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OBSERVATIONS ON THE PHYTOGEOGRAPHY OF THE LECYTHIDACEAE CLADE (BRAZIL NUT FAMILY)

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ABSTRACT

The Lecythidaceae clade of the order Ericales is distributed in Africa (including Madagascar), Asia in the broadest sense, and South and Central America. Distribution maps are included for the Lecythidaceae clade as follows: family maps for Napoleonaeaceae and Scytopetalaceae; subfamily maps for the Barringtonioideae, Foetidioideae, and Lecythidoideae, and maps for the subclades of Lecythidaceae subfam. Lecythidoideae. The following topics are discussed: (1) the difficulties using herbarium specimens for studies of phytogeography; (2) the worldwide distribution of the Lecythidaceae clade; (3) the migration of Lecythidaceae from the Old into the New World or *vice versa*; (4) the phytogeography of the New World subclades of Lecythidaceae; (5) the ability of some New World subclades of Lecythidaceae to occupy very large distributions; (6) the adaptations of New World Lecythidaceae to different habitats; (7) the Pleistocene refuge hypothesis; (8) the evolution of high species diversity of the family in eastern Central America/northwestern South America; (9) the possible migration of species from the Guayana lowlands and western Amazonia into Central Amazonia after large wetland areas drained after the Amazon River began to flow eastward; (10), the migration of Lecythidaceae into the Atlantic Forest of Brazil from both northeastern and southwestern Amazonia or *vice versa*; and (11) the worldwide distribution of floral symmetry of the Lecythidaceae clade.

The New World Lecythidaceae (Brazil nut family), related to members of the Old World Lecythidaceae (Figs. 1–2B), are best known for the edible seeds of the Brazil nut (*Bertholletia excelsa* Bonpl.) and the cultivation of the cannonball tree (*Couroupita guianensis* Aubl.) as an ornamental in tropical and subtropical botanical gardens. The Lecythidaceae lineage in the New World is recognized by its showy and morphologically diverse flowers with either actinomorphic or zygomorphic androecia (Figs. 3–7). In addition, the fruits are woody and dehiscent in most genera of the New World, (e.g., in the *Lecythis pisonis* clade, Figs. 8, 10J), indehiscent and berry-like (*Gustavia* clade, Fig. 8A), drupe-like (*Grias* clade), and some species are secondarily indehiscent (e.g., *Bertholletia excels*a, Fig. 9, 10C). The spectacular flowers and fruits show adaptations for pollination and dispersal (Prance & Mori 1998) by biotic and abiotic agents. The family is ecologically dominant in lowland forests in many parts of the Amazon Basin (Steege et al. 2006) and present, but less frequent, in periodically flooded forests, cloud forests, and savannas. Species of the family, the Brazil nut tree in particular, are icons of Amazonian trees (Mori 2001). In general, if numerous species of Lecythidaceae are present in lowland forests it is likely that those forests have not been drastically disturbed by humans in the recent past (Mori et al. 2001).

This family forms a clade in the Ericales (Schöenberger et al. 2005), referred to as the Lecythidaceae clade in this paper. The combined analysis of *ndh*F and *trn*L-F genes by Mori et al. (2007) and morphological data supports recognizing Napoleonaeaceae (Prance 2004) and Scytopetalaceae (Appel 1996, 2004) as related but separate families from Lecythidaceae. Authors in Kubitzki (2004) accept the division of Lecythidaceae into the subfamilies Foetidioideae, Barringtonioideae (not Planchonioideae fide Thorne 2000), and Lecythidoideae (Prance & Mori 2004). See Map 1 for the worldwide distribution of Lecythidaceae and Table I for the current family classification and number of species in each clade.

Current phylogenies do not prohibit recognizing the three subfamilies as the families Foetidiaceae, Barringtoniaceae, and Lecythidaceae. An argument for this point of view is that there are no apparent anatomical, cytological, or morphological characters uniting them into a single family. In contrast, there are key characters that can be used to separate the three subfamilies as families (see key below). We have not made the change to recognize the three families because some characters need to be confirmed by more sampling (e.g., the orientation of the xylem and phloem in cortical bundles), and because of the lack of data for other characters (e.g., chromosome counts for *Crateranthus*, *Foetidia* and all Scytopetalaceae except *Asteranthos brasiliensis* and molecular sequences for more taxa, especially for *Crateranthus*, and *Petersianthus*). In this paper, Lecythidaceae, instead of Lecythidaceae subfam. Lecythidoideae, is used when the family is mentioned for taxa of the New World whereas the Lecythidaceae clade refers to the Napoleonaeaceae, Scytopetalaceae, and Lecythidaceae.

In a large-scale ecological study of lowland Amazonian forests (Steege et al 2006), the Lecythidaceae ranked third in total number of trees. They are surpassed in number by Fabaceae (legumes) and Sapotaceae (chicle family), but *Eschweilera coriacea* (DC.) S.A Mori. is ranked as the most abundant of all tree species in the study. In another paper, Steege et al. (2013) concluded that there are 390 billion individual trees ≥10 cm DBH and 16,000 species of trees of that size in Amazonia. The study found that 227 species (including all families) accounted for nearly half of all of the trees sampled and demonstrated how important relatively few species of Lecythidaceae and other families are for maintaining ecosystem services of Amazonian forests. Other studies have documented large numbers of individuals as well as high species diversity of Lecythidaceae, especially in central Amazonia (Mori & Lepsch-Cunha 1995) and the Guianas (Mori & Boom 1987). A 100-hectare plot inventoried by Mori et al. (2001) in central Amazonia found that 10% of the individuals and 6% of the species belonged to Lecythidaceae. In higher-elevation cloud forests, periodically flooded forests and dry habitats, New World Lecythidaceae are present but at much lower densities and species richness than in lowland non-flooded forests.

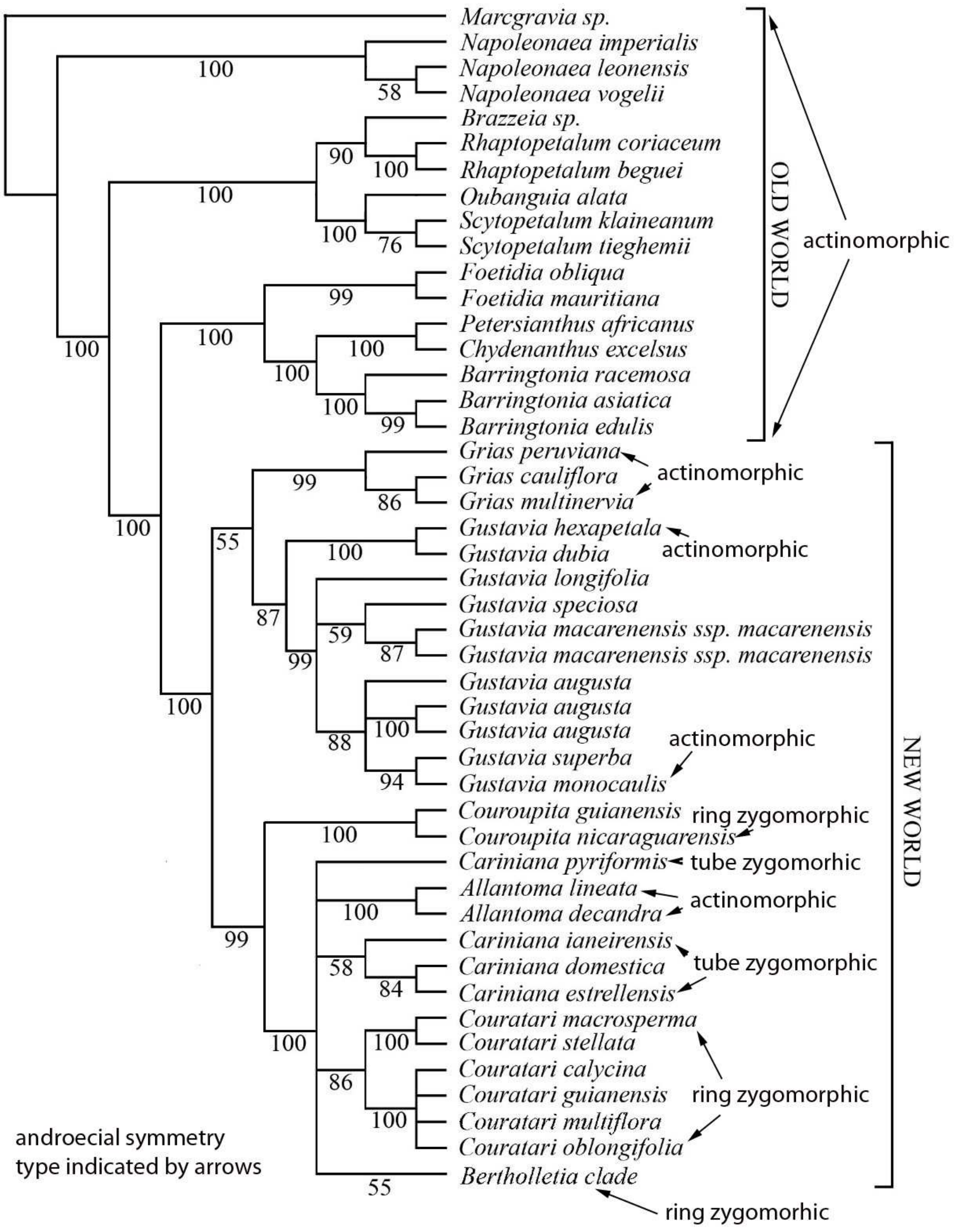

Figure 1. The non-*Bertholletia* grade. This cladogram includes most Old Word lineages (all with actinomorphic flowers), the actinomorphic-flowered genera of the New World, the only tubular zygomorphic-flowered genus in the clade, and two zygomorphic-flowered genera from the New World. The remaining zygomorphic-flowered genera in the New World belong to the *Bertholletia* clade (Figs. 2A–2B). The positions of the flower symmetry types are marked on the cladogram. This is a jackknife tree generated using Xac (Farris, 1997), which is based on a combination of *ndhF* and trnL-F sequences. From Mori et al. (2007) but modified by changing *Cariniana decandra* Ducke to *Allantoma decandra* (Huang *et al.* (2008).

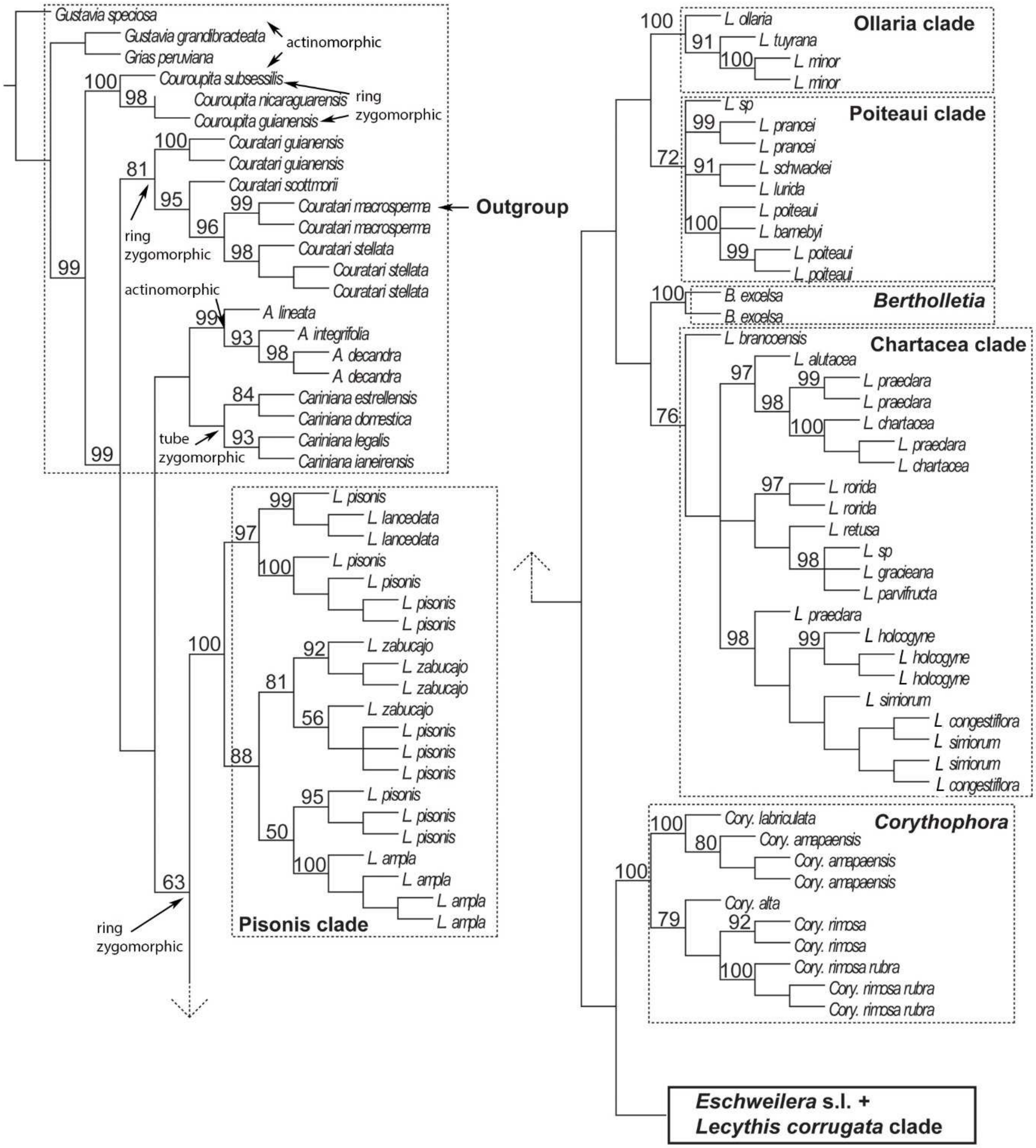

Figure 2A. The *Bertholletia* clade and its outgroup as recovered by Huang et al. (2015) are represented in this and Figure 2B. Old World species of the Lecythidaceae clade are not included in this cladogram. The cladogram is based on a strict consensus of 66 most parsimonious (MP) trees based on total evidence. Boot strap values (>50%) are given above the branches. The positions of the flower symmetry types are marked on the cladogram. *Eschweilera congestiflora* and *E. simiorum* have been changed to *Lecythis congestiflora* and *L. simiorum* to reflect the transfer of these species to *Lecythis*.

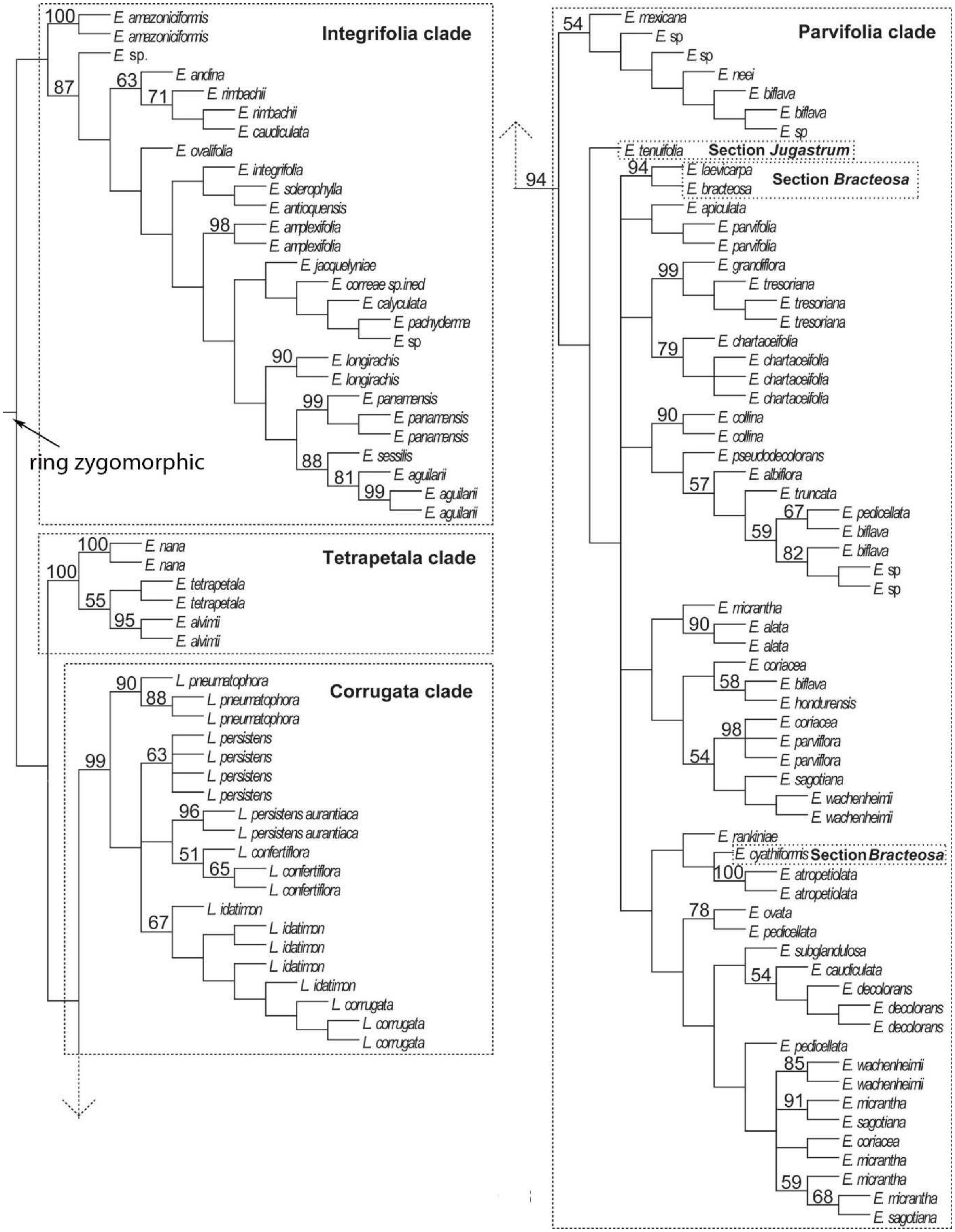

Figure 2B. Continuation from 2A.

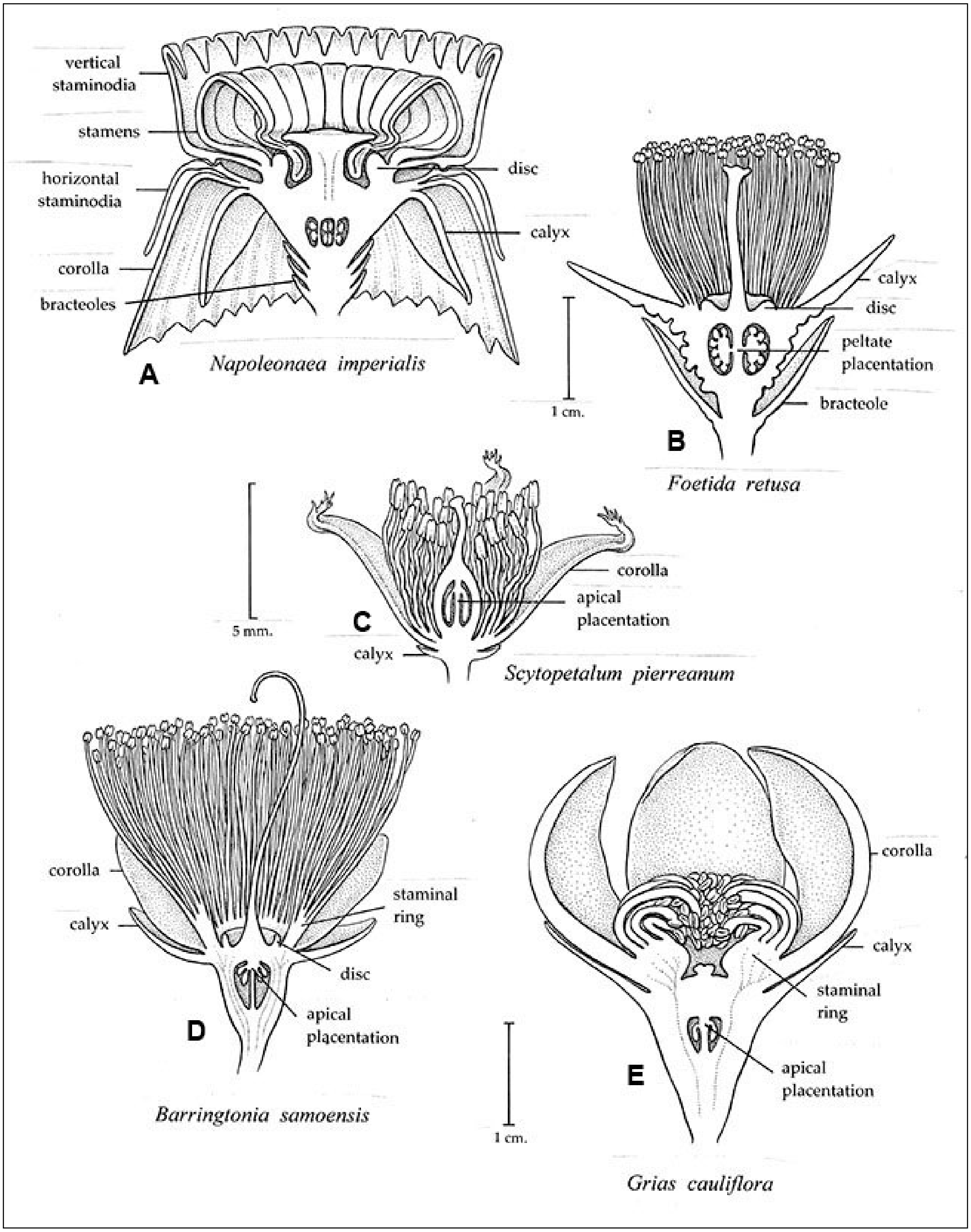

Figure 3. Flowers of the Lecythidaceae clade. A. Napoleonaeaceae. B. Foetidioideae. C. Scytopetalaceae. D. Barringtonioideae. E. Lecythidoideae. Drawings by B.Angell.

The distribution ranges of taxa of Lecythidaceae are driven by abiotic factors that isolate populations as well as create new habitats to which Lecythidaceae either adapt or become extinct. These factors include (1) formation of rivers, large lakes, or epicontinental seas and their changes over time; (2) uplift of mountains that create valleys and slopes, altitudinal differences, and different temperature regimes; and (3) soil moisture that ranges from always saturated (swamp forests), periodically saturated (along rivers), not saturated (non-flooded forests), and periodically dry areas (e.g., savannas and thorn scrub vegetation). Most species of New World Lecythidaceae grow in non-flooded forests but some have adapted to savanna, wet habitats, and cloud forests. Extreme rainfall, especially if a wet year is long and followed by consecutive wet years, can cause high mortality to species of Lecythidaceae adapted to lowland, non-flooded forests (Mori & Becker 1991). In contrast, we do not know of any species that grow in extremely dry areas such as the thorn-scrub vegetation (*caatinga*) in northeastern Brazil and the *Chacó* of Argentina or in cold areas such as the Araucaria Forests of Brazil and the *páramos* of the Andes.

In a paper about the origins of the flora of southern Brazil, Lyman Smith (1962) wrote

> “Ever since the first land plants evolved, the face of the earth has been changing constantly, so that we may safely assume that the flora of any given region today has arrived from somewhere else. In the case of land recently risen out of the sea, it is relatively easy to see whence its flora came, but in the case of a great center of distribution like the Amazon Basin it is difficult if not impossible to reconstruct its past.”

With the use of technologies not available to Lyman Smith, hypotheses about the geographical history of plants can now be addressed using up-to-date scientific tools. His paper represents the first step in understanding the historical biogeography of a region (eastern Brazil), whereas we present a review of the status of the phytogeography of the Lecythidaceae clade. Our goal is to make available what we have learned about this pantropical family of trees so that others can use our observations to develop and test hypotheses about the evolution and phytogeography of Lecythidaceae.

METHODS

Locality coordinates of Lecythidaceae were downloaded from The New York Botanical Garden’s Virtual Herbarium and other sources, such as the Global Biological Information Facility (GBIF 2016 accessed). The data were plotted using ArcGIS 10.4 (ESRI 2017). Cultivated specimens and specimens with incorrect coordinates (e.g., plotted in the incorrect hemisphere or in the ocean), were either corrected or filtered from the group. Metadata were taken from the collections and were assigned to the data points. The data were projected to the World Cylindrical Equal Area and were merged into one layer and saved in the project geodatabase. Using the ArcGIS geoprocessing tool Grid Index Features, a grid consisting of 10,000 km^2 units was created and overlaid on the data points, joining by both one-to-one and one-to-many relationships to count all points within a grid square (join count produced in one-to-one join) and to count all distinct variables within each grid square (one-to-many join). The one-to-many join enables the counting of distinct species per grid square by exporting the information from ArcGIS to an Excel spreadsheet and using the Pivot Tables tool in Excel to expedite the counting of distinct variables. Collection density and species richness are visualized using the spatially joined collection point data to grid square, based on distinct grid ID number (auto-populated by ArcGIS).

The families Napoleonaeaceae and Scytopetalaceae and the subfamilies Barringtonioideae, Foetidioideae, and Lecythidoideae are mapped to family and subfamily, respectively. In the maps of these lineages, a dot represents the presence of the family or subfamily at that locality. In contrast, the dots on the maps of the subclades of subfamily Lecythidoideae represent collections identified to species. In some maps (e.g., the maps of the *Gustavia* and the *Eschweilera parvifolia* clades) “heat maps” are used to indicate the number of species (number in grid) and number of collections (color of grid). This type of map is used because maps of high diversity clades become crowded and are difficult to read. Maps for all species can be viewed individually on the Lecythidaceae Pages (Mori et al. 2010). The New World subclades mapped in this paper are those recognized by Huang et al. (2015) and Mori et al. (2015).

In some maps, unrelated species grouped together illustrate congruent distributions. For example, different species with overlapping ranges in eastern Central America/northwestern South America suggest that geological events in this region caused similar distributions among numerous species (Map 23).

The presence of errors in the identification of collections (Mori 1998) and errors in mapping specimens make it difficult for botanists to accept or reject hypotheses based on data from some herbarium specimens (Steege et al. 2016). For example, Meyer et al. (2016) removed 53% of the 119 million collections studied because the discarded specimens lacked coordinates, the coordinates were incorrect, or the determinations were incomplete or obviously wrong. In this study, we corrected incorrect coordinates of some specimens (e.g., coordinates mapped in the sea) and did not include specimens with doubtful determinations.

There are two phylogenies referred to in this paper. Figure 1, based on Mori et al. (2007), represents the non-*Bertholletia* grade and its relationship with the *Bertholletia* clade. Thus, Figure 1 shows the relationships of Old and New World taxa and the placement of the *Bertholletia* clade. In the original publication by Mori et al. (2007) the non-*Bertholletia* grade was erroneously called a “clade” when it should have been called a “grade” because it is paraphyletic and the *Bertholletia* clade is derived from within it. The cladogram represented in Figures 2A–B includes only New World taxa (Huang et al. 2015).

Interactive Google maps are available for the New World species of Lecythidaceae on the Lecythidaceae Pages (Mori et al. 2010). These maps provide links to the data associated with the collections when the dot representing a collection is clicked.

RESULTS

The results of this project are the maps and their interpretations (Maps 1–27). The maps include families (e.g., Scytopetalaceae, Map 3), subfamilies (e.g., Lecythidaceae subfam. Lecythidoideae, Map 6), clades (e.g., *Lecythis pisonis* clade, Map 13), genera (e.g., *Gustavia*, Map 8), or species (e.g., *Allantoma*, Map 10). Descriptions and illustrations of the morphology of the clades belonging to the Lecythidaceae subfam. Lecythidoideae clade can be found in Huang et al. (2015) and Mori et al. (2015).

Key to the clades of Lecythidaceae *sensu lato*

1. Cortical bundles normally oriented (xylem inside phloem outside). Flowers with actinomorphic androecia and styles much shorter than stamens or flowers zygomorphic and styles shorter or only slightly projected beyond stamens; stigma small and not pentagonal; pollen tricolpate (Fig. 7A). Chomosome numbers x = 17. Native only to the Neotropics

.... **Lecythidaceae subfam. Lecythidoideae**

1. Cortical bundles normally or inversely oriented (xylem outside phloem inside). Flowers only with actinomorphic androecia and styles as long as or longer than the stamens, if shorter than stamens the stigma large and pentagonal; pollen tricolpate or syntricopate (Fig. 7B). Chromosome numbers x = 13, 16, 21, or unknown. All but one species (*Asteranthos brasiliensis* Desf. of the Scytopetalaceae) native to the Paleotropics.

2. Leaf blades with poorly defined secondary veins, the tertiary veins parallel to secondary veins. Calyx with 4, valvate, triangular lobes; petals absent; androecium with stamens free or nearly so. Fruits conical. Madagascar, surrounding islands, and nearby Africa
.... **Lecythidaceae subfam. Foetidioideae**

2. Leaf blades with well-defined secondary veins, the tertiary veins reticulate. Calyx with >4, valvate or imbricate, ovate lobes; petals present; androecium with stamens fused. Fruits globoid, ovoid, or fusiform.

3. Calyx-lobes with nectaries on margins; stamens 10, the filaments of stamens and staminodes fused at bases and apices but with slit-like openings in middle of staminal tube, markedly flattened, reflexed, the anthers positioned under stigma; stigma pentagonal ...**Napoleonaeaceae**

3. Calyx-lobes without nectaries on margins; stamens > 50, the filaments only fused at bases, without slit-like opening in middle of staminal tube, not markedly flattened, straight, the anthers positioned above stigma; stigma not pentagonal.

4. Cortical bundles inversely oriented. Annular nectary usually present; pollen syntricolpate; ovary inferior. Seeds without conspicuous endosperm
.... **Lecythidaceae subfam. Barringtonioideae**

4. Cortical bundles normally oriented. Annular nectary absent; pollen tricolpate; ovary superior. Seeds with ruminate endosperm .... **Scytopetalaceae**

Lecythidaceae clade (Map 1)

This map shows the distribution of Lecythidaceae *sensu lato* (all the families and subfamilies of the Lecythidaceae clade are mapped). The Lecythidaceae clade occurs in South and Central America, Africa, and Asia in the broadest sense (including Australia and the Pacific). The current numbers of known genera and species of this clade are found in Table I.

Napoleonaeaceae (BS 100%[Mori et al. 2007]; Figs.1, 3A; Map 2)

This is a monophyletic clade sister to Scytopetalaceae/Lecythidaceae.

This clade is recognized by the presence of normally oriented cortical bundles in the stem (xylem on inside); calyx lobes 5, not imbricate, with nectaries on margins; petals present (corona derived from petals, fide Ronse de Craene 2011); androecium actinomorphic, the stamens 10 (Frame & Durou 2001), filaments basally and apically fused but with window-like slits in middle, flat, the anthers laterally dehiscent, the pollen tricolpate *sensu lato* (Fig. 7A); intra staminal annular nectary absent (but nectar canal present, Frame & Durou 2001); ovary inferior, the style never as long as stamens, the anthers placed under stigma, the stigma, large, pentagonal; placentation not known; fruits drupes, seeds 1–20 per fruit (Liben 1971), endosperm absent, cotyledons 2, fleshy. x = 16 (Mangenot & Mangenot 1957, 1962), *Crateranthus* not known.

This West African family consists of *Napoleonaea* with eight species (Liben 1971) and *Crateranthos* with two species (Knuth 1939).

Based on descriptions and illustrations in Frame and Durou (2001), Knuth (1939), Prance (2004), and Prance and Jongkind (2015).

Scytopetalaceae (BS 100% [Mori et al. 2007]; Figs 1, 3C; Map 3)

This is a monophyletic clade sister to the three subfamilies of Lecythidaceae.

This clade is recognized by the following: presence of normally oriented vascular bundles in the stem (xylem inside); calyx fused, irregularly opening, not imbricate, rim-like or irregularly lobed, without nectaries; petals present (corona-like and interpreted to be derived from stamens by Appel, 1996); androecium actinomorphic, the stamens numerous 60–240 (Appel 1996), long, basally adnate to one another and to petals, a staminal tube scarcely developed, the anthers relatively long, with lateral or poricidal dehiscence, the pollen tricolpate (Fig. 7A); intra staminal annular nectary absent; ovary superior or semi-inferior, the style as long or longer than stamens, lobed (*Rhaptopetalum*) to slightly lobed at apex in other genera, the placentation variable, ovules axile, pendulous from apex of locule, arising along the length of the septum, or peltate-like; fruits globose or ovoid, elongate fusiform in *Pierrina*, indehiscent, drupes (exception is *Oubanguia* with loculicidal capsules), seeds 1 or very rarely 2–3 per fruit, endosperm present, ruminate in all genera except *Oubanguia*, the cotyledons flat, cordate or reduced in Asteranthos. x = 21 in *Asteranthos* (Kowal 1989) and unknown for other genera.

This family is restricted to West Africa, except for *Asteranthos brasiliensis*, which occurs in Amazonian Brazil and Venezuela. The family is divided into the subfamilies, Scytopetaloideae (*Asteranthos*, *Oubanguia*, and *Scytopetalum*) and Rhaptopetaloideae (*Brazzeia*, *Pierrina* and *Rhaptopetalum*).

Based on descriptions and illustrations in Appel (1996, 2004) and Prance and Jongkind (2015).

Lecythidaceae subfam. Foetidioideae (BS 99% [Mori et al. 2007]; Figs.1, 3B; Map 4).

This is a monophyletic group of a single genus sister to subfamily Barringtonioideae and these two clades together are sister to the New World Lecythidaceae.

The clade is recognized by the following: presence of inversely oriented cortical bundles of the stem (xylem outside); calyx 4-lobed, the lobes triangular, not imbricate, without nectaries; petals lacking, a corona not present; androecium actinomorphic, the stamens numerous (>200), not or only scarcely fused at base (i.e., staminal tube absent), the anthers small, with lateral dehiscence, the pollen tricolpate (Erdtman 1952); intrastaminal annular nectary absent; ovary inferior, truncate or slightly domed at apex, the style as long or longer than stamens, with 3–4 short lobes at apex, the placentation peltate, not apical, not pendulous; fruits obconical, thinly woody, indehiscent; seeds 1 per fruit, without endosperm, cotyledons not known. x = not known.

The secondary veins are obscure, depart from the midrib at about a 45° angle, run straight for most of distance to the margin, and the tertiary veins are parallel to the secondary veins. In the New World, all species of *Allantoma* and some species of *Cariniana* (*C. domestica* (Mart.) Miers and *C. micrantha* Ducke) also have this type of venation but the secondary veins of these species arch upward toward the margin.

The 17 narrowly distributed species of *Foetidia* are centered on the island of Madagascar. In addition, one species occurs in East Africa and two species occur in the Mascarene Islands (Prance 2008; Prance & Jongkind 2015).

Based on descriptions and illustrations in Knuth (1939), Prance (2008), and Prance and Jongkind (2015).

Lecythidaceae subfam. Barringtonioideae (BS 100% [Mori et al. 2007]; Figs.1, 3D, Map 5)

This is a monophyletic group sister to the Foetidioideae clade, both of which together are sister to the New World subfam. Lecythidoideae (Fig. 1).

This clade is recognized by the following: inversely oriented cortical bundles of the stem (xylem outside); calyx fused in bud (circumscissile or splitting irregularly at anthesis) or lobed from start, without nectaries on calyx; petals present, usually 4; androecium actinomorphic, the stamens numerous (>200), the filaments long, the anthers small, with lateral dehiscence, the pollen syntricolpate (Erdtman 1952; Tsou 1994); intrastaminal annular nectary present; ovary inferior, truncate at apex; style as long or longer than stamens, the stigma small, not lobed at apex, the placentation often with few ovules pendulous from summit of locule in *Barringtonia* but also along entire length of septum in *Careya*, and at base of septum in *Chydenanthus*; fruits indehiscent, narrowly fusiform to broadly fusiform in *Barringtonia* and *Chydenanthus*, globoid in *Planchonia* and *Careya*, and very narrowly fusiform with conspicuous wings in *Petersianthus*; seeds usually 1 per fruit in *Barringtonia* and *Chydenanthus*, numerous in *Careya* and one to numerous in *Planchonia*, not known for *Petersianthus*, cotyledons absent in *Barringtonia*, *Careya*, and *Chydenanthus*, leaf-like and plicate in *Planchonia* and not known in *Careya* and *Petersianthus*, endosperm absent or very sparse. x = 13 in *Barringtonia*, *Careya*, *Chydenanthus*, *Petersianthus*, *Planchonia* (Sobti & Singh 1961); Mehra 1972; Sakar et al. 1982; Singhal & Gill 1984; Morawetz 1986; Sarkar & Datta 1982; Kowal 1989; Prance & Kartawinata 2013) and x = 26 in *Barringtonia racemosa* (L.) Spreng. (Morawetz 1986; Sarkar 1982), *B. acutangula* (L.) Gaert. (Sarkar 1983), and *Petersianthus macrocarpus* (P. Beav.) Liben (Pl@ntUse 2017).

According to Prance (2012) the 69 species of *Barringtonia* have three areas of high species diversity: Malay Peninsula, Borneo, and New Guinea. There are four species of *Careya* native to India and Southeast Asia; two species of *Chydenanthus* native to Java and Sumatra; and two species of *Petersianthus*, one (*P. macrocarpus*) is African and the other (*P. quadrialatus* Merr.) is restricted to the Philippines. *Peteranthus* is the only native species of the Barringtonioideae found in west Africa where it is common and widespread. In addition, 14 species of *Planchonia* are native to tropical Asia and New Guinea.

Based on descriptions and illustrations in Kunth (1939), Kartawinata (1965), Prance (2010a 2010b, 2012), Prance and Kartawinata (2013), and Prance and Jongkind (2015).

According to Lindenmayer and Laurance (2016), *Petersianthus quadrialatus* is native to the the Philippines and, at 87.8 m, is one of the world's largest trees.

Lecythidaceae subfam. Lecythidoideae (BS 100% [Mori et al. 2007]; Figs. 2A–B, 4–10; Map 6)

This is a monophyletic group that is sister to the Foetidiodeae/Barringtonioideae clade and consists of all New World species except *Asteranthos brasiliensis* which is now placed in the Scytopetalaceae (Appel 1996 2004). The ten genera in this subfamily are restricted to the New World.

This clade is recognized by the following: presence of normally oriented cortical bundles of the stem (xylem inside); flowers with calyx only fused in bud (circumscissile or splitting irregularly at anthesis) in *Grias* (with the exception of *G. neuberthii* J.F. Macbr. which possesses 4 free calyx-lobes) or lobed from the start in other genera, without nectaries on calyx; petals present, 4 in *Grias*, 5 in *Allantoma*, and mostly 6 in other genera, androecium with four types of symmetry: (1) actinomorphic with a slightly carnose staminal tube bearing stamens along rim (*Gustavia*), (2) actinomorphic with markedly carnose staminal tube with stamens on rim and also on inner walls of the staminal tube (*Allantoma* and *Grias*), (3) obliquely zygomorphic with a slight prolongation on one side of a small membranous staminal tube and stamens inserted on the margin and inside of the tube, or (4) with a staminal ring (staminal tube absent) bearing fertile stamens and a ligular extension from one side of the staminal ring, the extension arches over the ovary and usually bears stamens or modified stamens (staminodes or vestigial stamens). The anthers usually open by lateral slits or by terminal pores (only in *Gustavia*), ovaries inferior (*Allantoma*, *Bertholletia*, *Cariniana*, *Corythophora*, *Couratari*, *Gustavia*, *Lecythis*) or half-inferior (*Couroupita*, *Eschweilera*, *Grias*), placentation variable (Mori et al. 2015), stigma usually not divided (slightly divided only in *Grias*), endosperm usually absent (found only in *Grias* but sparse). x = 17 (Mangenot & Mangenot, 1958; Kowal et al. 1977; Gibbs & Ingram 1982; Guerra 1986; Morawetz 1986; Kowal 1989), *Couroupita guianensis* has been recorded to have both x = 17 (Kowal et al. 1977; Morawetz 1986) and x = 18 (Sarkar et al. 1982; Sarkar 1983). *Gustavia augusta* L. is reported to have x = 36 which gives it a base number of x = 18 (Sarkar 1983). In summary, with a few exceptions, species of subfam. Lecythidoideae have base chromosome numbers of x = 17.

The generic relationships of this clade has been reviewed by Huang et al. (2015) and Mori et al. (2015) and the authors concluded that *Eschweilera* and *Lecythis* are not monophyletic; therefore, there may be realignments of these genera based on future studies.

Based on descriptions and illustrations in Huang et al. (2015), Mori et al. (2015), Mori and Prance (1990), and Prance and Mori (1979).

NON-BERTHOLLETIA GRADE

This is a paraphyletic grade of New World Lecythidaceae that has the *Bertholletia* clade nested within it (Fig. 2A–B).

Figure 1 shows relationships of worldwide members of the Lecythidaceae clade, whereas Figure 2 shows relationships of the New World taxa. The most recent phylogenies (Mori et al. 2007; Huang et al. 2015; Fig. 1, 2A) support the hypotheses that the actinomorphic-flowered genera *Grias*, *Gustavia*, and *Allantoma*, the tubular zygomorphic-flowered *Cariniana*, and the staminal zygomorphic-flowered *Couratari*, and *Couroupita* are monophyletic and correspond to the genera as circumscribed by Prance and Mori (1979) and Mori and Prance (1990). These conclusions are based on both morphological and molecular data (Huang et al. 2015; Mori et al. 2015).

The clades are discussed in the order they appear on the most recent phylogenetic trees (Figs. 1–2B), but bear in mind that relationships among the clades are not well resolved.

***Grias* clade** (99% BS [Mori et al. 2007]; Figs. 1, 3E, 5B; Map 7)

This clade is sister to the *Gustavia* clade. The 11 species in this clade range from Belize to central Peru (Prance & Mori 1979; Clark & Mori 2000; Cornejo & Mori 2010, 2011, 2012b; Mori et al. 2010). Most of the species are associated with the valleys and slopes of the Andes in southwestern Colombia and northwestern Ecuador but two, *G. neuberthii* J.F. Macbr. and *G. peruviana* Miers, occur in Amazonian Colombia, Ecuador, and Peru. *Grias cauliflora* L. is found mostly in Central America but also occurs in Jamaica where it was first described. *Grias peruviana* is disjunct between coastal Ecuador and Amazonian Ecuador and Peru.

***Gustavia* clade** (87% BS [Mori et al. 2007]; Figs. 1, 5A, 8; Map 8)

This clade is sister to the *Grias* clade. The 44 species of this clade (Prance & Mori 1979; Mori & Cornejo 2013) range from the Osa Peninsula of Costa Rica (*Gustavia brachycarpa* Pittier) to the state of Pernambuco in the Atlantic Forest of Brazil (*Gustavia augusta*). The genus is especially rich in species in Panama and northwestern Ecuador where as many as eight species have been collected from a grid square. Species of this genus are found in much of Amazonia with the exception of a large area including the llanos of Venezuela and Amazonian Colombia where they are rarely collected. In general, collecting records and species diversity for species of *Gustavia* in much of Amazonia and the Guianas are low—especially in the Guianas and eastern Amazonian Brazil where most of the area has only one to three species per grid square. In a grid square near Manaus, there are four species, and in the Atlantic Forest of Brazil the only species that has been collected is *Gustavia augusta*.

Couroupita clade (100% BS [Huang et al. 2015]; Figs. 1, 2A, 6A–6B; Map 9)

This monophyletic group is sister to the clade that contains *Cariniana*, *Couratari*, *Allantoma*, and the *Bertholletia* clade.

There are three well-defined species in the *Couroupita* clade. *Couroupita guianensis* has a periamazonian distribution (Granville 1992). In the north, collections of this species have been made in the Guianas, eastern Venezuela, and on the other side of the Andes in the Maracaibo Basin of Venezuela. In addition, numerous collections have been made in western Amazonia in Colombia, Ecuador, Peru, and Brazil. This species is often planted as an ornamental tree and sometimes it is difficult to determine if an individual is a cultivated or native tree. *Couroupita subsessilis* Pilg. runs along the Amazon River from eastern Amazonian Ecuador to near the border between the states of Amazonas and Pará. It has also been collected in the Brazilian state of Acre. This species has not been collected in the states of Pará and Amapá. *Couroupita nicaraguarensis* DC. is distributed from northwestern Nicaragua to coastal areas in northwestern Ecuador.

***Allantoma* clade** (99% BS [Huang et al. 2015]; Figs. 2A, 5B; 10E, Map 10)

This clade may be sister to the *Cariniana* clade, but we interpret this with caution given that the relationship has less than 50% BS support in the combined analyses of Huang et al. (2005; Fig. 2a). Nonetheless, a sister relationship between *Cariniana* and *Allantoma* was supported by Huang et al. (2008) based on morphological data alone.

Eight species belong to the *Allantoma* clade (Huang et al. 2008) and two of them, *A. decandra* (Ducke) S.A. Mori et al. and *A. lineata* (Mart. ex O.Berg) Miers, are widespread. The former species, ranging from southwestern to central Amazonia, is primarily found in well-drained lowland forests and the second, ranging from northwestern Amazonia, along the Rio Negro and the Amazon River to near its mouth, prefers riverine vegetation or wet areas along small streams. Species of this clade are limited to the Amazon Basin but are absent in the Guayana lowlands, northern Venezuela, in an area bounded in the north by the Amazon River, in the west by Amazonian Peru and Colombia, and in the east by the Madeira River.

***Cariniana* clade** (<50% BS [Huang et al. 2015]; Figs. 2A, 5C, 10D; Map 11)

Based on molecular data of Mori et al. (2007; Fig. 1), *Cariniana pyriformis* Miers falls outside of the *Cariniana* lineage, suggesting that the *Cariniana* clade may not be monophyletic. This species was unfortunately not included in the combined analyses of Huang et al. (2015; Fig. 2A), but in all morphological aspects it is clearly a species of *Cariniana* (Huang et al. 2008). A hypothesized sister group relationship between *Cariniana* and *Allantoma* was weakly supported (<50%) by Huang et al. (2015), and was also supported based on morphology alone (Huang et al. 2008).

The nine species of *Cariniana* (Huang et al. 2008) are found in either lowland forests or savanna habitats on well-drained soils. The overall distribution of this clade (Map 11) is central and southwestern Amazonia, the savanna habitat of central Brazil, and the Atlantic Forest of eastern Brazil. *Cariniana pyriformis* is found in northwestern Colombia, eastern Panama, and the Maracaibo Basin in Venezuela. Two species are disjunct (*C. estrellensis* (Raddi) Kuntze and *C. ianeirensis* R. Knuth) between southwestern Amazonia and the Atlantic Forest of eastern Brazil and one species (*C. pyriformis*) is found in lowlands west and north of the Andes in eastern Panama, northwestern Colombia, and the Maracaibo Basin of Venezuela. Species of *Cariniana* are not adapted to dry thorn scrub (= *caatinga*) of northeastern Brazil and cloud forests.

***Couratari* clade** (BS 81[Huang et al. 2015]; Figs. 2A, 6M; Map 12)

This monophyletic group falls in the clade that contains *Cariniana*, *Allantoma*, and the *Bertholletia* clade, but relationships of the genus are unresolved in Mori et al. (2007) and have <50% bootstrap support in Huang et al. (2015).

There are 19 species in this clade. Mori and Prance (1990) recognized three sections: *Couratari* sect. *Echinata*, *C.* sect. *Guianensis*, and *C.* sect. *Microcarpa*. There is support for retaining sect. *Echinata* but no support for maintaining the other two sections separate from one another (Mori et al. 2007). This clade is found throughout most of Amazonia and the Guianas except for a vast area in the south central and eastern Brazilian Amazon. In addition, two species, the widespread *C. guianensis* Aubl. and the Panamanian/Costa Rican endemic *C. scottmorii* Prance, are found west of the Andes where they occur from northwestern Colombia to the Osa Peninsula and nearby mainland of Costa Rica. In addition, four species have reached the Atlantic Forest where they range from southern Bahia to forests in the state of Rio de Janeiro. These species, *C. asterotricha* Prance, *C. asterophora* Rizzini, *C. pyramidata* (Vell.) R. Knuth, and *C. macrosperma* A.C. Sm., all belong to *Couratari* sect. *Echinata*. *Couratari macrosperma* is found in southwestern Amazonia and in eastern Brazil but further study may reveal that these disjunct populations represent two related species.

BERTHOLLETIA CLADE

Huang et al. (2015) described a species-rich New World clade that includes *Bertholletia*, *Corythophora*, *Eschweilera*, and *Lecythis* as circumscribed by Mori and Prance (1990). The *Bertholletia* clade has low molecular support (63% BS; Fig. 2A–2B). The neotropical genera with actinomorphic flowers (*Allantoma*, *Grias*, and *Gustavia*) and some of the zygomorphic genera (*Couratari*, *Couroupita*, *Allantoma*, and *Cariniana*) are the outgroup of this clade. Huang et al. (2015) concluded that *Corythophora* is monophyletic, *Bertholletia* is embedded in *Lecythis*, and that *Lecythis* and *Eschweilera* are not monophyletic, the former consisting of five and the latter of three clades.

The clades are discussed in the order they appear on the most recent phylogenetic trees (Huang et al. 2015; Fig. 2A) but bear in mind that relationships among and within the clades are not resolved. Do not confuse this clade with the monotypic *Bertholletia excelsa* clade described below.

***Lecythis pisonis* clade** (100% BS [Huang et al. 2015]; Figs. 2A, 4. 6C, 8, 10J; Map 13)

This clade consists of five species that range from Nicaragua to northern Ecuador, The Guayana lowlands, eastern and western Amazonia, and the Atlantic Forest of Brazil. Collections have not been made from north central Amazonia and south of the Amazon River in south central Amazonia. The seeds of species of this clade are edible, so their distribution has been influenced by humans moving plants from one area to another. The seeds of species of this clade are dispersed by bats that eat the basal, fleshy arils and drop the seeds on their way to or at their night roosts. The seed coats are too tough for the bats to open them to eat the embryo.

***Lecythis ollaria* L. clade** (100% BS [Huang et al. 2015]; Fig. 2A. , Map 14).

This clade consists of three species found in northwestern South America in Colombia and Venezuela and in eastern Panama. *Lecythis tuyrana* Pitter is a tall forest tree restricted to eastern Panama and extreme northwestern Colombia. The two other species, *L. minor* Jacq. and *L. ollaria*, are usually collected from dry savannah forests but are found in gallery forests within savanna where they are larger trees. *Lecythis ollaria* is separated from the other two species by the Andes.

***Lecythis poiteaui* O. Berg clade** (72% BS [Huang et al. 2015]; Fig. 2A; Map 15)

This clade consists of five species found in the Guayana lowlands, eastern Amazonia, and the Atlantic Forest. There is a wide dry band consisting of savanna and thorn scrub vegetation in northeastern Brazil that separates the Amazonian and the Atlantic Forest species of this clade. Only one of the species of this clade, *Lecythis lurida* (Miers) S.A. Mori, is disjunct between eastern Amazonia and the Atlantic forest.

***Bertholletia excelsa* clade** (100% BS [Huang et al. 2015]; Figs. 2A, 6G, 9, 10C; Map 16)

This clade consists only of *Bertholletia excelsa* and is embedded in the *L. ollaria*/*L. poiteaui/L. chartacea* O. Berg clades (Fig. 2A). Because of low resolution among these four clades, we are not able to determine if this clade should be recognized as a single genus or if the four weakly defined clades should be separated into different genera.

In Figure 2A, the *L. ollaria* clade is part of the weakly supported *L. ollaria*/ *L.poiteaui*/ *Bertholletia excelsa*/ *L. chartacea* clade. If this clade were circumscribed as *Lecythis* then *B. excelsa* would have to be transferred to *Lecythis* because the type of the genus (*Lecythis ollaria*) was published before any other Lecythidaceae (Dorr & Wiersema 2010a, 2010b). In contrast, if all subclades mentioned in this paragraph were considered as different genera *Lecythis* would be reduced to three instead of the 26 species recognized by Mori and Prance (1990). We hypothesize that future studies will support transferring the monotypic *Bertholletia* to *Lecythis.*

Today, Brazil nut trees grow throughout much of lowland Amazonia (Map 16). However, the current distribution of this species does not coincide with its original distribution because of dispersal by humans. Ducke and Black (1953) suggested that the overall distribution of *Hevea*, a historically important source of rubber, more-or-less defines the Amazonian hylaea, and Henderson (1995) defined the lowland Amazon Basin as the area below 500 m elevation. Eva and Huber (2005) defined the Amazon Basin based on hydrological, ecological, and biogeographical data. They recognized a large central Amazon basin surrounded by four peripheral areas, the Andes, Planalto, Gurupi, and Guayana subregions.

There are, however, large areas in southwestern Amazonia and another running east to west beneath the Guianas without collections. The linear series of collections along the Tapajós and other rivers indicate that Brazil nut trees are planted along rivers where humans cultivate the trees for their edible seeds. Maps of *Bertholletia excelsa* in Thomas et al. (2014) can be consulted for a more detailed discussion of the distribution of this species in both present and past times. The localities on their maps are based on herbarium collections and observations whereas our maps are based only on herbarium specimens. Because there is little possibility for misidentification of this species. The Thomas et al. (2014) maps give a better idea of the current distribution of the Brazil nut but make it difficult to know what trees are there because they are cultivated.

Figure 4. Zygomorphic flowers of the *sapucaia* tree (*Lecythis pisonis*) being pollinated by female carpenter bees (*Xylocopa* sp.). The bees are gathering sterile pollen from the inside of the androecial hood while fertile pollen of the staminal ring is placed on their dorsal surfaces. The sterile pollen is fed to their larvae and the fertile pollen is rubbed off onto the stigmas of other flowers on other trees visited thereby pollinating the flowers. Painting by M. Rothman.

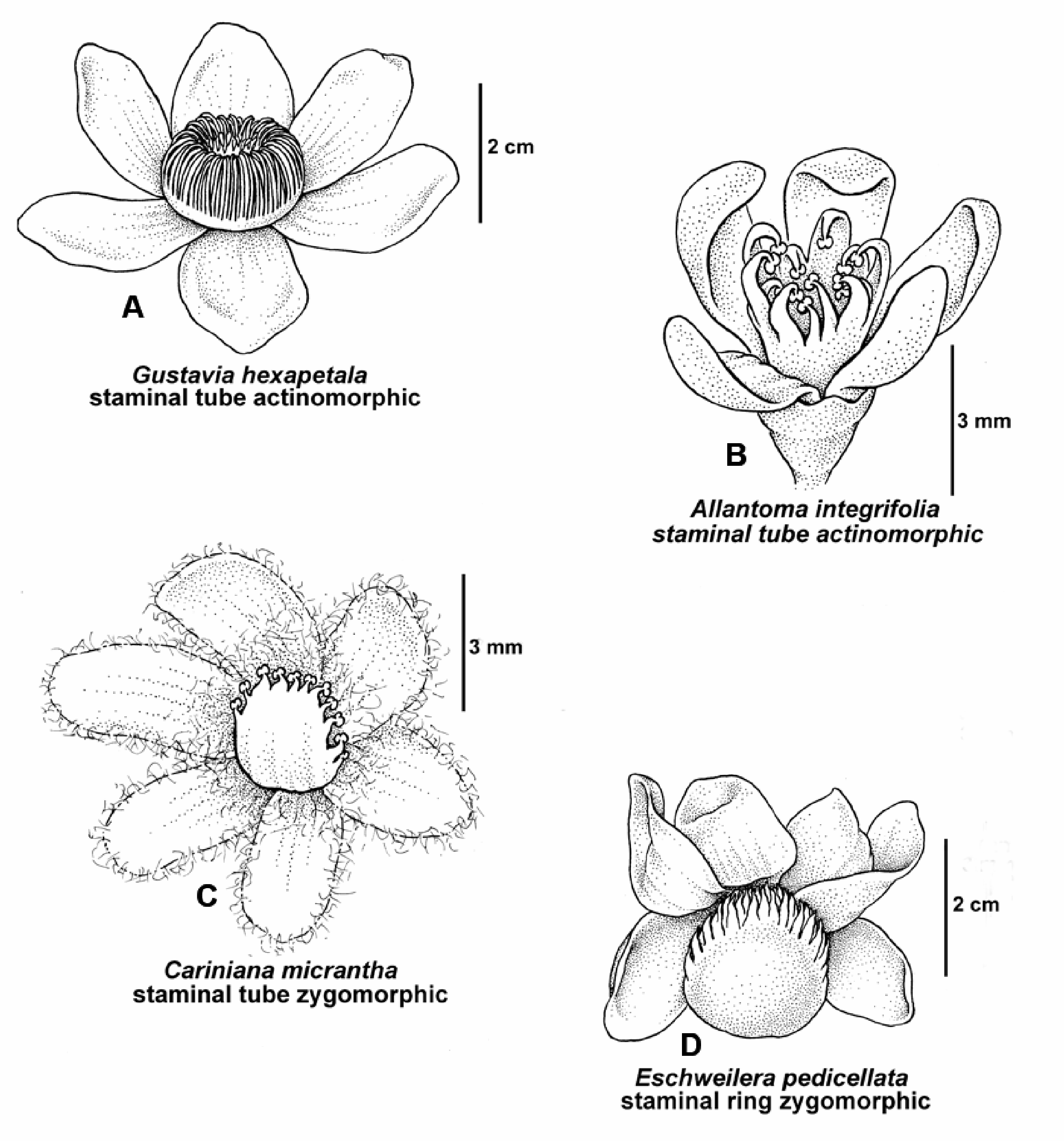

Figure 5. Examples of floral symmetry in the New World Lecythidaceae. A. *Gustavia* type, the androecium is relatively thin and actinomorphic and the stamens are erect, and inserted around the rim of the staminal tube (only in *Gustavia*). B. *Allantoma* type, the androecium is fleshy and actinomorphic and the stamens are reflexed and inserted on the inside and around the rim of the staminal tube (found also in *Grias*). C. *Cariniana* type, the androecium is membranous, the staminal tube is prolonged on one side, the stamens are not reflexed and are inserted around inside of the staminal tube and along its margin (only in *Cariniana*). D. *Lecythis* type, the androecium is fleshy, staminal tube absent, the stamens erect, arising from a staminal ring (found also in *Couroupita*, *Couratari*, *Corythophora,* and *Lecythis*). Drawings by B. Angell.

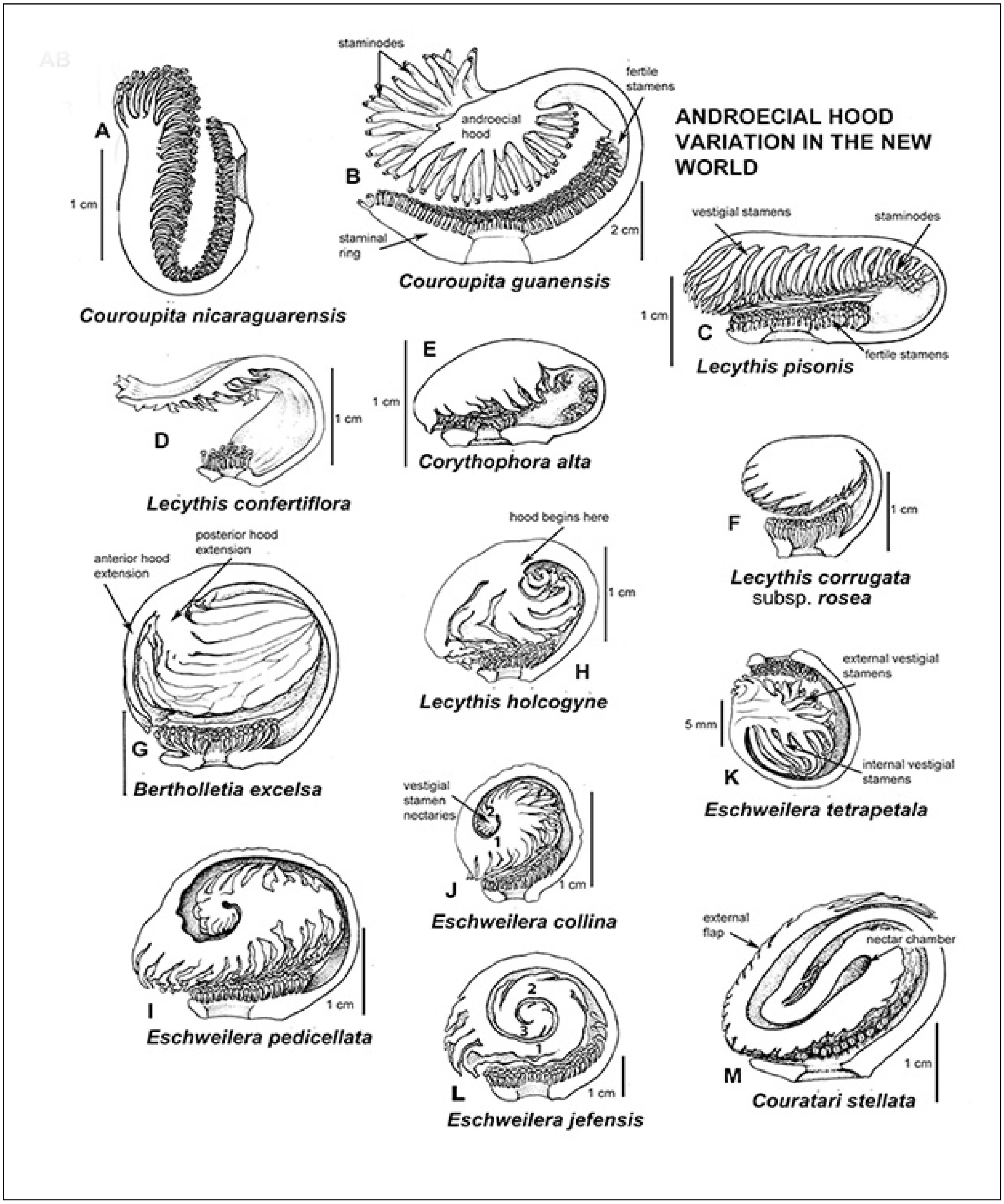

Figure 6. Variation of the androecium of staminal ring zygomorphic-flowered species of New World Lecythidaceae. The least complex androecium among the staminal ring zygomorphic genera is *Couroupita nicaraguarensis* (Fig. 6A) and the most complex is represented by *Couratari stellate* (all species of *Cariniana* have an external flap, Fig. 6M). The numbers in 6J and 6L indicate 2-coiled and 3-coiled androecial hoods, respectively. Drawings by B. Angell (E–F, H–L) and H. M. Fukuda (G, M).

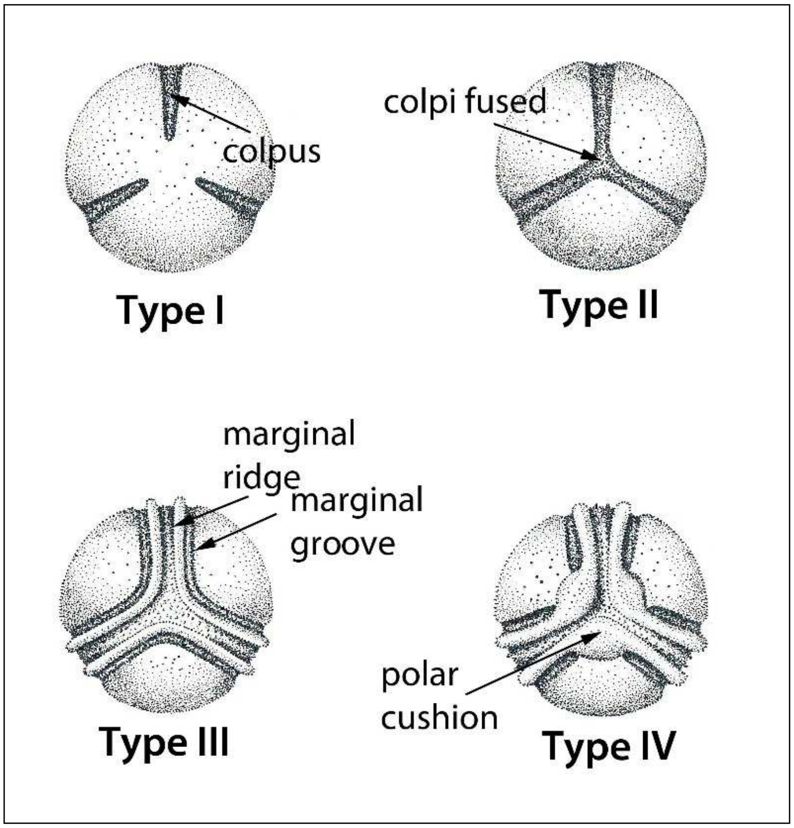

Figure 7. Comparison of the pollen of the Lecythidaceae clade. Type I. Tricolpate pollen found in the Napoleonaeaceae, Scyopetalaceae, Lecythidaceae subfam. Foetidioideae, and Lecythidaceae subfam. Lecythidoideae (the colpi do not fuse at the poles of the pollen grains). Type II. Syntricolpate pollen found in some species of subfam. Barringtonioideae (the colpi fuse at the poles of the pollen grain). Type III. Syntricolpate pollen found in some species of the subfam. Barringtonioideae (the colpi fuse at the poles of the pollen grains and marginal ridges and grooves are present), Type IV. Syntricolpate pollen found in some species of the subfam. Barringtonioideae (the colpi fuse at the poles of the pollen grains and marginal ridges, marginal grooves, and polar cushions are present). Pollen Types III and IV are good indicators of the presence of species of subfam. Barringtonioideae in the fossil record. Adapted from Tsou, 1994).

Lecy*this chartacea* clade (76% BS [Huang et al. 2015]; Figs. 2B, 6H; Map 17).

This clade consists of at least 11 species found throughout the Amazon and with one species in northwestern Colombia and eastern Panama into Costa Rica (*Lecythis mesophylla* S.A. Mori). The widespread *L. chartacea* may include more than one species. There are no species of this clade in the Atlantic Forest.

***Corythophora* clade** (100% BS [Huang et al. 2015]; Fig. 6E; Map 18)

There are four species in this clade, one of which (*Corythophora rimosa* W. Rodrigues) is treated as two subspecies (Mori & Prance 1990). *Corythophora rimosa* subsp. *rimosa* has green petals and is restricted to a small area in central Amazonian Brazil and *C. rimosa* subsp. *rubra* S.A. Mori has red petals and is found only in Amapá and French Guiana. This genus forms two distinct subclades, one consisting of *C. amapaensis* Pires ex S.A. Mori & Prance and *C. labriculata* (Eyma) S.A. Mori & Prance and the other of *C. alta* R. Knuth and *C. rimosa* (Huang et al. 2015). This clade has been collected in Surinam, French Guiana, eastern Amazonian Brazil around Bélem, Central Amazonian Brazil around Manaus, and northern Amazonian Brazil near the border with Guayana.

Within this area, there are large expanses without collections but we suspect that species of the genus are there but have not yet been collected.

***Eschweilera integrifolia* (Ruiz & Pav. ex Miers) R.Knuth clade** (<50% BS [Huang et al. 2015]; Figs. 2B, 6L; Map 19)

Huang et al. (2015) recovered a clade of *Eschweilera* species that differs from the Mori and Prance (1990) circumscription of *Eschweilera*. At least 15 species belong to this clade which differs from the *E. parvifolia* Mart. ex DC clade (the type of the genus) by having triple-coiled androecia (versus double-coiled androecial hoods) and arils that usually surround the entire seed (versus lateral arils). The latter feature is difficult to see because the aril is present only in fresh specimens of mature seeds (the lateral aril persists but the spreading aril usually disappears when specimens are dried). In addition, more than one-half of the species have pink to reddish petals but white to pale yellow petals are at least found in *E. aguilarii* S.A. Mori, *E. awaensis* Cornejo & S.A. Mori, *E. collinsii* Pittieri, and *E. ovalifolia* [DC.] Nied.).

Species of this clade range from south of the Costa Rican/Nicaraguan border to northern Bolivia. There are also two Amazonian species: *E. andina* (Rusby) J.F. Macbr. is found in western Amazonia paralleling the Andes from Ecuador to Bolivia; and the riverine *E. ovalifolia* ranges from western Amazonia in Bolivia and Peru and from there as far east as central Amazonia. Species circumscriptions in the Andean species of this clade have not been well established; nevertheless the map gives a good idea of the distribution of the entire clade.

***Eschweilera tetrapetala* S.A. Mori clade** (100% BS [Huang et al. 2015]; Figs. 2B, 6K, 10I; Map 20).

This clade includes seven known species. The basal species is the wide-spread *Eschweilera nana* (O. Berg) Miers, which is restricted to savanna vegetation in the Planalto of Brazil, and six other species endemic to forests of southern Bahia, Espírito Santo, and Rio de Janeiro. The species of this clade differs from the other clades of *Eschweilera* by single instead of double or triple androecial hood coils, more than one row instead of a single row of ovules, and basal instead of lateral or spreading arils.

***Lecythis corrugata* Poit. clade** (99% BS [Huang et al. 2015]; Figs. 2B, 6D, 6F; Map 21)

This clade consists of five species, two of which, are divided into subspecies (*Lecythis corrugata* subsp. *corrugata* and *L. corrugata* subsp. *rosea* (Spruce ex O. Berg) S.A. Mori and *L. persistens* Sagot subsp. *persistens* and *L. persistens* subp. *aurantiaca* S.A. Mori). The overall distribution of the clade is Guayanan but it is also found in eastern and central Amazonia south of the Amazon River. The ranges of the *L. corrugata* subspecies overlap near the Essequibo River and subsp. *rosea* also occurs north of the Venezuelan Andes in the Maracaibo Basin.

***Eschweilera parvifolia* clade** (94% BS [Huang et al. 2015]; Figs. 6I–J, 10G–H; Map 22)

The *Eschweilera parvifolia* clade is the most diverse clade of New World Lecythidaceae with approximately 69 species. Only the Old World Barringtonioideae clade with 69 species is as diverse. This figure was calculated by subtracting the 15 species that fall into the *E. integrifolia* clade, the seven species of the *E. tetrapetala* clade (which should be treated as a new genus), and two species now treated as *Lecythis* (*E. congestiflora* [Benoist] Eyma and *E. simiorum* [Benoist] Eyma) from the 83 species listed in Mori and Prance (1990) and then adding the 10 new species described since this monograph was published (Mori 1992, 1995, 2007; Mori & Lepsch-Cunha 1995; Cornejo & Mori 2011). There are, however, many species in this clade that have not yet been described.

Because of the high number of species in the *Eschweilera parvifolia* clade the map shows only the number of collections and number of species in each of the grids where species of the clade occur. Species of the *E. parvifolia* clade share coiled androecial hoods, vestigial stamen nectaries at the apices of the coils (also found in the *Couratari* clade), two locules (infrequently with 4 locules), and ovules arranged in a single row (Huang et al. 2015) with the *E. integrifolia* clade. This relationship, however, is not supported in phylogenetic studies based on molecular data (Mori et al. 2007; Huang et al. 2015).

The northern most species of this clade, and of New World Lecythidaceae in general, is *Eschweilera mexicana* Wendt et al. from Veracruz, Mexico. There have been no collections of this clade gathered from Belize, Guatemala, or El Salvador. Of the 11 species of Lecythidaceae on the Osa Peninsula of Costa Rica, five belong to this clade (Mori 2007). In Central America, the Osa is the last place where this clade plays a significant role in the ecology of an area of lowland forest (Aguilar et al. 2008). The southern limit of the clade is *E. ovata* (Cambess.) Mart. ex Miers in the androecial tube is relatively thin and actinomorphic, the stamens arise from the rim of the tube and are arched at the apex (only in *Gustavia*). B. *Allantoma* type, the androecium is fleshy and actinomorphic and the stamens are reflexed and inserted on the inside and around the rim of the staminal tube (found also in *Grias*). C. *Cariniana* type, the androecium is membranous, the staminal tube is prolonged on one side, the stamens are not reflexed and are inserted around inside of the staminal tube and along its margin (only in *Cariniana*). D. *Lecythis* type, the androecium is fleshy, a staminal tube is absent, and the erect stamens arise from a staminal ring (found also in *Couroupita*, *Couratari*, *Corythophora* and *Lecythis*). Drawings by B. Angell Figure 5. Examples of floral symmetry in the New World Lecythidaceae. A. *Gustavia* type, the. state of Espiríto Santo, Brazil. The most southern Lecythidaceae, however, is *Cariniana estrellensis* from southern Santa Catarina, Brazil.

There is a dry area ranging from Amazonian Colombia into the savannas of Venezuela where species of the *Eschweilera parvifolia* clade are extremely rare. In addition, the large arid area running in a southwestern direction from northeastern Brazil is not rich in Lecythidaceae. The only species of this clade in the Atlantic Forest is *E. ovata* which is also found in southeastern Amazonia.

DISCUSSION

Methodology

A major problem in determining the distributions of New World Lecythidaceae for phytogeographical studies is that collections are not available throughout the ranges of the species under study. Nelson et al. (1990) demonstrated that the collections of Amazonian species of *Inga* are most abundant in areas surrounding institutions with active herbaria or in areas where these institutions have ongoing projects. They also point out that this collecting bias compromises testing hypotheses such as the role that Pleistocene refuges (Prance & Elias 1977) played in the evolution of Amazonian species. Based on collection data taken from herbarium sheets, the highest number of species of Lecythidaceae found in a grid square corresponds to areas where the greatest numbers of specimens have been collected. Map 6 shows that eastern Central America (Costa Rica and Panama), Amazonian Peru, northwestern Ecuador, the Guianas, Manaus, Belém, southern Bahia, Espírito Santo, and Rio de Janeiro are regions with the highest number of specimens collected and the highest number of species recorded.

Like other tropical tree groups, Lecythidaceae are difficult to sample because of the remoteness of species-rich forests, the short time and irregularity of flowering and fruiting, and the work it takes to climb into the canopy to collect specimens. Collections of flowers and fruits from the same individuals are seldom gathered at the same time, so it is difficult to tell if the fruits from one tree belong to the same species as another tree in flower.

Once specimens have been collected, they need to be identified before they are mapped. For the most part, sterile specimens should not be collected as vouchers for DNA material nor as the source of coordinates for mapping because of the high rate of misidentification (Mori 1998). In long-term ecological studies with marked and mapped trees it is possible to wait for species only known by sterile specimens to flower and fruit but that is difficult and time consuming.

There are problems even with fertile collections of Lecythidaceae. Sometimes specimens with flowers and seeds lose their structure when they are dried over high heat and under excessive tightening of the plant press, thereby destroying the characters needed to identify the collection to species. For this reason, flowers and seeds need to be dried in paper bags under low heat (or preserved in alcohol) and accompanied by images of the taxonomically important parts of the plant (Mori & Prance 1987).

The difficulty of identifying sterile collections of Lecythidaceae, especially *Eschweilera*, makes sterile collections less desirable for species mapping and as vouchers for DNA collections. The simple, alternate leaves of different species of this genus are especially difficult to tell apart. For example, in an inventory of Lecythidaceae in a 100-hectare plot in central Amazonia (Mori et al. 2001) it was difficult to separate *E. collina* Eyma from *E. romeu-cardosoi* S.A. Mori and *E. truncata* A C. Sm. from *E. coriacea* until specimens from these species were gathered in both flower and fruit.

With additional time, more collections are made and the distributions of some species that were once thought to be endemic to small areas are documented to cover much larger areas. As an example, *Cariniana ianeirensis* (Map 25) was published in 1939 based on a few collections made in the vicinity of Rio de Janeiro. Subsequently this species was gathered in Bolivia in 1991 (*Quevado S. 502*) and then in southern Bahia in 2002 (*Fiaschi 1182*). This species is separated by wide expanses of savanna running from the southwest to the northeast through most of the Planalto of Brazil (Map 25). *Cariniana ianeirensis* grows as a tall tree in forests or as smaller trees in open areas on rocky slopes in the states of Rio de Janeiro and Espírito Santo (M. Lemes & R. Gribel, pers. comm.). The wide ecological amplitude of *C. ianeirensis* must have made it easier for this wind-dispersed species to migrate between the Atlantic Forest and Amazonian Bolivia.

Many species of Lecythidaceae have not yet received scientific names. For example, Prance and Mori (1979) recognized six species of *Grias* in the treatment of the genus in their Flora Neotropica monograph. Recent botanical exploration of the slopes and valleys of the Andes of northwestern Ecuador and southwestern Colombia has yielded six additional species added to these genus (Clark & Mori 2000; Cornejo & Mori 2010, 2011, 2012a, 12b; Mori et al. 2010).

Describing new species of tropical trees based on a finite number of collections from a seemingly infinite number of trees causes problems for defining new species. This slows down the process of publishing new species because taxonomists need to understand what characters separate new species from species already described. Most of the time, collections of new species and their closest relatives are not informative enough to determine the differences that distinguish new species from others that have already been described, a process that may take years to resolve. Bebber et al. (2013) determined that 1855 new species of flowering plants were published annually between 1970 and 2011. They calculated the average lag time between the first collection and publication of a new species took 35 years. A population of what one researcher (“a lumper”) calls a species may be interpreted as several species by another researcher (“a splitter”). For example, Dugand (1947) prepared a plate of fruit variation of *Lecythis minor* in which it first appears as if fruits from three species of *Lecythis* were illustrated on the same plate. However, the fruits were gathered from trees in proximity to one another in northwestern Colombia as well as from trees Dugand believed to represent the same species. We have seen the same variation in other species of Lecythidaceae to such an extent that fruits from a single tree of *Allantoma lineata* are variable enough to lead a splitter to describe several species based on fruits from the same tree (Prance & Mori 1979).

Changes in the identification of specimens need to be annotated on the herbarium sheets and the new names entered into a database. In addition, secondary material (e.g., DNA, pickled flowers and fruits, wood specimens, images, etc.) associated with herbarium specimens need to be correctly labelled on the specimens and corrected in the database. As an example, until recently two related species of *Lecythis* (identified as *Eschweilera congestiflora* [Benoist] Eyma and *E. simiorum* [Benoist] Eyma) were archived in the herbarium of The New York Botanical Garden. These two species, if left in *Eschweilera*, cause problems with the herbarium sheets and secondary specimens they voucher (i.e., if this is not done the herbarium sheets and all secondary collections will be misidentified). Likewise, phylogenies will have two species of *Eschweilera* embedded in *Lecythis* (Fig. 2A) and the two species will be mapped as *Eschweilera* instead of *Lecythis*. This problem goes beyond a single herbarium because similar changes have to be made on duplicate specimens and subsidiary objects archived in other herbaria. For the most part, trained herbarium staff are too few to keep up with this time-consuming work.

Interpreting biogeographic patterns depends on phylogenies with resolved and dated trees at the species level. Unfortunately, published phylogenies of Lecythidaceae (Mori et al. 2007; Huang et al. 2015) are not well resolved and have not been dated. In addition, it is difficult to understand the abiotic causes leading to the evolution of species without knowing when events, such as the formation and disappearance of large, inland Amazonian wetlands (such as the Lake Pebas system, Sacet 2014), took place. The resolution problem might be corrected when cladograms based on more species as well as more genes are used, but this is not guaranteed because missing links, caused by extinct and uncollected species, might cause incorrect interpretations of phylogenies. For example, *Lecythis poiteaui* is bat-pollinated (Mori et al. 1978) and was recovered as sister to the bee-pollinated *L. prancei* S.A. Mori (Mori et al., 2007). When another bat-pollinated species (*L. barnebyi* S.A. Mori), was added to the analysis ((Huang et al. 2015) it negated the sister relationship between *L. prancei* and *L. poiteaui* (Fig. 2A).

Ecology of New world Lecythidaceae

Trees of *Bertholletia excelsa* occur most frequently in formerly disturbed *terra firme* forests that develop on well-drained soils. Murça-Pires and Prance (1977) pointed out that *Eschweilera coriacea* (as *E. odora*), and *Lecythis idatimon* (as *L. amara* Aubl.) prefer *terra firme* forests. Mitchell and Mori (1987) demonstrated that even slight variations of altitude in *terra firme* forests make a difference on species distributions. For example, *Corythophora rimosa* and *Eschweilera micrantha* (O. Berg) Miers prefer ridge tops, and *Lecythis corrugata* and *Eschweilera coriacea* prefer the slopes and bottoms of hillsides in the forests of central French Guiana. In a study of the non-flooded forests of central Amazonian Brazil, 37 species of Lecythidaceae were found among the 7,791 individuals of Lecythidaceae documented in a 100-hectare plot of *terra firme* forest, indicating how important the Lecythidaceae are in that habitat (Mori et al. 2001). Approximately 70% of the New World species of Lecythidaceae are found in lowland, non-flooded forests.

Species such as *Allantoma lineata*, *Couratari gloriosa* Sandwith, *Couratari tenuicarpa* A.C. Sm., *Couroupita subsessilis*, *Eschweilera albiflora* (DC) Miers, *E. ovalifolia*, *E. parvifolia*, *E. tenuifolia* (O. Berg) Miers, *Lecythis pneumatophora* S.A. Mori, and *L. rorida* O. Berg (formerly treated as a synonym of *L. chartacea* by Mori & Prance 1990) prefer wetter areas along rivers or low wet areas within non-flooded forests. A few species of Lecythidaceae, such as *Gustavia augusta*, inhabit periodically flooded forest along the Amazon but are sometimes also found in wet areas within forests or even areas that are never inundated.

Black-water (Parolin et al. 2004) and white-water (Campbell et al. 1986) periodically flooded forests have fewer species than non-flooded forests (Arias et al. 2016) and this observation is confirmed by the small number of species of Lecythidaceae found in these habitats. Lower species diversity of Lecythidaceae in flood plain forests is probably caused by the difficulty of trees to adapt to both flooding and dry periods during the course of a year, especially when either the wet or the dry seasons are longer and more intense than normal or if extreme flooding or dry periods occur in consecutive years. An example is the prolonged flooding of a *terra firme* forest in central Amazonian Brazil from January to May 1989. In this case, many individuals of Lecythidaceae died in the flooded areas because the trees were weakened by the prolonged lack of oxygen in the soil. Wood-boring beetles attacked the trees and left piles of sawdust at their bases (Mori & Becker 1991) thereby increasing tree mortality of Lecythidaceae. The skeletal tree trunks along the Rio Cueiras in Amazonas, Brazil demonstrates that even trees adapted to periodic flooding are killed by excessively long periods of flooding, especially if they occur several years in a row (S.A. Mori, pers. obs.).

The most common species of Lecythidaceae found in savanna are *Eschweilera nana*, *E. subcordata* S.A. Mori, *L. minor*, *L. ollaria*, *L. schomburgkii* O. Berg, *L. brancoensis* (R. Knuth) S.A. Mori, and *L. schwackei* (R. Kunth) S.A. Mori. The *cerrado* biome of the Planalto of Brazil is a type of savanna that covers two million km^2 in Central Brazil. This vegetation type has been estimated to harbor as many as 6,429 to 10,500 species of vascular plants, of which 35% are endemic (Ratter et al. 2006; Fiaschi & Pirani 2009). Species of plants confined to *cerrado* have been estimated to be less than 10 mya old (Pennington & Lavin 2015) so it is likely an area of recent flowering plant diversification. Like many species of trees in the *cerrado, E. nana* is a small tree with thick bark and a relatively thick seed coat, both of which protect it from periodic savanna fires (see “Atlantic Forest”) for additional discussion of this species).

Species of Lecythidaceae occur in the cloud forests of the Andes of South America (e.g., *Eschweilera antioquensis* Dugand & Daniel and *E. sessilis* A.C. Sm.), eastern Panama (e.g., *E. jacquelyniae* S.A. Mori), and the coastal mountains of Venezuela (e.g., *E. perumbonata* Pittier). About five species of *Grias* grow in cloud forests. For the most part, only species of *Grias* and *Eschweilera* have been able to adapt to the cool, wet conditions of cloud forests. Because they are difficult to collect, many cloud forest species of the latter genus represent new species. Species of Lecythidaceae do not occur in higher vegetation types such as *páramo.*

Sometimes species of the same genus occur in adjacent flooded and *terra firme* forests; for example, *Allantoma lineata* grows mostly along periodically flooded rivers while *Allantoma decandra* (Map 10) is found in non-flooded forests. The former is water-dispersed with seeds possessing a vestigial unilateral wing and a corky seed coat, and the second is wind-dispersed with seeds possessing a well-developed unilateral wing (Ducke 1948). When the seeds of *A. lineata* are ripe they fall into the water and are carried downstream by river currents. The seeds survive in water for at least three months without losing their ability to germinate (Prance & Mori 1979).

Some of today’s Amazon riverine species may have pre-adapted to wet habitats while growing in hypothesized marshlands surrounding Lake Pebas (Sacet 2014). The Purus Arch in Central Amazonia started to erode about 11.8 mya and, because of continued erosion, the Amazon River reached its current configuration at about 2.4 mya (Figueredo et al. 2009). Caputo and Amaral Soares (2016), however, claim that the subsidence of the Gurupá Arch in the late Miocene had the most impact of the change of the Amazon River from the east to the west. During this time, plant species, such as *A. lineata* and those cited by Kubitzki and Ziburski (1994), became established along the banks of the newly formed periodically flooded Amazon River and its tributaries. The complexity of wetland habitats and their association with the Andean uplift (Hoorn 1993; Hoorn et al. 2010, 2017) most likely had an important role in the evolution of Amazonian Lecythidaceae as well as other plants.

Today, individuals of *Allantoma lineata* are common along rivers from northwestern Amazonia to the mouth of the Amazon (Map 10). We suggest that this species lost the unilateral seed wing and developed a corky seed coat as an adaptation to water dispersal. In contrast, *terra firme* species of *Allantoma* have winged seeds that facilitate dispersal by wind as do most species of *Cariniana* (Fig. 10D) and *Couratari* (Fig. 10F) but the species of these genera have not lost their seed wings even though several species of *Couratari* (*C. riparia* Sandwith and *C. tenuifolia*) are riverine species.

We hypothesize that *Allantoma lineata* first evolved in wet areas in northwestern Amazonia and from there dispersed downstream to near the mouth of the Amazon River. Even though back currents can carry seeds upstream, it seems unlikely that they could carry seeds upstream far enough to account for the current distribution of this species. It is also possible for fish to carry viable seeds upstream for very long distances (Anderson & Nuttle 2011) but only if the seeds are not masticated. For example, viable seeds are transported for long distances by frugivorous fish such as the *tambaqui* (*Colossoma macropomum*) (Anderson et al. 201l; Araújo-Lima & Goulding 1997) but this fish eats both the pulp of some species and crushes the seeds of other species (Gottsberger 1978). Long distance dispersal of the seeds of *A. lineata* by fish is unlikely because the only parts of the fruit for fish to eat are the embryos of the seeds (the pericarp is woody) so if the seeds are masticated as they pass through their digestive tracts they no longer germinate. Because it is difficult to identify the macerated seeds of *A. lineata* we have not seen reports of predation by fish of this species. On the other hand, the riverine *Gustavia augusta* (incorrectly reported as *G. speciosa* (Kunth) DC.) possesses hard seed coats embedded in pulp that have been reported to be dispersed by fish that eat the pulp and defecate intact seeds (Lucas 2008).

Although some species of Lecythidaceae have adapted to flooded forests, cloud forests, and savannas habitats, most of the New World species are adapted to non-inundated lowland rainforests. Kubitzki (1997) pointed out that biodiverse genera of flowering plant families often include widespread difficult to identify species found in lowland forests. In general, Lecythidaceae that occur in dry and flooded habitats have strong habitat selection (Sexton & Dickman 2016) and are less difficult to identify than species of widespread lowland rain forest species (Kubitzki 1977; Pennington & Lavin 2015).

Pleistocene refuges

Haffer (1969 2008) and Simpson and Haffer (1978) proposed that speciation of Amazonian forest birds was driven by oscillations between dry and wet periods. During glacial periods, considerable quantities of water were tied up in glacial ice which, in Haffer's model, allowed savannas to expand to such an extent that forested refuges became islands in a sea of savanna. According to this theory, when generalized to plants (Prance 1974), the expansion of dry vegetation in glacial periods fragmented populations of forest-adapted Lecythidaceae leading to allopatric divergence. With the arrival of an interglacial period water became available again and forests expanded such that drier areas were no longer an impediment to the migration of forest plants. When the original populations came together again they were: (1) not morphologically changed enough to be treated as separate species, (2) morphologically different but retained the ability to interbreed thereby creating hybrids, or (3) morphologically distinct enough to be recognized as new taxa.

The Pleistocene refuges hypothesis was originally supported in both studies of plants and animals (Simpson & Haffer 1978; Prance 1982, 1987). However, based on geological and paleoecological data, others challenged the hypothesis (Colinvaux et al. 1996, 2001). These authors claimed, "All geological data from Amazonia imply continuous humid weathering throughout late Tertiary and Quaternary times, with all claims for arid land processes shown to be in error." In addition, they noted, "no pollen data suggest increased coverage of savanna in glacial times." Endler (1982) added, "...many of the assumptions of the refuge hypotheses are not justified" and "The current distributions are consistent with geographic divergence and adaptation to present day ecogeographic factors." Recent studies of Pleistocene vegetation changes have demonstrated that oscillating water cycles in Amazonia did occur over the last 45,000 years, but they concluded that lowland wet forest did not change to large expanses of savanna during glacial periods (Bush 2017; Wang et al. 2017).

In contrast to the idea that there were no major changes in the extent of savanna during the Pleistocene, a study by Hammen and Absy (1994) found that some forests were replaced by savannas during interglacial periods. Hoorn et al. (2017) found that the presence of grass pollen suggest that dryer vegetation types were present from the late Miocene to Pleistocene. They emphasized that grass pollen percentages were much more common between 2.6 and 0.8 mya than they are today. Another question is why do biologists generally agree that forest expanded during interglacial periods and savannas became more prominent in glacial periods in Africa (Baker 2008)? It seems unlikely for forest plants and savanna plants of the Amazon to respond differently to the same environmental cues as those of tropical Africa. These studies support the idea that at least some areas of savanna and dryer forests replaced wet forests during glacial periods suggesting that the Pleisocene refuge hypothesis may have merit after all.

Prance (1974, 1987) recognized 8 Pacific coast, three Atlantic Forest, and 15 Amazon/Orinoco/Guayanan Pleistocene refuges. Even if these forest refuges did exist, they were not absolute barriers to the migration of Lecythidaceae because: (1) forests and savannas, as they do today, formed a mosaic of these two vegetation types and that would have facilitated movement from one forest refuge to another; (2) some species of Lecythidaceae, such as *Cariniana estrellensis* (Leite 2007), would have been able to move from one forest refuge to another by migrating along gallery forests; and 3) some species, such as *Cariniana ianeirensis* and *Couratari macrosperma*, prefer wet forested areas but can also tolerate dryer habitats.

In summary, distributions of New World Lecythidaceae do not support or negate the Pleistocene refuge hypothesis. Current distributions sometimes coincide with one or more places that have been hypothesized to be plant refuges (e.g., in the Guayana and Imataca refuges of the Guianas, in the Napo and East Peru refuges of western Amazonia, and the Chocó refuge of Eastern Panama and northwestern Colombia along the Pacific coast. Because there are so few species of New World Lecythidaceae in dry forests and savannas and their pollen grains are so similar to those of many other plant families it will be difficult to use this family to test the Pleistocene refuge hypothesis.

Two inexplicable distributions

Asteranthos brasiliensis (Map 3) is native in north central Amazonian Brazil and southern Venezuela where it grows in periodically flooded forests on white sand along the Negro and Orinoco river basins. This species has been treated as belonging to Lecythidaceae subfam. Napoleonaeaoideae (Prance & Mori 1979), as the monotypic family Asteranthaceae (Knuth 1939b), and most recently as a member of the Scytopetalaceae (Tsou 1994; Appel 1996, 2004). The latter placement is based on both molecular and morphological data (Morton et al. 1997, 1998), which make a strong case for the relationship between the Amazonian *A. brasiliensis* and the African species of Scytopetalaceae (Tsou 1994a; Apple 1996, 2004; Morton et al. 1997; Mori et al. 2007). There are no other species in the Lecythidaceae clade that share the combination of a corona derived from petals and ruminate endosperm as do *A. brasiliensis* and genera of the Scytopetalaceae. Although the origin of the corona is debated, Ronse de Craene (2011) argues that "In Napoleoneae (= Napoleonaeaceae) and Scytopetaloideae (= Scytopetalaceae), including *Asteranthos*, the petals are transformed into a plicate corolla closely linked to the androecium." Frame and Durou (2001) also interpret the showy corona of the flower of the related *Napoleonaea* as being derived from modified petals.

The wide disjunction between *A. brasiliensis* in central Amazonia and other Syctopetalaceae in western Africa is difficult to explain. This species has a single-seeded fruit dispersed by water aided by a calyx with a rim that keeps the fruit afloat. Thus, this disjunction might have been caused by long distance water dispersal from Africa to central Amazonia via sea embayments along the current Amazon and Essequibo Rivers (Frailey et al. 1988; Hovikoski et al. 2007).

The other disjunction is that of *Petersianthus* of the Barringtonioideae. One species, *Petersianthus africanus* (Welw. ex Benth. & Hook. f.) Merr., is found in Africa and the other, *P. quadrialatus* Merr, is limited to the Philippines. The numerous stamens with long filaments, inferior ovary, long style, and syntricolporate pollen suggests that this genus belongs in the Barringtonioideae but this needs confirmation because neither of the species have not yet been included in a molecular phylogeny of the Lecythidaceae clade.

Lecythidaceae and Gondwanaland

Distributions similar to those of the Lecythidaceae clade (Map 1) are sometimes explained as derived from widespread ancestral populations separated by the breakup of Gondwanaland (Raven & Axelrod 1972). As a matter of convenience, we include what is now Southeast Asia as part of Gondwanaland, a concept supported by Ridd (1971, 1972) but challenged by Stauffer and Gobbett (1972). Beaulieu et al. (2013) provide a useful literature review of this topic.

In addition to Lecythidaceae, other tropical tree families, such as Annonaceae, Bombacaceae, Burseraceae, Byttneriaceae (formerly part of Sterculiaceae), Cochlospermaceae, Combretaceae, Ebenaceae, Erythroxylaceae, Flacourtiaceae, Hernandiaceae, Hugoniaceae, Icacinaceae, Ixoxanthaceae, Lauraceae, Meliaceae, Memecylaceae, Monimiaceae, Myristicaceae, Ochnaceae, Olacaceae, Proteaceae, Putanjivaceae, Sapotaceae, Stemonuraceae, Simaroubaceae, and Theaceae have similar distributions (Heywood & Brummit 2007). This does not include families that are found today only in South America and Africa (e.g., Cecropiaceae and Chrysobalanaceae), families that appear only in South America and Southeast Asia (e.g., Symplocaceae), families that are widely distributed such as the Fabaceae (Heywood & Brummit 2007), families dominated by herb and shrub growth forms, and families represented by a few species disjunct between Africa and South America (e.g., *Sacoglottis* of the Humiriaceae, *Erismadelphus exsul* Mill. Br. and *Korupodendron songweanum* Litt & Cheek of the Vochysiaceae). This list indicates that there are many flowering plant tree families common to Central and South America, Africa, and Southeast Asia—but relatively few families that share species only between South America and Africa or between South America and Southeast Asia.

Gondwanaland presumably started to separate in the Jurassic, and Rufel et al. (2016) state that South America and Africa separated between 110–80 mya and the final connections between South America, Antarctica, and Australia were severed in the Cretaceous 55–41 mya. Using these dates, a mid-Cretaceous appearance of flowering plant families could have taken place before the break-up of Gondwanaland. As of yet, there are no phylogenies of the Lecythidaceae clade that support or negate this hypothesis.

In the early Cretaceous, some mammals evolved dental adaptations needed for feeding on flowering plants (Brusatte & Luo 2016). The sudden appearance of both the flowering plants and mammals in the fossil record of the Cretaceous supports the idea that diversification of both groups may have facilitated coevolution between them. Although Lecythidaceae have few mammal pollinators (all bats), many mammals disperse and/or prey on their seeds.

The origen of at least some flowering plant families has been calculated to be too young to have their distributions impacted by the separation of Gondwanaland (Davis et al. 2002; Ruhfel et al. 2016). In contrast, others conclude that the Gondwanaland break-up explains, at least in part, the current distributions of some flowering plant families. Some authors suggest that both continental separation combined with long-distance dispersal may explain intercontinental range disjunctions (Barker et al. 2007; Mennes et al. 2015). Sanmartín and Ronquist (2004) studied the biogeography of animals and plants of the southern hemisphere and concluded that some of the distributions may have been caused by Gondwana separation combined with long-distance dispersal; with long-distance dispersal playing a more significant role in plants than it does in animals.

Interchange between Old and New World Lecythidaceae

Old World Lecyythidaceae subfam. *Barringtonioideae* (= barringtonioids) and New World species of *Grias* share many morphological features. These characters are pachycaul growth forms; large leaves clustered at the ends of stems in many but not all species of either; a calyx that has well-defined lobes (only in *G. neuberthii* in the New Word) or, more frequently, a fused calyx that covers the bud and splits into irregularly shaped lobes at anthesis (ca. 60% of the species of *Barringtonia*, Payens 1967; Prance 2012); the presence of a ring nectary at the summit of the ovary (most barringtonioides and some *Grias*); pendulous ovules attached at the apex of the ovary in all species of both genera (not found in any other genus of New World Lecythidaceae); and universally single-seeded fruits with sparse endosperm. However, the flowers of *Grias* are thick and fleshy; have stamens placed on the inside of the staminal tube instead of only on the rim of the staminal tube; and possess a much shorter style than species of Barringtonioideae. Although *Gustavia* does not share some of the above features with species of the Barringtonioideae both usually have a pachycaul growth form, large leaves, and many stamens attached to the rim of a staminal tube. *Grias* and *Gustavia* and every other New World Lecythidaceae lack the long style of the barringtonioids and possess tricolpate pollen (Erdtman 1952; Muller 1979) whereas the barringtonioids have extremely long styles and syntricolpate pollen (Fig. 7; Erdtman 1952; Muller 1972, 1973, 1979, 1981; Tsou 1994b; Manchester et al 2015). The co-occurrence of many shared characters between barringtonioids and *Grias* and *Gustavia* could also be explained as symplesiomorphy or homoplasy given that *Barringtonia* is not particularly closely related to the latter two genera based on molecular data (Fig. 1).

We hypothesize that the ancestors of the New World Lecythidaceae originated in Southeast Asia, where all species of Lecythidaceae have actinomorphic flowers (Figs. 3A–D, and migrated from there into Africa (only a few species) and Central and South America or, as discussed above, are the results of the Gondwanaland breakup. African Napoleonaeaceae and Scytopetaceae have actinomorphic flowers but they are morphologically distinct from other species of the Lecythidaceae clade. In contrast, some of the New World species retain actinomorphic flowers similar to species of *Barringtonia* while others evolved zygomorphic flowers in response to pollination by robust, long proboscis bees, such as carpenter and euglossine bees (Huang 2010).

In addition to the breakup of Gondwanaland, another explanation for the current distribution of Lecythidaceae is long-distance dispersal. Some authors explain disjunct distributions as caused by the ability of plants and animals to disperse over long distances (Queiroz 2014), as is the case with Lecythidaceae. For example, the boreotropical migration route posits that tropical forests in Laurasia and Central America occurred further north into Europe and North America than today (Brusatte & Lou 2016). Davis et al. (2002) proposed that the Malpighiaceae originated in northern South America, repeatedly migrated into North America, and from there dispersed into the Old World via the North Atlantic land connection. They argue that vicariance cannot explain the presence of Malpighiaceae in both South America and Africa because the continents had separated long before the origin of Malpighiaceae. In a study of legumes, Lavin and Luckow (1993) hypothesized that a present-day center of diversity in tropical North America, and with an early Tertiary fossil record from any region there, has a high probability of having sister-group relatives in the Paleotropics and derived relatives in South America.

Fossil syntricolpate pollen similar to species of barringtoniods has been found in Germany from the Middle Eocene (Manchester et al. 2015) and in India from the Tertiary (Muller 1981). In addition, a fossilized barringtonioid fruit was discovered in India from the Tertiary (Mehrotra 2000). The endocarps of some barringtonioids are woody and preserve well; thus, their absence in the fossil record of western Laurasia does not support the idea that Lecythidaceae migrated across Laurasia, along the length of Central America, and into South America. Likewise, easy to identify syntricolpate pollen fossils of Lecythidaceae have not been discovered in the western parts of Laurasia. Nevertheless, it has been shown that northern tropical species are present in Mexico; for example, Wendt (1993) concluded that at least 25% of the tree species of the Mexican lowland rain forests are derived from "northern latitude tropical progenitors."

The dating of animal and plant fossils approximates the dates when taxa first evolved in the form of minimum ages (Beaulieu et al. 2013). For example, mammals are now considered to be older than they were previously thought to be (Brusatte & Luo 2016). Likewise, Hochuli and Feist-Burkhardt (2013) discovered angiosperm-like pollen grains in Switzerland from the Middle Triassic. Yin-Long et al. (1999) proposed that flowering plants dominated landscapes in the mid-Cretaceous as far back as 90 mya and Taylor et al. (2009) indicate that flowering plant fossils were scant before the Cretaceous. If flowering plants did appear in the fossil record that long ago then early lineages of Lecythidaceae could have been separated by the fragmentation of Gondwanaland. The oldest fossils of Lecythidaceae come from the Upper Cretaceous (Table II).

Another migratory route might have been long-distance water dispersal combined with island hopping from Asia along the southern hemisphere to the west coast of South America. Several species of Barringtonia (*B. asiatica* L. Kurz, *B. racemosa* and *B. acutangula*) have fruits with thick, coconut-like husks that facilitate water dispersal (Prance 2012). Today, drift currents flow in directions that make it possible for the fruits of these species to float to the western coast of northern South America and eastern Central America (Strub et al. 1998). If similar currents were present in the distant past then barringtonioids could have migrated from Asia to the Neotropics. However, the forests along this migration route at that time were probably temperate (e.g., *Nothofagus* forests) and, thus, this hypothesis does not support migration of tropical barringtonioid species over wide expenses of ocean under temperate climate conditions.

Although relatively few fossils of Lecythidaceae have been collected, fossil leaves, wood, a single flower, pollen, and fruits of Lecythidaceae have been described (Table II). Because of the difficulty in identifying fossil leaves and wood, previous determination as Lecythidaceae are not as reliable as determinations of fossil syntricolpate pollen, flowers, and fruits. A fossil flower, *Lecythidoanthus kugleri* Berry, was collected from Miocene deposits in Trinidad. In this fossil, the androecial hood is missing, but what remains looks similar to a species of *Couratari* as suggested by Knuth (1939a). One of the fossil fruits, *Barringtonia preracemosa* Mehrotra gathered from Oligocene deposits in India, is a good match for a fruit of *Barringtonia*. Another fossil fruit, *Lecythidopyxion girardotanum* Huertas collected in Cundinamarca, Colombia, is similar to some fruits of extant species of *Eschweilera* but the age of the stratum from which it was gathered was not provided (Huertas 1969). A carbonized Brazil-nut seed was discovered by Roosevelt et al. (1996) at the Pedra Pintada Cave near Monte Alegre in the state of Pará, Brazil. The cave was occupied nearly 11,000 years ago. Such a recent discovery is not useful for hypothesizing when the Brazil nut separated from its ancestors, but can be employed to test hypotheses about the time it took Brazil nut trees to migrate from hypothesized forest refuges to other areas during interglacial periods (Thomas et al. 2014).

Pollen grains offer the best opportunity to date evolutionary changes in Lecythidaceae because of the following: (1) the syntricolpate pollen of the barringtonioids, especially species with marginal grooves, marginal ridges, and polar cushions (Fig. 7, Types I–III; Muller 1972, 1973; Tsou 1994b; Manchester et al. 2015) are easy to distinguish from Lecythidaceae with tricolpate pollen (Fig. 7, Type I, Muller 1973, 1979); (2) syntricolpate pollen is extremely rare in other extant plant families (e.g., Caryocaraceae and some species of Myrtaceae; Erdtman 1952); (3) the age of syntricolpate pollen has been dated to at least the lower Eocene (Muller 1981) and Martínez-Millán (2010) dated the first Asterids, in which the Lecythidaceae are placed, as at least 89 mya; and (4) the interaction between species of Barringtonioideae and bats could give clues to estimating the age of pollen-type evolution in the Lecythidaceae clade. This assumes that the evolution of the large syntricolpate pollen in this group was the result of selection by large-sized fruit bats (the family Pteripodeae). The oldest known bat fossils were discovered in Europe, Africa, and Australia in the Eocene (Gunnell & Simmons 2005) and pollen of barringtonioids appeared in the fossil record in the Lower Eocene in India (Muller 1981) and the Middle Eocene in Germany (Manchester 2015). The high diversity of both large fruit bats and species of barringtonioids in Southeast Asia is consistent with the idea that large, syntricolpate pollen evolved as the result of coevolution with large fruit bats in the Old World. In contrast, pollinating bats in the New World Phyllostomideae are not nearly as large as their Old World (family Pteripodeae) counterparts (Fleming et al. 2009).

Stroo (2000) studied 130 plant species in 23 different families of which 75 species were bat-pollinated and 55 species were pollinated by other pollinating agents. In this study, the only parameter linked to bat-pollination was the larger size of the pollen grains; for example, in that study Lecythidaceae were represented by three New World species of *Lecythis* (21–29 microns) and four Old World species of subfamily Barringtonioideae (35–65 microns). The pollen size difference hints that larger Old World bat pollinators select plants with larger pollen whereas smaller New World bat pollinators collect smaller pollen. The small sample size used in the analysis requires that this suggestion be studied using a larger sample size of of pollen from all lineages of the Lecythidaceae clade.

Although species of barringtonioids are thought to be bat pollinated, there are only a few studies that have supported this hypothesis. Solomon Raju et al. (2004) observed a large fruit bat, two smaller bats, and birds visiting the flowers of *Careya arborea* Roxb. and concluded that the most efficient pollinators were large bats. Tanaka (2004) reported that moths visit the flowers of the widespread *Barringtonia racemosa* but pointed out that bats do not occur on the island where the study took place. Although we suggest that barringtonioid ancestors colonized the New World there are currently no native species with syntricolpate pollen from there, possibly because large fruit bats are absent in the New World. Among the New World Lecythidaceae only two species, *Lecythis poiteaui* (Mori & Prance 1990) and *L. barnebyi* (Mori & Lepsch-Cunha 1995), have been documented to be pollinated by bats. These relatively small bats (in comparison with Old World fruit bats) seek nectar as a reward when they are pollinating these two species. Inflorescence and floral characters and probable nocturnal flowering (N.P. Smith, pers. comm., 2017) of *L. brancoensis* is shared with the two preceding species suggesting that bats also pollinate this species. As mentioned above, the pollen of these species of *Lecythis* are small compared to the larger pollen grains collected by Old World bat pollinators (Stroo 2000).

Widespread distributions of New World Lecythidaceae

With enough time, suitable habitats, efficient dispersal systems, and the lack of major barriers to migration, some New World Lecythidaceae have achieved widespread distributions. Thomas et al. (2014) estimated the rate of *Bertholletia excelsa* migration which gives an idea of how fast this species of lowland Amazonian forests can migrate from one area to another. They assumed that a forest refuge harboring a Brazil nut population 400 to 500 km from another refuge would take at least 8,000 to 10,000 years to bridge the gap.

Species of *Allantoma* (with the exception of at least *A. lineata*), *Cariniana* (Fig. 10D), and *Couratari* have winged seeds (Fig. 10F) dispersed by the wind after the fruit opens and the seeds fall out. The wings are unilateral in the first two genera and surround the seed in the last genus (Tsou & Mori 2002). *Allantoma lineata* (Fig. 10E) and *Eschweilera tenuifolia* (Fig. 10G) have corky seed coats that facilitate water dispersal. The former species has a vestigial seed wing because it is no longer dispersed by the wind, as are most species of the genus. The latter has lost the lateral aril found in most species of the *Eschweilera parvifolia* clade which are dispersed by animals. *Lecythis rorida* is indehiscent so the fruits drop into the water with the seeds trapped inside. The fruits float away and do not release seeds until the pericarp rots. These last two species have lost their arils because they are dispersed by water and not by aril-eating mammals (e.g., bats).

Figure 8. Greater spear-nosed bat (*Phyllostomus hastatus*) removing a seed with its attached aril from the fruit of a *sapucaia* tree (*Lecythis pisonis*). The bat carries the seed away from the tree to its night roost and the seed is dispersed when it is accidently dropped in flight or when it falls to the ground under the night roost after the aril has been eaten. Painting by M. Rothman.

The *Lecythis pisonis* clade (Map 13) has woody fruits sometimes as large as a human head. This clade possesses fruits that open by an operculum that makes the seeds available for dispersal by bats. The seeds are large and fusiform with well-developed basal, white, edible arils that surround the funicles (Figs. 8, 10J). When the fruit opens, the seeds remain inside. Bats have been documented removing seeds from the fruit (Greenhall 1965) and flying away from the trees, presumably to their night roosts. The bats most likely drop some seeds by accident when flying but most of the time they probably eat the aril and the seeds fall to the ground under their roosts. Bats apparently do not eat the seeds because the seed coat is too hard for them to open to extract the embryo. This clade is widespread in Amazonia, occupies much of the length of the Atlantic Forest of Brazil, and ranges from northwestern Ecuador to Nicaragua. Because species of this clade are cultivated for their edible seeds, their current distributions have been altered. Today, local people living along the Amazon and Solimões rivers and their tributaries often have trees of the *sapucaia* planted on their property.

Another widespread species of Lecythidaceae is that of the monotypic *Bertholletia excelsa* native to Amazonia (Map 16). However, the distribution of this species does not include two vast areas, one south of the Amazon River in western, central, and eastern Amazonia and another in an east to west band north of the Amazon River running below the southern boundaries of Surinam, Guyana, and Venezuela). An understanding of the distribution of this species is complicated by the fact that Brazil nut trees are frequently planted by humans (Thomas et al. 2014). In addition, the linear distribution of many collections along rivers (Map 16) probably represents trees planted for their edible seeds. Shepard and Ramirez (2011), based on ecological, phytogeographical, genetic, linguistic, and archeological data, make the argument that the original distribution of the Brazil nut was in "northern/eastern Amazonia origen" from where it was subsequently spread by humans to southwestern Amazonia.

Figure 9. Dispersal of the Brazil nut (*Bertholletia excelsa*). The seeds are trapped inside of the fruit because the opercular opening (Fig. 10C) is smaller than the seeds. After the fruits fall to the ground mammals, such as the red-rumped agoutis (*Dasyprocta leporina*) illustrated here, remove the seeds from a fruit by gnawing around the edge of the opercular opening to make it large enough to remove the seeds. Some of the seeds are consumed but others are buried for future consumption and those that are not relocated may germinate and grow into adult trees. Painting by M. Rothman.

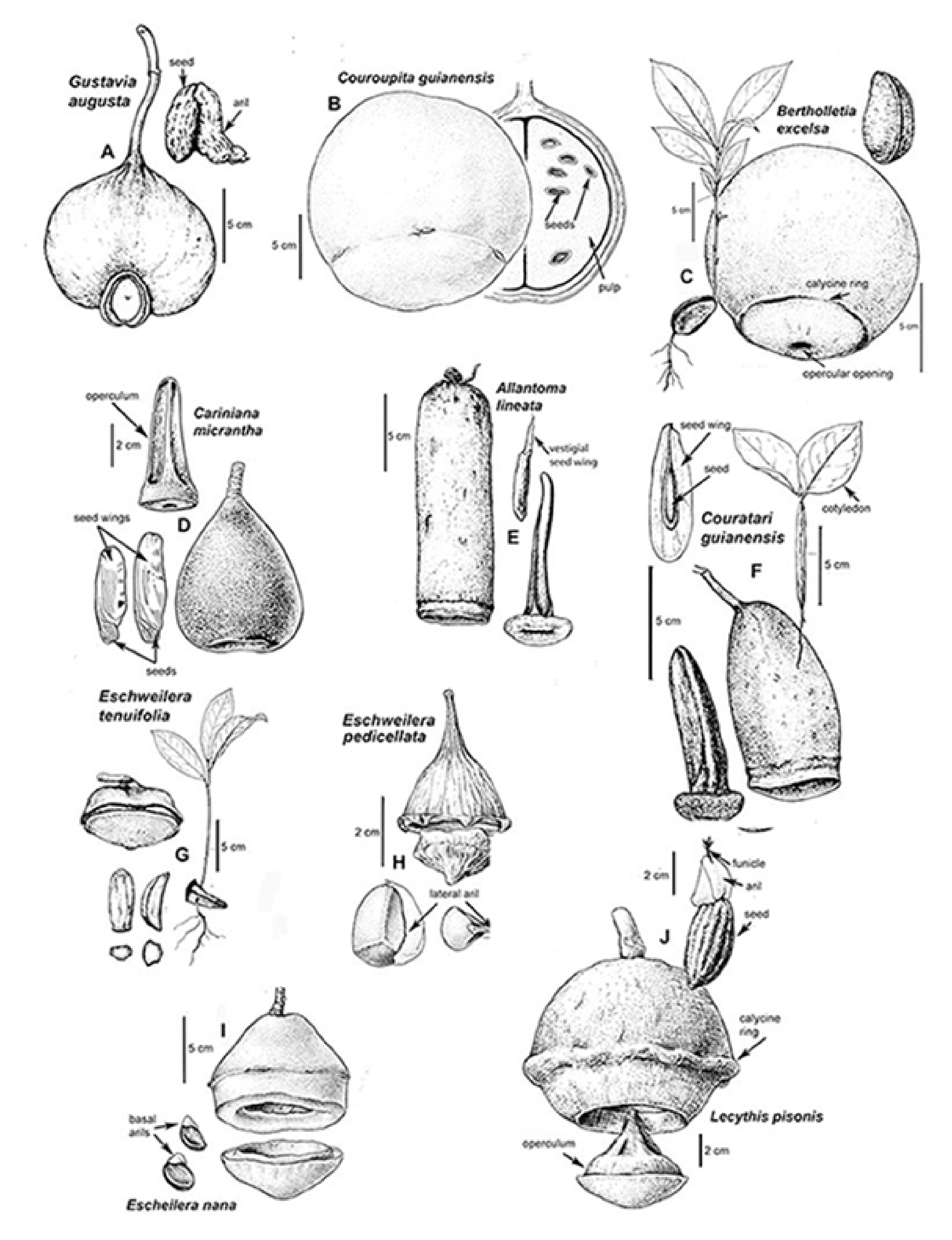

Figure 10**.** Fruits and seeds of New World Lecythidaceae. The fruits are indehiscent (A, B), secondarily indehiscent (C), or dehiscent (D–J). They are adapted for dispersal by animals (A, B, C, H–J), wind (D, F), and water (E, G). Drawings A, C, E–G. by H. M. Fukuda, D by A. Tangerini, and B, H–J. by B. Angell.

Reátegui-Zirena et al. (2009) concluded that trees they studied in seven populations using molecular data formed a panmictic population. They attributed this to the longevity of the species, an allogamous reproductive system, bee pollinators that can fly at least 20 km in a day (Janzen 1971), and the lack of barriers to seed dispersal by agoutis. As mentioned above, panmictic populations of this species could have also been created by the introduction of germplasm from trees planted by humans.

At maturity the large, round, woody fruits of the Brazil nut fall to the ground with 10 to 25 seeds trapped within the fruits. Agoutis (*Dasyprocta* spp.; Huber 1910), acouchis (*Myoprocta* spp.) and, less frequently squirrels (Tuck Haugaasen et al. 2010, 2012) gnaw open the fruits and remove the seeds from the capsules (Fig. 9). Because the seeds are protected by the woody pericarp and because the boney seed coats (Tsou & Mori 2002) are difficult to gnaw open, only animals with sharp teeth and a strong biting force are able to consume them. Agoutis and squirrels eat some of the seeds and cache others for future consumption. Subsequently some of the cached seeds are forgotten by the animals and it is these seeds that may germinate and grow into the next generation of trees.

Before phylogenies of Lecythidaceae were available, Mori and Prance (1990) hypothesized that *Bertholletia excelsa* was related to species like *Lecythis prancei* and *L. lurida*. This hypothesis was based on the following shared characters of these species with *B. excelsa*: the presence of cuticular papillae on the abaxial leaf blade surface; androecial hood appendages swept or curved inward without forming a complete coil; an anterior hood extension; yellow on the distal end of the androecial hood; and mature fruits that fall to the ground with the seeds inside. However, *B. excelsa* differs by possessing two calyx-lobes, thick woody fruits with such small openings that the seeds are trapped inside when the fruits fall, and seeds with thick and hard seed coats. All of these characters are not found in any other Lecythidaceae. For example, *L. prancei* and *L. lurida* have six calyx-lobes; the indehiscent fruits lack an opening; the pericarp is thin and easy to break open; and the seed coat is membranous and easy to remove.

The relationship of *Bertholletia excelsa* with *L. prancei* and *L. lurida* and other species of the *L. poiteaui* clade is not supported by the most recent cladograms of Huang et. al. (2015) (Fig. 2A). *Bertholletia excelsa* is embedded in the *L. ollaria/L. poiteaui/Bertholletia excelsa/L. chartacea* clade (Fig. 2A). The distributions of both the *L. poiteaui* (Map 15) and *L. chartacea* (Map 17) clades superimpose parts of the *B. excelsa* distribution.

Gustavia sect. *Hexapetala* (as defined by Mori in Prance & Mori 1979), of the *Gustavia* clade, is also widely distributed. The members of this group (*Gustavia hexapetala* Aubl., *G. brachycarpa*, *G. dubia* [Kunth] O. Berg, and *G. longifuniculata* S.A. Mori) possess calyx lobes with inverted y-shaped thickenings on their adaxial surfaces and winged hypanthia not found in other species of *Gustavia*.. Individuals of *Gustavia* with these features are widely distributed in the Guayana lowlands, the northern, eastern and western parts of Amazonia, and west of the Andes from northwestern Ecuador to Costa Rica. *Gustavia brachycarpa* is restricted to the Pacific slopes from central Costa Rica to western Panama, while *G. dubia* occurs on the Caribbean side of Central Panama into the Magdalena River valley of northwestern Colombia, and as far south on the western side of the Andes to northwestern Ecuador. The group is absent from the coastal forests of eastern Brazil as well as from southern Amazonian Brazil. There are no field observations on this group's dispersal biology but the presence of pulp surrounding the seeds and an aril suggests that the dispersal of species in this group are arboreal animals, probably monkeys and/or birds. Pieces found on the ground below fruiting trees indicate that mammals or birds or, perhaps both, are dispersal agents. The pulp surrounding the seeds of *Gustavia superba* (Kunth) O. Berg (not part of sect. *Hexapetala*) is consumed by many different animals (Sork 1977).

Couratari guianensis is distributed in the Brazilian Amazon; the Guayana lowlands; Amazonian Venezuela, northern Bolivia, Peru, Ecuador, and Colombia; and Central America as far north as San José, Costa Rica (Map 12). This species is found both south and north of the central cordillera in Central America. When its winged seeds are ripe, they fall from the fruits and are dispersed by the wind.

Allantoma lineata has a widespread linear distribution along major rivers in Amazonia (Map 10). The seeds of this species drop into the water and are carried downstream by river currents, but other species of this genus have well-developed winged seeds dispersed by the wind.

We conclude that at least some taxa of New World Lecythidaceae have the ability to establish themselves over wide areas regardless of their type of dispersal system. The present distribution of some Lecythidaceae on both sides of the Andes suggests that populations of some taxa were widely spread before the uplift of mountains, and then isolated from one another by the formation of mountain barriers such as the Andes. All of the taxa mentioned in this section are lowland species usually not found over 500 m elevation. Thus, it is unlikely that trans-Andean populations had contact with one another after the uplifted mountains reached higher elevations unless they migrated through mountain passes or along coastal areas when sea levels were lower during glacial periods (Scotti-Saintagne et al. 2013).

High species diversity in central Amazonia (Fig. 24)

The forests surrounding Manaus, Brazil, are rich in overall numbers of species and endemics of tree species, and this is also true for Lecythidaceae (Mori et al. 2001). The high diversity and high endemism is, at least in part, the result of intensive collecting by botanists associated with the *Instituto de Pesquisas da Amazônia*, especially because William Rodrigues, Ghillean T. Prance, Marlene Freitas da Silva, the senior author, and those who worked with them targeted Lecythidaceae for collection in this region over a long period of time. In Map 6, the number of collections and the number of species for each grid square shows that Manaus has the highest number of collections of Lecythidaceae from the New World and twice as many species as any other area of the New World tropics; thus, it is clear that biased sampling hinders phytogeographical studies (Nelson et al.,1990).

Oliveira and Daly (1999) and Oliveira and Mori (1999) agreed that high collection density must be considered but added that some of the increase was caused by the evolution of endemic species *in situ* as well as by species reaching the limits of their distributions in central Amazonia (Map 24). To address the hypothesis, Oliveira and Daly (1999) analyzed the distributions of 2,541 Amazonian tree species found in lowland *terra firme* forests in a 100 km radius surrounding Manaus. They found that 7.1% and 42.2% of the *terra firme* species were endemic or had their limits of distributions around Manaus, respectively. They did the same analysis centered on two other areas with high numbers of collections (Santarém and Belém, both in the state of Pará). In these two localities, the null hypothesis that these two areas have the same proportion of endemics and species with distribution limits as found near Manaus was rejected. This supports the idea that increased endemism and migration from different areas—not just the high number of collections— drive tree diversity in the Manaus area.

Additional support for this idea is provided by a comparison in which the presence of species of Lecythidaceae in central French Guiana (Mori 1991) was compared with the Lecythidaceae of a forest north of Manaus (Mori & Lepsch-Cunha 1995). The following species were recorded from both places: *Corythophora rimosa*, *Couratari guianensis*, *C. stellata* A. C. Sm., *Eschweilera collina*, *E. coriacea*, *E. grandiflora* Mart. ex DC., *E. laevicarpa* S.A. Mori, *E. micrantha*, *E. pedicellata* (Rich.) S.A. Mori, and *Lecythis poiteaui*. Ten of the 27 (37%) species in French Guiana also occur in the Amazonian forest, and four (14.8%) of these species, *C. rimosa*, *E. collina*, *E. pedicellata*, and *L. poiteaui*, reach the end of their distributions in the vicinity of Manaus.

The following species are examples of endemics occurring in central Amazonia within a radius of 200 km around Manaus: *Allantoma integrifolia* (Ducke) S.A.Mori et al. (Map 10), *Corythophora alta* and C. rimosa subsp. rimosa (Map 18), *Couratari longipedicellata* W.A. Rodrigues (Map 12), *Gustavia elliptica* S.A. Mori, *Eschweilera amazonica* R. Knuth, *E. amazoniciformis* S.A. Mori, *E. cyathiformis* S.A. Mori, *E. rhododendrifolia* (R. Knuth) A.C. Sm., and *L. barnebyi*. There are also numerous "endemic" species known from a single location that are not included in this list.

In addition, species from western Amazonian Brazil can also reach or nearly reach the central Brazilian Amazon. In the following list, those species reaching Manaus from western Amazonia are marked with an asterisk while those not marked occur only in western Amazonia: *Allantoma decandra**, *Cariniana micrantha**, *Couroupita subsessilis* (riverine)*, *Eschweilera albiflora** (riverine species), *E. andina*, *E. bracteosa** (Poeppig ex O. Berg) Miers, *E. gigantea* (R. Knuth) J.F. Macbr., *E. itayensis* R. Knuth, *E. juruensis* R. Knuth, *E. laevicarpa**, *E. ovalifolia** (riverine species), *E. rufifolia* S.A. Mori, *E. tessmanii* R. Knuth*, *Grias neuberthii* J.F. Macbr., *G. peruviana* Miers, and *Gustavia macarenensis* Philipson. The rich tree flora of western Amazonia reflects the high alpha-diversity from northern Bolivia to southern Colombia (Saatchi et al. 2008).

The occurrence of high species diversity in central Amazonia could be at least partially explained by the drying out of mega-wetlands in western Amazonia that persisted from at least the middle to the late Miocene (Shephard et al. 2010), the presence of sea embayments, and/or the drying out of hypothesized Pleistocene/Holocene Lago Amazonas that presumably covered large expanses of central Amazonia (Frailey et al. 1988; Mori 1991). Tuomisto et al. (1992), however, have debunked the presence of Lago Amazonas as described by Frailey et al. (1988). Over time, the Amazon Basin has experienced the formation and drying out of wetlands related to the uplift of the Andes (Hoorn et al. 2010), seawater embayments (Hovikoski et al. 2007), or the increase of water that occurs during interglacial periods.

Under this scenario, the breakthrough of the Amazon River to the east between 11.8 and 11.3 mya (Figueiredo et al. 2009) or 9.4 and 9 mya (Hoorn et al., 2017) drained the wetlands and opened central Amazonia to migration of Lecythidaceae from various directions, but especially from western Amazonia and the Guayanan lowland forests. In addition, endemic species could have evolved when satellite populations, isolated on large islands covered with *terra firme* forests, evolved into species distinct from the original populations. A possible example of this is the evolution of the endemic central Amazonian *Lecythis barnebyi* when water barriers separated it from widely distributed *L. poiteaui* (Map 15). Based on our most current phylogeny (Fig. 2B) these species are closely related.

Uplift of the Andes

Speciation of some clades and species of Lecythidaceae was driven by the uplift of the Andes. For example, nine of the 12 known species of *Grias* are endemic to the Andes of northwestern Ecuador and Colombia where they are limited to Andean valleys and slopes (Map 7). Because there were no high mountains before the Andean uplift (Gregory-Wodzicki 2000) the ancestors of the Andean species of *Grias* are assumed to have inhabited low elevations. Today, *G. neuberthii* and *G. peruviana* (usually found at 150 to 800 m altitude) are common along the base of the eastern slopes of the Andes, the latter also appears on the western side of the Andes in Ecuador (Map 7). The broadest distribution of a species in this genus is that of *Grias cauliflora* (Map 7), which occurs at low elevations on the western side of the Andes from northwestern Colombia to Belize with a disjunct population in Jamaica (Map 7). In lower Central America this species has populations on both sides of the Central American cordillera, but north of Costa Rica the species is only found on the Caribbean side (Map 7). Numerous, more widely distributed species of other families are disjunct between the Pacific and Caribbean slopes in Central America but most of these are also found in other areas of Central and South America (Cornejo et al. 2012; Dick et al., 2005, 2013), as are *Eschweilera coriacea* and *Couratari guianensis* (Map 12).

The endocarps of *Grias cauliflora* have been collected on the beaches of Florida and San José Island, Costa Rica (Ridley 1930; Johnston 1949; Gunn & Dennis 1976). According to Ridley (1930) the seeds remain viable after floating in fresh water for months but perish when they are exposed to salt water. Nevertheless, the presence of *G. cauliflora* in Jamaica seems most likely to be the result of long distance dispersal by water. The fleshy, edible mesocarp and large-sized, single-seeded fruits of this and other species of *Grias* suggest dispersal by mammals that eat the mesocarp. After the pulp is removed by animals, the endocarp and enclosed seed may be secondarily dispersed by water.

Jacaranda copia (Aubl.) D. Don (Bignoniaceae) is found on both sides of the Andes. This species consists of two subspecies: *J. copaia* subsp. *copaia* and *J. copaia* subsp. *spectabilis* (Mart. ex A. DC.) A.H. Gentry. The first is distributed in the Guayana lowlands and the second is widespread in lowland moist and wet forests from Belize to Bolivia. The low genetic variation between the *cis*/*trans* populations suggests that this disjunction did not arise from the separation of the Amazonian and *trans*-Andean populations caused by the uplift of the Andes (Scotti-Saintagne et al. 2013). These authors hypothesize that the progenitors of the *trans*-Andean population may have migrated around the northern part of the Andes when sea level was lower. Presumably, the exposed area would have been covered by savannas or dry forests. However, most Lecythidaceae are not adapted to savannas or dry forests (see section "Ecology of New world Lecythidaceae"). The broad ecological tolerance of some species of Lecythidaceae could have favored their dispersal through a dry northern dispersal corridor along the Caribbean coast but there are only a few extant species of Lecythidaceae in this region that tolerate dry habitats (e.g., *L. minor*). On the other hand, this and other species of various families may have circumvented Andean barriers by migrating through lowland passes (Scotti-Saintagne et al. 2013). These authors conclude that the trans-Andean distribution of taxa of *Jacaranda copia* is the result of recent events after the uplift of the Andes.

The *Lecythis ollaria* clade (Map 14) includes only three species—two (*L. ollaria* and *L. minor*) adapted to savannas and one (*L. tuyrana*) adapted to wet forests. In this case, it is also possible that the first two species adapted to a dryer climate from a progenitor similar to *Lecythis tuyrana* or *vice versa* but these scenarios are not supported by molecular data (Fig. 2A). *Cariniana pyriformis* (Map 11) is found in the Maracaibo Basin, in valleys in Northwestern Colombia, and Eastern Panama while all other species of the genus are *cis*-Andean (Map 11).

The *Gustavia* clade (Map 8) has high species diversity west of the Andes. Species of this clade are common in inter-Andean valleys and slopes, especially in the area from eastern Panama into northwestern Colombia as far south as northwestern Ecuador. Species of this genus are, however, found all over the Amazon basin but only the widespread *G. augusta* has reached the Atlantic Forest of eastern Brazil.

Gustavia has fewer species in eastern Amazonian Brazil and the Guianas than it does in the Andes. For example, there are only four species in the three Guianas (Mori & Prance 1993), two species in the Flora of Central French Guiana (Mori et al. 2002), and seven species in the Flora of Venezuelan Guayana (Mori & Prance 1999). In contrast, there are 13 species of *Gustavia* in Ecuador (Cornejo & Mori 2012a) and nine species in Panama (Mori et al. 2010), of which only one species is common to both areas. Eastern Panama, the Pacific coast of Colombia, and northwestern Ecuador harbor nearly 50% of the species of *Gustavia* (Map 23).

The *Eschweilera integrifolia* clade (Huang et al. 2015) has many poorly defined cloud forest species ranging from northwestern Ecuador on the slopes and in the valleys of the Andes into Costa Rica. There are only two well-defined species of this clade found east of the Andes in the lowlands of western Amazonia (Map 19): *Eschweileera andina* (with pink to purple petals and androecia) and *E. ovalifolia* (with light yellow petals and androecia). The former occurs along the foothills of the Andes and the latter is found there as well but its distribution extends as far east as the junction of the Negro and Amazon rivers. The two Amazonian lowland species of this clade could have been the ancestors of the Andean species because Andean habitats were not available until after the uplift of the Andes. Once the Andes surpassed 500 meters genetic interchange between the two lowland species and the evolving Andean species may no longer taken place. We assume that triple-coiled androecial hoods and spreading arils were preceded by ancestral species with double-coiled androecial hoods and lateral arils, i.e., the more complex character states are built upon the less complex character states. However, the evolutionary relationship between the *E. parvifolia* and *E. integrifolia* clades have not been supported by molecular based phylogenies (Mori et al. 2007; Huang et al. 2015).

We know that approximately 50% of the species of *Eschweilera* in Central America belong to the *E. parvifolia* clade. On the other hand, there are only the two species mentioned above of the *Eschweilera integrifolia* clade found in Amazonia. It is clear that the *parvifolia* clade dominates throughout the Amazon Basin whereas there are equal numbers of species of the *E. parvifolia* and *E. integrifolia* clades found west of the Andes into Central America.

The Venezuelan Andes have been a barrier to migrations of species of Lecythidaceae into the Maracaibo Basin where only five species of Lecythidaceae are known to occur (*Carinina pyriformis* [Map 11]; *Couroupita guianensis* [Map 9]; the poorly known *Gustavia tejerae* R. Knuth; *Lecythis corrugata* subsp. *rosea* [Map 21]; and *L. mino*r [Map 14]). The species found there could have migrated along the coast to the Maracaibo Basin, especially during times when water was tied up in glaciers and more forest paralleled the shoreline than today. On the other hand, these species could have crossed the Andes before the mountains were too high to block their passage into the Maracaibo Basin. It is surprising that both the *Eschweilera integrifolia* and *E. parvifolia* clades, together totaling more than 85 species, have apparently contributed no species to the Lecythidaceae flora of the Maracaibo Basin.

The *Couroupita* clade (Map 9) consists of three lowland species: *C. nicaraguarensis* is trans-Andean, *C. guianensis* is cis-Andean with a peri-Amazonian distribution (Granville 1992), and *C. subsessilis* is cis-Andean and mostly restricted to the banks of the Amazon River and its tributaries. These three species are found in lowland forests from near sea level to about 500 m elevation.

Huang et al. (2015) recovered *Couroupita subsessilis* as sister to the *C. nicaraguarensis*/*C. guianensis* clade (Fig. 2A). The androecial morphology of *C. nicaraguarensis* (Fig. 6A) is the least complex of the three species of the genus. This species has 100% fertile stamens in the staminal ring, progressively fewer fertile stamens along the ligule, and an increased number of staminodes toward the apex of the ligule. At the apex, nearly 100% of the appendages are sterile (Mori et al. 1980). In contrast, *C. subsessilis* and *C. guianensis* lack staminal appendages between the staminal ring and the apex of the ligule (Fig. 6B). The flowers of both *C. subsessilis* and *C. nicaraguarensis* have white petals, golden yellow anthers, and a tendency to have a cleft at the apex of the androecial hood. Based on these observations we hypothesized that *C. nicaraguarensis* and *C. subsessilis* were more closely related than either of these species are to *C. guianensis* but our molecular-based cladogram (Fig. 2A) does not support this hypothesis.

We hypothesize that the uplift of the Andes, including the Cordillera Central of Central America, had a major impact on the speciation of the *Couroupita*, *Grias*, *Gustavia*, and *Eschweilera integrifolia* clades. Bagley and Johnson (2014) point out that lower Central America is geologically complex and, as a result, populations of plants and animals were separated from one other (e.g., isolated on islands and in mountain valleys or by altitudinal differences).

This has resulted in high diversity of Lecythidaceae over a relatively small area in eastern Panama, northwestern Colombia, Pacific coastal Colombia, and northwestern Ecuador. Further south along the Pacific coast there are few, if any, species of Lecythidaceae, and, in Central America, the last significant population of Lecythidaceae to the northwest occurs on the Osa Peninsula where there are five genera and 11 species of the family (Aguilar, et al. 2008). Further to the north, the family becomes less-and-less common with five genera and six species in Nicaragua (Prance & Mori 2001) and only one species, *Eschweilera mexicana* Wendt et al., in Veracruz, Mexico (Wendt et al. 1985). The current distribution of Lecythidaceae indicates that it is a South American lineage that migrated into Central America.

Evolution of species of Lecythidaceae in northwestern South America/eastern Central America was probably driven by the following events: (1) the uplift of the Andes resulting in the evolution of *cis*- and *trans*-Amazonian species, (2) the formation of isolated Andean valleys where ecologically separated populations evolved into new species, (3) adaptation to the high altitudinal habitats of newly formed cloud forests, (4) the formation and inundation of islands before the closure of the Central American land bridge, and (5) the arrival of seeds carried by ocean currents from southeastern Asia to the Pacific coasts of South and Central America. These factors, in combination, contributed to the high diversity of Lecythidaceae in eastern Central America/northwestern South America as well in other plants (Cuatrcasas 1970) and animals (Bagley & Johnson 2014).

It has been suggested that the Andes uplift resulted in the diversification of plant species to such an extent that the coastal forests, valleys, and slopes of the Andes may be more species rich in plants than the Amazon Basin (Henderson et al. 1991). For trees, however, the high *alpha* diversity of Amazonia (up to 300 species over 10 cm DBH per hectare; Gentry 1982; Oliveira & Mori 1999) and the vast forested area of Amazonia make this seem unlikely. West of the Andes Lecythidaceae reach 20 species per grid square (only in Panama) whereas they frequently have over 20 and up to 60 species per grid square (only central Amazonia) east of the Andes in Amazonia (Map 6).

Lowland Guayana Floristic Province

This region is located in the northeastern part of South America bounded by the Atlantic Ocean in the northeast, the Amazon River in the south, the Rio Negro in the southwest, and the Rio Orinoco in the northwest (Mori 1991). The Guayana Highlands (Maguire 1970) are part of the Guayana Floristic Province but not included because there are no Lecythidaceae found at high elevations in the region. In this paper Guayana is used instead of Guiana or Guyana for three reasons: (1) Guyana is the name of a country, (2) the Guianas is a name for the three political units in northeastern South America (Guyana, Suriname, and French Guiana), and (3) two major botanical books, the Flora of the Guayana Highlands and the Flora of Guayanan Venezuela were published before botanists started to use Guiana in reference to this part of South America (Lindeman & Mori 1989).

The best example of a Guayana lowland distribution is the restriction of the 18 taxa of *Eperua* (Fabaceae Subfam. Caesalpinioideae) in the area described in the preceding paragraph (Cowan 1975). This distribution also occurs in species of birds (Haffer 1974; Cracraft & Prum 1988) and reptiles (Dixon 1979). One-third of the species of neotropical Chrysobalanaceae, 24 % of Meliaceae, and 22 % of Sapotaceae occur in the Guayana lowlands (Mori 1991) which suggests that this area harbors about one quarter of the tree species found in the New World tropics.

The *Lecythis corrugata* (Map 21) and *Corythophora* (Map 18) clades as well as individual species of other clades of New World Lecythidaceae (e.g., *Couratari calycina* Sandwith, *C. gloriosa*, *Eschweilera collina*, *E. subglandulosa* [Steud. ex O. Berg] Miers, *L. poiteaui*, *L. congestiflora*, and *L. simiorum*) are endemic to the Guayana Lowlands. In a study of the Lecythidaceae of Central French Guiana, Mori (1991) found that some of the species of Lecythidaceae occurring there reached the western limits of their distributions between the Essequibo River and the boundary between Guyana and Venezuela with only a few species (e.g., *E. sagotiana* Miers) distributed as far west as the mouth of the Orinoco River.

We hypothesize that in the past the distributions of Guayana lowland tree taxa may have been restrained by large inland lakes or epicontinental seas (Frailey et al. 1988; Mori 1991; Bush & Oliveira 2006; Sacet 2014). After the Amazon River broke through the Purus arch and reached its present shape and size some 2.4 mya (Figueredo et al. 2009; Shephard et al. 2010) the newly exposed lake bottoms in western and central Amazonia would have become available for colonization. Although Lake Pebas is well documented (Sacet 2014), Lago Amazonas may not have existed (Tuomisto et al. 1992), at least not in such a massive area.

Contemporary species of the *Lecythis corrugata* clade are confined to the Guayana lowland Floristic Province and adjacent Brazil (Map 21). *Lecythis corrugata* encompasses two subspecies, subsp. *corrugata* in the eastern and subp. *rosea* in the western parts of the Guayana lowlands (Map 21). The separation of these two subspecies may have been an adaption to dryer forest habitats in the western part of Guayana where subsp. *rosea* occurs. The main differences between the two subspecies are the more coriaceous leaves with striations on the upper surface of subsp. *rosea* and more chartaceous leaves without striations on the upper leaf surface of subsp. *corrugata*. The coriaceous leaves may be an adaptation for water conservation and, if so, the evolution of these two subspecies may have occurred because of ecological adaptation instead of a physical barrier. The border between the two subspecies is more-or-less along the Essequibo River and an embayment along that river may have contributed to the separation of these two subspecies from the original population.

Lecythis corrugata subsp. *rosea* has a widespread distribution in Amazonian Venezuela and north central Amazonian Brazil. It is absent in the savannas of Venezuela, reappears on the southern slopes of the Andes in Venezuela, and is found north of the Andes around Lake Maracaibo (Map 21). The *cis*- and *trans*-Andean populations may have been separated by the uplift of the western Venezuelan Andes and, after the mountains reached an elevation of 500 m altitude, there was no further genetic exchange.

The *Corythophora* clade (Map 18) is currently restricted to the eastern and central parts of the Guayana Floristic Province. Two species of the clade, *C. alta* (with reddish pink petals and androecial hoods) and *C. rimosa* subp. *rimosa* (with green petals and white androecial hoods), are found growing next to one another just north of Manaus. In French Guiana, *C. amapaensis* (with reddish-pink petals and androecial hoods) and *C. rimosa* subsp. *rubra* (with purple petals and white androecial hoods) also grow sympatrically. The sympatric distributions of the two species pairs suggest that the different flower colors may have evolved because of pollinator preferences. The other species, *C. labriculata* (with reddish pink petals and androecial hoods), is endemic to Surinam where no collections of other species of the genus have been collected.

Atlantic Forest (Mata Atlântica)

The forests of the eastern coast of Brazil range from Rio Grande do Norte State to Rio Grande do Sul State. These forests are found in a narrow strip paralleling the coast and ranging in width from several km in the north to 120–160 km in the south (Smith 1962; Bigarella et al. 1975; Andrade-Lima 1977; Mori 1989; Fiaschi & Pirani 2009). Although this phytogeographic domain is relatively small (1.5 million sq^2 km), it is estimated to have at least 14,000 (Zappi et al. 2015) to as many as 20,000 (Fiaschi & Pirani 2009) species of vascular plants. Because of high species diversity, significant endemism, and continuing deforestation, Myers et al. (1999) designated the Atlantic Forest as a biodiversity hotspot.

Forty-four (Thomas et al. 1998) to fifty-three percent (Mori et al. 1981) of the tree species and 49.5% of the seed plants (Zappi et al. 2015) of the Atlantic Forest may be endemic. For Lecythidaceae species in the Atlantic Forest, Smith et al. (2016) calculated that 50% of the species are endemic and threatened with extinction. The presence of only *Gustavia augusta* out of the 42 species of *Gustavia* (Map 8) as well as the total absence of the actinomorphic-flowered species of *Allantoma* (Map 10) and *Grias* (Map 7) in the Atlantic Forest demonstrates that actinomorphic-flowered species did not diversify in eastern Brazil.

Asymmetric distribution (i.e., high diversity in Amazonia and low diversity in the Atlantic Forest) also occurs in other clades of Lecythidaceae. *Eschweilera ovata* is the only species of the *E. parvifolia* clade in the Atlantic Forest, which has over 65 species in South and Central America. Another clade with a similar distribution is the *L. poiteaui* (Map 15) clade. The asymmetric distributions of these clades suggest that they migrated into the Atlantic Forest via a northern route from Amazonia during a time when the dry thorn scrub forest and savanna were covered by more humid forests (Costa 2003). The *L. pisonis* clade (Map 13) has equal numbers in the Atlantic Forest as it does outside this area.

Another hypothesis is that species of Lecythidaceae could have migrated stepwise along higher, wetter areas (called *brejos*) from Amazonia into the Atlantic Forest (Andrade-Lima 1977), or *vice versa*. This suggestion seems unlikely because it would have been difficult for seeds from at least two trees to disperse from one *brejo* to another and arrive in close enough proximity to cross-pollinate. Individual trees would infrequently produce seeds because of the low survival rate of self-pollination in Lecythidaceae (Moritz 1984).

Eschweilera nana of the *E. tetrapetala* clade is a widespread savanna species of planalto of central Brazil (Map 20) that shares morphologically distinct characters with six Atlantic Forest endemics. Huang et al. (2015) retrieved *Eschweilera nana* as sister to *E. tetrapetala* and *E. alvimii*, which are morphologically similar to four species not included in the molecular analysis (*E. complanata* S.A. Mori, *E. compressa* [Vellozo] Miers, *E. mattos-silvae* S.A. Mori, and *E. sphaerocarpa* M. Ribeiro et al, [Ribeiro et al. 2016]).

The species of the *tetrapetala* clade differ from the *Eschweilera integrifolia* and *E. parvifolia* clades in the following features: presence of a single-coiled vs. at least a double-coiled androecial hood; the lack of vestigial stamen nectaries vs. the presence of vestigial stamen nectaries; more than a single row vs. a single row of ovules in each locule; seed coats with impressed primary veins vs. seed coats without impressed primary veins; seeds with higher order veins not showing between the primary veins vs. higher order veins showing between the primary veins; and a basal instead of a lateral or spreading aril. The *E. tetrapetala* clade is the only clade confined to the Atlantic Forest and adjacent Brazilian savannas.

The migratory route of species into or out of the Atlantic Forest from southwestern Amazonia is located at the level of the states of Rio de Janeiro/Espírito Santo/southern Bahia. One example is the disjunct distribution between southwestern Amazonia and the Atlantic Forest of *Couratari macrosperma* (Map 25). The two populations appear morphologically similar but might represent two closely related species. In addition, there are three other Atlantic Forest endemics of the *Couratari* clade (*C. asterotricha*, *C. asterophora*, and *C. pyramidata* that belong to *Couratari* sect. *echinata* as defined by Prance (Mori & Prance 1990). We hypothesize that *C. macrosperma* originally consisted of a large population that extended from southwestern Amazonia to the Atlantic Forest and was then isolated by the expansion of dryer vegetation thereby leaving one population in southwestern Amazonia and another in the Atlantic Forest. After the split the ancestor of *C. macrosperma* split into four lineages in eastern Brazil, a somewhat modified *C. macrosperma* and the morphologically distinct *C. asterotricha*, *C. asterophora*, and *C. pyramidata*. Other possibilities are that *C. macrosperma*, which is able to grow in both forest and disturbed habitats (Mori, Smith & Ribeiro, pers. obs.), may have moved from southwestern Amazonia to the Atlantic Forest or by migrating along gallery forests from Amazonia to the Atlantic Forest.

Cariniana estrellensis and *C. ianeirensis* have disjunct distributions between southwestern Amazonia and the central and southern parts of the Atlantic Forest (Maps 11, 25). The ability of species like *C. estrellensis* to migrate along gallery forests (Leite 2001) facilitates crossing savanna barriers. In contrast, *C. legalis* is restricted to the Atlantic Forest from Paraíba to Rio de Janeiro and from there arches inward in the state of São Paulo. The overall distribution of this species forms a “J” shape (Map 11). *Cariniana ianeirensis* ranges from southern Bahia to Rio de Janeiro and occurs disjunct in NW Bolivia and adjacent Mato Grosso. *Cariniana parvifolia* is endemic to the Atlantic Forest with a very limited distribution in northern Espírito Santo and southern Bahia.

In summary, compared to Amazonian Lecythidaceae, the Atlantic Forest has few species and all but one species (*Gustavia augusta*) have zygomorphic flowers. We conclude that Lecythidaceae migrated into the area when the dry areas between it and Amazonia were occupied by wetter forest. Once there new species, especially in the *Eschweilera tetrapetala* and *Couratari* clades, evolved. Today, 50% of the species of Lecythidaceae are endemic to the Atlantic Forest (Smith et al., 2016).

Evolution of floral zygomorphy in New World Lecythidacdeae

There are striking differences in androecial symmetry (Figs. 5–6) within the Lecythidaceae clade *sensu lato*. In the Old World, the Napoleonaeaceae (Map 2), Scytopetalaceae (Map 3), Lecythidaceae subfam. Foetidioideae (Map 4), and Lecythidaceae subfam. Barringtonioideae (Map 5) possess actinomorphic flowers. In contrast, the New World Lecythidaceae subfam. Lecythidoideae (Map 6) have three major types of androecial symmetry. *Allantoma*, *Grias*, and *Gustavia* have actinomorphic flowers (Fig. 5A) while the other genera have two types of zygomorphic flowers—one limited to the obliquely zygomorphic flowers of *Cariniana* (Fig. 5C) and the other includes zygomorphic genera with an androecial extension (= ligule) arising from a staminal ring (Fig. 5D, 6). Tsou and Mori (2007) have shown that the one-sided extension of a staminal tube (as in *Cariniana*) or from a staminal ring (all other species of zygomorphic-flowered Lecythidaceae) occurs on the abaxial side of the flower and suggest that this is caused by auxins stimulating growth on that side. There is one known example of a reversal from a zygomorphic to an actinomorphic androecium in *Corythophora rimosa* subsp. *rimosa* showing that changes in floral symmetry sometimes occur (N.P. Smith, pers. comm. 2015). Huang et al. (2015) and Mori et al. (2015) illustrate the floral features of all clades of New World Lecythidaceae.

Because no zygomorphic-flowered species occur in the Old World we assume that zygomorphy evolved in the New World from actinomorphic-flowered ancestors similar to species of subfam. *Barringtonioideae*. As mentioned above, species of barringtonioids have a broad staminal tube with many stamens arising from the rim thereby causing the androecium to resemble species of *Gustavia*; however, species of *Grias* share more morphological features in common with species of the subfam. *Barringtonioideae* (see “Worldwide distribution”).

Once in the New World, floral zygomorphy of Lecythidaceae most likely evolved in response to pollination by bees. However, two New World Lecythidaceae, *Lecythis poiteaui* (Mori et al. 1978) and *L. barnebyi* (Mori & Prance 1990) are documented as bat-pollinated and, based on floral aromas, *Grias peruviana* may be pollinated by beetles because it possesses floral compounds similar to those found in other plants pollinated by them (Knudsen & Mori 1996). New World Lecythidaceae offer fertile pollen, sterile pollen, and nectar as pollinator rewards (Mori et al. 1987).

Species of *Gustavia* have the least complex flowers in the New World and are visited by the greatest diversity of bees (Huang 2010). Species of this genus have poricidal anthers (not found in other species of New World Lecythidaceae) and, thus, are most efficiently pollinated by buzz-pollinating bees. Other bees, such as species of trigonids, are pollen robbers that are not efficient pollinators because they fill their pollen baskets and return directly to their nest without visiting other flowers (Mori & Boeke 1987; Potascheff et al. 2013). However, more robust trigonid bees are known to be pollinators of Lecythidaceae (Mori & Boeke, 1987). (Pollinators have not been recorded for *Allantoma* but the staminal tube suggests that nectar accumulates in the tube and serves as a reward to attract pollinators. The faintly scented flowers of *Cariniana estrellensis* open before dawn and pollinator visitation intensifies one hour after sunrise (Leite 2007). The nectar reward and aroma of this species most likely attracts relatively small bee pollinators.

Huang (2010) suggested that selection for pollination by large bees is the key to understanding the evolution of zygomorphic flowers in New World Lecythidaceae. She found that individuals of large-bodied species of *Xylocopa* (carpenter bees) visit both actinomorphic and zygomorphic flowers and hypothesized that species similar to this genus were the initial drivers of evolution of zygomorphic flowers in Lecythidaceae. Subsequently, long-tongued euglossine bees (Mori & Boeke 1987) also became important pollinators of New World Lecythidaceae.

Morphological adaptations present in at least some New World Lecythidaceae with staminal ring, zygomorphic flowers are the: (1) petals that press against the androecium to block entry into the flower by pollen and nectar robbers; (2) closure of the androecial hood opening against the staminal ring to stop entry into the flower by nectar and pollen robbers (Fig. 5D); (3) yellow honey guide spots at the entrance into the androecium; (4) formation of coiled androecial hoods (Fig. 6I–J, 6L–M) to limit nectar removal to bees with long proboscises; (5) change from fertile stamens (Fig. 6C) to staminodes (Fig. 6B) that provide sterile pollen for bees to feed their larvae; (6) yellow color of antherodes to direct bees to sterile pollen rewards; (7) change from fertile stamens to vestigial stamen nectaries (Fig. 6J) that provide nectar; (8) an obliquely oriented style that places the stigma in a position that receives pollen from pollinator before new pollen is collected, and (9) the formation of an external flap (Fig. 6M) in the *Couratari* clade. The *Couratari* flap overlaps the androecial hood and, thus, provides another layer that robber bees have to drill through to gather nectar. Evidence for this is that androecial hoods of species of *Couratari* are seldom perforated by trigonid bees, whereas the hoods of other groups, such as the *Eschweilera integrifolia* and *E. parvifolia* clades, are often perforated.

Huang (2011) pointed out that the evolution of the different zygomorphic flower types is more complex than originally proposed by Prance and Mori (1979), Mori et al. (1978), and Mori and Boeke (1987). According to Huang, the androecial types of New World Lecythidaceae do not provide clear examples of linear floral evolution; for example, Mori and Prance (1990) suggested that an ancestral *Cariniana* was the first step in the evolution of zygomorphy in New World Lecythidaceae. Based on current cladograms (Fig. 2A), the *Couroupita* clade is basal to all other zygomorphic-flowered genera as well as the actinomorphic-flowered species of the *Allantoma* clade, which in turn is sister to the *Cariniana* clade (Fig. 2A). It is more likely that the flowers of the *Cariniana* clade did not lead to more advanced zygomorphic flower innovations. In addition, the *Couratari* clade possesses the most complex flowers of New World Lecythidaceae but molecular trees do not support the hypothesis that this clade is evolutionarily most advanced.

The current distributions of the different floral symmetry types of New World Lecythidaceae await interpretation about where zygomorphic flowers evolved and how they migrated to different parts of the New World tropics. We hope that others will address the following questions:

(1) Did actinomorphic-flowered Old World Lecythidaceae colonize the New World? This hypothesis is based on the morphological similarity between *Grias* and *Gustavia* with the barringtonioids (see "Interchange between Old and New World Lecythidaceae"). The molecular data (Fig. 1) indicates that the relationship between *Grias* and *Gustavia* with the Barringtonoioideae is either plesiomorphic or homoplasious.

(2) Eastern Amazonia, the Guayana lowland biome, and the Atlantic Forest have relatively few actinomorphic-flowered species of Lecythidaceae (Map 26). Can we assume that these areas are not where actinomorphic-flowered species reached the New World.

(3) Species with small, membranous, tubular, zygomorphic androecia (also called tubular or obliquely zygomorphic, Fig. 5C) are found only in *Cariniana*. This genus is most diverse in southern Amazonia and has one *trans*-Andean species (*C. pyriformis*) found in eastern Panama near the boundary with Colombia, northwestern Colombia, and the Maracaibo Basin of Venezuela. There are no species in the Guayana lowlands and eastern Amazonia Brazil (Map 11). We propose that this type of androecium probably evolved from ancestors related to *Allantoma* (Fig. 5B) because of the similarity of the androecia in the two genera. However, *Cariniana* differs from *Allantoma* by its membranous *vs*. fleshy staminal tube and six instead of four or five petals. Are we justified in believing that the tubular zygomorphic androecium is an evolutionary dead end (Huang 2010), *i.e.*, it is not a precursor of more complex androecia as implied by Prance and Mori (1979)?

(4) Because zygomorphic-flowered Lecythidaceae only occur in the New World tropics, can we assume that this flower type evolved there?

(5) The variation of staminal ring zygomorphic flowers is greater in the Amazon than it is in any part of the New World. Of the 12 staminal ring zygomorphic clades (Figs. 1A–B), the following 11 clades are present in Amazonia: the *Couroupita* clade (Fig. 6A–B, 10B, Map 9), *Couratari* clade (Fig. 6M, 10F, Map 12), *Lecythis pisonis* clade (Fig. 6C, 10J, Map 13), *Bertholletia excelsa* clade (Figs. 6G, 10C, Map 16), *L. poiteaui* clade (Map 15), *L. chartacea* clade (Fig. 6H, Map 17), *Corythophora* clade (Fig. 6E, Map 18), *Eschweilera integrifolia* clade (Fig. 6L, Map 19), *E. tetrapetala* clade (Fig. 6K, 10I, Map 20), *L. corrugata* (Figs. 6D, 6F, Map 21), and *E. parvifolia* clade (Fig. 6I–6J, Map 22). The only clade outside of Amazonia with this type of androecium is the *Lecythis ollaria* clade (Map 14). Did staminal ring zygomorphy first evolve in the Guayana lowlands and surrounding Amazonian lowlands?

(6) Several Amazonian clades with staminal ring zygomorphic flowers have one or two trans-Andean species that reach the other side of the Andes: *Couratari guianensis* (widespread) and *C. scottmorii* (*trans*-Andean endemic); *Couroupita nicaraguarensis* (*trans*-Andean endemic); *Lecythis ampla* Miers (*trans*-Andean endemic), *L. tuyrana* (*trans*-Andean endemic), *L. mesophylla* (*trans*-Andean endemic), and *L. corrugata* subsp. rosea (widespread). Did this flower type migrate from Amazonia into northwestern South America and eastern Central America?

CONCLUSIONS

Taxonomic changes

The three subfamilies of Lecythidaceae merit family status as the Foetidiaceae, Barringtoniaceae, and Lecythidaceae. These three clades are separated by differences in their distributions, morphology, and by the results of phylogenetic analyses (Fig. 1). The Napoleonaeaceae (Prance 2004) and the Scytopetalaceae (Appel 2004) are already recognized as separate families, but the Angiosperm Phylogeny Group (Stevens 2004) still maintains five subfamilies in the Lecythidaceae.

We suggest that the *Eschweilera tetrapetala* clade (Fig. 2B) merits recognition as a separate genus based on its recovery as a highly supported clade based on molecular data and the possession of morphological features not found in the other two clades of *Eschweilera*. Michel Ribeiro, a doctoral candidate at the School of Tropical Botany of the Rio de Janeiro Botanical Garden, is studying this clade. The other two clades of *Eschweilera* (*E. integrifolia* and *E. parvifolia* clades) (Fig. 2B) have distinct morphological characters in common but the two clades are not retrieved as sister taxa based on molecular data (Huang et al. 2015) (Fig. 2B). We suggest that these two clades remain in *Eschweilera* until further information about their relationship is resolved. If the clades turn out to be sisters then they should be recognized as subgenera in order to show their close relationship as well as to avoid name changes. On the other hand, if they are not sisters they will have to be recognized as separate genera.

Two of the five clades of *Lecythis* have unique morphological characters and molecular data that set them apart from other clades of New World Lecythidaceae as defined by Mori and Prance (1990); thus, the *L. pisonis* and *L. corrugata* clades merit consideration as separate genera.

The *Lecythis ollaria*/ *L. poiteaui*/ *Bertholletia excelsa*/ *L. chartacea* clade (Fig. 2A) has <50% BS support and is difficult to differentiate by morphological features. If this clade is recognized as a single genus, then *Bertholletia excelsa* has to be transferred to *Lecythis* because the type, *L. ollaria*, was published earlier than other species in the clade (Dorr & Wiersema 2010a, 2010b).

Many species of *Eschweilera*, as currently circumscribed (Mori & Prance 1990) are difficult to distinguish. The first step in further study of this genus is to establish the relationship between the *E. integrifolia* and *E. parvifolia* clades as defined by Huang et al. (2015). If the separation of these clades is supported, the *E. integrifolia* clade should be recognized as a new genus and it should be monographed first because it has fewer species found in a more limited area (Map 19) than the *E. parvifolia* clade (Map 22).

Phytogeographic questions

In this study, we have described phytogeographic patterns of Lecythidaceae. Based on our observations, we suggest that future research addresses the following questions:

(1) How was the current tropical distribution of the Lecythidaceae clade *sensu lato* achieved (Map 1)?

(2) Is there a close relationship between the barringtonioids of the Old World and the actinomophic-flowered New World Lecythidaceae?

(3) How can the extreme disjunctions of (1) *Asteranthos brasiliensis* (Map 3) in the Amazon with other Scytopetalaceae in Africa and (2) *Petersianthus monocarpus* in Africa and *P. quadrialatus* in the Philippines be explained?

(4) Does the Pleistocene refuge theory play a major role in the diversification of New World Lecythidaceae?

(5) What impact did the uplift of the Andes have in the speciation and distribution of Lecythidaceae (Map 23)?

(6) What are the phylogenetic relationships between the *Eschweilera integrifolia* and *E. parvifolia* clades; e.g., did ancestral species of the *Eschweilera. parvifolia* clade give rise to the *E. integrifolia* clade?

(7) How did the appearance and disappearance of large bodies of water, such as lakes, wetlands, and sea embayments influence speciation of Lecythidaceae?

(8) Did species of Lecythidaceae migrate from both southeastern and southwestern Amazonia into the Atlantic Forest?

(9) Where did zygomorphic flowers evolve in the New World Lecythidaceae?

(10) Vicariance and long-distance dispersal are important drivers of speciation in Lecythidaceae but how are these events related to other drivers of speciation, e.g., pollination and dispersal?

Importance of conservation

Species of New World Lecythidaceae are ecologically dominant in many lowland primary forests, especially in the Amazon Basin (Steege et al. 2013). The more disturbed primary forests become the fewer species of Lecythidaceae they harbor. This and other associated tree families (e.g., Arecaceae, Burseraceae, Chrysobalanaceae, Fabaceae, Sapotaceae, etc.) form an Amazonian guild that provides ecosystem services upon which life on earth depends. Extinction of trees, like the death of “canaries in a coal mine,” should warn humans that the negative impacts on the world’s ecosystem services would continue to get worse if primary forests of all types are not more rigorously protected.

Over the last 20 years, deforestation of tropical forests has continued unabated. Over this period, human population has increased by 23% and economic growth has soared by 153% (Venter et al. 2016). Watson et al. (2016) calculate that 10% of the wilderness areas of the world have been lost during the last two decades, especially in South America where that figure is 30%. It is obvious, that the planet is already experiencing global warming; air, water, and soil pollution; crop failure; and increasing human conflicts over the use of natural resources.

Ferry Silk et al. (2015) estimated that there are at least 40,000 but perhaps as many as 53,000 tree species found in tropical forests. These authors compare tropical tree diversity with the 124 species of trees that grow in temperate Europe, demonstrating the overwhelming tree diversity of the tropics. In contrast, a study in Central Amazonian Brazil recorded 300 species of trees greater than 10 cm DBH in a plot of just 100 hectares (Oliveira & Mori 1998). In order to save tropical trees, the survival of plants and animals that depend upon them, and the ecosystem services they provide, it is essential to protect currently established biological reserves as well as continue to establish governmental, NGO, and private preserves as fast as possible. However, this strategy will not work unless human population and excessive consumption are also controlled!

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that makes it possible to publish papers that might not be accepted in other journals because they are too long or because hypotheses are not tested. This is especially important for senior botanists because it allows them to leave a more complete legacy of what they have accomplished during their careers.

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TABLES

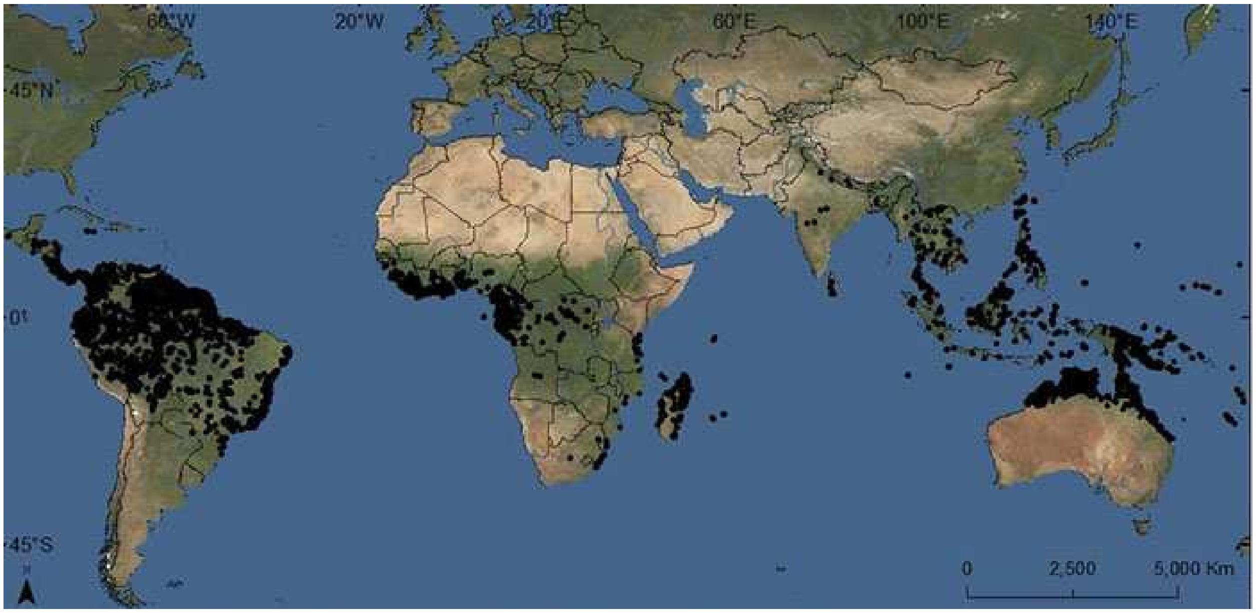
Table I. The number of species in each of the subclades of the Lecythidaceae clade. The clades correspond to those circumscribed by Huang et al. (2015) and Mori et al. (2015). Note that Huang et al. (2015) recognize clades within *Eschweilera* and *Lecythis* that were previously delimited by Mori and Prance (1990) but these two genera are not monophyletic. In order to determine the total number of species in *Eschweilera* fide Mori and Prance (1990) the species in the *Eschweilera parvifolia*, *E. integrifolia*, and *E. tetrapetala* clades need to be added together. Likewise, the number of species in *Lecythis* fide Mori and Prance (1990) is the sum of the number of species in the *L. pisonis*, *L. ollaria*, *L. poiteaui*, *Bertholletia excelsa*, and *L. chartacea* clades.

Family	**Subfamily**	**Genus/clade**	**Species**	**Distribution**	**References**
Napoleonaeaceae					Kunth, 1939; Liben, 1971; Prance & Jongkind, 2015
		Napoleonaea clade	15–17	West & Central Africa	
		Crateranthos	04	West Africa	
Scytopetalaceae					Apple, 1996, 2004
	Scytopetaloideae				
		Scytopetalum clade	04	West Africa	
		Oubanguia clade	03	West Africa	
		Asteranthos clade	01	Central Amazonia	
	Rhaptopetaloideae				
		Rhaptopetalum clade	10	West Africa	
		Pierrina clade	01	West Africa	
		Brazzeia clade	03	West Africa	
Lecythidaceae					
	Foetidioideae			West Africa, Madagascar, and Mascarene islands	
		Foetidia clade	17	Madagascar and several species on islands around Madagascar, 1 in East Africa	Prance, 2008; Prance & Jongkind, 2015
	Barringtonioideae			Southeast Asia	
		Barringtonia clade	69	Southeast Asia	Prance, 2012
		Careya clade	04	Southeast Asia	Prance & Kartawinata, 2013
		Chydenanthus clade	01	Southeast Asia	Prance & Kartawinata, 2013

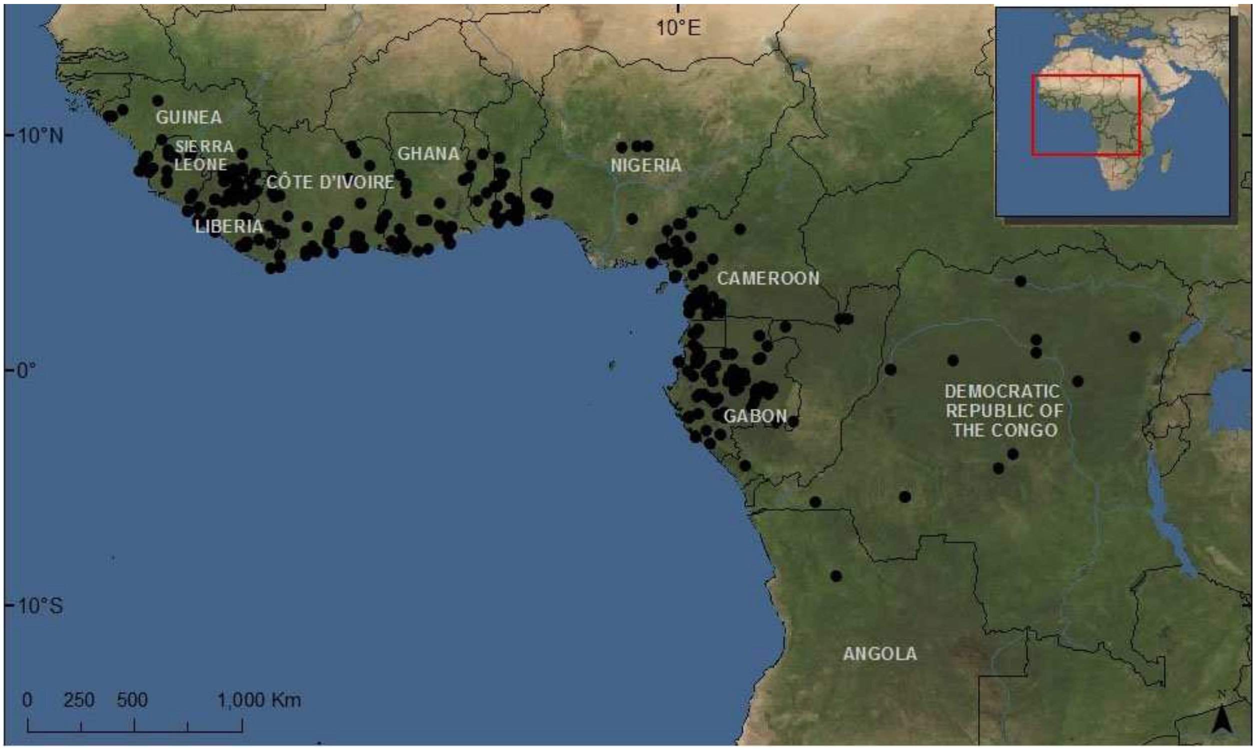
		Petersianthus clade	02	1 in Africa, 1 in Philippines	Prance & Jongkind, 2015
		Planchonia clade	06	Southeast Asia	Prance & Kartawinata, 2013
	Lecythidoideae			New World tropics	
		Allantoma clade	07		Huang et al., 2008
		Bertholletia clade	01		Mori & Prance, 1990
		Cariniana clade	09		Huang et al., 2008; Mori, 1995
		Corythophora clade	04		Mori & Prance, 1990
		Couratari clade	19		Mori & Prance, 1990
		Couroupita clade	03		Mori & Prance, 1990
		Eschweilera	three clades = 84 spp.		
		E. integrifolia clade	ca. 19		Huang et al., 2015
		E. parvifolia clade	ca. 58		Huang et al., 2015
		E. tetrapetala clade	07		Mori & Prance, 1990; Ribeiro & Smith (2016)
		Grias clade	12		Prance & Mori, 1979; Clark & Mori, 2000; Mori et al., 2010; Cornejo & Mori, 2011, 2012
		Gustavia clade	44		Prance & Mori, 1979; Mori & Cornejo, 2013
		Lecythis	total in 5 clades = 30		
		L. chartacea clade	ca. 11		Mori & Prance, 1990
		L. corrugata clade	05		Huang et al., 2015
		L. ollaria clade	03		Huang et al., 2015
		L. pisonis clade	05		Huang et al. 2015; Smith et al., 2012
		L. poiteaui clade	06		Huang et al., 2015; Smith et al., 2016

Table II. Lecythidaceae fossil record. Arranged in chronological order of publication.

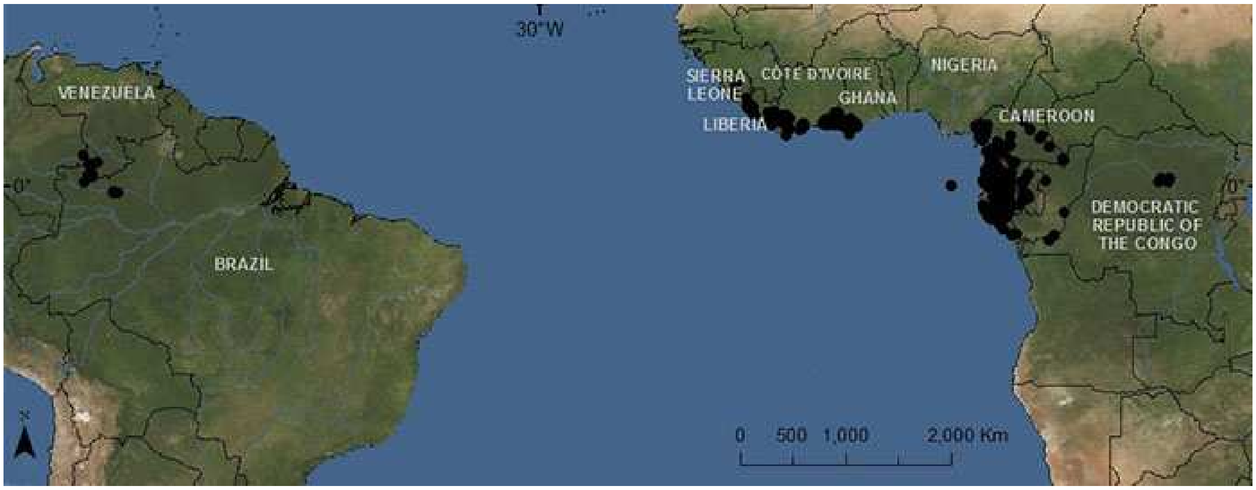
Taxon	Organ	Age	Distribut.	Citation
Lecythis neriifolia	Leaves	Tertiary	Chile	Englehardt 1891
Couratari tertiaria	Leaves	Tertiary	Ecuador	Englehard 1895
Lecythidophyllum	Leaves	Miocene	Southern Mexico	Berry, 1923
Lecythidoanthus kugleri	Flower	Miocene	Trinidad	Berry 1924
Couroupita ovata	Leaves	Late Tertiary	Bahia, Brazil	Hollick & Berry, 1924
Lecythioxylon brasiliense	Wood	Cretaceous	Piauí, Brazil	Milanez, 1935
Couroupita santanderiensis	Leaves	Miocene	Santander, Colombia	Berry 1936
Barringtonioxlon deccanense	Wood	Upper Cretaceous to Early Eocene	India	Shallom 1960
Barringtonioxlon eopterocarpum	Wood	Upper Cretaceous to Early Eocene	India	Prakkash & Dayal 1965
Marginipollis coccinus	Pollen	Upper Tertiary	Nigeria	Clarke & Frederiksen 1968
Rostriapollenites kuchensis	Pollen	Eocene	India	Venkatachala & Kar 1968
Lecythidopyon girardotanum	Fruit	Not cited	Cundinamarca Colombia	Huertas 1969
Barringtonia sp.	Leaves	Eocene	Alaska	Wolfe 1972
Planchoniidites areolatoideus	Pollen	Tertiary	New Guinea	Khan 1976
Barringtonia sp.	Pollen	Lower Eocene	India	Muller 1981
Barringtonia assamicum	Wood	Oligocene	India	Agarwall et al. 2000
Barringtonia preracemos	Fruit	Tertiary	India	Mehrotra 2000
Carinianoxylon, brasiliense	Wood	Tertiary	Maranhão, Brazil	Selmeier 2003
Cariniana & Eschweilera	Wood	Middle Eocene	Pebas formation, Brazil	Pons & de Franceschi 2007
Barringtonia sp.	Pollen	Middle Eocene	Germany	Manchester et al. 2015



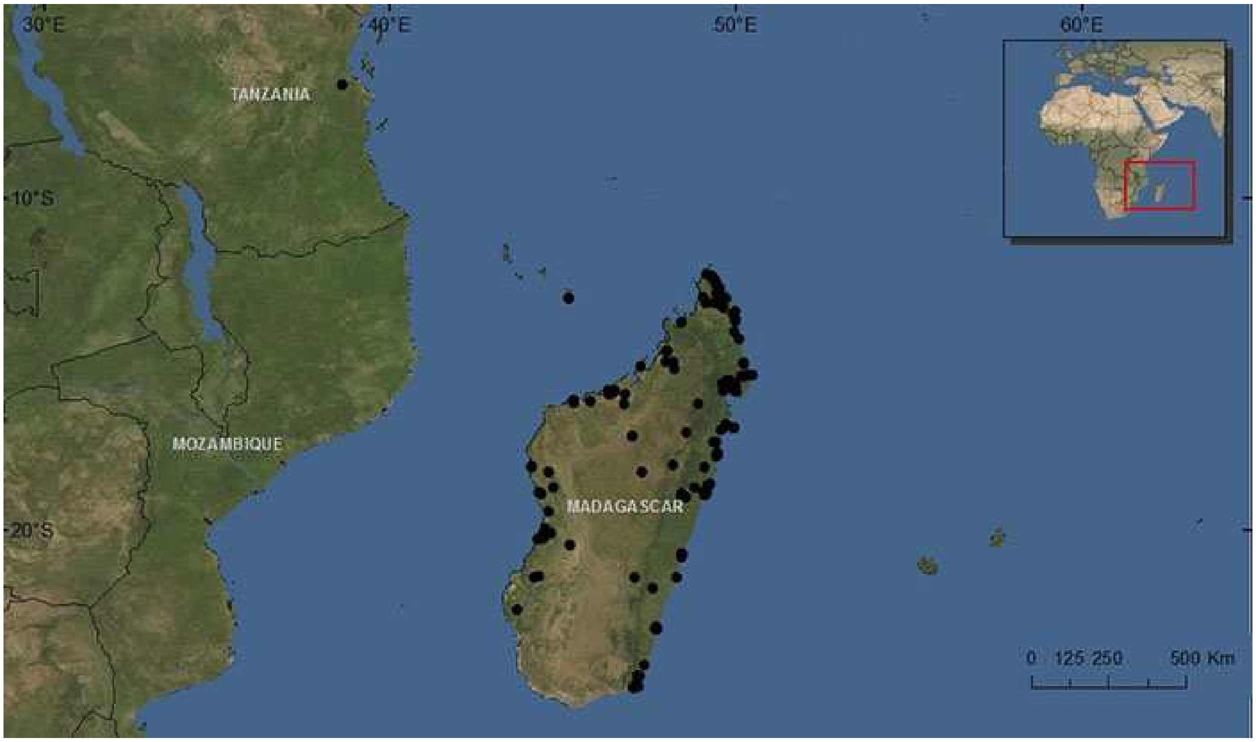
MAP 1. The Lecythidaceae clade (including Napoleonaeaceae, Scytopetalaceae, Lecythidaceae subfam. Foetidioideae, Lecythidaceae subfam. Barringtonioideae, and Lecythidaceae subfam. Lecythidoideae) are native to Central and South America, Africa, and Asia.



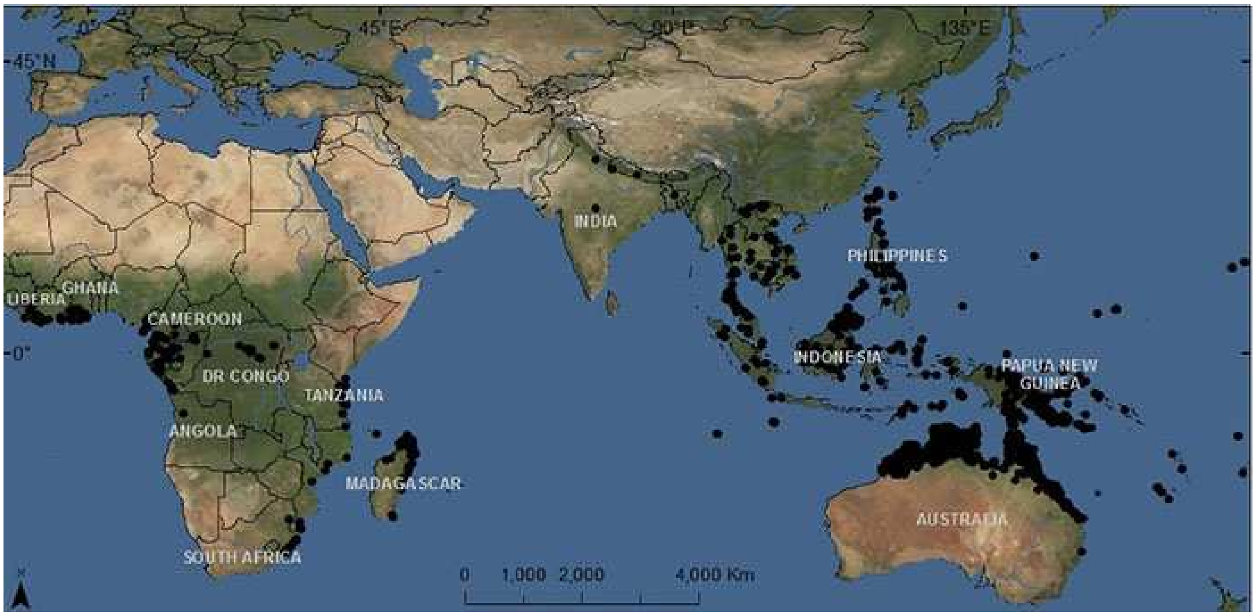
MAP 2. Distribution of the Napoleonaeaceae. This family is found only in western and central Africa.



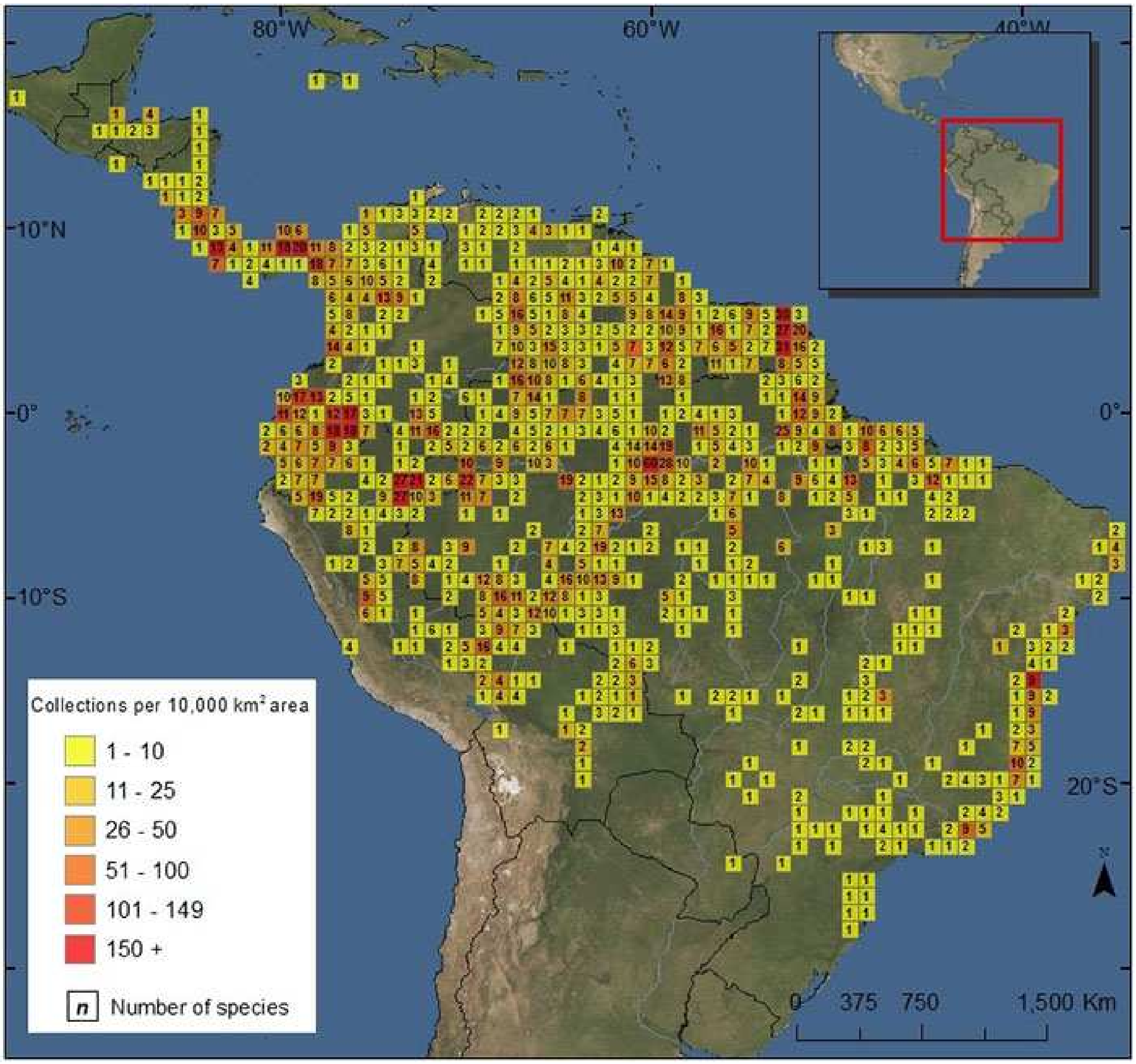
MAP 3. Distribution of Scytopetalaceae. This family is found in western and central Africa and one species, *Asteranthos brasiliensis*, is limited to northwestern Amazonian Brazil and adjacent Venezuela.



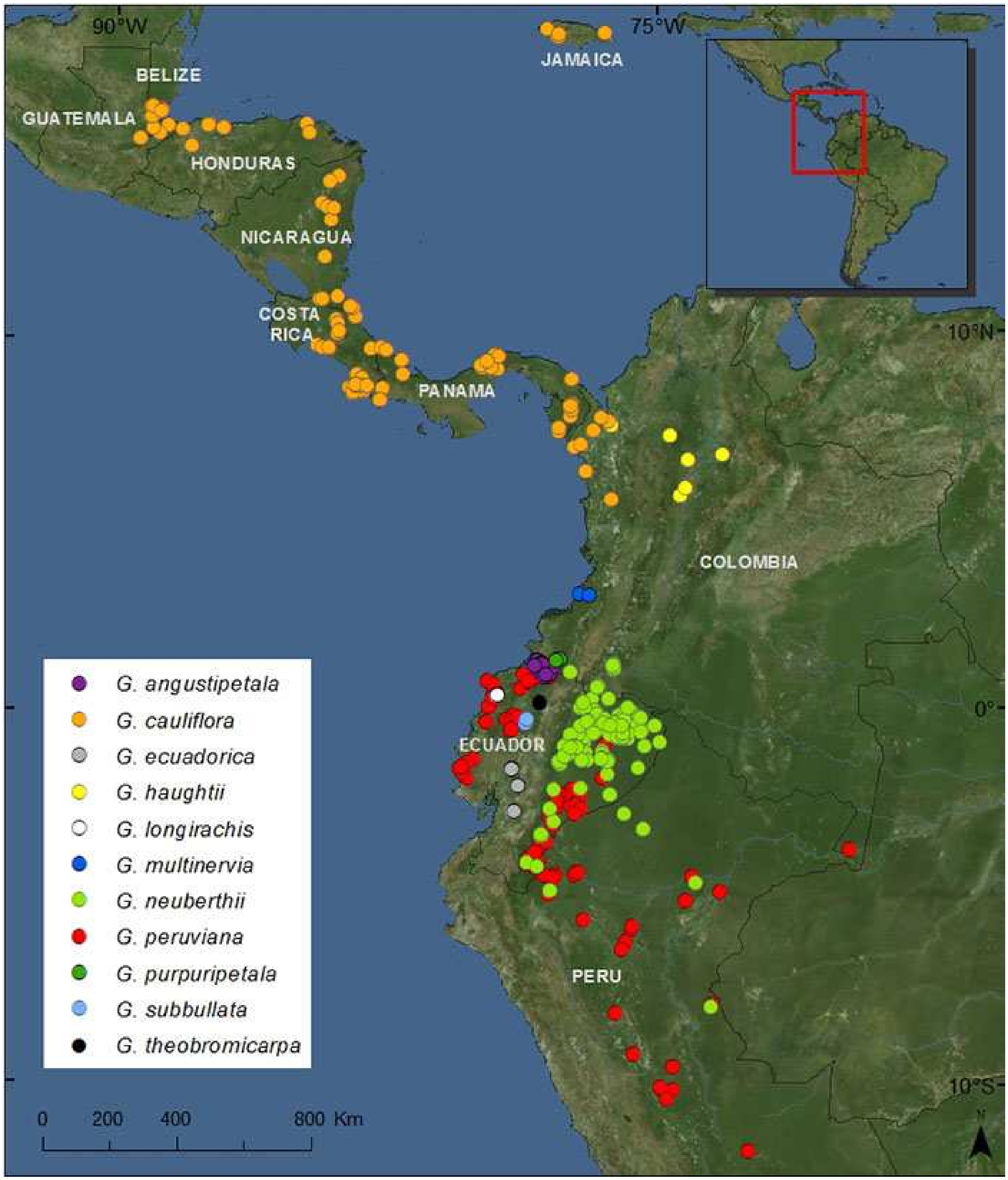
MAP 4. Distribution of Lecythidaceae subfam. Foetidioideae. This monogeneric subfamily is represented by 14 species in Madagascar, three species in the Mascarene Islands, and 1 species in western Africa (Prance, 2008).



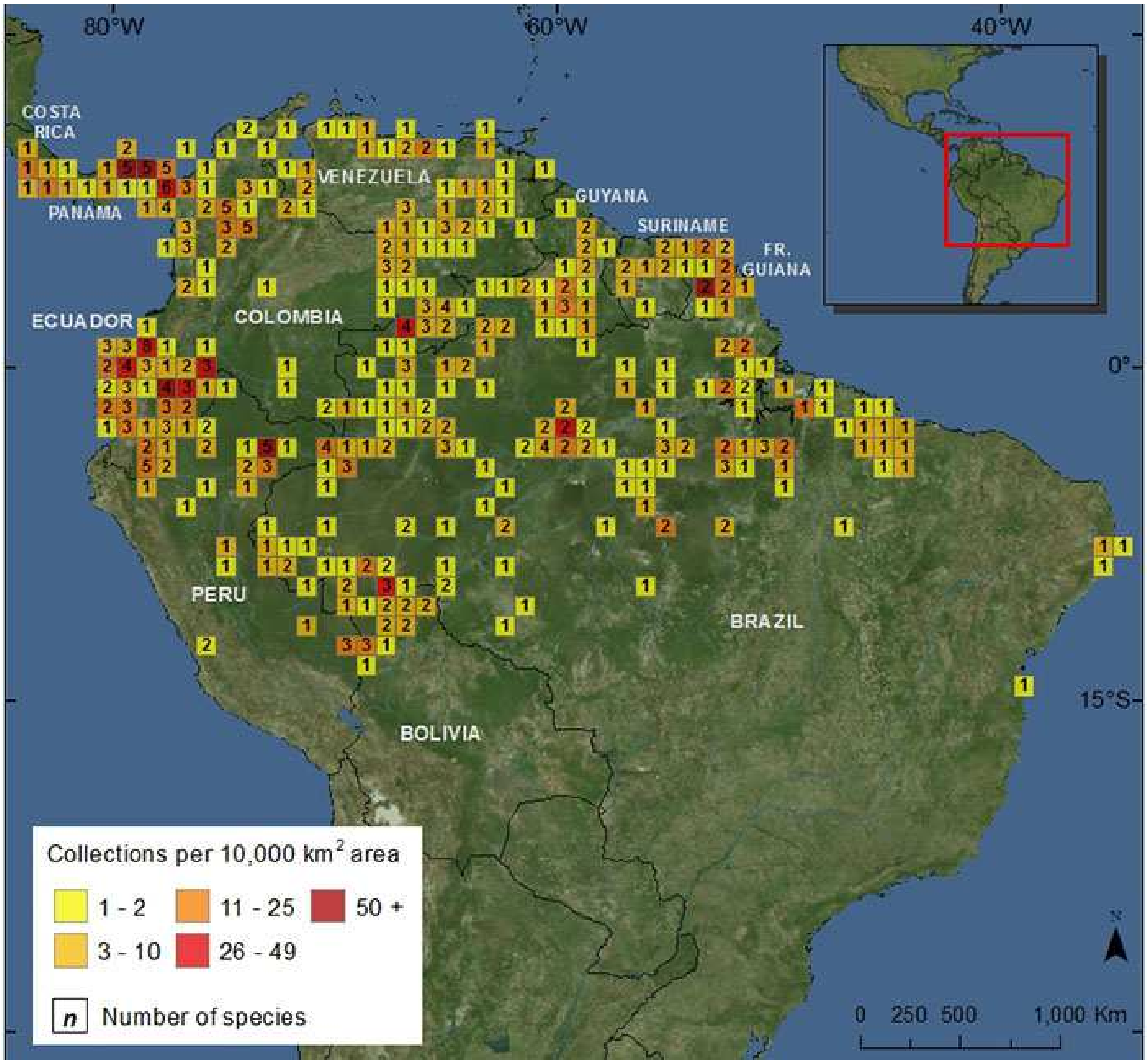
MAP 5. Distribution of Lecythidaceae subfam. Barringtonioideae. This subfamily is well represented in India, northern Australia, and southern Asia. In eastern Africa it is represented by two species (*Barringtonia asiatica* and *B. racemosa*), both of which have fruits that float. In addition, the common and widespread *Petersianthus macrocarpus* is the only species of subfam. Barringtonioideae that occurs in eastern and central Africa. The other species of *Petersianthus quadrialatus* is endemic to the Phillipines (Prance, 2012). There are no native barringtonioids in the New World and nearly all of the cultivated individuals are *Barringtonia asiatica*.



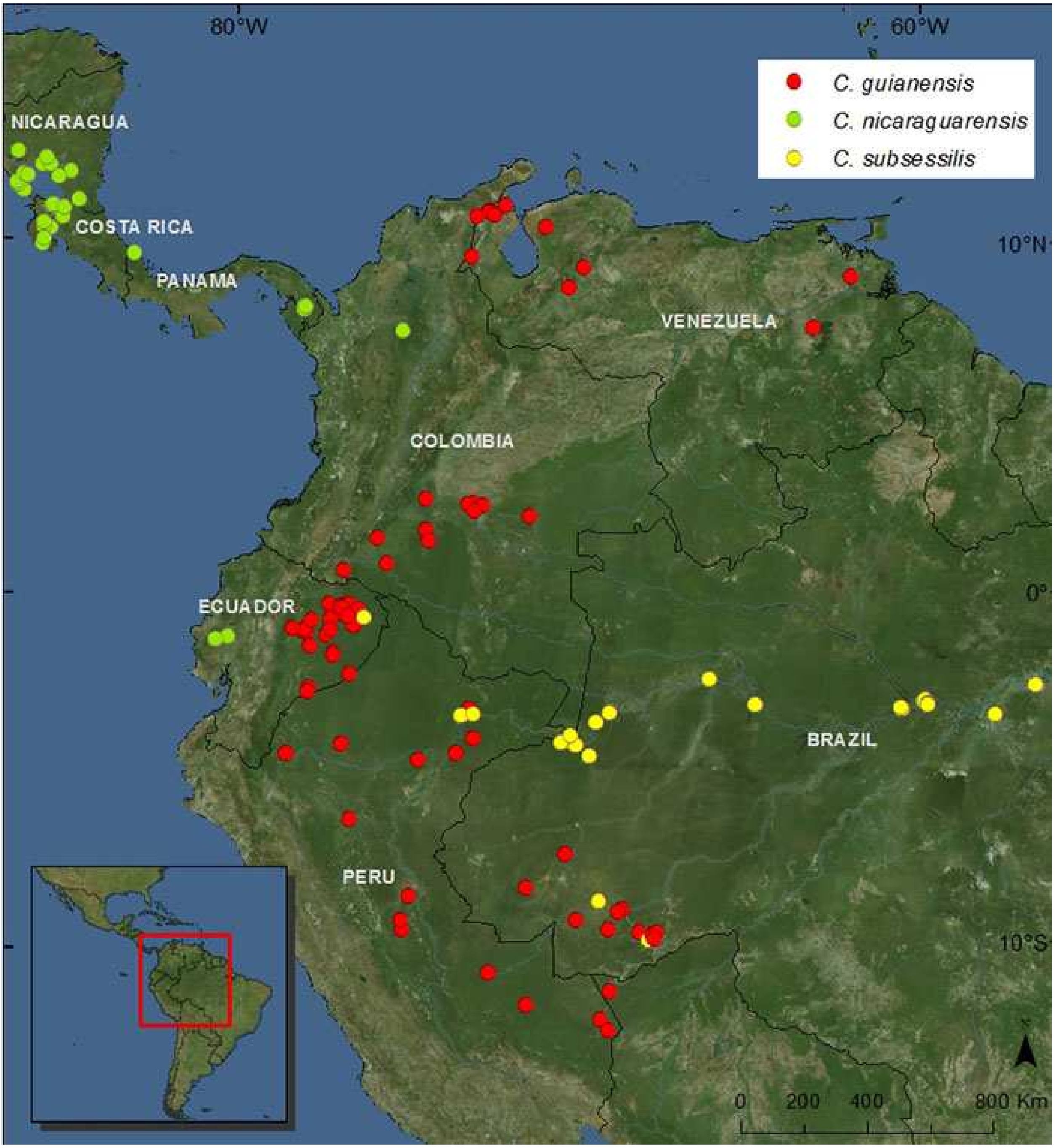
MAP 6. Distribution of Lecythidaceae subfam. Lecythidoideae. This subfamily is restricted to the New World tropics ranging from southern Brazil (*Cariniana estrellensis*) to Veracruz, Mexico (*Eschweilera mexicana*).



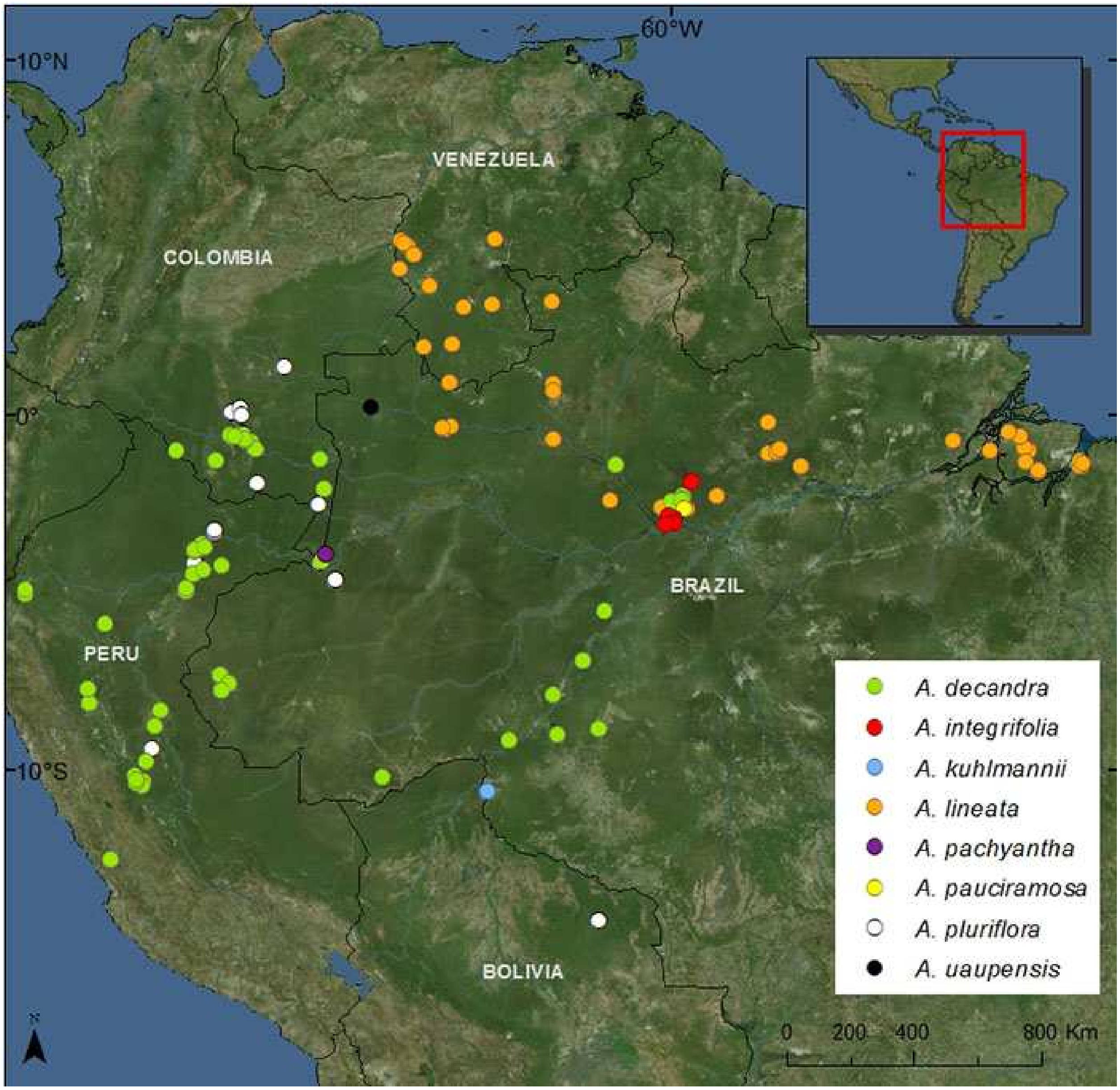
MAP 7. Distribution of the actinomorphic-flowered, monophyletic *Grias* clade. This genus is found mostly in the northwestern Andes but two species occur in western Amazonia (*G. neuberthii* and *G. peruviana*) and one species, the widespread *G. cauliflora*, is disjunct between Central America and Jamaica.



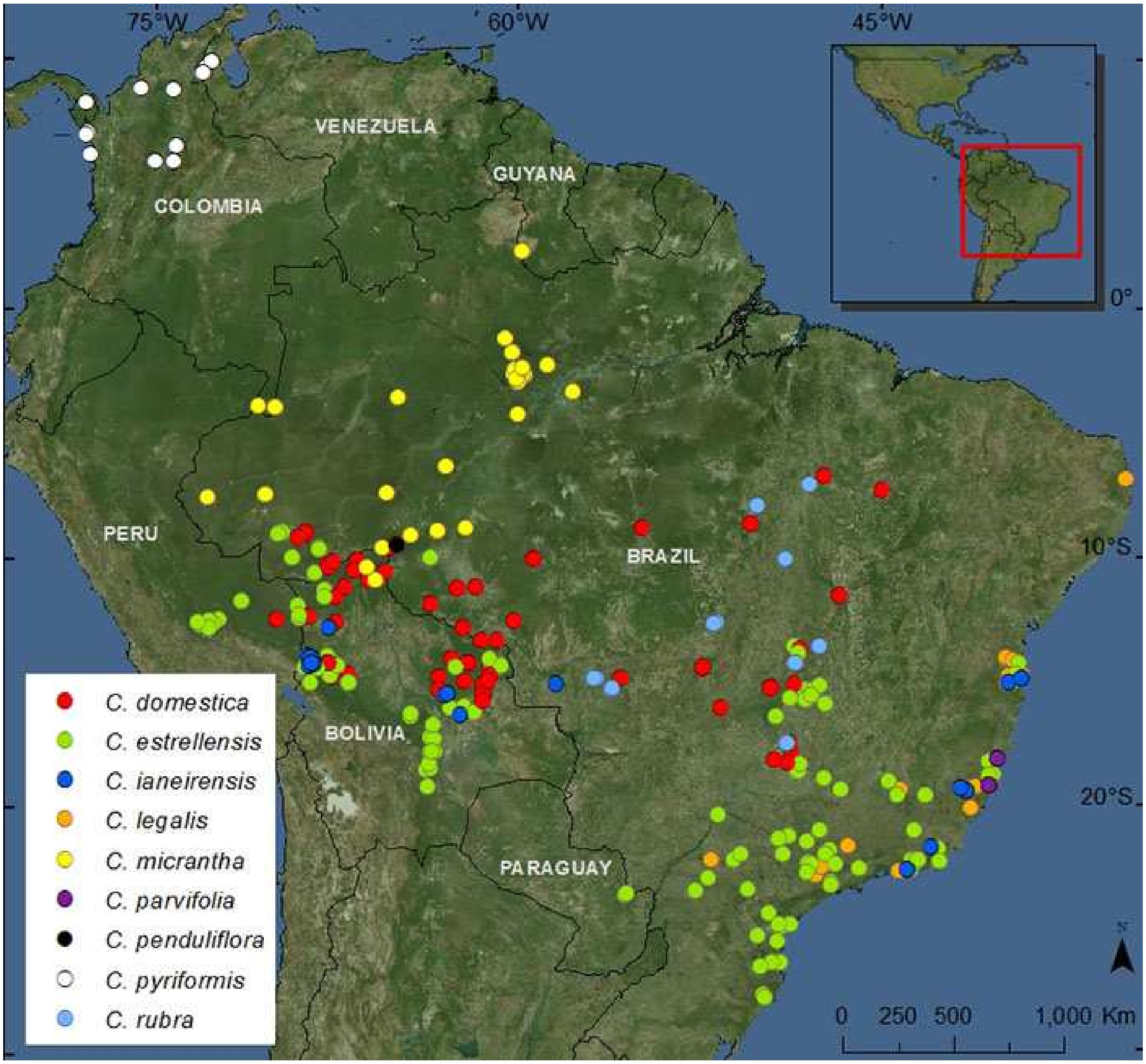
MAP 8. Distribution of the actinomorphic-flowered, monophyletic *Gustavia* clade. This genus occurs throughout most of the New World tropics. However, only one species is found in the Atlantic Forest of Brazil and diversity is low throughout the Guianas and eastern Amazonian Brazil. High diversity of this clade is found from eastern Panama to northwestern Ecuador.



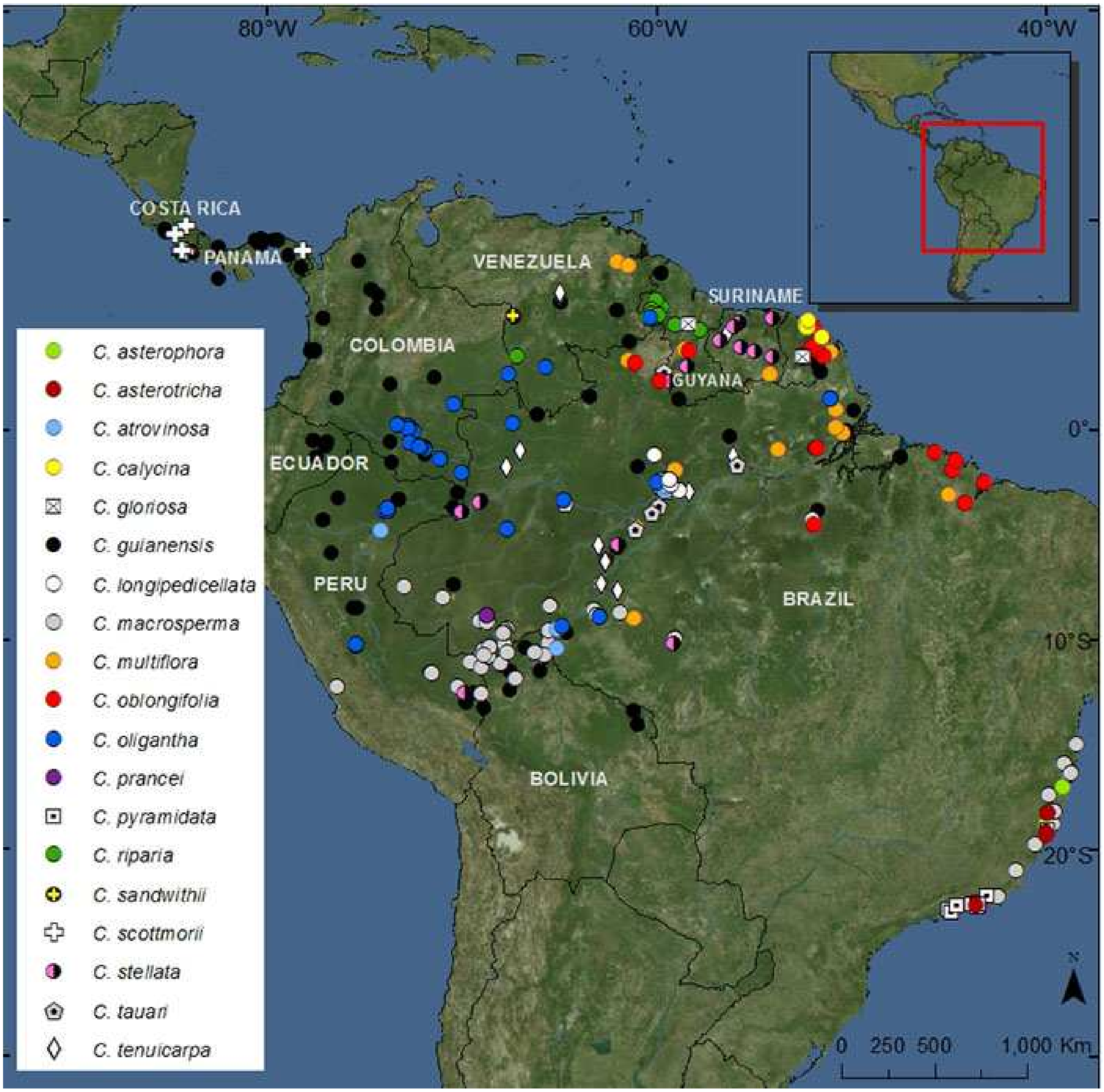
MAP 9. Distribution of the zygomorphic-flowered, monophyletic *Couroupita* clade. There are three species in this clade, two east of the Andes (*Couroupita guianensis* and *C. subsessilis*) and one west of the Andes (*C. nicaraguarensis*). Collections of cultivated species are not included on this map.



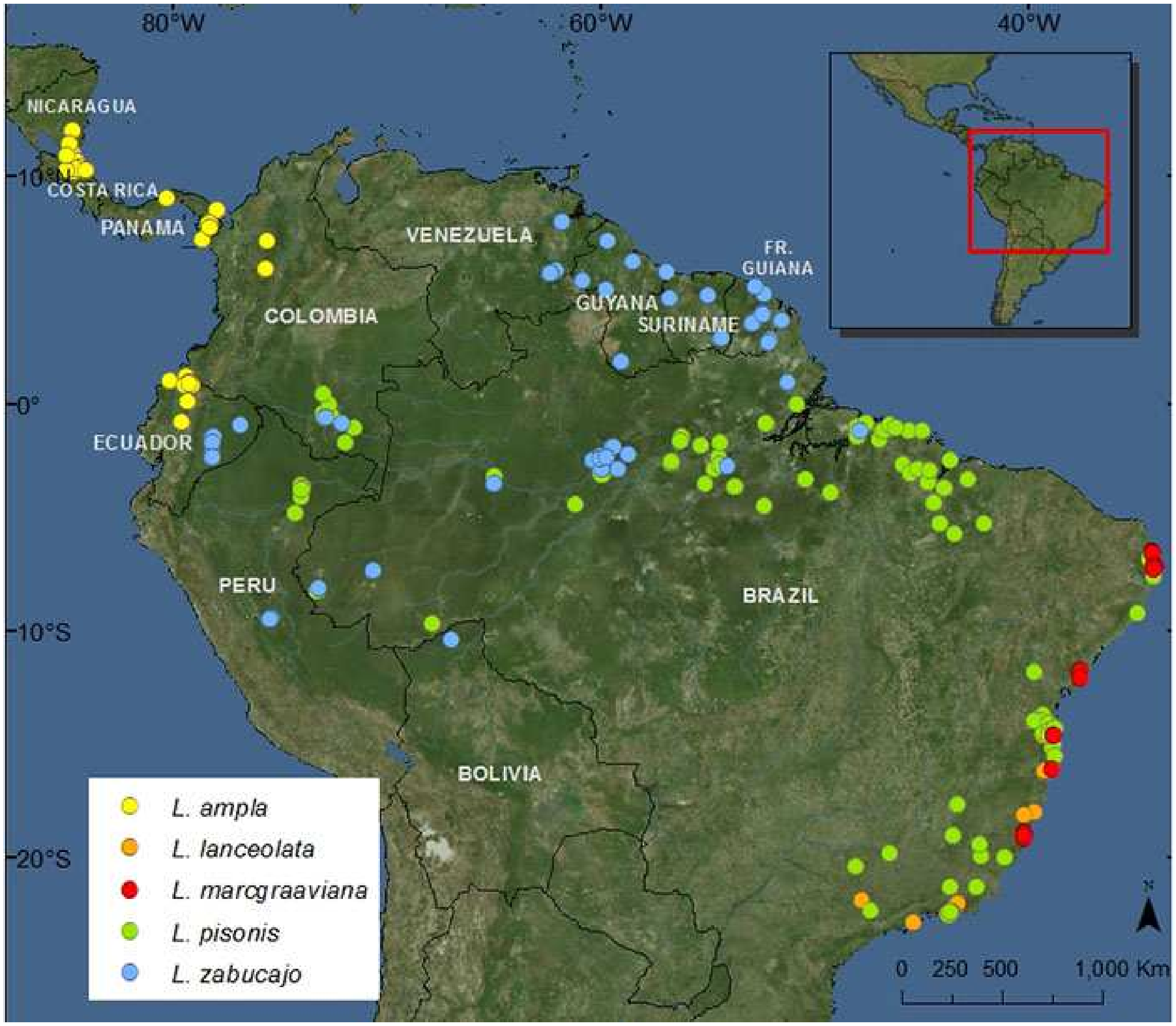
MAP 10. Distribution of the actinomorphic, monophyletic *Allantoma*. The greatest species diversity of this genus is in the northwestern Amazon. It is absent in the Guayana lowland flora, southeastern Amazonia, and the Atlantic Forest of Brazil. The disjunct collection from Bolivia is correctly identified as a species of *Allantoma* but the species has not been determined.



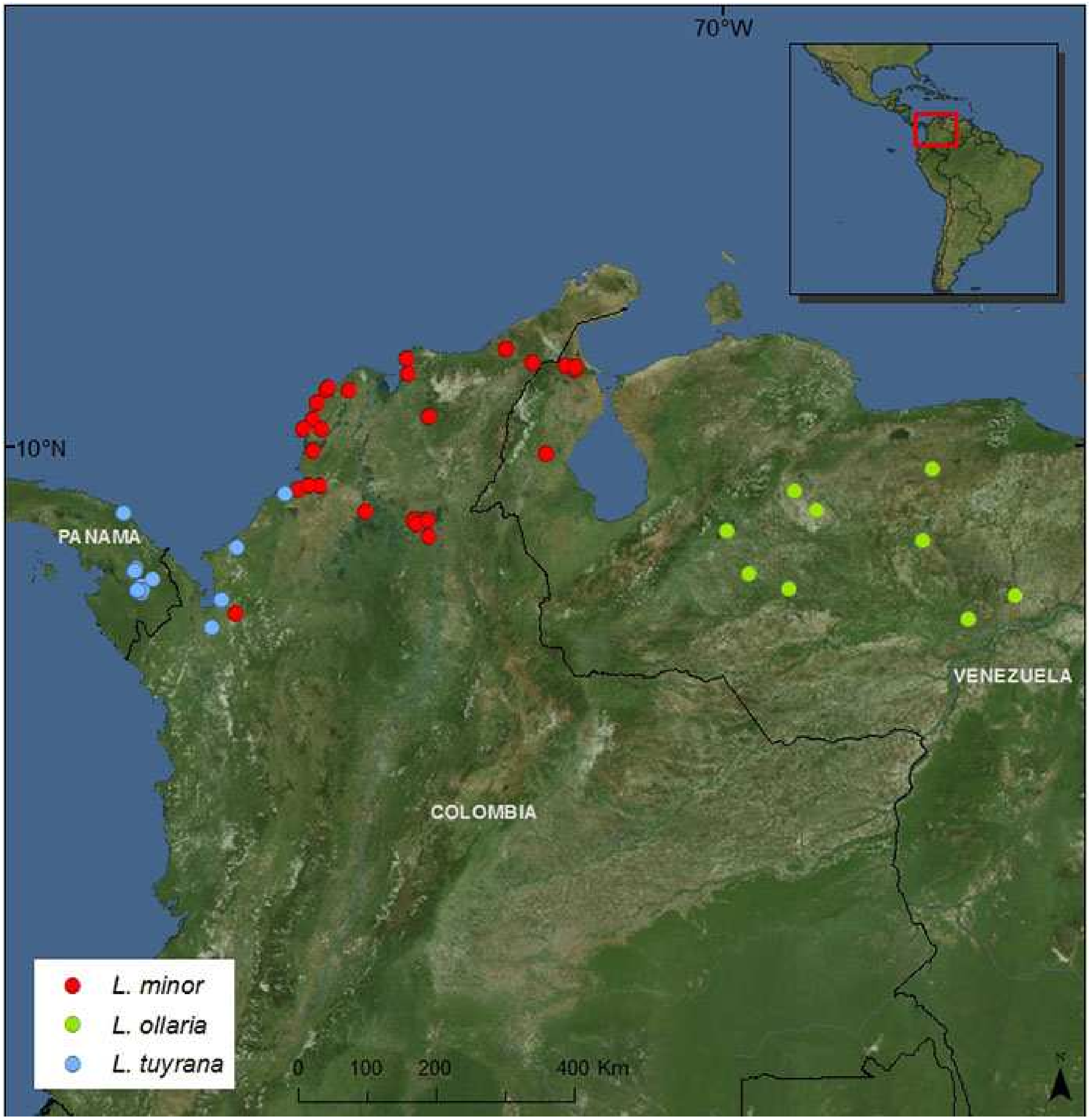
MAP 11. Distribution of the zygomorphic-flowered, monophyletic *Cariniana* clade. This genus is most speciose in a band from southwestern Amazonia to the Atlantic Forest of Brazil. Species of this clade are absent in eastern Amazonia, the Guayana lowlands, Venezuela, and Ecuador. *Cariniana pyriformis* occurs in northwestern Colombia, eastern Panama, and the Maracaibo Basin of Venezuela.



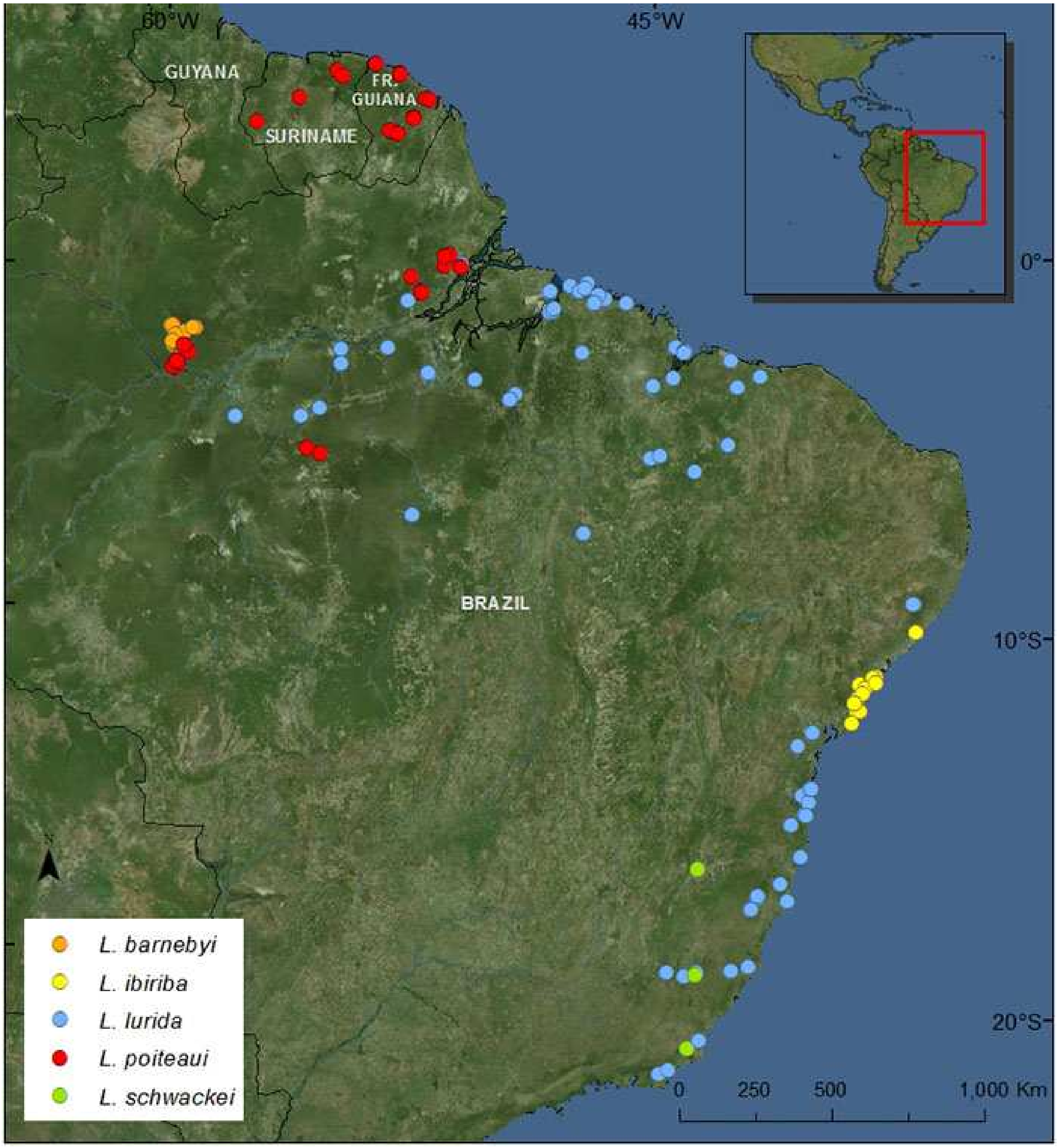
MAP 12. Distribution of the zygomorphic-flowered, monophyletic *Couratari* clade. Species of this clade appear in most lowland forests of the New World tropics but are usually absent from dryer areas. There is one trans-Andean species (*C. guianensis*), one Central America endemic (*C. scottmorii*), and four species in the Atlantic Forest of Brazil (*C. asterophora*, *C. asterotricha*, *C. macosperma*, and *C. pyramidata*).



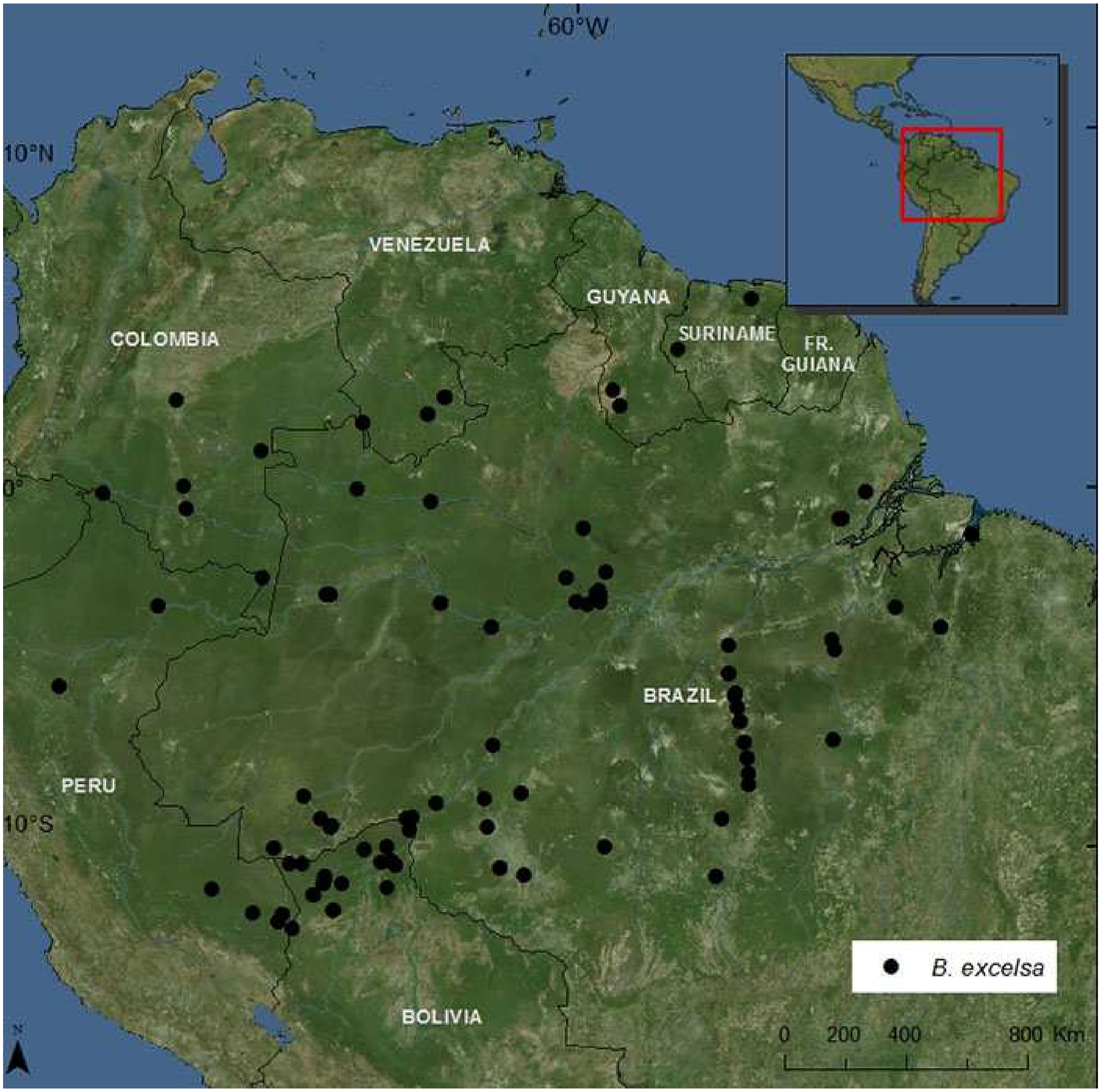
MAP 13. Distribution of the zygomorphic-flowered, monophyletic *Lecythis pisonis* clade (Huang et al., 2015). This clade is found in most of the lowland forests of lower Central America and South America but is usually absent from savanna, dry thorn scrub, and cloud forest vegetation types. *Lecythis pisonis* is cultivated so it is difficult to determine if some collections represent native plants.



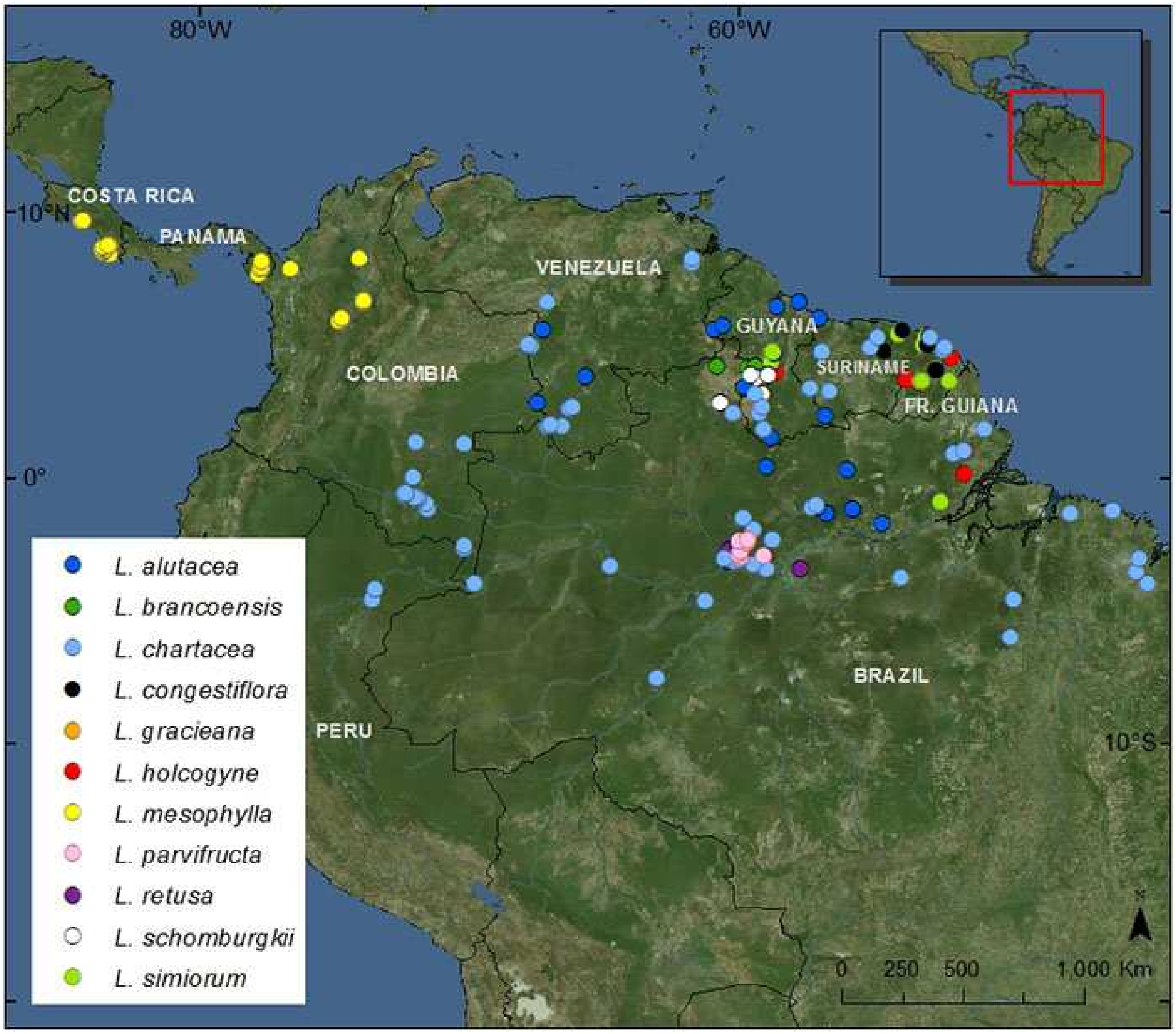
MAP 14. Distribution of the zygomorphic-flowered, non-monophyletic *Lecythis ollaria* clade (Huang et al., (2015). There are only three species in this clade: *Lecythis ollaria* (the type of *Lecythis*) found in savannas south of the Andes in Venezuela, *L. minor* in dry areas in northeastern Colombia, and *L. tuyrana* in lowland forests ranging from the Chocó of Panama into the Magdalena valley of Colombia.



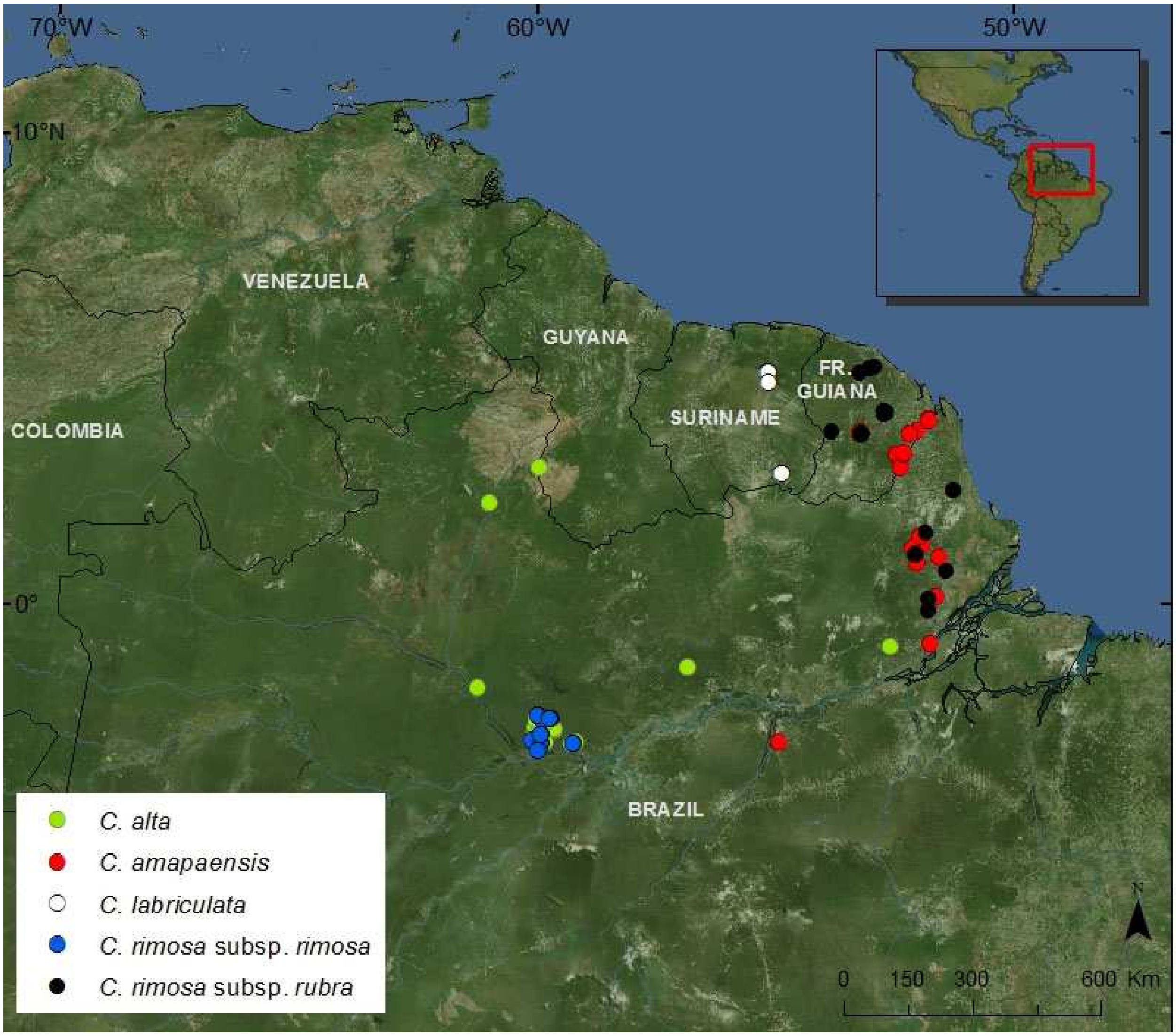
MAP 15. Distribution of the zygomorphic-flowered, non-monophyletic *Lecythis poiteaui* clade (Huang et al. 2015). This clade is found in the Guayana lowlands, central and eastern Amazonian Brazil, and the Atlantic Forests of Brazil. The Amazonian and Atlantic Forest species of this clade are currently separated by thorn scrub forest and savanna.



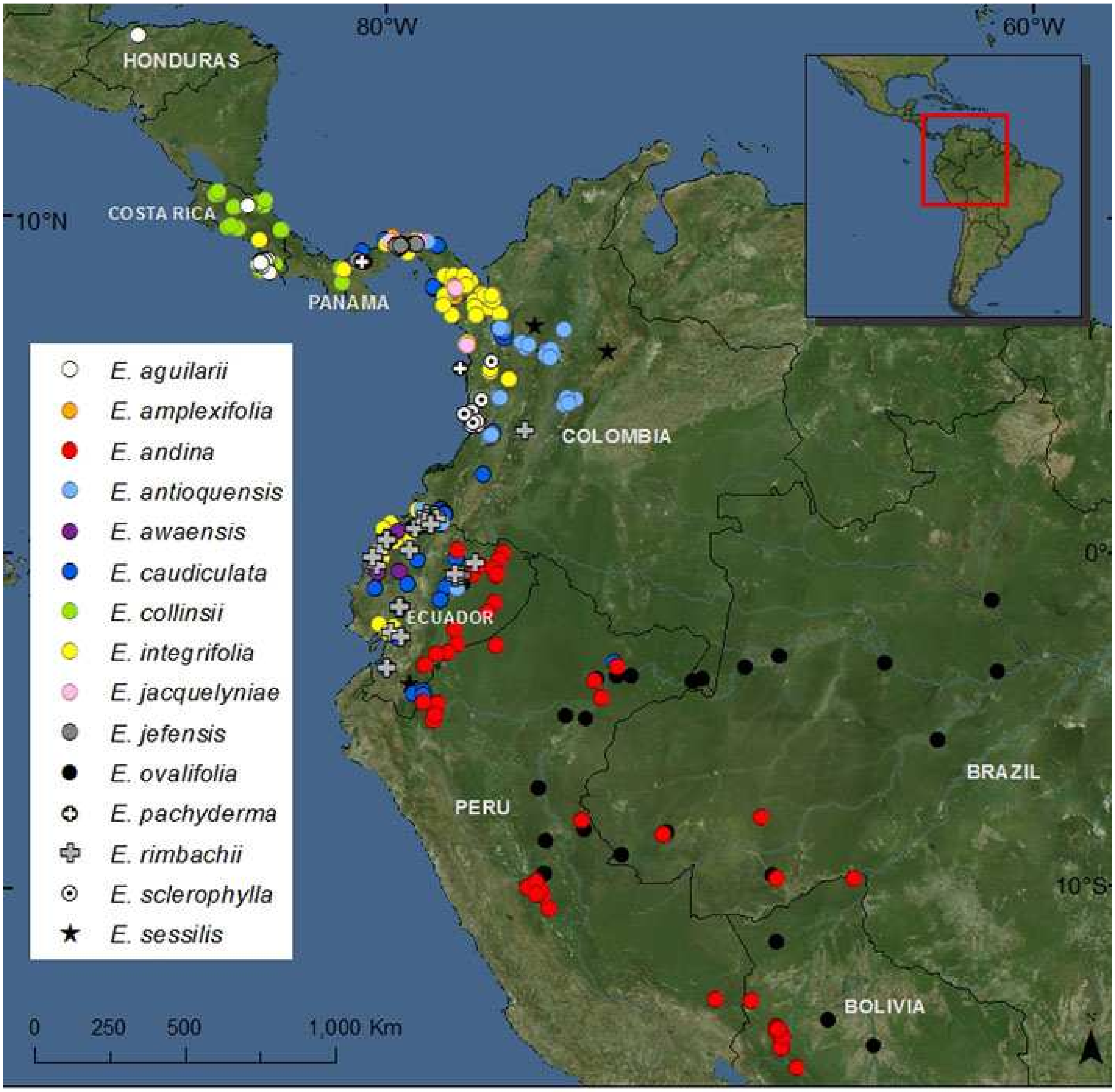
Map 16. Distribution of the zygomorphic-flowered, monotypic, non- phylogenetic *Bertholletia excelsa* clade. This clade is restricted to the Amazon Basin. Because of its edible seeds it has been carried from one region of the Amazon Basin to other parts of the Basin by humans; thus, the native distribution of this species is difficult to determine.



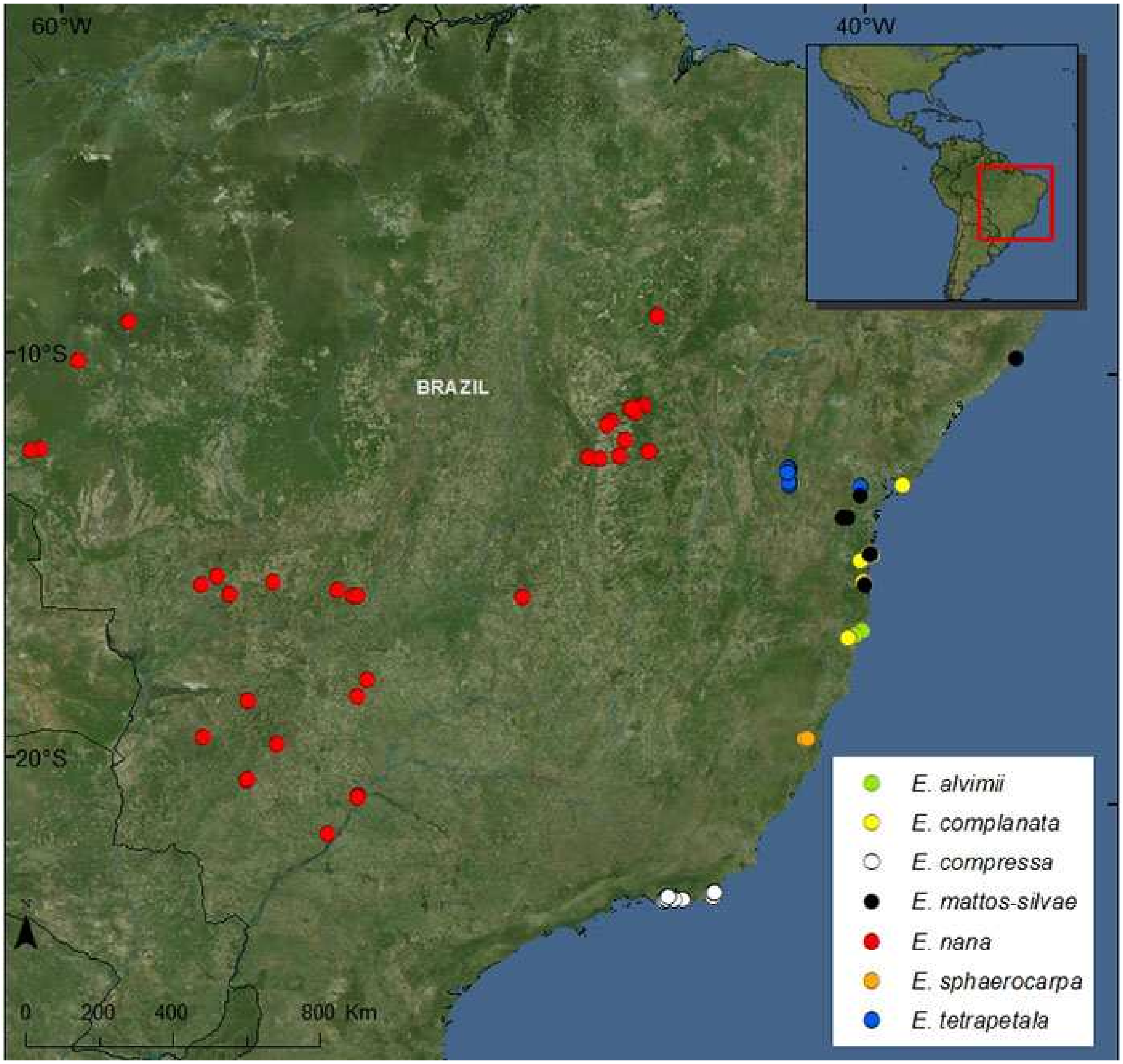
MAP 17. Distribution of the zygomorphic-flowered, non-monophyletic *Lecythis chartacea* clade. We now consider *Eschweilera congestiflora* and *E. simiorum* to be synonyms of *Lecythis congestiflora* Benoist and *L. simiorum* Benoist. This clade is distributed widely in Amazonia and is represented in eastern Panama and northwestern Colombia by *Lecythis mesophylla*. It is absent from the Atlantic Forest of Brazil.



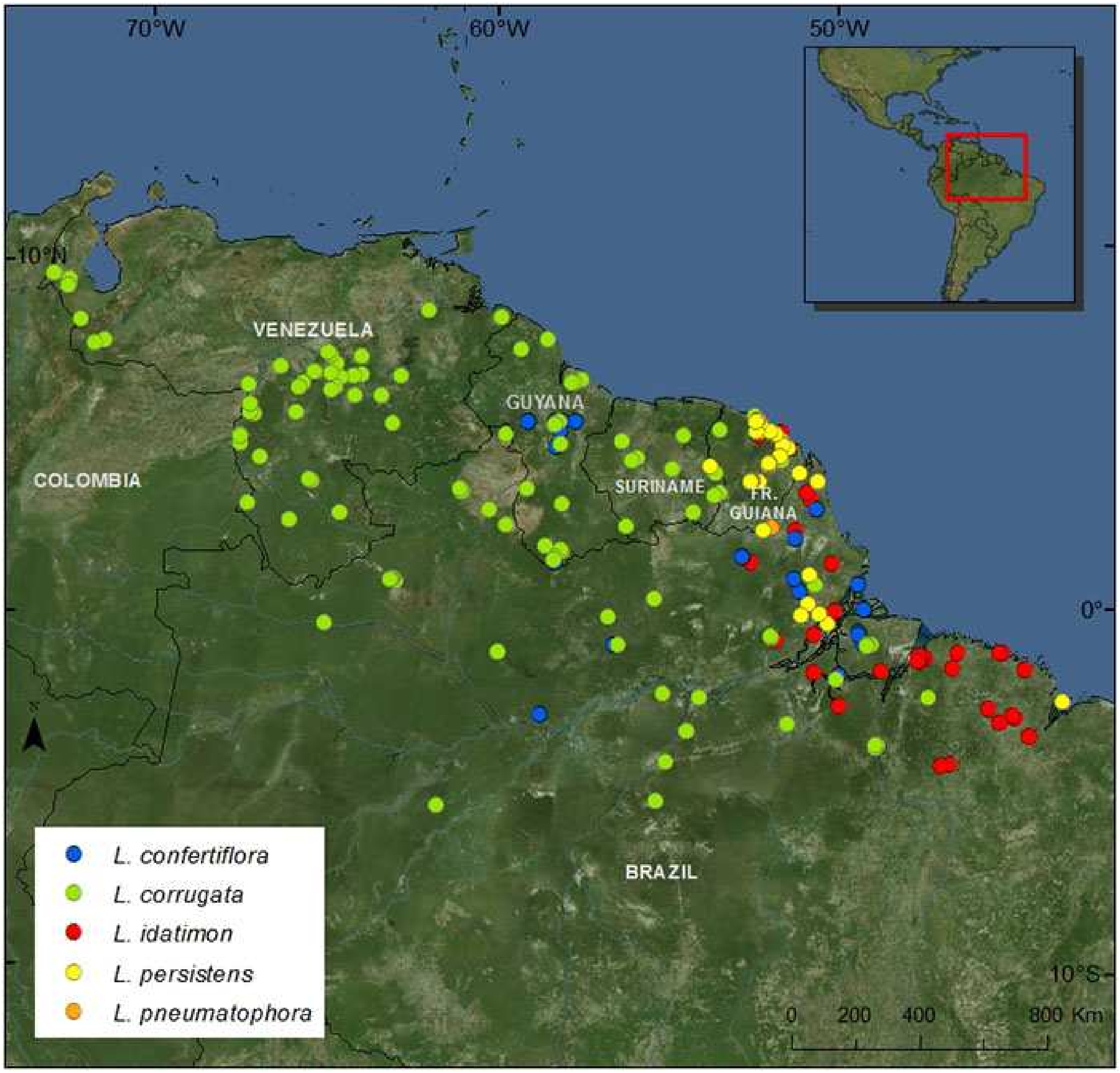
MAP 18. Distribution of the zygomorphic-flowered, monophyletic *Corythophora* clade. This clade is limited to the Guayana lowlands.



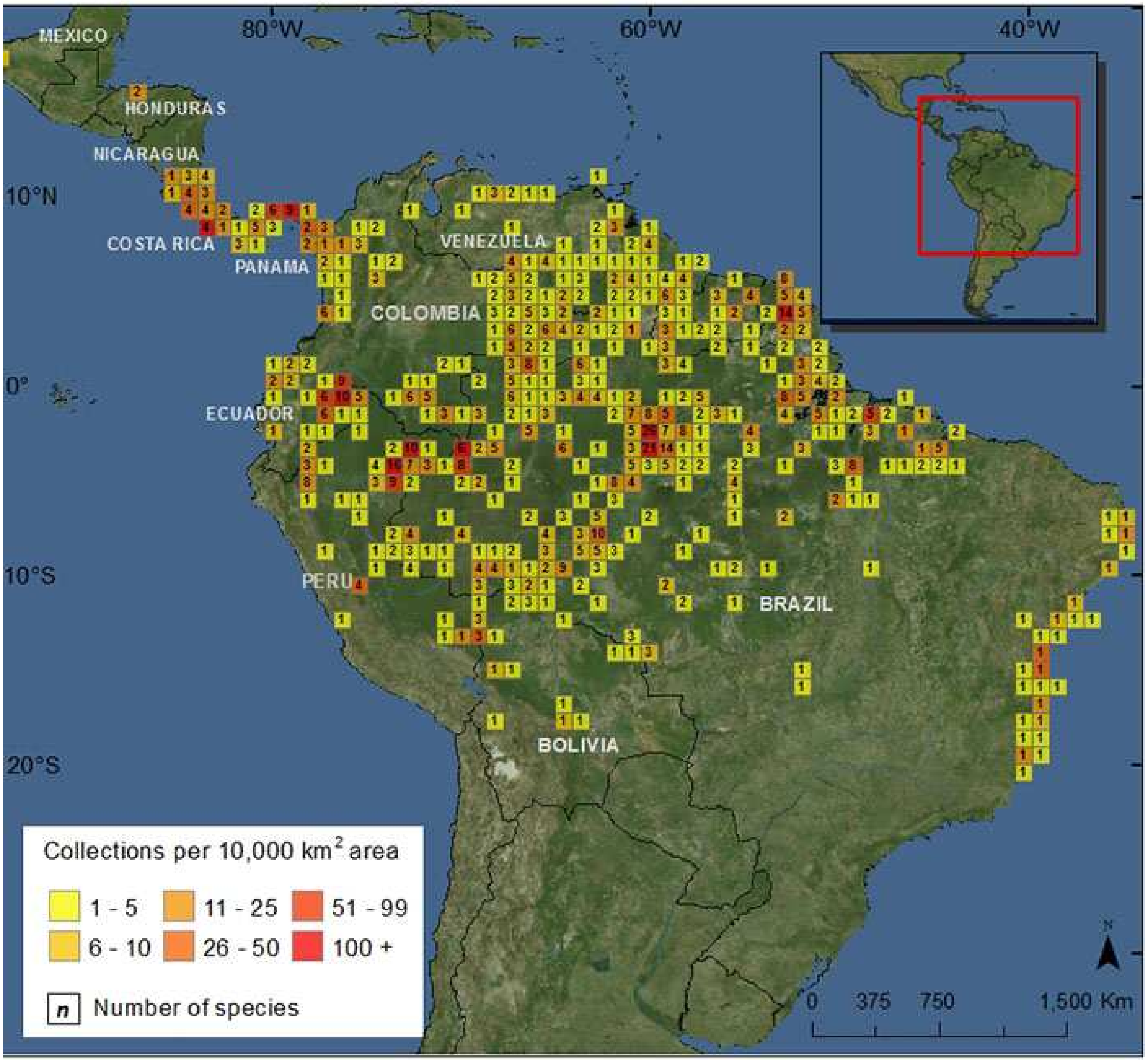
MAP 19. Distribution of the zygomorphic-flowered, non-phylogenetic *Eschweilera integrifolia* clade. This clade has two species found east of the Andes, the well-defined *E. ovalifolia* and *E. andina*, as well as numerous, poorly-defined species associated with the Andes into Central America as far north as Costa Rica.



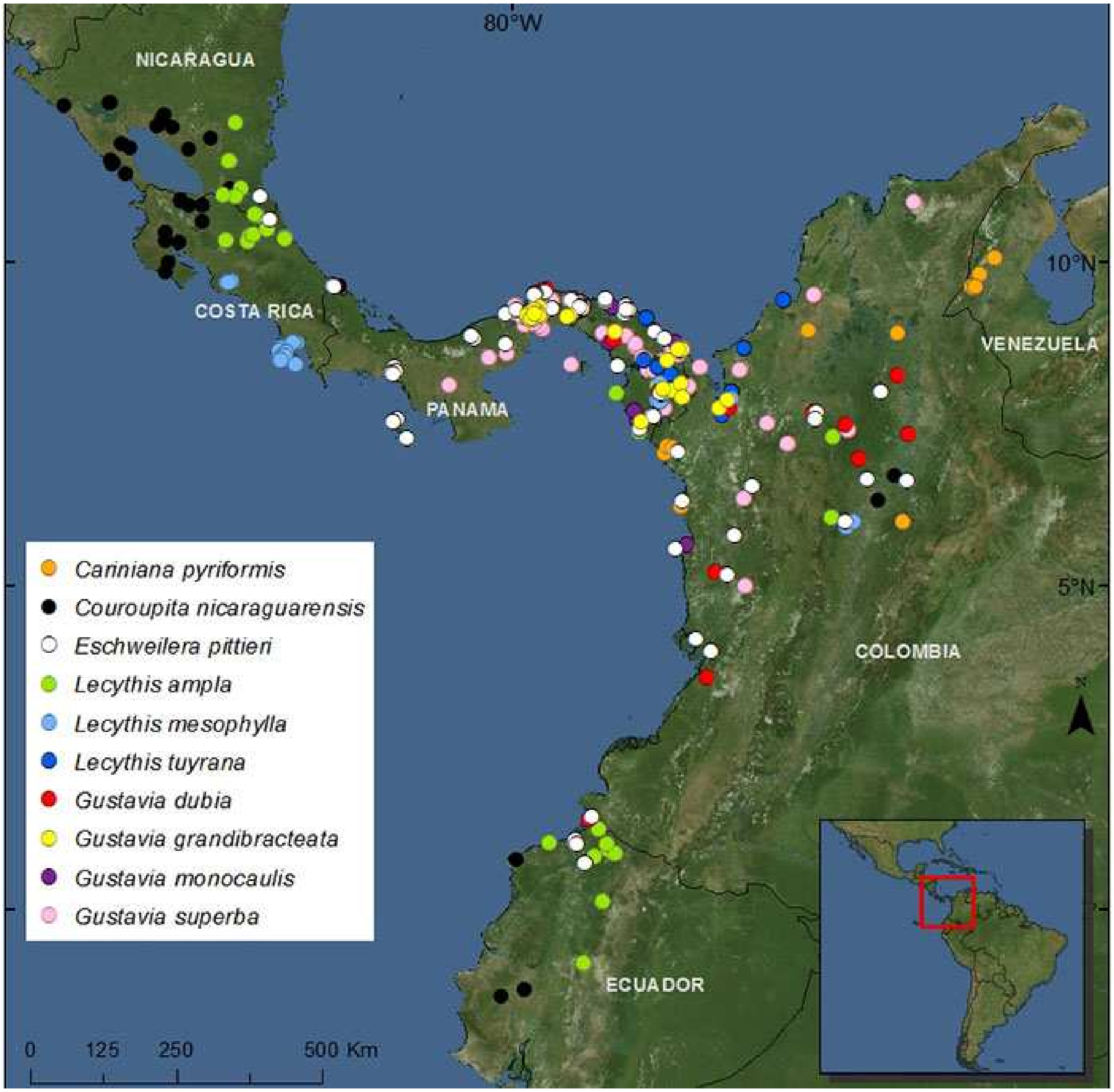
MAP 20. Distribution of the zygomorphic-flowered, monophyletic *Eschweilera tetrapetala* clade. This clade has one widespread species in the savannas of central Brazil and six described species with limited distributions in the Atlantic Forest of eastern Brazil.



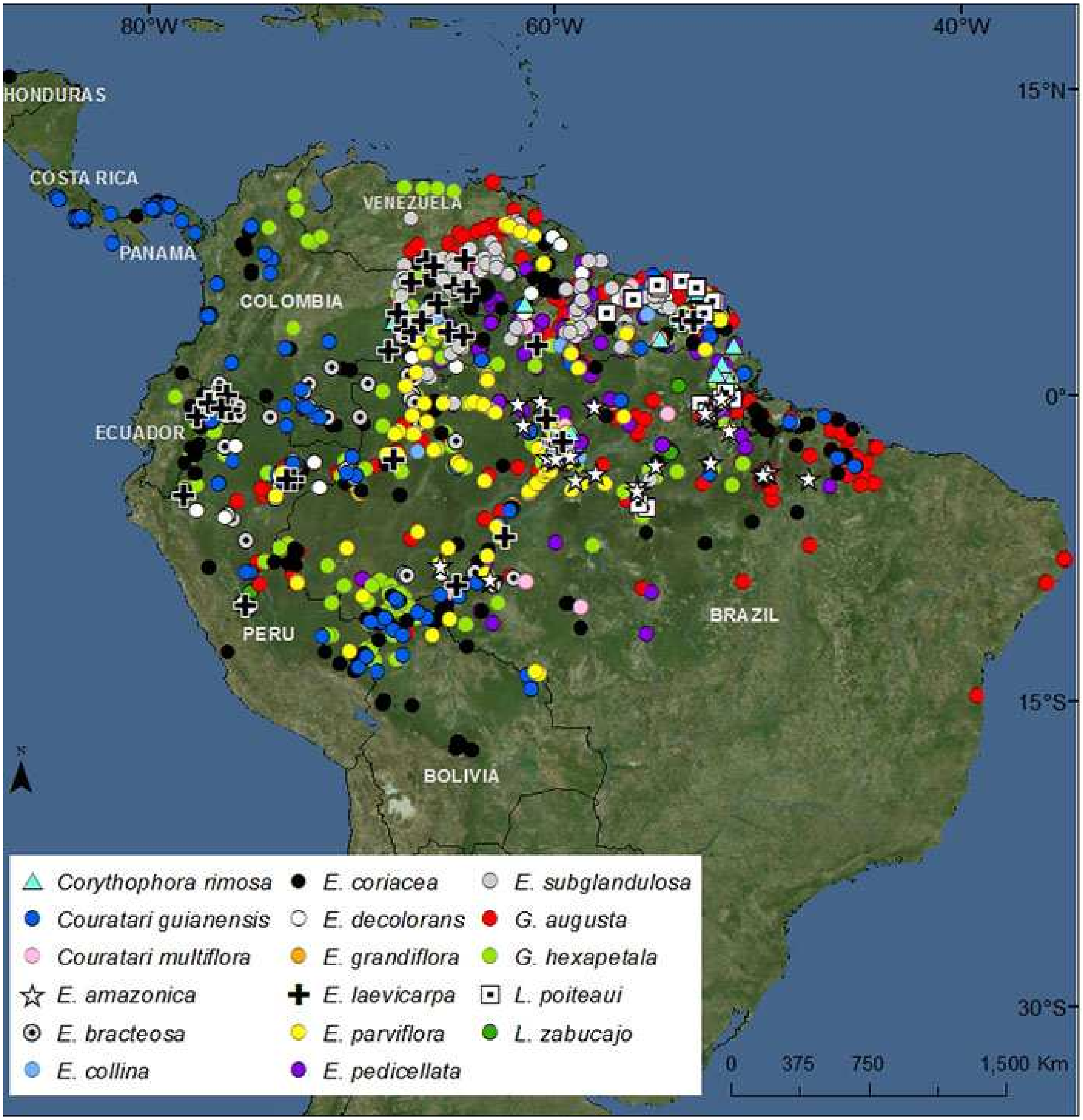
MAP 21. Distribution of the zygomorphic-flowered, non-monophyletic *Lecythis corrugata* clade. Species of this clade are mostly found in lowland Guayanan forests but some collections have been gathered south of the Amazon River.



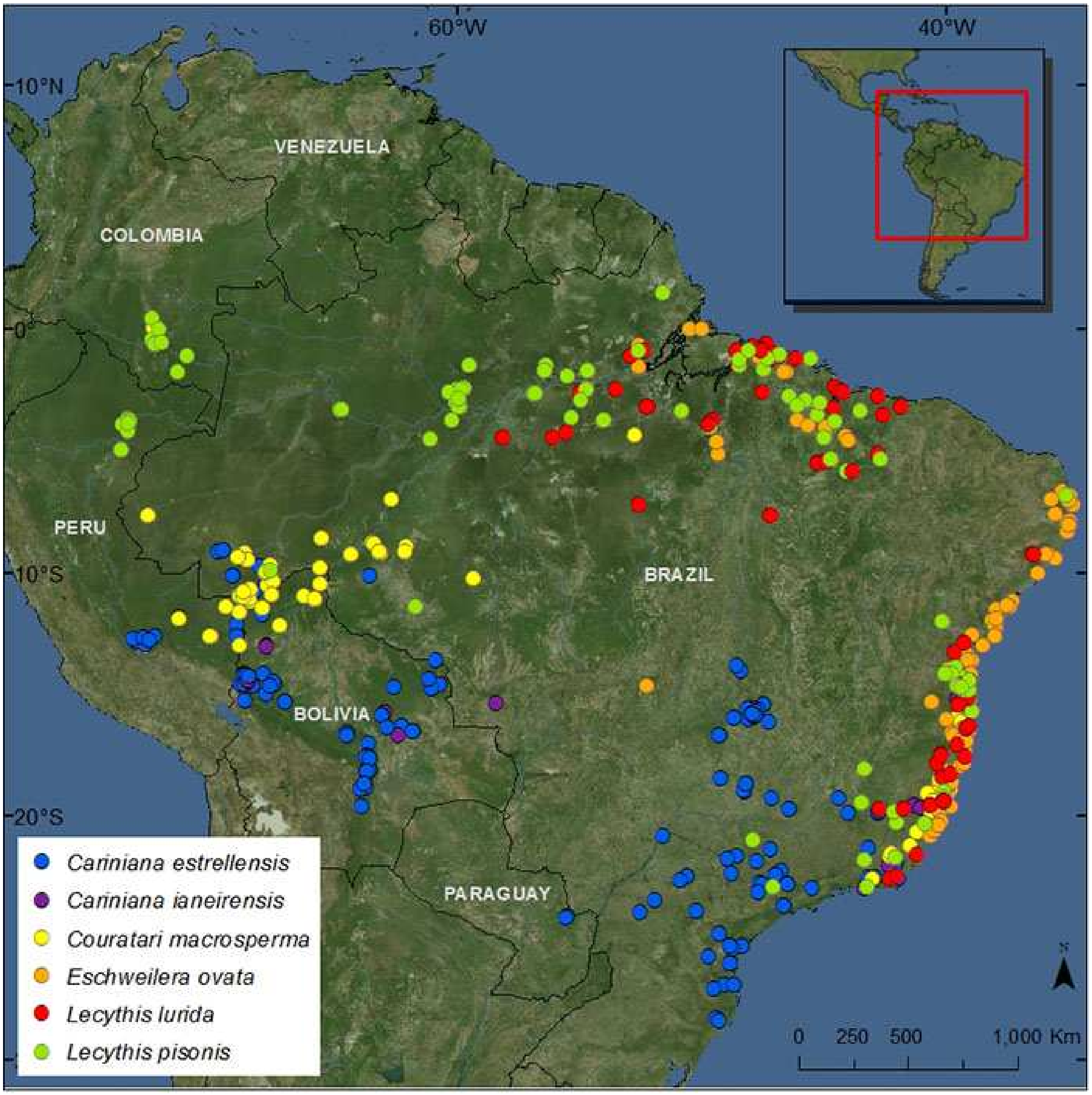
MAP 22. Distribution of the zygomorphic, non-monophyletic *E. parvifolia* clade. This clade is widely distributed throughout the Amazon, the Guayana lowlands, west of the Andes, and the Atlantic Forest where there is only one species of this species clade (*E. ovata*).



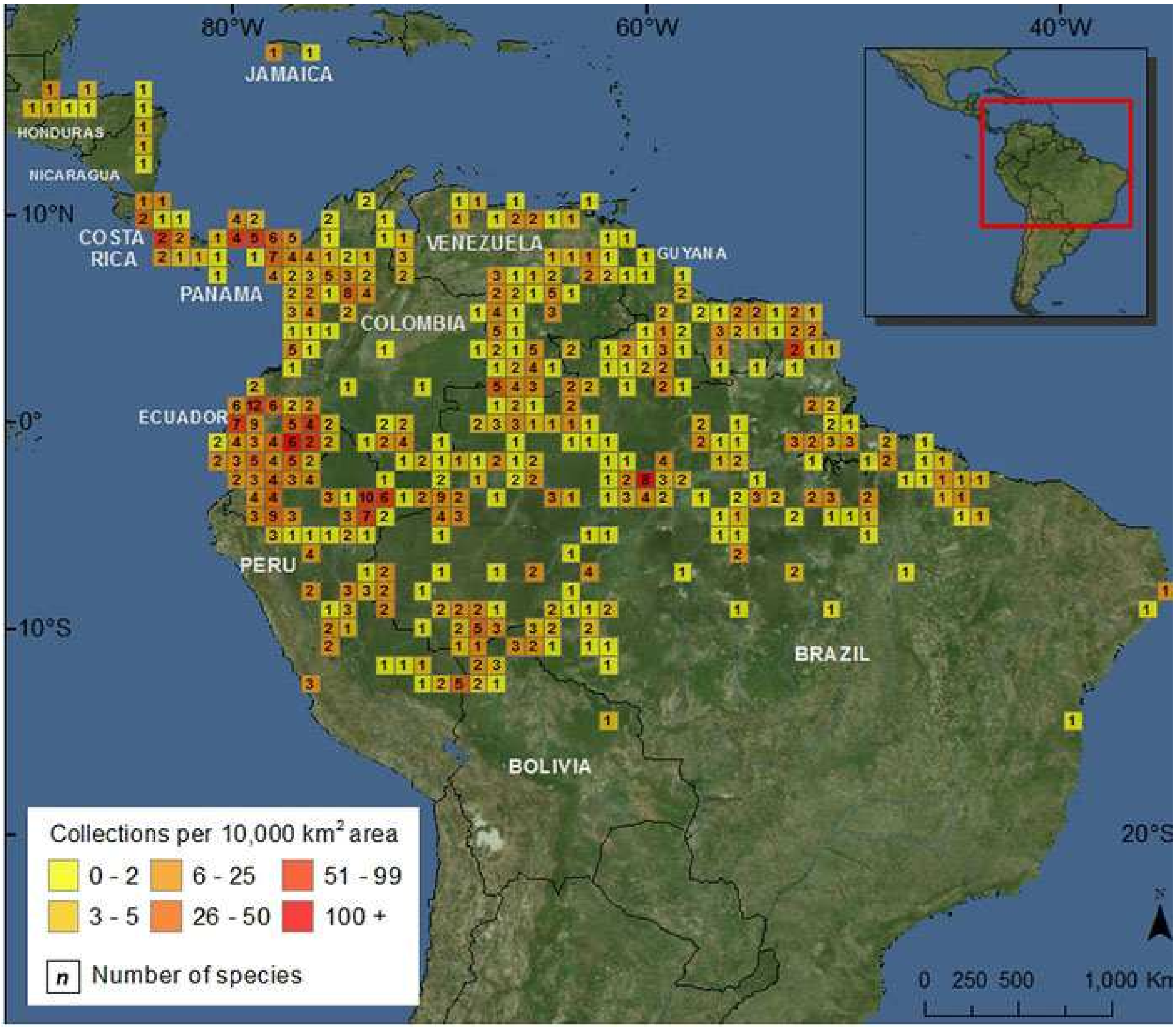
MAP 23. Distributions of selected species found in eastern Panama and northwestern South America. Such high diversity in this relatively small area appears to be promoted by the uplift of the Andes and the closing of the connection between North and South America.



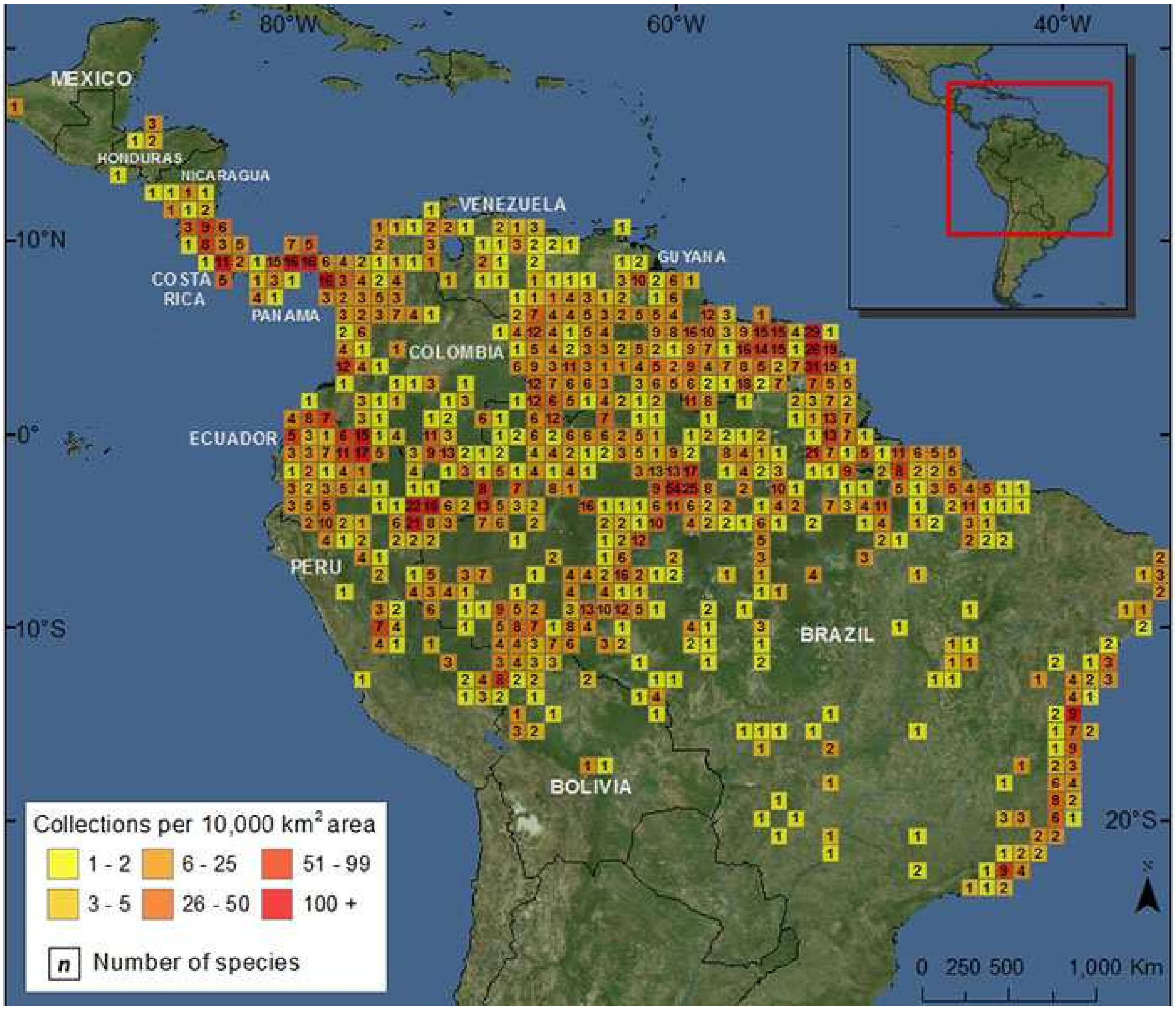
Map 24. Selected species of Lecythidaceae found in Central Amazonia. The diversity found in this area may have developed when lakes and oceanic intrusions receded and formed open habitats into which species of Lecythidaceae migrated from non-flooded areas such as the Guayanan lowlands (e.g., *L. barnebyi*, Map 15) and far western Amazonian (e.g., *E. tessmanii*. Map 19). In addition, other species may have been isolated on islands where they evolved *in situ* (e.g., *Lecythis barnebyi*).



Map 25. Distributions of selected species of Lecythidaceae found in the Atlantic Forest of Brazil as well as in either the Planalto of Brazil, eastern Amazonia, or southwestern Amazonia.



Map 26. Overall distributions of New World genera of Lecythidaceae with actinomorphic flowers (*Allantoma*, *Grias*, *Gustavia*). This map shows the colored coded collection density and the numbers indicate the number of species with this type of flower symmetry per degree grid square.



Map 27. Overall distribution of species with staminal ring zygomorphic flowers. Species of the following clades have this type of floral zygomorphy: *Bertholletia*, *Corythophora*, *Couratari*, *Couroupita*, *Eschweilera* (consists of three subclades and is not monophyletic), and *Lecythis* (consists of five subclades and is not monophyletic).