Madagasikaria (Malpighiaceae): A New Genus from Madagascar with Implications for Floral Evolution in Malpighiaceae

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The Malpighiaceae are a medium-sized family of tropical and subtropical flowering plants that are widely distributed across the forests and savannas of both the Old and New Worlds. They comprise approximately 1250 species in 65 genera, with approximately 130 species belonging to the 15 Old World genera (W. Anderson, University of Michigan, unpublished data). The only overlap between the Malpighiaceae in the two hemispheres consists of two species of predominantly New World genera that also occur in west Africa (Anderson, 1990; see also Cameron et al., 2001 and Davis, Anderson, and Donoghue, 2001). The Old World taxa do not form a clade and are represented in as few as six or as many as nine independent clades that are each more closely related to New World lineages (Davis, Anderson, and Donoghue, 2001). Of the Old World clades, about 71 are endemic to Madagascar and belong to eight genera (Arènes, 1950; Anderson, 2001b), which are represented in at least four of these disparate Old World clades.

Fruits have long been a major criterion for recognizing genera in the Malpighiaceae (Anderson, 2001a), with floral and vegetative characters contributing additional (in some cases primary) characters. In most cases, molecular data have supported the monophyly of traditionally recognized genera (Cameron et al., 2001; Davis, Anderson, and Donoghue, 2001). On a recent expedition to Madagascar, I discovered a previously unknown plant that I am describing here as a new genus and species. *Madagaskaria andersonii* C. Cav. Davis has a distinctive winged fruit not present among other Malpighiaceae. It also has large leaf-like stipules that are rare in the family and only present in distantly related taxa.

To estimate the phylogenetic relationships of *Madagaskaria*, I have obtained DNA sequence data from four gene regions: ndhF, trnL-F, PHYC, and ITS. Data from chloroplast ndhF and trnL-F sequences have been informative for inferring phylogenetic relationships among genera of Malpighiaceae (Davis, Anderson, and Donoghue, 2001). The phytochrome gene family (*PHYB*) is phylogenetically informative among grasses (Mathews, Tsai, and Kellogg, 2000), resolving 67% of the nodes with bootstrap values of >91%. In some angiosperm taxa, gene duplications have occurred in the phytochrome A and B (*PHYA* and *PHYB*) subfamilies (Mathews and Sharrock, 1996), but there is no evidence of duplications in *PHYC* (Donoghue and Mathews, 1998; Mathews and Donoghue, 1999; C. C. Davis, unpublished data), making it a reasonable choice for this study. Nuclear ribosomal DNA from the internal transcribed spacer region (ITS) has proven useful for resolving phylogenetic relationships at lower taxonomic levels in plants due to high interspecific nucleotide variation (Baldwin et al., 1995) and may be appropriate for inferring
phylogenetic relationships among closely related genera of Malpighiaceae.

MATERIALS AND METHODS

Taxon sampling—Madagaskaria was placed into an existing ndhF and trnL-F data set (Davis, Anderson, and Donoghue, 2001) to estimate its approximate phylogenetic position. Madagaskaria and the previously unsampled Malagasy endemic genus Microsteira Baker belong to the malpighioid clade (sensu Davis, Anderson, and Donoghue, 2001). The malpighioids represent a lineage of approximately 110 species in nine genera, which are all paleotropical, save the most species rich genus Malpighia L. (about 40 species) and Mascagnia (Bartero ex DC.) Colla sensu stricto (about 5 species), which are neotropical. Nine species (ten accessions) of Malpighiaceae, representing all of the known genera of the malpighioid clade were sampled (voucher, source, and accession information has been archived at the Botanical Society of America website; http://ajbsupp.botany.org/v89). There is morphological evidence to suggest that the monotypic Malagasy genus Digonioperis Aréaz may also be a member of the malpighioid clade, but it was not possible to obtain material for this species. Mascagnia dipholiphylla Small (Bullock) and Stignaphyllon pabueron (Rich.) Adr. Juss. were identified as putative out-groups (see Davis, Anderson, and Donoghue, 2001) to this clade and used for rooting purposes. Twelve ndhF sequences were included, eight of which are from Davis, Anderson, and Donoghue (2001; http://ajbsupp.botany.org/v89) and four were newly generated. Twelve trnL-F sequences were included, eight of which were previously sampled (Davis, Anderson, and Donoghue, 2001) and four were newly generated. Eleven and 12 new sequences of PHYC and ITS were generated, respectively.

DNA amplification, cloning, and sequencing—Total genomic DNA was extracted primarily with a hot cetyltrimethylammonium bromide (CTAB) extraction method (Doyle and Doyle, 1987; see Davis, Anderson, and Donoghue, 2001). The DNA of some samples was extracted by using the DNEasy Plant Mini Kit protocol (QIAGEN, Valencia, California, USA).

ndhF and trnL-F—ndhF and trnL-F were amplified and sequenced in accordance with the protocols outlined in Davis, Anderson, and Donoghue (2001). Double-stranded polymerase chain reaction (PCR) products were sequenced in both directions with dye terminators and cycle sequencing protocols (Perkin Elmer, Wellesley, Massachusetts, USA). Sequences were obtained with an ABI model 377 or an ABI model 3100 automated sequencer (Applied Biosystems, Foster City, California, USA) and edited with the computer program Sequencher 3.0 (Gene Codes Corporation, Ann Arbor, Michigan, USA). Both strands were sequenced with a minimum overlap of 75% of the total sequence length. All sequences were submitted to GenBank (http://ajbsupp.botany.org/v89/davis.pdf).

PHYC—A 1.2-kilobase (kb) region of the PHYC gene was amplified in all cases using a stepdown PCR protocol (Hecker and Roux, 1996) beginning at 58° or 60°C. The PHYC locus-specific amplification primer pairs are described in Matthes and Donoghue (1999). The degenerate upstream primer listed in Matthes and Donoghue (1999) was used to obtain clones from some of the taxa.

PHYC PCR products were excised after electrophoresis and extracted from a 1.0% agarose gel with the QIAquik gel extraction protocol (QIAGEN). Cloning procedures followed that of Matthes, Tsai, and Kellogg (2000). PHYC fragments were ligated into pGEM-T or pGEM-T Easy vectors (Promega, Madison, Wisconsin, USA) while incubating overnight at 4°C. XL1-Blue Epicurian Coli competent cells (Stratagene, LaJolla, California, USA) were transformed with these ligation products and incubated overnight at 37°C. Colonies were cultured overnight in nutrient broth, and plasmid DNA was subsequently isolated using the QIAprep Spin Miniprep Kit (QIAGEN). Five to ten clones were screened for several species of Malpighiaceae (C. C. Davis, unpublished data) using EcoRI restriction enzyme digestion. Preliminary results from Malpighiaceae indicate that multiple copies are not present in PHYC. ABI PRISM DyeDeoxy terminator cycle sequencing of positive clones was performed as above by using the vector-based primers f7 (5'-AATAGCACTCAGTATAAGAAG-3') and s6 (5'-GATTAGGGACACATATAG-3') and the internal sequence-specific primer mdf0: 5'-ATGGAYTNGF-NAARTGYGATGG-3'.

ITS—The ITS region was amplified with the primers ITS4 (White et al., 1990) and ITSLEU (Baum, Small, and Wendel, 1998) by following the protocols described in Davis et al. (in press). To date, PCR has yielded only single bands for ITS. Bands were excised and cleaned as above. Two to four clones have been sequenced for several accessions for a study of Acridocarpus (Malpighiaceae) by the author (unpublished data). Preliminary results from Acridocarpus indicate that polymorphisms in ITS (e.g., Wendel, Schnabel, and Seelanan, 1995; Buckler and Holtsford, 1996; Campbell et al., 1997) are not present in Malpighiaceae. Sequences were obtained by using the amplification primers and the internal sequence specific primers ITS2 and ITS3B (Baum, Small, and Wendel, 1998).

Phylogenetic analyses—Nucleotide sequences were aligned easily by eye. Phylogenetic analyses were conducted with PAUP* (version 4.0b8; Swofford, 1999). Parsimony analyses of the data were conducted for each gene independently (results not shown) and in combination by using all taxa (ten in groups in all). All searches for equally parsimonious trees were implemented with the branch-and-bound option selected. Nucleotide substitutions were weighted equally; gaps were treated as missing by PAUP* and included in the analyses. Bootstrap support (Felsenstein, 1985) for each clad was estimated from 1000 heuristic search replicates with the simple taxon addition and tree-reconstruction-recombination (TBR) branch-swapping options selected. To assess congruence between each independent data set, the incongruence length difference test (ILD) (Farris et al., 1994; implemented as the partition homogeneity test in PAUP*) was conducted. The same heuristic search strategy as that presented for the bootstrap analysis was conducted with 999 random repetitions employed, and only ten trees from each replicate were retained to generate the distribution.

Scanning electron microscopy (SEM)—Pollen grains of Madagaskaria andersonii and Rhynchotheca philippsonii W. R. Anderson were examined by using SEM. Air-dried pollen grains were extracted from anthers and placed onto SEM stubs using double-stick conductive tape followed by sputter-coating with 1–2 nm gold/palladium in a Technics Hummer Sputter Corder (Technics, Alexandria, Virginia, USA). Pollen grains were viewed with an AMRAY Model 1000 Scanning Electron Microscope at 20 kV.

RESULTS

Sequences/matrices—Sequences of the 3′ region of ndhF are 637 nucleotides (nt) long and required no gaps in the alignment. The ndhF matrix provides 15 parsimony-informative sites to the combined data set (7.00% of the total informative sites), along with 38 variable but uninformative sites and 584 invariant sites. Sequences of trnL-F are 974 nt long. Sequences of trnL-F were the most length-variable of the genes studied, with several gap regions (from 1 to 225 nt long) inserted into the sequences to produce the alignment. One A-T rich region totalling 35 nt was difficult to align and was excluded from the analyses. The trnL-F matrix provides 18 parsimony-informative sites to the combined data set (8.41% of the total informative sites), along with 51 variable but uninformative sites and 905 invariant sites. The aligned sequences for PHYC were 1127 nt long and required no gaps in the alignment. The PHYC matrix provides 59 parsimony-informative sites to the combined data set (27.6% of the total informative sites), along with 113 variable but uninformative sites and 955 invariant sites. The aligned ITS sequences were 716 nt long with several small indel regions ranging from 1 to 29 nt long. The ITS
Fig. 1. Phylogram of one of the two equally parsimonious trees generated from the combined data set. Length = 735 steps; consistency index, including all variable characters = 0.8259, excluding uninformative characters = 0.6816; retention index = 0.7016. Arrow indicates clade not recovered in the strict consensus tree. Bootstrap values are given for those clades supported at >50%. The designated informal names correspond to clades discussed in this analysis.

matrix provides 122 parsimony-informative sites to the combined data set (57.0% of the total informative sites), along with 101 variable but uninformative sites and 493 invariant sites.

The combined data set consists of 3454 nt of aligned sequence and 214 parsimony-informative characters. The combined data set contains ten ingroup taxa (http://ajbsupp.botany.org/v89). The highest pairwise distance within the ingroup occurs between Caucanthus auriculatus (Radlk.) Nied. and Rhynchophora phillipsonii (142 steps; 4.11% of the total sites). The highest overall distance is 239 steps (6.91% of the total sites), between Caucanthus auriculatus and Stigmaphyllon puberum (one of the outgroup taxa). There are 303 variable but uninformative sites and 2937 invariant sites. The ILD test results revealed no significant difference ($P = 0.6160$) between the partitions defined by the four genes and random partitions of the same size as these four genes, but drawn from the combined data set.

**Phylogenetic analyses**—Analysis of the combined data set resulted in two equally parsimonious trees of 735 steps (Fig. 1). The New World species Mascagnia sepium (Adr. Juss. in A. St.-Hil.) Griseb. in Mart. is sister to all of the other malpighioids. The New World genus Malpighia is monophyletic (100%) and strongly supported (90%) as sister to the remain-
of the malpighioids, which are all Old World taxa. The latter clade is moderately well supported (76%) and consists of two clades. One of these is a weakly supported (63%) clade containing the genera Triaspis Burch., Aspidopterys Adr. Juss., and Caucanthus Forssk. The other, here named madagasikarioiids, forms a strongly supported clade (100%) and contains the genera Microsteira, Madagasikaria, and Rhynchophora Arénes. The madagasikarioiids are all Malagasy endemics.

**TAXONOMY**

*Madagasikaria andersonii* C. Cav. Davis, gen. et sp. nov.—

**Type:** MADAGASCAR. Toliara: southwest of Andranovory, along Route National 7, sandy soil in deciduous seasonally dry western forest, 235 m, 23°09'41"S, 44°05'41"E, 20 Jan. 2001 fl/ft, C. C. Davis, K. Abdul-Salim, and J. Andriantiana 20-01 (holotype: A; isotypes: MICH, MO, PBZT).

*Madagasikaria* C. Cav. Davis; genus novum *Digionopteridis, Microsteira*, et *Rhynchophora* affine, a quibus stipulis binatis magnis ovatis et fructu schizocarpico quaque samara ala laterali elliptica nucem circumdanti et ala dorsali replicata instructa differt; genus monotipicum, ex *M. andersonii* C. Cav. Davis constans.

Woody vine; stems glabrate to glabrous, the hairs white to translucent. Leaves opposite; lamina of larger leaves 5.5–13.3 cm long, 2.2–5.2 cm wide, narrowly elliptical to ovate, obtuse to (less frequently) rounded at base, acute to (often) apiculate at apex, glabrous above and below, eglandular or bearing small button-shaped glands on the lamina and near margin at base on abaxial surface on one or both sides of midrib, with 4–7 pairs of principal lateral veins, the veins and reticulum prominent below, obscure above; petiole 7–12 (–17) mm long, glabrate, eglandular or often with 1–2 small glands near apex; mature stipules 4–12 (–14) mm long, 3–6 (–8) mm wide, elliptical to obovate, reticulum prominent below, borne on stem adjacent to leaf bases, ± persistent. Inflorescence loosely sericeous, axillary, flowers ultimately borne in racemes; bracts 0.5–1 mm long, subulate or very narrowly triangular, abaxially sericeous, adaxially glabrate, occasionally bearing a small gland at the abaxial base, ± persistent; peduncle 1–2 mm long; bracteoles like bracts but only 0.5–0.6 mm long, borne at or slightly below apex of peduncle; pedicel 13–16 mm long. Flowers radially symmetrical, bisexual. Sepals 5, alike, ± 1.5–2 mm long, 1–1.25 mm wide, distinct, ovate to lanceolate, acute to rounded at apex, eglandular, glabrous to glabrous at anthesis. Petals 5, white, glabrous, spreading at anthesis, the claw 1–1.25 mm long, the limb 10.3–11 mm long, 3.25–5.5 mm wide, flat or (generally) concave, ovate or broadly elliptical, entire or somewhat erose or denticulate near the base. Stamens 10, glabrous, alternating in height (one short, one long), filaments tapering toward apex, straight, short-connate only at base, 0.75–0.85 mm long in short filaments, 1.5–2 mm long in long filaments; anthers 1.2–1.5 mm long, opening longitudinally, basifixid, the locules separated on a wide flat connate, becoming twisted with age. Gynoecium 3-carpellate; ovary about 2.25 mm long, densely sericeous, 3-locular, each locule containing 1 ovule; styles 3, about 2.5 mm long, of uniform thickness their whole length, arcuate-ascending, the stigma terminal, large, sagittate to reniform, stigmatic over the whole upper surface. Fruit schizocarpic, breaking apart into three samaras borne on a short pyramidal torus; samara glabrous at maturity, the lateral wing fully developed and completely encircling the nut, the dorsal wing folded over nut, rendering a flap-like appearance to the wing; lateral wing about 16 mm high and 11 mm wide on each side of the nut, elliptical, entire or undulate at margin; dorsal wing elliptical and appressed to nut, about 10 mm wide, 14 mm long, the margin notched and undulate; nut 8 mm high, 5 mm wide.

**Etymology**—Madagascar has been a source of inspiration for numerous biologists. This genus is named for Madagascar, using the Malagasy spelling. The specific epithet honors William R. Anderson, my mentor, collaborator, and friend. He has worked tirelessly on Malpighiaceae for the past 30 yr to better understand the evolution and diversity of this most exciting group.

**DISCUSSION**

*Madagasikaria* C. Cav. Davis forms a strongly supported clade with the Malagasy endemic genera *Rhynchophora* Arénes and *Microsteira* Baker and is most closely related to *Rhynchophora* (Fig. 1). *Microsteira* is a genus of 21 species (Arénes, 1950) widely distributed across Madagascar. *Rhynchophora* contains two species and occurs sympatrically with *Madagasikaria* in the deciduous seasonally dry forests of southwestern Madagascar. I tentatively refer to this well-supported clade as the madagasikarioiids herein. There are several morphological features that support the monophyly of this lineage. These taxa all have large reniform stigmas (Fig. 2g) and unusually wide anther connectives (Fig. 2f), characters which are unique within the Malpighiaceae. Additionally, the madagasikarioiids are all apparently androdioecious (Arénes, 1946, 1950; Anderson, 2001b; see below), producing both staminate and bisexual individuals, a condition that is rare in the Malpighiaceae. A staminate individual of *Madagasikaria* is not known for this species. Based on pollen morphology (discussed below), however, I would expect *Madagasikaria* to also be morphologically androdioecious. The small, white, radially symmetrical flowers produced by members of this clade are nearly identical and make it difficult to distinguish these taxa in flower (see also Anderson, 2001b). In contrast, fruits are very distinctive between all three genera (see Fig. 3b–d).

**Generic status**—Genera of the Malpighiaceae have traditionally been recognized primarily on the basis of fruit type (see Anderson, 2001a). *Madagasikaria* has a distinctive schizocarpic fruit in which each mericarp has an elaborate lateral wing, which completely encircles the nut, and a peculiar dorsal wing, which is folded over on itself (see Fig. 2h–i). The recognition of *Madagasikaria* at the rank of genus is warranted on the basis of its distinctive folded dorsal wing, which occurs in no other species of Malpighiaceae. Furthermore, *Madagasikaria* produces unusually large leaf-like stipules (Fig. 2b), unlike other members of the madagasikarioiids, which bear rather small linear stipules (or are estipulate).

In contrast to *Madagasikaria*, the schizocarpic fruit of *Microsteira* breaks apart at maturity into three samaras, each with a small dorsal crest and a three-lobed Y-shaped lateral wing (Fig. 3c). In this case, the unusual shape of each mericarp is a putative synapomorphy for the genus. In *Rhynchophora*, the three or four carpels are connate and apparently indehiscent. At maturity, each carpel bears a single elliptical wing that is neither dorsal nor lateral, but at right angles to the dorsiventral...
plane of the carpel. The result is a three- or four-winged fruit that resembles a helicopter (Anderson, 2001b; Fig. 3d).

Of the other Malagasy Malpighiaceae (Arènes, 1950), the fruit of *Madagasikaria* most resembles that of *Digoniopterys* Arènes, in which each mericarp has a lateral wing similar to *Madagasikaria* (Fig. 3a). *Digoniopterys* is a monotypic genus that occurs on the dunes around Tulear in southwestern Madagascar. The distribution of *Digoniopterys* does not appear to overlap with *Madagasikaria*. I was unable to include *Digoniopterys* in this study, but in future analyses I would expect these two taxa to be close relatives (if not sister taxa) because *Digoniopterys* appears to be functionally dioecious (Arènes, 1950) and bears flowers similar to other members of the madagasikarioids. Despite the similar lateral wing, *Madagasikaria* is distinct from *Digoniopterys* in several aspects. The mericarps of *Digoniopterys* have a dorsal crest that is perpendicular
encircles the nut. The molecular phylogenetic data indicate that members of *Triaspis* are not included within the madagasikarioid clade. Moreover, species of *Triaspis* differ from any of the other madagasikarioids in a number of notable floral features, including the presence of large ornately imbricate petals, entirely bisexual flowers, long arched styles, and unusually elongated stigmas. These characteristics, combined with the phylogenetic placement of *Triaspis*, suggest that *Madagasikaria* should not be recognized as a segregate species within *Triaspis*.

**Fruit evolution**—*Rhynchophora* has a particularly unusual indehiscent fruit, unlike other winged species of Malpighiaceae (Anderson, 2001b: Fig. 3d). The position and morphological nature of the single wing borne on each carpel has prompted repeated speculation as to its homology. Arènes (1946) suggested that the single wing in *Rhynchophora* is homologous with the single lower lobe of the three-lobed wing of *Microsteira* (Fig. 3c). This would mean that the two upper lateral lobes have been completely reduced and that the lower lobe must have shifted position from the base of the fruit to the middle or apex, consistent with the position of extant species of *Rhynchophora*. Anderson (2001b) suggested instead that the single wing is homologous with the upper two lateral wings of *Microsteira*, which are in a position and orientation similar to the single wing of *Rhynchophora*. He expressed caution in his assessment because the wings of *Rhynchophora* are apparently never notched, nor is their venation double, which, under Anderson’s scenario, would most likely result from the fusion of the two upper lateral wings in *Microsteira*.

The sister relationship of *Madagasikaria* with *Rhynchophora* helps clarify the nature of wing homology in *Rhynchophora*. Given the folded aspect of the dorsal wing in *Madagasikaria* it is possible that this wing has rotated and shifted upward into the position found in *Rhynchophora*. This scenario requires a great deal of wing realignment, however, and on that basis it seems more likely that the unusual wing in *Rhynchophora* represents a reduced lateral wing similar to that found in *Madagasikaria*. This suggests that the lateral wing in the lineage leading to *Rhynchophora* may have been reduced proximally and folded over at the apex, a scenario that is consistent with the wing venation and lack of lobing in *Rhynchophora*. These hypotheses should be tested with further comparative developmental data, but from this discovery we can (1) reliably infer that the wing in *Rhynchophora* is most likely not homologous with any single lobe in *Microsteira* as previously speculated and (2) provide more convincing evidence that the wing in *Rhynchophora* is indeed most likely lateral in nature.

**Floral evolution**—Neotropical Malpighiaceae are principally pollinated by specialized (Neff and Simpson, 1981) oil-

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**Table 1.** Summary of major morphological features for distinguishing madagasikarioid genera.

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<th>Leaf shape</th>
<th>Stipules</th>
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<td><em>Digionioptrys</em></td>
<td>Shrub</td>
<td>Linear</td>
<td>Absent</td>
<td>Dehiscent; each mericarp ± circular with the lateral wing completely encircling the nut; dorsal crest greatly reduced and perpendicular to carpel wall</td>
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<tr>
<td><em>Madagasikaria</em></td>
<td>Vine</td>
<td>Elliptic-ovate</td>
<td>Elliptic-obovate; persistent</td>
<td>Dehiscent; each mericarp ± ellipsoid with the lateral wing completely encircling the nut; dorsal crest prominent and folding over on itself</td>
</tr>
<tr>
<td><em>Rhynchophora</em></td>
<td>Vine</td>
<td>Elliptic-ovate</td>
<td>Subulate; often deciduous</td>
<td>Indehiscent; each carpel with a single elliptic wing</td>
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collecting anthophorine bees of the tribe Centridini and exhibit highly conserved floral morphology (Vogel, 1974; Anderson, 1979) despite tremendous diversity in fruit morphology and habit (Anderson, 1979). The oil-collecting bees, which visit neotropical malpighs, are absent from the paleotropics (Vogel, 1990), where most Malpighiaceae species lack the oil glands and typical flower orientation crucial to pollination by oil-collecting bees. Given the scattered phylogenetic distribution of Old World taxa (Davis, Anderson, and Donoghue, 2001) and the great diversity of floral variation among these species (C. C. Davis, unpublished data), Old World Malpighiaceae provide an excellent opportunity to examine the ecological consequences of shifts in the pollinator selective regime. The madagasikarioids apparently represent one such shift away from the characteristic neotropical pollination syndrome.

Anderson (2001b) reported that individuals of *Rynchophora philippsonii* bear either wholly staminate flowers or her-