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

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Abstract

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

Introduction

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

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

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

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

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