



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 Napoleoniaeoidae) 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 Schönenberger *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), Napoleoniaeoidae, Scytopetaloidae, Foetidioideae, and Lecythidoideae (Morton, 1998).

Others have treated the Napoleoniaeaceae (Prance, 2004) and Scytopetalaceae (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., Barringtonioideae), characters that could be used to separate them as families. Two other options would be to recognize all clades as separate families, Napoleoniaeaceae, Scytopetalaceae, Foetidiaceae, 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 *trnL-F* 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.

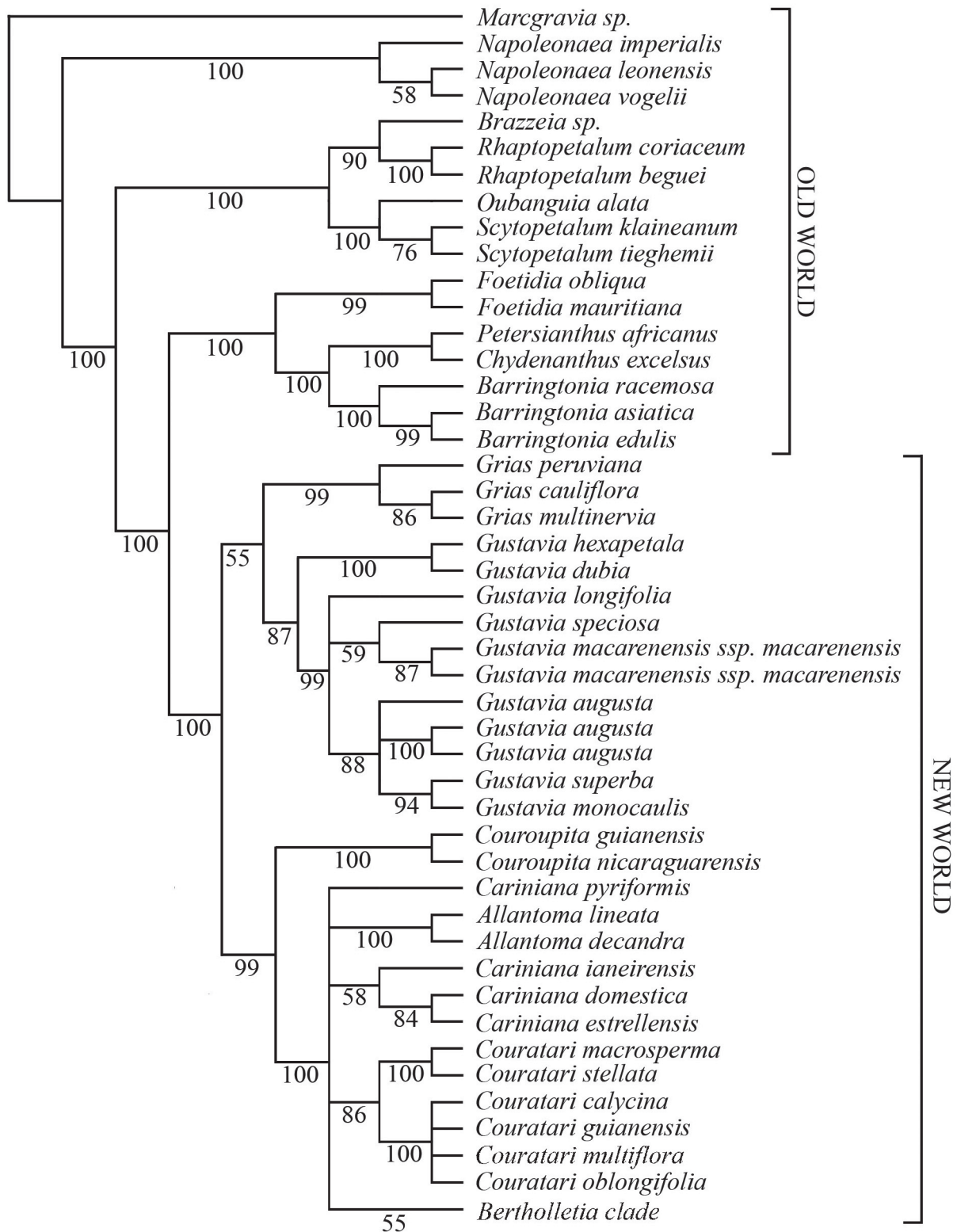


FIGURE 1. Part of a jackknife tree generated using Xac (Farris, 1997) which is based on a combination of *ndhF* and *trnL-F* sequences. Only the clades treated in this paper are shown in this cladogram (Mori *et al.*, 2007). The families and subfamilies making up the Lecythidaceae and its close relatives discussed in this paper and the genera representing them are the following: family Napoleonaeaceae (*Napoleonaea*), family Scytopetalaceae (*Brasseia*, *Rhapsopetalum*, *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 pachycaulous 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 placentae 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 pachycauls that can be unbranched (e.g., *G. monocalis* 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 leptocauls with medium-sized leaves, robust twigs (from 5–10 mm diam.), and densely ovate crowns; and others are leptocauls with more slender twigs (usually 5 or less mm diam.), relatively small leaves and dense but not necessarily ovate crowns. The pachycaul 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 septate), apically expanded placentae (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 pachycaul and leptocaul types. The twigs are thick (ca. 5 mm diam.) and the leaves are tightly congested as in pachycauls. The trees have many orders of branching and the narrowly obovate leaves are medium-sized (usually 30–40 cm long) as in most other leptocauls. 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

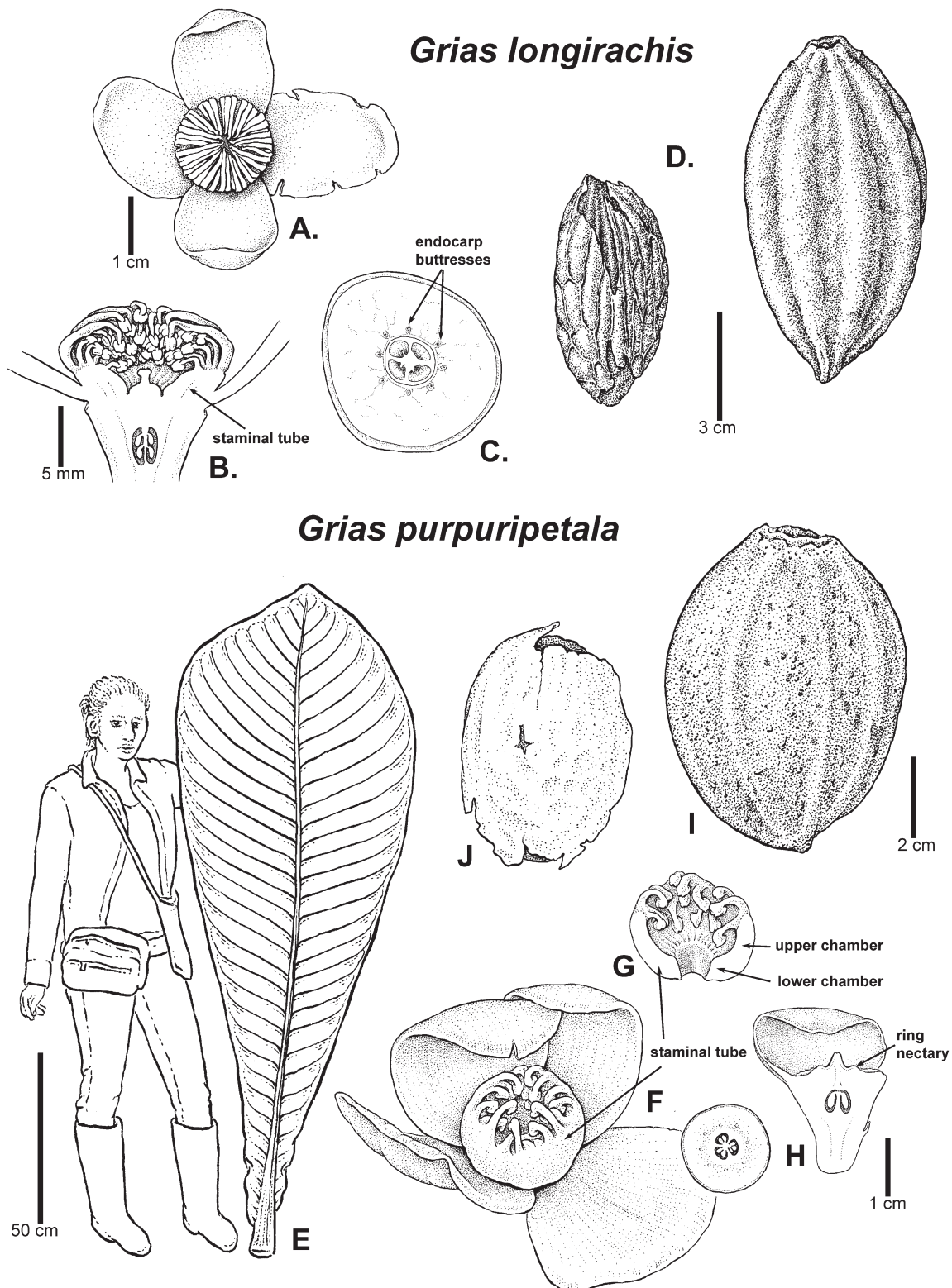


FIGURE 2. The *Grias* clade. A–D. *G. longirachis* (Clark & Mori, 2000 for vouchers). E–J. *G. purpuripetala* (see Mori *et al.*, 2010 for vouchers). A. Apical view of a flower. All species of this clade have four petals. B. Medial longitudinal section of a flower. All species of this clade have a thick 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.

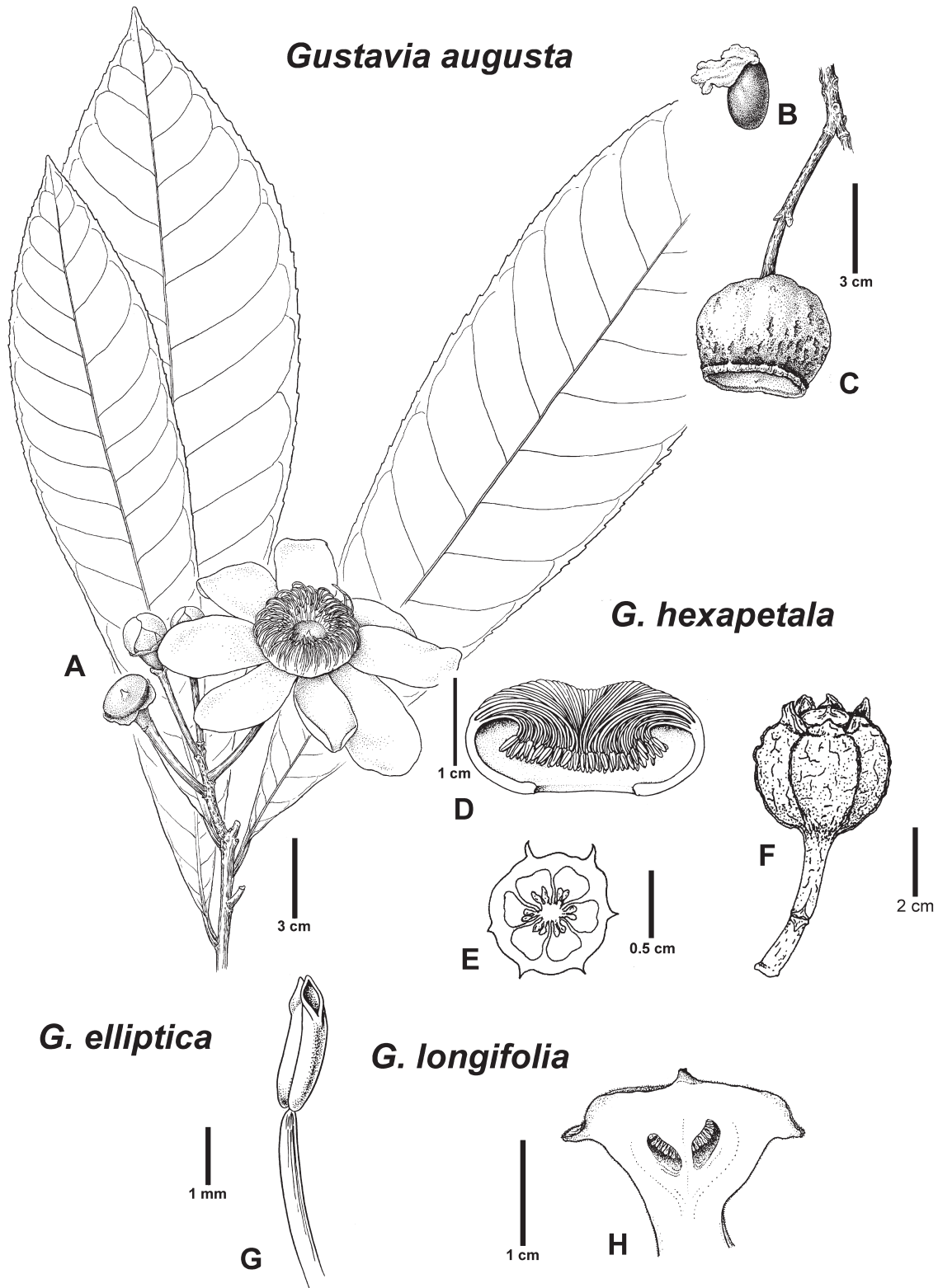


FIGURE 3. The *Gustavia* clade. A–D. *Gustavia augusta* (see Mori, 1995 for vouchers). E–F. *G. hexapetala* (see Mori & Prance, 1993 for vouchers). F. *G. elliptica* (see Mori & Lepsch-Cunha, 1995 for vouchers). G. *G. longifolia* (Cornejo 8092). A. Actinomorphic flower (note that the stamens arise from 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.

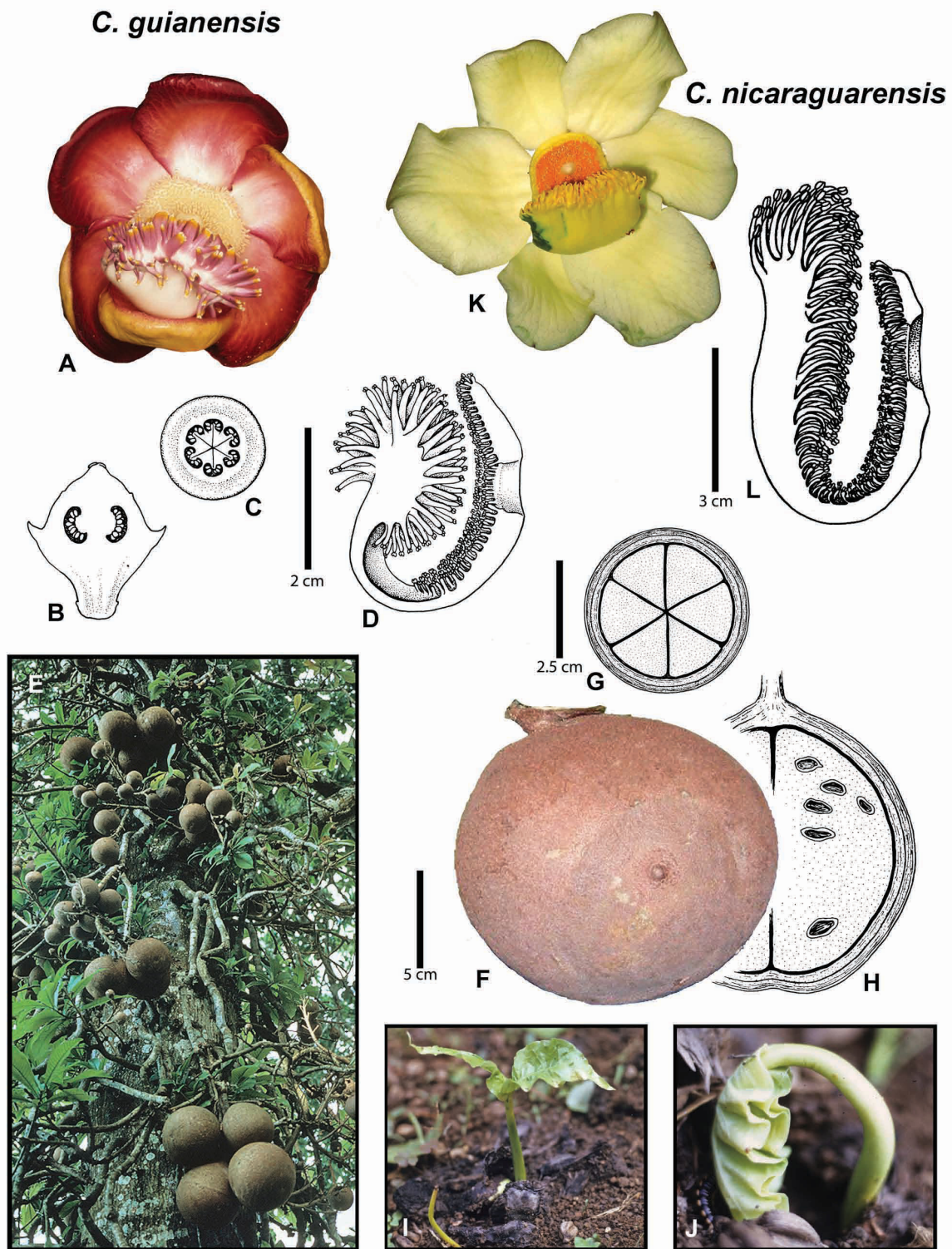


FIGURE 4. The *Couroupita* clade. A–J. *C. guianensis*. K–L. *C. nicaraguarens*. A. Flower (Mori *et al.* 25755, photos only). B. Medial longitudinal section of an ovary (see Mori & Prance, 1990 for vouchers for B, C, and D). Note that the placentae are located on the septa in the middle of the locule. 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 (unvouchered photo taken in Costa Rica). F. A mature fruit (unvouchered 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 vouchered by Mori & Kallunki 3263). J. Seedling just after pulling free from the seed coat. Note the foliaceous cotyledons (I and J vouchered by Mori & Kallunki 3263). 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, leptocaul 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), leptocaul trees with trunks that are cylindrical 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 zygomorphic (Figs. 6A, 6F, 6M; all other Lecythidaceae with zygomorphic 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 zygomorphic 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, leptocaul 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. 7I, 7J), 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 styler 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 *Corythophora*; 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

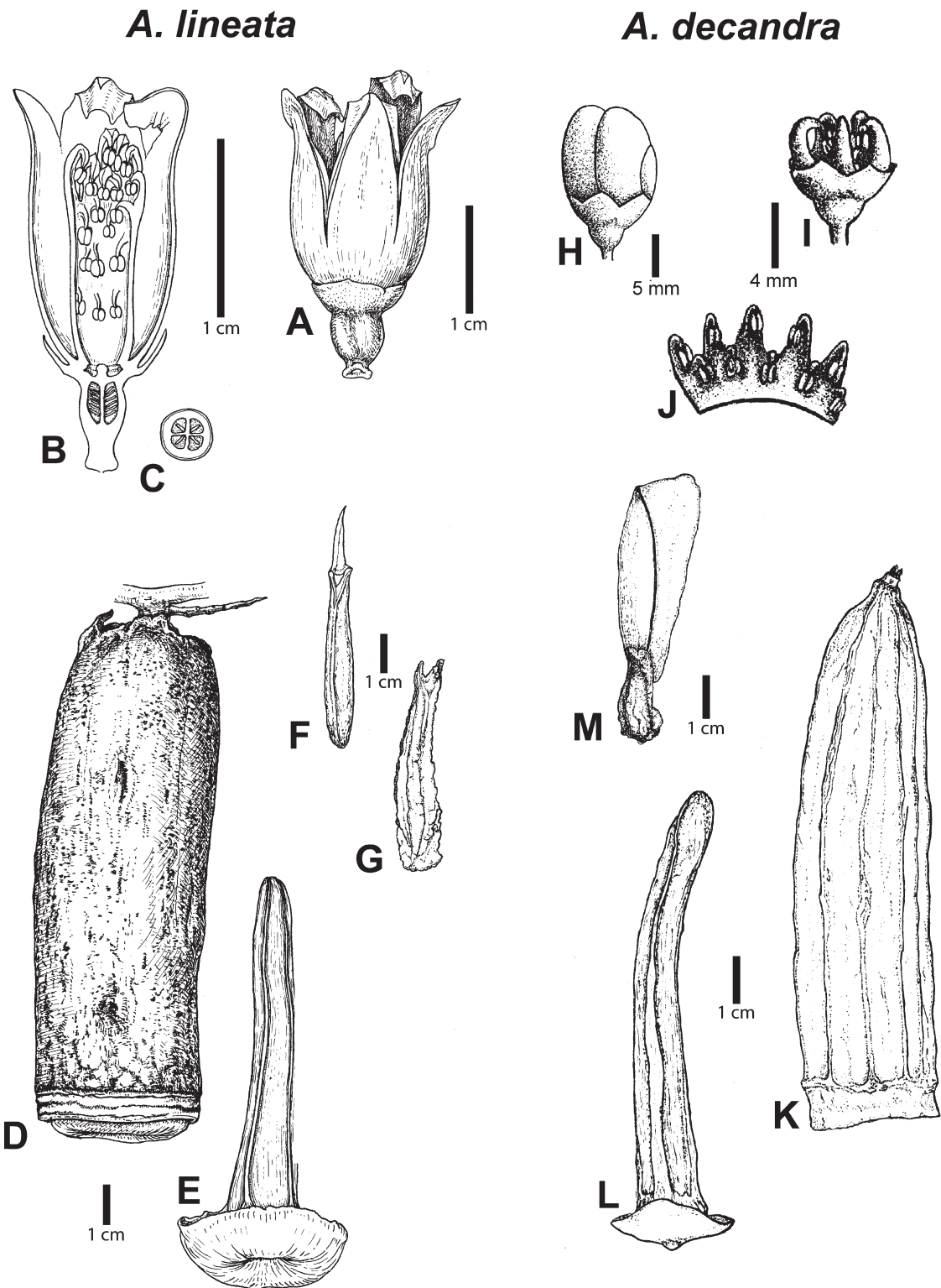


FIGURE 5. The *Allantoma* clade. A–G. *A. lineata* (see Prance & Mori, 1979 for vouchers for all but G based on Prance *et al.* 11618). H–M. *A. decandra* (H–J based on Ducke, 1925, vouchers not cited; K–M based on Krukoff 7193). A. Entire flower. All species of *Allantoma* have 5 petals. Note that the 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.

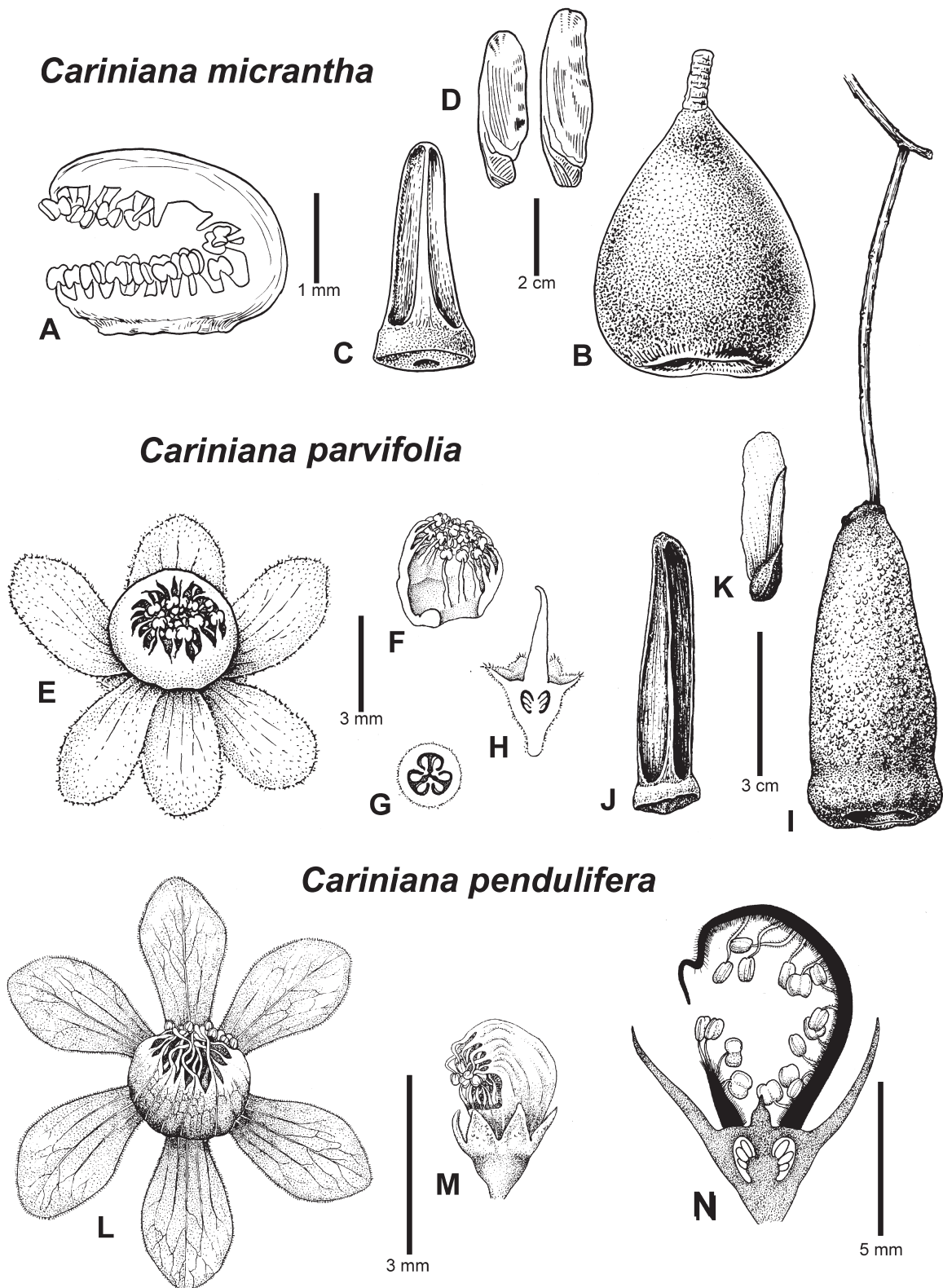


FIGURE 6. The *Cariniana* clade. A–D. *C. micrantha* (see Mori & Lepsch-Cunha, 1995 for vouchers). E–K. *C. parvifolia* (see Mori, 1995 for vouchers). L–N. *C. pendulifera* (see Prance in Mori & Prance, 1979 for vouchers). A. Lateral view of an androecium. This species has a very short staminal tube. B. Lateral view of a turbate fruit. C. Operculum with its long columella. D. Seeds with unilateral wings, which adapts the seeds for wind dispersal. E. Apical view of a flower. All species of *Cariniana* have six petals. F. Medial section of an androecium. This species has a staminal tube extension. G. Cross-section of a 3-locular ovary. All species of this genus are predominantly 3-locular. H. Medial section of an ovary showing the long, erect style and placentation on a slightly expanded lower septum. I. Lateral view of a fruit. J. Lateral view of an operculum and its columella. K. Seed with a unilateral wing. The line running through the wing is thought to be the funicle. L. Apical view of a flower. M. Lateral view of a flower with the petals removed. The staminal tube and staminal tube extension are well developed. N. Lateral view of a medial longitudinal section of a flower. Drawings A–D by A. Tangerini, E–K by B. Angell, and L–N by B. Moyer.

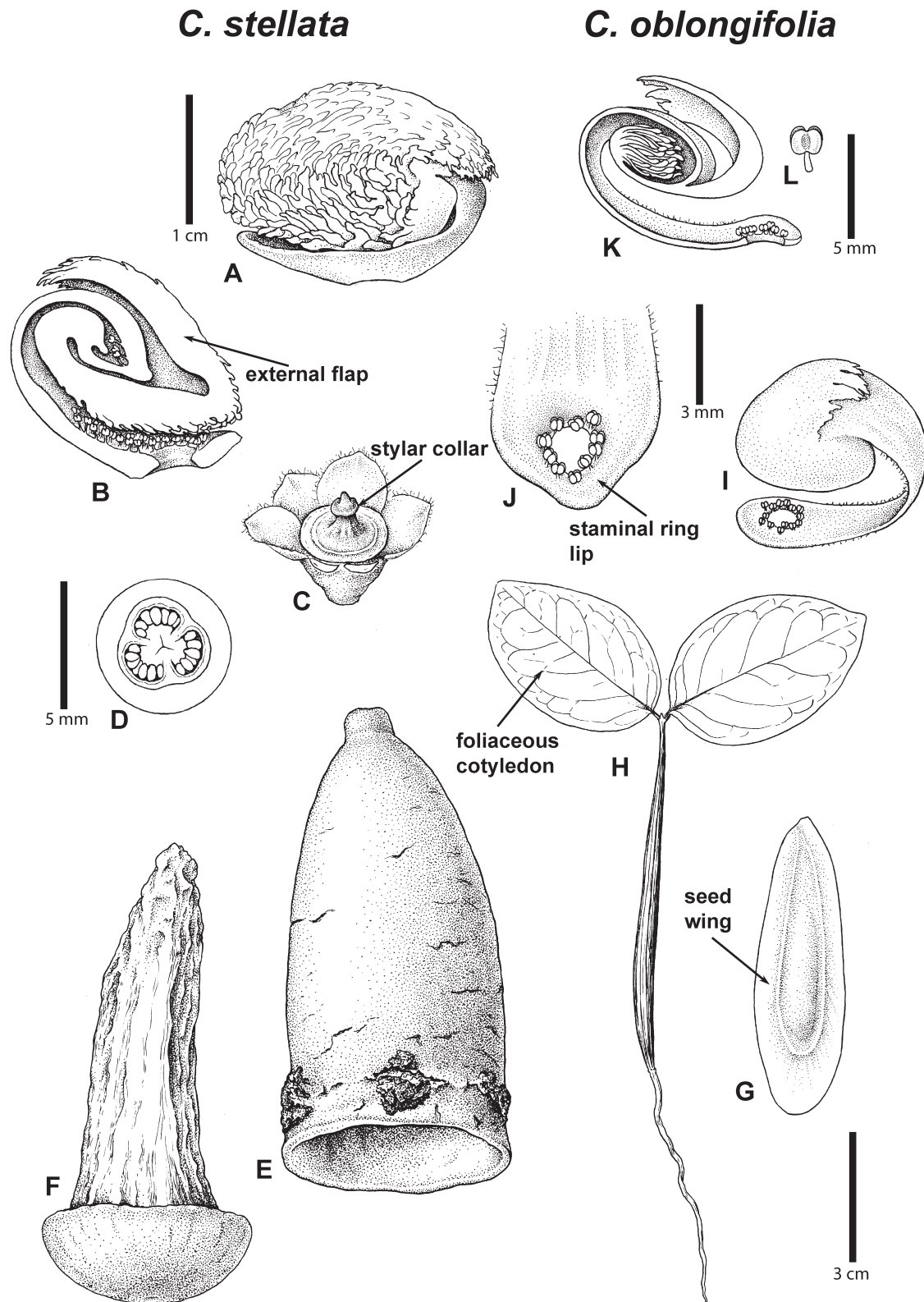


FIGURE 7. The *Couratari* clade. A–H. *C. stellata* (see Mori & Prance, 1990 for vouchers). I–L. *C. oblongifolia* (Fróes 1763). A. Androecium. Note the echinate exterior of the androecial hood. B. Medial longitudinal section of an androecium. Note the external flap. C. Lateral view of an ovary with two of the six calyx-lobes removed. Note the stylar collar. D. Cross-section of a 3-locular ovary which is characteristic of all species of *Couratari*. E. Base of a fruit. F. Operculum. Note the long columella. G. Seed with circumferential wing. H. Seedling with flattened stem and foliaceous cotyledons. I. Androecium. J. Staminal ring. Species of *Couratari* have fewer stamens than any other species of zygomorphic-flowered Lecythidaceae. Note the staminal ring lip. K. Medial longitudinal section of an androecium. Note the vestigial stamen nectaries at the apex of the coil. *Eschweilera* sensu lato is the only other genus with vestigial stamen nectaries. L. A stamen. Note the very short filament. Drawings by Bobbi Angell.

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 trigonid 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) androecia2
- Flowers with zygomorphic (bilaterally symmetrical or monosymmetric) androecia4
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 buttresses). 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 buttresses. 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-like5
5. Androecial hood flat, without vestigial stamens curved inwards or without coils6
- Androecial hood not flat, with vestigial stamens and/or staminodes curved inward or with one, two, or three coils9
6. Stems thick (>5 mm diam.), slightly swollen in area of leaf attachment, petiole scars touching one another. Inflorescences cauline (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 petioles scars usually not touching one another. Inflorescences seldom cauline or, if cauline, the rachises < 20 cm long. Flowers usually 2-, 3-, or 4-locular, ovules

- on placentae inserted on lower septum toward base of locule or on horizontally expanded placentae 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 cylindrical*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 conical8
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 corrugata* clade (Fig. 14 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 pisonis* clade (Fig. 4 in Huang *et al.*, 2015).
9. Androecial hood with external flap, stamens usually < 60, the filaments filiform. Fruits cylindrical 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 developed10
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 Lecythydaceae, 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 poiteaui* 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 ovules14
- 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 seed15
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.

Acknowledgements

The senior author is grateful to the NSF-OPUS program for supporting the synthesis of the research he and his collaborators have contributed to the systematics and ecology of the Brazil nut family. In addition, this research has received support for mapping New World Lecythidaceae as part of a collaborative grant (*Dimensions US-Biota-São Paulo: Assembly and evolution of the Amazon biota and its environment: an integrated approach*) provided by the US National Science Foundation (NSF), National Aeronautics and Space Administration (NASA), and the Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP). We thank Bobbi Angell for most of the line drawings and Alice Tangerini and H. M. Fukuda for other drawings as indicated in the figure legends. We are grateful to Fermin Hernández and Carol A. Gracie for permitting us to use their images of *Couroupita* as indicated on the plate and Xavier Cornejo for his review of the manuscript.

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