



Toward a Phylogenetic-based Generic Classification of Neotropical Lecythidaceae— II. Status of *Allantoma*, *Cariniana*, *Couratari*, *Couroupita*, *Grias* and *Gustavia*

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Abstract

The morphological features of all clades of neotropical Lecythidaceae subfam. Lecythidoideae (Brazil nut family) with actinomorphic androecia (*Allantoma*, *Grias*, *Gustavia*) as well as three clades with zygomorphic androecia (*Cariniana*, *Couroupita*, and *Couratari*) are described. These clades are those that were recovered by a phylogeny based on molecular data, and all, except *Allantoma* and *Cariniana*, have been recognized as genera without changes for over a hundred years. The latter two genera have recently been circumscribed such that they now also represent monophyletic clades; thus, the authors conclude that the clades discussed in this paper represent well-defined genera based on both morphological and molecular data. Morphological descriptions of these six clades of the non-*Bertholletia* clade are included and a key to the 16 clades of New World Lecythidaceae is presented.

Introduction

The use of anatomical, morphological, and molecular data to produce cladograms has advanced the study of neotropical Lecythidaceae. For the first time in the history of classification of neotropical Lecythidaceae, higher order classification, from the generic level to the placement of the family among the angiosperms, is being developed based on testable hypotheses.

The first Lecythidaceae cladograms produced were published by Chih-Hua Tsou in 1994. The emphasis of her study was to determine the value of morphological, anatomical, and embryological features to discern higher order relationships among the 20 worldwide genera of Lecythidaceae. Tsou (1994) also contributed valuable embryological descriptions and illustrations (including androecial features) for most of the genera in both the Old World and New World and produced the first hand-generated cladograms of Lecythidaceae based on embryological and morphological characteristics for the subfamily Barringtonioideae (erroneously called the Planchonioideae fide Thorne, 2000). She concluded the following: 1) the family concept of Lecythidaceae should be limited to the Old World Barringtonioideae and Foetidioideae, and the New World Lecythidoideae; 2) Lecythidaceae and Scytopetalaceae have embryological features in common; and 3) the central Amazonian *Asteranthos brasiliensis* Desfontaines (1820: 9) (formerly placed in the African Napoleoniaeideae) is part of the Scytopetalaceae, a family otherwise limited to Africa. The last conclusion was subsequently supported by molecular (Morton *et al.*, 1997) and morphological (Apple, 1996, 2004) data.

The next step forward was taken by Morton *et al.* (1997, 1998) who analyzed the relationships of Lecythidaceae using cladistics based on anatomical, morphological, and molecular data. The major result of this study was that Lecythidaceae belong to a large clade with other families that are now considered to belong to the Ericales, a conclusion that has been supported by the molecular studies of Anderberg *et al.* (2002) and Schönenberger *et al.* (2005). The relationship of Lecythidaceae to taxa of Ericales has been recovered so many times in molecular studies that its position there is well established. It is, however, perplexing that there are no convincing anatomical or morphological characters that Lecythidaceae share with Ericales. Morton followed up their original paper (Morton *et al.*, 1997) with another study in which they recognized the following subfamilies of Lecythidaceae: Barringtonioideae (= their Planchonioideae), Napoleoniaeideae, Scytopetaloidae, Foetidioideae, and Lecythidoideae (Morton, 1998).

Conclusions

We conclude that the six clades of Lecythidaceae treated in this paper represent monophyletic groups that merit continued recognition as the following genera: *Allantoma*, *Cariniana*, *Couratari*, *Couroupita*, *Grias*, and *Gustavia*. The morphological features described and illustrated for each of these clades facilitate their identification to clades. In addition, molecular data (Mori *et al.*, 2007) confirm this conclusion for *Grias*, *Gustavia*, *Couroupita*, and *Couratari* (Fig. 1) and Huang *et al.* (2008) make a strong case for recognizing *Cariniana* and *Allantoma* as distinct genera. In this scenario, *Couroupita* is basal to the remaining zygomorphic-flowered species (the *Bertholletia* clade) and the actinomorphic-flowered *Allantoma* is nested within what is otherwise a zygomorphic-flowered clade (Fig. 1). Further study is needed to resolve the relationships of the *Cariniana*, *Allantoma*, and *Couratari* clades.

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