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THE UTILITY OF PLACENTATION IN THE CIRCUMSCRIPTION OF GENERA OF NEW WORLD LECYTHIDACEAE (BRAZIL NUT FAMILY)

SCOTT A. MORI
Institute of Systematic Botany
The New York Botanical Garden
Bronx, New York 10458-5126
smori@nybg.org

CAROL CAROLLO MATOS[1]
Institute of Systematic Botany
The New York Botanical Garden
Bronx, New York 10458-5126
carolcarollo@hotmail.com

YA-YI HUANG
Biodiversity Research Center
Academia Sinica
Taipei 11529, Taiwan
lecy.yhuang@gmail.com

NATHAN P. SMITH
Institute of Systematic Botany
The New York Botanical Garden
Bronx, New York 10458-5126
nathansmit@gmail.com

C. DE MORAES POTASCHEFF
Instituto de Biociência
Universidade Estadual Paulista
Rio Claro, São Paulo, BraSil
Caixa Postal 199, CEP 13506-900
carolpotas@yahoo.com.br

ABSTRACT

The utility of placentation in the circumscription of genera of New World Lecythidaceae (Brazil nut family). The placentation of the 16 known clades of New World Lecythidaceae and several species of Old World *Barringtonia* are illustrated and described. The authors conclude that the family possesses axile placentation but an SEM study of flower development may modify that conclusion. They also restrict the term placenta to all tissue derived from the same carpel to which the ovules are attached. The more basal genera are often defined by placental features as well as by morphological apomorphies and sometimes by molecular data. In contrast, *Eschweilera* and *Lecythis*, based on molecular data, are made up of three and five different clades, respectively. Of the three *Eschweilera* clades, the *Eschweilera tetrapetala* clade can be separated from the two other clades of the genus by having more than one row of ovules per locule. In contrast, the other two clades of *Eschweilera* (the *E. integrifolia* and *E. parvifolia* clades) posses a single row of ovules in each locule. We conclude that placental data support the segregation of the *E. tetrapetala* clade as a separate genus while the segregation of the latter two clades is not supported by placental data, even though morphological data support their separation at some taxonomic level. Within the currently circumscribed *Lecythis*, the *Lecythis pisonis*. and *L. corrugata* clades are supported by weak placental data; nevertheless, morphological and molecular data support recognizing them as distinct genera. The *Lecythis ollaria* clade, which includes the type species, is supported by morphological and molecular (100% bootstrap support) data and, if *Lecythis* were restricted to this clade, the genus would be reduced from 26 to three species. In contrast, the *L. poiteaui* and *L. chartacea* clades recovered in this study are not supported by placental or molecular data and morphological support

for these clades is weak. The *Bertholletia excelsa* clade is supported by placental, morphological, and molecular data but retaining it as a monotypic genus, recognizing the *L. ollaria* clade as a genus with three species, and segregating the *L. poiteaui* and *L. chartacea* clades into separate genera await further phylogenetic study because there is poor r6esolution among the clades of these groups of *Lecythis*. Although there may be additional placental features that help define genera, we conclude that they will only be accurately defined if serial sections and SEM developmental sequences are used in future studies. Finally, the relationship between New World and Old World Lecythidaceae through *Grias* is supported by placentation features that do not occur in other New World Lecythidaceae but that are present in species of *Barringtonia*.

Thompson (1921, 1927) was the first to use medial sections of flowers to show the structure and development of the androecium of New World Lecythidaceae and illustrated the placentation of selected actinomorphic- and zygomorphic-flowered species. His carefully prepared drawings illustrate placentation of species of the following genera: *Barringtonia*, *Grias*, *Cariniana* (as species of *Couratari*), *Couratari* (as species of *Lecythopsis*), *Couroupita* , and *Bertholletia*, which represent genera as circumscribed by Prance and Mori (1979) and Mori and Prance (1990). In addition, he studied *Lecythis zabucajo* Aubl., which belongs to the *L. pisonis* Cambess. clade of *Lecythis* as suggested by Huang et al. (in press), and *Asteranthos brasiliensis* Desf., which is now placed in the Scytopetalaceae (Tsou 1994; Appel 1996, 2004).

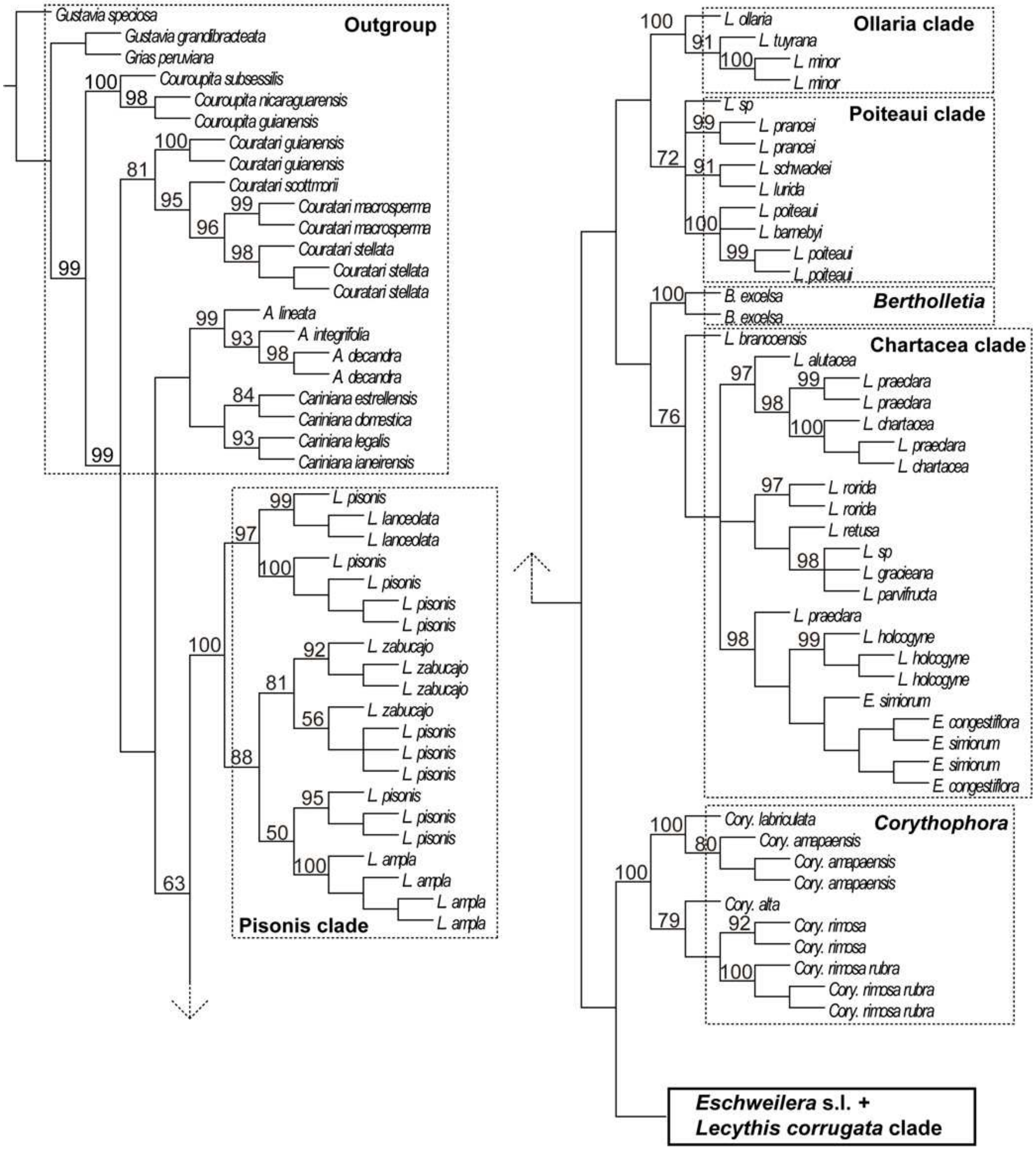
The meticulous studies of fruit development of *Couroupita guianensis* Aubl. published by Schoenberg (1983a, 1983b, 1983c) provide considerable information about placentation of one of the best known species of New World Lecythidaceae.

An important step forward in the knowledge of the placentation of Lecythidaceae was made by Tsou (1994) in her worldwide review of its embryology and the relationship of embryological features with reproductive morphology and systematics. This study also provided outstanding images of the placentation that show similarities of some Old World species with some New World species. For example, species of Old World *Abdulmajida* (placed in *Barringtonia* by Prance 2010, 2012), *Planchonia*, and *Barringtonia* possess placentae that are similar to those of the New World *Grias*, and the placentation of *Careya arborea* Roxb. is similar to some species of New World *Gustavia* (Tsou 1994). The pendulous ovules at the apex of the locules of the erstwhile *Abdulmajidia* are consistent with the transfer of its species into *Barringtonia*. In addition, Tsou and Mori (2007) studied androecial development, provided SEM images and images of sections of pickled flowers, and discussed the development of the ovaries of New World Lecythidaceae.

In contrast, Tsou's (1994) images of the placentation of the Old World *Foetidia oblique* Blume, *Petersianthus quadrialatus* Merr., and *Napoleonaea imperialis* P. Beauv. do not appear to have similarities with taxa of New World Lecythidaceae. A more detailed comparison between the placentation of Old World and New World Lecythidaceae might provide data that could shed light on the relationships between New and Old World genera of the family.

In spite of previous studies, placentation characters have been infrequently used for defining genera and preparing phylogenetic analyses of Lecythidaceae. Their main use has been in keys, but this has been limited to locule number and the type of placentae in *Couroupita guianensis*. On the hand cotyledon development is useful for distinguishing some taxa; i.e., in some genera the cotyledons are leaf-like (*Cariniana*, *Couroupita*, and *Couratari*), in another they are fleshy and irregular (*Gustavia*), and in the remaining genera there are no apparent cotyledons (*Bertholletia*, *Corythophora*, *Eschweilera*, *Grias*, and *Lecythis*) (Prance & Mori 1979, 1983; Mori & Prance 1990).

The purpose of the present study has been to determine the following for New World Lecythidaceae (1) type of placentation (axile or parietal), (2) nature of the placenta, (3) use of placentation features in the generic classification of New World Lecythidaceae, (4) use of placentation features in the clades recognized by Huang et al. (in press) and Mori et al. (in press), and (5) recommendations of the clades that we judge to be stable and those that might have to be recognized as separate taxa in the future. An example of a stable genus with distinct placentation features is *Grias* and of the latter is *Lecythis* (as defined by Prance & Mori 1979; Mori & Prance1990).



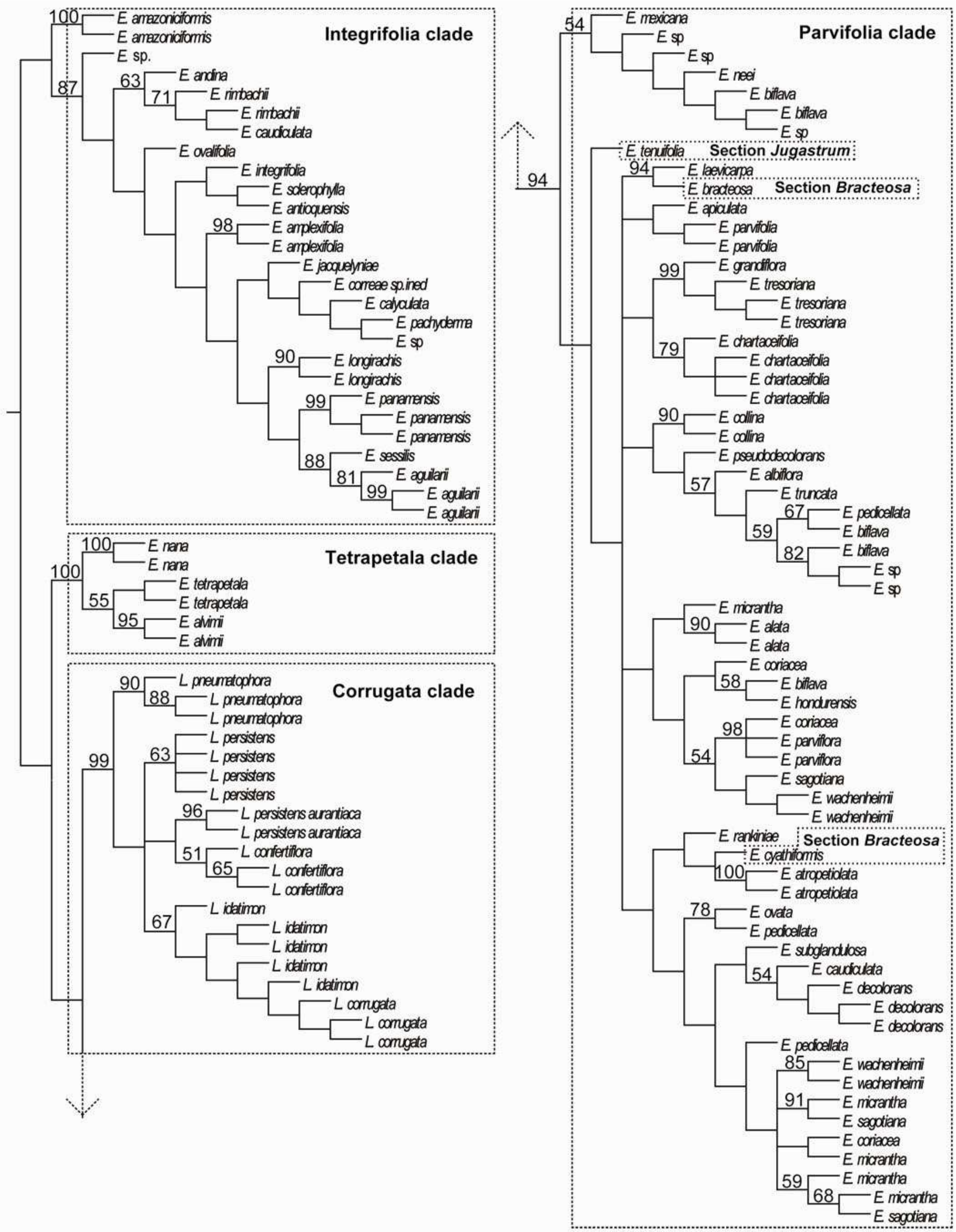


Figure 1A–1B. This cladogram represents a strict consensus of 66 most parsimonious (MP) trees based on total evidence. Bootstrap values (>50%) are given above the branches. The cladogram consists of the outgroup, the non-*Bertholletia* clades (*Gustavia*, *Grias*, *Couroupita*, *Cariniana*, *Allantoma*, *Couratari*) and the *Bertholletia* clades (*Lecythis pisonis*, *L. ollaria*, *Bertholletia excelsa*, *L. poiteaui*, *Corythophora*, *Eschweilera integrifolia*, *E. tetrapetala*, *L. corrugata*, and *Eschweilera parvifolia* clades). This figure was taken from Huang (2010).

Figure 1 provides an overview of the non-*Bertholletia* clade based on molecular data (Mori et al. 2007) and for the *Bertholletia* clade based on both molecular and morphological data (Huang 2010). Images of placental features are provided in Figures 2–26. Because of the difficulty in understanding the morphological features used to distinguish the clades of New World Lecythidaceae, we recommend reading and studying the plates of the clades in Huang et al. (in press) and Mori et al. (in press). The terminology used to describe Lecythidaceae can also be consulted on the Lecythidaceae Pages (Mori et al. 2010 onward).

METHODS

Buds from the pickled (usually in 50% or 70% ETOH) collection of Lecythidaceae at The New York Botanical Garden (NY) and from fresh flowers were hand sectioned in cross- and longitudinal sections (Figs. 3, 4). If pickled material was not available, buds from herbarium specimens were sectioned after being boiled in water with a few drops of detergent until they were soft. In many cases, buds are so damaged in the collecting process that they do not yield informative sections, especially if they are dried with too much pressure and heat. In contrast, buds that have been slowly dried in paper bags outside of the press usually assume their original form after boiling in water with several drops of dishwashing detergent. Each of the collections sectioned is vouchered by a herbarium collection listed in the figure legends. Those collections with specimens at The New York Botanical Garden are not indicated with the NY acronym while those archived in other herbaria are indicated by the acronyms of where they are stored (Thiers, 2014 onward).

The best results from cross-sections (Fig. 3) were obtained just below the apex or of the placentae—a section made at the very apex of the locule may not show the manner in which the ovules are inserted on the placenta and might not even show the septa joining at their inner apices. Likewise, a section at the base of the ovary might cut through a space in which there are no ovules. It is, however, useful to know if the ovules are attached all of the way along the placenta to the base of the locule. A longitudinal section that removes the outer wall of a locule was made to determine the number of columns and rows and the position of ovules on the placenta (Figs. 6–7). In addition a medial longitudinal section, cut down the middle of the ovary (this section should cut at least part of the style), was made to show the relationship of the placenta with the septum as well as the way the upper septum articulates with the lower septum (Fig. 2).

It is extremely difficult to section buds that are comparable with one another because it is hard to select buds that are at the same developmental stage and to make hand sections at the same location of the ovary. For these reasons, we only used characters that we evaluated as not changing significantly in spite of different bud sizes and different positions of the sections. Thus, we do not report absolute lengths and shapes but relate the size of a structure as a percentage of a larger structure (e.g., the length of the lower septum as a percentage of the overall length of the lower/upper septum. For example, Fig. 4I shows an upper septum longer than the lower septum, Figure 4G shows a lower septum longer than the upper septum, and Fig. 2K shows lower and upper septa equal in length. Other clades seem to lack upper septa (Fig. 4A, E, H) but these may have arms that extend upward from the lower septum along the stylar canal (Figs. 2J).

We sectioned a small number of flowers compared to the numbers of flowers found on an individual tree, on different individuals in a population, and on individuals from other populations Unfortunately, almost all characters vary to some extent; thus, a species with a 4-locular ovary almost always produces some flowers with 3- and 5-locular ovaries—and this varies within and between individuals. The greatest difficulty in circumscribing plant taxa is determining how much morphological (including placental) and molecular data variation is allowed before populations of individuals are assigned to a different taxon. All studies suffer, at least to some extent, because of small sample size.

The Huang et al. (in press) and the Mori et al. (in press) papers provide descriptions and plates of the morphological features of the 15 clades of New World Lecythidaceae currently recovered. The cladograms upon which this paper is based are found in Huang et al. (in press). Reading these papers in conjunction with this paper facilitates understanding of how placentation features relate to the generic classification of New World Lecythidaceae. A major problem with the most recent morphological and molecular analyses of Lecythidaceae is that many of the clades within the Bertholleita and non-Bertholletia clade are not resolved (Huang 2010; Huang et al., in press; Mori et al. 2007, in review) and it is likely that the resolution of the clades included in the currently circumscribed *Eschweilera* and *Lecythis* (Mori & Prance 1990) may change in such a way that splitting these two taxa into additional genera may not be justified. Therefore, we only recommend segregating the clades recovered in the most recent molecular studies (Huang et al., in press; Mori et al. 2007) into genera if the clades are strongly supported by both molecular and morphological data.

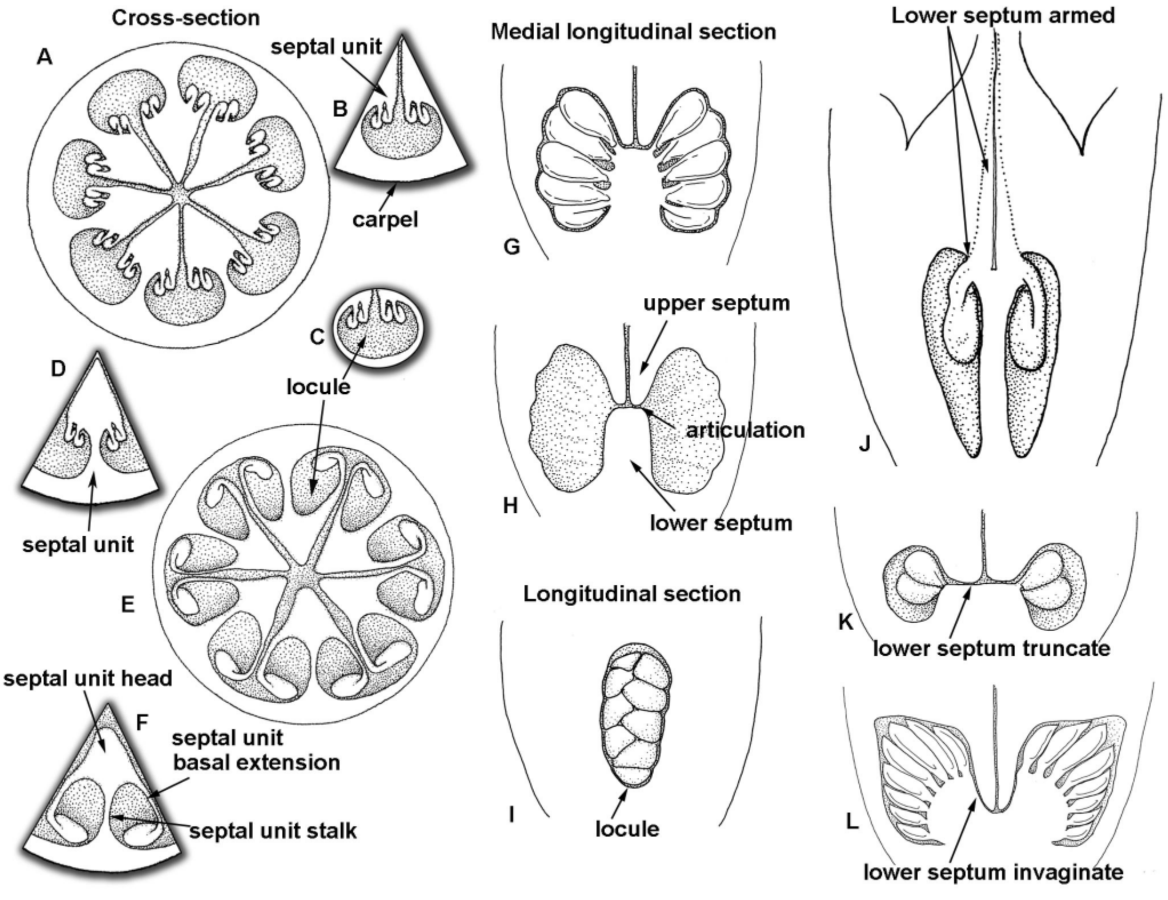


Figure 2. General placentation terms. A. Cross-section of an ovary with the septal units spear-shaped. B. One of seven carpels of the ovary illustrated in the preceding drawing. C. One of the six locules of the ovary as indicated by the arrow. D. One of the seven septal units of the ovary illustrated in the preceding drawing. Note that a septal unit consists of tissue from adjacent carpels. E. Cross-section of an ovary with long septal unit head basal extensions. F. One of the seven septal units illustrated in the A. G. Medial longitudinal section. Note that this type of section goes through the middle of the ovary and, thus, usually cuts at least part of the style (not visible here). H. The same as G but with the ovules removed. Note the upper and lower septa and the articulation between them. I. Longitudinal section that does not go through the middle of the ovary and only cuts off the outside of the ovary wall. This type of section is good for determining the number of rows and columns of ovules per locule. J. An armed lower septum. In species with this type of septum the upper septum is poorly developed or absent. K. A truncate lower septum possessing a flat apex. L. An invaginate lower septum in which the upper septum appears to push into the lower septum.

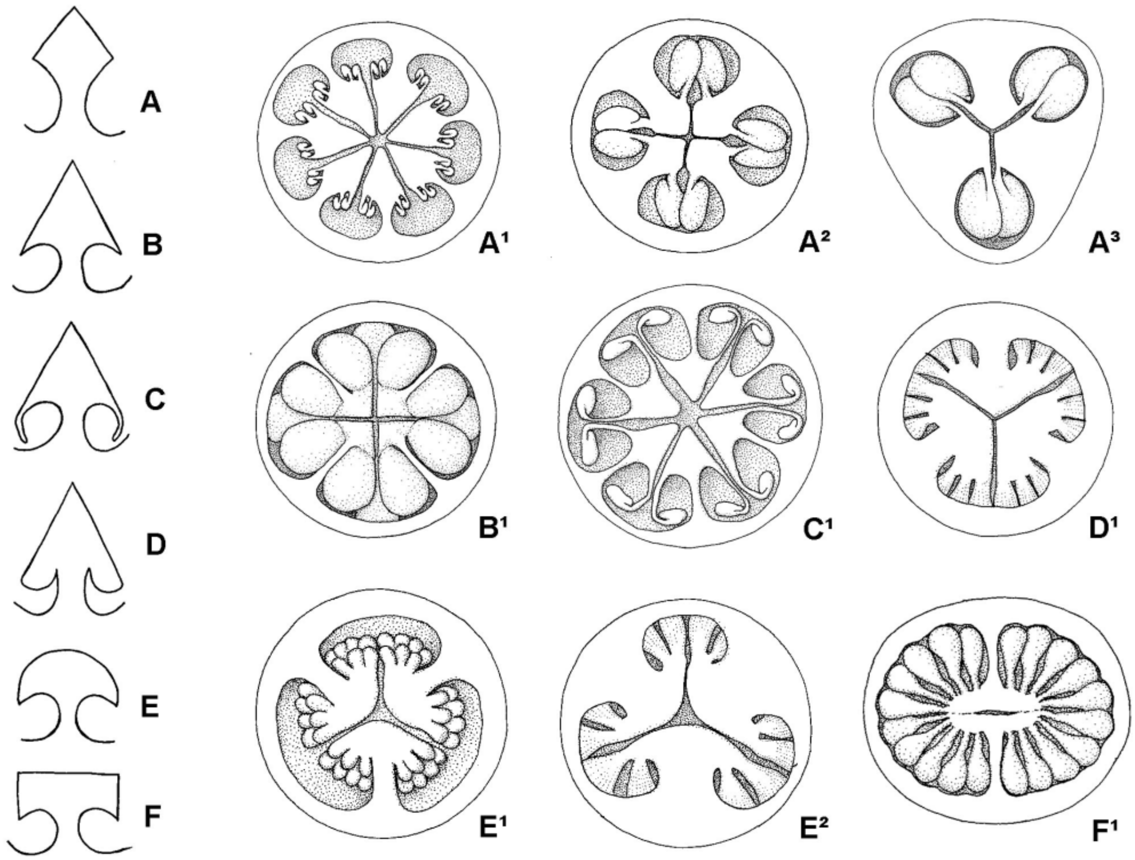


Figure 3. Septal unit heads as seen in cross-section. A. Spear-shaped septal unit head. A^1–A^3. Cross-sections of ovaries showing examples of spear-shaped septal unit heads. B. Arrowhead-shaped septal unit head. B^1. Cross-section of an ovary showing arrowhead-shaped septal unit heads with poorly developed septal unit basal extensions. C. Arrowhead-shaped septal unit head with well-developed septal unit basal extensions. C^1. Cross-section of an ovary with very long septal head basal extensions. D. Arrowhead-shaped septal unit head with thick basal extensions. D^1. A Cross-section of an ovary showing thick septal unit basal extensions. E. Anchor-shaped septal unit head. E^1–E^2. Cross-section of an ovary showing anchor-shaped septal unit heads. F. Anvil-shaped septal unit head. F^1. Cross-section of an ovary showing anvil-shaped septal unit heads.

RESULTS

In this section, we describe the placentation of the clades of Lecythidaceae as defined in Huang et al. (in press) and Mori et al. (in review) and summarize support for the clades based on molecular (Fig. 1) and morphological (Figs. 2–25) data. The clades are presented in alphabetic order. If a cited figure is found in another publication the reference to it is preceded by "see." For example "(see Fig. 21 in Huang 1990)."

***Allantoma* clade** (Fig. 7)

Ovary (3)4-locular. Septal units as seen in cross-section through placentae: spear-shaped (B–C). Locule orientation and width as seen in longitudinal section: vertical (E), width intermediate (E). Lower septum: truncate at apex (E), occupying ca. 50% of upper/lower septum length (E). Placentae as seen in longitudinal section: narrow columnar (E). Ovules as seen in cross- and longitudinal sections: not pendulous, not flattened, ca. 10–18 per locule, in 2 columns (B, C) and 5-8 rows, (D–E), inserted along most of length of lower septum, with short ovule-free area below ovule insertion (E).

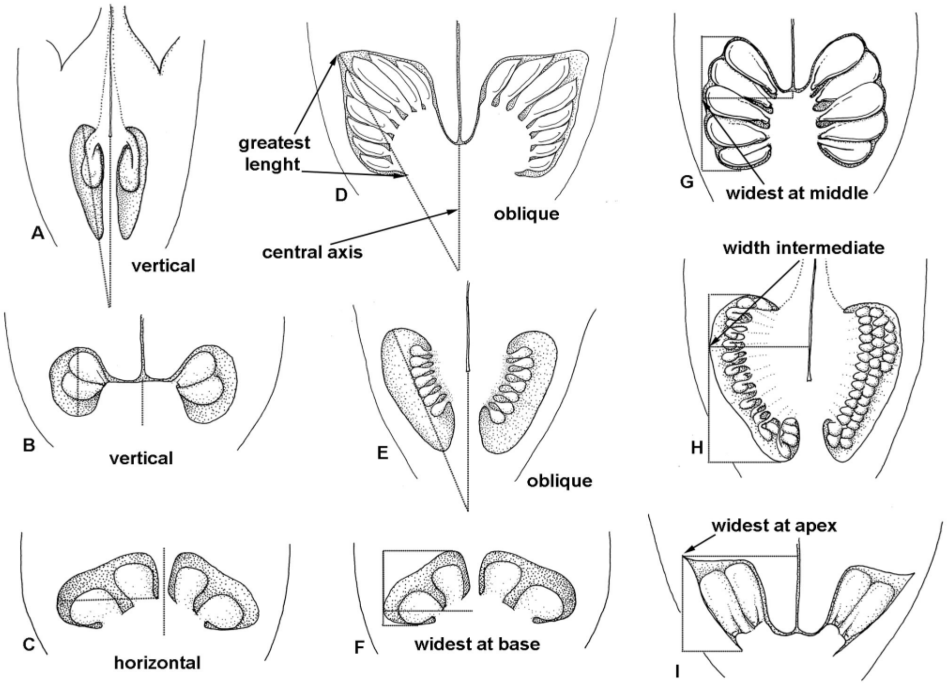


Figure 4. Locule orientation seen in medial longitudinal section. A. Vertically oriented locules. B. Vertically oriented locules. C. Horizontally oriented locules. D. Obliquely oriented locules. E. Obliquely oriented locules. F. Locules widest at base. G. Locules widest at middle. H. Locules with intermediate width (between the middle and apex of the locule). I. Locules widest at apex.

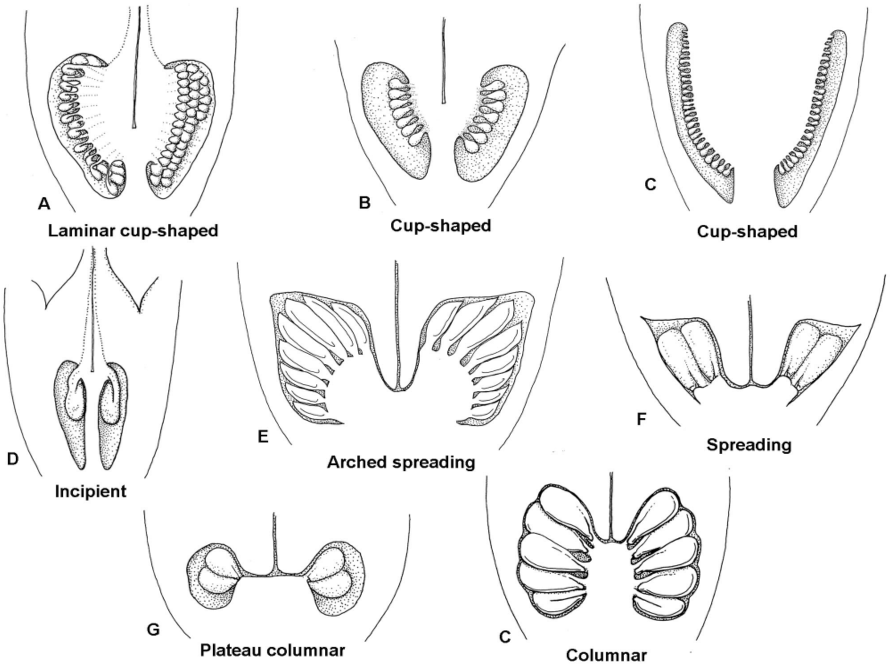


Figure 5. Placentation types as seen in medial longitudinal section. A. Laminar cup-shaped (e.g., in the *Couroupita* clade). B─C. Cup-shaped (in the *Gustavia* clade). D. Incipient (in the *Grias* clade). E. Arched spreading (e.g., in the *Couratari* clade). F. Spreading (e.g., in the *Corythophora, Eschweilera*, *Lecythis chartacea and Lecythis corrugata* clades). G. Plateau columnar (e.g., in the *Bertholletia excelsa* clade). H. Columnar (e.g., in the *Allantoma*, *Cariniana, Lecythis pisonis*, *and Lecythis poiteaui* clades).

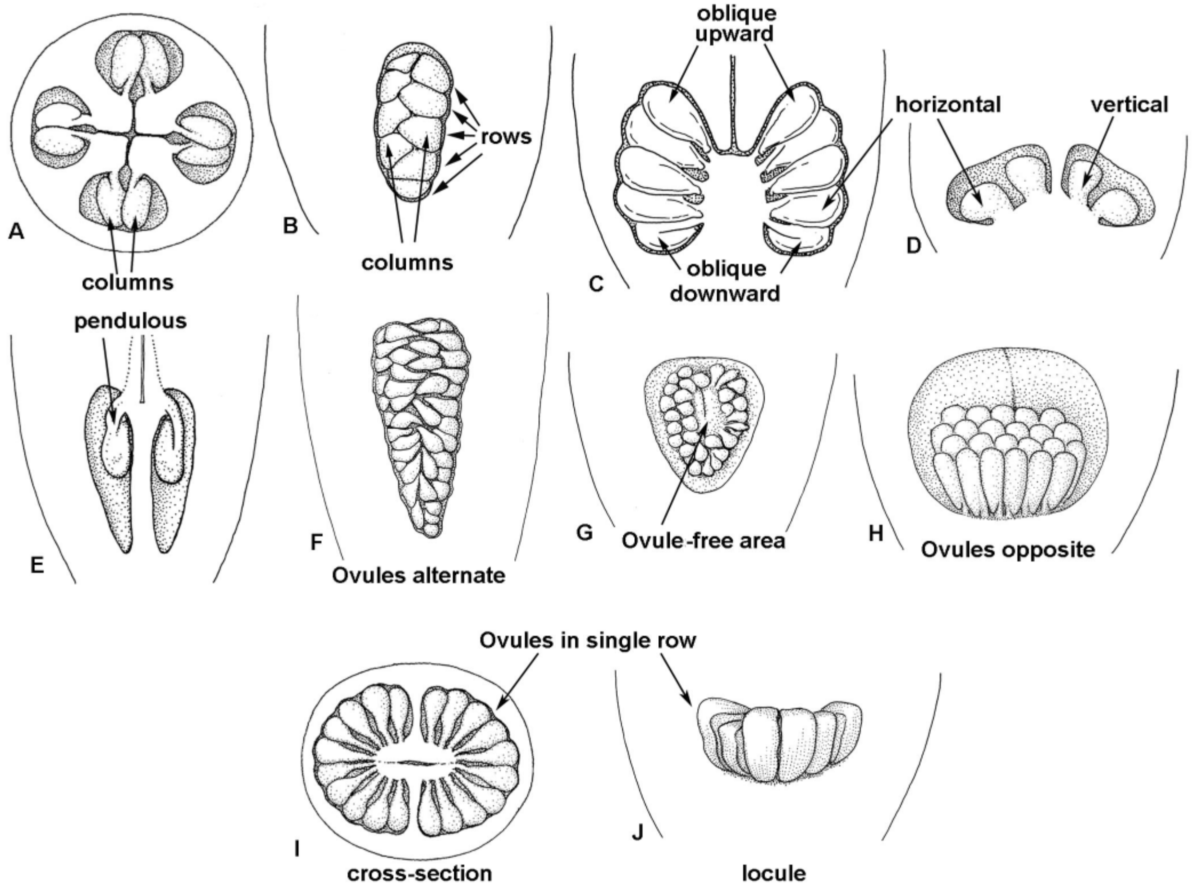


Figure 6. Ovule attachment and orientation as seen in cross and longitudinal sections. A. Cross-section showing ovules in 2 columns. B. Longitudinal section showing ovules in 1–2 columns and 5 rows. The ovules are alternately arranged. C. Medial longitudinal section showing the upper ovules oriented obliquely upward, some of the middle ovules oriented horizontally, and the lower ovules oriented obliquely downward. D. Longitudinal section showing vertically and obliquely upward oriented ovules. E. Medial longitudinal section showing pendulous ovules (a feature restricted to species of *Barringtonia* and *Grias*). F. Longitudinal section showing numerous, alternately arranged ovules. G. Longitudinal section showing an ovule-free area in the middle (found in some species of *Gustavia*. H. Longitudinal section showing ovules in 6 columns and 4 rows. I. Cross-section showing the ovules in ca. 10 columns and a single row (a feature restricted to the *Eschweilera integrifolia* and *Eschweilera parviflora* clades). J. Longitudinal section showing the ovules in 6 columns and a single row per locule.

Barringtonia clade (Fig. 8)

Ovary 4-locular. Septal units as seen in cross-section through placentae: arrowhead-shaped (B) or spear-shaped (G), the basal extensions thick (B) or absent (G). Locule orientation and width as seen in longitudinal section: vertical (D, I–J), width intermediate (D, I). Lower septum: truncate? or slightly arched? at apex, occupying 100% of lower/upper septum length (D–E, I–J). Placentae as seen in cross- and longitudinal sections: incipient (D–E, I–J). Ovules as seen in cross- and longitudinal sections: mostly pendulous (D–E, I–J), sometimes horizontal (D, apical row), not flattened, ca. 2–5 per locule, in 2 columns (B–C and 1 row (D–E, I–J); inserted at apex of lower septum, with long ovule-free area below ovule insertion (Figs. D–E, I–J).

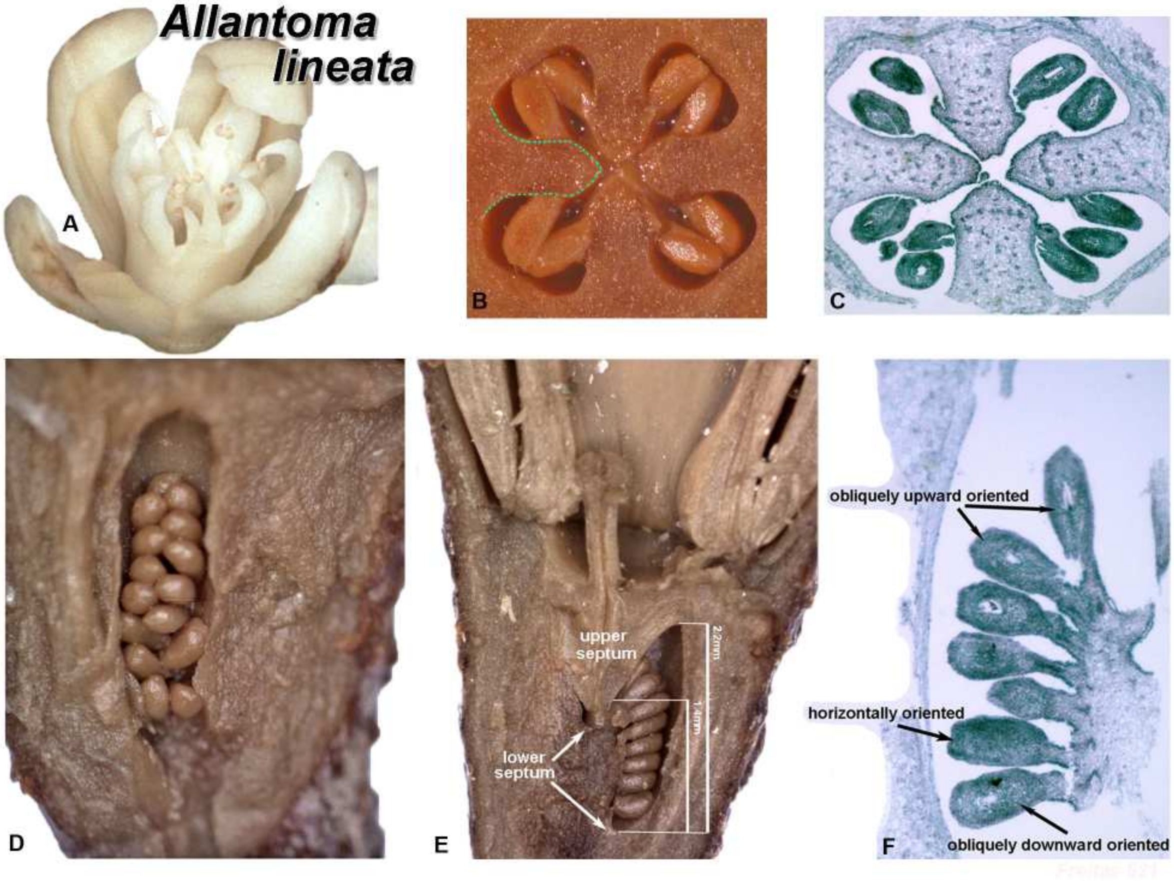


Figure 7. *Allantoma* clade. A. *Allantoma integrifolia* (Ducke) S.A. Mori, Y.-Y. Huang & Prance. B─F. *Allantoma lineata.* A. Flower. B. Cross-section of an ovary showing 2 columns of ovules per locule. C. Cross-section of an ovary showing spear-shaped septal unit heads. D. Longitudinal section of an ovary showing ca.16 ovules in 2 columns. E. Medial longitudinal section showing the columnar placenta and articulation between the lower and upper septa. F. Longitudinal section of an ovary showing ovule orientation. A. Photo by M. Hopkins based on *PA 89* at INPA. B, D–E. Photos by C.M. C. M. de Potascheff and C. Carollo Matos based on *Freitas 521*. F. Photos by C. Carollo Matos based on *Prance 17549*.

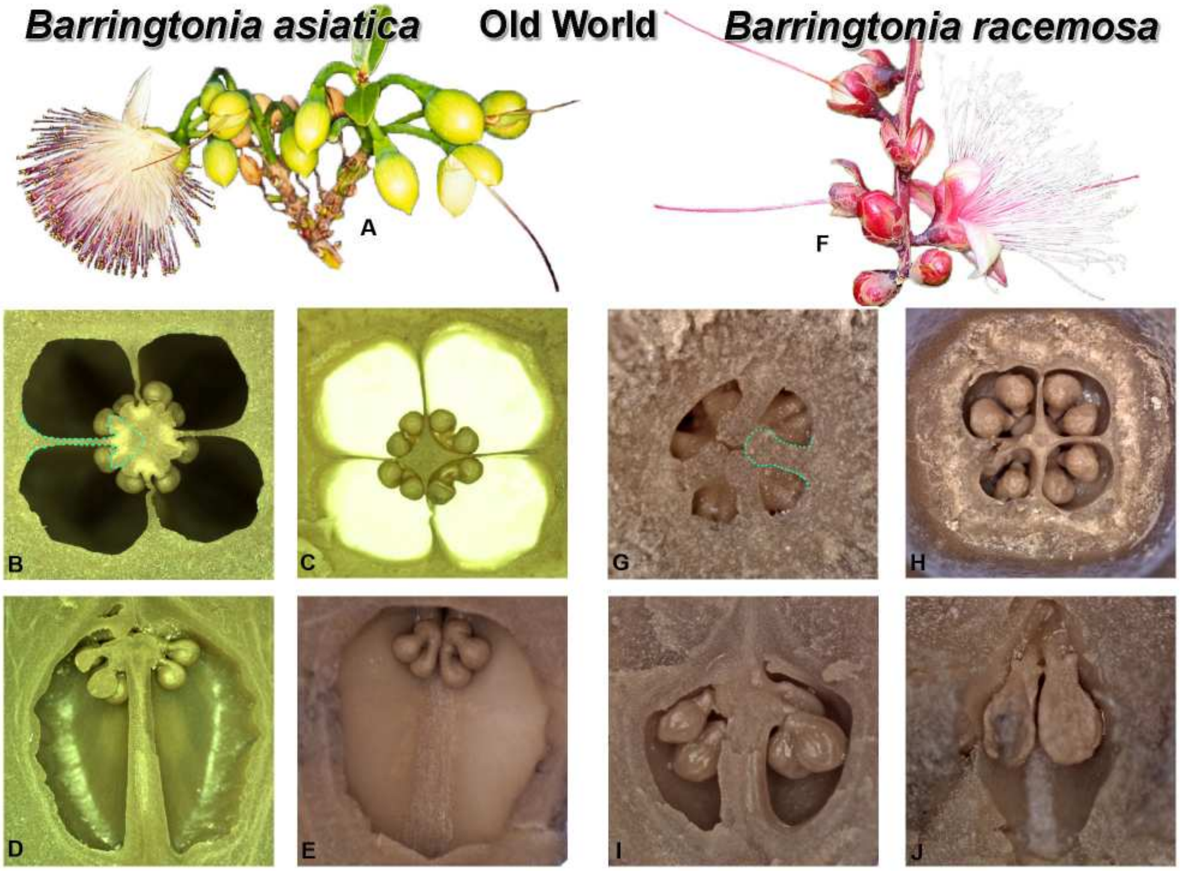


Figure 8. *Barringtonia* clade. A–E. *Barringtonia asiatica* (L.) Kurz. F–J. *Barringtonia racemosa* (L.) Sprengel. A. Part of an inflorescence showing buds and an open flower. B. Cross-section of an ovary (apical view) showing arrowhead-shaped septal unit heads and thin septal head stalks. C. Cross-section of an ovary (basal view) showing 4 locules. D. Medial longitudinal section of an ovary showing 2 locules with pendulous ovules. E. Longitudinal section of an ovary showing a locule with 4 ovules attached to the incipient placentae. F. Part of an inflorescence showing buds, an open flower, and 2 flowers that have lost their petals. G. Cross-section of an ovary (apical view) above point of ovule attachment. H. Cross-section of an ovary (basal view) showing pendulous ovules and arrowhead-shaped septal unit heads. I. Longitudinal section of an ovary showing the pendulous ovules attached at the apex of the lower septum and the incipient placentae. J. Longitudinal section of an ovary showing a locule with 2 pendulous ovules. A. Photo by Mori based on *Mori et al. 25013* (collection is a photograph only). B–E. Photo by C. Carollo Matos based on an unvouchered collection by an unknown collector from Indonesia. F. Photo by C.A. Gracie based an unvouchered tree cultivated at the Royal Botanic Gardens, Kew. G–J. Photos by C. Carollo Matos based on an unvouchered collection by C.-H. Tsou in Sri Lanka.

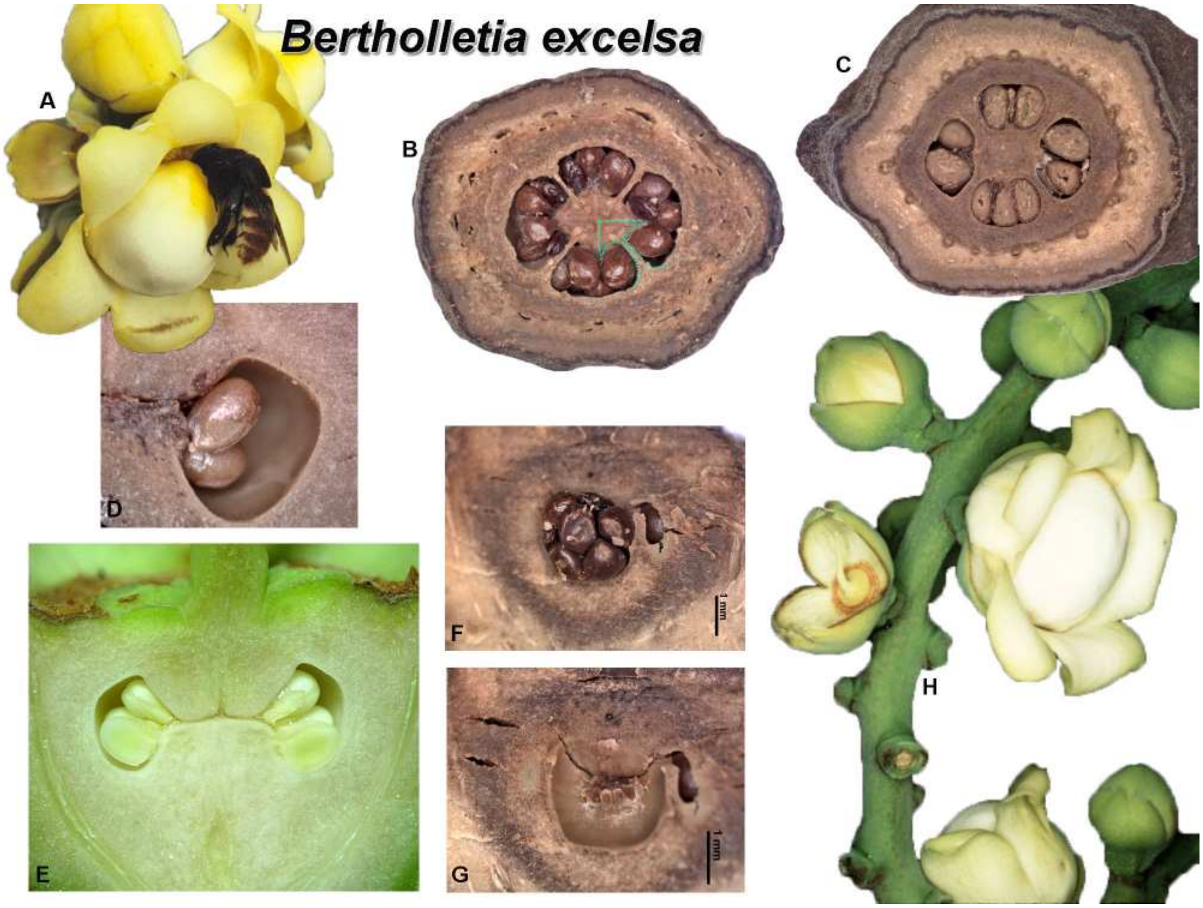


Figure 9. B*ertholletia excelsa* clade. A–H. *Bertholletia excelsa*. A. Flowers and buds. B. Cross-section of an ovary (apical view) showing the arrowhead-shaped septal unit heads. C. Cross-section of an ovary (basal view) showing the 4 locules of this species. D. Longitudinal section of an ovary showing the ovule attachments. E. Medial longitudinal section showing the columnar plateau placentae and the truncate apex of lower septum. F. Longitudinal section of an ovary showing a locule and some of the ovules. G. Ovules removed from locule to show funicular scars. H. Part of an inflorescence. A. Photo by A.J. Henderson based on *J.F. Ramos P20205*. B–D, F. Photos by C. Carollo Matos based on *Freitas 511* (assumed to be at INPA). E. Photo by N.P. Smith based on *N.P. Smith 397* (at INPA). H. Photo by Mori based on *Mori et al. 17503*.

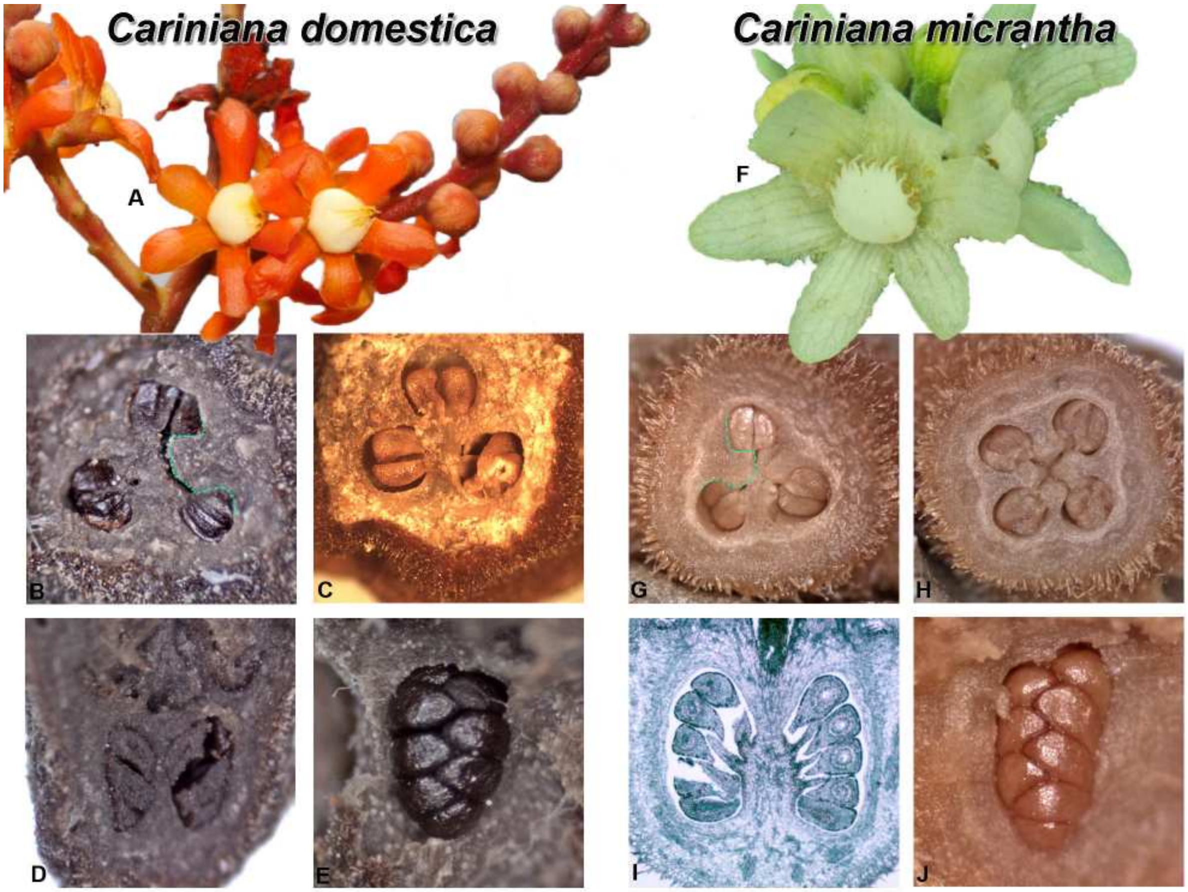


Figure 10. *Cariniana* clade. A–E. *Cariniana domestica* (Mart.) Miers. F–J. *Cariniana micrantha* Ducke. A. Flowers and buds. B. Cross-section of an ovary (apical view) showing the spear-shaped septal unit heads. C. Cross-section of an ovary (basal view) showing 3 locules and 2 columns of ovules. D. Longitudinal section of an ovary of *Cariniana domestica* showing lower septum and ovule orientations. E. Longitudinal section of an ovary showing a locule and alternately arranged ovules. F. Flowers. G. Cross-section of an ovary (basal view) showing the spear-shaped septal unit heads, 3-locular ovary, and 2 columns of ovules. H. Cross-section of an ovary (basal view) showing 4-locular ovary from same collection as in G. with a 3-locurlar ovary. I. Medial longitudinal section of an ovary showing the columnar placentae and ovules extending nearly along the full length of the lower septum. J. Longitudinal section of an ovary showing alternately arranged ovules. A. Photo by M. Nee based on *Nee 58876*. B, D–E. Photos by C. Carollo Matos based on *Prance et al. 7967*. C. Photo by N.P. Smith based on *Prance et al. 8834*. F. Photo by Mori based on *Mori 20191*. G–J. Photos by C. Carollo Matos based on *Mori 20191*.

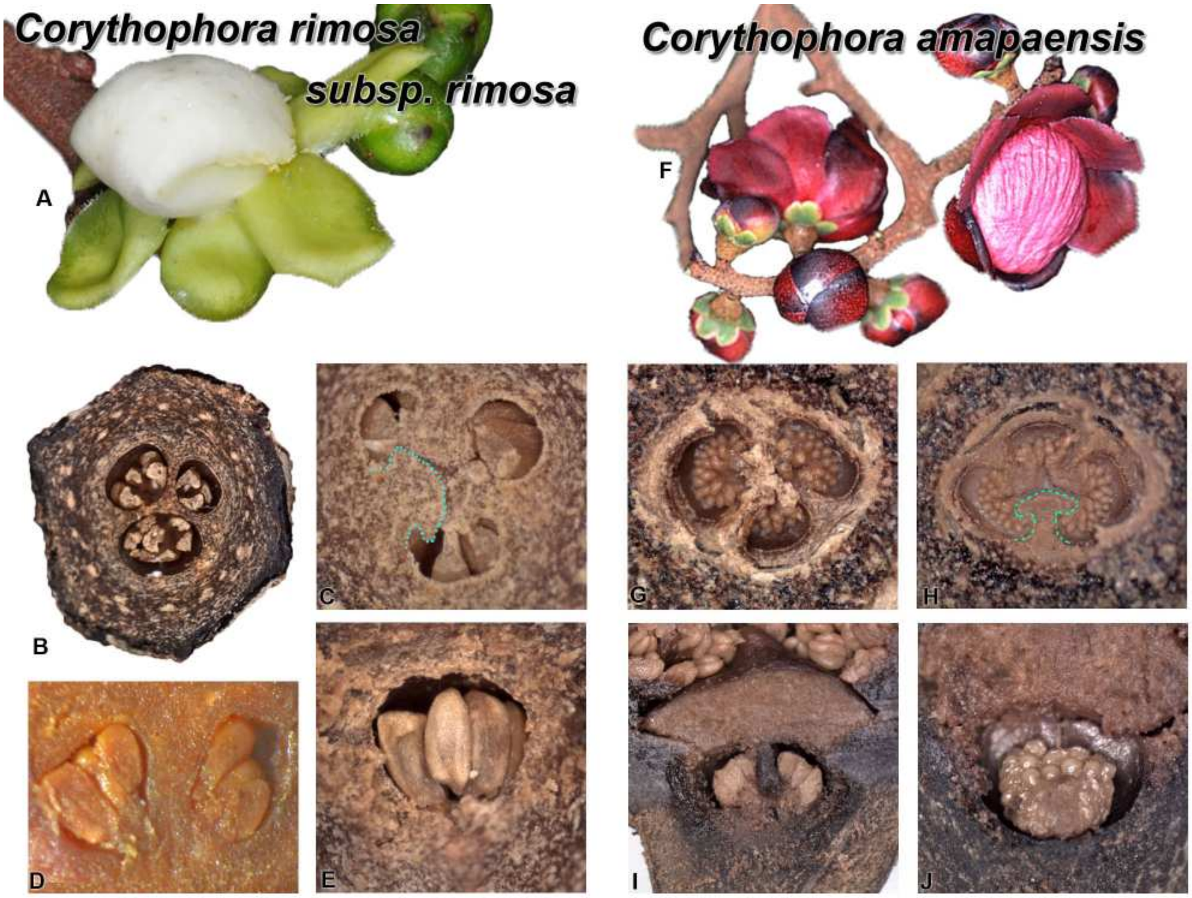


Figure 11. *Corythophora* clade. A–E. *Corythophora rimosa* W. Rodrigues subsp. *rimosa*. F–J. *Corythophora amapaensis* Pires ex S.A. Mori & Prance. A. Flower and buds. B. Cross-section of an ovary (apical view) showing 3 locules. C. Cross-section of an ovary (basal view) showing anchor-shaped septal unit heads. D. Medial longitudinal section of an ovary showing the spreading placentae. E. Longitudinal section of an ovary showing the attachment of the ovules and the spreading placenta. F. Flower and buds. G. Cross-section of an ovary (apical view) showing 3 locules and numerous ovules. H. Cross-section of an ovary (apical view) showing the anchor-shaped septal unit heads. I. Medial longitudinal section of an ovary showing the spreading placentae. J. Longitudinal section of an ovary showing the attachment of the ovules. A. Photo by M.J.G. Hopkins based on *Smith & Hopkins 367* (at INPA). B–C, E. Photos by C. Carollo Matos based on Prance et al. 10417. D. Photo by C.M.de Potascheff based on *Mori & Pereira 20525*. F. Photos by C. Gracie based on *Mori et al. 22640*. G–J. Photos by C. Carollo Matos based on *Mori et al. 18550*.

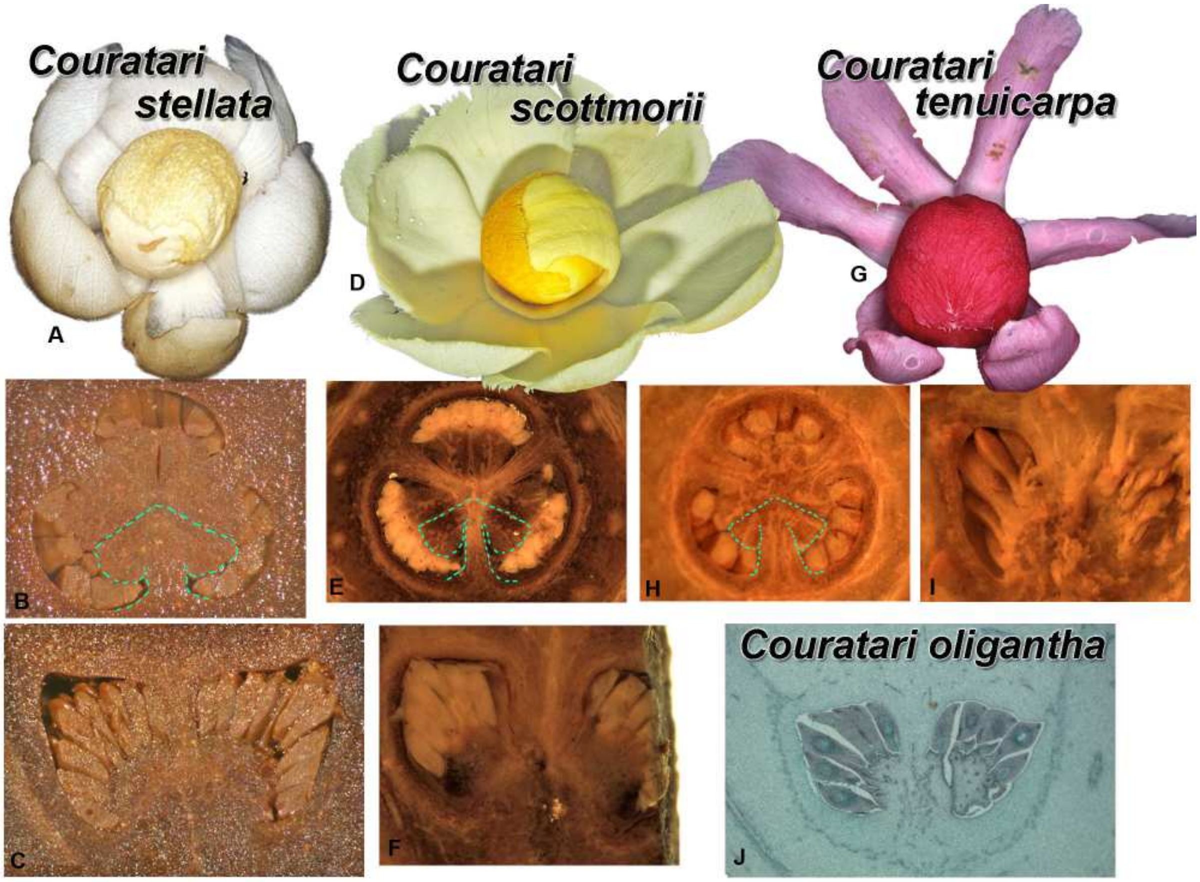


Figure 12. *Couratari* clade. A–C. *Couratari stellata* A.C. Sm. D–F. *Couratari scottmorii* Prance. G–I. *Couratari tenuicarpa* A.C. Sm. J. *Couratari oligantha* A.C. Sm. A. Flower. B. Cross-section of an ovary (basal view) showing the arrowhead-shaped septal unit heads, the thick septal unit head basal extensions, and the 3-locular ovary. *C.* Longitudinal section of an ovary showing the placentae arched spreading. D. Flower. E. Cross-section of an ovary (apical view) showing the arrowhead-shaped septal unit heads, the thick septal unit head basal extensions, and the 3-locular ovary. F. Medial longitudinal section of an ovary showing the placentae arched spreading and invaginated lower septum. G. Flower. H. Cross-section of an ovary (basal view) showing the arrowhead-shaped septal unit heads, the thick septal unit head basal extensions, and the 3-locular ovary. I. Longitudinal section of an ovary showing the placentae arched spreading and invaginated lower septum. J. Medial longitudinal section of an ovary showing the flattened ovules. A. Photo by C. Gracie based on *Mori et al. 22750*. B–C. Photos by C.M. C. M. de Potascheff based on *Prance et al. 22900*. D. Photo by R. Aguilar based on *Aguilar 10259*. E–F. Photo by N.P. Smith based on pickled flowers of *Cornejo 8043* (from same tree as *Aguilar 11108* at CR). G. Photo by C. Gracie based on an unvouchered tree. H–I. Photos by N.P. Smith based on *Mori et al. 20331*. J. Photo by C. Carollo Matos based on *Plowman 12546*.

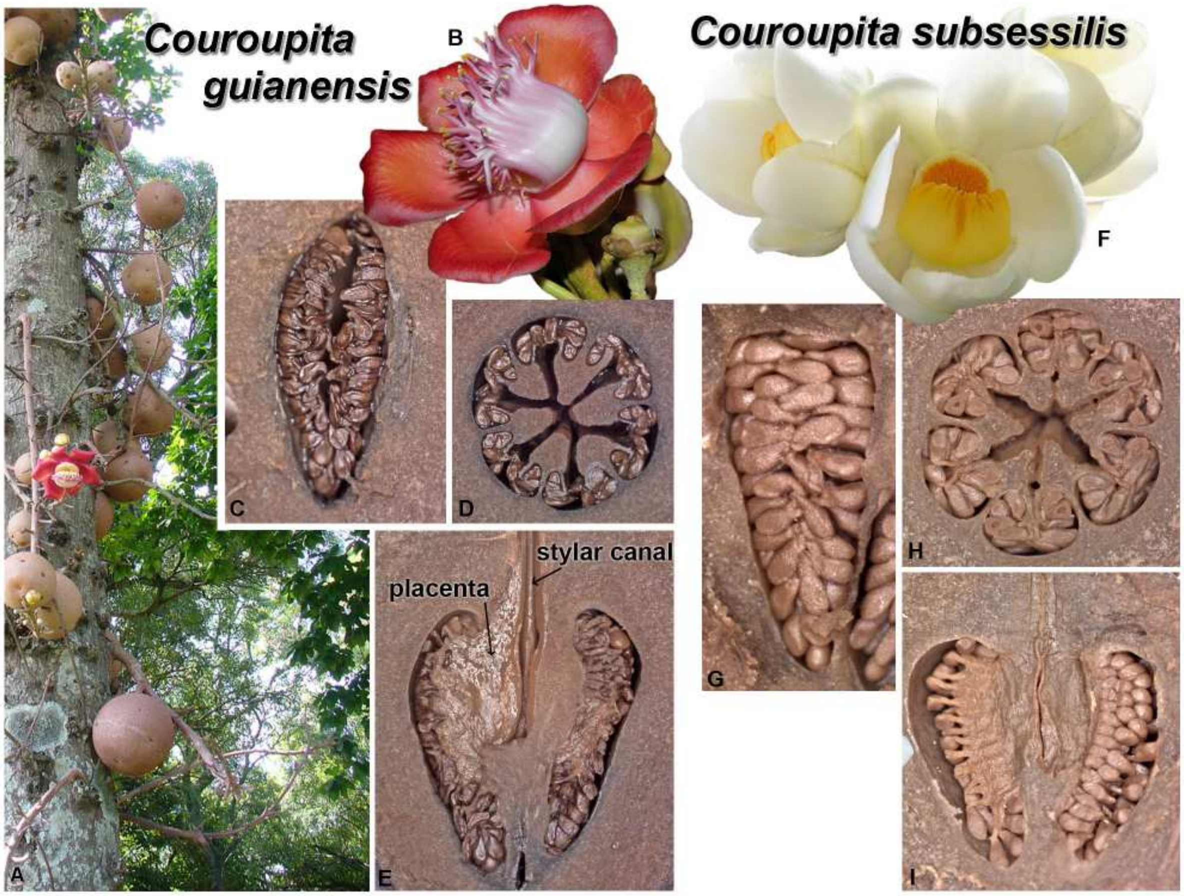


Figure 13. *Couroupita* clade. A–E. *Couroupita guianensis*. F–I. *Couroupita subsessilis*. A. Tree bearing fruits and flower on the trunk. B. Flower. C. Longitudinal section of an ovary showing the locule and numerous ovules with many rows. D. Cross-section of an ovary (apical view) showing the arrowhead-shaped septal heads and the long septal head basal extensions. E. Medial longitudinal section of an ovary showing the placentae laminar cup-shaped. F. Flowers. G. Longitudinal section of an ovary showing the locule and numerous alternately arranged ovules. H. Cross-section of an ovary (apical view) showing the arrowhead-shaped septal unit heads and the long septal head basal extensions. I. Medial longitudinal section of an ovary showing the laminar placentae laminar cup-shaped. A. Photo by S. Zona based on an unvouchered tree. B. Photo by R. Aguilar based on *R. Aguilar 13743* (at CR). C–E. Photos by C. Carollo Matos based on an unvouchered pickled collection made by C─H. Tsou from the Fairchild Tropical Garden, Florida, USA. F. Photo by M. Geschneider based on an unvouchered plant cultivated in the conservatory of the University of Ulm, Germany. G–I. Photos by C. Carollo Matos based on *Lleras 16883* from Amazonas, Brazil.

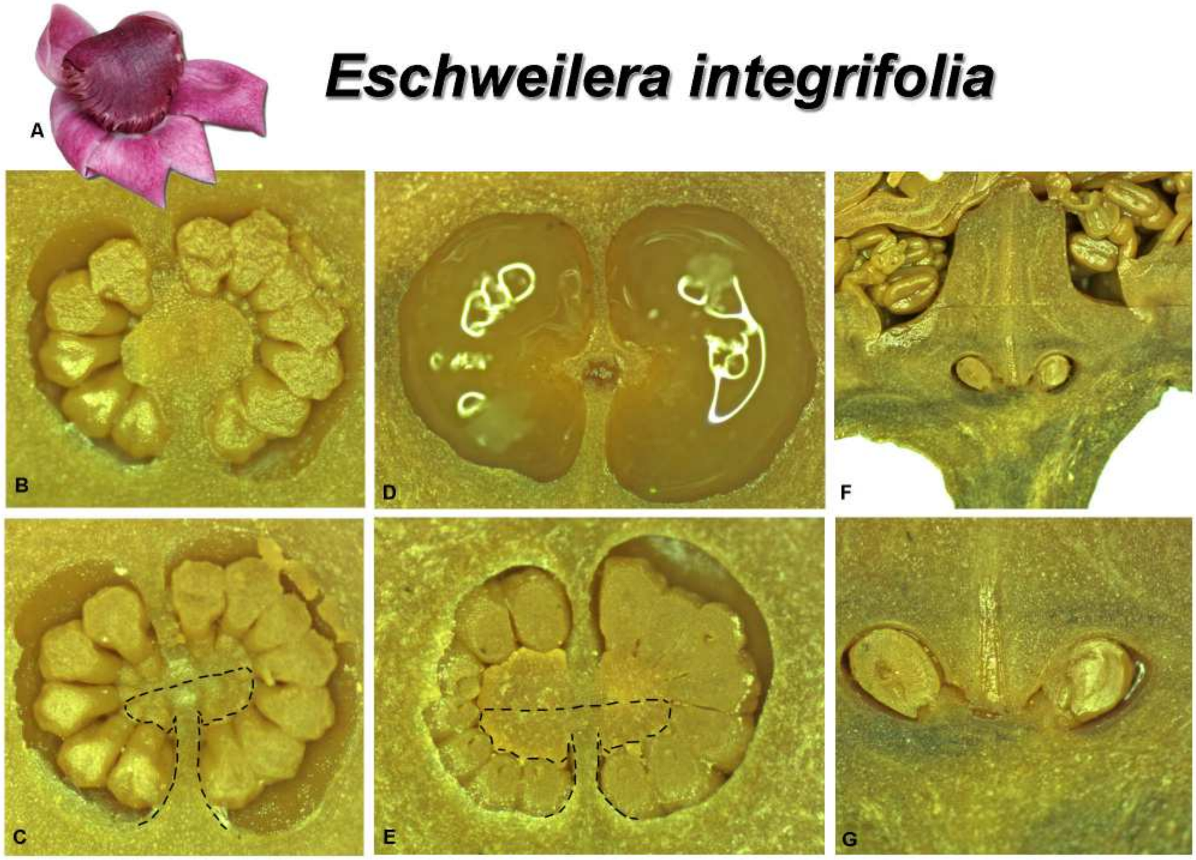


Figure 14. *Eschweilera integrifolia* clade. Plate 1: A─G. *Eschweilera integrifolia*. A. Flower. B. Cross-section of an ovary (apical view) showing the 2-locular ovary each with a single row of ovules. C. Cross-section of an ovary (apical view) showing the anvil-shaped septal unit heads. D. Cross-section of an ovary (basal view) with the ovules removed and showing the upper septum (= above the placentae) and the septal articulations. E. Cross-section of an ovary (basal view) showing the lower septum and the anvil-shaped septal unit. F. Medial longitudinal section showing the spreading placentae. G. Medial longitudinal section showing the invaginate lower septum. A. Photo by X. Cornejo based on *Cornejo & Bonifaz 8018.* B–G. Photos by C. Carollo Matos based on *Cornejo & Bonifaz 8018.*

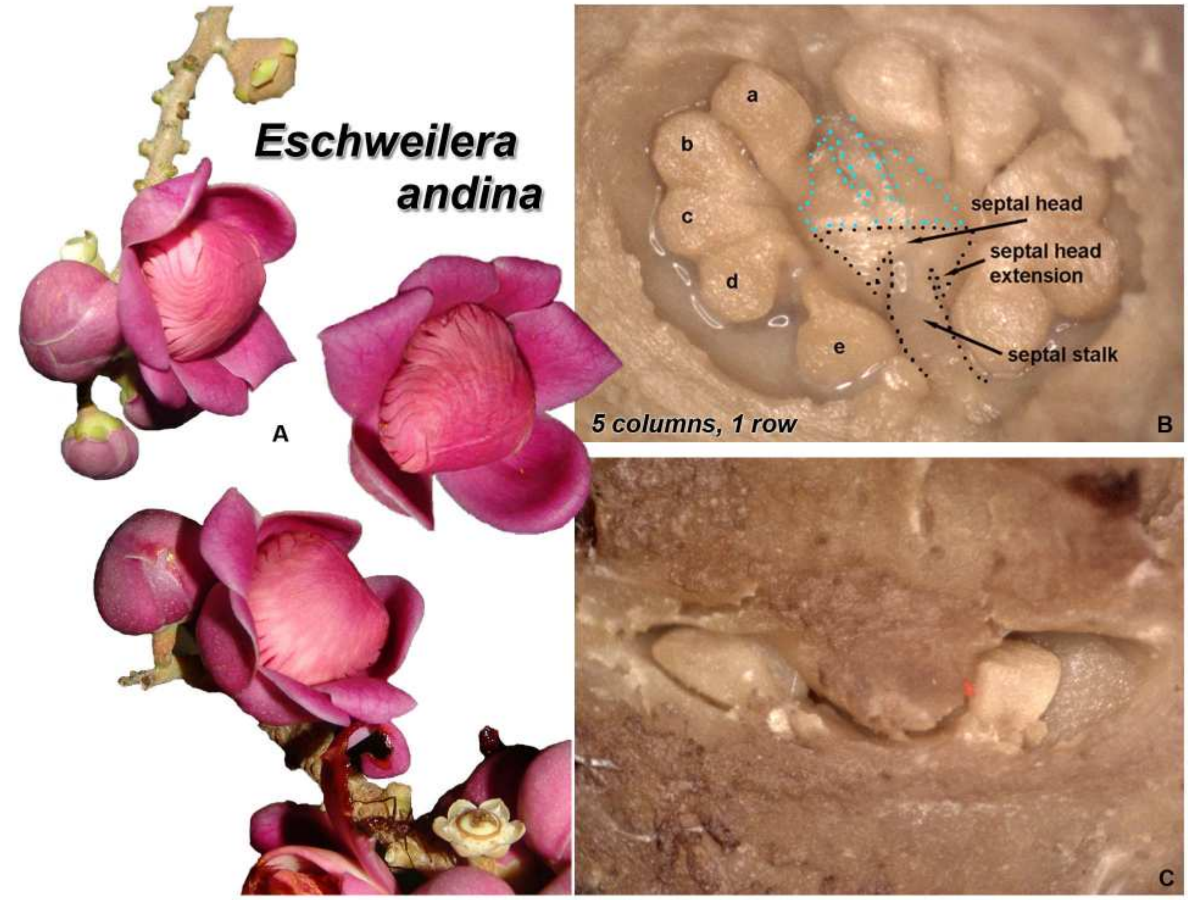


Figure 15. *Eschweilera intregrifolia* clade. Plate 2: A─C. *Eschweilera andina* (Rusby) J.F. Macbr. A. Buds, flowers, and very young fruit. B. Cross-section of an ovary (apical view) showing the anvil-shaped septal unit heads. C. Longitudinal section of an ovary showing the spreading placentae and invaginated lower septum. A. Photo by C. Davidson based on *Araujo-Murakami 1110* from La Paz, Bolivia. B–C. Photo by C. Carollo Matos based on *Pitman 5892* from Napo, Ecuador.

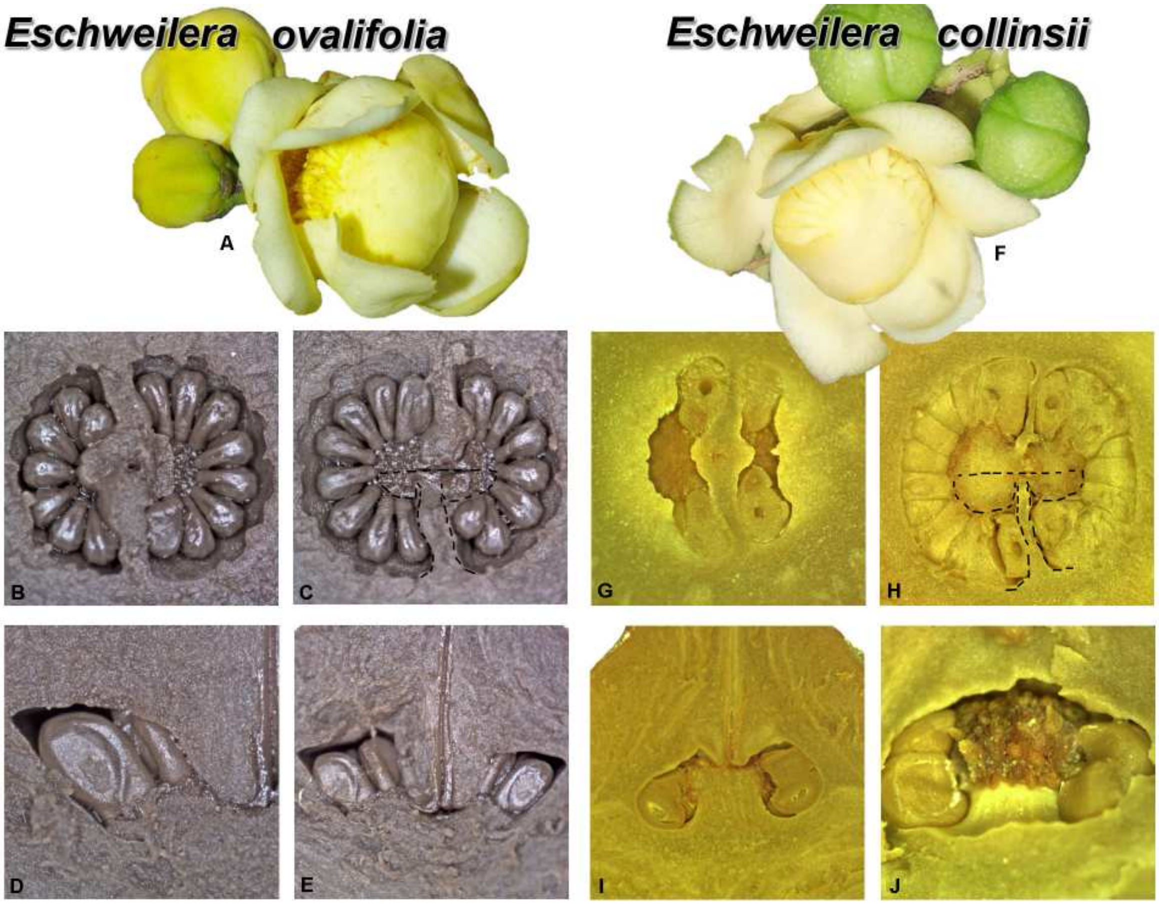


Figure 16. *Eschweilera integrifolia* clade. Plate 3: A─E. *Eschweilera ovalifolia* (DC.) Nied. F─J. *Eschweilera collinsii*. A. Flowers and buds. B. Cross-section of an ovary (apical view) showing lower part of the upper septum. C. Cross-section of an ovary (apical view) showing the anvil-shaped septal unit heads. D. Medial longitudinal section showing the obliquely upward oriented ovules. E. Medial longitudinal section of an ovary showing the invaginate lower septum and the spreading placentae. F. Flower and buds. G. Cross-section of an ovary (apical view) through upper septum showing 2-locular ovary. H. Cross-section of an ovary (apical view) showing the anvil-shaped septal unit heads. I. Medial longitudinal section of an ovary showing columnar placentae and the space between the base of the lower septum and the attachment of the ovules. J. A few ovules removed from locule to show funicular scars. A. Photo by T.L.P. Couvreur based on *Couvreur 240* from La Paz, Bolivia. B–E. Photos by C. Carollo Matos based on *Prance et al. 24390*. F. Photo by R. Aguilar based on *R. Aguilar 8857* (at CR). G–J. Photos by C. Carollo Matos based on *Mori & Kallunki 3172*.

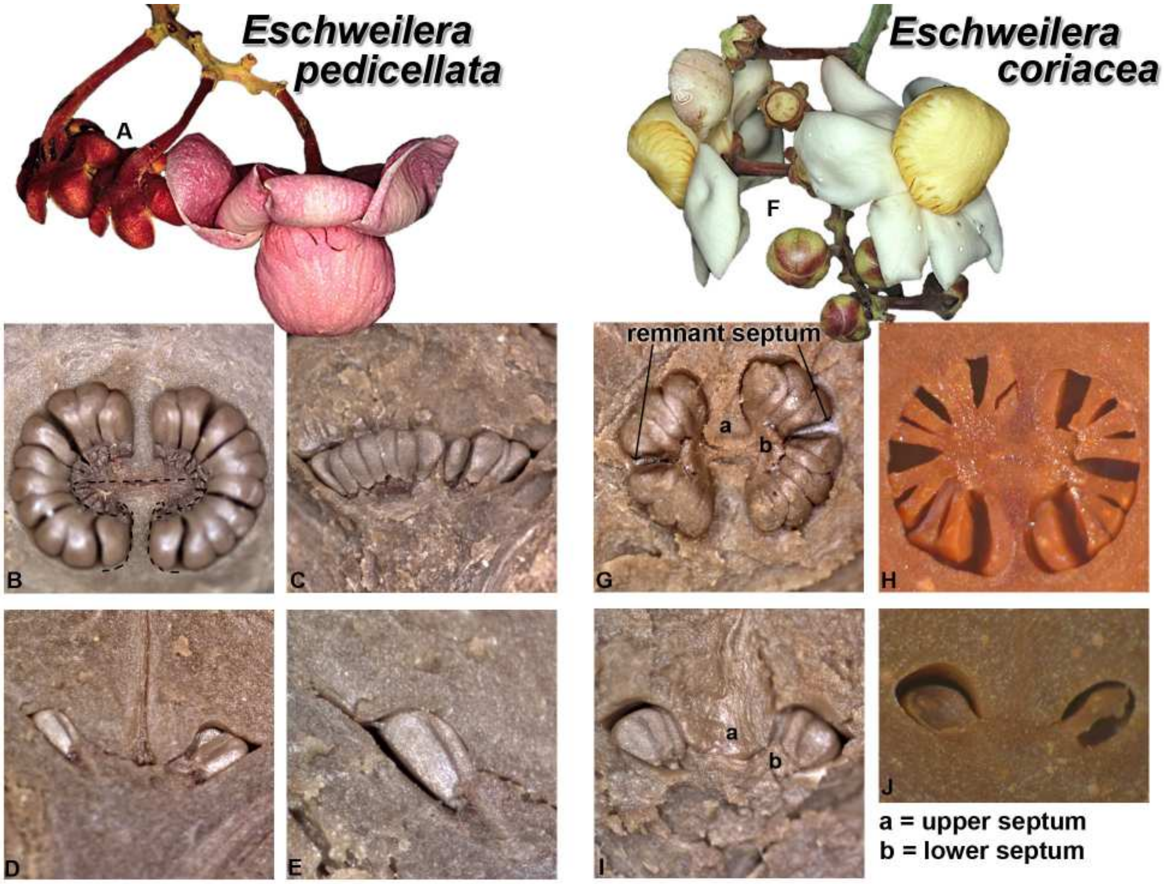


Figure 17. *Eschweilera parvifolia* clade. A–E. *Eschweilera pedicellata* (Rich.) S.A. Mori. F–J. *Eschweilera coriacea* (DC.) S.A. Mori. A. Flower and immature fruits. B. Cross-section of an ovary (apical view) showing anvil-shaped septal unit heads. C. Longitudinal section of an ovary showing the single rows of ovules. D. Medial longitudinal section of an ovary showing spreading placentae. E. Medial longitudinal section showing obliquely upward oriented locule and ovules. F. Flowers and buds. G. Cross-section of an ovary (apical view) showing remnant septum indicating that 2-locular ovaries may have evolved from an ancestor with 4-locular ovaries. H. Cross-section of an ovary (basal view) showing anvil-shaped septal unit heads. I. Medial longitudinal section of an ovary showing the spreading placentae and the slightly invaginate lower septum. J. Longitudinal section of an ovary showing the spreading placentae. A. Photo by Mori based on *Mori et al. 25648*. B–E. Photos by C. Carollo Matos based on *N. Cunha 389*. F. Photo by C.A. Gracie based on *Mori et al. 22651*. G, I. Photos by C. Carollo Matos based on *Cunha 452*. H, J. Photos by C.M. de Potascheff based on *Prance et al. 22837*.

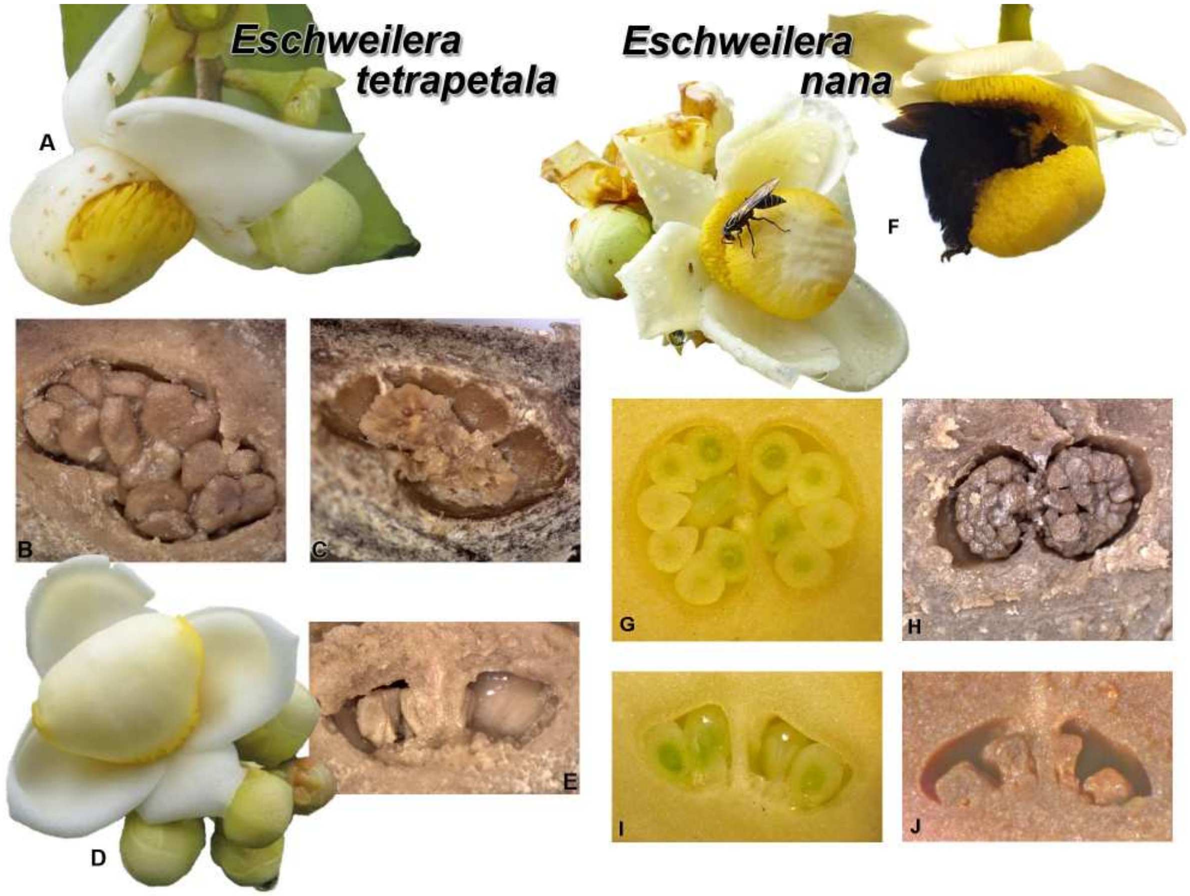


Figure 18. *Eschweilera tetrapetala* clade. A–E. *Eschweilera tetrapetala*. F–J. *Eschweilera nana* (O. Berg) Miers. A. Lateral view of flower. B. Cross-section of an ovary (apical view) showing more than a single row of ovules in each locule. C. Cross-section of an ovary (apical view) showing the placenta with the ovules removed. D. Apical view of flower and buds. E. Medial longitudinal section of an ovary showing the spreading placentae. F. Flower being visited by a non-pollinating hymenoptera (left) and a large *Centris scopipes* bee pollinator visiting a flower (right). G. Cross-section of an ovary (apical view) showing 4–5 columns of ovules. H. Cross-section of an ovary (apical view) showing more than on row of ovules. I. Longitudinal section of an ovary showing spreading placentae and 2─3 rows of ovules. J. Longitudinal section of an ovary showing locule widest at the base. A, D. Photos by N.P. Smith based on *N.P. Smith et al. 116*. B–C, E. Photos by C.M. de Potascheff based on *Hatschbach & Kummrow 48060*. F, G, I. Photos by C.M. de Potascheff based on *C..M. de Potascheff 001*. H. Photo by C. Carollo Matos based on *Anderson 36667*. J. Photo by C.M. de Potascheff based on *Maguire et al. 56555*.

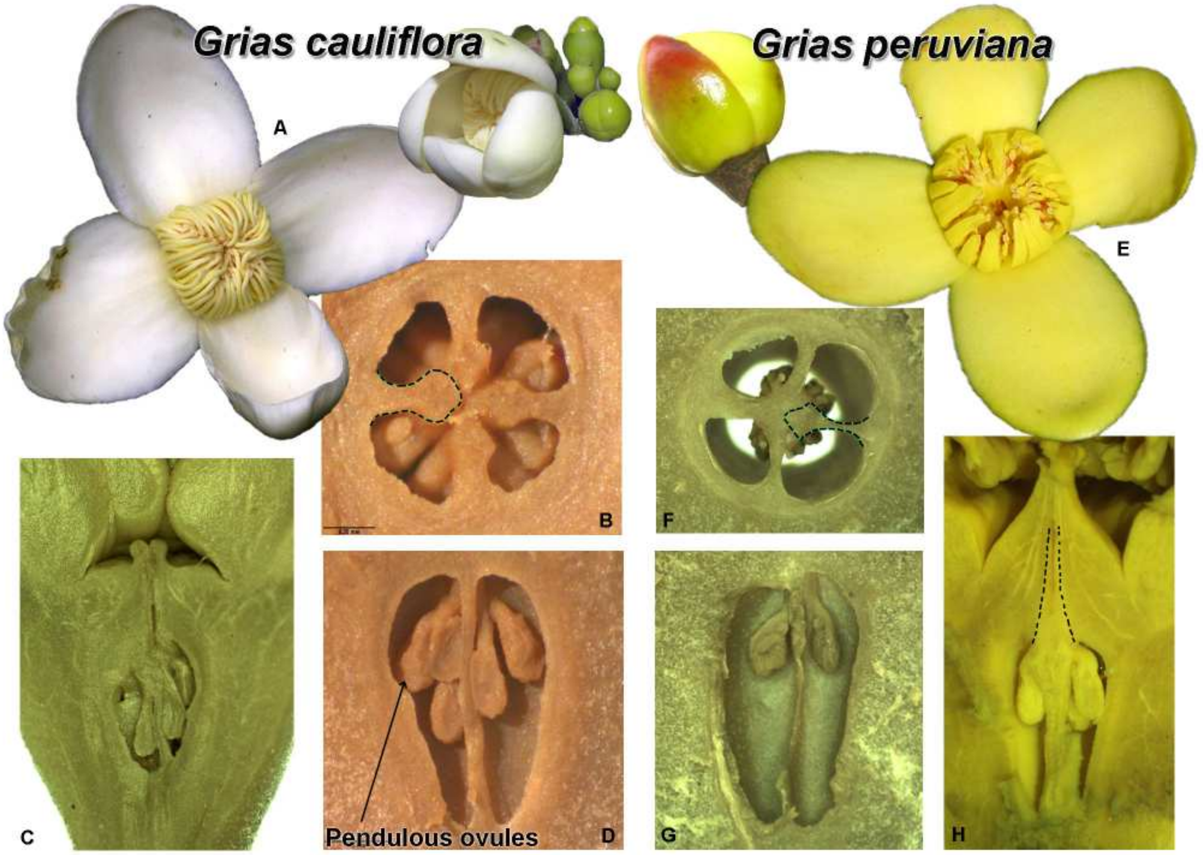


Figure 19. *Grias* clade. A–D. *Grias cauliflora* L. E–H. *Grias peruviana* Miers. A. Flowers and buds. B. Cross-section of an ovary (apical view) showing the spear-shaped septal unit heads. C. Medial longitudinal section of an ovary showing the pendulous ovules and the incipient placentae. D. Longitudinal section of an ovary showing the pendulous ovules and the long ovule-free area between the base and apex of the lower septum. E. Flower and bud. F. Cross-section of an ovary (apical view) showing the spear-shaped septal unit heads, 4 locules, and the thin septal stalks. G. Longitudinal section of an ovary showing the pendulous ovules and the long ovule-free area between the base and apex of the lower septum. H. Medial longitudinal section of an ovary showing the incipient placentae and the faint outline of the armed lower septum. A. Photo by L. Raz based on *L. Raz 400* (at FTG). B–D. Photos by C.M. de Potascheff based on *Nee & Mori 3574*. E. Photo by X. Cornejo based on *Cornejo & C. Medina 8220*. F. Photo by C. Carollo Matos based on *C. Peters 84-55*. H. Photo by X. Cornejo based on *C. Peters 84-55*.

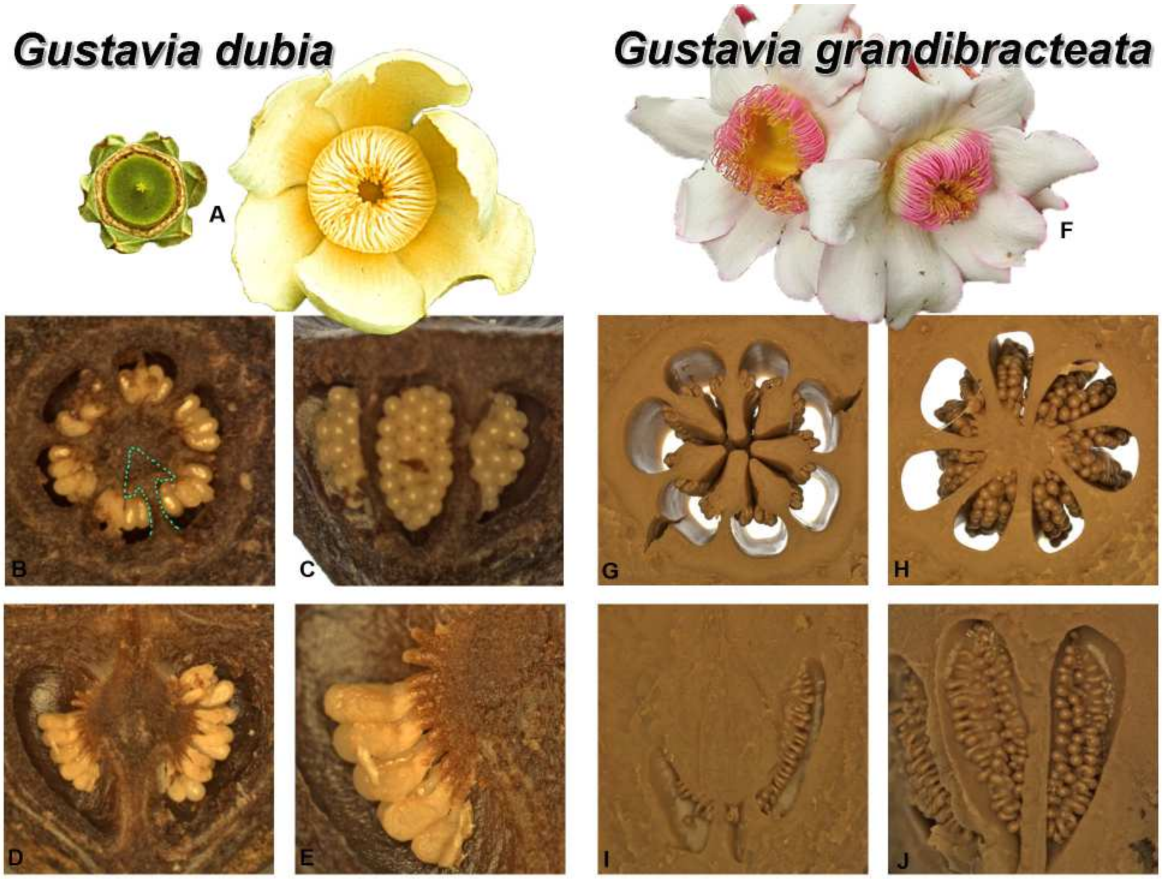


Figure 20. *Gustavia* clade. A–E. *Gustavia dubia* (Kunth) O. Berg. F–J. *Gustavia grandibracteata* Croat & S.A. Mori. A. Flower and immature fruit. B. Cross-section of an ovary (apical view) showing the arrowhead-shaped septal unit heads. C. Longitudinal section of the ovule attachments in three locules. D. Medial longitudinal section of an ovary showing the laminar cup-shaped placenta. E. Close-up of the preceding showing the outward and downward orientation of the ovules. F. Flowers. G. Cross-section of an ovary (apical view) showing the spear-shaped septal unit heads not fused at the apex of the ovary. H. Cross-section of an ovary (basal view) showing the fused carpels at the base of the placenta. I. Longitudinal section of an ovary showing the cup-shaped placentae. J. Longitudinal section of an ovary showing the high number of ovule rows per locule. A. Photo by P.M.J. Maas based on *Maas et al. 2801*. B–E. Photos by C. Carollo Matos based on *Mori 7704*. F. Photo by C. Galdames based on *Galdames et al. 9541*. G–J. Photos by C. Carollo Matos based on *Mori & Kallunki 5612*.

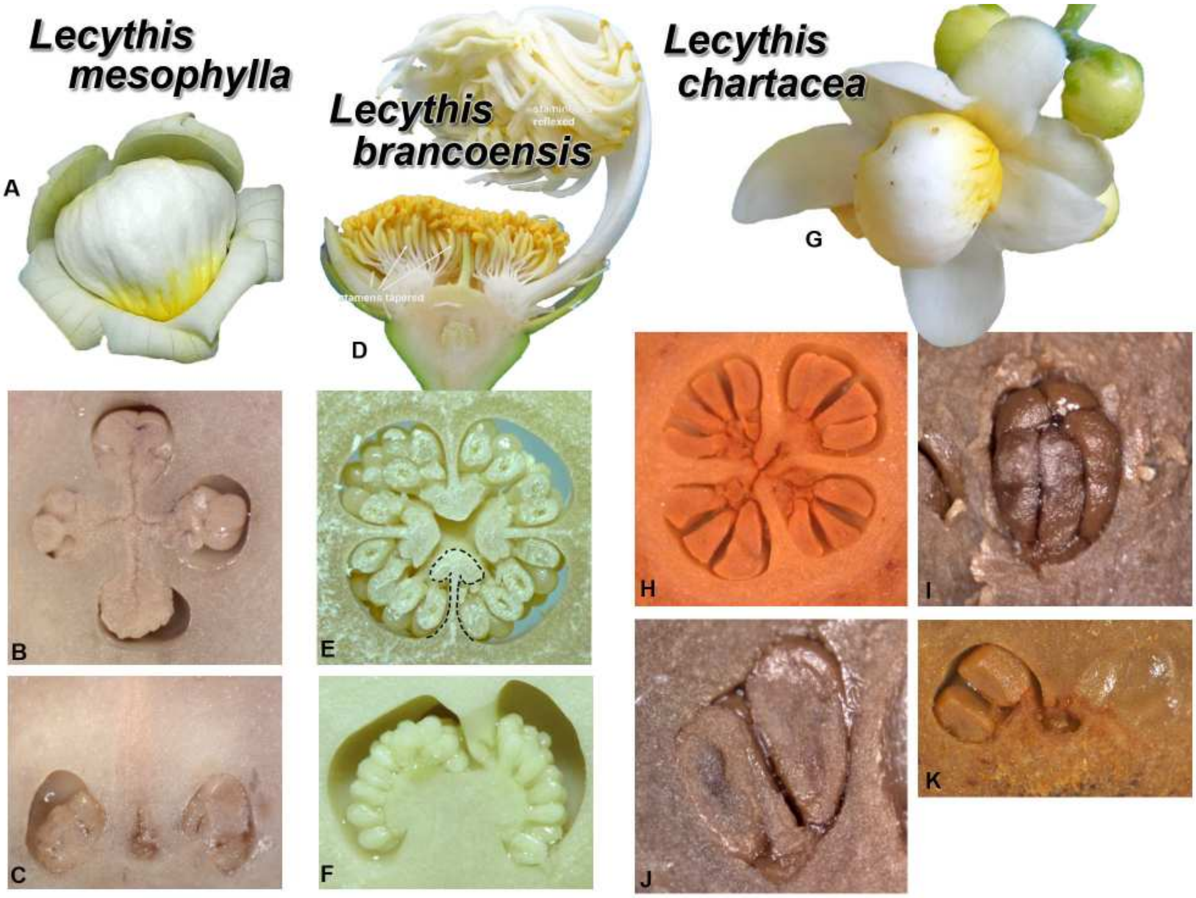


Figure 21. *Lecythis chartacea* clade. A–C. *Lecythis mesophylla* S.A. Mori. D–F. *Lecythis brancoensis*. G–K. *Lecythis chartacea*. A. Flower. B. Cross-section of an ovary (apical view) showing the arrowhead-shaped septal unit heads and 4 locules. C. Medial longitudinal section of an ovary showing invaginate lower septum and spreading placentae. D. Medial longitudinal section of a mature bud (with petals removed). E. Cross-section of an ovary (apical view) showing the arrowhead-shaped septal unit heads. F. Longitudinal section of an ovary showing the columnar placentae. G. Buds and a flower. H. Cross-section of an ovary (apical view) showing 3 to 4 columns of ovules. I. Longitudinal section of an ovary showing 3 columns and 3 rows of ovules. J. Longitudinal section showing one obliquely upward and outward ovule and one vertically oriented ovule. K. Medial longitudinal section of an ovary showing the spreading placenta and the invaginate lower septum. A. Photo by R. Aguilar based on *Aguilar 13712*. B–C. Photos by C. Carollo Matos based on *Aguilar 1177*. D. Photo by N.P. Smith based on *N.P. Smith 380*. E. Photo by N.P. Smith based on *N.P. Smith 381*. F. Photo by N.P. Smith based on *N P. Smith 379*. G. Photo by C. Bhikhi based on *C.B. Bhikhi 100*. H, K. Photos by C.M. de Potascheff. based on *Berg et al. BG706*. I, J. Photos by C. Carollo Matos based on *Lleras et al. P19664*.

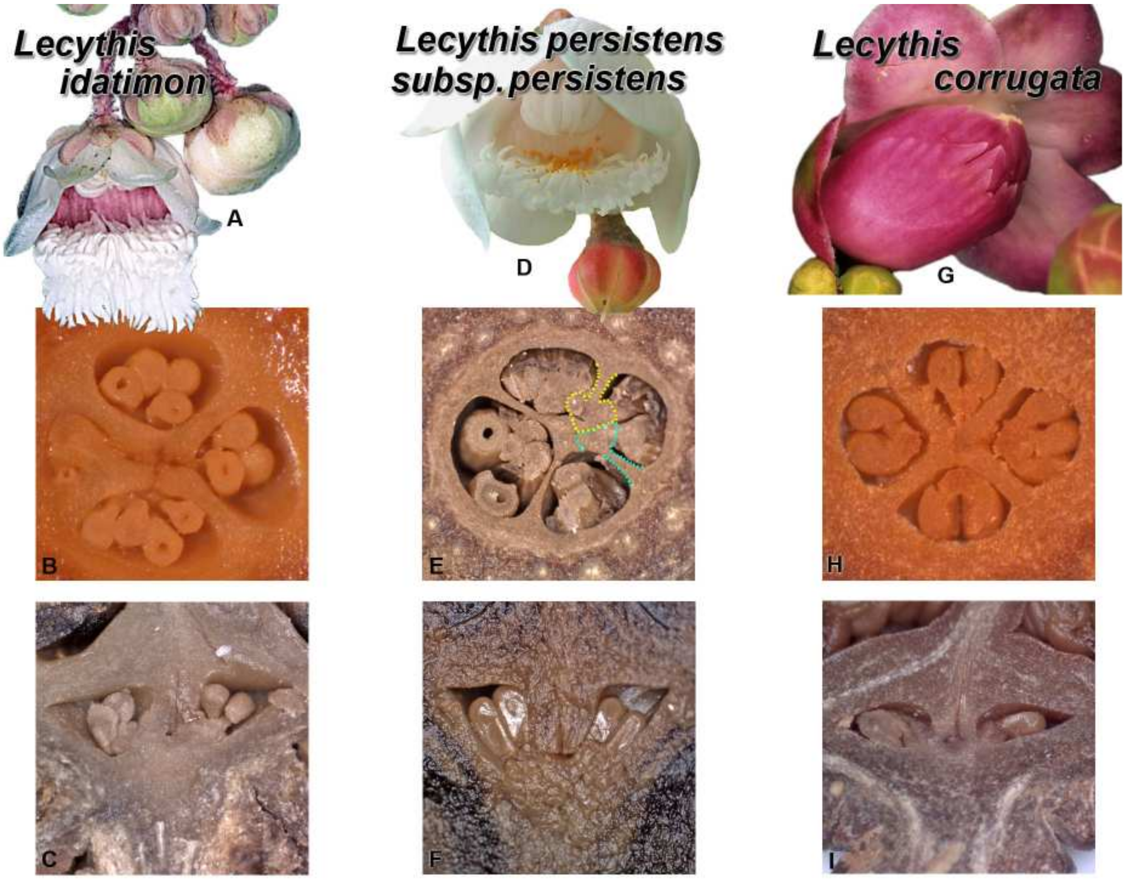


Figure 22. *Lecythis corrugata* clade. A–C. *Lecythis idatimon* Aubl. D–F. *Lecythis persistens* Sagot. G─I. *Lecythis corrugata*. A. Buds and flower. B. Cross-section of an ovary (apical view) showing the 4 locules common to this clade. C. Medial longitudinal section of an ovary showing the spreading placentae and locules wider at apices. D. Flower and bud. E. Cross-section of an ovary (basal view) showing the arrowhead-shaped septal unit heads. F. Medial longitudinal section of an ovary showing the spreading placentae, the locules wider at apices, and the obliquely upward and outward oriented ovules. G. Flower. H. Cross-section of an ovary showing 4 locules and 2–3 columns of locules. I. Medial longitudinal section of an ovary showing the spreading placentae and the invaginate lower septum. A. Photo by Mori based on *Mori et al. 17739* (at IAN). B. Photo by C.M. de Potascheff based on *Prévost & Sabatier 4776*. C. Photo by C. Carollo Matos based on *Prévost & Sabatier 4776*. D. Photo by Mori based on *Mori 25523*. E–F. Photos by C. Carollo Matos based on *Mori & J.J. de Granville 8810*. G. Photo by Mori based on *Mori et al. 25730*. H. Photo by C.M. de Potascheff based on *Tinde van Andel et al. 2636*. I. Photo by C. Carollo Matos based on *Tinde van Andel et al. 2636*.

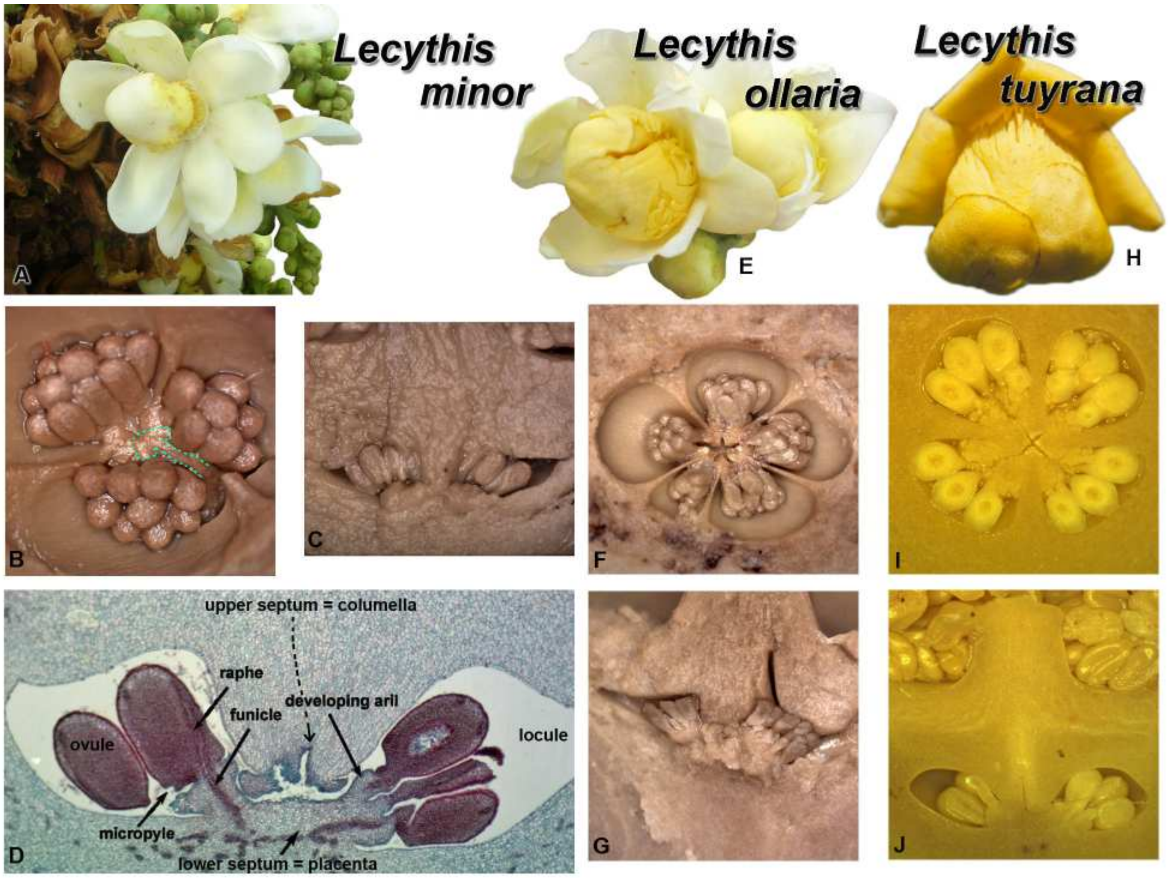


Figure 23. *Lecythis ollaria* clade. A–D. *Lecythis minor* Jacq. E–G. *Lecythis ollaria*. H─J. *Lecythis tuyrana* Pittier. A. Flowers and buds. B. Cross-section of an ovary (apical view) showing the arrowhead-shaped septal unit heads. C. Longitudinal section of an ovary showing the spreading placentae and the locules widest at apex. D. Medial longitudinal section of an ovary (microscope slide) showing spreading placentae and invaginate lower septum. E. Flower (the flower has an abnormal split in the androecial hood). F. Cross-section of an ovary (apical view) showing the arrowhead-shaped septal unit head and thin septal unit stalks. G. Medial longitudinal section of an ovary showing the spreading placentae and locules widest at the apex. H. Flower. I. Cross-section of an ovary (apical view) showing the arrowhead-shaped septal unit heads. J. Medial longitudinal section of an ovary showing the spreading placentae. A. Photo by A. de Sedas based on *A. de Sedas 219*. B–C. Photos by C. Carollo Matos based on *Prance et al. 23155*. D. Photo by C. Carollo Matos based on *Nee 7226*. E. Photo by G. Aymard based on *Aymard et al. 12786*. F–G. Photos by C. Carollo Matos based on *Aymard & Ferrera 13088*. H. Photo by Mori based on. *Mori & Kallunki 5772*. I–J. Photos by C. Carollo Matos based on *Galdames 5766*.

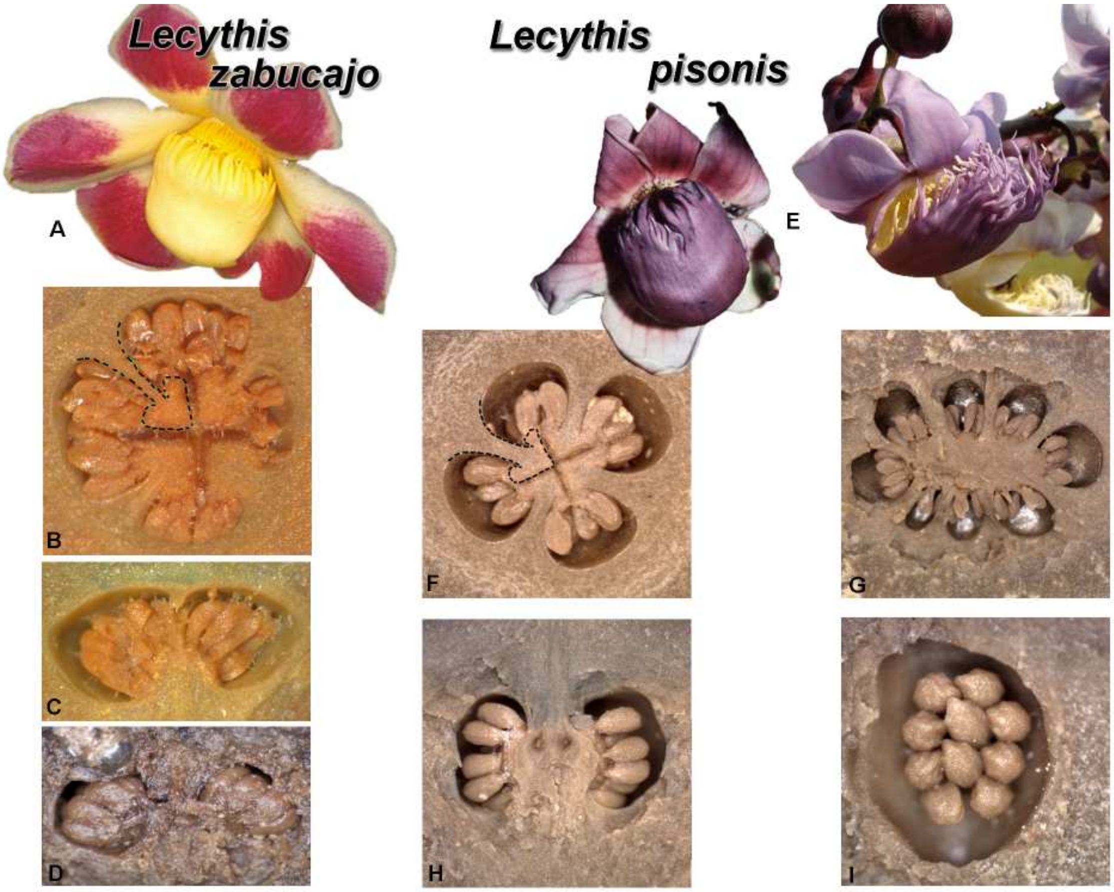


Figure 24. *Lecythis pisonis* clade. A–D. *Lecythis zabucajo*. E–I. *Lecythis pisonis*. A. Flower. B. Cross-section of an ovary (apical view) showing the arrowhead-shaped septal unit heads. C. Longitudinal section of an ovary showing the obliquely upward oriented ovules and the columnar placentae. D. Longitudinal section of an ovary showing the truncate lower septum and the ovule orientations. E. Flower and buds. F. Cross-section of an ovary (apical view) showing the arrowhead-shaped septal unit heads and 4-locular ovary. G. Cross-section of an unusual 8-locular ovary. H. Longitudinal section of an ovary showing the columnar placentae. I. Longitudinal section showing the ovules attached in 2–3 columns and 4 rows. Note that there is an ovule-free space above and below the ovules. A. Photo by Mori based on *Mori et al. 25034*. B–C. Photos by C.M. de Potascheff based on *Mori et al. 8106*. D. Photo by C. Carollo Matos based on *Mori &* Bolten 8381. E. Photos by Mori (left) based on *Mori et al. 16527* and C.M. de Potascheff (right) based an unvouchered cultivated tree. F–I. Photos by C. Carollo Matos based on *Prance et al. 14730*.

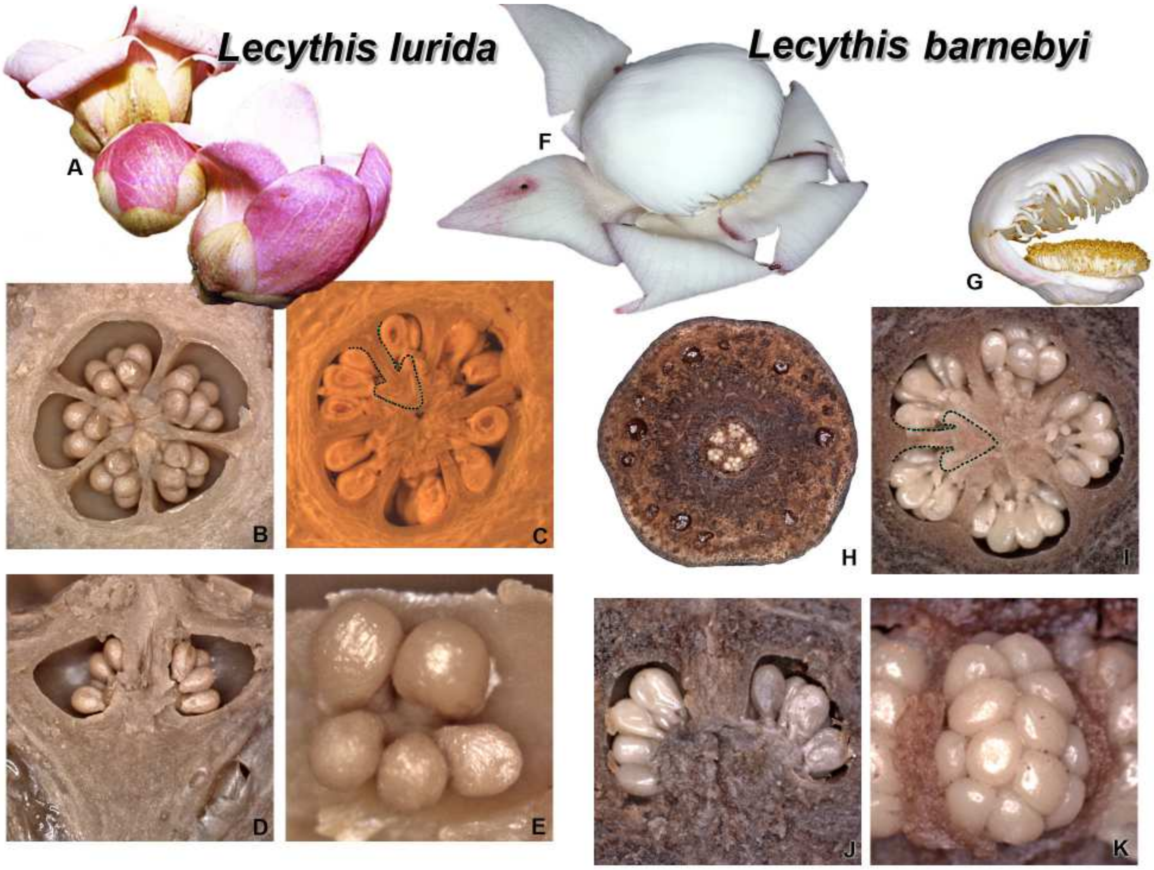


Figure 25. *Lecythis poiteaui* clade. A–E. *Lecythis lurida.* F–K. *Lecythis barnebyi*. A. Flowers and bud. B. Cross-section of an ovary (apical view) showing the arrowhead-shaped septal unit heads. C. Cross-section of an ovary (basal view) showing the arrowhead-shaped septal unit heads. D. Medial longitudinal section of an ovary showing locules widest in the middle and the columnar placenta. E. Longitudinal section of an ovary showing 4 rows of ovules in locule. F. Flower. G. Androecium of flower. H. Cross-section of an ovary (apical view) showing mucilage ducts in the hypanthium. I. Cross-section of an ovary (apical view) showing arrowhead-shaped septal unit heads. J. Medial longitudinal section of an ovary showing columnar placentae. K. Longitudinal section with the outer wall of ovary removed showing up to 4 columns and 5 rows of ovules per locule. A, C. Photos by Mori (A) and N.P. Smith (C) based on *Mori & Mendes 13270*. B, D–E. Photos by C. Carollo Matos based on *Prance & Silva 24237*. F–G. Photos by C. Gracie based on *Mori et al. 20629*. H–K. Photos by C. Carollo Matos based on *M. Freitas 598* (specimen at INPA).

***Bertholletia excelsa* Bonpl. clade** (Fig. 9)

Ovary 4-locular. Septal units as seen in cross-section through placentae: arrowhead-shaped, the basal extensions short and thin (B). Locule orientation and width as seen in longitudinal section: vertical, widest at middle (E) or width intermediate (D). Lower septum: truncate at apex, occupying ca. 50–60% of lower/upper septum length (D, E). Placentae as seen in longitudinal section: plateau columnar (E). Ovules as seen in cross- and longitudinal sections: not pendulous, not flattened, ca. 7 per locule, in ca. 2 columns (B) and 2 rows (E), inserted at apex of lower septum, with distinct ovule-free area below ovule insertion (D, E).

***Cariniana* clade** (Fig. 10)

Ovary 3(4)-locular. Septal units as seen in cross-section through placentae: spear-shaped (G–H). Locule orientation and width as seen in longitudinal section: vertical (D, I), widest at middle (I). Lower septum truncate at apex (D, I), occupying ca. 60% of lower/upper septum length (I). Placentae as seen in longitudinal section: narrow columnar (I). Ovules as seen in cross- and longitudinal sections: not pendulous, not flattened, ca. 8 per locule, in 2 columns (C, H) and 5 rows (E, J), inserted along most of lower septum, with very short ovule-free area below ovule insertion (E, I, J).

***Corythophora* clade** (Fig. 11)

Ovary (2)3(4)-locular. Septal units as seen in cross-section through placentae: anchor-shaped, the head rounded, the basal extensions thick (C, H). Locule orientation and width as seen in longitudinal section: oblique (D), widest at middle (I). Lower septum: invaginate at apex, (I), occupying ca. 30–40% of lower/upper septum length (D, I). Placentae as seen in longitudinal section: spreading (D, I). Ovules as seen in cross- and longitudinal sections: not pendulous, not flattened, ca. 3–24 per locule, in 26 columns (C–G), and 2–4 rows (D, I–J), without apparent ovule-free area at base of lower septum (D, I).

***Couratari* clade** (Fig. 12)

Ovary 3–locular. Septal units as seen in cross-section through placentae: arrowhead-shaped, the basal extensions thick (B, E, H). Locule orientation and width as seen in longitudinal section: oblique (C–F), widest at apex (C, F, J). Lower septum: invaginate at apex (F, J), occupying ca. 50–70% of lower/upper septum length (C, F, I—J). Placentae as seen in longitudinal section: arched columnar (C, F, I—J). Ovules as seen in cross- and longitudinal sections: not pendulous, distinctly flattened, ca. 10–50 per locule, in 4–8 columns (B, E, H) and 4—9 rows (C, F, I–J), without apparent ovule-free area at base of lower septum (C, F, I–J).

***Couroupita* clade** (Fig. 13)

Ovary 6-locular. Septal units as seen in cross-section through placentae: arrowhead-shaped, the basal extensions long and thin (D, H). Locule orientation and width as seen in longitudinal section: vertical (C, E, I), width intermediate (E, I). Lower septum: armed at apex (E), occupying ca. 90% of upper/lower septum length (E, I). Placentae as seen in cross- and longitudinal sections: laminar cup-shaped (E, I). Ovules as seen in cross- and longitudinal sections: not pendulous, not flattened, ca. 40–90 per locule, in 4–6 columns (C, G) and ca. 10–25 rows (C, G, I), inserted along most of lower septum, with short ovule-free area below ovule insertion (E, G, I).

Eschweilera integrifolia clade (Figs. 14–16)

Ovary 2(3)-locular. Septal units as seen in cross-section through placenta: anvil-shaped, the head truncate, the basal extensions thick (14C–E, 15B, 16C). Locule orientation and width as seen in longitudinal section: oblique (Fig. 14F–G, 15C, 16D–E), width intermediate (Fig. 14G), widest at apex (Fig. 15C), or at middle (Fig. 16I). Lower septum: invaginate (Figs 14G, 15C, 16D–E) to nearly truncate at apex (Fig. 16I), occupying 25–60% (Fig. 16J) of lower/upper septum length. Placenta as seen in cross- and longitudinal sections: spreading (Figs. 14G, 15C, 16E) or plateau columnar (Figs.

16J). Ovules as seen in cross- and longitudinal sections: not pendulous, not flattened, ca. 5–12 per locule, in 5–10 columns (14B–C, 15B, 16B) and 1 row (Figs. 14F–G, 15C, 16D–E), without apparent ovule-free area at base of lower septum (Figs 14F, 15C, 16D–F) or infrequently with distinct ovule-free area below ovule insertion (e.g., *E. collinsii*, Figs. 16I–J).

***Eschweilera parvifolia* Mart. ex DC. clade** (Fig. 17)

Ovary 2-locular. Septal units as seen in cross-section through placenta: anvil-shaped, the head truncate, basal extensions scarcely developed (16B). Locule orientation as seen in longitudinal section: oblique (D–E, I–J), width intermediate (I–J) or widest at apex (D). Lower septum: invaginate (D, I), occupying ca. 10–30% of lower/upper septum length (E, I–J). Placenta as seen in longitudinal section: spreading (D, I–J). Ovules as seen in cross- and longitudinal sections: not pendulous, not flattened, 4–11 per locule, in 4–10 columns (B, G) and 1 row (B–C), without apparent ovule-free area at base of lower septum (Figs. E, I—J).

***Eschweilera tetrapetala* S.A. Mori clade** (Fig. 18)

Ovary 2-locular. Septal units as seen in cross-section through placentae: anvil-shaped, the head truncate, the basal extensions not well-developed (C, difficult to see). Locule orientation and width as seen in longitudinal section: oblique (E, J), width widest at apex (E, I—J). Lower septum: truncate at apex, occupying ca. 20–30% of lower/upper septum length (E). Placentae as seen in longitudinal section: spreading? Ovules as seen in both cross- and longitudinal sections: not pendulous, not flattened, ca. 6–15 per locule, in 2–6 columns (B–H) and 2–3 rows (B, H—I), without apparent ovule-free area at base of lower septum (E, I—J).

***Grias* clade** (Fig. 19)

Ovary (3)4-locular. Septal units as seen in cross-section through placentae: spear-shaped (B, F). Locule orientation and width as seen in longitudinal sections: vertical (C–D, G–H), width intermediate (D—G). Lower septum: armed at apex (H), occupying nearly 100% of upper/lower septum length not including lower septum arms (D, G—H). Placentae as seen in longitudinal section: incipient (D, G—H). Ovules as seen in cross- and longitudinal sections: pendulous (C—D, G—H), not flattened, 2–3 per locule, in 2 columns (B) and 1–2 rows (B, G—H), inserted at apex of lower septum, with long ovule-free area below ovule insertion (D, G—H).

***Gustavia* clade** (Fig. 20)

Ovary 4–8 locular. Septal units as seen in cross-sections through placentae: spear-shaped (G) or arrowhead-shaped (B, only in *Gustavia* sect. *Hexapetala*), the basal extensions short. Locule orientation and width as seen in longitudinal section: vertical (J) or oblique (D–E), width intermediate (D, J). Lower septum: armed at apex (no image), occupying most of upper/lower septum length (C–D, I–J). Placentae as seen in longitudinal section: cup-shaped (I) or laminar cup-shaped (D—E). Ovules as seen in cross- and longitudinal sections: not pendulous, ca. 25–50 per locule, in 4 columns (B—C) and ca. 6–8 (in *Gustavia* sect. *Hexapetala*) and ca. 20 rows (I—J), inserted from near middle or less to apex of lower septum, with distinct ovule-free area below ovule insertion (D, I—J).

***Lecythis chartacea* O. Berg clade** (Fig. 21)

Ovary (3)4(5)-locular. Septal units as seen in cross-sections through placentae: arrowhead-shaped, the basal extensions thick (E). Locule orientation and width as seen in longitudinal section: vertical (C, F) or oblique (J—K), widest at middle (C, F, J—K). Lower septum: truncate (F) or invaginate (C, K), occupying ca. 50–60% (C, J—K) of upper/lower septum length. Placentae as seen in longitudinal section: spreading (C, J—K), or plateau columnar (F, only in *L. brancoensis* (R. Knuth) S.A. Mori). Ovules as seen in cross- and longitudinal sections: not pendulous, not flattened, ca. 4–28 per locule, in 2–4 columns (H—I) and 4–7 rows (C, F, I, J—K), without apparent ovule-free area at base of lower septum (C, J─K) or infrequently with short ovule-free area below ovule insertion (F, e.g., *L. brancoensis*).

Lecythis corrugata **Poit. clade** (Fig. 22)

Ovary 4(5)-locular. Septal units as seen in cross-sections: arrowhead-shaped, the basal extensions thick (E). Locule orientation as seen in longitudinal section: horizontal (I) or oblique (C, F), widest at apex (C, F) or at middle (I). Lower septum: invaginate at apex (C, F, I), occupying 10–50% (C, F, I) of upper/lower septum length. Placentae as seen in longitudinal section: spreading (C, F, I). Ovules as seen in cross and longitudinal sections: not pendulous, not flattened, ca. 4–8 per locule, in 2–4 columns (B, H) and 1–2 rows (C, F, I), without apparent ovule-free area at base of lower septum (C, F, I).

Lecythis ollaria **L. clade** (Fig. 23)

Ovary (3)4(5)-locular. Septal units as seen in cross-sections through placentae: arrowhead-shaped, the basal extensions thick (B). Locule orientation and width as seen in longitudinal section: horizontal (C) or oblique (D, G, J), widest at apex (C, D, G) or at middle (J). Lower septum: invaginate at apex (D, G), occupying ca. 30–40% of lower/upper septum length (C–D, G). Placentae as seen in longitudinal section: spreading (C–D, G, J). Ovules as seen in cross and longitudinal sections: not pendulous, not flattened, ca. 3–11 per locule, in 3–4 columns (B, F, I) and 2–4 rows (B–D), without apparent ovule-free area at base of lower septum (C–D, G).

Lecythis pisonis **clade** (Fig. 24)

Ovary 4-locular. Septal units as seen in cross-sections: arrowhead-shaped, the basal extensions thick (B, F). Locule orientation and width as seen in longitudinal section: oblique (D) or vertical (H), widest at middle (C, D, H). Lower septum: truncate at apex (D, H), occupying ca. 40–80% of upper/lower septum length (C–D, H). Placentae as seen in longitudinal section: Laminar cup-shaped (C, H). Ovules as seen in cross and longitudinal sections: not pendulous, not flattened, ca. 8–24 per locule, in ca. 3 columns (F, I) and 3–4 rows (C, H–I), inserted along most of lower septum, with short ovule-free area above and below ovule insertion (D, H–I).

Lecythis poiteaui **O. Berg clade** (Fig. 25)

Ovary (3)4(6)-locular. Septal units as seen in cross-sections through placenta: arrowhead-shaped, the basal extensions short, thick (C, I). Locule orientation and width as seen in longitudinal section: vertical (J) or oblique (D), widest at middle (D) or width intermediate (J). Lower septum: truncate at apex, occupying ca. 50% of lower/upper septum length (D, J). Placentae as seen in longitudinal section: arched spreading (D, J). Ovules as seen in cross and longitudinal sections: not pendulous, not flattened, ca. 6–20 per locule, in 2–4 columns (B–C, I) and 3–5 rows (D, J–K), inserted from apex of lower septum to near base, with very short ovule-free area below ovule insertion.

THE OVARY

The placentae of New World Lecythidaceae appear axile as seen in a cross-sections through the area of the placenta to which the ovules are attached although the carpels are sometimes not entirely fused (Fig. 2). A cross-section at this level also shows the number of locules in an ovary, the relationship of the placentae to the septa, and the manner in which the ovules arise from the placenta. If a section is made above the ovule attachment, the septa may not be fused at their apices and, as a result, the placentation appears parietal or intruded parietal. This has been pointed out by Schoenberg (1983a) and Monteiro-Scanavacca (1975) for *Couroupita guianensis.* Because this decision is arbitrary, we conclude that the placentation of this family should continue to be classified as axile. We also base this conclusion on the fact that where the ovules are attached the apices of the septa are usually fused together or are in very close approximation as seen in cross-sections. The evolution of placentation in New World Lecythidaceae has not been adequately addressed and, thus, it is not known if the ovary is derived from an ancestor with parietal placentation and the apical placentae have not fused or if the ancestor had axile placentae in which the septa in the upper part of the ovary separated to form what looks like parietal placentation toward the apex of the ovary. It is not unusual among flowering plants to have placentation that appears axile toward the base and parietal toward the apex, which is often interpreted as a stage in the evolution of axile from parietal placentation. In addition, it has been observed that species with axile placentation at anthesis often show parietal placentation in early bud development stages (Gunderson 1939) and that fusion of the carpels develops from the base to the apex of the ovary (Endress 1994).

The septa (the walls that divide the ovary into different chambers [locules]) are generally considered to have evolved from proto-angiosperms in the early evolution of angiosperms. The origin of the ovary of angiosperms and whether it has evolved once or more than once is still under debate. Whatever their origin, the structures that form the ovary are called carpels and their number is usually revealed by counting the number of locules, the number of stigmatic lines or lobes, or the number of valves making up the outer walls of the ovary. In Lecythidaceae, the number of carpels forming an ovary based on the number of valves does not work because the valves are surrounded by a hypanthium, thus the sutures of the ovary walls are not apparent. In New World Lecythidaceae, the style is only divided in some species of *Grias* and the number of stigmatic lines is only apparent in species of *Gustavia* and *Couroupita*. Both Monteiro-Scanavacca (1974) and Schoenberg (1983a) concluded that the hypanthium is appendicular, i.e., it originated from fused sepal, petal, and stamen tissue. According to Schoenberg (1983a), the hypanthium does not participate in the development of the fruit.

A medial longitudinal section of the ovary shows that the septae are divided into a lower and upper septum separated by a septal articulation (Fig. 2G, K). The placentae always arise from the lower septum We hypothesize that there are no known selective advantages for ovaries that produce indehiscent fruits to develop an upper septum and therefore suggest that it is usually vestigial in species with fruits that do not dehisce (e.g., species of *Gustavia*, *Grias*, and *Couroupita*). Species of this group usually fall to the ground and are generally dispersed by animals. In most dehiscent-fruited species the upper septum develops into a woody projection that protrudes from the inside of the operculum and is called the columella. The most developed columellae are associated with cylindrical fruits (*Allantoma*, *Cariniana*, and *Couratari*) that possess winged seeds and are usually dispersed by the wind. Less markedly developed columellae are found in the dehiscent fruited *Lecythis pisonis* clade that is dispersed by bats seeking the well-developed aril as a reward. The remaining clades lack a columella but sometimes the septal walls tightly surround the basal part of the seed and the operculum and the seeds fall to the ground together (e.g., in relatively few species of the *Eschweilera parvifolia* clade).

We use *Couroupita* (Figs. 2A–F, Fig. 4) to illustrate the terms employed for describing the placentation of New World Lecythidaceae because its placentae possess most of the characters found or modified from this genus. The three species of *Couroupita* have 6-locular ovaries, and unlike species of other genera, the locules seldom vary in number. The septa of the ovary are made up of what we hypothesize to be tissue derived from two adjacent carpels. We call the non-expanded part of the septum the septal stalk, the enlarged apex the septal unit head, and extensions from the base of the septal unit head, the septal unit extensions (Fig. 2E, Fig. 4). Septal unit heads differ in shape to a greater or lesser extent among genera as seen in cross-sections — in *Couroupita* the septal unit head is arrowhead-shaped. In this genus the septal unit consists of the non-differentiated septal stalk, the septal unit head, and relatively long septal unit extensions. In contrast, an individual locule is formed by a single carpel that forms the inner wall of a locule; thus there are six curved inward walls and six carpels in species of *Couroupita*. The placental tissue that bears the ovules is formed at the apical ends of each carpel, and each is called a placental unit; thus there are two placental units within a locule derived from a single carpel (Figs. 14D, H) and together they make up what we call the placenta.

Nevertheless, there are three choices for what could be considered the placenta in *Couroupita* and other New World Lecythidaceae: (1) all of the tissue in a ovary to which ovules are attached, i.e., the combined placental tissue of all six locules; (2) all of the tissue associated with a single septal unit head, i.e., the combined tissue from two adjacent carpels (Figs. 2D); or (3) all of the tissue to which ovules are attached within a given locule, i.e., the combined placental tissue of a single carpel which in turn represents two placental units (Fig. 2B). We have elected to consider the latter as the placenta in Lecythidaceae because this definition is based on placental tissue derived from a single carpel.

USE OF PLACENTATION IN SEPARATING CLADES

In this section we discuss what placentation characters contribute to confirming or rejecting genera as circumscribed in the last monographs of New World Lecythidaceae (Mori & Prance 1990; Prance & Mori 1979). The clades presented are those recognized by Huang et al. (in press) and Mori et al. (in press), which are presented in alphabetical order in the following discussion.

***Allantoma* clade** (Fig. 7)

This clade includes the eight species of *Allantoma* (Huang et al. 2008; Mori et al., in press) for which an infrageneric classification has not been proposed. The description presented here is based only on *A. lineata* (Mart. ex Miers) O. Berg, which is the largest-flowered species of the genus. Once smaller-flowered species are studied, parts of the description in the **RESULTS** will change because the flowers of other species are very small (e.g., *Allantoma decandra* (Ducke) S.A. Mori, Y.-Y. Huang & Prance. This clade is characterized by the following combination of placentation characters: spear-shaped septal units; vertical locule orientation; upper septum truncate; narrow columnar placentae; and ovules arranged in 5–10 rows and two columns. These placental features are similar to those of the *Cariniana* clade. The clade is supported by morphology (Huang et al. 2008; Mori et al., in press) but the *Allantoma* clade is not resolved forming a polytomy with the *Cariniana* and *Couratari* clades (Fig. 1). Nevertheless, we hypothesize that *Allantoma* merits continued recognition as a distinct genus because of morphological differences in the leaves and flowers (Mori et al., in press).

The species of *Allantoma*, as circumscribed by Huang et al. (2008), are found mostly in western and central Amazonia but *Allantoma lineata* grows along the Rio Orinoco, Rio Negro, and the Amazon from its junction with the Rio Negro to the mouth of the Amazon (map not available). Species of *Allantoma* are absent from the Guianas, eastern Amazonia (except for *A. lineata*), and the forests of eastern Brazil.

Barringtonia clade (Fig. 8)

This clade includes 69 species (Prance 2012). The clade is characterized by the following combination of placentation characters: ovary 4-locular; ovules few and pendulous; and very long lower septum in comparison with the upper septum. These features are also found in species of *Grias* in the New World and we hypothesize the ancestor of these two genera to be the connection between the Old World and New World Lecythidaceae.

Additional study of the placentation of the genera of Old World Lecythidaceae is needed to determine if placentation features can contribute to an understanding of intergeneric relationships as well as to the relationships between Old and New World Lecythidaceae.

The species of *Barringtonia* are found in eastern Africa (including Madacascar), Southeast Asia, and Australia.

***Bertholletia excelsa* clade** (Fig. 9)

This species belongs to a monotypic clade that should not be confused with the more widely defined *Bertholletia* clade; the latter includes all of the zygomorphic-flowered clades except *Cariniana*, *Couratari*, and *Couroupita* clades (Huang et al., in press; Mori et al., in press). The following combined placentation features support the recognition of the *Bertholletia excelsa* clade: 4-locular ovaries; septal units arrowhead-shaped, the basal extensions short and thin; plateau columnar placentae; ovules in two rows; the lower septum truncate at apex; and an ovule-free area below the ovule attachments. Morphological (Huang et. al, in review) data support the recognition of the *Bertholletia excelsa* clade as a monotypic genus, but molecular data does not support or negate this conclusion because the genus is monotypic (Huang 2010). This type of placentation is also found in *Lecythis brancoensis* (R. Knuth) S.A. Mori that, based on molecular and morphological (Fig. 1) evidence, is placed in the *Lecythis chartacea* clade.

Bertholletia excelsa occupies most of the Amazon Basin (see Fig. 21 in Mori & Prance 1990) but this is probably because Amerindians planted the edible seeds everywhere they travelled, an idea supported by the discovery that there is little genetic variation among individuals throughout its range (Reis et al. 2009). Shepard and Ramirez (2011), linguistic data, suggest that the Brazil nut originated in the north-central Brazilian Amazon.

***Cariniana* clade** (Fig. 10)

This clade includes the nine species of *Cariniana* recognized by Huang et al. (2008) for which an infrageneric classification has not been proposed (Prance & Mori 1979). Huang et al. (2008) placed a number of species formerly part of *Cariniana* as defined by Prance in Prance and Mori (1979) in *Allantoma*. This clade is characterized by the following combination of placentation characters: 3-locular ovaries; spear-shaped septal unit heads; vertical locule orientation; narrow columnar placentae; ovules arranged in two columns and ca. 5 rows; and ovules alternately arranged as seen in longitudinal section when the locule wall is removed. These placental features are similar to those of the *Allantoma* clade. The clade is supported by morphological (Huang et al. 2008; Mori et al., in press) and weak molecular data (58% bootstrap support in Mori et al. 2007). Nevertheless, we conclude that it merits continued recognition as a genus separate from *Allantoma* and other New World Lecythidaceae because of morphological differences in the leaves, flowers, and fruits (Huang et al 2008), even though its relationships with that of other clades is not resolved.

The species of the *Cariniana* clade are found in the forests of the *Cerrado* of eastern Brazil into southeastern Bolivia and throughout western and southern Amazonia. *Cariniana pyriformis* Miers is the only species found both east and west of the Andes around Lake Maracaibo of Venezuela and northwestern Colombia (see Fig. 67 in Prance & Mori 1979). The genus is not represented in eastern Venezuela, the Guianas, and extreme eastern Amazonia (map not available) and has only recently been collected in Central America in eastern Panama.

***Corythophora* clade** (Fig. 11)

This clade includes the four species of *Corythophora* as circumscribed by Mori and Prance (1990). This genus has not been divided into subgenera which includes two clades — one with *C. amapaensis* Pires ex S.A. Mori & Prance and *C. labriculata* (Eyma) S.A. Mori & Prance (many ovules) and the other with *C. alta* R. Knuth and *C. rimosa* W.A. Rodrigues (few ovules), the latter with two subspecies (Huang et al. 2008, 2011). The anchor-shaped septal units are unique to this clade which is also supported by (Huang et al., in press) and molecular data (100% bootstrap support, Huang 2010); thus this clade merits continued recognition as a separate genus.

This clade is distributed in the Guianas and from central to eastern Amazonia. All collections come from north of the Amazon River (see Fig. 23 in Mori & Prance 1990).

***Couratari* clade** (Fig. 12)

This clade includes the 19 species of *Couratari* (Huang 2010; Huang et al. 2011; Mori et al., in press). The following combined placentation features support the recognition of the *Couratari* clade: 3-locular ovaries; septal units arrowhead-shaped; the basal extensions thick truncate at ends; and flattened ovules. This clade is also supported by morphological (Huang et al. 2011, in press) and molecular data (86% bootstrap support, Huang 2008) and merits continued recognition as a separate genus.

Prance in Mori & Prance (1990) recognized three sections in *Couratari*. Morphological (Huang et al. 2011, in press) and molecular data (Mori et al. 2007) support the recognition of *Couratari* sect. *Echinata.* The differences between *Couratari* sect. *Guianensis* and *Couratari* sect. *Microcarpa* may not be sufficient to merit their recognition.

The species of *Couratari* are found throughout the Amazonian Basin, the Guianas into Venezuela, in Central America from Panama to Costa Rica, and in the forests and savannas of eastern Brazil (see Fig. 24 in Mori & Prance 1990).

***Couroupita* clade** (Fig. 13)

This clade includes the three species of *Couroupita* (Mori et al., in press) for which an infrageneric classification has not been proposed. The clade is characterized by the following combination of placentation characters: 6-locular ovaries; ca. 40–90 ovules per locule; arrowhead-shaped septal units with long, thin basal extensions, lower septum armed, and an ovule-free area below the ovules. The clade is also supported by morphological (Mori et al., in press) and molecular data (100% bootstrap support, Mori et al. 2007) and merits continued recognition as a genus.

Couroupita nicaraguarensis DC. is distributed west of the Andes from northwestern Ecuador to Nicaragua, *C. guianensis* encircles the Amazon in what has been called a periamazonian distribution by Jean-Jacques de Granville (1992), and *C. subsessilis* Pilg. is found along the Amazon River and some of its major tributaries (see Fig. 23 in Mori & Prance 1990).

***Eschweilera integrifolia* (Ruiz & Pav. ex Miers) R. Knuth** (Figs. 14–17)

The approximately 15 species of this group were first recognized as a clade by Huang (2010) based on morphological and molecular data. This clade had previously been placed in the more broadly defined *Eschweilera* sect. *Eschweilera* by Mori and Prance (1990). The *E. integrifolia* (Ruiz & Pav. ex Miers) R. Knuth clade can be recognized by the combination of the following placentation features: 2-locular ovaries, anvil-shaped septal units; lower septum invaginate; spreading placentae; and a single row of ovules. These features are also shared with the *E. parvifolia* clade. There is strong morphological (Huang et al., in press) and moderate molecular data (76% bootstrap support, Huang et al. 2010) supporting the recognition of this clade at some taxonomic level.

Eschweilera collinsii Pittier differs from other members of the *E. integrifolia* clade by having a narrow columnar placenta, truncate at the apex of the lower septum, and a single row of ovules that are not inserted in a single plane, i.e., they are placed at different levels along the placenta to form an upward oriented arch of ovules. This is the only species (with the exception of the *Bertholletia excelsa* clade, Fig. 10E) that we have studied in the broadly defined *Eschweilera* that has a columnar placenta and several rows of ovules (Fig. 17J).

Species of this clade are distributed in Central America as far north as the Osa Peninsula, in the Andean valleys and slopes of northwestern South America, and in western Amazonia.

***Eschweilera parvifolia* DC. ex Miers clade** (Fig. 17).

The approximately 70 species of this clade belong to *Eschweilera* sect. *Eschweilera* as recognized by Mori and Prance (1990). *Eschweilera parvifolia*, the type of the genus, belongs in this clade. This clade can be recognized by the combination of the following placentation features: 2-locular ovaries, anvil-shaped septal units; spreading placentae; and a single row of ovules. These features are shared with most of the species of the *Eschweilera integrifolia* clade but that relationship was not recognized by Mori and Prance (1990). There are strong morphological (Huang et al., in press) and weak molecular data (Huang et al. 2010) supporting the recognition of this clade, which excludes the *E. integrifolia* and *E. tetrapetala* clades (which were included as part of *Eschweilera* by Mori and Prance 1990).

The approximately 70 known species of this clade are distributed throughout northern South America and Central America, reaching Mexico in the north, and the area around Rio de Janeiro in the south (see Fig. 18 in Huang 2010).

***Eschweilera tetrapetala* clade** (Fig. 18)

The five species of this clade were placed in *Eschweilera* Sect. *Tetrapetala* by Mori and Prance (1990). The clade is recognized by the combination of the following placentation features: 2-locular ovaries, anvil-shaped septal units; invaginate lower septum; spreading placentae; and more than one row of ovules. The presence of anvil-shaped septal units is found only in this and the *E. integrifolia* and *E. parvifolia* clades but these clades have multiple rows of ovules per locule (Fig. 15) instead of a single row of ovules found in the latter clades (Figs. 14–17). Morphological (Huang et al. 2011, in press) and molecular data (99% bootstrap support in Huang 2010) support the recognition of this clade as separate from the other clades of *Eschweilera* but it is not resolved with other members or the larger *Bertholletia* clade.

The species of this clade are restricted to the coastal forests and adjacent savanna (*cerrado*) vegetation of eastern Brazil (see Fig. 16 in Huang 2010).

***Grias* clade** (Fig. 19)

This clade includes all 11 species of the genus (Cornejo & Mori 2012) for which an infrageneric classification has not been proposed (Prance & Mori 1979). This clade is characterized by the following combination of placentation characters: upper septum reduced, lower septum long and armed; incipient placentae; pendulous ovules; and a long ovule-free area below the ovules. The clade is supported by morphological (Cornejo & Mori 2010) and molecular (99% bootstrap support, Huang 2010) data and merits continued recognition as a genus.

Species of the *Grias* clade are the only New World Lecythidaceae with very few pendulous ovules located at the summit of the ovary which are also found in *Barringtonia* and some of its relatives in the Old World subfamily Barringtonioideae. Numerous drawings of the pendulous ovaries of *Barringtonia* are illustrated in Payens (1967).

The species of *Grias* are mostly found in the Andean valleys and slopes of northwestern South America, but two occur in western Amazonia, and another ranges from Central America into northwestern South America (a disjunct distribution of it occurs in Jamaica) (see Fig. 20 in Mori & Prance 1990).

***Gustavia* clade** (Fig. 20)

This clade includes the 43 species of *Gustavia* as defined by Mori and Cornejo (2013). The clade is characterized by the following combination of placentation characters: upper septum reduced or absent; cup-shaped or laminar cup-shaped placentae; lower septum armed or not armed at apex; and well-defined ovule-free area below the insertion of ovules. Morphological (Mori & Cornejo 2013) and molecular data (100% bootstrap support, Mori et al. 2007) also support its continued recognition as a separate genus. However, Prance and Mori (1979) recognized the following sections of the genus: *G*. sect. *Hexapetala*, *G*. sect. *Grandibracteata*, and *G*. sect. *Gustavia*. The first section is supported by molecular data (Mori et al. (2007, Jackknife support of 100%) but most morphological data does not support its segregation from the rest of the genus. Placental features (septal heads arrowhead-shaped (instead of spear-shaped); lack of lower septal arms (instead of septal arms present); and laminar cup-shaped placentae (instead of cup-shaped) differ from other species of the genus. There is no support for separating the other two sections of the genus because only one species of the *G.* sect. *Grandibracteata* was used in the molecular based study (Mori et al. 2007).

Species of *Gustavia* are found throughout Amazonia into Central America as far north as western Panama, the greatest diversity is associated with the Andes of northwestern South America and the mountains and lowlands of Panama. The widespread *G. augusta* L. is the only species that reaches the coastal forest of eastern Brazil and then it is restricted to the northern part of that phytogeographic area (see Fig. 26 in Mori & Prance 1990).

***Lecythis chartacea* clade** (Fig. 21)

The approximately nine species belonging to this clade were assigned to *Lecythis* sect. *Lecythis* by Mori & Prance (1990) which also includes the following clades recovered by Huang et al. (2010, in press): *L. ollaria*, *L. pisonis*, and *L. poiteaui*. There are no combined placentation features, only weak morphological differences, and weak molecular (73% bootstrap support, Huang 2010) data defining this clade; thus, there is insufficient support for recognizing the clade as a separate genus. Additional species, morphological characters, and genes should be included in a phylogenetic analysis to determine the placement and validity of this clade.

Although *L. brancoensis* (R. Knuth) S.A. Mori falls into the *L. chartacea* clade, the following placentation features do not support this placement: vertical locule orientation; plateau columnar placenta, an ovule-free area below ovule insertion, and the lower septum occupying ca. 80% of the lower/upper septum length. These are features shared by *Bertholletia excelsa*.

The species of this clade are mostly distributed in eastern Amazonian Brazil and the Guianas into Venezuela. There are, however, a few collections that have been gathered in western Amazonia (see Fig. 12 in Huang et al. 2010).

***Lecythis corrugata* clade** (Fig. 22)

The five species of this clade were placed in *Lecythis* sect. *Lecythis* by Mori in Mori and Prance (1990). This clade is characterized by the following combination of placentation characters: arrowhead-shaped septal head units; thick basal septal head extensions; lower septum invaginate; and spreading placentae. It is also supported by morphological (Huang et al., in press) and molecular data (99% bootstrap support, Huang 2010).

This clade is distributed in the Guianas and northeastern Amazonia in the states of Amapá, eastern Pará, and *Lecythis corrugata* is disjunct in the state of Amazonas around Manaus and in the Maracaibo basin in Venezuela (see Fig. 17 in Huang 2010). These species are only found south of the Amazon River in eastern Pará.

***Lecythis ollaria* clade** (Fig. 23)

The three species belonging to this clade (Huang 2010; Huang et al. 2011, in review) were placed by Mori in Mori and Prance (1990) in *Lecythis* sect. *Lecythis*. This clade is weakly characterized by the following combination of placentation characters: arrowhead-shaped septal units; thick basal extensions; and lower septum invaginate. In addition, this clade possesses an apomorphic morphological character (single-coiled androecial hoods with vestigial stamens only on the exterior of the coil [Huang et al., in press]) and molecular support for the clade [100% bootstrap support, Huang 2010]).

If *Lecythis*, as defined by Mori and Prance (1990), were redefined to include only the *Lecythis ollaria* clade the genus would be reduced to three instead of 26 species. This decision, however, should be deferred until additional species, morphological characters, and genes are included in a phylogeny analysis.

The species of the clade are found only in eastern Panama, northern Colombia, and north-central Venezuela (see Fig. 10 in Huang 2010 as the *Lecythis s.s.* clade).

***Lecythis pisonis* Clade** (Fig. 24)

The five species belonging to this clade (Huang 2010; Huang et al. 2011, in press) were recognized by Mori in Mori & Prance (1990) as *Lecythis* Sect. *Pisonis*. The following combined placentation features support the recognition of the *Lecythis pisonis* clade: 4-locular ovaries; septal units arrowhead-shaped; the septal head basal extensions thick; and laminar cup-shaped placentae. This clade is also supported by morphological (Huang et al., in press) and molecular data (100% bootstrap support, Huang 2010), which suggests that, with further study, the clade could be recognized as a separate genus.

The species of this clade are found in lowland forests of the Atlantic coastal forest of eastern Brazil, the Brazilian and Peruvian Amazon, the Guianas and adjacent Venezuela, and the Andean valleys of northwest Colombia into Central America as far north as Nicaragua (see Fig. 9 in Huang 2010 as the *Pachylecythis* clade).

***Lecythis poiteaui* clade** (Fig. 25)

The following species are known or hypothesized to belong to this clade: *L. barnebyi* S.A. Mori, *L. ibiriba* (Miers) N.P. Smith et al., *L. lurida* (Miers) S.A. Mori, *L. prancei* S.A. Mori, *L.* poiteaui, and *L. schwackei* (R. Knuth) S.A. Mori. There are no combined placentation features that separate this clade from other clades and molecular data is weak (73% bootstrap support, Huang 2010). Possible morphological features are dendritic and slightly impressed seed venation and absent or vestigial versus well-developed basal arils (Huang et. al., in review).

The species of this clade are found from central to eastern Amazonia and in the Atlantic coastal forest of eastern Brazil (see Fig. 13 in Huang 2010, as the *Holopyxidium* clade).

DISCUSSION

A significant obstacle to this study was the difficulty of obtaining buds of the same size for study. We do not know how much placentation characters as seen in sectioned buds change over the course of development; thus, if changes in form and position do take place comparing buds at one stage with buds at another stage may lead to false conclusions about placentation differences among clades. In addition, making sections consistently through the same place in different buds, even if they are at the same stage of development, makes it difficult to compare the sections; for example, a medial longitudinal section (Fig. 5) of a bud may differ in locule shape from another bud sectioned in longitudinal section in a slightly different place. However, the greatest problem in this study is the small sample size used. Even though NYBG has more pickled flowers of Lecythidaceae than has ever been assembled, there are still not enough buds and flowers to determine how much variation takes place within an individual, among individuals of a population, and among individuals of different populations, a problem with almost all studies of plant systematics.

Because most collections of Lecythidaceae are dried under too much pressure and heat, our efforts to use buds and flowers from herbarium specimens often yielded sections too distorted and carbonized to show placentation features. On the other hand, buds that are dried in paper bags on low heat allow making acceptable sections after they have been boiled in water. Liquid preserved collections and fresh flowers sectioned in the field, however, give the best results.

In spite of the difficulty in making sections, placentation features of some genera of Lecythidaceae are so different that genera can be recognized based on placentation alone. In addition, placentation data adds information for future testing of the validity of genera as proposed in the latest monographs (Mori & Prance 1990; Prance & Mori 1979). For example, *Grias* (Cornejo & Mori 2010) encompasses the only New World species with a few pendulous ovules per locule and an incipient placenta (Fig.19) and this type of placentation is also found in species of Old World *Barringtonia* (Fig. 7). One can recognize species of *Grias* from species of *Barringtonia* based on geography and tricolpate vs. syntricolpate pollen but could conclude that there may be a relationship between species of *Grias* and *Barringtonia* because of their striking similarity in placentation and some morphological features. This hypothesis waits testing by preparing a more detailed species level phylogeny of both New World and Old World Lecythidaceae based on molecular data (Fig. 1). Note that species of *Gustavia* also have some floral features (e.g., a broad staminal tube with at least most of the stamens arising from the rim of a staminal tube) in common with some species of *Barringtonia* but the placentation of the two genera is different (compare Figs. 20 of *Gustavia* with Fig. 8 of *Barringtonia*) based on the few species we have examined or have been described and illustrated in the literature (Thomson 1921; Tsou 1994). The similarities of *Barringtonia* with *Grias* and *Gustavia* suggest links between the Old World tropics and New World tropics among these genera.

Most species of *Gustavia* can be recognized by their spear-shaped septal unit heads as seen in cross-section (Fig. 20G) and their cup-shaped placentae as seen in medial longitudinal section (Fig. 20I–J). However, *Gustavia* Sect. *Hexapetala* lacks these features — their septal unit heads are arrowhead-shaped (Fig. 20B). The placentae of this section (Fig. 20 D), however, are similar to species of *Couroupita* (Figs. 13D–E, H–I). Recognizing *Gustavia* sect. *Hexapetala* as a separate genus is not supported by floral morphology because sect. *Hexapetala* possesses actinomorphic flowers with a broad staminal tube and poricidal anthers, features not found in any other genus of Lecythidaceae but occurring in all other species of *Gustavia*. The similar placentation of *G.* sect. *Hexapetala* and the *Couroupita* clade suggest that the evolution of zygomorphy (excluding the obliquely zygomorphic *Cariniana* clade), which was first manifested in *Couroupita*, may have evolved from an actinomorphic-flowered ancestor similar to species of *G.* sect. *Hexapetala* clade. Supporting this idea is our field observations that some species of *Gustavia* are often very slightly zygomorphic even though they do not have a staminal ring extension as in other species of zygomorphic-flowered New World Lecythidaceae.

Recently some species of *Cariniana* were transferred to *Allantoma* based on several characters, the most significant being floral texture, symmetry, and texture (androecium membranous and zygomorphic and petals flat at apices in *Cariniana* and androecium fleshy and actinomorphic and petals hooked at apices in *Allantoma*). In addition, and leaves are different (tertiary veins usually reticulate in *Cariniana* and percurrent in *Allantoma*). The presence of unilaterally winged seeds (Mori et al., in press) is common to both genera. This is also supported by the nearly identical placentae of *Allantoma* (Fig. 7) and *Cariniana* (Fig. 10). Those species with membranous, zygomorphic flowers remained in *Cariniana* and those with fleshy, actinomorphic flowers were transferred to *Allantoma* by Huang et al. (2008). Based on morphological data, *Cariniana* and *Allantoma* were recovered as sister clades (Huang et al. 2008) but when molecular data were added their relationship was not resolved.

The monotypic *Bertholletia excelsa* clade (Huang et al., in press) possesses morphological features (2-lobed calyces [Fig. 9F], a unique type of secondarily indehiscent fruit, and bony seed coats) that allow this species to be easily separated from other Lecythidaceae. However, these characters may not be good indicators of relationships. For example, the 2-lobed calyces are clearly evolved from ancestors with 6-lobed calyces (Tsou & Mori 2007) and secondary fruit indehiscence is found is several other species and seems to be a response to different dispersal agents, in this case rodents such as agoutis (Mori & Prance 1990). The bony seed coat, even though it is found only in *B. excelsa*, also appears to be an adaptation to seed dispersal by rodents. The plateau columnar placentation (Fig. 4B, Fig. 9E) also supports maintaining *Bertholletia* as a genus; however, *Lecythis brancoensis* of the *L. chartacea* clade, possesses a similar type of placenta (Fig. 21F) but with more rows of ovules than found in *B. excelsa*. With further studies, if *Bertholletia excelsa* (Bonpland 1808) were found to be embedded in a clade including only species currently placed in *Lecythis* the *Bertholletia* clade (Fig. 2) would have to be recognized as *Lecythis* because that genus was published before the publication of all other New World genera (Loefling 1758).

In addition to the unilaterally winged seeds of *Allantoma* and *Cariniana*, the only other genus with winged seeds is *Couratari* but the wings of species of this clade are circumferential versus unilateral and have a different origin (flattened aril in the former two genera and flattened seed in the latter genus) (Tsou & Mori 2007). The placentation of the *Allantoma* and *Cariniana* clades differ from the *Couratari* clade by the columnar placenta of the first two genera (Figs. 7C, 10D, I;) versus arched columnar placentae of *Couratari* (Fig. 12C, F, J), and spear-shaped (Figs. 7B–C) versus thick septal head extensions (Figs. 12B, E, H).

The *Corythophora* clade forms a monophyletic group supported by morphological (Huang et al., in press) and molecular data (Fig. 1). However, the morphological features need to be applied in combination using the following characters: squamose inflorescence rachises, non-coiled androecial hoods, the presence of both fertile and sterile (= fodder) pollen, and thick-walled campanulate or cylindric fruits. On the other hand, the anchor-shaped septal unit heads (Fig. 3E) are not found in any of the other clades of New World Lecythidaceae.

The three clades of *Eschweilera*, as circumscribed by Mori and Prance (1990), were recovered by Huang (2010). These are the *E. tetrapetala* (= *E.* sect. *Tetrapetala* in Mori & Prance, 1990), *E. integrifolia*, and *E. parvifolia* (includes the type *E. parvifolia*) clades. The *E. tetrapetala* clade is similar in placentation to the other two clades in its 2-locular ovaries and anvil-shaped septal head unit but the ovules are arranged in several rows (Fig. 18B–H) instead of in a single row as they are in the *E. integrifolia* (Fig. 14B–C, E) and *E. parvifolia* (Fig. B, G) clades (Huang et al., in press). With the insight provided by a better understanding of placentation, we discovered that the *E. tetrapetala* clade also differs in having a single-coiled instead of double-coiled (*E. parvifolia* clade), or triple-coiled (*E. integrifolia* clade) androecial hood (Huang et al., in press) and a short, basal aril instead of a lateral aril as found in the type of the genus and the *E. parvifolia* clade in general; thus, based on these differences we hypothesize that the *E. tetrapetala* clade represents generic status.

The presence of triple-coiled androecial hoods and spreading arils (a few species, e.g., *E. antioquensis* Dugand & Daniel and *E. jacquelynieae* S.A. Mori may have neither spreading or lateral arils) characterize the *E. integrifolia* clade while double-coiled androecial hoods and lateral arils separate the *E. parvifolia* clade. These two clades are the only ones with a single row of ovules (e.g., Figs. 14C, 15B, 16(B), 17(B). An exception is *Eschweilera collinsii*, which has triple-coiled androecial hoods and spreading arils and falls within the *E. integrifolia* clade based on these characters and molecular data (Huang, in review), but its placentation differs from the *E. integrifolia E. parvifolia* clades by having more than one row of ovules and by possessing a distinct space between the attachment of the ovules and the base of the lower/upper septum (Fig. 16K).

Within *Lecythis* as defined by Mori and Prance (1990), Huang et al. (in press) recovered the following clades: *L. chartacea*, *L. corrugata*, *L. ollaria*, *L. pisonis*, and *L. poiteaui* clades (Fig. 1). There is morphological (Huang et al., in press) and molecular (Huang, 2010) support for recognizing the *L. corrugata*, *L. ollaria*, and *L. pisonis* clades as separate genera but placentation characters do little to support or negate these hypotheses.

Based on the studies of Mori et al. (2007) and Huang et al. (in press) it has become apparent that the generic concepts of *Eschweilera* and *Lecythis* are not monophyletic as intimated by Mori and Prance (1990). The placentation data reported in this paper add support to this suggestion and are also useful in confirming the generic status of other genera in other genera of New World Lecythidaceae.

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TABLE LEGENDS

Table I. Terms used to describe the placentation of New World Lecythidaceae. These terms are illustrated in Figures 3 to 7 and in the remaining figures used to illustrate the placentation of the currently recognized clades of Lecythidaceae.

TABLE I
TERMS USED TO DESCRIBE THE PLACENTATION OF NEW WORLD LECYTHIDACEAE

The terms are arranged in groups of characters and not alphabetically. Each group of terms is defined under the section heading.

SECTIONS

Sections are made either at right angles to the main axis of the ovary (Fig. 2A), parallel through the main axis of the ovary (Fig. 2G), or parallel but not through the main axis of the ovary (Fig. 2I). All of the data obtained for this study were made with one or the other or a combination of these three types of sections.

Cross (= transverse) **section**. A section made at right angles to the long axis of an ovary (Fig. 2A). This type of section facilitates determining the number of locules, number of ovules per locule, the number of columns of ovules on the placenta, the relationship of the septa to the placentae, and the attachment of the ovules to the placenta. The most complete information is obtained by making a section through the middle of the placenta.

Medial longitudinal section. A section through the middle and parallel to the long axis of an ovary such that the stylar canal is visible (Fig. 2G). This type of section facilitates determining the shape and orientation of the locules, numbers of ovules per locule, the attachment of the ovules to the placenta, the shape of the placentae, and the relationship of the lower to the upper septum (i.e., what percent the lower septum of the lower/upper septum occupies when viewed in this section).

Longitudinal section. A section along the long axis of an ovary but not through the middle of the ovary. This type is useful for removing the outer wall of the ovary to reveal the number of columns and rows of ovules (Figs. 2I).

SEPTUM (pl. = septa)

A wall-like partition that divides an ovary into chambers called locules (Fig. 2A, C). The septa are made up of the walls of adjacent carpels (Fig. 2D).

Lower septum. A wall-like partition of a locule located basally to an articulation best seen in medial longitudinal section of an ovary (Fig. 2G). The upper septum is sometimes not apparent.

Upper septum. A wall-like partition of a locule located apically to an articulation as seen in a medial longitudinal section of an ovary (Fig. 2G). The upper septum is sometimes not apparent.

Lower/upper septum. The combined lengths of the lower and the upper septa as seen best in medial longitudinal section of an ovary; the two septa are divided by a septal articulation (Fig. 2H). The lower septum gives rise to the placenta and the upper septum, when present, develops into the columella of the fruit.

Lower/upper septum articulation. A joint located between the lower septum and the upper septum as seen in a medial longitudinal section of an ovary. The articulation can be represented by a thin line or a narrow gap (Fig. 2H)

Apex of lower septum truncate. The apical end of the lower septum forms a horizontal line or gap as seen in a medial longitudinal section (Fig. 2K). This feature is not obvious in species that have armed lower septa, e.g., species of *Grias*, *Gustavia*, and *Couroupita.*

Apex of lower septum invaginate. The apical end of the lower septum forms a slight depression into which the upper septum is inserted as seen in medial longitudinal section (Fig. 2L).

Apex of lower septum armed. The apical end of the lower septum is separated into two prolongations (the dashed lines in Fig. 2J) upward as seen in medial longitudinal section. The arms of the lower septum surround the stylar canal.

Septal unit. The shape of a septum is revealed in crosssection (Fig. 1D– F). The septal unit consists of tissue from adjacent carpels and includes the septal unit stalk, the septal unit head, and sometimes basal extensions from the septal unit head. There are 4 septal units in a 4-locular ovary, 6 in a 6-locular ovary, etc.

Septal unit stalk. The part of the septum that departs from its departure from the wall of the ovary to the point at which it expands into the septal unit head (Fig. 2F). The septal unit stalk is derived from the walls of adjacent carpels and, with the septal unit head, makes up the septal unit. This character is observed in cross-section.

Septal unit head. The expanded part located at the apex the septal unit (Fig. 2F). One-half of the septal unit head is derived from one carpel and the other half is derived from the adjacent carpel. This character is seen in cross-sections.

Basal extensions. Referring to basal extensions from a septal unit head to which the ovules are attached (Fig. 2F). There are two basal extensions in a septal unit, each of which is derived from an adjacent carpel. This character is seen in cross-sections. Some species may not have basal extensions.

SEPTAL UNIT SHAPES

This section refers to shape of the septal unit head and their basal extensions (when present) as seen in cross-sections. In order to observe this character the section must be made through the middle of the placenta where the ovules are attached.

Septal unit anchor-shaped. A septal unit in which the sepal unit head expands at the apex to form a broad and rounded head that appears anchor-like as seen in cross-sections of an ovary (Fig. 3E─E^2).

Septal unit anvil-shaped. A septal unit in which the septal unit head is truncate at the apex as seen in cross-sections (Fig. 3F). This type is only found in species with 2-locular ovaries.

Septal unit arrowhead-shaped. A septal unit head that possesses basal extensions. (Fig. 3). Combined with the septal unit stalk the entire structure looks like an arrow.

Septal unit spear-shaped. A septal unit head that expands at the apex to form a triangle and tapers at the base to the septal unit stalk (Fig. 3A– A^3). Species that have equal sides, i.e., appearing like a diamond, are also classified as spear-shaped.

LOCULES

Locules are the chambers of an ovary (Fig. 2C). The number of locules is observed in a cross-section of the ovary while all other characters of locules are observed in a medial longitudinal section.

Locule number. The number of chambers as they appear in a cross-sections of an ovary (Figs. C, E). In order to reveal the correct number of locules the section should be made through the middle of the placenta. The locules are shaded in Fig. 3A.

Locule orientation (Fig. 4A–E). The orientation of a locule as it appears in relation to the main axis of the ovary. This feature is seen in a medial longitudinal section.

Locule orientation horizontal (Fig. 4C). A locule oriented horizontally to the central axis of the ovary at an angle of more than 60 degrees as seen in a medial longitudinal section. A perfectly horizontally oriented locule would have an angle of 90 degrees.

Locule orientation oblique (Figs. 4D). A locule oriented obliquely with the central axis of the ovary at an angle between 30 and 60 degrees as seen in a medial longitudinal section.

Locule orientation vertical (Figs. 4A–B). A locule oriented vertically to the main axis of the ovary or at an angle less than 30 degrees as seen in medial longitudinal section.

Locule width (Fig. 4F–I). The location of the greatest width of a locule measured between the outside and inside walls as seen in medial longitudinal section.

Locule width at apex (Fig. 4F) The greatest width of a locule occurs at the apex of the locule as seen in medial longitudinal section.

Locule width intermediate (Fig. 4I). The greatest width of a locule occurs between the middle and the apex of the locule as seen in medial longitudinal section.

Locule width at middle (Fig. 4G). The greatest width of a locule occurs at the middle of the locule as seen in medial longitudinal section.

Locule width at base (Fig. 4F). The greatest width of a locule occurs at the base of the locule as seen in medial longitudinal section.

PLACENTATION

In the broadest sense the tissue to which ovules are attached within an ovary. We consider New World Lecythidaceae to possess axile placentation limited to the tissue derived from a single carpel.

Placenta (pl. = placentae) (Fig. 5). Tissue derived from a single carpel to which the ovules are attached. Under our definition, the number of placentae in an ovary is the same as the number of locules.

Placental unit (Fig. 2B). One of two parts of a placenta located in the same locule and derived from the same carpel. Do not confuse this with septal unit.

Placenta incipient (Fig. 4A, 5D). A placenta barely expanded from the septum and with a very long ovule-free area from the base of the lower septum to the first ovules as seen in medial longitudinal section. This type of placentation is associated with apical, pendulous ovules.

Placenta laminar cup-shaped (Figs. 5A). A type of placenta in which the ovules are attached to long basal extensions of the septal unit heads as seen in cross-sections (arrow-head shaped, Fig. 3C) and with an ovule-free area from the base of the lower septum to the attachment of the first ovules as seen in medial longitudinal section. The placentae in two adjacent locules arch or curve from the base to form long septal unit bases.

Placenta cup-shaped (Fig. 5B, C). Same as the preceding except the septal unit basal extensions are absent making them spear-shaped in cross-sections (Fig. 3A). In medial longitudinal section the combined septa appear cup-shaped. This type of placenta is similar to laminar cup-shaped placentae but the basal extensions of the septal unit heads are absent (Fig. 3A–A^1).

Placenta narrow columnar (Fig. 4G). A type of placenta that is narrow throughout the length of the lower septum and with a short ovule-free area on the lower septum from the base of the locule to attachment of the first ovules as seen in medial longitudinal section. In this type, the area where ovules are attached along the lower septum is relatively long (Figs. 6C).

Placenta plateau columnar (Fig. 5G). A type of placenta that has parallel sides and is truncate at apex of the lower septum. In this type, the area where the ovules are attached at the summit of the lower septum is relatively short (Figs. 9E).

Placenta spreading (Figs. 5F). A type of placenta derived from a horizontally expanded lower septum as seen in medial longitudinal section. The ovules all appear attached to the floor or near to the floor of the locule.

Placenta arched spreading (Fig. E). A type of placenta derived from a horizontal to slightly slightly horizontally septum as seen in medial longitudinal section. This type differs from spreading aril but has more ovules that appear to arch from the base of the lower septum to its apex (it curves from the base to the apex of the lower septum).

OVULES

An ovule is the organ that contains the egg and, after fertilization, develops into the seed. The ovules are included within locules of an ovary and may differ in their orientation along the lower septum. In Lecythidaceae the ovules always arise from the lower septum.

Ovule insertion (Fig. 6). This feature describes the orientation of the ovules in relation to the main axis of the ovary as seen in medial longitudinal section. Ovules may have different orientations along the same lower septum. They can be oriented vertically (2J), horizontally (Fig. 6D), obliquely outward and upward (Fig. 6C at the apex), obliquely outward and downward (Fig. 6C at the base).

Ovule columns. Vertically oriented lines of ovules as they appear in a locule of an ovary. This feature is seen in a longitudinal section that removes the outside wall of the ovary (Figs. 6B, F–H) or in a cross-sections (Fig. 6I). Because there are usually fewer columns at the base and apex of the count should be made in the middle of the placenta.

Ovule rows (Fig. 6B). Horizontally oriented lines of ovules as they appear in a locule of an ovary. A longitudinal section that removes the outside wall of a locule allows this feature to be seen with the most accuracy. It can also be observed in medial longitudinal sections.

Ovule orientation pendulous (Figs. 6E, 8I–J). Downward oriented ovules as seen in medial longitudinal sections of an ovary. Only *Barringtonia* and *Grias* have this type of ovule orientation.

Ovule orientation not pendulous. Ovules that are oriented in the following way: vertical, obliquely upward and outward, horizontally, and obliquely downward and outward oriented. These types of orientation are related to the type of placentation and the position on the placenta where the ovules are attached. All ovule orientation, except in species of *Barringtonia* and *Grias*, are is included in this category.