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**Madagasikaria (Malpighiaceae): a new genus from Madagascar with implications for floral evolution in Malpighiaceae**

CHARLES C. DAVIS

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*Madagasikaria andersonii* is described here as a new genus and species of Malpighiaceae from Madagascar. The phylogenetic placement of *Madagasikaria* was estimated by using combined data from *ndhF* and *trnL-F* chloroplast sequences and phytochrome (*PHYC*) and ITS nuclear sequences. It forms a strongly supported clade with the Malagasy endemic genera *Rhynchophora* and *Microsteira*. Despite nearly identical floral morphology among species in this clade (here called the madagasikarioid clade), these genera are easily distinguishable on the basis of their fruits. The schizocarpic fruits of *Madagasikaria* have distinctive mericarps. Each mericarp has a lateral wing, which completely encircles the nut, and a peculiar dorsal wing, which folds over on itself. The morphology of this fruit suggests that the homology of the unusual wing in *Rhynchophora* is lateral in nature and represents a reduced wing similar to the lateral wing in *Madagasikaria*. Taxa in the madagasikarioid clade all appear to be morphologically androdioecious and functionally dioecious, producing both staminate and “bisexual” (i.e., functionally carpellate) individuals. This condition appears to be exceedingly rare in flowering plants and has important implications for floral evolution within Malpighiaceae. Neotropical Malpighiaceae are pollinated by specialized oil-collecting anthophorine bees of the tribe Centridini and exhibit highly conserved floral morphology despite tremendous diversity in fruit morphology and habit. These oil-collecting bees are absent from the paleotropics, where most members of the Malpighiaceae lack both the oil glands and the typical floral orientation crucial to pollination by neotropical oil-collecting bees. The madagasikarioids represent one shift from the neotropical pollination syndrome among Old World Malpighiaceae.

**Key words:** morphological androdioecy; breeding system; floral evolution; functional dioecy; *Madagasikaria andersonii*; Malpighiaceae; molecular systematics; phylogeny.

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 genera, 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. *Madagasikaria 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 *Madagasikaria*, 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 Microsteoe 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 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://ajb supp.botany.org/v89). There is morphological evidence to suggest that the monotypic Malagasy genus Digoniopitys Arneses may also be a member of the malpighioid clade, but it was not possible to obtain material for this species. Mascagnia diphyphylla Small (Bullock) and Stigmaphyllon paberum (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://ajb supp.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 DNAeasy 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://ajb supp.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 Mathews and Donoghue (1999). The degenerate upstream primer listed in Mathews 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 Mathews, 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’-AAATACGACTCATATAG) and sp6 (5’-AGTATTAGTGACACTATAG-3’) and the internal sequence-specific primer mdf3r: 5’-ATGGAYYTNGF-NAARTGYYGATGG-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 Seelanun, 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 100 heuristic search replicates with the simple taxon addition and tree-bisection-reconnection (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)—Pollens grains of Madagasikaria andersonii and Rhynchophora 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 Coater (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

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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 Caucanthis auriculatus (Radl.) Nied. and Rhynchophora philipsonii (142 steps; 4.11% of the total sites). The highest overall distance is 239 steps (6.91% of the total sites), between Caucanthis auriculatus and Stigmaphyllum 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-
der 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 madagasikarioids, forms a strongly supported clade (100%) and contains the genera Microsteira, Madagasikaria, and Rhynchophora Arènes. The madagasikarioids are all Malagasy endemics.

**TAXONOMY**


_C. Cav._ Davis, gen. et sp. nov.—Madagasikaria C. Cav. Davis; genus novum DIGONIOPTERYDAE, Microsteirae, et Rhynchopterae affine, a quibus stipulis binatis magnis ovatis et fructu schizocarpico quaque samara (holotype: A; isotypes: MICH, MO, PBZT).

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 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 and 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 glabrate, the hairs white to translucent. 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, basifixte, 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* Arênes and *Microsteira* Baker and is most closely related to *Rhynchophora* (Fig. 1). *Microsteira* is a genus of 21 species (Arênes, 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 madagasikarioids 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 madagasikarioids are all apparently androdioecious (Arênes, 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 stigmas (Fig. 2b), unlike other members of the madagasikarioids, which bear rather small linear stigmas (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 madagasikaroids. Despite the similar lateral wing, Madagasikaria is distinct from Digoniopterys in several aspects. The mericarps of Digoniopterys have a dorsal crest that is perpendicular
to the carpel wall and does not bend (Fig. 3a), and each mericarp is nearly half the size of those found in Madagasikaria. Moreover, Digoniopterys is a microphyllous shrub without stipules (Arènes, 1946). In contrast, Madagasikaria has relatively large laminate leaves, has large ovate stipules, and is a vine. See Table 1 for a summary of the salient differences between madagasikarioid genera. 

Although the stipules of Madagasikaria are unique to the madagasikarioids they are nearly identical to those found in some species of Triaspis Burch. (e.g., T. stipulata Oliv. and T. macropteron Oliv.). Triaspis is a genus of approximately 15 species distributed widely across Africa (Niedenzu, 1928) and is closely related to the madagasikarioids (Fig. 1). Like Madagasikaria, some species of Triaspis produce schizocarpic fruits in which the lateral wing of the mericarp completely 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 fimbriate 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>
<th>Fruit</th>
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<td><em>Digoniopterys</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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<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 malpighis, 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 sequences of shifts in the pollinator selective regime. The madagasikarioids apparently maintained anthers with fodder pollen to ensure that pollinators visit the pistillate flowers often enough to effect pollination. I was unable to locate a staminate individual of Madagasikaria, but the nature of the pollen found in the type collection (Fig. 4a) combined with its phylogenetic placement strongly suggest that this species is dioecious and produces both “bisexual” and staminate individuals. The functionally carpellate flowers of Madagasikaria bear very large pollen like that of Rynchophora described above, which is also inaperturate. Future collections of Madagasikaria should yield staminate individuals similar to those found in Rynchophora and Microsteira.

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