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A COMPLETE GENERIC PHYLOGENY OF MALPIGHIACEAE INFERRED FROM NUCLEOTIDE SEQUENCE DATA AND MORPHOLOGY¹

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- **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, stigmaphyllid, 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 tricarpetate gynoecium 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 (Niedenau, 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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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 Hiraecae and in subtribe Sphegamnocarpaceae 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., *Callicola* W. R. Anderson & C. Davis, *Camarea* A. St.-Hil., *Christianella* W. R. Anderson, *Clonodia* Griseb., *Digoniopterys* 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; Tokuyama 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 Sequencer 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+ Γ]. A mixed model was applied to our combined analyses to accommodate the morphological data: GTR+I+ Γ 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+ Γ 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 (≥ 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*, *Callicola* 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*,

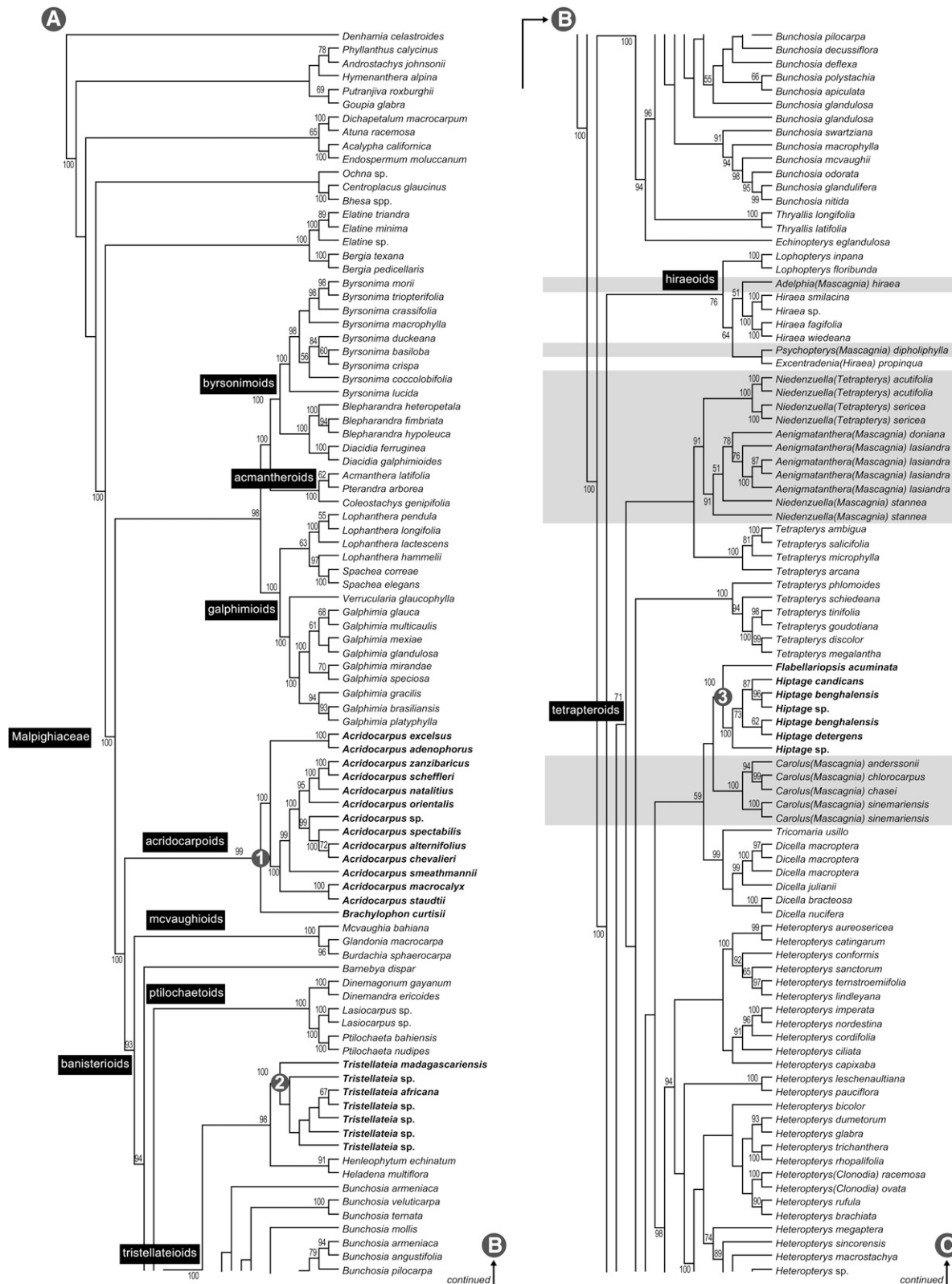
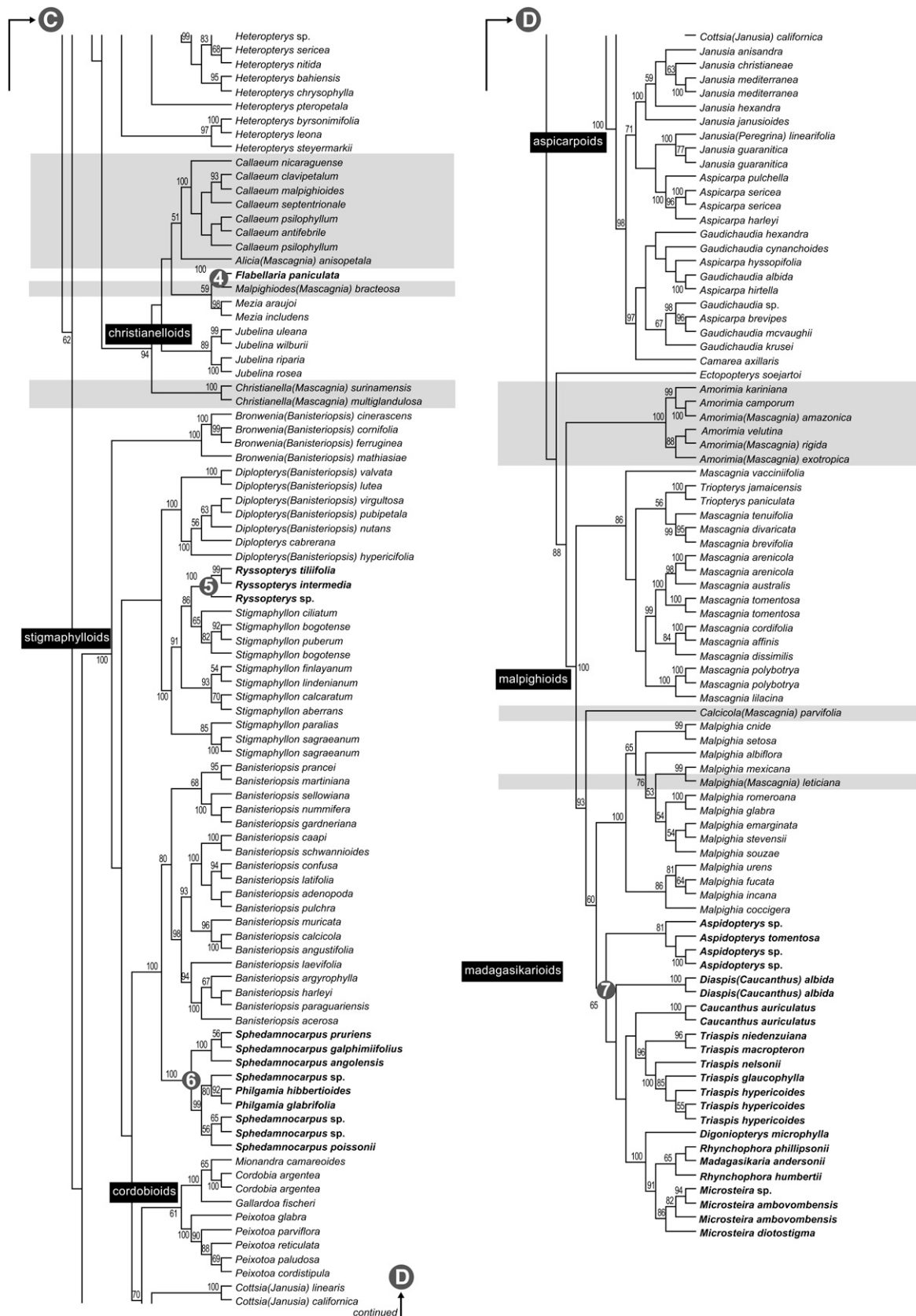


Fig. 1. One of the maximum likelihood (ML) topologies based on the four-gene-plus-morphology data set. ML bootstrap percentages >50 are indicated at the nodes. Generic names in parentheses reflect the previous taxonomic placement for those species. Former members of *Mascagnia* are highlighted in gray. 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.



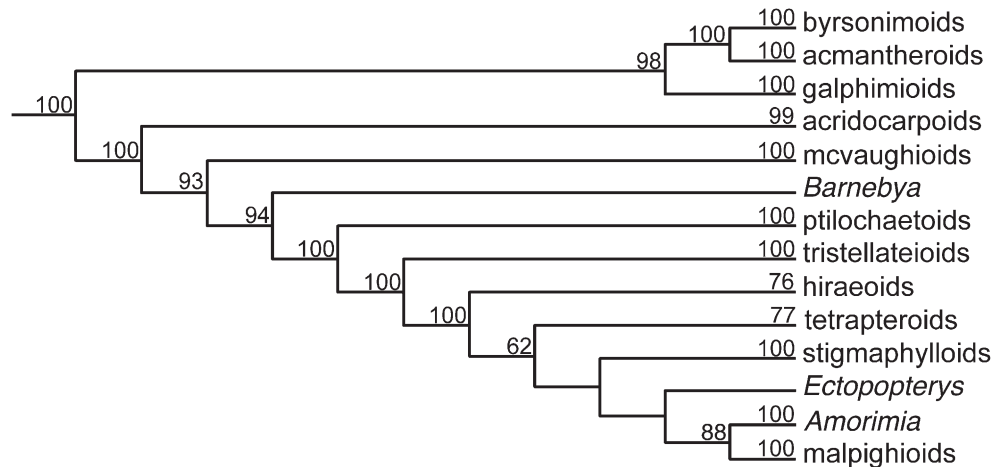


Fig. 2. Summary of major clades of Malpighiaceae emerging from this study derived from Fig. 1. Maximum likelihood bootstrap percentages >50 are indicated at nodes.

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

Triopteris—*Triopteris* 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*, *Tetrapteris*, and *Mascagnia* s.s., respectively. Our tree (Fig. 1) shows that *Triopteris* 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 *Triopteris* 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 *Tetrapteris*. 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 sub-distinct 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 stigmaphyllioids (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.

Tetrapteryx—Even after the segregation of *Niendenzuella* (discussed above) from *Tetrapteryx*, 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 (≥ 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

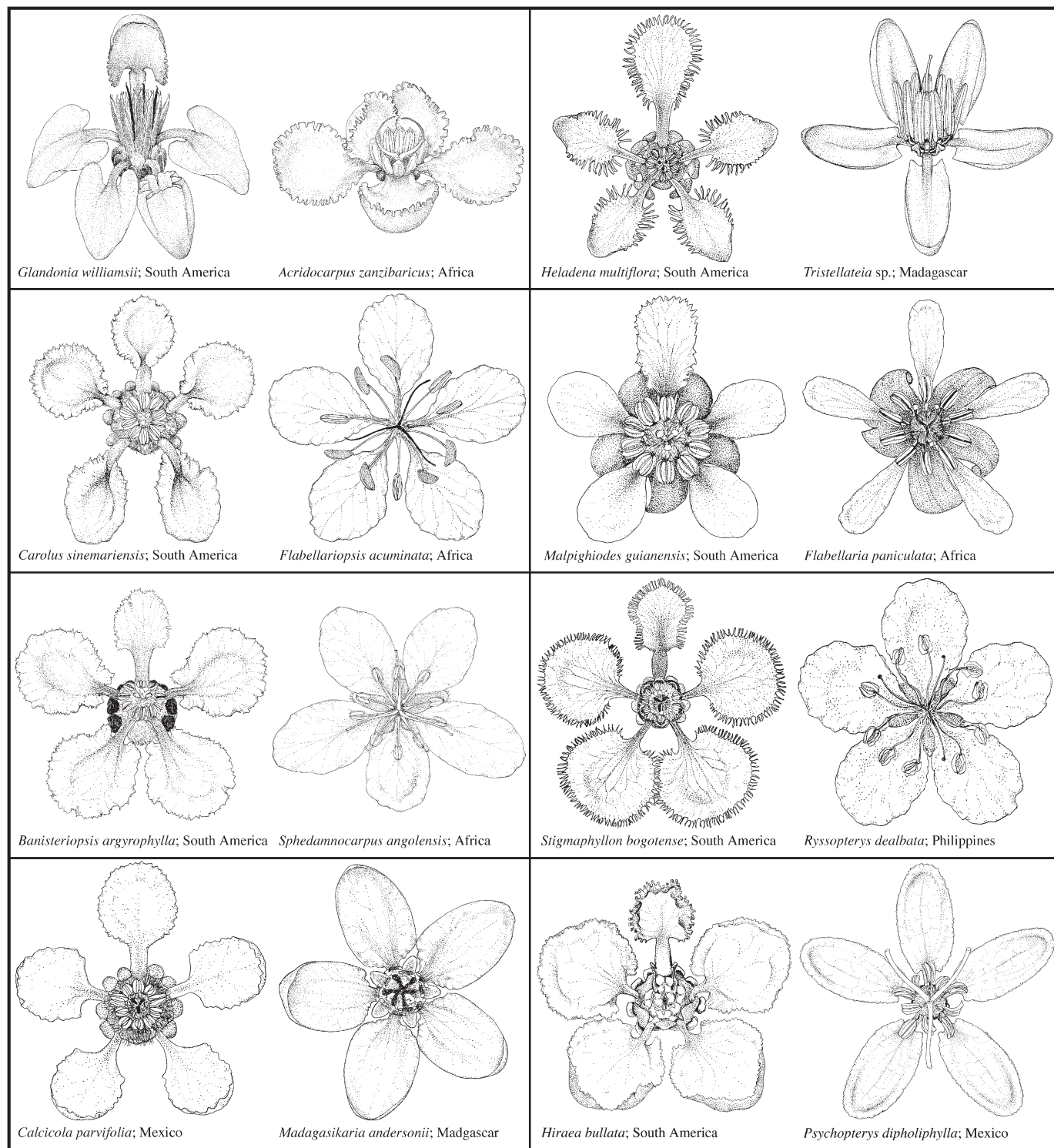


Fig. 3. Corolla morphology of Malpighiaceae of the seven New and Old World sister clades highlighted in Fig. 1. Seven panels (all but that at lower right) illustrate the New World flower morphology contrasted with a representative from its Old World sister clade on the right. None of those Old World 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 *Sphegamnocarpus*) 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 hiraecoid 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).

LITERATURE CITED

- ANDERSON, C. 1997. Monograph of *Stigmaphyllon* (Malpighiaceae). *Systematic Botany Monographs* 51: 1–313.
- ANDERSON, C. 2001. The identities of two water-dispersed species of *Heteropterys* (Malpighiaceae): *H. leona* and *H. platyptera*. *Contributions from the University of Michigan Herbarium* 23: 35–47.
- ANDERSON, C. 2007. Revision of *Galphimia* (Malpighiaceae). *Contributions from the University of Michigan Herbarium* 25: 1–82.
- ANDERSON, C. In press. Revision of *Ryssopterys* and transfer to *Stigmaphyllon* (Malpighiaceae). *Blumea*.
- ANDERSON, W. R. 1979. Floral conservatism in neotropical Malpighiaceae. *Biotropica* 11: 219–223.
- ANDERSON, W. R. 1981. Malpighiaceae in the botany of the Guayana Highland—Part XI. *Memoirs of the New York Botanical Garden* 32: 21–305.
- ANDERSON, W. R. 1982. Notes on neotropical Malpighiaceae—I. *Contributions from the University of Michigan Herbarium* 15: 93–136.
- ANDERSON, W. R. 1987. Notes on neotropical Malpighiaceae—II. *Contributions from the University of Michigan Herbarium* 16: 55–108.
- ANDERSON, W. R. 1990. The origin of the Malpighiaceae—The evidence from morphology. *Memoirs of the New York Botanical Garden* 64: 210–224.
- ANDERSON, W. R. 2004. Malpighiaceae (Malpighia family). In N. Smith, S. A. Mori, A. Henderson, D. W. Stevenson, and S. V. Heald [eds.], *Flowering plants of the neotropics*, 229–232. Princeton University Press, Princeton, New Jersey, USA, in association with The New York Botanical Garden, Bronx, New York, USA.
- ANDERSON, W. R. 2006. Eight segregates from the neotropical genus *Mascagnia* (Malpighiaceae). *Novon* 16: 168–204.
- ANDERSON, W. R. 2007. Malpighiaceae. In B. E. Hammel, M. H. Grayum, C. Herrera, and N. Zamora [eds.], *Manual de plantas de Costa Rica*, vol. 6, 253–312. Monographs in Systematic Botany from the Missouri Botanical Garden, vol. 111. Missouri Botanical Garden, St. Louis, Missouri, USA.
- ANDERSON, W. R., C. ANDERSON, AND C. C. DAVIS. 2006 onward [continuously updated]. Malpighiaceae [online]. Website <http://herbarium.lsa.umich.edu/malpigh> [accessed 05 November 2009].
- ANDERSON, W. R., AND S. CORSO. 2007. *Psychopterys*, a new genus of Malpighiaceae from Mexico and Central America. *Contributions from the University of Michigan Herbarium* 25: 113–135.
- ANDERSON, W. R., AND C. C. DAVIS. 2005a. The *Mascagnia cordifolia* group (Malpighiaceae). *Contributions from the University of Michigan Herbarium* 24: 33–44.
- ANDERSON, W. R., AND C. C. DAVIS. 2005b. Transfer of *Mascagnia letici-ana* to *Malpighia* (Malpighiaceae). *Contributions from the University of Michigan Herbarium* 24: 45–49.
- ANDERSON, W. R., AND C. C. DAVIS. 2006. Expansion of *Diplopterys* at the expense of *Banisteriopsis* (Malpighiaceae). *Harvard Papers in Botany* 11: 1–16.
- ANDERSON, W. R., AND C. C. DAVIS. 2007. Generic adjustments in neotropical Malpighiaceae. *Contributions from the University of Michigan Herbarium* 25: 137–166.
- BELDADE, P., K. KOOPS, AND P. M. BRAKEFIELD. 2002. Developmental constraints versus flexibility in morphological evolution. *Nature* 416: 844–847.
- BRAKEFIELD, P. M., AND J. C. ROSKAM. 2006. Exploring evolutionary constraints is a task for an integrative evolutionary biology. *American Naturalist* 168: S4–S13.
- CAMERON, K. M., M. W. CHASE, W. R. ANDERSON, AND H. G. HILLS. 2001. Molecular systematics of Malpighiaceae: Evidence from plastid *rbcL* and *matK* sequences. *American Journal of Botany* 88: 1847–1862.
- DARWIN, C. 1862. On the various contrivances by which orchids are fertilized by insects. John Murray, London, UK.
- DAVIS, C. C. 2002. *Madagasikaria* (Malpighiaceae): A new genus from Madagascar with implications for floral evolution in Malpighiaceae. *American Journal of Botany* 89: 699–706.
- DAVIS, C. C., W. R. ANDERSON, AND M. J. DONOGHUE. 2001. Phylogeny of Malpighiaceae: Evidence from chloroplast *ndhF* and *trnL-F* nucleotide sequences. *American Journal of Botany* 88: 1830–1846.
- DAVIS, C. C., C. D. BELL, P. W. FRITSCH, AND S. MATHEWS. 2002a. Phylogeny of *Acridocarpus-Brachylophon* (Malpighiaceae): Implications for Tertiary tropical floras and Afroasian biogeography. *Evolution* 56: 2395–2405.
- DAVIS, C. C., C. D. BELL, S. MATHEWS, AND M. J. DONOGHUE. 2002b. Laurasian migration explains Gondwanan disjunctions: Evidence from Malpighiaceae. *Proceedings of the National Academy of Sciences, USA* 99: 6833–6837.
- DAVIS, C. C., AND M. W. CHASE. 2004. Elatinaceae are sister to Malpighiaceae; Peridiscaceae belong to Saxifragales. *American Journal of Botany* 91: 262–273.

- DAVIS, C. C., P. W. FRITSCH, C. D. BELL, AND S. MATHEWS. 2004. High latitude Tertiary migrations of an exclusively tropical clade: Evidence from Malpighiaceae. *International Journal of Plant Sciences* 165: S107–S121.
- DAVIS, C. C., C. O. WEBB, K. J. WURDACK, C. A. JARAMILLO, AND M. J. DONOGHUE. 2005. Explosive radiation of Malpighiales supports a mid-Cretaceous origin of tropical rain forests. *American Naturalist* 165: E36–E65.
- DAVIS, C. C., M. LATVIS, D. L. NICKRENT, K. J. WURDACK, AND D. A. BAUM. 2007. Floral gigantism in Rafflesiaceae. *Science* 315: 1812.
- FRENOPOULO, C. 2005. The ritual use of ayahuasca. *Journal of Psychoactive Drugs* 37: 237–239.
- GAGLIANONE, M. C. 2005. Nesting biology, seasonality, and flower hosts of *Epicharis nigrata* (Fries, 1900) (Hymenoptera: Apidae: Centridini), with a comparative analysis for the genus. *Studies on Neotropical Fauna and Environment* 40: 191–200.
- GATES, B. 1982. *Banisteriopsis*, *Diplopterys* (Malpighiaceae). *Flora Neotropica Monograph* 30: 1–237.
- GRANT, V., AND K. A. GRANT. 1965. Flower pollination in the phlox family. Columbia University Press, New York, New York, USA.
- HOLMGREN, P. K., N. H. HOLMGREN, AND L. C. BARNETT. 1990. Index herbariorum, part 1: The herbaria of the world. New York Botanical Garden, Bronx, New York, USA.
- HUELSENBECK, J. P., AND F. RONQUIST. 2001. MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* 17: 754–755.
- HUTCHINSON, J. 1967. The genera of flowering plants. Clarendon Press, Oxford, UK.
- JIAN, S. G., P. S. SOLTIS, M. A. GITZENDANNER, M. J. MOORE, R. LI, T. A. HENDRY, Y. L. QIU, ET AL. 2008. Resolving an ancient, rapid radiation in Saxifragales. *Systematic Biology* 57: 38–57.
- LEWIS, P. O. 2001. A likelihood approach to estimating phylogeny from discrete morphological character data. *Systematic Biology* 50: 913–925.
- LOBREAU-CALLEN, D. 1989. Les Malpighiaceae et leurs pollinisateurs: Coadaptation ou coévolution. *Bulletin du Muséum National d'Histoire Naturelle, série 4, B, Adansonia* 11: 79–94.
- MADDISON, W. P., AND D. R. MADDISON. 2000. MacClade version 4: Analysis of phylogeny and character evolution. Sinauer, Sunderland, Massachusetts, USA.
- MICHENER, C. D. 2000. The bees of the world. Johns Hopkins University Press, Baltimore, Maryland, USA.
- NIEDENZU, F. 1928. Malpighiaceae. *Das Pflanzenreich IV* 141: 1–870.
- POSADA, D., AND T. R. BUCKLEY. 2004. Model selection and model averaging in phylogenetics: Advantages of Akaike information criterion and Bayesian approaches over likelihood ratio tests. *Systematic Biology* 53: 793–808.
- POSADA, D., AND K. A. CRANDALL. 1998. MODELTEST: Testing the model of DNA substitution. *Bioinformatics* 14: 817–818.
- SIGRIST, M. R., AND M. SAZIMA. 2004. Pollination and reproductive biology of twelve species of neotropical Malpighiaceae: Stigma morphology and its implications for the breeding system. *Annals of Botany* 94: 33–41.
- STAMATAKIS, A. 2006. RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22: 2688–2690.
- STEBBINS, G. L. 1974. Flowering plants: Evolution above the species level. Harvard University Press, Cambridge, Massachusetts, USA.
- TAYLOR, D. W., AND W. L. CREPET. 1987. Fossil floral evidence of Malpighiaceae and an early plant–pollinator relationship. *American Journal of Botany* 74: 274–286.
- TOKUOKA, T., AND H. TOBE. 2006. Phylogenetic analyses of Malpighiales using plastid and nuclear DNA sequences, with particular reference to the embryology of Euphorbiaceae sens. str. *Journal of Plant Research* 119: 599–616.
- VAN DER PIJL, L., AND H. DODSON. 1966. Orchid flowers: Their pollination and evolution. University of Miami Press, Coral Gables, Florida, USA.
- VOGEL, S. 1974. Ölblumen und ölsammelnde Bienen. *Tropische und Subtropische Pflanzenwelt* 7: 283–547.
- VOGEL, S. 1990. History of the Malpighiaceae in the light of pollination ecology. *Memoirs of the New York Botanical Garden* 55: 130–142.
- WIENS, J. J. 2006. Missing data and the design of phylogenetic analyses. *Journal of Biomedical Informatics* 39: 34–42.
- WIENS, J. J., J. W. FETZNER, C. L. PARKINSON, AND T. W. REEDER. 2005. Hylid frog phylogeny and sampling strategies for speciose clades. *Systematic Biology* 54: 778–807.
- WURDACK, K. J., AND C. C. DAVIS. 2009. Malpighiales phylogenetics: Gaining ground on one of the most recalcitrant clades in the angiosperm tree of life. *American Journal of Botany* 96: 1551–1570.
- XI, Z., B. R. RUHFEL, K. J. WURDACK, A. AMORIM, AND C. C. DAVIS. 2010. Complete plastid genomes do not resolve deep relationships in Malpighiales. Botany 2010: Annual meeting of the Botanical Society of America, Providence, Rhode Island, USA [online abstract, website <http://2010.botanyconference.org/engine/search/index.php?func=detail&aid=581>].
- YAMPOLSKY, C., AND H. YAMPOLSKY. 1922. Distribution of sex forms in the phanerogamic flora. *Bibliotheca Genetica* 3: 1–62.
- ZHANG, L.-B., AND M. P. SIMMONS. 2006. Phylogeny and delimitation of the Celastrales inferred from nuclear and plastid genes. *Systematic Botany* 31: 122–137.
- ZHANG, W., E. M. KRAMER, AND C. C. DAVIS. 2010. Floral symmetry genes and the origin and maintenance of zygomorphy in a plant–pollinator mutualism. *Proceedings of the National Academy of Sciences, USA* 107: 6388–6393.

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

Taxon	Distr. ^a	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
Centroplocaceae*						
<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>Centroplocus 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>Hymenanthra 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 hiraia</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'Donnell & Lourteig†	NW	Anderson 13614 (MICH)	AF351026	AF344528	AF344458	HQ246960

APPENDIX 1. Continued

Taxon	Distr. ^a	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) [<i>Chase M239</i> (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 schwannoides</i> (Griseb.) B. Gates	NW	Mori et al. 21590 (MICH)	HQ246764	HQ247212	HQ247445	HQ246982
<i>Banisteriopsis sellowiana</i> (Adr. Juss.) B. Gates	NW	Menendro 278 (MICH)	HQ246765			HQ246983
<i>Barnebya dispar</i> (Griseb.) W. R. Anderson & B. Gates†	NW	Leoni 1473 (MICH)	AF351073	AF344531	AJ402924/ 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. ^a	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>Callicola 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		HQ247023
<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> (Radlk.) 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 galphimoides</i> (Maguire) W. R. Anderson	NW	Berry et al. 5275 (MICH)	HQ246811	HQ247257	HQ247476	HQ247032
<i>Diaspis albida</i> Nied.†	OW	De Wilde 5920 (MO)	HQ246813	HQ247259	HQ247478	HQ247034
<i>Diaspis albida</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>Digoniopterys 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	HQ247265	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>Echinopterys 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>Gallardoa 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. ^a	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>Heladenia 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 byrsionimifolia</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 wiedeana</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. ^a	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 leticiana</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 souzai</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>Mezias araujoii</i> Nied.†	NW	Anderson 13672 (MICH)	AF351051	AF344569	AF344502	HQ247123
<i>Mezias 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	Rabenantoandro 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 stannea</i> (Griseb.) W. R. Anderson†	NW	Anderson 13804 (MICH)	AF351056	HQ247368	AF344500	AF500560
<i>Niedenzuella stannea</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. ^a	Voucher	Plastid			Nuclear <i>PHYC</i>
			<i>ndhF</i>	<i>matK</i>	<i>rbcL</i>	
<i>Philgamia hibernioides</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 & 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 & 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>Phillipson 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 & 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 phlomoides</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 & 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 & 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 & 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 & Rakotozafy 2682</i> (P)	HQ246943	HQ247411		HQ247172
<i>Tristellateia</i> sp.	OW	<i>Leeuwenberg & Rafamantanansoa 14477</i> (MO)	HQ246942	HQ247410		HQ247171
<i>Verrucularia glaucophylla</i> A. Dr. Juss.†	NW	<i>Amorim 3662</i> (MICH)	AY499108	HQ247414	HQ247602	AY499080

^a 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 suffrutescent; 2: trailing suffrutescent; 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 (μm)—0: ≤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