



# A Complete Generic Phylogeny of Malpighiaceae Inferred from Nucleotide Sequence Data and Morphology

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**A COMPLETE GENERIC PHYLOGENY OF MALPIGHIACEAE  
 INFERRED FROM NUCLEOTIDE SEQUENCE DATA  
 AND MORPHOLOGY<sup>1</sup>**

CHARLES C. DAVIS<sup>2,4</sup> AND WILLIAM R. ANDERSON<sup>3</sup>

<sup>2</sup>Department of Organismic and Evolutionary Biology, Harvard University Herbaria, 22 Divinity Avenue, Cambridge, Massachusetts 02138 USA; and <sup>3</sup>University of Michigan Herbarium, 3600 Varsity Drive, Ann Arbor, Michigan 48108 USA

- *Premise of the study:* The Malpighiaceae include ~1300 tropical flowering plant species in which generic definitions and inter-generic relationships have long been problematic. The goals of our study were to resolve relationships among the 11 generic segregates from the New World genus *Mascagnia*, test the monophyly of the largest remaining Malpighiaceae genera, and clarify the placement of Old World Malpighiaceae.
- *Methods:* We combined DNA sequence data for four genes (plastid *ndhF*, *matK*, and *rbcL* and nuclear *PHYC*) from 338 ingroup accessions that represented all 77 currently recognized genera with morphological data from 144 ingroup species to produce a complete generic phylogeny of the family.
- *Key results and conclusions:* The genera are distributed among 14 mostly well-supported clades. The interrelationships of these major subclades have strong support, except for the clade comprising the wing-fruited genera (i.e., the malpighioid+*Amorimia*, *Ectopopterys*, hiraoid, stigmaphylloid, and tetrapteroid clades). These results resolve numerous systematic problems, while others have emerged and constitute opportunities for future study. Malpighiaceae migrated from the New to Old World nine times, with two of those migrants being very recent arrivals from the New World. The seven other Old World clades dispersed much earlier, likely during the Tertiary. Comparison of floral morphology in Old World Malpighiaceae with their closest New World relatives suggests that morphological stasis in the New World likely results from selection by neotropical oil-bee pollinators and that the morphological diversity found in Old World flowers has evolved following their release from selection by those bees.

**Key words:** biogeography; floral symmetry; Malpighiaceae; *matK*; mutualism; *ndhF*; *PHYC*; phylogeny; pollination biology; *rbcL*; systematics.

The Malpighiaceae are an angiosperm family of trees, shrubs, and vines in the tropical and subtropical forests and savannas of the New and Old Worlds. They comprise ~1300 species in 77 genera, with ~150 species belonging to 17 exclusively Old World genera. The majority of the genera and species are found in the New World, and the only members of the family found in both hemispheres are two species of New World genera that also occur in coastal western Africa. New World Malpighiaceae typically have unicellular, 2-branched hairs, simple opposite leaves, bilaterally symmetrical flowers with two large oil glands on the abaxial surface of four or all five sepals, five clawed petals, 10 stamens, and a tricarpeolate gynoeceum with one ovule

per locule (Anderson, 2004). Some of these characteristics have been lost in Old World members of the family. Malpighiaceae produce a variety of dry or fleshy, indehiscent or dehiscent fruits that are smooth-walled, bristly, or winged (Davis et al., 2001). This diversity in fruits, coupled with the relative uniformity of the flowers of New World Malpighiaceae (Anderson, 1979), led earlier workers to define genera and tribes principally on the basis of fruit morphology (Nieden zu, 1928). Published phylogenetic studies (Cameron et al., 2001; Davis et al., 2001, 2002b, 2004) have highlighted the problematic nature of this single-character taxonomy. Some of the largest traditionally recognized genera have been shown to be polyphyletic [e.g., *Mascagnia* (DC.) Colla, Cameron et al., 2001; Davis et al., 2001; and Discussion later], and Davis et al. (2001) concluded that all tribes previously recognized for the family (Hutchinson, 1967) were polyphyletic except Gaudichaudieae, whose members ironically bear diverse fruit types, but exhibit distinctive floral features. These data suggest that there have been several origins of very similar fruit types within the family. Reconstructions of fruit evolution (Davis et al., 2001) established that winged fruits evolved early in Malpighiaceae from a smooth-walled ancestor and that there were at least three reversals to smooth-walled fruits from within the large heterogeneous wing-fruited clade, which constitutes the majority of Malpighiaceae species. Bristly fruits are similarly homoplastic and evolved at least three (and more likely four) times in clades with wing-fruited ancestors.

A major goal of our work since 2001 has been to improve the resolution of the Malpighiaceae phylogeny by sequencing

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<sup>4</sup> Author for correspondence (e-mail: cdavis@oeb.harvard.edu)

representatives of the genera that were missing from our previous studies plus a much broader sampling of the larger and more problematic genera. Our aims for this study were to (1) resolve relationships among the 11 segregates from the New World genus *Mascagnia* sensu lato (s.l.), (2) test the monophyly of the largest remaining Malpighiaceae genera, and (3) clarify the placement of Old World Malpighiaceae. To achieve this goal, we included 309 species of Malpighiaceae, representing about a fourth of the total species diversity in this large tropical clade. We sampled these species across four gene regions that have previously been shown to be phylogenetically informative in the family but have never been analyzed simultaneously (i.e., plastid [pt] *matK*, *ndhF*, *rbcL*, and the low-copy nuclear phytochrome gene *PHYC*). We also added a morphological data set for representatives of all the genera and integrated those data into our molecular phylogenetic analyses. This expanded sampling has enabled us to present here a greatly improved phylogeny of the family, which has made it possible to further untangle some of the problems caused by the traditional classifications based mainly on fruit morphology. Working back and forth between molecular and morphological approaches, we are achieving a synergy that is leading not only to new phylogenetic insights for this group, but also to the translation of those insights into a revised classification for the family. The progress of those revisions is summarized in the discussion and on our website for the family (Anderson et al., 2006 onward).

In addition to fruit morphology, biogeography has also been important for circumscribing major groups within the family. Niedenzu (1928) placed the Old World Malpighiaceae (not including the two more recently introduced species from the New World) in subtribe Aspidopteryginae within his lateral-winged tribe Hiraeeae and in subtribe Sphehamnocarpaceae within his dorsal-winged tribe Banisterieae. While each of these wing-fruited tribes has previously been shown to be polyphyletic (Cameron et al., 2001; Davis et al., 2001), the precise New World relatives of these Old World clades have remained elusive. In previous studies, the Old World genera were shown to represent six to nine different clades, each of which was more closely related to a New World clade than to other Old World clades. Alternative topologies in which these Old World species were forced to form a single clade were strongly rejected. More recent investigations of the biogeographic history of Malpighiaceae (Davis et al., 2002a, b, 2004) have better clarified the placement of many of these Old World lineages, but the identity of the closest New World relatives of several Old World clades remains problematic due to low support and/or incomplete taxon sampling. These difficulties are magnified by our subsequent discovery of several previously unsampled, mostly New World, phylogenetic lineages identified here. Resolving the number of Old World lineages and discerning their placement among the many newly recognized New World members of the family will aid in future biogeographic studies of the family.

Finally, establishing the placement of most Malpighiaceae genera will help to clarify patterns of floral evolution within the family. Malpighiaceae exhibit a highly stereotyped floral morphology characterized by an elegant suite of floral characters that appears to be closely tied to their oil-bee pollinators (Vogel, 1974, 1990; Anderson, 1990). These bees, however, do not exist in the Old World where most of these unique floral features have been lost (Davis, 2002). Malpighiaceae thus provide an excellent opportunity to examine the origin and maintenance of morphological stasis in the Tree of Life.

## MATERIALS AND METHODS

**Taxon sampling**—Three hundred thirty-eight accessions representing all 77 currently recognized genera of Malpighiaceae (Anderson et al., 2006) plus 19 outgroup accessions were included in our analyses (see Appendix 1). Our sampling builds greatly on our past efforts (Cameron et al., 2001; Davis et al., 2001, 2002b, 2004). In particular, the following genera have been added since our last studies: *Aenigmatanthera* W. R. Anderson, *Amorimia* W. R. Anderson, *Bronwenia* W. R. Anderson & C. Davis, *Banisteriopsis* C. B. Rob. s.s., *Calcolica* W. R. Anderson & C. Davis, *Camarea* A. St.-Hil., *Christianella* W. R. Anderson, *Clonodia* Griseb., *Digoniapterys* Arènes, *Henleophytum* H. Karst., *Madagasikaria* C. Davis, *Microsteira* Baker, *Philgamia* Baill., and *Verrucularia* Adr. Juss. In addition, we have greatly expanded our sampling in the largest and most heterogeneous genera, including *Banisteriopsis*, *Bunchosia* H.B.K., *Byrsonima* H.B.K., *Heteropterys* H.B.K., *Janusia* Adr. Juss. and its close relatives (herein referred to as the aspicarpoid clade), *Malpighia* L., *Mascagnia* s.l., and *Tetrapterys* Cav. These taxa were targeted primarily because they were either shown to be nonmonophyletic in previous studies (e.g., *Mascagnia* s.l., and several aspicarpoid genera) or were suspected of being nonmonophyletic on the basis of recent morphological investigations (e.g., *Banisteriopsis*, *Heteropterys*, *Malpighia*, and *Tetrapterys*). *Bunchosia* and *Byrsonima* were not suspected of being nonmonophyletic but are two of the largest genera in the family, with 68 and 130 species, respectively. We included more species of these two genera to make our sampling more reflective of Malpighiaceae diversity, which will be important for future evolutionary studies in the group.

Broader phylogenetic analyses based on several genes have independently confirmed the sister group relationship of Malpighiaceae and Elatinaceae (Davis and Chase, 2004; Tokuoka and Tobe, 2006; Wurdack and Davis, 2009), and more recent analyses that include denser taxon and character sampling across the order Malpighiales indicate that the newly recognized family Centroplacaceae (Zhang and Simmons, 2006; Wurdack and Davis, 2009) is sister to Elatinaceae-Malpighiaceae (Wurdack and Davis, 2009; Xi et al., 2010). Members of Elatinaceae and Centroplacaceae were, therefore, included as outgroups. In addition, we included several more distant outgroups to help stabilize the ingroup topology, including other Malpighiales (Chrysobalanaceae, Dichapetalaceae, Euphorbiaceae, Goupiaceae, Ochnaceae, Phyllanthaceae, Picramniaceae, Putranjivaceae, and Violaceae), Celastrales (Celastraceae), and Saxifragales (Peridiscaceae). *Peridiscus lucidus* Benth. (Peridiscaceae) was used for rooting purposes.

**Molecular methods**—Total cellular DNAs were prepared using the protocol of Davis et al. (2002a) or were obtained from other sources (see Acknowledgments). Voucher information is listed in Appendix 1.

Amplification and sequencing protocols for obtaining *matK* followed Cameron et al. (2001), using their primers 400F, *trnK*-2R, and 842F; *ndhF* followed Davis et al. (2001); *rbcL* followed Cameron et al. (2001); and *PHYC* followed Davis et al. (2002b) with the addition of forward primer int-1F (5'-CCAGCTACTGATATACCWCARGCTTC-3'), which when paired with reverse primer 623r/cdo produced an ~800 base-pair (bp) amplicon.

Double-stranded polymerase chain reaction (PCR) products were primarily gel-extracted and purified using the QIAquick Gel Extraction Kit. PCR products were sequenced in both directions using dye terminators and sequencing protocols at the University of Michigan DNA facility (Ann Arbor, Michigan, USA) and at MWG Biotechnology (High Point, North Carolina, USA). Chromatograms were assembled into contiguous sequences and checked for accuracy using the software program Sequencher 4.7 (Gene Codes Corp., Ann Arbor, Michigan, USA). All newly generated sequences were submitted to GenBank (see Appendix 1).

**Morphological scoring**—Morphological data were recorded for 144 ingroup species that represented all genera of Malpighiaceae, plus six outgroup taxa. Seventy-five discrete (binary or multistate) morphological characters were scored, representing vegetative and reproductive structures (see Appendix 2). We have indicated representative voucher specimens for each of the species that were scored in Appendix 1, but in many cases additional specimens were needed to adequately score all of the relevant data.

**Phylogenetic analyses**—Nucleotide sequences were aligned by eye with the program MacClade 4.0 (Maddison and Maddison, 2000); the ends of sequences were trimmed from each data set to maintain complementary



data between taxa. The aligned *pt matK*, *ndhF*, *rbcL*, and *nu PHYC* data sets included 1194, 867, 1414, and 1180 bp, respectively; 75 morphological characters were also included as part of the alignment. Data matrices are available in Treebase (no. 10998, <http://www.treebase.org>) and from C. C. Davis.

Maximum likelihood (ML) bootstrap consensus trees and Bayesian posterior probabilities from all individual analyses of the five data partitions revealed no strongly supported incongruent clades (i.e., >80 ML bootstrap percentage [BP]) and were thus analyzed simultaneously using the search strategies described below. Searches using the combined data were conducted using a data set that included 357 accessions (338 ingroup and 19 outgroup).

The optimal model of molecular evolution for the individual and combined analyses was determined by the Akaike information criterion (AIC) using the program Modeltest ver. 3.7 (Posada and Crandall, 1998; Posada and Buckley, 2004). In each case, the optimal model was the general time reversible model, with rate heterogeneity modeled by assuming that some sites are invariable and that the rate of evolution at other sites is modeled using a discrete approximation to a gamma distribution [GTR+I+ $\Gamma$ ]. A mixed model was applied to our combined analyses to accommodate the morphological data: GTR+I+ $\Gamma$  for the molecular data and the Mk1 model for the morphological data (Lewis, 2001). Maximum likelihood (ML) analyses of the individual and combined matrices were implemented in the program RAxML 7.1.0 (Stamatakis, 2006) (distributed by A. Stamatakis at <http://icwww.epfl.ch/~stamatak/index-Dateien/Page443.htm>) starting from random trees and using the default parameters. Analyses were rerun at least three times. ML BP values were estimated from 100 bootstrap replicates. We subsequently conducted analyses not presented here using RAxML 7.2.6 in which GTR+I+ $\Gamma$  was enforced for all partitions, including morphology. Those topologies were very similar to the ones presented here, but were slightly better resolved. Bayesian analyses were similarly implemented in the parallelized version of MrBayes ver. 3.1.2 (Huelsenbeck and Ronquist, 2001) following Davis et al. (2005). Bayesian posterior probabilities (BPP) were calculated from five restarts with a burn-in period of 400 000 generations.

## RESULTS

We increased the ingroup taxonomic sampling by a factor of ~4.3 over that used in preparing our earlier phylogeny of the family (Davis et al., 2001). This sampling includes representatives of all the genera currently recognized in the family and many of the species groups in the most diverse genera. For the 45 genera for which we sampled multiple species, 35 (or 78%) are monophyletic. For the sake of space, we present the ML results from the combined data here (Fig. 1, but see Appendix S1 online at <http://www.amjbot.org/cgi/content/full/ajb.1000146/DC1> for BPP). A tree summarizing the major ingroup clades is also presented for simplicity in Fig. 2.

Several broad generalizations can be made about our new phylogeny of Malpighiaceae. We have obtained far greater resolution of the family than in our previous studies (Cameron et al., 2001; Davis et al., 2001). In addition to identifying several novel relationships, our findings largely confirm these previous results, but often with greatly increased support (e.g., the placements of *Barnebya* W. R. Anderson & B. Gates and *Lophopterys* Adr. Juss.). Bootstrap support along the spine of the tree (Fig. 2), and for all of the major subclades, is mostly very (>90 BP) to moderately ( $\geq 71$  BP) strong. The exception is that the tetrapteroid, stigmaphylloid, and malpighioid clades, as well as *Ectopopterys* W. R. Anderson, are not well resolved with respect to one another. Furthermore, within each of the 14 major subclades identified (Figs. 1, 2), there is generally strong support for internal clades, with the exception of the christianelloids, cordobioids, hiraeoids, and madagasikarioids.

## DISCUSSION

This is the first complete generic-level analysis of Malpighiaceae and one of the largest to date for a major tropical angiosperm clade. Furthermore, it is one of the largest phylogenetic studies to include a companion, morphological data set. The morphological data set will be invaluable for ongoing taxonomic revisions of the family and for future analyses of floral evolution (see below). Importantly, the results presented here meet the goals of our study to (1) resolve relationships among the 11 segregates from the New World genus *Mascagnia* s.l., (2) test the monophyly of the largest remaining Malpighiaceae genera, and (3) clarify the placement of Old World Malpighiaceae. We shall summarize the most novel developments here and highlight areas where new challenges have arisen.

**I. *Mascagnia* s.l.**—*Mascagnia* s.l. contains all Malpighiaceae species with lateral-winged samaras, 10 fertile stamens, and internal stigmas that do not readily fit among other taxa with similar morphologies, including *Hiraea* Jacq., *Jubelina* Adr. Juss., *Mezia* Nied., *Tetrapteryx*, and *Triopteryx* L. (Anderson, 2006). It has been known that *Mascagnia* s.l. is not monophyletic (Cameron et al., 2001; Davis et al., 2001), but the number and placement of its constituent subclades have been unclear, and until very recently morphology has similarly not provided a clear direction for dividing this group into monophyletic subunits (Anderson, 2006).

On the basis of our preliminary phylogenetic results and morphology, W. Anderson (2006) and his colleagues (Anderson and Davis, 2007; Anderson and Corso, 2007) recognized 10 generic segregates from *Mascagnia*: *Adelphia* W. R. Anderson, *Aenigmatanthera* W. R. Anderson, *Alicia* W. R. Anderson, *Amorimia*, *Calcolica* W. R. Anderson & C. Davis, *Carolus* W. R. Anderson, *Christianella* W. R. Anderson, *Malpighiodes* Nied., *Niendenzuella* W. R. Anderson, and *Psychopteryx* W. R. Anderson & S. Corso. We show here for the first time that these former members of *Mascagnia*, plus *Malpighia leticiiana* W. R. Anderson and *Callaeum* Small, which have previously been included in *Mascagnia*, belong to 11 clades variously scattered across Malpighiaceae (in Fig. 1, *Callaeum* and *Alicia* form a clade that has little support [51 BP], and so we are considering them separately in this calculation). All of the new generic segregates of *Mascagnia* s.l. that have been sampled with two or more species are monophyletic with >78 BP, with the exception of *Niendenzuella* (see below). *Mascagnia* s.s. is now greatly reduced and consists of about 37 species. These species are vines with interpetiolar stipules, and they possess glands impressed in the abaxial surface of the lamina, glabrous petals exposed in the bud, orbicular membranous samaras with arching and anastomosing veins in the lateral wing, and a three-lobed disc that subtends the fruit (Anderson and Davis, 2005a). There is not space to discuss all of these many new generic segregates here. Instead, we refer the reader to recently published morphological and taxonomic accounts of these groups (Anderson and Davis, 2005a, b; Anderson, 2006; Anderson and Corso, 2007; Anderson and Davis, 2007).

*Niendenzuella*—*Niendenzuella* comprises former members of *Mascagnia* and *Tetrapteryx* (Anderson, 2006) and forms a well-supported (91 BP) clade with *Aenigmatanthera*. This is supported by their many shared morphological traits, including decussate pseudoracemes, marginal leaf glands, tiny epipetiolar stipules, and yellow petals (Anderson, 2006). *Niendenzuella*,

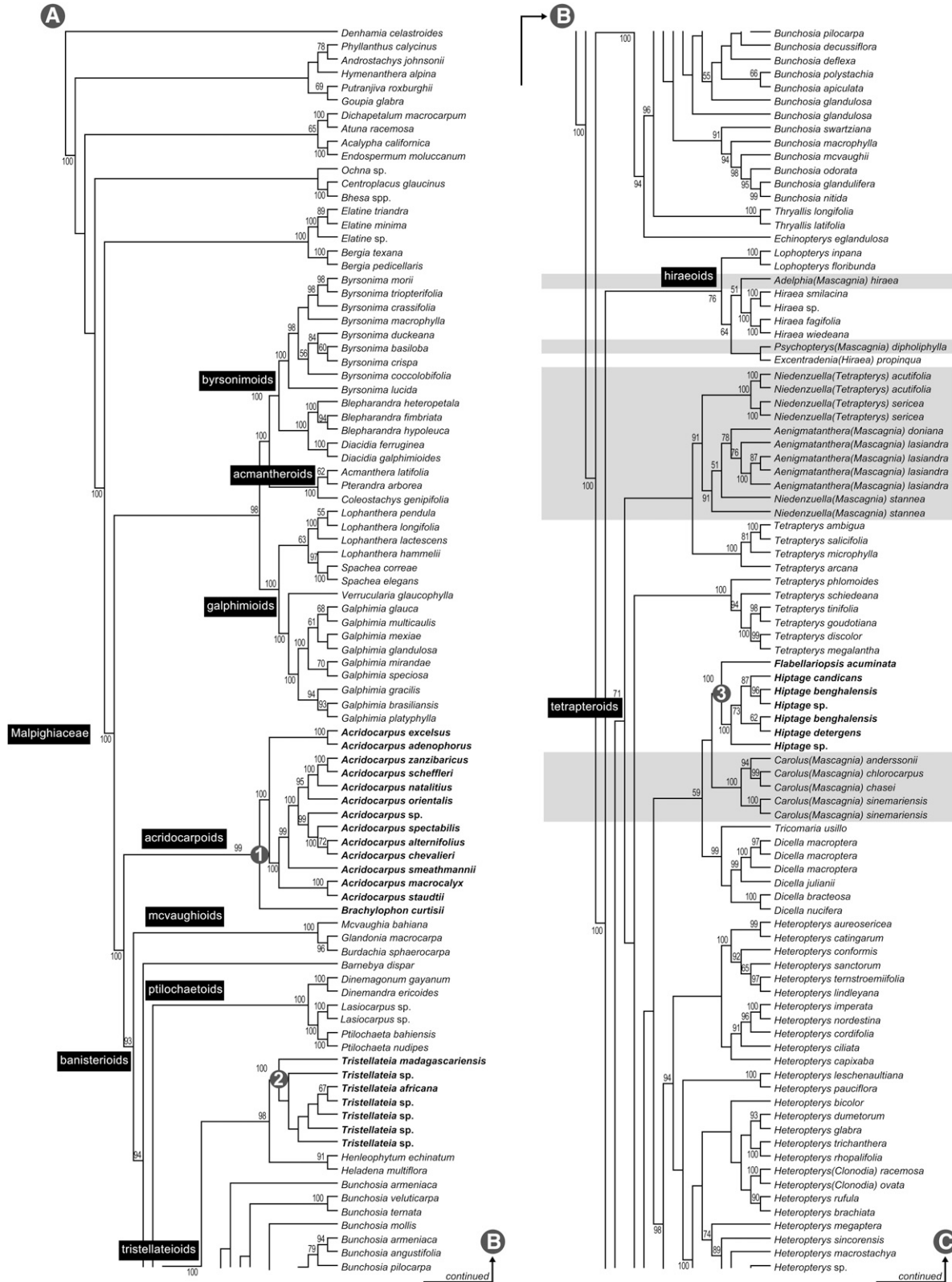
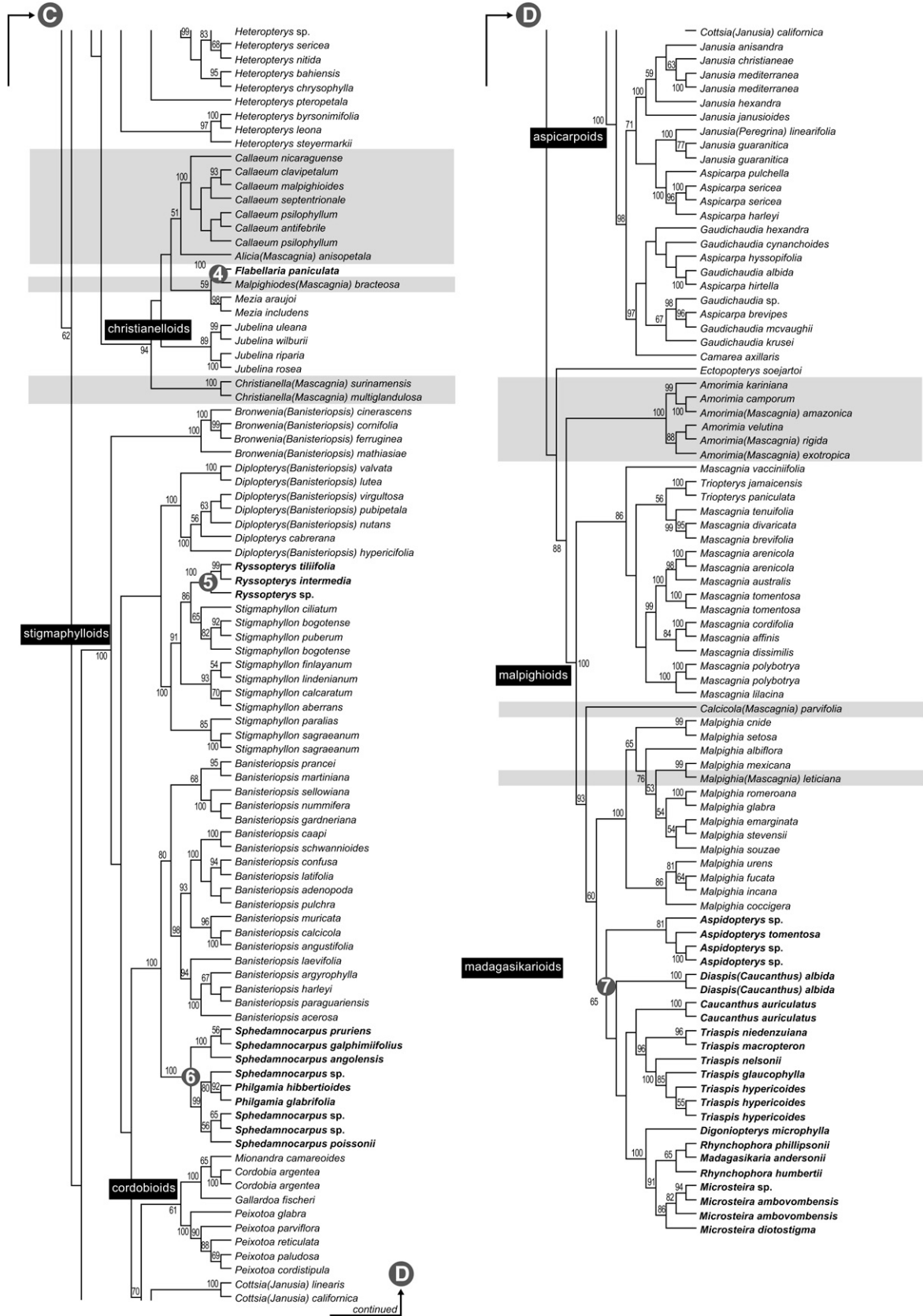


Fig. 1. One of the maximum likelihood (ML) topologies based on the four-gene-plus-morphology data set. ML bootstrap percentages >50 are indicated at the nodes. Generic names in parentheses reflect the previous taxonomic placement for those species. Former members of *Mascagnia* are highlighted in gray. The seven ancient, Old World clades are numbered; Old World species are shown in boldface. For Bayesian posterior probabilities see Appendix S1 in the Supplemental Data accompanying the online version of this article. Three hundred fifty-seven accessions were included for this analysis, but only 356 are shown; *Peridiscus lucidus* Benth. was used for rooting, but has been removed for brevity.





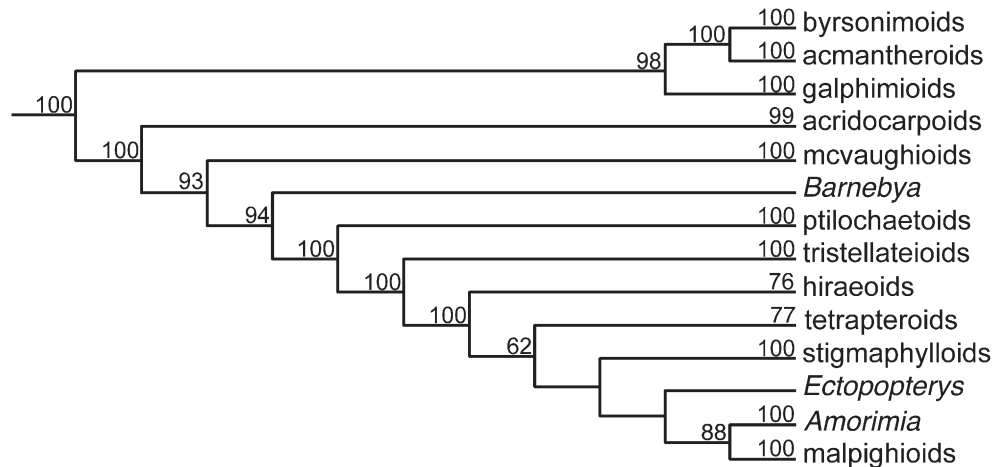


Fig. 2. Summary of major clades of Malpighiaceae emerging from this study derived from Fig. 1. Maximum likelihood bootstrap percentages >50 are indicated at nodes.

however, is not monophyletic—*N. stannea* is more closely related to *Aenigmatanthera* with 91 BP than it is to the remaining species of *Niendenzuella*. To avoid a proliferation of generic names, we intend to expand *Niendenzuella* and reduce *Aenigmatanthera* to a synonym of the former.

*Triopterys*—*Triopterys* consists of five species restricted to the West Indies. It has been distinguished from other genera principally on the basis of its Y-shaped samaroid fruit, vs. the butterfly-shaped, X-shaped, or orbicular samaras of *Hiraea*, *Tetrapterys*, and *Mascagnia* s.s., respectively. Our tree (Fig. 1) shows that *Triopterys* is well placed (86 BP) in the *Mascagnia* s.s. clade. We intend to combine the two genera under the name *Mascagnia* and propose conserving that name against the older name *Triopterys* in the near future.

**II. Testing the monophyly of the largest remaining genera of Malpighiaceae**—Beyond *Mascagnia* s.l., all of the other large genera of Malpighiaceae, with the exception of *Bunchosia* and *Byrsonima*, are not monophyletic as traditionally circumscribed (Fig. 1). These include *Aspicarpa* Rich. (and its related genera, in the aspicarpoid clade), *Banisteriopsis*, *Heteropterys*, *Malpighia*, *Sphedamnocarpus* Hook. f., *Stigmaphyllon* Adr. Juss., and *Tetrapterys*. Three of these genera, all of which are distantly related members of the large wing-fruited banisterioid clade, merit discussion together: *Heteropterys*, *Banisteriopsis*, and *Sphedamnocarpus*. These large genera bear a single prominent dorsal wing on each of their mericarps but otherwise resemble small genera whose mericarps bear a minimal dorsal crest or none at all, such that the mericarp resembles a nutlet instead of a samara. Our results demonstrate that these putative sister genera are not reciprocally monophyletic. Instead, each genus with wingless species is nested within a genus with winged fruits, rendering the latter nonmonophyletic: *Clonodia* is nested within *Heteropterys* with 100 BP, *Diplopterys* Adr. Juss. is nested within one of the major subclades of *Banisteriopsis* sensu Gates (1982) with 100 BP, and *Philgamia* is nested within *Sphedamnocarpus* with 99 BP. In each of these cases, it appears that the principal wing has been secondarily lost or greatly reduced. We will consider each of these instances below and follow with discussion of the remaining large or problematic genera of Malpighiaceae.

*Heteropterys*—The sampling of this large genus was greatly expanded here, with the result that the monophyly of the genus receives 98 BP. This contrasts with previous results that indicated very low support for the monophyly of *Heteropterys* (Cameron et al., 2001; Davis et al., 2001). In addition, for the first time, we were able to include the wingless *Clonodia*, whose phylogenetic affinities have long been problematic (Anderson, 1981). Species of *Clonodia* resemble some species of *Mascagnia*, most notably in their alate pink and white petals and racemose inflorescences. However, the same features are found in some species of *Heteropterys*, which also share the lenticels and subdistinct carpels of *Clonodia*. On this basis, Anderson (1981) thought that an origin of *Clonodia* from a *Heteropterys*-like ancestor was more likely. Our analyses indicate that *Clonodia* is indeed sister to two pink-flowered members of *Heteropterys* series *Rhodopetalis* Nied., *H. brachiata* and *H. rufula* (Fig. 1). Although support for the placement of *Clonodia* with the mostly pink-flowered *Heteropterys* is not strong (<50 BP), it is well nested (100 BP) within *Heteropterys*, and as such, its continued recognition would make *Heteropterys* nonmonophyletic. To remedy this problem, we have treated *Clonodia* as a synonym of *Heteropterys* (Anderson and Davis, 2007).

*Banisteriopsis*—*Banisteriopsis* sensu Gates (1982) is not monophyletic—its members belong to three distinct and well-supported (>80 BP) clades within the stigmaphylloids (Fig. 1), which correspond to the three subgenera recognized by Gates: subg. *Banisteriopsis*, subg. *Hemiramma* (Griseb.) B. Gates, and subg. *Pleiopterys* (Nied.) B. Gates. The wingless *Diplopterys* (represented in Fig. 1 by *D. cabrerana*) is nested within *Banisteriopsis* subg. *Pleiopterys*. To remedy this situation, we transferred members of subgenus *Pleiopterys* to an expanded *Diplopterys*, which now includes both wingless and wing-fruited species (Anderson and Davis, 2006). Members of Gates's subg. *Hemiramma* are now recognized as the genus *Bronwenia* (Anderson and Davis, 2007), whose species are characterized by marginal leaf glands (if any), flowers borne in short, dense pseudoracemes, calyx glands attached below the free part of the sepals, yellow, usually glabrous petals, and samaras with the nut smooth or bearing a single ridge or winglet, and the carphophore absent or short. Members of subg. *Banisteriopsis* s.s. comprise the largest number of species of *Banisteriopsis* s.l. and

retain the generic name *Banisteriopsis*. *Banisteriopsis* s.s. includes *Banisteriopsis caapi*, which is an important religious totem of many Amazonian Indian groups (Frenopoulo, 2005). *Banisteriopsis* s.s. is a well-supported (100 BP) sister to the Old World clade *Sphedamnocarpus* Hook. f. plus *Philgamia*.

*Sphedamnocarpus*—*Sphedamnocarpus* is disjunctly distributed between Africa and Madagascar; the wingless *Philgamia* is wholly Malagasy. The African species [*Sphedamnocarpus angolensis* (Adr. Juss.) Oliv., *S. galphimifolius* (Adr. Juss.) Szyszyl., and *S. pruriens* (Adr. Juss.) Szyszyl. in Fig. 1] form a well-supported subclade (100 BP), the Malagasy species of *Sphedamnocarpus* and *Philgamia* form a sister subclade with similar support (99 BP), and the two subclades together form a clade with similarly high support (100 BP). These results are reinforced by floral morphology: Malagasy *Sphedamnocarpus* and *Philgamia* have white, radial flowers, while those of the African *Sphedamnocarpus* are yellow or cream-colored and zygomorphic. Biogeography is obviously an important indicator of relationships in this clade. Under the circumstances, the later name *Philgamia* will have to be reduced to synonymy under *Sphedamnocarpus* unless all the Malagasy species of *Sphedamnocarpus*, including *Philgamia*, are determined to merit recognition at the level of genus. In that case, the Malagasy genus will bear the name *Philgamia*.

*Stigmaphyllon*—Members of the Old World Australasian clade *Ryssopterys* are well nested (86 BP) within the large, well-supported (100 BP) New World clade *Stigmaphyllon* (Fig. 1). *Ryssopterys* species resemble *Stigmaphyllon* in most aspects of their morphology: the two groups have nearly identical leaves, usually consisting of a long petiole bearing a pair of conspicuous glands at the apex and a large, often cordate lamina. In both, the flowers are borne in umbels or pseudoracemes disposed in a dichasial inflorescence, and the samaras are identical (Anderson, 1997). The principal difference between them is that in *Ryssopterys* the sepals lack abaxial glands, the corolla is radial, and the styles have terminal stigmas, whereas in *Stigmaphyllon* the lateral sepals bear large paired abaxial glands, the corolla is strongly bilateral, and the styles are stigmatic on the internal angle of the apex and often bear an abaxial foliole that gives the genus its name (Anderson, 1997). *Ryssopterys* is also notable for having in each species some plants with staminate flowers and others with morphologically bisexual flowers (Yampolsky and Yampolsky, 1922; Christiane Anderson, personal communication, University of Michigan), while species of *Stigmaphyllon* bear only bisexual flowers (Anderson, 1997). Christiane Anderson has recently revised *Ryssopterys* and will soon publish a treatment that will resolve both the generic status and the species taxonomy of this group (Anderson, in press).

*The aspicarpoid clade*—Members of this well-supported (100 BP) stigmaphylloid subclade include the genera *Aspicarpa*, *Gaudichaudia* H.B.K., *Janusia*, and *Peregrina* W. R. Anderson. The aspicarpoid clade is well supported by morphology and is distinguished by the loss of four or all five of the stamens opposite the petals and the possession of a single style borne on the anterior carpel.

*Janusia* s.l. is disjunctly distributed between North and South America (Anderson, 1982, 1987). However, the North American species of *Janusia* are not most closely related to the South American species of *Janusia*. Instead, *Janusia* in North America is sister to all of the remaining aspicarpoids. To correct this

problem, we resurrected the generic name *Cottisia* Dubard & Dop for the North American species of *Janusia* (Anderson and Davis, 2007). In addition, we have adopted here the already-published combination *Janusia linearifolia* (A. St.-Hil.) Adr. Juss. for *Peregrina linearifolia* (A. St.-Hil.) W. R. Anderson. Despite these taxonomic improvements, however, *Aspicarpa*, *Gaudichaudia*, and the remaining members of *Janusia* s.s. are not monophyletic. The best course of treatment of this group remains to be determined and will be a focus of our future research.

*Malpighia*—Our results demonstrate that the peculiar species *Mascagnia leticiana* W. R. Anderson is nested (76 BP) within *Malpighia* (Fig. 1). *Mascagnia leticiana* shares a combination of characters that link it either to *Malpighia* or to *Mascagnia* s.s., including similar stipules, leaf glands, petal color, androecium, and gynoecium (Anderson and Davis, 2005b). On the other hand, the needle-like hairs of *M. leticiana* and its tree habit make it a bad fit with *Mascagnia* s.s. and a better fit with *Malpighia*. The difficulty of placing *Mascagnia leticiana* in *Malpighia*, however, is that its fruits are strikingly different from those of *Malpighia*. Whereas the fruit is indehiscent and fleshy in *Malpighia* (i.e., drupelike) and dry, dehiscent, and samaroid in *Mascagnia*, the fruit of *Mascagnia leticiana* is intermediate, i.e., it is small and rather fleshy, but conspicuously winged. Given the phylogenetic placement of *M. leticiana*, it would appear that this represents a striking reversal to a presumably dehiscent *Mascagnia*-like fruit within a lineage of indehiscent fleshy-fruited species. Anderson and Davis (2005b) transferred *M. leticiana* to *Malpighia*, on the basis of these results.

*Tetrapterys*—Even after the segregation of *Niendenzuella* (discussed above) from *Tetrapterys*, the genus may not be monophyletic: its two constituent well-supported (100 BP) subclades may not be each other's closest relatives (Fig. 1). This is not entirely surprising given the morphological diversity of the species that have traditionally been assigned to this genus. Resolution of this problem will have high priority among the things we do next and should be done carefully with additional data from morphology and molecular sequences.

*Lophanthera*—*Lophanthera* Adr. Juss. and *Spachea* Adr. Juss. are sister genera and present an interesting problem. *Lophanthera* comprises five species, four in Amazonian South America and one in the lowlands of Costa Rica (Anderson et al., 2006). *Spachea* comprises six species: five in northern South America, Panama, and the lowlands of Costa Rica and Nicaragua and one in Cuba (Anderson et al., 2006). The two genera are both distinguished by putative morphological synapomorphies, so it was a surprise to find the Central American species of *Lophanthera*, *L. hammelii* W. R. Anderson, more closely related to *Spachea* than to other species of *Lophanthera* (Fig. 1). It is intriguing that *L. hammelii* and *S. correae* Cuatrec. & Croat are sympatric in Costa Rica (W. Anderson, 2007), but we do not want to read too much into those distributions or into the fact that *L. hammelii* is disjunct from its Amazonian congeners. Other similar disjunctions involving monophyletic taxa are known within the family (e.g., *Dicella* Griseb. in Costa Rica, W. Anderson, 2007). Moreover, it is very rare for us to encounter cases where there is such a disagreement between evidence from morphology and molecular sequences, so we do not intend to propose any taxonomic adjustments until this group receives more thorough study.



### III. Phylogenetic placement of Old World Malpighiaceae—

One of our most significant findings is the placement of the Old World clades of Malpighiaceae. We identified seven Old World clades and their closest New World relatives, in nearly all instances with 85 BP or greater (Fig. 1). Except for the acridocarpoid clade, all of these Old World clades are scattered deep within the predominantly New World banisterioid clade. If we also include the New World species *Heteropterys leona* (Cav.) Exell and *Stigmaphyllon bannisterioides* (L.) C. Anderson, which are native to the New World but have representative populations in coastal West Africa, the total number of Old World clades increases to nine. These findings will greatly help to produce an improved knowledge of the biogeography and floral evolution within the family, which we discuss below, and will be critical for future studies.

**Biogeography of Malpighiaceae**—Anderson (1979, 1990) argued on morphological grounds that the Malpighiaceae originated in South America in isolation from Africa. Molecular analyses (Cameron et al., 2001; Davis et al., 2001, 2002b, 2004) have similarly supported a likely New World origin for the family. In our previous studies (Cameron et al., 2001; Davis et al., 2001), there was still uncertainty about how many times the Malpighiaceae migrated from the New World to the Old World, because the placement of the Old World clades was not fully resolved.

It is now clear from the results presented here that the Malpighiaceae reached the Old World a total of nine times (Fig. 1). Two of those migrants are the species *Heteropterys leona* and *Stigmaphyllon bannisterioides*, both members of large New World genera and both found on the Atlantic coasts of Central America, the Caribbean, and South America as well as on the coast of West Africa. Those species have fruits that appear to be adapted for dispersal by water (e.g., arechymatous fruit walls and/or dissected outgrowths on the fruit wall that presumably trap air and promote buoyancy; Anderson, 1997, 2001). These two species may have reached Africa via water dispersal across the Atlantic relatively recently, but long enough ago for both to have established extensive populations in coastal Africa (for a map showing the African distribution of *H. leona*, see Anderson et al., 2006).

The seven other Old World clades have diverged significantly from their New World relatives, suggesting much earlier arrivals in the Old World, likely during the Cenozoic (Davis et al., 2002b, 2004). Six of these clades, all consisting of only one or two genera, receive 99–100 BP. The madagasikarioids are the seventh and by the far the largest Old World clade, comprising eight genera. That clade is moderately supported (65 BP) here, but well supported elsewhere with increased taxon sampling and more rapidly evolving gene regions (Davis, 2002). Six of these Old World clades are well placed ( $\geq 86$  BP) with their closest New World relatives (Fig. 1), while the placement of the seventh, the hiptageoid clade, has less support (59 BP) but is likely to be closely related to the New World genera *Carolus*, *Dicella*, and *Tricomaria*.

Anderson (1990) has suggested that the Malpighiaceae reached the Old World by dispersing across the southern Atlantic (without suggesting when that occurred or how great a gap existed at the time). Davis et al. (2002b, 2004) have argued that long-distance dispersal across the southern Atlantic is unlikely. Instead, they suggested that Malpighiaceae dispersed into North America from South America via the Caribbean Basin, crossed the North Atlantic into Eurasia, and subsequently reached the Old World tropics when paleoland and paleoclimatic configurations could have facilitated this migration. These ideas are testable,

and the way forward lies in combining additional information from DNA sequences, morphology, fossils, and past and present-day distributions of the many New and Old World clades identified here. This study will allow us to better focus our ongoing efforts to obtain a much more thoughtful geographic sampling of species, especially from within those predominantly New World clades that also include Old World taxa. Such an approach will allow us to make better inferences on the routes followed by Malpighiaceae following their departure from South America.

**IV. Floral evolution**—Specialist pollination systems are often invoked as key factors underlying floral diversification as suggested, for example, in studies of orchids (Darwin, 1862; van der Pijl and Dodson, 1966) and Polemoniaceae (Grant and Grant, 1965; Stebbins, 1974). In some cases, however, specialized pollination systems may constrain floral morphological evolution. Neotropical species of Malpighiaceae may illustrate this pattern. Most are pollinated by specialist oil-collecting bees (Vogel, 1974), a relationship that appears to be ancient (Taylor and Crepet, 1987) and show relatively little floral diversity in contrast to diverse fruit structure and habit type (Anderson, 1979). A major question of evolutionary biologists is how such conserved morphologies are maintained over long periods of time, even in the face of diversification into different ecological roles (Beldade et al., 2002; Brakefield and Roskam, 2006). Are they the result of intrinsic genetic and developmental constraints, or are they labile and actively maintained by extrinsic factors (in this case, their oil-bee pollinators) over millions of years?

Malpighiaceae are a natural laboratory for testing these hypotheses because they comprise multiple sister-pairs of New World lineages that have maintained their oil-bee pollinators and Old World lineages that have lost them (the oil-bees that pollinate most New World Malpighiaceae are not present in the Old World; Vogel, 1990; Michener, 2000). New World Malpighiaceae are especially species-rich, yet they exhibit a conserved floral morphology (Fig. 3), which appears to be tightly associated with their oil-bee pollinators (Vogel, 1974, 1990; Anderson, 1979, 1990; Sigrist and Sazima, 2004; Gaglianone, 2005). In contrast, the Old World genera are relatively species-poor, yet they display a diverse array of floral morphologies (Fig. 3). The majority of these Old World species lack most of the characteristic floral features critical to the pollination syndrome of New World Malpighiaceae, including especially the unique bilateral symmetry of the corolla (one dorsal petal functioning as a flag and the four lateral petals forming mirror-image pairs) and paired oil glands on the abaxial side of four or all five sepals. In the few Old World species that maintain some calyx glands (viz., African *Acridocarpus* Guill. & Perr. and Australasian *Hiptage* Gaertn.), the glands have shifted from producing oil to sugar (Lobreau-Callen, 1989). In most Old World Malpighiaceae, the only obvious reward for pollinators is pollen.

These observations suggest that the stereotyped New World flower may be maintained by selection by their oil-bee pollinators, not by intrinsic genetic constraints, and that when lineages migrated to the Old World where those pollinators were not found their floral morphology soon departed from that of their ancestors. This conclusion is also supported by (1) recent developmental and genetic data indicating that these changes may be relatively labile at the genetic level (Zhang et al., 2010) and (2) by those few New World Malpighiaceae species that have apparently abandoned pollination by oil-bees. An excellent example is *Psychopterys*, a Mexican/Central American genus of

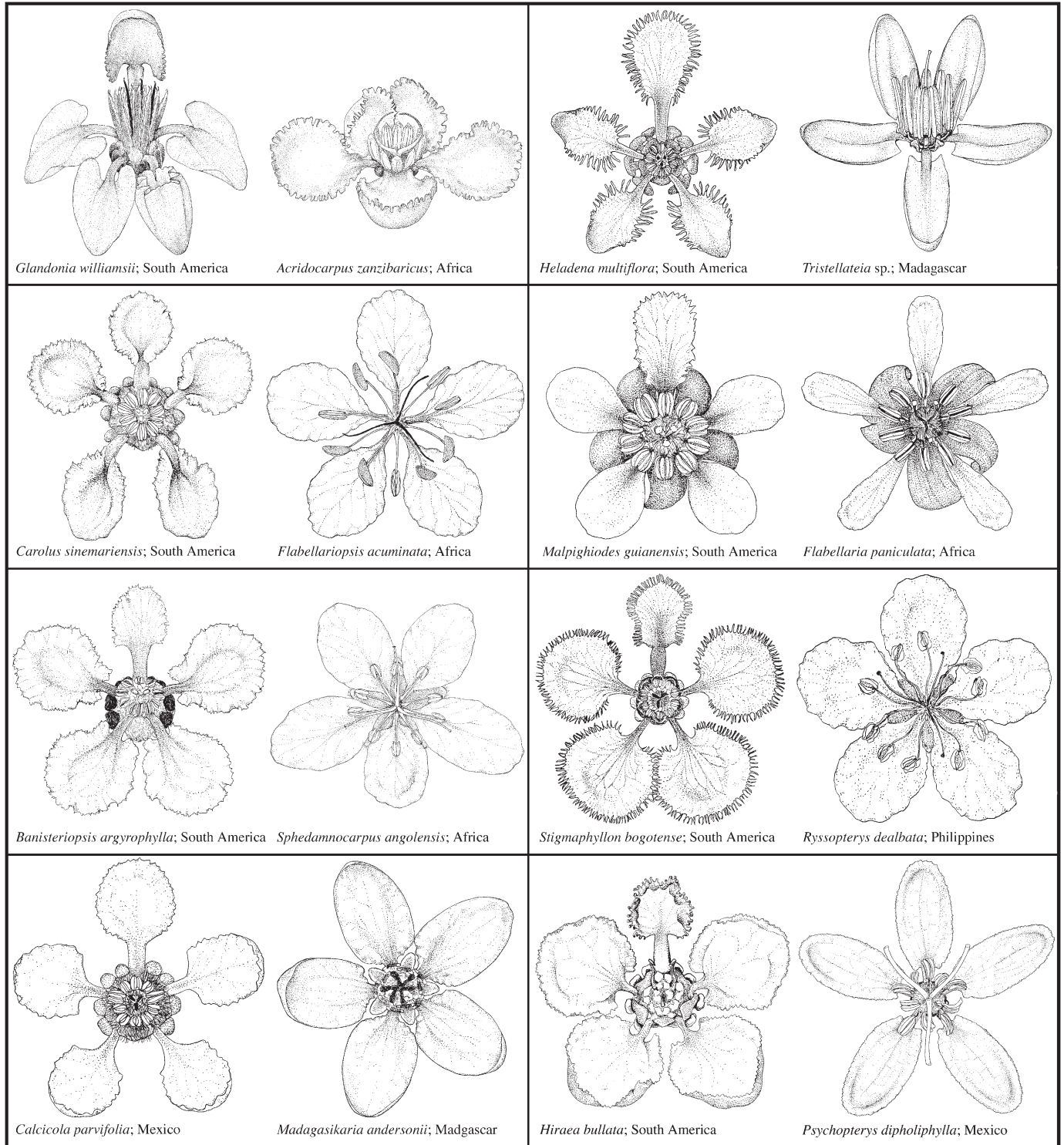


Fig. 3. Corolla morphology of Malpighiaceae of the seven New and Old World sister clades highlighted in Fig. 1. Seven panels (all but that at lower right) illustrate the New World flower morphology contrasted with a representative from its Old World sister clade on the right. None of those Old World clades have maintained the stereotypical corolla symmetry of their New World sisters, which is ancestral in the family (Zhang et al., 2010). The three Old World genera that have bilaterally symmetrical corollas (*Acridocarpus*, *Tristellateia* Thouars, and *Sphedamnocarpus*) possess two dorsal petals (vs. only one in the New World) and one ventral petal, so the whole appearance of the flower is radically different from what a pollinator sees on approaching a flower in the New World. In the other four Old World genera (*Flabellariopsis* Wilczek, *Flabellaria* Cav., *Ryssopterys*, and *Madagasikaria*), the corolla is radially symmetrical. The eighth panel (lower right) compares two New World genera in the same clade: *Hiraea*, with a bilaterally symmetrical corolla and calyx glands for pollination by oil-bees, and *Psychopterys*, with a radially symmetrical corolla and eglandular sepals.



the hiraoid clade that completely lacks calyx glands and has radially symmetrical corollas, quite different from those of other genera of that clade, which have the typical New World morphology (Fig. 3; Anderson and Corso, 2007). In *Galphimia* Cav., C. Anderson (2007) found something similar: the calyx glands are rudimentary or absent, and while it is often still possible to identify which is the flag petal, the overall symmetry of the corolla is much closer to radial than that of most New World Malpighiaceae. A final example is the Mexican genus *Lasio-carpus* Liebm. and its South American sister, *Ptilochaeta* Turcz. In this case, both genera lack calyx glands and possess radially symmetrical corollas (W. Anderson and C. Davis, unpublished data).

To more thoroughly address the question of developmental and genetic constraints vs. active maintenance, we need to integrate these morphological and phylogenetic insights into a strong analytical framework. Furthermore, it will be crucial to further examine the underlying genetic architecture of the floral morphology in Malpighiaceae (cf. Zhang et al., 2010). The phylogenetic results we present here represent an essential step toward making these kinds of evolutionary analyses possible and are a major focus of inquiry in Davis's laboratory.

**Future directions**—The analyses reported here have done a great deal to resolve infrafamilial relationships in the Malpighiaceae, but as described above, there remains a need for better resolution in several parts of the tree, especially in the tetrapteroids and stigmaphylloids. We are hopeful that progress can be achieved using two approaches to resolve these problems. The first will be to continue to expand character sampling across many members of the family using additional low copy nuclear genes, which have been shown to be very informative for resolving infrafamilial relationships in Malpighiaceae (Davis, 2002; Davis et al., 2002b) and relationships within the larger clade Malpighiales (Davis and Chase, 2004; Wurdack and Davis, 2009). One candidate is exon 9 of *EMB2765*, which has been useful for resolving relationships across the order Malpighiales (Wurdack and Davis, 2009). The second will be to greatly expand the number of characters using a phylogenomic approach, i.e., sampling a very large number of characters across a carefully selected subset of taxa representing all major clades within the family. These placeholder taxa can then be combined as a “scaffold” (Wiens et al., 2005; Wiens, 2006; Xi et al., 2010) with data sets that include greater taxon sampling (but far fewer characters) and analyzed simultaneously as a large supermatrix. The addition of a large number of more slowly evolving gene regions has been especially helpful in resolving rapid radiations deeper in Malpighiales (Davis et al., 2007), as well as in Saxifragales (Jian et al., 2008).

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APPENDIX 1. Taxa sequenced with distribution, voucher information, and GenBank accession numbers. Herbarium acronyms follow *Index herbariorum* (Holmgren et al., 1990).

| Taxon   | Distr. <sup>a</sup> | Voucher                         | Plastid     |             |             | Nuclear     |
|---|---------------------|---------------------------------|-------------|-------------|-------------|-------------|
|   |                     |                                 | <i>ndhF</i> | <i>matK</i> | <i>rbcL</i> | <i>PHYC</i> |
| Celastraceae*   |                     |                                 |             |             |             |             |
| <i>Denhamia celastroides</i> (F. Muell.) Jessup               | OW                  | Chase 2050 (K)                  | AY425043    | EF135526    | AJ402941    | AY425097    |
| Centroplacaceae*  |                     |                                 |             |             |             |             |
| <i>Bhesa archiboldiana</i> (Merr. & L. M. Perry) Ding Hou     | OW                  | Takeuchi & Ama 16456 (GH)       | FJ670065    |             |             |             |
| <i>Bhesa paniculata</i> Arn.†                                 | OW                  | Sugumaran 118 (US)              |             |             |             | FJ669883    |
| <i>Bhesa robusta</i> (Roxb.) Ding Hou                         | OW                  | Laman 283 (L)                   |             | FJ670001    | AY935723    |             |
| <i>Centroplacus glaucinus</i> Pierre†                         | OW                  | White 128, ser. 1 (MO)          | FJ670066    | FJ670002    | AY663646    | FJ669884    |
| Chrysobalanaceae*   |                     |                                 |             |             |             |             |
| <i>Atuna racemosa</i> Raf.                                    | OW                  | Chase 2118 (K)                  | AY425030    | EF135503    | AF089758    | AY425088    |
| Dichapetalaceae*  |                     |                                 |             |             |             |             |
| <i>Dichapetalum macrocarpum</i> Engl.                         | OW                  | Fisson s.n. 10/8/93 (K)         | AY425044    | EF135527    | AF089764    | AY425098    |
| Euphorbiaceae*  |                     |                                 |             |             |             |             |
| <i>Acalypha californica</i> Benth.                            | NW                  | Levin 2192 (SD)                 | AY425027    | EF13549     | AY380341    | AY425087    |
| <i>Endospermum moluccanum</i> (Teijsm. & Binn.) Kurz          | OW                  | Chase 1258 (K)                  | AY425051    | EF135533    | AJ402950    | AY425106    |
| Elatinaceae*  |                     |                                 |             |             |             |             |
| <i>Bergia pedicellaris</i> (F. Muell.) Benth.†                | OW                  | Harwood 1285 (A)                | HQ246766    | HQ247213    | HQ247446    | HQ246984    |
| <i>Bergia texana</i> Seub. ex Walp.†                          | NW                  | Sanders et al. 13525 (MICH)     | AY425033    | EF135506    | AY380344    | AY425091    |
| <i>Elatine minima</i> (Nutt.) Fisch. & C. A. Mey.†            | NW                  | Oldham 16691 (MICH)             | HQ246824    |             |             | HQ247048    |
| <i>Elatine triandra</i> Schkuhr†                              | NW                  | Burton et al. 13384 (MICH)      | AY425049    | EF135532    | AY380348    | AY425104    |
| <i>Elatine</i> sp.  | OW                  | Qiu 99051 (Z)                   | HQ246825    | HQ247273    |             | HQ247049    |
| Goupiaceae*   |                     |                                 |             |             |             |             |
| <i>Goupia glabra</i> Aubl.                                    | NW                  | Prevost 3031 (CAY)              | AY425054    | EF135544    | AJ235780    | AY425108    |
| Ochnaceae*  |                     |                                 |             |             |             |             |
| <i>Ochna</i> sp.  | OW                  | Davis 31-01 (A)                 | AY425073    | FJ670031    | AY380354    | AY425123    |
| Peridiscaceae*  |                     |                                 |             |             |             |             |
| <i>Peridiscus lucidus</i> Benth.                              | NW                  | Soares 205 (CEPEC)              | AY425076    | DQ411570    | AY380356    | AY425125    |
| Phyllanthaceae*   |                     |                                 |             |             |             |             |
| <i>Phyllanthus calycinus</i> Labill.                          | OW                  | Chase 2163 (K)                  | EU002250    | EF135580    | AY663603    | AY579869    |
| Picrodendraceae*  |                     |                                 |             |             |             |             |
| <i>Androstachys johnsonii</i> Prain                           | OW                  | Chase 1904 (K)                  | AF500495    |             | AJ402922    | AF500522    |
| Putranjivaceae*   |                     |                                 |             |             |             |             |
| <i>Putranjiva roxburghii</i> Wall.                            | OW                  | Wurdack D57 (US)                | AY425048    | EF135530    | M95757      | AY425102    |
| Violaceae*  |                     |                                 |             |             |             |             |
| <i>Hymenanthera alpina</i> (Kirk) W. R. B. Oliv.              | OW                  | Chase 501 (K)                   | AY425059    | EF135552    | Z75692      | AY425112    |
| Malpighiaceae   |                     |                                 |             |             |             |             |
| <i>Acmanthera latifolia</i> (Adr. Juss.) Griseb.†             | NW                  | Anderson 13771 (MICH)           | AF351013    | AF344524    | AF344454    | AF500528    |
| <i>Acridocarpus adenophorus</i> Adr. Juss.†                   | OW                  | McPherson 14406 (MICH)          | AY137243    | HQ247173    | HQ247415    | AY499049    |
| <i>Acridocarpus alternifolius</i> (Schumach. & Thonn.) Nied.  | OW                  | Davis 99-16 (A)                 | HQ246730    | HQ247174    | HQ247416    | HQ246944    |
| <i>Acridocarpus chevalieri</i> Sprague                        | OW                  | Davis 99-15 (A)                 | AY137247    | HQ247175    | HQ247417    | AY499050    |
| <i>Acridocarpus excelsus</i> Adr. Juss.                       | OW                  | Rakotomalaza et al. 378 (MO)    | AY137248    | HQ247176    | HQ247418    | AY499051    |
| <i>Acridocarpus macrocalyx</i> Engl.                          | OW                  | Davis 99-09 (A)                 | AF351017    | HQ247177    | HQ247419    | AF500532    |
| <i>Acridocarpus natalitius</i> Adr. Juss.†                    | OW                  | Goldblatt s.n. (PRE)            | AF351016    | AF344525    | AF344455    | AF500531    |
| <i>Acridocarpus orientalis</i> Adr. Juss.                     | OW                  | Popov 85 (MO)                   | AY137255    | HQ247178    | HQ247420    | AY499052    |
| <i>Acridocarpus scheffleri</i> Engl.                          | OW                  | Mlangwa et al. 1417 (MO)        | HQ246731    |             | HQ247421    | HQ246945    |
| <i>Acridocarpus smeathmannii</i> (DC.) Guill. & Perr.         | OW                  | Davis 99-13 (A)                 | AY137261    | HQ247179    | HQ247422    | AY499053    |
| <i>Acridocarpus</i> sp.                                       | OW                  | Bourobou 939 (MO)               | HQ246732    | HQ247180    |             | HQ246946    |
| <i>Acridocarpus spectabilis</i> (Nied.) Doorn-Hoekm.          | OW                  | GC 47679 (MO)                   | HQ246733    | HQ247181    | HQ247423    | HQ246947    |
| <i>Acridocarpus staudtii</i> (Engl.) Hutch. & Dalziel         | OW                  | Davis 99-7 (A)                  | HQ246734    | HQ247182    | HQ247424    | HQ246948    |
| <i>Acridocarpus zanzibaricus</i> Adr. Juss.                   | OW                  | Davis 99-23 (A)                 | AY137264    | HQ247183    | HQ247425    | AY499054    |
| <i>Adelphia hiraea</i> (Gaertn.) W. R. Anderson†              | NW                  | Anderson 13802 (MICH)           | AF351059    | AF344566    | AF344498    | AF500563    |
| <i>Aenigmatanthera doniana</i> (Griseb.) W. R. Anderson       | NW                  | Prance & Henriques 29888 (MICH) | HQ246735    |             | HQ247426    | HQ246949    |
| <i>Aenigmatanthera lasiandra</i> (Adr. Juss.) W. R. Anderson† | NW                  | Dubs 1460 (MICH)                | HQ246737    |             | HQ247428    | HQ246951    |
| <i>Aenigmatanthera lasiandra</i> (Adr. Juss.) W. R. Anderson† | NW                  | Dubs 2371 (MICH)                | HQ246736    | HQ247184    | HQ247427    | HQ246950    |
| <i>Aenigmatanthera lasiandra</i> (Adr. Juss.) W. R. Anderson† | NW                  | Fonseca et al. 1912 (MICH)      | HQ246738    | HQ247185    | HQ247429    | HQ246952    |
| <i>Alicia anisopetala</i> (Adr. Juss.) W. R. Anderson†        | NW                  | Anderson 13598 (MICH)           | AF351053    | AF344562    | AF344494    | AF500557    |
| <i>Amorimia amazonica</i> (Nied.) W. R. Anderson†             | NW                  | Steinbach 339 (MICH)            | HQ246739    | HQ247186    | HQ247430    | HQ246953    |
| <i>Amorimia camporum</i> W. R. Anderson                       | NW                  | Campos & Díaz 2490 (MICH)       | HQ246740    | HQ247187    | HQ247431    | HQ246954    |
| <i>Amorimia exotropa</i> (Griseb.) W. R. Anderson             | NW                  | Vanni et al. 2903 (MICH)        | HQ246741    | HQ247188    |             | HQ246955    |
| <i>Amorimia kariniana</i> W. R. Anderson                      | NW                  | Asplund 16617 (S)               | HQ246742    | HQ247189    | HQ247432    | HQ246956    |
| <i>Amorimia rigida</i> (Adr. Juss.) W. R. Anderson†           | NW                  | Anderson 13691 (MICH)           | AY499101    | HQ247190    | HQ247433    | AY499075    |
| <i>Amorimia velutina</i> W. R. Anderson                       | NW                  | Shepherd et al. 4409 (NY)       | HQ246743    | HQ247191    |             | HQ246957    |
| <i>Aspicarpa brevipes</i> (DC.) W. R. Anderson†               | NW                  | Cházaro 6295 (MICH)             | AF351082    | AF344526    | AF344456    | AF500581    |
| <i>Aspicarpa harleyi</i> W. R. Anderson†                      | NW                  | Anderson 13696 (MICH)           | HQ246744    | HQ247192    | HQ247434    | HQ246958    |
| <i>Aspicarpa hirtella</i> Rich.†                              | NW                  | Anderson 13525 (MICH)           | AF351033    | AF344527    | AF344457    | AF500541    |
| <i>Aspicarpa hyssopifolia</i> A. Gray                         | NW                  | Anderson 13321 (MICH)           | HQ246745    | HQ247193    |             | HQ246959    |
| <i>Aspicarpa pulchella</i> (Griseb.) O'Donell & Lourteig†     | NW                  | Anderson 13614 (MICH)           | AF351026    | AF344528    | AF344458    | HQ246960    |

## APPENDIX 1. Continued

| Taxon  | Distr. <sup>a</sup> | Voucher                               | Plastid     |             |                       | Nuclear     |
|--|---------------------|---------------------------------------|-------------|-------------|-----------------------|-------------|
|  |                     |                                       | <i>ndhF</i> | <i>matK</i> | <i>rbcL</i>           | <i>PHYC</i> |
| <i>Aspicarpa sericea</i> Griseb.†  | NW                  | Anderson 13586 (MICH)                 | HQ246747    |             | HQ247436              | HQ246962    |
| <i>Aspicarpa sericea</i> Griseb.†  | NW                  | Krapovickas & Schinini 39191 (MICH)   | HQ246746    | HQ247194    | HQ247435              | HQ246961    |
| <i>Aspidopterys</i> sp.†   | OW                  | Larsen & Larsen 34311 (P)             | HQ263253    | HQ263254    |                       | HQ263255    |
| <i>Aspidopterys</i> sp.  | OW                  | Bogor XVI.G.110 (BO) [Chase M239 (K)] | AF351019    | AF344529    | AF344459              | AF436796    |
| <i>Aspidopterys</i> sp.  | OW                  | Srisanga 1137 (P)                     | HQ246748    | HQ247195    | HQ263252              | HQ246963    |
| <i>Aspidopterys tomentosa</i> (Blume) Adr. Juss.†                        | OW                  | Tsi Zhanhuo 92-121 (MO)               | HQ246749    | HQ247196    | HQ247437              | HQ246964    |
| <i>Banisteriopsis acerosa</i> (Nied.) B. Gates                           | NW                  | Guala 1370 (MICH)                     |             | HQ247197    |                       | HQ246965    |
| <i>Banisteriopsis adenopoda</i> (Adr. Juss.) B. Gates                    | NW                  | Silva 1109 (MICH)                     | HQ246750    |             | HQ247438              | HQ246966    |
| <i>Banisteriopsis angustifolia</i> (Adr. Juss.) B. Gates                 | NW                  | Carvalho 80 (MICH)                    | HQ246751    | HQ247198    |                       | HQ246967    |
| <i>Banisteriopsis argyrophylla</i> (Adr. Juss.) B. Gates                 | NW                  | Silva et al. 3548 (MICH)              | HQ246752    | HQ247199    | HQ247439              | HQ246968    |
| <i>Banisteriopsis caapi</i> (Griseb.) C. V. Morton†                      | NW                  | Anderson 13791 (MICH)                 | HQ246753    | HQ247200    | HQ247440              | HQ246969    |
| <i>Banisteriopsis calcicola</i> B. Gates                                 | NW                  | Lombardi 1690 (MICH)                  | HQ246754    | HQ247201    |                       | HQ246970    |
| <i>Banisteriopsis confusa</i> B. Gates                                   | NW                  | Krapovickas & Cristóbal 44854 (MICH)  | HQ246755    | HQ247202    |                       | HQ246971    |
| <i>Banisteriopsis gardneriana</i> (Adr. Juss.) W. R. Anderson & B. Gates | NW                  | Azevedo & Lopes 313 (MICH)            |             | HQ247203    |                       | HQ246972    |
| <i>Banisteriopsis harleyi</i> B. Gates                                   | NW                  | Carvalho 87 (MICH)                    | HQ246756    | HQ247204    |                       | HQ246973    |
| <i>Banisteriopsis laevifolia</i> (Adr. Juss.) B. Gates†                  | NW                  | Anderson 13631 (MICH)                 | HQ246757    | HQ247205    | HQ247441              | HQ246974    |
| <i>Banisteriopsis latifolia</i> (Adr. Juss.) B. Gates                    | NW                  | Azevedo 698 (MICH)                    | HQ246758    | HQ247206    |                       | HQ246975    |
| <i>Banisteriopsis martiniana</i> (Adr. Juss.) Cuatrec.†                  | NW                  | Chase 90161 (MICH)                    | HQ246759    | HQ247207    | HQ247442              | HQ246976    |
| <i>Banisteriopsis muricata</i> (Cav.) Cuatrec.†                          | NW                  | Anderson 13799 (MICH)                 | HQ246760    | HQ247208    | HQ247443              | HQ246977    |
| <i>Banisteriopsis nummifera</i> (Adr. Juss.) B. Gates                    | NW                  | Harley 54681 (MICH)                   | HQ246761    | HQ247209    | HQ247444              | HQ246978    |
| <i>Banisteriopsis paraguayensis</i> B. Gates                             | NW                  | Ferrucci et al. 1624 (MICH)           | HQ246762    | HQ247210    |                       | HQ246979    |
| <i>Banisteriopsis prancei</i> B. Gates                                   | NW                  | Anderson 9910 (MICH)                  |             |             |                       | HQ246980    |
| <i>Banisteriopsis pulchra</i> B. Gates                                   | NW                  | Dubs 2258 (MICH)                      | HQ246763    | HQ247211    |                       | HQ246981    |
| <i>Banisteriopsis schwannioides</i> (Griseb.) B. Gates                   | NW                  | Mori et al. 21590 (MICH)              | HQ246764    | HQ247212    | HQ247445              | HQ246982    |
| <i>Banisteriopsis sellowiana</i> (Adr. Juss.) B. Gates                   | NW                  | Menendo 278 (MICH)                    | HQ246765    |             |                       | HQ246983    |
| <i>Barnebya dispar</i> (Griseb.) W. R. Anderson & B. Gates†              | NW                  | Leoni 1473 (MICH)                     | AF351073    | AF344531    | AJ402924/<br>AJ403020 | AF500574    |
| <i>Blepharandra fimbriata</i> MacBryde†                                  | NW                  | Anderson 13882 (MICH)                 | HQ246767    |             | HQ247447              | HQ246985    |
| <i>Blepharandra heteropetala</i> W. R. Anderson†                         | NW                  | Anderson 13782 (MICH)                 | AF351008    | AF344532    | AF344461              | AF500523    |
| <i>Blepharandra hypoleuca</i> (Benth.) Griseb.                           | NW                  | Anderson 13844 (MICH)                 | HQ246768    | HQ247214    | HQ247448              | HQ246986    |
| <i>Brachylophon curtisii</i> Oliv.†                                      | OW                  | Middleton et al. 387 (A)              | AF351018    | HQ247215    | HQ247449              | AY137337    |
| <i>Bronwenia cinerascens</i> (Benth.) W. R. Anderson & C. Davis          | NW                  | Nee 48570 (MICH)                      | HQ246769    | HQ247216    |                       | HQ246987    |
| <i>Bronwenia cinerascens</i> (Benth.) W. R. Anderson & C. Davis          | NW                  | Nee 48324 (MICH)                      |             |             | HQ247450              |             |
| <i>Bronwenia cornifolia</i> (H. B. K.) W. R. Anderson & C. Davis†        | NW                  | Clark 1 (MICH)                        | HQ246770    | HQ247217    | HQ247451              | HQ246988    |
| <i>Bronwenia ferruginea</i> (Cav.) W. R. Anderson & C. Davis             | NW                  | Amorim et al. 3222 (MICH)             | HQ246771    | HQ247218    | HQ247452              | HQ246989    |
| <i>Bronwenia mathiasiae</i> (W. R. Anderson) W. R. Anderson & C. Davis†  | NW                  | Nelson et al. 518 (MICH)              | HQ246772    | HQ247219    | HQ247453              | HQ246990    |
| <i>Bunchosia angustifolia</i> Adr. Juss.                                 | NW                  | Coimbra S. 766 (MICH)                 | HQ246773    | HQ247220    |                       | HQ246991    |
| <i>Bunchosia apiculata</i> Huber   | NW                  | Gentry et al. 50215 (MICH)            | HQ246774    | HQ247221    |                       | HQ246992    |
| <i>Bunchosia armeniaca</i> (Cav.) DC.†                                   | NW                  | FTG 77-999C (FTG)                     | AF351045    | AF344533    | Z75274                | AF500550    |
| <i>Bunchosia armeniaca</i> (Cav.) DC.†                                   | NW                  | Nee 41995 (MICH)                      | HQ246775    | HQ247222    |                       | HQ246993    |
| <i>Bunchosia decussiflora</i> W. R. Anderson                             | NW                  | de Granville 4905 (MICH)              | HQ246776    | HQ247223    |                       | HQ246994    |
| <i>Bunchosia deflexa</i> Triana & Planch.                                | NW                  | Gentry et al. 54765 (MICH)            | HQ246777    | HQ247224    |                       | HQ246995    |
| <i>Bunchosia glandulifera</i> (Jacq.) H. B. K.                           | NW                  | Anderson 13761 (MICH)                 | HQ246778    | HQ247225    | HQ247454              | HQ246996    |
| <i>Bunchosia glandulosa</i> (Cav.) DC.                                   | NW                  | Correll 50038 (MICH)                  |             |             |                       | HQ246998    |
| <i>Bunchosia glandulosa</i> (Cav.) DC.                                   | NW                  | Goldman 3697 (GH)                     | HQ246779    | HQ247226    |                       | HQ246997    |
| <i>Bunchosia macrophylla</i> Rose  | NW                  | Hammel 17747 (CR)                     | HQ246780    | HQ247227    | HQ247455              | HQ246999    |
| <i>Bunchosia mcvaughii</i> W. R. Anderson                                | NW                  | Evans s.n. (MICH)                     | HQ246781    | HQ247228    | HQ247456              | HQ247000    |
| <i>Bunchosia mollis</i> Benth.   | NW                  | Jansen-Jacobs et al. 3958 (MICH)      | HQ246782    | HQ247229    |                       | HQ247001    |
| <i>Bunchosia nitida</i> (Jacq.) DC.                                      | NW                  | Silverstone-Sopkin & Paz 7096 (MICH)  | HQ246783    |             |                       | HQ247002    |
| <i>Bunchosia odorata</i> (Jacq.) DC.                                     | NW                  | Flora Falcón 791 (MICH)               | HQ246784    | HQ247230    |                       | HQ247003    |
| <i>Bunchosia pilocarpa</i> Rusby   | NW                  | Smith et al. 14020 (MICH)             | HQ246785    | HQ247231    |                       | HQ247004    |
| <i>Bunchosia polystachia</i> (Andrews) DC.                               | NW                  | Ernst 1960 (MICH)                     | HQ246786    | HQ247232    |                       | HQ247005    |
| <i>Bunchosia swartziana</i> Griseb.                                      | NW                  | Webster & Wilson 4820 (MICH)          |             | HQ247233    |                       | HQ247006    |
| <i>Bunchosia ternata</i> Dobson  | NW                  | Anderson 13806 (MICH)                 | HQ246787    | HQ247234    | HQ247457              | HQ247007    |
| <i>Bunchosia veluticarpa</i> W. R. Anderson                              | NW                  | Anderson 13805 (MICH)                 | HQ246788    | HQ247235    | HQ247458              | HQ247008    |
| <i>Burdachia sphaerocarpa</i> Adr. Juss.†                                | NW                  | Anderson 13774 (MICH)                 | AF351071    | AF344534    | AF344462              | AF500572    |
| <i>Byrsonima basiloba</i> Adr. Juss.                                     | NW                  | Anderson 13671 (MICH)                 | HQ246789    | HQ247236    | HQ247459              | HQ247009    |
| <i>Byrsonima coccolobifolia</i> H. B. K.†                                | NW                  | Anderson 13661 (MICH)                 | HQ246790    | HQ247237    | HQ247460              | HQ247010    |
| <i>Byrsonima crassifolia</i> (L.) H. B. K.†                              | NW                  | FTG 81-680A (MICH)                    | AF351011    | AF344535    | L01892                | AF500526    |



## APPENDIX 1. Continued

| Taxon  | Distr. <sup>a</sup> | Voucher                                | Plastid     |             |             | Nuclear     |
|--|---------------------|--|-------------|-------------|-------------|-------------|
|  |                     |  | <i>ndhF</i> | <i>matK</i> | <i>rbcL</i> | <i>PHYC</i> |
| <i>Byrsonima crispa</i> Adr. Juss.   | NW                  | Anderson 13755 (MICH)                  | HQ246791    | HQ247238    | HQ247461    | HQ247011    |
| <i>Byrsonima duckeana</i> W. R. Anderson   | NW                  | Anderson 13765 (MICH)                  | HQ246792    | HQ247239    |             | HQ247012    |
| <i>Byrsonima lucida</i> (Mill.) DC.  | NW                  | FTG 85-139 (MICH)                      | HQ246793    | HQ247240    | HQ247462    | HQ247013    |
| <i>Byrsonima macrophylla</i> (Pers.) W. R. Anderson                              | NW                  | Anderson 13647 (MICH)                  | HQ246794    | HQ247241    |             | HQ247014    |
| <i>Byrsonima morii</i> W. R. Anderson  | NW                  | Harley 26462 (MICH)                    | HQ246795    |             | HQ247463    | HQ247015    |
| <i>Byrsonima triopterifolia</i> Adr. Juss.                                       | NW                  | Anderson 13702 (MICH)                  | HQ246796    | HQ247242    | HQ247464    | HQ247016    |
| <i>Calpicola parvifolia</i> (Adr. Juss.) W. R. Anderson & C. Davis†              | NW                  | Salinas T. 5444 (MICH)                 | HQ246797    | HQ247243    | HQ247465    | HQ247017    |
| <i>Callaeum antifebrile</i> (Griseb.) D. M. Johnson                              | NW                  | Morawetz & Wallnöfer 117-161085 (MICH) | HQ246798    | HQ247244    | HQ247466    | HQ247018    |
| <i>Callaeum clavipetalum</i> D. M. Johnson                                       | NW                  | Acosta C. 812 (MICH)                   | HQ246799    | HQ247245    | HQ247467    | HQ247019    |
| <i>Callaeum malpighioides</i> (Turcz.) D. M. Johnson                             | NW                  | Ventura A. 19165 (MICH)                | HQ246800    | HQ247246    | HQ247468    | HQ247020    |
| <i>Callaeum nicaraguense</i> (Griseb.) Small                                     | NW                  | Moreno 25336 (MICH)                    | HQ246801    | HQ247247    | HQ247469    | HQ247021    |
| <i>Callaeum psilophyllum</i> (Adr. Juss.) D. M. Johnson†                         | NW                  | FTG 61-291 (FTG)                       |             | HQ247248    |             | HQ247022    |
| <i>Callaeum psilophyllum</i> (Adr. Juss.) D. M. Johnson†                         | NW                  | Krapovickas & Cristóbal 44674 (MICH)   | HQ246802    | HQ247249    | HQ247470    | HQ247022    |
| <i>Callaeum septentrionale</i> (Adr. Juss.) D. M. Johnson†                       | NW                  | Anderson 13491 (MICH)                  | AF351058    | AF344536    | AF344463    | AF500562    |
| <i>Camarea axillaris</i> A. St.-Hil.†  | NW                  | Amorim 3659 (CEPEC)                    | AY499081    | HQ247250    | HQ247471    | AY499055    |
| <i>Carolus anderssonii</i> (W. R. Anderson) W. R. Anderson                       | NW                  | Homeier & Werner 1308 (MICH)           | HQ246803    | HQ247251    |             | HQ247024    |
| <i>Carolus chasei</i> (W. R. Anderson) W. R. Anderson†                           | NW                  | Anderson 13710 (MICH)                  | AF351054    | AF344564    | AF344496    | AF500558    |
| <i>Carolus chlorocarpus</i> (Adr. Juss.) W. R. Anderson                          | NW                  | Azevedo et al. 1147 (MICH)             | HQ246804    | HQ247252    |             | HQ247025    |
| <i>Carolus sinemariensis</i> (Aubl.) W. R. Anderson†                             | NW                  | Cochrane et al. 12331 (MICH)           | HQ246806    | HQ247253    | HQ247472    | HQ247027    |
| <i>Carolus sinemariensis</i> (Aubl.) W. R. Anderson†                             | NW                  | Henkel 1832 (MICH)                     | HQ246805    |             |             | HQ247026    |
| <i>Caucanthus auriculatus</i> (Radlk.) Nied.†                                    | OW                  | Kindeketa et al. 1527 (MO)             | HQ246807    | HQ247254    | HQ247473    | HQ247028    |
| <i>Caucanthus auriculatus</i> (Griseb.) Nied.†                                   | OW                  | Knox 2128 (MICH)                       | AF351020    | AF344537    | AF344464    | AF436797    |
| <i>Christianella multiglandulosa</i> (Nied.) W. R. Anderson†                     | NW                  | Hahn 1736 (MICH)                       | HQ246808    | HQ247255    | HQ247474    | HQ247029    |
| <i>Christianella surinamensis</i> (Kosterm.) W. R. Anderson                      | NW                  | Killeen et al. 7674 (MICH)             | HQ246809    | HQ247256    | HQ247475    | HQ247030    |
| <i>Coleostachys genipifolia</i> Adr. Juss.†                                      | NW                  | Anderson 13752 (MICH)                  | AF351012    | AF344538    | AF344465    | AF500527    |
| <i>Cordobia argentea</i> (Griseb.) Nied.†  | NW                  | Anderson 13583 (MICH)                  | AF351081    | AF344539    | AF344466    | HQ247031    |
| <i>Cordobia argentea</i> (Griseb.) Nied.†  | NW                  | Zardini & Duarte 49837A (MICH)         | HQ246810    |             |             |             |
| <i>Cottisia californica</i> (Benth.) W. R. Anderson & C. Davis†                  | NW                  | Anderson 12539 (MICH)                  | AF351031    | AF344554    | AF344486    | AF500539    |
| <i>Cottisia linearis</i> (Wiggins) W. R. Anderson & C. Davis†                    | NW                  | Anderson 12540 (MICH)                  | AF351030    | AF344555    | AF344487    | AF500538    |
| <i>Diacidia ferruginea</i> (Maguire & K. D. Phelps) W. R. Anderson†              | NW                  | Berry et al. 4987 (MICH)               | AF351010    | AF344540    | AF344467    | AF500525    |
| <i>Diacidia galphimioides</i> (Maguire) W. R. Anderson                           | NW                  | Berry et al. 5275 (MICH)               | HQ246811    | HQ247257    | HQ247476    | HQ247032    |
| <i>Diaspis albidia</i> Nied.†  | OW                  | De Wilde 5920 (MO)                     | HQ246813    | HQ247259    | HQ247478    | HQ247034    |
| <i>Diaspis albidia</i> Nied.†  | OW                  | Robertson 5045 (MO)                    | HQ246812    | HQ247258    | HQ247477    | HQ247033    |
| <i>Dicella bracteosa</i> (Adr. Juss.) Griseb.                                    | NW                  | Kallunki et al. 576 (MICH)             | HQ246814    | HQ247260    | HQ247479    | HQ247035    |
| <i>Dicella julianii</i> (J. F. Macbr.) W. R. Anderson                            | NW                  | Burnham 1903 (MICH)                    | HQ246815    | HQ247261    | HQ247480    | HQ247036    |
| <i>Dicella macroptera</i> Adr. Juss.†  | NW                  | Fonseca et al. 2257 (MICH)             | HQ246816    |             |             | HQ247037    |
| <i>Dicella macroptera</i> Adr. Juss.†  | NW                  | Fonseca et al. 2404 (MICH)             | HQ246817    | HQ247262    |             | HQ247038    |
| <i>Dicella macroptera</i> Adr. Juss.†  | NW                  | Pereira 2047 (MICH)                    |             | HQ247263    |             | HQ247039    |
| <i>Dicella nucifera</i> Chodat†  | NW                  | Anderson 13607 (MICH)                  | AF351048    | AF344541    | AJ235802    | AF500553    |
| <i>Digonopteris microphylla</i> Arènes†  | OW                  | Du Puy et al. MB68 (P)                 | HQ246818    | HQ247264    | HQ247481    | HQ247040    |
| <i>Dinemagonum gayanum</i> Adr. Juss.†   | NW                  | Simpson 83-10-23-2c (MICH)             | AF351084    | AF344565    | AF344468    | HQ247041    |
| <i>Dinemandra ericoides</i> Adr. Juss.†  | NW                  | Dillon & Teillier 5103 (MICH)          | AF351069    | AF344542    | AF344469    | AF500570    |
| <i>Diplopterys cabrerana</i> (Cuatrec.) B. Gates†                                | NW                  | Burnham 1774 (MICH)                    | AF351039    | HQ247266    | HQ247482    | AF500582    |
| <i>Diplopterys hypericifolia</i> (Adr. Juss.) W. R. Anderson & C. Davis†         | NW                  | Anderson 13638 (MICH)                  | AF351037    | AF344530    | AF344460    | HQ247042    |
| <i>Diplopterys lutea</i> (Griseb.) W. R. Anderson & C. Davis†                    | NW                  | FTG 60-85 (FTG)                        | HQ246819    | HQ247267    | HQ247483    | HQ247043    |
| <i>Diplopterys nutans</i> (Nied.) W. R. Anderson & C. Davis                      | NW                  | Matezki 175 (MICH)                     | HQ246820    | HQ247268    | HQ247484    | HQ247044    |
| <i>Diplopterys pubipetala</i> (Adr. Juss.) W. R. Anderson & C. Davis             | NW                  | Salino 3472 (MICH)                     | HQ246821    | HQ247269    | HQ247485    | HQ247045    |
| <i>Diplopterys valvata</i> (W. R. Anderson & B. Gates) W. R. Anderson & C. Davis | NW                  | Lombardi 2203 (MICH)                   | HQ246822    | HQ247270    | HQ247486    | HQ247046    |
| <i>Diplopterys virgultosa</i> (Adr. Juss.) W. R. Anderson & C. Davis             | NW                  | Fonseca et al. 2866 (MICH)             | HQ246823    | HQ247271    |             | HQ247047    |
| <i>Echinopteris eglandulosa</i> (Adr. Juss.) Small†                              | NW                  | Van Devender 98-178 (MICH)             | AF351047    | AF344543    | AF344470    | AF500552    |
| <i>Ectopopterys soejartoi</i> W. R. Anderson†                                    | NW                  | Callejas 11806 (MICH)                  | AF351064    | HQ247272    | AF344471    | AF500565    |
| <i>Excentradenia propinqua</i> (W. R. Anderson) W. R. Anderson†                  | NW                  | Lindeman et al. 51 (MICH)              | AF351062    |             |             | AF350995    |
| <i>Flabellaria paniculata</i> Cav.†  | OW                  | Congdon 414 (K)                        | AF351083    |             | AF344472    |             |
| <i>Flabellariopsis acuminata</i> (Engl.) Wilczek†                                | OW                  | Luke & Robertson 2683 (MO)             | HQ246826    | HQ247274    | AF344473    | HQ247050    |
| <i>Gallardoia fischeri</i> Hicken†   | NW                  | Anderson 13580 (MICH)                  | AF351035    | AF344544    | AF344474    | AF500543    |
| <i>Galphimia brasiliensis</i> (L.) Adr. Juss.                                    | NW                  | Alencar 3 (MICH)                       | HQ246827    | HQ247275    | HQ247487    | HQ247051    |
| <i>Galphimia glandulosa</i> Cav.   | NW                  | Anderson & Anderson 5849 (MICH)        | HQ246828    |             |             | HQ247052    |
| <i>Galphimia glauca</i> Cav.†  | NW                  | Ventura & López 8481 (MICH)            |             |             |             | HQ247053    |
| <i>Galphimia gracilis</i> Bartl.†  | NW                  | FTG 79-235 (FTG)                       | AF351015    | AF344545    | AF344475    | AF500530    |

## APPENDIX 1. Continued

| Taxon  | Distr. <sup>a</sup> | Voucher                              | Plastid     |             |             | Nuclear     |
|--|---------------------|--------------------------------------|-------------|-------------|-------------|-------------|
|  |                     |                                      | <i>ndhF</i> | <i>matK</i> | <i>rbcL</i> | <i>PHYC</i> |
| <i>Galphimia mexiae</i> C. E. Anderson                       | NW                  | Anderson & Anderson 6122 (MICH)      | HQ246829    |             |             | HQ247054    |
| <i>Galphimia mirandae</i> C. E. Anderson                     | NW                  | Cabrera s.n. (ENCB)                  | HQ246830    | HQ247276    |             | HQ247055    |
| <i>Galphimia multicaulis</i> Adr. Juss.                      | NW                  | Díaz B. 4760 (MICH)                  | HQ246831    |             | HQ247488    | HQ247056    |
| <i>Galphimia platyphylla</i> Chodat                          | NW                  | Schinini & Marmorì 30112 (MICH)      | HQ246832    |             |             | HQ247057    |
| <i>Galphimia speciosa</i> C. E. Anderson                     | NW                  | Anderson 12991 (MICH)                | HQ246833    | HQ247277    | HQ247489    | HQ247058    |
| <i>Gaudichaudia albida</i> Schlechtend. & Cham.†             | NW                  | Anderson 13309A (MICH)               | AF351034    | AF344546    | AF344476    | AF500542    |
| <i>Gaudichaudia cynanchoides</i> H. B. K.                    | NW                  | Koch 82260 (MICH)                    | HQ246834    |             | HQ247490    | HQ247059    |
| <i>Gaudichaudia hexandra</i> (Nied.) Chodat                  | NW                  | Haber 3782 (MICH)                    | HQ246835    | HQ247278    |             | HQ247060    |
| <i>Gaudichaudia krusei</i> W. R. Anderson                    | NW                  | Jessup 4064 (MICH)                   | HQ246836    | HQ247279    |             | HQ247061    |
| <i>Gaudichaudia mcvaughii</i> W. R. Anderson†                | NW                  | Anderson 12699C (MICH)               | AF351032    | AF344547    | AF344477    | AF500540    |
| <i>Gaudichaudia</i> sp.                                      | NW                  | Anderson 13291B, C (MICH)            | HQ246837    | HQ247280    | HQ247491    | HQ247062    |
| <i>Glandonia macrocarpa</i> Griseb.†                         | NW                  | Anderson 13776 (MICH)                | AF351072    | AF344548    | AF344478    | AF500573    |
| <i>Heladena multiflora</i> (Hook. & Arn.) Nied.†             | NW                  | Anderson 13599 (MICH)                | AF351044    | AF344549    | AF344479    | AF500549    |
| <i>Henleophytum echinatum</i> (Griseb.) Small†               | NW                  | Curtiss 688 (NY)                     | HQ246838    | HQ247281    | HQ247492    |             |
| <i>Heteropterys aureosericea</i> Cuatrec.                    | NW                  | Burnham 3344 (MICH)                  | AY499082    | HQ247282    | HQ247493    | AY499056    |
| <i>Heteropterys bahiensis</i> Nied.                          | NW                  | Amorim 3664 (CEPEC)                  | AY499083    | HQ247283    | HQ247494    | AY499057    |
| <i>Heteropterys bicolor</i> Adr. Juss.                       | NW                  | Amorim 2710 (MICH)                   | AY499084    | HQ247284    | HQ247495    | AY499058    |
| <i>Heteropterys brachiata</i> (L.) DC.†                      | NW                  | FTG PRC-105 (MICH)                   | HQ246839    | HQ247285    | HQ247496    | HQ247063    |
| <i>Heteropterys bysonimifolia</i> Adr. Juss.                 | NW                  | Amorim 3663 (CEPEC)                  | AY499085    | HQ247286    | HQ247497    | AY499059    |
| <i>Heteropterys capixaba</i> Amorim                          | NW                  | Amorim 3317 (MICH)                   | AY499086    | HQ247287    | HQ247498    | AY499060    |
| <i>Heteropterys catingarum</i> Adr. Juss.                    | NW                  | Sousa 455 (CEPEC)                    | AY499087    | HQ247288    | HQ247499    | AY499061    |
| <i>Heteropterys chrysophylla</i> (Lam.) DC.                  | NW                  | Amorim 3097 (CEPEC)                  | AY499088    | HQ247289    | HQ247500    | AY499062    |
| <i>Heteropterys ciliata</i> Nied.†                           | NW                  | Anderson 13778 (MICH)                | AF351049    | AF344550    | AF344480    | AF500554    |
| <i>Heteropterys conformis</i> W. R. Anderson                 | NW                  | Amorim 3583 (MICH)                   | HQ246840    | HQ247290    | HQ247501    | HQ247064    |
| <i>Heteropterys cordifolia</i> Adr. Juss.                    | NW                  | Amorim 3087 (MICH)                   | HQ246841    | HQ247291    | HQ247502    | HQ247065    |
| <i>Heteropterys dumetorum</i> (Griseb.) Nied.†               | NW                  | Iuppo s.n. (CEPEC 96908)             | HQ246842    | HQ247292    | HQ247503    | HQ247066    |
| <i>Heteropterys glabra</i> Hook. & Arn.†                     | NW                  | Anderson 13590 (MICH)                | HQ246843    | HQ247293    | HQ247504    | HQ247067    |
| <i>Heteropterys imperata</i> Amorim                          | NW                  | Amorim 3128 (CEPEC)                  | HQ246844    | HQ247294    | HQ247505    | HQ247068    |
| <i>Heteropterys leona</i> (Cav.) Exell                       | NW & OW             | Davis 99-5 (A)                       | AF351050    | HQ247295    | HQ247506    | AF500555    |
| <i>Heteropterys leschenaultiana</i> Adr. Juss.               | NW                  | Amorim 3352 (MICH)                   | HQ246845    | HQ247296    | HQ247507    | HQ247069    |
| <i>Heteropterys lindleyana</i> Adr. Juss.                    | NW                  | Amorim 3375 (MICH)                   | AY499089    | HQ247297    | HQ247508    | AY499063    |
| <i>Heteropterys macrostachya</i> Adr. Juss.                  | NW                  | Anderson 13788 (MICH)                | HQ246846    | HQ247298    |             | HQ247070    |
| <i>Heteropterys megaptera</i> Adr. Juss.                     | NW                  | Amorim 3667 (CEPEC)                  | AY499090    | HQ247299    | HQ247509    | AY499064    |
| <i>Heteropterys nitida</i> (Lam.) DC.                        | NW                  | Amorim 3327 (CEPEC)                  | AY499091    | HQ247300    | HQ247510    | AY499065    |
| <i>Heteropterys nordestina</i> Amorim                        | NW                  | Amorim 3229 (CEPEC)                  | HQ246847    | HQ247301    | HQ247511    | HQ247071    |
| <i>Heteropterys ovata</i> (Nied.) W. R. Anderson & C. Davis† | NW                  | Beck 15105 (MICH)                    | HQ246848    |             | HQ247512    |             |
| <i>Heteropterys pauciflora</i> (Adr. Juss.) Adr. Juss.       | NW                  | Amorim 3623 (CEPEC)                  | AY499092    | HQ247302    | HQ247513    | AY499066    |
| <i>Heteropterys pteropetala</i> Adr. Juss.†                  | NW                  | Anderson 13637 (MICH)                | HQ246849    | HQ247303    | HQ247514    | HQ247072    |
| <i>Heteropterys racemosa</i> Adr. Juss.†                     | NW                  | Rabelo et al. 3685 (MICH)            | HQ246850    | HQ247304    | HQ247515    |             |
| <i>Heteropterys rhopalifolia</i> Adr. Juss.†                 | NW                  | Amorim 2879 (MICH)                   | AY499093    | HQ247305    | HQ247516    | AY499067    |
| <i>Heteropterys rufula</i> Adr. Juss.†                       | NW                  | Amorim 3666 (CEPEC)                  | HQ246851    |             | HQ247517    | HQ247073    |
| <i>Heteropterys sanctorum</i> W. R. Anderson                 | NW                  | Amorim 3653 (MICH)                   | AY499094    | HQ247306    | HQ247518    | AY499068    |
| <i>Heteropterys sericea</i> (Cav.) Adr. Juss.                | NW                  | Amorim 3342 (MICH)                   | AY499095    | HQ247307    | HQ247519    | AY499069    |
| <i>Heteropterys sincorensis</i> W. R. Anderson               | NW                  | Queiroz 7145 (CEPEC)                 | AY499096    | HQ247308    | HQ247520    | AY499070    |
| <i>Heteropterys</i> sp.                                      | NW                  | Amorim 3671 (CEPEC)                  | HQ246852    |             | HQ247521    | HQ247074    |
| <i>Heteropterys steyermarkii</i> W. R. Anderson              | NW                  | Maguire & Politi 27524 (MICH)        | AY499097    | HQ247309    | HQ247522    | AY499071    |
| <i>Heteropterys ternstroemiifolia</i> Adr. Juss.             | NW                  | Amorim 3619 (MICH)                   | AY499098    | HQ247310    | HQ247523    | AY499072    |
| <i>Heteropterys trichanthera</i> Adr. Juss.†                 | NW                  | Amorim 3019 (CEPEC)                  | AY499099    | HQ247311    | HQ247524    | AY499073    |
| <i>Hiptage benghalensis</i> (L.) Kurz†                       | OW                  | Averyanov et al. VH 1381 (P)         | HQ246853    | HQ247312    |             | HQ247075    |
| <i>Hiptage benghalensis</i> (L.) Kurz†                       | OW                  | Herbst 9221 (MICH)                   | AF351057    | HQ247313    | HQ247525    | AF500561    |
| <i>Hiptage candicans</i> Hook. f.                            | OW                  | Johnson 2059A (MICH)                 | HQ246854    | HQ247314    | HQ247526    | HQ247076    |
| <i>Hiptage detergens</i> Craib                               | OW                  | Middleton et al. 2095 (MICH)         | HQ246855    | HQ247315    | HQ247527    | HQ247077    |
| <i>Hiptage</i> sp.   | OW                  | Middleton 2496 (A)                   | HQ246856    | HQ247316    | HQ247528    | HQ247079    |
| <i>Hiptage</i> sp.   | OW                  | Middleton 2556 (A)                   |             |             |             | HQ247078    |
| <i>Hiraea fagifolia</i> (DC.) Adr. Juss.†                    | NW                  | Anderson 13593 (MICH)                | AF351060    | AF344552    | AF344483    | AF500564    |
| <i>Hiraea smilacina</i> Standl.†                             | NW                  | Anderson 13794 (MICH)                | AF351061    |             | AF344484    | HQ247080    |
| <i>Hiraea</i> sp.  | NW                  | Anderson 13813 (MICH)                | HQ246857    | HQ247317    | HQ247529    | HQ247081    |
| <i>Hiraea wiedeanae</i> Adr. Juss.                           | NW                  | Anderson 13622 (MICH)                | HQ246858    | HQ247318    | HQ247530    | HQ247082    |
| <i>Janusia anisandra</i> (Adr. Juss.) Griseb.†               | NW                  | Anderson 13694 (MICH)                | AF351028    | AF344553    | AF344485    | AF500536    |
| <i>Janusia christianeae</i> W. R. Anderson                   | NW                  | Silva et al. 1364 (MICH)             | HQ246859    | HQ247319    |             | HQ247083    |
| <i>Janusia guaranitica</i> (A. St.-Hil.) Adr. Juss.†         | NW                  | Cristóbal & Schinini 2498 (MICH)     | HQ246860    | HQ247321    |             | HQ247084    |
| <i>Janusia guaranitica</i> (A. St.-Hil.) Adr. Juss.†         | NW                  | Krapovickas & Cristóbal 46736 (MICH) | HQ246861    | HQ247322    | HQ247531    | HQ247085    |
| <i>Janusia hexandra</i> (Vell.) W. R. Anderson               | NW                  | Thomas et al. 11423a (MICH)          | HQ246862    | HQ247320    | HQ247532    | HQ247086    |
| <i>Janusia janusioides</i> (Adr. Juss.) W. R. Anderson†      | NW                  | McDaniel et al. 2690 (US)            |             | HQ247323    |             |             |
| <i>Janusia janusioides</i> (Adr. Juss.) W. R. Anderson†      | NW                  | Anderson 13759 (MICH)                | HQ246863    |             | HQ247533    | HQ247087    |
| <i>Janusia linearifolia</i> (A. St.-Hil.) Adr. Juss.†        | NW                  | Krapovickas & Cristóbal 46451 (MICH) | AY499102    | AF344572    | AF344505    | AF500535    |

## APPENDIX 1. Continued

| Taxon   | Distr. <sup>a</sup> | Voucher                              | Plastid     |             |             | Nuclear     |
|---|---------------------|--------------------------------------|-------------|-------------|-------------|-------------|
|   |                     |                                      | <i>ndhF</i> | <i>matK</i> | <i>rbcl</i> | <i>PHYC</i> |
| <i>Janusia mediterranea</i> (Vell.) W. R. Anderson†                   | NW                  | Anderson 13686 (MICH)                | AF351029    | AF344556    | AF344488    | AF500537    |
| <i>Janusia mediterranea</i> (Vell.) W. R. Anderson†                   | NW                  | Ferrucci et al. 1636 (MICH)          | HQ246864    | HQ247324    |             | HQ247088    |
| <i>Jubelina riparia</i> Adr. Juss.                                    | NW                  | Mori & Souza 17320 (MICH)            | HQ246865    | HQ247325    | HQ247534    | HQ247089    |
| <i>Jubelina rosea</i> (Miq.) Nied.†                                   | NW                  | Mori 23855 (MICH)                    | AF351079    | AF344557    | AF344489    | HQ247090    |
| <i>Jubelina uleana</i> (Nied.) Cuatrec.                               | NW                  | Burnham 1573 (MICH)                  | HQ246866    | HQ247326    | HQ247535    | HQ247091    |
| <i>Jubelina wilburii</i> W. R. Anderson†                              | NW                  | Anderson 13789 (MICH)                | AY499100    | HQ247327    | HQ247536    | AY499074    |
| <i>Lasiocarpus</i> sp.†   | NW                  | Anderson 13828 (MICH)                | HQ246867    | HQ247328    | HQ247537    | HQ247092    |
| <i>Lasiocarpus</i> sp.†   | NW                  | Anderson 13834 (MICH)                | AF351066    | AF344558    | AF344490    | AF500567    |
| <i>Lophanthera hammelii</i> W. R. Anderson†                           | NW                  | Schatz 1034 (MICH)                   | HQ246868    | HQ247329    | HQ247538    |             |
| <i>Lophanthera hammelii</i> W. R. Anderson†                           | NW                  | Hammel 17748 (MICH)                  |             |             |             | HQ247093    |
| <i>Lophanthera lactescens</i> Ducke†                                  | NW                  | Anderson 13781 (MICH)                | AF351009    | AF344559    | AF344491    | AF500524    |
| <i>Lophanthera longifolia</i> (H. B. K.) Griseb.†                     | NW                  | Zimmermann 27 (MICH)                 | HQ246869    | HQ247330    | HQ247539    | HQ247094    |
| <i>Lophanthera pendula</i> Ducke                                      | NW                  | Lima & Lima 3185 (MICH)              | HQ246870    | HQ247331    | HQ247540    | HQ247095    |
| <i>Lophopterys floribunda</i> W. R. Anderson & C. Davis†              | NW                  | Anderson 13754 (MICH)                | AF351078    | AF344560    | AF344492    | AF500579    |
| <i>Lophopterys inpana</i> W. R. Anderson                              | NW                  | Morawetz & Wallnöfer 11-27888 (MICH) | HQ246871    | HQ247332    |             | HQ247096    |
| <i>Madagasikaria andersonii</i> C. Davis†                             | OW                  | Davis 20-01 (A)                      | AF436790    | HQ247333    | HQ247541    | AF436800    |
| <i>Malpighia albiflora</i> (Cuatrec.) Cuatrec.†                       | NW                  | Anderson 13815 (MICH)                | HQ246872    | HQ247334    | HQ247542    | HQ247097    |
| <i>Malpighia cnide</i> Spreng.  | NW                  | García & Pimentel 747 (MICH)         | HQ246873    |             |             | HQ247098    |
| <i>Malpighia coccigera</i> L.†  | NW                  | UMBG 20626 (MICH)                    | HQ246874    | HQ247335    | HQ247543    | HQ247099    |
| <i>Malpighia emarginata</i> DC.†                                      | NW                  | Anderson 13621 (MICH)                | AF351023    | AF344561    | AF344493    | AF436799    |
| <i>Malpighia fucata</i> Ker Gawl.                                     | NW                  | Proctor 23111 (MICH)                 | HQ246875    | HQ247336    |             | HQ247100    |
| <i>Malpighia glabra</i> L.†   | NW                  | FTG X-12-104 (FTG)                   | HQ246876    | HQ247337    | HQ247544    | HQ247101    |
| <i>Malpighia incana</i> Mill.†  | NW                  | Houghton 1152 (MICH)                 | HQ246877    | HQ247338    | HQ247545    | HQ247102    |
| <i>Malpighia leuciana</i> (W. R. Anderson) W. R. Anderson & C. Davis† | NW                  | Torres C. 629 (MICH)                 | HQ246878    | HQ247339    | HQ247546    | HQ247103    |
| <i>Malpighia mexicana</i> Adr. Juss.                                  | NW                  | Calzada et al. 18581 (MICH)          | HQ246879    | HQ247340    |             | HQ247104    |
| <i>Malpighia romeroana</i> Cuatrec.                                   | NW                  | Wendt et al. 3982 (MICH)             | HQ246880    | HQ247341    |             | HQ247105    |
| <i>Malpighia setosa</i> Spreng.                                       | NW                  | Bartlett 17568 (MICH)                | HQ246881    | HQ247342    |             | HQ247106    |
| <i>Malpighia souzæ</i> Miranda  | NW                  | Zembrano C. 1252 (MICH)              | HQ246882    | HQ247343    |             | HQ247107    |
| <i>Malpighia stevensii</i> W. R. Anderson†                            | NW                  | Davis 1019 (MICH)                    | AF351022    | HQ247344    | HQ247547    | AF436798    |
| <i>Malpighia urens</i> L.   | NW                  | Bartlett 17518 (MICH)                | HQ246883    | HQ247345    |             | HQ247108    |
| <i>Malpighiodes bracteosa</i> (Griseb.) W. R. Anderson†               | NW                  | Anderson 13777 (MICH)                | AF351055    | AF344563    | AF344495    | AF500559    |
| <i>Mascagnia affinis</i> W. R. Anderson & C. Davis                    | NW                  | Gerlach et al. 19/01 (MICH)          | HQ246884    | HQ247346    |             | HQ247109    |
| <i>Mascagnia arenicola</i> C. E. Anderson†                            | NW                  | Chase 90160 (MICH)                   | AF351025    | AF344567    | AF344499    | AF436804    |
| <i>Mascagnia arenicola</i> C. E. Anderson†                            | NW                  | Chase 90165 (MICH)                   | HQ246885    | HQ247347    | HQ247548    | HQ247110    |
| <i>Mascagnia australis</i> C. E. Anderson†                            | NW                  | Anderson 13592 (MICH)                | HQ246886    | HQ247348    | HQ247549    | HQ247111    |
| <i>Mascagnia brevifolia</i> Griseb.†                                  | NW                  | Nee 51409 (MICH)                     | HQ246887    | HQ247349    | HQ247550    | HQ247112    |
| <i>Mascagnia cordifolia</i> (Adr. Juss.) Griseb.†                     | NW                  | Anderson 13626 (MICH)                | HQ246888    | HQ247350    | HQ247551    | HQ247113    |
| <i>Mascagnia dissimilis</i> C. V. Morton & Moldenke                   | NW                  | Wallnöfer 114-291088 (MICH)          | HQ246889    | HQ247351    | HQ247552    | HQ247114    |
| <i>Mascagnia divaricata</i> (H. B. K.) Nied.†                         | NW                  | Anderson 13604 (MICH)                | HQ246890    | HQ247352    | HQ247553    | HQ247115    |
| <i>Mascagnia lilacina</i> (S. Watson) Nied.                           | NW                  | Anderson & Anderson 4656 (MICH)      | HQ246891    | HQ247353    | HQ247554    | HQ247116    |
| <i>Mascagnia polybotrya</i> (Adr. Juss.) Nied.†                       | NW                  | Anderson & Laskowski 4098 (MICH)     | HQ246892    | HQ247354    | HQ247555    | HQ247117    |
| <i>Mascagnia polybotrya</i> (Adr. Juss.) Nied.†                       | NW                  | McVaugh 24004 (MICH)                 | HQ246893    | HQ247355    | HQ247556    | HQ247118    |
| <i>Mascagnia tenuifolia</i> Nied.                                     | NW                  | Webster 23307 (MICH)                 | HQ246894    | HQ247356    |             | HQ247119    |
| <i>Mascagnia tomentosa</i> C. E. Anderson                             | NW                  | Cortes 728 (MICH)                    | HQ246895    | HQ247357    | HQ247557    | HQ247120    |
| <i>Mascagnia tomentosa</i> C. E. Anderson                             | NW                  | Neill 7103 (MICH)                    | HQ246896    | HQ247358    |             | HQ247121    |
| <i>Mascagnia vacciniifolia</i> Nied.†                                 | NW                  | Anderson 13797 (MICH)                | HQ246897    | HQ247359    | HQ247558    | HQ247122    |
| <i>Mcvaughia bahiana</i> W. R. Anderson†                              | NW                  | Anderson 13690 (MICH)                | AF351070    | AF344568    | AF344501    | AF500571    |
| <i>Mezium araujoii</i> Nied.†   | NW                  | Anderson 13672 (MICH)                | AF351051    | AF344569    | AF344502    | HQ247123    |
| <i>Mezium includens</i> (Benth.) Cuatrec.†                            | NW                  | Anderson 13784 (MICH)                | HQ246898    | HQ247360    | HQ247559    | HQ247124    |
| <i>Microsteira ambovombensis</i> Arènes†                              | OW                  | Davis 38-01 (A)                      | AF436791    | HQ247361    | HQ247560    | AF436803    |
| <i>Microsteira ambovombensis</i> Arènes†                              | OW                  | Rabantoandro et al. 750 (MO)         | HQ246899    | HQ247362    | HQ247561    | HQ247125    |
| <i>Microsteira diotostigma</i> (Baill.) Dubard & Dop                  | OW                  | CTFT 262085F (P)                     | HQ246900    | HQ247363    |             | HQ247126    |
| <i>Microsteira</i> sp.  | OW                  | Randrianaivo et al. 365 (P)          | HQ246901    |             |             | HQ247127    |
| <i>Mionandra camareoides</i> Griseb.†                                 | NW                  | Anderson 13585 (MICH)                | AF351080    | AF344570    | AF344503    | AF500580    |
| <i>Niedenzuella acutifolia</i> (Cav.) W. R. Anderson†                 | NW                  | Amorim 1574 (MICH)                   | HQ246903    | HQ247365    | HQ247563    | HQ247129    |
| <i>Niedenzuella acutifolia</i> (Cav.) W. R. Anderson†                 | NW                  | Amorim 3350 (MICH)                   | HQ246902    | HQ247364    | HQ247562    | HQ247128    |
| <i>Niedenzuella sericea</i> (Adr. Juss.) W. R. Anderson†              | NW                  | Anderson 13611 (MICH)                | HQ246904    | HQ247366    | HQ247564    | HQ247130    |
| <i>Niedenzuella sericea</i> (Adr. Juss.) W. R. Anderson†              | NW                  | Heringer et al. 1524 (MICH)          | HQ246905    | HQ247367    | HQ247565    | HQ247131    |
| <i>Niedenzuella stanæa</i> (Griseb.) W. R. Anderson†                  | NW                  | Anderson 13804 (MICH)                | AF351056    | HQ247368    | AF344500    | AF500560    |
| <i>Niedenzuella stanæa</i> (Griseb.) W. R. Anderson†                  | NW                  | Prance et al. 26362 (MICH)           | HQ246906    | HQ247369    | HQ247566    | HQ247132    |
| <i>Peixotoa cordistipula</i> Adr. Juss.†                              | NW                  | Gerlach et al. 26/01 (MICH)          | HQ246907    | HQ247370    | HQ247567    | HQ247133    |
| <i>Peixotoa glabra</i> Adr. Juss.†                                    | NW                  | Anderson 13636 (MICH)                | AF351036    | AF344571    | AF344504    | AF500544    |
| <i>Peixotoa paludosa</i> Turcz.                                       | NW                  | Anderson 9197 (MICH)                 |             | HQ247371    |             | HQ247134    |
| <i>Peixotoa parviflora</i> Adr. Juss.                                 | NW                  | Hatschbach et al. 67158 (MICH)       | HQ246908    | HQ247372    |             | HQ247135    |
| <i>Peixotoa reticulata</i> Griseb.                                    | NW                  | Ferrucci et al. 1678 (MICH)          | HQ246909    | HQ247373    |             | HQ247136    |
| <i>Philgamia glabrifolia</i> Arènes                                   | OW                  | Schatz et al. 4098 (P)               | HQ246910    | HQ247374    | HQ247568    | HQ247137    |



## APPENDIX 1. Continued

| Taxon  | Distr. <sup>a</sup> | Voucher   | Plastid     |             |             | Nuclear     |
|--|---------------------|---|-------------|-------------|-------------|-------------|
|  |                     |   | <i>ndhF</i> | <i>matK</i> | <i>rbcL</i> | <i>PHYC</i> |
| <i>Philgamia hibbertioides</i> Baill.†                               | OW                  | <i>Du Puy et al. M635</i> (P)                       | HQ246911    | HQ247375    | HQ247569    | HQ247138    |
| <i>Psychopterys dipholiphylla</i> (Small) W. R. Anderson & S. Corso† | NW                  | <i>Anderson 13816</i> (MICH)                        | AF351063    | AF344565    | AF344497    | AF436795    |
| <i>Pterandra arborea</i> Ducke†                                      | NW                  | <i>Anderson 13766</i> (MICH)                        | AF351014    | AF344573    | AF344506    | AF500529    |
| <i>Ptilochaeta bahiensis</i> Turcz.†                                 | NW                  | <i>Anderson 13725</i> (MICH)                        | AF351068    | AF344574    | AF344507    | AF500569    |
| <i>Ptilochaeta nudipes</i> Griseb.†                                  | NW                  | <i>Anderson 13588</i> (MICH)                        | AF351067    | HQ247376    | HQ247570    | AF500568    |
| <i>Rhynchophora humbertii</i> Arènes†                                | OW                  | <i>Davis 18-01M</i> (A)                             | HQ246912    | HQ247377    | HQ247571    | HQ247139    |
| <i>Rhynchophora phillipsonii</i> W. R. Anderson†                     | OW                  | <i>Davis 23b-01</i> (A)                             | AF436793    | HQ247378    | HQ247572    | AF436802    |
| <i>Ryssopterys intermedia</i> Hochr.†                                | OW                  | <i>Chase M241</i> (K)                               | AF351040    |             | AF344509    | AF500545    |
| <i>Ryssopterys</i> sp.   | OW                  | <i>Motley &amp; Cameron 2215</i> (NY)               | HQ246913    | HQ247379    | HQ247573    | HQ247140    |
| <i>Ryssopterys tiliifolia</i> (Vent.) A. Dr. Juss.†                  | OW                  | <i>Chase M240</i> (K)                               | HQ246914    |             | HQ247574    | HQ247141    |
| <i>Spachea correae</i> Cuatrec. & Croat†                             | NW                  | <i>Hammel 17746</i> (MO)                            | AF351074    | AF344575    | AF344510    | AF500575    |
| <i>Spachea elegans</i> (G. Mey.) A. Dr. Juss.†                       | NW                  | <i>Jansen-Jacobs et al. 3907</i> (MICH)             | HQ246915    | HQ247380    | HQ247575    | HQ247142    |
| <i>Sphedamnocarpus angolensis</i> (A. Dr. Juss.) Oliv.               | OW                  | <i>Brummitt &amp; Pope 19597</i> (MICH)             | HQ246916    | HQ247381    | HQ247576    | HQ247143    |
| <i>Sphedamnocarpus galphimifolius</i> (A. Dr. Juss.) Szyszyl.        | OW                  | <i>Steiner 2275</i> (MICH)                          | AF351041    | AF344576    | AF344511    | HQ247144    |
| <i>Sphedamnocarpus poissonii</i> Arènes                              | OW                  | <i>Dorr 3959</i> (P)                                | HQ246917    | HQ247382    | HQ247577    | HQ247145    |
| <i>Sphedamnocarpus pruriens</i> (A. Dr. Juss.) Szyszyl.†             | OW                  | <i>Goldblatt s.n.</i> (MO)                          |             | HQ247383    | HQ247578    | HQ247146    |
| <i>Sphedamnocarpus</i> sp.   | OW                  | <i>Davis 03-01</i> (A)                              | AY499104    | HQ247385    | HQ247579    | AF500546    |
| <i>Sphedamnocarpus</i> sp.   | OW                  | <i>Davis 39-01</i> (A)                              | AY499105    | HQ247386    | HQ247580    | AY499077    |
| <i>Sphedamnocarpus</i> sp.   | OW                  | <i>Phillips 2957</i> (P)                            | HQ246918    | HQ247384    |             | HQ247147    |
| <i>Stigmaphyllon aberrans</i> C. E. Anderson                         | NW                  | <i>Rojas et al. 2347</i> (MICH)                     | HQ246919    | HQ247387    | HQ247581    | HQ247148    |
| <i>Stigmaphyllon bogotense</i> Triana & Planch.                      | NW                  | <i>Rojas et al. 3058</i> (MICH)                     | HQ246920    | HQ247388    | HQ247582    | HQ247149    |
| <i>Stigmaphyllon bogotense</i> Triana & Planch.                      | NW                  | <i>Woytkowski 7035</i> (MICH)                       | HQ246921    | ??          |             |             |
| <i>Stigmaphyllon calcaratum</i> N. E. Br.                            | NW                  | <i>Anderson 13595</i> (MICH)                        | HQ246922    | HQ247389    | HQ247583    | HQ247150    |
| <i>Stigmaphyllon ciliatum</i> (Lam.) A. Dr. Juss.                    | NW                  | <i>Anderson 13739</i> (MICH)                        | HQ246923    | HQ247390    | HQ247584    | HQ247151    |
| <i>Stigmaphyllon finlayanum</i> A. Dr. Juss.                         | NW                  | <i>Chase 90163</i> (MICH)                           | HQ246924    | HQ247391    | HQ247585    | HQ247152    |
| <i>Stigmaphyllon lindenianum</i> A. Dr. Juss.                        | NW                  | <i>Anderson 13796</i> (MICH)                        |             | HQ247392    | HQ247586    | HQ247153    |
| <i>Stigmaphyllon paralias</i> A. Dr. Juss.†                          | NW                  | <i>Anderson 13693</i> (MICH)                        | AF351065    | AF344577    | AF344513    | AF500566    |
| <i>Stigmaphyllon puberum</i> (Rich.) A. Dr. Juss.†                   | NW                  | <i>Anderson 13793</i> (MICH)                        | AF351038    | HQ247393    | AF344514    | AF436794    |
| <i>Stigmaphyllon sagraeanum</i> A. Dr. Juss.                         | NW                  | <i>FTG 375A</i> (FTG)                               | HQ246925    | HQ247395    | HQ247587    | HQ247154    |
| <i>Stigmaphyllon sagraeanum</i> A. Dr. Juss.                         | NW                  | <i>FTG X-1-6</i> (FTG)                              | AF351077    | HQ247394    | AF344512    | AF500578    |
| <i>Tetrapteryx ambigua</i> (A. Dr. Juss.) Nied.†                     | NW                  | <i>Kral &amp; Wanderley 75016</i> (MICH)            | HQ246926    |             | HQ247588    | HQ247155    |
| <i>Tetrapteryx arcana</i> C. V. Morton†                              | NW                  | <i>Daniel 9558</i> (MICH)                           | HQ246927    | HQ247396    |             | HQ247156    |
| <i>Tetrapteryx discolor</i> (G. Mey.) DC.†                           | NW                  | <i>Chase 90158</i> (MICH)                           | AF351076    | AF344578    |             | AF500577    |
| <i>Tetrapteryx goudotiana</i> Triana & Planch.                       | NW                  | <i>Anderson 13800</i> (MICH)                        | HQ246928    | HQ247397    | HQ247589    | HQ247157    |
| <i>Tetrapteryx megalantha</i> W. R. Anderson                         | NW                  | <i>Mori et al. 21584</i> (MICH)                     | HQ246929    | HQ247398    | HQ247590    | HQ247158    |
| <i>Tetrapteryx microphylla</i> (A. Dr. Juss.) Nied.†                 | NW                  | <i>Anderson 13644</i> (MICH)                        | AF351052    | AF344579    | AF344515    | AF500556    |
| <i>Tetrapteryx phlomooides</i> (Spreng.) Nied.†                      | NW                  | <i>Anderson 13685</i> (MICH)                        | HQ246930    | HQ247399    | HQ247591    | HQ247159    |
| <i>Tetrapteryx salicifolia</i> (A. Dr. Juss.) Nied.                  | NW                  | <i>Anderson 13616</i> (MICH)                        | HQ246931    |             | HQ247592    | HQ247160    |
| <i>Tetrapteryx schiedeana</i> Schlechtend. & Cham. †                 | NW                  | <i>Anderson 13811</i> (MICH)                        | HQ246932    | HQ247400    | HQ247593    | HQ247161    |
| <i>Tetrapteryx tinifolia</i> Triana & Planch.†                       | NW                  | <i>Anderson 13792</i> (MICH)                        | HQ246933    | HQ247401    | HQ247594    | HQ247162    |
| <i>Thryallis latifolia</i> (Bartl.) Kuntze                           | NW                  | <i>Lombardi 2213</i> (MICH)                         | HQ246934    | HQ247402    |             | HQ247163    |
| <i>Thryallis longifolia</i> Mart.†                                   | NW                  | <i>Anderson 13657</i> (MICH)                        | AF351046    | AF344580    | AF344516    | AF500551    |
| <i>Triaspis glaucophylla</i> Engl.                                   | OW                  | <i>Goldblatt &amp; Manning 10130</i> (MO)           | HQ246935    | HQ247403    | HQ247595    | HQ247164    |
| <i>Triaspis hypericoides</i> Burch.†                                 | OW                  | <i>Immelman 650</i> (PRE)                           | AF351021    | AF344581    | AF344517    | AF500533    |
| <i>Triaspis hypericoides</i> Burch.†                                 | OW                  | <i>P. Raal &amp; G. Rall 2429BB</i> (M)             | HQ246936    | HQ247404    | HQ247596    | HQ247165    |
| <i>Triaspis macropteron</i> Oliv.                                    | OW                  | <i>Kuchar 23017</i> (MO)                            | HQ246937    | HQ247405    | HQ247597    | HQ247166    |
| <i>Triaspis nelsonii</i> Oliv.                                       | OW                  | <i>Gleiss &amp; Müller 13967</i> (M)                | HQ246938    | HQ247406    | HQ247598    | HQ247167    |
| <i>Triaspis niedenzuiana</i> Engl.                                   | OW                  | <i>Belsky 584</i> (MO)                              | HQ246939    |             |             | HQ247168    |
| <i>Tricomaria usillo</i> Hook. & Arn.†                               | NW                  | <i>Anderson 13581</i> (MICH)                        | AF351075    | AF344582    | AF344518    | AF500576    |
| <i>Triopteryx jamaicensis</i> L.†                                    | NW                  | <i>Hammel 17816</i> (MICH)                          | AF351024    | AF344583    | AF344519    | AF500534    |
| <i>Triopteryx paniculata</i> (Mill.) Small†                          | NW                  | <i>Veloz et al. 862</i> (MICH)                      | HQ246940    | HQ247407    | HQ247599    | HQ247169    |
| <i>Tristellateia africana</i> S. Moore                               | OW                  | <i>Davis 99-25</i> (A)                              | AF351043    | HQ247408    | HQ247600    | AF500548    |
| <i>Tristellateia madagascariensis</i> Poir.†                         | OW                  | <i>McPherson 14398</i> (MICH)                       | AF351042    | AF344584    | AF344520    | AF500547    |
| <i>Tristellateia</i> sp.   | OW                  | <i>Bourgeois 16</i> (MO)                            | HQ246941    | HQ247409    |             | HQ247170    |
| <i>Tristellateia</i> sp.   | OW                  | <i>Davis 19-01</i> (A)                              | AY499106    | HQ247412    |             | AY499078    |
| <i>Tristellateia</i> sp.   | OW                  | <i>Davis 29-01</i> (A)                              | AY499107    | HQ247413    | HQ247601    | AY499079    |
| <i>Tristellateia</i> sp.   | OW                  | <i>Lucile &amp; Rakotozafy 2682</i> (P)             | HQ246943    | HQ247411    |             | HQ247172    |
| <i>Tristellateia</i> sp.   | OW                  | <i>Leeuwenberg &amp; Rafamantanansoa 14477</i> (MO) | HQ246942    | HQ247410    |             | HQ247171    |
| <i>Verrucularia glaucophylla</i> A. Dr. Juss.†                       | NW                  | <i>Amorim 3662</i> (MICH)                           | AY499108    | HQ247414    | HQ247602    | AY499080    |

<sup>a</sup> Distribution: NW = New World, OW = Old World.

\* Outgroups

† Taxa scored for morphology

## APPENDIX 2. Morphological characters scored for 144 species representing all genera of Malpighiaceae, plus six outgroup taxa.

1. Habit—0: tree or woody shrub; 1: erect suffrutex; 2: trailing suffrutex; 3: vine; 4: herb
2. Stems rooting at nodes—0: no; 1: yes
3. Vegetative hairs—0: unicellular; 1: multicellular
4. Vegetative hairs—0: 2-branched; 1: basifixed; 2: stellate
5. Phyllotaxy—0: opposite or whorled; 1: alternate
6. Stipule position—0: stem between petioles or beside petiole; 1: petiole margin; 2: petiole inner face; 3: not present
7. Stipule connation—0: distinct; 1: connate, same leaf; 2: connate, opposite leaves; 3: connate, opposite and same leaves; 4: not present
8. Stipule persistence—0: long-persistent; 1: soon-deciduous; 2: not present
9. Stipules enclosing buds—0: no; 1: yes
10. Petiole glands—0: absent; 1: present
11. Lamina margin—0: without true teeth; 1: toothed
12. Lamina glands—0: absent; 1: abaxial surface; 2: margin or very slightly within; 3: adaxial surface
13. Inflorescence position—0: terminal or terminal and axillary; 1: axillary
14. Inflorescence ultimate units—0: pseudoraceme or thyrse; 1: umbel of (2)4(6) flowers; 2: umbel of >6 flowers; 3: 1(2) flower(s); 4: verticil of 4 flowers; 5: spike; 6: consistently 2 flowers
15. Inflorescence decussate—0: mostly not; 1: all or mostly yes; 2: proximally decussate, distally not; 3: too tight to tell; 4: single flowers
16. Cincinni—0: 1-flowered; 1: 2-several-flowered
17. Bract and bracteole size—0: full-sized leaves; 1: much reduced; 2: apparently absent
18. Bracts and bracteoles scalelike—0: no; 1: yes; 2: absent
19. Bract persistence—0: persistent; 1: deciduous; 2: absent
20. Peduncle—0: 0–1 mm long; 1: >1 mm long
21. Pedicel—0: well developed, > bracteoles; 1: absent or very short, < bracteoles
22. Bracteole glands—0: eglandular; 1: 1 or both glandular; 2: bracteoles absent
23. Bracteole persistence—0: persistent; 1: deciduous; 2: absent
24. Bracteoles enclosing buds—0: no; 1: yes; 2: absent
25. Cleistogamous flowers—0: absent; 1: present
26. Breeding system—0: bisexual; 1: morphologically bisexual, functionally unisexual; 2: morphologically bisexual or male; 3: unisexual, dioecious
27. Sepal number—0: 5; 1: 2–4
28. Sepal aestivation—0: imbricate; 1: valvate
29. Sepal margin, glands—0: absent; 1: present
30. Calyx in anthesis—0: erect or appressed; 1: revolute; 2: reflexed
31. Calyx in fruit—0: hardly enlarged; 1: enlarged, papery
32. Calyx glands—0: none; 1: 10 on 5 sepals; 2: 8 on lateral 4 sepals; 3: 4 (fused) on lateral 4 sepals; 4: up to 5 glands; 5: 6 on lateral 4 sepals
33. Calyx gland attachment—0: completely on free sepals; 1: half or more on free sepals; 2: mostly below free sepals; 3: not present
34. Calyx glands long-stalked—0: no; 1: yes; 2: not present
35. Petal number—0: 5; 1: 2–4
36. Petals in bud—0: exposed; 1: concealed by sepals
37. Petal color—0: yellow; 1: pink (+white); 2: white; 3: lilac
38. Petals clawed—0: yes; 1: no
39. Petal hairs—0: absent; 1: present, abaxial surface; 2: present, adaxial surface; 3: present, margin
40. Corolla symmetry—0: nearly radial; 1: bilateral, NW type; 2: bilateral, *Acridocarpus* type
41. Disc—0: absent; 1: present
42. Stamen number (in bisexual or male flowers)—0: >10; 1: 10; 2: 7–9; 3: 6 opposite sepals + posterior petal; 4: 5 opposite sepals; 5: 1–4
43. Stamens sterile (in bisexual or male flowers)—0: none; 1: staminodes opposite 5 sepals; 2: staminodes opposite anterior-lateral sepals; 3: posterior 3 staminodes; 4: filament opposite posterior petal without anther; 5: staminodes opposite posterior-lateral sepals; 6: staminodes opposite petals, posterior-lateral sepals; 7: staminodes opposite 3 anterior sepals; 8: staminodes opposite 5 petals
44. Filament sizes (fertile)—0: subequal; 1: longer opposite sepals; 2: longer opposite some or all petals; 3: longer opposite sepals, posterior-lateral petals; 4: anterior 3 shorter; 5: posterior 3 shorter; 6: shorter opposite posterior-lateral petals; 7: very long opposite anterior sepal; 8: stouter opposite posterior-lateral petals; 9: anterior 1 shorter
45. Filament fusion—0: distinct; 1: connate at base or higher
46. Anther hairs—0: absent; 1: present
47. Anther bristles, apex—0: absent; 1: present
48. Anther wings—0: absent; 1: present
49. Anther dehiscence—0: longitudinal slits; 1: apical or subapical pores
50. Connective extended, fleshy (fertile anthers)—0: no; 1: yes
51. Anther size (fertile)—0: subequal; 1: larger opposite sepals; 2: larger opposite petals; 3: larger opposite posterior-lateral petals; 4: posterior 3 smaller; 5: smaller opposite anterior-lateral petals; 6: anterior 3 smaller; 7: anterior 1 larger; 8: larger opposite 3 anterior sepals; 9: anterior 3 larger
52. Androecium symmetry—0: nearly radial; 1: strongly bilateral
53. Pollen symmetry—0: radial; 1: global
54. Pollen ectoapertures—0: present; 1: absent
55. Pollen endoapertures, number—0: 3; 1: 4–12
56. Pollen diameter ( $\mu\text{m}$ )—0:  $\leq 22$ ; 1:  $> 22$
57. Receptacle hairs between filaments and gynoecium—0: absent or nearly so; 1: present, abundant
58. Carpel number (chasmogamous flowers)—0: 3; 1: 2; 2: 5
59. Ovules per locule—0: 1 (or none); 1: 2 or more
60. Carpels sterile—0: none; 1: anterior; 2: 1 posterior; 3: anterior + 1 posterior
61. Carpel fusion in ovary—0: distinct or connate at base only; 1: connate whole ventral face or axis
62. Style number (chasmogamous flowers)—0: as many as carpels; 1: 1 on anterior carpel; 2: 2 on posterior carpels; 3: 2 on anterior carpel + 1 posterior carpel
63. Style fusion—0: distinct; 1: connate in styles; 2: connate in stigmas
64. Gynoecium symmetry—0: nearly radial; 1: strongly bilateral
65. Style thickness—0: subulate, slender; 1: uniform, thick; 2: uniform, slender
66. Stigma—0: terminal or nearly so, tiny; 1: internal, short, large; 2: internal, long-decurrent, large; 3: internal, tiny; 4: terminal, large, capitate or truncate; 5: terminal, large, reniform; 6: terminal, large, elongated
67. Style dorsal extension—0: none; 1: angle to hook; 2: foliole
68. Styles distally—0: entire; 1: bifid
69. Fruit texture—0: dry; 1: fleshy
70. Fruit dehiscence—0: schizocarpic, not releasing seed; 1: indehiscent; 2: loculicidally dehiscent, releasing seeds; 3: septicidally dehiscent, releasing seeds
71. Fruit wall—0: smooth; 1: setiferous; 2: dorsal wing dominant; 3: lateral wing(s) dominant; 4: winglets, ruffles; 5: aculeate; 6: dorsal or dorsal+lateral crest(s)
72. Carpophore—0: absent; 1: present
73. Eumascagnoid disk—0: absent; 1: present
74. Aril—0: absent; 1: present
75. Endosperm—0: absent; 1: present