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Phylogeny of the complex Vanguerieae (Rubiaceae) genera *Fadogia*, *Rytigynia*, and *Vangueria* with close relatives and a new circumscription of *Vangueria*

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Abstract. The phylogeny of the Vanguerieae genera *Fadogia*, *Rytigynia*, *Vangueria*, and closely related genera is investigated using nuclear rDNA ITS sequences and plastid *trn*T-F and *rpl*16 sequences. Individual and combined analyses reveal several strongly supported clades. There are indications that *Fadogia, Rytigynia, Tapiphyllum*, and *Vangueria* are para- or polyphyletic and only *Multidentia* is strongly supported as monophyletic. Several taxa are found to have incongruent positions in the ITS and chloroplast phylogenies, and possible reasons behind these incongruencies are discussed. For *Ancylanthos rubiginosus* a chloroplast capture event can explain the incongruent position. In the *Fadogia-Rytigynia* group the incongruence is more widespread and cannot be attributed to a single taxon or a few taxa, but hybridization and introgression is the most likely explanation for the incongruence. It is concluded that the genera *Ancylanthos, Lagynias, Pachystigma*, and *Tapiphyllum* and the three species *Fadogia agrestis, Rytigynia fuscosetulosa*, and *Rytigynia induta* should be transferred to *Vangueria*.

Key words: *Fadogia*, hybridization, phylogeny, Rubiaceae, *Rytigynia*, taxonomy, *Vangueria*, Vanguerieae.

Introduction

Until recently, the tribe Vanguerieae of the Rubiaceae remained one of the poorest understood larger groups in the family concerning the phylogeny of the group. Recent studies (Lantz et al. 2002, Lantz and Bremer 2004) have improved our knowledge and now there is a good general knowledge of the phylogeny. The monophyly of the tribe has rarely been doubted (Verdcourt 1958). A very distinct and easily recognized character, a pollen presenter at the apex of the style is of great diagnostic value and makes it easy to distinguish between members of Vanguerieae and other Rubiaceae tribes also in the field. Eastern and southern tropical African taxa have so far received the most attention (Verdcourt and Bridson 1991, Bridson 1998). Around 600 species are currently recognized, but the delimitation of many of these is uncertain, especially for the poorly known species from Madagascar and South East Asia.

An earlier study (Lantz and Bremer 2004) identified one subclade of the tribe in which the generic limits were especially unclear. Due to

the slightly longer corolla tubes and lobes present in this group compared to other members of Vanguerieae, the group was given the informal name 'the large-flowered group'. This group is the focus of the present study. The large-flowered group is with few exceptions restricted to Africa south of Sahara, but a few *Rytigynia* and *Vangueria* species are found on Madagascar. Two subgroups of the large-flowered group had earlier been identified (Lantz et al. 2002), i.e. the *Vangueria* group and the *Fadogia-Rytigynia* group. Included in the *Vangueria* group is the type genus of the tribe, *Vangueria*, together with *Ancylanthos* (tentatively included), *Lagynias*, *Pachystigma*, and *Tapiphyllum* (Lantz et al. 2002, Lantz and Bremer 2004). These genera are considered some of the most problematic in the tribe, concerning delimitation of species as well as genera (Bridson 1998). The four genera *Fadogia*, *Fadogiella*, *Hutchinsonia*, and *Rytigynia* form the species-rich *Fadogia-Rytigynia* group (Lantz et al. 2002) with just above 100 species. *Cuviera*, *Multidentia*, *Pygmaeothamnus, Robynsia*, *Vangueriopsis* and a single species of *Canthium*, *C. oligocarpum*, also belong to the large-flowered group, but their phylogenetic affinities are more uncertain (Lantz and Bremer 2004). In total, over 180 species are currently recognized in the group, but a number of these, especially in *Rytigynia*, are known from very few collections.

The work of Robyns (1928) has been especially important for the classification of the group. With the exclusion of *Cuviera* and the large genus *Canthium*, Robyns revised all species of Vanguerieae, and made over a hundred new combinations and descriptions of species in the large-flowered group. He also described several new genera, of which *Fadogiella*, *Hutchinsonia*, *Pygmaeothamnus*, *Tapiphyllum*, and *Vangueriopsis* are known to belong to the large-flowered group (Lantz and Bremer 2004). Later authors (e.g. Verdcourt 1981, 1987; Bridson 1996, 1998) have added new species to the genera in the group, and also performed several synonymizations.

Over 180 species representing thirteen genera are currently recognized in the large-flowered group. Most of the genera are hard to delimit morphologically, good diagnostic characters are usually lacking. In earlier studies covering the whole tribe (Lantz et al. 2002, Lantz and Bremer 2004), but with a rather small sample of the large-flowered group, we were unable to resolve the relationships in the group. With this study we aim to resolve the phylogeny with strong support by greatly increasing the sample size and adding an extra data set to the already existing data. The new data set consists of sequences of the *rpl*16 intron, one of the fastest evolving chloroplast regions (Small et al. 1998) and is likely to add support for the close relationships in this difficult group. We intend to use the phylogeny to test the monophyly of the genera as currently conceived and if necessary base a new classification on the results. Some incongruence between chloroplast and nuclear phylogenies was noted in an earlier publication (Lantz and Bremer 2004), and we also aim to quantify the extent to which the different genera are affected by this.

Material and methods

Taxon sampling. Our strategy was to include as many species as possible from all genera known to belong in the large-flowered clade (Lantz and Bremer 2004). Sixty-six ingroup (of 180) taxa were sampled. The availability of material largely determined which species were included. A majority of the in-group species sampled occur in eastern and southern Africa, but five species from West Africa, one from Central Africa, and two from Madagascar are also included (see Fig. 1) . The distributions of the taxa detailed only to major geographical regions are given in Fig. 1. This information is added only to give an indication of the distribution of the taxa. The taxa are in many cases restricted to smaller areas within these regions and can also in some small amount occur outside of the mentioned areas. Eight representatives of *Canthium* s. str., shown to be the closest relative of the ingroup (Lantz et al. 2002, Lantz and Bremer 2004), were chosen as outgroup. Several of these were only

Table 1. Voucher information and EMBL accession numbers. Herbarium abbreviations according to Holmgren et al. (1990). - indicates sequences not included due to sequencing difficulties. Sequences new for this study are underlined.

Species	Voucher	EMBL number ITS/*trn*T-F/*rpl*16
Canthium coromandelicum (Burm. f.) Alston	Andreasen 36 (UPS)	AJ315081/AJ620122/AJ876810
Canthium glaucum Hiern ssp. *glaucum*	Kuchar 17410 (UPS)	AJ617752/AJ620124/AJ876811
Canthium inerme (L.f.) Kuntze	Bremer & Bremer 3686 (UPS)	AJ315120/AJ620125/AJ876812
Canthium tetraphyllum (Schweinf. ex Hiern) Baill.	Bremer 3074 (UPS)	AJ315083/AJ620149/AJ876813
Canthium armatum (K. Schum.) Lantz	Bremer & Bremer 3790 (UPS)	AJ315082/AJ620155/AJ876814
Pygmaeothamnus cf. *chamaedendrum* (Kuntze) Robyns	Bremer & Bremer 3800 (UPS)	AJ315119/AJ620165/AJ876815
Canthium bugoyense (K. Krause) Lantz	Rwburindore 3536 (UPS)	AJ315084/AJ620172/AJ876816
Canthium stenosepalum Lantz	Merello et al. 1494 (K)	AJ315085/AJ620182/AJ876817
Ancylanthos rubiginosus Desf.	Zimba et al. 776 (UPS)	AJ617747/AJ620119/-
Canthium oligocarpum Hiern ssp. *captum* (Bullock) Bridson	Borhidi et al. 85449 (UPS)	AJ617755/AJ620129/AJ876818
Cuviera angolensis Welw. ex K. Schum.	McPherson 16297 (MO)	AJ315088/AJ620134/-
Fadogia agrestis Schweinf. ex Hiern	Madsen 5495 (S)	AJ874980/AJ874942/AJ876819
Fadogia ancylantha Hiern	Chapman & Chapman 9109 (UPS)	AJ315103/AJ620136/AJ876820
Fadogia arenicola K. Schum. & K. Krause	Gereau et al. 6011 (UPS)	AJ874981/AJ874943/AJ876821
Fadogia cienkowskii Schweinf.	Lantz 101 (UPS)	-/AJ620137/AJ876822
Fadogia elskensii De Wild.	Taylor et al. 8318 (UPS)	AJ315118/AJ719191/AJ876823
Fadogia stenophylla Hiern	Mwangoka 1742 (UPS)	-/AJ875117/AJ876824
Fadogia tetraquetra K. Krause	Bremer & Bremer 3799 (UPS)	AJ315099/AJ620139/AJ876825
Fadogia triphylla Baker	Bidgood et al. 589 (UPS)	AJ874982/AJ874944/AJ876826
Fadogia verdcourtii Tennant var. *verdcourtii*	Gereau et al. 6010 (UPS)	AJ315116/AJ620140/AJ876827
Fadogiella stigmatoloba (K. Schum) Robyns	Lawton 1318 (S)	AJ315100/AJ620141/AJ876828
Hutchinsonia barbata Robyns	Adam 20599 (UPS)	AJ315102/AJ620142/AJ876829
Lagynias dryadum (S. Moore) Robyns	Bremer & Bremer 3811 (UPS)	AJ315090/AJ620146/AJ876830
Lagynias lasiantha (Sond.) Bullock	Bremer & Bremer 3792 (UPS)	AJ315089/AJ620147/AJ876831
Lagynias monteiroi (Oliv.) Bridson	Bremer et al. 4297 (UPS)	AJ874983/AJ874945/AJ876832
Lagynias pallidiflora Bullock	Ntemi Sallu et al. 309 (UPS)	AJ874984/AJ874946/AJ876833

Table 1. (Continued)

Species	Voucher	EMBL number ITS/*trn*T-F/*rpl*16
Multidentia concrescens (Bullock) Bridson & Verdc.	Bidgood et al. 845 (K)	AJ315086/AJ620150/AJ876834
Multidentia crassa (Hiern) Bridson & Verdc.	Lantz 150 (UPS)	AJ874985/AJ874947/AJ876835
Multidentia fanshawei (Tennant) Bridson	Lovett et al. 3311 (K)	AJ315087/AJ620151/AJ876836
Multidentia sclerocarpa (K. Schum.) Bridson	Luke 9442 (UPS)	AJ874986/AJ874948/AJ876837
Pachystigma gillettii (Tennant) Verdc.	Gilbert & Thulin 128 (UPS)	AJ874987/AJ874949/AJ876838
Pachystigma latifolium Sond.	Bremer et al. 4304 (UPS)	-/AJ874950/AJ876839
Pachystigma loranthifolium (K. Schum.) Verdc.	Luke 9464 (UPS)	AJ874988/AJ874951/AJ876840
Pachystigma pygmaeum Robyns	Pawek 12335 (BR)	AJ315091/AJ620152/AJ876841
Pachystigma schumannianum (Robyns) Bridson & Verdc.	Mlangwa & Mbuso 1274 (UPS)	AJ874989/AJ874952/AJ876842
Pygmaeothamnus zeyheri (Sond.) Robyns var. *zeyheri*	Bremer et al. 4356 (UPS)	AJ617773/AJ620166/AJ876843
Robynsia glabrata Hutchinson	Hall & Amponsah 46545 (K)	AJ617774/AJ620170/-
Rytigynia adenodonta (K. Schum.) Robyns var. *reticulata* (Robyns) Verdc.	Lantz 108 (UPS)	AJ874990/AJ874953/AJ876844
Rytigynia bagshawei (S. Moore) Robyns var. *bagshawei*	Borhidi et al. 84439 (UPS)	AJ315101/AJ620171/AJ876845
Rytigynia beniensis (De Wild.) Robyns	Festo 1151 (UPS)	AJ874991/AJ874954/AJ876846
Rytigynia celastroides (Baillon) Verdc.	Mwangoka & Maingo 1514 (UPS)	AJ874992/AJ874955/AJ876847
Rytigynia decussata (K. Schum.) Robyns	Rulangaranga et al. 95 (MO)	AJ874993/AJ874956/AJ876848
Rytigynia eickii (K. Schum. & K. Krause) Bullock	Borhidi et al. 84003 (UPS)	AJ874994/AJ874957/AJ876849
Rytigynia fuscosetulosa Verdc.	Frimodt Moller et al. NG117 (K)	AJ315097/AJ620173/-
Rytigynia hirsutiflora Verdc.	Luke et al. 9189 (UPS)	AJ874995/AJ874958/AJ876850
Rytigynia induta (Bullock) Verdc.	Luke 9051 (UPS)	AJ874996/AJ874959/AJ876851
Rytigynia lichenoxenos (K. Schum.) Robyns	Luke et al. 9104 (UPS)	AJ874997/AJ874960/AJ876852
Rytigynia longicaudata Verdc.	Borhidi & Pocs 85206 (UPS)	-/AJ874961/AJ876853
Rytigynia longipedicellata Verdc.	Bidgood et al. 1577 (UPS)	-/AJ874962/AJ876854
Rytigynia monantha (K. Schum.) Robyns	Hedrén et al. 308 (UPS)	-/AJ874963/AJ876855
Rytigynia neglecta (Hiern) Robyns	Gilbert et al. 7937 (UPS)	-/AJ874964/AJ876856

Table 1. (Continued)

Species	Voucher	EMBL number ITS/*trn*T-F/*rpl*16
Rytigynia parvifolia Verdc.	Luke 8345 (UPS)	AJ874998/AJ874965/AJ876857
Rytigynia pseudolongicaudata Verdc.	Kayombo 1953 (UPS)	AJ874999/-/-
Rytigynia sambavensis Cavaco	Davis 2157 (K)	AJ875000/AJ874966/-
Rytigynia senegalensis Blume	van den Berghen 8746 (BR)	AJ315104/AJ620175/AJ876858
Rytigynia seyrigii Cavaco	Gereau et al. 5731 (MO)	AJ875001/AJ874967/-
Rytigynia sp. L of F.T.E.A.	Luke 9039 (UPS)	AJ875002/AJ874968/-
Rytigynia uhligii (K. Schum. & K. Krause) Verdc.	Borhidi et al. 84458 (UPS)	AJ875003/AJ874969/AJ876859
Rytigynia umbellulata (Hiern) Robyns	Gobbo & Gilagiza 860 (UPS)	AJ875004/AJ874970/AJ876860
Rytigynia xanthotricha (K. Schum.) Verdc.	Borhidi et al. 87353 (UPS)	AJ875005/AJ874971/AJ876861
Tapiphyllum cinerascens (Welw. ex Hiern) Robyns var. *cinerascens*	Milne-Redhead 3292 (BR)	AJ315096/AJ620177/AJ876862
Tapiphyllum obtusifolium (K. Schum.) Robyns	Gereau et al. 6669 (UPS)	AJ875006/AJ874972/AJ876863
Tapiphyllum velutinum (Hiern) Robyns	Emanuelsson 672 (S)	AJ315098/AJ620178/AJ876864
Vangueria apiculata K. Schum.	Kårehed & Odhult 161 (UPS)	AJ315095/AJ620179/AJ876865
Vangueria esculenta S. Moore	Lantz 145 (UPS)	AJ875007/AJ874973/AJ876866
Vangueria infausta Burch.	Bremer et al. 4254 (UPS)	AJ617777/AJ620180/AJ876867
Vangueria madagascariensis J. F. Gmelin	Bremer 3077 (UPS)	AJ224839/AJ620184/AJ876868
Vangueria parvifolia Sond.	Bremer & Bremer 3771 (UPS)	AJ315092/AJ620181/AJ876869
Vangueria praecox Verdc.	Luke 9357 (UPS)	AJ875008/AJ874974/AJ876870
Vangueria proschii Briq.	Blomberg et al. BMP 466 (UPS)	AJ875009/AJ874975/AJ876871
Vangueria randii S. Moore	Luke 5161 (EA)	AJ875010/AJ874976/AJ876872
Vangueria soutpansbergensis N. Hahn	Bremer et al. 4324 (UPS)	AJ875011/AJ874977/AJ876873
Vangueria volkensii K. Schum.	Borhidi et al. 85162 (UPS)	AJ875012/AJ874978/AJ876874
Vangueriopsis cf. *longiflora* Verdc.	Luke 8316 (UPS)	AJ617778/AJ620183/AJ876875

recently transferred to *Canthium* (Lantz and Bremer 2004).

Molecular methods. DNA was extracted using the CTAB method (Doyle and Doyle 1987) from herbarium material, fresh, or silica-dried material. The DNA was purified using either QiaQuick PCR purification kit (QIAGEN) or caesium chloride/ethidium bromide gradient centrifugation. PCR amplification and sequencing for the ITS and *trn*T-F region were performed as in Lantz and Bremer (2004). Amplification and sequencing of *rpl*16 were performed as for the *trn*T-F region, but used the following primers: L16exon1 (Downie et al. 2000) and 1067F (C. Asmussen; pers. comm.) for the PCR amplification and primers1067F and rpl16-18R (Asmussen 1999) for sequencing.

Phylogenetic methods. Sequences were aligned manually. Informative insertion/deletion events (indels) were coded manually using the simple method of Simmons and Ochoterena (2000). The phylogenies were constructed using parsimony with the program PAUP* (Swofford 2002). All three data sets (ITS, *trn*T-F, and *rpl*16) were run together in a combined analysis as well as separately. A chloroplast data set (*trn*T-F + *rpl*16) was also analyzed. Incongruence between the ITS and chloroplast data sets was assessed by the comparison of bootstrap values from the separate analyses.

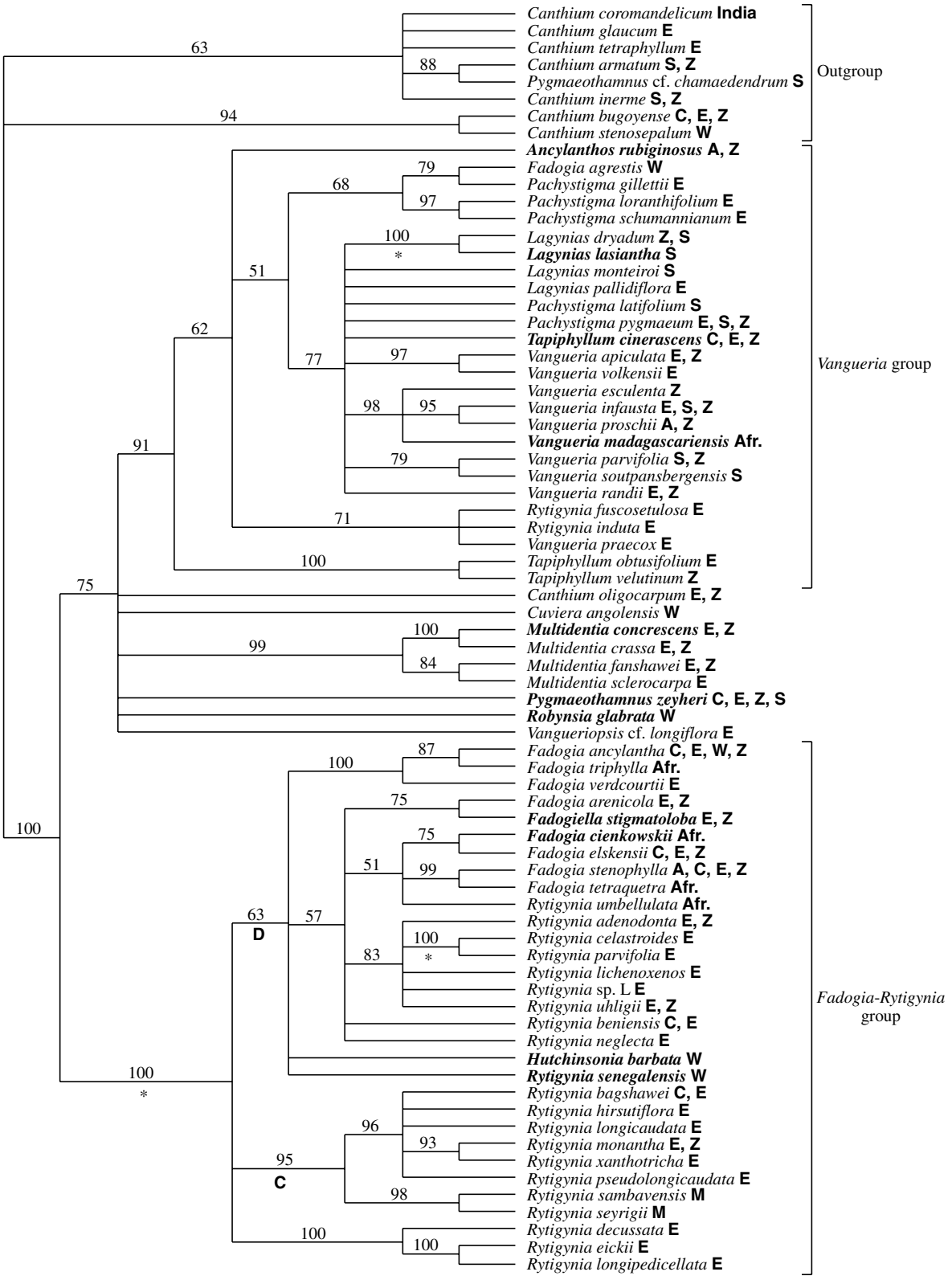

Canthium coromandelicum India
Canthium glaucum E
Canthium tetraphyllum E
Canthium armatum S, Z
Pygmaeothamnus cf. chamaedendrum S
Canthium inerme S, Z
Canthium bugoyense C, E, Z
Canthium stenosepalum W
Outgroup
Ancylanthos rubiginosus A, Z
Fadogia agrestis W
Pachystigma gillettii E
Pachystigma loranthifolium E
Pachystigma schumannianum E
Lagynias dryadum Z, S
Lagynias lasiantha S
Lagynias monteiroi S
Lagynias pallidiflora E
Pachystigma latifolium S
Pachystigma pygmaeum E, S, Z
Tapiphyllum cinerascens C, E, Z
Vangueria apiculata E, Z
Vangueria volkensii E
Vangueria esculenta Z
Vangueria infausta E, S, Z
Vangueria proschii A, Z
Vangueria madagascariensis Afr.
Vangueria parvifolia S, Z
Vangueria soutpansbergensis S
Vangueria randii E, Z
Rytigynia fuscosetulosa E
Rytigynia induta E
Vangueria praecox E
Tapiphyllum obtusifolium E
Tapiphyllum velutinum Z
Vangueria group
Canthium oligocarpum E, Z
Cuviera angolensis W
Multidentia concrescens E, Z
Multidentia crassa E, Z
Multidentia fanshawei E, Z
Multidentia sclerocarpa E
Pygmaeothamnus zeyheri C, E, Z, S
Robynsia glabrata W
Vangueriopsis cf. longiflora E
Fadogia ancylantha C, E, W, Z
Fadogia triphylla Afr.
Fadogia verdcourtii E
Fadogia arenicola E, Z
Fadogiella stigmatoloba E, Z
Fadogia cienkowskii Afr.
Fadogia elskensii C, E, Z
Fadogia stenophylla A, C, E, Z
Fadogia tetraquetra Afr.
Rytigynia umbellulata Afr.
Rytigynia adenodonta E, Z
Rytigynia celastroides E
Rytigynia parvifolia E
Rytigynia lichenoxenos E
Rytigynia sp. L E
Rytigynia uhligii E, Z
Rytigynia beniensis C, E
Rytigynia neglecta E
Hutchinsonia barbata W
Rytigynia senegalensis W
Rytigynia bagshawei C, E
Rytigynia hirsutiflora E
Rytigynia longicaudata E
Rytigynia monantha E, Z
Rytigynia xanthotricha E
Rytigynia pseudolongicaudata E
Rytigynia sambavensis M
Rytigynia seyrigii M
Rytigynia decussata E
Rytigynia eickii E
Rytigynia longipedicellata E
Fadogia-Rytigynia group
D
C

Table 2. Data set characteristics

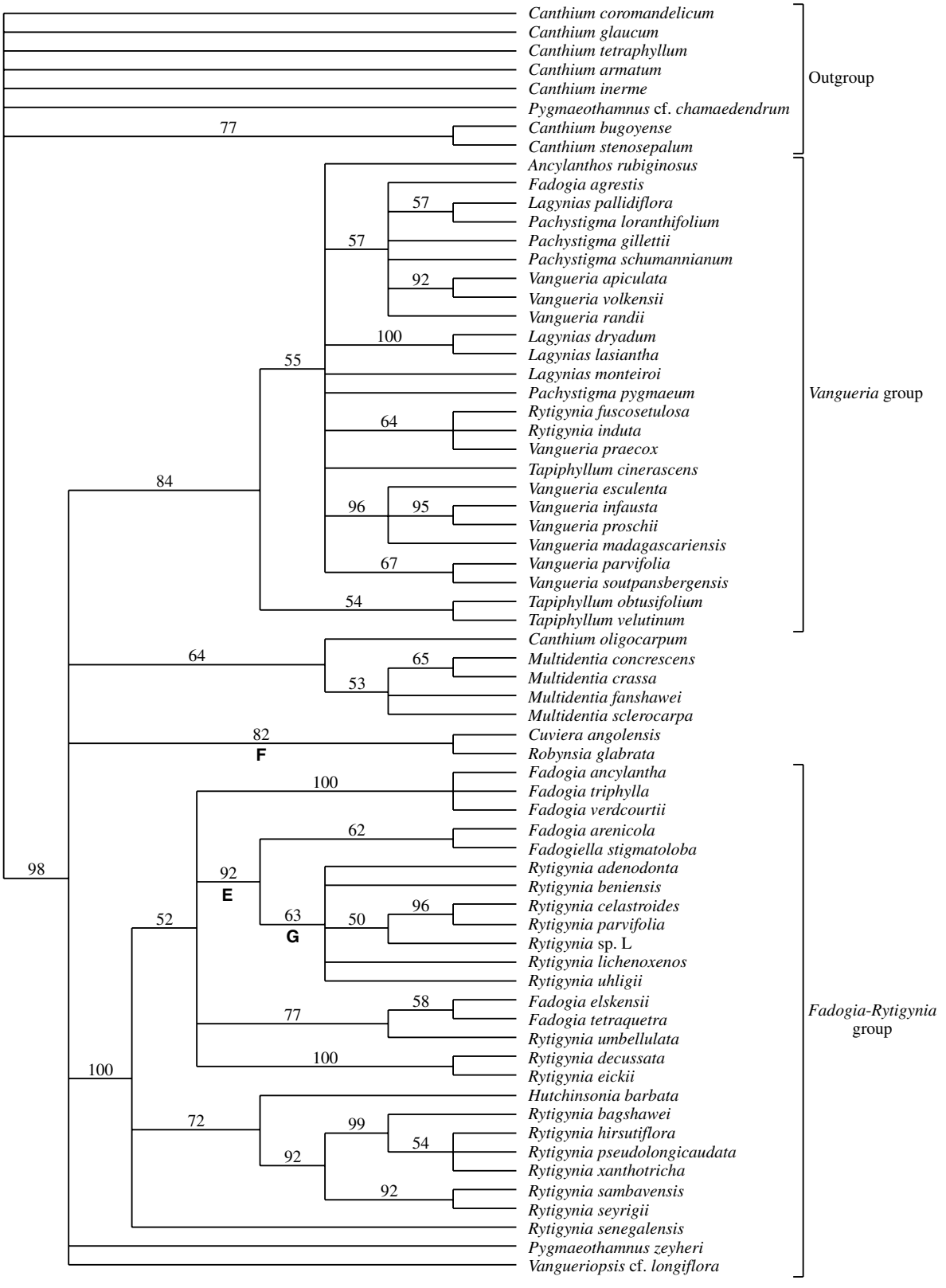
Data set	Number of taxa	Number of characters	Informative characters (including indels)	Informative indel characters
ITS	67	712	157	20
*trn*T-F	73	2096	111	22
*rpl*16	66	854	60	7
*trn*T-F + *rpl*16	73	2950	171	29
ITS + *trn*T-F + *rpl*16	74	3662	328	49
ITS + *trn*T-F + *rpl*16, incongruent taxa removed	69	3662	311	46

When strongly incongruent taxa had been identified (see results), all data sets were analyzed again but with the incongruent taxa removed. A heuristic search with 100 random addition replicates and TBR branch-swapping was performed to find the most parsimonious trees. Support was measured by the bootstrap option as implemented by PAUP* using 10000 bootstrap replicates, each with 5 random addition replicates, TBR branch-swapping and MULTREES off.

Results

The number of taxa, total number of characters, number of informative characters, and number of indel-characters for each of the six data sets are presented in Table 2. We were unable to get ITS sequences for seven species, *trn*T-F sequences for one species, and *rpl*16 sequences for eight species (Table 1). The ITS data set has the highest number of informative characters followed by *trn*T-F, and *rpl*16. The comparison is, however, likely influenced by the uneven sample sizes of the different data sets. About half of the informative characters stem from the ITS data set. For all of the analyses, the number of most parsimonious trees was too large to be saved and the analyses did not run to completion. We therefore choose to present the majority rule consensus trees from the bootstrap analyses. Results from four of the analyses are presented; the combined analysis (ITS + *trn*T-F + *rpl*16; Fig. 1), ITS (Fig. 2), the chloroplast tree (*trn*T-F + *rpl*16; Fig. 3), and a combined analysis with strongly incongruent taxa removed (Fig. 4). We found no cases of topological incongruence between the phylogenies based on the *trn*T-F and *rpl*16 data sets (results not

Fig. 1. Majority rule consensus tree from the bootstrap analysis of the combined (ITS + *trn*T-F + *rpl*16) data set. Bootstrap support ≥50 is included above nodes. Letters in the tree refer to clades discussed in the text. Letters added after the taxa names indicate geographical distribution (see material and methods), i.e. *Afr.* = Subsaharan Africa, *A* = Angola with Namibia, *C* = Central Africa, *E* = East Africa, *M* = Madagascar, *S* = South Africa, *Z* = Zambia with Botzwana, Malawi, Mozambique, and Zimbabwe (Zambesian distribution), *W* = West Africa. Types of genera are indicated in **bold**. Clades which receive strong support both from the plastid and nuclear data sets are indicated by an *


Canthium coromandelicum
Canthium glaucum
Canthium tetraphyllum
Canthium armatum
Canthium inerme
Pygmaeothamnus cf. chamaedendrum
Canthium bugoyense
Canthium stenosepalum
Outgroup
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Pachystigma loranthifolium
Pachystigma gillettii
Pachystigma schumannianum
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Vangueria randii
Lagynias dryadum
Lagynias lasiantha
Lagynias monteiroi
Pachystigma pygmaeum
Rytigynia fuscosetulosa
Rytigynia induta
Vangueria praecox
Tapiphyllum cinerascens
Vangueria esculenta
Vangueria infausta
Vangueria proschii
Vangueria madagascariensis
Vangueria parvifolia
Vangueria soutpansbergensis
Tapiphyllum obtusifolium
Tapiphyllum velutinum
Vangueria group
Canthium oligocarpum
Multidentia concrescens
Multidentia crassa
Multidentia fanshawei
Multidentia sclerocarpa
Cuviera angolensis
Robynsia glabrata
F
Fadogia ancylantha
Fadogia triphylla
Fadogia verdcourtii
Fadogia arenicola
Fadogiella stigmatoloba
Rytigynia adenodonta
Rytigynia beniensis
Rytigynia celastroides
Rytigynia parvifolia
Rytigynia sp. L
Rytigynia lichenoxenos
Rytigynia uhligii
Fadogia elskensii
Fadogia tetraquetra
Rytigynia umbellulata
Rytigynia decussata
Rytigynia eickii
E
G
Hutchinsonia barbata
Rytigynia bagshawei
Rytigynia hirsutiflora
Rytigynia pseudolongicaudata
Rytigynia xanthotricha
Rytigynia sambavensis
Rytigynia seyrigii
Rytigynia senegalensis
Pygmaeothamnus zeyheri
Vangueriopsis cf. longiflora
Fadogia-Rytigynia group

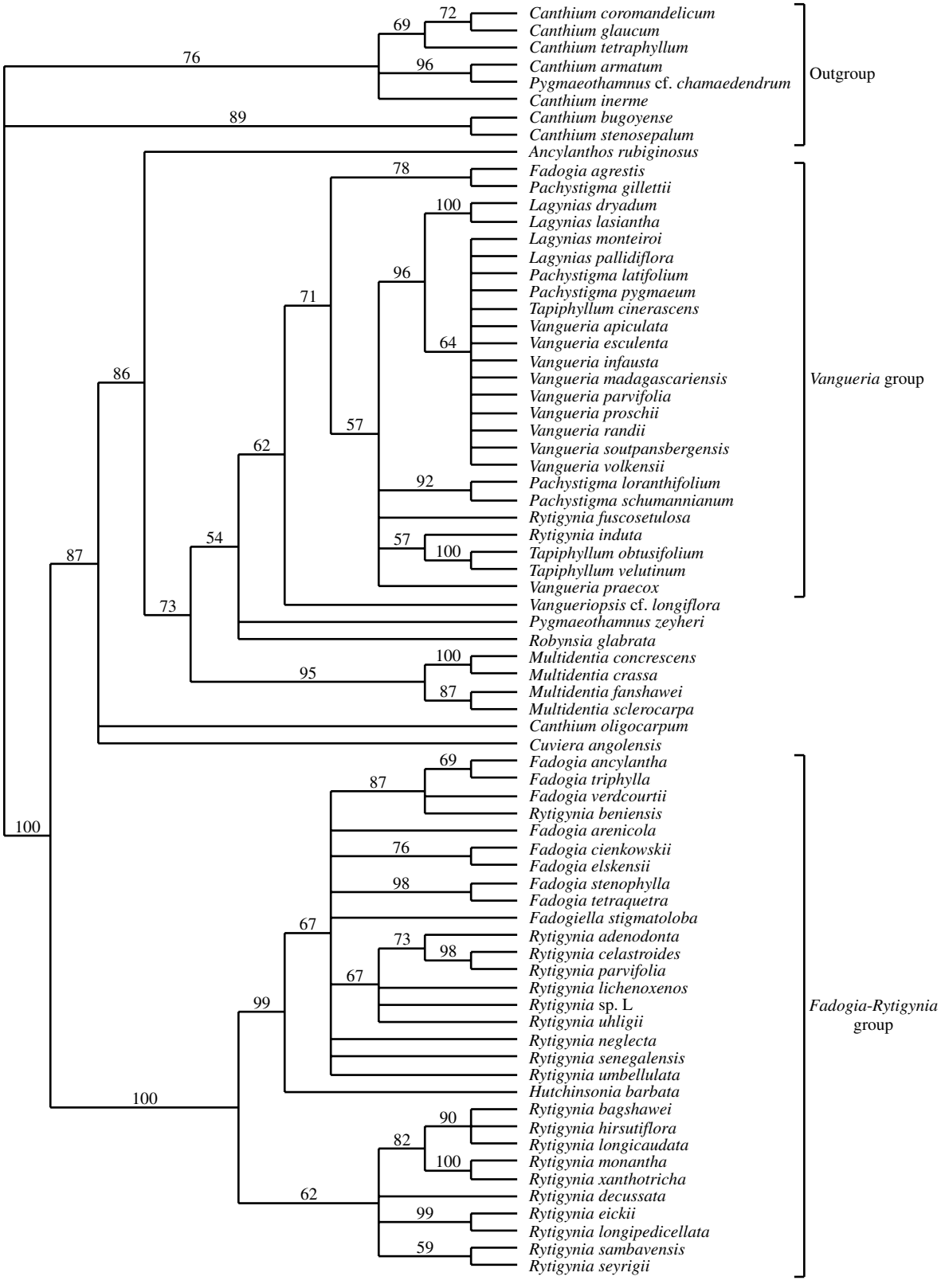
shown). Since both genes are from the plastid genome they are likely to share the same evolutionary history. We therefore combined the two data sets into a single chloroplast data set and only present the results from the bootstrap analysis of this data set. Compared to the phylogenies of the individual (*trn*T-F and *rpl*16) data sets, the combined chloroplast tree has both increased resolution and support.

There are strongly supported clades in all presented phylogenies. Comparing the ITS and chloroplast phylogenies, both include a similar number of strongly supported clades (above 90% bootstrap), but only in three instances are clades supported strongly from both data sets (see Fig. 1). Comparisons are, however, made difficult by the uneven sample sizes of the chloroplast and ITS data sets. This is especially true in the *Fadogia-Rytigynia* group in which seven taxa are present in only one of the data sets (Table 1). There are also several cases of incongruence in the comparison between the ITS and chloroplast phylogenies. Most incongruencies are weakly supported (e.g. the position of *Rytigynia induta*), but there are some that are more strongly supported, i.e. situations where a strongly supported node in one of the phylogenies is contradicted by an at least moderately supported node in the other. In the *Fadogia-Rytigynia* group the positions of *Hutchinsonia barbata*, *Rytigynia beniensis*, and the clade consisting of *R. decussata* and *R. eickii* are strongly incongruent. In the *Vangueria* group, no taxon is strongly incongruent as defined above, but *Ancylanthos rubiginosus* has significantly different positions in the two trees. In the ITS tree, *Ancylanthos rubiginosus* has an internal position in the group, but is in the chloroplast tree sister to a clade consisting not only of the other members of the *Vangueria* group but also *Multidentia*, *Pygmaeothamnus*, *Robynsia*, and *Vangueriopsis*.

Cases where taxa have an unresolved position in one of the phylogenies and a resolved in the other (e.g. the positions of *Cuviera angolensis* and *Robynsia glabrata*) could possibly be influenced by incongruence, but the unresolved position in one of the phylogenies makes any comparisons uninformative. Of more importance are strongly supported nodes which collapse when the data sets are combined. In the *Vangueria* group, no strongly supported clades present in the chloroplast or ITS phylogenies collapse in the combined phylogeny, although clade A (Figs. 3 and 4) is more strongly supported (bp = 96) in the chloroplast phylogeny than in the combined phylogeny (bp = 79), indicating some conflict. Of greater concern are the strongly supported clades present in the ITS phylogeny for a clade in the *Fadogia-Rytigynia* group (clade E; Fig. 2) and the moderately supported clade of *Cuviera* and *Robynsia* (clade F; Fig. 2) that collapses in the combined phylogeny (Fig. 1). These clades are not present in the chloroplast phylogeny (Fig. 3) and the incongruence can therefore not be attributed to a single taxon or a single clade such as in the above mentioned examples.

After we identified *Ancylanthos rubiginosus*, *Hutchinsonia barbata*, *Rytigynia beniensis*, *R. decussata*, and *R. eickii* as strongly incongruent, these taxa were removed from further analyses (results only shown for the combined data set with incongruent taxa removed; Fig. 4). Comparing the results from the combined analyses with incongruent taxa included or excluded (Fig. 1 and Fig. 4 resp.), little was changed in the phylogeny for the *Vangueria* group, although the support for the node separating the clade consisting of *Tapiphyllum obtusifolium* and *T. velutinum* from the other taxa in the group was increased from 62 to 85 and the support for the *Vangueria* group from 91 to 99. In the *Fadogia-Rytigynia* group the

Fig. 2. Majority rule consensus tree from the bootstrap analysis of the ITS data set. Bootstrap support ≥ 50 is included above nodes. Letters in the tree refer to clades discussed in the text


Canthium coromandelicum
Canthium glaucum
Canthium tetraphyllum
Canthium armatum
Pygmaeothamnus cf. chamaedendrum
Canthium inerme
Canthium bugoyense
Canthium stenosepalum
Outgroup
Ancylanthos rubiginosus
Fadogia agrestis
Pachystigma gillettii
Lagynias dryadum
Lagynias lasiantha
Lagynias monteiroi
Lagynias pallidiflora
Pachystigma latifolium
Pachystigma pygmaeum
Tapiphyllum cinerascens
Vangueria apiculata
Vangueria esculenta
Vangueria infausta
Vangueria madagascariensis
Vangueria parvifolia
Vangueria proschii
Vangueria randii
Vangueria soutpansbergensis
Vangueria volkensii
Pachystigma loranthifolium
Pachystigma schumannianum
Rytigynia fuscosetulosa
Rytigynia induta
Tapiphyllum obtusifolium
Tapiphyllum velutinum
Vangueria praecox
Vangueria group
Vangueriopsis cf. longiflora
Pygmaeothamnus zeyheri
Robynsia glabrata
Multidentia concrescens
Multidentia crassa
Multidentia fanshawei
Multidentia sclerocarpa
Canthium oligocarpum
Cuviera angolensis
Fadogia ancylantha
Fadogia triphylla
Fadogia verdcourtii
Rytigynia beniensis
Fadogia arenicola
Fadogia cienkowskii
Fadogia elskensii
Fadogia stenophylla
Fadogia tetraquetra
Fadogiella stigmatoloba
Rytigynia adenodonta
Rytigynia celastroides
Rytigynia parvifolia
Rytigynia lichenoxenos
Rytigynia sp. L
Rytigynia uhligii
Rytigynia neglecta
Rytigynia senegalensis
Rytigynia umbellulata
Hutchinsonia barbata
Rytigynia bagshawei
Rytigynia hirsutiflora
Rytigynia longicaudata
Rytigynia monantha
Rytigynia xanthotricha
Rytigynia decussata
Rytigynia eickii
Rytigynia longipedicellata
Rytigynia sambavensis
Rytigynia seyrigii
Fadogia-Rytigynia group

changes in support and resolution were more significant to the point of making comparisons difficult. However, a clade of *Rytigynia* species where all but *R. seyrigii* have long appendages on the corolla lobes (clade C; Figs. 1 and 4) is supported in both phylogenies, but the support is lowered from 95 to 57 when the incongruent taxa are removed. The large clade in which *Hutchinsonia* is included (clade D; Fig. 1) has weak support (63), but this is increased to 95 (clade D; Fig. 4) when the incongruent taxa are removed, although these two clades are not identical and the results are possibly influenced not only by incongruence but also by sampling effects.

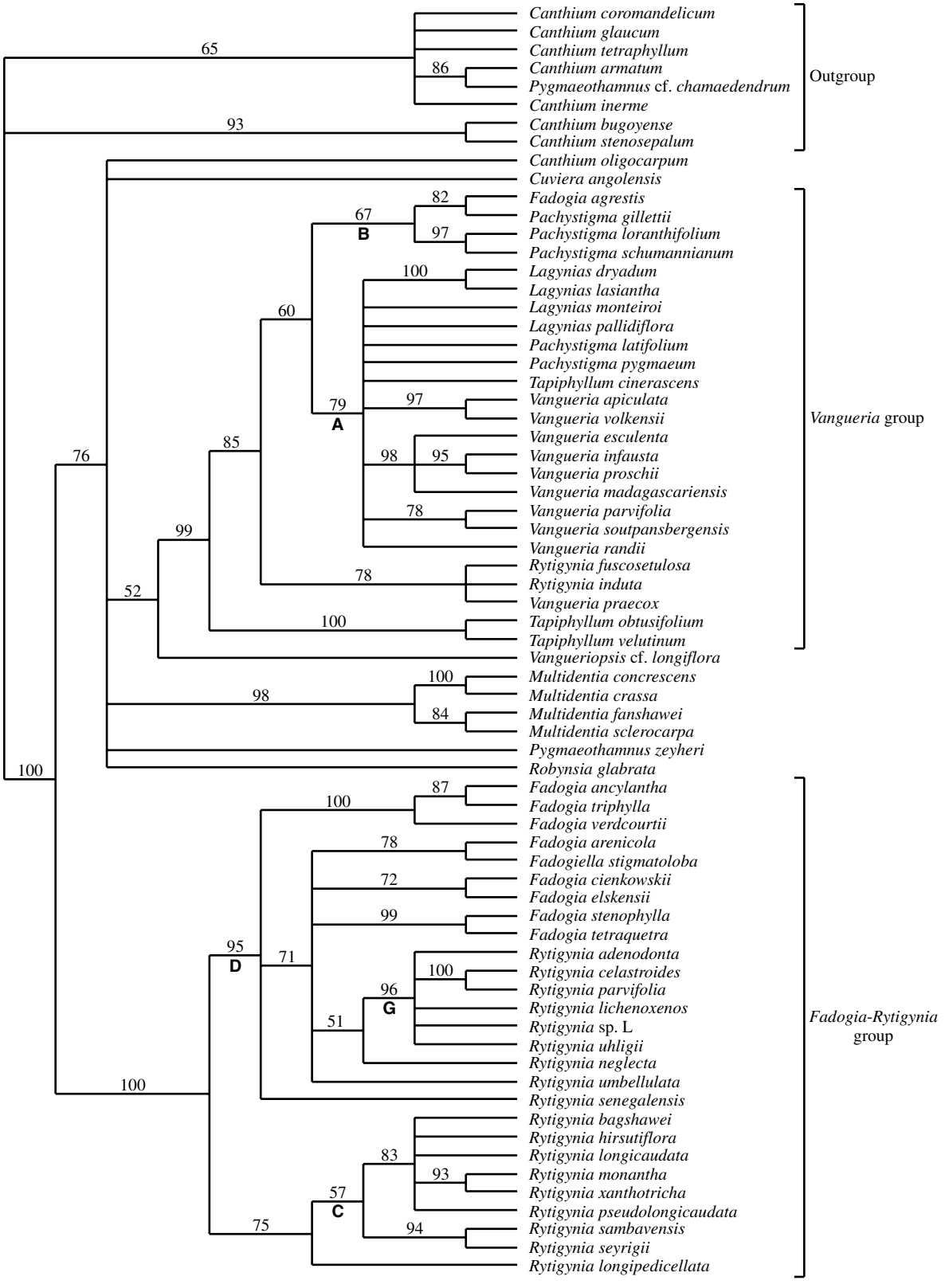
Comparing the phylogenies based on the individual data sets with and without incongruent taxa (results only shown for phylogenies with incongruent taxa included; Figs. 2 and 3), only minor changes in support occur by the removal of taxa for nodes at which the incongruent taxa were not attached, and comparisons of support can equally well be done with the incongruent taxa included (Figs. 2 and 3).

The *Vangueria* group as circumscribed by Lantz and Bremer (2004) is supported in the ITS and combined phylogenies but not in the chloroplast phylogeny due to the incongruent position of *Ancylanthos rubiginosus*. The *Fadogia-Rytigynia* group is strongly supported in all trees. In the chloroplast phylogeny (Fig. 3), the clade is sister to a clade consisting of all other taxa, and this result is also favoured by the combined analyses, but is unresolved in the ITS phylogeny (Fig. 2). *Rytigynia* and *Fadogia* are polyphyletic in all four phylogenies and there are indications that this is true also for *Pachystigma*, *Tapiphyllum* and *Vangueria*. *Pygmaeothamnus* is present both in the outgroup and in the ingroup and is thus also polyphyletic, but this has been discussed elsewhere (Lantz and Bremer 2004) and will not be investigated in detail here. Within the *Fadogia-Rytigynia* group the situation is complex. The taxa with incongruent positions and the low supported or unresolved nodes hamper our ability to draw conclusions, but *Fadogia* and *Rytigynia* are not supported as monophyletic in any of the trees. *Multidentia* is the only genus which is monophyletic in all four phylogenies, although with weak support in the ITS phylogeny.

Discussion

We will divide the discussion into two major parts. In the first part we discuss the results of the phylogenetic analyses. Morphological characters of importance for the delimitation of the clades and genera are also discussed, but we restrict the discussion to characters found to be informative in Lantz and Bremer (2004). In the second part we try to explain the incongruencies noticed in the comparisons between the individual analyses. We base our discussion on the phylogeny in which the strongly incongruent taxa have been removed (Fig. 4), unless otherwise noted. This phylogeny exhibits increased support and resolution in comparison to the analyses based on the individual data sets. Although the taxa with most strongly incongruent positions have been removed, it is possible that the phylogeny still is influenced by incongruence. Indeed, in two cases did the combination of data sets with taxa removed result in significantly lowered bootstrap support for a node, indicating conflicting phylogenetic signals. With this in mind, we refrain from making changes to the classification in situations not unequivocally supported by all data sets, unless support from morphology can corroborate any of the phylogenies. We often choose to use the term

Fig. 3. Majority rule consensus tree from the bootstrap analysis of the chloroplast (*trn*T-F + *rpl*16) data set. Bootstrap support ≥ 50 is included above nodes. Letters in the tree refer to clades discussed in the text. *Ancylanthos rubiginosus* is supported as a member of the *Vangueria* group in the ITS and combined trees (Figs. 1, 2, and 4)


Canthium coromandelicum
Canthium glaucum
Canthium tetraphyllum
Canthium armatum
Pygmaeothamnus cf. chamaedendrum
Canthium inerme
Canthium bugoyense
Canthium stenosepalum
Outgroup
Canthium oligocarpum
Cuviera angolensis
Fadogia agrestis
Pachystigma gillettii
Pachystigma loranthifolium
Pachystigma schumannianum
Lagynias dryadum
Lagynias lasiantha
Lagynias monteiroi
Lagynias pallidiflora
Pachystigma latifolium
Pachystigma pygmaeum
Tapiphyllum cinerascens
Vangueria apiculata
Vangueria volkensii
Vangueria esculenta
Vangueria infausta
Vangueria proschii
Vangueria madagascariensis
Vangueria parvifolia
Vangueria soutpansbergensis
Vangueria randii
Rytigynia fuscosetulosa
Rytigynia induta
Vangueria praecox
Tapiphyllum obtusifolium
Tapiphyllum velutinum
Vangueriopsis cf. longiflora
Vangueria group
Multidentia concrescens
Multidentia crassa
Multidentia fanshawei
Multidentia sclerocarpa
Pygmaeothamnus zeyheri
Robynsia glabrata
Fadogia ancylantha
Fadogia triphylla
Fadogia verdcourtii
Fadogia arenicola
Fadogiella stigmatoloba
Fadogia cienkowskii
Fadogia elskensii
Fadogia stenophylla
Fadogia tetraquetra
Rytigynia adenodonta
Rytigynia celastroides
Rytigynia parvifolia
Rytigynia lichenoxenos
Rytigynia sp. L
Rytigynia uhligii
Rytigynia neglecta
Rytigynia umbellulata
Rytigynia senegalensis
Rytigynia bagshawei
Rytigynia hirsutiflora
Rytigynia longicaudata
Rytigynia monantha
Rytigynia xanthotricha
Rytigynia pseudolongicaudata
Rytigynia sambavensis
Rytigynia seyrigii
Rytigynia longipedicellata
Fadogia-Rytigynia group
A
B
C
D
G

'incongruent taxon/taxa' rather than the bulkier but more correct 'taxon/taxa with incongruent positions' fully aware of the fact that a taxon (when represented by a single terminal) cannot be incongruent in itself, but prefer the shorter, less cumbersome term.

The *Vangueria* group. This group was first identified in Lantz et al. (2002) and also investigated in Lantz and Bremer (2004). *Lagynias*, *Pachystigma*, *Tapiphyllum*, *Vangueria*, and one species of *Rytigynia*, *R. fuscosetulosa*, were identified as belonging to this clade, and also *Ancylanthos rubiginosus*, but with some hesitation due to the incongruent positions for this taxon supported by the plastid and nuclear data sets. All of these genera have plurilocular ovaries, a character traditionally used to distinguish between *Vangueria* and the bilocular genus *Canthium*, the two first described genera in the tribe. The group is identical to 'Gattungskomplex *Vangueria'* suggested by Igersheim (1989) with the exception of *R. fuscosetulosa*. In the present study, the ITS and chloroplast phylogenies support a similar circumscription of the *Vangueria* group, with the exception of *Ancylanthos rubiginosus*. Of the two possible positions for *A. rubiginosus* suggested by the ITS and chloroplast phylogenies, the internal position in the *Vangueria* group seen in the ITS phylogeny is better supported by morphology. Also in the *Vangueria* group are *Pachystigma pygmaeum* and *Tapiphyllum cinerascens*. All three are geofrutices and sometimes have ternate leaves, and both *A. rubiginosus* and *T. cinerascens* have short, stiff external indumentum on the corollas. Geofrutescent habit and ternate leaves are otherwise rare features in the *Vangueria* group, but external indumentum on the corollas is more common (e.g. Bridson 1998). The inclusion of *Ancylanthos* in the *Vangueria* group is thus supported by morphology and by the ITS phylogeny. To conclude, we consider the *Vangueria* group to comprise the genera *Ancylanthos*, *Lagynias*, *Pachystigma*, *Tapiphyllum*, *Vangueria*, and the three species *Fadogia agrestis*, *Rytigynia fuscosetulosa,* and *R. induta*.

Nine of the included *Vangueria* species, all in subgenus *Vangueria*, form a moderately supported clade (A; Fig. 4) together with four species of *Lagynias, Pachystigma latifolium*, *P. pygmaeum*, and *Tapiphyllum cinerascens*. A tenth species, *V. praecox*, tentatively included in *Vangueria* and the single member of subgenus *Itigi* (Verdcourt 1981), instead forms a clade with *Rytigynia fuscosetulosa* and *R. induta* at a more basal position in the *Vangueria* group. *Vangueria* subgenus *Vangueria* has traditionally been recognized by a combination of large leaves and lax many-flowered inflorescences, but is in the most recent circumscription (Verdcourt 1981, Bridson 1998) morphologically heterogeneous. *Vangueria parvifolia* and *V. soutpansbergensis* both have small leaves and few-flowered, shortly pedunculate and dense inflorescences and form a moderately supported clade in the combined phylogeny (Fig. 4). *Vangueria parvifolia* was earlier included in *Tapiphyllum* but was found to be atypical of that genus and was transferred (Bridson 1998) shortly after the morphologically similar South African endemic *V. soutpansbergensis* was described (Hahn 1997). Two other clades formed by the *Vangueria* species are well delimited by type of calyx lobes, a character earlier suggested to be of importance in the classification of *Vangueria* (Bridson 1998). The type species *V. madagascariensis* forms a strongly supported clade together with *V. esculenta*, *V. infausta*, and *V. proschii*, all of which have triangular to narrowly oblong calyx lobes. *Vangueria apiculata* and *V. volkensii*, both with narrowly oblong to linear calyx lobes, group together with strong support. Surprisingly *V. randii*, a

Fig. 4. Majority rule consensus tree from the bootstrap analysis of the combined data set (ITS + *trn*T-F + *rpl*16) with putative hybrids removed. Bootstrap support ≥ 50 is included above nodes. Letters in the tree refer to clades discussed in the text

third species with similar elongate calyx lobes, does not group with these species but has an unresolved position in the same clade. *Lagynias* is a genus of five species distributed in eastern and southern Africa characterized by well-developed often oblong or narrowly obovate calyx lobes and usually reflexed corolla lobes in the mature flower (Bullock 1931). Two species of *Lagynias*, *L. dryadum* and *L. lasiantha*, form a strongly supported group, but *Lagynias* as a genus is not supported as monophyletic. *Tapiphyllum cinerascens* is a highly variable species (Verdcourt and Bridson 1991) which in the phylogeny (Fig. 4) is distanced from the two other included species of *Tapiphyllum*. The genus is considered ill-defined (Bridson 1998) and is diagnosed principally by a thick indumentum, dense inflorescences, and mostly elongate calyx lobes.

Sister to the clade including most of the *Vangueria* species (clade A; Fig. 4) is a weakly supported clade (B; Fig. 4) consisting of three species of *Pachystigma* and one representative of *Fadogia*, *F. agrestis*. *Pachystigma* is thus represented in two clades, a division supported by type of habit. *Pachystigma latifolium* and *P. pygmaeum* are both geofrutices while the three other species are shrubs or small trees. *Fadogia agrestis* is a West African species obviously misplaced in *Fadogia*, differing from the species of *Fadogia* present in the *Fadogia-Rytigynia* group by its large ovate to triangular calyx lobes and consistently paired leaves. As shown by the phylogeny and also supported by morphology, *Pachystigma* contains smaller groups of closely related species, but is as a genus united by little but an absence of the characters used to delimit *Tapiphyllum* and *Vangueria*. The problematic circumscription of the genus has also been discussed elsewhere (e.g. Verdcourt 1981, Bridson 1996).

The already mentioned clade of *Rytigynia fuscosetulosa*, *R. induta*, and *Vangueria praecox* is interesting in that all three species were tentatively included in their genera, but a close relationship between the three has never been proposed. *Rytigynia fuscosetulosa* is a member of the small (two species) subgenus *Sali* (Verdcourt 1987, Verdcourt and Bridson 1991) and was when described mentioned as intermediate between several genera and with pyrenes similar to *Vangueria* (Verdcourt 1981). *Rytigynia induta* has been suggested to be misplaced in the genus (D. Bridson, pers. comm.) and *Vangueria praecox* was tentatively included in *Vangueria* (Verdcourt 1981). All three species have few-flowered and shortly pedunculate inflorescences, but this is not unknown from other species in the *Vangueria* group (e.g. *Vangueria parvifolia* and *V. soutpansbergensis*) and we can find no unique morphological synapomorphy for the clade.

Two species of *Tapiphyllum* form a strongly supported clade as sister to the other taxa of the *Vangueria* group. *Tapiphyllum obtusifolium* is restricted to Tanzania and *T. velutinum* has a Zambesian distribution. These species are both shrubs or small trees in contrast to the type species of *Tapiphyllum*, the geofrutex *T. cinerascens* (clade B; Fig. 4). They otherwise share a number of features with *T. cinerascens* such as a thick indumentum on the leaves, dense inflorescences, and elongate often linear calyx lobes, and would based on morphology be suspected to be more closely related.

None of the genera in the *Vangueria* group are supported as monophyletic, and indeed, the weak internal nodes in the clade do not either enable us to tell with certainty if the genera are paraphyletic or polyphyletic. However, there are indications that *Pachystigma*, *Tapiphyllum*, and *Vangueria* are not monophyletic. Moreover, there is little morphological support for the current circumscriptions of the genera. The genera are not homogeneous in their current circumscriptions. All genera include groups of species clearly closely related but there are also a number of species often tentatively included and clearly dissimilar from the other species. These are also quite often intermediate in generic characters. The here included *Vangueria parvifolia* and *V. soutpansbergensis*, or *Lagynias monteiroi*, are examples of such species but there are more we have not

been able to include such as *Tapiphyllum schliebenii* Verdc., a species of *Tapiphyllum* with lax inflorescences. With the addition of two species currently included in *Rytigynia* and one in *Fadogia*, as discussed earlier, the generic characters of the genera in the *Vangueria* group break down even further. The problematic circumscription of these genera has also been noted by other authors. Verdcourt (1981) wrote (about *Pachystigma*) 'There are no constant technical characters to distinguish it from *Vangueria* save facies.'. He goes on to state that '*Tapiphyllum* is no more than a velvety *Pachystigma* and some South African species are certainly intermediate in character…'. Bridson (1996) noted in the discussion on *Ancylanthos monteiroi* Oliv. (now *Lagynias monteiroi* (Oliv.) Bridson) that 'The distinction between *Pachystigma* and *Lagynias* is in need of clarification…'. We agree with these views and consider a new classification for the genera in the *Vangueria* group to be desirable. The best solution is to consider the whole *Vangueria* group as one genus; a classification that receives support both from the phylogeny and from morphological characters. *Vangueria* is the oldest name in the group (Jussieu 1789), and would have priority. With the exception of *Ancylanthos*, this clade is present in all phylogenies. An alternative solution would be to recognize the smaller clades present (i.e. A, B etc; Fig. 4) as genera, but these clades are likely to change with the addition of new species and we are also unable to find morphological support for any of the clades. *Vangueria* in this new sense is recognized by a combination of the following characters: domatia rarely present, inflorescences usually borne at nodes from which the leaves have fallen, bracteoles small (present on secondary branches, usually not more than 1 mm in length), smooth retrorse hairs in the corolla (Lantz and Bremer 2004), and large fruits (above 1 cm in length) with 3 to 5 locules. This combination of characters is not known from any other currently recognised genus in the tribe and will greatly facilitate the identification of Vanguerieae genera. Below, we make combinations at the genus level and also at the species level for all currently recognised species.

The *Fadogia-Rytigynia* group. This group was identified by Lantz et al. (2002), and is identical in circumscription to 'Gattungskomplex *Rytigynia'* suggested by Igersheim (1989) on morphological grounds. For this group there exists no conflict as regards the circumscription, it is strongly supported in all phylogenies (Figs. 1, 2, 3, and 4). Internally however, the phylogeny is strongly affected by incongruence between the chloroplast and ITS data sets as enumerated above. The great extent of these incongruencies greatly hinders our ability to draw conclusions about the phylogeny of the group. We can, however, make comparisons with morphology and see to which extent the phylogenies support the current classification. As a general rule, the *Fadogia-Rytigynia* group can be distinguished from the *Vangueria* group or any of the other genera in the large-flowered clade by a presence of domatia and a calyx without or with poorly developed calyx lobes, although this rule is not without exceptions.

None of the included genera are supported as monophyletic in any of the phylogenies, but the small genera *Fadogiella* (three species) and *Hutchinsonia* (two species) are both sampled by one species each and we are thus unable to test the monophyly of these genera. *Fadogiella stigmatoloba* was in an earlier analysis with a smaller sample (Lantz et al. 2002) nested within *Fadogia*, but this result is not corroborated here. It groups with *Fadogia arenicola* with weak support in the ITS and combined analysis, a position supported by the thick indumentum of both species. *Hutchinsonia* is morphologically close to *Rytigynia* and is mainly distinguished by its long and slender corolla tubes. *Fadogia* and *Rytigynia* are the two largest genera in the group, both comprising at least 50 species. *Fadogia* is diagnosed by a geofrutescent habit and leaves at least sometimes in whorls of three (or more). *Rytigynia* is much harder to diagnose and is recognized mainly by a shrubby habit and

absence of the characters typical of the genera in the *Vangueria* group or *Fadogia*. As shown here, and earlier (Lantz et al. 2002, Lantz and Bremer 2004), *Rytigynia* is polyphyletic with species included also in the spiny group (the present outgroup) and in the *Vangueria*-group. The majority of the currently recognized species in *Rytigynia* belong in the *Fadogia-Rytigynia* group and we consider these to constitute *Rytigynia* s. str. The characters most useful to distinguish between *Rytigynia* s.str. and the species incorrectly included in *Rytigynia* (such as the here sampled *R. fuscosetulosa* and *R. induta*) is the development of the calyx lobes and the size of the fruits. *Rytigynia* s. str. has a truncate or very shortly toothed calyx and fruits rarely more than 10 mm in diameter. *Rytigynia induta* has short calyx lobes and is in many ways morphologically similar to *Rytigynia* s. str. but has much larger fruits (20 mm in diameter compared to usually below 10 mm). *R. fuscosetulosa* has elongate calyx lobes. As often is the case in Vanguerieae, even distantly related species can be closely similar morphologically and it is only with the aid of a phylogeny the distinguishing characters can be found.

A clade consisting of *Fadogia ancylantha*, *F. triphylla*, and *F. verdcourtii* is consistently recovered in all phylogenies although with the addition of *Rytigynia beniensis* in the chloroplast phylogeny. All three *Fadogia* species have corollas of 5 mm or more and have in contrast to the other included species of *Fadogia* sometimes paired leaves, especially on the younger parts of the branches. This character has not been considered of importance earlier, but is strongly supported here. *Fadogiella stigmatoloba* is the only geofrutex sampled here which otherwise has both paired or whorled leaves. *Rytigynia beniensis* does not share any of these characters or any other characters used to delimit *Fadogia*. The ITS phylogeny groups *R. beniensis* with several species of *Rytigynia* in a weakly supported clade (clade G; Fig. 1), a position much better supported by morphology. Also included in the same clade is *R. celastroides*, a species which shares the rare character branches sometimes in whorls of three with *R. beniensis*. However, *R. umbellulata*, considered very close to *R. beniensis* (Verdcourt 1987), instead forms a moderately supported clade with *Fadogia elskensii* and *F. tetraquetra* in the same phylogeny. The two *Fadogia* species are considered close (Verdcourt 1981) but the relationship with *R. umbellulata* is quite unexpected. In the combined analysis (Fig. 4) *F. tetraquetra* groups with *F. stenophylla* with strong support, *F. elskensii* forms a moderately supported clade with *F. cienkowskii*, and *R. umbellulata* has unresolved position in a moderately supported clade. *Fadogia cienkowskii* and *F. stenophylla* were, however, not sequenced for ITS. The clade in which *R. beniensis* was supported to belong by the ITS phylogeny receives strong support in both of the combined analyses (clade G; Figs. 1 and 4), and the support is strongest when the incongruent taxa are not included (Fig. 4). None of the taxa in the clade have long appendages (over 2 mm) on the corolla lobes, a character otherwise common in another clade (C; Fig. 4). Appendages are also missing from *R. longipedicellata*, *R. neglecta*, *R. senegalensis*, *R. umbellulata*, and two of the taxa identified as strongly incongruent, *R. decussata* and *R. eickii*. *Rytigynia longipedicellata* is morphologically similar to *R. eickii*, and forms a strongly supported clade with this species in the chloroplast phylogeny (Fig. 3), but was not sequenced for ITS and the position in the combined phylogeny (Fig. 4) as sister to the clade with long appendages is thus only based on chloroplast data. *Hutchinsonia barbata* also has appendages on the corolla lobes and the position indicated by the ITS phylogeny (Fig. 2) is thus better supported by morphology. The two Malagasy specimens *R. sambavensis* and *R. seyrigii* group together in all phylogenies, but only with weak support in the chloroplast phylogeny. The clade is strongly supported as sister to the other taxa in the appendaged clade by the combined phylogeny with incongruent taxa included (Fig. 1), but this support is greatly decreased when the incongruent taxa

are removed (Fig. 4). In the combined analysis with incongruent taxa removed, the *Fadogia-Rytigynia* group is divided into two clades, one of which is strongly supported (clade D; Fig. 4. Apart from the partial congruence with presence or absence of appendages on the corolla lobes, we see little support for this division from morphology.

We can thus find morphological support for clades present in both the chloroplast and ITS phylogenies and none of the two phylogenies agree with morphology better than the other. The widespread incongruence for these genera puts all phylogenies in some doubt, and we are not prepared to make any changes to the classification. The phylogenies do not enable us to present any classification which would result in monophyletic and unequivocally supported genera. In addition, several of the strongly supported clades lack morphological support. The inclusion of the whole clade in one genus would result in a monophyletic but morphologically heterogeneous genus. At this point, when a number of the currently recognized species are poorly known, especially those occurring in West and Central Africa, we prefer to stress the morphological and geographical variation present within the group by retaining the genera rather than hide it within one very large genus.

Other genera in the large-flowered group. In the chloroplast and combined phylogenies, *Canthium oligocarpum*, *Cuviera*, *Multidentia*, *Pygmaeothamnus zeyheri*, *Robynsia*, and *Vangueriopsis* form a weakly to moderately supported clade together with the *Vangueria* group as sister to the *Fadogia-Rytigynia* group. Their relationships to the *Vangueria* group or to each other are however weakly supported. The only relationship which receives support here is the moderately supported clade formed by *Cuviera* and *Robynsia* in the ITS phylogeny (clade F, Fig. 2). *Cuviera* is a morphologically distinct genus centred in West Africa but with some few representatives also in central and East Africa. Diagnostic for the genus are large and many-flowered inflorescences with linear to lanceolate or even elliptic bracts and bracteoles, and many species also have hairs on the styles, sometimes in combination with peculiar swellings (Hallé 1959). The calyx lobes are also often large and foliose, usually similar to the bracts and bracteoles. Today the genus includes around 20 species (Bridson 1998). The monotypic genus *Robynsia* (Hutchinson 1931) has very similar inflorescences to *Cuviera*, but has long and slender corolla tubes not known in *Cuviera*. A relationship between *Cuviera* and *Robynsia* is thus supported by morphology, but the clade collapses in the combined phylogenies, possibly due to incongruence.

Canthium oligocarpum is a member of the small (three species) subgenus *Lycioserissa*. It is clearly distanced both from the type species of *Canthium*, *C. coromandelicum* and the type species of subgenus *Lycioserissa*, *C. inerme*, both of which are represented in the outgroup, but is of uncertain position in the large-flowered group. It is similar in leaf morphology to some species of *Multidentia* (e.g. *M. sclerocarpa*), and is in the ITS phylogeny (Fig. 2) weakly supported as sister to that genus, but lacks the morphological synapomorphies of *Multidentia* and should no be transferred until its phylogenetic position can be ascertained with better support.

Multidentia is one of the best delimited genera in Vanguerieae (Bridson 1987). Eleven species are known, and the genus has a wide distribution in tropical Africa. The genus is easily recognized by a combination of vague tertiary nerves, a well-developed calyx limb tube, and thickly woody pyrenes. The sample here includes most of the morphological variation in the genus and the monophyly of *Multidentia* is strongly supported.

Pygmaeothamnus is a genus of two geofrutices of which *P. chamaedendrum* is restricted to South Africa and *P. zeyheri* has a wide essentially Zambesian distribution. A combination of a geofrutescent habit and bilocular ovaries is the major morphological character used to delimit the genus. The genus is polyphyletic and is represented both in the outgroup and in the large-flowered group.

Vangueriopsis includes four species and is recognized by long (over 15 mm) and linear corolla lobes, long exserted stamens, and hairs usually present on stamens. The specimen here sampled is a fruiting specimen tentatively identified to *Vangueriopsis longiflora* (see also Lantz and Bremer 2004) but is without doubt a member of the genus.

Even though not really tested here, we find it highly unlikely that the *Vangueria* group is nested within any of these genera. The monophyly of *Multidentia* is strongly demonstrated here (Fig. 4), *Cuviera* and *Vangueriopsis* are strongly delimited in a morphological sense, *Robynsia* is monotypic and *Pygmaeothamnus* is known to be represented only by the type species *P. zeyheri* in the large-flowered group. The phylogenetic affinities of *Canthium oligocarpum* remain unknown and, as was concluded also in an earlier study (Lantz and Bremer 2004), the species cannot remain in *Canthium* but neither morphology nor phylogeny enables us to suggest how to deal with the species.

Incongruencies. As discussed above, the ITS (Fig. 2) and chloroplast (Fig. 3) trees are partly incongruent. Phylogenetic incongruence can be caused by a number of phenomena, some reflecting biological processes such as hybridization or lineage sorting, but there are also technical causes such as taxon sampling or insufficient data which can lead to incongruence (Wendel and Doyle 1998). A common case of incongruence is when weakly supported clades contradict each other. An example of this is the position of *Rytigynia induta*. Such weakly supported results are not necessarily reflecting the evolutionary history of the taxa studied, but can be the result of homoplasy (e.g. Kellogg et al. 1996) and are therefore usually not taken into account in a discussion on phylogeny. However, there are also some strongly supported incongruencies in this study, and these cannot easily be dismissed as artefacts caused by technical phenomena.

In the *Vangueria* group we are able to identify a single taxon, *Ancylanthos rubiginosus*, as incongruent in the comparison between the ITS and chloroplast phylogenies. Based on comparisons with morphology (see above) the internal position in the *Vangueria* group suggested by the ITS phylogeny is the most likely for the organism. The incongruent position of *Ancylanthos rubiginosus* in the chloroplast phylogeny in comparison to the position supported by both the nuclear phylogeny and morphology can be explained by a chloroplast capture event (e.g. Soltis et al. 1996). In chloroplast capture, hybridization and introgression results in a cytoplasmic transfer with little or no transfer of nuclear DNA (Rieseberg and Soltis 1991). An additional factor that potentially could explain the incongruence is the different ITS paralogues known to exist for this species (Lantz and Bremer 2004). As these paralogues do not share the same evolutionary history, their presence can result in erroneous phylogenies (Sanderson and Doyle 1992, Buckler et al. 1997). However, it was concluded that the variation did not pass the species boundary (Lantz and Bremer 2004; see also Razafimandimbison et al. 2004 for a similar situation). It is therefore unlikely that it is the presence of different ITS paralogues that are causing the incongruence.

The incongruence in the *Fadogia-Rytigynia* group is more complex, especially if comparisons with morphological characters also are made. Four taxa, i.e. *Hutchinsonia barbata*, *Rytigynia beniensis*, *R. decussata*, and *R. eickii* have strongly supported incongruent positions in the ITS (Fig. 2) and chloroplast (Fig. 3) phylogenies. There are also strongly supported nodes present in the individual phylogenies which collapse when the data sets are combined. Morphological support exists for some of the strongly supported clades, but not all. In the *Fadogia-Rytigynia* group, we cannot find a single plausible explanation for the incongruence as we could in the *Vangueria* group, but we find it most likely that the incongruence has a similar origin; hybridization and introgression. Chloroplast capture is also in this group a possibility, and there is also an additional

phenomenon known to exist for repetitive DNA such as ITS. The ITS region exists in a multitude of copies, and concerted evolution operates on these copies to homogenize them (e.g. Baldwin 1992). Following a hybridization it is likely that the hybrids have a mix of the paralogues present in the parent species, and if the concerted evolution homogenizes the ITS region to different paralogues in different hybrid lineages, phylogenies based on these paralogous ITS sequences are likely to give misleading inferences of the organismal phylogenies. This has been shown to occur in *Gossypium* (Wendel et al. 1995). Concerted evolution can also cause DNA to be exchanged between the paralogues, creating even more complex reticulate relationships between the paralogues (Hillis et al. 1991). A process which does not include hybridization but is known to cause incongruence is lineage sorting (Pamilo and Nei 1988, Wendel and Doyle 1998). In this process an ancestral polymorphism fails to survive a speciation event, so that not all of the descendant species share the polymorphism. As a result of this, alleles (or paralogues in the case of ITS) from different species may be more closely related to each other than alleles within the same species.

A study including also other parts of the tribe (Lantz and Bremer 2004) using ITS and *trn*T-F data did not find any incongruencies outside of the large-flowered group. An interesting correlation between phylogeny and morphology is that most of the genera in the large-flowered group are known to have a special kind of pollen presenter (type 2; Igersheim 1993). Genera in the large-flowered group known to have this type are *Ancylanthos*, *Fadogia*, *Fadogiella*, *Lagynias*, *Pachystigma*, *Tapiphyllum*, *Vangueria*, and part of *Rytigynia* (Igersheim 1989, Bridson 1996). Before the flower bud opens, when the pollen is deposited on the presenter, the stigmatic lobes are exposed but covered by sterile apical appendages present on the anthers (Igersheim 1993). This is in contrast to type 1 (Igersheim 1993), where the stigmatic lobes are tightly pressed together and do not open until the flower has opened and the style is fully elongated. This correlation between exposed stigmatic lobes and the presence of incongruence for these genera raises the question whether the exposed stigmatic lobes somehow might facilitate hybridization. We cannot see why this would be the case unless the type 2 pollen presenter is also coupled with weak barriers to hybridization. No studies on hybridization in Vanguerieae have been performed, so we can only guess that this could be the case. However, it is more likely that the exposed stigmatic lobes could increase the possibility for self-fertilization. The pollen sacs of the anthers and the stigmatic surfaces are spatially separated (Igersheim 1993), but the pollen sacs are nevertheless close and if the sterile apical appendages of the anthers fail to cover the stigmatic surfaces completely, it is possible that pollen could be deposited there in the bud stage. Selfing has been suggested to promote establishment of hybrid species (see e.g. discussion in Rieseberg 1997) and this could in part explain why we see possible cases of hybridization in the large-flowered group and not in other parts of Vanguerieae. At present, this is little more than speculation, since it is not known whether any Vanguerieae species are self-fertilizing or whether they are self-compatible or not.

We can thus conclude that the *Vangueria* group, as circumscribed here, should be given generic rank (as *Vangueria*). In the *Fadogia-Rytigynia* group, the presence of several taxa with incongruent positions complicates any conclusions about the phylogeny. *Fadogia* (including *Fadogiella*) is morphologically distinct, and should not be combined with *Rytigynia* before the reasons behind the incongruencies are known. We consider diagnosability to be a major desirable feature of classification, second only to the criterion of monophyly and would prefer to describe morphologically well-delimited genera. The phylogenies present some possible answers to why the genera and species of the *Fadogia-Rytigynia* group have proven to be difficult to delimit using morphological criteria (Verdcourt 1987).

Hybridization can lead to intermediate morphologies (McDade 1990) and this could explain why these species and genera are hard to delimit morphologically. Surprisingly enough, the possibility for hybridization in Vanguerieae has rarely been discussed. We know of only a single report of a possible hybrid in Vanguerieae (between *Vangueria apiculata* and *V. madagascariensis*; Verdcourt 1981). However, the hybridization events may be old and the species might not hybridize today. Nevertheless, studies on self-compatibility and hybridization in Vanguerieae would be a most welcome addition to the complex issue of the evolution of Vanguerieae.

Taxonomy of Vangueria

Vangueria Juss., Gen. pl.: 206. 1789. Type: *V. madagascariensis* Gmelin in Syst. Nat., ed. 13, 2: 367. 1791.

Ancylanthos Desf., Mém. Mus. Hist. Nat. 4: 5. 1818, syn. nov. Type: *A. rubiginosus* Desf.

Pachystigma Hochst., Flora 25: 234. 1842, syn. nov. Type: *P. venosum* Hochst.

Tapiphyllum Robyns, Bull. Jard. Bot. État. 11: 101. 1928, syn. nov. Type: *T. cinerascens* (Hiern) Robyns.

Lagynias E. Mey. ex Robyns, Bull. Jard. Bot. État. 11: 312. 1928, syn. nov. Type: *L. lasiantha* (Sond.) Bullock.

Lagynias E. Mey. ex Robyns subgen. *Bembea* Verdc. in Kew Bull. 42: 141. 1987, syn. nov. Type: *L. rufescens* (E.A. Bruce) Verdc.

Vangueria Juss. subgen. *Itigi* Verdc. in Kew Bull. 42: 186. 1987, syn. nov. Type: *V. praecox* Verdc.

Small trees, shrubs, or geofrutices. Unarmed, or very rarely with paired spines. Leaves usually deciduous, paired or (for geofrutices) in whorls of three, glabrous to thickly pubescent; domatia absent, or very rarely present; stipules triangular or with a broad base and a narrow apex, hairs present within. Flowers 5(6)-merous in axillary pedunculate or rarely fasciculate inflorescences, secondary axes well-developed or not, with 1–30 flowers; bracts and bracteoles inconspicuous. Calyx glabrous to densely pubescent, limb tube short, not equalling disk or more developed exceeding the disk; lobes variable but always well developed, triangular, oblong, lanceolate, spatulate, or linear. Corolla usually white to green, less often yellow or orange, externally glabrous to densely pubescent; tube cylindrical to campanulate, with diffusely spreading hairs at throat and retrorse straight hairs in a well defined ring inside, usually clearly distanced from hairs present at throat; lobes equalling tube or shorter, rarely longer, often apiculate or shortly appendaged. Stamens inserted at throat; anthers ovate or oblong, apiculate, usually shortly exserted. Ovary 3-5-locular, each locule with a single pendulous ovule; style shortly exserted or sometimes long exserted; pollen presenter cylindrical or sometimes coroniform. Fruit large, above 1 cm in length, only rarely below 1 cm, subglobose or globose, glabrous or pubescent, calyx lobes often persistent; 3–5 pyrenes, or rarely less due to faulty development.

A genus of over 50 species distributed in Africa south of the Sahara with one species occurring in Madagascar (*V. madagascariensis*). The centre of diversity is in East Africa (Kenya, Tanzania) and it is rare in West Africa.

Robyns (1928) revised all of the then recognized species and later also described additional species, especially in *Tapiphyllum* (Robyns 1931, 1962). The East African and Zambesian species were revised in conjunction with the production of the Vanguerieae volumes for Flora of Tropical East Africa and Flora Zambesiaca (Verdcourt 1981, 1987; Verdcourt and Bridson 1991; Bridson 1996, 1998), but the other species have not recently been revised. Several of these taxa are poorly known, especially the ones from Angola and Western/Central Africa, and are possibly not worth maintaining. Unless suggested by other authors (see *V. infausta*, *V. macrocalyx*, and *V. venosa*), we do not address the delimitation of any of the included species here, but it should be noted that further studies are

certainly needed. The genus is in this circumscription made more variable in comparison to how it earlier was conceived, especially concerning inflorescence and floral morphology. However, the genus is now easily distinguished from its closest relatives by the following combination of characters (also listed above): domatia rarely present, inflorescences usually borne at nodes from which the leaves have fallen, bracteoles small (present on secondary branches, usually not more than 1 mm in length), smooth retrorse hairs in the corolla (Lantz and Bremer 2004), and large fruits (above 1 cm in length) with 3 to 5 locules.

Here follows a list of all currently recognized species of *Vangueria* in the circumscription suggested above. New combinations are made when necessary, but infraspecific names are given only for taxa here transferred to *Vangueria*. Basionyms and most recently accepted names are listed, full synonyms are not included.

Vangueria apiculata K. Schum. in Pflanzenw. Ost-Afrikas, C: 384. 1895.

Vangueria agrestis (Schweinf. ex Hiern) Lantz, comb. nov. *Fadogia agrestis* Schweinf. ex Hiern in Fl. trop. Afr. 3: 154. 1877.

Vangueria albosetulosa (Verdc.) Lantz, comb. nov.

Pachystigma albosetulosum Verdc. in Kew Bull. 42: 139. 1987.

Vangueria bicolor K. Schum. in Bot. Jahrb. Syst. 34: 332. 1904.

Vangueria bowkeri (Robyns) Lantz, comb. nov.

Pachystigma bowkeri Robyns in Bull. Jard. Bot. État. 11: 128. 1928.

Vangueria burnettii (Tennant) Lantz, comb. nov.

Tapiphyllum burnettii Tennant in Kew Bull. 19: 280, Fig. 1. 1965.

Vangueria burttii (Verdc.) Lantz, comb. nov.

Pachystigma burttii Verdc. in Kew Bull. 36: 545, Fig. 11. 1981.

subsp. *burttii*.

subsp. *hirtiflora* (Verdc.) Lantz, comb. nov.

Pachystigma burttii subsp. *hirtiflorum* Verdc. in in Fl. Trop. E. Afr., Rubiaceae: 769. 1991.

Vangueria chariensis A. Chev. ex Robyns in Bull. Jard. Bot. État. 11: 299.

Vangueria cinerascens (Welw. ex Hiern) Lantz, comb. nov.

Ancylanthos cinerascens Welw. ex Hiern in Fl. trop. Afr. 3: 159. 1877.

Tapiphyllum cinerascens (Welw. ex Hiern) Robyns in Bull. Jard. Bot. État. 11: 107. 1928.

var. *cinerascens*.

var. *inaequalis* (Robyns) Lantz, comb. nov. *Tapiphyllum inaequale* Robyns in Bull. Jard. Bot. Brux. 32: 145. 1962.

Tapiphyllum cinerascens var. *inaequale* (Robyns) Verdc. in Kew Bull. 42: 144. 1987.

var. *laeta* (Robyns) Lantz, comb. nov. *Tapiphyllum laetum* Robyns in Bull. Jard. Bot. Brux. 32: 143. 1962.

Tapiphyllum cinerascens var. *laetum* (Robyns) Verdc. in Kew Bull. 42: 145. 1987.

var. *laevior* (K. Schum.) Lantz, comb. nov. *Vangueria velutina* Hiern var. *laevior* K. Schum. in Bot. Jahrb. Syst. 28: 494. 1900. *Tapiphyllum cinerascens* var. *laevius* (K. Schum.) Verdc. in Kew Bull. 42: 144. 1987.

var. *richardsii* (Robyns) Lantz, comb. nov. *Tapiphyllum richardsii* Robyns in Bull. Jard. Bot. Brux. 32: 142. 1962.

Tapiphyllum cinerascens var. *richardsii* (Robyns) Verdc. in Kew Bull. 42: 145. 1987.

Vangueria cistifolia (Welw., ex Hiern) Lantz, comb. nov.

Ancylanthus cistifolius Welw. ex Hiern in Fl. trop. Afr. 3: 159. 1877. *Tapiphyllum cistifolium* (Welw.) Robyns in Bull. Jard. Bot. État. 11: 108. 1928.

var. *cistifolia*.

var. *latifolia* (Verdc.) Lantz.

Tapiphyllum cistifolium (Welw. ex Hiern) Robyns var. *latifolium* Verdc. in Fl. Zamb. 259. 1998.

Vangueria coerulea (Robyns) Lantz, comb. nov. *Pachystigma coeruleum* Robyns in Bull. Jard. Bot. État. 11: 129. 1928.

Vangueria cyanescens Robyns in Bull. Jard. Bot. État. 11: 284. 1928.

Vangueria discolor (De Wild.) Lantz, comb. nov.

Fadogia discolor De Wild. in Feddes Repert. 13: 138. 1914.

Tapiphyllum discolor (De Wild.) Robyns in Bull. Jard. Bot. État. 11: 105. 1928.

Vangueria dryadum S. Moore in J. Linn. Soc., Bot. 40: 93. 1911.

Lagynias dryadum (S. Moore) Robyns in Bull. Jard. Bot. État. 11: 315. 1928.

Vangueria esculenta S Moore in J. Linn. Soc., Bot. 40: 91. 1911.

Vangueria fulva (Robyns) Lantz, comb. nov.

Tapiphyllum fulvum Robyns in J. Bot. 69: 186. 1931.

Vangueria fuscosetulosa (Verdc.) Lantz, comb. nov.

Rytigynia fuscosetulosa Verdc. in Fl. Trop. E. Afr., Rubiaceae: 836. 1991.

Vangueria gillettii (Tennant) Lantz, comb. nov.

Rytigynia gillettii Tennant in Kew Bull. 19: 279. 1965.

Pachystigma gillettii (Tennant) Verdc. in Kew Bull. 42: 140. 1987.

Vangueria gossweileri (Robyns) Lantz, comb. nov.

Tapiphyllum gossweileri Robyns in J. Bot. 69: 185. 1931.

Vangueria induta (Bullock) Lantz, comb. nov.

Rytigynia induta (Bullock) Verdc. & Bridson in Kew Bull. 42: 169. 1987.

Canthium indutum Bullock in Kew Bull. 1932: 366. 1932.

Vangueria infausta Burchell in Trav. S. Africa 2: 258. 1824.

Vangueria velutina Hook. in Bot. Mag. 57, t. 3014. 1830, syn. nov.

Vangueria velutina Hook. has been suggested earlier (Verdcourt 1981) to be a synonym of *V. infausta* Burchell, but has not been formally listed as such. From the excellent illustration in Hooker's description with detail of the calyx lobes there can be no doubt that the specimen depicted indeed is the same taxon as *Vangueria infausta* Burchell. See also *Vangueria zambesiaca* Lantz below.

Vangueria lasiantha (Sond.) Sond. in Fl. Cap. 3: 14. 1865.

Pachystigma lasianthum Sond. in Linnaea 23: 55. 1850.

Lagynias lasiantha (Sond.) Bullock in Bull. Misc. Inform. Kew 1931: 274. 1931.

Vangueria latifolia (Sond.) Sond. in Fl. Cap. 3: 15. 1864.

Pachystigma latifolium Sond. in Linnaea 23: 56. 1850.

Vangueria loranthifolia K. Schum. in Pflanzenw. Ost-Afrikas, C: 385. 1895.

Pachystigma loranthifolium (K. Schum.) Verdc. in Kew Bull. 42: 140. 1987.

subsp. *loranthifolia*.

subsp. *salaense* (Verdc.) Lantz, comb. nov.

Pachystigma lorantifolium subsp. *salaense* Verdc. in Kew Bull. 42: 140. 1987.

Vangueria macrocalyx Sond. in Linnaea 23: 59. 1850.

Vangueria caffra Sim in Forest fl. Cape: 244. 1907, syn. nov.

Pachystigma caffrum (Sim) Robyns in Bull. Jard. Bot. État. 11: 120. 1928, syn. nov.

Pachystigma macrocalyx (Sond.) Robyns in Bull. Jard. Bot. État. 11: 130. 1928.

We agree with the view in Retief (2003) that *Pachystigma caffrum* (Sim) Robyns should be considered a synonym of *Pachystigma macrocalyx* (Sond.).

Vangueria madagascariensis J.F. Gmelin in Syst. Nat., ed. 13, 2: 367. 1791.

Vangueria micropyren (Verdc.) Lantz, comb. nov. *Pachystigma micropyren* Verdc. in Kew Bull. 42: 139. 1987.

Vangueria mollis (Robyns) Lantz, comb. nov. *Tapiphyllum molle* Robyns in J. Bot. 69: 186. 1931.

Vangueria monteiroi (Oliv.) Lantz, comb. nov.

Ancylanthos monteiroi Oliv. in Icon. pl. 8: 7. 1877.

Lagynias monteiroi (Oliv.) Bridson in Kew Bull. 51: 351. 1996.

Vangueria obtusifolia K. Schum. in Bot. Jahrb. Syst. 28: 493. 1900.

Tapiphyllum obtusifolium (K. Schum.) Robyns in Bull. Jard. Bot. État. 11: 115. 1928.

Vangueria pachyantha (Robyns) Lantz, comb. nov.

Tapiphyllum pachyanthum Robyns in Bull. Jard. Bot. Brux. 32: 150. 1962.

Vangueria pallidiflora (Bullock) Lantz, comb. nov.

Lagynias pallidiflora Bullock in Kew Bull. 1931: 273. 1931.

Vangueria parvifolia Sond. in Linnaea 23: 58. 1850.

Vangueria praecox Verdc. in Kew Bull. 36: 554. 1981.

Vangueria proschii Briq. in Annuaire Conserv. Jard. Bot. Genève. 6: 7. 1902.

Vangueria psammophila (K. Schum.) Lantz, comb. nov.

Fadogia psammophila K. Schum. in Bot. Jahrb. Syst. 32: 147. 1902.

Tapiphyllum psammophilum (K. Schum.) Robyns in Bull. Jard. Bot. État. 11: 105. 1928.

Vangueria pygmaea Schlecht. in J. Bot. 35: 342. 1897.

Pachystigma pygmaeum (Schlecht.) Robyns in Bull. Jard. Bot. État. 11: 122. 1928.

Vangueria quarrei (Robyns) Lantz, comb. nov.

Tapiphyllum quarrei Robyns in Bull. Jard. Bot. Brux. 32: 144. 1962.

Vangueria randii S. Moore in J. Bot. 40: 252. 1902.

Vangueria rhodesiaca (Tennant) Lantz, comb. nov.

Ancylanthos rhodesiacus Tennant in Kew Bull. 19: 283. 1965.

Tapiphyllum rhodesiacum (Tennant) Bridson in Kew Bull. 51: 351. 1996.

Vangueria rubiginosa (Desf.) Lantz, comb. nov.

Ancylanthos rubiginosus Desf. in Mém. Mus. Hist. Nat. 4: 5 1818, (as *rubiginosa*).

Vangueria rufescens (E.A. Bruce) Lantz, comb. nov.

Ancylanthos rufescens E.A. Bruce in Kew Bull. 1936: 477. 1936.

Lagynias rufescens (E.A. Bruce) Verdc. in Kew Bull. 42: 143. 1987.

subsp. *rufescens*.

subsp. *angustiloba* (Verdc.) Lantz, comb. nov.

Lagynias rufescens (E.A. Bruce) Verdc. subsp. *angustiloba* Verdc. in Kew Bull. 42: 143. 1987.

Vangueria schliebenii (Verdc.) Lantz, comb. nov.

Tapiphyllum schliebenii Verdc. in Kew Bull. 36: 534. 1981.

Vangueria schumanniana (Robyns) Lantz, comb. nov.

Tapiphyllum schumannianum Robyns in Bull. Jard. Bot. État. 11: 109. 1928. *Pachystigma schumannianum* (Robyns) Bridson & Verdc. in Fl. Trop. E. Afr., Rubiaceae: 768. 1991.

subsp. *schumanniana* subsp. *mucronulata* (Robyns) Lantz, comb. nov.

Pachystigma schumannianum (Robyns) Bridson & Verdc. subsp. *mucronulatum* in Fl. Trop. E. Afr., Rubiaceae: 768. 1991.

Vangueria solitariiflora (Verdc.) Lantz, comb. nov.

Pachystigma solitariiflorum Verdc. in Kew Bull. 36: 541, Fig. 9. 1981.

Vangueria soutpansbergensis N. Hahn in Bothalia 27: 45. 1997.

Vangueria thamnus (Robyns) Lantz, comb. nov.

Pachystigma thamnus Robyns in Bull. Jard. Bot. État. 11: 121. 1928.

Vangueria triflora (Robyns) Lantz, comb. nov.

Pachystigma triflorum Robyns in Bothalia 3: 184. 1937.

Vangueria venosa (Hochst.) Sond. in Fl. Cap. 3: 14. 1864.

Pachystigma venosum Hochst. in Flora 25: 235. 1842.

Pachystigma cymosum Robyns in Bull. Jard. Bot. État. 11: 127. 1928, syn. nov.

Pachystigma cymosum Robyns is listed as a synonym of *Pachystigma venosum* Hochst. in Retief (2003), and we agree with that view.

Vangueria verticillata (Robyns) Lantz, comb. nov.

Tapiphyllum verticillatum Robyns in Bull. Jard. Bot. Brux. 32: 141. 1962.

Vangueria volkensii K. Schum. in Pflanzenw. Ost-Afrikas, C: 384. 1895.

Vangueria zambesiaca Lantz, nom. nov. *Vangueria velutina* Hiern in Fl. trop. Afr. 3: 151. 1877, nom. illegit. *Tapiphyllum velutinum* (Hiern) Robyns Bull. Jard. Bot. État. 11: 111. 1928.

Vangueria velutina Hook. (1830) precedes *Vangueria velutina* Hiern (1877) and the latter name is thus a later homonym and should not be used. The species epithet used here is derived from the strictly Zambesian distribution of the species (Bridson, 1998). *Vangueria velutina* Hook. is above combined under *V. infausta* Burchell.

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References

Asmussen C. B. (1999) Toward a chloroplast DNA phylogeny of the tribe Genomeae (Palmae). Mem. New York Bot. Gard. 83: 121–129.

Baldwin B. G. (1992) Phylogenetic utility of the internal transcribed spacers of nuclear ribosomal DNA in plants: an example from the Compositae. Molec. Phylogenet. Evol. 1:3–16.

Bridson D. M. (1987) The recognition and recircumscription of the African genus *Multidentia* (Rubiaceae-Vanguerieae). Kew Bull. 42: 641–654.

Bridson D. M. (1996) The tropical African genus *Ancylanthos* (Rubiaceae-Vanguerieae) reconsidered. Kew Bull. 51: 343–352.

Bridson D. M. (1998) Rubiaceae (Tribe Vanguerieae). In: Pope G. V. (ed.) Flora Zambesiaca. Royal Botanic Gardens, Kew, London, pp. 211–377.

Buckler IV E. S., Ippolito A., Holtsford T. P. (1997) The evolution of ribosomal DNA: divergent paralogues and phylogenetic implications. Genetics 145: 821–832.

Bullock A. A. (1931) Tropical African Plants: VIII. Bull. Misc. Inform. No. 5: 270–275.

Desfontaines M. (1818) Nouveau genre de la famille des Rubiacées: *Ancylanthos*. Mém. Mus. Hist. Nat. 4: 5–7.

Downie S. R., Katz-Downie D. S., Watson M. F. (2000) A phylogeny of the flowering plant family Apicaeae based on chloroplast DNA *rpl*16 and rpoc1 intron sequences: towards a suprageneric classification of subfamily Apioideae. Amer. J. Bot. 87: 273–292.

Doyle J. J., Doyle J. L. (1987) A rapid DNA isolation procedure for small quantities of fresh leaf tissue. Phytochem. Bull. Bot. Soc. Amer. 19: 11–15.

Hahn N. (1997) Rubiaceae: A new species of Vangueria from the Soutpansberg. Bothalia 27: 45–48.

Hallé N. (1959) Sur les *Cuviera* (Rubiacées) d'Afrique intertropicale et description pour ce genre de deux espèces et de deux variétés nouvelles. Bull. Soc. Bot. France 7–8: 342–348.

Hillis D. M., Moritz C., Porter C. A., Baker R. J. (1991) Evidence for biased geneconversion in concerted evolution of ribosomal DNA. Science 251: 308–309.

Holmgren P. K., Holmgren N. H., Barnett L. C. (1990) Index herbariorum, Part 1: The herbaria of the world, 8th edn. New York Botanical Garden, New York.

Hutchinson J. (1931) *Robynsia*. In: Hutchinson J., Dalziel J. M. (eds.) Flora of West Tropical Africa. The Crown Agents for the Colonies, London, pp. 108–109.

Igersheim A. F. (1989) Beiträge zur Klärung der Gattungsabgrenzungsprobleme innerhalb der Rubiaceae-Vanguerieae. Ph. D. Thesis. Universität Wien.

Igersheim A. F. (1993) Gynoecium development in Rubiaceae-Vanguerieae, with particular reference to the "stylar-head"-complex and secondary pollen presentation. Pl. Syst. Evol. 187: 175–190.

Jussieu A. L. de (1789) Genera Plantarum Secundum Ordines Naturales Disposita. Paris.

Kellogg E. A., Appels R., Mason-Gamer R. J. (1996) When genes tell different stories: the

diploid genera of Triticeae (Gramineae). Syst. Bot. 21: 321–347.

Lantz H., Andreasen K., Bremer B. (2002) Nuclear rDNA ITS data used to construct the first phylogeny of Vanguerieae (Rubiaceae). Pl. Syst. Evol. 230: 173–187.

Lantz H., Bremer B. (2004) Phylogeny inferred from morphology and DNA data: characterizing well-supported groups in Vanguerieae (Rubiaceae). Bot. J. Linn. Soc. 146: 257–283.

McDade L. (1990) Hybrids and phylogenetic systematics I. Patterns of character expression in hybrids and their implications for cladistic analysis. Evolution 44: 1685–1700.

Pamilo P., Nei M. (1988) Relationships between gene trees and species trees. Mol. Biol. Evol. 5: 568–583.

Razafimandimbison S., Kellogg E., Bremer B. (2004) Recent origin and phylogenetic utility of divergent ITS putative pseudogenes: a case study from Naucleeae (Rubiaceae). Syst. Biol. 53: 177–192.

Retief E. (2003) Rubiaceae. In: Germishuizen G., Meyer N. L. (eds.) Plants of southern Africa: an annotated checklist. Strelitzia 14: 825–841. National Botanical Institute, Pretoria.

Rieseberg L. H., Soltis D. E. (1991) Phylogenetic consequences of cytoplasmic gene flow in plants. Evol. Trends Pl. 5: 65–84.

Rieseberg L. H. (1997) Hybrid origins of plant species. Annual Rev. Ecol. Syst. 28: 359–389.

Robbrecht E. (1988) Tropical woody Rubiaceae. Opera Bot. Belg. 1: 1–271.

Robyns W. (1928) Tentamen Monographiae Vanguerieae Generumque Affinium. Bull. Jard. Bot. État. 11: 1–359.

Robyns W. (1931) Vanguerieae Gossweilerianae. J. Bot. 69: 189–190.

Robyns W. (1962) Contribution a l'étude du genre *Tapiphyllum* Robyns. Bull. Jard. Bot. État. 32: 133–153.

Sanderson M. J., Doyle J. J. (1992) Reconstruction of organismal and gene phylogenies from data on multigene families: concerted evolution, homoplasy, and confidence. Syst. Biol. 41: 4–17.

Simmons M. P., Ochoterena H. (2000) Gaps as characters in sequence-based phylogenetic analyses. Syst. Biol. 49: 369–381.

Small R. L., Ryburn J. A., Cronn R. C., Seelanan T., Wendel J. F. (1998) The tortoise and the hare: choosing between noncoding plastome and nuclear *ADH* sequences for phylogeny reconstruction in a recently diverged plant group. Amer. J. Bot. 85: 1301–1315.

Soltis D. E., Johnson L. A., Looney C. (1996) Discordance between ITS and chloroplast topologies in the *Boykinia* group (Saxifragaceae). Syst. Bot. 21: 169–185.

Swofford D. L. (2002) PAUP*. Phylogenetic Analysis Using Parsimony (*and other methods). Version 4. Sinauer Associates, Sunderland, Massachusetts.

Verdcourt B. (1958) Remarks on the classification of the Rubiaceae. Bull. Jard. Bot. État. 28: 209–281.

Verdcourt B. (1981) Notes on African Rubiaceae. Kew Bull. 36: 493–557.

Verdcourt B. (1987) Notes on African Rubiaceae-Vanguerieae. Kew Bull. 42: 123–199.

Verdcourt B., Bridson D. M. (1991) Rubiaceae (Part 3). In: Polhill R. M. (ed.) Flora of Tropical East Africa. A.A. Balkema, Rotterdam/Brookfield, pp. 749–956.

Wendel J. F., Schnabel A., Seelanan T. (1995) Bidirectional interlocus concerted evolution following allopolyploid speciation in cotton (*Gossypium*). Proc. Natl. Acad. Sci. USA 92: 280–284.

Wendel J. F., Doyle J. J. (1998) Phylogenetic incongruence: window into genome history and molecular evolution. In: Soltis P. S., Soltis D. E., Doyle J. J. (eds.) Molecular systematics of plants, 2nd edn. Chapman and Hall, New York, pp. 265–296.

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