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Evolution and trends in the Psychotrieae alliance (Rubiaceae)—A rarely reported evolutionary change of many-seeded carpels from one-seeded carpels

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ABSTRACT

Bayesian and parsimony analyses of five plastid gene and nrITS regions from 58 Rubioideae (Rubiaceae) taxa further support the sister-group relationship between the African monotypic genus *Schizocolea* and the Psychotrieae alliance sensu Bremer & Manen. Our analyses show that the Psychotrieae alliance can be subdivided into in four well-supported clades: *Schizocolea*, (Schradereae(Gaertnereae(Mitchelleae–Morindeae s.s.))), Palicoureeae–Psychotrieae s.s., and Craterispermeae–Prismatomerideae. The relationships between the latter three clades remain unsettled. Our study further reveals much higher numbers of molecular autapomorphies of the tribes compared with those of molecular synapomorphies of two sister tribes or groups of tribes. Within the newly delimited Psychotrieae alliance a one-seeded carpel was inferred as ancestral and many- and two-seeded carpels evolved once each. We describe Mitchelleae to accommodate *Damnacanthus* and *Mitchella* and restrict Morindeae to include only *Appunia, Coelospermum, Gynochthodes, Morinda, Pogonolobus*, and *Syphonandrium*. Mitchelleae is characterized e.g., by placentae inserted near the top of the septum and a single campylotropous ovule per carpel, while Morindeae s.s. has massive and T-shaped placentae inserted in the middle of the septum and two anatropous ovules per carpel.

1. Introduction

Rubioideae Verdc. (Verdcourt, 1958), the largest subfamily in the coffee family (Rubiaceae) with ca. 7475 species (Govaerts et al., 2006), is a well-defined monophyletic group that can easily be diagnosed by the presence of raphide idioblasts, valvate corolla aestivation and often heterostylous flowers. Our knowledge of the subfamily has recently been improved as a result of a series of independent molecular phylogenetic studies of Rubiaceae (Bremer, 1996a; Andersson and Rova, 1999; Bremer and Manen, 2000; Robbrecht and Manen, 2006). For examples, the sister-group relationship between the African monotypic genus *Colletoecema* Petit (1963) and the remaining Rubioideae was shown for the first time by Robbrecht and Manen (2006). The tribes Lasiantheae Bremer and Manen (2000) and Coussareeae Hooker (1873) were demonstrated to be successive sister groups to the large Psychotrieae and Spermacoceae alliances (both sensu Bremer and Manen, 2000), which are in turn sisters (e.g., Andersson and Rova, 1999; Bremer and Manen, 2000). Despite the largely congruent results from these independent studies, there were some noticeable discrepancies such as, the phylogenetic positions of the tribes Urophylleae Bremek. ex Verdc. and Ophiorrhizeae Bremek. ex Verdc. (Verdcourt, 1958) and the tribal delimitations and relationships within the Psychotrieae alliance (see Fig. 1A–D). This latter group is the main focus of the present study.

The Psychotrieae alliance sensu Bremer and Manen (2000) [also known as Psychotrieae s.l., Bremer (1996a); the Gaertnereae-Morindeae–Psychotrieae complex, Andersson and Rova (1999); supertribe Psychotriidinae, Robbrecht and Manen (2006)] is mostly tropical, with the exception of the East Asian *Damnacanthus* C.F.Gaertn. and the North American and East Asian *Mitchella* L., which are restricted to the temperate regions. The alliance is characterized by its fleshy (drupes or berries) fruits, which are considered important food sources for many tropical frugivorous birds (Snow, 1981). It is a predominantly woody group consisting of ca. 3000 species (ca. 1/4 of Rubiaceae) (Govaerts et al., 2006) belonging to ca. 54 genera, which have previously been classified in four to six tribes (see Table 1). These tribes are morphologically distinct and apparently share no obvious morphological synapomorphies. As a result, the tribal relationships within the Psychotrieae alliance have always been unsettled (see Fig. 1A–D) and are the major issues in the recent discussions about the classification

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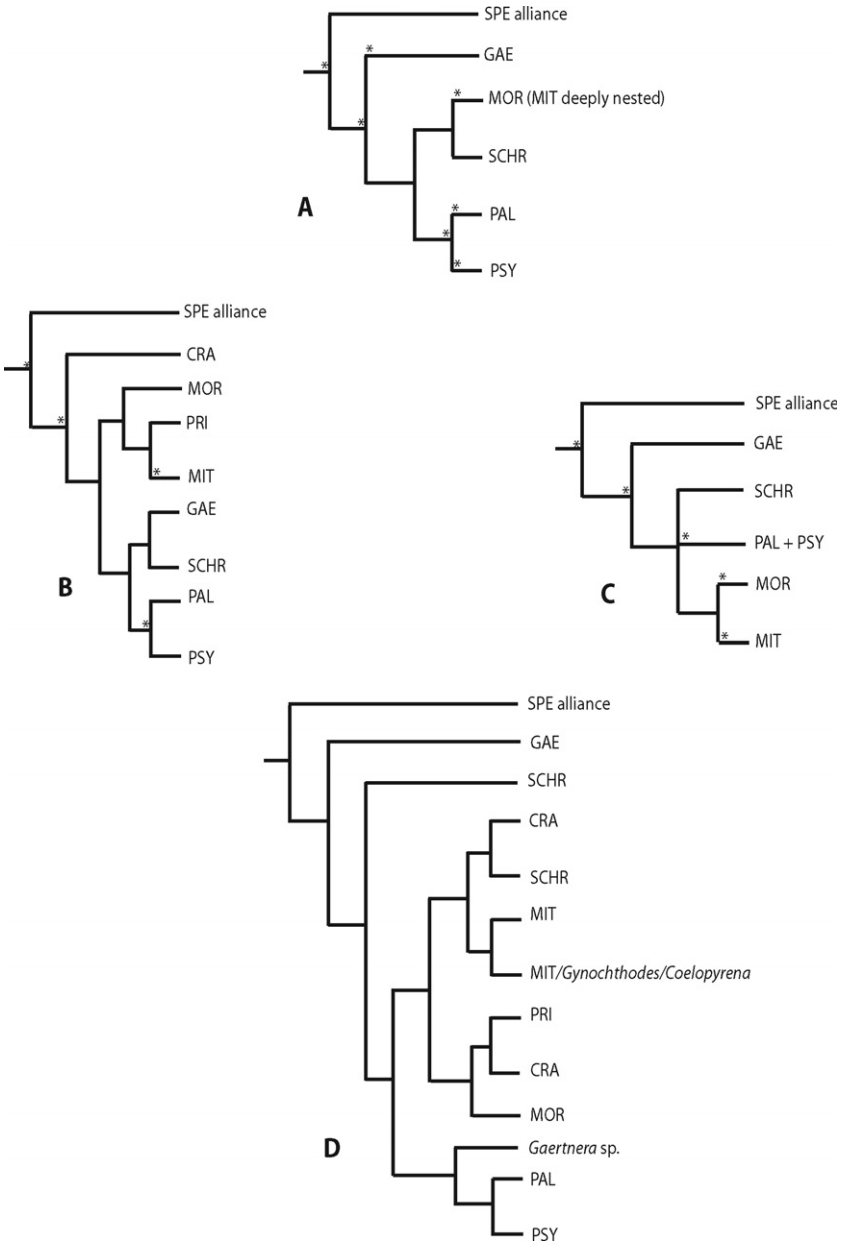

Fig. 1. Intertribal phylogenetic relationships in the Psychotrieae alliance, as inferred in three different studies. CRA, Craterispermeae; GAE, Gaertnereae; MIT, *Mitchella* group; MOR, Morindeae s.s.; PRI, Prismatomerideae; and SCHR, Schradereae. Branches marked by an asterisk correspond to clades supported by bootstrap or jackknife values ⩾80%. (A) *rps*16 tree from Andersson and Rova (1999: Fig. 5); (B) combined *atp*B-*rbc*L/*rbc*L tree from Bremer and Manen (2000: Fig. 3); (C) combined *atp*B-*rbc*L/*rbc*L/*rps*16 tree from Bremer and Manen (2000: Fig. 4); (D) and supertree based *atp*B-*rbc*L/*rbc*L/*rps*16/*trn*L-F data from Robbrecht and Manen (2006: Fig. 4C).

Table 1
Tribal circumscriptions of the Psychotrieae alliance based the recent molecular phylogenetic studies

Andersson and Rova (1999)	Bremer and Manen (2000)	Robbrecht and Manen (2006)	Razafimandimbison et al. (this study)
	Craterispermeae[5]	Craterispermeae[5]	Craterispermeae[5]
Gaertnereae[1]	Gaertnereae[1]	Gaertnereae[1]	Gaertnereae[1]
			Mitchelleae trib. nov.
Morindeae s.l.[2]	Morindeae s.l.[2]	Morindeae s.l.[2]	Morindeae s.s.
		Paliocoureeae[6]	Paliocoureeae[6]
			Prismatomerideae[7]
Psychotrieae s.l.[3]	Psychotrieae s.l.[3]	Psychotrieae s.s.[6]	Psychotrieae s.s.[6]
Schradereae[4]	Schradereae[4]	Schradereae[4]	Schradereae[4]
			Schizocolea

[1]Darwin (1976); [2]including the *Mitchella* group and Prismatomerideae sensu Robbrecht et al. (1991); [3]including Paliocoureeae sensu Robbrecht and Manen (2006); [4]Puff and Buchner (1998); Puff et al. (1998a,b); [5]Verdcourt (1958); [6]Robbrecht and Manen (2006); and [7]Robbrecht et al. (1991).

of Rubioideae. Almost all morphological (including anatomical and palynological) studies focusing on one or more tribes of the Psychotrieae alliance (e.g., Robbrecht et al., 1991; Igersheim, 1992; Puff et al., 1993; Igersheim et al., 1994; Jansen et al., 1996) seemed