 2004b). Initial alignments of *nad1B-C* and *ndhF* used the program CLUSTAL_W (as implemented in CLUSTAL_X version 1.83; Thompson et al., 1997) followed by extensive manual optimization in Se-Al. Gaps were treated as missing data. Ambiguously aligned regions were excluded from analyses (Appendix S1, see Supplemental Data with the online version of this article), as were autapomorphic insertions greater than 4 bp in length. The latter greatly reduced the amount of missing data owing to large indel regions. The highly variable 3′ end of the *trnK* intron (i.e., *matK–trnK*) was also excluded due to alignment ambiguity. In 18S rDNA, the few small excluded regions corresponded to those detailed by Soltis et al. (1997). The divergent 18S rDNA domains V2 and V4 in Rafflesiaceae (Nickrent and Starr, 1994; Davis and Wurdack, 2004) were included in our analyses; their inclusion or exclusion had no effect on the placement of Rafflesiaceae in combined analyses. A number of taxa contained other small divergent sequence elements, especially short, continuous strings (up to 6 bp) of positionally unambiguous apomorphic changes in *matR* and *rps3*. These features likely represent single mutational events such as small structural changes, and some are microinversions. We did not exclude these regions but point out that the occurrence of such structural changes in protein-coding exons that resemble changes seen in introns (Kelchner, 2000, 2002) deserves further study both for their molecular evolution and to assess their impact on phylogenetic inference. The aligned combined matrix with details of the excluded ambiguous regions is archived in the database TreeBASE (http://www.treebase.org/treebase/index.html) under study accession SN4370 and is available from the authors.

Phylogenetic analyses—We applied maximum likelihood (ML; Felsenstein, 1973) methods, which are expected to have higher accuracy in data sets with widely varying rates of sequence evolution and taxa with long branches (Anderson and Swofford, 2004; Bergsten, 2005). Nucleotide substitution models for each gene were the general time reversible model (GTR), or submodels of GTR, as determined by the program Modeltest version 3.6 (Posada and Crandall, 1998) using the Akaike information criterion (Akaike, 1974). Maximum likelihood optimization was implemented in the program GARLI version 0.951 (Zwickl, 2006) using a minimum of five independent runs from a random starting tree and using the automated stopping criterion (i.e., a stable –ln score for 20 000 generations). The version of GARLI used did not support partitioned analyses so combined analyses were parameterized using the GTR+I+Γ model as a single partition across each data set of interest. Because alternate runs sometimes produced slightly different optimal topologies in weakly supported parts of the tree, we focus our discussion primarily on those clades that receive >70 bootstrap percentage (BP; Felsenstein, 1985). ML bootstrap support values were estimated from 100 replicates using GARLI and the automated stopping criterion.

Bayesian MCMC analyses (Yang and Rannala, 1997) were implemented in the program MrBayes version 3.1.2 (Huelsenbeck and Ronquist, 2001; Altekar et al., 2004) under the GTR+I+Γ model with default priors for the rate matrix,

branch lengths, gamma shape parameter (Yang, 1993), and the proportion of invariant sites (Reeves, 1992). Five separate analyses were performed on the data to assess clade stability. A Dirichlet distribution was used for the base frequency parameters and an uninformative prior was used for the tree topology. Fourteen chains were initiated with a random starting tree and run for two million generations sampled every 1000 generations. Following a burn-in period of 500 000 generations, trees were sampled from the posterior distribution to calculate Bayesian posterior probabilities (PP). Stationarity (i.e., a plateau in log-likelihood values) was verified using the program Tracer version 1.4 (Rambaut and Drummond, 2003–2007).

Parsimony analyses were implemented in the program PAUP* version 4.0b10 (Swofford, 2002) using several search strategies: (1) the two stage method in Wurdack et al. (2005) and searches were swapped to completion or to a limit of 20 000 trees, (2) 1000 random addition sequences (RAS) with no limits (Multrees ON), or (3) five iterations of 200 replicates of the parsimony ratchet (Nixon, 1999) using the program PRAP version 2 (Müller, 2004). Uninformative characters were included in analyses except for the calculation of tree statistics. Bootstrap support was evaluated with 1000 replicates, each with five RAS and tree-bisection-reconnection (TBR) swapping, holding 10 trees at each step, and either without search limits or saving no more than 10 trees per iteration.

Our analyses involved considerable exploration of the data sets with preliminary searches to identify rogue sequences (e.g., misidentifications, chimeric sequences, or incorrect orthology assignments) and to examine the effects of missing data and different data exclusion sets (i.e., regions of ambiguous alignment or third position sites). In particular, mixtures of sequences of two very different lengths were present in *ndhF* (34% of the sequences had an additional 356 bp) and *PHYC* (32% had an additional 548 bp) because of the original primer combinations used in PCR. Test analyses using different partition lengths to examine the impact of these missing data demonstrated that some support values declined with these data excluded so we opted to use the full-length data sets in both cases. ML and parsimony searches were performed on each individual gene region, on each genome (i.e., plastid, mitochondrial, or nuclear), and on three variations of 13 genes including, (1) total evidence, (2) removing third codon positions globally, and (3) removing third positions from the most rapidly evolving protein-coding nuclear genes, *PHYC* and *EMB2765*. This last data set (i.e., 3) was our preferred final one, and the one on which Bayesian analyses were conducted. *PHYC* and *EMB2765* have a high proportion of synonymous substitutions and have the potential for saturation (Maynard Smith and Smith, 1996) at their third codon positions. Saturation can be problematic for inferring phylogenetic relationships of lineages that have very accelerated rates of nucleotide substitution. Although it is clear that third positions do have information content for some tips of our trees, the goals of our study are to identify deeper branching patterns where such saturation is likely to have a very negative impact (see review by Whitfield and Lockhart, 2007).

To evaluate a competing hypothesis for the sister group to Malpighiales, we performed an alternative topology test on the combined data by applying a monophyly constraint placing Celastrales sister to Malpighiales. Relationships were otherwise freely estimated by ML analysis and rival topologies were compared for incongruence using the approximately unbiased test (AU test; Shimodaira, 2002) as implemented in the program CONSEL version 0.1i (Shimodaira and Hasegawa, 2001).

RESULTS

Our combined data set included 13 genes and ~2.5 megabases of sequence data. A comparison of the data set and tree measures for our analyses is provided in Appendix S1 (see Supplemental Data in online version of this article). Well-supported relationships (i.e., those >85 BP) were congruent between analyses of individual gene trees (in both ML and parsimony), and the data were thus analyzed in combination. Our best overall depiction of phylogenetic relationships in Malpighiales was achieved with ML using all 13 gene regions and excluding third codon positions from the two most rapidly evolving nuclear regions, *PHYC* and *EMB2765* (Figs. 2, 3; see also Discussion). The removal of those sites resulted in increased support (≥5 BP) for 26 clades relative to combined analyses including or excluding all third positions. Support values for clades deeper in the tree appear to be particularly negatively impacted by including these more rapidly evolving sites (Appendices S2, S3, see online Supplemental Data). In addition, although topologies were very similar in all analyses, the use of parsimony resulted in a sharp decline in branch support deeper in the tree where support from ML and Bayesian analyses was otherwise very high (see Discussion; online Appendices S4, S5).

Molecular evolution—We observed widely varying branch lengths, indicative of heterogeneity in substitution rates among the taxa sampled. This variation was consistent within lineages regardless of the genomic partition, with the longest branches occurring in Rafflesiaceae and in the clusioid clade (especially in Podostemaceae). Gene loss is hypothesized to explain failed amplifications of *PHYC* (i.e., Passifloraceae s.l., and some Achariaceae and Salicaceae), despite attempts with multiple primer combinations. We could more clearly ascertain gene loss for *matR* in sister taxa *Croizatia* and *Lachnostylis* (Phyllanthaceae) where we recovered only flanking *nad1D* sequence; *nad1i728* and resident *matR* were completely lost. Preferential amplification of an intronless pseudogene is unlikely given the multiple internal primers we tried and the conserved nature of *matR*, but this loss should be corroborated in the future by Southern blot analysis. For *nad6* in *Paropsia* (Passifloraceae), a presumably functional copy (i.e., no stop codons present) and a second pseudogenic copy were obtained; the latter appears to be a fusion of *nad6* with a 279-bp region that is homologous to *atp9*. Celastrales contain a conspicuous deletion (aligned length of 549 bp) at the 3′ end of the *nad1B-C* intron that did not occur in any other taxa. This deletion is the broadest (i.e., in terms of taxonomic breadth) structural change that we observed but it unfortunately does not help to clarify relationships between Celastrales, Oxalidales and Malpighiales.

DISCUSSION

Resolving relationships of an ancient rapid radiation: Rapidly evolving sites and the utility of parsimony—We observed that support values for critical nodes deeper in the tree declined with the inclusion of the most rapidly evolving sites (i.e., third positions in *PHYC* and *EMB2765*). Although such sites are likely to change on a short internode (i.e., capture the branching pattern in a rapid radiation), they are also likely to be subsequently "overwritten" and become saturated (reviewed by Whitfield and Lockhart, 2007). This problem will be especially exacerbated if there is a delay in the appearance of crown groups that we are able to sample for phylogenetic study. In Malpighiales, saturation may be particularly relevant as there appear to be several, mostly family level crown group clades, that emerged well after the origin of their stem lineages (Davis et al., 2005b). On these grounds, we believe that slowly evolving sites may provide better resolution of rapid radiations, such as in Malpighiales. Slowly evolving sites are less likely to change, but when they do, are less prone to be "overwritten." Thus, they have the distinct advantage of being less homoplastic, but the disadvantage that a far greater number of characters are necessary to obtain a relatively small number of phylogenetically informative sites.

The method of data analysis is also an important consideration in resolving relationships in an ancient and rapid radiation. This problem poses special analytical challenges that may be more amenable to ML and Bayesian approaches, (e.g., heterogeneous evolution owing to lineage and gene-specific rate variation;

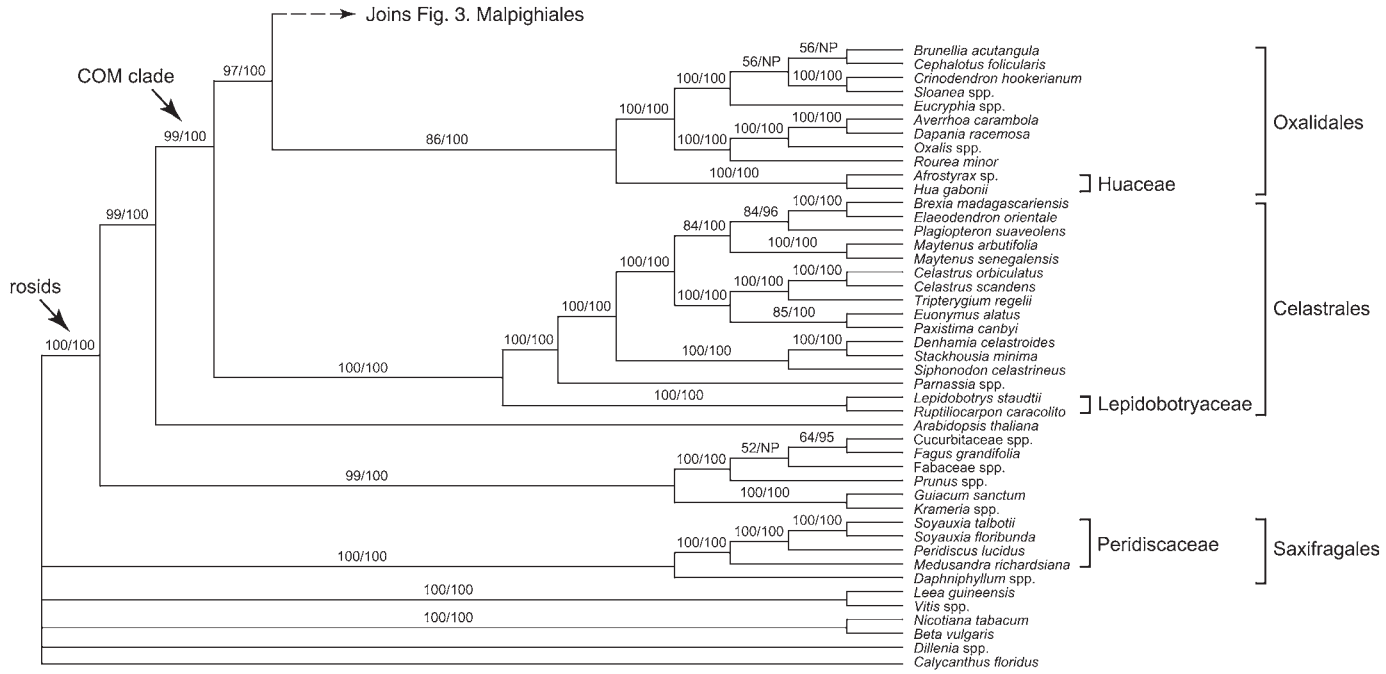


Fig. 2. Maximum likelihood (ML) bootstrap majority-rule consensus tree based on the combined 13-gene, 190 taxon, data set with third positions removed from *PHYC* and *EMB2765*. ML bootstrap/Bayesian posterior probabilities >50% are indicated. NP = not present in Bayesian analysis; spp. = composite terminals with multiple species. Sensu lato families follow APG II (2003). Tree continued in Fig. 3.

Gadagkar and Kumar, 2005; Whitfield and Lockhart, 2007; Whitfield and Kjer, 2008). We have placed less emphasis on parsimony in our discussion because it routinely produced lower support values deeper in the tree (online Appendix S4, S5), despite high ML and Bayesian support (>85 BP or 100 PP, respectively). This loss of support was especially pronounced in the euphorb clade and for the placement of Ctenolophonaceae as sister to Erythroxylaceae + Rhizophoraceae (<50 parsimony BP). Not only are these clades otherwise very strongly supported using ML and Bayesian methods, they are also supported on the basis of morphology (discussed later). A similar decrease in support is also observed in the placement of Oxalidales as sister to Malpighiales (53 parsimony BP). For these reasons, our subsequent discussion focuses on the 13-gene ML analysis with the most rapidly evolving sites removed (Figs. 2, 3), which better meets the objectives of this study and is not prone to artificially inflated support values as has been observed with Bayesian methods (Suzuki et al., 2002; Douady et al., 2003; Simmons et al., 2004).

Oxalidales + Huaceae is the sister group to Malpighiales—The COM (i.e., Celastrales, Oxalidales, and Malpighiales; sensu Matthews and Endress, 2006) + Huaceae clade has previously been found to have strong support, but resolution among its subclades has been unclear. Oxalidales (Davis and Wurdack, 2004; Davis et al., 2005a, b, 2007; Zhu et al., 2007; Wang et al., 2009) and Celastrales (Zhang and Simmons, 2006; Soltis et al., 2007b) have both been recovered as sisters to Malpighiales. Oxalidales + Celastrales as the sister to Malpighiales has also been inferred elsewhere, but is without strong support (Savolainen et al., 2000a; Hilu et al., 2003).

Our combined topology recovers Huaceae + Oxalidales as the strongly supported (97 BP, 100 PP) sister group to Malpighiales. Moreover, our alternative topology test rules out the placement of Celastrales as sister to Malpighiales (AU test, $P < 0.0001$). Studies of floral morphology indicate that Malpighiales share more features with Celastrales than with Oxalidales (Matthews and Endress, 2002, 2005). In particular, Lepidobotryaceae, which is the sister to the remaining Celastrales, shares several floral features with Malpighiales (Matthews and Endress, 2005). However, these features may be plesiomorphic in the COM clade. Until the early-diverging lineages of Malpighiales are better characterized; however, it will likely remain difficult to interpret patterns of character evolution between these orders to identify synapomorphies.

Huaceae contain the small tropical African genera *Hua* and *Afrostyrax* (both sampled here). The family has been placed with Malvales or Malpighiales on the basis of morphology (Baas, 1972; Cronquist, 1981; Takhtajan, 1997), and APG II (2003) treated the group as a member of the eurosid I clade without ordinal affiliation. Molecular phylogenetic studies have weakly supported this taxon as either sister to the entire COM clade or as sister to each of its three constituent orders (Nandi et al., 1998; Savolainen et al., 2000a, b; Soltis et al., 2000, 2003, 2007b; Davis and Wurdack, 2004; Davis et al., 2005b; Zhu et al., 2007; Wang et al., 2009). Here we recover a strongly supported (86 BP, 100 PP) placement of Huaceae as sister to Oxalidales (congruent with the results of Zhang and Simmons, 2006; Davis et al., 2007). We propose that the circumscription of Oxalidales should be expanded to include Huaceae, as opposed to adding another order to the COM clade (i.e., Huales; Doweld, 2001). Nonmolecular synapomorphies for Oxalidales are still poorly known, and Huaceae are especially unusual in their basal placentation and glandular leaves.

Medusandra belongs in Saxifragales—*Medusandra* and *Soyauxia* have either been united in Medusandraceae (Brenan, 1954) or considered distant relatives, with *Medusandra* placed

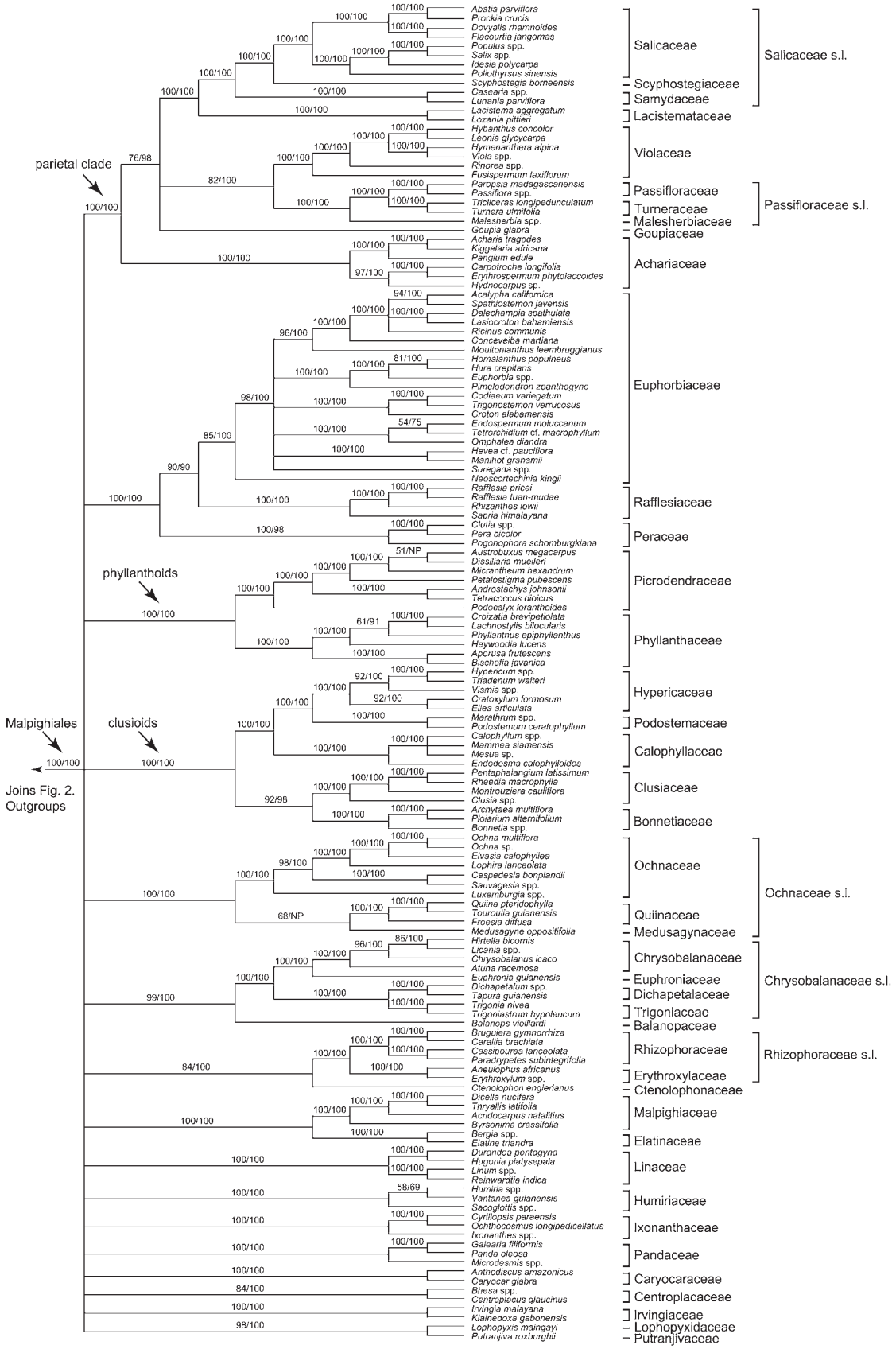


Fig. 3. Continuation of Fig. 2. Maximum likelihood majority-rule bootstrap consensus tree based on the combined 13-gene data set.

in Santalales and *Soyauxia* placed in Passifloraceae or Flacourtiaceae (Cronquist, 1981; Takhtajan, 1997). *Soyauxia* was recently included with Peridiscaceae in Saxifragales (Bayer, 2007; Soltis et al., 2007a; Jian et al., 2008), and *Medusandra* has been placed in Malpighiales near Passifloraceae based on unpublished molecular data (Soltis et al., 2005; Haston et al., 2007). APG II (2003) considered both genera as unplaced, presumably reflecting the uncertainty of their close relations to one another.

Our results do not support the placement of *Medusandra* in Malpighiales and instead we obtain strong support (100 BP, 100 PP) for the placement of *Medusandra* with Saxifragales as sister to Peridiscaceae (i.e., *Soyauxia* + *Peridiscus*). Our analyses using the three-gene angiosperm data set of Soltis et al. (2000, 2007a) also recover a strongly supported sister group relationship of this taxon with Peridiscaceae (results not shown).

We believe that our sequences are authentic given the great care in obtaining these data (see Materials and Methods) and the correct identity of the source herbarium collection. Moreover, this phylogenetic result is in much better agreement with morphology. An association of *Medusandra* with Passifloraceae is not supported by wood anatomy, palynology, or floral features (Brenan, 1952, 1954; Melcalfe, 1952), but agrees well with its placement with other Peridiscaceae (see Davis and Chase, 2004; Soltis et al., 2005, 2007a; Bayer, 2007), which share similar floral features (unilocular ovary with free central placentation and pendulous ovules, and separate stylodia with minute punctate stigmas that lack papillae or protruberances) and seed structure (similar seed coat anatomy and small embryos; Stevens, 2001 onward). *Medusandra* also contains an insertion in 18S rDNA (a single adenosine) that is synapomorphic for Saxifragales (Soltis et al., 1997). Based on these data, *Medusandra* is best included in an expanded Peridiscaceae comprising four genera (*Medusandra*, *Peridiscus*, *Soyauxia*, and *Whittonia*), rather than treated as the monogeneric Medusandraceae.

Monotypic *Whittonia* is the sole unsampled member of the order. Its previous placement with Malpighiales (Savolainen et al., 2000b) was based on contaminated *rbcL* data (Wurdack, 2002; Davis and Chase, 2004). Although authentic *Whittonia* data has yet to be included in any phylogenetic study (as it is only known from the type collection), its close association with *Peridiscus* seems likely based on their many shared morphological and anatomical features (Metcalfe, 1962; Sandwith, 1962; Davis and Chase, 2004). The type locality of *Whittonia* below Kaieteur Falls in Guyana is still relatively pristine, but the plant was not located after a search in August 2006 by one of us (K.J.W.). Rediscovering this taxon would be helpful for future studies of Peridiscaceae. A more comprehensive sampling of Peridiscaceae may be especially interesting for future biogeographic studies: the West African *Medusandra* and *Soyauxia* are successive sisters to the New World members of the family, suggesting a possible origin of the group in Africa. Peridiscaceae are not only notable in their transoceanic disjunction but also for inhabiting regions and biomes (i.e., wet, tropical rainforests) that are otherwise rare in Saxifragales. Given the age of Saxifragales (Hermsen et al., 2006; Jian et al., 2008), this trans-Atlantic disjunction may be due to ancient vicariance, rather than more recent long-distance dispersal from Africa to South America.

The relationships among the rapidly diverged Saxifragales have been difficult to resolve. It now appears that Peridiscaceae may be sister to the rest of the order (Davis and Chase, 2004; Soltis et al., 2005, 2007a; Jian et al., 2008), making the reconstruction of phylogenetic relationships and patterns of character evolution in this family important for understanding Saxifragales evolution. Peridiscaceae possess many plesiomorphic features identified for Saxifraglales (e.g., woody habit; alternate, simple, pinnately veined leaves, with anomocytic or paracytic stomata; bisexual flowers with a pentamerous perianth, petals, free stamens, basifixed anthers, free styles, and terminal stigmas; Soltis et al., 2005; Hermsen et al., 2006). However, they differ in gynoecial structure, which has been considered a feature of special interest in the order. Saxifragales are inferred to ancestrally possess two partly free carpels (i.e., basally syncarpous and apically free) and appendicular epigyny (Soltis et al., 2005, 2007a). In contrast, Peridiscaceae are apocarpous, three-carpellate, and hypogynous. Although Peridiscaceae have been characterized as "half-inferior" (Soltis et al., 2007a), presumably owing to a conspicuous disc of uncertain homology surrounding the gynoecium of *Peridiscus*, morphological observations by one of us (K.J.W.) indicate that all members of the family possess perianth parts inserted below the ovary (i.e., hypogyny). Understanding the origin of tricarpelly and hypogyny in Peridiscaceae may better inform our understanding of character evolution in Saxifragales. It may be that traits previously thought to be synapomorphic for the order (i.e., bicarpelly and appendicular epigyny) are instead associated with a subclade of Saxifragales. A better understanding of the directionality of these evolutionary trends (e.g., carpel gain in Peridiscaceae vs. carpel loss in the rest of Saxifragales) will require increased resolution of the sister group to Saxifragales.

Malpighiales—Malpighiales form a well-supported (100 BP, 100 PP) clade in our analyses (Fig. 3). Most traditionally recognized families and small groups of related families are resolved with a high degree of support, but relationships involving the deepest subclades are still poorly supported. Changes to the circumscription of Malpighiales since APG II (2003) include the additions of Rafflesiaceae s.s. (Barkman et al., 2004, 2007; Davis and Wurdack, 2004; Nickrent et al., 2004; Davis et al., 2007), *Aneulophus* (Schwarzbach and Ricklefs, 2000), *Bhesa* (Zhang and Simmons, 2006), *Centroplacus* (Wurdack et al., 2004), *Ploiarium* (Wurdack, 2002), and *Trichostephanus* (not sampled here; see Alford, 2005). These taxa are confirmed as Malpighiales in our trees, as is *Cyrillopsis,* which we resolve as a member of Ixonanthaceae. Previous suggestions on the affiliation of *Cyrillopsis* have included Cyrillaceae, Irvingiaceae, Ixonanthaceae, or Linaceae (Robson and Airy Shaw, 1962).

Nonmolecular synapomorphies for Malpighiales remain unclear and the taxon sampling for characters of interest needs to be expanded and appropriately framed within a phylogenetic context to better discern patterns of character evolution deeper in the tree. Levels of homoplasy appear to be high for most morphological characters that have been investigated in the order, however, suggesting that the elucidation of synapomorphies for the order may be difficult to uncover. We cannot begin to better understand the evolution of these morphologies and evaluate correlated patterns of diversification, until we can identify how and when putatively adaptive traits evolved, and if their origin coincided with rapid bursts of species diversification. It may be that their early occupation of tropical rain forest understories best explains their rapid diversification (Davis et al., 2005b) as opposed to single "key innovations." Shifts in diversification rates, possibly associated with movement into

new environments have recently been implicated in playing an important role in the diversification of Dipsacales (Moore and Donoghue, 2007).

Centroplacaceae expanded to include Bhesa—*Centroplacus,* a rather nondescript monotypic West African genus, has been considered as a member of Euphorbiaceae s.l. and associated with the segregate clades Pandaceae (Takhtajan, 1997; Wurdack et al., 2004) or Phyllanthaceae (Webster, 1994; Radcliffe-Smith, 2001). It was unplaced by APG II (2003), and this uncertainty was translated into the recognition of the family Centroplacaceae (Hoogland and Reveal, 2005). Our analyses do not support the association of Centroplacaceae with any of the six euphorb lineages but instead indicate that the family should be expanded to include its well-supported (84 BP, 100 PP) sister, *Bhesa,* which was only recently placed in Malpighiales (Zhang and Simmons, 2006). Support for the *Bhesa* + *Centroplacus* clade is markedly stronger (>95 BP) in other combined analyses (i.e., including third positions, excluding all third positions, and parsimony; online Appendices S2–S5).

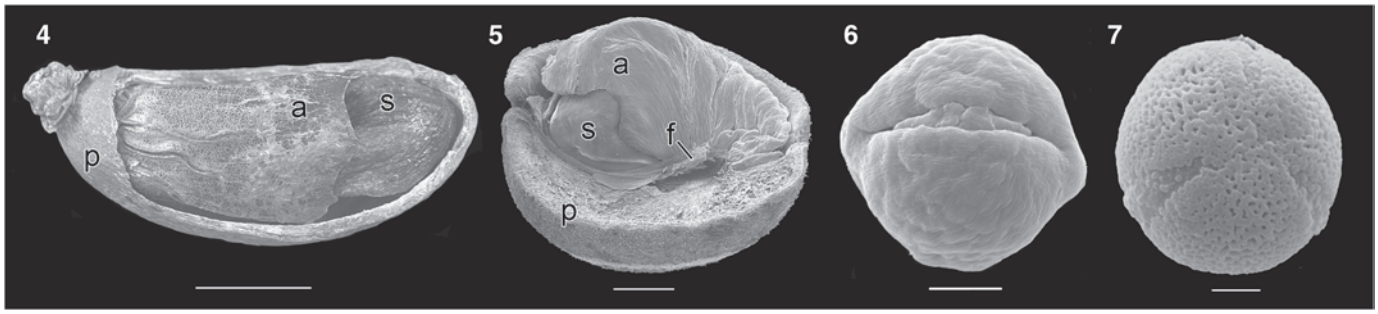
Bhesa includes six species of Indo-Malesian trees and has been traditionally classified in Celastraceae, but is aberrant there based on gross morphology (i.e., venation, sheathing stipules, and separate styles) and nodal and wood anatomy (Pierre, 1894; Ding Hou, 1962; Zhang et al., 1990; Simmons and Hedin, 1999; Simmons, 2004a). *Bhesa* and *Centroplacus* share alternate, stipulate, leaves; pentamerous, haplostemonous flowers with petals and articulated pedicels; similar oppositisepalous stamens; two collateral ovules per locule; separate styles with small stigmas; a floral disc; and loculicidal fruits with one arillate seed per locule (due to abortion of the other ovule). Many of these features are present elsewhere in the order and may be plesiomorphic, but their aril is unique in Malpighiales and therefore almost certainly synapomorphic for this clade. They both possess brightly colored, fleshy, sheet-like arils that arise at the exostome and envelop or nearly envelop the entire seed (Figs. 4, 5). These arils presumably aid in seed dispersal by animals and are orange or red in *Bhesa* (Corner, 1976) and red in *Centroplacus* (fide *McPherson 13734*, NY); other Malpighiales arils are usually cream or white.

We examined the pollen of both genera using SEM to compare their exine structures that were previously poorly resolved in light microscope observations (Punt, 1962; Köhler, 1965; Lobreau-Callen, 1977). We found that both have tricolporate pollen but very different exine patterns (Figs. 6, 7). Despite the similarities previously noted, *Bhesa* and *Centroplacus* are morphologically very distinct from each other. *Centroplacus* is dioecious, has leaves with small teeth and reticulate venation, small persistent stipules without colleters, a trilocular ovary with subapical epitropous ovules, and perforate pollen. *Bhesa* is bisexual, has leaves with entire margins and distinctive scalariform tertiary venation, caducous sheathing stipules with colleters, a bilocular (rarely unilocular) ovary with erect apotropous ovules, and finely striate pollen. Based on these numerous morphological differences, it is tempting to place *Bhesa* in its own family as has been previously suggested (Zhang et al., 1990; Zhang and Simmons, 2006). We prefer, however, to include *Bhesa* in Centroplacaceae to better reflect the new affinities we have uncovered here. Finally, it may be worth noting that combined analyses consistently place Centroplacaceae as sister to the Malpighiaceae + Elatinaceae clade, albeit with weak (<50 BP) support.

Phyllanthoids (Phyllanthaceae + Picrodendraceae)—Phyllanthaceae and Picrodendraceae are strongly supported (100 BP, 100 PP) as sister clades in our analyses. This pairing has either been unresolved or poorly supported in many previous molecular studies (Savolainen et al., 2000b; Wurdack, 2002; Chase et al., 2002; Davis and Chase, 2004; Wurdack et al., 2004; Davis and Wurdack, 2004; Davis et al., 2005b; but supported in Tokuoka and Tobe, 2006; Davis et al., 2007; Korotkova et al., in press). A close affiliation between these two groups has long been accepted on morphological grounds when both were formerly subfamilies of Euphorbiaceae s.l. (i.e., Phyllanthoideae and Oldfieldioideae; Webster, 1994; Radcliffe-Smith, 2001; Wurdack et al., 2004). The families share unisexual flowers, details of embryology (two epitropous ovules per locule, obturator, and nucellar beak), and explosively dehiscent capsular fruits; they are distinguished from one another principally based on palynology and the presence/absence of arils (Wurdack et al., 2004; Sutter et al., 2006). Picrodendraceae have mostly carunculate seeds and echinate brevicolporate pollen with 4–20 apertures, whereas Phyllanthaceae are ecarunculate and have tricolporate and nonechinate pollen. *Podocalyx* from Amazonian South America represents the first-diverging lineage of Picrodendraceae (see also Wurdack, 2002) and has morphological links to Phyllanthaceae, notably ecarunculate seeds and similar wood anatomy (Hayden, 1994; Levin and Simpson, 1994). Other putative early-diverging (sensu Levin and Simpson, 1994) members of Picrodendraceae sampled here are placed elsewhere (i.e., *Croizatia* in Phyllanthaceae, and *Paradrypetes* in Rhizophoraceae) in our analyses.

The absence of *matR* in *Croizatia* and *Lachnostylis*, both members of Bridelieae (subclade F2 sensu Wurdack et al., 2004; Hoffmann et al., 2006), is the first reported loss of this maturase gene (Adams et al., 2002; Qiu and Palmer, 2004). Maturases such as *matR* or *matK* are thought to be intron-splicing factors for transcript maturation and are expected to be conserved (Hausner et al., 2006; Barthet and Hilu, 2007). Angiosperm mitochondrial genomes contain up to 23 group II introns and *matR* is the only native maturase (Sugiyama et al., 2005). The loss of this seemingly important gene requires further investigation and, in particular, to determine whether it is associated with the loss of additional mitochondrial introns. At present, we can say that the loss of *matR* has not resulted in complete mitochondrial intron loss because our data indicate *Croizatia* and *Lachnostylis* retain *nad1B-C*.

Ctenolophonaceae with Erythroxylaceae + Rhizophoraceae—Ctenolophonaceae have been suggested as allied to Humiriaceae, Linaceae, or Malpighiaceae (Saad, 1962; Cronquist, 1981; van Hooren and Nooteboom, 1984; Link, 1992; Takhtajan, 1997). We show instead that the family is well supported (84 BP, 100 PP) as sister to Erythroxylaceae + Rhizophoraceae. These three families share opposite leaves with sheathing, interpetiolar stipules, that are rare features in the order and likely synapomorphic for this clade. Monogeneric Ctenolophonaceae have a relictual disjunct distribution with three species presently in West Africa and Malaysia: fossil evidence starting from the Upper Cretaceous indicates its distribution was formerly much wider, with its distinctive pollen occurring across South America, India, Africa, and Malaysia (Saad, 1962; van der Ham, 1989; Schrank, 1994). Erythroxylaceae and Rhizophoraceae share tropane and pyrrolidine alkaloids, unique sieve-element plastids (PVc type; Behnke, 1988a), colleters (Thiebaut and Hoffmann, 2005), cymose inflorescences,



Figs. 4–7. Fruits and pollen of Centroplacaceae. **4.** Fruit of *Bhesa ceylanica* with valve removed to show single erect seed surrounded by aril. *Bernardi 15754*, US. **5.** Fruit of *Centroplacus glaucinus* with valve and a second seed removed to show aril and central, subapical placenta. *McPherson 13734*, NY. **6.** Equatorial view of pollen of *Bhesa nitidissima*. *Balakrishnan 1173*, US. **7.** Polar view of pollen of *Centroplacus glaucinus*. *Reitsma 2610*, NY. All figures are of untreated dried herbarium material; (5–7) scanning electron micrographs; (4–5) in same orientation. Scale bars: Fig. 4 = 5 mm; Fig. 5 = 1 mm; Fig. 6 = 5 μm; Fig. 7 = 2 μm. *Abbreviations*: a, aril; f, funiculus; p, pericarp; s, seed.

floral morphology (Matthews and Endress, 2007), chlorophyllous embryos, and thickened inner integuments. These synapomorphies do not appear to extend to Ctenolophonaceae, however, phytochemistry and sieve-element plastid type have not been examined in this taxon to date.

Aneulophus was unplaced by APG II (2003), but its traditional affiliation with Erythroxylaceae is confirmed by our data (also Schwarzbach and Ricklefs, 2000; Wurdack, 2002). *Paradrypetes* is an enigmatic genus with two widely disjunct species in Brazil and Ecuador and was once considered a early-diverging member of Euphorbiaceae s.l. subfamily Oldfieldioideae (=Picrodendraceae) due to similar echinate pollen (Levin and Simpson, 1994). Our data indicate that it is well supported (100 BP, 100 PP) as a member of Rhizophoraceae (also Wurdack, 2002; Davis et al., 2005b). Although the genus is morphologically distinct from other Malpighiales in possessing epipetiolar inflorescences, leaves with spinose teeth, and raphides, it shares several features with other Rhizophoraceae including opposite leaves, sheathing interpetiolar stipules with colleters, and chlorophylous embryos. Like Ctenolophonaceae, its phytochemistry and sieve-element plastid type are also unknown.

Clusioids and the resurrection of Calophyllaceae—Family circumscriptions (except for Podostemaceae) and interfamilal relationships for this clade have been difficult to establish (Weitzman and Stevens, 1997; Savolainen et al., 2000a; Gustafsson et al., 2002; Davis and Wurdack, 2004; Notis, 2004; Davis et al., 2007). The difficulty in resolving relationships within the clusioids most likely relates to the fact that the clade is quite ancient (their fossil record dates back ~90 Myr; Crepet and Nixon, 1998) and members appear to display accelerated rates of molecular evolution (Adams et al., 2002; Davis et al., 2007). We recover a strongly supported clusioid clade containing Bonnetiaceae, Hypericaceae, Podostemaceae, and a polyphyletic Clusiaceae. The two subfamilies of Clusiaceae s.l., recognized on morphological grounds (Metcalfe and Chalk, 1950; Weitzman and Stevens, 1997; Notis, 2004; Stevens, 2007), do not form a clade: subfamily Kielmeyeroideae are sister to Hypericaceae + Podostemaceae, and subfamily Clusioideae are sister to Bonnetiaceae. Monophyletic family circumscriptions for the group require either uniting all of the clusioids as a heterogenous Clusiaceae s.l. (Gustafsson et al., 2002; Soltis et al., 2005) or reinstating Calophyllaceae J. Agardh for Clusiaceae-Kielmeyeroideae. We prefer the latter and herein add Calophyllaceae as an additional family of Malpighiales that contains 14 genera and ~476 species (Stevens, 2007). The clusioids notably share multiple types of secretory structures that are sites for the accumulation and/or synthesis of secondary products such as resin, latex, and xanthones. Pellucid-punctate dots (resin/latex cavities sensu Notis, 2004) are a potential synapomorphy for Hypericaceae and Calophyllaceae. Although the other families apparently do not have pellucid dots, Podostemaceae and Clusiaceae s.s. contain canals and Bonnetiaceae produce xanthones (Weitzman and Stevens, 1997; Cook and Rutishauser, 2007; Stevens, 2007).

Ploiarium contains three Southeast Asian species and has been presumed to be the sole Old World vicariant of the otherwise neotropical Bonnetiaceae. Savolainen et al. (2000b) placed *Ploiarium* in Thymelaeaceae (Malvales), but this appears to be an artifact of misidentification (their sample is most likely from a *Gonystylus*, but the voucher from Mt. Kinabalu is lost; K. Cameron, University of Wisconsin, Madison, personal communication). Our analyses using new data recover *Ploiarium* with Bonnetiaceae (also with partial *rbcL* in Wurdack, 2002) as the well-supported (100 BP, 100 PP) sister to neotropical *Archytaea*, which it closely resembles based on morphology (Prakash and Lau, 1976; Dickison and Weitzman, 1996, 1998; Weitzman and Stevens, 1997).

An embedded placement of Podostemaceae within a paraphyletic Hypericaceae has been previously suggested (Gustaffson et al., 2002; Davis and Wurdack, 2004; Notis, 2004). However, our analyses, which include representatives of all three tribes of Hypericaceae, show that Hypericaceae and Podostemaceae are both monophyletic. Links have been drawn between the fully aquatic Podostemaceae and the genus *Hypericum* based on "transitional" semiaquatic species and remarkable vegetative diversity in the latter (Stevens, 2007). In the current study, a connection between Podostemaceae and *Hypericum* is not supported. Instead, our analyses support *Hypericum* as firmly nested within Hypericaceae. Podostemaceae are so specialized (i.e., thalloid plant body of great diversity in form, highly modified flowers, absence of double fertilization and endosperm) that establishing homologies between the family and Hypericaceae or other clusioids is extremely challenging (Cook and Rutishauser, 2007; Moline et al., 2007). Moreover, a linkage of Podostemaceae and Hypericaceae through semiaquatic Elatinaceae (i.e., Gustafsson et al., 2002) is not supported here; Elatinaceae are supported as sister to Malpighiaceae (here, and in Davis and Chase, 2004). Elatinaceae and the clusioids both have seeds with sinuous-walled

exotegmic cells, but this character is homoplasious and has also evolved independently within Phyllanthaceae (Tokuoka and Tobe, 2001, 2006).

Parietal clade—The strongly supported (100 BP, 100 PP) parietal clade unites 10 families in our trees (i.e., Achariaceae, Goupiaceae, Lacistemataceae, Malesherbiaceae, Passifloraceae, Salicaceae, Samydaceae, Scyphostegiaceae, Turneraceae, and Violaceae). Most of its members share parietal placentation, which is independently derived elsewhere in the order (e.g., in Rafflesiaceae, some clusioids, and Ochnaceae). Until strong support for the parietal clade emerged (Davis et al., 2007; Soltis et al., 2007b), prior phylogenies showed members of this group variously scattered in several smaller subclades or only weakly united (Nandi et al., 1998; Savolainen et al., 2000b; Soltis et al., 2000; Chase et al., 2002; Wurdack, 2002; Davis and Chase, 2004; Davis and Wurdack, 2004; Tokuoka and Tobe, 2006). We follow the alternative classification of Alford (2005) and recognize the two segregates of Salicaceae s.l., Samydaceae (tribe Samydeae with *Casearia* and *Lunania*, sampled here) and monotypic Scyphostegiaceae (*Scyphostegia*), that are successive sisters to Salicaceae sensu stricto. *Scyphostegia* from Borneo is morphologically unusual with its telescoping floral bracts and basal placentation.

Placement of Rafflesiaceae—Rafflesiaceae s.s. include three Southeast Asian genera (*Rafflesia*, *Rhizanthes*, and *Sapria*) and ~20 species that are holoparasites on *Tetrastigma* (Vitaceae). They are remarkable not only in their narrow host specificity and reduced plant body, but also in possessing the world's largest flowers (Meijer, 1993, 1997; Nais, 2001). The family was recently placed in Malpighiales and disassociated from other holoparasitic lineages previously grouped in Rafflesiaceae s.l. and Rafflesiales (Cronquist, 1981; Meijer, 1993; Barkman et al., 2004, 2007; Davis and Wurdack, 2004; Nickrent et al., 2004; Davis et al., 2007). In the current study, we recover a strongly supported (90–100, BP and PP) relationship of Rafflesiaceae within a paraphyletic Euphorbiaceae, congruent with prior results (i.e., Davis et al., 2007). The nested Euphorbiaceae placement was evident in earlier analyses with *matR* (see Davis and Wurdack, 2004, fig. S1), but combined (i.e., *matR*, *PHYC*, and 18S) analyses yielded a different, albeit weakly supported (<50 parsimony BP), placement near Clusiaceae.

Our 13-gene data set includes eight genes that are potentially informative for the placement of Rafflesiaceae (five of six mitochondrial and all three nuclear genes are sampled for Rafflesiaceae). Although these species apparently possess plastids (Behnke, 1988b), no plastid genes have been identified from Rafflesiaceae (also Nickrent et al., 1997; Davis and Wurdack, 2004) and are thus missing from our data set; *nad1B-C* was excluded for Rafflesiaceae because only horizontally transferred copies have been identified from these species (see Materials and Methods; Davis and Wurdack, 2004). Character reconstructions on our combined tree reveal that the support for this placement is largely attributable to mitochondrial data, but signal is also present in nuclear *PHYC*. Although the nuclear data analyzed alone are not in conflict with our placement of Rafflesiaceae, they are inconclusive. ML analyses of those data with third codon positions removed, however, do place Rafflesiaceae as a subclade of Euphorbiaceae, but with very low support (<50 BP). The addition of slowly evolving protein-coding nuclear genes is needed to further corroborate the mitochondrial placement.

Rafflesiaceae s.s. offer limited or highly modified morphological features for comparison to Euphorbiaceae or other Malpighiales, but details of Rafflesiaceae embryology are not inconsistent with Malpighiales (Bouman and Meijer, 1994; Igersheim and Endress, 1998). A feature shared by Rafflesiaceae and Euphorbiaceae is the presence of unisexual flowers. The sole exceptions in Rafflesiaceae are *Rhizanthes zippelii* and *R. lowii,* which appear to have bisexual flowers, in addition to unisexual ones (Meijer and Veldkamp, 1988; Bänziger and Hansen, 2000; Bänziger et al., 2007). The observation of bisexual flowers in these two species merits further investigation, especially as to whether they are functionally bisexual, but is not at odds with a euphorb placement. Many unisexual Euphorbiaceae maintain vestiges of the other sex, and semiperfect euphorb flowers have been observed (e.g., occasional anthers on pistillate flowers). Comparisons of Rafflesiaceae with Passifloraceae (Barkman et al., 2004) based on gross floral structure (i.e., corona and parietal placentation) and limited taxon sampling are not supported (also Davis and Wurdack, 2004; Nickrent et al., 2004).

Rafflesiaceae flowers are fly pollinated and mimic carrion—they lure pollinators through deceit (i.e., offer no reward), thus acting as dual parasites on their pollinators and their *Tetrastigma* hosts (Bänziger, 1996; Nais, 2001). The evolution of floral gigantism and other traits associated with carrion mimicry (e.g., color, texture, scent, and endothermy) are likely related to this specialized pollination biology (Davis et al., 2008). This suite of floral characters appears to be under selection for a more faithful resemblance to the mimicked carrion model. The greatest rate of floral size evolution in Rafflesiaceae occurred along its stem lineage rather than within the crown group (Davis et al., 2007, 2008). Surprisingly, crown-group Rafflesiaceae, whose flowers range in size from ~8–100 cm in diameter, were shown to exhibit a rate of floral size evolution comparable to their small-flowered euphorb relatives. Most Euphorbiaceae flowers are <1 cm in diameter, with the largest ones encountered in petaliferous members of subfamily Crotonoideae (e.g., *Ostodes* at up to 4 cm in diameter) or in the apetalous pistillate flowers of *Hura* (subfamily Euphorbioideae; up to 1.5 cm in diameter). Those large-flowered Euphorbiaceae, however, are well embedded within that family and are phylogenetically distant from Rafflesiaceae (see Wurdack et al., 2005). Subsequent investigations by Barkman et al. (2008), indicate that dramatic changes in floral size have also occurred within crown group Rafflesiaceace (see also Davis, 2008).

The vegetative body of Rafflesiaceae is a host-embedded endophyte consisting of mostly uniseriate parenchymetous filaments (Brown, 1912; Cartellieri, 1926) and is remarkably similar to endophytes in distantly related holoparasites (e.g., Cytinaceae [De Vega et al., 2007] and Hydnoraceae [Tennakoon et al., 2007]). Although homologies for this structure are not yet established, it has root-like behavior (i.e., probable secretory capacity for intercellular intrusive growth and absorptive capacity for nutrient and water transfer). In light of the euphorb placement, a tantalizing hypothesis to consider is that the endophyte might be derived from laticifers. Laticifers share with the endophyte the characteristic of intrusive intercellular growth and are widely distributed in the Euphorbiaceae (Rudall, 1987; Wurdack et al., 2005). Could it be that the presence of laticifers facilitated the origin of holoparasitism in these species? Similarly, given the diversity and systematic importance of chemical characters in Euphorbiaceae (Seigler, 1994), phytochemistry may be fertile ground for identifying shared features between these two groups.

Euphorbiaceae and the resurrection of Peraceae—Euphorbiaceae are the largest family of Malpighiales with over 246 genera and ~6300 species. Except for the first-branching nodes, relationships between the nine major lineages (sensu Wurdack et al., 2004) are mostly poorly resolved. We do establish one new well-supported (96 BP, 100 PP) relationship with *Moultonianthus* (tribe Erismantheae) sister to the rest of subfamily Acalyphoideae. This approaches its traditional classification (Webster, 1994; Radcliffe-Smith, 2001) and is contrary to the recent unsupported placement near subfamily Euphorbioideae (Wurdack et al., 2005).

The first-branching node of Euphorbiaceae was recently delimited as a new subfamily, Peroideae, which contains five genera and ~130 species (Wurdack et al., 2005). We propose the elevation of this clade to familial status (i.e., Peraceae; see Radcliffe-Smith, 1987) to accommodate Rafflesiaceae without making Euphorbiaceae paraphyletic. Most Peraceae share unique fruit and seed coat morphologies, but their association with Euphorbiaceae s.s. have otherwise never been contested on account of the many other morphological features uniting the two families (Webster, 1994; Radcliffe-Smith, 2001; Tokuoka and Tobe, 2003; Wurdack et al., 2005). *Pogonophora* more closely resembles the rest of Euphorbiaceae in fruit and seed features, but the genus is clearly sister (100 BP, 98 PP) to the remaining Peraceae despite questions about its euphorb affinities (close morphological resemblance to Icacinaceae; see Webster, 1994) and recent concerns about its exact phylogenetic position (Tokuoka and Tobe, 2006; Tokuoka, 2007).

Evolution and utility of EMB2765—This newly developed low-copy nuclear gene produces phylogenetic results that are largely congruent with our combined analyses, although strong support is confined to relationships within or between closely related families (online Appendix S6). We believe that this gene may be especially useful at resolving intrafamilial relationships and has the added benefit that the primers we designed are general enough for amplifications from a wide range of angiosperm groups. We easily isolated the gene from most of our outgroups including far removed *Calycanthus*, and GenBank searches indicate homologs occur broadly across angiosperms and in other land plants (i.e., *Physcomitrella*). In *Populus*, *EMB2765* is located on chromosome LGIII and spans 10 335 bp with a predicted protein-coding length of 4665 bp (*Arabidopsis* is 7376 bp and 4530 bp, full length and coding, respectively). It has a conserved gene structure between *Populus* and *Arabidopsis* with 14 exons. Whole-genome projects (e.g., *Arabidopsis*, *Medicago*, *Oryza*, and *Populus*) indicate the gene is usually single copy. However, *Vitis* has a duplication, and some of our sequences contain polymorphic sites (including our *Vitis* data), which suggest the possibility of additional duplications that warrant further investigation. Gene expression for *EMB2765* is confirmed in *Populus* and *Arabidopsis* based on available EST libraries (GenBank and PopulusDB databases, http://www.populus.db.umu.se/). *EMB2765* needs experimental study, but limited characterization has shown *Arabidopsis* mutants produce embryo defective phenotypes (SeedGenes database, http://www.seedgenes.org), and database annotations indicate an RNA helicase gene model.

Conclusions and future directions—Nonmolecular synapomorphies for Malpighiales are poorly known, and the sampling for characters of interest needs to be expanded and appropriately framed in a phylogenetic context to determine which characters define the order and its major subclades. Among the most promising areas for further investigation are comparative embryology (Sutter and Endress, 1995), floral structure and development (Endress and Matthews, 2006; Matthews and Endress, 2006, 2008), seed anatomy (Corner, 1976; Stuppy, 1996; Tokuoka and Tobe, 2001, 2003), wood anatomy (Hayden and Hayden, 2000), and chemotaxonomy (Seigler, 1994).

We believe that greatly expanding the number of informative molecular characters using a phylogenomic approach is necessary to further resolve relationships among the deepest nodes in Malpighiales. In particular, we intend to sample a very large number of characters from slowly evolving regions that exhibit low homoplasy (e.g., mitochondrial or plastid inverted repeat genes). This approach has improved resolution in ancient, rapidly diverged lineages (Moore et al., 2007; Jian et al., 2008), including Malpighiales (Davis et al., 2007). Larger character sets from a carefully selected subset of taxa representing all major Malpighiales clades can then be analyzed simultaneously with our existing taxon/character-rich data set as a large supermatrix.

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APPENDIX 1. Voucher information and GenBank accession numbers for sequences used in this study. New data have GenBank numbers beginning with FJ, and accessions in brackets are from a different extraction or taxon source. A dash (—) indicates that the sequence was unavailable; underlined accession numbers are additional supporting data that was discussed but not used in phylogenetic analyses (i.e., pseudogenes and evidence for *matR* loss). Herbaria acronyms follow Holmgren and Holmgren (1998).

FAMILY. **Species**, *voucher*, (herbarium), GenBank accessions: *atpB*, *matK*, *ndhF*, *rbcL*, *ccmB*, *cob*, *matR*, *nad1B–C*, *nad6*, *rps3*, 18S, *EMB2765*, *PHYC*.

ACHARIACEAE. ***Acharia tragodes*** Thunb., *Cloete s.n.* (BOL), AF209520, EF135498, AY425028, AF206728, EF135075, EF135183, AY674472, AY674643, EF135311, EF135413, AF206728, FJ669724, FJ669878; ***Carpotroche longifolia*** Benth., *Alford* & *Grandez 3117* (BH), —, EF135514, FJ670059, —, —, EF135198, FJ670349, AY674661, EF135326, EF135426, —, —, —; ***Erythrospermum phytolaccoides*** Gardn., *Chase 1277* (K), FJ669964, EF135535, FJ670060, AJ402951, EF135110, EF135216, FJ670350, FJ670411, EF135345, EF135443, FJ669684, FJ669725, —; ***Hydnocarpus* sp.** (originally misidentified as ***Ixonanthes icosandra*** Jack), *Chase 1301* (K), AF209607, EF135551, AY425058, AF206783, EF135126, FJ670266, EF135298, AY674714, EF135359, FJ669582, AF206941, FJ669726, FJ669879; ***Kiggelaria africana*** L., *Alford* & *Lewis 3028* (BH), AY788231, EF135555, FJ670061, AY788180, EF135129, EF135234, AY674527, AY674719, EF135362, EF135456, AY674609, [*Chase 5607* (K), FJ669727], —; ***Pangium edule*** Reinw., *Chase 1285* (K), AF209644, FJ669998, FJ670062, AF206801, FJ670188, FJ670267, FJ670351, AY674742, FJ669491, FJ669583, AF206979, FJ669728, FJ669880.

AMARANTHACEAE. ***Beta vulgaris*** L., *NPGS PI 467870*, [DQ067451], [DQ116790], [AY858633], [DQ067450], FJ670262, [NC_006581], [NC_002511], [BA000009], [BA000024], [BA000009], FJ669720, FJ669871, —.

BALANOPACEAE. ***Balanops vieillardi*** Baill., *Chase 1816* (K), AF209534, EF135505, AY425032, AF089760, EF135081, EF135188, AY674479, AY674652, EF135317, EF135418, AF206860, FJ669729, AY425090.

BONNETIACEAE. ***Archytaea multiflora*** Benth., *Kubitzki* & *Feuerer 97-26* (HBG), AY788202, —, AY425029, AY380342, EF135078, —, AY674475, FJ670412, EF135314, —, AY674574, FJ669730, —; ***Bonnetia sessilis*** Benth., *Berry s.n. 25/7/98* (MO), FJ707526, EF135509, [***B. ahogadoi*** (Steyer.) A.L. Weitzman & P.F. Stevens, AY425035], [***B. roraimae*** Oliv. in Thurn., AJ402930], —, FJ670268, EF135292, FJ670413, FJ669492, —, FJ707523, FJ669731, FJ669881; ***Ploiarium alternifolium*** Melchoir, *Sugumaran 165* (US), FJ669965, FJ669999, FJ670063, FJ670161, FJ670189, FJ670269, FJ670352, FJ670414, FJ669493, —, FJ669685, FJ669732, —.

BRASSICACEAE. ***Arabidopsis thaliana*** (L.) Heynh., NC_000932, NC_000932, NC_000932, NC_000932, NC_001284, Y08501, NC_001284, X98301, NC_001284, NC_001284, NC_003071, NM_179966, X17343.

BRUNELLIACEAE. ***Brunellia acutangula*** Humb. & Bonpl., *Stergios 20646* (US), FJ669993, EF135512, FJ670136, FJ707536, FJ670243, FJ670326, DQ110330, AY674657, FJ669556, FJ669656, FJ669718, FJ669845, FJ669942.

CALOPHYLLACEAE. ***Calophyllum soulattrie*** Burm. f., *Chase 1217* (K), —, —, AY425037, [***C.* sp**. Z75672], EF135088, EF135196, AY674484, AY674659, EF135324, —, AY674580, —, AY425093; ***Endodesma calophylloides*** Benth., *Burgt 762* (WAG), FJ669967, FJ670005, FJ670069, FJ670163, FJ670195, FJ670274, FJ670356, FJ670418, FJ669498, FJ669588, FJ669688, FJ669740, FJ669887; ***Mesua* sp.** (probably ***Kayea* sp.,** fide Notis, 2004), *Coode 7884* (K), AF209627, EF135567, AY425069, AF206794, EF135140, EF135246, AY674540, AY674735, EF135374, —, AF206962, FJ669741, AY425118.

CALYCANTHACEAE. ***Calycanthus floridus*** L., *Wen 894* (A), [NC_004993], [NC_004993], [NC_004993], [NC_004993], FJ670265, FJ670348, [AF197777], [AY832126], FJ669580, FJ669683, [U38318], FJ669874, FJ669963.

CARYOCARACEAE. ***Anthodiscus amazonicus*** Gleason & A.C. Sm., *van der Werff 13889* (MO), FJ669966; FJ670000, FJ670064, FJ670162, FJ670190, FJ6702270, FJ670353, FJ670415, FJ669494, FJ669584, FJ669686, FJ669733, —; ***Caryocar glabrum*** Pers., *Mori 22997* (NY), AF206745, EF135515, AY425039, Z75671, EF135089, EF135199, AY674486, AY674662, EF135327, EF135427, AF206881, FJ669734, FJ669882.

CELASTRACEAE. ***Brexia madagascariensis*** Thouars, *Wurdack D764* (US), [AJ235419], EF135510, FJ670144, [L11176], EF135086, EF135193, AY674482, AY674655, EF135321, EF135422, [U42543], FJ669851, FJ669950; ***Celastrus orbiculatus*** Thunb., *Simmons 1773* (BH), AY788263, EF135517, FJ670145, AY788194, EF135091, —, EF135295, AY674664, EF135329, EF135429, AY788162, —, FJ669951; ***Celastrus scandens*** L., *Simmons 1783* (BH), AY788264, FJ670050, FJ670146, AY788195, —, —, AY674488, AY674665, —, —, AY674581, —, AY674449; ***Denhamia celastroides*** (F. Muell.) L.W. Jessup, *Chase 2050* (K), AY788267, EF135526, AY425043, AJ402941, EF135100, EF135209, EF135297, AY674680, EF135336, —, AY674591, —, AY425097; ***Elaeodendron orientale*** Jacq., *Chase 1213* (K), AY788269, EF135531, —, AY380347, EF135106, —, AY674506, AY674689, EF135341, EF1354439, AY674593, —, AY425103; ***Euonymus alatus*** Siebold, *Simmons 1772* (BH), AY788270, EF135537, FJ670147, AY788197, [EF135112], [EF135218], AY674511, AY674694, [EF135347], [EF1354445], AY788164, —, AY674453; ***Maytenus arbutifolia*** (Hochst. ex A. Rich.) R.Wilczek, *Collenette 2/93* (K), AY788271, EF135565, FJ670148, AY380352, EF135138, EF135244, AY674538, AY674732, EF135372, FJ669662, AY674616, FJ669852, AY425116; ***Maytenus senegalensis*** (Lam.) Exell, *Collenette 4/93* (K), AY788272, EF135566, AY425068, AY380353, EF135139, EF135245, EF135301, AY788286, EF135373, FJ669663, AY788165, FJ669853, AY425117; ***Paxistima canbyi*** A. Gray, *Simmons 1775* (BH), AY788273, FJ670051, FJ670149, AY788198, —, —, AY674548, AY674746, —, —, AY674623, —, —; ***Plagiopteron suaveolens*** Griff., *Chase 1335* (K), AJ235562, FJ670052, FJ670150, FJ670182, FJ670250, FJ670332, FJ670399, AY674751, FJ669562, FJ669664, AF206993, FJ669854, FJ669952; ***Siphonodon celastrineus*** Griff., *Chase 2097* (K), AF209676, FJ670053, FJ670151, FJ670183, —, FJ670333, FJ670400, AY674771, FJ669563, FJ669665, AF207021, FJ669855, FJ669953; ***Stackhousia minima*** Hook. f., *Molloy s.n.* (CHR), AJ235610, EF135596, —, FJ670184, EF135170, EF135276, AY674564, AY674773, FJ669564, EF135487, AF207026, FJ669856, AY425131; ***Tripterygium regelii*** Sprague & Takeda, *Simmons 1776* (BH), AY788260, FJ670054, FJ670152, AY788193, —, [*Chase 1003*

(K), FJ670334], AY674568, AY674781, —, [*Chase 1003* (K), FJ669666], AY788161, [*Chase 1003* (K). FJ669857], [*Chase 1003* (K), FJ669954].

CENTROPLACACEAE. ***Bhesa robusta*** (Roxb.) Ding Hou, *Laman 283* (L), [AY935826], [AY935898] + FJ670001, [***B. archboldiana*** (Merr. & L.M. Perry) Ding Hou, *Takeuchi & Ama 16456* (GH), FJ670065], [AY935723], [***B. paniculata*** Arn., *Sugumaran 118* (US), FJ670191], [***B. paniculata*** Arn., *Sugumaran 118* (US), FJ670271], [***B. paniculata*** Arn., *Sugumaran 118* (US), FJ670354], FJ670416, FJ669495, [***B. archboldiana*** (Merr. & L.M.Perry) Ding Hou, *Takeuchi & Ama 16456* (GH), FJ669585], [AY929341], [***B. paniculata*** Arn., *Sugumaran 118* (US), FJ669735], [***B. paniculata*** Arn., *Sugumaran 118* (US), FJ669883]; ***Centroplacus glaucinus*** Pierre, *White 128, ser. 1* (MO), AY788207, FJ670002, FJ670066, AY663646, [*Wieringa 5505* (WAG), FJ670192], [*Wieringa 5505* (WAG), FJ670272], FJ670355, AY788277, [*Wieringa 5505* (WAG), FJ669496], FJ669586, AY674582, [*Wieringa 5505* (WAG), FJ669736], FJ669884.

CEPHALOTACEAE. ***Cephalotus folicularis*** Labill., *Chase 147* (NCU), AY788265, FJ670045, —, L01894, FJ670244, —, AY674489, AY674666, FJ669557, —, U42515, FJ669846, FJ669943.

CHRYSOBALANACEAE. ***Atuna racemosa*** Rafin., *Chase 2118* (K), AY788203, EF135503, AY425030, AF089758, EF135079, EF135186, AY674476, AY674650, EF135315, EF135416, AY674575, —, AY425088; ***Chrysobalanus icaco*** L., *Wurdack D711* (US), [AF209562], EF135519, FJ670067, [L11178], EF135093, EF135202, AY674491, [AY674668], EF135331, EF135431, [U42519], FJ669737, FJ669885; ***Hirtella bicornis*** Mart. & Zucc., *Ducke Res. 2-303Z.489* (K?), AY788225, FJ670003, AY425055, AF089756, FJ670193, EF135227, AY674520, AY674706, EF135354, EF135451, AY674603, FJ669738, AY425109; ***Licania michauxii*** Prance, *Wurdack D788* (US), [***L. tomentosa*** Fritsch, AF209617], FJ670004, FJ670068, [***L. tomentosa*** Fritsch, L11193], FJ670194, FJ670273, AY674532, FJ670417, FJ669497, FJ669587, [***L. tomentosa*** Fritsch, U42520], FJ669739, FJ669886.

CLUSIACEAE. ***Clusia gundlachii*** Stahl, *Chase 341* (NCU), AY788209, EF135520, AY425041, Z75673, [***C. rosea*** Jacq., EF135094], [***C. rosea*** Jacq., EF135203], AY674493, —, [***C. rosea*** Jacq., EF135332], [***C. rosea*** Jacq., EF135332], AY674584, —, AY425095; ***Mammea siamensis*** T. Anderson, *Chase 1216* (K), FJ669968, FJ670006, FJ670070, [AY625028], FJ670196, FJ670275, FJ670357, FJ670419, FJ669499, FJ669589, FJ669689, —, FJ669888; ***Montrouziera cauliflora*** Planch. & Triana, *Lowry 5601* (MO), FJ669969, FJ670007, FJ670071, FJ670164, FJ670197, FJ670276, FJ670358, —, FJ669500, FJ669590, FJ669690, FJ669742, FJ669889; ***Pentaphalangium latissimum*** Lauterb., *Chase 2100* (K), FJ669970, FJ670008, FJ670072, AF518386, FJ670198, FJ670277, FJ670359, —, FJ669501, FJ669591, FJ669691, FJ669743, FJ669890; ***Rheedia macrophylla*** Planch. & Triana, *Chase 1219* (K), FJ669971, —, FJ670073, FJ670165, FJ670199, FJ670278, FJ670360, —, FJ669502, FJ669592, FJ669692, FJ669744, FJ669891.

CONNARACEAE. ***Rourea minor*** Leenh., *Chase 1221* (K), AJ235585, EF135591, FJ670137, FJ707537, FJ670245, FJ670327, DQ110357, AY674764, FJ669558, FJ669657, EF135603, FJ669847, FJ669944.

CTENOLOPHONACEAE. ***Ctenolophon englerianus*** Mildbr., *McPherson 16911* (MO), AY788215, EF135524, FJ670074, [AJ402940], EF135098, [EF135207], [AY674499], AY674676, [EF135335], [EF135436], [AY674589], FJ669745, FJ669892.

CUCURBITACEAE. ***Cucumis sativus*** L., *NPGS Ames 7736*, [AJ970307], [AJ970307], [AJ970307], [AF206755], FJ670257, FJ670341, [***Cucurbita pepo*** L., AY453101], [***Gurania megistantha*** Donn. Sm., AY256881], FJ669571, FJ669674, [***Cucurbita pepo*** L., AF206895], FJ669865, FJ669961.

CUNONIACEAE. ***Eucryphia milliganii*** Hook. f., *Chase 2528* (K), [***E. lucida*** (Labill.) Baill., AF209584], FJ670046, FJ670138, [***E. lucida*** (Labill.) Baill., L01918], FJ670246, FJ670328, AY674510, AY674693, FJ669559, FJ669658, [***E. lucida*** (Labill.) Baill., U42533], FJ669848, FJ669945.

DAPHYNIPHYLLACEAE. ***Daphyniphyllum macropodum*** Miquel, *Wurdack 4532* (US), [***D.* sp.**, AF092118], [***D.* sp.**, AF274612], FJ670160, [***D.* sp.**, L01901], FJ670264, FJ670347, [*Qiu 01-102*, FJ670407], [AY674679], FJ669579, FJ669682, [***D.* sp.** U42531], FJ669873, [AY674452].

DICHAPETALACEAE. ***Dichapetalum macrocarpum*** Engl., *Fisson s.n. 10/8/93* (K), [***D. brownii*** Baill., AJ235455], EF135527, AY425044, AF089764, EF135102, [***D. brownii*** Baill., *Chase 624* (K), FJ670279], AY674502, [***D. brownii*** Baill. AY674683], EF135338, [***D. brownii*** Baill., *Chase 624* (K), FJ669587], AF206902, [***D. brownii*** Baill., *Chase 624* (K), FJ669746], AY425098; ***Tapura guianensis*** Aubl., *Ducke Res. 4-557* (K), FJ669972, [*Neill 6508* (NY), FJ670009], FJ670075, AF089763, EF135171, EF135277, [*Neill 6508* (NY), FJ670361], [*Neill 6508* (NY), FJ670420], EF135401, FJ669594, FJ669693, —, FJ669893.

DILLENIACEAE. ***Dillenia philippinensis*** Rolfe, *Chase 2102* (K), AY788268, EF135602, AY425045, L01903, EF135177, —, [***D. indica*** L., AY163747], AY674684, EF135408, —, AY788163, —, AY425099.

ELAEOCARPACEAE. ***Crinodendron hookerianum*** Gay, *Chase 909* (K), AF209570, AY491655, FJ670139, AF206754, FJ670247, FJ670329, AY674497, AY674673, FJ669560, FJ669659, AF206893, FJ669849, FJ669946; ***Sloanea berteroana*** Choisy ex DC., *Chase 343* (NCU), [***S. latifolia*** K. Schum., AJ235603], FJ670047, FJ670140, [***S. latifolia*** K. Schum., AF022131], FJ670248, FJ670330, FJ670397, AY674772, FJ669561, FJ669660, [***S. latifolia*** K. Schum., U42826], —, FJ669947.

ELATINACEAE. ***Bergia texana*** Seub. ex Walp., *Sanders et al. 13525* (MICH), FJ707527, EF135506, AY425033, AY380344, [EF135083], EF135190, AY674480, —, [EF135318], [***B. pedicellaris*** F. Muell., EF135420], AY674577, [*McKenzie 2046* (MO), FJ669747], AY425091; ***Elatine triandra*** Schkuhr, *Burton et al. 13384* (MICH), [AY788219], [EF135532], AY425049, [AY380349], EF135107, [***E. hexandra*** DC., *Chase 2978* (K), FJ670280], AY674507, [AY674690], EF135342, [EF135440], AY674594, [***E. hexandra*** DC., *Chase 2978* (K), FJ669748], AY425104.

ERYTHROXYLACEAE. ***Aneulophus africanus*** Benth., *White 825* (MO), FJ669973, FJ670010, FJ670076, [*McPherson 16920* (MO), FJ670166], FJ670200, FJ670281, FJ670362, FJ670421, FJ669503, FJ669595, FJ669694, FJ669749, FJ669894; ***Erythroxylum coca*** Lam., *Wurdack D713* (US), [***E. confusum*** Britton, AJ235466], EF135536, FJ670077, [***E. confusum*** Britton, L13183], EF135111, EF135217, AY674509, AY674692, EF135346, [***E.* sp.**, EF135444], [***E. confusum*** Britton, AF206909], FJ669750, —.

EUPHORBIACEAE. ***Acalypha californica*** Benth., *Levin 2192* (SD), AY788199, EF135499, AY425027, AY380341, EF135074, EF135182, EF135289, AY674642, FJ669504, EF135413, AY674571, FJ669751, AY425087; ***Codiaeum variegatum*** (L.) Blume, *Wurdack s.n.* (US), AY788211, EF135522, FJ670079, AY788169, EF135096, EF135205, AY674495, AY674670, FJ669505, EF135434, AY674586, FJ669753, FJ669895; ***Conceveiba martiana*** Baill., *Bell 93-176* (US), AY788212, FJ670011, FJ670080, AY788170, FJ670201, FJ670282, AY674496, AY674671, FJ669506, FJ669596, AY674587, FJ669754, —; ***Croton alabamensis* var. *alabamensis*** E.A. Smith ex Chapman, *Wurdack D8* (US), AY788214, EF135523, AY425042, AY788171, EF135097, EF135206, AY674498, AY674675, EF135334, EF135435, AY674588, —, AY425096; ***Dalechampia spathulata*** (Scheidw.) Baill., *Wurdack D10* (US), AY788216, EF135525, FJ670081, AY788172, FJ670202, FJ670283, EF135296, AY674677, FJ669507, FJ669597, AY788149, FJ669755, —; ***Endospermum moluccanum*** (Teijsm. & Binn.) Kurz, *Chase 1258* (K), AY788220, EF135533, AY425051, AJ402950, EF135108, EF135214, AY674508, AY674691, EF135343, EF135441, AY674595, FJ669756, AY425106; ***Euphorbia epithymoides*** L. (as ***E. polychroma*** Kern.), *Chase 102* (NCU), AJ235472, EF135539, [***E. esula*** L., AF538229], AY788174, EF135114, [***E. abyssinica*** J.F. Gmel, EF135219], AY674512, AY674695, FJ669508, EF135447, [***E. pulcherrima*** Willd. ex Klotzsch, U42535], FJ669757, —; ***Hevea* cf. *pauciflora*** (Spruce ex Benth.) Müll. Arg., *Gillespie 4272* (US), AY788223, EF135547, FJ670082, AY788175, FJ670203, FJ670284, AY674519, AY674703, FJ669509, FJ669598, AY674601, —, FJ669896; ***Homalanthus populneus*** (Geiseler) Pax, *Chase 1266* (K), AY788226, EF135548, AY425056, AY380350, EF135122, FJ670285, AY674521, AY674707, EF135355, EF135452, AY674604, FJ669758, AY425110; ***Hura crepitans*** L., *Wurdack D89* (US), AY788228, FJ670012, FJ670083, AY788177, FJ670204, FJ670286, FJ670363, AY674711, FJ669510, FJ669599, AY674606, FJ669759, FJ669897; ***Lasiocroton bahamiensis*** Pax & K. Hoffm., *Wurdack D58* (US), AY788233, FJ670013, FJ670084, AY788181, FJ670205, FJ670287, FJ670364, AY674723, FJ669511, FJ669600, AY788152, FJ669760, —; ***Manihot grahamii*** Hook., *Wurdack s.n.* (US), FJ707528, FJ670014,

FJ670085, AY94875, FJ670206, FJ670288, FJ670365, FJ670422, FJ669512, FJ669601, FJ707524, FJ669761, FJ669898; ***Moultonianthus leembruggianus*** (Boerl. & Koord.) Steenis, *Challen et al. 3* (K), FJ669974, FJ670015, FJ670086, AY794982, FJ670207, FJ670289, FJ670366, FJ670423, FJ669513, FJ669602, FJ669695, FJ669762, FJ669899; ***Neoscortechinia kingii*** (Hook. f.) Pax & K. Hoffm., *Chase 1265* (K), AY788239, EF135571, AY425071, AJ402977, EF135144, EF135251, AY674543, AY674738, EF135378, EF135467, AY674619, FJ669763, AY425121; ***Omphalea diandra*** L., *Chase 570* (K), AY788241, FJ670016, FJ670087, AY788183, FJ670208, FJ670290, FJ670367, AY674740, FJ669514, FJ669602, AY674622, FJ669764, FJ669900; ***Pimelodendron zoanthogyne*** J.J. Sm., *Chase 1268* (K), AY788247, EF135582, AY425079, AJ418812, EF135154, FJ670291, EF135303, AY674750, EF135385, FJ669604, AY674628, FJ669766, AY425128; ***Ricinus communis*** L., *Wurdack D9* (US), AY788253, EF135590, FJ670089, AY788188, EF135163, EF135270, AY674560, AY674763, FJ669515, EF135482, AY674633, FJ669768, —; ***Spathiostemon javensis*** Blume, *Chase 1261* (K), AY788227, FJ670017, FJ670090, AY788176, FJ670209, FJ670292, FJ670368, AY674708, FJ669516, FJ669606, AY788151, FJ669769, —; ***Suregada glomerulata*** (Blume) Baill., *Chase 1272* (K), [***S. boiviniana*** Baill., AY788255], FJ670018, FJ670091, [***S. boiviniana*** Baill., AY788189], FJ670210, FJ670293, FJ670369, [***S. boiviniana*** Baill., AY788284], FJ669517, FJ669607, [***S. boiviniana*** Baill., AY788157], FJ669770, [***S. boiviniana*** Baill., *Rakotomalaza et al. 1292* (MO). FJ669901]; ***Tetrorchidium* cf. *macrophyllum*** Müll. Arg., *Bell 93-204* (US), AY788257, FJ670019, FJ670092, AY788191, FJ670211, FJ670294, FJ670370, AY674777, FJ669518, FJ669608, AY788159, FJ669771, FJ669902; ***Trigonostemon verrucosus*** J.J. Sm., *Chase 1274* (K), AY788259, FJ670020, FJ670093, AY788192, FJ670212, FJ670295, FJ670371, AY674780, FJ669519, FJ669609, AY788160, FJ669772, FJ669903.

EUPHRONIACEAE. ***Euphronia guianensis*** (R.H. Schomb.) H. Hallier, *Mori 23699* (NY), AY788221, EF135540, AY425052, AF089762, EF135115, EF135220, AY674513, AY674696, EF135348, FJ669610, AY674597, FJ669773, FJ669904.

FABACEAE. ***Heterostemon otophorus*** Sandwith, *Redden 4283* (US), [***Lotus japonicus*** (Regel) K. Larsen, NC_002694], [***Lotus japonicus*** (Regel) K. Larsen, NC_002694], [***Lotus japonicus*** (Regel) K. Larsen, NC_002694], [***Lotus japonicus*** (Regel) K. Larsen, NC_002694], FJ670258, FJ670342, [***Pisum sativum*** L., AY453078], [***Cercis chinensis*** Bunge, DQ110265], FJ669572, FJ669675, [***Pisum sativum*** L., U43011], FJ669866, —.

FAGACEAE. ***Fagus grandifolia*** Ehrh., *Kress 06-8043* (US), [AY935855], [***F. sylvatica*** L., AB046507], [AY586361], [AY935745], FJ670260, FJ670343, [AY263909], [AY968480], FJ669574, FJ669677, [AF206910], FJ669868, FJ669962.

GOUPIACEAE. ***Goupia glabra*** Aubl., *Prevost 3031* (CAY), AJ235484, EF135544, AY425054, AJ235780, EF135119, EF135224, AY674516, AY674699, EF135352, FJ669611, AF206920, FJ669774, AY425108.

HUACEAE. ***Afrostyrax* sp.**, *Cheek 5007* (K), AJ235385, EF135501, FJ670155, AJ235771, FJ670253, FJ670337, AY674473, AY674645, FJ669567, FJ669670, AF206840, FJ669861, FJ669957; ***Hua gabonii*** Pierre ex De Wild., *Wieringa 3177* (WAG), FJ669995, FJ670056, FJ670156, FJ670185, FJ670254, FJ670338, FJ670403, FJ670449, FJ669568, FJ669671, FJ669719, FJ669862, FJ669958.

HUMIRIACEAE. ***Humiria balsamifera*** Aubl., *Anderson 13654* (MICH), AJ235495, EF135549, AF351007, L01926, [Humiria wurdackii Cuatrec., EF135124], EF135229, AY674523, [***H. wurdackii*** Cuatrec., AY674710], EF135357, EF135454, AF206930, —, [***H. wurdackii*** Cuatrec., *Wurdack s.n.* (US). FJ669905]; ***Sacoglottis gabonensis*** Urb., *Stone 3283* (MO), [***S.* sp.**, AB233682], FJ670021, FJ670094, [***S.* sp.**, AB233890], FJ670213, FJ670296, FJ670372, FJ670424, FJ669520, FJ669612, FJ669696, FJ669775, FJ669906 ***Vantanea guianensis*** Aubl., *Pennington 13855* (K), AY788261, EF135600, AY425086, Z75679, EF135175, EF135282, AY674570, AY674783, EF135406, FJ669613, AY674639, FJ669776, AY425132.

HYPERICACEAE. ***Cratoxylum formosum*** (Jack) Benth. & Hook. f. ex Dyer, *Chase 1218* (K), FJ669975, FJ670022, FJ670095, AF518395, —, FJ670297, FJ670373, FJ670425, FJ669521, FJ669614, FJ669697, FJ669777, FJ669907, $\tilde{\Psi}$ *EMB2765* FJ669876, $\tilde{\Psi}$ *EMB2765* FJ669877; ***Eliea articulata*** Cambess., *Razakamalala 295* (MO), FJ669976, FJ670023, FJ670096, FJ670167, —, FJ670298, FJ670374, FJ670426, FJ669522, FJ669615, FJ669698, FJ669778, FJ669908; ***Hypericum empetrifolium*** Willd., *Chase 837* (K), [***H. perforatum*** L., AF209602], [***H. perforatum*** L., DQ168438], AY425060, [***H. perforatum*** L., AF206779], —, EF135232, AY674525, [***H. hypericoides*** Crantz, AY674715], EF135360, [***H. hypericoides*** Crantz, *Wurdack D492* (US), FJ669616], [***H. perforatum*** L., AF206934], [***H. hypericoides*** Crantz, *Wurdack D492* (US), FJ669779], AY425113; ***Triadenum walteri*** (J.F. Gmel.) Gleason, Brant 4792 (MO), FJ669977, —, FJ670097, FJ670168, FJ670214, FJ670299, FJ670375, FJ670427, FJ669523, FJ669617, FJ669699, FJ669780, FJ669909; ***Vismia* sp.**, *Miller et al. 9313* (MO), [***V. rubescens*** Oliver, *Niangadou 374* (MO), FJ669978], EF135601, FJ670098, FJ670169, —, FJ670300, AY674571, AY674784, [EF135407], [***V. rubescens*** Oliver, *Niangadou 374* (MO), FJ669618], AY674640, FJ669781, FJ669910.

IRVINGIACEAE. ***Irvingia malayana*** Oliv., *Simpson 2638* (K?), AF209605, EF135553, AY425061, AF123278, EF135128, EF135233, EF135300, AY674717, EF135361, FJ669619, AF206939, FJ669782, —; ***Klainedoxa gabonensis*** Pierre, *Bradley et al. 1092* (MO), AY788232, EF135556, FJ670099, AY663630, EF135130, EF135235, AY674528, AY674720, EF135363, EF135457, AY674610, FJ669783, AY674456.

IXONANTHACEAE. ***Cyrillopsis paraensis*** Kuhl., *Hentrich 68* (NY), FJ669979, FJ670024, FJ670100, FJ670170, FJ670215, FJ670301, FJ670376, FJ670428, FJ669524, FJ669620, FJ669700, FJ669784, —; ***Ixonanthes reticulata*** Jack, *Sugumaran 149* (US), [***I. chinensis*** Champ., AY788230], [***I. chinensis*** Champ., EF135554], [***I. chinensis*** Champ., AY425062], [***I. chinensis*** Champ., AY788179], FJ670216, FJ670302, [***I. chinensis*** Champ., AY674526], [***I. chinensis*** Champ., AY674718], FJ669525, FJ669621, FJ669701, FJ669785, [***I. chinensis*** Champ., AY674455]; ***Ochthocosmus longipedicellatus*** Steyerm. & Luteyn, *Berry 6561* (MO), FJ707529, EF135573, FJ670101, FJ707535, FJ670217, FJ670303, AY674545, FJ670429, FJ669526, FJ669622, AY674621, FJ669786, FJ669911.

KRAMERIACEAE. ***Krameria lanceolata*** Torr., *Simpson 88-05-1-1* (MICH), [***K. ixine*** L., AJ235514], FJ670058, FJ670158, Y15032, FJ670256, FJ670340, [AY453089], AY674721, FJ669570, FJ669673, [***K. ixine*** L., AF206948], FJ669864, FJ669960.

LACISTEMATACEAE. ***Lacistema aggregatum*** Rusby, *Pennington et al. 583* (K), [AF935858], FJ670025, AY425064, AF206787, FJ670218, FJ670304, AY674529, AY674722, FJ669527, FJ669623, AF206949, FJ669787, FJ669912; ***Lozania pittieri*** (Blake) L.B. Sm., *Pennington et al. 584* (K), FJ669980, FJ670026, FJ670102, AJ418804, FJ670219, FJ670305, FJ670377, FJ670430, FJ669528, FJ669624, FJ669702, FJ669788, FJ669913.

LEEACEAE. ***Leea guineensis*** G. Don, *Wurdack D841* (US), [AJ235520], [AF274621], FJ670159, [AJ235783], —, [EF135285], AY674530, AY674724, [EF135409], [EF135494], AY674612, FJ669869, AY674457.

LEPIDOBOTRYACEAE. ***Lepidobotrys staudtii*** Engl., *Ewango 658* (WAG), [AY935831], [AY935904], —, [AJ402966], FJ670251, FJ670335, FJ670401, FJ670448, FJ669565, FJ669667, [AY929346], FJ669858, FJ669955; ***Ruptiliocarpon caracolito*** Hammel & Zamora, *Hammel 19102* (MO), AY788275, FJ670055, FJ670153, [AJ402997], FJ670252, FJ670336, FJ6703402, AY674765, FJ669566, FJ669668, AY788166, FJ669859, —.

LINACEAE. ***Durandea pentagyna*** K. Schum., *Takeuchi 7103* (MO), AY788218, FJ670027, FJ670103, AY788173, —, FJ670306, FJ670378, AY674688, FJ669529, FJ669625, AY788150, —, FJ669914; ***Hugonia platysepala*** Welw. ex Oliv., *Gereau et al. 5201* (MO), —, —, AY425057, Z75678, EF135123, EF135228, AY674522, AY674709, EF135356, EF135453, —, —, AY425111; ***Linum arboreum*** L., *Chase 478* (K), [***L. perenne*** L. AJ235521], EF135559, AY425066, AY380351, [***L. perenne*** L., *Chase 111* (NCU), FJ670220], EF135238, AY674533, AY674726, EF135366, EF135460, [***L. perenne*** L. L24401], [***L. perenne*** L., *Chase 111* (NCU), FJ669789], [***L. perenne*** L., *Chase 111* (NCU), FJ669915]; ***Reinwardtia indica*** Dumort., *Chase 230* (NCU), AJ235577, AB048380, FJ670104, L13188, FJ670221, EF135268, AY674559, AY674762, EF135394, EF135481, AF207005, FJ669790, AY674462.

LOPHOPYXIDACEAE. ***Lophopyxis maingayi*** Hook. f., *Adelbai P-10203* (US), AY788235, EF135560, FJ670105, AY663643, EF135133, —, AY674534, AY674728 + FJ670431, FJ669530, FJ669626, AY674614, FJ669791, —.

MALESHERBIACEAE. ***Malesherbia linearifolia*** Poir., *Chase 609* (K), AF209622, EF135562, AY425067, AF206792, EF135135, EF135240, AY674536, AY674731, EF135368, EF135462, AF206957, [***M. weberbaurei*** Gilg, *Weigend 2000-365* (NY), FJ669792], —.

MALPIGHIACEAE. ***Acridocarpus natalitius*** Adr. Juss., *Goldblatt s.n.* (PRE), AY788200, AF344525, AF351016, AF344455, EF135076, EF135184, EF135290, AY674644, EF135311, —, AY674573, —, AF500531; ***Byrsonima crassifolia*** Kunth, *FTG 81-680A* (MICH), AY788206, AF344535, AF351011, L01892, EF135087, EF135195, EF135293, AY674658, EF135323, EF135424, AY674579, —, AF500526; ***Dicella nucifera*** Chodat, *Anderson 13607* (MICH), AJ235453, AF344541, AF351048, AJ235802, EF135101, EF135210, AY674501, AY674681, EF135337, EF135437, AF206901, FJ669793, AF500553; ***Thryallis longifolia*** Mart., *Anderson 13657* (MICH), AY788258, AF344580, AF351046, AF344516, EF135172, EF135278, AY674566, AY674778, EF135402, EF135489, AY674638, —, AF500551.

MEDUSAGYNACEAE. ***Medusagyne oppositifolia*** Baker, *Kew 1981-2059 Fay s.n.* (K), AJ235530, FJ670030, FJ670109, [Z75670], FJ670225, FJ670310, AY674539, AY674733, FJ669534, FJ669630, AF206959, FJ669796, FJ669920.

OCHNACEAE. ***Cespedesia bonplandii*** Goudot, *Chase 1325* (K), AY788208, EF135518, AY425040, AJ420168, EF135092, EF135201, AY674490, AY674667, EF135330, EF135430, AY674583, —, AY425094; ***Elvasia calophyllea*** DC., *Amaral s.n.* (K?), FJ669981, FJ670028, FJ670106, FJ670171, FJ670222, FJ670307, FJ670380, FJ670432, FJ669531, FJ669627, FJ669703, —, FJ669917; ***Lophira lanceolata*** Tiegh., *Schmidt 1902* (MO), FJ669982, FJ670029, FJ670107, FJ670172, FJ670223, FJ670308, FJ670381, FJ670433, FJ669532, FJ669628, FJ669704, FJ669794, FJ669918; ***Luxemburgia octandra*** A. St.-Hil., *Batista dos Santos 0013* (US), FJ669983, —, FJ670108, [***L. ciliosa*** (Mart.) Tiegh., Z75685], FJ670224, FJ670309, FJ670382, FJ670434, FJ669533, FJ669629, FJ669705, FJ669795, FJ669919; ***Ochna multiflora*** DC., *Chase 229* (NCU), AJ235546, EF135572, AY425072, Z75273, EF135145, EF135252, EF135302, AY788280, EF135379, EF135468, AF206974, FJ669797, AY425122; ***Ochna* sp.**, *Davis 31-01* (A), AY788240, FJ670031, AY425073, AY380354, —, —, AY674544, AY674739, —, —, AY674620, —, AY425123; ***Sauvagesia erecta*** L., *Miller 8852* (MO), FJ669984, EF135593, FJ670110, [***S. calophylla*** (Boerl.) M.C.E. Amaral, Z75686], [EF135167], FJ670311, EF135306, FJ670435, [EF135398], FJ669631, EF135604, FJ669798, —.

OXALIDACEAE. ***Averrhoa carambola*** L., *Chase 214* (NCU), AJ235404, FJ670048, FJ670141, L14692, FJ707532, FJ707533, AY674478, AY674651, FJ707534, FJ669661, AF206859, FJ669850, FJ669948; ***Dapania racemosa*** Korth., *Ambri & Arifin 1014* (K), AY788266, FJ670049, FJ670142, AY788196, —, —, AY674500, AY674678, —, —, AY674590, —, FJ669949; ***Oxalis acetosella*** L., *Fay 440* (K), FJ707531, [***O. stricta*** L., AY935936 + AF542605], FJ670143, FJ670181, [***O. violacea*** L., *Kress 04-7463* (US), FJ670249], [***O. violacea*** L., *Kress 04-7463* (US), FJ670331], FJ670398, [***O. stricta*** L., AY968484], —, —, [***O. dillenii*** Jaq., AF206978], —, —.

PANDACEAE. ***Galearia filiformis*** (Blume) Boerl., *Chase 1334* (K), AY788222, EF135542, AY425053, AJ418818, EF135117, EF135222, AY674515, AY674698, EF135350, EF135448, AY674598, FJ669799, AY425107; ***Microdesmis puberula*** Hook. f. ex Planch., *Cheek 5986* (K), [***M. pierlotiana*** J. Léonard, AY788238], EF135570, AY425070, [***M. pierlotiana*** J. Léonard, AJ402975 + AJ403029], [***M. pierlotiana*** J. Léonard, *Gereau et al. 5654* (MO), FJ670226], EF135249, AY674542, AY674737, EF135376, EF135465, [***M. pierlotiana*** J. Léonard, AY674618], [***M. pierlotiana*** J. Léonard, *Gereau et al. 5654* (MO), FJ669800], AY425120; ***Panda oleosa*** Pierre, *Schmidt et al. 2048* (MO), AY788242, FJ670032, FJ670111, AY663644, FJ670227, FJ670312, FJ670383, AY788281, FJ669535, FJ669632, AY788153, FJ669801, FJ669921.

PARNASSIACEAE. ***Parnassia grandifolia*** DC., *Wurdack D795* (US), [***P. palustris*** L., AJ235552], EF135575, FJ670154, [***P. palustris*** L., AY935731], EF135147, EF135254, AY674546, AY674743, EF135381, EF135470, [***P. palustris*** L., AY929352], FJ669860, FJ669956.

PASSIFLORACEAE. ***Paropsia madagascariensis*** (Baill.) H. Perrier, *Zyhra 949* (WIS), AF209645, EF135576, FJ670112, AF206802, EF135148, EF135255, AY674547, AY674744, FJ669536, EF135471, AF206980, FJ669802, —, $\tilde{\Psi}$ *nad6* FJ669581; ***Passiflora coccinea*** Aubl., *Chase 2475* (K), AJ235553, EF135577, AY425074, L01940, EF135149, EF135256, [***P. edulis*** Sims, AY453071], AY674745, EF135382, EF135472, [***P. standleyi*** Killip, AF206981, FJ669803, —.

PERACEAE. ***Clutia pulchella*** L., *Chase 5876* (K), [***C. tomentosa*** L., AY788210], EF135521, FJ670078, [***C. tomentosa*** L., AY788168], [***C. myricoides*** Jaub. & Spach., EF135095], [***C. myricoides*** Jaub. & Spach., EF135204], AY674494, [***C. tomentosa*** L. AY674669], [***C. myricoides*** Jaub. & Spach., EF135333], [***C. myricoides*** Jaub. & Spach., EF135433], [***C. tomentosa*** L., AY674585], FJ669752, —; ***Pera bicolor*** (Klotzsch) Müll. Arg., *Gillespie 4300* (US), AY788244, EF135578, AY425075, AY380355, EF135150, EF135257, AY674549, AY674747, EF135383, EF135473, AY674624, FJ669765, AY425124; ***Pogonophora schomburgkiana*** Miers ex Benth., *Larpin 1022* (US), AY788250, EF135585, FJ670088, AY788185, [EF135157], [EF135262], EF135305, AY674755, [EF135388], FJ669605, AY788156, FJ669767, —.

PERIDISCACEAE. ***Medusandra richardsiana*** Brenan, *Nemba & Thomas 536* (MO), FJ669996, —, —, FJ670186, —, —, FJ670405, —, FJ669576, FJ669679, FJ669721 + FJ669722, —, —; ***Peridiscus lucidus*** Benth., *Soares 205* (CEPEC), AY372816, DQ411570, AY425076, AY380356, FJ670263, FJ670346, AY674550, AY674748, FJ669577, FJ669680, AY372815, FJ669872, AY425125; ***Soyauxia floribunda*** Hutch., *Kpadeyeah 20* (WAG), FJ669997, —, —, FJ670187, —, —, FJ6703406, —, FJ669578, FJ669681, FJ669723, —, —; ***Soyauxia talbotii*** Baker f., *Cheek 10617* (K), AM111357, —, —, AM111356, —, —, —, —, —, —, AM111355, —, —.

PHYLLANTHACEAE. ***Aporusa frutescens*** Blume, *Chase 1251* (K), AY788201, AY552430, FJ670113, Z75674, FJ670228, FJ670313, FJ670384, AY674647, FJ669537, FJ669633, AY788147, FJ669804, AY579835; ***Bischofia javanica*** Blume, *Levin 2200* (SD), AY788205, EF135508, FJ670114, AY663571, EF135085, EF135191, AY674481, AY674654, EF135320, EF135421, AY674578, FJ669805, [AY579838]; ***Croizatia brevipetiolata*** (Secco) Dorr, *Dorr & Yustiz 8555* (US), AY788213, FJ670033, AY830310, AY663579, FJ670229, —, —, AY674674, FJ669538, FJ669634, AY788148, FJ669806, FJ669922, *nad1D* FJ670409; ***Heywoodia lucens*** Sim, *Saufferer et al. 1544* (US), AY788224, AY552430, FJ670115, AY663587, —, FJ670314, —, AY674704, FJ669539, FJ669635, AY674602, FJ669807, [AY579851]; ***Lachnostylis bilocularis*** R.A. Dyer, *Kurzweil 83/88* (K), AY830218, FJ670034, AY425063, LB1418813, FJ670230, FJ670315, —, FJ670436, FJ669540, FJ669636, AY674611, FJ669808, AY425114, *nad1D* FJ670410; ***Phyllanthus epiphyllanthus*** L., *Wurdack D56* (US), AY788246, EF135581, AY425078, AY663604, EF135153, EF135260, AY674552, AY674749, FJ669541, EF135476, AY674627, FJ669809, AY425127.

PICRODENDRACEAE. ***Androstachys johnsonii*** Prain, *Chase 1904* (K), AF209527 + AJ402922, EF135502, AF500495, AJ402922, EF135077, EF135185, AY674474, AY674646, EF135313, EF135415, AF206848, FJ669810, AF500522; ***Austrobuxus megacarpus*** P.I. Forster, *Forster 21239* (BRI), AY788204, EF135504, AY425031, AY380343, EF135080, EF135187, AY674477, AY788276, EF135316, EF135417, AY674576, FJ669811, AY425089; ***Dissiliaria muelleri*** Baill., *Forster 14629* (BRI), FJ707530, EF135528, AY425046, AY380346, EF135103, EF135211, AY674503, AY674685, EF135339, EF135438, FJ669707, FJ669812, AY425100; ***Micrantheum hexandrum*** Hook. f., *Chase 1940* (K), AY788237, EF135569, FJ670116, AJ418816, EF135142, EF135248, AY674541, AY674736, EF135375, EF135464, AY674617, FJ669813, AY425119; ***Petalostigma pubescens*** Domin, *Clifford s.n.* (BRI), AY788245, EF135579, AY425077, AY380357, EF135151, EF135258, AY674551, AY788283, EF135384, EF135474, AY674626, FJ669814, AY425126; ***Podocalyx loranthoides*** Klotzsch, *Berry & Aymard 7226* (MO), AY788248, EF135583, FJ670117, AY663647, EF135155, EF135261, AY674553, AY674752, EF135386, EF135477, AY674629, FJ669815, FJ669923, Ψ*–EMB2765* FJ669875; ***Tetracoccus dioicus*** Parry, *Levin 2202* (DUKE), AY788256, FJ670035, FJ670118, AY788190, FJ670231, FJ670316, FJ670385, AY674774, FJ669542, FJ669637, AY788158, FJ669816, FJ669924.

PODOSTEMACEAE. ***Marathrum* c.f. *oxycarpum*** Tul., *Gabriel da Cachoeirc 9/1996* (AM), FJ669985, EF135564, —, [***M. oxycarpum*** Tul., AJ402971], —, EF135243, AY674537, FJ670437, EF135371, FJ669638, [***M. rubrum*** A. Novelo & C.T. Philbrick, AF206958], FJ669817, —; ***Podostemum***

ceratophyllum Michx., *Horn & Wurdack s.n.* (DUKE), [AY788249], [EF135584], —, [AJ418819], EF135156, —, EF135304, AY674754, EF135387, FJ669639, AY674630, FJ669818, —.

PUTRANJIVACEAE. ***Putranjiva roxburghii*** Wall. (as ***Drypetes roxburghii*** [Wall.] Hurus.), *Wurdack D57* (US), [AF209578], EF135530, [AY425048], [M95757], [EF135105], EF135213, [AY674505], FJ670438, [EF135340], —, [U42534], FJ669819, AY425102.

QUIINACEAE. ***Froesia diffusa*** Gereau & R. Vásquez, *Macia et al. 1172* (MO), FJ669986, FJ670036, FJ670119, FJ670173, FJ670232, FJ670317, FJ670386, FJ670439, FJ669543, FJ669640, FJ669709, FJ669820, FJ669925; ***Quiina pteridophylla*** (Radlk.) Pires, *Pires* (CPATU), AF209664, EF135589, AY425081, Z75689, EF135161, EF135266, AY674558, AY674759, EF135392, EF135479, AF207003, FJ669821, FJ669926; ***Touroulia guianensis*** Aubl., *Pires 18034* (K), FJ669987, FJ670037, FJ670120, Z75690, FJ670233, FJ670318, FJ670387, FJ670440, FJ669544, FJ669641, FJ669710, FJ669822, FJ669927.

RAFFLESIACEAE. ***Rafflesia pricei*** Meijer, *Nickrent 4034*, —, —, —, —, EF135162, EF135267, AY739008, —, EF135393, EF135480, AY739083, —, —; ***Rafflesia tuan-mudae*** Becc., *Davis 07-35* (GH), —, —, —, —, FJ670234, FJ670319, FJ670388, —, FJ669545, FJ669642, FJ669711, FJ669823, FJ669928; ***Rhizanthes lowii*** (Becc.) Harms, *Davis 07-24* (GH), —, —, —, —, —, FJ670320, FJ670389, —, FJ669546, FJ669643, FJ669712, FJ669824, —; ***Sapria himalayana*** Griff., *Kocyan 180*, —, —, —, —, EF135166, EF135273, [AY674561], —, EF135397, EF135484, [AY674634], FJ669825, [AY674464].

RHIZOPHORACEAE. ***Bruguiera gymnorhiza*** Lam., *Chase 12838* (K), [AF209547], EF135511, AY425036, [AF127693], —, EF135194, AY674483, AY674656, EF135322, EF135423, [AF206875], —, FJ669929; ***Carallia brachiata*** (Lour.) Merr., *Chase 2151* (K), AJ235425, EF135513, AY425038, AF206744, FJ670235, EF135197, AY674485, AY674660, EF135325, EF135425, FJ707525, FJ669826, AY674448; ***Cassipourea lanceolata*** Tul., *Schatz 3689* (MO), FJ669988, FJ670038, FJ670121, FJ670174, FJ670236, FJ670321, FJ670390, FJ670441, FJ669547, FJ669644, FJ669713, FJ669827, FJ669930; ***Paradrypetes subintegrifolia*** G.A. Levin, *Acevedo-Rdgz. & Cedeño 7560* (US), AY788243, FJ670039, FJ670122, FJ670175, FJ670237, FJ670322, FJ670391, AY788282, FJ669548, FJ669645, AY788154, FJ669828, FJ669931.

ROSACEAE. ***Prunus caroliniana*** (Mill.) Aiton, *Wen 7177* (US), [***P. persica*** (L.) Batsch. AF209660], [***P. persica*** (L.) Batsch, AF288117], [***P. persica*** (L.) Batsch., AY968518], [***P. persica*** (L.) Batsch., AF206813], FJ670259, —, FJ670404, [***P. persica*** (L.) Batsch., AY968485], FJ669573, FJ669676, [***P. persica*** (L.) Batsch., L28749], FJ669867, —.

SALICACEAE. ***Abatia parviflora*** Ruiz & Pav., *Pennington 676* (K), AF209519, EF135498, FJ670123, AF206726, EF135073, EF135181, AY674471, AY674641, FJ669549, FJ669646, AF206836, —, —; ***Dovyalis rhamnoides*** Burch. ex Harv. & Sond., *Chase 271* (NCU), AY788217, EF135529, AY425047, Z75677, EF135104, EF135212, AY674504, AY674686, —, —, AY674592, —, AY425101; ***Flacourtia jangomas*** Steud., *Chase 2150* (K), AF209588, EF135541, FJ670125, AF206768, EF135116, EF135221, AY674514, AY674697, EF135349, FJ669647, AF206912, FJ669830, FJ669933; ***Idesia polycarpa*** Maxim., *Wurdack D22* (US), [AF209604], FJ670040, FJ670126, [AB021924], FJ670238, FJ670323, FJ670392, AY674716, FJ669550, FJ669648, [AF206936], FJ669831, FJ669934; ***Poliothyrsis sinensis*** Oliver, *Borgardt 1322* (BH), AY788251, EF135586, FJ670128, AY788186, EF135158, EF135263, AY674555, AY674756, EF135389, FJ669649, AY674631, [Wurdack s.n. (US). FJ669832], —; ***Populus maximowiczii*** Henry, *Chase 996* (K), [***P. tremuloides*** Michx., AF209658], EF135587, AY425080, AJ418836, EF135159, EF135264, AY674556, AY674757, EF135390, EF135478, [***P. tremuloides*** Michx., AF206999, [***P. trichocarpa*** Torr. & Gray, AARH00000000], —; ***Prockia crucis*** L., *Alford & Manuyama 3132* (BH), AY788252, EF135588, FJ670129, AY788187, EF135160, EF135265, AY674557, AY674758, EF135391, —, AY674632, —, FJ669936; ***Salix reticulata*** L., *Chase 840* (K), AJ235590, EF135592, AY425082, AJ235793, EF135165, EF135272, [***S. babylonica*** L., AY453072], AY674767, EF135396, EF135483, AF207011, [***S. przewalski*** E.L.Wolf, *Chase 993* (K), FJ669833], —.

SAMYDACEAE. ***Casearia sylvestris*** Sw., *Alford 2999* (BH), [***C. javitensis*** Kunth, AY935851], [***C. nitida*** (L.) Jacq., EF135516], [***C. nitida*** (L.) Jacq., *FTG 72496*, FJ670124], AY788167, EF135090, EF135200, [***C. nitida*** (L.) Jacq., AY674487], AY674663, EF135328, EF135428, [AF206882], [***C. nitida*** (L.) Jacq., *FTG 72496*, FJ669829], [***C. nitida*** (L.) Jacq., *FTG 72496*, FJ669930]; ***Lunania parviflora*** Spruce ex Benth., *Alford & Grandez 3114* (BH), AY788236, EF135561, FJ670127, AY788182, EF135134, EF135239, AY674535, AY674729, EF135367, EF135461, AY674615, —, FJ669935.

SCYPHOSTEGIACEAE. ***Scyphostegia borneensis*** Stapf, *Beaman 911* (BH), AY788254, EF135594, AY425083, AJ403000, EF135168, EF135274, AY674562, AY674770, EF135399, FJ669650, AY674635, FJ669834, —.

SOLANACEAE. ***Nicotiana tabacum*** L., NC_001879, NC_001879, NC_001879, NC_001879, NC_006581, NC_006581, NC_006581, NC_006581, NC_006581, AJ236016, —, —.

TRIGONIACEAE. ***Trigonia nivea*** Cambess., *Anderson 13656* (MICH), AF209691, EF135598, AY425084, AF089761, FJ670239, EF135280, AY674567, AY674779, EF135404, EF135491, AF207047, FJ669835, FJ669937; ***Trigoniastrum hypoleucum*** Miq., *Og B128* (L), FJ669989, FJ670041, FJ670130, FJ670176, FJ670240, FJ670324, FJ670393, FJ670442 + FJ670443, FJ669551, FJ669651, FJ669714, FJ669836, FJ669938.

TURNERACEAE. ***Tricliceras longipedunculatum*** (Mast.) R. Fern., *Kanji et al. 304* (NY), FJ669990, FJ670042, FJ670131, FJ670177, FJ670241, FJ670325, FJ670394, FJ670444, FJ669552, FJ669652, FJ669715, FJ669837, —; ***Turnera ulmifolia*** L., *Chase 220* (NCU), AJ235634, EF135599, AY425085, Z75691, EF135174, EF135281, AY674569, [AY674782], EF135405, EF135492, U42817, [*Wurdack D307* (US). FJ669838], —.

VIOLACEAE. ***Fusispermum laxiflorum*** Hekking, *Hammel 20491* (MO), FJ669991, FJ670043, FJ670132, FJ670178, FJ670242, —, FJ670395, FJ670445, FJ669553, FJ669653, FJ669716, FJ669839, FJ669939; ***Hybanthus concolor*** Spreng., *Alford 3056* (BH), AY788229, EF135550, FJ670133, AY788178, EF135125, EF135230, AY674524, AY674712, EF135358, [*Wurdack D148* (US), FJ669654], AY674607, [*Wurdack D148* (US), FJ669840], [*Wurdack D148* (US), FJ669940]; ***Hymenthera alpina*** (Kirk) W.R.B. Oliv., *Chase 501* (K), AJ235499, EF135552, AY425059, Z75692, EF135127, EF135231, EF135299, AY674713, FJ669554, EF135455, AF206933, FJ669841, AY425112; ***Leonia glycycarpa*** Ruiz. & Pav., *Pennington 13852* (K), AY788234, EF135558, AY425065, FJ670179, EF135132, EF135237, AY674531, AY674725, EF135365, EF135459, AY674613, FJ669842, AY425115; ***Rinorea bengalensis*** Kuntze, *Chase 2148* (K), AJ235584, FJ670044, FJ670134, [***R. crenata*** S.F. Blake, AJ237591], [***R. pubiflora*** (Benth.) Sprague & Sandwith, EF135164], [***R. pubiflora*** (Benth.) Sprague & Sandwith, EF135271], FJ670396, FJ670446, [***R. pubiflora*** (Benth.) Sprague & Sandwith, EF135395], FJ669655, [***R. pubiflora*** (Benth.) Sprague & Sandwith, AY929373], FJ669843, FJ669941; ***Viola pubescens*** Aiton, *Wells 4886* (US), FJ669992, [***V. chaerophylloides*** Makino, AB038188], FJ670135, [***V.* sp.**, AJ247621], [***V. kitaibeliana*** Roem. & Schult., EF135176], [***V. kitaibeliana*** Roem. & Schult., EF135283], [***V. cucullata*** Aiton, AY453070], [***V.* sp.**, *Davis 13-03* (A), FJ670447], FJ669555, [***V. kitaibeliana*** Roem. & Schult., EF135493], FJ669717, FJ669844, —.

VITACEAE. ***Vitis aestivalis*** Michx., *Wen 7158* (US), [AJ235643], [***V. vinifera*** L. AJ429274], [***V. vinifera*** L., DQ424856], [***V. rotundifolia*** Michx., AJ419718], FJ670261, FJ670345, [***V. riparia*** Michx., AY453123], [***V.* sp.**, AY674785], FJ669575, FJ669678, [***V.* sp.**, AF207053], FJ669870, [***V.* sp.**, AY674470].

ZYGOPHYLLACEAE. ***Guaiacum sanctum*** L., *Chase 133* (NCU), AJ235485, FJ670058, FJ670157, AJ1311770, FJ670255, FJ670339, AY674517, AY674700, FJ669569, FJ669672, AY674599, FJ669863, FJ669959.