



## Phylogeny of the Henriquezieae-Posoquerieae-Sipaneeae, a Guayanan-centered clade of Rubiaceae: implications for morphological evolution<sup>#</sup>

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### Abstract

The Henriquezieae-Posoquerieae-Sipaneeae clade (Rubiaceae) is centered in the Guayana Region of Northern South America. The Henriquezieae and Sipaneeae contain a large number of taxa that are endemic to the Guayana Region, while the Posoquerieae exhibits a wider distribution throughout the Neotropics. In order to evaluate the phylogenetic relationships within this clade, and assess the evolution of selected morphological characters potentially important in its diversification, we performed parsimony analyses of ITS, *trnL-F*, *rps16* and morphology, Bayesian Markov chain Monte Carlo analyses of the molecular data, and optimized six morphological characters on cpDNA trees. Results confirm the monophyly of each of the tribes, and that of the genera included in the study. The Sipaneeae are the earliest diverging lineage, sister to a well-supported Henriquezieae-Posoquerieae clade. Henriquezieae have many traits unique or atypical in Rubiaceae, a tendency observed in other lineages endemic to the Guayana Region, suggesting strong selection for morphological novelties necessary to colonize the extremely poor soils of this region. The pollen catapult mechanism originated in the *Molopanthera-Posoqueria* clade is perhaps unique in angiosperms, and may represent a novel strategy that played an important role in the early divergence that gave rise to both genera, and to the early radiation of the genus *Posoqueria*. Diversification of *Posoqueria* outside the Guayana Region probably was accompanied by a shift from capsular to baccate fruits that facilitated colonization of understory forests. Habit specialization may be considered a consistent factor in the diversification of the Guayanan-centered clade of the Rubiaceae.

**Key words:** Character evolution, *Gleasonia*, *Henriquezia*, *Platycarpum*, Systematics

### Introduction

Rubiaceae is one of the most diverse families in the Guayana Region of Northern South America (Berry *et al.* 1995, Berry & Riina 2005). This region is one of the most geologically ancient cores on earth, characterized mainly by isolated table mountains, very poor sandy soils, and high levels of endemism (Maguire 1970, Berry *et al.* 1995, Huber 1995). The Rubiaceae is the richest family in the Guayana Region in terms of endemism at the generic level with 20 endemic or near endemic genera (Berry *et al.* 1995). When looking these levels of endemism in the two (Robbrecht & Manen 2006) or three main lineages of the family (Bremer & Eriksson 2009), subfamily Ixoroideae (supertribe Ixoridinae, *sensu* Robbrecht & Manen (2006)) includes 10 endemic or near endemic genera to the Guayana Region, with ca. 52 species, while subfamily Rubioideae is represented only by four genera and five species, and subfamily Cinchonoideae (supertribe Cinchonidinae, *sensu* Robbrecht & Manen (2006)) includes just six genera with eight species. In the Ixoroideae, one of the recognized clades of the subfamily contains nine of these endemic genera, here referred to as the Guayanan-centered clade, or the HPS clade, because it contains the tribes Henriquezieae Bentham & Hooker (1873: 8), Posoquerieae Delprete (2004: 23), and Sipaneeae Bremekamp (1934: 253). Most Guayanan endemics are found in the tribes Henriquezieae (HEN) and Sipaneeae (SIP), while most species of the tribe Posoquerieae (POS) are distributed outside the Guayana Region, particularly in the Andes, but in general in Central and Tropical South America. The HPS clade includes a total of 15 genera and about 86 species. Genera of this clade indicating total number of species, number of species endemic to the Guayana Region, and geographic distribution are shown in Table 1.