Toward a Phylogenetic-based Generic Classification of Neotropical Lecythidaceae—
II. Status of Allantoma, Cariniana, Couratari, Couroupita, Grias and Gustavia

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Abstract

The morphological features of all clades of neotropical Lecythidaceae subfam. Lecythidoideae (Brazil nut family) with actinomorphic androecia (Allantoma, Grias, Gustavia) as well as three clades with zygomorphic androecia (Cariniana, Couroupita, and Couratari) are described. These clades are those that were recovered by a phylogeny based on molecular data, and all, except Allantoma and Cariniana, have been recognized as genera without changes for over a hundred years. The latter two genera have recently been circumscribed such that they now also represent monophyletic clades; thus, the authors conclude that the clades discussed in this paper represent well-defined genera based on both morphological and molecular data. Morphological descriptions of these six clades of the non-Bertholletia clade are included and a key to the 16 clades of New World Lecythidaceae is presented.

Introduction

The use of anatomical, morphological, and molecular data to produce cladograms has advanced the study of neotropical Lecythidaceae. For the first time in the history of classification of neotropical Lecythidaceae, higher order classification, from the generic level to the placement of the family among the angiosperms, is being developed based on testable hypotheses.

The first Lecythidaceae cladograms produced were published by Chih-Hua Tsou in 1994. The emphasis of her study was to determine the value of morphological, anatomical, and embryological features to discern higher order relationships among the 20 worldwide genera of Lecythidaceae. Tsou (1994) also contributed valuable embryological descriptions and illustrations (including androecial features) for most of the genera in both the Old World and New World and produced the first hand-generated cladograms of Lecythidaceae based on embryological and morphological characteristics for the subfamily Barringtonioideae (erroneously called the Planchonioideae fide Thorne, 2000). She concluded the following: 1) the family concept of Lecythidaceae should be limited to the Old World Barringtonioideae and Foetidioideae, and the New World Lecythidoideae; 2) Lecythidaceae and Scytopetalaceae have embryological features in common; and 3) the central Amazonian Asteranthos brasiliensis Desfontaines (1820: 9) (formerly placed in the African Napoleonaeoideae) is part of the Scytopetalaceae, a family otherwise limited to Africa. The last conclusion was subsequently supported by molecular (Morton et al., 1997) and morphological (Apple, 1996, 2004) data.

The next step forward was taken by Morton et al. (1997, 1998) who analyzed the relationships of Lecythidaceae using cladistics based on anatomical, morphological, and molecular data. The major result of this study was that Lecythidaceae belong to a large clade with other families that are now considered to belong to the Ericales, a conclusion that has been supported by the molecular studies of Anderberg et al. (2002) and Schönberger et al. (2005). The relationship of Lecythidaceae to taxa of Ericales has been recovered so many times in molecular studies that its position there is well established. It is, however, perplexing that there are no convincing anatomical or morphological characters that Lecythidaceae share with Ericales. Morton followed up their original paper (Morton et al., 1997) with another study in which they recognized the following subfamilies of Lecythidaceae: Barringtonioideae (= their Planchonioideae), Napoleonaeoideae, Scytopetaloidae, Foetidioideae, and Lecythidoideae (Morton, 1998).
Others have treated the Napoleonaeoideae (Prance, 2004) and Scytopetaloidae (Appel, 1996, 2004) as separate families and the Lecythidaceae as consisting of the subfamilies Barringtonioideae (as the Planchonioideae), Foetidioideae, and Lecythidoideae (Prance & Mori, 2004; Mori et al., 2007). Retaining these clades together as a family results in a broadly circumscribed Lecythidaceae (Fig. 1) with so many disparate characters that it is difficult to separate them in a key no matter what rank they are placed in. Even the inclusion of the monogeneric Foetidioideae in the Lecythidaceae sensu lato is not convincing when only anatomical and morphological data are considered; however, treating the Foetidioideae as a separate family would also require recognizing the Barringtonioideae as a family and require that all New World species, except Asteranthos brasiliensis, be treated as a narrowly defined Lecythidaceae. One option would be to include Foetidia Comm. ex Lamarck (1788: 2) in the Barringtoniaceae, which can be defended based on molecular data because these two groups are sister to one another (Mori et al., 2007). However, this requires grouping taxa that lack petals and have a poorly developed staminal ring (all species of Foetidia) with those with petals and well-developed staminal rings (e.g., Barringtoniaceae), characters that could be used to separate them as families. Two other options would be to recognize all clades as separate families, Napoleonaeaceae, Scytopetalaceae, Foetidiaeae, Barringtoniaceae, and Lecythidaceae, or to recognize all clades as separate subfamilies as is done by the Angiosperm Phylogeny Group (Stevens, 2001; Angiosperm Phylogeny Group, 2009).

The next phase had the goal of evaluating the monophyly of the Neotropical genera. An initial study by Mori et al. (2007) revealed that all actinomorphic-flowered genera, except Cariniana Casaretto (1842: 35), formed well-defined clades or subclades. Cariniana was recovered as paraphyletic and included two groups of species by Huang et al. (2008). The first group has zygomorphic androecia, brochidodromous secondary leaf veins, and six membranous petals. The second has actinomorphic androecia, eucamptodromous secondary leaf veins, and five fleshy petals. The latter group possesses the same characters as Allantoma lineata (Mart. ex O. Berg [1858: 508]; Miers (1874: 297); thus, Huang et al. (2008) transferred the species with actinomorphic androecia to Allantoma Miers (1874: 291) and retained the species with zygomorphic androecia in Cariniana. With that change, both Allantoma and Cariniana also formed well-defined clades.

In addition, Mori et al. (2007) recovered a large clade with zygomorphic androecia that was subsequently called the Bertholletia Bonpland (1808: 122) clade by Huang (2010). The ten subclades comprising the Bertholletia clade were morphologically described by and evaluated for the possibility of treating them as separate genera by Huang et al. (2015). The other genera with zygomorphic androecia (the redefined Cariniana, Couroupita Aublet [1775: 708], and Couratari Aublet [1775: 723]) are not treated by Huang et al. (2015); thus, the goal of this paper is to 1) describe the clades of neotropical Lecythidaceae not treated by Huang et al. (2015) (i.e., the actinomorphic-flowered Allantoma, Grias, and Gustavia) and the zygomorphic-flowered (Cariniana, Couratari, and Couroupita), 2) analyze their generic status, and 3) provide a key to the 16 clades found in the New World tropics.

Materials and methods

This paper is based on the phylogenetic trees published in Mori et al. (2007) and Huang et al. (2015). The morphological and anatomical characters are defined in the Flora Neotropica monographs on Lecythidaceae (Prance & Mori, 1979; Mori & Prance 1990), the notes of the senior author and his colleagues, and data and images from the Lecythidaceae Pages (Mori et al., 2010).

Results

This paper is based on the phylogenies reported in two papers (Mori et al., 2007) and another paper in this volume (Huang et al., 2015). In a strict consensus tree based on a combined analysis of ndhF and rnlF sequences (Mori et al., 2007), the following clades and subclades, excluding those of the Bertholletia clade (Huang et al., 2015), with jackknife support values >50% were recovered: Grias Linnaeus (1759: 1075); Gustavia Linnaeus (1775: 12, 17, 18); and Couroupita (Fig. 1). Subsequently Huang et al. (2008), in a study based on morphology, transferred the seven actinomorphic-flowered species in the Allantoma lineata/Cariniana clade to Allantoma and retained the nine species with zygomorphic flowers in Cariniana. The new “Allantoma” and “Cariniana” clades had jackknife support values >50%. Figure one in this paper was modified to reflect this change.
FIGURE 1. Part of a jackknife tree generated using Xac (Farris, 1997) which is based on a combination of ndhF and trnL-F sequences. Only the clades treated in this paper are shown in this cladogram (Mori et al., 2007). The families and subfamilies making up the Lecythidaceae and its close relatives discussed in this paper and the genera representing them are the following: family Napoleonaeaceae (Napoleonaea), family Scytopetalaceae (Brasseia, Rhaiptpetalum, Oubanguia, and Scytopetalum), subfamily Foetidioideae (Foetidia), subfamily Barringtonioideae (Petersianthus, Chydenanthus, Barringtonia), and subfamily Lecythidoideae (all remaining genera). This cladogram was modified by changing Cariniana decandra Ducke to Allantoma decandra by Huang et al. (2008).
The Allantoma/Cariniana/Couratari/Bertholletia clade has poor resolution and is in need of future study to resolve such enigmas as why the actinomorphic-flowered Allantoma is embedded in a clade with other taxa that possess zygomorphic flowers, and why the Couratari clade, which possesses the most complex flowers in the New World taxa, does not appear in the Bertholletia clade, which also possesses morphologically complex flowers.

**Discussion**

**Grias** clade (Mori, 1979a)—species of Grias have a pachycalycaul growth form, cylindrical trunks to the ground, thick twigs usually greater than 10 mm diam. (as measured here and throughout these descriptions directly below the insertion of the leaves), and very long leaves that range from 50 cm to two meters (Fig. 2E). The buds are surrounded by calyx-lobes fused together in bud that irregularly split apart when opening (the exception is G. neuberthii with 6 free calyx-lobes). Although there are sporadic species with four petals in a few other genera, Grias always has flowers with four petals, actinomorphic androecia (Fig. 2A), and a fleshy staminal tube that differs from the other genera by having a lower, narrower chamber that surrounds the ovary and an upper wider chamber that slants (Fig. 2B) or arches (Fig. 2G) outward. The staminal tube in Allantoma is also fleshy and is the same diameter throughout its length. The stamens of Grias are always curved inward and the filaments are fleshy and more-or-less angular in cross-section. In addition, Grias flowers usually have four locules (Fig. 2C) (although some have three [Fig. 2H] or more than four), with only a few, pendulous ovules at the apex of the locules and placenta that are not expanded (i.e., they are the same thickness throughout their length when viewed in a medial longitudinal section). All species of Grias have fruits with a single massive seed and a very strongly ribbed endocarp (the ribs are called endocarp buttresses) (Fig. 2C–D). The embryo is macropodial (i.e., it lacks cotyledons).

**Gustavia** clade (Mori, 1979b)—the growth form of species of Gustavia is variable; some species are pachycalycauls that can be unbranched (e.g., G. monocaulis S. A. Mori [1976: 289]) or with several orders of branching (e.g., G. superba (Kunth [1825: 426]) O. Berg (1854: 444), with very thick twigs (greater than 10 mm diam.) and long leaves (>50 cm long); some species are leptocalycauls with medium-sized leaves, robust twigs (from 5–10 mm diam.), and densely ovate crowns; and others are leptocalycauls with more slender twigs (usually 5 or less mm diam.), relatively small leaves and dense but not necessarily ovate crowns. The pachycalycaul species usually have very long leaves that approximate the lengths, but do not usually surpass those of most species of Grias. The trunk is cylindrical to the ground in all species. Although eight petals (Fig. 3A) are most common in this genus, there can be as few as six (e.g., G. hexapetala (Aubl.) Smith [1811: 2] or, as many as 12[18] in G. romeroi S. A. Mori & Garcia-Barriga [1975: 51]). The androecia of all species of Gustavia are actinomorphic (Fig. 3A) and possess a thin, broad staminal tube (ca. 2 mm thick and 3–6 cm or more in diameter). The filaments arise from the rim of the staminal tube and are much longer than those of any other neotropical Lecythidaceae; however, the paleotropical Barringtonioideae have similar androecia. Gustavia is the only genus of Lecythidaceae that has apically poricidal anthers >2 mm long (Fig. 3G), which suggest buzz pollination (Boeke & Mori, 1987), pubescent ovary summits (the simple trichomes are sepalate), apically expanded placenta (Fig. 3H), and embryos with fleshy, irregular-shaped cotyledons. In addition, the fruits of Gustavia are indehiscent and are usually globose in shape (Figs. 3C, 3F). Seed sizes vary: the smaller ones with relatively thick seed coats and funicles surrounded by a thick, yellow or orangish, contorted aril (e.g., G. augusta Linnaeus [1775: 12, 17, 18], Fig. 3B) and the larger ones with membranous seed coats and inconspicuous funicles surrounded by a tubular aril (e.g., G. nana Pittier [1927: 5] subsp. rhodantha (Standley [1929: 239] S. A. Mori [1979: 173] and G. superba).

**Couroupita** clade (Prance, 1990a)—the growth form of the three species of this genus (Prance, 1990a) is intermediate between pachycalycaul and leptocalycaul types. The twigs are thick (ca. 5 mm diam.) and the leaves are tightly congested as in pachycalycauls. The trees have many orders of branching and the narrowly obovate leaves are medium-sized (usually 30–40 cm long) as in most other leptocalycauls. In addition the leaves often have tufts of trichomes in the axils between the midrib and the secondary veins abaxially. The trunk is cylindrical to the ground. The flowers possess six petals, the androecia are zygomorphic (Fig. 4A), and the stamens arise from a staminal ring (Figs. 4D, 4L), a character common to all zygomorphic species except those of Cariniana (see below). Several characters are found in all species of Couroupita but infrequently in other neotropical Lecythidaceae: the strictly cauline or ramiflorous inflorescences (Fig. 4E) are not found in other species of large trees although they do occur in the smaller trees of Grias, Gustavia, and some species of Eschweilera; the 6-locular ovary (Fig. 4C) of species of Couroupita also occurs consistently only in species of Gustavia related to G. hexapetala group; the presence of staminodes (Fig. 4D) is also found in all species of Corythophora, usually in species related to Lecythis pisonis Cambessèdes (1829: 377) and
FIGURE 2. The *Grias* clade. A–D. *G. longirachis* (Clark & Mori, 2000 for vouchers). E–J. *G. purpuripetala* (see Mori et al., 2010 for vouchers). A. Apical view of a flower. All species of this clade have four petals. B. Medial longitudinal section of a flower. All species of this clade have a thick and fleshy staminal tube with a lower and an upper chamber. In this species the lower chamber is very short. C. Cross-section of an immature fruit. All species of this clade have endocarp buttresses and usually have 4-locular ovaries. D. Fruit on the right and seed on the left. Note the endocarp buttresses showing in this dried fruit and the single seed with a very fragile seed coat. E. Large leaf characteristic of all species in this clade. F. Apical view of a flower on the left and cross-section of an ovary on the right. This flower is 3-locular but most likely it is a variant from the normal 4-locular ovary common to species of the genus. G. Medial longitudinal section of the androecium showing the stamens and the upper and lower chambers of the staminal tube. In this species the lower chamber is well developed. H. Medial longitudinal section of an ovary. All species of this clade have a few pendulous ovules from near the apex of the septum. This species appears to have a ring nectary but this characteristic is not apparent in all species of the clade. Drawings by B. Angell.
FIGURE 3. The *Gustavia* clade. A–D. *Gustavia augusta* (see Mori, 1995 for vouchers). E–F. *G. hexapetala* (see Mori & Prance, 1993 for vouchers). F. *G. elliptica* (see Mori & Lepsch-Cunha, 1995 for vouchers). G. *G. longifolia* (Cornejo 8092). A. Actinomorphic flower (note that the stamens arise from the rim of a broad, thin-walled staminal tube, a combination of features found only in this clade) and leaves. B. Seed with aril. At maturity the seed is black and the aril is yellow. Only a few species have a conspicuous aril such as found in this species. C. Fruit. The fruit is indehiscent. D. Longitudinal section of an androecium. E. Cross-section of an ovary. Note that the ovary is 6-locular and alate—within the *Gustavia* clade, these are features found only in a group of species related to the *G. hexapetala* group. F. Lateral view of a fruit of *G. hexapetala*. G. Stamen with poricidally dehiscent anther, a character found only in this clade. H. Medial longitudinal section of an ovary. Note that the ovules are inserted on apical, expanded placentae, features found only in this clade. Drawings A–C by B. Angell, D–E by C. A. Gracie, F by A. Tangerini, and G by C. Carollo Matos.
FIGURE 4. The Couroupita clade. A–J. C. guianensis. K–L. C. nicaraguarensis. A. Flower (Mori et al. 25755, photos only). B. Medial longitudinal section of an ovary (see Mori & Prance, 1990 for vouchers for B, C, and D). Note that the placentae are located on the septa in the middle of the locule. C. Cross-section of an ovary. Note that the ovary is 6-locular. D. Medial longitudinal section of an androecium. Note that there is an appendage-free area between the staminal ring and the androecial hood. E. A tree showing the cauline infructescences and the cannon-ball shaped indehiscent fruits (unvoucheded photo taken in Costa Rica). F. A mature fruit (unvoucheded photo). Note the faint ring near the apex of the fruit indicating where the calyx-lobes were attached—this is called the calycine ring. The pimple-like structure in the middle of the apex of the fruit is the remnant style. G. Cross-section of a fruit (see Mori & Prance, 1990 for vouchers for G and H). Note that the interior of the fruit consists of six wedges that represent the six locules of the ovary. H. Medial longitudinal section of a fruit. Note the seeds embedded in the pulp. I. A seedling with expanded foliaceous cotyledons (I and J voucheded by Mori & Kallunki 3263). J. Seedling just after pulling free from the seed coat. Note the foliaceous cotyledons. K. Flower (Hernández et al. 661). L. Medial longitudinal section of an androecium (see Fig. 35 in Mori & Prance 1990 for vouchers). Note there are appendages along the entire length of the ligule and, thus, this species has continuous stamens from the staminal ring to the end of the staminal hood. Line drawings by B. Angell. Photos A, I, and J. by S. A. Mori, photo E. Photo by C. A. Gracie, and photo K by F. Hernández.
others related to *L. corrugata* Poiteau (1825: 146); oxidation of flowers and fruits to bluish-green also occurs in the *L. pisonis* group and a few species of *Eschweilera* (e.g., *E. decolorans* Sandwith [1932: 214]); and foliaceous, opposite cotyledons also occur in *Cariniana* and *Couratari*. In contrast, bilamellar placentae attached throughout the middle of the locules (the *Lecythis hexapetala* group also has this type of placentation) (Fig. 4B); spherical (cannonball-like), indehiscent fruits (Fig. 4F) that fall to the ground at maturity, seeds embedded in fruit pulp (Figs. 4G, 4H), and pubescent seed coats (Tsou & Mori, 2002) are mostly limited to *Couroupita*.

*Allantoma* clade ([Prance, 1979a])—most species of this genus are understory to canopy, leptocal trees found in both lowland non-flooded and periodically inundated forests. The leaves have closely spaced percurrent secondary veins. Although other genera have percurrent secondary veins, they are usually more widely spaced than in *Allantoma*. The androecia are actinomorphic (Fig. 5A), the staminal tube, which can be long (e.g., *A. lineata*, Fig. 5B) or short (e.g., *A. decandra* [Ducke [1925: 153]]) S. A. Mori et al. [in Huang et al. 2008: 80], Fig. 5J), is thick and fleshy as in *Grias*, the stamens are reflexed (Figs. 5B, 5J) as they are in *Grias*, and the seeds possess a unilateral wing (Fig. 5F, 5M) as in species of *Cariniana*. The horizontally oriented ovules (at least in *A. lineata*) occur in vertically oriented locules from slightly expanded placentae along the entire length of the lower septum as seen in medial longitudinal sections. The seed wing is vestigial in the water-dispersed *A. lineata* and winged in *terra firme* species (e.g., *A. decandra*) (Fig. 5M), a feature that was observed by Ducke (1948) who recognized some of the species now placed in *Allantoma* as species of *Cariniana* (Huang et al., 2008). Characters that distinguish *Allantoma* from *Cariniana* are as follows: leaves with percurrent secondary venation versus usually reticulate secondary venation in *Cariniana*; five petals that are hooked at their apices (Fig. 5A) in contrast to six petals that are not hooked at their apices in *Cariniana* (Fig. 6E, L); and fleshy petals and androecia versus membranous petals and androecia in *Cariniana*.

*Cariniana* clade—([Prance, 1979b; Huang et al., 2008])—most species of this genus are very large, canopy or emergent trees (with the exception of the savanna species *C. rubra* Gard. ex Miers [1874: 288], which reaches only 15 m in height), leptocal trees with trunks that are cylindric to the ground, fissured external bark, thick outer bark, and reddish inner bark. *Cariniana* species are the most sought after Lecythidaceae for timber by loggers, who prefer that of *albarco* (*C. pyriformis* Miers [1874: 290]) from northwestern South America (Colombia and Venezuela) and species of *jequitiba* (*C. estrellensis* Raddi [1820: 403] Kuntze [1898: 89] and *C. legalis* [Martius [1837: 88]) Kuntze [1898: 89]) of the coastal forests of eastern Brazil. The flowers in this clade have six membranous petals (Fig. 6E, 6L), zygomorphic androecia (Figs. 6A, 6F, 6M), and leaf-like cotyledons. Obliquely upward oriented ovules (at least in *C. micrantha* Ducke [1930: 175]) are found in vertically oriented locules along the entire length of the lower septum, the ovules arise from expanded placentae that are wider at the base than at the apex of the lower septum. For the most part, the genus differs from all others by its relatively small flowers (usually <2.5 cm diam.); membranous petals (only the petals of *C. ianeirensis* R. Knuth [1939: 38] are somewhat thicker); a thin-walled staminal tube that is extended on one side to make the androecium zygomorph (Figs. 6A, 6F, 6M); all other Lecythidaceae with zygomorph androecia possess a prolongation that arises from a fleshy staminal ring [Tsou & Mori, 2002]); and stamens that arise from all over the inside of both the staminal tube and the extension of the tube (Figs. 6F, 6M, 6N). We have also noted that at least some species are pubescent on the filaments and the inside of the staminal tube (Fig. 6N), a feature not known to us in other species of Lecythidaceae. To distinguish the two types of zygomorph androecia we call the *Cariniana* type “staminal tube zygomorphic” whereas the type that arises from a low staminal ring is called “staminal ring zygomorphic.” The degree of zygomorphy varies among species of *Cariniana*, e.g., the staminal tube extension is scarcely developed in *C. parvifolia* S. A. Mori (1995: 8) (Fig. 6E) and pronounced in *C. micrantha* (Fig. 6A) and *C. penduliflora* [Prance [in Prance & Anderson 1976: 298] (Fig. 6N).

*Couratari* clade (Prance, 1990b)—most species of this genus are very large, canopy or emergent trees with tall or short buttresses found in lowland rain forests; the exceptions are those that occur in flooded forests (e.g., *Couratari riparia* Sandwith [1955: 473], *C. sandwithii* [Prance 1981:19] and *C. tenuicarpa* A. C. Smith [1936:158]). The flowers in this clade possess six petals, zygomorphic androecia (Figs. 7A, 7B, 7I), a staminal ring lip (Figs. 7J, 7I), and have fewer stamens (Fig. 7I) than most other zygomorphic neotropical Lecythidaceae. In species of *Couratari*, there are vestigial stamen nectaries which are also present in all species of *Eschweilera*; the ovaries are 3-locular (Fig. 7D), a feature also found consistently in species of *Cariniana*; at least some of the species possess stylar collars, a character that also occurs in the *Lecythis pisonis* clade; the locules are vertically oriented and the ovules arise from placentae that cover the entire length of the lower septum; the fruits are very narrowly campanulate (i.e., they taper toward the base, Fig. 7E) and not as cylindrical, as they are in species of *Allantoma*, or broadly campanulate, as they are in some species of *Cariniana* and *Corinthophora*; the columella is tack-shaped (i.e., possesses a long, woody prolongation that extends into the fruit, Fig. 7F); and the cotyledons are leaf-like and opposite (Fig. 7H), which also occur in species of *Cariniana* and *Couroupita*. Two features are present in species of *Couratari* that are not present in any other clade.
FIGURE 5. The Allantoma clade. A–G. *A. lineata* (see Prance & Mori, 1979 for vouchers for all but G based on Prance et al. 11618). H–M. *A. decandra* (H–J based on Ducke, 1925, vouchers not cited; K–M based on Krukoff 7193). A. Entire flower. All species of *Allantoma* have 5 petals. Note that the petals are curved downward at apices. B. Medial longitudinal section of a flower. Note that the stamens turn downward and that they are inserted both on the rim of the staminal tube as well as on the inside of the tube. C. Cross-section of the ovary. Note that it is usually 4-locular. D. Fruit base. Note that it is cylindrical throughout. E. Operculum with its long, tapered columella (= tack-shaped). F. Immature seed. Note that it has a vestigial unilateral seed wing. G. Mature seed. Note that the vestigial wing has disappeared and that there is a notch where it was once attached. H. Bud. I. Bud with petals removed showing the broadly triangular calyx-lobes and the longest stamens. J. Androecium cut and spread open. Note that there are two sets of stamens, an alternating long set and a shorter set, and that both sets arise from the staminal tube rim and curve downward. K. Fruit base. Note that it tapers at the base and is slightly costate (at least when the fruits are dry). L. Operculum with its long columella. M. Mature seed with a well-developed unilateral wing at maturity. Drawings A–F by H. M. Fukuda and G, K–M by C. Carollo Matos. The artist for H–J is not known.
of the family. One is an androecium that coils inward and then outward to form an external flap (Fig. 7B, 7K). Slight invaginations of the androecial hood also occur in species of other clades (e.g., Couroupita subsessilis Pilger [1905: 163], Eschweilera cyathiformis S. A. Mori [1989: 20], and E. ovalifolia (DC [1828:292]) Niedenzu [1892: 40] but these taxa do not have a fully developed external flap as in all species of Couratari. We hypothesize that the well-developed external flap of Couratari protects the nectar from robbers such as trignonid bees. In support of this suggestion, we have observed that neotropical Lecythidaceae without external flaps often have their androecial hoods perforated by nectar robbers while the hoods of relatively few flowers of species of Couratari are perforated. The second defining character is seeds with a circumferential wing (Fig. 7G), which we hypothesize to be derived from flattened seeds because the wings and seed have the same seed coat anatomy (Tsou & Mori, 2002).

**Key to hypothesized clades**

This key is based on the clades recovered by Mori et al. (2007), Huang (2011), and Huang et al. (2015). Some of the clades represent well-established genera for which we envision no further changes and others have been previously included in a more widely circumscribed Lecythis and Eschweilera (Mori and Prance, 1990).

The terms used in the key are illustrated in the figures presented in this paper, the illustrations in another paper in this volume by Huang et al. (2015), and in an online specialized glossary of Lecythidaceae available on the Lecythidaceae Pages (Mori et al., 2010 onward).

Images in Huang et al (2015) are cited in the key to help the reader understand the terminology of the clades not discussed in this paper (i.e., the Bertholletia clade).

1. Flowers with actinomorphic (radially symmetric) androecia .................................................................2
- Flowers with zygomorphic (bilaterally symmetrical or monosymmetric) androecia .........................................................4

2. Staminal tube thin, membranous, broad (≥3 cm diam.), stamens >500, all arising from rim of staminal tube, filaments terete in cross-section, anthers > 1.5 mm long, dehiscence poricidal at apex. Fruits indehiscent, subglobose to globose, not woody or thin and somewhat woody. Seeds < 10 per fruit, but usually >1; cotyledons present, fleshy, irregularly shaped ........ Gustavia (Fig. 3)
- Staminal tube thick, fleshy, narrow (<1.5 cm diam.), stamens <100, arising from rim and inside of staminal tube, filaments angular in cross-section, anthers <1.5 mm long, dehiscence lateral. Fruits indehiscent or dehiscent, fusiform, pyriform, or cylindrical (not globose), not woody (Grias) or woody (Allantoma). Seeds 1 or >20 per fruit; cotyledons absent or fleshy, when fleshy not irregularly shaped..........................3

3. Petals 4, the apices not hooked ; staminal tube 2-chambered (the lower surrounding the ovary, the upper flared outward or arched when viewed in medial longitudinal section). Fruits very broadly fusiform or pyriform, indehiscent, endocarp with butresses). Seeds 1 per fruit, not winged, the seed coat smooth, thin (ca. 1 mm thick), embryo shorter than wide.................Grias (Fig. 2)
- Petals 5, the apices hooked, staminal tube 1-chambered. Fruits cylindrical, dehiscent, endocarp without butresses. Seeds >20 per fruit, unilaterally winged (the wing sometimes vestigial in riverine species), the seed coat rough, thick (>2 mm thick), embryo longer than wide ..............................................................Allantoma (Fig. 5).

4. Flowers <2 cm diam., staminal tube present, the tube thin, membranous, extended on one side (i.e., staminal tube zygomorphic), fertile stamens on inside of tube and on rim of tube extension. Fruits pyriform or very narrowly turbinate. Seeds with unilateral wing; cotyledons leaf-like ..........................................................................................Cariniana (Fig. 6).
- Flowers >2 cm diam., staminal ring present, the ring thick, fleshy, prolonged on one side (i.e., staminal ring zygomorphic), fertile stamens on staminal ring. Fruits usually globose, not pyriform or very narrowly turbinate. Seeds without wings or with wing surrounding entire seed; cotyledons absent or leaf-like ........................................5

5. Androecial hood flat, without vestigial stamens curved inwards or without coils ..............................................6
- Androecial hood not flat, with vestigial stamens and/or staminodes curved inward or with one, two, or three coils ...............9

6. Stems thick (>5 mm diam.), slightly swollen in area of leaf attachment, petiole scars touching one another. Inflorescences cauleine (on main trunk or low branches in crown), at least some rachises > 20 cm long. Flowers with 6-locular ovary, ovules on placenta in middle of locules as viewed in medial longitudinal section. Fruits indehiscent, cannon-ball like, falling intact from tree at maturity. Seeds embedded in pulp that oxidizes bluish-green when exposed to air, the seed coat with long trichomes; cotyledons leaf-like..........................................................Couroupita (Fig. 4)
- Stems usually thinner or, if thicker, the twigs not swollen in area of leaf attachment and the petiole scars usually not touching one another. Inflorescences seldom cauleine or, if cauleine, the rachises < 20 cm long. Flowers usually 2-, 3-, or 4-locular, ovules...
on placenta inserted on lower septum toward base of locule or on horizontally expanded placenta that make them appear as if arising from base of locule. Fruits usually dehiscent, not cannon-ball like, usually not falling from tree at maturity. Seeds not embedded in pulp, the seed coat without trichomes; cotyledons not differentiated.---------------------7

7. Androecial hood tightly pressed against summit of ovary; hypanthium smooth. Inflorescence rachises with horizontally oriented scales. Fruits campanulate or cylindric .......................................................... "Corythophora" (Fig. 10 in Huang et al., 2015). ..

- Androecial hood open (except for Lecythis corrugata); hypanthium smooth, rugose or tuberculate. Inflorescence rachises usually without horizontally oriented scales. Fruits globose or conical ..........................................................8

8. Flower and fruit parts never turning bluish-green when bruised. Appendage-free ligule with flanges (except for L. corrugata), hypanthium and pedicels rugose or tuberculate; style without collar. Fruits conical, < 5 cm diam., with rugose or tuberculate exterior. Seeds not markedly sulcate, aril relatively small, less than one-half length of seed .........................................................."Lecythis pisonis" clade (Fig. 4 in Huang et al., 2015). ..

- Flower and fruit parts usually turning bluish-green when bruised. Appendage-free ligule without flanges, hypanthium smooth, style with collar. Fruits globose, > 5 cm diam., with smooth exterior. Seeds markedly sulcate, aril very large, more than one-half length of seed .........................................................."Lecythis chartacea" clade (Fig. 14 in Huang et al., 2015). ..

9. Androecial hood with external flap, stamens usually < 60, the filaments filiform. Fruits cylindric to very narrowly campanulate, thin-walled (< 3 mm thick) (Fig. 7E), columella of operculum tack-shaped. Seeds flattened, surrounded by wing, cotyledons leaf-like: .........................................................."Couratari" (Fig. 7). ..

- Androecial hood without external flap, stamens usually > 70, at least some of filaments clavate or gradually increasing in diameter from base to apex. Fruits usually not narrowly campanulate, thicker-walled (> 3 mm thick), columella of operculum absent or poorly developed. Seeds not winged, cotyledons not developed ..........................................................10

10. Petals often pressed against sides of androecial hood. Androecial hood with vestigial stamens and staminodes curved inward, the hood not coiled as seen in medial longitudinal section. ........................................................................................................11

- Petals infrequently pressed against sides of androecial hood. Androecial hood with one, two, or three coils as seen in medial longitudinal section. ........................................................................................................13

11. Calyx lobes 2. Fruits secondarily indehiscent (opercular opening ca. 1 cm diam.), perfectly globose. Seeds larger than opercular opening, trapped inside when fruit falls, seed coat boney, harder and thicker than that of other species of Lecythidaceae, aril absent .........................................................."Bertholletia excelsa" clade (Fig. 7 in Huang et al., 2015) ..

- Calyx lobes 6. Fruits usually dehiscent (opercular opening > 3 cm diam.), rarely indehiscent, not perfectly globose. Seeds smaller than opercular opening, seed coat not boney, aril present, sometimes vestigial. ........................................................................................................12

12. Inflorescence with rachises often with horizontally oriented scales. Seeds with thin seed coat (< 1 mm thick), often breaking free from embryo when dried, venation reticulate, plane or impressed ..........."Lecythis poiteau" Poit. clade (Fig. 6 in Huang et al., 2015). ..

- Inflorescence rachises without horizontally oriented scales. Seeds with thicker seed coat (>2 mm thick), not breaking free from embryo when dried, major veins running length of seed (i.e., not reticulate), salient .........................................................."Lecythis chartacea" O. Berg clade (Fig. 8 in Huang et al., 2015). ..

13. Androecial hood with one coil as seen in medial longitudinal section, vestigial stamen nectaries absent. Aril basal. Ovary with more than 1 row of ovules ..........................................................14

- Androecial hood with two or three coils as seen in medial longitudinal section, vestigial stamen nectaries present at apex of coils, ovary with 1 row of ovules. Aril lateral or spreading over entire seed ..........................15

14. Vestigial stamens only on exterior surface of coil. Seeds with major veins usually plane with seed surface. Ovary usually 4-locular. Seeds with long, basal aril (≥1 cm long). .........................................................."Lecythis ollaria" Loefl. clade (Fig. 5 in Huang et al., 2015). ..

- Vestigial stamens on both exterior and interior surfaces of coil. Seeds with major veins impressed. Ovary usually 2-locular. Seeds with short, basal aril (<1 cm long). ............................................................................................................ Eschweilera tetrapetala S. A. Mori clade (Fig. 13 in Huang et al., 2015). ..

15. Androecial hood with two coils as seen in medial longitudinal section. Aril lateral but not overlapping ends of seeds ..........................Eschweilera parvifolia Mart. ex DC. clade (Fig. 15 in Huang et al., 2015). ..

- Androecial hood with three coils as seen in medial longitudinal section. Aril spreading over entire seed or lateral with ends overlapping ends of seeds .........................................................."Eschweilera integrifolia" (Ruiz & Pav. [vol. 8: 529] ex Miers [1874: 225]) R. Knuth (1939: 97) clade (Fig. 11 in Huang et al., 2015).
Conclusions

We conclude that the six clades of Lecythidaceae treated in this paper represent monophyletic groups that merit continued recognition as the following genera: Allantoma, Cariniana, Couratari, Couroupita, Grias, and Gustavia. The morphological features described and illustrated for each of these clades facilitate their identification to clades. In addition, molecular data (Mori et al., 2007) confirm this conclusion for Grias, Gustavia, Couroupita, and Couratari (Fig. 1) and Huang et al. (2008) make a strong case for recognizing Cariniana and Allantoma as distinct genera. In this scenario, Couroupita is basal to the remaining zygomorphic-flowered species (the Bertholletia clade) and the actinomorphic-flowered Allantoma is nested within what is otherwise a zygomorphic-flowered clade (Fig. 1). Further study is needed to resolve the relationships of the Cariniana, Allantoma, and Couratari clades.

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References


