Systematics of Lecythidoideae (Lecythidaceae) with emphasis on *Bertholletia*, *Corythophora*, *Eschweilera*, and *Lecythis*

by

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fulfillment of the requirements for the degree of Doctor of Philosophy,
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ABSTRACT

Systematics of Lecythidoideae (Lecythidaceae): with emphasis on *Bertholletia*, *Corythophora*, *Eschweilera*, and *Lecythis*

by

Ya-Yi Huang

Advisor: Scott A. Mori, Ph.D.

Phylogenetic analyses based on morphological and DNA sequence data were generated to test the monophyly of *Eschweilera* and *Lecythis* and to investigate the relationships of these two genera and their close relatives (*Bertholletia* and *Corythophora*). The final results were applied to questions of taxonomic rearrangements and character evolution in traits related to pollination.

A cladistic analysis based on morphology indicates that *Bertholletia*, *Corythophora*, *Eschweilera*, and *Lecythis* form a clade (the *Bertholletia* clade), but the resolution within the clade is too poor to elucidate the phylogenetic relationships among the genera. Nonetheless, the data support the monophyly of *Corythophora*. *Eschweilera* is divided into two clades: *Eschweilera* section *Tetrapetala* and *Eschweilera* s.s. Whether or not the two clades form a clade remains as unresolved. *Lecythis* is not resolved as monophyletic, but each of the Sections *Corrugata*, *Pisonis*, and *Poiteaui* is monophyletic.

A combined analysis based on morphology and nuclear ITS and plastid *ndhF*, *trnL-F*, and *trnH-psbA* sequence data was conducted to improve the resolution of the phylogenetic tree. The results support the generic circumscriptions of *Bertholletia* and *Corythophora* based on morphology, but suggest the revision of *Eschweilera* and *Lecythis*. *Eschweilera* is paraphyletic and divided into three clades: the *Eschweilera* section *Tetrapetala* clade, the *Eschweilera andina* clade, and the core *Eschweilera* clade. *Lecythis* is polyphyletic and consists of five clades: the *Lecythis* s.s. clade, the *Pachylecythis* clade, the *Lecythis chartacea* clade, the *Holopyxidium* clade, and the Section *Corrugata* clade. Based on the results of these analyses, Section *Tetrapetala* clade merits recognition as an independent genus and should be segregated from *Eschweilera*. On the other hand, the five clades of *Lecythis* are distinct from each other and should be recognized as five separate genera.

Androecial evolution inferred from the resulting phylogeny demonstrates that features such as floral zygomorphy, closed androecia, coiled ligules, and the production of nectar are homoplasious. Evolution of these characters most likely is because of the adaptation in response to pollinator shift and does not simply represent a process of morphological transformation from a simpler to a more complicated structure as previously suggested.

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INTRODUCTION

The Lecythidoideae (Lecythidaceae) are understory, canopy, or emergent trees confined to tropical America (Prance & Mori, 1979). Currently ten genera and about 210 species are recognized in this subfamily (Prance & Mori, 1979; Mori & Prance, 1990b; Mori, 1992, 1995a, 1995b, 2007; Huang et al., 2008). The best-known species of Lecythidoideae is the Brazil nut, *Bertholletia excelsa*, with its edible seeds (Mori & Prance, 1990a). Members of Lecythidoideae encompass endemics with narrow distributions and widespread taxa. They are most abundant and diverse in non-flooded primary forest, but are also found in periodically flooded forest, savanna, gallery forest, and dry forest (Mori & Prance, 1990b). Phylogenetic analyses based on anatomical, cytological, morphological, and plastid sequence data indicate that Lecythidoideae are monophyletic (Morton et al., 1998; Mori et al., 2007).

Traditional taxonomy of Lecythidoideae places great emphasis on floral features, especially on the androecial structure, which is assumed as a likely driving force in floral evolution within the family (Mori et al., 1978; Mori & Boeke, 1987). The ten genera of Lecythidoideae are divided into two groups based on androecial symmetry (Prance & Mori, 1979; Mori & Prance, 1990b; Huang et al., 2008): *Gustavia*, *Grias*, and *Allantoma* have actinomorphic androecia while *Cariniana*, *Couroupita*, *Corythophora*, *Bertholletia*, *Couratari*, *Eschweilera*, and *Lecythis* have zygomorphic androecia. Within each group the genera are distinguished by complexity of the androecial structure supplemented with number of ovary locules and fruit and seed features. Generic concepts established upon these morphological characters were tested in a phylogenetic study based on plastid *ndhF* and *trnL-F* sequence data (Mori et al., 2007). Two main questions arising from that study are that two of the genera (*Eschweilera* and *Lecythis*) may not be monophyletic and that the phylogenetic relationships among major clades are unresolved (Fig. 1 in Mori et al., 2007).

Eschweilera and *Lecythis* represent the largest and the second largest zygomorphic-flowered genera of Lecythidoideae. These two genera, along with *Bertholletia* and *Corythophora*, form the largest clade, which is called the *Bertholletia* clade (Mori et al., 2007). The *Bertholletia* clade is the most diverse of all clades of Lecythidoideae in terms of species richness and morphology (Mori & Prance, 1990b). Traditionally the four genera of the *Bertholletia* clade can be distinguished by two or six sepals, a coiled or non-coiled androecial hood, a two or four-locular ovary, the absence or presence of hood anthers, and the absence or presence of a lateral, basal, or spreading aril (Mori & Prance, 1990b). Generic concepts based on these characters might be problematic because of convergent evolution, which results in the uncertainty of monophyly of *Eschweilera* and *Lecythis* as indicated by Mori et al. (2007). However, the results presented in their study are not sufficient for taxonomic rearrangements due to the lack of resolution in their phylogenetic tree. Therefore this dissertation aims at resolving the problems of generic circumscriptions addressed by Mori et al. (2007) and targets the *Bertholletia* clade recognized in their study.

The objectives of this dissertation are the following: (1) test the monophyly of the *Bertholletia* clade; (2) test the monophyly of *Eschweilera* and *Lecythis*; (3) resolve the phylogenetic relationships within the *Bertholletia* clade; and (4) use the phylogeny as a framework to examine androecial evolution of Lecythidoideae. The dissertation consists of two chapters. In the first chapter, morphological characters used for generic circumscription in Prance and Mori (1979) and Mori and Prance (1990b) were reexamined and those that are parsimony informative were divided into two or more discrete states. A cladistic analysis based on these parsimony-informative characters was conducted to test the monophyly of the *Bertholletia* clade and the monophyly of each of the genera within the clade. In the second chapter, more taxa were added to the data matrix of Mori et al. (2007) and two additional

DNA markers (nuclear ITS & plastid *trnH-psbA* spacers) were included in the analysis. In the final stage, a combined analysis of four DNA markers and morphological characters of the first chapter was conducted. The resulting phylogeny is discussed in relation to geographic distributions of the clades and is used to infer character evolution in floral traits considered important in previous classification.

CHAPTER ONE

A morphological cladistic analysis of Lecythidoideae with emphasis on *Bertholletia*, *Corythophora*, *Eschweilera* and *Lecythis*

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Abstract — A cladistic analysis was conducted to test the monophyly of *Eschweilera* and *Lecythis* as well as to examine the relationships of these two genera and their close relatives: *Bertholletia* and *Corythophora*. The study included 86 species, representing all four genera and covering the range of taxonomic and morphological variation in genera. The data matrix included 41 characters derived from vegetative, floral, fruit, and seed morphology and anatomy. The results based on consensus of all most parsimonious trees indicate that *Bertholletia*, *Corythophora*, *Eschweilera* and *Lecythis* form a clade supporting by stamens arising from the surface of a flat cushion, fertile stamens more than 100, and the presence of an aril. Within the clade, the resolution is not sufficient to establish the monophyly of *Eschweilera* or *Lecythis* or to elucidate the relationships of the clades. Nonetheless, the data support the monophyly of *Corythophora*, which is characterized by a non-coiled ligule, anther dimorphism, and the absence of nectar. *Eschweilera* is divided into two major clades: the *Eschweilera* section *Tetrapetala* clade, which is characterized by the presence of appendages on both the inner and outer surface of the ligule, and the *Eschweilera* s.s. clade,

which is characterized by the presence of a double or triple-coiled ligule. *Lecythis* is not resolved as monophyletic in the analysis, but three sections of *Lecythis* are monophyletic: Section *Corrugata*, which is characterized by a rugose/tuberculate pedicel and hypanthium and anther dimorphism; Section *Pisonis*, which is characterized by oxidation of wounded tissue, a stout style with an annular expansion right below the apex, and sulcate seeds; and Section *Poiteaui*, which is characterized by the presence of leaf papillae on abaxial surface. *Bertholletia* and species of *Lecythis* section *Lecythis* remain unresolved.

INTRODUCTION

Lecythidaceae are small to large trees common in lowland rainforest (Mori & Prance, 1990b). This family comprises three subfamilies (Mori et al., 2007): Foetidioideae, Planchonioideae, and Lecythidoideae. The Foetidioideae have 17 species in one genus. These species are found in East Africa, Madagascar and Mauritius (Mori et al., 2007). The Planchonioideae consist of 59 species in six genera. They are found in tropical Asia, tropical Africa, Australia, and the Pacific Islands (Mori et al., 2007). The Lecythidoideae contain 210 species in ten genera (Prance & Mori, 1979; Mori & Prance, 1990, 1992; Mori, 1995a, 1995b, 2007; Mori et al., 2007; Huang et al., 2008). Species of the Lecythidoideae are confined to tropical America. The Lecythidaceae are monophyletic and each of the subfamilies is monophyletic (Morton et al., 1998; Mori et al., 2007). However, the relationships within the subfamilies are not fully understood, especially within the Lecythidoideae.

Lecythidoideae includes endemics with narrow distribution and widespread taxa. They occupy diverse habitats but are most abundant in non-flooded primary forests (Mori & Prance, 1990b). Species of Lecythidoideae are characterized by fibrous bark; simple, alternate leaves; actinomorphic or zygomorphic androecia; numerous stamens; inferior or half-inferior ovaries; bitegmic ovules; and the presence of cortical bundles (Prance & Mori, 1979).

The taxonomy of Lecythidoideae places great emphasis on floral features, especially on the structure of the androecium. The ten genera of Lecythidoideae can be divided into two groups based on androecial symmetry. Three genera have actinomorphic androecia: *Allantoma* Miers (eight species; Huang et al., 2008), *Grias* L. (nine species; Mori 1979b; Clark & Mori, 2000; Cornejo & Mori, 2010; Mori et al., 2010), and *Gustavia* L. (41 species in three sections; Mori, 1979a; Mori et al., 2007). On the other hand, seven genera have zygomorphic androecia: *Bertholletia* Bonpl. (one species; Prance, 1990b), *Cariniana* Casar. (nine species; Huang et al., 2008), *Corythophora* R. Knuth (four species; Mori & Prance, 1990c), *Couratari* Aubl. (19 species in three sections; Prance, 1990c), *Couroupita* Aubl. (three species; Prance, 1990a), *Eschweilera* Mart. *ex* DC. (93 species in four sections; Mori & Prance, 1990d; Mori, 1992, 1995, 2007), and *Lecythis* Loefl. (27 species in four sections; Mori, 1990, 1995b). Based on comparative morphology, Mori et al. (2007) hypothesized that the actinomorphic androecium is the plesiomorphic state in the Lecythidoideae. Most actinomorphic-flowered genera have their greatest diversity west of the Andes or in western Amazonia, whereas the zygomorphic-flowered genera are most diverse in central Amazonia and the Guianas.

Morton et al. (1998) constructed a phylogenetic analysis to test the monophyly of Lecythidaceae and the monophyly of each of the three subfamilies based on morphological, anatomical, cytological, and plastid *rbcL* and *trnL* sequence data. This study included one species to represent each genus and one individual was sampled for each species. The results indicated that Lecythidaceae are monophyletic and each of the three subfamilies is monophyletic (Fig. 1 in Morton et al., 1998). Mori et al. (2007) performed another analysis to test the monophyly of genera of the subfamily Lecythidoideae based on plastid *ndhF* and *trnL-F* sequence data. This study incorporated more species into the analysis. However, the type species of *Eschweilera* and *Lecythis* were not included and some of the representatives were missing, e.g., *Eschweilera* section *Tetrapetala* S. A. Mori. In addition, *Bertholletia*, *Corythophora*, *Eschweilera*, and *Lecythis* together were monophyletic (the *Bertholletia* clade), but the phylogenetic relationships among them were not fully understood (Fig. 1 in Mori et al., 2007). Within the *Bertholletia* clade, the results further indicated that *Eschweilera* and *Lecythis* may not be monophyletic. My dissertation focuses on systematics of the *Bertholletia* clade and phylogenetic relationships within the *Bertholletia* clade.

Of the four genera, *Bertholletia* was described by Bonpland (1807). *Bertholletia excelsa* Bonpl. (the Brazil nut) is the only species of the genus. It is also the best known species of the entire family because of its edible seeds (Prance, 1990b). *Bertholletia excelsa* can be easily distinguished from the other three genera by two instead of six calyx lobes, operculum falling inside instead of outside the fruit, and by the absence instead of the presence of a fleshy aril. It is widespread throughout Amazonia and the Guianas (Fig. 21 in Mori & Prance, 1990b).

Knuth (1939) established *Corythophora* based on *Corythophora alta* R. Knuth. He separated *Corythophora* from *Lecythis* because all the hood appendages of *C. alta* possess anthers, whereas most species of *Lecythis* do not have hood anthers or only part of the hood appendages have anthers (Mori & Prance, 1990c). He separated *Corythophora* from *Couroupita* by its dehiscent versus indehiscent fruits (Mori & Prance, 1990c). Species of *Corythophora* are limited to Surinam, French Guiana, and Brazilian Amazonia from Manaus to Amapá, where they are found mostly north of the Amazon River (Fig. 23 in Mori & Prance, 1990b).

Eschweilera was first described by De Candolle (1828). Martius (1837) accepted *Eschweilera* as a genus and listed several features of *Eschweilera* distinct from *Lecythis* (e.g., bi-locular ovary). However, many subsequent authors still considered *Eschweilera* as part of *Lecythis* (Endlicher, 1840; Berg, 1856, 1857, 1858). In 1874, Miers maintained the generic status of *Eschweilera* and provided a list of features that distinguished *Eschweilera* from *Lecythis*. The generic status of *Eschweilera* has not changed since then. *Eschweilera* is the largest and the most widely distributed genus of Lecythidoideae. Species of *Eschweilera* range from Veracruz, Mexico, to Rio de Janeiro, Brazil (Fig. 25 in Mori & Prance, 1990b).

In 1758, two years after Loefling died, Linnaeus published Loefling's description of a new genus and a new species, *Lecythis ollaria* Loefl. This was the first valid publication of Lecythidaceae, even before the family status was established. *Lecythis* is the third largest genus of Lecythidoideae, however, it is the most diverse of all genera in terms of floral and fruit features (Mori, 1990c). Species of *Lecythis* are distributed from Nicaragua to Rio de Janeiro, Brazil (Fig. 27 in Mori & Prance, 1990b)

In this study I conducted a phylogenetic analysis of the *Bertholletia* clade based on morphological and anatomical characters. The main purposes of this study are to test the monophyly of *Eschweilera* and *Lecythis* and to address the phylogenetic relationships within the *Bertholletia* clade. To carry out these objectives I included more taxa than the previous studies (Morton et al., 1998; Mori et al., 2007) and added more parsimony-informative characters.

METHODOLOGY

Sampling

This study included 86 ingroup taxa, representing *Bertholletia*, *Corythophora*, *Eschweilera*, and *Lecythis*. Taxon sampling covers the range of morphological variation in genera and sections recognized by Mori and Prance (1990b). Fourteen species were included as outgroup taxa, representing *Gustavia*, *Grias*, *Allantoma*, *Cariniana*, *Couroupita*, and *Couratari*. The selection of the outgroup taxa followed the molecular analysis of plastid *ndhF* and *trnL-F* sequence data, but with fewer species for each genus (Mori et al., 2007). The taxonomy follows Prance and Mori (1979) and Mori and Prance (1990b). The sampled taxa are listed in Table 1.

Data collection

Morphological and anatomical characters were collected based on original observations in the field or based on the images available on the Lecythidaceae Pages (http://sweetgum.nybg.org/lp/index.html). Some characters were derived from herbarium specimens at INB, INPA, MO, NY, and US or pickled collections at NY; and some were derived from the literature.

Leaf fragments used for study of venation patterns and stomata were placed in vials with 50% alcohol and bathed in boiling water for ten minutes. This procedure was repeated two or three times until no further color leached into the solution. After cooling to room temperature, samples were washed with water two or three times, and then changed to a 2% NaOH solution. The NaOH solution was replaced every day until the mesophyll of the leaf became transparent. After clearing, the samples were washed with water to remove NaOH residue. The specimens were then mounted in Hoyer's mounting medium. Alternatively samples were put in a 5% bleach solution until the stomata were visible when viewed with a compound microscope. Anatomical and morphological leaf features followed the terminology of Hickey (1973) and the Leaf Architecture Working Group (1999).

Pollen morphology was studied using scanning electron microscopy (SEM). Pollen samples were taken from herbarium specimens with mature flowers or flower buds at an advanced stage of development. Flowers were boiled until softened and then observed with the dissecting microscope. Anthers were taken from the ligule and the staminal ring for species that have ligular anthers. The anthers were air-dried and pollen was then shed and mounted directly onto a SEM stub and coated with gold. The coated pollen was observed with a Hitachi S2700-SEM.

Characters were divided into two or more discrete states. All multistate characters were coded as non-additive. The following 41 characters were included in the analysis. The data matrix is shown in Table 2.

1. Wood color. 0= sapwood not distinct from heartwood, 1= sapwood distinct from heartwood. Wood color is pale yellow to tan without distinction between sapwood and heartwood in *Gustavia*, *Grias*, *Couroupita* and *Couratari*. In contrast, the heartwood varies from reddish to chocolate brown and the sapwood is pale in *Allantoma*, *Cariniana*, *Corythophora*, *Bertholletia*, *Eschweilera*, and *Lecythis* (Zeeuw, 1990).
2. Oxidation of wounded tissues. 0= absent, 1= present. Wounded tissues oxidize and turn blue in species of *Couroupita*, some species of *Lecythis* (e.g., *Lecythis pisonis* Cambess. and its relatives), and a few species of *Eschweilera* (e.g., *Eschweilera decolorans* Sandwith). The color change is most distinct in wounded flowers and fruits.
3. Leaf pubescence, abaxial surface. 0= absent, 1= present. Some species of *Couratari* section *Echinata* Prance and *Couratari* section *Couratari* Prance have stellate hairs on

the abaxial leaf surface. The abaxial leaf surface is glabrous in all other species of the Lecythidoideae, including species of *Couratari* section *Microcarpa* Prance.

4. Leaf punctate, abaxial surface. 0= absent, 1= present. Many species of *Eschweilera* have black, brown, or reddish-brown dots on the abaxial leaf surface. These dots sometimes are referred as cork warts (Roth, 1984; Fig. VII-4 in Mori & Black, 1987).
5. Leaf papillae, abaxial surface (Fig. 1). 0= absent, 1= present. Papillae are outgrowths of the cuticle. This character is found in *Bertholletia*, some species of *Lecythis* (e.g., *Lecythis poiteaui* O. Berg), and some species of *Eschweilera* (e.g., *Eschweilera congestiflora* (Benoist) Eyma). Mori and Black (1987) hypothesized that papillae may have adaptive value in reducing water loss through the stomata.
6. Domatia. 0= absent, 1= present. Domatia are small cavities at the junction of the secondary vein with the primary vein (Fig. 2). These cavities are often lined with hairs and inhabited by mites (pers. obs.). Domatia are only found in some species of *Cariniana* (e.g., *Cariniana estrellensis* (Raddi) Kuntze).
7. Venation type. 0= eucamptodromous, 1= brochidodromous. In eucamptodromous venation, the secondary veins curve upward and gradually diminish apically inside the margin without forming prominent arches (Fig. 3; Leaf Architecture Working Group, 1990). In brochidodromous venation, the secondary veins join together in a series of prominent arches (Fig. 3; Leaf Architecture Working Group, 1999). The eucamptodromous venation pattern is found in species of *Allantoma*. All other genera have brochidodromous venation pattern.
8. Tertiary venation. 0= percurrent, 1= reticulate. In percurrent tertiary venation, the tertiary veins cross between adjacent secondary veins in parallel paths without branching (Fig. 4A; Leaf Architecture Working Group, 1999). In reticulate tertiary venation, the tertiary veins

join with other tertiary or secondary veins at random angles (Fig. 4B; Leaf Architecture Working Group, 1999). The tertiary venation of species of *Allantoma* and some species of *Gustavia*, *Grias*, *Couroupita* and *Couratari* are percurrent. The tertiary venation of other species of the Lecythidoideae is reticulate.

9. Quaternary venation. 0= dichotomizing, 1= regular polygonal reticulate. In the dichotomizing type the fourth-order veins branch freely, i.e., they do not unite with other veins and are the finest order of venation that the leaf exhibits (Fig. 5A; Leaf Architecture Working Group, 1999). In the regular polygonal reticulate type, the fourth-order veins join to form polygons of similar size and shape (Fig. 5B; Leaf Architecture Working Group, 1999). Fifth order veins are the finest venation in this type. The fourth-order venation of *Allantoma* is dichotomizing. The fourth-order venation of all other species of the Lecythidoideae is regular polygonal reticulate.
10. Areolation. 0= not well developed, 1= well-developed. Areoles are the smallest areas of leaf tissue surrounded by veins of any order (Leaf Architecture Working Group, 1999). The areoles are defined as poorly developed if they are highly irregular in size and shape (Leaf Architecture Working Group, 1999; Fig. 5A); the areoles are well-developed with four or five sides (Fig. 6). The former is found in species of *Allantoma* and the latter is found in all other species of Lecythidoideae.
11. Stomatal type. 0= brachyparacytic, 1= anomocytic. In brachyparacytic stomata, two cells are parallel to the long axis of the guard cells but not completely enclosing them (Fig. 7A; Leaf Architecture Working Group, 1999). In anomocytic stomata, five or more cells surround the guard cells and the cells adjacent to the guard cells are not differentiated in any way from other epidermal cells (Fig. 7B; Leaf Architecture Working Group, 1999). Brachyparacytic stomata are found in *Allantoma*, *Corythophora*, *Bertholletia*,

Eschweilera, *Lecythis*, and some species of *Couratari*. Anomocytic stomata are found in *Gustavia*, *Grias*, *Cariniana*, *Couroupita*, and some species of *Couratari*.

12. Inflorescence scales. 0= absent, 1= present. The rachis of the inflorescence is squamate in *Eschweilera alvimii* S. A. Mori, *Eschweilera nana* (O. Berg) Miers, *Eschweilera tetrapetala* S. A. Mori and species of *Corythophora*.
13. Pedicel. 0= absent, 1= present. Pedicels are absent in species with spike or spike-like inflorescences; pedicels are present in species with racemose or fasciculate inflorescences; pedicels may or may not be present in species that have paniculate inflorescences.
14. Pedicel/hypanthium surface. 0= rugose/tuberculate, 1= not rugose/tuberculate. Species of *Lecythis* section *Corrugata* S. A. Mori have rugose/tuberculate pedicels and hypanthia. This character is not found in any other species of Lecythidoideae.
15. Bract and bracteole persistence. 0= caducous, 1= persistent. The Lecythidoideae have one bract and two smaller bracteoles that enclose young flower buds. The bract is located at the base of the pedicel while bracteoles usually are on the pedicel between the base and the articulation of the pedicel or are located at the base of the pedicel just above the bract. The bract and bracteoles are caducous in most species, but in a few species they are persistent at anthesis (e.g., *Eschweilera bracteosa* (Poepp. ex O. Berg) Miers).
16. Calyx lobe number. 0= entire, 1= two, 2= four, 3= five, 4= six. *Bertholletia excelsa* has two calyx lobes. *Grias neuberthii* J. F. Macbr. and *Eschweilera amazoniciformis* S. A. Mori have four calyx lobes; species of *Allantoma* have five calyx lobes; and species of *Cariniana*, *Couroupita*, *Couratari*, *Lecythis*, and most species of *Eschweilera* have six calyx lobes. Most species of *Grias* have calyces that completely enclose the bud and open circumscissilely or irregularly (Prance & Mori, 1979). For example, the calyces of *Grias*

peruviana are entire or are split into two or four irregular lobes (Mori, 1979b). The calyces of species of *Gustavia* are entire or four or six lobed (Mori, 1979a).

17. Mucilage ducts in sepals (Fig. 8). 0= absent, 1= present. Several species of *Lecythis* section *Lecythis* S. A. Mori have mucilage-bearing ducts in the sepals (e.g., *Lecythis alutacea* (A. C. Sm.) S. A. Mori). The composition and function of the mucilage is unknown.
18. Petal number. 0= four, 1= five, 2= six, 3= eight. Species of *Grias* and some species of *Eschweilera* (e.g., *E. tetrapetala*) have four petals; species of *Allantoma* have five petals; species of *Cariniana*, *Corythophora*, *Couratari*, *Couroupita*, *Lecythis*, and most species of *Eschweilera* have six petals; and species of *Gustavia* have six, eight, or twelve petals.
19. Petal texture. 0= fleshy, 1= not fleshy. When the flowers are fresh, the veins are invisible in fleshy petals when viewed with transmitted light. In contrast, the veins are visible in non-fleshy petals. The fleshy petals are found in *Allantoma* and *Grias*. The remaining genera of Lecythidoideae, with a few exceptions, have non-fleshy petals.
20. Androecial symmetry. 0= actinomorphic, 1= zygomorphic, 2= obliquely zygomorphic. In Lecythidoideae, *Gustavia*, *Grias*, and *Allantoma* have actinomorphic androecia while the remaining genera have zygomorphic androecia. Characteristic of actinomorphic androecium is that the basal portions of the filaments fuse and elongate to form a tube (Fig. 9A). Within genera that have zygomorphic androecia, the androecium of *Cariniana* is only slightly zygomorphic. The androecium of *Cariniana* also forms a tube, which differs from the tube of actinomorphic species in that one side of the tube elongates more than the other (Fig. 9B). This type of androecium is called obliquely zygomorphic. In *Bertholletia*, *Corythophora*, *Couratari*, *Couroupita*, *Eschweilera*, *Lecythis*, the androecium consists of a flat, donut-shaped cushion and a strap-like structure, which is

expanded from one side of the cushion. The strap-like structure curves over the summit of the ovary (Fig. 9C) and is called the ligule.

21. Stamen attachment. 0= on the rim of the tube, 1= on the rim and upper inner surface of the tube, 2= on the inner surface and the rim of the tube, 3= on the surface of a flat cushion. The stamens arise directly from the rim of the staminal tube in *Gustavia* (Fig. 9A); the stamens arise from the rim and the upper inner surface of the staminal tube in *Grias*; the stamens arise from the rim and the entire inner surface of the tube in *Allantoma* and *Cariniana* (Fig. 9B); and the stamens of zygomorphic androecium arise from the flat, donut-shape cushion. Stamens of zygomorphic androecia surround the style and form a staminal ring (Fig. 10A). In most species the distal part of the ligule bears appendages, which are separated from the staminal ring by a stamen/appendage-free area. The appendages may or may not bear anthers. The only known exception is found in *Couroupita nicaraguarensis* DC., which possesses a ligule without a stamen/appendage-free area (Fig. 10B). The appendages-bearing area of the ligule is defined as the hood in Mori and Prance (1990b).
22. Fertile stamens. 0= less than 50, 1= more than 100. Fertile stamens are less than 50 in *Allantoma* and most species of *Cariniana*, except *Cariniana ianeirensis* R. Knuth, which has about 150 fertile stamens. There are less than 100 fertile stamens in *Couratari*. All other genera of Lecythidoideae have more than 100 fertile stamens. Species of *Cariniana* and *Couratari* included in this study have less than 50 fertile stamens. Therefore this character is divided into two states: less than 50 and more than one 100.
23. Ligule. 0= not coiled, 1= single-coiled, 2= double or triple-coiled, 3= single or double-coiled with an external flap. The ligule is only found in zygomorphic-flowered genera. It is absent in *Gustavia*, *Grias*, *Allantoma*, and *Cariniana* and is coded as inapplicable for

these four genera. The ligule is not coiled (Fig. 11A) in all species of *Couroupita*, *Bertholletia*, *Corythophora*, and most species of *Lecythis*. A single coil (Fig. 11B) is found in some species of *Eschweilera* (e.g., *E. alvimii*) and *Lecythis* (e.g., *Lecythis minor* Jacq.). Double or triple coils of ligule (Fig. 11C) are characteristic of most species of *Eschweilera*. In *Couratari*, the ligule curves inward to form a single or a double coil and then curves outward to form an external flap (Fig. 11D).

24. Ligule appendages position. 0= on one side of the ligule, 1= on both sides of the ligule, 2= at apex of the ligule. Ligule appendages are located only on the inner surface of a non-coiled ligule in species of *Couroupita*, *Corythophora*, and some species of *Lecythis* (Fig. 10B); or only on the outer surface of the ligule coils in *Couratari*, most species of *Eschweilera*, and a few species of *Lecythis* (Fig. 11C); on both the inner and outer surfaces of the ligule in *Eschweilera nana* and species of *Eschweilera* section *Tetrapetala* (Fig. 11B); and at the apex of the ligule in *Bertholletia excelsa*, two species of *Eschweilera* (*E. congestiflora* & *E. simiorum* (Benoist) Eyma) and most species of *Lecythis* section *Lecythis* (Fig. 11A).
25. Anthers in the ligule. 0= absent, 1= present. *Bertholletia excelsa*, *Corythophora amapaensis* Pires ex S. A. Mori & Prance, *Corythophora labriculata* (Eyma) S. A. Mori & Prance, *Lecythis corrugata* Poit., *Lecythis confertiflora* (A. C. Sm.) S. A. Mori, and *Lecythis pneumatophora* S. A. Mori, and species of *Couratari*, *Eschweilera*, and *Lecythis* section *Lecythis* lack anthers in the ligule while *Corythophora alta*, *Corythophora rimosa* W. A. Rodrigue, *Lecythis persistens* Sagot, and species of *Couroupita*, *Lecythis* section *Pisonis* S. A. Mori and *Lecythis* section *Poiteaui* S. A. Mori have anthers in the ligule. Morphologically pollen of the ligular anthers may or may not differ from pollen of the anthers in the staminal ring. In *Couroupita guianensis* Aubl. and *C. nicaraguarensis*,

pollen of the ligular anthers has a rugose surface and remains in tetrads whereas its pollen of the staminal ring has a smooth surface and is released in monads (Mori et al., 1980; Tsou, pers. commun.). In *Lecythis pisonis* and *Lecythis zabucajo* Aubl., ligular pollen does not differ from pollen of the staminal ring in morphology. However, ligular pollen turns black later at anthesis, whereas pollen of the staminal ring does not change color (Mori et al., 1980; pers. obs.). Ligular pollen in species of *Corythophora* and *Lecythis* section *Poiteaui* (pers. obs.) is not in tetrads and does not change color during anthesis. *In vitro* experiments indicate that ligular pollen of *Couroupita guianensis* and *Lecythis pisonis* does not germinate while 21% of the pollen of the staminal ring in the former species and 48% in the latter species germinate (Mori et al., 1980). It is not known if the ligular pollen of other species is sterile.

26. Closed androecium. 0= absent, 1= present. Species of *Gustavia*, *Grias*, *Allantoma*, *Cariniana*, *Couroupita*, and some species of *Lecythis* (e.g., *Lecythis idatimon* Aubl.) have open androecia that allow potential pollinators and predators to reach the pollinator rewards easily. In contrast, species of *Bertholletia*, *Corythophora*, *Couratari*, and *Eschweilera*, and some species of *Lecythis* (e.g., *L. ollaria*) have closed androecia. The hood of these species presses against the staminal ring and limits the entry to pollinators with enough strength to open the hood. The degree of limitation depends on the tightness of the hood against the ring. Only pollinators of the right body size have enough strength to push their way into the flowers. An example was described in a pollination study of *Corythophora amapaensis* and *C. rimosa* (Mori & Boeke, 1987). Flowers of the former species are larger and effective pollinators tend to be larger bees than those that pollinate the latter species. Mori and Boeke (1987) observed that smaller trigonid bees similar to the pollinators of *C. rimosa* were not able to enter the flowers of *C. amapaensis*.

27. Pollen aggregation. 0= monads, 1= tetrads. Most species of the Lecythidoideae have pollen in monads. Pollen in tetrads is only found in the ligule of *Couroupita guianensis* and *C. nicaraguarensis* (Mori et al., 1980; Tsou, pers. comm.). *In vitro* experiments demonstrated that pollen in tetrads does not germinate (Mori et al., 1980).
28. Anther dimorphism. 0= absent, 1= present. When the flowers are fresh, all of the anthers in the same flower have the same color in most species of Lecythidoideae. The only known exceptions are found in species of *Corythophora* and *Lecythis* section *Corrugata*. *Corythophora alta*, *C. rimosa*, and *Lecythis persistens* have anthers in the ligule. The ligular anthers of these species are yellow or orange while their anthers in the staminal ring are white. *Corythophora amapaensis*, *C. labriculata*, *Lecythis corrugata*, *L. confertiflora*, *L. idatimon*, and *L. pneumatophora* do not have ligular anthers. In the staminal ring, anthers of the innermost few rows (near ligule) of these species are orange or dark yellow while the remaining anthers are white or light yellow.
29. Nectar. 0= absent, 1= present. Nectar is found in *Bertholletia excelsa*, *Couratari*, *Eschweilera*, and some species of *Lecythis*, e.g., *L. confertiflora*. In *Couratari* and *Eschweilera*, nectar is produced from the modified appendages located at the apex of the ligule coil (Prance, 1990c; Mori & Prance, 1990c); in *Bertholletia excelsa*, nectar is produced from the base of ligular appendages (pers. obs.); in species of *Lecythis*, nectar is produced from the base of ligular appendages (e.g., *L. confertiflora*) or from the base of the stamens of the staminal ring (*Lecythis persistens* Sagot subsp. *aurantiaca* S. A. Mori; Mori & Boeke, 1987).
30. Style. 0= absent, 1= slender, 2= stout. The style is absent in *Allantoma lineata* (Mart. ex O. Berg) Miers and some species of *Gustavia* (Fig. 12A); the style is slender in species of *Lecythis* sections *Corrugata* and *Poiteaui*, some species of *Cariniana*, *Allantoma*, and

Lecythis section *Lecythis* (Fig. 12B); and the style is stout in species of *Couroupita*, *Couratari*, *Eschweilera*, *Lecythis* section *Pisonis*, and some species of *Allantoma*, *Cariniana*, *Grias*, and *Gustavia* (Fig. 12C).

31. Style apex. 0= with annular expansion, 1= without annular expansion. An annular expansion right below the apex of the style (Fig. 13) is only found in species of *Lecythis* section *Pisonis* and some species of *Couratari* (e.g., *Couratari stellata* A. C. Sm.) have.
32. Ovary locules. 0= two, 1= three, 2=four, 3= five or six. Most species of *Corythophora* and most species of *Eschweilera* are two-locular; species of *Couratari*, *Cariniana*, and most species of *Allantoma* are three-locular; species of *Grias*, *Corythophora labriculata*, and *Lecythis*, and some species of *Eschweilera* and *Gustavia* are four-locular. *Allantoma lineata* is four or five-locular; and *Couroupita* and some species of *Gustavia* are six-locular.
33. Operculum. 0= absent, 1= present. The operculum is absent in species of *Gustavia*, *Grias*, and *Couroupita*; the operculum is present in species of *Allantoma*, *Cariniana*, *Couratari*, *Corythophora*, *Bertholletia*, *Eschweilera*, and *Lecythis*.
34. Operculum dehiscence. 0= indehiscent, 1= dehiscent. In species of *Allantoma*, *Cariniana*, *Couratari*, *Corythophora*, and *Eschweilera* and most species of *Lecythis*, the operculum falls spontaneously from the fruit and release the seeds. In *Bertholletia excelsa*, the operculum is also dehiscent, however, it falls inside the fruit and the opening is smaller than the seeds. The seeds of *B. excelsa* remain inside the fruit at maturity. The operculum is indehiscent in *Lecythis gracieana* S. A. Mori, *Lecythis parvifructa* S. A. Mori, and *Lecythis prancei* S. A. Mori.
35. Seeds embedded in pulp (Fig. 14). 0= absent, 1= present. This character is only found in species of *Couroupita*. The seeds of *Couroupita* cannot be easily separated from the

surrounding pulp, which is derived from the proliferation of the septa and the placentae (Schoenberg, 1983). Although the seeds of *Gustavia* and *Grias* are surrounded by pericarp, it is not juicy and pulpy and the seeds can be easily removed from the fruit.

36. Seeds sulcate. 0= absent, 1= present. The seeds of species of the *Lecythis* section *Pisonis* have longitudinal grooves or furrows (sulci; Fig. 15). This character is not found in any other species of the Lecythidoideae.
37. Seed trichomes. 0= absent, 1= present. Seed trichomes are an outgrowth of the exotesta (Tsou & Mori, 2002). This character is only found in species of *Couroupita*.
38. Unilateral seed wing (Fig. 16A). 0= absent, 1= present. *Allantoma* (except *A. lineata*), *Cariniana*, and *Couratari* are the only genera of Lecythidoideae that have seed wings. Tsou and Mori (2002) have demonstrated that unilateral seed wings in *Allantoma*/*Cariniana* and circumferential seed wings in *Couratari* are different, both in origins and structures. Thus, seed wings are coded as two different characters. The unilateral seed wing originates from the mesophyll of the outer integument of the ovule, there is no exotesta in the seed wing, and the seed coat has branched vascular bundles but no fibers (Tsou & Mori, 2002). This character is found in species of *Cariniana* and *Allantoma*, with the exception of *A. lineata*. Seeds of *A. lineata* have no unilateral wings but have rich oil content, which allows them to float for at least six months (Ducke, 1948). Species of *Cariniana* and *Allantoma* that have seed wings are wind dispersed, whereas *A. lineata* is water dispersed. A cladistic study of *Cariniana* and *Allantoma* indicated that the seed wing has been lost in *A. lineata* (Huang et al., 2008), however, a vestigial wing is observed (Fig. 16B). This suggests that the loss of seed wing is probably because of adaptation for water dispersal.

39. Circumferential seed wing (Fig. 16C). 0= absent, 1= present. The circumferential seed wing originates from both the exotesta and the outer layers of mesotesta of the seed body, the seed wing has an exotesta, and the seed coat has unbranched vascular bundles and fibers (Tsou & Mori, 2002). This character is only found in species of *Couratari*.
40. Aril (Fig. 17). 0= absent, 1= lateral, 2= spreading, 3= basal. In most species of Lecythidoideae, the seeds are attached to the ovary wall through a well-developed funicle that may or may not be surrounded by a fleshy aril. Arils are not developed in species of *Grias*, *Allantoma*, *Couroupita*, *Cariniana*, *Bertholletia excelsa*, *Couratari*, *Eschweilera tenuifolia* (O. Berg) Miers, most species of *Gustavia*, and a few species of *Lecythis* (Prance & Mori, 1979; Mori & Prance, 1990b). For species that have a well-developed aril, the position of the aril is of taxonomic importance. Most species of *Eschweilera* have an aril running along the side of the seed (lateral) and some species of *Eschweilera* have an aril spreading around the seeds (spreading). The spreading aril may cover only the bottom part of the seed or it may cover the whole seed. Some species of *Gustavia*, all species of *Corythophora*, a few species of *Eschweilera*, and most species of *Lecythis* have an aril at the base of the seed (basal).
41. Cotyledons. 0= undifferentiated or small scales, 1= leaf-like, 2= fleshy. Cotyledons are undifferentiated or reduced to small scales in *Allantoma lineata*, *Bertholletia excelsa*, and all species of *Corythophora*, *Eschweilera*, and *Lecythis*. Species of *Allantoma* (except *A. lineata*), *Cariniana*, *Couratari* and *Couroupita* have leaf-like cotyledons; and species of *Gustavia* have fleshy cotyledons.

Excluded characters

Several characters were explored for possible use, but were excluded from the analysis. Characters of calyx imbrication and orientation and fruit shape and size are too variable and the variation is continuous and inconsistent. It is difficult to divide the variation into discrete states and code each taxon accurately. Flower color is useful in many occasions, but is difficult to code. For example, many zygomorphic-flowered species have a petal color different from the androecium; some have different colors at different parts of the petals (e.g., white petals with pink margins/apex); and some have different color at different stages of anthesis, e.g., flowers of *Lecythis pisonis* are purple at early stage and become completely white when flowers are older. Characters of seed veins are very distinct in some species of *Lecythis*, however, variation of those characters is not fully understood and many taxa do not have any information for character coding. Another excluded character is resin residue on the surface of the flowers or immature fruits. The presence of resin was not formally recorded in Lecythidoideae, but was only mentioned occasionally on the labels of a few herbarium specimens. It was first found in dry fruits of species of the *Lecythis* section *Corrugata*, but more was discovered in species of *Eschweilera*. More study is needed before this character can be used for phylogenetic analysis.

Phylogenetic analysis

WinClada (Nixon, 1999) was used to create the data matrix. Characters were equally weighted and all multistate characters are coded as non-additive. The parsimony-based program “Tree analysis using New Technology” (TNT) was used to generate phylogenetic trees (Goloboff, 2008). A Maximum of 1,000 trees was held. The combination of the following algorithms was applied for tree search: Ratchet (RAT), Tree-Drifting (DFT), Sectorial-Searches (SS), and Tree-Fusing (TF). The search strategy included two stages. The purpose of the first stage was to find the shortest tree with the optimal score by performing 200 replicates of RAT, 50 replicates of DFT, and random SS. The resulting trees were then submitted to perform five runs of TF. The purpose of the second stage was to test the correctness of the consensus by finding the optimal score 20 times. Characters were optimized using the fast option of Winclada. Branch support was constructed by Bootstrap analysis with 1000 replications, 10 random taxon entry sequences per replication, and one tree saved per replication.

RESULTS

There are 41 characters included in morphological data matrix. All characters are informative. Cladistic analysis generated 125 equally parsimonious trees of 105 steps with a consistency index (CI) of 0.53 and a retention index (RI) of 0.88. One of these trees is shown in Fig. 18, and the strict consensus of all 125 trees is shown in Fig. 19. The topology of strict consensus indicates that *Bertholletia*, *Corythophora*, *Eschweilera*, and *Lecythis* together (the *Bertholletia* clade) are monophyletic (Fig. 19). Within the *Bertholletia* clade, the resolution further supports the monophyly of *Corythophora* and the monophyly of a large clade of *Eschweilera* that includes all species except species of *Eschweilera* section *Tetrapetala* and *Eschweilera congestiflora*, *E. nana*, and *E. simiorum*. Species of *Eschweilera* section *Tetrapetala* along with *E. nana* form a clade separate from most species of *Eschweilera*. *Lecythis* is not resolved as monophyletic in the analysis, but *Lecythis* sections *Corrugata*, *Pisonis*, and *Poiteaui* are monophyletic; *Bertholletia excelsa*, *Eschweilera congestiflora*, *E. simiorum* and species of *Lecythis* section *Lecythis* remained as unresolved (Fig. 19; *Lecythis*/*Bertholletia* complex).

DISCUSSION

The monophyly of the ingroup — The strict consensus tree supports the monophyly of the *Bertholletia* clade. This relationship is congruent with previous molecular analysis of plastid *ndhF* and *trnL-F* sequences (Mori et al., 2007). Most clades recognized in each of the most parsimonious (MP) trees are similar; however, the relationships among these clades may be different in different MP trees because of different tree topology. Different tree topology changes the character optimization in different MP trees and results in different synapomorphies that support the monophyly of the *Bertholletia* clade. Nonetheless, many of the MP trees show that the monophyly of the *Bertholletia* clade is supported by the following synapomorphies: stamens arising from the surface of a flat cushion (Fig. 18-1; character 21), more than 100 fertile stamens (22), and the presence of an aril (40).

Clades and the supporting synapomorphies — Within the *Bertholletia* clade, seven clades are recognized, but the relationships among these clades are not fully resolved. The clades and their supporting synapomorphies are described in the following paragraphs.

Corythophora – This clade includes all four species of *Corythophora* recognized by Mori and Prance (1990c). Synapomorphies of this clade include a non-coiled ligule (Fig. 18-2; character 23), anther dimorphism (28), and the absence of nectar (29). The monophyly of *Corythophora* is congruent with Mori and Prance (1990c) and previous phylogenetic analysis of plastid *ndhF* and *trnL-F* sequences (Mori et al., 2007).

Eschweilera section *Tetrapetala* – This clade includes four species: all three species of *Eschweilera* section *Tetrapetala* (*E. alvimii*, *Eschweilera compressa* (Vell.) Miers, and *E. tetrapetala*) recognized by Mori (1990a) and *Eschweilera nana*, which was included in *Eschweilera* section *Eschweilera* Mori and Prance (Mori & Prance, 1990e). This clade is supported by one synapomorphy (Fig. 18-2): the presence of appendages on both the inner and outer surface of the ligule (24), which is unique to this clade. Within the clade, *E. nana* is sister to the other three species. Character that distinguishes *E. nana* from the other three species is the petal number (18). *Eschweilera nana* has six petals while the other three species have four petals. The sister relationship of *E. nana* and species of Section *Tetrapetala* is a new finding of the present study. Mori (1990a) established Section *Tetrapetala* to accommodate three species that differ from all other species of *Eschweilera* in having four instead of six petals (18), a non-coiled instead of a double or triple-coiled ligule (23), and a basal instead of a lateral or spreading aril (40). The last two characteristics are also shared by *E. nana*. A non-coiled ligule combined with a basal aril occurs in many species of *Lecythis* (Mori, 1990c). All four species of Section *Tetrapetala* in the present study were placed in *Eschweilera* because that they have a two-locular ovary (32), which is an important characteristic of most species of *Eschweilera*. However, the present study does not resolve whether or not *Eschweilera* section *Tetrapetala* and *Eschweilera* s.s. are monophyletic (Fig. 19).

Eschweilera s.s. – This clade includes 48 species: two species of *Eschweilera* Section *Bracteosa* S. A. Mori (*E. bracteosa* & *Eschweilera cyathiformis* S. A. Mori), one species of the monotypic *Eschweilera* Section *Jugastrum* Prance and Mori (*E. tenuifolia*), and 45 species of Section *Eschweilera*. This clade is supported by a synapomorphy of the presence of a double or triple-coiled ligule (Fig. 18-3; character 23), which is unique to this clade. In Mori and Prance's treatment (1990d), *Eschweilera* includes four sections. Section *Tetrapetala* is discussed in the last paragraph. Mori (1990b) described Section *Bracteosa* to accommodate four species that have a bract and two smaller bracteoles persistent at anthesis (15). Section *Jugastrum* includes only one species, *E. tenuifolia*, which differs from other species of *Eschweilera* in having seed without an aril (40) and the seed germinates from the side instead of from the end (Prance & Mori, 1990). The latter character is not included in the present analysis because it is not parsimony informative. Section *Eschweilera* includes most species of the genus (ca. 85 sp.). Mori and Prance (1990e) defined that species in this section possess all of the following features: six petals, a fully coiled androecial hood (referred as a ligule (23) in the present study), caducous bracts and bracteoles, and apical seed germination. In the present study, the segregation of Sections *Bracteosa* and *Jugastrum* from Section *Eschweilera* is not supported because both sections are nested within Section *Eschweilera* (Fig. 18-3). However, no further taxonomic conclusion can be made because of the lack of resolution within *Eschweilera* s.s.

Traditionally species of *Eschweilera* are characterized by a fully coiled androecial hood (23), antherless hood appendages (25), a bilocular ovary (32), and seeds with a lateral aril (40; Mori & Prance; 1990d). These features are all homoplasious in the present study (Fig. 18). The monophyly of *Eschweilera* was tested in a molecular study of Mori et al. (2007) and in the present study. Section *Tetrapetala* was not included in Mori et al. (2007). Section *Eschweilera* was divided into three clades in their study and Sections *Bracteosa* and *Jugastrum* were nested in the largest clade of Section *Eschweilera* (Fig. 1 in Mori et al., 2007). In the present study, *E. nana* and Section *Tetrapetala* form a clade and all the remaining species of *Eschweilera* form another clade (Fig. 19). Nonetheless, both studies demonstrate that *Eschweilera* may not be monophyletic and that the segregation of Sections *Bracteosa* and *Jugastrum* is not necessary.

Lecythis section *Corrugata* – This clade includes all five species of Section *Corrugata* recognized by Mori (1990c). Synapomorphies of this clade are the presence of a pedicel (Fig. 18-1; character 13), rugose/tuberculate pedicels and hypanthia (14), and anther dimorphism (28). Mori (1990c) established *Lecythis* Section *Corrugata* to accommodate five species that have rugose/tuberculate pedicels and hypanthia. The monophyly of Section *Corrugata* in the present study is congruent with Mori (1990c) and previous molecular study (Mori et al., 2007).

Lecythis section *Pisonis* – This clade includes all four species of Section *Pisonis* recognized by Mori (1990c). Synapomorphies of this clade include the presence of oxidation of wounded tissues (Fig. 18-1; character 2), a stout style (30), an annular expansion right below the apex of the style (31), and sulcate seeds (36). Mori (1990c) established Section *Pisonis* to accommodate four species that are characterized by a group of features. Some of the features are not included in the present study. For example, traits such as large trees, brownish bark with pronounced vertical fissures, and laminated outer bark are excluded from the analysis because they are not parsimony informative. The trait of fruit size is excluded because the variation is continuous and inconsistent. Nonetheless, the monophyly of Section *Pisonis* in the present study is congruent with Mori (1990c) and Mori et al. (2007).

Lecythis section *Poiteaui* – This clade includes all three species of Section *Poiteaui* that was recognized by Mori (1990c). There is one synapomorphy supporting this clade (Fig. 18-1): the presence of leaf papillae on abaxial surface (5). Mori (1990c) established Section *Poiteaui* to accommodate three species that have a terminal inflorescence, flat androecial hood (referred as a ligule in the present study) with antheriferous appendages, and densely packed stamens (up to 1,000) on the staminal ring. *Lecythis poiteaui* was sister to *L. prancei* in Mori et al. (2007), and, together they were sister to a clade that consisted of *L. minor* and *L. tuyrana* (Fig. 1 in Mori et al., 2007). The monophyly of Section *Poiteaui* in the present study is congruent with Mori (1990c). However, the sister relationship of Section *Poiteaui* and *L. prancei* and its close relatives as indicated in Mori et al. (2007) is not confirmed in the present study because of the poor resolution among the clades.

Lecythis prancei clade – This clade includes three species: *L. gracieana*, *L. parvifructa*, and *L. prancei*. All three species were included in Section *Lecythis* (Mori, 1990c). The only synapomorphy of this clade is the indehiscent operculum (Fig. 18-2; character 34), which is unique to this clade and distinguishes the three species from other species of Section *Lecythis*. In addition, the three species differ from other species of Section *Lecythis* in the absence of an aril (40), which is also characteristic of *Bertholletia excelsa*, *Eschweilera tenuifolia*, and most of the outgroup genera.

Traditionally species of *Lecythis* have been characterized by a four-locular ovary (32), a well-defined style (30), and ovules that are attached toward the base of the septum (Mori, 1990c). The first two features are homoplasious in the present study. The last feature is not included in the analysis because it is not parsimony informative. Mori et al. (2007) demonstrated that two of the Sections (*Corrugata* and *Pisonis*) recognized by Mori (1990c) are monophyletic; Section *Lecythis* is divided into three clades; and one representative of Section *Poiteaui* (*L. poiteaui*) is nested within one of the three clades of Section *Lecythis* (Fig. 1 in Mori et al., 2007). The present study supports the monophyly of Sections *Corrugata*, *Pisonis*, and *Poiteaui* (Fig. 19). Except for the three species of the *Lecythis prancei* clade, all other species of Section *Lecythis* along with *B. excelsa*, *Eschweilera congestiflora*, and *E. simiorum* remain as unresolved in the present study (*Bertholletia*/*Lecythis* complex; Fig. 19).

The close relationship of *B. excelsa* and *Lecythis* was suggested by Mori and Prance (1990a) based on their morphological similarity. For example, in Lecythidoideae, the presence of leaf papillae (5) on the abaxial surface is only found in *B. excelsa*, three species of Section *Poiteaui*, and a few species of Section *Lecythis*. In addition, *B. excelsa* has a non-coiled ligule (23) and the presence of the appendages at the apex of the ligule (24), which is also only found in some species of Section *Lecythis*. However, whether *B. excelsa* and Section *Lecythis* are monophyletic is not resolved in the present study or in Mori et al. (2007) due to the lack of resolution.

Eschweilera congestiflora and *E. simiorum* were included in *Eschweilera* section *Eschweilera* (Mori & Prance, 1990d). Both species have a non-coiled ligule (23), the appendages locating at the apex of the ligule (24), a four-locular ovary (32), and seeds with a basal aril (40). Although the monophyly of *E. congestiflora*, *E. simiorum* and species of Section *Lecythis* is not resolved in the present study, both species were included in a clade that consisted of four species of Section *Lecythis* in previous molecular study (Fig. 1 in Mori et al., 2007). It is almost certain that both *E. congestiflora* and *E. simiorum* were placed in the wrong genus. However, more study is needed to determine the genus to which these two species belong.

Table 1. List of sampled taxa (No. of sampled/No. of total species). Taxa with * are type species of the genus or section; taxa with ** are type species of both section and genus.

- *Bertholletia* Bonpl. (1/1)
  - *B. excelsa* Bonpl.
- *Corythophora* R. Knuth (4/4)
  - *C. alta* R. Knuth*
  - *C. amapaensis* Pires ex S. A. Mori & Prance
  - *C. labriculata* (Eyma) S. A. Mori & Prance
  - *C. rimosa* W. Rodrigues subsp. *rimosa*
  - *C. rimosa* W. Rodrigues subsp. *rubra* S. A. Mori
- *Eschweilera* Mart. ex DC (55/93)
  - Section *Tetrapetala* S. A. Mori (3/3)
    - *E. alvimii* S. A. Mori
    - *E. tetrapetala* S. A. Mori*
    - *E. compressa* (Vellozo) Miers
  - Section *Bracteosa* S. A. Mori (2/4)
    - *E. bracteosa* (Poeppig ex O. Berg) Miers*
    - *E. cyathiformis* S. A. Mori
  - Section *Jugastrum* Prance & S. A. Mori (1/1)
    - *E. tenuifolia* (O. Berg) Miers*
  - Section *Eschweilera* S. A. Mori & Prance (49/85)
    - *E. aguilarii* S. A. Mori
    - *E. alata* A. C. Sm.
    - *E. albiflora* (DC.) Miers
    - *E. amazonica* R. Knuth
    - *E. amazoniciformis* S. A. Mori
    - *E. amaplexifolia* S. A. Mori
    - *E. andina* (Rusby) J. F. Macbr.
    - *E. antioquensis* Dugand & Daniel
    - *E. apiculata* (Miers) A. C. Sm.
    - *E. atropetiolata* S. A. Mori
    - *E. biflava* S. A. Mori
    - *E. calyculata* Pittier
    - *E. caudiculata* R. Knuth
    - *E. chartaceifolia* S. A. Mori
    - *E. collina* Eyma
    - *E. congestiflora* (Benoist) Eyma
    - *E. coriacea* (DC) S. A. Mori
    - *E. correae* sp. ined.
    - *E. decolorans* Sandwith

Table 1. Continued. List of sampled taxa (No. of sampled/No. of total species). Taxa with * are type species of the genus or section; taxa with ** are type species of both section and genus.

- *E. grandiflora* (Aubl.) Sandwith
- *E. hondurensis* Standley
- *E. integrifolia* (Ruiz & Pav. ex Miers) R. Knuth
- *E. jacquelyniae* S. A. Mori
- *E. juruensis* R. Knuth
- *E. laevicarpa* S. A. Mori
- *E. longirachis* S. A. Mori
- *E. mexicana* T. Wendt, Mori & Prance
- *E. micrantha* (O. Berg) Miers
- *E. nana* (O. Berg) Miers
- *E. neei* S. A. Mori
- *E. ovalifolia* (DC) Nied.
- *E. ovata* (Cambess.) Mart. ex Miers
- *E. panamensis* Pittier
- *E. parviflora* (Aubl.) Miers
- *E. parvifolia* Mart. *ex* DC.**
- *E. pedicellata* (Richard) S. A. Mori
- *E. pittieri* R. Knuth
- *E. pseudodecolorans* S. A. Mori
- *E. rankiniae* S. A. Mori
- *E. rimbachii* Standl.
- *E. sagotiana* Miers
- *E. sessilis* A. C. Sm.
- *E. simiorum* (Benoist) Eyma
- *E. subglandulosa* (Steud. ex O. Berg) Miers
- *E. tessmannii* R. Knuth
- *E. tresoriana* sp. ined.
- *E. truncata* A. C. Sm.
- *E. wachenheimii* (Benoist) Sandwith

Lecythis Loefling (25/27)

- Section *Corrugata* S. A. Mori (5/5)
  - *L. confertiflora* (A. C. Sm.) S. A. Mori
  - *L. corrugata* Poit.*
  - *L. idatimon* Aubl.
  - *L. persistens* Sagot subsp. *aurantiaca* S. A. Mori
  - *L. persistens* Sagot subsp. *persistens*
  - *L. pneumatophora* S. A. Mori

Table 1. Continued. List of sampled taxa (No. of sampled/No. of total species). Taxa with * are type species of the genus or section; taxa with ** are type species of both section and genus.

- Section *Pisonis* S. A. Mori (4/4)
  - *L. ampla* Miers
  - *L. lanceolata* Poiret
  - *L. pisonis* Cambess.*
  - *L. zabucajo* Aubl.
- Section *Poiteaui* S. A. Mori (3/3)
  - *L. barnebyi* S. A. Mori
  - *L. brancoensis* (R. Knuth) S. A. Mori
  - *L. poiteaui* O. Berg*
- Section *Lecythis* S. A. Mori (13/15)
  - *L. alutacea* (R. Knuth) S. A. Mori
  - *L. chartacea* O. Berg
  - *L. gracieana* S. A. Mori
  - *L. holcogyne* (Sandwith) S. A. Mori
  - *L. lurida* (Miers) S. A. Mori
  - *L. mesophylla* S. A. Mori
  - *L. minor* Jacq.
  - *L. ollaria* Loefling**
  - *L. parvifructa* S. A. Mori
  - *L. prancei* S. A. Mori
  - *L. retusa* Spruce ex O. Berg
  - *L. schomburgkii* O. Berg
  - *L. tuyrana* Pittier

Outgroup taxa

- *Gustavia speciosa* (Kunth) DC.
- *Grias peruviana* Miers
- *Allantoma decandra* (Ducke) S. A. Mori, Y.-Y. Huang & Prance
- *Allantoma integrifolia* (Ducke) S. A. Mori, Y.-Y. Huang & Prance
- *Allantoma lineata* (Mart. ex O. Berg) Miers
- *Cariniana estrellensis* (Raddi) Kuntez
- *Cariniana pyriformis* Miers
- *Couratari guianensis* Aubl.
- *Couratari macrosperma* A. C. Sm.
- *Couratari multiflora* (Sm.) Eyma
- *Couratari stellata* A. C. Sm.
- *Couroupita guianensis* Aubl.
- *Couroupita nicaraguianensis* DC.
- *Couroupita subsessilis* Pilg.

Table 2. Data matrix for phylogenetic analysis

	CHARACTER																				
Taxon	1				5					10					15					20	
Bertholletia excelsa	1	0	0	0	1	0	1	1	1	1	0	0	0	1	0	1	0	2	1	1	3
Corythophora alta	1	0	0	0	0	0	1	1	1	1	0	1	0	1	0	4	0	2	1	1	3
C. amapaensis	1	0	0	0	0	0	1	1	1	1	0	1	0	1	0	4	0	2	1	1	3
C. labriculata	1	0	0	0	0	0	1	1	1	1	0	1	0	1	0	4	0	2	1	1	3
C. rimosa	1	0	0	0	0	0	1	1	1	1	0	1	0	1	0	4	0	2	1	1	3
C. rimosa rubra	1	0	0	0	0	0	1	1	1	1	0	1	0	1	0	4	0	2	1	1	3
Eschweilera aguilarii	1	0	0	1	0	0	1	1	1	1	0	0	1	1	0	4	0	2	1	1	3
E. alata	1	0	0	0	0	0	1	1	1	1	0	0	1	1	0	4	0	2	1	1	3
E. albiflora	1	0	0	1	0	0	1	1	1	1	0	0	1	1	0	4	0	2	1	1	3
E. alvimii	1	0	0	0	0	0	1	1	1	1	0	1	0	1	0	4	0	0	1	1	3
E. amazonica	1	0	0	0	0	0	1	1	1	1	0	0	0	1	0	4	0	2	1	1	3
E. amazoniciformis	1	0	0	0	0	0	1	1	1	1	0	0	0	1	0	2	0	0	1	1	3
E. amplexifolia	1	0	0	1	0	0	1	1	1	1	0	0	0	1	0	4	0	2	1	1	3
E. andina	1	0	0	1	0	0	1	1	1	1	0	0	0	1	0	4	0	2	1	1	3
E. antioquensis	1	0	0	1	0	0	1	1	1	1	0	0	1	1	0	4	0	2	1	1	3
E. apiculata	1	0	0	0	0	0	1	1	1	1	0	0	1	1	0	4	0	2	1	1	3
E. atropetiolata	1	0	0	0	0	0	1	1	1	1	0	0	1	1	0	4	0	2	1	1	3
E. biflava	1	0	0	0	0	0	1	1	1	1	0	0	1	1	0	4	0	2	1	1	3
E. bracteosa	1	0	0	0	0	0	1	1	1	1	0	0	1	1	1	4	0	2	1	1	3
E. calyculata	1	0	0	1	0	0	1	1	1	1	0	0	0	1	0	4	0	2	1	1	3
E. caudiculata	1	0	0	1	0	0	1	1	1	1	0	0	1	1	0	4	0	2	1	1	3
E. chartaceifolia	1	0	0	0	0	0	1	1	1	1	0	0	1	1	0	4	0	2	1	1	3
E. collina	1	0	0	1	0	0	1	1	1	1	0	0	1	1	0	4	0	2	1	1	3
E. compressa	1	0	0	0	0	0	1	1	1	1	0	0	1	1	0	4	0	0	1	1	3
E. coriacea	1	0	0	1	0	0	1	1	1	1	0	0	1	1	0	4	0	2	1	1	3
E. congestiflora	1	0	0	0	1	0	1	1	1	1	0	0	0	1	0	4	1	2	1	1	3
E. correae sp.ined	1	0	0	1	0	0	1	1	1	1	0	0	1	1	0	4	0	2	1	1	3
E. cyathiformis	1	0	0	0	0	0	1	1	1	1	0	0	1	1	1	4	0	2	1	1	3
E. decolorans	1	1	0	0	0	0	1	1	1	1	0	0	1	1	0	4	0	2	1	1	3
E. grandiflora	1	0	0	1	0	0	1	1	1	1	0	0	1	1	0	4	0	2	1	1	3
E. hondurensis	1	0	0	0	0	0	1	1	1	1	0	0	1	1	0	4	0	2	1	1	3
E. integrifolia	1	0	0	1	0	0	1	1	1	1	0	0	0	1	0	4	0	2	1	1	3
E. jacquelyniae	1	0	0	1	0	0	1	1	1	1	0	0	1	1	0	4	0	2	1	1	3
E. juruensis	1	0	0	0	0	0	1	1	1	1	0	0	0	1	0	4	0	2	1	1	3
E. laevicarpa	1	1	0	0	0	0	1	1	1	1	0	0	1	1	0	4	0	2	1	1	3

Table 2. Data matrix for phylogenetic analysis - continued

	CHARACTER																			
Taxon				25					30					35					40	
Bertholletia excelsa	1	0	2	0	1	0	0	1	1	1	2	1	1	0	0	0	0	0	0	0
Corythophora alta	1	0	0	1	1	0	1	0	2	1	0	1	1	0	0	0	0	0	3	0
C. amapaensis	1	0	0	0	1	0	1	0	2	1	0	1	1	0	0	0	0	0	3	0
C. labriculata	1	0	0	0	1	0	1	0	2	1	2	1	1	0	0	0	0	0	3	0
C. rimosa	1	0	0	1	1	0	1	0	2	1	0	1	1	0	0	0	0	0	3	0
C. rimosa rubra	1	0	0	1	1	0	1	0	2	1	0	1	1	0	0	0	0	0	3	0
Eschweilera aguilarii	1	2	0	0	1	0	0	1	2	1	0	1	1	0	0	0	0	0	2	0
E. alata	1	2	0	0	1	0	0	1	2	1	0	1	1	0	0	0	0	0	1	0
E. albiflora	1	2	0	0	1	0	0	1	2	1	0	1	1	0	0	0	0	0	1	0
E. alvimii	1	1	1	0	1	0	0	1	2	1	0	1	1	0	0	0	0	0	3	0
E. amazonica	1	2	0	0	1	0	0	1	2	1	0	1	1	0	0	0	0	0	1	0
E. amazoniciformis	1	2	0	0	1	0	0	1	2	1	0	1	1	0	0	0	0	0	3	0
E. amplexifolia	1	2	0	0	1	0	0	1	2	1	0	1	1	0	0	0	0	0	2	0
E. andina	1	2	0	0	1	0	0	1	2	1	0	1	1	0	0	0	0	0	2	0
E. antioquensis	1	2	0	0	1	0	0	1	2	1	0	1	1	0	0	0	0	0	1	0
E. apiculata	1	2	0	0	1	0	0	1	2	1	0	1	1	0	0	0	0	0	1	0
E. atropetiolata	1	2	0	0	1	0	0	1	2	1	0	1	1	0	0	0	0	0	1	0
E. biflava	1	2	0	0	1	0	0	1	2	1	0	1	1	0	0	0	0	0	1	0
E. bracteosa	1	2	0	0	1	0	0	1	2	1	0	1	1	0	0	0	0	0	1	0
E. calyculata	1	2	0	0	1	0	0	1	2	1	0	1	1	0	0	0	0	0	2	0
E. caudiculata	1	2	0	0	1	0	0	1	2	1	0	1	1	0	0	0	0	0	1	0
E. chartaceifolia	1	2	0	0	1	0	0	1	2	1	0	1	1	0	0	0	0	0	1	0
E. collina	1	2	0	0	1	0	0	1	2	1	0	1	1	0	0	0	0	0	1	0
E. compressa	1	1	1	0	1	0	0	1	2	1	0	1	1	0	0	0	0	0	3	0
E. coriacea	1	2	0	0	1	0	0	1	2	1	0	1	1	0	0	0	0	0	1	0
E. congestiflora	1	0	2	0	1	0	0	1	1	1	2	1	1	0	0	0	0	0	3	0
E. correae sp.ined	1	2	0	0	1	0	0	1	2	1	0	1	1	0	0	0	0	0	1	0
E. cyathiformis	1	2	0	0	1	0	0	1	2	1	0	1	1	0	0	0	0	0	1	0
E. decolorans	1	2	0	0	1	0	0	1	2	1	0	1	1	0	0	0	0	0	1	0
E. grandiflora	1	2	0	0	1	0	0	1	2	1	0	1	1	0	0	0	0	0	1	0
E. hondurensis	1	2	0	0	1	0	0	1	2	1	0	1	1	0	0	0	0	0	1	0
E. integrifolia	1	2	0	0	1	0	0	1	2	1	0	1	1	0	0	0	0	0	2	0
E. jacquelyniae	1	2	0	0	1	0	0	1	2	1	0	1	1	0	0	0	0	0	1	0
E. juruensis	1	2	0	0	1	0	0	1	2	1	0	1	1	0	0	0	0	0	1	0
E. laevicarpa	1	2	0	0	1	0	0	1	2	1	0	1	1	0	0	0	0	0	1	0

Table 2. Data matrix for phylogenetic analysis - continued

	CHARACTER																				
Taxon	1				5					10					15					20	
E. longirachis	1	0	0	1	0	0	1	1	1	1	0	0	1	1	0	4	0	2	1	1	3
E. mexicana	1	0	0	1	0	0	1	1	1	1	0	0	1	1	0	4	0	2	1	1	3
E. micrantha	1	0	0	0	0	0	1	1	1	1	0	0	1	1	0	4	0	2	1	1	3
E. nana	1	0	0	0	0	0	1	1	1	1	0	1	0	1	0	4	0	2	1	1	3
E. neei	1	0	0	1	0	0	1	1	1	1	0	0	1	1	0	4	0	2	1	1	3
E. ovalifolia	1	0	0	0	0	0	1	1	1	1	0	0	0	1	0	4	0	2	1	1	3
E. ovata	1	0	0	0	0	0	1	1	1	1	0	0	1	1	0	4	0	2	1	1	3
E. panamensis	1	0	0	1	0	0	1	1	1	1	0	0	1	1	0	4	0	2	1	1	3
E. parviflora	1	0	0	1	0	0	1	1	1	1	0	0	1	1	0	4	0	2	1	1	3
E. parvifolia	1	0	0	0	0	0	1	1	1	1	0	0	1	1	0	4	0	2	1	1	3
E. pedicellata	1	0	0	0	0	0	1	1	1	1	0	0	1	1	0	4	0	2	1	1	3
E. pittieri	1	0	0	1	0	0	1	1	1	1	0	0	1	1	0	4	0	2	1	1	3
E. pseudodecolorans	1	0	0	0	0	0	1	1	1	1	0	0	1	1	0	4	0	2	1	1	3
E. rankiniae	1	0	0	0	0	0	1	1	1	1	0	0	1	1	0	4	0	2	1	1	3
E. rimbachii	1	0	0	1	0	0	1	1	1	1	0	0	1	1	0	4	0	2	1	1	3
E. sagotiana	1	0	0	0	0	0	1	1	1	1	0	0	1	1	0	4	0	2	1	1	3
E. sessilis	1	0	0	1	0	0	1	1	1	1	0	0	1	1	0	4	0	2	1	1	3
E. simiorum	1	0	0	0	1	0	1	1	1	1	0	0	0	1	0	4	1	2	1	1	3
E. subglandulosa	1	0	0	0	0	0	1	1	1	1	0	0	1	1	0	4	0	2	1	1	3
E. tenuifolia	1	0	0	0	0	0	1	1	1	1	0	0	0	1	0	4	0	2	1	1	3
E. tessmannii	1	0	0	0	0	0	1	1	1	1	0	0	0	1	0	4	0	2	1	1	3
E. tetrapetala	1	0	0	0	0	0	1	1	1	1	0	1	1	1	0	4	0	0	1	1	3
E. tresoriana	1	0	0	1	0	0	1	1	1	1	0	0	1	1	0	4	0	2	1	1	3
E. truncata	1	0	0	0	0	0	1	1	1	1	0	0	1	1	0	4	0	2	1	1	3
E. wachenheimii	1	0	0	1	0	0	1	1	1	1	0	0	1	1	0	4	0	2	1	1	3
Lecythis alutacea	1	0	0	0	0	0	1	1	1	1	0	0	0	1	0	4	1	2	1	1	3
L. ampla	1	1	0	0	0	0	1	1	1	1	0	0	0	1	0	4	0	2	1	1	3
L. barnebyi	1	0	0	0	1	0	1	1	1	1	0	0	0	1	0	4	0	2	1	1	3
L. brancoensis	1	0	0	0	1	0	1	1	1	1	0	0	0	1	0	4	0	2	1	1	3
L. chartacea	1	0	0	0	0	0	1	1	1	1	0	0	1	1	0	4	0	2	1	1	3
L. confertiflora	1	0	0	0	0	0	1	1	1	1	0	0	1	0	0	4	0	2	1	1	3
L. corrugata	1	0	0	0	0	0	1	1	1	1	0	0	1	0	0	4	0	2	1	1	3
L. idatimon	1	0	0	0	0	0	1	1	1	1	0	0	1	0	0	4	0	2	1	1	3
L. gracieana	1	0	0	0	0	0	1	1	1	1	0	0	0	1	0	4	0	2	1	1	3
L. holcogyne	1	0	0	0	0	0	1	1	1	1	0	0	0	1	0	4	1	2	1	1	3

Table 2. Data matrix for phylogenetic analysis - continued

									CHARACTER											
Taxon				25					30					35					40	
E. longirachis	1	2	0	0	1	0	0	1	2	1	0	1	1	0	0	0	0	0	2	0
E. mexicana	1	2	0	0	1	0	0	1	2	1	0	1	1	0	0	0	0	0	1	0
E. micrantha	1	2	0	0	1	0	0	1	2	1	0	1	1	0	0	0	0	0	1	0
E. nana	1	1	1	0	1	0	0	1	2	1	0	1	1	0	0	0	0	0	3	0
E. neei	1	2	0	0	1	0	0	1	2	1	0	1	1	0	0	0	0	0	1	0
E. ovalifolia	1	2	0	0	1	0	0	1	2	1	0	1	1	0	0	0	0	0	2	0
E. ovata	1	2	0	0	1	0	0	1	2	1	0	1	1	0	0	0	0	0	1	0
E. panamensis	1	2	0	0	1	0	0	1	2	1	0	1	1	0	0	0	0	0	2	0
E. parvifolia	1	2	0	0	1	0	0	1	2	1	0	1	1	0	0	0	0	0	1	0
E. parviflora	1	2	0	0	1	0	0	1	2	1	0	1	1	0	0	0	0	0	1	0
E. pittieri	1	2	0	0	1	0	0	1	2	1	0	1	1	0	0	0	0	0	1	0
E. pedicellata	1	2	0	0	1	0	0	1	2	1	0	1	1	0	0	0	0	0	1	0
E. pseudodecolorans	1	2	0	0	1	0	0	1	2	1	2	1	1	0	0	0	0	0	1	0
E. rankiniae	1	2	0	0	1	0	0	1	2	1	0	1	1	0	0	0	0	0	1	0
E. rimbachii	1	2	0	0	1	0	0	1	2	1	0	1	1	0	0	0	0	0	1	0
E. sagotiana	1	2	0	0	1	0	0	1	2	1	0	1	1	0	0	0	0	0	1	0
E. sessilis	1	2	0	0	1	0	0	1	2	1	0	1	1	0	0	0	0	0	2	0
E. simiorum	1	0	2	0	1	0	0	1	1	1	2	1	1	0	0	0	0	0	3	0
E. subglandulosa	1	2	0	0	1	0	0	1	2	1	0	1	1	0	0	0	0	0	1	0
E. tenuifolia	1	2	0	0	1	0	0	1	2	1	0	1	1	0	0	0	0	0	0	0
E. tessmannii	1	2	0	0	1	0	0	1	2	1	0	1	1	0	0	0	0	0	1	0
E. tetrapetala	1	1	1	0	1	0	0	1	2	1	0	1	1	0	0	0	0	0	3	0
E. tresoriana	1	2	0	0	1	0	0	1	2	1	0	1	1	0	0	0	0	0	1	0
E. truncata	1	2	0	0	1	0	0	1	2	1	0	1	1	0	0	0	0	0	1	0
E. wachenheimii	1	2	0	0	1	0	0	1	2	1	0	1	1	0	0	0	0	0	1	0
Lecythis alutacea	1	0	2	0	1	0	0	1	1	1	2	1	1	0	0	0	0	0	3	0
L. ampla	1	0	0	1	0	0	0	0	2	0	2	1	1	0	1	0	0	0	3	0
L. barnebyi	1	0	0	1	0	0	0	1	1	1	2	1	1	0	0	0	0	0	3	0
L. brancoensis	1	0	2	1	0	0	0	1	1	1	2	1	1	0	0	0	0	0	3	0
L. chartacea	1	0	2	0	1	0	0	1	1	1	2	1	1	0	0	0	0	0	3	0
L. confertiflora	1	0	0	0	0	0	1	1	1	1	2	1	1	0	0	0	0	0	3	0
L. corrugata	1	0	0	0	1	0	1	1	1	1	2	1	1	0	0	0	0	0	3	0
L. idatimon	1	0	0	0	0	0	1	1	1	1	2	1	1	0	0	0	0	0	3	0
L. gracieana	1	0	2	0	1	0	0	1	1	1	2	1	0	0	0	0	0	0	0	0
L. holcogyne	1	0	2	0	1	0	0	1	1	1	2	1	1	0	0	0	0	0	3	0

Table 2. Data matrix for phylogenetic analysis - continued

	CHARACTER																				
Taxon	1				5					10					15					20	
L. lanceolata	1	1	0	0	0	0	1	1	1	1	0	0	1	1	0	4	0	2	1	1	3
L. mesophylla	1	0	0	0	0	0	1	1	1	1	0	0	0	1	0	4	0	2	1	1	3
L. minor	1	0	0	0	0	0	1	1	1	1	0	0	0	1	0	4	0	2	1	1	3
L. ollaria	1	0	0	0	0	0	1	1	1	1	0	0	0	1	0	4	0	2	1	1	3
L. parvifructa	1	0	0	0	0	0	1	1	1	1	0	0	0	1	0	4	?	2	1	1	3
L. persistens	1	0	0	0	0	0	1	1	1	1	0	0	1	0	0	4	0	2	1	1	3
L. persistens aurantiaca	1	0	0	0	0	0	1	1	1	1	0	0	1	0	0	4	0	2	1	1	3
L. pisonis	1	1	0	0	0	0	1	1	1	1	0	0	1	1	0	4	0	2	1	1	3
L. pneumatophora	1	0	0	0	0	0	1	1	1	1	0	0	1	0	0	4	0	2	1	1	3
L. poiteaui	1	0	0	0	1	0	1	1	1	1	0	0	0	1	0	4	0	2	1	1	3
L. prancei	1	0	0	0	0	0	1	1	1	1	0	0	0	1	0	4	0	2	1	1	3
L. retusa	1	0	0	0	0	0	1	1	1	1	0	0	0	1	0	4	1	2	1	1	3
L. rorida	1	0	0	0	1	0	1	1	1	1	0	0	0	1	0	4	0	2	1	1	3
L. schomburgkii	1	0	0	0	0	0	1	1	1	1	0	0	1	1	0	4	1	2	1	1	3
L. tuyrana	1	0	0	0	0	0	1	1	1	1	0	0	0	1	0	4	0	2	1	1	3
L. zabucajo	1	1	0	0	0	0	1	1	1	1	0	0	0	1	0	4	0	2	1	1	3
Allantoma. decandra	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	3	0	1	0	0	2
A . lineata	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	3	0	1	0	0	2
A. integrifolia	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	3	0	1	0	0	2
Cariniana estrellensis	1	0	0	0	0	1	1	1	1	1	1	0	1	1	0	4	0	2	1	2	2
C. pyriformis	1	0	0	0	0	1	1	1	1	1	1	0	1	1	0	4	0	2	1	2	2
Couratari guianensis	0	0	1	0	0	0	1	1	1	1	1	0	1	1	0	4	0	2	1	1	2
C. macrosperma	0	0	1	0	0	0	1	1	1	1	?	0	1	1	0	4	0	2	1	1	3
C. multiflora	0	0	0	0	0	0	1	1	1	1	1	0	1	1	0	4	0	2	1	1	3
C. stellata	0	0	1	0	0	0	1	1	1	1	0	0	1	1	0	4	0	2	1	1	3
Couroupita guianensis	0	1	0	0	0	0	1	0	1	1	1	0	1	1	0	4	0	2	1	1	3
C. nicaraguarebsis	0	1	0	0	0	0	1	1	1	1	1	0	1	1	0	4	0	2	1	1	3
C. subsessilis	0	1	0	0	0	0	1	0	1	1	1	0	0	1	0	4	0	2	1	1	3
Grias peruviana	0	0	0	0	0	0	1	-	1	1	1	0	1	1	0	0,1,2	0	0	0	0	1
Gustavia speciosa	0	0	0	0	0	0	1	-	1	1	1	0	1	1	0	0,2	0	2,3	1	0	0

Inapplicable characters are indicated with dashes "-", and unknown character states are indicated with question marks "?".

Table 2. Data matrix for phylogenetic analysis - continued

	CHARACTER																			
Taxon				25					30					35					40	
L. lanceolata	1	0	0	1	0	0	0	0	2	0	2	1	1	0	1	0	0	0	3	0
L. mesophylla	1	0	2	0	1	0	0	1	1	1	2	1	1	0	0	0	0	0	3	0
L. minor	1	1	0	0	1	0	0	1	2	1	2	1	1	0	0	0	0	0	3	0
L. ollaria	1	1	0	0	1	0	0	1	2	1	2	1	1	0	0	0	0	0	3	0
L. parvifructa	1	0	2	0	1	0	0	1	1	1	2	1	0	0	0	0	0	0	0	0
L. persistens	1	0	0	1	0	0	1	1	1	1	2	1	1	0	0	0	0	0	3	0
L. persistens aurantiaca	1	0	0	1	0	0	1	1	1	1	2	1	1	0	0	0	0	0	3	0
L. pisonis	1	0	0	1	0	0	0	0	2	0	2	1	1	0	1	0	0	0	3	0
L. pneumatophora	1	0	0	0	0	0	1	1	1	1	2	1	1	0	0	0	0	0	3	0
L. poiteaui	1	0	0	1	0	0	0	1	1	1	2	1	1	0	0	0	0	0	3	0
L. prancei	1	1	0	0	1	0	0	1	2	1	2	1	0	0	0	0	0	0	3	0
L. retusa	1	0	0	0	1	0	0	1	1	1	2	?	?	0	0	0	0	0	?	0
L. rorida	1	0	2	0	1	0	0	1	1	1	2	?	?	0	0	0	0	0	?	0
L. schomburgkii	1	0	2	0	1	0	0	1	1	1	2	1	1	0	0	0	0	0	3	0
L. tuyrana	1	0	2	0	1	0	0	1	1	1	2	1	1	0	0	0	0	0	3	0
L. zabucajo	1	0	0	1	0	0	0	0	2	0	2	1	1	0	1	0	0	0	3	0
Allantoma lineata	0	-	-	-	0	0	0	0	1	1	1	1	1	0	0	0	1	0	0	1
A. integrifolia	0	-	-	-	0	0	0	0	0	1	2,3	1	1	0	0	0	0	0	0	0
A. decandra	0	-	-	-	0	0	0	0	1	1	1	1	1	0	0	0	1	0	0	1
Cariniana estrellensis	0	-	-	-	0	0	0	0	2	1	1	1	1	0	0	0	1	0	0	1
C. pyriformis	0	-	-	-	0	0	0	0	2	1	1	1	1	0	0	0	1	0	0	1
Couratari guianensis	0	3	0	0	1	0	0	1	2	0	1	1	1	0	0	0	0	1	0	1
C. macrosperma	0	3	0	0	1	0	0	1	2	0	1	1	1	0	0	0	0	1	0	1
C. multiflora	0	3	0	0	1	0	0	1	2	0	1	1	1	0	0	0	0	1	0	1
C. stellata	0	3	0	0	1	0	0	1	2	0	1	1	1	0	0	0	0	1	0	1
Couroupita guianensis	1	0	0	1	0	1	0	0	2	1	3	0	-	1	0	1	0	0	0	1
C. nicaraguarebsis	1	0	0	1	0	1	0	0	2	1	3	0	-	1	0	1	0	0	0	1
C. subsessilis	1	0	0	1	0	?	0	0	2	1	3	0	-	1	0	1	0	0	0	1
Grias peruviana	1	-	-	-	0	0	0	0	2	1	2	0	-	0	0	0	0	0	0	0
Gustavia speciosa	1	-	-	-	0	0	0	0	2	1	3	0	-	0	0	0	0	0	0	2

Inapplicable characters are indicated with dashes "-", and unknown character states are indicated with question marks "?".

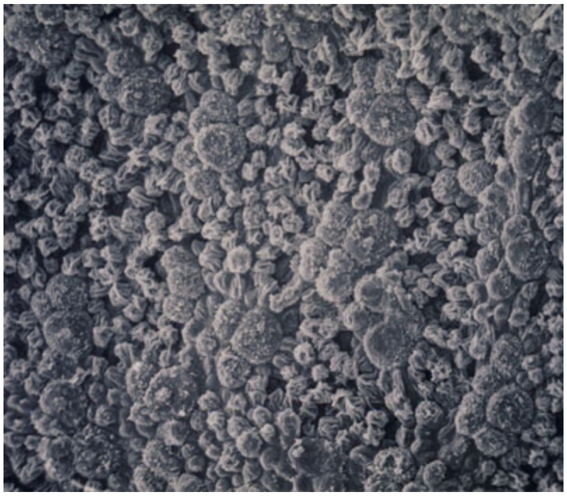

Fig. 1. *Bertholletia excelsa*, leaf papillae on abaxial surface (photo by C. Gracie).

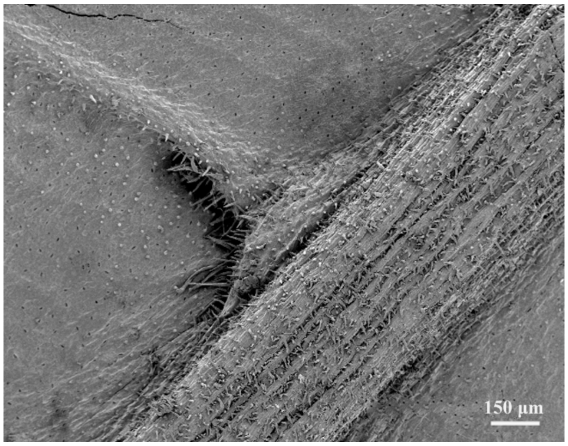

Fig. 2. *Cariniana domestica* (*Eiten* 4304), leaf domatia.

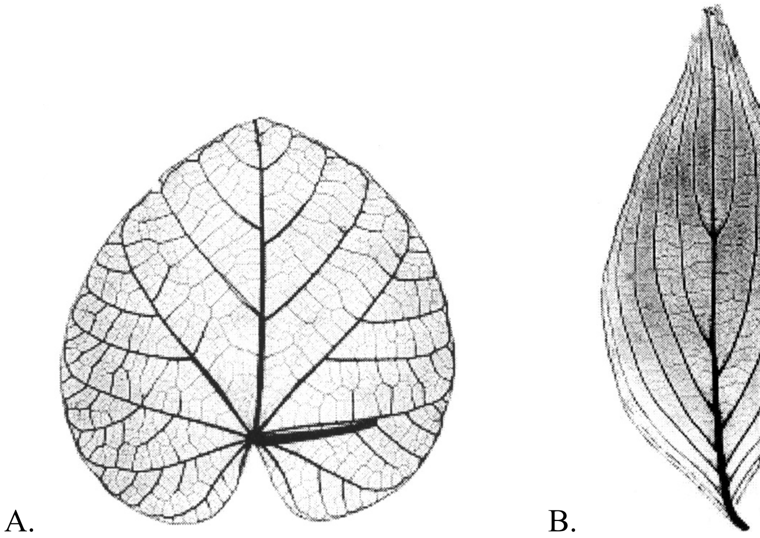

Fig. 3. Venation type. A. Brochidodromous. B. Eucamptodromous. Drawings are from Leaf Architecture Working Group (1999).

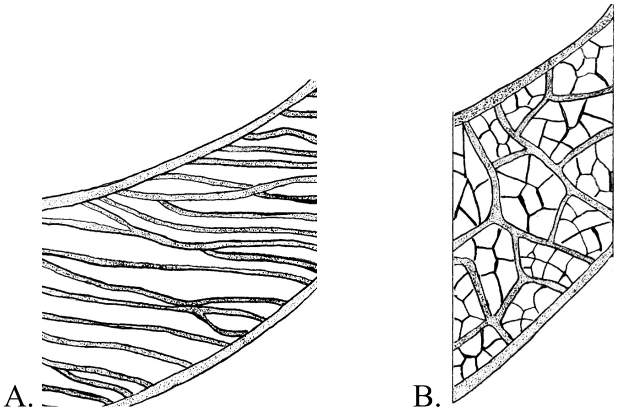

Fig. 4. Tertiary venation. A. *Allantoma lineata* (*Prance* 10454), percurrent tertiary venation. B. *Cariniana estrellensis* (*Nee* 42078), reticulate tertiary venation.

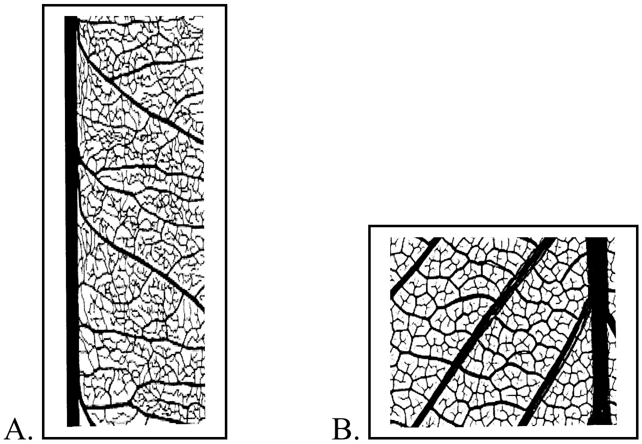

Fig. 5. Quaternary venation. A. Dichotomizing type. B. Regular polygonal reticulate type. Drawings are from Leaf Architecture Working Group (1999).

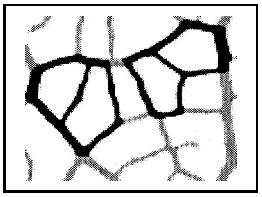

Fig. 6. Areoles. The areoles are well-developed with five or more sides. Drawing is from Leaf Architecture Working Group (1999).

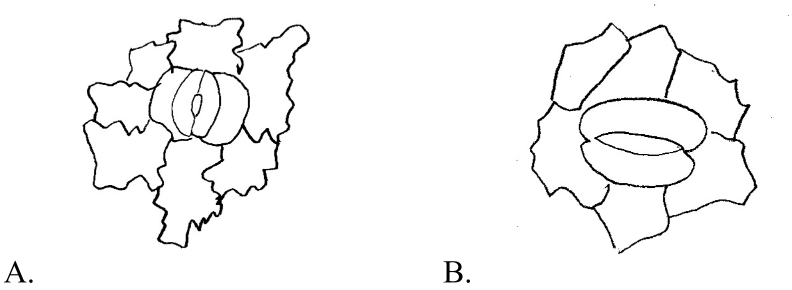

Fig. 7. Stomatal type. A. *Cariniana decandra* (*Thomas* 6408), brachyparacytic stomata. B. *Cariniana rubra* (*Kuhlmann* s.n.), anomocytic stomata.

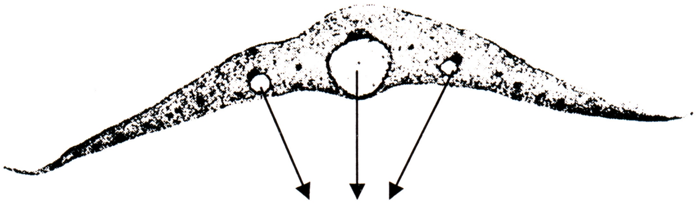

Fig. 8. Cross section of sepal. The mucilage-bearing ducts are longitudinally oriented (from Mori, 1990). *Lecythis schomburgkii* (*Schomburgk* 792).

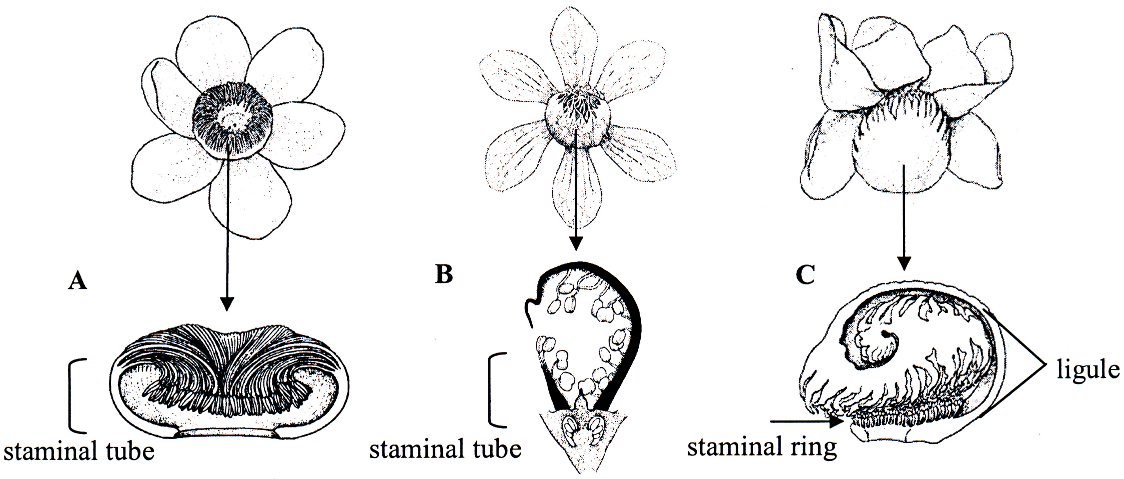

Fig. 9. Androecial symmetry. A. Actinomorphic androeciaum, *Gustavia hexapetala*. B. Obliquely zygomorphic androecium, *Cariniana penduliflora*. C. Zygomorphic androecium, *Eschweilera pedicellata*. Drawings modified from Prance and Mori (1979) and Mori and Prance (1990b).

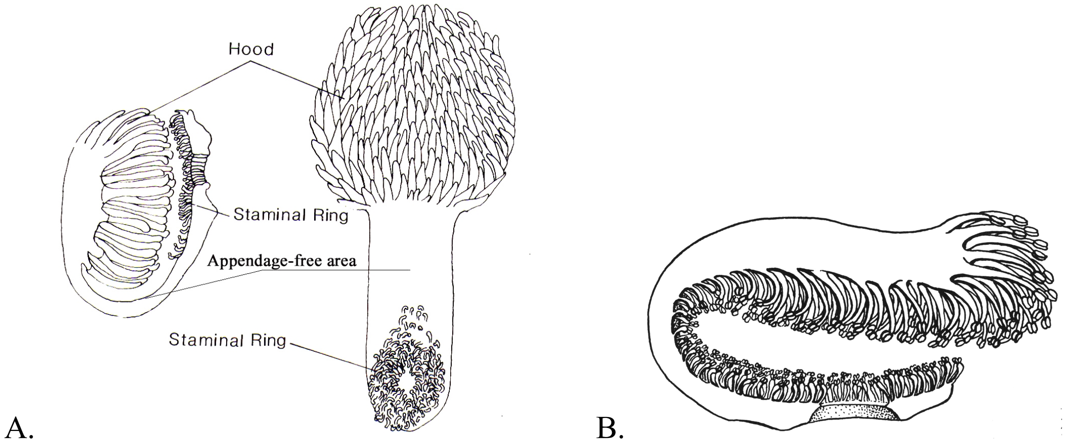

Fig. 10. Structure of zygomorphic androecium. A. Androecium of most zygomorphic-flowered species (Fig. 30C *in* Mori & Prance, 1990b). B. Androecium of *Couroupita nicaraguarensis*. Note that there is no appendage-free area (Fig. 34C *in* Mori & Prance, 1990b).

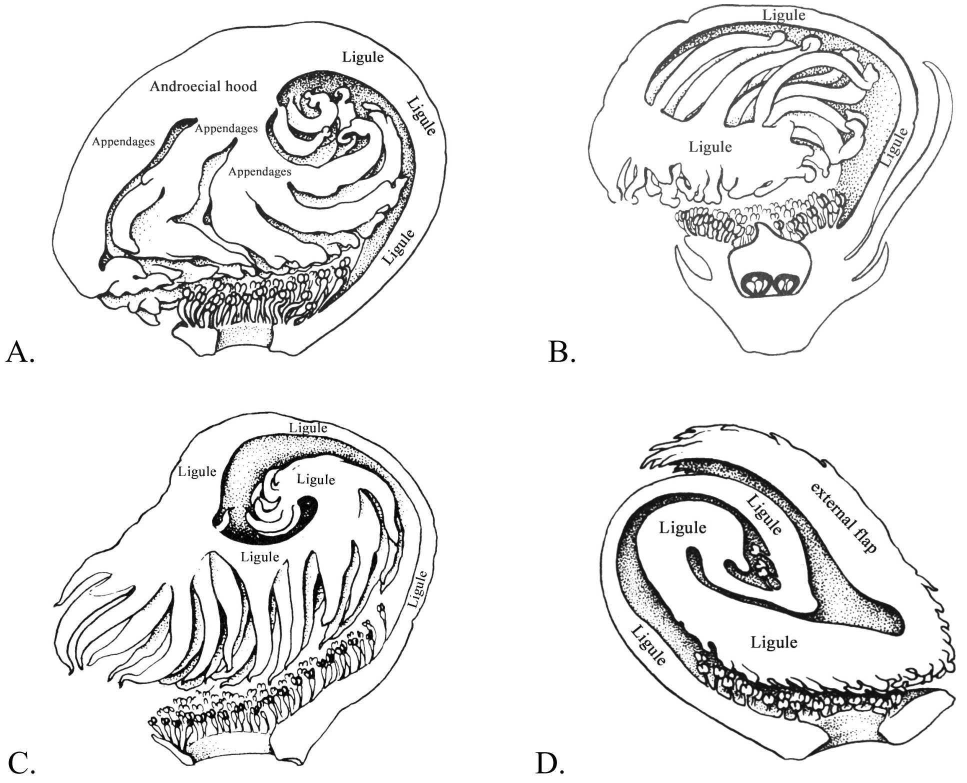

Fig. 11. Ligules of zygomorphic-flowered species. A. Non-coiled ligule. *Lecythis holcogyne*. B. Single-coiled ligule. *Eschweilera alvimii*. C. Double-coiled ligule. *Eschweilera ovata*. D. Single or double-coiled with an external flap. *Couratari stellata*. All the images are modified from Mori and Prance (1990b).

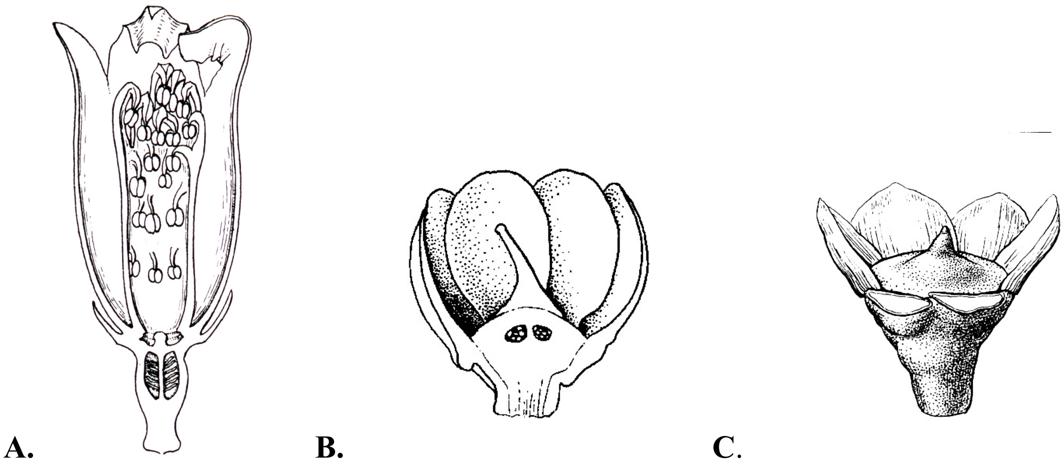

Fig. 12. Style. A. Style is absent. *Allantoma lineata* (Fig. 62B in Prance & Mori, 1979). B. Slender style. *Lecythis lurida* (Fig. 105E in Mori & Prance, 1990). C. Stout style. *Eschweilera tetrapetala* (Fig. 63D in Mori & Prance, 1990).

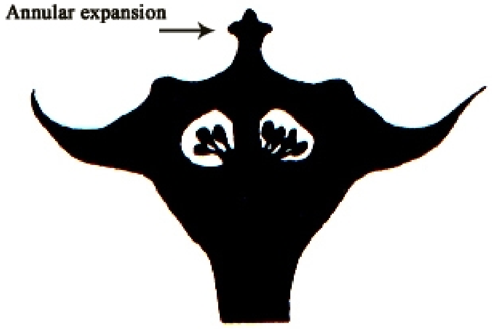

Fig. 13. Annular ring at the apex of style. *Lecythis pisonis* (Fig. 101E in Mori & Prance, 1990).

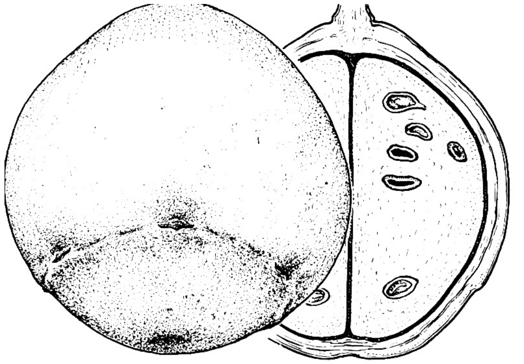

Fig. 14. Seeds embeded in pulp. *Couroupita guianensis* (Fig. 36G in Mori & Prance, 1990).

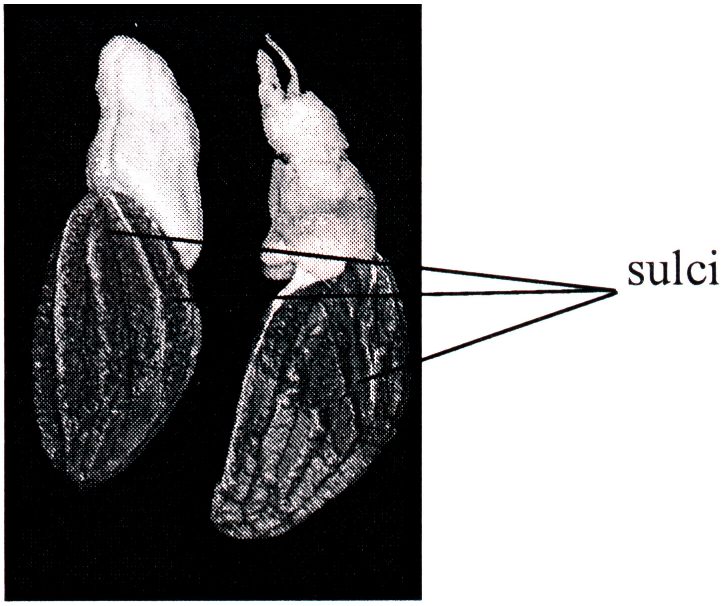

Fig. 15. Sulcate seeds. *Lecythis pisonis*. Photo by C. Gracie.

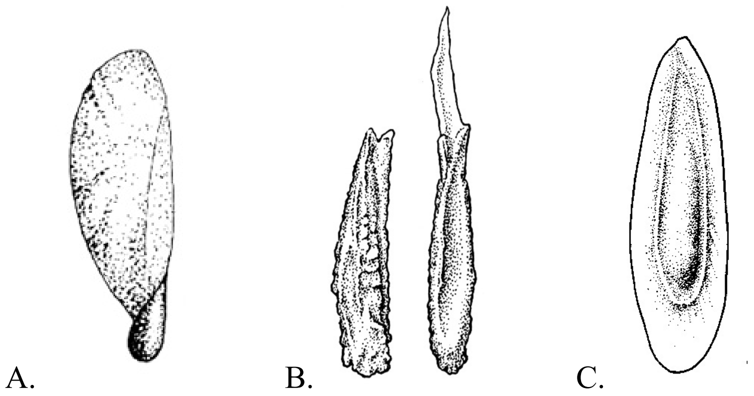

Fig. 16. Winged seeds. A. Unilateral winged seed. *Allantoma decandra* (Fig. $66B_2$ *in* Prance & Mori, 1979). B. Seed with vestigial seed wing. *A. lineata* (Fig. 1O *in* Tsou & Mori, 2002). C. Circumferential winged seed. *Couratari stellata* (Fig. 51G *in* Mori & Prance, 1990).

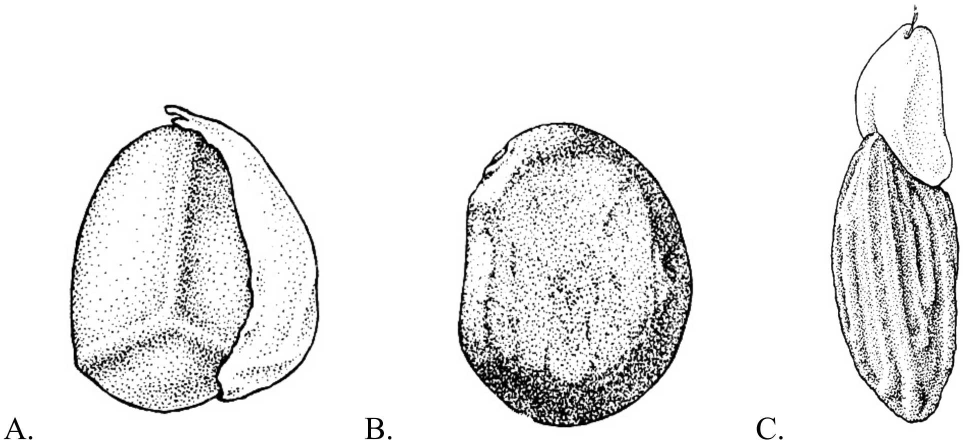

Fig. 17. Arils. A. Lateral aril. *Eschweilera pedicellata*. B. Spreading aril. *E. ovalifolia*. C. Basal aril. *Lecythis pisonis*. Images are from Tsou and Mori (2002).

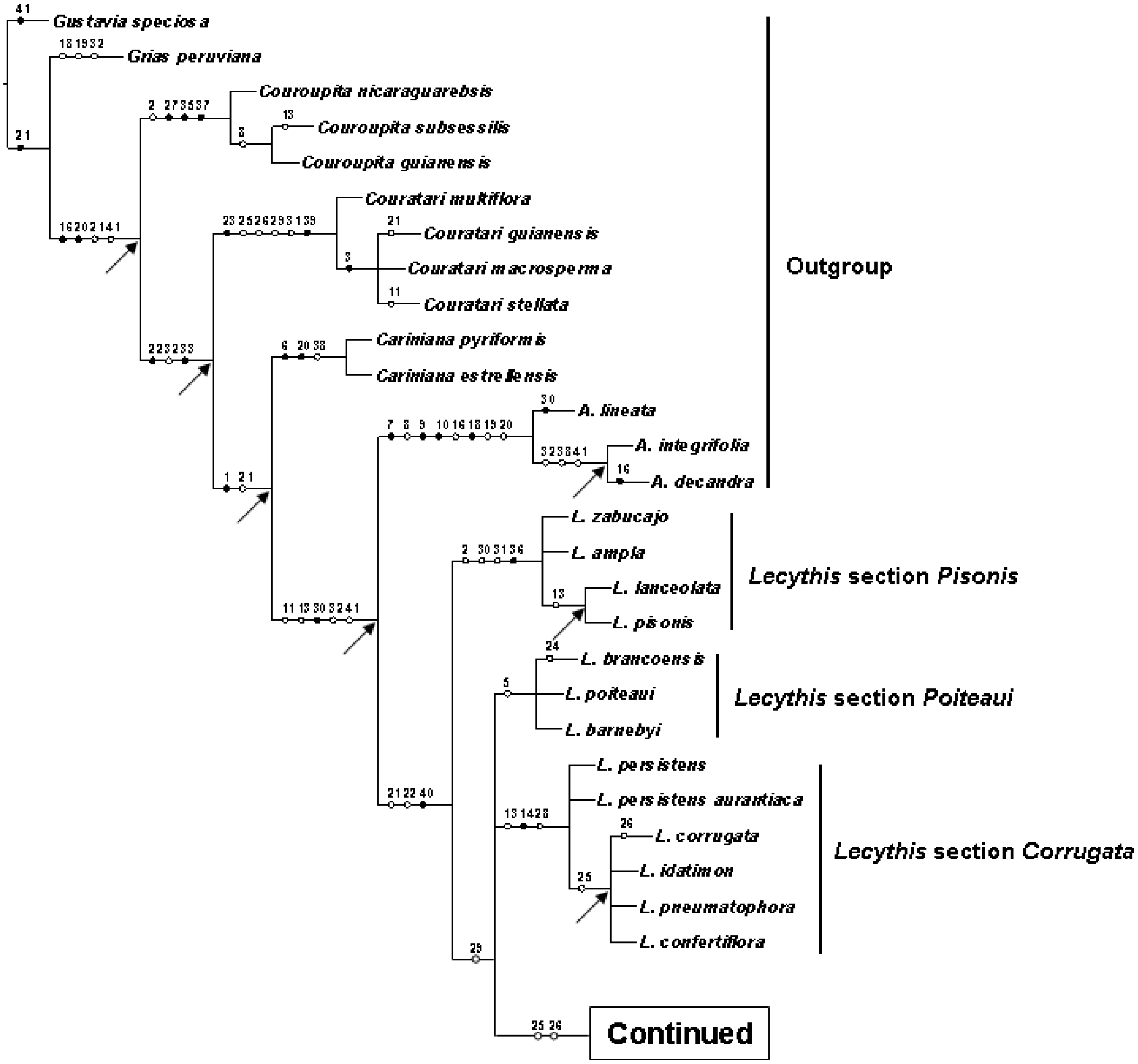

Fig 18-1. One of 125 equally parsimonious trees based on 41 informative characters. The tree length is 105 steps, the consensus index (CI) is 0.53 and the retention index (RI) is 0.88. Characters are optimized onto the tree using fast option of Winclada. Supporting characters are shown on branches. Branches without supporting characters were collapsed. Arrows indicate nodes collapsed in strict consensus. White elipses are homoplasious and black elipses are non-homoplasious characters.

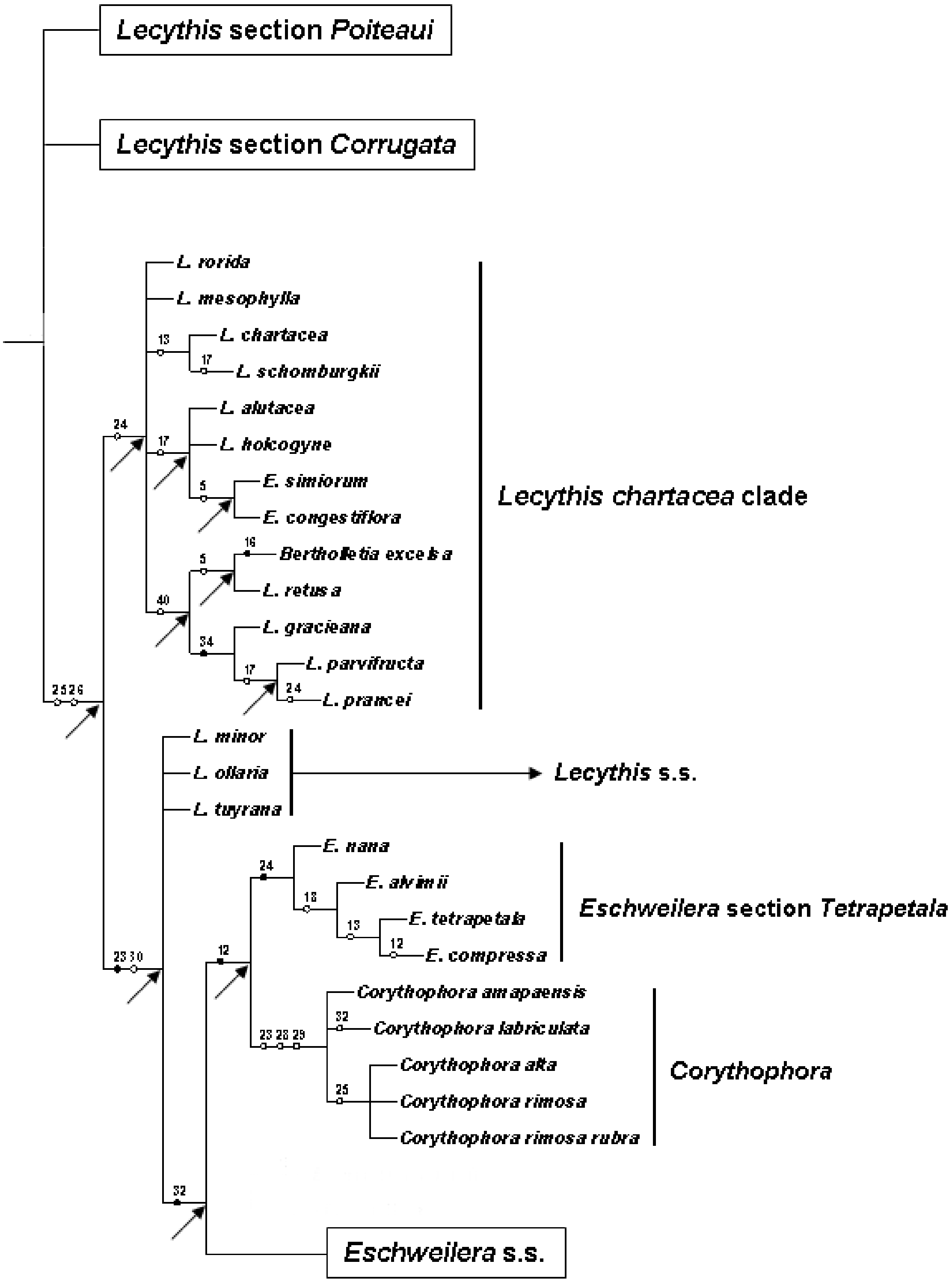

Fig 18-2. One of 125 equally parsimonious trees-continued. Supporting characters are shown on branches. Branches without supporting characters were collapsed. Arrow-pointed nodes collapsed in strict consensus. White elipses are homoplasious and black elipses are non-homoplasious characters.

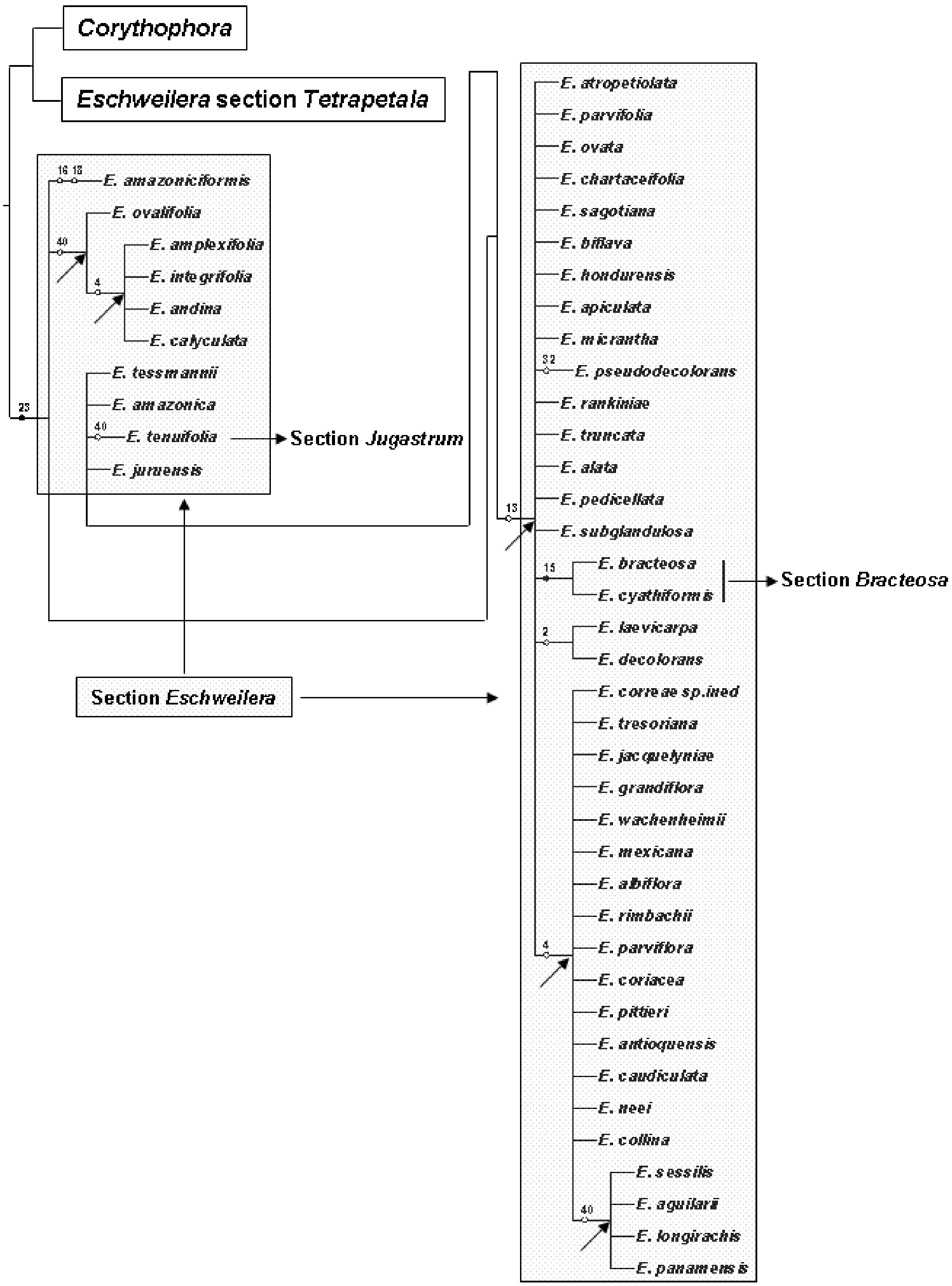

Fig 18-3. One of 125 equally parsimonious trees-continued. Supporting characters are shown on branches. Branches without supporting characters were collapsed. Arrow-pointed nodes collapsed in strict consensus. White elipses are homoplasious and black elipses are non-homoplasious characters.

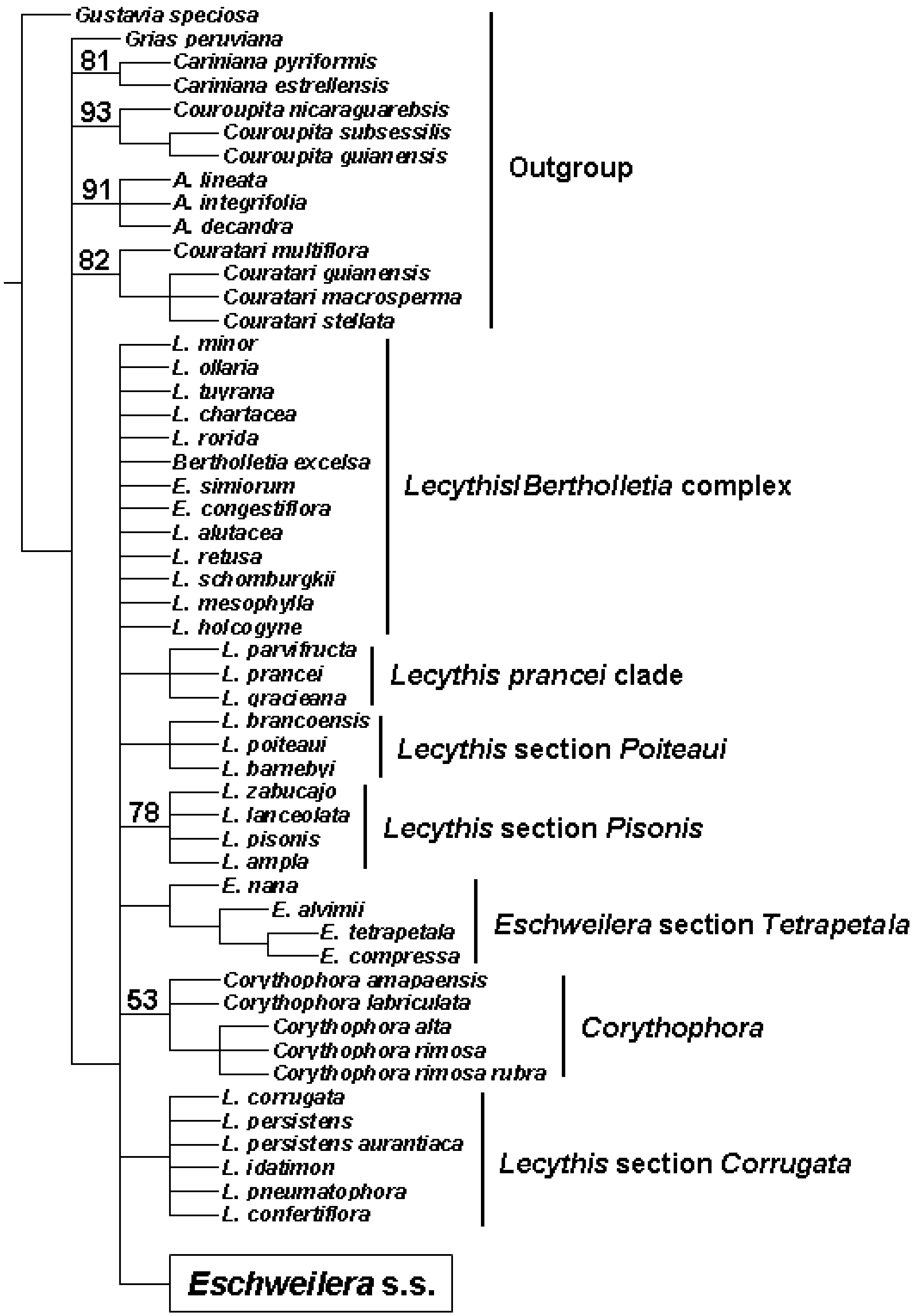

Fig. 19-1. Strict consensus of 125 maximum parsimonious (MP) trees. Bootstrap values (>50%) are given above the branches. The details of the outgroup and most ingroup (except *Eschweilera* s.s.) are shown in this figure.

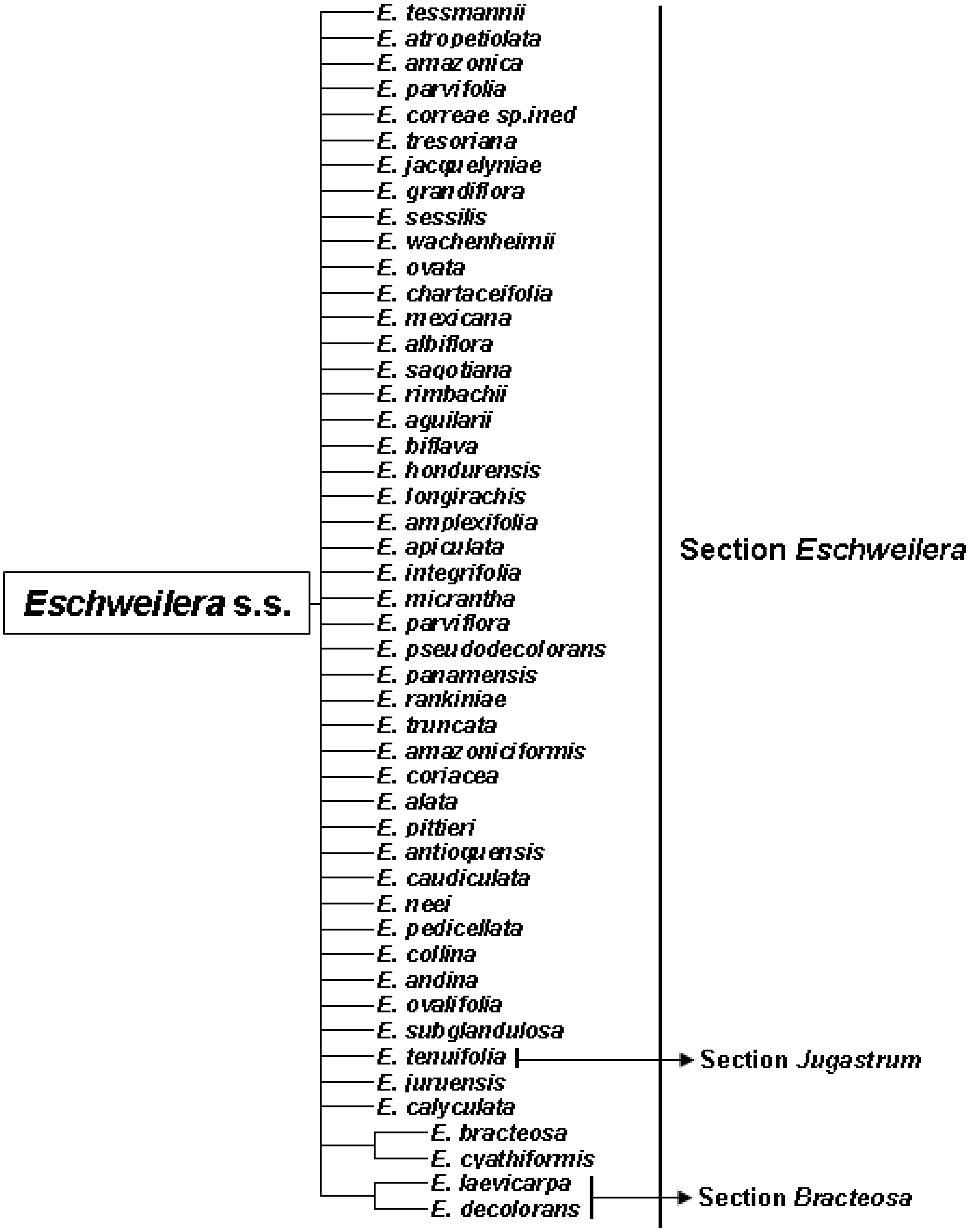

Fig. 19-2. Strict consensus of 125 MP trees – *Eschweilera* s.s. The resolution within *Eschweilera* s.s. is poorly resolved. Sections *Bracteosa* and *Jugastrum* are nested in Section *Eschweilera*.

CHAPTER TWO

A phylogenetic study of Lecythidoideae based on morphological and DNA sequence data: emphasis on *Bertholletia*, *Corythophora*, *Eschweilera* and *Lecythis*

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Abstract — Phylogenetic analyses based on morphology and plastid DNA indicate that *Bertholletia*, *Corythophora*, *Eschweilera*, and *Lecythis* form a clade (the *Bertholletia* clade) and within this clade *Eschweilera* and *Lecythis* may not be monophyletic. In order to improve the resolution within the *Bertholletia* clade, a combined analysis of morphological and molecular sequence data was conducted and more terminals were sampled in the present study. Forty-one morphological characters and sequences of nuclear ITS and plastid *ndhF*, *trnL-F*, and *trnH-psbA* regions were included in the analysis. The results support the generic circumscription of *Bertholletia* and *Corythophora* but suggest revisions for *Eschweilera*, which is paraphyletic, and *Lecythis*, which is polyphyletic. Consequently this study recommends reinstatement of two genera and recognition of three new genera in Lecythidoideae. Character optimization onto the consensus tree demonstrates that androecial evolution is more likely an adaptation in response to pollinator shift and is less likely a process of morphological transformation from a simpler to a more complicated form.

INTRODUCTION

The Lecythidoideae is the largest subfamily of the pantropical tree family Lecythidaceae. Currently there are ten genera and 210 species in the Lecythidoideae (Prance & Mori, 1979; Mori & Prance, 1990b; Mori, 1992, 1995a, 1995b, 2007; Huang et al., 2008). Phylogenetic analyses based on anatomical, cytological, morphological, and molecular sequence data indicate that the Lecythidoideae are monophyletic (Morton et al., 1998; Mori et al., 2007; APG III, 2009). A non-molecular synapomorphy unique to the Lecythidoideae is a basic chromosome number of x = 17 (Morton et al., 1998). Species of the Lecythidoideae are small to large trees characterized by the following characters that may or may not be synapomorphic: actinomorphic or zygomorphic flowers; tricolpate/tricolporate pollen; ovary with two, three, four, or six locules; dehiscent or indehiscent fruits; secondary xylem with cortical bundles normally oriented (Morton et al., 1998). Members of the Lecythidoideae range from Jamaica and Veracruz, Mexico to Santa Catarina, Brazil (Mori & Prance, 1990b). They are most diverse and abundant in lowland primary rainforests.

Traditionally the taxonomy of Lecythidoideae has been based on a combination of morphological characters such as androecial symmetry, number of ovary locules, and fruit and seed features, etc. These characters may or may not be parsimony-informative. The ten genera can be divided into two groups based on androecial symmetry. The first group consists of three genera that have actinomorphic androecia: *Gustavia* L., *Grias* L., and *Allantoma* Miers. The second group has seven genera that have zygomorphic androecia: *Cariniana* Casar., *Couroupita* Aubl., *Corythophora* R. Knuth, *Bertholletia* Bonpl., *Couratari* Aubl., *Eschweilera* Mart. ex DC., and *Lecythis* Loefl. (Prance & Mori, 1979; Mori & Prance, 1990b; Huang et al., 2008). Mori et al (2007) conducted a phylogenetic analysis based on plastid *ndhF* and *trnL-F* sequence data to test the monophyly of the genera of

Lecythidoideae. In this study the ten genera of Lecythidoideae were divided into two distinct clades. The first clade included two actinomorphic-flowered genera: *Gustavia* and *Grias*. The second clade included all zygomorphic-flowered genera and *Allantoma*. Within the first clade, the resolution further supported the monophyly of both *Gustavia* and *Grias*. Within the second clade, *Couroupita* was sister to all other genera. The latter were further divided into four clades, but the relationships among the four clades were unresolved. These clades were *Allantoma lineata*/*Cariniana decandra*, *Cariniana* s.s., *Couratari*, and the *Bertholletia* clade. The *Bertholletia* clade consisted of *Bertholletia*, *Corythophora*, *Eschweilera*, and *Lecythis* (Fig. 1 in Mori et al., 2007). Within the *Bertholletia* clade, the monophyly of *Corythophora* was supported by the data, but the monophyly of *Eschweilera* and the monophyly of *Lecythis* were uncertain. In addition, the phylogenetic relationships within the *Bertholletia* clade were not fully understood (Fig. 1 in Mori et al., 2007). The purpose of the present study is to investigate the systematics of the *Bertholletia* clade and the phylogenetic relationships within the clade. Genera of the *Bertholletia* clade and their taxonomic status at present are described in the following paragraphs.

Eschweilera is the largest genus of Lecythidoideae with 93 species (Mori & Prance, 1990d; Mori, 1992, 1995a, 1995b, 2007). Traditionally species of *Eschweilera* are characterized by the following features: six calyx lobes and petals, an androecial hood (referred as ligule in the present study) with double or triple coils, antherless ligule appendages, a two-locular ovary, dehiscent fruits, and seeds with a lateral or spreading aril (Mori & Prance, 1990b). Mori and Prance (1990d) further divided *Eschweilera* into four sections: *Eschweilera* section *Tetrapetala* S. A. Mori includes three species that have four petals, a non-coiled ligule, and seeds with basal arils; *Eschweilera* section *Bracteosa* S. A. Mori includes four species that have one bract and two smaller bracteoles persistent at anthesis; *Eschweilera* section *Jugastrum* Prance and S. A. Mori includes one species that has wedge-shaped seeds that lack an aril and the germinate from the sides; and *Eschweilera* section *Eschweilera* S. A. Mori and Prance includes ca. 85 species that have six petals, a fully coiled ligule, caducous bracts and bracteoles, and apical seed germination.

Lecythis is the third largest genus of Lecythidoideae (Prance & Mori, 1979). Currently there are 27 species in *Lecythis* (Mori & Prance, 1990b; Mori, 1995b). *Lecythis* is the most diverse of all genera in terms of floral and fruit features (Mori & Prance, 1990b). Traditionally species of *Lecythis* are characterized by six calyx lobes and petals, a non-coiled ligule, ligule appendages with or without anthers, a four-locular ovary, dehiscent or indehiscent fruits, and seeds with a basal aril (Mori & Prance, 1990b). Mori (1990c) further divided *Lecythis* into four sections: *Lecythis* section *Corrugata* S. A. Mori includes five species that have rugose/tuberculate pedicels and hypanthia; *Lecythis* section *Pisonis* S. A. Mori includes four species that have wounded tissues turning bluish, ligular anthers, an annular expansion right below the apex of the style, and sulcate seeds; *Lecythis* section *Poiteaui* S. A. Mori includes three species that have leaf papillae on the abaxial surface, terminal inflorescences that are not branched, ligular anthers, and numerous stamens (ca. 1,000) on the staminal ring; and *Lecythis* section *Lecythis* includes 15 species that have antherless ligular appendages and these appendages sweep inward without forming a complete coil.

Bertholletia is a monotypic genus. The only species, *Bertholletia excelsa*, is the best-known species of the entire family because of its edible seeds (Prance, 1990b). *Bertholletia excelsa* is characterized by the following features: two calyx lobes, six petals, ovary with four locules, antherless ligule appendages that sweep inward without forming a complete coil, style geniculate, opening of the operculum smaller than the seeds, and seeds with a woody testa (Prance, 1990b). The androecial structure of *B. excelsa* resembles the ones found in the species of *Lecythis* section *Lecythis*, especially *Lecythis lurida* (Miers) S. A. Mori and its close relatives (Mori & Prance, 1990a). Therefore Mori and Prance (1990a) suggested that the closest relatives of *B. excelsa* lie in *Lecythis* section *Lecythis*.

Corythophora consists of four species characterized by the following features: presence of squamulae on the inflorescence rachis, six calyx lobes and petals, non-coiled ligule, anther dimorphism, ovary with two or four locules, and seeds with a basal aril (Mori & Prance, 1990c). The androecia of *Corythophora amapaensis* Pires ex S. A. Mori & Prance and *Corythophora labriculata* (Eyma) S. A. Mori & Prance resemble that of *Lecythis corrugata* Poit. in that the ligule is dorsiventrally thickened, the antherless appendages are fused, and the androecial hood presses against the staminal ring. Thus Mori (1990c) hypothesized that *L. corrugata* is the link between *Corythophora* and *Lecythis*.

The monophyly of the *Bertholletia* clade was weakly supported (55% bootstrap value) in the previous molecular study (Mori et al., 2007). Within the clade, although the monophyly of *Eschweilera* and the monophyly of *Lecythis* were ambiguous, the type species of both genera (*Eschweilera parvifolia* Mart. ex DC. & *Lecythis ollaria* Loefl.) were not included in the analysis. In addition, not all sections were represented (e.g., *Eschweilera* section *Tetrapetala*), and only one individual was sampled for some species that have widespread distributions. In order to further understand the systematics of the *Bertholletia* clade and the phylogenetic relationships within the clade, these sampling problems need to be solved and more data need to be included in the analysis.

In chapter two a morphological cladistic analysis based on morphological and anatomical characters was built to examine the monophyly of the *Bertholletia* clade and the phylogenetic relationships within the clade. The monophyly of the *Bertholletia* clade was supported in that analysis. Synapomorphies of the clade include stamens arising from the surface of a flat cushion, the presence of more than 100 fertile stamens on the staminal ring, and the presence of an aril. Phylogenetic relationships are not fully understood within the clade because of poor resolution. Nonetheless, the monophyly of *Corythophora* is supported. The monophyly of *Eschweilera* and the monophyly of *Lecythis* remain unresolved, but the following clades are supported by the results: *Eschweilera* section *Tetrapetala*, a clade of *Eschweilera* that includes most of the species, and *Lecythis* sections *Corrugata*, *Pisonis*, *Poiteaui*, and a small clade that consists of three species of Section *Lecythis*.

In the present study a molecular phylogeny is conducted and combined with the one based on morphological and anatomical data. The objectives of this study are to: (1) further test the monophyly of the *Bertholletia* clade; (2) further test the monophyly of *Eschweilera* and the monophyly of *Lecythis*; (3) resolve the relationships within the *Bertholletia* clade; and (4) use the phylogenetic reconstruction as a framework to infer character evolution. I expand the current dataset of plastid *ndhF* and *trnL-F* sequences by adding more taxa, especially those critical taxa that were missing in Mori et al. (2007), e.g., the type species of the genera and sections. In addition, I add two more genetic markers into the dataset: nuclear ITS and plastid *trn*H-*psb*A regions.

METHODOLOGY

Sampling — DNA sequences were collected from 185 individuals (84 species), representing *Bertholletia*, *Corythophora*, *Eschweilera*, and *Lecythis* (ingroup). Taxon sampling covers the range of morphological variation in the genera and sections as circumscribed by Mori and Prance (1990b). Priority was given to type species of each genus; representatives of each section; species with atypical morphological characters, e.g., *Eschweilera nana*; and species that have been difficult to assign to genus, e.g., *Eschweilera congestiflora* and *E. simiorum*. More individuals were sampled for geographically widespread species, e.g., *Eschweilera coriacea* (DC.) S. A. Mori, *E. pedicellata* (Rich.) S. A. Mori, *Lecythis chartacea* O. Berg, and *Lecythis pisonis* Cambess. etc. Twenty two individuals (17 species) were included as outgroups, representing *Allantoma*, *Grias*, *Gustavia*, *Cariniana*, *Couratari*, and *Couroupita*. The selection of the outgroup taxa followed the molecular analysis of plastid *ndhF* and *trnL-F* sequence data, but with fewer species for each genus (Mori et al., 2007). Voucher information and GenBank accession for the sampled taxa are provided in Table 1.

Morphological Data — The morphological data matrix contains 41 characters, representing wood anatomy; leaf venation and stomata characteristics; and floral, fruit, and seed features. Character coding and the complete data matrix are presented in Chapter One.

Molecular data — Four genetic markers were used in this study: internal transcribed spacer from the region of the 18S-26S nuclear ribosomal DNA (ITS), the *ndhF* plastid gene that encodes the subunit of NADH dehydrogenase in the small single-copy region, the plastid *trnL-trnF* non-coding region (*trnL-F*) and plastid *trnH-psbA* non-coding region. ITS was chosen because it could be easily amplified using universal primers and preliminary data showed great potential for resolving interspecific relationships. The *ndhF* gene and *trnL-F* region were chosen because they had shown appropriate variation for resolving the intergeneric relationships (Mori et al., 2007) and because many sequences could be downloaded from GenBank. The *trnH-psbA* region was chosen because the primers specific for amplifying the samples of Lecythidoideae had been designed by Hamilton (1999) and preliminary analysis showed great potential for understanding the phylogenetic relationships within the study ingroup.

Genomic DNA was isolated from silica-dried leaves or herbarium specimens using Qiagen DNeasy plant mini kit following the manufacturer's protocols or modified CTAB methods as described by Doyle and Doyle (1990). Target loci were amplified in 25 µL volumes using standard polymerase chain reaction (PCR) protocols. For ITS amplification extra reagent Dimethyl Sulfoxide (DMSO) was added (1.25 µL) to break the secondary structure. The whole ITS region was amplified using primers 18S-1830F (Howarth et al., 2003), 26S-25R (Luton et al., 1992), and ITS5angio (ITS5A) and 241 R (Stanford et al., 2000). Samples that failed to amplify in one piece were amplified in two pieces by adding internal primers 5.8S-32F and 5.8S-32R (Downie & Downie, 1996) and Huang (5' - GAAGAACGTAGCGAAATGCG - 3' & 5' - GCATCGATGAAGAACGTAGC - 3'). The *ndhF* region was amplified in two or three pieces using different combinations of the primers 1b, 10 R, and 16 R used in Mori et al. (2007) and 972, 1318, 536 R, 972 R, and 1955 R used in Olmstead and Sweere (1994). The *trn*L-F region was amplified using primers C (B49317), F (A50272), and E (B49873) used in Taberlet et al. (1991). The *trn*H-*psbA* region was amplified using primers *trnH* (GUG) and *psbA* designed by Hamilton et al. (2003). The complete primer sequences are listed in Table 2. The PCR conditions for ITS sequences were performed with the following program: initial incubation at 94˚C for 5 minutes; 36 to 40 cycles of denaturation at 94˚C for 30 seconds, annealing at 50˚C - 55˚C for 30 seconds, and 72˚C for 45 seconds; and a final extension at 72˚C for 10 minutes. Similar protocols with different annealing temperature were applied to amplify the *ndhF*, *trnL-F* and *trnH-psbA* regions. The annealing temperature was 48˚C - 50˚C for *ndhF*, 50˚C for *trnL-F*, and 53˚C -55˚C for *trnH-psbA*. The PCR products were purified with the polyethylene glycol (PEG; Rosenthal et al., 1993). Purified PCR products were sequenced in the laboratory of the Institute of Plant and Microbial Biology, Academia Sinica, Taipei, Taiwan.

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

Phylogenetic analyses — Different DNA regions were analyzed independently, and then were combined for simultaneous analysis. The program Tree analysis using New Technology (TNT) was performed to generate phylogenetic trees based on parsimony criteria (Goloboff et al., 2008). The following algorithms were applied for tree search: Rachet (RAT), Tree-Drifting (DFT), Sectorial Search (SS) & Tree fusing (TF). Tree search strategy included two stages. The purpose of the first stage was to find the shortest tree with the optimal score by performing 200 replicates of RAT, 50 replicates of DFT, and random SS. The resulting trees were then submitted to perform five runs of TF. The purpose of the second stage was to test the correctness of the consensus by finding the optimal score 20 times. A strict consensus tree was calculated in Winclada. Branch support was assessed by bootstrap (BS) re-sampling with 1,000 replications, ten random taxon entry sequences per replication, and one tree saved per replication.

RESULTS

Molecular data — In total, 216 ITS, 163 *ndhF*, 161 *trnL-F*, and 167 *trnH-psbA* sequences were generated for this study. An additional 50 *ndhF* and 50 *trnL-F* sequences were downloaded from GenBank. Characteristics of different DNA regions and the combined datasets are summarized in Table 3. Of all four genetic markers, the nuclear ITS region possesses the largest number and highest percentage of parsimony-informative characters (48%). Among the three plastid markers, the *trnH-psbA* region is the most variable (37%), followed by the *trnL-F* region (20%), and then the *ndhF* gene (13%). The combined dataset of three plastid DNA has 864 parsimony-informative characters (20%); and the combined dataset of ITS and the three plastid DNA has 1581 parsimony-informative characters (27%). Only informative characters were included in the analyses. The monophyly of the *Bertholletia* clade is supported by the independent analysis of each genetic marker and by the analyses of combined datasets. The results of phylogenetic analyses of each genetic marker and the combined datasets are described in the following paragraphs.

The analysis of ITS sequences generated 105 most parsimonious (MP) trees with a length of 2662 steps, a CI of 0.36, and a RI of 0.80 (not shown). The strict consensus of all 105 MP trees is shown in Fig. 1. Within the *Bertholletia* clade the ingroup is divided into five major clades, among which the relationships are unresolved: *Bertholletia excelsa*, *Lecythis* s.s., *Pachylecythis*, a clade of *Lecythis* that consists of two sister clades (*Holopyxidium* & *Lecythis chartacea* clade), and a large clade that includes *Corythophora*, *Lecythis* section *Corrugata*, and *Eschweilera*. Within the last clade there are three subclades. The first subclade consists of *Eschweilera amazoniciformis*, *E. nana*, and the *Corythophora* clade; the second subclade includes two sister clades: *Eschweilera* section *Tetrapetala* and *Lecythis* section *Corrugata*; and the third subclade encompasses most species of *Eschweilera*. The clade of *Eschweilera* is further divided into the *Eschweilera mexicana*, *Eschweilera andina*, and *Eschweilera* s.s. clades (Fig. 1-3).

The analysis of *ndhF* sequences generated 148 MP trees with a length of 474 steps, a CI of 0.60, and a RI of 0.90 (not shown). The strict consensus of all 148 MP trees is shown in Fig. 2. Within the *Bertholletia* clade the ingroup is divided into six clades, among which the relationships are unresolved: *Bertholletia excelsa*, a small clade that includes three species of *Eschweilera* (*E. amazoniciformis*, *E. alvimii*, & *E. nana*), *Pachylecythis*, a clade of *Lecythis* that consists of two sister clades (*Lecythis* s.s. & *Holopyxidium*), a clade that contains *Lecythis chartacea* clade and *Eschweilera andina* clade, and a large clade that encompasses three subclades (*Corythophora*, *Lecythis* section *Corrugata*, and *Eschweilera* s.s.). Within the last clade *Lecythis* section *Corrugata* is sister to *Eschweilera* s.s., and together, they are sister to *Corythophora*.

The analysis of *trnL-F* sequences generated 67 MP trees with a length of 527 steps, a CI of 0.56, and a RI of 0.89 (not shown). The strict consensus of all 67 MP trees is shown in Fig. 3. Within the *Bertholletia* clade the ingroup is divided into two major clades. Within the first major clade *Eschweilera andina* is sister to a clade that includes three subclades: *Bertholletia excelsa*, *Eschweilera amazoniciformis*, and *Lecythis chartacea* clade. The relationships of the three subclades are unresolved (Fig. 3-1). The second major clade is further divided into two subclades. Within the first subclade *Lecythis* s.s. is sister to *Eschweilera* section *Tetrapetala*, and together, they are sister to *Holopyxidium*. The second subclade consists of three clades, among which the relationships are unresolved (Fig. 3-2): *Corythophora*, *Pachylecythis*, and a clade that includes two sister clades (*Lecythis* section *Corrugata* & *Eschweilera* s.s.).

The analysis of *trnH-psbA* sequences generated 53 MP trees with a length of 1319 steps, a CI of 0.42, and a RI of 0.83 (not shown). The strict consensus of all 53 MP trees is shown in Fig. 4. The first major clade is divided into two subclades. Within the *Bertholletia* clade the ingroup is divided into two major clades. The first clade is divided into two subclades. Within the first subclade *Bertholletia excelsa* is sister to *Lecythis* s.s. Within the second subclade *Corythophora* 1 is sister to *Lecythis* section *Corrugata* and together they are sister to *Eschweilera* s.s. The second major clade is also divided into two subclades. Within the first subclade *Corythophora* 2 is sister to *Lecythis chartacea* clade, and together, they are sister to *Eschweilera andina* clade. Within the second subclade *Pachylecythis* is sister to a clade that consists of two sister clades (*Holopyxidium* & *Eschweilera* section *Tetrapetala*).

The combined analysis of plastid DNA generated 77 MP trees with a length of 2297 steps, a CI of 0.45, and a RI of 0.80 (not shown). The strict consensus of all 77 MP trees is shown in Fig. 5. Within the *Bertholletia* clade the ingroup is divided into three major clades, among which the relationships are unresolved. Within the first major clade *Bertholletia* is sister to a clade that consists of two sister clades (*Eschweilera amazoniciformis* and *Eschweilera* section *Tetrapetala*). Within the second major clade *Lecythis chartacea* clade is sister to *Eschweilera andina* clade. The third major clade is further divided into two clades. Within the first clade *Lecythis* s.s. is sister to *Holopyxidium*. Within the second clade *Lecythis mesophylla* is sister to a clade that includes four subclades: *Pachylecythis*, *Corythophora*, *Lecythis* section *Corrugata*, and *Eschweilera* s.s. Among the four subclades *Pachylecythis* is sister to the other three subclades. Within the latter *Lecythis* section *Corrugata* is sister to *Eschweilera* s.s., and together, they are sister to *Corythophora* (Fig. 5-2).

The combined analysis of ITS and plastid DNA generated 115 MP trees with a tree length of 6089 steps, a CI of 0.35, and a RI of 0.75 (not shown). The strict consensus of all 115 MP trees is shown in Fig. 6. Within the *Bertholletia* clade the ingroup is divided into two major clades. The first major clade consists of two sister clades: *Lecythis* s.s. and *Pachylecythis*. The second major clade is further divided into two clades. Within the first clade *Bertholletia excelsa* is sister to *Eschweilera andina* clade. Within the second clade there are two subclades. The first subclade includes two sister clades: *Holopyxidium* and

Lecythis chartacea clade. The second subclade includes four clades: *Corythophora*, *Eschweilera* section *Tetrapetala*, *Lecythis* section *Corrugata*, and *Eschweilera* s.s. Among the four clades, *Corythophora* is sister to the other three clades. Within the later the relationship is unresolved (Fig. 6-2).

Total evidence — The combined analysis of morphological and molecular sequence data generated 132 MP trees with a tree length of 6114 steps, a CI of 0.36, and a RI of 0.76. One of the MP trees is shown in Fig. 7. The morphological characters are optimized and the resulting synapomorphies of clades are shown along the branches (Fig. 7). The strict consensus of all 132 MP trees is shown in Fig. 8. Within the *Bertholletia* clade the ingroup is divided into three clades: *Lecythis* s.s., *Pachylecythis*, and a large clade that includes all the remaining clades (Fig. 8-1). The relationships among the three clades are unresolved. Within the large clade there are two clades. The first clade consists of two sister clades: *Bertholletia* and *Lecythis chartacea* clade. Within the second clade *Holopyxidium* is sister to a clade that consists of five subclades: *Corythophora*, *Eschweilera andina* clade, *Eschweilera* section *Tetrapetala* (including *E. nana*), *Lecythis* section *Corrugata*, and *Eschweilera* s.s. (Fig. 8-2). Among the five subclades, *Corythophora* is sister to all others. Within the latter, *Eschweilera andina* clade is sister to the remaining three subclades. Within the remaining subclades, *Lecythis* section *Corrugata* is sister to *Eschweilera* s.s., and together, they are sister to *Eschweilera* section *Tetrapetala*. Although the strict consensus tree based on total evidence does not have the best resolution, it has the best overall support (bootstrap value; BS) for each clade. Therefore the following taxonomic discussion is based on the strict consensus tree of total evidence.

DISCUSSION

The monophyly of the ingroup — The *Bertholletia* clade contains four genera recognized by Mori and Prance (1990b): *Bertholletia*, *Corythophora*, *Eschweilera*, and *Lecythis*. The monophyly of the *Bertholletia* clade is weakly supported in the present study (60% BS; Fig. 8). Character optimization using fast option of Winclada shows that non-molecular synapomorphies supporting the monophyly of the *Bertholletia* clade include the presence of more than 100 fertile stamens (Fig. 7; character 22), a two or four-locular ovary (32), the presence of an aril (40), and undifferentiated cotyledons (41). The monophyly of the *Bertholletia* clade in the present study is congruent with the cladistic analysis of morphology in chapter two and previous molecular study based on plastid *ndhF* and *trnL-F* sequence data (Mori et al., 2007). Within the *Bertholletia* clade there are three major clades (Fig. 8): *Lecythis* s.s., *Pachylecythis*, and a clade that consists of *Bertholletia*, *Lecythis chartacea* clade, *Holopyxidium*, *Corythophora*, *Eschweilera andina* clade, *Eschweilera* section *Tetrapetala*, *Lecythis* section *Corrugata*, and *Eschweilera* s.s. The relationship among these three clades remains as unresolved.

Comparisons between different datasets — Different datasets may have different evolutionary histories or different evolutionary rates, which may result in different tree topologies and create incongruence. Most clades discovered in the strict consensus tree of total evidence are also recognized in each individual marker, except for *Corythophora* and *Eschweilera* section *Tetrapetala* (including *E. nana*). The monophyly of *Corythophora* is not supported by *trnH-psbA* (Fig. 4) and the monophyly of *Eschweilera* section *Tetrapetala* is not supported by ITS (Fig. 1-2). In addition to the incongruence of the supporting clade, the positions of *B. excelsa* and *E. amazoniciformis* are inconsistent among datasets. *Bertholletia excelsa* remains as unresolved in the analyses of ITS region (Fig. 1-1) and *ndhF* gene (Fig. 2-1); it forms a clade with the *Lecythis chartacea* clade in the analyses of the *trnL-F* region

(Fig. 3-1) and the total evidence dataset (Fig. 8-1); it is sister to *Lecythis* s.s. in the analysis of the *trnH-psbA* region (Fig. 4); it forms a clade with *Eschweilera* section *Tetrapetala* in the combined analysis of three plastid DNA (Fig. 5-1); and it is sister to the *E. amazoniciformis*/*Eschweilera andina* clade in the combined analysis of all four genetic markers (Fig. 6-1). On the other hand, *E. amazoniciformis* forms a clade with *Corythophora* in the analysis of the ITS region (Fig. 1-2); it is sister to *Eschweilera* section *Tetrapetala* in the analyses of the *ndhF* gene (Fig. 2-1) and the combined dataset of three plastid DNA (Fig. 5-1); it forms a clade with *B. excelsa* and *Lecythis chartacea* clade in the analysis of the *trnL-F* region (Fig. 3-1); and it is sister to *Eschweilera andina* clade in the analyses of the combined datasets of four DNA markers (Fig. 6-1) and total evidence (Fig. 8-2).

The inconsistency also occurs in the phylogenetic relationships among the clades. For example, the analyses of the *ndhF* (Fig. 2-1) and the combined dataset of three plastid DNA (Fig. 5-1) support the sister relationship of *Lecythis* s.s. and *Holopyxidium*. In the analysis of the *trnL-F* region, however, *Lecythis* s.s. is sister to *Eschweilera* section *Tetrapetala*, and together, they are sister to *Holopyxidium* (Fig. 3-1); in the analysis of the *trnH-psbA* region *Lecythis* s.s. is sister to *Bertholletia excelsa* (Fig. 4); and in the analysis of the combined dataset of four genetic markers *Lecythis* s.s. is sister to *Pachylecythis* (Fig. 6-1). In addition to being sister to *Lecythis* s.s., *Holopyxidium* is sister to the *Lecythis chartacea* clade in the analyses of ITS (Fig. 1-1) and the combined dataset of four genetic markers (Fig. 6-1). Another example is found in the sister relationship of the two *Eschweilera* clades. The sister relationship of the *Eschweilera andina* clade and *Eschweilera* s.s. is supported by ITS. However, the *Eschweilera andina* clade is sister to the *Lecythis chartacea* clade in both the independent and the combined analyses of plastid DNA; and it is sister to *Eschweilera amazoniciformis*, and together, they are sister to *Bertholletia excelsa* in the combined analysis of all four molecular markers. On the other hand, most datasets (except ITS) support the sister relationship of *Eschweilera* s.s. and *Lecythis* section *Corrugata*.

Clades and supporting synapomorphies — In spite of the incongruence of some supporting clades among different datasets and the ambiguity of the sister relationships, each clade is well supported by total evidence (Fig. 8). The clades and synapomorphies supporting the clades are described in the following paragraphs.

Pachylecythis (100% BS; Fig. 8) —This clade comprises all four species of *Lecythis* section *Pisonis* recognized by Mori (1990c). The four species are widespread throughout lowland rainforests in tropical America (Fig. 9). Non-molecular synapomorphies of *Pachylecythis* include the presence of wounded tissue oxidation (Fig. 7-1; character 2), presence of ligule anthers (25), an annular expansion right below the apex of the style (31), and sulcate seeds (35). The sulcate seeds are unique to species of *Pachylecythis*. The monophyly of *Pachylecythis* in this study is congruent with Mori (1990c) and the morphological cladistics in chapter two. It is also congruent with previous molecular study based on plastid *ndhF* and *trnL-F* sequence data (Mori et al., 2007). Although the monophyly of *Pachylecythis* is strongly supported, however, the taxonomy within the clade is problematic, especially for the species of *L. pisonis*. *Lecythis pisonis* has disjunct distribution in both flooded (várzea) and non-flooded forests (terra firme) in the Amazon Basin and in terra firme in eastern Brazil (Mori & Prance, 1990d). Mori and Prance (1981) recognized the populations of the Amazon Basin as *Lecythis pisonis* Cambess. subsp. *usitata* (Miers) S. A. Mori & Prance and the populations of eastern Brazil as *Lecythis pisonis* Cambess. subsp. *pisonis*. In the most recent monograph Mori (1990c) treated populations of both areas as a single species based on his conclusion that the characters used for separating the subspecies were continuous and inconsistent (e.g., hypanthium pubescence and fruit size etc.). However, the result of the present study shows that samples of *L. pisonis* from different populations appear in three different positions in the cladogram. Samples from terra firme in eastern Brazil form a clade with *L. lanceolata* (96% BS; Fig. 8), which is endemic to the coastal forests in eastern Brazil; samples from várzea in the Amazon Basin form a clade with *L. ampla* (55% BS), which is only found west of the Andes; and samples from terra firme in the Amazon Basin form a clade with *L. zabucajo* (83%), which is widespread in the Guayana floristic province and Amazonia. This result indicates that disjunct populations of *L. pisonis* may represent different species.

Lecythis s.s. (100% BS; Fig. 8) — This clade consists of three species that have narrow distributions: *Lecythis ollaria* (the type species of *Lecythis*) is restricted to north-central Venezuela; *Lecythis minor* Jacq. ranges from the Maracaibo Basin of Venezuela to the northern coast of Colombia; and *L. tuyrana* Pittier is distributed from eastern Panama south into northern coast of Ecuador (Fig. 10). The three species were included in *Lecythis* section *Lecythis* (Mori, 1990c). One non-molecular synapomorphy of *Lecythis* s.s. is the presence of a single-coiled ligule (Fig. 7-2; character 23), which is also found only in the *Eschweilera* section *Tetrapetala* clade. A single-coiled ligule distinguishes the three species of *Lecythis* s.s. from other species of Section *Lecythis*, which all have non-coiled ligules. The monophyly of *Lecythis* s.s. is a new finding of this study. The sister relationship of *L. minor* and *L. tuyrana* was recognized in previous molecular study based on plastid *ndhF* and *trnL-F* sequence data, in which *L. ollaria* was not included in the analysis (Mori et al. 2007). Morphologically *L. ollaria* is similar to *L. minor*. Mori (1990c) hypothesized that these two species are closely related based on the morphological similarity. This hypothesis is supported in the present study.

Lecythis section *Lecythis* recognized by Mori (1990c) have an androecial hood (referred to ligule (23) in the present study) that is slightly expanded at the apex and the appendages sweep inward without forming a coil. In addition, the hood appendages of these species lack anthers (Mori, 1990c). The type species of the genus, *L. ollaria*, is in this section. The monophyly of Section *Lecythis* is not supported in the present study. It is divided into three clades: *Lecythis* s.s., the *Lecythis chartacea* clade, and *Holopyxidium* (Figs. 8-1, 8-2). In addition to the presence of a single-coiled ligule (23), species of *Lecythis* s.s. also differ from species of the other two clades in the following characteristics: the presence of appendages on the outer surface (24) instead of the inner surface of the ligule (*Holopyxidium*) or at the apex of the ligule (*Lecythis chartacea* clade) and a stout instead of a slender style (30). The *Lecythis chartacea* clade and *Holopyxidium* are described in the following two paragraphs.

Bertholletia/*Lecythis chartacea* clade (<50% BS; Fig. 8) — This clade contains 13 species that are characterized by two non-molecular synapomorphies: the presence of leaf papillae on the abaxial surface (5) and appendages located at the apex of the ligule (24). Within the clade, *Bertholletia excelsa* is sister to all other species (*Lecythis chartacea* clade). *Bertholletia excelsa* is the only species of the monotypic *Bertholletia* and is found in Amazonia and the Guianas (Fig. 11). It differs from other species of the clade in having two calyx lobes (16) and seeds without an aril (40). Mori and Prance (1990a) hypothesized that *B. excelsa* is closely related to some species of *Lecythis*, especially *Lecythis lurida* (Miers) S. A. Mori. The hypothesis was made based on the following features that are shared by both species (Mori & Prance, 1990a): the presence of leaf papillae on the abaxial surface (5), hood appendages swept inward without forming a complete coil (referred to ligule appendage position (24) in the present study), and the mature fruits that fall to the ground with the seeds remaining inside (referred to operculum (33) and operculum dehiscence (34) in the present study). The first two character states are synapomorphies of the *Bertholletia*/*Lecythis chartacea* clade, but they are also found in some species of *Holopyxidium*. The topology of the strict consensus tree supports the close relationship of *B. excelsa* and some species of *Lecythis*. However, *L. lurida* is not among those species, but is included in the *Holopxidium* clade (Fig. 8-2).

The *Lecythis chartacea* clade (73% BS; Fig. 8) consists of 12 species that are distributed in Amazonia and the Guianas (Fig. 14). There is no non-molecular synapomorphy supporting the monophyly of the *Lecythis chartacea* clade. Within the clade, *L. brancoensis* is sister to all other species. *Lecythis brancoensis* was included in *Lecythis* section *Poiteaui* (Mori, 1990c). It differs from other species of the *Lecythis chartacea* clade in the presence of the ligular anthers (Fig. 7; character 25) and the absence of a closed androecium (26). The sister relationship of *L. brancoensis* and other species of the *Lecythis chartacea* clade is a new finding of the present study. Mori (1990c) established Section *Poiteaui* to accommodate three species (*Lecythis barnebyi* S. A. Mori, *L. brancoensis* & *Lecythis poiteaui* O. Berg) that have terminal inflorescence, flat androecial hoods with antheriferous appendages, and densely packed stamens (up to 1,000) on the staminal ring. *Lecythis brancoensis* was not included in previous molecular study (Mori et al. 2007). In the cladistic analysis of the morphological dataset, it formed a clade with the other two species of Section *Poiteaui*. However, the close relationship of *L. brancoensis* and the other two species of Section *Poiteaui* is not supported in the present study.

The remaining species of the *Lecythis chartacea* clade consist of two species of *Eschweilera* (*E. congestiflora* and *E. simiorum*) and nine species of *Lecythis*. The former were included in *Eschweilera* section *Eschweilera* (Mori & Prance, 1990d) and the latter were included in *Lecythis* section *Lecythis* (Mori, 1990c). These species are united by the absence of leaf papillae on abaxial surface (5). Both two species of *Eschweilera* (*E. congestiflora* and *E. simiorum*) in this group have a non-coiled ligule (23), appendages locating at the apex of the ligule (24), a four-locular ovary (32), a slender style (30), and seeds with a basal aril (40). These features combined together are diagnostic for species of the *Lecythis chartacea* clade. Mori et al. (2007) pointed out that both species were possibly placed in the wrong genus because of the close relationship of both species and the *Lecythis chartacea* clade as indicated in their analysis of plastid *ndhF* and *trnL-F* sequences (Fig. 1 in Mori et al., 2007). The present study further confirms the result of Mori et al. (2007).

Holopyxidium (72% BS; Fig. 8) — This clade consists of six species that are found in central and eastern Amazonia or in eastern Brazil (Fig. 13). There is no non-molecular synapomorphy supporting the monophyly of *Holopyxidium*. Within the clade, the six species form two distinct clades. The first clade consists of *L. barnebyi* and *L. poiteaui*. Both species were included in *Lecythis* section *Poiteaui* (Mori, 1990c). Synapomorphies of this clade include the presence of leaf papillae on abaxial surface (Fig. 8; character 5) and ligular anthers (25), and the absence of a closed androecium (26). Section *Poiteaui* recognized by Mori (1990c) consisted of three species. Cladistic analysis of morphology in chapter two supported the monophyly of Section *Poiteaui*, but in the present study, the monophyly of Section *Poiteaui* is not supported because one of the species (*L. brancoensis*) is included in the *Lecythis chartacea* clade.

The second clade contains four species of *Lecythis*: *L. lurida*, *Lecythis schwackei* (R. Knuth) S. A. Mori, *Lecythis prancei* S. A. Mori, and one undescribed species of *Lecythis*. The first three species were included in *Lecythis* section *Lecythis* (Mori, 1990c). One non-molecular synapomorphy of this clade is the presence of mucilage ducts in the sepals (Fig. 8; character 17), which is also found only in a few species of the *Lecythis chartacea* clade. Mori

(1995) recognized the four species in this clade along with *Lecythis gracieana* S. A. Mori, *Lecythis parvifructa* S. A. Mori, and *Lecythis retusa* Spruce ex O. Berg. as the *jarana* group, which was characterized by an androecial hood that swept inward and the fruit that falls to the ground with the seeds remaining inside. *Jarana* is the common name of *L. lurida* (Mori & Prance, 1990a). Mori (1995) placed these species in the *jarana* group because morphologically they all resemble *L. lurida*. However, when these species are further examined, the four species in *Holopyxidium* have appendages on the inner surface of the ligule (24) while *L. gracieana*, *L. parvifructa*, and *L. retusa* have appendages at the apex of the ligule. Moreover, species of the former tend to have reticulate and impressed seed veins while the latter three species have salient seed veins. The seed-veined character is not included in the analysis because variation of this character is not fully understood. The tree topology of the present study shows that *L. gracieana*, *L. parvifructa*, and *L. retusa* are included in *Lecythis chartacea* clade while the other four species are included in *Holopyxidium*. Therefore the monophyly of the *jarana* group as described by Mori (1995) is not supported.

The inclusion of two species of Section *Poiteaui* in *Holopyxidium* in the present study is surprising because morphologically species of these two groups are very different, especially in terms of the androecial structure. For example, two species of Section *Poiteaui* have hood anthers (25) and open androecia (26). In contrast, other species of *Holopyxidium* lack hood anthers and possess closed androecia. Nonetheless, the sister relationship of *L. prancei* and *L. poiteaui* was first inferred and strongly supported in the molecular analysis of plastid *ndhF* and *trnL-F* sequences (Fig. 1 in Mori et al., 2007). In the present study more species are included in the analysis and the close relationship of Section *Poiteaui* and other species of *Holopyxidium* is further confirmed.

Corythophora (100% BS; Fig. 8) — This clade includes all four species of *Corythophora* recognized by Mori and Prance (1990c). Species of *Corythophora* are restricted to Surinam, French Guiana, and central and eastern Amazonian Brazil (Fig. 14). Non-molecular synapomorphies of *Corythophora* include the presence of squamulae on the surface of the inflorescence rachis (Fig. 7; character 12), the presence of anther dimorphism (28), and the absence of nectar (29). Within the clade, four species are divided into two subclades: one with *C. labriculata* sister to *C. amapaensis* and the other with *C. alta* sister to *C. rimosa*. Species of the former subclade lack ligule anthers while species of the latter subclade possess ligule anthers (25). The monophyly of *Corythophora* in this study is congruent with the classification of Mori and Prance (1990c) and the cladistic analysis of morphology in chapter two. It is also congruent with previous molecular study (Mori et al., 2007).

Eschweilera amazoniciformis/*Eschweilera andina* clade (<50% BS; Fig. 8) — This clade contains 19 species of *Eschweilera* recognized by Mori and Prance (1990d). These species were included in *Eschweilera* section *Eschweilera* (Mori & Prance, 1990e). Within the clade, *Eschweilera amazoniciformis* S. A. Mori is sister to the *Eschweilera andina* clade. However, there is no non-molecular synapomorphy supporting this relationship. *Eschweilera amazoniciformis* is endemic to central Amazonia. It differs from species of the *Eschweilera andina* clade in the presence of four instead of six calyx lobes (Fig. 7; character 16) and petals (18) and seeds with a basal instead of a lateral or spreading aril (39).

Most species of the *Eschweilera andina* clade are found west of the Andes, with the exceptions of *Eschweilera andina* (Rusby) J. F. Macbr., *Eschweilera ovalifolia* (DC.) Nied., and *Eschweilera tessmannii* R. Knuth, which are found in western Amazonia (Fig. 15). The monophyly of the *Eschweilera andina* clade is well supported by the data (Fig. 8; 87% BS).

However, there is only one non-molecular synapomorphy supporting the monophyly of this clade: the presence of a lateral or spreading aril (Fig. 7; character 40).

Eschweilera section *Tetrapetala* (99% BS; Fig. 8) — This clade consists of three species: *Eschweilera alvimii* S. A. Mori, *Eschweilera tetrapetala* S. A. Mori, and *Eschweilera nana* (O. Berg) Miers. The first two species were included in *Eschweilera* section *Tetrapetala* (Mori, 1990a). They are endemic to the coastal forests in eastern Brazil (Fig. 16). *Eschweilera nana* was included in *Eschweilera* section *Eschweilera* by Mori and Prance (1990e). It is widely distributed in the Central Plateau into northeastern Brazil and southwestern Amazonia (Fig. 16). Synapomorphies of this clade include the presence of squama on the inflorescence rachis (Fig. 7; character 12), a single-coiled ligule (23), and appendages on both the inner and outer surface of the ligule (24). The last character state is unique to this clade. The monophyly of Section *Tetrapetala* in the present study is congruent with the result of the morphological cladistics in chapter two.

The present study indicates that the inclusion of Section *Tetrapetala* in *Eschweilera* is problematic. The morphological cladistics in chapter two did not resolve whether or not Section *Tetrapetala* and *Eschweilera* s.s. (including *Eschweilera andina* clade & core *Eschweilera*) together are monophyletic. In the present study, however, Section *Tetrapetala* is sister to a clade that consists of *Lecythis* section *Corrugata* and core *Eschweilera* (Fig. 8), and thus, the inclusion of Section *Tetrapetala* in *Eschweilera* is not supported. In addition, both morphological cladistics in chapter two and the present study show that species of Section *Tetrapetala* have a single-coiled ligule (23), a two-locular ovary (32), and a basal aril (40). The first feature is also found only in *Lecythis* s.s.; the second feature is found in most species of *Eschweilera*; and the third feature is found in species of *Pachylecythis*, *Lecythis* s.s., *Holopyxidium*, *Corythophora*, and *Lecythis* section *Corrugata*. Both the morphological and molecular data suggest that Section *Tetrapetala* should be treated as an independent genus.

Lecythis section *Corrugata* (99% BS; Fig. 8) — This clade includes all five species of *Lecythis* Section *Corrugata* recognized by Mori (1990c). Species of Section *Corrugata* are mostly found in eastern Venezuela, the Guianas, and eastern Amazonia (Fig. 17). One synapomorphy unique to this clade is the presence of rugose/tuberculate pedicel and hypanthium (Fig. 7; character 14). Other synapomorphies include the presence of a non-coiled ligule (23), an open androecium (26), anther dimorphism (28), a slender style (30), and a four-locular ovary (32). The monophyly of Section *Corrugata* in the present study is congruent with Mori (1990c) and the cladistic analysis of morphology in chapter two. It is also congruent with previous molecular study (Mori et al., 2007). However, the sister relationship of Section *Corrugata* and core *Eschweilera* has not been suggested before.

Morphologically species of Section *Corrugata* are more closely related to *Corythophora*, especially in terms of floral and seed features. For example, species of Section *Corrugata* and *Corythophora* both have a non-coiled ligule (23), appendages on the inner surface of the ligule (24), anther dimorphism (28), and seeds with a basal aril (40). In general, species of Section *Corrugata* can be distinguished from species of *Corythophora* by an open instead of a closed androecium (26) and a four instead of a two-locular ovary (32). However, one species of Section *Corrugata* (*L. corrugata*) also has a closed androecium that resembles the one of *Corythophora*; and a four-locular ovary is also found in one species of *Corythophora* (*C. labriculata*). Mori (1990c) pointed out the androecial resemblance between *L. corrugata* and species of *Corythophora* and hypothesized the close relationship of Section *Corrugata* and *Corythophora* through the link of *L. corrugata*. In the present study, however, Section

Corrugata is sister to core *Eschweilera* (Fig. 8-2), and thus, the close relationship of Section *Corrugata* and *Corythophora* is not supported.

Core *Eschweilera* (95% BS; Fig. 8) — This clade consists of 29 species of *Eschweilera* recognized by Mori and Prance (1990d). Among these species, *Eschweilera tenuifolia* (O. Berg) Miers was the only species of the monotypic Section *Jugastrum* (Prance & Mori, 1990); *Eschweilera bracteosa* (Poepp ex. O. Berg) Miers and *Eschweilera cyathiformis* S. A. Mori were included in Section *Bracteosa* (Mori, 1990b); and the remaining 26 species were included in Section *Eschweilera* (Mori & Prance, 1990e). The type species, *E. parvifolia*, is in this clade. Species of core *Eschweilera* range from Veracruz, Mexico to Rio de Janeiro, Brazil (Fig. 18). One synapomorphy of core *Eschweilera* is the presence of a lateral aril (Fig. 7; character 40). Within the clade, *E. tenuifolia* is sister to all other species of core *Eschweilera* and differs from them in the absence of a pedicel (13) and an aril (40). Species of the latter are further divided into *Eschweilera mexicana* clade and *Eschweilera* s.s. However, there are no non-molecular synapomorphies supporting the sister relationship of the *Eschweilera mexicana* clade and *Eschweilera* s.s. *Eschweilera* s.s. is further divided into three subclades, but the relationships of the three subclades are unresolved (Fig. 8-3). The two representatives of Sections *Bracteosa* are nested separately in the largest subclade of *Eschweilera* s.s. (Fig. 8-3).

Eschweilera is divided into four sections in current classification (Mori & Prance, 1990d): Sections *Tetrapetala* (3sp.), *Bracteosa* (4 sp.), *Jugastrum* (1 sp.), and *Eschweilera* (ca. 85 sp.). Both morphological cladistics in chapter two and the previous molecular study (Mori et al., 2007) indicate that *Eschweilera* may not be monophyletic. In the present study, *Eschweilera* is divided into three clades: *Eschweilera* section *Tetrapetala*, the *Eschweilera andina* clade, and core *Eschweilera*. The three clades of *Eschweilera* along with *Lecythis* section *Corrugata* form a clade, which makes *Eschweilera* paraphyletic (Fig. 8). Therefore the monophyly of *Eschweilera* is further rejected in the present study. Among the four sections of *Eschweilera*, the data only supports the monophyly of Section *Tetrapetala*. Section *Eschweilera* is divided into two separate clades: the *Eschweilera andina* clade and core *Eschweilera*. Both Sections *Jugastrum* and *Bracteosa* are included in core *Eschweilera* (Fig. 8). The inclusion of Sections *Jugastrum* and *Bracteosa* in Section *Eschweilera* in the present study is congruent with the morphological cladistics in chapter two and the previous molecular study (Mori et al., 2007). The segregation of the two sections from Section *Eschweilera* is further rejected in the present study.

Character evolution and pollination implication — Prance and Mori (1979) suggested that floral evolution in Lecythidoideae has occurred, for the most part, in the androecium. The ten genera of Lecythidoideae can be divided into two major groups based on the androecial symmetry: *Gustavia*, *Grias*, and *Allantoma* have actinomorphic androecia and *Cariniana*, *Couroupita*, *Corythophora*, *Bertholletia*, *Couratari*, *Eschweilera* and *Lecythis* have zygomorphic androecia (Prance & Mori, 1979; Mori & Prance, 1990b; Huang et al., 2008). The androecium in *Cariniana* is only slightly zygomorphic, and thus, is referred as oblique zygomorphy in the present study. Prance and Mori (1979) assumed that the evolution of the androecium in Lecythidoideae follows a trend of increasing zygomorphy and then follows a trend of increasing ligular complexity within zygomorphic-flowered genera. They also assumed that the increasing zygomorphy is accompanied by the reduction of stamens and the production of nectar (Mori & Prance, 1979). Based on these assumptions, I hypothesize that the evolution of the androecium in Lecythidoideae follows the rule of linear morphological transformation. This hypothesis predicts that the androecium in Lecythidoideae evolved from actinomorphy to oblique zygomorphy and then to zygomorphy.

In addition, it also predicts that within the zygomorphic-flowered genera, the open androecium with a non-coiled ligule in *Couroupita*, *Lecythis* sections *Corrugata* (excluding *L. corrugata*), *Pisonis*, and *Poiteaui* is the most primitive; the second most primitive androecium is the closed androecium with a non-coiled ligule in *Bertholletia excelsa*, *Lecythis corrugata*, species of *Corythophora* and *Lecythis* section *Lecythis* (excluding *L. minor*, *L. ollaria*, and *L. tuyrana*); the third is the closed androecium with a single-coiled ligule in *Eschweilera nana*, *Lecythis minor*, *L. ollaria*, *L. tuyrana*, and species of *Eschweilera* section *Tetrapetala*; the fourth is the closed androecium with a double or triple-coiled ligule in most species of *Eschweilera*; and the most advanced is the closed androecium with a single or double-coiled ligule and an external flap in *Couratari*.

In order to test the hypothesis of floral evolution in Lecythidoideae, selected characters were optimized onto the phylogenetic trees using parsimonious criteria. The results may be different because of different resolution of the trees and/or different optimization of the characters. For example, the optimization of androecial symmetry (20) shows that actinomorphic androecia of *Gustavia* and *Grias* are plesiomorphic, both zygomorphic and obliquely zygomorphic androecia are derived character state, and actinomorphic androecia of *Allantoma* are reversals of zygomorphic androecia (Fig. 19). The androecial symmetry evolved three times in Lecythidoideae: once evolved from actinomorphy (state 0) to zygomorphy (state 1), once evolved from zygomorphy to actinomorphy, and once evolved from actinomorphy or zygomorphy to oblique zygomorphy (state 2). In Figure 19 characters are optimized onto the consensus tree using fast option of Winclada. It shows that obliquely zygomorphic androecia of *Cariniana* are derived from zygomorphic androecia (Fig. 19). The prediction of androecial symmetry evolving from actinomorphy to oblique zygomorphy and then to zygomorphy is not supported by the result. This result is congruent with previous molecular study based on plastid *ndhF* and *trnL-F* sequence data (Mori et al., 2007), but is incongruent with the one based on morphological and anatomical data (Huang et al., 2008). In the former study the most parsimonious solution for androecial symmetry included three changes: one change from actinomorphy to zygomorphy in one clade that consists of all zygomorphic-flowered genera plus *Allantoma*, one change from zygomorphy to oblique zygomorphy in *Cariniana*, and one change from zygomorphy to actinomorphy in *Allantoma*. In the latter study androecial symmetry evolved three times: twice from actinomorphy to zygomorphy in *Couroupita* and in *Couratari* and once from actinomorphy to oblique zygomorphy in *Cariniana*.

A closed androecium (state 1; character 26) is derived from an open androecium and is found in *Couratari* and most species of the *Bertholletia* clade. The closed androecia of *Couratari* may or may not evolve independently from the *Bertholletia* clade. Within the *Bertholletia* clade four reversals occurred in the *Pachylecythis* clade, *Lecythis brancoensis* of the *Lecythis chartacea* clade, Section *Poiteaui* of the *Holopyxidium* clade, and *Lecythis* section *Corrugata* clade (Fig. 20).

Optimization of the ligule (23) demonstrates that this character evolved five times in Lecythidoideae (Fig. 21): once from a non-coiled (0) to a coiled ligule with an external flap (state 3), once from a non-coiled to a single-coiled ligule (state 1), once from a non-coiled to a double or triple-coiled ligule (state 2), once from a double or triple-coiled to a single-coiled ligule, and once from a double or triple-coiled to a non-coiled ligule. In this scenario, the first appearance of the coiled ligule evolved three times independently in the *Couratari* clade, the *Lecythis* s.s. clade, and the clade that consists of the three clades of *Eschweilera* and the *Lecythis* section *Corrugata* clade (Fig. 21). Two reversals occurred after the first appearance of the coiled ligule: once in *Eschweilera* section *Tetrapetala* (from state 2 to state 1) and the other happened in *Lecythis* section *Corrugata* (from state 2 to state 0). The results of the evolution of a closed androecium and the ligule reject the stepwise evolution of the androecium from a simpler toward a more complicated form.

According to the hypothesis of linear morphological transformation, actinomorphic-flowered *Gustavia* is the most primitive while the highly zygomorphic-flowered *Couratari* is the most advanced in Lecythidoideae. Although many species of *Gustavia* have numerous fertile stamens (up to 1200; Mori & Boeke, 1987) and most species of *Couratari* have fewer than 50 fertile stamens, a general survey of number of fertile stamens shows that genera that have more advanced androecia do not always have fewer stamens (character 22; Fig. 22). In addition to *Couratari*, distinct stamen reduction is only found in *Allantoma* and *Cariniana*. Most species of *Allantoma* have fewer than 20 stamens (Prance, 1979a, 1979b) and most species of *Cariniana* have fewer than 50 stamens (Prance, 1979b). The former have actinomorphic androecia and the latter have obliquely zygomorphic androecia. Therefore the association of stamen reduction with the increasing zygomorphy is not supported in the present study. Likewise, although nectar (29) is known to occur only in zygomorphic-flowered genera, it does not always occur in genera that have a more complicated androecium (Fig. 23). For example, both species of *Corythophora*, *Lecythis* sections *Corrugata*, and *Poiteaui* have a non-coiled ligule, but the androecia of *Corythophora* are closed while the androecia of Section *Corrugata* and *Poiteaui* are open. Closed androecium is more advanced than open androecium based on the hypothesis of linear morphological transformation. However, nectar is absent in species of *Corythophora* but is present in species of *Lecythis* Sections *Corrugata* and *Poiteaui*. Therefore the association of nectar production with increasing zygomorphy is not supported in the present study either.

As discussed in the previous paragraphs, the characters of fertile stamens (22), ligule (23), closed androecium (26), and nectar (29) are homoplasious in Lecythidoideae (Figs. 20-23). Instead of following the trend of increasing zygomorphy, evolution of these characters is probably a process of adaptation in response to different pollinators. Except for a few cases of bat or beetle pollination, the principal pollinators of Lecythidoideae are bees (Mori et al., 1978; Mori & Boeke, 1987). The flowers of Lecythidoideae provide pollen or nectar or both as pollinator rewards and are visited by many kinds of bees (Prance & Mori, 1979). The following bees are among the most frequent visitors: euglossine bees (*Euglossa* & *Eufriesea*), carpenter bees (*Xylocopa*), bumblebees (*Bombus*), trigonid bees (*Trigona*), *Epicharis*, *Centris*, *Ceratina*, and *Megalopta* (Mori & Boeke, 1987). Euglossine bees have large body size and a curved long tongue; carpenter bees, bumblebees, *Epicharis*, and *Centris* also have large body size, but they do not have a curved long tongue; and trigonid bees, *Ceratina*, and *Megalopta* are small bees. Some of these bees are further identified as the principal pollinators of some species of Lecythidoideae (Jackson & Salas, 1965; Mori & Kallunki, 1976; Mori et al., 1978; Müller et al., 1980; Ormond et al., 1981; Nelson et al., 1985; Yarsick et al., 1986; Mori & Boeke, 1987). Based on pollination studies of some representative species, the important visiting bees are mapped onto the phylogenetic tree (Fig. 24).

As indicated in Fig. 24, *Trigona*, *Bombus*, and *Megalopta* were seen visiting the flowers of *Gustavia*, the only actinomorphic-flowered clade that has pollination information. *Gustavia* is the only genus that has poricidal anthers in Lecythidoideae and fertile pollen is the only pollinator reward in *Gustavia*. Although the trigona bees visit the flowers of *Gustavia* frequently, they are not efficient pollinators (Mori & Boeke, 1987). Alternatively, buzz pollination performed by *Bombus cayennensis* in *G. hexapetala* (Mori & Boeke, 1987) suggests that bumblebees are probably the principal pollinators of *Gustavia* because of the presence of the poricidal anthers. Buzz pollination by bees is found in many other plants (e.g., Melastomataceae) that have poricidal anthers (Buchmann & Hurley, 1978).

On the other hand, of all the visiting bees, carpenter bees were seen visiting all of the zygomorphic-flowered clades (Fig. 24). Carpenter bees may collect pollen or nectar from the zygomorphic-flowered Lecythidoideae (Mori & Boeke, 1987). In *Couroupita* and *Pachylecythis*, carpenter bees are further identified as the principal pollinators (Mori et al., 1980; Ormond et al., 1981). *Couroupita* diverged from all other zygomorphic-flowered clades early in the evolutionary history of Lecythidoideae. Since carpenter bees are the principal pollinators of *Couroupita* and they appear in all other zygomorphic-flowered clades, pollination by carpenter bees is plesiomorphic in zygomorphic-flowered Lecythidoideae.

In addition to pollen, many zygomorphic-flowered clades produce nectar as the pollinator reward. Most of these clades have a closed androecium (e.g., *Bertholletia*, *Lecythis* s.s. etc,), which may offer protection against nectar robbers. Some clades enhance the protection by the increasing ligule complexity such as a double or triple-coiled ligule in *Eschweilera* s.s. or a single or double-coiled ligule along with an external flap in *Couratari*. As shown in Fig. 24, small bees (e.g., *Trigona*) are less frequently seen visiting the clades that have a closed androecium than the large bees (e.g., carpenter bees & euglossine bees etc.). Apparently small body size does not provide enough strength for the small bees to force open the closed androecia. Among clades that have a closed androecium, flowers that have a highly coiled ligule (*Couratari* & *Eschweilera*) are visited by fewer kinds of bees than flowers that have a non-coiled (e.g., *Corythophora*; Fig. 24) or a less coiled ligule (e.g., Section *Tetrapetala*). In addition, although large bees are able to enter the flowers, clades that have a closed androecium and a coiled-ligule are visited more frequently by euglossine bees than by carpenter bees or other large bees (Mori & Boeke, 1987). This is probably because the possession of a curved, long tongue enables euglossine bees to extract nectar from the apex of the ligular coil more successfully than other bees. It is possible that the evolution of the highly coiled ligule is a morphological adaptation that enables the pollinator shift from carpenter bees (or others) to euglossine bees.

Another pollinator shift occurred in Section *Poiteaui* of *Holopyxidium*. Instead of bee pollination, flowers of Section *Poiteaui* are bat-pollinated (Mori, 1990c). Species of Section *Poiteaui* have the largest flowers (ca. 11 cm in diameter) of all zygomorphic-flowered clades and provide both pollen and nectar as pollinator rewards. Unlike most nectar producing clades, however, flowers of Section *Poiteaui* have an open androecium and are nocturnal. The terminal inflorescences are not branched and the numerous stamens (up to 1,000) are densely packed on the staminal ring. Moreover, the flowers emit a musty odor at anthesis. These features indicate the adaptation of Section *Poiteaui* to bat pollination.

In summary, this study demonstrates that (1) the obliquely zygomorphic androecium of *Cariniana* is not an intermediate state, but is a derived character state evolved from a zygomorphic androecium; (2) the evolution of the most complicated androecium in *Couratari* is independent from the evolution of other zygomorphic-flowered clades; (3) stamen reduction and nectar production are not necessarily associated with increasing zygomorphy; (4) the evolution of the androecium in Lecythidoideae is closely related to the principal pollinators. In conclusion, the evolution of the androecium in Lecythidoideae is more likely the process of adaptation due to pollinator shift. It is less likely the process of a linearly morphological transformation from a simpler to a more complicated structure.

Taxonomic implication — The present study favors the maintenance of *Bertholletia* and *Corythophora*, but clearly shows that the revision is needed for the circumscriptions of *Eschweilera* and *Lecythis*. The topology of the consensus tree indicates that *Eschweilera* as circumscribed by Mori and Prance (1990d) is paraphyletic and consists of three clades: Section *Tetrapetala* clade, *Eschweilera andina* clade (including *E. amazoniciformis*), and core *Eschweilera* clade (Fig. 8-2). Based on the present phylogeny it is reasonable to treat the three clades as three separate genera. Of the three clades, species of Section *Tetrapetala* possess several morphological features that are distinct from species of the other two clades. In addition, Section *Tetrapetala* is never sister to the *Eschweilera andina* clade or to the core *Eschweilera* clade in any dataset. Therefore the segregation of Section *Tetrapetala* from *Eschweilera* is preferred in the present study. Although the present study favors the segregation of the *Eschweilera andina* clade from the core *Eschweilera* clade, whether or not these two clades represent two genera is questionable. Unlike Section *Tetrapetala*, there are no distinct morphological features that can distinguish these two clades. Moreover, the nuclear ITS sequence data supports the sister relationship of these two clades (Fig. 1-3). Consequently a better solution at present is to retain both the *Eschweilera andina* clade and the core *Eschweilera* clade in *Eschweilera*.

On the other hand, *Lecythis* as circumscribed by Mori (1990c) is polyphyletic and consists of the following clades: *Lecythis* s.s., *Pachylecythis*, *Holopyxidium*, Section *Corrugata*, and *Lecythis chartacea* clade. The results conclusively show that these clades are distinct from each other and each clade can be treated as individual genus. Based on the present phylogeny the three species of *Lecythis* s.s. should be retained in *Lecythis* Loefl. because the type species of the genus (*L. ollaria*) is in this clade. *Pachylecythis* as circumscribed by Ledoux (1964) should be reinstated to accommodate *Lecythis pisonis* and its close relatives. Ledoux (1964) established *Pachylecythis* based on *Pachylecythis egleri* Ledoux, which was treated as a synonym of *Lecythis pisonis* by Mori (1990c). *Lecythis pisonis* is the type species of *Lecythis* section *Pisonis* (Mori, 1990c) and the monophyly of Section *Pisonis* is strongly supported by the data (100% BS; Fig. 8). Therefore all four species of Section *Pisonis* recognized by Mori (1990c) will be transferred to *Pachylecythis*. *Holopyxidium* as circumscribed by Ducke (1925) will be reinstated to accommodate *L. lurida* and its close relatives. Ducke published *Holopyxidium* based on *Holopyxidium jarana* Ducke, which was treated as a synonym of *Lecythis lurida* (Mori, 1990c). *Lecythis lurida* along with another five species of *Lecythis* form a clade in the analysis. Although the clade lacks supporting synapomorphy and most character states shared by these species are plesiomorphic (e.g., non-coiled ligule, four-locular ovary etc.), these species cannot be included in any other clade because they lack the diagnostic features of these clades. In addition, in every molecular dataset these species always form a clade, never nested within other clades. Therefore *L. lurida* along with *L. schwackei*, *L. prancei*, *L. poiteaui*, *L. barnebyi*, and the unknown species in the clade will be transferred to *Holopyxidium*.

The distinctness and the monophyly of Section *Corrugata* are strongly supported by the data (Figs. 7-8), and thus, Section *Corrugata* merits a separate genus from all other clades. *Chytroma* as circumscribed by Miers (1874) probably can be applied to Section *Corrugata*. Miers (1874) established *Chytroma* based on *Chytroma amara* (Aubl.) Miers, which was treated as a synonym of *L. idatimon* by Mori (1990c). However, whether or not *C. amara* is indeed *L. idatimon* is questionable (Mori, pres. comm). Based on the illustration and description, *C. amara* is more likely a species of *Eschweilera* than *L. idatimon* (Mori, 1990c). In order to apply *Chytroma* to accommodate species of Section *Corrugata*, it is necessary to establish the identity of *C. amara* by studying the type specimen using molecular sequence data. If *C. amara* is really a species of *Eschweilera*, a new name, instead of *Chytroma*, should be established for Section *Corrugata*.

Most character states shared by species of the *Lecythis chartacea* clade are plesiomorphic, except the presence of leaf papillae on abaxial surface (character 5; Fig. 7) and the appendages locating at the apex of the ligule (24). Both character states are synapomorphies of the *Lecythis chartacea* clade and *Bertholletia excelsa*. The distinctness of *B. excelsa* is supported by the results and its generic maintenance is favored in the present study. On the other hand, the monophyly of the *Lecythis chartacea* clade is supported by all molecular datasets. Therefore a new genus will be established to accommodate the species of the *Lecythis chartacea* clade.

Table 1. List of sampled taxa and their voucher information and GenBank accession (No. of sampled/No. of total species). Taxa with * are type species of section or genus; taxa with ** are type species of both section and genus.

Taxa	Locality	Voucher information	*ndhF* GenBank Acc.	*trnL-F* GenBank Acc.
Bertholletia Bonpl. (1/1)				
B. excelsa Bonpl.	Peru, Madre de Dios	NY/S. A. Mori 25637		
		Janovec 2508		
Corythophora R. Knuth (4/4)				
C. alta R. Knuth*	Brazil, Amazonus	NY/S. A. Mori 27246		
C. amapaensis Pires *ex* S. A. Mori & Prance	French Guiana, Saül	NY/S. A. Mori 24146		
		NY/S. A. Mori 24147		
		NY/S. A. Mori 24148	DQ388189	DQ417942
C. labriculata (Eyma) S. A. Mori & Prance	Suriname, Brownsberg Nature Reserve	NY/S. A. Mori 25518	DQ388190	DQ417943
C. rimosa W. A. Rodrigues subsp. *rimosa*	Brazil, Manaus, Amazonas	NY/S. A. Mori 27227		
		NY/S. A. Mori 27282		
C. rimosa W. A. Rodrigues subsp. *rubra* S. A. Mori	French Guiana, Saül	NY/S. A. Mori 24327		
		NY/S. A. Mori 24328		
		NY/S. A. Mori 25475	DQ388191	DQ417944
Eschweilera Mart. *ex* DC. (54/93)				
Section *Tetrapetala* S. A. Mori (2/3)				
E. alvimii S. A. Mori	Brazil, Bahia	NY/W. W. Thomas 10300		
		NY/A. Morim 2634		
E. tetrapetala S. A. Mori*	Brazil, Bahia	NY/S. C. de Sant'Ana 316		
		NY/G. Hatschbach 48060		
Section *Bracteosa* S. A. Mori (2/4)				
E. bracteosa (Poepp. *ex* O. Berg) Miers*	Brazil, Manaus, Amazonas	NY/S. A. Mori 27239		
E. cyathiformis S. A. Mori	Brazil, Manaus, Amazonas	NY/S. A. Mori 27229		
Section *Jugastrum* Prance & S. A. Mori (1/1)				
E. tenuifolia (O. Berg) Miers*	Brazil, Manaus, Amazonas	NY/L. V. Ferreira 135	DQ388255	DQ417982
Section *Eschweilera* S. A. Mori & Prance (49/85)				
E. aguilarii S. A. Mori	Costa Rica, Puntarenas, Osa	INB/R. Aguilar 6521	DQ388234	DQ417965
		INB/R. Aguilar 11109		
		INB/R. Aguilar 11110		
E. alata A. C. Sm.	French Guiana, Forêt domaniale de Crique Plomb	NY/M.-F. Prévost 4607		
		NY/M.-F. Prévost 4615		
E. albiflora (DC.) Miers	Brazil, Amazonus	NY/S. A. Mori 9199	DQ388226	DQ417954
E. amazoniciformis S. A. Mori	Brazil, Amazonus	NY/S. A. Mori 27244		
		NY/S. A. Mori 27270		
E. amaplexifolia S. A. Mori	Panama, Colón	NY/F. Hernández 262		
		NY/F. Hernández 263		
E. andina (Rusby) J. F. Macbr.	Ecuador, Napo, Orellana	NY/N. A. C. Pitman 5892	DQ388229	DQ417956
E. antioquensis Dugand & Daniel	Colombia, Antioquia, Frontino	MO/P. Acevedo 1321		
E. apiculata (Miers) A. C. Sm.	French Guiana, Piste de St. Elite	NY/S. A. Mori 25897		
E. atropetiolata S. A. Mori	Brazil, Manaus, Amazonas, Amazonas	NY/S. A. Mori 27225		
		NY/S. A. Mori27237		
E. biflava S. A. Mori	Costa Rica, Puntarenas, Osa	INB/R. Aguilar 11103		
		INB/R. Aguilar 11104		
		INB/R. Aguilar 11111		
		INB/R. Aguilar 11123		
		INB/R. Aguilar 11124		
E. calyculata Pittier	Panama, Colón	Toribio 78		
E. caudiculata R. Knuth	Ecuador, Carchi	NY/Aulestia 817		
	Ecuador, Esmeraldas, San Lorenzo	NY/Clark 7156		
E. chartaceifolia S. A. Mori	French Guiana, Saül	NY/S. A. Mori 24088		
	French Guiana, Nouragues Field Station	NY/S. A. Mori 25556		
	French Guiana, Camp Arataï on Arataye River	NY/S. A. Mori 25676		
	French Guiana, Piste de St. Elite	NY/M.-F. Prévost 4498	DQ388231	DQ417959
E. collina Eyma	French, Guiana, Pic Maté cho	NY/S. A. Mori 25145	DQ388232	DQ417960
	French Guiana, Montagnes Plomb	NY/M.-F. Prévost 4588		
E. congestiflora (R. Benoist) Eyma	French Guiana, Paracou	NY/J.-F. Molino 2019	DQ388225	DQ417961
	French Guiana, Nouragues Field Station	NY/S. A. Mori 25766		

Table 1. Continued. List of sampled taxa and their voucher information and GenBank accession (No. of sampled/No. of total species). Taxa with * are type species of section or genus; taxa with ** are type species of both section and genus.

Taxa	Locality	Voucher information	*ndhF* GenBank Acc.	*trnL-F* GenBank Acc.
E. coriacea (DC.) S. A. Mori	Panama, Colón	NY/F. Hernández 271		
	French Guiana, Saül	NY/S. A. Mori 24084		
	French Guiana, Nouragues Field Station	NY/S. A. Mori 25420A	DQ388246	DQ417962
E. correae sp. ined.	Panama, Veraguas, Santa Fé	NY/F. Hernández 193		
E. decolorans Sandwith	Guyana, Potaro-Siparuni	NY/S. A. Mori 24494		
	French Guiana, Nouragues Field Station	NY/S. A. Mori 25451		
		NY/S. A. Mori 25452	DQ388247	DQ417963
E. grandiflora (Aubl.) Sandwith	French Guiana, Nouragues Field Station	NY/S. A. Mori 25435	DQ388251	DQ417964
E. hondurensis Standl.	Costa Rica, Puntarenas, Osa	INB/R. Aguilar 11128		
E. integrifolia (Ruiz & Pav. *ex* Miers) R. Knuth	Ecuador, Guayas	NY/Cornejo 8018		
	Costa Rica, Puntarenas, Osa	INB/R. Aguilar 11140		
	Panama, Veraguas, Santa Fé	NY/F. Hernández 314		
E. jacquelyniae S. A. Mori	Panama, Panamá	NY/F. Hernández 315		
E. juruensis R. Knuth	Brazil, Acre	NY/Daly 10998	DQ388242	DQ417966
E. laevicarpa S. A. Mori	French Guiana, Saül	NY/S. A. Mori 24325		
E. longirachis S. A. Mori		R. Aguilar 7966		
		R. Aguilar 7967	DQ388266	DQ417968
E. mexicana T. Wendt, S. A. Mori & Prance	Mexico, Veracruz, Jesús Carranza	NY/T. L. Wendt 4180	DQ388269	DQ417969
E. micrantha (O. Berg) Miers		Clark 4209		
	French Guiana, Saül	NY/S. A. Mori 24711		
	French Guiana, Nouragues Field Station	NY/S. A. Mori 25448	DQ388248	DQ417970
	French Guiana, Trésor Nature Reserve	NY/S. A. Mori 25652		
	French Guiana, Patawa	NY/S. A. Mori 25931		
E. nana (O. Berg) Miers	Brazil, Mato Grosso	Potascheff 1		
		NY/M. do C. B. Teixeira 0874	DQ388271	DQ417971
E. neei S. A. Mori	Costa Rica, Puntarenas, Osa	CR/R. Aguilar 6517	DQ388253	DQ417972
E. ovalifolia (DC.) Nied.	Bolivia, Cochabamba	NY/G. Navarro 1759		
E. ovata (Cambess.) Mart. *ex* Miers	Brazil, Bahia	NY/W. W. Thomas 111060	DQ388224	DQ417974
E. pachyderma Cuatre.	Colombia, Choco, Nuqúi	NY/Acevedo 6881		
E. panamensis Pittier	Costa Rica, Puntarenas, Osa	CR/R. Aguilar 11106		
		CR/R. Aguilar 11107		
		CR/R. Aguilar 11121		
E. parviflora (Aubl.) Miers	French Guiana, Nouragues Field Station	NY/S. A. Mori 25437		
		NY/S. A. Mori 25458	DQ388223	DQ417975
E. parvifolia Mart. *ex* DC.**	Brazil, Manaus, Amazonas, Amazonas	NY/S. A. Mori 27043A		
		NY/S. A. Mori 27277		
E. pedicellata (Rich.) S. A. Mori	French Guiana, Saül	NY/S. A. Mori 24085		
	Guyana, Potaro-Siparuni	NY/S. A. Mori 24381		
	French Guiana, Camp Arataï on Arataye River	NY/S. A. Mori 25597		
E. pseudodecolorans S. A. Mori	Brazil, Manaus, Amazonas, Amazonas	NY/S. A. Mori 27224		
E. rankiniae S. A. Mori	Brazil, Manaus, Amazonas, Amazonas	NY/S. A. Mori 27333		
E. rimbachii Standl.	Ecuador, Carchi, Tulcan	NY/J. L. Clark 6380	DQ388233	DQ417977
	Ecuador, Los Rios Samama	S/B. Stahl 5930	DQ388235	DQ417978
E. sagotiana Miers	Guyana, Potaro-Siparuni	NY/S. A. Mori 24493		
	French Guiana, Nouragues Field Station	NY/S. A. Mori 25470	DQ388249	DQ417979
	French Guiana, Camp Arataï on Arataye River	NY/S. A. Mori 25712		
E. sclerophylla Cuatrec.	Colombia, Valle del Cauca, Buenaventura	NY/A. H. Gentry 53722		
E. sessilis A. C. Sm.	Panama, Panamá	NY/F. Hernández 209		
E. simiorum (Benoist) Eyma	French Guiana, Nouragues Field Station	NY/S. A. Mori 25507	DQ388227	DQ418980
	French Guiana, Piste de St. Elite	NY/M.-F. Prévost 4250		
	Mont Grand Matoury	NY/D. R. L. Sabatier 4804	DQ388243	DQ417981
E. subglandulosa (Steud. *ex* O. Berg) Miers	Guyana, Potaro-Siparuni	NY/S. A. Mori 24380		
E. tessmannii R. Knuth	Peru, Madre de Dios	NY/S. A. Mori 25642	DQ388268	DQ417983
E. tresoriana sp. ined.	French Guiana, Trésor Nature Reserve	NY/S. A. Mori 25577		
		NY/S. A. Mori 25645		
		NY/S. A. Mori 25649		
E. truncata A. C. Sm.	Brazil, Manaus, Amazonas, Amazonas	NY/S. A. Mori 27234		

Table 1. Continued. List of sampled taxa and their voucher information and GenBank accession (No. of sampled/No. of total species). Taxa with * are type species of section or genus; taxa with ** are type species of both section and genus.

Taxa	Locality	Voucher information	*ndhF* GenBank Acc.	*trnL-F* GenBank Acc.
E. wachenheimii (R. Benoist) Sandwith	French Guiana, Nouragues Field Station	NY/S. A. Mori 25570		
	French Guiana, Camp Arataï on Arataye River	NY/S. A. Mori 25591		
		NY/S. A. Mori 25664		
	French Guiana, Piste de St. Elite	NY/M.-F. Prévost 4252	DQ388254	DQ417984
E. sp.	Costa Rica, Puntarenas, Osa	CR/R. Aguilar 6572		
E. sp.		CR/R. Aguilar 11102		
E. sp.		CR/R. Aguilar 11105		
E. sp.		CR/R. Aguilar 11112		
Lecythis Loefl. (25/27)				
Section *Corrugata* S. A. Mori (5/5)				
L. confertiflora (A. C. Sm.) S. A. Mori	French Guiana, Saül	NY/S. A. Mori 24320		
	French Guiana, Nouragues Field Station	NY/S. A. Mori 25411	DQ388210	DQ418014
	French Guiana, Montagnes Plomb	NY/M.-F. Prévost 4597		
L. corrugata Poit.*	French Guiana, Saül	NY/S. A. Mori 24265	DQ388211	DQ418015
		NY/S. A. Mori 24271		
	French Guiana, Saut Athanase tourist camp	NY/S. A. Mori 25730		
L. idatimon Aubl.	French Guiana, Nouragues Field Station	NY/S. A. Mori 25430	DQ388214	DQ418018
		NY/S. A. Mori 25498	DQ388215	DQ418019
	French Guiana, L'Auberge des Orpailleurs	NY/S. A. Mori 25745		
	French Guiana, Trésor Nature Reserve	NY/S. A. Mori 25754		
	French Guiana, Cayenne	NY/M.-F. Prévost 4776		
L. persistens Sagot subsp. *aurantiaca* S. A. Mori	French Guiana, Saül	NY/S. A. Mori 24724		
	French Guiana, Nouragues Field Station	NY/S. A. Mori 25436	DQ388218	DQ418023
L. persistens Sagot subsp. *persistens*	French Guiana, Nouragues Field Station	NY/S. A. Mori 25391		
		NY/S. A. Mori 25523		
	French Guiana, Trésor Nature Reserve	NY/S. A. Mori 25651		
	French Guiana, Matiti	NY/M.-F. Prévost 4285	DQ388239	DQ418024
L. pneumatophora S. A. Mori	French Guiana, Saut Athanase tourist camp	NY/S. A. Mori 25728		
	French Guiana, Trésor Nature Reserve	NY/S. A. Mori 25748		
	French Guiana, Piste de St. Elite	NY/M.-F. Prévost 4261	DQ388220	DQ418025
Section *Pisonis* S. A. Mori (4/4)				
L. ampla Miers		R. Aguilar 7958	DQ388238	DQ418012
		R. Aguilar 7968		
		R. Aguilar 7970		
		R. Aguilar 7975		
L. lanceolata Poir.	Brazil, Bahia	NY/A. M. de Carvalho 5824		
	Brazil, São Paulo	NY/G. T. Prance25917	DQ388213	DQ418020
L. pisonis Cambess.*	Brazil, Pará	NY/C. A. Cid Ferreira 1696		
	Brazil, Manaus, Amazonas, Amazonas	NY/S. A. Mori 27268		
		NY/S. A. Mori 27272		
		NY/S. A. Mori 27290		
		NY/S. A. Mori 27291		
	Brazil, Pará, Belém	NY/G. T. Prance23703		
		Smith 51		
		Smith 52		
		Smith 53		
		Smith 54		
	Brazil, Bahia	NY/W. W. Thomas 10896		
L. zabucajo Aubl.	French Guiana, Saül	NY/S. A. Mori 24287		
	French Guiana, Nouragues Field Station	NY/S. A. Mori 25472		
	Brazil, Manaus, Amazonas, Amazonas	NY/S. A. Mori 27271		
	French Guiana, Matiti	NY/M.-F. Prévost 4331		
Section *Poiteaui* S. A. Mori (3/3)				
L. barnebyi S. A. Mori	Brazil, Manaus, Amazonas, Amazonas	NY/S. A. Mori 27228		
L. brancoensis (R. Knuth) S. A. Mori	Guyana, Upper Takutu-Upper Essequibo	NY/B. Hoffman 1084		
L. poiteaui O. Berg*	French Guiana, Saül	NY/S. A. Mori 24178		
	Brazil, Manaus, Amazonas	NY/S. A. Mori 27279		
	French Guiana, Station de la Piste de St. Elite	NY/M.-F. Prévost 4502		

Table 1. Continued. List of sampled taxa and their voucher information and GenBank accession (No. of sampled/No. of total species). Taxa with * are type species of section or genus; taxa with ** are type species of both section and genus.

Taxa	Locality	Voucher information	*ndhF* GenBank Acc.	*trnL-F* GenBank Acc.
Section *Lecythis* S. A. Mori (13/15)				
L. alutacea (R. Knuth) S. A. Mori	Guyana, Potaro-Siparuni	NY/S. A. Mori 24622	DQ388244	DQ418011
L. chartacea O. Berg	French Guiana, Emerald Jungle Village	NY/S. A. Mori 25364	DQ388209	DQ418013
	French Guiana, Paracou	NY/S. A. Mori 26485		
L. gracieana S. A. Mori	Brazil, Manaus, Amazonas	NY/M. G. M. Van Roosmalen L-79		
L. holcogyne (Sandwith) S. A. Mori	French Guiana, Station de la Piste de St. Elite	NY/M.-F. Prévost 4505		
		NY/M.-F. Prévost 4508	DQ388212	DQ418016
		NY/M.-F. Prévost 4511	DQ388236	DQ418017
L. lurida (Miers) S. A. Mori	Brazil, Amazonas	NY/G. T. Prance 23702		
L. mesophylla S. A. Mori	Costa Rica, Puntarenas, Osa	NY/R. Aguilar 8449		
		NY/R. Aguilar 11119		
L. minor Jacq.	Hawaii, Oahu Island	NY/T. J. Motley 2895		
	Panama, Panamá	NY/A. de Sedas 219		
L. ollaria P. Loefl.**	Venezuela, Portuguesa	NY/G. Aymard C. 11847		
L. parvifructa S. A. Mori	Brazil, Manaus, Amazonas	NY/S. A. Mori 27231		
L. prancei S. A. Mori	Brazil, Manaus, Amazonas	NY/S. A. Mori 27226		
		NY/S. A. Mori 27260		
L. retusa Spruce *ex* O. Berg	Brazil, Manaus, Amazonas	NY/S. A. Mori 27273		
L. rorida O. Berg	Brazil, Manaus, Amazonas	NY/S. A. Mori 27276		
L. schwackei (R. Knuth) S. A. Mori	Brazil, Minas Gerais	NY/E. T. Neto 2501		
L. tuyrana Pittier	Panama, Panamá	NY/A. de Sedas 216		
Outgroup				
Cariniana estrellensis (Raddi) Kuntze	Bolivia, Santa Cruz	NY/M. Nee 38522	DQ388187	DQ417937
Cariniana domestica (Mart.) Miers	Bolivia, Beni	NY/Solomon7848	DQ388186	DQ417936
Cariniana ianeirensis R. Knuth	Bolivia, Santa Cruz	NY/J. Justiniano12	DQ388184	DQ417938
Couratari macrosperma A. C. Sm.	Peru, Madre de Dios	NY/S. A. Mori 25634	DQ388194	DQ417947
Couratari stellata A. C. Sm.	French Guiana, Saül	NY/S. A. Mori 24092	DQ388196	DQ417950
Couroupita guianensis Aubl.	Costa Rica, Guanacaste, Bagaces	NY/R. C.-H. Tsou 1550	DQ388182	DQ417951
Couroupita nicaraguarensis DC.	Costa Rica, Guanacaste, Bagaces	NY/R. Aguilar 8041	DQ388183	DQ417952
Couroupita subsessilis Pilg.	Brazil, Paraná do Limão, Amazonas	NY/Mori27298		
Grias peruviana Miers	Ecuador, Zamora-Chinchipe, Zamora	NY/J. L. Clark 6426	DQ388178	DQ417999
Gustavia grandibracteata Croat & S. A. Mori	Panama, Panamá	NY/Hernández 261		
Gustavia speciosa (R. Knuth) DC.	Ecuador, Los Rios Samama	S/B. Stahl 5902	DQ388204	DQ418009

Table 2 . List of Primers for DNA amplification and sequencing

Markers		Name	Sequences	References
ITS	F	18S-1830F	5' - AACAAGGTTTCCGTAGGTGA - 3'	Howarth et al. 2003
	R	26S-25R	5' - ACCCGCTGAYTTTAAGCATA - 3'	Luton et al. 1992
	F	ITS5angio (ITS5A)	5' - CCTTATCATTTAGAGGAAGGAG - 3'	K. Wurdack from Standfor et al.2000
	R	241 R	5' - TGTCGCACCACGAGGCACTG - 3'	Ken Wurdack in Michelangeli et al. 2004
	F	5.8S-32F	5' - GCATCGATGAAGAACGTAGC - 3'	Downie & Downie, 1996
	R	5.8S-32R	5' - GCATCGATGAAGAACGTAGC - 3'	Downie & Downie, 1996
	F	NY 760	5' - GAAGAACGTAGCGAAATGCG - 3'	designed by Y.-Y. Huang
	R	NY 762	5' - GCATCGATGAAGAACGTAGC - 3'	designed by Y.-Y. Huang
trnL-F	F	C (B49317)	5' - CGAAATCGGTAGACGCTACG - 3'	Taberlet et al., 1991
	R	F (A50272)	5' - CTCGTGTCACCAGTTCAAAT - 3'	Taberlet et al., 1991
	F	E (B49873)	5' - GGTTCAAGTCCCTCTATCCC - 3'	Taberlet et al., 1991
ndhF	F	1b F	5' - TGGGACTTCTTCTTTTTCC - 3'	Mori et al., 2007
	R	16 R	5' - GTCAGAATATGGTGCTTATGGGAGGTTTAAC - 3'	Mori et al., 2007
	R	10 R	5' - GGAGAAGGTATCAAATATYTAGGGGG - 3'	Mori et al., 2007
	F	972 F	5' - GTCTCAATTGGGTTATATGATG - 3'	Olmstead & Sweere, 1994
	R	536 R	5' - TTGTAACTAATCGTGTAGGGGA - 3'	Olmstead & Sweere, 1994
	R	972 R	5' - GTCTCAATTGGGTTATATGATG - 3'	Olmstead & Sweere, 1994
	R	1155 R	5' - AATATGATTGGTCATATAATCG 3'	Olmstead & Sweere, 1994
	F	1318 F	5' - GGATTAACYGCATTTTATATGTTTCG - 3'	Olmstead & Sweere, 1994
trnH-psbA	F	*trnH* (GUG)	5' - ACTGCCTTGATCCACTTGGC - 3'	Hamilton, 1999
	R	*psbA*	5' - CCATTTGTAGATGGAGCTTCG - 3'	Hamilton, 1999

Table 3. Tree statistics of separate and combined DNA matrices

	ITS	*ndhF*	*trnL-F*	*trnH-psbA*	cpDNA	combined DNA	morphology	total evidence
Taxa	205	164	190	161	203	209	100	207
L (bp)	610-688	1,994-2,014	905-952	405-451	3304-3417	3914-4105	-	-
AL (sites)	1258	1956	1382	1113	4321	5766	41	-
PI (sites)	608	257	273	413	864	1581	41	1603
Indels (sites)	202	8	66	137	116	400	-	202
VS (%)	48%	13%	20%	37%	20%	27%	-	-
Tn	105	148	67	53	77	115	125	132
TL	2662	474	527	1319	2297	6089	105	6114
CI	0.36	0.60	0.56	0.42	0.45	0.35	0.53	0.36
RI	0.80	0.90	0.89	0.83	0.80	0.75	0.88	0.76

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

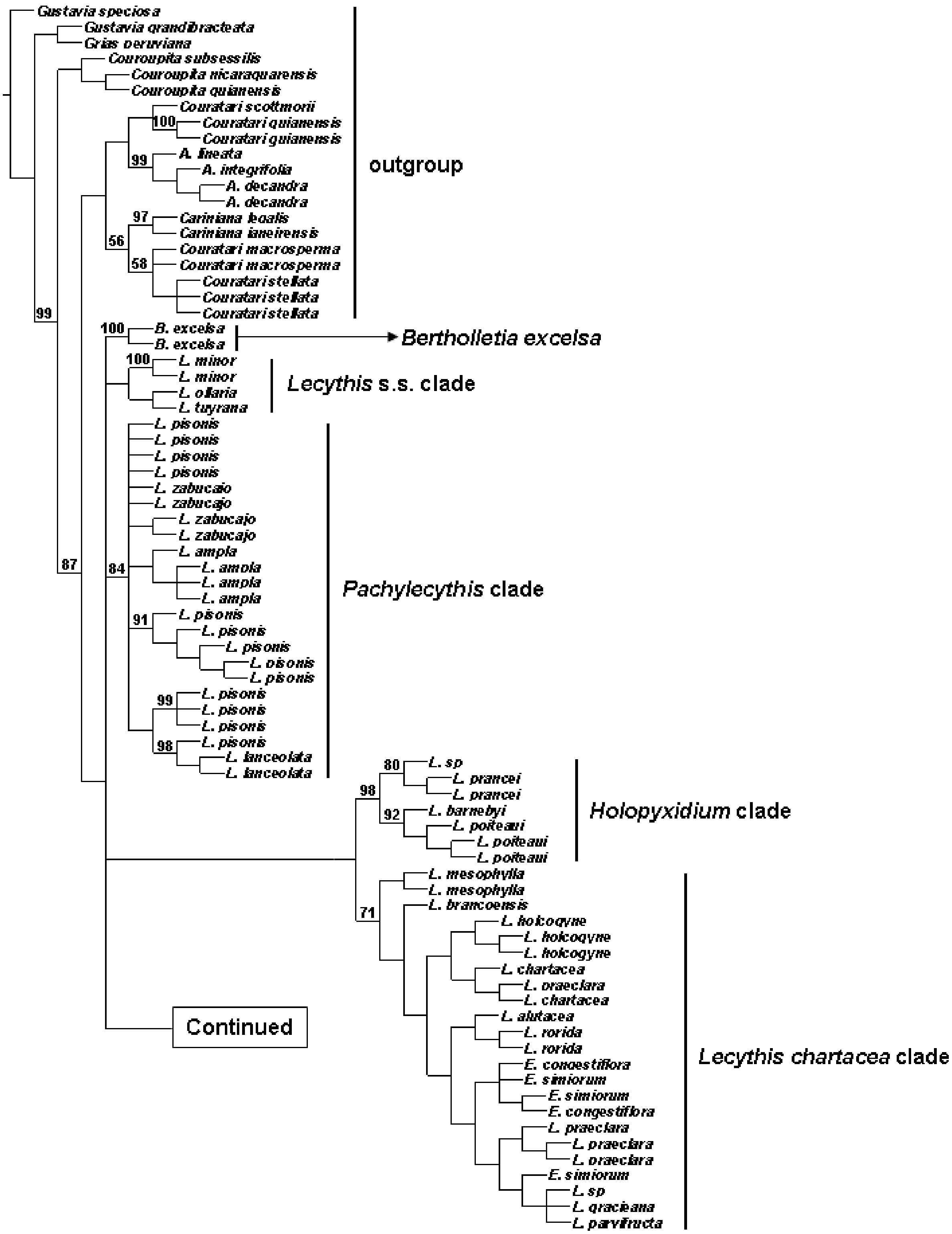

Fig. 1-1. Strict consensus of 105 most parsimonious (MP) trees based on ITS sequences. Bootstrap values (>50%) are given above the branches. Details of the outgroups and *Bertholletia excelsa*, *Lecythis* s.s., *Pachylecythis*, and *Lecythis chartacea* clade of the ingroup are shown in this figure.

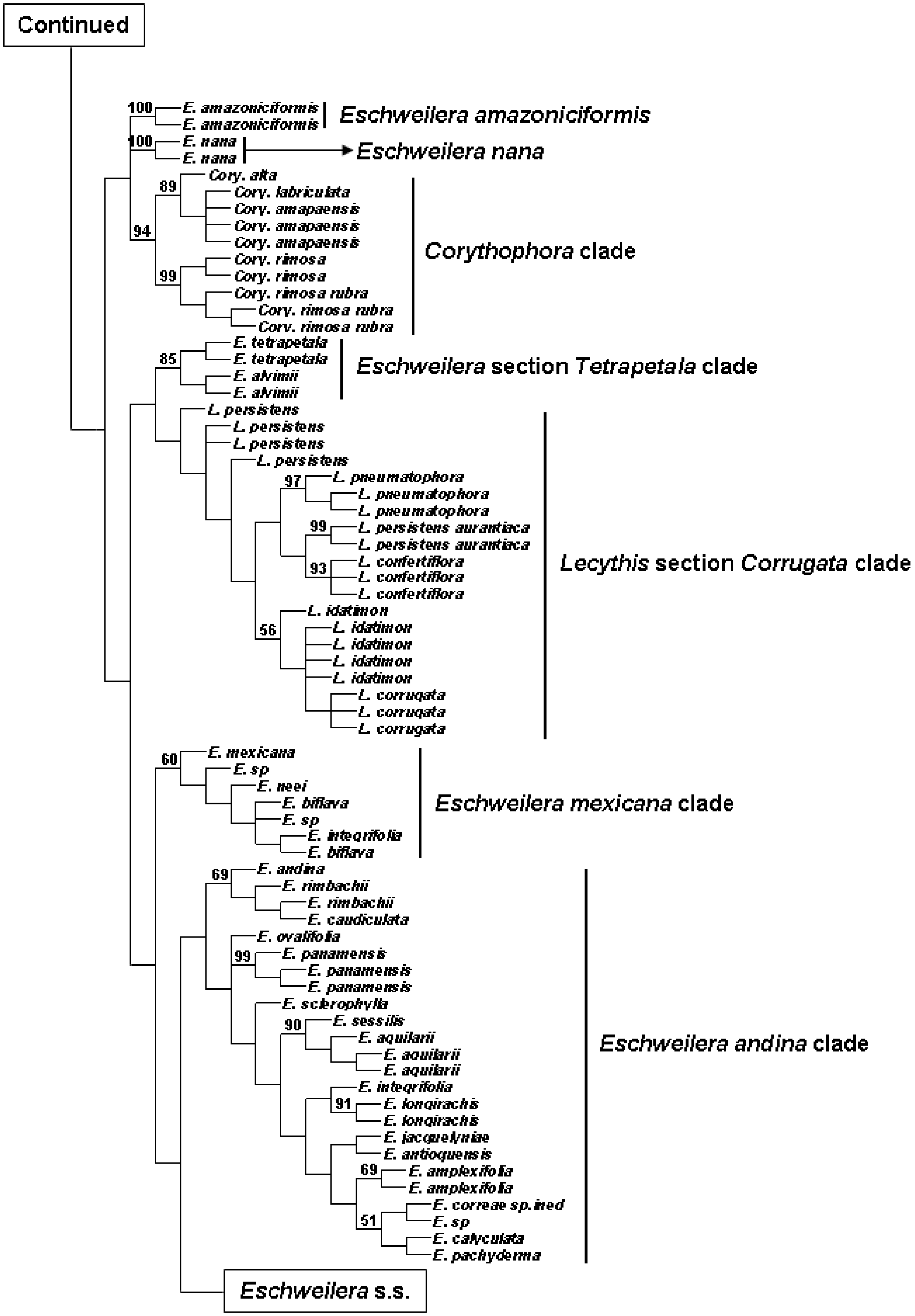

Fig. 1-2. Strict consensus of 105 MP trees based on ITS sequences — continued. *Eschweielra amazoniciformis*, *E. nana*, *Eschweilera* section *Tetrapetala*, *Lecythis* section *Corrugata*, *Eschweilera mexicana*, and *Eschweilera andina* clade are shown in this figure.

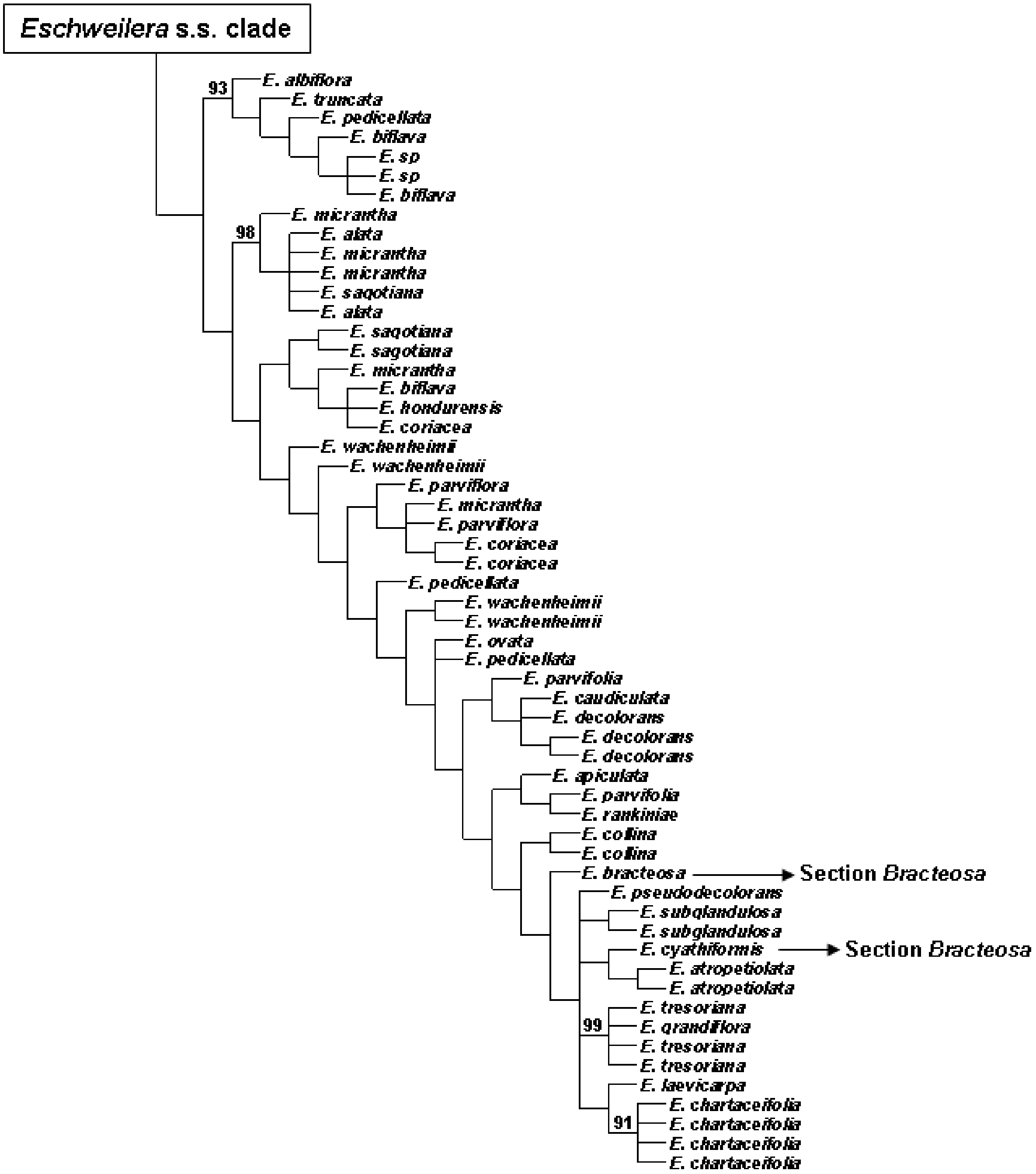

Fig. 1-3. Strict consensus of 105 MP trees based on ITS sequences — continued. Details of *Eschweilera* s.s. are shown in this figure. Sections *Bracteosa* and *Jugastrum* are nested separately in *Eschweilera* s.s.

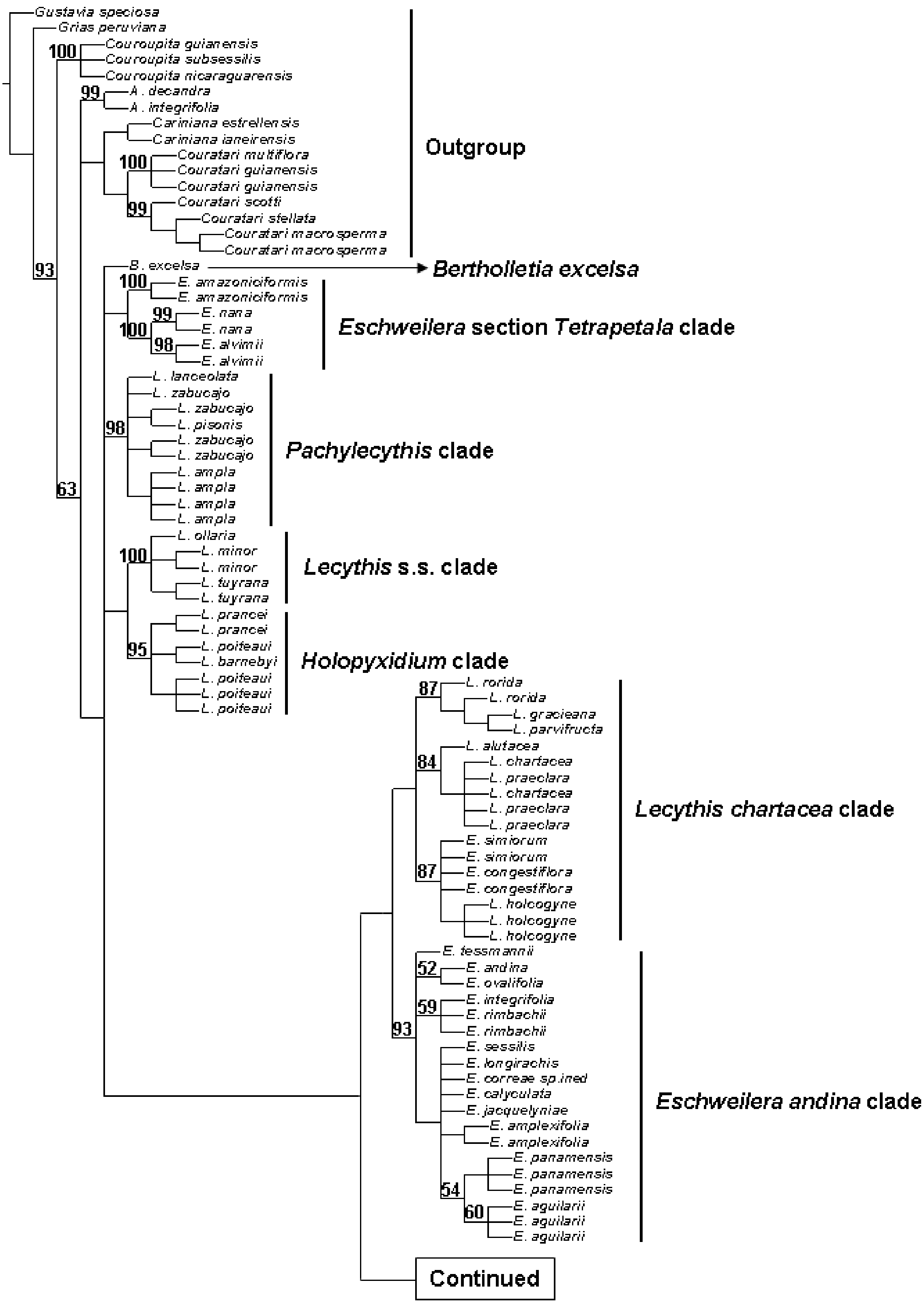

Fig. 2-1. Strict consensus of 148 most parsimonious (MP) trees based on *ndhF* sequences. Bootstrap values (>50%) are given above the branches. Details of the outgroups and *Bertholletia excelsa*, *Eschweilera* section *Tetrapetala*, *Pachylecythis*, *Lecythis* s.s., *Holopyxidium*, *Lecythis chartacea* clade, and *Eschweilera andina* clade of the ingroup are shown in this figure.

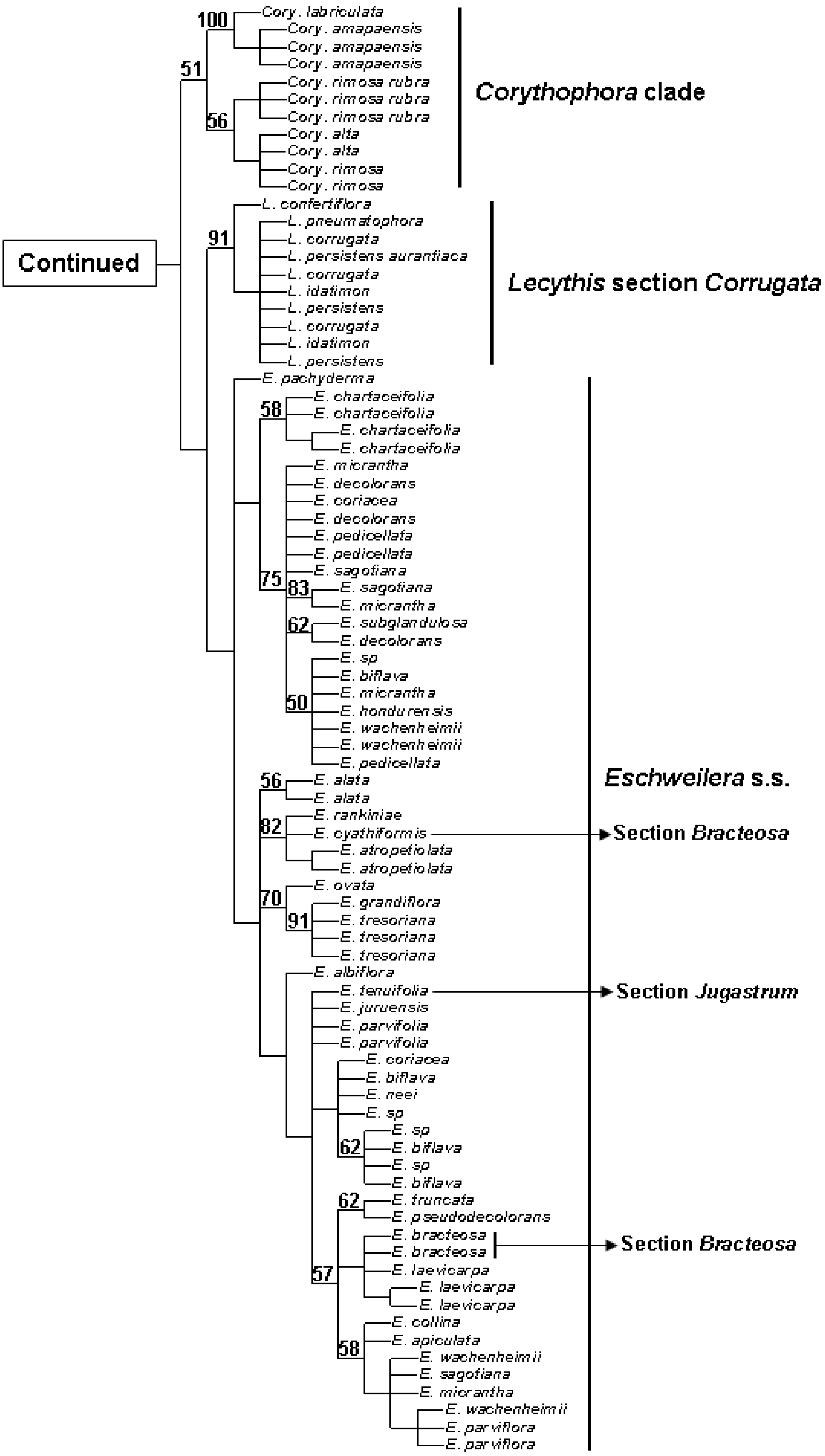

Fig. 2-2. Strict consensus of 148 MP trees based on *ndhF* sequences — continued. *Corythophora*, *Lecythis* section *Corrugata*, and *Eschweilera* s.s. of the ingroup are shown in this figure.

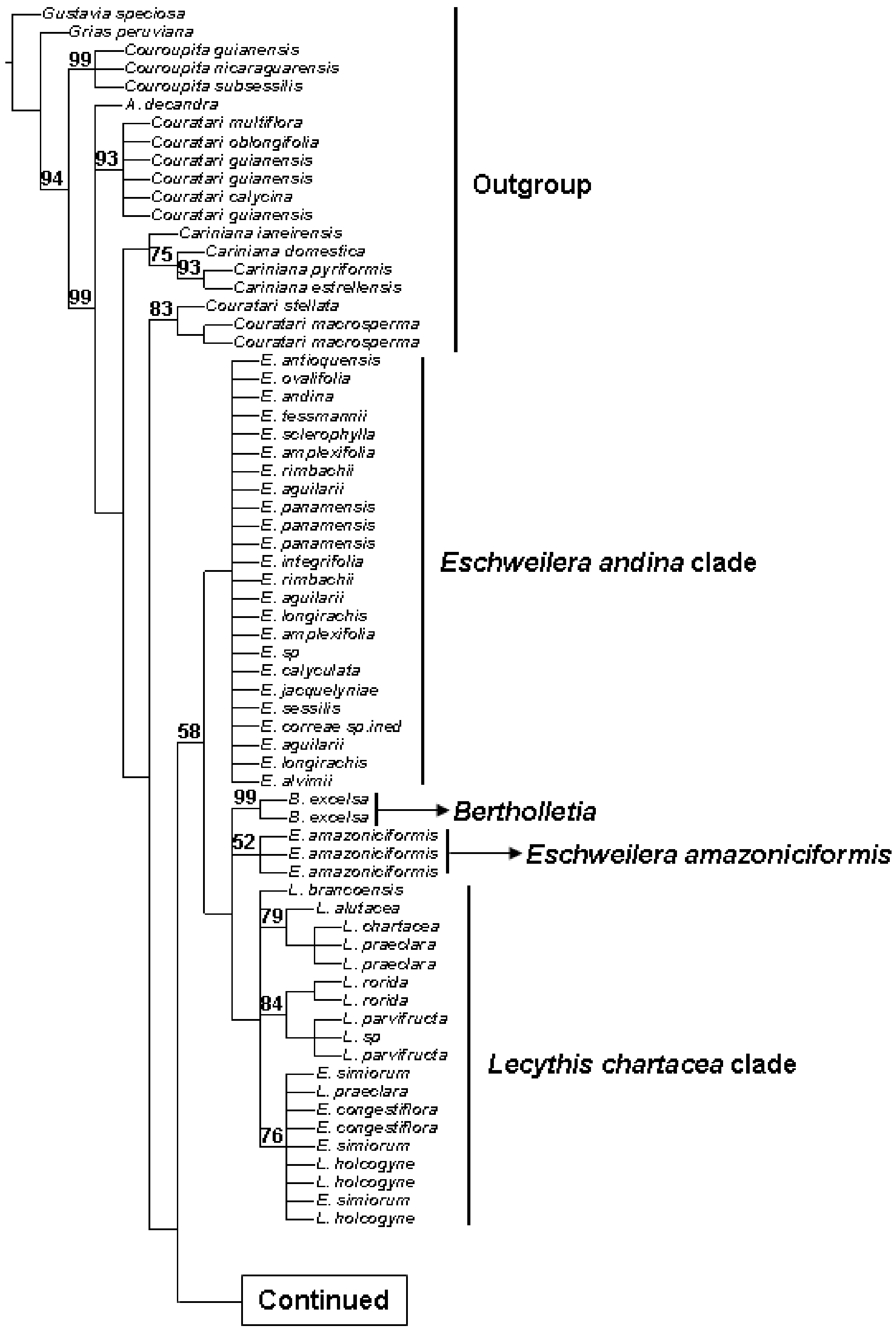

Fig. 3-1. Strict consensus of 67 most parsimonious (MP) trees based on *trnL-F* sequences. Bootstrap values (>50%) are given above the branches. Details of the outgroup and *Eschweilera andina* clade and *Lecythis chartacea* clade of the ingroup are shown in this figure.

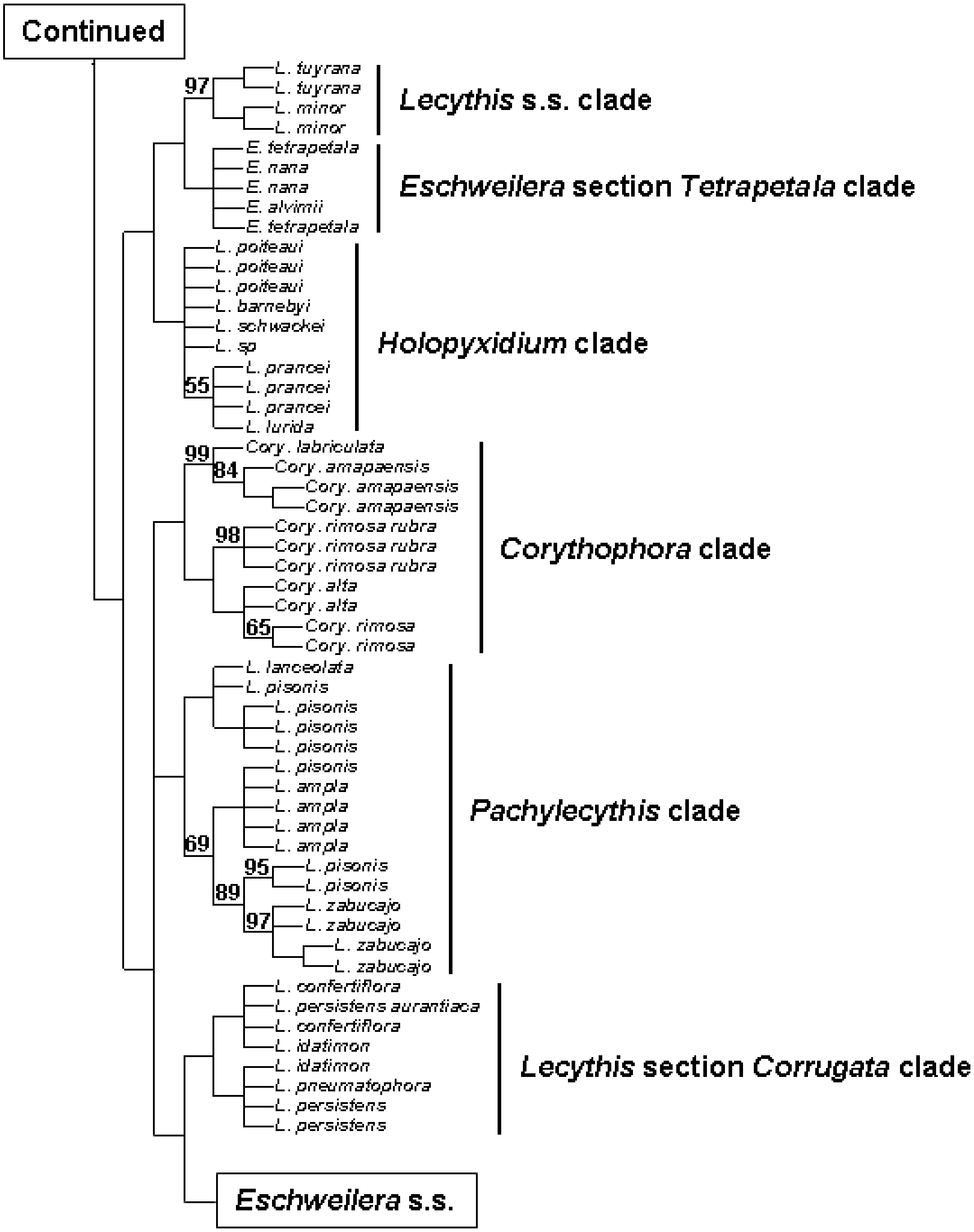

Fig. 3-2. Strict consensus of 67 MP trees based on *trnL-F* sequences — continued. Details of *Lecythis* s.s., *Eschweilera* section *Tetrapetala*, *Holopyxidium*, *Corythophora*, *Pachylecythis*, and *Lecythis* section *Corrugata* are shown in this figure.

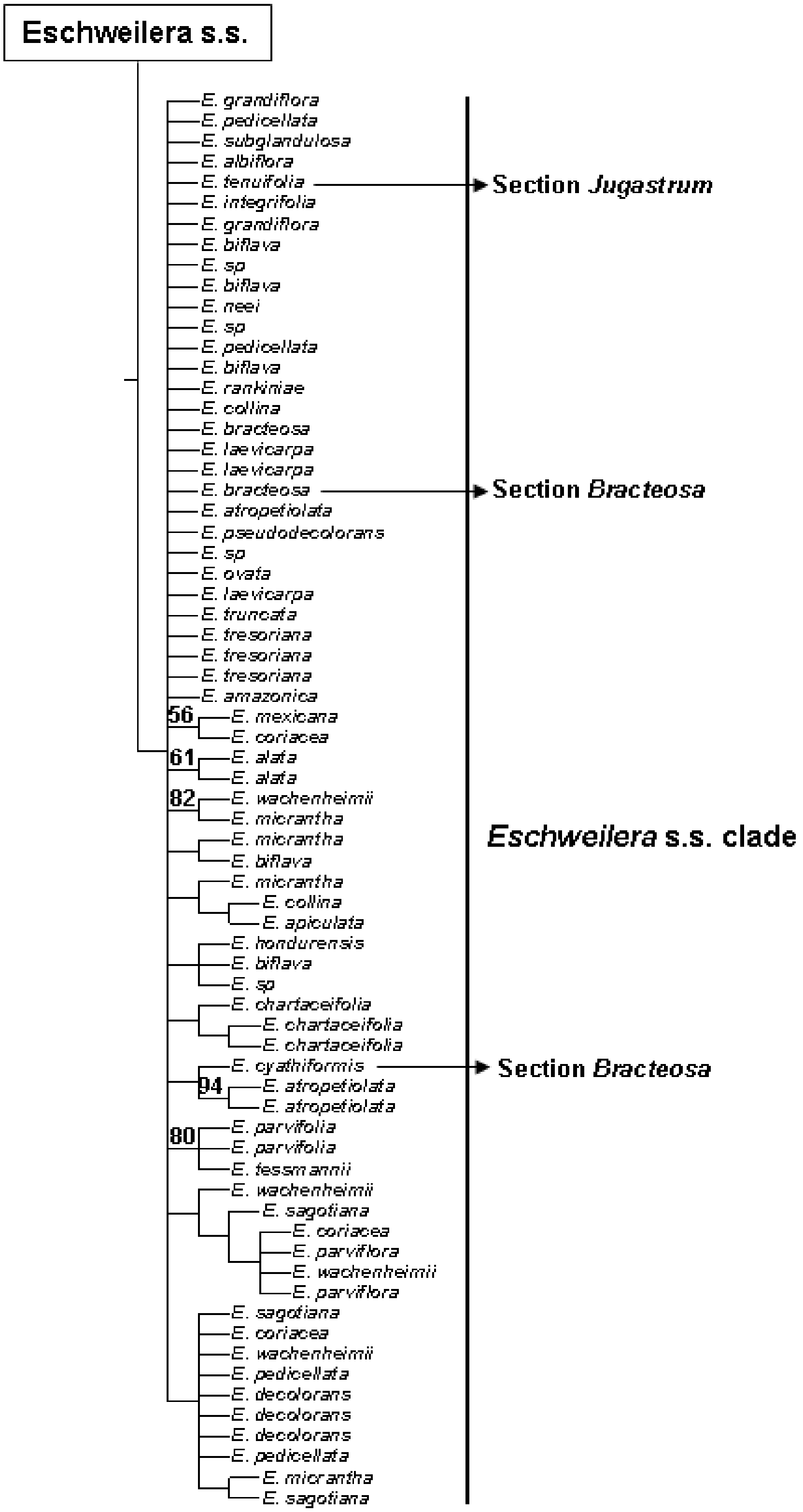

Fig. 3-3. Strict consensus of 67 MP trees based on *trnL-F* sequences — continued. Details of *Eschweilera s.s.* are shown in this figure.

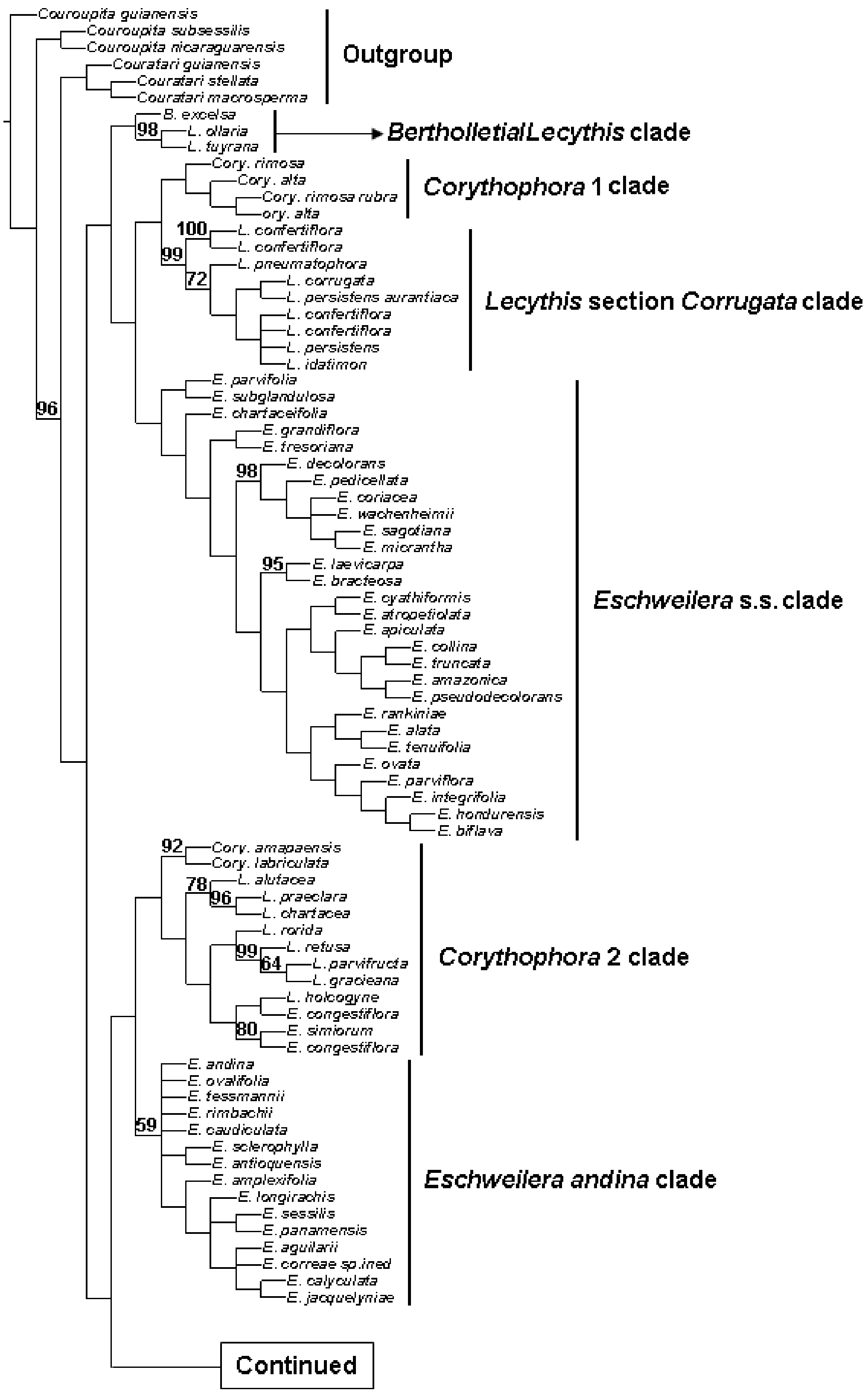

Fig. 4-1. Strict consensus of 53 most parsimonious (MP) trees based on *trnH-psbA* sequences. Bootstrap values (>50%) are given above the branches. Details of the outgroup and most of the ingroup (except *Holopyxidium*, *Eschweilera* section *Tetrapetala*, and *Pachylecythis*) are shown in this figure.

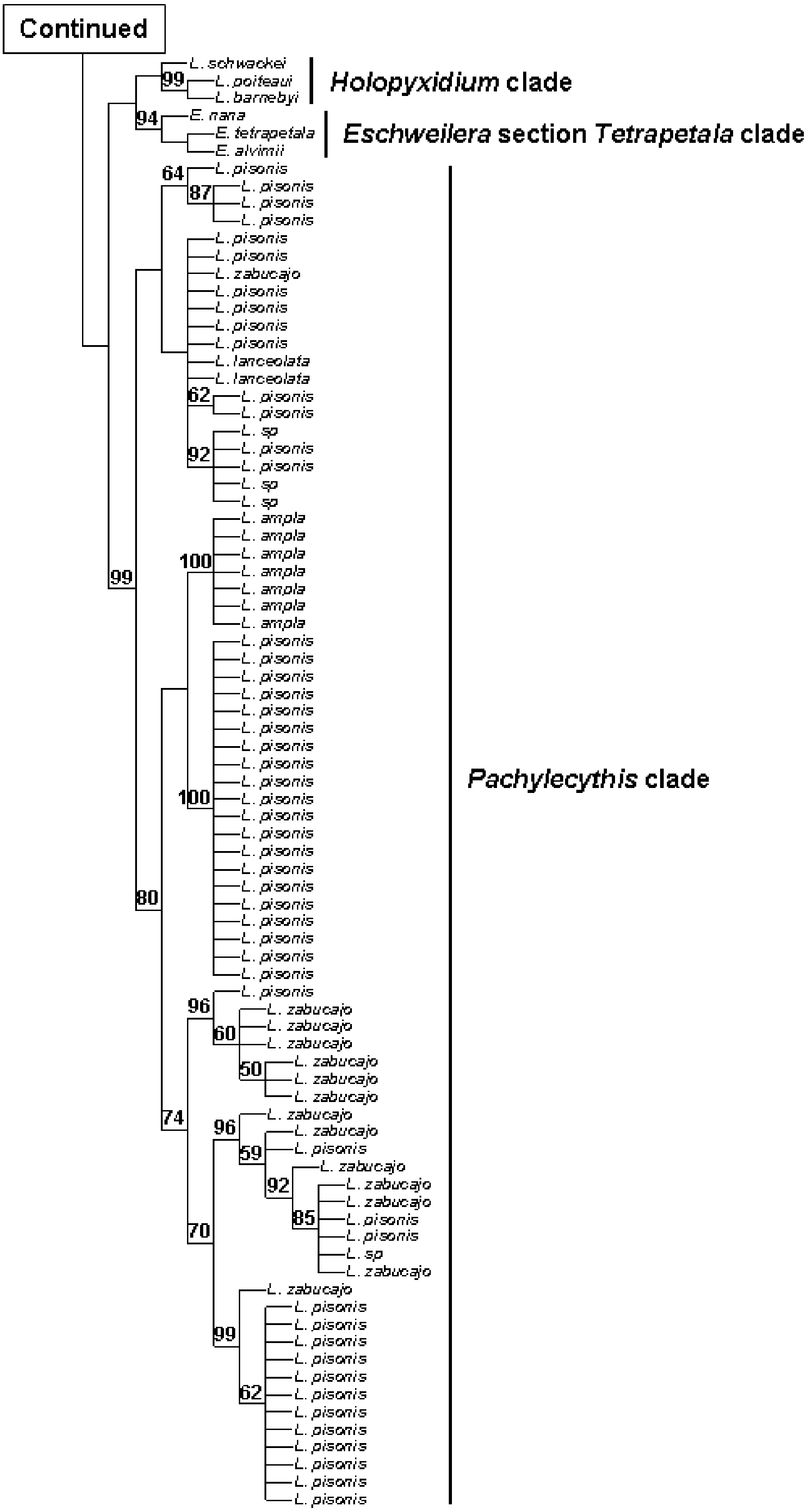

Fig. 4-2. Strict consensus of 53 MP trees based on *trnH-psbA* sequences — continued. Details of *Holopyxidium*, *Eschweilera* section *Tetrapetala*, and *Pachylecythis* are shown in this figure.

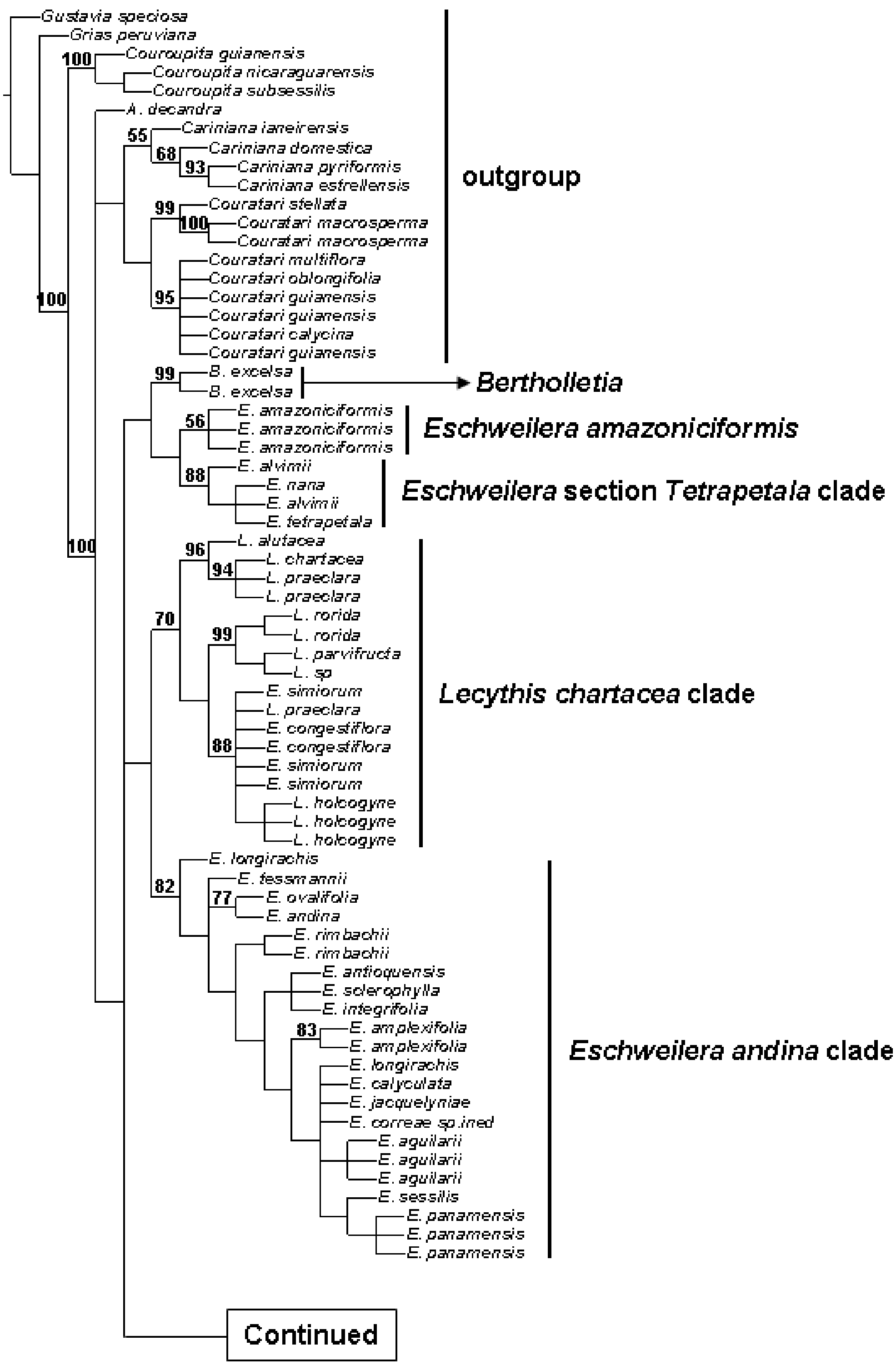

Fig. 5-1. Strict consensus of 77 most parsimonious (MP) trees based on combined analysis of three plastid DNA sequences. Bootstrap values (>50%) are given above the branches.Details of the outgroups and *Bertholletia*, *Eschweilera* section *Tetrapetala*, *Lecythis chartacea* clade, and *Eschweilera andina* clade of the ingroup are shown in this figure.

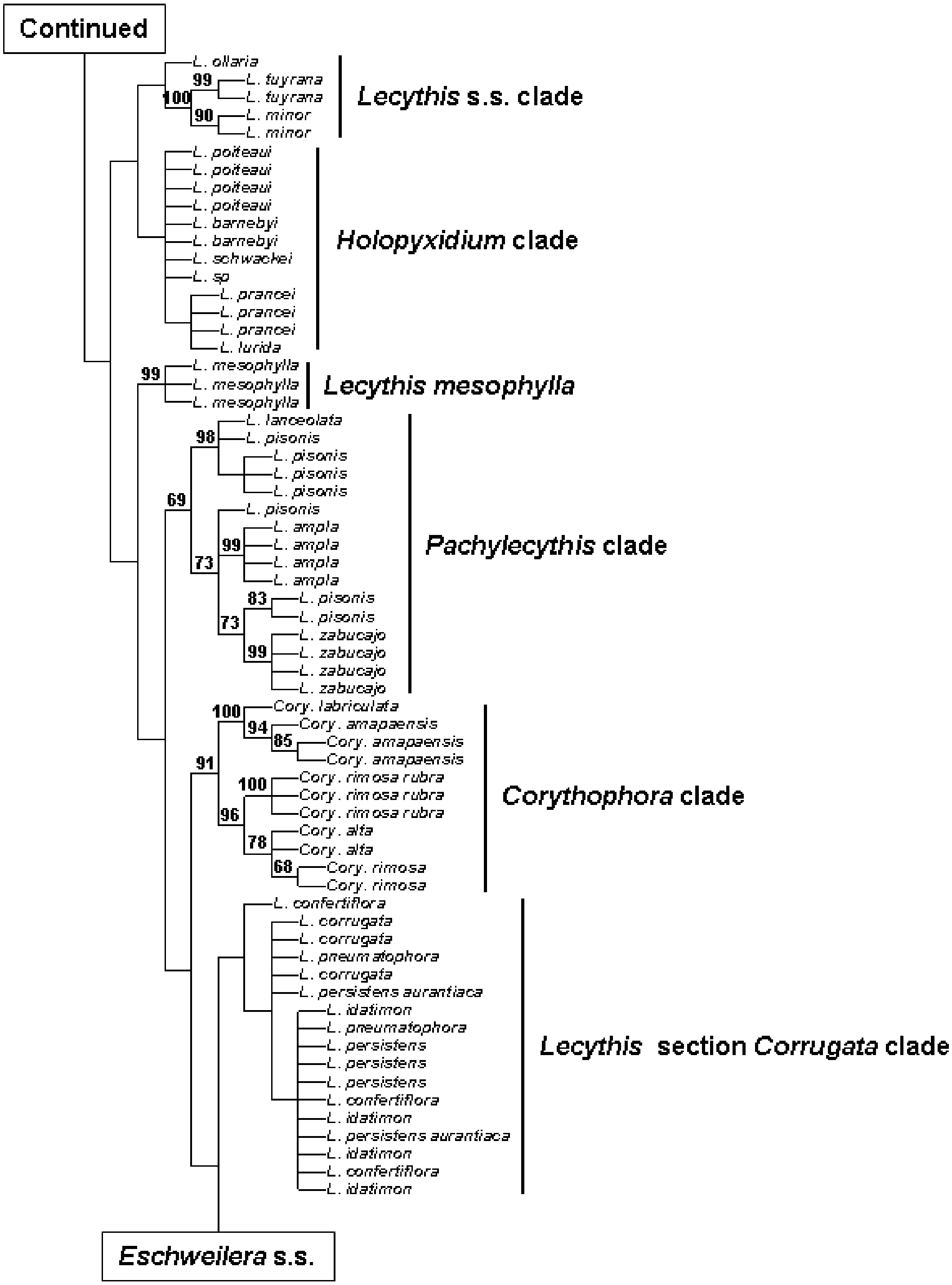

Fig. 5-2. Strict consensus of 77 MP trees based on combined analysis of three plastid DNA sequences — continued. Details of *Lecythis* s.s., *Holopyxidium*, *Pachylecythis*, *Corythophora*, *Lecythis* section *Corrugata* and *Eschweilera* s.s. are shown in this figure.

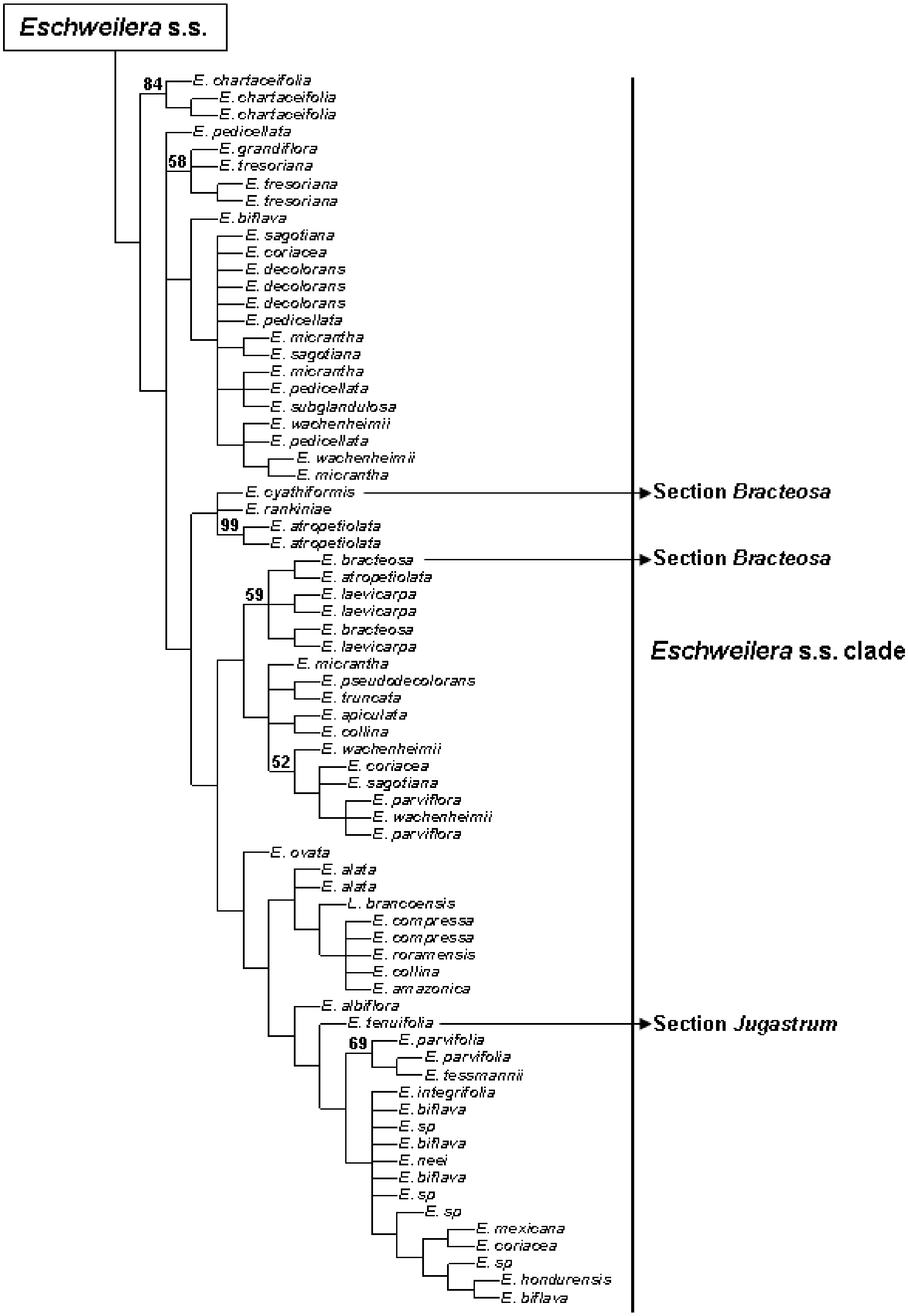

Fig. 5-3. Strict consensus of 77 MP trees based on combined analysis of three plastid DNA sequences — continued. Details of *Eschweilera* s.s. are shown in this figure. *Eschweilera* sections *Bracteosa* and *Jugastrum* are nested within *Eschweilera* s.s.

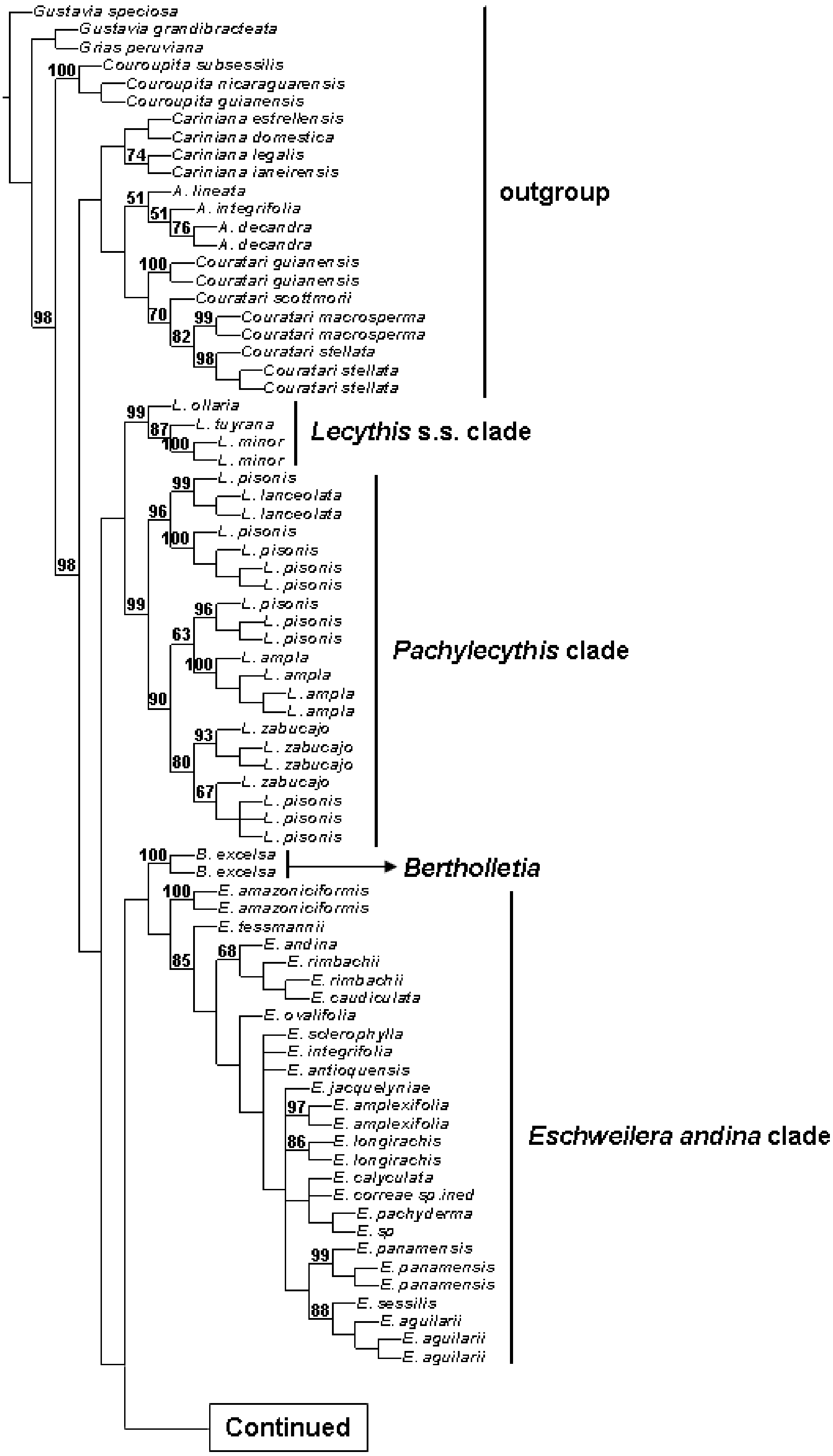

Fig. 6-1. Strict consensus of 115 most parsimonious (MP) trees based on combined analysis of ITS, *ndhF*, *trnL-F*, and *trnH-psbA* sequences. Bootstrap values (>50%) are given above the branches.The ingroup is divided into two major clades. Details of the outgroup and *Lecythis* s.s., *Pachylecythis*, *Bertholletia*, and *Eschweilera andina* clade of the ingroup are shown in this figure.

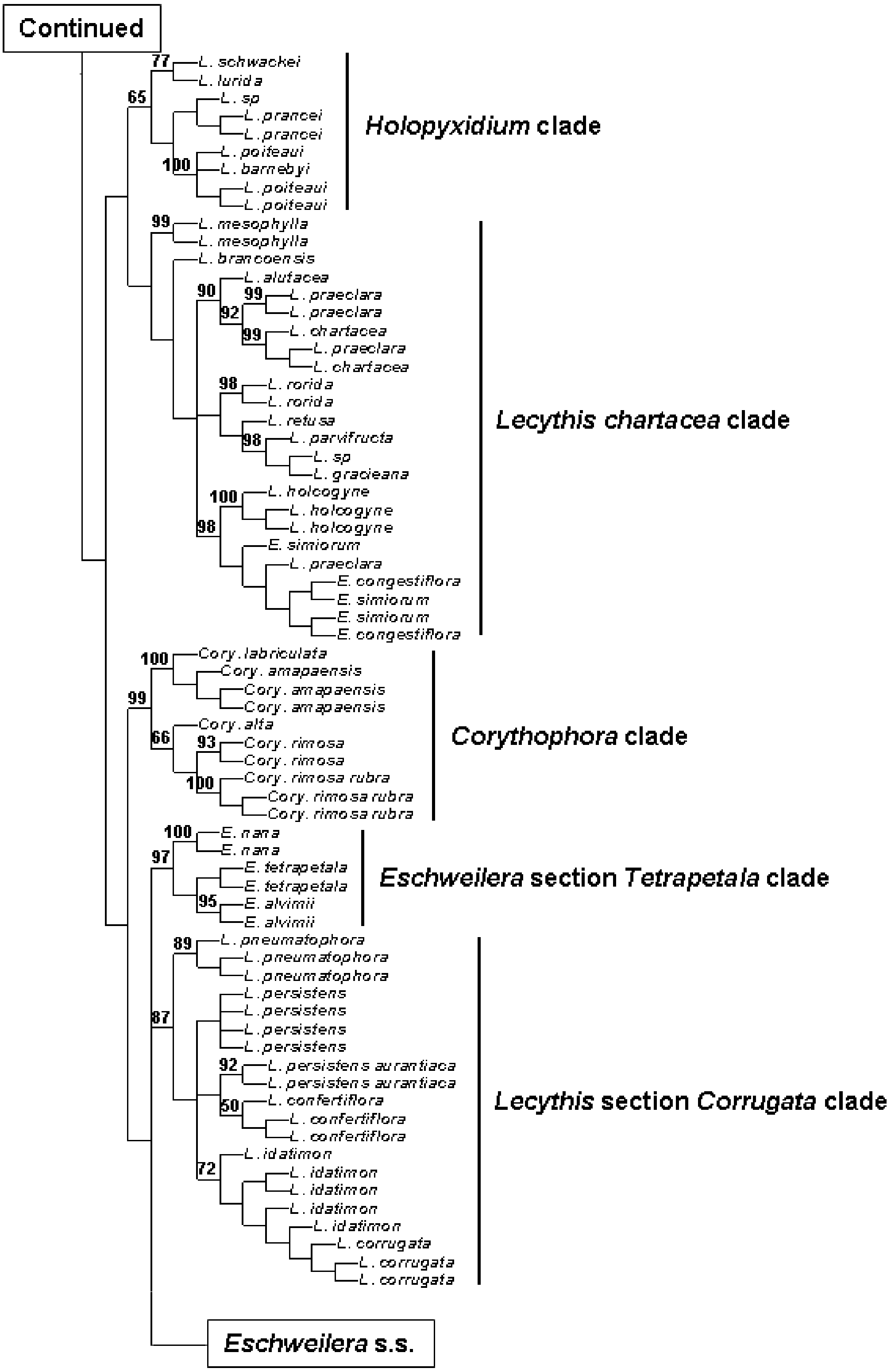

Fig. 6-2. Strict consensus of 115 MP trees based on combined analysis of ITS, *ndhF*, *trnL-F*, and *trnH-psbA* sequences — continued. Details of *Holopyxidium*, *Lecythis chartacea* clade, *Corythophora*, *Eschweilera* section *Tetrapetala*, and *Lecythis* section *Corrugata* are shown in this figure.

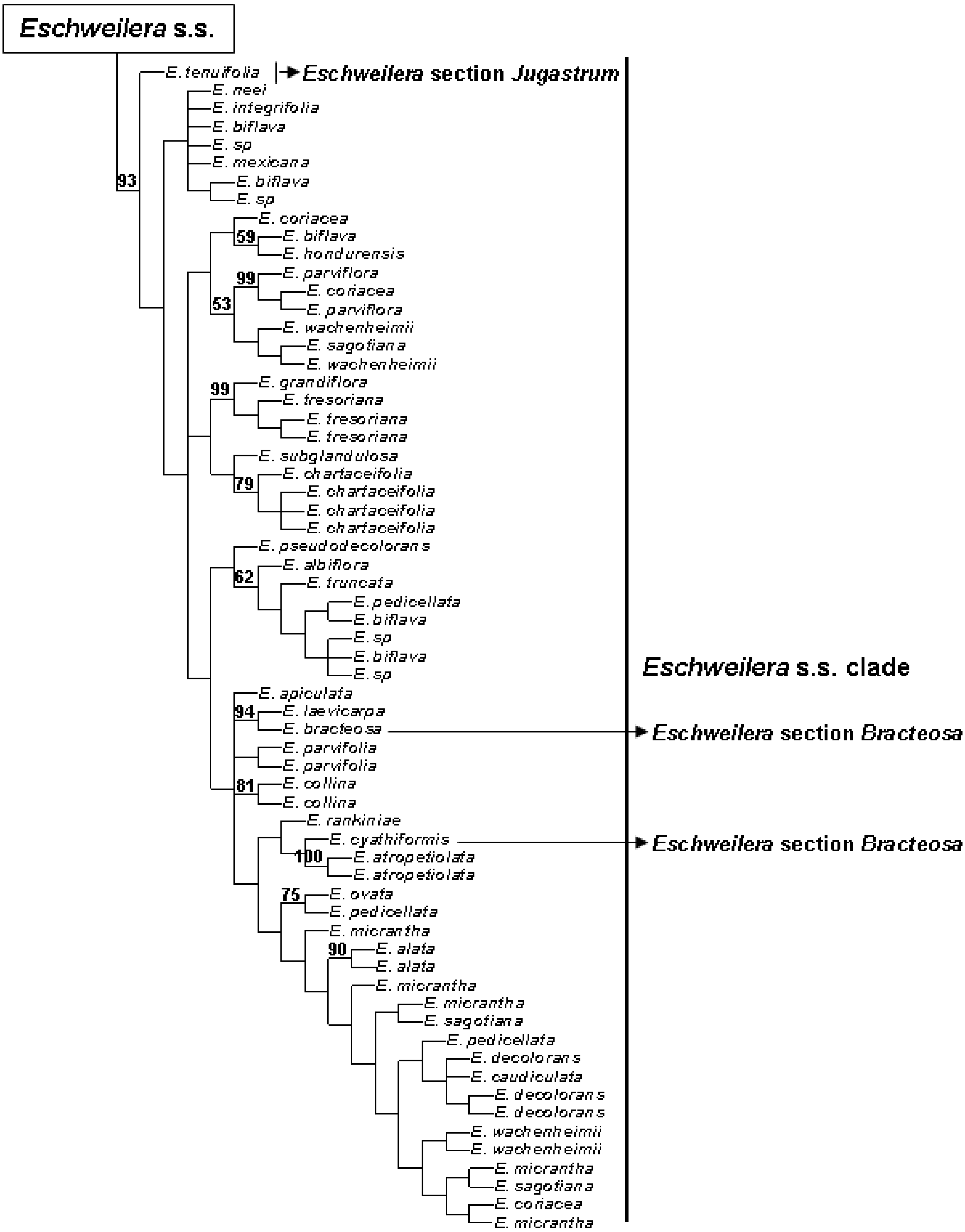

Fig. 6-3. Strict consensus of 115 MP trees based on combined analysis of ITS, *ndhF*, *trnL-F*, and *trnH-psbA* sequences — continued. Details of *Eschweilera* s.s. are shown in this figure. *Eschweilera* sections *Bracteosa* and *Jugastrum* are nested within this clade.

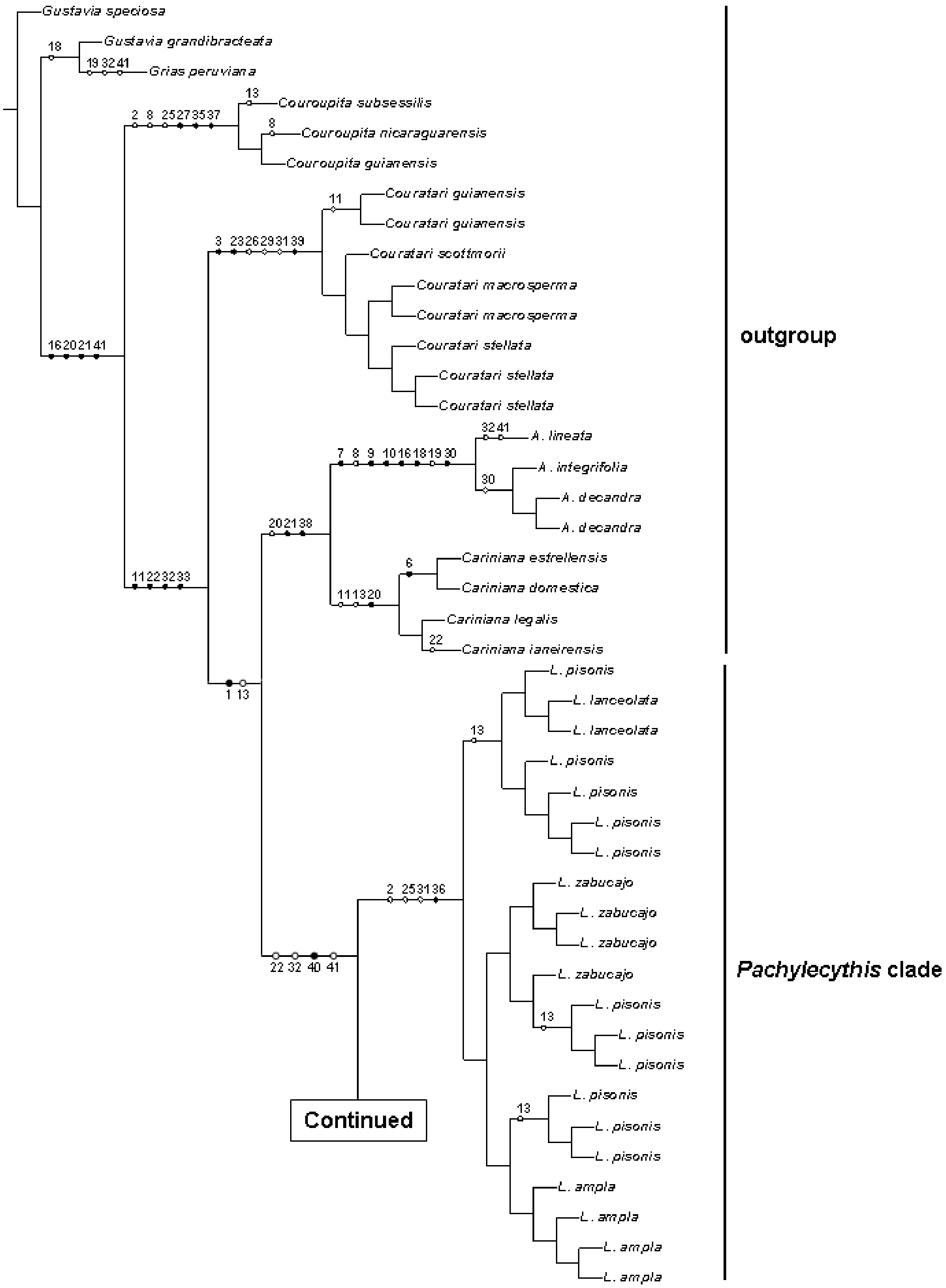

Fig. 7-1. One of 132 most parsimonious (MP) trees based on total evidence (L= 6114, CI= 0.36, RI= 0.76). Morphological characters are optimized onto the tree using fast option of Winclada. Supporting characters are shown on branches. White elipses are homoplasious and black elipses are non-homoplasious characters. The details of the outgroup and *Pachylecythis* of the ingroup are shown in this figure.

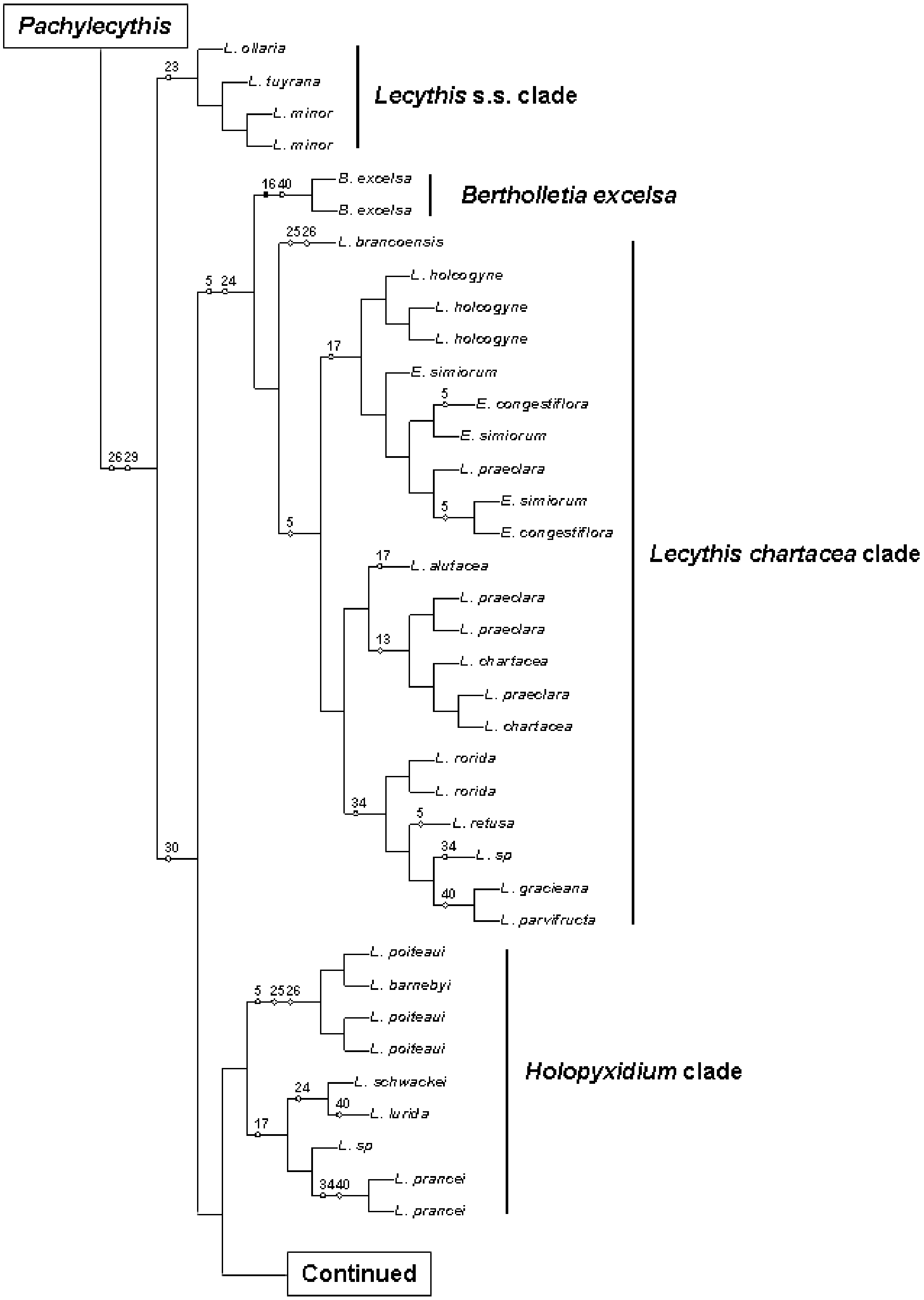

Fig. 7-2. One of 132 MP trees based on total evidence (L= 6114, CI= 0.36, RI= 0.76) — continued. Supporting characters are shown on branches. White elipses are homoplasious and black elipses are non-homoplasious characters. The Details of *Lecythis* s.s., *Bertholletia excelsa*, *Lecythis chartacea* clade, and *Holopyxidium* are shown in this figure.

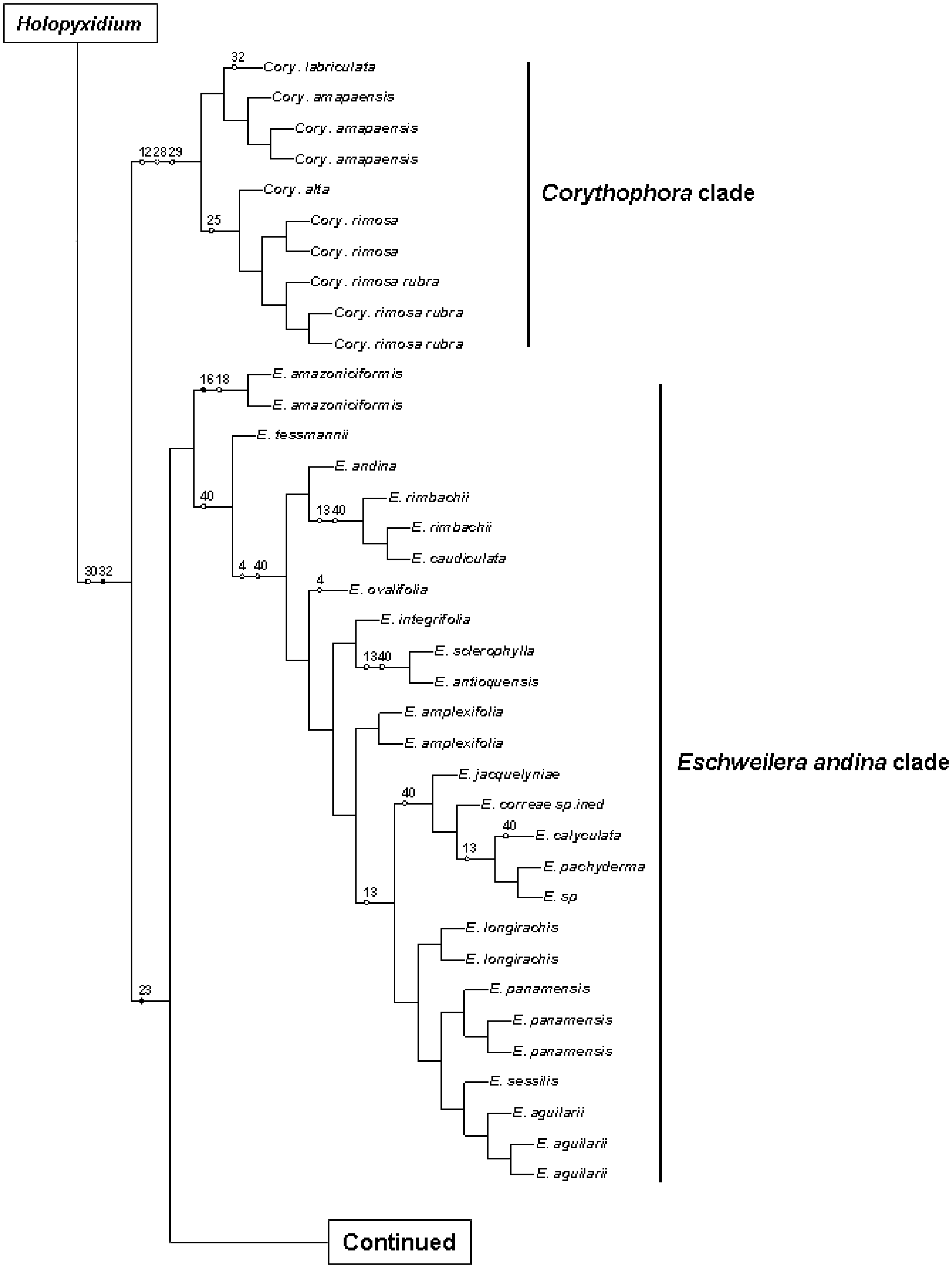

Fig. 7-3. One of 132 MP trees based on total evidence (L= 6114, CI= 0.36, RI= 0.76) — continued. Supporting characters are shown on branches. White elipses are homoplasious and black elipses are non-homoplasious characters. The details of *Corythophora* and *Eschweilera andina* clade are shown in this figure.

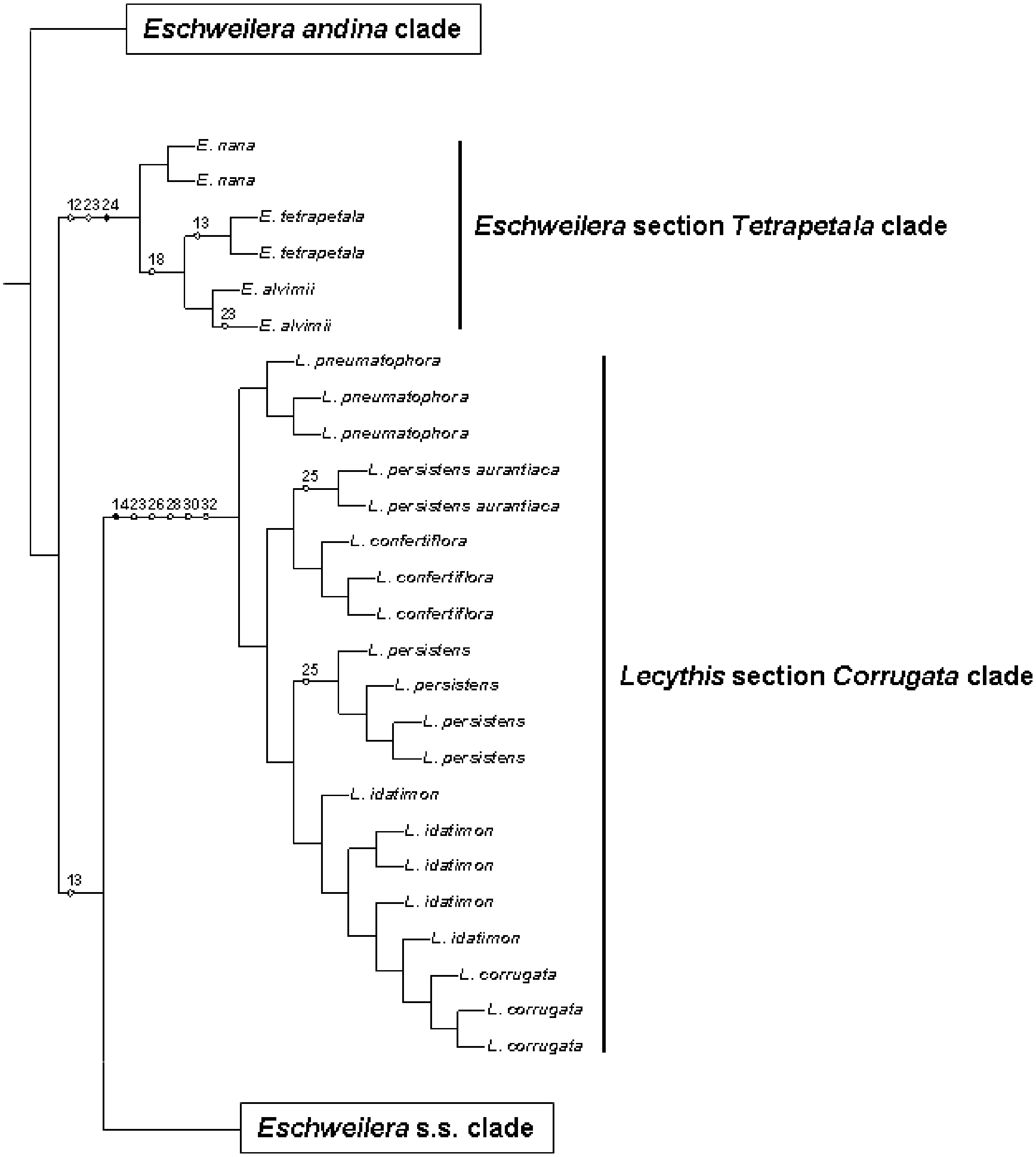

Fig. 7-4. One of 132 MP trees based on total evidence (L= 6114, CI= 0.36, RI= 0.76) — continued. Supporting characters are shown on branches. White elipses are homoplasious and black elipses are non-homoplasious characters. The details of *Eschweilera* section *Tetrapetala* clade and *Lecythis* section *Corrugata* clade are shown in this figure.

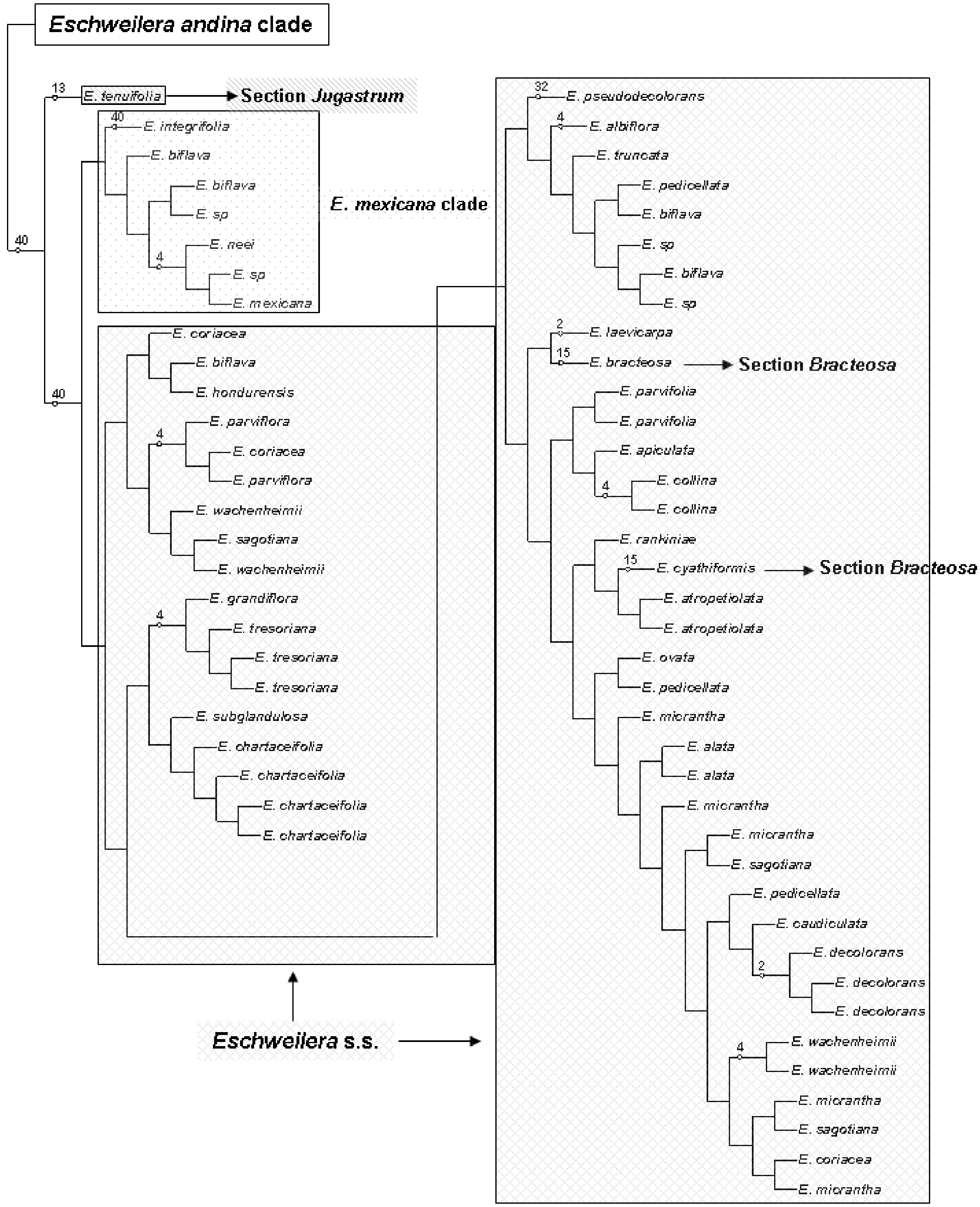

Fig. 7-5. One of 132 MP trees based on total evidence (L= 6114, CI= 0.36, RI= 0.76) — continued. Supporting characters are shown on branches. White elipses are homoplasious and black elipses are non-homoplasious characters. The details of core *Eschweilera* are shown in this figure.

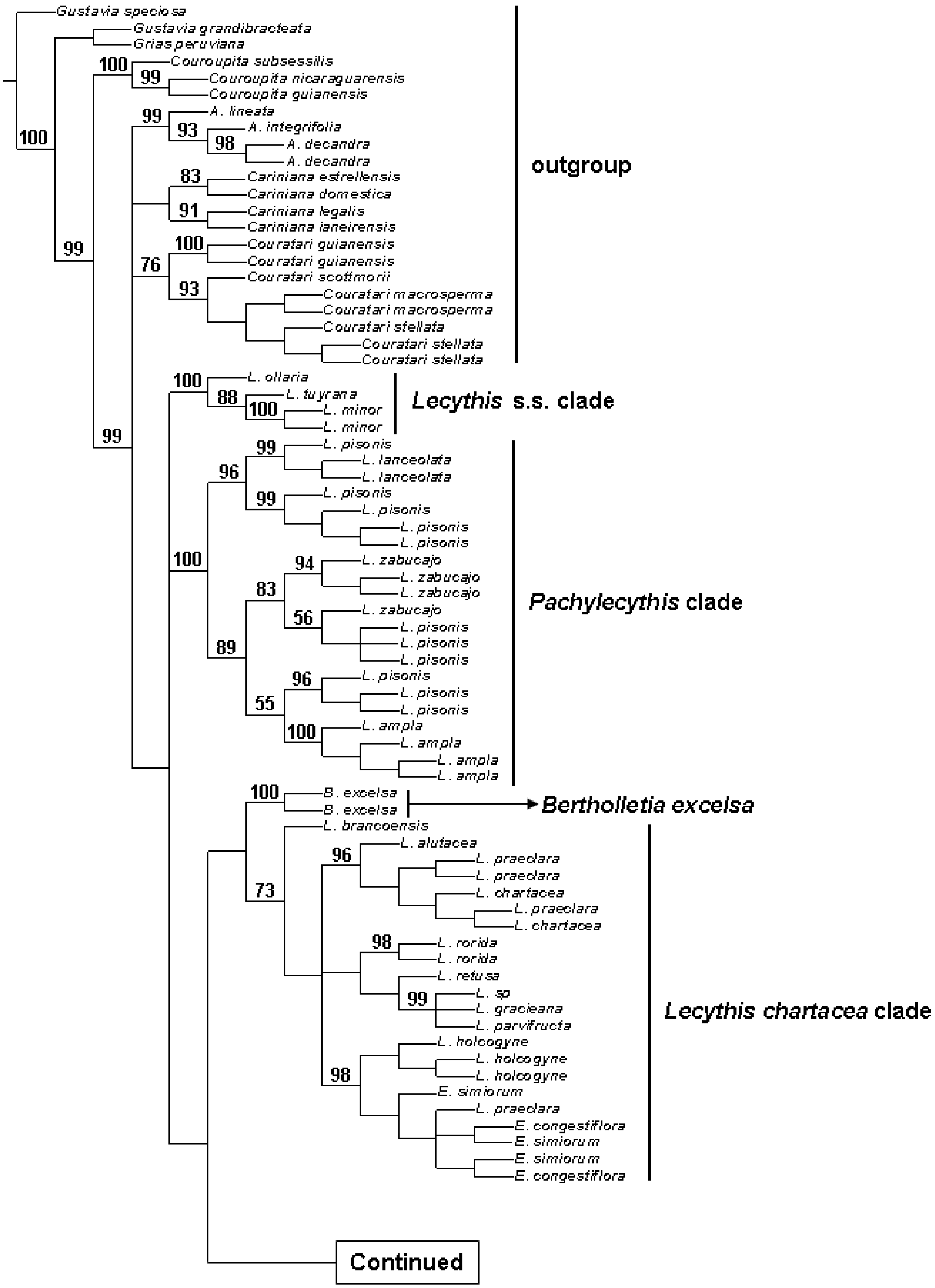

Fig. 8-1. Strict consensus of 132 most parsimonious (MP) trees based on total evidence. Bootstrap values (>50%) are given above the branches. The details of the outgroup, *Lecythis* s.s., *Pachylecythis*, *Bertholletia excelsa*, and *Lecythis chartacea* clade of the ingroup are shown in this figure.

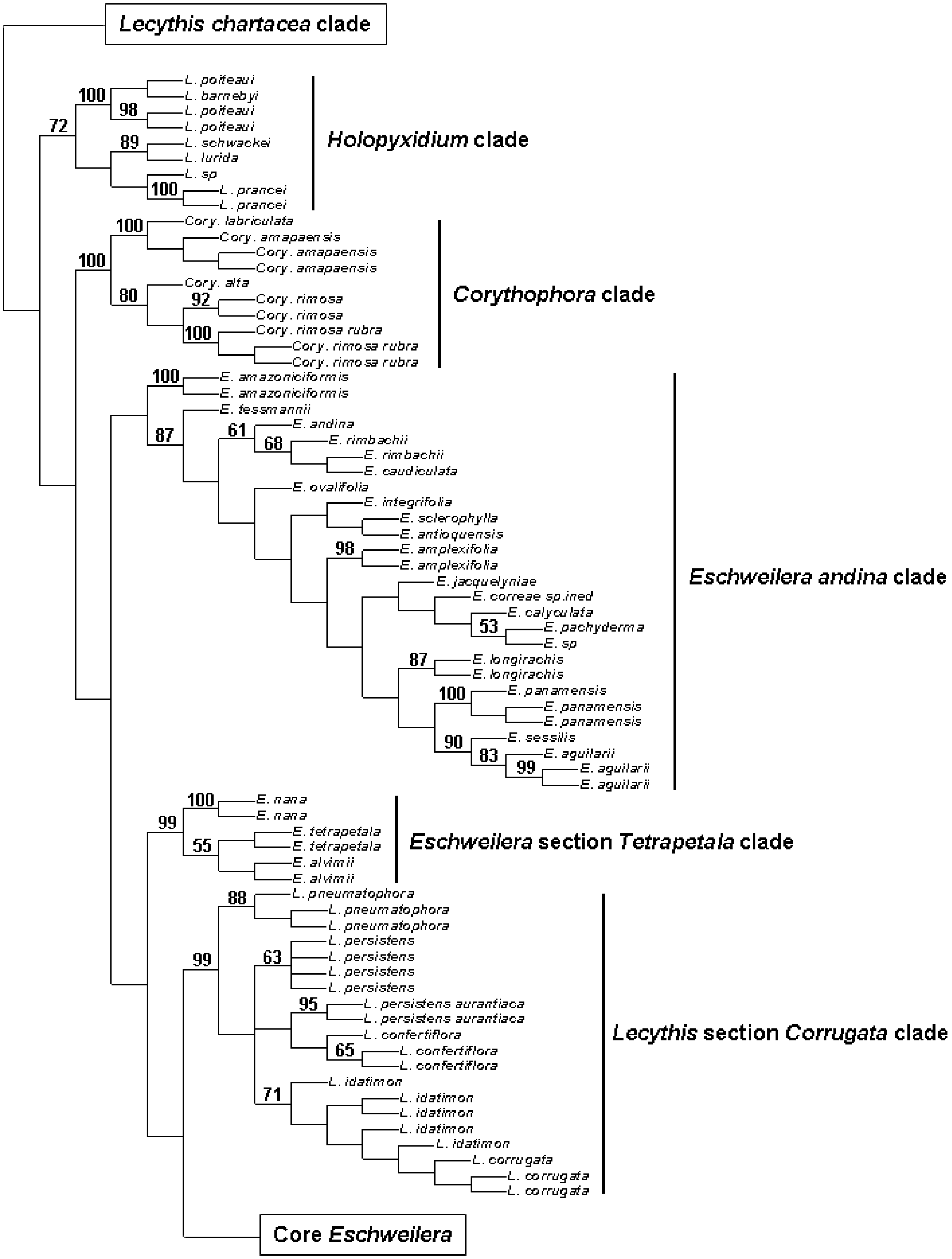

Fig. 8-2. Strict consensus of 132 MP trees based on total evidence. Bootstrap values (>50%) are given above the branches. The details of *Holopyxidium*, *Corythophora*, *Eschweilera andina* clade, and *Lecythis* section *Corrugata* of the ingroup are shown in this figure.

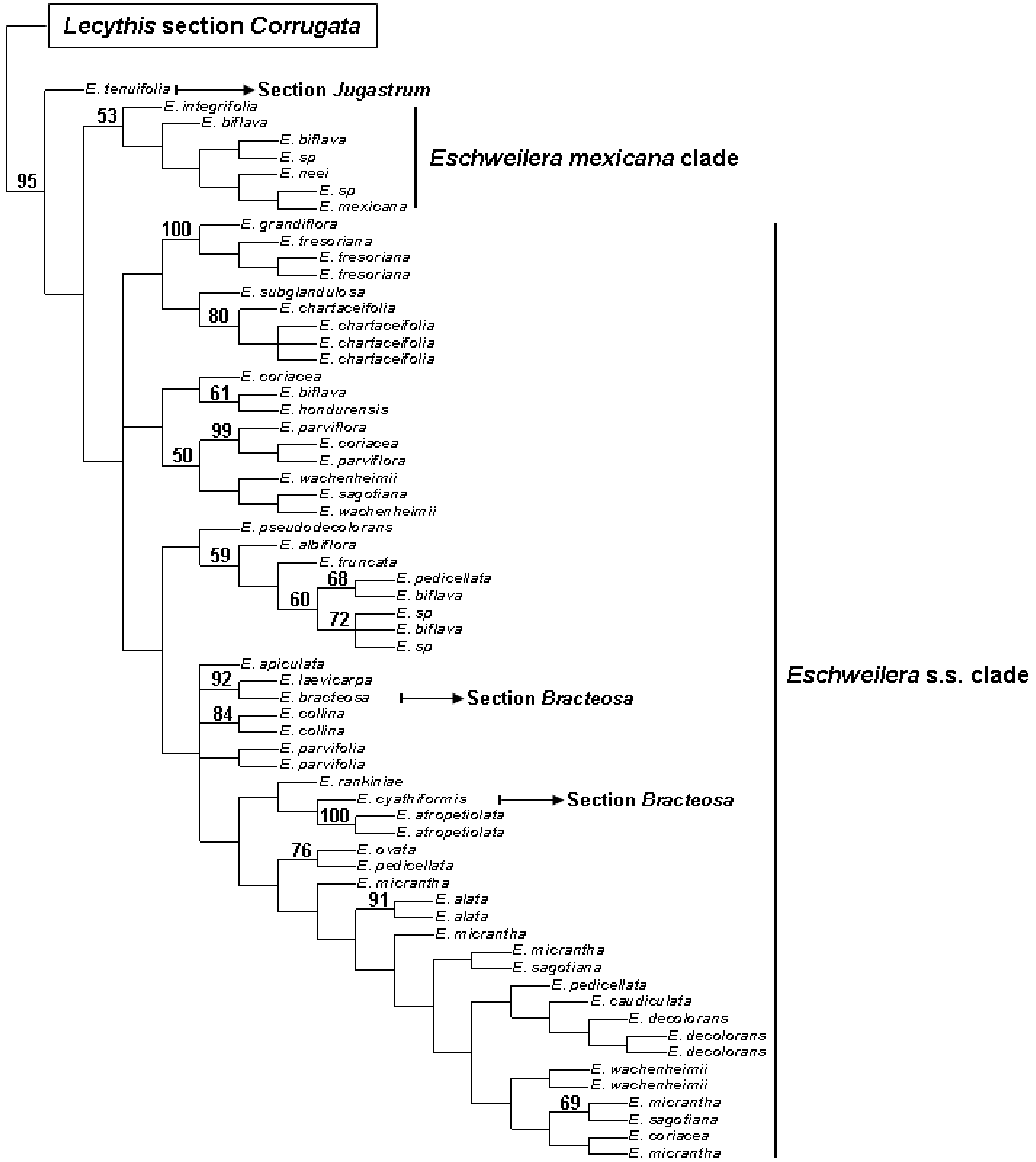

Fig. 8-3. Strict consensus of 132 MP trees based on total evidence. Bootstrap values (>50%) are given above the branches. The details of core *Eschweilera* of the ingroup are shown in this figure.

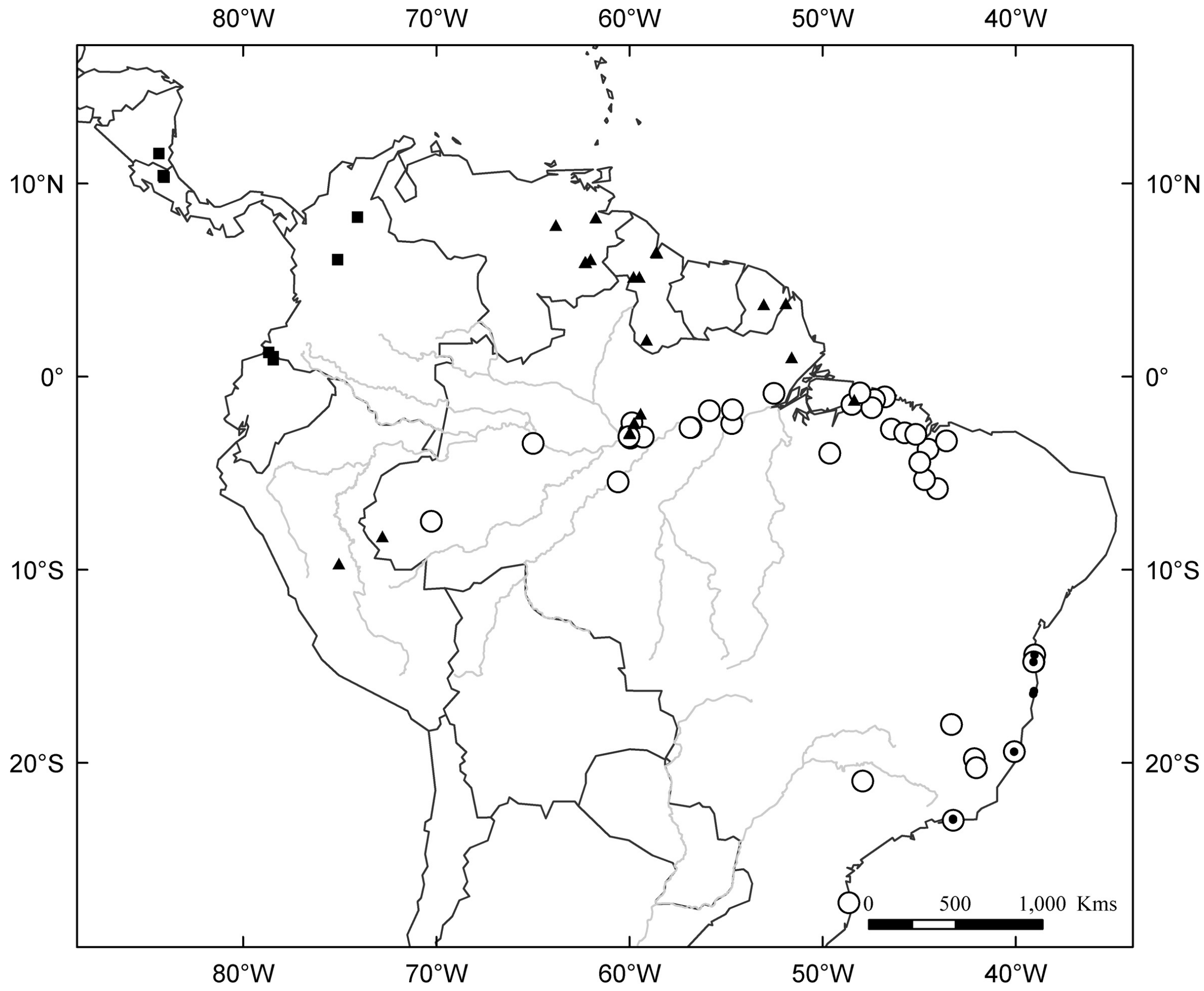

Fig. 9. Distribution of the *Pachylecythis* clade. Black squares represent *Lecythis lanceolata*; black triangles represent *L. zabucajo*; black circles represent *L. lanceolata*; and white circles represent *L. pisonis*. White circle with black dot means coexistence of *L. pisonis* and *L. lanceolata*; and white circle with black triangle means coexistence of *L. pisonis* and *L. zabucajo*.

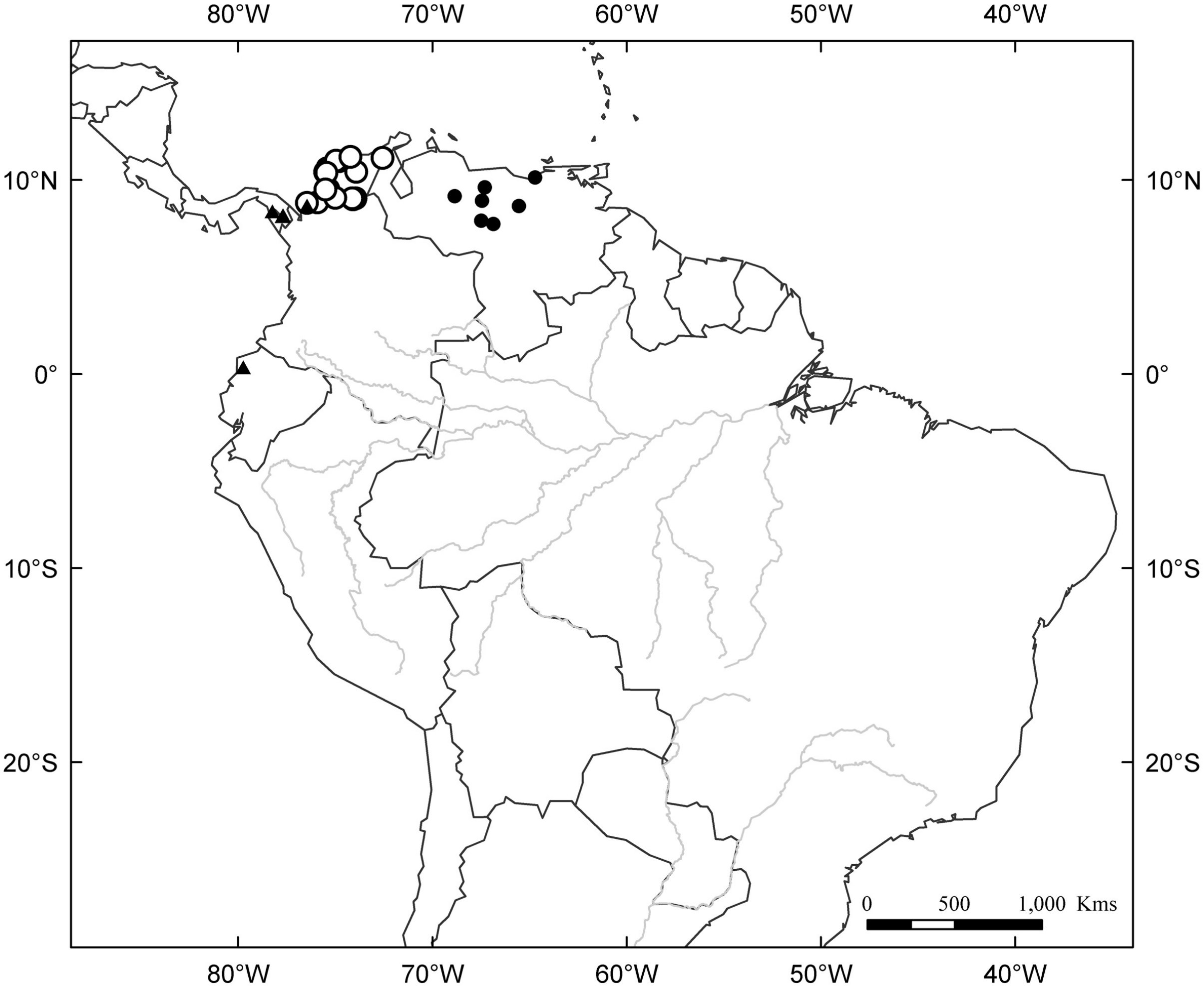

Fig. 10. Distribution of the *Lecythis* s.s. Clade. Black triangles represent *Lecythis tuyrana*; black circles represent *L*. *ollaria*; and white circles represent *L*. *minor*. White circle with black triangle means coexistence of *L*. *tuyrana* and *L*. *minor*.

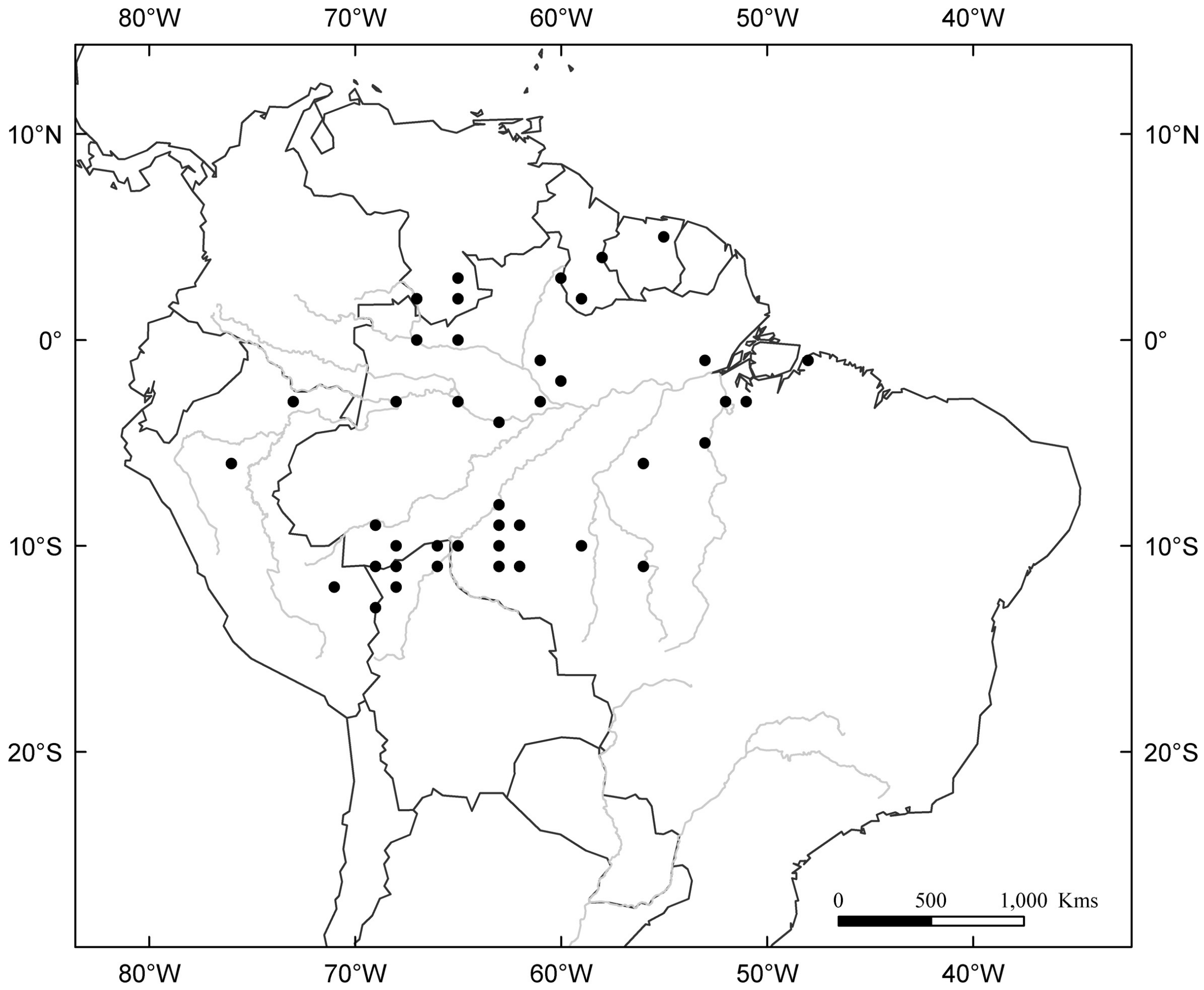

Fig. 11. Distribution of *Bertholletia excelsa*.

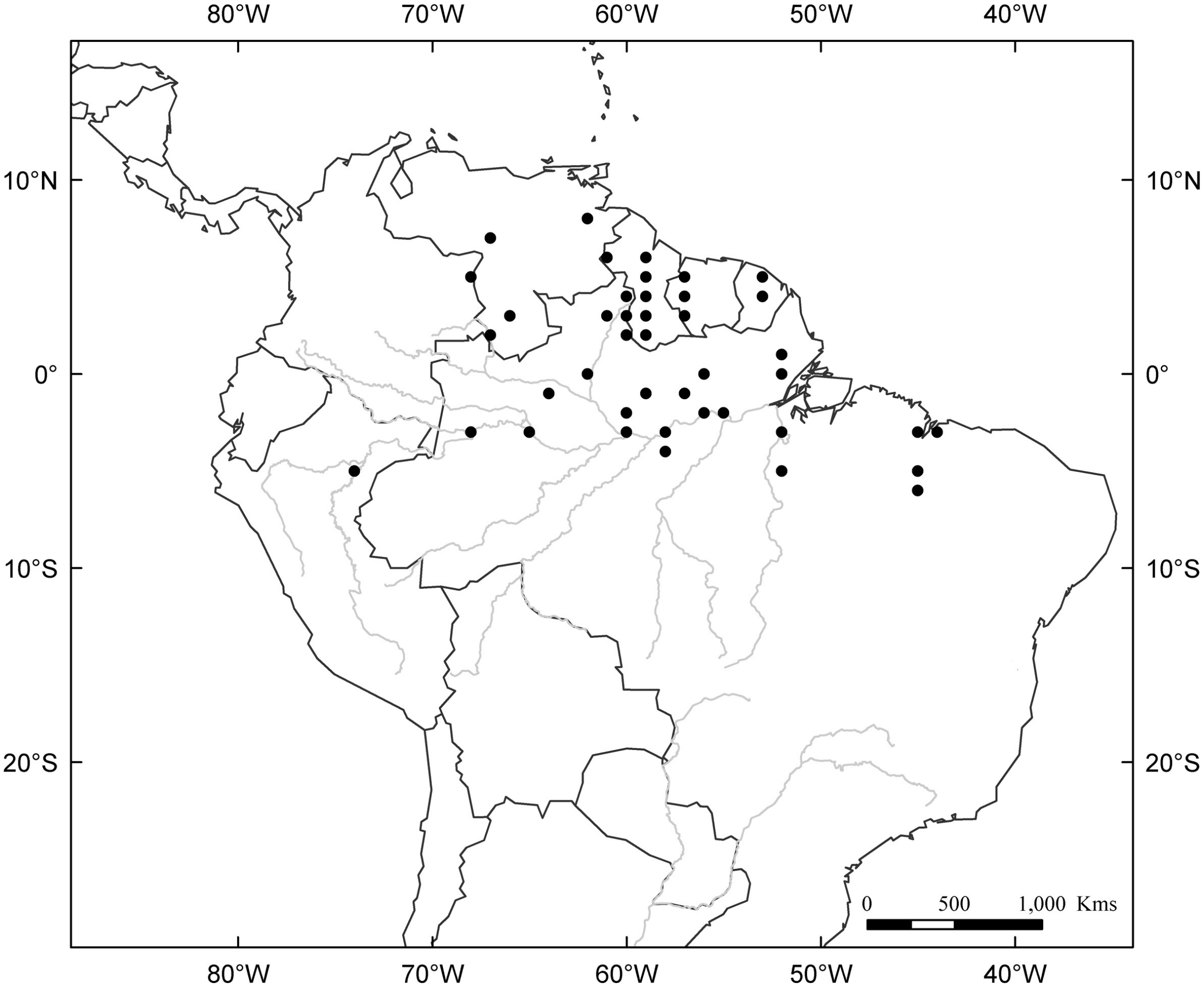

Fig. 12. Distribution of the *Lecythis chartacea* clade.

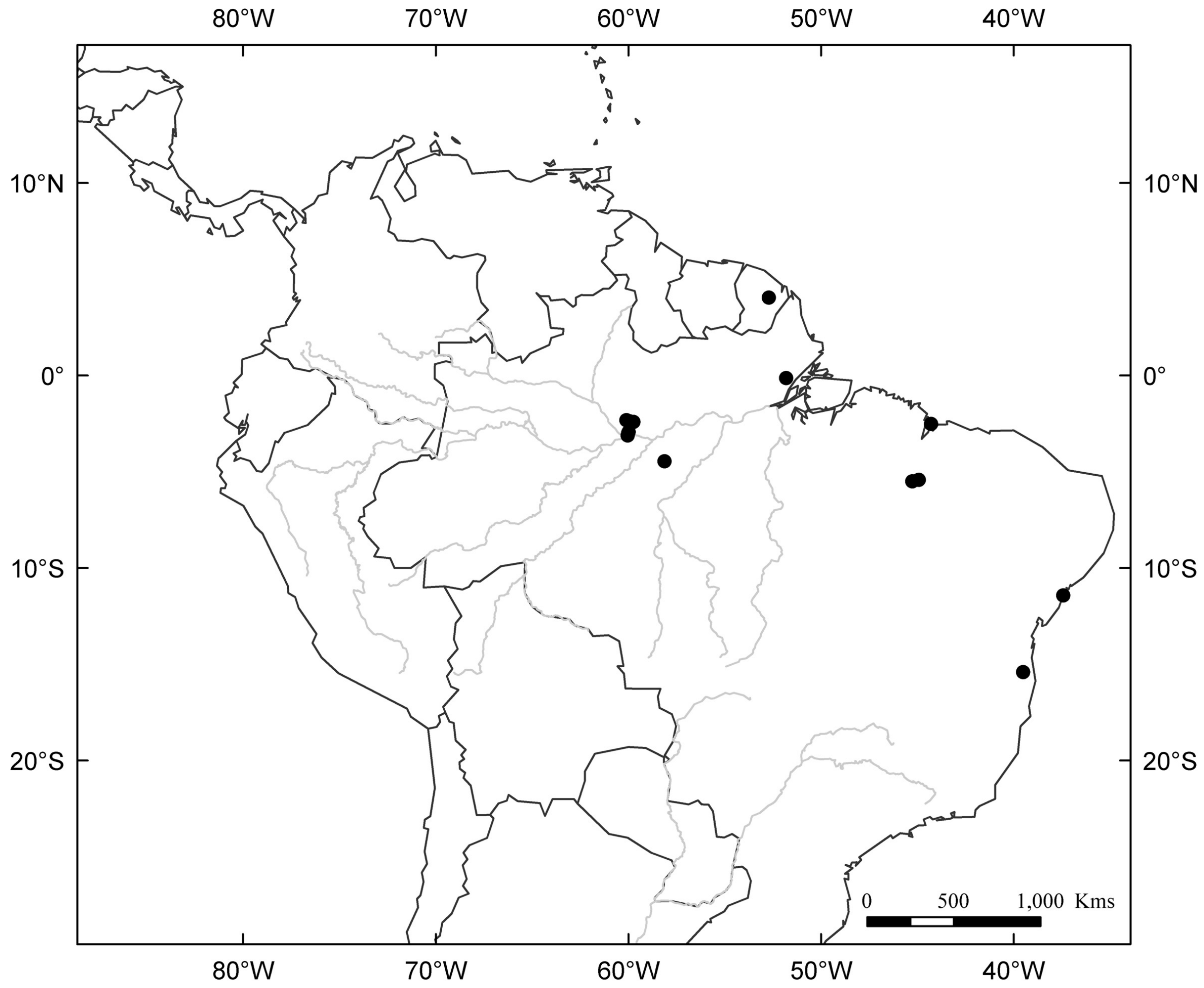

Fig. 13. Distribution of the *Holopyxidium* clade.

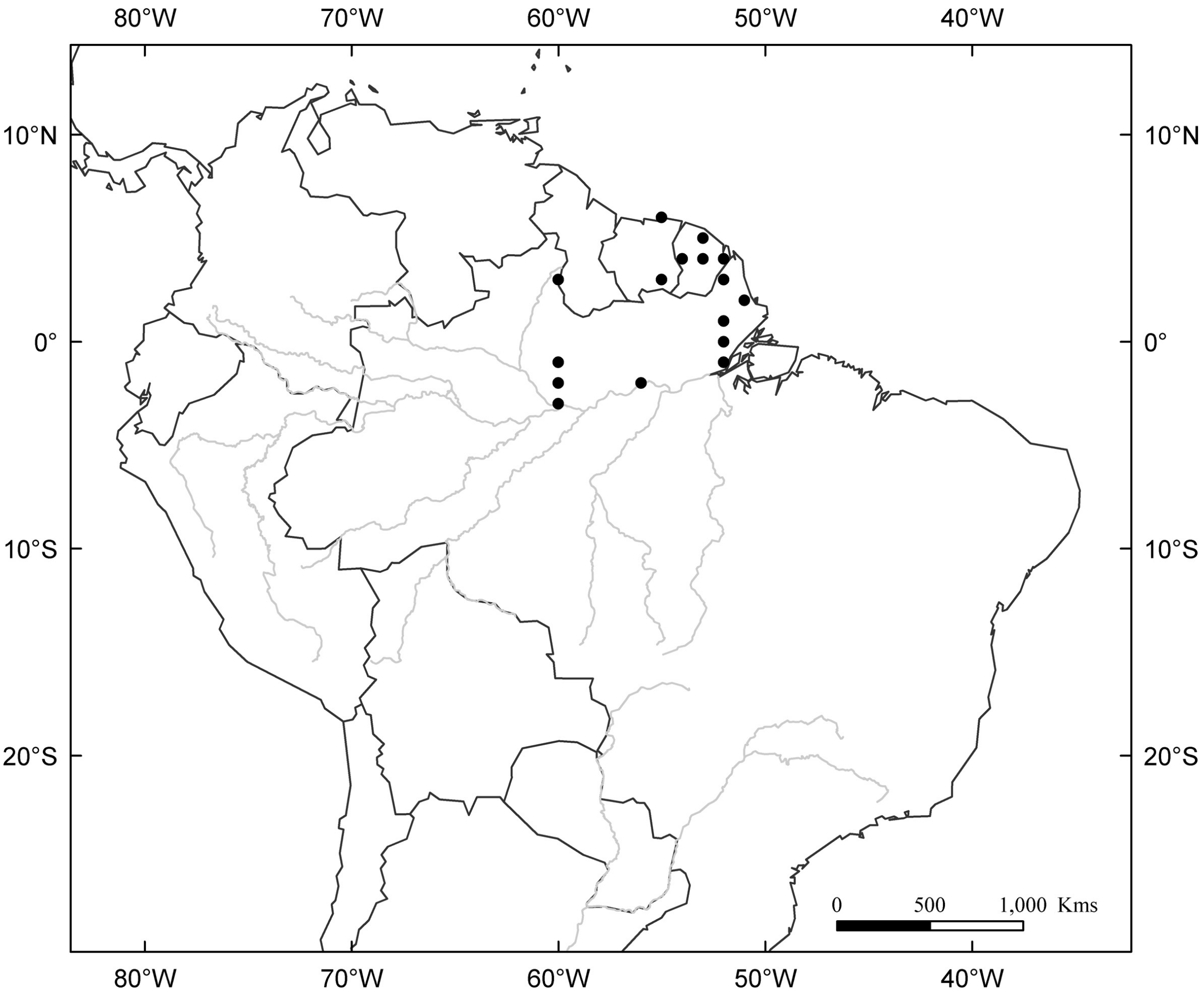

Fig. 14. Distribution of the *Corythophora* clade.

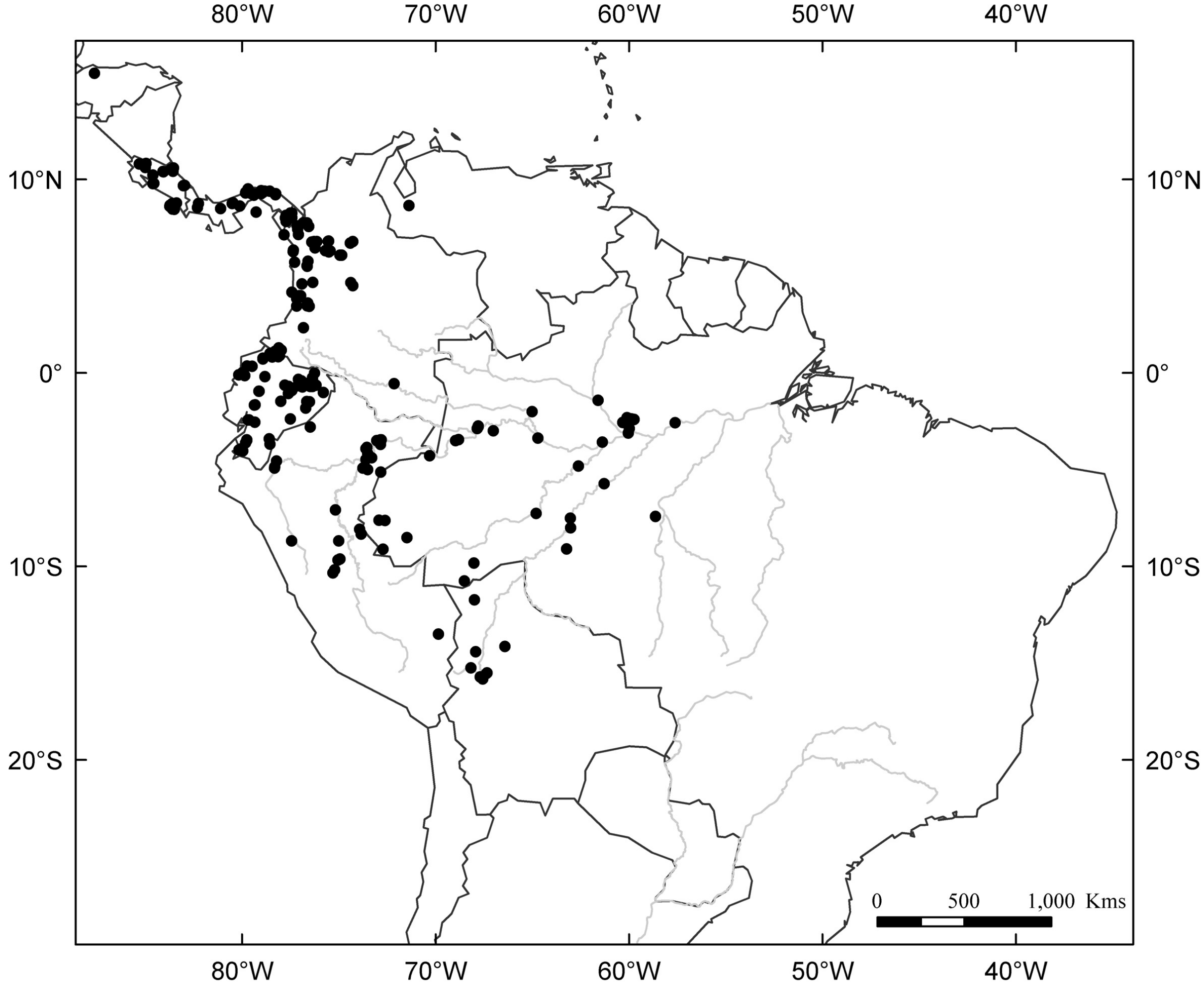

Fig. 15. Distribution of the *Eschweilera amazoniciformis*/*Eschweilera andina* clade.

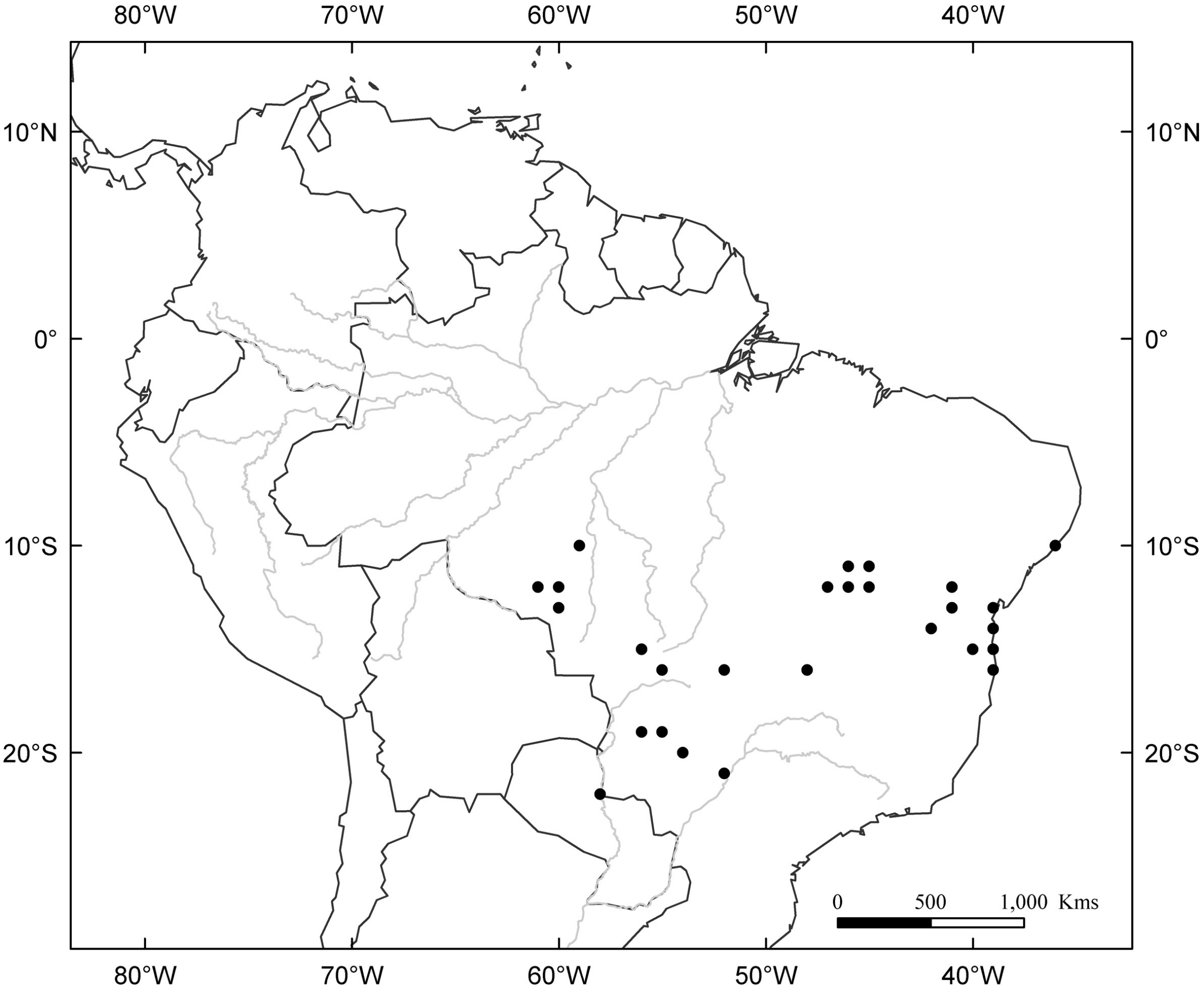

Fig. 16. Distribution of the *Eschweilera* section *Tetrapetala* clade.

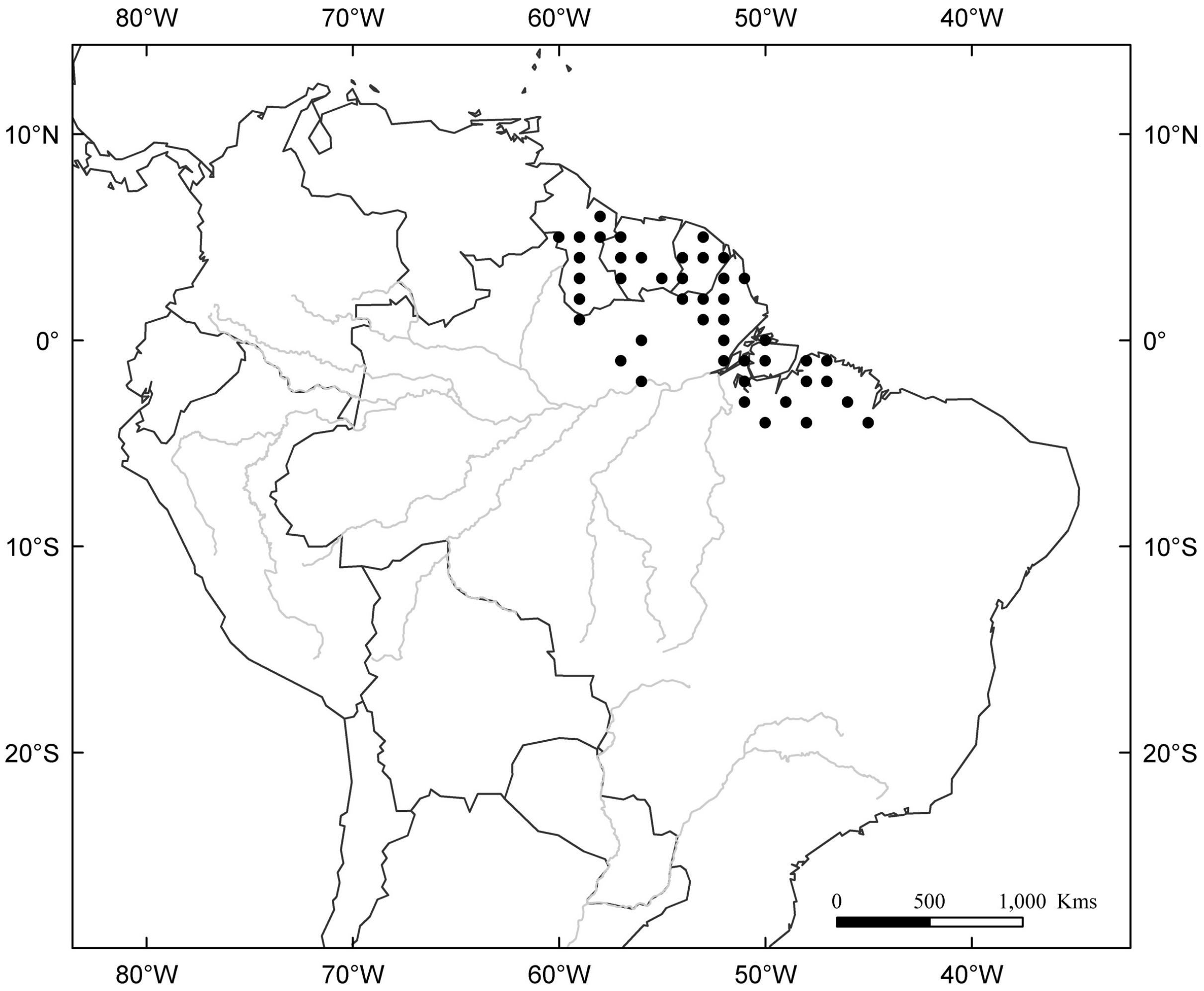

Fig. 17. Distribution of the *Lecythis* section *Corrugata* clade.

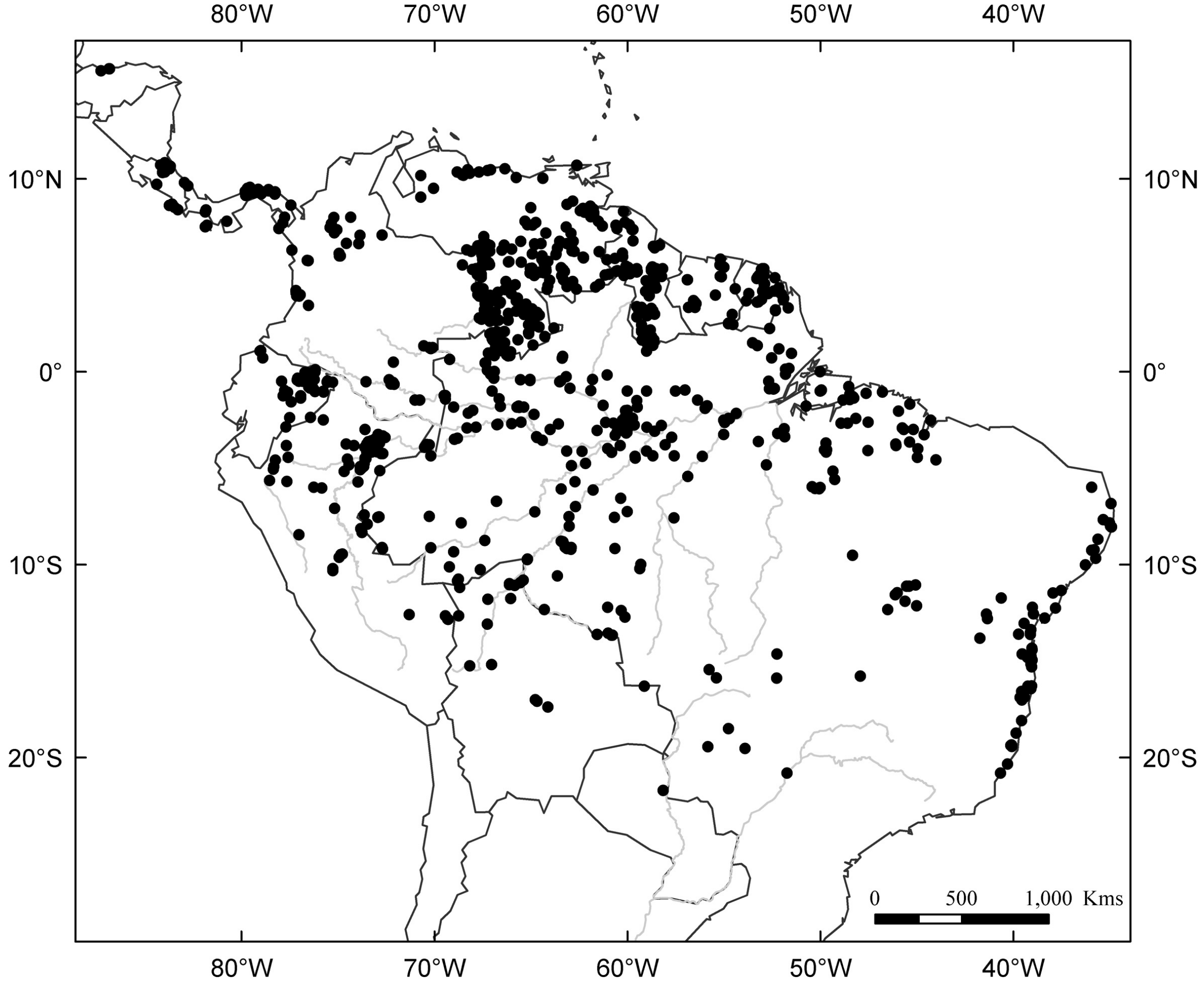

Fig. 18. Distribution of the core *Eschweilera* clade.

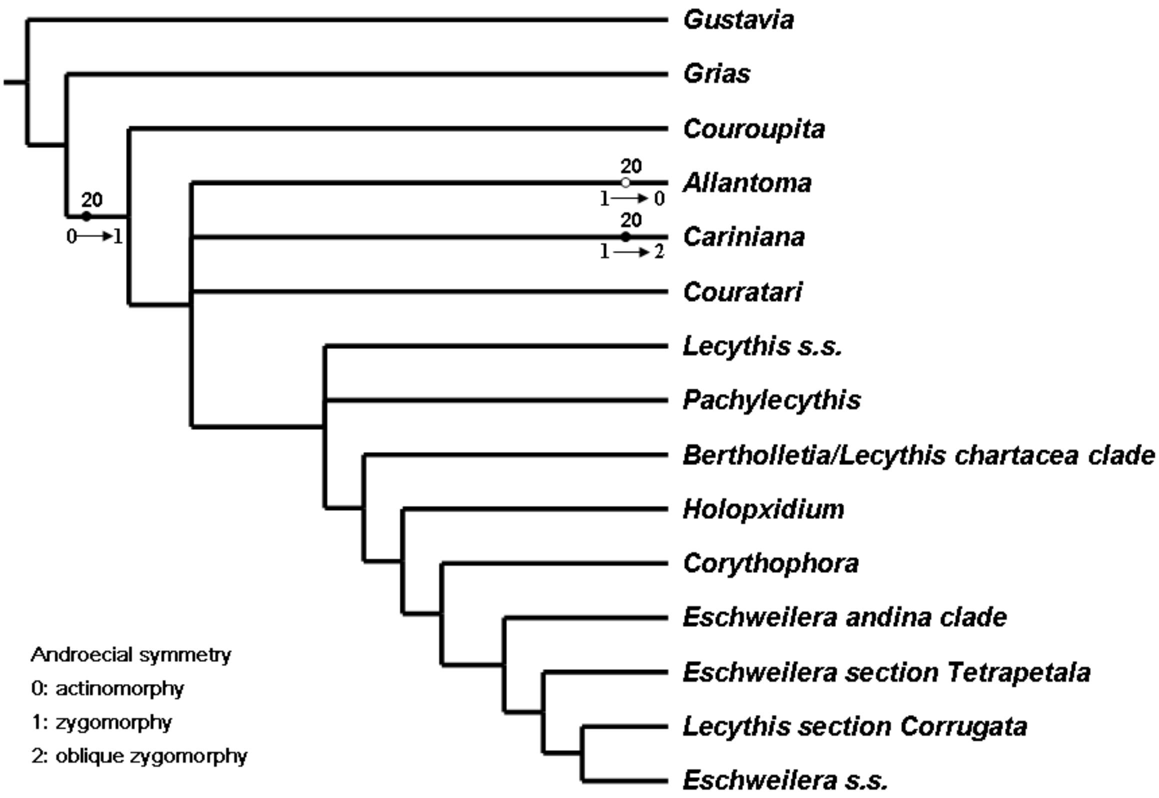

Fig. 19. Evolution of androecial symmetry in Lecythidoideae. The androecial symmetry evolved three times in Lecythidoideae. Numbers below the branches represent character states and arrows indicate the direction of the state change. White elipses are homoplasious and black elipses are non-homoplasious.

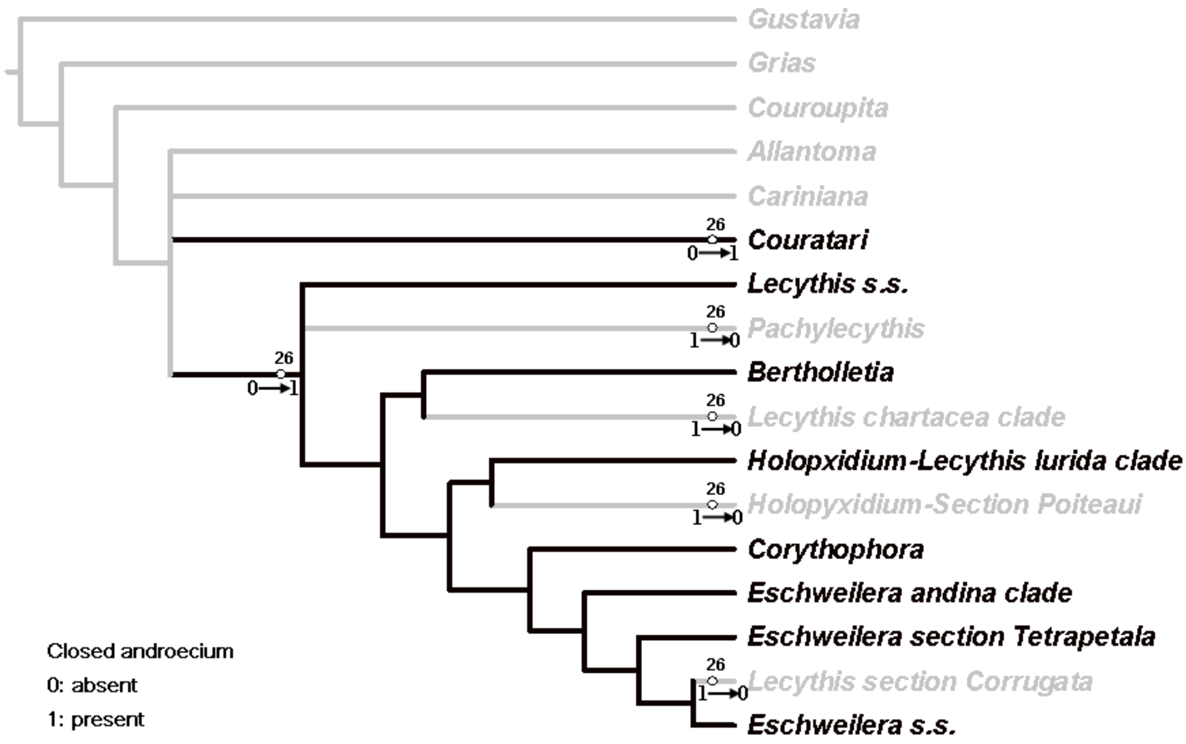

Fig. 20. Evolution of closed androecium. Clades in gray have open androecia and clades in black have closed androecia. Although the *Lecythis chartacea* clade is marked in grey, an open androecium is only found in *Lecythis brancoensis*. The remaining species the *Lecythis chartacea* clade have closed androecia. Numbers below the branches represent character states and arrows indicate the direction of the state change. White elipses are homoplasious.

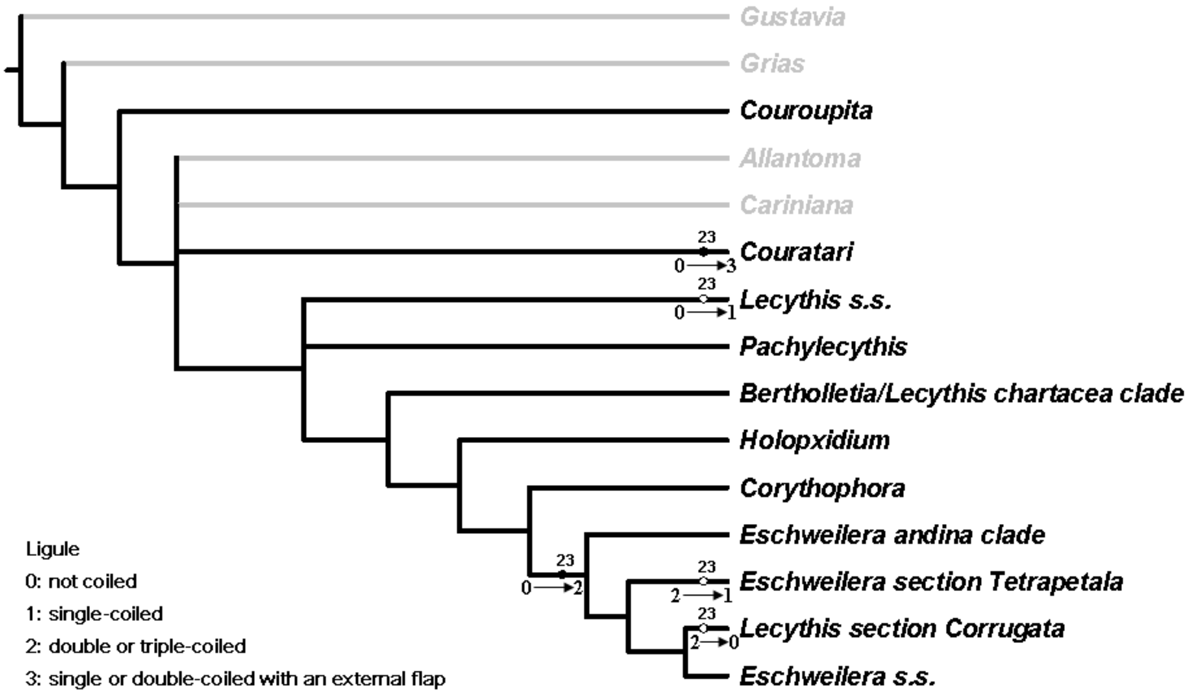

Fig. 21. Evolution of ligule. The ligule evolved five times in Lecythidoideae. Clades in grey do not have a ligule and is coded as inapplicable. Clades in black have a ligule. Numbers below the branches represent character states and arrows indicate the direction of the state change. White elipses are homoplasious and black elipses are non-homoplasious.

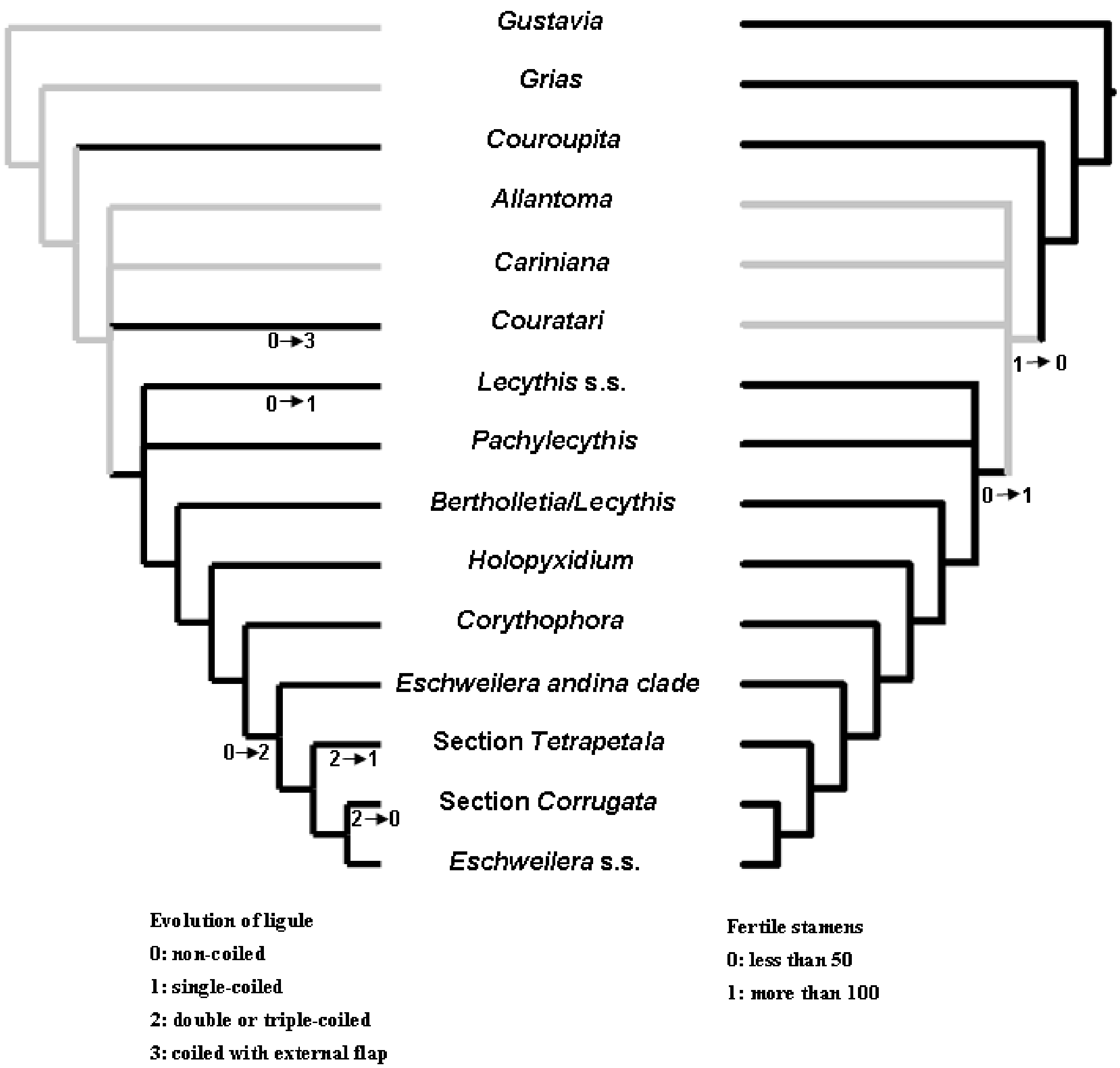

Fig. 22. Evolution of ligule versus fertile stamens. On the left, clades in grey do not have a ligule while clades in black have a ligule. On the right, clades in grey have fewer than 50 fertile stamens and clades in black have more than 50 fertile stamens. Numbers below the branches represent character states and arrows indicate the direction of the state change.

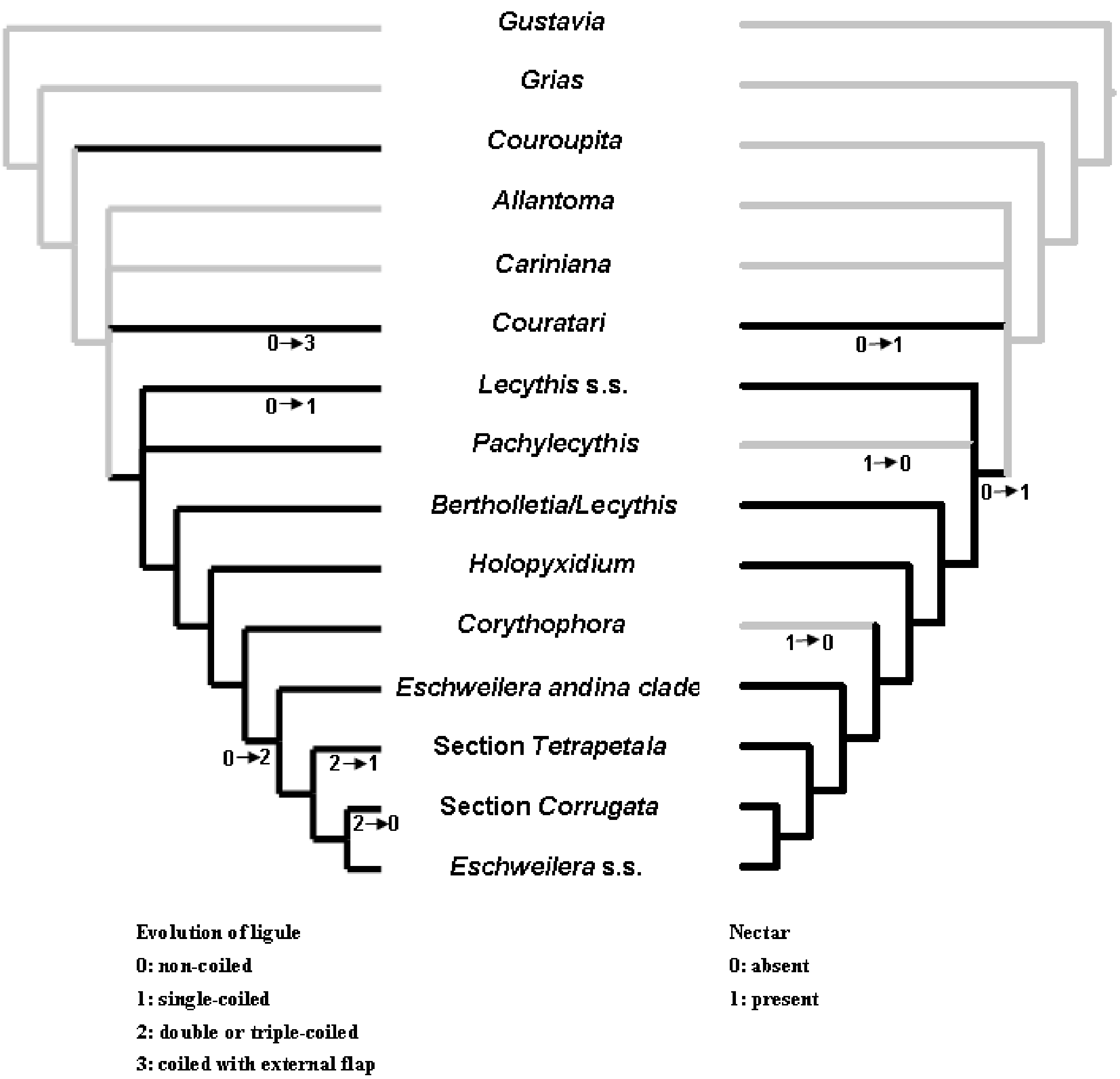

Fig. 23. Evolution of ligule and nectar. On the left, clades in grey do not have a ligule while clades in black have a ligule. On the right, clades in grey do not have nectar and clades in black have nectar. Numbers below the branches represent character states and arrows indicate the direction of the state change.

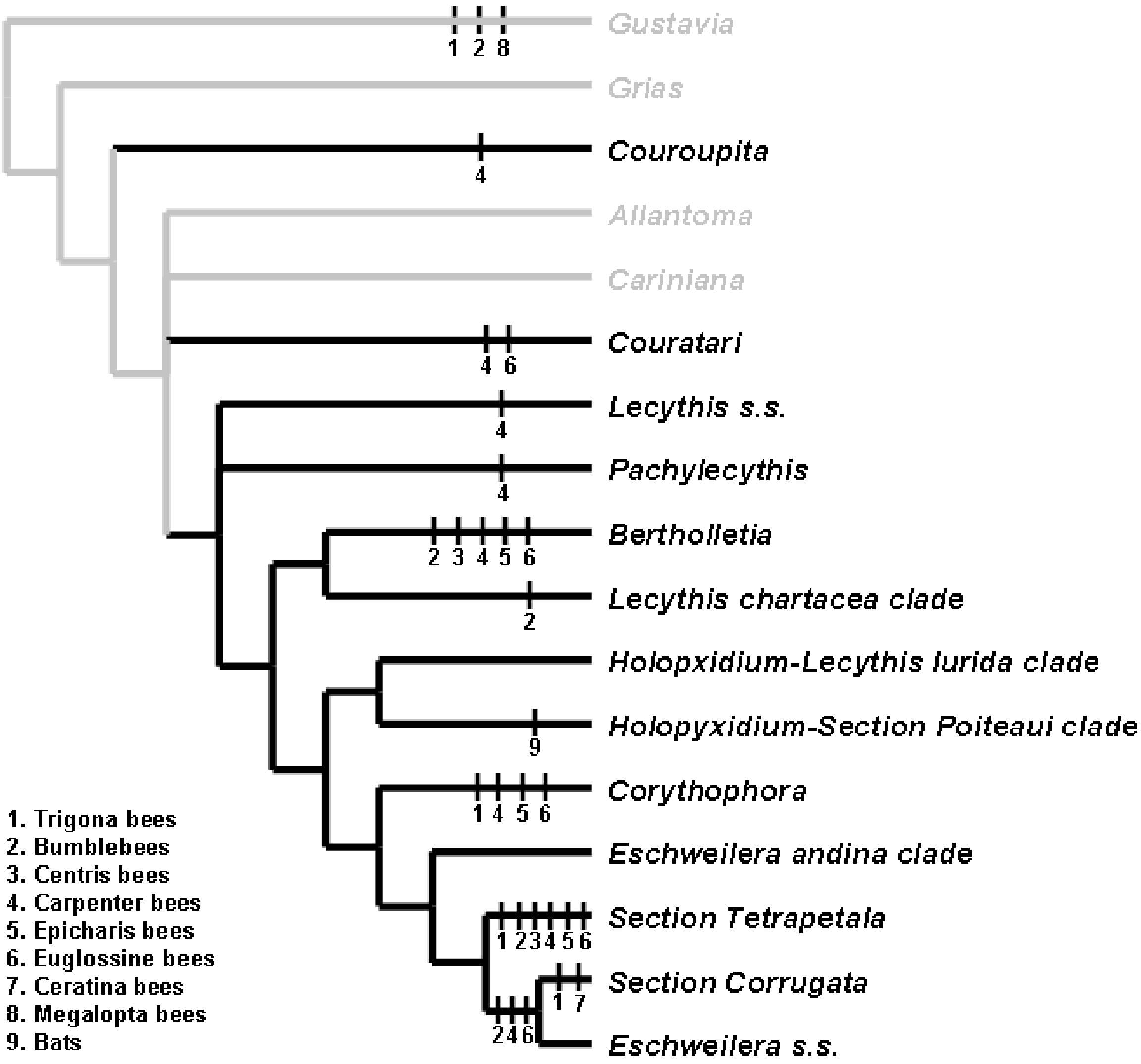

Fig. 24. Reported pollinators of the clades. Observations were based on some species in each clade. Clades in grey do not have a ligule while clades in black have a ligule. Information of the bees and their visiting plants are from Mori and Boeke (1987).

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