Nuclear rDNA ITS sequence data used to construct the first phylogeny of Vanguerieae (Rubiaceae)

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Abstract. The morphologically homogenous tribe Vanguerieae was investigated phylogenetically using sequence data from the Internal Transcribed Spacer (ITS) region in the nuclear ribosomal DNA. Sequences from 41 Vanguerieae species representing 19 genera were produced, and a parsimony analysis was performed. The phylogenetic analysis has several clades with strong support, among which three new informal groups are discussed, i.e. the Vangueria group, the Fadogia-Rytigynia group and the Spiny group. Also found monophyletic with strong support are Multidentia, Keetia, Lagynias, and Pyrostria. Canthium and Rytigynia are revealed as polyphyletic; Vangueria, Tapiphylum, and Fadogia are paraphyletic. Results from this first phylogenetic analysis of the tribe clearly demonstrate a need for new circumscriptions of several genera. Morphological characters are discussed and putative synapomorphies are mentioned. Jackknife, bootstrap, and Bremer support are calculated and differences found in support are discussed.

Key words: Rubiaceae, Ixoroideae, Vanguerieae, ITS, phylogeny, support.

Although a widespread and common group in the paleotropics, Vanguerieae are a tribe that has received little attention. They are a member of the large and important family Rubiaceae, a family of mostly woody species distributed over large parts of the world, but centred in the tropics. Rubiaceae are perhaps best known for coffee (Coffeea sp.), but also include many ornamentals and are an important constituent of many tropical habitats. The main characteristics of the family are opposite leaves, interpetiolar stipules, sympetalous corollas and inferior ovaries. While many phylogenies for the family have been produced in the last ten years, all from the subfamilial level down to genera, no phylogeny has so far been produced for Vanguerieae. This might in part be due to a strong morphological similarity between the taxa in the tribe, which has made the tribe a very difficult group to work with. The taxonomy has in recent years become refined, but no real consensus has been reached on how to delimit the genera.

Consisting of about 600 species (Robyns 1928, Cavaco 1969, Smith and Darwin 1988, Bridson 1998), Vanguerieae are among the larger tribes in the family Rubiaceae. The major part of the described taxa can be found in Africa (almost all parts south of the Sahara), but some can also be found in southern Asia, the Pacific, and Australia.
As Vangueriaceae are delimited today they form a strongly supported monophyletic group (Bremer et al. 1995, Andreasen and Bremer 1996). Dumortier first mentioned the tribe in 1829 (as “Vaugneriaceae”; Dumortier 1829). He included not only “Vaugneria” but also several other genera that now have been excluded from the tribe. Later authors also had opinions on Vangueriaceae that deviate from the present classification (e.g. Hooker 1873, Hieron 1877), and it was not until 1958 that Verdcourt finally delimited the tribe as it is known today (Verdcourt 1958). Several subfamilial placements have been suggested, e.g. Cinchonoideae (including Xyloloideae; Verdcourt 1958) and Antirhineoideae (Robbrecht 1988), but now most studies place it in Xyloloideae (e.g. Bremer et al. 1995, Andersson and Rova 1999).

The tribe is easily identified by a combination of characters: axillary inflorescences, valvate aestivation, single pendulous ovules and above all, the apex of the style swollen into a pollen presenter serving in secondary pollen presentation. This way of presenting pollen to the pollinator is a rather common phenomenon in the family (Puff et al. 1996), especially in the subfamily Xyloloideae of which Vangueriaceae are a member, and was also used as a character to circumscribe the subfamily (Brenekamp 1954). However, in the case of Vangueriaceae the pollen presenter is represented by a ‘styril head’-complex (Igersheim 1993), a character unique for the tribe (see Fig. 1). The complex consists of both the pollen presenting tissue and of the stigma lobes and is in most cases globose to cylindrical, often with the style retracted into the structure. Furthermore, several anatomical characters support the complex as a unique structure (Igersheim 1993). However, following the example set in Flora of Tropical East Africa (F.T.E.A.; Verdcourt and Bridson 1991) and Flora Zambesiaca (Bridson 1998), the more general term pollen presenter will be used here.

Of genera later to be included in Vangueriaceae, the two first were Canthium (Lamarck 1783) and Vangueria (Jussieu 1789). Canthium was partly defined by having two locules and Vangueria by five. The number of locules was the main character used when later species were described; species with two locules were placed in Canthium (or Electronia, an invalid synonym; Hieron 1898) and species with more than two locules were placed in Vangueria. New genera were later described, sometimes including species earlier described as Canthium or Vangueria, and today 28 generic names are in use. For a more complete discussion on the history of Vangueriaceae, see Verdcourt (1987).

In the last 20 years a vast amount of work on Vangueriaceae has been produced for the F.T.E.A. and Flora Zambesiaca projects (Verdcourt and Bridson 1991, Bridson 1998). These publications have greatly helped the understanding of the complicated groupings within the tribe. However, very few studies have attempted to study Vangueriaceae as a whole. Only two general works have been produced. The first one is ‘Tentamen Monographiae Vangueriaceae’ by Robyns (1928). In this study Robyns describes many new species and genera but avoids many problems by not dealing with Cuviera and the large genus Canthium, which is perhaps the most problematic one. The other study is the thesis of