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A detailed investigation of the Pterocarpus clade (Leguminosae: Dalbergieae): *Etaballia* with radially symmetrical flowers is nested within the papilionoid-flowered *Pterocarpus*

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ABSTRACT

The pantropical genus *Pterocarpus* (Leguminosae: Dalbergieae) with papilionoid flowers, and allied genera in the Pterocarpus clade were sampled for the five molecular markers ITS2, *trnL-F*, *ndhF-rpL32*, *matK*, and *rbcL*, as part of our ongoing systematic studies in the clade. For wider analyses of the Pterocarpus clade the remaining 14 members of this clade were also sampled for *matK*. Phylogenetic analyses were performed under the maximum likelihood criterion (ML) and Bayesian criteria. In the five-marker analysis of the core Pterocarpus clade (including 106 accessions) two robustly supported clades were resolved. The first clade includes *Centrolobium*, *Etaballia*, *Inocarpus*, *Maraniona*, *Paramachaerium*, *Pterocarpus*, *Ramorinoa*, and *Tipuana*. The second includes all species of *Pterocarpus* (except *P. acapulcensis*), *Etaballia* with radially symmetric flowers, and *Paramachaerium*. *Paramachaerium* is placed as sister to the several *Pterocarpus* species from South America, while *Etaballia* is resolved within the clade containing the African and Asian species of *Pterocarpus*. The wider sampled *matK* data set includes 199 accessions. *Discolobium* and *Riedeliella* are recovered as sister to the remaining Pterocarpus clade. *Platymiscium* is strongly supported as sister to the rest of the members of the clade, and *Pterocarpus acapulcensis* is also here resolved in a separate lineage from the remaining *Pterocarpus* accessions. We used the phylogenies to investigate patterns of floral evolvability in the Pterocarpus clade, which include four genera with actinomorphic flowers (*Acosmium s.s.*, *Etaballia*, *Inocarpus* and *Riedelliela*). Our results reinforce the hypothesis that flower evolvability is high in early-branching legume lineages, and that actinomorphy has evolved independently four times in the Pterocarpus clade. In light of our results, the taxonomic status of the monospecific genus *Etaballia dubia* Benth. was revisited, and the species is synonymized as belonging to *Pterocarpus*, under the name *Pterocarpus dubius* Spreng., published in 1827, but hiding in synonymy for nearly two centuries.

1. Introduction

The decrease in costs and increase in methodological efficiency in molecular techniques in the past decade have resulted in an explosion in molecular phylogenetic research in general, including studies focused on the legume family. Among flowering plant families, Leguminosae encompasses one of the widest ranges in geographic distribution, habitat preference, habit type, leaf, flower and fruit morphology, thus the family serves as an excellent model for evolutionary studies [e.g. Dalbergioids (Lavin et al., 2001), *Aeschynomene* (Ribeiro et al., 2007), *Acosmium* (Cardoso et al., 2012a), *Lonchocarpus* (da Silva et al., 2012), *Steinbachiella* (Lewis et al., 2012)]. Phylogenetic studies within the Leguminosae have not only contributed to a much better understanding of relationships among legume genera, but they have also sometimes highlighted cases where a recircumscription of the generic and/or tribal concepts was necessary [e.g. Dalbergioids (Lavin et al., 2001), *Aeschynomene* (Ribeiro et al., 2007), *Acosmium* (Cardoso et al., 2012a), *Lonchocarpus* (da Silva et al., 2012), *Steinbachiella* (Lewis et al., 2012)]. Similarly, these studies have often required a rethink of widely accepted views about habitat preference and morphological evolvability (e.g. Cardoso et al., 2012a,b,c; Lavin et al., 2001; McMahon and Hufford, 2004; Pennington et al., 2000;

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Saslis-Lagoudakis et al., 2008, 2011). Pennington et al. (2000) first drew attention to 23 papilionoid genera with radially symmetric flowers, representing nine reversals from zygomorphy to actinomorphy in their phylogenetic analyses of early-diverging papilionoids. This number increased to twelve with the additional three discovered subsequently by Lavin et al. (2001) within the relatively early-branching Dalbergioid clade. These taxa were thought to be “primitive” by authors of earlier legume classifications (e.g. Polhill, 1981, 1994; Yakovlev, 1975), but showed to be scattered among early-branching papilionoid lineages including mainly genera with “less primitive” papilionoid flowers (Lavin et al., 2001; Pennington et al., 2000, 2001). Those authors also noted that despite apparent multiple origins of actinomorphic flowers in these lineages, the non-papilionoid flower morphologies do not occur in more derived lineages of the Papilionoideae. Explaining this phylogenetic pattern in the distribution of actinomorphic flowers, Pennington and co-authors (2000) suggested that in groups where papilionoid flowers have become more canalized (e.g. a zygomorphic corolla with fusion of petals and stamens, often seen in the more derived legume taxa such as *Medicago* spp., *Pisum* spp., and *Swainsona* spp.), it is more difficult to revert to a non-papilionoid flower morphology. Furthermore, zygomorphy might be conserved in late-branching lineages, as it has been a key innovation associated with high diversification rates in various lineages (e.g. Arroyo, 1981; Citerne et al., 2010; Endress, 1999, 2001; Sargent, 2004). Recently, this evolutionary pattern of repeated reversal from zygo- to actinomorphy has proven even more widespread among the early-branching papilionoids (Boatwright et al., 2008; Cardoso et al., 2012a, 2012b, 2013).

Since Bronn ex De Candolle (1825) coined the tribe name Dalbergieae it has taken several shapes and guises until Lavin et al.'s (2001) groundbreaking paper united 44 genera, previously thought to belong to five different tribes, in one monophyletic group. They called this expanded group the “Dalbergioid clade”, and subdivided it into three well-supported subclades: the Adesmia, Pterocarpus, and Dalbergia clades. This paper also formed the basis for the circumscription of the Dalbergieae (Klitgård and Lavin, 2005) in Legumes of the World (Lewis et al., 2005). Since 2005, three new genera have been added to the group, increasing the number of genera assigned to the Dalbergieae to a current total of 47 members. *Steinbachiella* Harms was reinstated and placed in the Dalbergia clade (Lewis et al., 2012), while the Pterocarpus clade acquired two new additions: the monospecific *Maraniona lavinii* C.E. Hughes, G.P. Lewis, Daza & Reynel., a new discovery from the interandean valleys of Peru (Hughes et al., 2004), and *Acosmium* Schott *s.s.* (three spp.) joining the Pterocarpus clade segregated from the other members of *Acosmium* which are placed in the Bowdichia clade of the Genistioids under the new generic names *Leptolobium* and *Guianodendron* (Cardoso et al., 2012a). In the Pterocarpus clade a number of genera have been the focus of recent species level phylogenetic studies: *Platymiscium* (Klitgård, 2005; Saslis-Lagoudakis et al., 2008); *Centrolobium* (Pirie et al., 2009); *Pterocarpus* (Saslis-Lagoudakis et al., 2011); and *Acosmium* (Cardoso et al., 2012a), which have improved the resolution of the core Pterocarpus clade. Nevertheless, infrageneric relationships within the wider Pterocarpus clade are still not well-resolved.

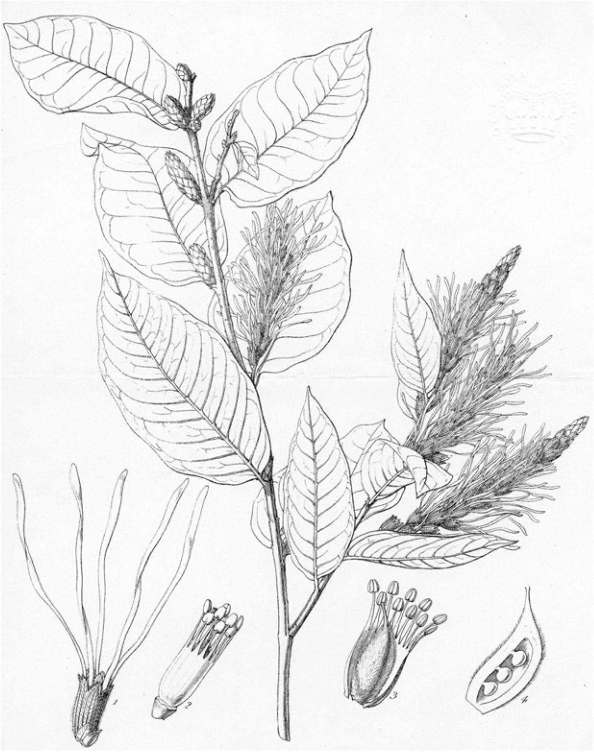

Fig. 1. *Pterocarpus dubius* Spreng. (= *Etaballia dubia* (Kunth) Rudd [as *Etaballia guianensis* Benth.]), plates first published in Hooker's Icones (1842).

Etaballia Benth. is a monospecific legume tree genus, restricted to periodically inundated humid tropical rainforests of Brazil, the Guianas, and Venezuela, and has recently also been recorded from Pando in the Bolivian Amazon (voucher *Klitgård et al. 1394*; Figs. 1–2). Largely due to its unusual morphology with unifoliolate leaves, radially symmetric flowers and samaroid fruits, *Etaballia* has had a turbulent taxonomic history, since Bentham (1840a) first published *Etaballia guianensis* Benth. [=*E. dubia* (Kunth) Rudd] as a member of the Bauhinieae, “allied to [the genus] *Schnella*…”. In Genera Plantarum (Bentham, 1865), *Etaballia* was placed in synonymy under *Inocarpus* Forst., a Southeast Asian monospecific genus also with unifoliolate leaves and radially symmetric flowers, but with drupaceous fruits, and placed as “genus anomalum” in tribe Dalbergieae. Subsequently, most authors have given *Etaballia* independent generic status in the tribe Dalbergieae (Dalla Torre and Harms, 1900–1907; Ducke, 1949; Funch and Santos, 1997; Klitgård and Lavin, 2005; Lavin et al., 2001; Polhill, 1981), while some have placed it elsewhere in the legume family: intermediate between subfamilies Mimosoideae and Papilionoideae (Kuhlmann, 1949); in a “primitive position” in tribe Sophoreae or Cadieae (Hutchinson, 1964 — in synonymy under *Inocarpus*; Polhill, 1994; Yakovlev, 1975); and between subfamilies Caesalpinioideae and Papilionoideae (Barroso et al., 1984). Some authors have commented on the resemblance of the fruits of *Etaballia dubia* to those of the two amphiatlantic species, *Pterocarpus officinalis* Jacq. [e.g. Kunth, 1824 — when publishing *Hecastaphyllum dubia* Kunth (=*E. dubia*); Rudd, 1970], and *P. santalinoides* DC. (Rojo, 1972), which share a samaroid (sometimes appearing drupaceous) fruit with a narrow wing encircling 1/3 to 2/3 of the circumference of the seed chamber (Fig. 2).

Another member of the Pterocarpus clade which has had a complex taxonomic history is *Paramachaerium* Ducke, currently consisting of five species distributed in the Amazonian regions of the Guianas, Venezuela, Brazil, Peru, and Panama (Klitgård and Lavin, 2005; Rudd, 1981). In 1925 Ducke segregated *Machaerium schomburgkii* Benth. (Bentham, 1840b) [synonymous with *Pterocarpus kuhlmannii* Ducke (Ducke, 1922)] from *Machaerium*, published the genus *Paramachaerium* and based it on the type species *Paramachaerium schomburgkii* (Benth.) Ducke. In 1935 he added *Paramachaerium ormosioides* Ducke [=*Pterocarpus ormosioides* Ducke (Ducke, 1922)]. To-date three additional