Article

Toward a phylogenetic-based Generic Classification of Neotropical Lecythidaceae—I. Status of *Bertholletia*, *Corythophora*, *Eschweilera* and *Lecythis*

YA-YI HUANG[1], SCOTT A. MORI[2] & LAWRENCE M. KELLY[3]

[1]*Institute of Plant and Microbial Biology, Academia Sinica, 128 Sec. 2, Academia Road, Taipei 11529, Taiwan; lecy.yhuang@gmail.com*
[2]*Author for correspondence: Institute of Systematic Botany, The New York Botanical Garden, Bronx, New York, USA 10458-5126; smori@nybg.org*
[3]*The New York Botanical Garden, Bronx, New York, USA 10458-5126; lkelly@nybg.org*

Abstract

Lecythidaceae subfam. Lecythidoideae is limited to the Neotropics and is the only naturally occurring subfamily of Lecythidaceae in the New World. A subset of genera with zygomorphic flowers—*Bertholletia*, *Corythophora*, *Eschweilera* and *Lecythis*—comprises a group of about 125 species called the *Bertholletia* clade. A previous study based on plastid *ndhF* and *trnL-F* genes supported the monophyly of *Corythophora* but suggested that *Eschweilera* and *Lecythis* are not monophyletic. Using this study as a baseline, we sampled more taxa and sequenced more loci to address the taxonomic problems of the ambiguous genera and to determine relationships within the *Bertholletia* clade. Our results support the monophyly of the *Bertholletia* clade as previously circumscribed. In addition, *Corythophora* is monophyletic, and the two accessions of *Bertholletia excelsa* come out together on the tree. Results of the simultaneous analysis do not support the monophyly of *Lecythis* or *Eschweilera*. *Lecythis* consists of four main groups (the *Lecythis pisonis*, *L. poiteaui*, *L. chartacea*, and *L. corrugata* clades), the last of which is nested within *Eschweilera*, and *Eschweilera* consists of three clades (the *Eschweilera integrifolia*, *E. tetrapetala*, and *Eschweilera parvifolia* clades). We compare our results with the generic classification presented in the latest monograph of neotropical Lecythidaceae and make recommendations for a revised generic classification of the *Bertholletia* clade of Lecythidaceae.

Introduction

We consider the Lecythidaceae (Brazil nut family) to consist of three subfamilies, the Old World Barringtonioideae (previously incorrectly called the Planchonioideae fide Thorne, 2000) and Foetidioideae, and the New World Lecythidoideae (Prance & Mori, 2004; Mori *et al*., 2007). In addition, the Angiosperm Phylogeny Group (2009) also includes the Napoleonaeoideae and Scytopetaloideae as subfamilies of Lecythidaceae. Regardless of how the Lecythidaceae are classified, these five groups form a strongly supported clade in the Ericales (Morton *et al*., 1997, 1998; Anderberg *et al*., 2002; Schönenberger *et al*., 2005).

The New World Lecythidaceae consist of ten genera and 210 described species (Prance & Mori, 1979; Mori & Prance, 1990; Mori, 1992, 1995, 2007; Mori & Lepsch-Cunha, 1995; Huang *et al*., 2008), and are limited to the Neotropics—moreover, no species of the other two subfamilies occurs naturally anywhere in Central America, South America, or the Caribbean (Mori *et al*., 2007). Thus, when we mention Lecythidaceae in this paper, we are referring to the species found naturally in the tropics of the western hemisphere, i.e., Lecythidaceae subfamily Lecythidoideae.

The greatest species diversity of Lecythidaceae in the New World is found in the Amazon Basin (Kincaid *et al*., 2001) where they flourish and often dominate lowland primary rainforests, especially those of non-flooded forests (*terra firme*). In Amazonia (Mori *et al*., 2001) and the Guianas (Mori & Boom, 1987), Lecythidaceae often rank as one of the ecologically most dominant families of the Amazonian tree flora (ter Steege *et al*., 2013). Although species are also found as far south as Paraguay and as far north as Mexico, and they inhabit other vegetation types such as periodically flooded forests, cloud forests, and savannas, they are never as numerous in these localities and habitats as they are in Amazonian and Guianan lowland rainforests.

Neotropical Lecythidaceae are small to large trees with fibrous bark; normally oriented cortical bundles, i.e., the xylem is on the inside and the phloem is on the outside of the bundles (Prance & Mori, 1979; Morton *et al*., 1998);

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caducous stipules (difficult if not impossible to see in adult plants because they are very small and short lived); simple, alternate leaves; actinomorphic or zygomorphic androecia; stamens arising from a staminal tube (see Figs. 2–7 *in* Mori *et al*., 2015) or a staminal ring; stamens usually numerous (50–1200); tricolpate/tricolporate pollen (Tsou 1994); inferior to half-inferior (i.e., the summit of the ovary projects beyond the hypanthium) ovaries; axile placentation at least at the base of the ovary (Mori *et al*., 2015); bitegmic, tenuinucellate ovules (Tsou, 1994a); and dehiscent or indehiscent fruits. Phylogenetic analyses based on anatomical, cytological, morphological, and DNA sequence data indicate that Lecythidaceae subfam. Lecythidoideae is monophyletic (Morton *et al*., 1998; Stevens, 2001; Mori *et al*., 2007; APG III, 2009). A non-molecular synapomorphy unique to the Lecythidoideae is the presence of a basic chromosome number of x = 17 (Morton *et al*., 1998). If the Lecythidaceae are treated as comprising three subfamilies (Mori *et al*., 2007; Prance & Mori, 2004), the tricolpate or tricolporate pollen types of the subfamilies Lecythidoideae and Foetidioideae are markedly different than the syntricolpate pollen (Tsou, 1994) of subfamily Barringtonioideae.

Traditionally the generic delimitation of Lecythidaceae is based on flower size; sepal and petal number; androecial features including symmetry, presence or absence of a staminal tube or a staminal ring, number of stamens, anther size and dehiscence, presence or absence of sterile pollen in addition to fertile pollen, and morphology of the androecial hood; number of locules and placentation types; fruit dehiscence, size, and shape; seed features such as number of seeds per fruit, shape, presence or absence of seed wings, presence or absence of arils, position of arils when present, and type of seed coat; and cotyledon presence, absence, and type (Prance & Mori, 1979; Mori & Prance, 1990). Many of these features have been hypothesized to be adaptations to pollinators (Mori & Boeke, 1987a; Mori *et al*., 1978) or dispersal agents (Prance & Mori, 1978).

In the two most recent monographs (Prance & Mori, 1979; Mori & Prance, 1990), 11 genera of neotropical Lecythidaceae were recognized. Tsou (1994) and Appel (1996, 2004) subsequently pointed out that *Asteranthos* Desfontaines (1820: 9) is better placed in the Scytopetalaceae. The remaining ten genera were placed by Prance & Mori (1979) and Mori & Prance (1990) in two groups based on androecial symmetry. The first included the three genera with actinomorphic androecia (*Gustavia* Linnaeus [1775: 12, 17, 18], *Grias* Linnaeus [1759: 1075], and *Allantoma* Miers [1874: 291]). *Cariniana* Casaretto (1842: 35), which at the time included two groups of species, one with actinomorphic and the other with a zygomorphic androecia, was also placed here. Since then, Huang *et al*. (2008) transferred the *Cariniana* species with actinomorphic androecia to *Allantoma*. The second group included the six genera with zygomorphic androecia (*Couroupita* Aublet [1775: 708], *Corythophora* R. Knuth [1939: 50], *Bertholletia* Bonpland [1808: 122], *Couratari* Aublet [1775: 723], *Eschweilera* Mart. ex Candolle [1828: 293], and *Lecythis* Loefling [1758: 189]). Although the newly circumscribed *Cariniana* would now be placed with the zygomorphic genera, the androecium is not the same as that of the other six genera because the androecial zygomorphy is caused by a unilateral extension from a staminal tube, and not by a unilateral extension from a staminal ring (Fig. 1 in Huang *et al*. 2008).

Using plastid *ndhF* and *trnL-F* sequence data, Mori *et al*. (2007) tested the morphological-based classification of Prance & Mori (1979) and Mori & Prance (1990). Their results supported the monophyly of most genera, but raised questions about the monophyly of *Eschweilera* and *Lecythis*. The type species of these two genera, however, were not included in their analysis. In order to test the monophyly of *Eschweilera* and *Lecythis*, as well as to determine their relationships with *Bertholletia* and *Corythophora*, Huang (2011) chose to study these four genera herein informally called the *Bertholletia* clade, because the relationships within the clade were unresolved (Fig. 2 in Mori *et al*., 2007). A study by Huang (2010) suggested that *Eschweilera* is monophyletic only if *Eschweilera congestiflora* (Benoist 1915: 177) Eyma (1932: 71) and *Eschweilera simiorum* (Benoist 1915: 178) Eyma (1932: 81) are excluded from the genus and that, except for Section *Tetrapetala* S. A. Mori (1990: 169), the segregation of sections *Bracteosa* S. A. Mori (1990a: 172) and *Jugastrum* Prance & S. A. Mori (1990: 177) from section *Eschweilera* S. A. Mori & Prance (1990: 181) is not supported (Fig. 6 in Huang *et al*., 2011). *Lecythis*, on the other hand, is paraphyletic (Fig. 6 in Huang *et al*., 2011), but three sections of *Lecythis* (*Corrugata* S. A. Mori [1990b: 277], *Pisonis* S. A. Mori [1990b: 289], and *Poiteaui* S. A. Mori [1990b: 298]) recognized by Mori (1990b) are monophyletic.

In this study, we improved the sampling of Mori *et al*. (2007) by including the type species of all four genera and sections within each genus as recognized by Mori & Prance (1990). In addition, we incorporated DNA sequence data into the morphological data set of Huang *et al*. (2011), and sequenced more loci and included more taxa than was done by Mori *et al*. (2007).

The goal of this paper is to contribute to a phylogeny-based classification of the genera in the *Bertholletia* clade, which includes *Bertholletia*, *Corythophora*, *Eschweilera*, and *Lecythis* as defined by Mori & Prance (1990). Thus, our objectives are to (1) examine the monophyly of the ambiguous taxa in the *Bertholletia* clade (i.e., *Eschweilera* and *Lecythis*) and evaluate the validity of the sections within these two genera, (2) identify morphological synapomorphies

for the supported clades, (3) make suggestions for generic changes, and (4) make recommendations for further phylogenetic study of neotropical Lecythidaceae.

Materials and methods

Sampling

DNA sequences representing the ingroup taxa were collected from 185 individuals (84 species), representing *Bertholletia*, *Corythophora*, *Eschweilera*, and *Lecythis*. Taxon sampling covers the range of morphological variation in the genera and sections as circumscribed by Mori & Prance (1990). Priority was given to type species of each genus, representatives of each section, species with atypical morphological characters (e.g., *Eschweilera nana* [O. Berg 1858: 617] Miers [1874: 261]), and species that have been difficult to assign to genus (e.g., *Eschweilera congestiflora* and *E. simiorum*). More individuals were sampled from geographically widespread species (e.g., *Eschweilera coriacea* (Candolle 1828: 291) S. A. Mori [in Mori & Prance 1990: 203], *Eschweilera pedicellata* (Richard [1792: 111]) S. A. Mori [1987: 34], *Lecythis chartacea* O. Berg [1856: 450], and *Lecythis pisonis* Cambessèdes [1829: 377]). Twenty two individuals (17 species) were included as outgroup taxa, representing *Allantoma*, *Grias*, *Gustavia*, *Cariniana*, *Couratari*, and *Couroupita*. The selection of the outgroup taxa followed the molecular analysis of Mori *et al*. (2007), but with fewer species from each genus. A complete list of samples along with voucher information and GenBank accession numbers are provided in Appendix 1.

Morphological data

The data matrix consisted of 49 characters, representing wood anatomy, leaf venation, stomata characteristics, and floral, fruit, and seed features. Details of character coding and the complete data matrix are presented in Huang *et al*. (2011).

Molecular data

We sequenced nuclear ITS and plastid *ndhF*, *trnL-F*, and *trnH-psbA* for phylogenetic analysis. Genomic DNA was isolated from silica-dried leaves or herbarium specimens using Qiagen DNeasy plant mini kit following the manufacturer's protocols or modified CTAB methods as described by Doyle and Doyle (1990). Target loci were amplified in 25 μL volumes using standard polymerase chain reaction (PCR) protocols. Extra reagent Dimethyl Sulfoxide (DMSO) was added (1.25 μL) to amplify ITS in one or two pieces using primers described in Luton *et al*. (1992), Downie and Katz-Downie (1996), Howarth *et al*. (2003), Stanford *et al*. (2000), and those designed by the first author (5' - GAAGAACGTAGCGAAATGCG - 3' & 5' - GCATCGATGAAGAACGTAGC - 3'). Three plastid loci were amplified using primers described in Taberlet *et al*. (1991), Olmstead & Sweere (1994), Hamilton (1999), and Mori *et al*. (2007). PCR was performed with an initial denaturation at 94°C for 5 minutes, followed by 36 to 40 cycles at 94°C for 30 seconds, a range between 50°C–55°C for 30 seconds, and 72°C for 45 seconds, plus a final extension at 72°C for 10 minutes. PCR products were purified with the polyethylene glycol (PEG; Rosenthal *et al*., 1993). Purified PCR products were sequenced in the laboratory of the Institute of Plant and Microbial Biology, Academia Sinica, Taipei, Taiwan.

The resulting sequences were first assembled and trimmed in Sequencher 4.5 (Gene Code Corporation, 2005) and then submitted to BLAST to verify their identities. After confirmation, sequences were aligned with the program Muscle (Edgar, 2004) and manually adjusted with BioEdit (Hall, 1999). Insertions and deletions (indels) longer than one base pair were coded for absence or presence using the method of simple gap coding (Simmons & Ochoterena, 2000) and the program 2xread (Little, 2005).

Phylogenetic analyses

The parsimony based computer program "Tree analysis using New Technology (TNT)" by Goloboff *et al*. (2008) was used to construct phylogenetic trees. Only parsimony informative characters were included in the analyses. All four algorithms incorporated into TNT program were applied to finding the most parsimonious trees, using TNT's "New technology search" with the following parameters: 500 iterations of Rachet (RAT), 500 cycles of Tree-Drifting (DFT), Sectorial Search (SS) with RSS and CSS chosen, and five runs of Tree fusion (TF). Once the minimum score was found, an extra search of finding the minimum score 20 times was performed to test the accuracy of the consensus. If a shorter tree was found during the consensus test, the search procedure restarted and the shorter tree found in

the previous search was used as the starting tree. After all equally parsimonious trees were found, a strict consensus of these trees was calculated in Winclada (Nixon, 1999). Branch support was assessed using standard bootstrap (BS) re-sampling with 1,000 replications, ten random taxon entry sequences per replication, and one tree saved per replication. The morphological data set and different DNA loci were each analyzed independently, and additional analyses of combined three plastid loci as well as combined DNA data were performed. Finally a simultaneous analysis of combined morphological data and all four DNA loci was conducted, and the results of the simultaneous analysis served as the basis for our conclusions. In order to establish morphological synapomorphies for each supporting clade, morphological characters were then optimized onto the trees inferred from the simultaneous analysis using the unambiguous option of Winclada.

Naming of clades
Clades are named using the following methodology: (1) clades are given the name of the genus if the clade is monophyletic and all of the taxa included were treated as belonging to the genus by Mori & Prance (1990), which applies only to the *Corythophora* clade; (2) clades are named after the type species of a genus (the *Bertholletia excelsa* Bonpland [1807: 122] and *Eschweilera parvifolia* Mart. ex Candolle [1828: 293] clades) or section (the *Eschweilera tetrapetala* S. A. Mori [1981: 467], *Lecythis corrugata* Poiteau [1825: 146], *L. ollaria* Linnaeus [1759: 1071], and *L. pisonis* clades); or (3) the earliest name of a species included in the recovered clade is applied if there are no other names available for it (the *Eschweilera integrifolia* [Ruiz & Pav. ex Miers 1874: 225] R. Knuth [1939: 97], *Lecythis chartacea* and *L. poiteaui* O. Berg [1858: 615] clades). In order to avoid confusion, it is important to remember that the *Bertholletia* clade includes all of the genera mentioned in this paragraph and that the *B. excelsa* clade is a monotypic clade within the *Bertholletia* clade.

Terminology

Students of neotropical Lecythidaceae have developed a large vocabulary to describe variation in vegetative, flower, fruit, seed, and seedling features and, thus, an understanding of these terms is needed to comprehend the morphological characters used in this paper. A matrix of the anatomical and morphological characters used in this study, along with their definitions and discussion of the coding, is presented in Huang *et al*. (2011). In this paper, a number in parentheses refers to the number of a character in the Huang *et al*. (2011) paper; for example "(character 31)" refers to apical ligular appendages (also called hood appendages). In the current paper, we have included illustrations of the morphological features of each of the clades (Figs. 4–15). For additional help with the definition of terms, the reader can refer to an illustrated glossary of terms for neotropical Lecythidaceae available on the Lecythidaceae Pages at http://sweetgum. nybg.org/lp/.

Results

Analyses based on 41 morphological characters generated 125 equally parsimonious trees with a tree length of 105 steps, a consistency index (CI) of 0.53 and a retention index (RI) of 0.88 (Table 1). Details of the morphological analyses are presented in Huang *et al*. (2011). Characteristics of four DNA loci and results of tree searches based on individual loci and combined loci are provided in Table 1. :

The combined analysis of ITS and three cpDNA generated 115 MP trees with a tree length of 6089 steps, a CI of 0.35, and a RI of 0.75. The strict consensus of all 115 MP trees is shown in Fig. 1. Within the *Bertholletia* clade the ingroup is divided into two major clades. The first major clade consists of two sister clades: The Ollaria clade and the Pisonis clade. The second major clade is further divided into two clades. Within the first clade *Bertholletia excelsa* is sister to the E. integrifolia clade. Within the second clade there are two clades. The first clade consists of two sister clades: the Poiteaui clade and the Chartacea clade. The second clade consists of four clades: *Corythophora*, the Tetrapetala clade, the Corrugata clade, and the Parvifolia clade. Among the four clades, *Corythophora* is sister to the latter three, and relationships among the latter three clades are unresolved.
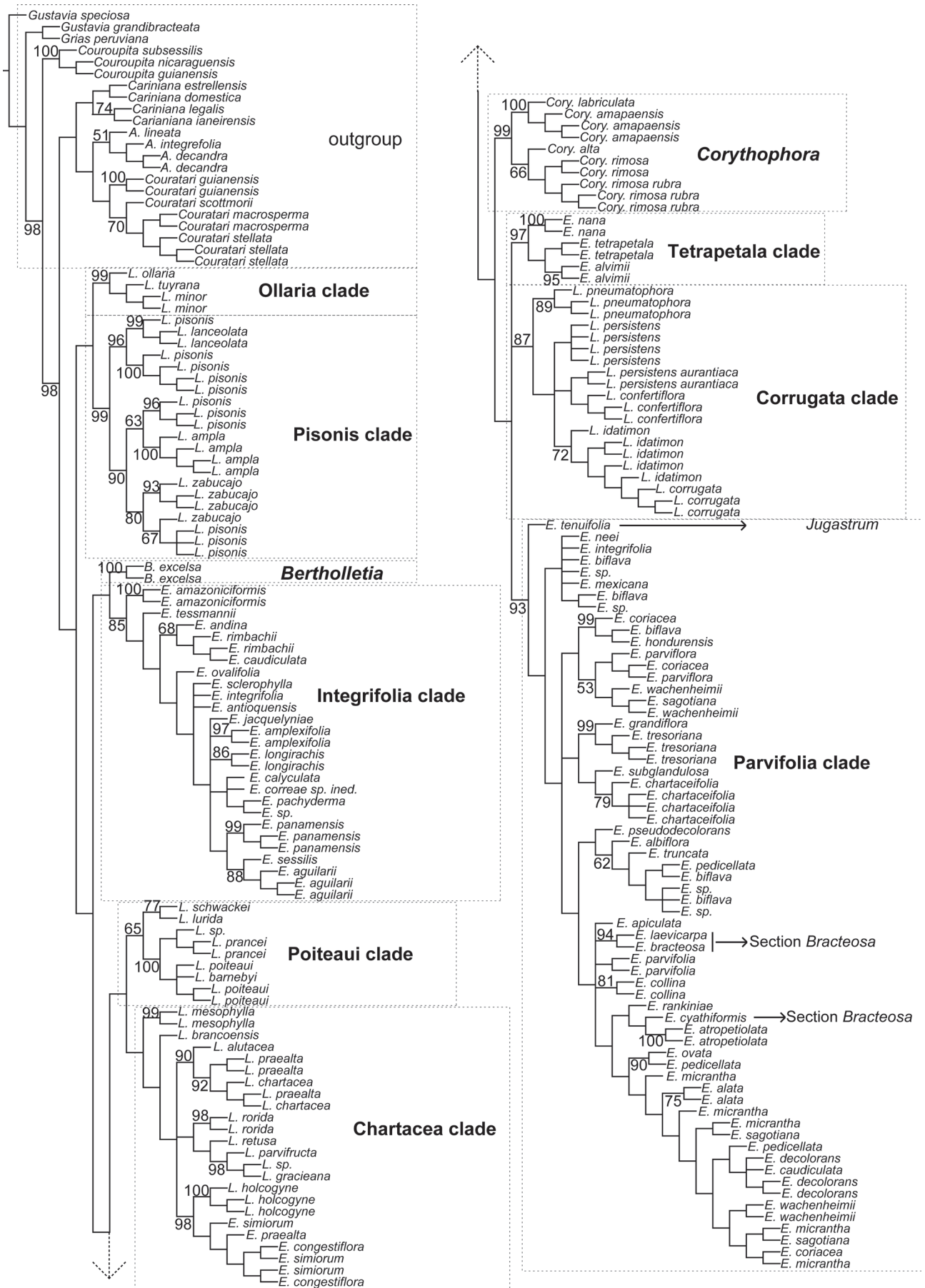
FIGURE. 1. Strict consensus of 115 most parsimonious (MP) trees based on combined analysis of ITS, *ndh*F, *trn*L-F, and *trn*H-*psb*A sequences. Bootstrap values (>50%) are given above the branches. All clades in this figure are part of the *Bertholletia* clade.

The strict consensus tree (Fig. 2) from the simultaneous analysis shows support for the monophyly of the *Bertholletia* clade (63%), which includes *Lecythis*, *Corythophora*, *Bertholletia*, and *Eschweilera*. In addition, *Corythophora* is monophyletic (100%), and the two accessions of *Bertholletia excelsa* come out together on the tree (100%). Results of the simultaneous analysis do not support the monophyly of *Lecythis* or *Eschweilera*. *Lecythis* consists of five main clades: the *L. pisonis* (100%), *L. ollaria* (100%), *L. poiteaui* (72%), *L. chartacea* clade (76%), *L. corrugata* (99%) clades. The *L. pisonis* clade is sister to all remaining members of the *Bertholletia* clade (*Lecythis*, *Bertholletia*, *Corythophora*, and *Eschweilera*). The *L. chartacea* clade is sister to *Bertholletia excelsa*, and together these two clades are sister to the *L. ollaria* + *L. poiteaui* clades. The *L. corrugata* clade is nested within *Eschweilera*. *Eschweilera* consists of three clades: the *E. integrifolia* clade, the *E. tetrapetala* clade (100%), and the *E. parvifolia* clade (94%). The *E. parvifolia* clade is sister to the *Lecythis corrugata* clade, these two clades together are sister to the *E. tetrapetala* clade, and this entire grouping is sister to the *E. integrifolia* clade.

TABLE 1. Tree statistics of separate and combined data matrices.

	ITS	*ndhF*	*trnL-F*	*trnH-psbA*	cpDNA	combined DNA	morphology	total evidence
Taxa	205	164	190	161	203	209	100	207
L (bp)	610–688	1994–2014	905–952	405–451	3304–3417	3914–4105	-	-
AL (sites)	1258	1956	1382	1113	4321	5766	41	-
PI (sites)	608	257	273	413	864	1581	41	1603
Indels (sites)	202	8	66	137	116	400	-	202
VS (%)	48%	13%	20%	37%	20%	27%	-	-
Tn	105	148	67	53	77	115	125	132
TL	2662	474	527	1319	2297	6089	105	6114
CI	0.36	0.60	0.56	0.42	0.45	0.35	0.53	0.36
RI	0.80	0.90	0.89	0.83	0.80	0.75	0.88	0.76

L = sequence length before alignment; AL = sequence length after alignment; PI = parsimony-informative sites; Indels = insertions or deletions; VS = % of variable sites (no. of variable base pairs (bps) /no. of total bps); Tn = number of trees; TL = tree length; CI = consistency index; RI = retention index.

The individual analyses provided moderate resolution, with none of the individual data sets or loci obviously outperforming any other in terms of number of nodes resolved or bootstrap support values (Table 2). The combined analyses of all the DNA data (Fig. 1) and the DNA data + morphology (Fig. 2) are more resolved (and with higher support values) than any of the individual analyses. Groups that are supported in every analysis are the *Bertholletia* clade, the *Lecythis pisonis* clade, and the *Lecythis corrugata* clade. Clades that are supported in the morphological analysis and in all except one of the molecular analyses are *Corythophora* (not supported by trnH-psbA) and the *Eschweilera tetrapetala* clade (not supported by ITS).

Eschweilera and *Lecythis* are not monophyletic in any analysis of the data (none of the individual partitions, none of the combined analyses). Three clades of *Lecythis* (*L. pisonis* clade, *L. chartacea* clade, *L. corrugata* clade) are each supported in all of the molecular analyses. The sister group relationship of the *L. ollaria* and L. *poiteaui* clades is not supported in some of the DNA analyses, but the *L. ollaria* clade and the *L. poiteaui* clade are individually supported in all of the molecular analyses. Two clades of *Eschweilera* (E. *tetrapetala* clade, *E. parvifolia* clade) are supported in all individual analyses except that which includes only ITS data, which does not support either of these clades. The *Eschewilera integrifolia* clade is not supported in most of the individual analyses of molecular data, but the molecular data support the *E. integrifolia* clade minus *E. amazoniciformis* S. A. Mori [in Mori & Prance 1990: 227] in all analyses.

Several of the larger clades are supported in the strict consensus of the simultaneous analysis, but do not appear in most of the individual analyses. For example, the sister group relationship of *Bertholletia* to the *Lecythis chartacea* clade and the monophyly of the larger group that contains *Lecythis ollaria*/*poiteaui*, *Bertholletia*, and the *L. chartacea* clade only occur on the strict consensus of the simultaneous analysis (and not in any of the individual analyses). In addition, the sister group relationship of the *Lecythis corrugata* clade to the *Eschweilera parvifolia* clade and the monophyly of the group that contains *Corythophora*, *Eschweilera*, and the *Lecythis corrugata* clade only appear in the ITS analysis and the simultaneous analysis. The monophyletic group that contains the *Eschweilera tetrapetala* clade, the *Lecythis corrugata* clade, and the *Eschweilera parvifolia* clade only appears in the analyses of all DNA data and the simultaneous analysis, not in the analyses of any individual loci (or morphology).

TABLE 2. Clades that are supported in the strict consensus of the simultaneous analysis. Presence (+) or absence (-) of each clade is indicated for the individual analyses (based on strict consensus). Bootstrap values >50% are given in parentheses.

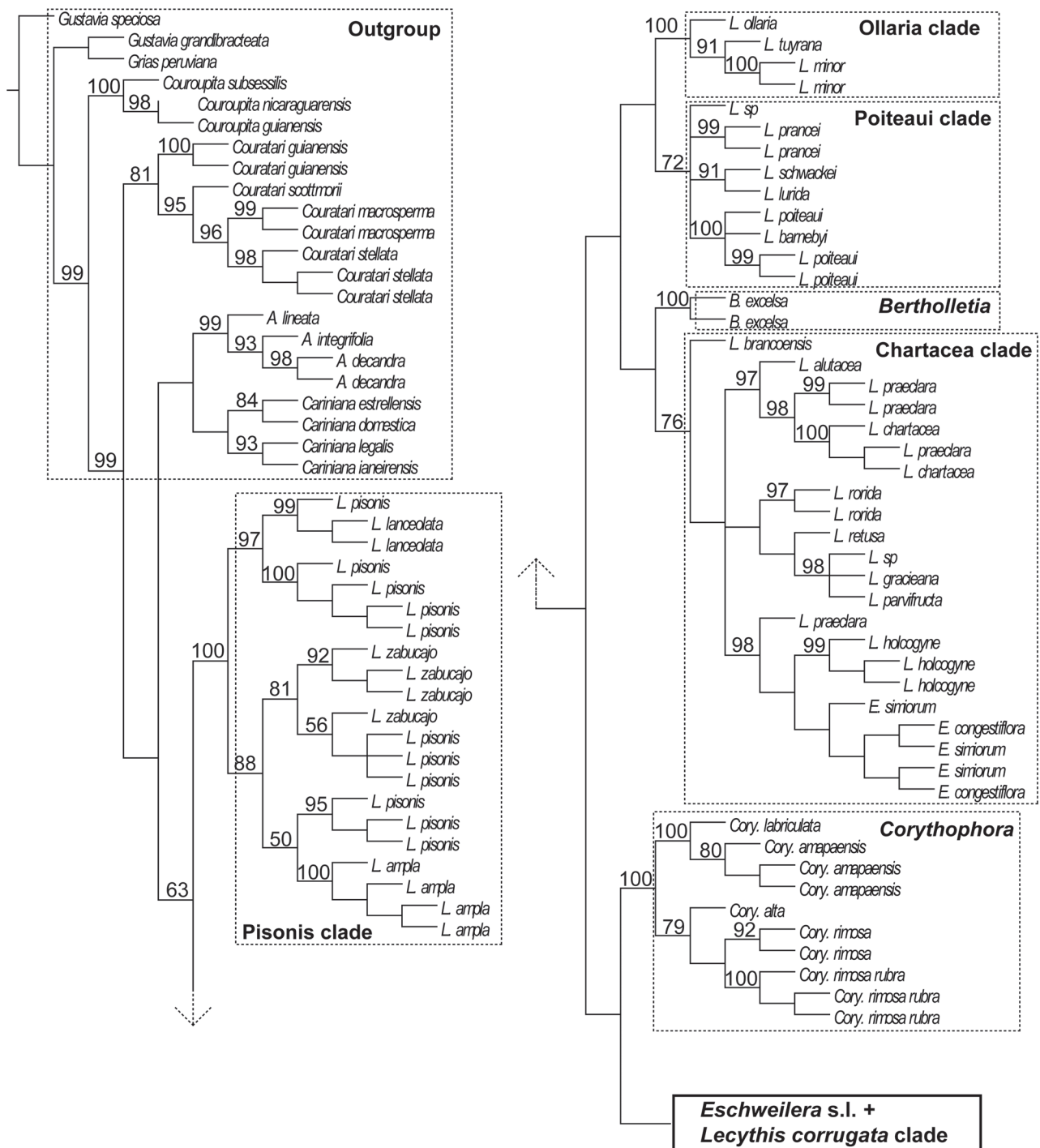| Clade names	morph	ITS	*ndhF*	*trnL-F*	*trnH-psbA*	Plastid: *ndhF/ trnL-F/trnH-psbA*	all DNA	morph + DNA
					Data source			
Bertholletia clade	+	+	+	+	+	+	+	+ (63%)
Lecythis pisonis	+ (78%)	+ (84%)	+ (98%)	+	+ (99%)	+ (69%)	+	+ (100%)
Lecythis ollaria / poiteaui	-	-	+	-	-	+	-	+
Lecythis ollaria	-	+	+ (100%)	+ (97%)	+ (98%)	+ (100%)	+ (99%)	+ (100%)
Lecythis poiteaui	-	+ (98%)	+ (95%)	+	+	+	+ (65%)	+ (72%)
Lecythis chartacea	-	+ (71%)	+	+ (55%)	+	+ (70%)	+	+ (76%)
Bertholletia + Lecythis ollaria / poiteaui + L. chartacea	-	-	-	-	-	-	-	+
Bertholletia + Lecythis chartacea	-	-	-	-	-	-	-	+
Corythophora	+ (52%)	+ (94%)	+ (51%)	+	-	+ (91%)	+ (99%)	+ (100%)
Corythophora + Eschweilera + Lecythis corrugata	-	+	-	-	-	-	-	+
Lecythis corrugata + Eschweilera	-	+	-	-	-	-	-	+
Eschweilera integrifolia	-	-	-	-	+	-	+ (85%)	+
E. integrifolia minus *E. amazoniciformis*	-	+	+ (93%)	+ (58%)	+ (59%)	+ (82%)	+	+ (87%)
Eschweilera tetrapetala	+ (54%)	-	+ (100%)	+	+ (94%)	+ (88%)	+ (97%)	+ (100%)
Lecythis corrugata	+ (52%)	+	+ (91%)	+	+ (94%)	+	+ (87%)	+ (99%)
Eschweilera parvifolia	-	-	+	+	+	+	+ (93%)	+ (94%)
Eschweilera tetrapetala + Lecythis corrugata + Eschweilera parvifolia	-	-	-	-	-	-	+	+
Lecythis corrugata + Eschweilera parvifolia	-	-	+	+	-	+	-	+

Discussion

Clades and supporting synapomorphies

In spite of the incongruence of some supporting clades among different datasets, many clades recognized by simultaneous analysis have strong branch support and are also recovered by analyses with different datasets (Figs. 2A, 2B). The morphological features of each of the clades are illustrated (Figs. 4–15) and described in the following paragraphs. In the following discussion, numbers are provided for characters that were included in the analysis. In addition, we integrate information for characters that were not included in the analysis. In some cases, such characters provide useful descriptive or biological information about clades, even though they may not have been included in the analysis because of continuous variation, within-terminal polymorphism, missing data, or difficulties defining and coding states. In many cases, such excluded characters were discussed (2011).

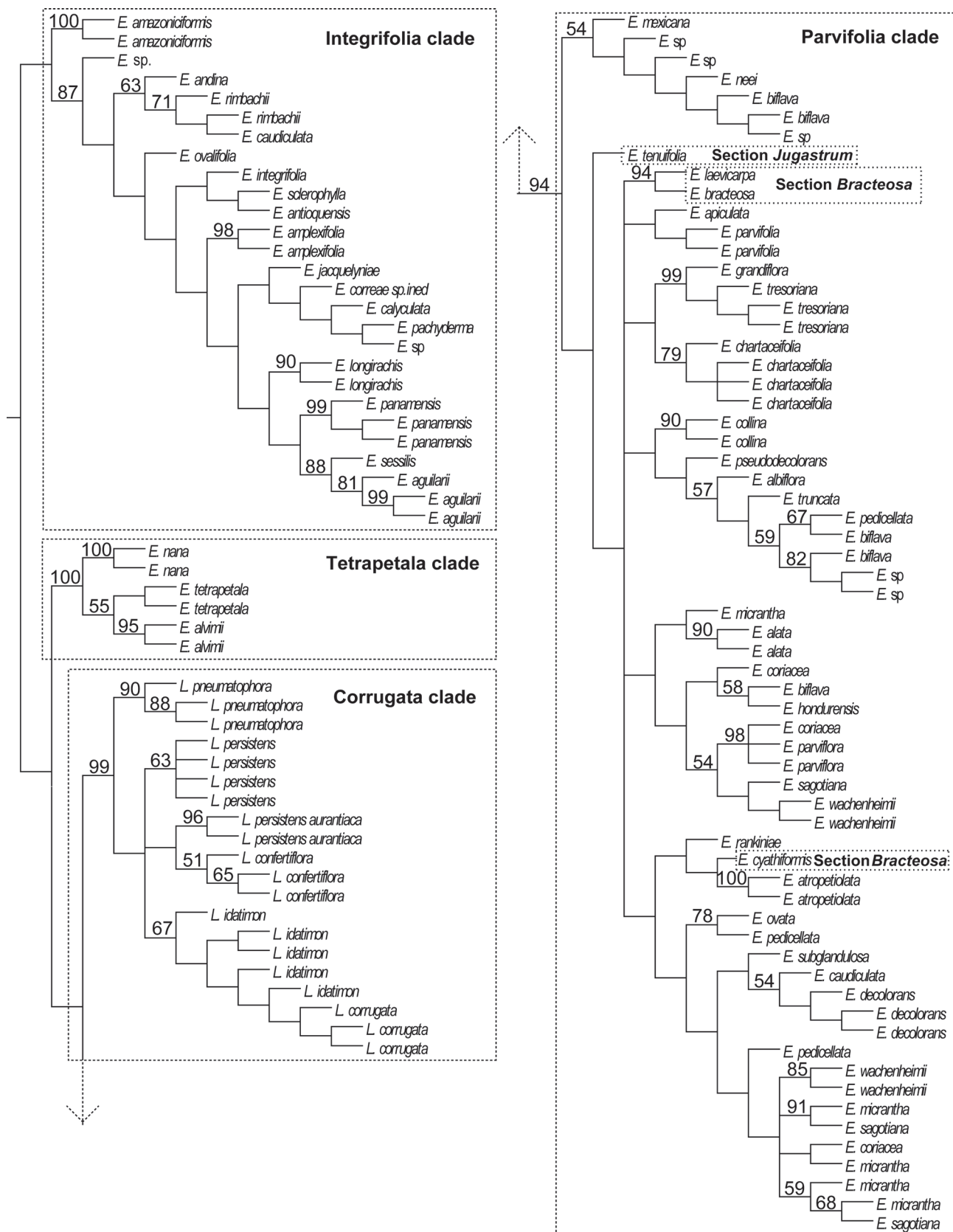### *Bertholletia* clade (63% BS; Figs. 2, 4–15)

Our results support the monophyly of the *Bertholletia* clade, which includes *Bertholletia*, *Corythophora*, *Eschweilera* and *Lecythis* as defined in Mori & Prance (1990), and the results are congruent with Mori *et al*. (2007) and Huang *et al*. (2011). The *Bertholletia* clade has a distinctive combination of its own synapomorphies and character states shared with some of the outgroup taxa. Character optimization using the unambiguous option of Winclada shows that

morphological synapomorphies supporting the monophyly of the clade include the presence of a two or four-locular ovaries (character 39), the presence of an aril (character 47), and the absence of cotyledons (character 49). In addition, flowers of the *Bertholletia* clade have a distinctive combination of androecium features shared with some outgroup taxa, including zygomorphy (character 20), presence of a hood (= coiled ligule, character 26), the presence of stamens in the hood (character 32; called "vestigial" stamens because they lack anthers), and the absence of an external flap (character 25). None of the outgroup taxa has this combination of characters; all are either actinomorphic or all of the appendages on the hood are either staminodes (species of *Couroupita*) or vestigial stamen nectaries as in *Couratari*. In addition, there are no species in the *Bertholletia* clade with staminal tubes, as in species of *Allantoma*, *Cariniana*, and *Gustavia* (character 21).
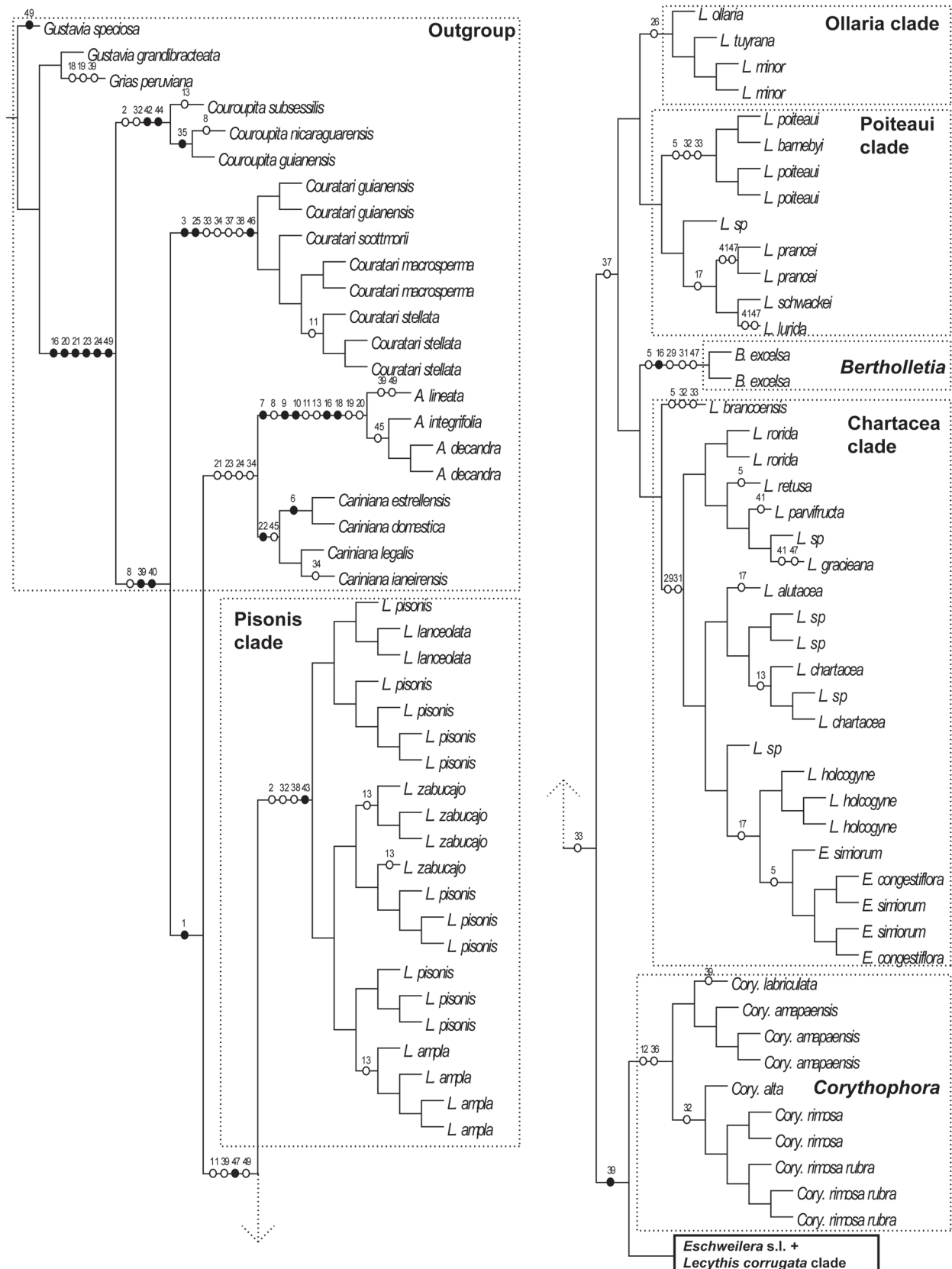

FIGURE 2A. Strict consensus of 66 most parsimonious (MP) trees based on total evidence. Bootstrap values (>50%) are given above the branches. All clades in this figure are part of the *Bertholletia* clade. The *Lecythis pisonis*, *L. ollaria*, *Bertholletia excelsa*, *L. poiteaui*, and *Corythophora* clades of the *Bertholletia* clade are shown.
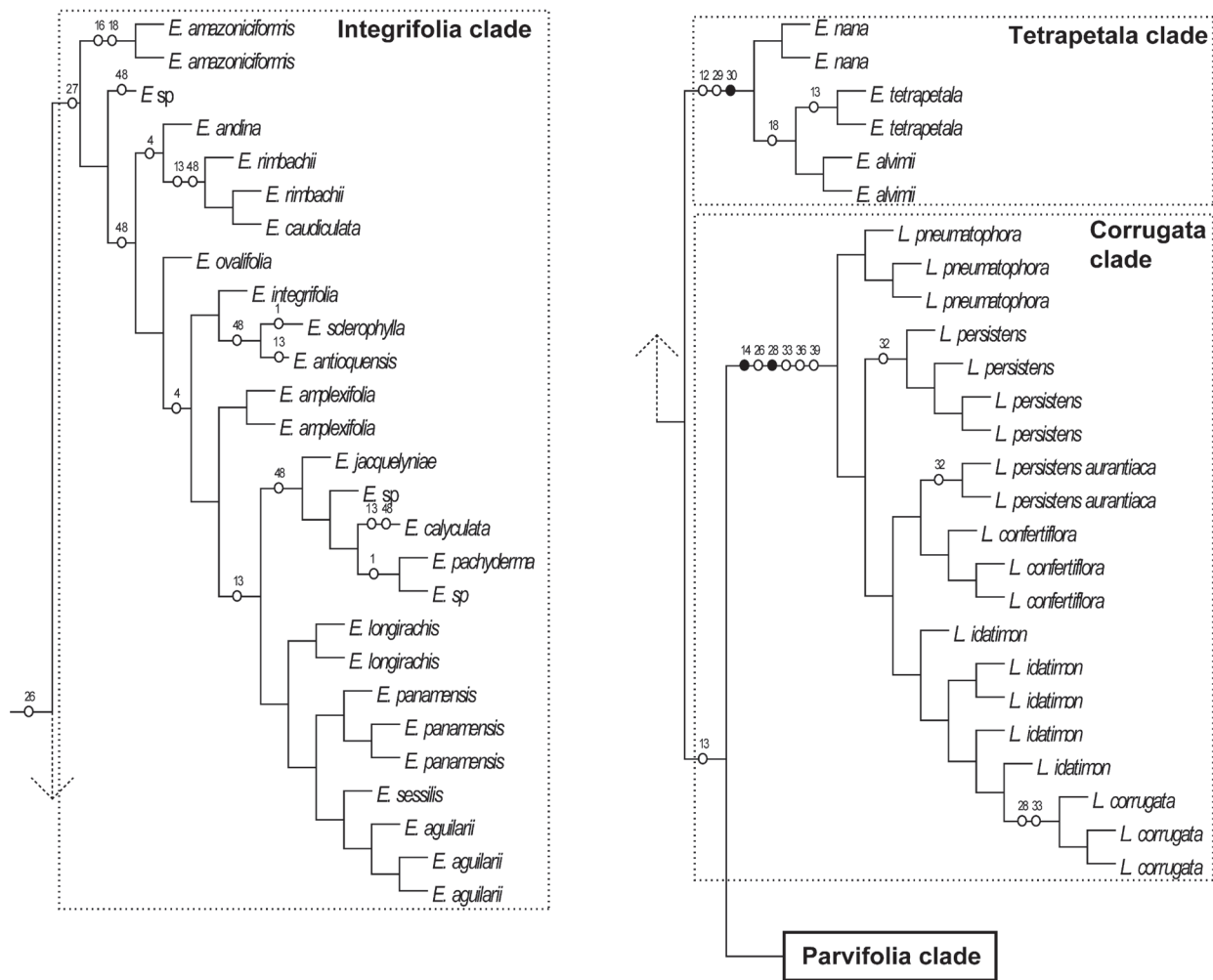
FIGURE 2B. Strict consensus of 66 most parsimonious (MP) trees based on total evidence. Bootstrap values (>50%) are given above the branches. All clades in this figure are part of the *Bertholletia* clade. The *Eschweilera integrifolia*, *E. tetrapetala*, *L. corrugata*, and *Eschweilera parvifolia* clades are shown.

FIGURE 3A. One of 66 most parsimonious trees based on total evidence (L = 6134, CI = 0.35, RI = 0.76). Morphological characters are optimized onto the tree using the unambiguous option of Winclada. Supporting characters are shown on branches. White ellipses are homoplasious and black ellipses are non-homoplasious characters. All clades in this figure are part of the *Bertholletia* clade. The *Lecythis pisonis*, *L. ollaria*, *Bertholletia excelsa*, *L. poiteaui*, and *Corythophora* clades are shown.
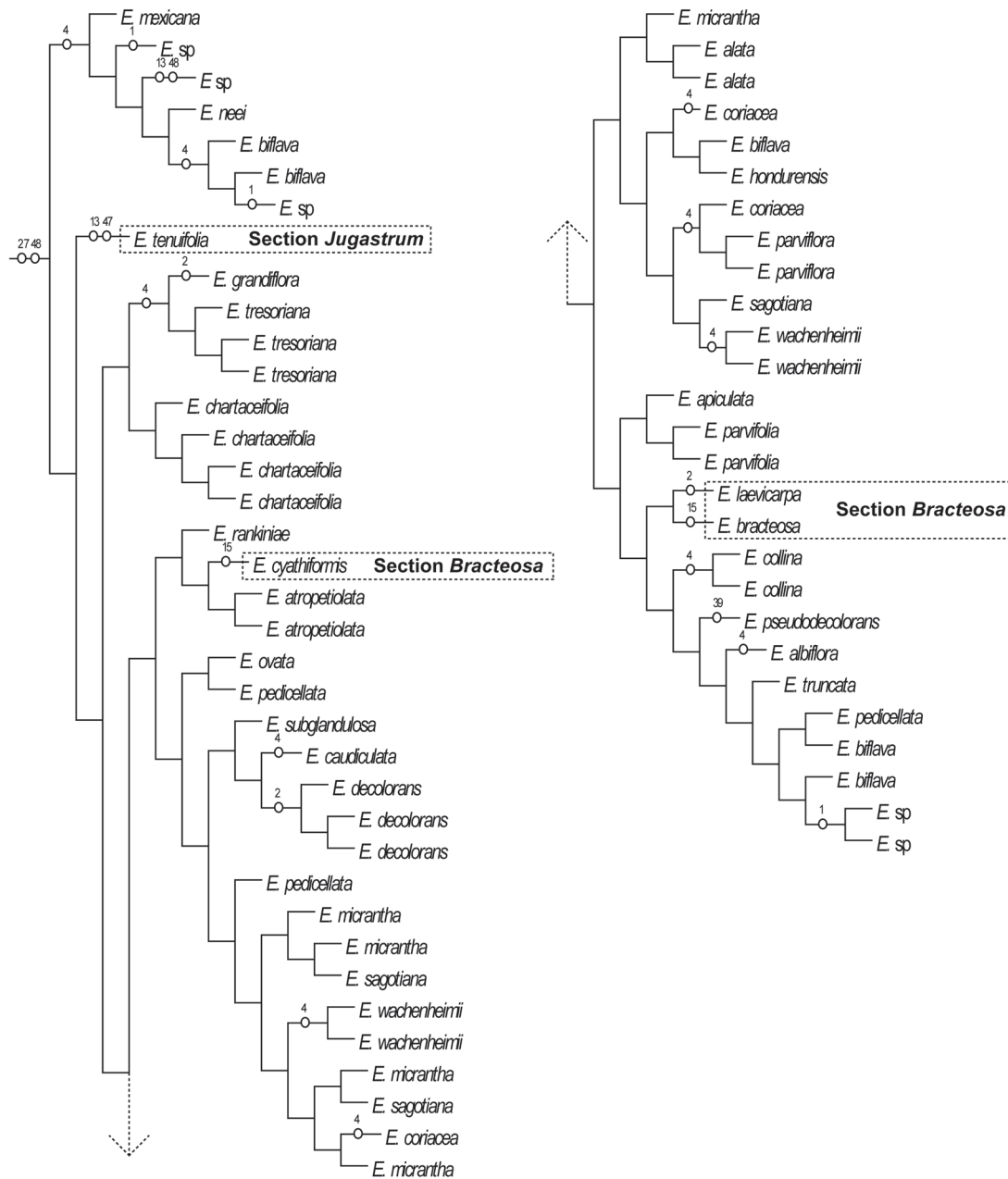
FIGURE 3B. One of 66 most parsimonious trees based on total evidence (L = 6134, CI = 0.35, RI = 0.76). Morphological characters are optimized onto the tree using the unambiguous option of Winclada. Supporting characters are shown on branches. White ellipses are homoplasious and black ellipses are non-homoplasious characters. All clades in this figure are part of the *Bertholletia* clade. The *Eschweilera integrifolia*, *E. tetrapetala*, and *L. corrugata* clades are shown.

There are also seed features that separate the *Bertholletia* clade from the outgroup. For example, there are no species in the *Bertholletia* clade with linear seeds with a notch at the base (cf. *Allantoma lineata* [Mart. ex O. Berg [1858: 508]] Miers [1874: 297]), and none have fleshy cotyledons (cf. *Gustavia*; character 49), winged seeds (unilaterally winged in *Allantoma* and *Cariniana*, circumferentially winged in *Couratari*; character 45), seeds with long trichomes extending from the seed coat (cf. *Couroupita*; character 44) (Tsou & Mori, 2002), or seeds with leaf-like cotyledons (cf. *Cariniana*, *Couratari*, and *Couroupita*; character 49). The only genus outside of the *Bertholletia* clade with a ligule extending from a staminal ring, a feature common to all members of the *Bertholletia* clade, is *Couroupita* (character 24). Within the *Bertholletia* clade, the four genera are divided into the ten clades described and illustrated below (Figs. 4–14).

Lecythis pisonis **clade** (100% BS; Figs. 2A, 4)

This clade comprises all four species of *Lecythis* section *Pisonis* recognized by Mori & Prance (1981) and Mori (1990b) and several other species that were included in synonymy by these authors but represent distinct species that have not yet been resurrected (Mori, unpubl. data). The species of this clade are found throughout lowland rainforests in Central and South America but at low densities. Morphological synapomorphies include the presence of a bluish-green color caused by the oxidation of wounded tissue (character 2), an annular expansion below the apex of the

style (character 38; Fig. 4C), and sulcate seeds (character 43; Fig. 4G). The sulcate seeds are unique to this clade. In addition to these features, the bark is deeply fissured and laminated and the fruits (Fig. 4F) are larger than found in any group of Lecythidaceae. The monophyly of Section *Pisonis* found in this study is congruent with previous studies (Mori, 1990b; Mori *et al.*, 2007; Huang *et al.*, 2011). Although the monophyly of the *Lecythis pisonis* clade is strongly supported, species circumscriptions within the clade are problematic, especially for *L. pisonis* as circumscribed by Mori (1990b).
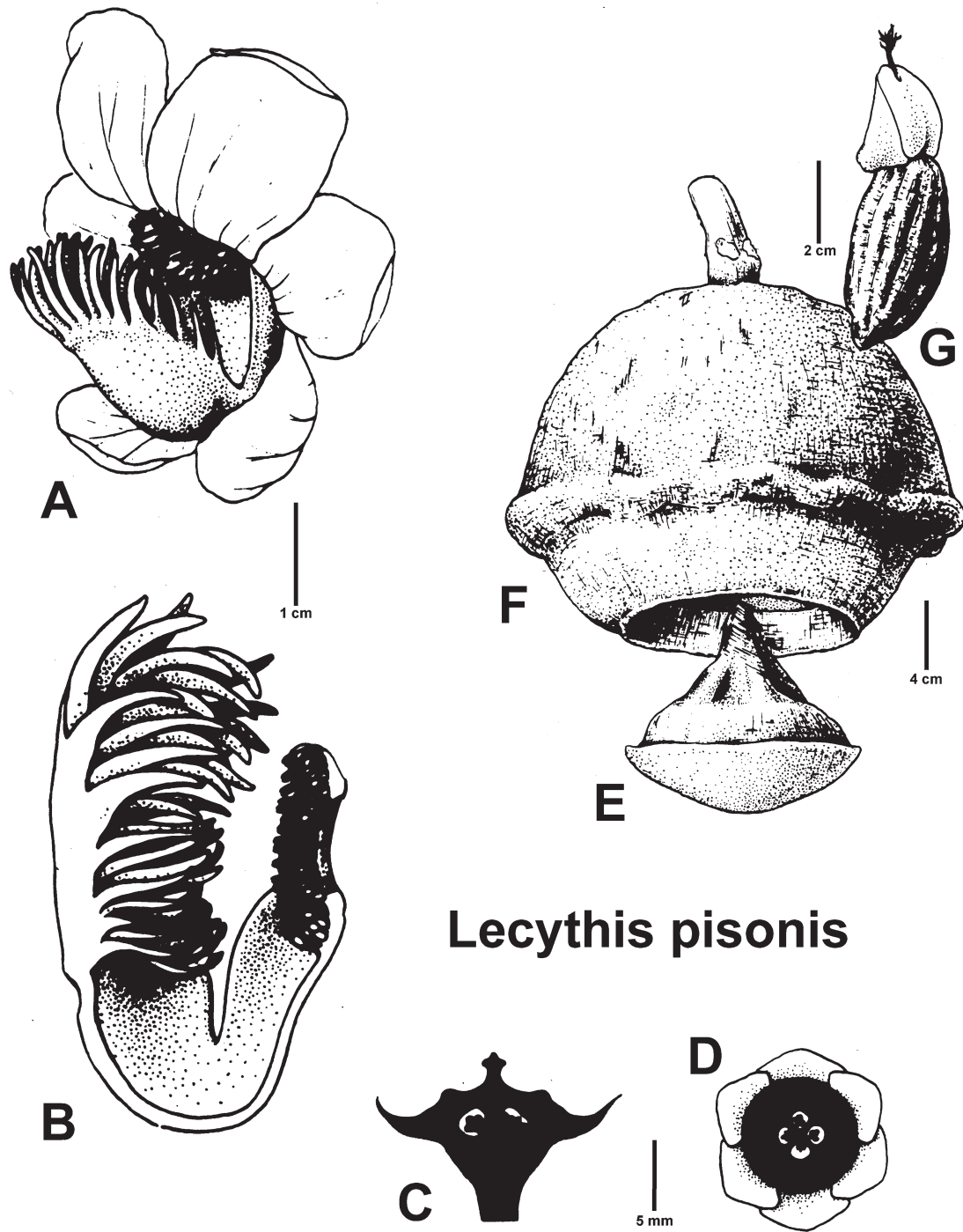

FIGURE 3C. One of 66 most parsimonious trees based on total evidence (L = 6134, CI = 0.35, RI = 0.76). Morphological characters are optimized onto the tree using the unambiguous option of Winclada. Supporting characters are shown on branches. White ellipses are homoplasious and black ellipses are non-homoplasious characters. All clades in this figure are part of the *Bertholletia* clade. The *Eschweilera parvifolia* clade is shown.

Lecythis ollaria clade (100% BS; Figs. 2A, 5, 9A–C)

The three species of this clade have a narrow distribution limited to northwestern South America (Huang, 2010). The
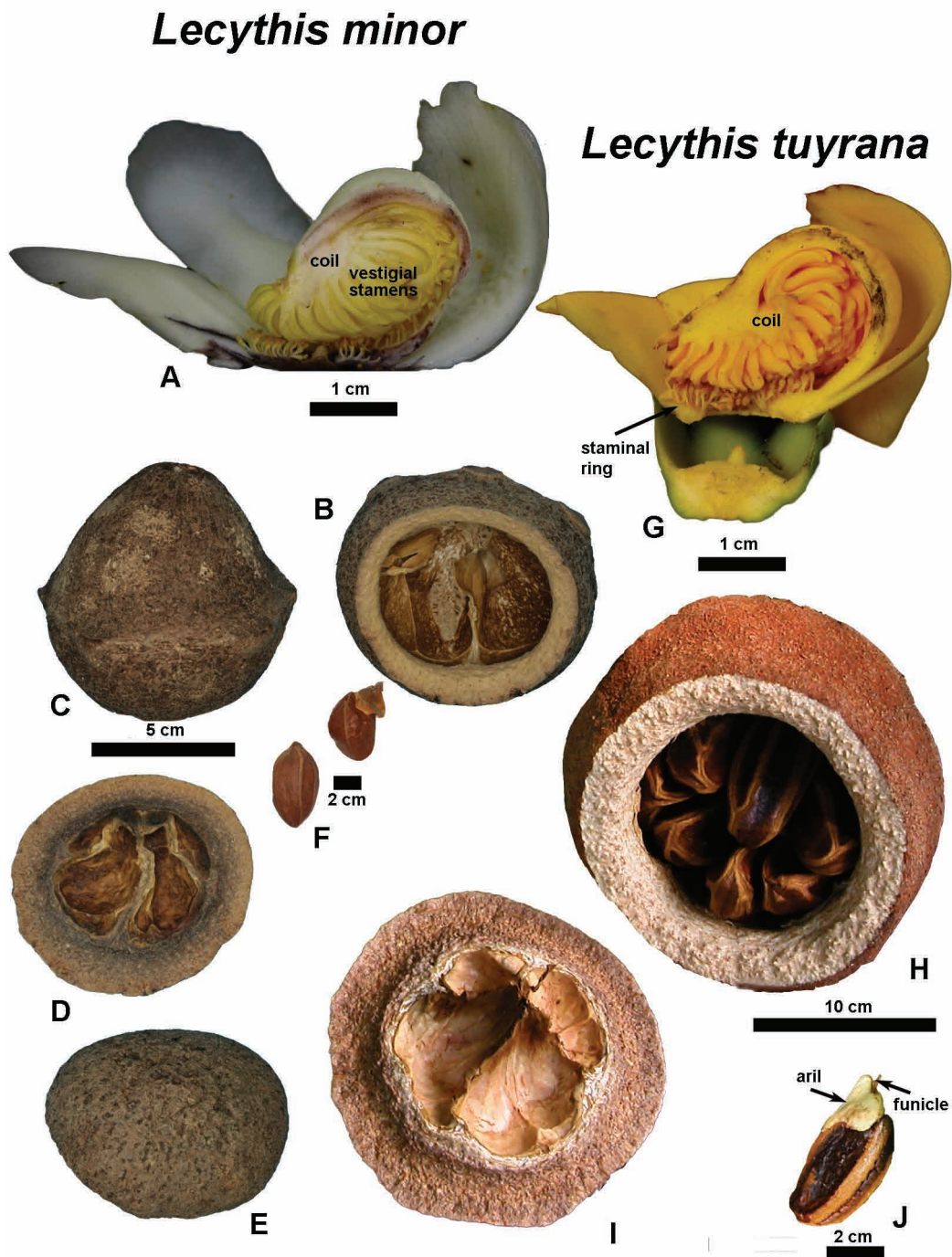
three sampled species were included in *Lecythis* Section *Lecythis* by Mori (1990b), in which he placed an additional 11 species.

FIGURE 4. The *Lecythis pisonis* clade (see Fig. 101 in Mori & Prance, 1990 for vouchers). A. Flower with an open androecial hood. B. Medial longitudinal section of flower with flat androecial hood. The androecial hood possesses a proximal group of staminodes for about one-quarter of its length (not distinguishable in this image) and vestigial stamens for the rest of the length. C. Medial longitudinal section of ovary. Note the stylar collar located just under the stigma. D. Cross-section of 4-locular ovary. E. Operculum with a woody columella that projects into the fruit. F. Fruit base. The fruits of this clade are the largest of all Lecythidaceae. G. Sulcate seed with a long basal aril. Note the funicle projecting from the bottom of the aril. Drawing by B. Angell.

A morphological synapomorphy for the *Lecythis ollaria* clade is the presence of a single coiled ligule with vestigial stamens found only on the exterior part of the coil (character 26, Fig. 5A, G). In addition, the style is short and erect (Fig. 5G; not coded in Huang *et al.*, 2011), the seeds have a well-developed basal aril (character 48; Figs. 5J, 9A, B),

and the major seed veins are plane or slightly impressed and the areas between the veins appear to be free of connecting veins and are smooth (Figs. 5J, 9A–C).

FIGURE 5. The *Lecythis ollaria* clade. A–F. *L. minor* (A based on *Galdames 5768*; B–F. based on *Nee & Mori 3580*). G–J. *L. tuyrana* (based on *Galdames 5766*). A. Medial longitudinal section of flower showing the single coil and the vestigial stamens limited to the exterior of the coil. B. Apical view of dehisced fruit. C. Lateral view of fruit. D. Basal view of operculum. E. Apical view of operculum. F. Seeds with basal arils. G. Medial longitudinal section of flower showing single but short coil. H. Apical view of fruit with operculum removed and showing seeds inside. I. Basal view of operculum. Note that the columella is not developed. J. Seed with basal aril (above). Note funicle protruding from aril. Photos A and G–J by C. Galdames and photos B–F by S. A. Mori.

***Lecythis poiteaui* clade** (72% BS; Figs. 2A, 6)

This clade is found from central to eastern Amazonia and disjunct in the coastal forests of eastern Brazil (Huang, 2010). It is sister to the *L. ollaria* clade but the five species recovered in it lack the single coil (character 26, Fig. 6C, D, F, K) of that clade. None of the coded morphological characters provide synapomorphies for the *L. poiteaui* clade, but its members possess a long, oblique or geniculate (Fig. 6G) instead of an erect style; roundish (Fig. 6J, P) instead of longer than broad seeds of the *L. chartacea* clade (e.g., Fig. 9D, E); dendritic seed venation (Fig. 9M–P); and absent (Fig. 6J) or vestigial aril (Fig. 6P) versus a more developed basal aril of other clades (characters 47 and 48; Figs. 4G, 5F, 9A, B). The species of this clade generally have the androecial hood closed (= closed androecium, character 33, Figs. 6D, F, K) and petals that are tightly pressed against the androecium, presumably to stop entry into the flowers by non-pollinators. In addition the entrance into the apex of androecial hood is yellow, a color that usually directs bees to a pollinator reward.
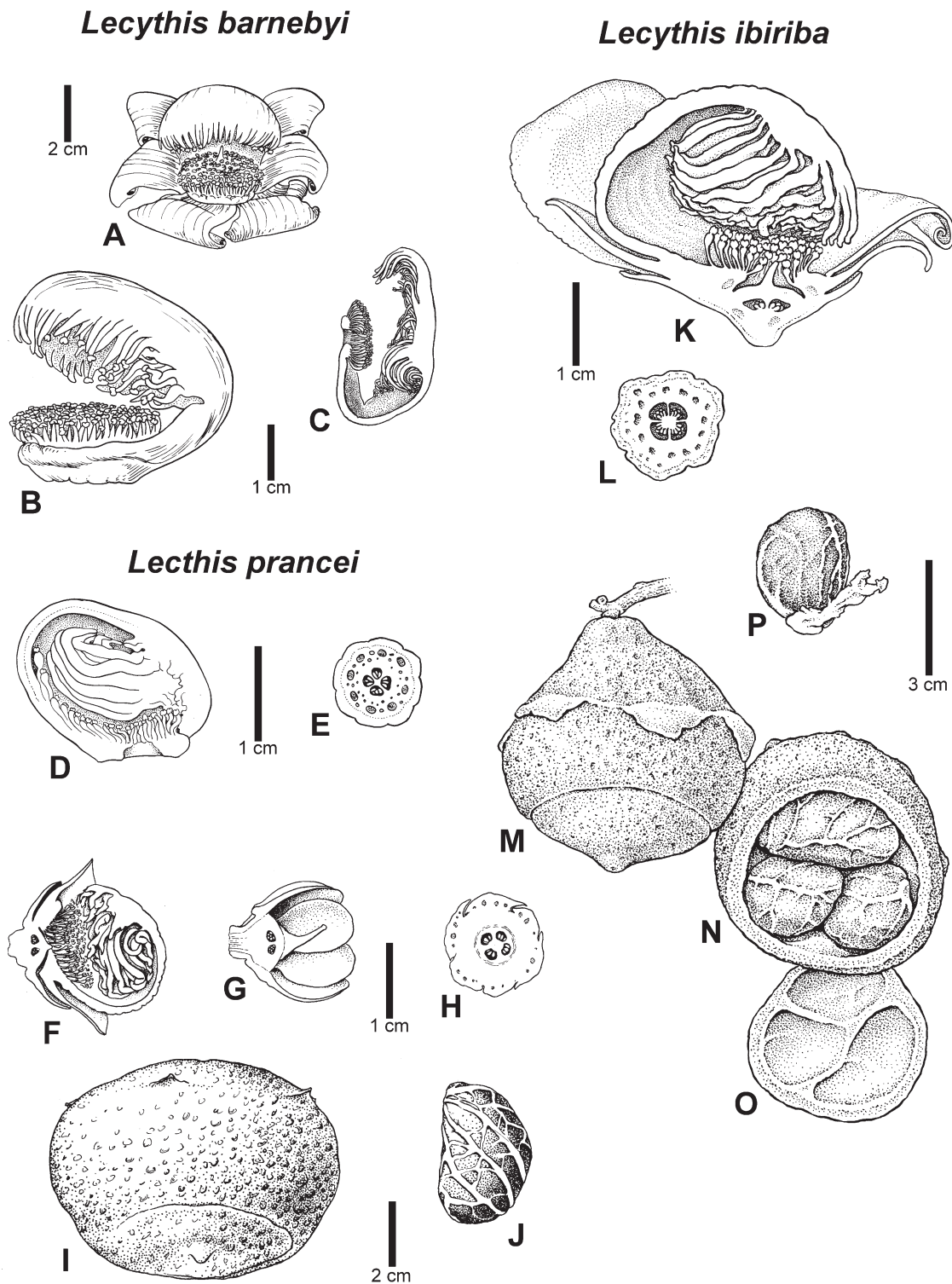
 Species of the *Lecythis poiteaui* clade that are not bee pollinated are *Lecythis barnebyi* S. A. Mori (1981a: 360) (Fig. 6A) and *L. poiteaui*. These two species are nocturnal and bats have been observed taking nectar from their flowers; thus, they are presumed to be bat-pollinated (Mori & Prance, 1990). These two species also possess similar cuticular papillae on the abaxial leaf blade surface (character 5), a massive number of stamens (character 34; Fig. 6A, B), open androecia (character 33; Figs. 6A, B), petals not pressed against the androecium (Fig. 6A), and the presence of at least some anthers (or possibly antherodes) on the hood (character 32). Mori (1990b) placed *L. brancoensis* (R. Knuth 1939: 84) S. A. Mori (1981a: 359), along with the two other bat-pollinated species, in *Lecythis* sect. *Poiteaui*, and this relationship was supported by Huang *et al*. (2011). In contrast, this study places *L. brancoensis* in the *Lecythis chartacea* clade. Thus, if *L. brancoensis* is found to be bat-pollinated as suggested by Mori (1990b), our results indicate that bat pollination may have evolved twice in New World Lecythidaceae.

***Bertholletia excelsa* clade** (100% BS; Figs. 2A, 7)

This clade includes only *Bertholletia excelsa*, which is distributed throughout Amazonia and parts of the Guianas (see Fig. 21 in Prance & Mori, 1990). In the present study, *B. excelsa* is sister to the *Lecythis chartacea* clade. It differs from species of that clade by having two calyx lobes (character 16; Fig. 7B), seeds without an aril (character 47; Fig. 7G), and a type of secondary indehiscence in which the seed is larger than the opercular opening (character 41; Fig. 7E, F). *Bertholletia excelsa* provides good examples of petals pressed against the androecium (character 33; Fig. 7A) and, as seen in the field or in color images, of the yellow color on the androecial hood at the entrance into the flower. *Bertholletia* is the only genus of the family with a boney seed testa and the complete absence of an aril (Fig. 7G). It does, however, share features with species of the *L. poiteaui* and *L. chartacea* clades, including similar androecia with swept in appendages (Fig. 7D), 4-locular ovaries (Fig. 7C), and long, slender, oblique or geniculate styles (Fig. 7B).
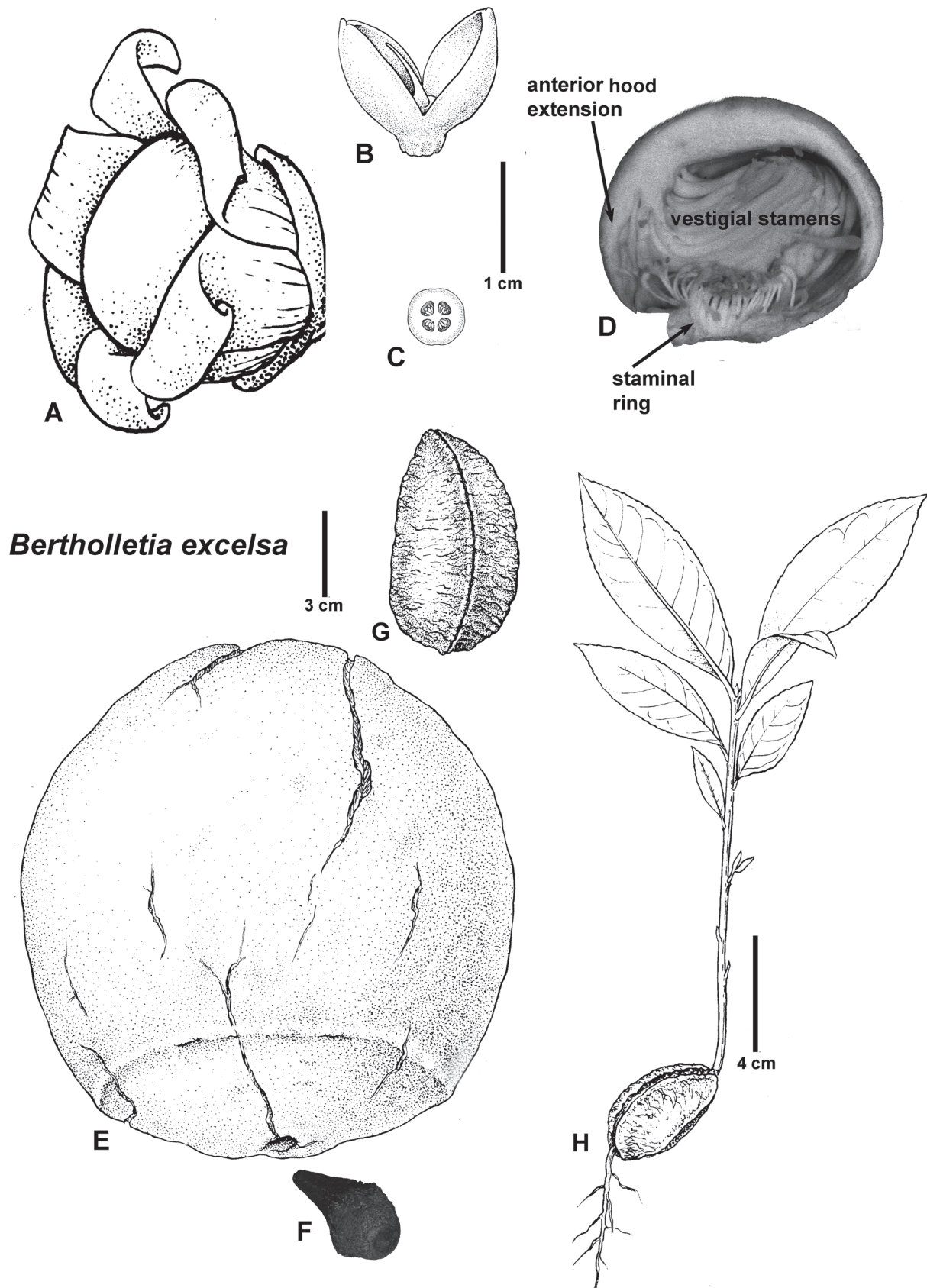
 Mori & Prance (1990) hypothesized that *B. excelsa* is related to *Lecythis lurida* (Miers 1874: 262) S. A. Mori (1981a: 362). This hypothesis was based on the following shared characters of the two species (Mori & Prance, 1990): the presence of cuticular papillae on the abaxial leaf blade surface (character 5; see Fig. 96 in Mori & Prance, 1990), hood appendages swept or curved inward without forming a complete coil (character 31; Fig. 7D), mature fruits that fall to the ground with the seeds remaining inside (character 40), a unique dehiscence (character 41; Fig. 7E, F) in *Bertholletia*, and fruits that do not open at all in *L. lurida*. The relationship of *B. excelsa* with *L. lurida* and related species of the *L. poiteaui* clade is not supported by this study (Fig. 3A).

 There are no other species of Lecythidaceae with fruits morphologically similar to those of *B. excelsa*. The fruits of *B. excelsa* have thicker and woodier pericarps and are, in fact, dehiscent but the opercular opening is smaller in diameter than that of the seeds, and the operculum falls into the fruit when it dehisces (Tsou & Mori, 2002) (Fig. 7E, F). It has been hypothesized that this type of dehiscence is related to selection for dispersal by rodents, especially agoutis (Ducke, 1948; Prance & Mori, 1978). In neotropical Lecythidaceae, shifts to different dispersal agents and accompanying morphological changes have occurred a number of times (Tsou & Mori, 2002). For example, in *Allantoma* there has been a shift from wind-dispersal facilitated by a unilateral seed wing in most *terra firme* species to the water-dispersed *A. lineata* with only a vestigial seed wing (Huang *et al*., 2008). Another shift has been from the *terra firme* dehiscent-fruited, arillate seeded, animal-dispersed *L. chartacea* to the riverine, indehiscent-fruited, non arillate-seeded, water-dispersed *L. rorida* O. Berg (1858: 488) (Kubitzki & Ziburski, 1994). Thus, species of neotropical Lecythidaceae may belong to the same genus even though the morphological adaptations for seed dispersal by different dispersal agents may be quite different.

Lecythis barnebyi

Lecythis ibiriba

Lecthis prancei

FIGURE 6. The *Lecythis poiteaui* clade. A–C. *L. barnebyi* (A–B see Mori & Lepsch-Cunha, 1995 for vouchers and C see Mori 1990c for voucher). D–E. *L. prancei* (see Mori, 1990c for vouchers). F–J. *L. lurida* (see Mori, 1990c for vouchers). K–L. *L. ibiriba* (K–L based on *Popovkin 496*, M based on *Popovkin 497*, N–P based on *Cardoso 2338*). A. Anterior view of flower showing open androecial hood. B. Lateral view of flower showing open androecial hood. C. Medial section of androecium. Note that innermost hood appendages arise from slight expansion of hood, there is a long anterior hood extension, and all of the appendages are swept inward. D. Medial section of androecium. Note that the appendages are swept inward. E. Cross-section of ovary showing mucilage ducts in the ovary wall. F. Medial section of flower. Note that hood appendages are swept inward. G. Medial section of calyx and ovary. Note that style is obliquely oriented and long. H. Cross-section of ovary. Note mucilage ducts in the calyx-lobes. I. Indehiscent fruit, operculum facing downward. J. Seed with dendritic venation and without well-developed aril. K. Medial section of flower. Note that hood appendages are swept inward. L. Cross-section of ovary showing mucilage ducts in ovary wall. M. Lateral view of fruit. N. Apical view of open fruit with seeds inside. O. Basal view of operculum. P. Seed with dendritic venation and poorly-developed aril. Drawings A–B by A. Tangerini and all others by B. Angell.

FIGURE 7. The *Bertholletia excelsa* clade (see Fig. 45 in Mori & Prance, 1990 for vouchers except for B which is vouchered by *Mori et al. 17503*). A. Flower showing petals tightly pressed against androecium and turned downward at their apices. B. Calyx, ovary, and style. Note that the calyx consists of two lobes, the ovary is inferior and very short and the style is oblique. C. Cross-section of 4-locular ovary. D. Medial section of androecium showing swept in vestigial stamens and the anterior ligular extension. E. Fruit showing that the opercular opening is smaller in diameter than the diameter of the seeds. F. Operculum. Note that it drops into the inside of the fruit a maturity. G. Seed. This is the only neotropical Lecythidaceae with a ligneous seed coat. H. A seedling. The embryo lacks cotyledons and is mostly composed of the hypocotyl. This monotypic clade is part of the larger *Bertholletia* clade. Drawings by B. Angell and photo by S.A. Mori.

Other morphological characters that would suggest relationships between *B. excelsa* and some species of *Lecythis* may be misleading and are homoplasious on our trees. For example many species of Amazonian Lecythidaceae have thick cuticles and papillae that arise from them, most likely to reduce water loss from the leaves—thus, the presence or absence of papillae should not be given much weight in predicting evolutionary relationships in this family. Even the unique two-lobed calyx (Fig. 7B) of *B. excelsa* is not an absolute indicator of evolutionary relationships because nearly all zygomorphic-flowered neotropical Lecythidaceae (including *B. excelsa*) have six calyx-lobe primordia in early floral development (see Fig. 78 in Tsou & Mori, 2007).
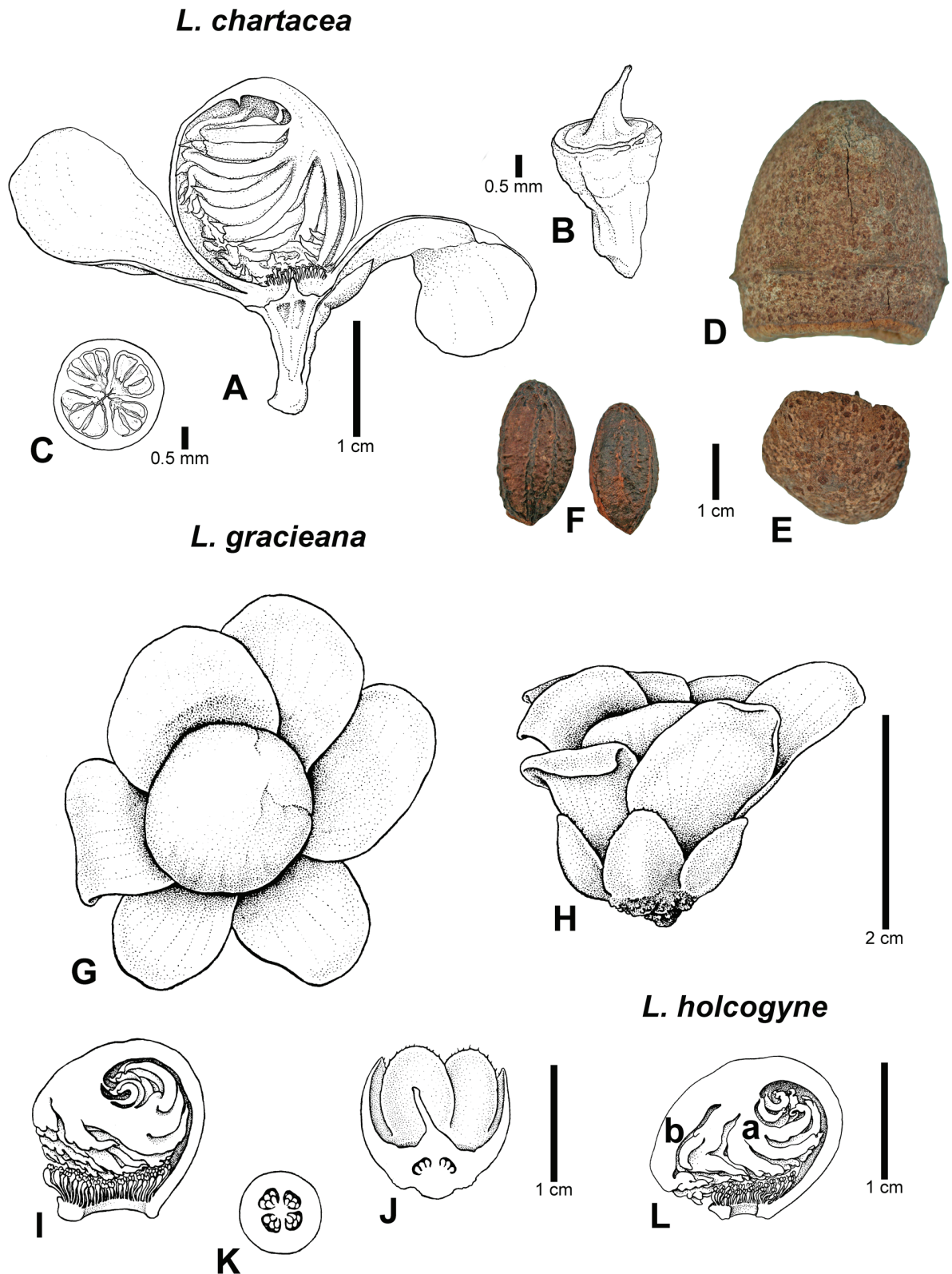
Lecythis chartacea clade (76% BS; Figs. 2A, 8)

This clade is distributed in Amazonian Venezuela, the Guianas, and in western to eastern Amazonian Brazil (Huang, 2010). None of the morphological characters that were included in the analysis provide synapomorphies for this clade, and the only apparent morphological distinction for the clade is the more-or-less fusiform seeds with salient longitudinally oriented major veins and the areas between them with salient higher order veins (Figs. 8F). These seeds differ from the smooth inter-venal areas of the seeds of the *L. ollaria* clade (Fig. 9A–C), the dendritically arranged pattern and plane or impressed veins of the *L. poiteaui* clade (Fig. 9M–P), and the hard seed coat of the *Bertholletia excelsa* clade (Fig. 7G). Members of the *L. chartacea* clade possess an androecial hood with swept in appendages (Figs. 8A, I, L) as do some of the species of the *L. poiteaui* (Fig. 6D) and *B. excelsa* (Fig. 7D) clades. The hood of the *L. ollaria* clade differs from these clades in its possession of a single coil (Fig. 5A, G). In addition, zygomorphic-flowered species with these types of androecial hoods do not possess obvious vestigial stamen nectaries, like those of the *Eschweilera integrifolia* (Figs. 11B, F) and *E. parvifolia* (Figs 15B, H) clades and the outgroup genus *Couratari*. The presence of mucilage ducts in the ovary and/or the calyx lobes (character 17) is found in both the *L. poiteaui* (Figs. 6E, H, L) and *L. chartacea* clades but they are more common in the former clade; relatively long, obliquely oriented or geniculate styles occur in the *L. poiteaui* (Fig. 6G), *B. excelsa* (Fig. 7B), and *L. chartacea* (Figs. 8B, 8J) clades; indehiscent fruits are found in some of the species of the *L. poiteaui*, *B. excelsa*, and some of the species of the *L. chartacea* clades. Moreover, there are both dehiscent- and indehiscent-fruited species in the *L. poiteaui* and *L. chartacea* clades. In these clades, the fruits are of two types: they can be large with a relatively thin pericarp and fall to the ground without dehiscing (e.g., *L. lurida* and *L. prancei* Mori [1990b: 304], Fig. 6I) or the fruits dehisce but do not release the seeds, which are so large that they do not fall from the fruit (e.g., *L. ibiriba* (Miers 1874: 236) Smith *et al*. [2013: 447], Fig. 6N). In the Lecythis poiteaui clade, regardless of fruit type (whether truly indehiscent or with seeds that remain stuck inside the fruit), the seeds are large, more-or-less round (i.e., not markedly longer than broad), have plane or slightly impressed, dendritic veins, and a vestigial (Fig. 6P) aril or no sign of an aril (Figs. 6J, 9M–P).
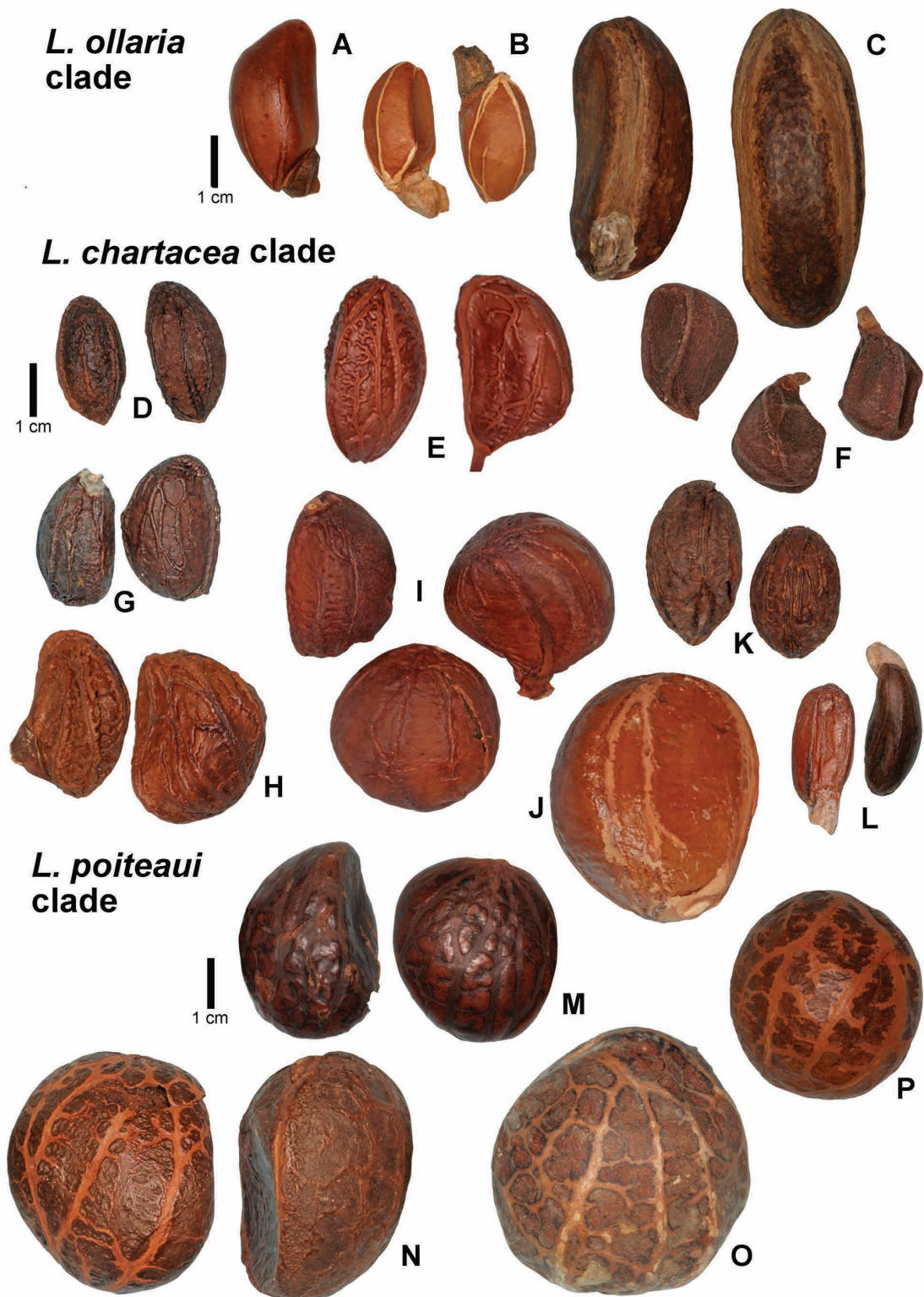
Indehiscent fruits of the *L. chartacea* clade are possessed by the riverine species *L. rorida* (mistakenly treated as a synonym of *L. chartacea* by Mori, 1990b), which has fruits that usually drop into the water with the non-arillate seeds trapped inside, and the *terra firme* species *L. gracieana* S. A. Mori (*in* Mori & Lepsch-Cunha 1995: 47) and *L. parvifructa* S. A. Mori (1990b: 312), which have relatively small, single-seeded fruits that fall to the ground at maturity without dehiscing. All of the remaining species sampled in the *L. chartacea* clade have dehiscent fruits and seeds with well-developed basal arils.

Lecythis brancoensis is sister to all other species of the *L. chartacea* clade (Fig. 2A), but was included in *Lecythis* Section *Poiteaui* by Mori (1990b). It differs from other species of the *L. chartacea* clade in the presence of anthers or antherodes (character 32) on the innermost appendages of the androecial hood and the absence of a closed androecium (character 33). It was placed in *Lecythis* sect. *Poiteaui* based on the hypothesis that *L. brancoensis* is also bat-pollinated, which is supported by its unbranched terminal inflorescence and very large numbers of stamens, In addition, *L. brancoensis* shares a papillate abaxial leaf surface with the bat-pollinated *L. barnebyi* and *L. poiteaui*. In Huang *et al*. (2011), *L. brancoensis* was recovered as a clade with the two known bat-pollinated species of *Lecythis* sect. *Poiteaui*; however, the current study does not support the relationship between the bat-pollinated species of the *Lecythis poiteaui* clade (Fig. 2A) and the hypothetical bat-pollinated *L. brancoensis* of the *L. chartacea* clade.

Eschweilera congestiflora and *E. simiorum* were placed in *Eschweilera* Section *Eschweilera* by Mori & Prance (1990) but these two species possess features that are common for species of the *L. chartacea* clade, e.g., a non-coiled ligule (character 26; Fig. 8C, I, L), curved inward appendages arising from the apex of the ligule (character 31), a 4-locular ovary (character 39), and seeds with a basal aril (characters 47, 48; Fig. 9L). Mori *et al*. (2007) pointed out that these two species were placed in the wrong genus as indicated by molecular data. In this study, these two species are embedded in the *L. chartacea* clade, but new combinations will not be needed because they were originally described as *L. congestiflora* Benoist (1915: 177) and *L. simiorum* Benoist (1915: 178) (Fig. 2 in Mori *et al*., 2007).
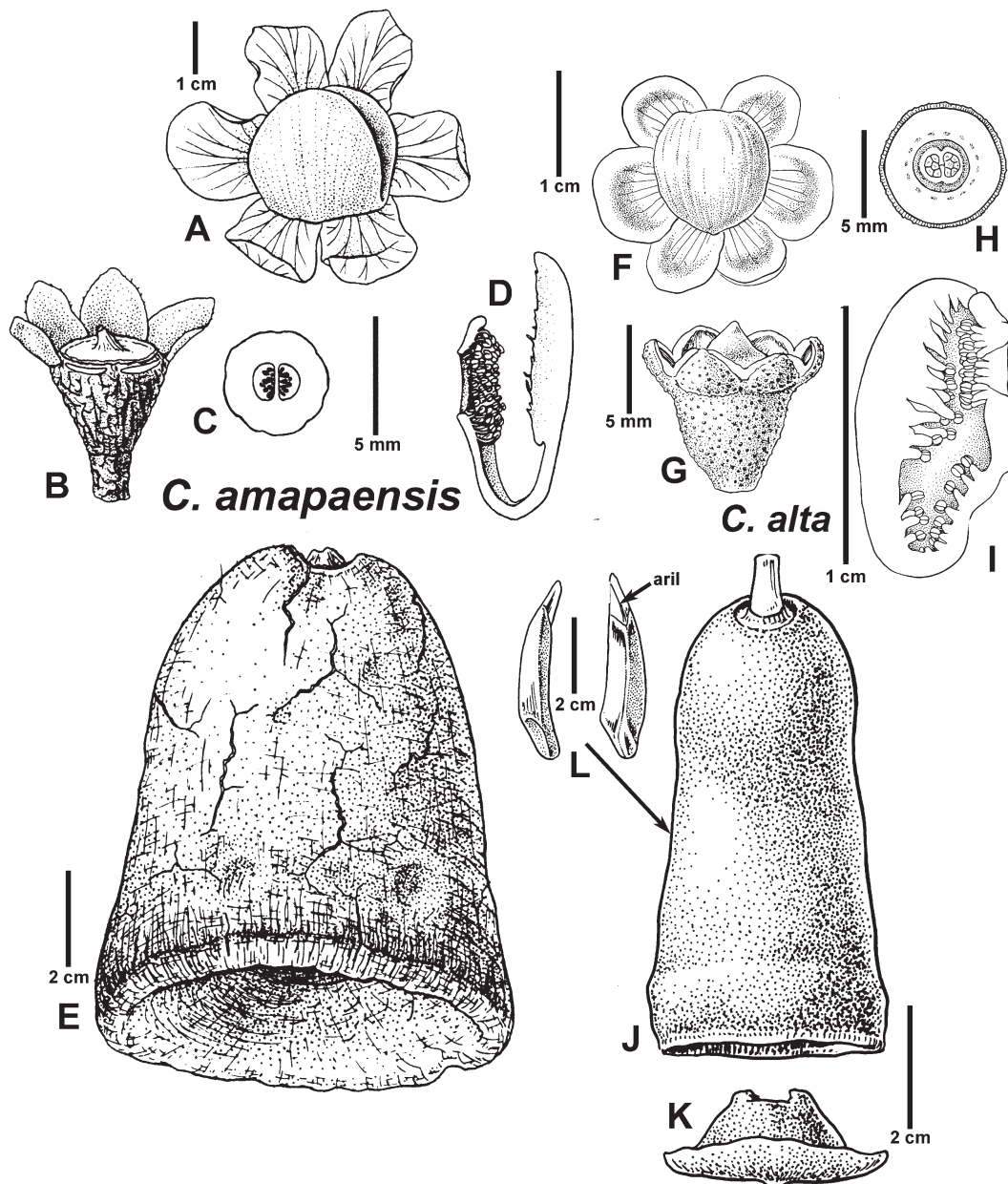
FIGURE 8. The *Lecythis chartacea* clade. A–E. *L. chartacea* (A–C based on *Mori et al. 26485*, D–F based on *Nee & Mori 4199*). G–K. *L. gracieana* (see Fig. 19 in Mori & Lepsch-Cunha, 1995 for vouchers). L. *L. holcogyne* (see Fig. IV-1 in Mori, 1987 for voucher). A. Medial section of flower. Note that the vestigial stamens arise from the apex of the ligule and are swept inwards. B. Lateral view of ovary with all other floral parts removed. Note the geniculate style. C. Cross-section of 4-locular ovary. D. Lateral view of fruit. E. Operculum. F. Two seeds. The salient major veins run parallel to the main axis of the seed and the secondary veins depart from them into the area between the major veins. G. Apical view of flower. H. Lateral view of flower showing petals tightly pressed against androecium making it difficult for all but robust bees to enter the flower. I. Medial section of an androecium showing vestigial stamens swept inward. J. Medial section of ovary. Note obliquely oriented style. K. Cross-section of 4-locular ovary. L. Medial section of androecium showing swept inward vestigial stamens (a) and anterior hood extension (b). Drawings A–C by C. Carollo, the remaining by B. Angell, and the photographs by S. A. Mori.

FIGURE 9. Seeds of the *Lecythis ollaria* (A–C), *L. chartacea* (D–L), and *Lecythis poiteaui* (M–P) clades. *Lecythis ollaria* clade—A. *L. ollaria* (*Davidse & González 12096A*). B. *L. minor* (*Prance 23172*). C. *L. tuyrana* (not vouchered). All species in this clade have a tendency toward more-or-less fusiform seeds, plane primary veins, major veins oriented along length of seeds, and higher order veins absent, i.e., the areas between the major veins are smooth. Most of the veins of *L. ollaria* and *L. minor* only extend for part of the length of the seeds while those of *L. tuyrana* extend from the base to the apex of the seed. *Lecythis chartacea* clade—D. *L. chartacea* (*Nee & Mori 4199*). E. *L. alutacea* (*Redden et al. 1732*). F. *L. brancoensis* (*Silva 48*). G. *Lecythis rorida* (*Mori et al. 20428*). H. *L. retusa* (Ramos s.n. NY barcode 00684323). I. *L. gracieana* (*Freitas et al. 745*). J. *Lecythis parvifructa* (*Freitas et al. 726*). K. *L. holcogyne* (*Mori & Pipoly 15493*). L. *Eschweilera. simiorum* (*Clark 4333*). Most species in this clade have fusiform or, less frequently, globose seeds, salient primary veins, major veins oriented along the entire length of the seeds, and salient higher order veins. The seeds associated with indehiscent fruits (e.g., those of *L. gracieana* (I) and *L. parvifructa* (J), tend to be more globose. *Lecythis poiteaui* clade—M. *L. barnebyi* (*Costich & dos Santos 836*). N. *Lecythis ibiriba* (*Carvalho et al.* 6026). O. *L. lurida* (*Prance 26574*). P. *L. prancei* (*Mori 20286*). All species in this clade have more-or-less globose seeds, plane or impressed veins, and the overall dendritic venation pattern. Photos by S. A. Mori.
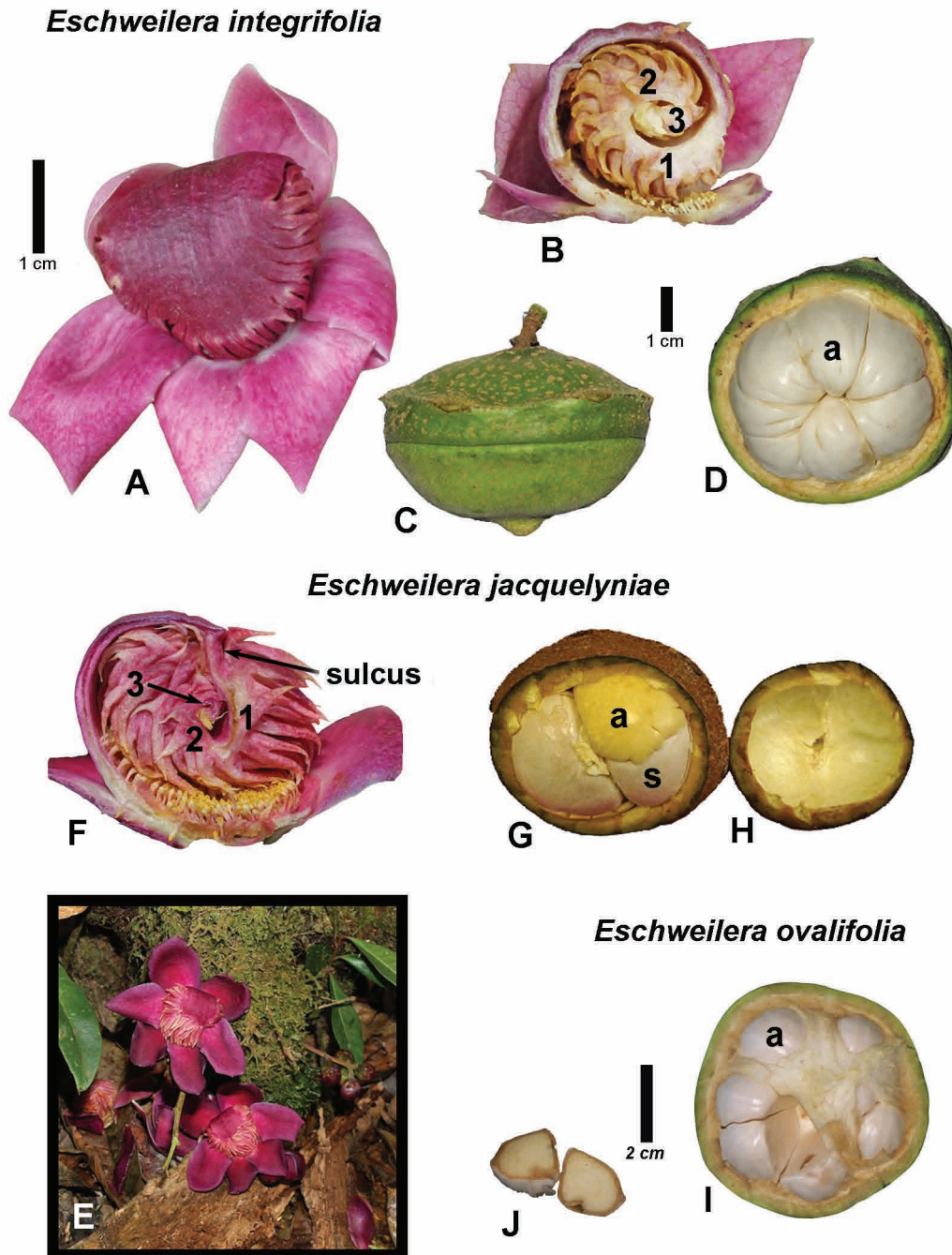
Corythophora clade (100% BS; Fig. 2A, 10)

This clade includes all four species of *Corythophora* recognized by Mori & Prance (1990). Species of *Corythophora* are restricted to Surinam, French Guiana, and central and eastern Amazonian Brazil (Huang, 2010). Morphological synapomorphies of *Corythophora* include the presence of squamae on the surface of the inflorescence rachis (character 12, Fig. 3A) and anther dimorphism (character 36). In addition, the species of *Corythophora* possess dorsiventrally thickened and closed androecial hoods (character 33; Fig. 10A, D, F, I). Within the clade, the species are divided into two subclades (Fig. 2A): one with *C. labriculata* (Eyma 1932: 75) S. A. Mori & Prance (Mori 1981a: 365) and *C. amapaensis* Pires ex S. A. Mori & Prance (Mori 1981a: 365), and the other with *C. alta* R. Knuth (1939: 51) and *C. rimosa* Rodrigues (1974: 5). The latter subclade differs from the former by the presence of ligular (character 32) instead of staminal ring antherodes, non-imbricate calyx-lobes, and a hypanthium and calyx-lobes that are not differentiated in texture and color. The monophyly of *Corythophora* in this study is congruent with previous studies (Mori & Prance, 1990; Mori *et al.*, 2007; and Huang *et al.*, 2011).

FIGURE 10. The *Corythophora* clade. A–E. *C. amapaensis* (see Fig. 42 in Mori & Prance, 1990 for vouchers), F–L. *C. alta* (see Fig. 12 in Mori & Lepsch-Cunha, 1995 for vouchers) A. Apical view of flower. Note the closed androecial hood typical of all species in this clade. B. Inferior ovary with all but four calyx-lobes removed. Note that the calyx-lobes are strongly imbricate. C. Cross-section of 2-locular ovary. D. Medial section of an androecium with the androecial hood dorsiventrally thickened. E. Campanulate fruit base. F. Apical view of flower. G. Ovary, calyx, and style of a very young fruit. Note that the calyx-lobes are not imbricate. H. Cross-section of 2-locular ovary. I. Medial longitudinal section of androecium with dorsiventrally thickened hood. J. Cylindrical fruit. K. Operculum without a columella. L. Seeds with basal arils. The seeds of this clade are oblong to fusiform. Drawings A–E by B. Angell and F–L by A. Tangerini.
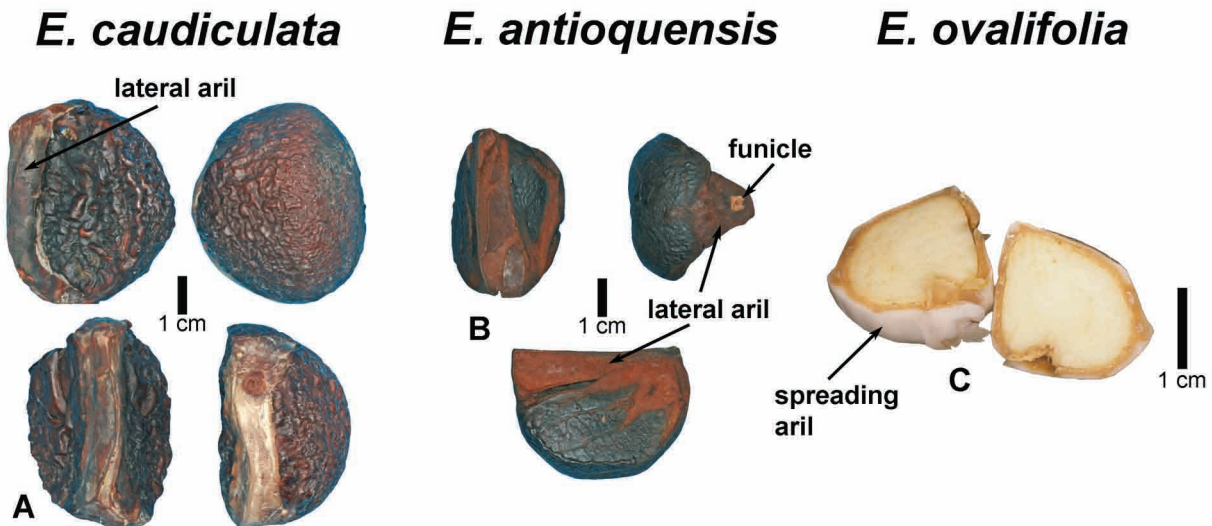
This clade comprises 19 sampled species of *Eschweilera* included in *Eschweilera* section *Eschweilera* by Mori & Prance (1990). Species of this group are found from central to western Amazonian Brazil, the Andes, forests of the Pacific coasts of Colombia, Ecuador, and Central America as far north as Costa Rica.

FIGURE 11. The *Eschweilera integrifolia* clade. A–D. *E. integrifolia* (based on *Cornejo 8111*). E–H. *E. jacquelyniae* (E–F based on *Hernández 828* and G–H based on *Galdames 6142*). I–J. *E. ovalifolia* (based on an unvouchered photo by S. A. Mori). A. Apical view of flower. Note the closed androecial hood typical of all species of this clade. B. Medial section of triple-coiled androecial hood. Note that there are three coils, a feature common to this clade, and that the coils are oriented horizontally. C. Lateral view of fruit. D. Apical view of a fruit with "a" marking a seed completely surrounded by the aril (= spreading aril). E. Cauline inflorescences. Note that this inflorescence is very near to the ground but other inflorescences of this species may also occur on the branches. F. Medial section of triple coiled androecium. Note that the coils are oriented vertically. G. Apical view of opened fruit with "a" marking a seed with a spreading aril. The aril is pale yellow and the immature seeds are white. H. Inside view of operculum. I. Apical view of open fruit. Note that the seeds are completely surrounded by arils. J. Cross-section of seed. Note the white layer on the outside (= aril), the seed coat, and the solid embryo which does not have differentiated cotyledons. Photos A–D by X. Cornejo, E–H by F. Hernández, and I–J by S. A. Mori.

This clade is defined by a triple coil (characters 26, 27) with vestigial stamen nectaries at the apex of the last coil (not coded; Fig. 11B, F). In addition, most of the species (e.g., *E. aguilarii* S. A. Mori [2007: 903], *E. amplexifolia* S. A. Mori [Mori & Prance 1990: 201], *E. andina* (Rusby 1896: 37) Macbride [1941: 246]*, E. collinsii* Pittier (1908: 97)*, E. integrifolia, E. ovalifolia* (Candolle 1828: 292) Niedenzu [1892: 40]*,* and *E. sessilis* A. C. Smith 1933: 21) have a spreading aril that completely surrounds the seed (character 48; Figs. 11D, G, I, 12C), but several species (e.g., *E. antioquensis* Dugand & Daniel [1938: 1], *E. caudiculata* R. Knuth [1939: 95], and *E. rimbachii* Standley [1935: 31]) possess arils that are lateral but differ from the lateral arils of the *E. parvifolia* clade by having their ends extend around the base and apex of the seed (Fig. 12A, B); one species (*E. jacquelyniae* S. A. Mori [Mori & Prance 1990: 192]) has very large and fleshy lateral arils (Fig. 11D).
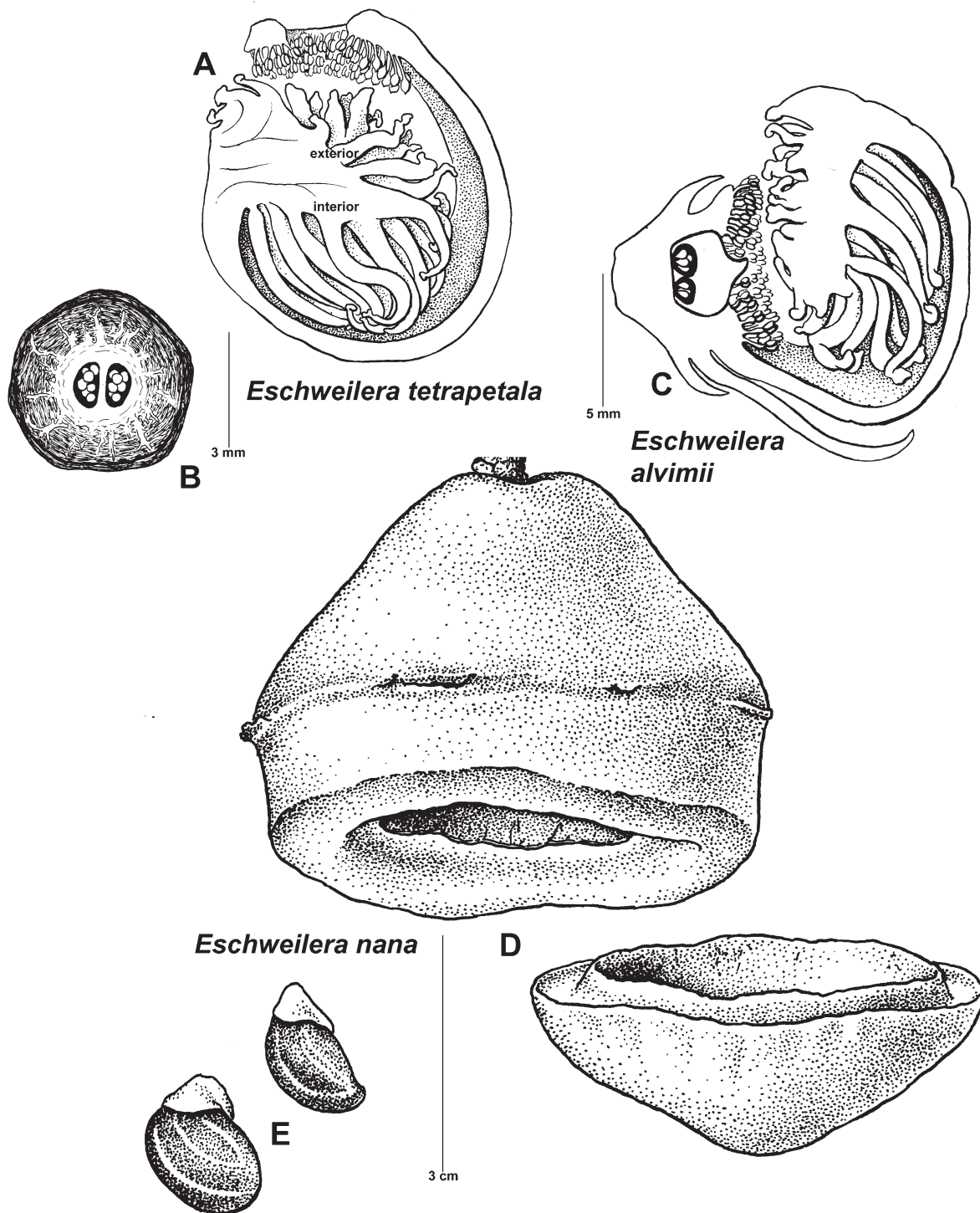

FIGURE 12. Arils found in the *Eschweilera integrifolia* clade. A. *E. caudiculata* (Cornejo 8106). B. *E. antioquensis* (*Luteyn & Callejas 12025*). C. *E. ovalifolia* (S. A. Mori photo only). A. Top left: Side view of seed showing lateral aril. Note that this type of lateral aril extends onto both ends of the seed. Top right: Rounded side of hemispherically-shaped seed. Bottom left: Lateral aril of wedge-shaped seed. Bottom right: Flat side (left) and round side (right) of hemispherically shaped seed. B. Three different views of wedge-shaped seed. C. Cross-section of seed with spreading aril. Note that the next layer is the seed coat, and the center is filled with an undifferentiated (= macropodial) embryo. Photos by S. A. Mori.

Eschweilera amazoniciformis, endemic to central Amazonian Brazil, is sister to the remaining species of the clade (Fig. 2B). This species is distinguished by the presence of four instead of six calyx-lobes (character 16) and four instead of six petals (18). In addition, it is the only known species of neotropical Lecythidaceae with the combination of a triple-coiled androecial hood and fusiform seeds with a well-developed basal aril.

Most of the species of the *E. integrifolia* clade are found in western Amazonia and the mountain valleys and slopes of the Andes, with the exception of the central Amazonian *E. amazoniciformis* and *Eschweilera ovalifolia*. The Andean and western Amazonian species possess predominantly red flowers, but some species, for example, the coastal Ecuadorean species *E. awaensis* S. A. Mori & Cornejo (2011: 470) and the western to central Amazonian species *E. ovalifolia*, have yellow flowers.

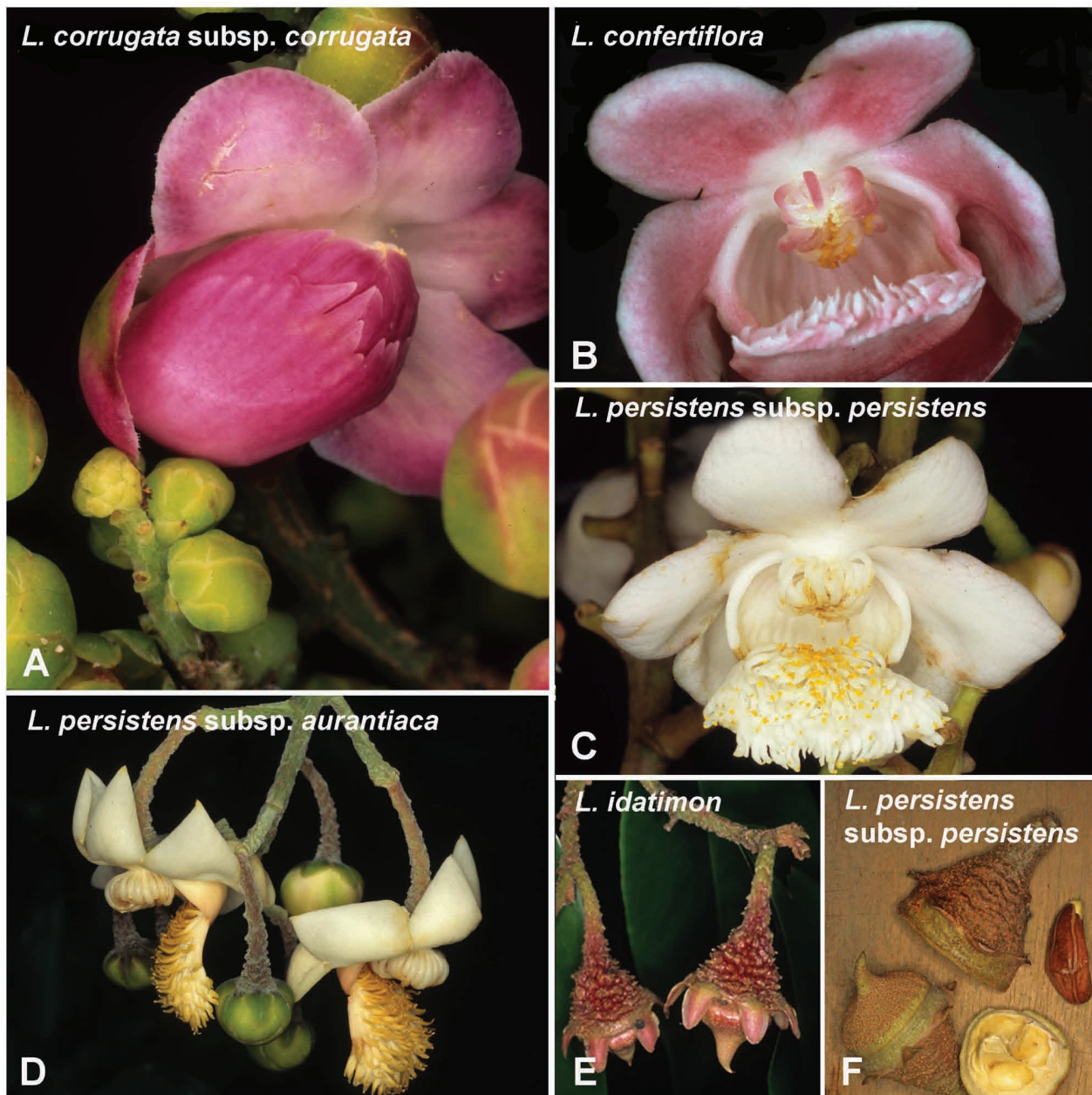**Eschweilera tetrapetala clade** (100% BS; Figs. 2B, 13)

This small clade consists of three sampled species (*E. alvimii* S. A. Mori [1981: 469], *E. tetrapetala*, and *E. nana* and three additional species (*E. complanata* S. A. Mori [1995: 16], *E. compressa* (Vellozo 1829: 222) Miers [1874: 248], and *E. mattos-silvae* S. A. Mori [1995: 22]) and several unnamed species that were not included in this study. *Eschweilera alvimii* and *E. tetrapetala* were included in *Eschweilera* section *Tetrapetala* (Mori, 1990) and *Eschweilera nana* was included in *Eschweilera* section *Eschweilera* by Mori & Prance (1990). *Eschweilera nana* has a wide distribution in the Brazilian *cerrado* but the other species have narrow distributions and are endemic to the coastal forests of eastern Brazil (Huang, 2010).

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FIGURE 13. The *E. tetrapetala* clade. A–B. *E. tetrapetala* (see Fig. 63 in Mori & Prance, 1990 for vouchers), C. *E. alvimii* (see Fig. 65 in Mori & Prance, 1990 for vouchers). D–E. *E. nana* (see Fig.8 in Prance & Mori, 1991 for vouchers). A. Medial section of androecium. Note that the androecial hood has a single coil and that there are vestigial stamens on both the exterior and interior of the coil, a feature unique to all species of this clade. B. Cross-section of 2-locular ovary, a feature common to all species of this clade. C. Medial section of androecium of *E. alvimii*. D. Fruit base and operculum. Note that the operculum lacks a columella. E. Seeds with basal arils. Drawings by B. Angell.

Synapomorphies of this clade include the presence of squamae on the inflorescence rachises (Fig. 3B; character 12) and appendages on both the interior and exterior surfaces instead of only on the exterior surface of the single androecial hood coil (character 29; Fig. A, C). The latter character is unique to this clade. The monophyly of Section *Tetrapetala* in the present study is congruent with Huang *et al*. (2011). In addition, species of the *E. tetrapetala* clade have a single androecial hood coil, a two-locular ovary (character 39; Fig. 13B), and a basal aril (characters 47, 48; Fig. 13E).

FIGURE 14. The *Lecythis corrugata* clade. A. *L. corrugata* subsp. *corrugata* (*Mori et al. 25730*). B. *L. confertiflora* (*Mori et al. 20801*). C. *L. persistens* subsp. *persistens* (*Mori et al. 25651*). D. *L. persistens* subsp. *aurantiaca* (*Mori et al. 24724*). E. *Lecythis idatimon* (*Mori et al. 25745*). F. *L. persistens* subsp. *persistens*. A. Apical view of flower. Note that this is the only species in this clade with a closed androecial hood and without lateral flanges. B. Anterior view of flower. Note that this species has an open androecium and the sides of the ligule with lateral flanges. C. Anterior view of flower. Note that his species has an open androecium and the sides of the ligule possess lateral flanges. D. Lateral view of flowers. Note that this species has an open androecium and the sides of the ligule with lateral flanges. E. Young fruits with tuberculate pedicels and hypanthia. F. Young fruits with rugose pericarp and fusiform seeds with a small aril at their base. Photos by S. A. Mori (A, C–F) and C. Gracie (B).

Lecythis corrugata (99% BS; Fig. 14)

This clade includes all five species of *Lecythis* section *Corrugata* recognized by Mori (1990b). Species of *L.* section *Corrugata* are found in the Guianas, eastern Amazonian Brazil, and on the other side of the Andes in the Lake Maracaibo area (Huang, 2010).

Synapomorphies for this clade are the presence of rugose/tuberculate pedicels and hypanthia (character 14; Figs. 14E, F) and ligular flanges (absent in *L. corrugata*) (character 28, Fig. 14B, D). Other synapomorphies include the presence of a non-coiled ligule (character 26; Fig. 14B–D), an open androecium (absent in *L. corrugata*, character 33; Fig. 14B–D), anther dimorphism (character 36), and four-locular ovaries (character 39). The monophyly of the *L. corrugata* clade in the present study is consistent with Mori (1990b), Mori *et al.* (2007), and Huang *et al.* (2011). However, recovering the *L. corrugata* clade as sister to the *E. parvifolia* clade has not been suggested before.

FIGURE 15. The *Eschweilera parvifolia* clade. A–G. *E. pedicellata* (see Fig. 85 in Mori & Prance, 1990 for vouchers). H–J. *E. ovata* (see Fig. 87 in Mori & Prance for vouchers). K. *E. romeu-cardosoi* (see Mori & Lepsch-Cunha, 1995 for vouchers). A. Apical view of flower. Note that this and all species of this clade have a closed androecium. B. Medial longitudinal section of an androecium. Note the incipient third coil in contrast to the double coil of most species of this clade. C. Cross-section of 2-locular ovary. Although most species of this clade have 2-locular ovaries there are a few species that are 4-locular. D. Base of fruit. E. Operculum of fruit. F. Lateral view of seed with lateral aril. G. Basal view of seed showing position of lateral aril. H. Medial longitudinal section of androecial hood showing double coil. I. Stamen showing clavate filament. J. Medial longitudinal section of ovary showing basal insertion of the ovules. K. Seedling. Note that the embryo remains inside of the seed coat upon germination. Line drawings by B. Angell..

Within this clade *L. corrugata* is morphologically similar to species of *Corythophora*, especially to the two species in the *C. amapaensis/C. labriculata* clade, as indicated by dorsi-ventrally thickened, closed androecial hoods (character 33; Figs. 10D, 10I, 14A). Huang *et al*. (2011) pointed out that the *L. corrugata* and *Corythophora* clades have non-coiled ligules (character 26; Figs. 14A–C), reduced or well-developed appendages on the interior side of the ligule (character 29, Fig. 14A–C), anther dimorphism (character 36, Fig. 14C), and seeds with basal arils (characters 47, 48; Figs. 10L, 14F). However, all species in this clade (other than *L. corrugata*) are easily separated from *Corythophora* by an open instead of a closed androecium, the presence of lateral flanges, and four instead of a two-locular (except *C. labriculata*) ovaries. In this study, the close relationship of the *L. corrugata* and *Corythophora* clades is not supported. A close relationship of these clades was supported by Huang *et al*. (2011), but the only synapomorphy was the presence of anther dimorphism (character 36; Fig. 14C).

Eschweilera parvifolia clade (94% BS; Fig. 2B, Fig. 15)

This clade consists of a sample of 29 of the approximately 63 species (minus the species now considered as belonging to the *E. integrifolia* clade) recognized by Mori & Prance (1990). Species of this clade are found nearly everywhere in the Neotropics, ranging from Veracruz, Mexico to Rio de Janeiro, Brazil (Huang, 2010).

The sections of *Eschweilera*, as defined by Mori & Prance (1990), include *Eschweilera* sect. *Tetrapetala* (our *E. tetrapetala* clade discussed above); *Eschweilera* sect. *Jugastrum*, consisting only of *E. tenuifolia* (O. Berg 1858: 502) Miers (1874: 266); *Eschweilera* sect. *Bracteosa*, consisting of the sampled *E. bracteosa* (Poepp ex. O. Berg (1856: 455) Miers (1874: 274), *E. laevicarpa* S. A. Mori (1987: 32), and *E. cyathiformis* S. A. Mori (1989: 20), and the non-sampled *E. rabeliana* S. A. Mori (1989: 21) and *E. revoluta* S. A. Mori (*in* Mori & Prance 1990: 174); and *Eschweilera* section *Eschweilera* with the remaining species (minus those found in the *E. integrifolia* clade). The type, *E. parvifolia* (Mori & Prance, 1990), is found in this clade.

Mori & Prance (1990d) included species of our *E. integrifolia* (described above), *E. tetrapetala* (described above), and the *E. parvifolia* clades in their concept of *Eschweilera*. Based on our results, *Eschweilera* is not monophyletic.

The most useful morphological synapomorphy of the *E. parvifolia* clade is the presence of a lateral aril (character 48, Fig. 15F). Although there are a few species with lateral arils in the *E. integrifolia* clade, most of those species have spreading arils (Fig. 12C) and the ones with lateral arils are either much larger and/or wrap around the ends of the seeds (Figs. 12A, 12B, see above discussion of the *E. integrifolia* clade). In addition, this is the only clade with consistently double-coiled androecial hoods (Fig. 15B–H) in contrast to the consistently single-coiled androecial hoods of the *Eschweilera tetrapetala* and the triple-coiled androecial hoods of the *E. integrifolia* clades. The species of the *Eschweilera parvifolia* and *E. integrifolia* clades are the only species to have vestigial stamen nectaries in the *Bertholletia* clade, a feature that is also found outside of the clade in *Couratari* (Mori et. al., 2015).

Eschweilera tenuifolia differs from the other species of this clade because it lacks pedicels (character 13) and its seeds do not have an aril (character 47). Other defining features are wedge-shaped seeds; a corky seed coat; and seed germination from the sides (Fig. 18M in Prance & Mori, 1979) instead of the ends of the seeds (not coded). The flowers of *E. tenuifolia* have a double-coiled androecial hood identical to the other species of the *E. parvifolia* clade. This species was the only one included in *E.* section *Jugastrum* by Mori & Prance (1990) and can only be recognized as a separate section if the poorly understood basal clade (the *E. mexicana* clade) is also recognized as a section but that clade has no differences from the other species of the *Eschweilera parvifolia* clade. In this study, the representatives of *Eschweilera* section *Bracteosa* fall into two unresolved clades. Whether this section should be recognized is open to question, but it is unlikely that the persistent bracts and bracteoles in the inflorescences are stable enough for use in defining taxonomic groups (Fig. 2B).

Taxonomic implications

Phylogenetic study based on combined evidence derived from morphological and molecular data will continue to contribute to a phylogenetic classification of the genera of neotropical Lecythidaceae (Morton *et al*. 1998; Mori *et al*., 2007; Huang *et al*., 2011). Our goal in this paper has been to determine if the generic classification within the *Bertholletia* clade as recovered in this study is congruent with the generic classification of Mori & Prance (1990). This study does not address the evolutionary relationships of the actinomorphic-flowered (*Allantoma, Grias*, or *Gustavia*) or the zygomorphic-flowered (*Cariniana, Couratari, Couroupita*) genera because they are not part of the *Bertholletia* clade. These genera are discussed in a paper by Mori *et al*. (2015).

The topology of our consensus tree indicates that *Eschweilera*, as circumscribed by Mori & Prance (1990), is paraphyletic (Fig. 2B) and that *Lecythis*, as defined by Mori (1990b), is polyphyletic. In the paragraphs below, we discuss the implications that this study has on the generic classification of neotropical Lecythidaceae, and we present options for circumscribing genera. The clades are discussed in the order they appear on our trees.

A. The monophyly of Section *Pisonis* (*Lecythis pisonis* clade) is strongly supported by the data (100% BS; Fig. 2A). In addition, this clade has a combination of features that allow it to be easily recognized. Ledoux (1964) established *Pachylecythis* Ledoux based on *Pachylecythis egleri* Ledoux (1964: 2), which was treated as a synonym of *Lecythis pisonis* by Mori (1990b). Therefore, all species of Section *Pisonis* recognized by Mori (1990) would have to be transferred to *Pachylecythis* if this clade is recognized as a separate genus.

B. The relationships among and within the taxa of the *Lecythis ollaria, L. poiteaui, Bertholletia excelsa,* and *L. chartacea* clades are still incompletely understood. Our trees provide several options upon which to base a generic classification, but only the two extreme possibilities will be discussed here. The first option is to recognize all of the clades as *Lecythis*, which would require treating *Bertholletia excelsa* as a species of *Lecythis*. With some exceptions, the morphological features defining this clade are an androecial hood with swept in appendages (in all taxa except the *Lecythis ollaria* clade which has a single coil) and basal arils in all except the indehiscent-fruited species. This "new *Lecythis*" would include all the species of *Lecythis* sect. *Lecythis* minus the *L. pisonis* and *L. corrugata* clades. The other extreme would be to recognize all of the clades as separate genera, as follows:

1) The *L. ollaria* clade would remain as *Lecythis*, but with the number of species reduced to three. Defining characters would be a single-coiled androecial hood with only exterior appendages (Figs. 5A, G), an erect short style (Fig. 5G), and seeds with plane or impressed major veins running the length of the seed and no evident veins between the major veins (Figs., 5F, J, 9A–C).

2) The *Lecythis poiteaui* clade is supported in every analysis that includes molecular data, but does not have morphological synapomorphies among the characters included in the analysis. Members of the clade can be recognized by the lack of a single coil (but with swept inward appendages); a long, slender, obliquely oriented or geniculate style; indehiscent or dehiscent fruits, with the indehiscent taxa lacking an aril; plane or impressed seed veins that do not parallel the length of the seed but are dendritically arranged (Figs. 6, 9M–P).

Ducke published *Holopyxidium* (Ducke 1925: 152) based on *Holopyxidium jarana* (Ducke 1925: 152) which was treated as a synonym of *Lecythis lurida* (Mori, 1990b), so that generic name is available for naming this clade if future studies support its recognition as a genus.

3) The monotypic *Bertholletia excelsa* clade defined by a two-lobed calyx, a unique type of fruit dehiscence, a boney seed coat, and total absence of an aril (Fig. 7). This clade would be retained as a monotypic genus.

4) The *L. chartacea* clade is supported in every analysis based on molecular data. Morphologically, the clade possesses features similar to those of the *L. poiteaui* clade, but the seeds are more-or-less fusiform, the major veins are salient and run the length of the seed, and cross veins depart from the major veins into the area between the veins (Figs. 8, 9D–L). Segregation of *Lecythis chartacea* clade into a separate genus should only be done if further study supports this action. The name *Cercophora* Miers (1874), previously established as a monotypic genus, may available for the *Lecythis chartacea* clade, but the identity and status of the type of *Cercophora anomala* Miers (1874: 302) is uncertain and needs to be resolved.

C. The *Corythophora* clade is supported by both morphological (Fig. 10) and molecular data and is congruent with Mori & Prance (1990); thus, no changes are needed.

D. The *Eschweilera integrifolia* clade. The separation of this clade from the *E. parvifolia* clade is supported by separation of these two clades in our trees (Fig. 2) and by the following morphological characters: three-coiled androecial hoods (Fig. 11B, F) and seeds surrounded by a spreading aril (Fig. 11D, H, I) or lateral aril that differs from the typical lateral aril of the *E. parvifolia* clade (Fig. 15F) because it curves around the base and apex of the seed (Fig. 11A, B).

The nature of the aril in this clade has to be studied in more detail because the group potentially possesses three different types: one that completely surrounds the seed (Fig. 11C), one that is lateral but curves around the ends of the seed (Fig. 11A, B), and another that is very thick and also curves around the end of the seed (only seen in *E. jacquelyniae*, see image on the Lecythidaceae Pages [Mori *et al.*, 2010]). These problems point out the need for a study focused on the *Eschweilera integrifolia* clade in which more taxa, more morphological characters, and additional genes are employed.

E. The *Eschweilera tetrapetala* clade. The species of this clade conform to *Eschweilera* sect. *Tetrapetala* (Mori, 1990) and have 4 or 6 petals, a single-coiled androecial hood with vestigial stamens on both the exterior and interior of the coil (Fig. 13A, C), 2-locular ovaries (Fig. 13B), impressed seed veins (Fig. 13E), and short basal arils (Fig. 13E). In addition, some species have a calycine rim (i.e., calyx-lobes that are fused at their bases to form a rim, e.g., *E. compressa*), and other species lack a calycine rim (e.g., *E. nana*)

There is no support for retaining *E*. sect. *Tetrapetala* (Mori, 1990) as part of either the *E. integrifolia* or the

E. parvifolia clades because both options would necessitate including the *L. corrugata* clade, along with the *E. integrifolia* and *E. parvifolia* clades, into a more broadly defined genus that would not have defining morphological features. In contrast treating these four clades separately results in genera that are relatively well supported and have unique morphological features.

F. The *Lecythis corrugata* clade. This clade conforms to *Lecythis* sect. *Corrugata* S. A. Mori. The clade has high support and all of its species have either tuberculate or rugose hypanthia (Fig. 14E, F), long styles, and basal arils (14F). In addition, all species except *L. corrugata* have flat, open androecial hoods (Fig. 14B–D) and lateral flanges (Fig. 14B–D). The androecial hood of *L. corrugata* is also flat but it is dorsiventrally thickened, closed, and the ligule lacks lateral flanges (Fig. 14A). *Chytroma*, as circumscribed by Miers (1874), includes species that would be placed in our *Eschweilera tetrapetala*, *E. parvifolia*, *Lecythis corrugata*, *L. ollaria*, and *L. poiteaui* clades—thus, including most of the variation of the *Bertholletia* clade. However, Miers (1874) selected *Chytroma amara* (Aublet 1775: 716) Miers (1874: 231) as the type of the genus (a synonym of *L. idatimon* fide Mori, 1990b), and this species possesses the features of the species except some of those of *Lecythis corrugata* as mentioned above.

G. The *Eschweilera parvifolia* clade. Mori & Prance (1990) included the species of our *E. integrifolia*, *E. tetrapetala*, and *E. parvifolia* clades in their broadly defined *Eschweilera*. Our study supports recognizing only the *Eschweilera parvifolia* clade as *Eschweilera* because it contains the type and is separated from the *E. integrifolia*, *E. tetrapetala*, and *L. corrugata* clades by both morphological and molecular characters as discussed above. However, our trees do not justify recognizing any of the sections published by Mori & Prance (1990), because they are either not monophyletic or because recognizing them would leave behind a large paraphyletic assemblage of species.

Conclusions

We conclude that the *Bertholletia* clade informally recognized by Mori *et al.* (2007) and confirmed by Huang (2010) consists of ten zygomorphic flowered clades of Neotropical Lecythidaceae currently placed in *Bertholletia*, *Corythophora*, *Eschweilera*, and *Lecythis* as circumscribed by Mori and Prance (1990). Three other zygomorphic flowered genera (*Cariniana*, *Couratari*, and *Couroupita*) fall outside of the *Bertholletia* clade and these genera, along with three actinomorphic-flowered genera (*Allantoma*, *Grias*, and *Gustavia*), are discussed separately (Mori *et al.*, 2015). Among the ten clades recognized in this paper, only *Corythophora* is monophyletic as defined by Mori and Prance (1990). *Eschweilera* is recovered as three separate clades (the *E. tetrapetala*, *E. integrifolia*, and the *E. parvifolia* clades) and *Lecythis* is recovered as five separate clades (the *L. pisonis*, *L. ollaria*, *L. poiteaui*, *L. chartacea*, and *L. corrugata* clades). *Bertholletia excelsa* is embedded within the *L. ollaria/ L. poiteaui/B. excelsa/L. chartacea* clade. Morphological and molecular data support the continued recognition of *Corythophora* as a genus and the possibility of recognizing the *E. tetrapetala*, *E. integrifolia*, *E. parvifolia* (encompasses the type), *L. pisonis*, and *L. corrugata* clades as separate taxa. In contrast, all six genera of the non *Bertholletia* clade are well-defined molecularly and morphologically and do not need generic changes. A key to the 16 clades of neotropical Lecythidaceae is included in Mori *et al.* (2015).

Another challenge in the systematics of neotropical Lecythidaceae is reaching a more complete understanding of the species and their relationships within the clades of this group. This information will provide the framework for determining how species of Lecythidaceae interact with their abiotic and biotic environments which, in turn, will facilitate future studies on the evolution, ecology, and conservation of this ecologically dominant group of Amazonian-centered trees.

Acknowledgements

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APPENDIX 1. Voucher information and GenBank accession numbers for taxa used in this study. Voucher specimens are deposited in the following herbaria: CAY Herbier de Guyane, CR Herbario Nacional de Costa Rica, INB Costa Rican National Biodiversity Institute, MO Missouri Botanical Garden, NY New York Botanical Garden.

For each taxon, the information is displayed in the following sequence: taxa—GenBank accession: *ITS*, *ndhF*, *trnL-F*, *trnH-psbA*; voucher specimen, site of collection, country of collections, herbarium. When two separate accessions belong to one region, the two accessions are connected by an ampersand (&). Missing sequences are denoted with a dash (-). Accession numbers starting with DQ were downloaded from GenBank while those starting with JN were generated in this study.

Allantoma decandra (Ducke) S. A. Mori, Y.-Y. Huang & Prance—JN222224,-,-,-; Mori 25635, Peru, NY. *A. decandra*—JN222210,-,-,-; Janovec2509, Los Amigos, Peru, NY. *A. integrifolia* (Ducke) S. A. Mori, Y.-Y. Huang & Prance—JN222201, JN222089,-, JN221813; Mori 27286, Ducke Reserve, Brazil, NY. *A. lineata* (Mart. ex O. Berg) Miers—JN222140 & JN222141,-,-,-; Goeldi s.n., Belém, Brazil, NY.

Bertholletia excelsa BonpL.—JN222278, JN222007 & JN222008, JN221870, JN221778; Mori 25637, Madre de Dios, Peru, NY. *B. excelsa*—JN222114, JN607441,-,-; Janovec 2508, Los Amigos, Peru.

Cariniana estrellensis (Raddi) Kuntze—-, DQ388187, DQ417937, JN221808; Nee 38522, Santa Cruz, Bolivia, NY. *C. domestica* (Mart.) Miers—JN222204, DQ388186, DQ417936,-; Solomon7848, Beni, Bolivia, NY. *C. ianeirensis* R. Knuth—JN222138 & JN222139, DQ388184, DQ417938, JN221809; Justiniano12, Santa Cruz, Bolivia, NY. *C. legalis* (Mart.) Kuntze—JN222194,-,-,-; Prance 23705, Pará, Brazil, NY.

Corythophora alta R. Knuth—JN222180, JN222053, JN221985, JN221817; Mori 27246, Amazonus, Brazil, NY. *C. amapaensis* Pires ex S. A. Mori & Prance—JN222256, JN222022 & JN222023, JN221871,-; Mori 24146, Saül, French Guiana, NY. *C. amapaensis*—JN222257, JN222028, JN221872,-; Mori 24147, Saül, French Guiana, NY. *C. amapaensis*—JN222314, DQ388189, DQ417942, JN221801; Mori 24148, Saül, French Guiana, NY. *C. labriculata* (Eyma) S. A. Mori & Prance—JN222258, DQ388190, DQ417943, JN221823; Mori 25518, Brownsberg Nature Reserve, Suriname, NY. *C. rimosa* W. A. Rodrigues subsp. *rimosa*—JN222174, JN222096, JN221837,-; Mori 27227, Manaus Amazonas, Brazil, NY. *C. rimosa* subsp. *rimosa*—JN222181, JN222054, JN221986, JN221818; Mori 27282, Manaus Amazonas, Brazil, NY. *C. rimosa* W. A. Rodrigues subsp. *rubra* S. A. Mori—JN222299, JN222029, JN221883,-; Mori 24327, Saül, French Guiana, NY. *C. rimosa* subsp. rubra—JN222259, JN222030, JN221926, JN221739; Mori 24328, Saül, French Guiana, NY. *C. rimosa* subsp. *rubra*—JN222300, DQ388191, DQ417944,-; Mori 25475, Saül, French Guiana, NY.

Couratari guianensis Aubl.—JN222150, JN222055, JN221929,-; Prévost 4687, French Guiana, CAY. *C. guianensis*—JN222151, JN222040, JN221930, JN221750; Prévost 4690, French Guiana, CAY. *C. macrosperma* A. C. Sm.—JN222225 & JN222226, DQ388194, DQ417947, JN221812; Mori 25634, Madre de Dios, Peru, NY. *C. scottmorii* Prance—JN222153 & JN222154, JN222086,-,-; Aguilar11108, Osa, Costa Rica, NY. *C. stellata* A. C. Sm.—JN222109 & JN222110,-,-,-; Mori24111, Saül, French Guiana, NY. *C. stellata*—JN222339,-,-,-; Mori24093, Saül, French Guiana, NY. *C. stellata*—JN222105, DQ388196, DQ417950, JN221800; Mori24092, Saül, French Guiana, NY.

Couroupita guianensis Aubl.—JN222143 & JN222144, DQ388182, DQ417951, JN221741; Tsou1550, Guanacaste Bagaces, Costa Rica, NY. *C. nicaraguarensis* DC.—JN222279, DQ388183, DQ417952, JN221786; Aguilar 8041, Guanacaste Bagaces, Costa Rica, NY. *C. subsessilis* Pilg.—JN222118, JN222097, JN221987, JN221773; Mori 27298, Paraná do Limão Amazonas, Brazil, NY.

Eschweilera aguilarii S. A. Mori—JN222241, DQ388234, DQ417965,-; Aguilar 6521, Puntarenas Osa, Costa Rica, INB. *E. aguilarii*—JN222260, JN222059, JN221848, JN221754; Aguilar 11109, Puntarenas Osa, Costa Rica, INB. *E. aguilarii*—JN222264, JN222087, JN221874,-; Aguilar 11110, Puntarenas Osa, Costa Rica, INB. *E. alata* A. C. Sm.—JN222316, JN222051 & JN222052, JN221912,-; Prévost 4607, Forêt domaniale de Crique Plomb, French Guiana, NY. *E. alata*—JN222108, DQ388262, JN221842, JN221804; Prévost 4615, Forêt domaniale de Crique Plomb, French Guiana, NY. *E. albiflora* (DC.) Miers—JN222341, DQ388226, DQ417954,-; Mori 9199, Amazonus, Brazil, NY. *E. alvimii* S. A. Mori—JN222128, JN222061 & JN222062, JN221940, JN221762; Thomas 10300, Bahia, Brazil, NY. *E. alvimii*—JN222127, JN222101 & JN222102, JN221939,-; Morim 2634, Brazil, NY. *E. amazoniciformis* S. A. Mori—JN222172 & JN222173, JN222070, JN221981,-; Mori 27244, Amazonus, Brazil, NY. *E. amazoniciformis*—JN222142, JN222071, JN221982, JN221816; Mori 27270, Amazonus, Brazil, NY. *E. amplexifolia* S. A. Mori—JN222280, JN222018, JN221884, JN221791; Hernández 262, Colón, Panama, NY. *E.*

amplexifolia—JN222227 & JN222228, JN222081,-, JN221859; Hernández 263, Colón, Panama, NY. *E. andina* (Rusby) J. F. Macbr.—JN222106 & JN222107, DQ388229, DQ417956, JN221745; Pitman 5892, Napo Orellana, Ecuador, NY. *E. antioquensis* Dugand & Daniel—JN222206, JN607442, JN221964, JN221760; Acevedo 1321, Antioquia Frontino, Colombia, MO. *E. apiculata* (Miers) A. C. Sm.—JN222281, JN222034, JN221921, JN221799; Mori 25897, Piste de St. Elite, French Guiana, NY. *E. atropetiolata* S. A. Mori—JN222167, JN222065, JN221974,-; Mori 27225, Manaus Amazonas, Brazil, NY. *E. atropetiolata*—JN222117, JN222075, JN221978, JN221771; Mori 27237, Manaus Amazonas, Brazil, NY. *E. biflava* S. A. Mori—JN222318, JN222084, JN221954,-; Aguilar 11103, Puntarenas Osa, Costa Rica, INB. *E. biflava*—JN222319, JN222085, JN221849,-; Aguilar 11104, Costa Rica, INB. *E. biflava*—JN222261, JN222011, JN221850,-; Aguilar 11111, Costa Rica, INB. *E. biflava*—JN222298, JN222024 & JN222025, JN221856, JN221756; Aguilar 11123, Costa Rica, INB. *E. biflava*—JN222262, JN607443, JN221851,-; Aguilar 11124, Costa Rica, INB. *E. calyculata* Pittier—JN222282, JN222019, JN221860, JN221792; Toribio 78, Colón, Panama. *E. caudiculata* R. Knuth—JN222337,-,-,-; Aulestia 817, Carchi, Ecuador, NY. *E. caudiculata*—JN222338,-,-, JN221785; Clark 7156, Esmeraldas San Lorenzo, Ecuador, NY. *E. bracteosa* (Poepp. ex O. Berg) Miers—JN222207, JN222068, JN221979, JN221772; Mori 27239, Manaus Amazonas, Brazil, NY. *E. cyathiformis* S. A. Mori—JN222168, JN222066, JN221975, JN221831; Mori 27229, Manaus Amazonas, Brazil, NY. *E. chartaceifolia* S. A. Mori—JN222301, JN222003, JN221904,-; Mori 24088, Saül, French Guiana, NY. *E. chartaceifolia*—JN222248, JN222014 & JN222015, JN221923, JN221748; Mori 25556, Nouragues Field Station, French Guiana, NY. *E. chartaceifolia*—JN222322, JN222080, JN221924,-; Mori 25676, Camp Arataï on Arataye River, French Guiana, NY. *E. chartaceifolia*—JN222332, DQ388231, DQ417959,-; Prévost 4498, Piste de St. Elite, French Guiana, NY. *E. collina* Eyma—JN222254, DQ388232, DQ417960, JN221802; Mori 25145, Guiana Pic Maté cho, French, NY. *E. collina* Eyma—JN222315,-, JN221885,-; Prévost 4588, Montagnes Plomb, French Guiana, NY. *E. congestiflora* (R. Benoist) Eyma—JN222324, DQ388225, DQ417961, JN221824; Molino 2019, Paracou, French Guiana, NY. *E. congestiflora*—JN222317, JN222031, JN221873, JN221826; Mori 25766, Nouragues Field Station, French Guiana, NY. E. coriacea (DC.) S. A. Mori—JN222211, JN222103 & JN222104, JN221861,-; Hernández 271, Colón, Panama, NY. *E. coriacea* (DC.)—JN222302, JN607445, JN221845,-; Mori 24084, Saül, French Guiana, NY. *E. coriacea* (DC.)—JN222303, DQ388242, DQ417966, JN221822; Mori 25420A, Nouragues Field Station, French Guiana, NY. *E. decolorans* Sandwith—JN222304, JN222027, JN221886, JN221740; Mori 24494, Potaro-Siparuni, Guyana, NY. *E. decolorans*—JN222305, JN222077, JN221888,-; Mori 25451, Nouragues Field Station, French Guiana, NY. *E. decolorans*—JN222193, DQ388247, DQ417963,-; Mori 25452, French Guiana, NY. *E. grandiflora* (Aubl.) Sandwith—JN222311, DQ388251, DQ417964, JN221807; Mori 25435, Nouragues Field Station, French Guiana, NY. *E. hondurensis* Standl.—JN222263, JN222037, JN221852, JN221757; Aguilar 11128, Puntarenas Osa, Costa Rica, INB. *E. integrifolia* (Ruiz & Pav. ex Miers) R. Knuth—JN222320, JN222017, JN221953,-; Cornejo 8018, Guayas, Ecuador, NY. *E. integrifolia*—JN222283,-, JN221798, JN221862; Hernández 314, Veraguas Santa Fé, Panama, NY. E. jacquelyniae S. A. Mori—JN222223, JN222041, JN221863, JN221793; Hernández 315, Panamá, Panama, NY. *E. juruensis* R. Knuth—JN222205, DQ388242, DQ417966,-; Daly 10998, Acre, Brazil, NY. *E. laevicarpa* S. A. Mori—JN222284, JN222016, JN221875, JN221753; Mori 24325, Saül, French Guiana, NY. *E. longirachis* S. A. Mori—JN222266, JN607444, JN221936,-; Aguilar 7966, Costa Rica. *E. longirachis*—JN222265, DQ388266, DQ417968, JN221781; Aguilar 7967, Costa Rica. *E. mexicana* T. Wendt, S. A. Mori & Prance—JN222178 & JN222179, DQ388269, DQ417969,-; T. L. Wendt 4180, Veracruz Jesús Carranza, Mexico, NY. *E. micrantha* (O. Berg) Miers—JN222288,-, JN221876,-; Clark 4209. *E. micrantha*—JN222285, JN222001, JN221905,-; Mori 24711, Saül, French Guiana, NY. *E. micrantha*—JN222323, DQ388248, DQ417970,-; Mori 25448, Nouragues Field Station, French Guiana, NY. *E. micrantha*—JN222286, JN222056 & JN222057, JN221925,-; Mori 25652, Trésor Nature Reserve, French Guiana, NY. *E. micrantha*—JN222287, JN222032, JN221864, JN221790; Mori 25931, Patawa, French Guiana, NY. *E. nana* (O. Berg) Miers—JN222175 & JN222176, JN222098, JN221984,-; Potascheff 1, Mato Grosso, Brazil. *E. nana*—JN222148 & JN222149, DQ388271, DQ417971, JN221747; Teixeira 0874, Brazil, NY. *E. neei* S. A. Mori—JN222145, DQ388253, DQ417972,-; Aguilar 6517, Puntarenas Osa, Costa Rica, CR. *E. ovalifolia* (DC.) Nied.—JN222158 & JN222159, JN607446, JN221938, JN221761; Navarro 1759, Cochabamba, Bolivia, NY. *E. ovata* (Cambess.) Mart. ex Miers—JN222239, DQ388224, DQ417974, JN221821; Thomas 111060, Bahia, Brazil, NY. *E. pachyderma* CuatrE.—JN222187, JN607447,-,-; Acevedo 6881, Choco Nuqúi, Colombia, NY. *E. panamensis* Pittier—JN222267, JN222042, JN221853,-; Aguilar 11106, Puntarenas Osa, Costa Rica, CR. *E. panamensis*—JN222268, JN222035, JN221854,-; Aguilar 11107, Puntarenas Osa, Costa Rica, CR. *E. panamensis*—JN222269, JN221988, JN221855, JN221755; Aguilar 11121, Puntarenas Osa, Costa Rica, CR. *E. parviflora* (Aubl.) Miers—JN222289, JN222044, JN221887, JN221743; Mori 25437, Nouragues Field Station, French

Guiana, NY. *E. parviflora*—JN222290, DQ388223, DQ417975,-; Mori 25458, French Guiana, NY. *E. parvifolia* Mart. ex DC.—JN222212, JN222033, JN221865, JN221752; Mori 27043A, Manaus Amazonas, Brazil, NY. *E. parvifolia*—JN222186, JN222072, JN221952,-; Mori 27277, Brazil, NY. *E. pedicellata* (Rich.) S. A. Mori—JN222306,-, JN221889,-; Mori 24085, Saül, French Guiana, NY. *E. pedicellata*—JN222240, JN222004, JN221903,-; Mori 24381, Potaro-Siparuni, Guyana, NY. *E. pedicellata*—JN222313, JN222026, JN221916, JN221825; Mori 25597, Camp Arataï on Arataye River, French Guiana, NY. *E. pseudodecolorans* S. A. Mori—JN222165 & JN222166, JN222074, JN221973, JN221769; Mori 27224, Manaus Amazonas, Brazil, NY. *E. rankiniae* S. A. Mori—JN222169 & JN222170, JN222067, JN221976, JN221815; Mori 27333, Manaus Amazonas, Brazil, NY. *E. rimbachii* Standl.—JN222249, DQ388233, DQ417977,-; Clark 6380, Carchi Tulcan, Ecuador, NY. *E. rimbachii*—JN222111 & JN222112, DQ388235, DQ417978, JN221810; Stahl 5930, Los Rios Samama, Ecuador. *E. sagotiana* Miers—JN222244, JN222076, JN221935,-; Mori 24493, Potaro-Siparuni, Guyana, NY. *E. sagotiana*—JN222312, DQ388249, DQ417979,-; Mori 25470, Nouragues Field Station, French Guiana, NY. *E. sagotiana*—JN222291, JN222010, JN221877, JN221784; Mori 25712, Camp Arataï on Arataye River, French Guiana, NY. *E. sclerophylla* Cuatrec.—JN222129, JN607448, JN221941, JN221763; Gentry 53722, Valle del Cauca Buenaventura, Colombia, NY. *E. sessilis* A. C. Sm.—JN222229 & JN222230, JN222048, JN221866, JN221795; Galdames 5779, Panamá, Panama, NY. *E. simiorum* (Benoist) Eyma—JN222190, DQ388227, DQ418980,-; Mori 25507, Nouragues Field Station, French Guiana, NY. *E. simiorum*—JN222147,-, JN221928,-; Prévost 4250, Piste de St. Elite, French Guiana, NY. *E. simiorum*—JN222113, DQ388243, DQ417981, JN221779; Sabatier 4804, Mont Grand Matoury, NY. *E. subglandulosa* (Steud. ex O. Berg) Miers—JN222307, JN222099, JN221906,-; Mori 24380, Potaro-Siparuni, Guyana, NY. *E. tenuifolia* (O. Berg) Miers—JN222182 & JN222183, DQ388255, DQ417982, JN221746; Ferreira 135, Manaus Amazonas, Brazil, NY. *E. tessmannii* R. Knuth—JN222208 & JN222209, DQ388268, DQ417983, JN221780; Mori 25642, Madre de Dios, Peru, NY. *E. tetrapetala* S. A. Mori—JN222157, JN607449, JN221967,-; Sant'Ana 316, Bahia, Brazil, NY. *E. tetrapetala*—JN222156, JN607450, JN221966, JN221828; Hatschbach 48060, Brazil, NY. *E. truncata* A. C. Sm.—JN222171, JN222095, JN221977, JN221770; Mori 27234, Manaus Amazonas, Brazil, NY. *E. wachenheimii* (R. Benoist) Sandwith—JN222231 & JN222232, JN221991 & JN221992, JN221891,-; Mori 25570, Nouragues Field Station, French Guiana, NY. E. *wachenheimii*—JN222293, JN222050, JN221894,-; Mori 25591, Camp Arataï on Arataye River, French Guiana, NY. *E. wachenheimii*—JN222233 & JN222234, JN222047, JN221900, JN221782; Mori 25664, French Guiana, NY. *E. wachenheimii*—JN222253, DQ388254, DQ417984,-; Prévost 4252, Piste de St. Elite, French Guiana, NY. *E.* sp.—JN222213, JN222082, JN221868, JN221797; Hernández 193, Veraguas Santa Fé, Panama, NY. *E.* sp.—JN222273, JN222012, JN221857,-; Aguilar 11140, Puntarenas Osa, Costa Rica, INB. *E.* sp.—JN222343, JN222043, JN221913,-; Mori 25577, Trésor Nature Reserve, French Guiana, NY. *E.* sp.—JN222214, JN221989 & JN221990, JN221899,-; Mori 25645, French Guiana, NY. *E.* sp.—JN222292, JN222009, JN221901, JN221783; Mori 25649, French Guiana, NY. *E.* sp.—JN222242, DQ388264, DQ417990,-; Aguilar 6572, Puntarenas Osa, Costa Rica, CR. *E.* sp.—JN222270, JN222083, JN221878,-; Aguilar 11102, Puntarenas Osa, Costa Rica, CR. *E.* sp.—JN222271, JN222058, JN221922,-; Aguilar 11105, Puntarenas Osa, Costa Rica, CR. *E.* sp.—JN222272, JN222049, JN221879,-; Aguilar 11112, Puntarenas Osa, Costa Rica, CR.

Grias peruviana Miers—JN222215, DQ388178, DQ417999,-; Clark 6426, Zamora-Chinchipe Zamora, Ecuador, NY.

Gustavia grandibracteata Croat & S. A. Mori—JN222216,-, JN221867,-; Hernández 261, Panamá, Panama, NY. G. speciosa (R. Knuth) DC.—JN173348, DQ388204, DQ418009,-; Stahl 5902, Los Rios Samama, Ecuador.

Lecythis alutacea (R. Knuth) S. A. Mori—JN222188, DQ388244, DQ418011, JN221803; Mori 24622, Potaro-Siparuni, Guyana, NY. *L. ampla* Miers—JN222329, DQ388238, DQ418012, JN221665; Aguilar 7958, Costa Rica. *L. ampla*—JN222152, JN607451, JN221897, JN221666; Aguilar 7968, Costa Rica. *L. ampla*—JN222115, JN607452, JN221846, JN221667; Aguilar 7970, Costa Rica. *L. ampla*—JN222327, JN222038, JN221898, JN221668; Aguilar 7975, Costa Rica. *L. barnebyi* S. A. Mori—JN222200, JN607453, JN221858, JN221830; Mori 27228, Manaus Amazonas, Brazil, NY. *L. brancoensis* (R. Knuth) S. A. Mori—JN222185, JN607454, JN221832,-; Hoffman 1084, Upper Takutu-Upper Essequibo, Guyana, NY. *L. chartacea* O. Berg—JN222294, DQ388209, DQ418013,-; Mori 25364, Emerald Jungle Village, French Guiana, NY. *L. chartacea*—JN222217, JN221993 & JN221994, JN221869, JN221789; Mori 26485, Paracou, French Guiana, NY. *L. confertiflora* (A. C. Sm.) S. A. Mori—JN222218, JN222002, JN221927, JN221673; Mori 24320, Saül, French Guiana, NY. *L. confertiflora*—JN222309, DQ388210, DQ418014, JN221677; Mori 25411, Nouragues Field Station, French Guiana, NY. *L. confertiflora*—JN222247, JN607455,-,-; Prévost 4597, Montagnes Plomb, French Guiana, NY. *L. corrugata* Poit.—JN222219, DQ388211, DQ418015, JN221805; Mori 24265, Saül, French Guiana, NY. *L. corrugata*—JN222274, JN222060,

JN221908,-; Mori 24271, French Guiana, NY. *L. corrugata*—JN222275, JN607456, JN221962,-; Mori 25730, Saut Athanase tourist camp, French Guiana, NY. *L. lanceolata* Poir.—JN222191,-,-, JN221672; de Carvalho 5824, Bahia, Brazil, NY. *L. lanceolata*—JN222243, DQ388213, DQ418020,-; Prance25917, São Paulo, Brazil, NY. *L. gracieana* S. A. Mori—JN222164, JN222064, JN221768,-; Van Roosmalen L-79, Manaus Amazonas, Brazil, NY. *L. holcogyne* (Sandwith) S. A. Mori—JN222295, JN222006, JN221896,-; Prévost 4505, Station de la Piste de St. Elite, French Guiana, NY. *L. holcogyne*—JN222245, DQ388212, DQ418016,-; Prévost 4508, Station de la Piste de St. Elite, French Guiana, NY. *L. holcogyne*—JN222246, DQ388236, DQ418017, JN221811; Prévost 4511, Station de la Piste de St. Elite, French Guiana, NY. *L. idatimon* Aubl.—JN222310, DQ388214, DQ418018, JN221806; Mori 25430, Nouragues Field Station, French Guiana, NY. *L. idatimon*—JN222276, DQ388215, DQ418019,-; Mori 25498, French Guiana, NY. *L. idatimon*—JN222325, JN607458, JN221932,-; Mori 25745, L'Auberge des Orpailleurs, French Guiana, NY. *L. idatimon*—JN222326, JN607459,-,-; Mori 25754, Trésor Nature Reserve, French Guiana, NY. *L. idatimon*—JN222296, JN607457, JN221880,-; Prévost 4776, Cayenne, French Guiana, NY. *L. lurida* (Miers) S. A. Mori—JN607475, JN607460, JN221958,-; Prance 23702, Amazonas, Brazil, NY. *L. minor* Jacq.—JN222235 & JN222236, JN221995 & JN221996, JN221895,-; Motley 2895, Oahu Island, Hawaii, NY. *L. minor*—JN222297, JN222021, JN221881,-; de Sedas 219, Panamá, Panama, NY. *L. ollaria* P. Loefl.—JN222177, JN222045 & JN222046, JN221957, JN221788; Aymard11847, Portuguesa, Venezuela, NY. *L. parvifructa* S. A. Mori—JN222203, JN222092, JN221946, JN221765; Mori 27231, Manaus Amazonas, Brazil, NY. *L. persistens* Sagot subsp. *aurantiaca* S. A. Mori—JN222220, JN607461, JN221909,-; Mori 24724, Saül, French Guiana, NY. *L. persistens* Sagot subsp. *aurantiaca*—JN221742, DQ388218, DQ418023, JN222251; Mori 25436, Nouragues Field Station, French Guiana, NY. *L. persistens* Sagot subsp. *persistens*—JN222250,-,-,-; Mori 25391, Nouragues Field Station, French Guiana, NY. *L. persistens* subsp. *persistens*—JN222221, JN222039, JN221892,-; Mori 25523, French Guiana, NY. *L. persistens* subsp. *persistens*—JN222255,-, JN221933,-; Mori 25651, Trésor Nature Reserve, French Guiana, NY. *L. persistens* subsp. *persistens*—JN222277, DQ388239, DQ418024, JN221744; Prévost 4285, Matiti, French Guiana, NY. *L. pisonis* Cambess.—JN222196,-,-, JN221671; Cid 1696, Pará, Brazil, NY. *L. pisonis*—JN222132 & JN222133, JN607462, JN221969, JN221700; Mori 27268, Manaus Amazonas, Brazil, NY. *L. pisonis*—JN222130 & JN222131, JN607463, JN221970, JN221703; Mori 27272, Manaus Amazonas, Brazil, NY. *L. pisonis*—JN222199, JN222090,-, JN221708; Mori 27290, Manaus Amazonas, Brazil, NY. *L. pisonis*—JN222136 & JN222137, JN607465, JN221971, JN221709; Mori 27291, Manaus Amazonas, Brazil, NY. *L. pisonis*—JN222116, JN607464,-, JN221682; Prance23703, Pará Belém, Brazil, NY. *L. pisonis*—JN222119, JN607466, JN221942, JN221726; Smith 51, Brazil. *L. pisonis*—JN222120, JN607467, JN221943, JN221727; Smith 52, Brazil. *L. pisonis*—JN222121, JN607468, JN221944, JN221728; Smith 53, Brazil. *L. pisonis*—JN222122, JN607469, JN221955, JN221729; Smith 54, Brazil. *L. pisonis*—JN222197,-,-, JN221827; Thomas 10896, Bahia, Brazil, NY. *L. pneumatophora* S. A. Mori—JN222222, JN607470, JN221961, JN221751; Mori 25728, Saut Athanase tourist camp, French Guiana, NY. *L. pneumatophora* S. A. Mori—JN222237 & JN222238, JN607471,-,-; Mori 25748, Trésor Nature Reserve, French Guiana, NY. *L. pneumatophora* S. A. Mori—JN222252, DQ388220, DQ418025,-; Prévost 4261, Piste de St. Elite, French Guiana, NY. *L. poiteaui* O. Berg—JN222328, JN221997 & JN221998, JN221890,-; Mori 24178, Saül, French Guiana, NY. *L. poiteaui* O. Berg—JN222162 & JN222163, JN222073,-, JN221767; Mori 27279, Manaus Amazonas, Brazil, NY. *L. poiteaui* O. Berg—JN222336, JN222013, JN221847,-; Prévost 4502, Station de la Piste de St. Elite, French Guiana, NY. *L. prancei* S. A. Mori—JN222124, JN222091, JN221956, JN221764; Mori 27226, Manaus Amazonas, Brazil, NY. *L. prancei*—JN222126, JN607472, JN221949,-; Mori 27260, Manaus Amazonas, Brazil, NY. *L. retusa* Spruce ex O. Berg—JN222189,-, JN221972, JN221766; Mori 27273, Manaus Amazonas, Brazil, NY. *L. rorida* O. Berg—JN222192, JN222094, JN221950,-; Mori 27276, Manaus Amazonas, Brazil, NY. *L. rorida*—JN222160 & JN222161, JN222063, JN221951, JN221814; Mori 27278, Manaus Amazonas, Brazil, NY. *L. schwackei* (R. Knuth) S. A. Mori—JN222155, JN607473, JN221959, JN221759; Tameirão 2501, Minas Gerais, Brazil, NY. *L. tuyrana* Pittier—JN222335, JN222020, JN221882, JN221796; Sedas 216, Panamá, Panama, NY. *L. zabucajo* Aubl.—JN222340,-,-, JN221676; Mori 24287, Saül, French Guiana, NY. *L. zabucajo*—JN222333 & JN222334, JN222078, JN221910, JN221679; Mori 25472, Nouragues Field Station, French Guiana, NY. *L. zabucajo*—JN222198, JN222088,-, JN221702; Mori 27271, Manaus Amazonas, Brazil, NY. *L. zabucajo*—JN222146, JN607474, JN221911, JN221680; Prévost 4331, Matiti, French Guiana, NY. *L.* sp.—JN222344 & JN222345, JN221999 & JN222000, JN221749, JN221915; Mori 25582, French Guiana, NY. *L.* sp.—JN222134 & JN222135, JN222005, JN221914,-; Mori 25580, French Guiana, NY. *L.* sp.—JN222321, JN222100,-,-; Mori 25753, French Guiana, NY. *L.* sp.—JN222125,-, JN221948,-; Mori 27259, Manaus Amazonas, Brazil, NY. *L.* sp.