



## Phylogenetic relationships and new tribal delimitations in subfamily Ixoroideae (Rubiaceae)

KENT KAINULAINEN<sup>1,2\*</sup>, SYLVAIN G. RAZAFIMANDIMBISON<sup>1,2</sup> and BIRGITTA BREMER<sup>1,2</sup>

<sup>1</sup>*Bergius Foundation, The Royal Swedish Academy of Sciences, SE-106 91 Stockholm, Sweden*

<sup>2</sup>*Department of Ecology, Environment and Plant Sciences, Stockholm University, SE-106 91 Stockholm, Sweden*

Received 4 April 2012; revised 2 October 2012; accepted for publication 31 January 2013

Subfamily Ixoroideae is one of three major lineages in Rubiaceae, with approximately 4000 species. Previous molecular phylogenetic studies have indicated that many genera and tribes previously placed in other subfamilies are better considered as part of Ixoroideae. However, the internal resolution and clade support have generally been low, and several genera found to be nested in the subfamily do not appear to be associated with any described tribe. In order to resolve the phylogeny and assess the tribal delimitations in the expanded Ixoroideae, phylogenetic reconstructions were performed using Bayesian and parsimony analyses of six plastid DNA regions and a broad sampling of genera from all tribes of the subfamily. In the inferred phylogenetic hypotheses, the tribal relationships were mostly well supported, with Ixoroideae consisting of the Coffeae and the Vanguerieae alliances as sister groups and a grade comprising Condamineae, Henriquezieae, Posoquerieae, Retiniphyllae, Sipaneeae and the genus *Steenisia*. A revised tribal classification, including the description of five new tribes, Airospermeae, Augusteae, Scyphiphoreae, Steenisieae and Trailliaedoxeae, is provided. © 2013 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2013, **173**, 387–406.

**ADDITIONAL KEYWORDS:** Airospermeae – Augusteae – molecular phylogenetics – Scyphiphoreae – Steenisieae – systematics – Trailliaedoxeae.

### INTRODUCTION

With >13 000 species (Davis *et al.*, 2009), Rubiaceae is one of the largest and most diverse families of angiosperms. Well-known representatives include *Coffea* L., *Ixora* L. and *Gardenia* J.Ellis, all part of Ixoroideae, a subfamily comprising about 4000 species of pantropical and subtropical distributions. Ixoroideae, as recognized by Bremekamp (1952, 1966), included taxa characterized by secondary pollen presentation ('ixoroid pollination mechanism'), a feature that Bremekamp considered to be of high taxonomic value because of its requirement for a combination of characters for functionality. Included were tribes Acranthereae, Chiococceae, Coptosapelteae, Cremasporeae, Gardenieae, Ixoreae and Vanguerieae. Verdcourt (1958), however, considered pollen presentation to be of less importance, and preferred to

include Ixoroideae in a wide Cinchonoideae (see also Robbrecht & Manen, 2006). In a comprehensive classification of the family, Robbrecht (1988) restricted Ixoroideae to include genera with contorted corolla lobe aestivation and fleshy fruits. In his system, Ixoroideae comprised tribes Cremasporeae, Gardenieae and Ixoreae *sensu* Bremekamp (the correct name of which would have been Coffeae; Darwin, 1976), i.e. Aulacocalyceae, Coffeae, Gardenieae, Octotropideae and Pavetteae. For an overview of the changes in the classification of Ixoroideae, the reader is referred to Andreasen & Bremer (2000).

Results of molecular phylogenetic studies have since then indicated many unknown relationships and also, consequently, possible improvements in the classification of Rubiaceae. This includes the expansion of Ixoroideae, as many additional tribes or segregates of tribes and a number of taxa of uncertain taxonomic placement have been shown to be associated with the subfamily. *Ixora*, the type of the subfamily, was shown

\*Corresponding author. E-mail: kent@bergianska.se

to form a clade with Vanguerieae (Bremer *et al.*, 1999), confirming the position of Vanguerieae in Ixoroideae, as suggested by Bremekamp (1952, 1966), and supporting the exclusion of *Ixora* from Pavetteae. Andreasen & Bremer (2000) resurrected Ixoreae and provided new circumscription for several other tribes in the subfamily. Many additional taxa have been found to be associated with Ixoroideae *sensu* Robbrecht (1988), including *Bertiera* Aubl. (Bremer, Andreasen & Olsson, 1995), Mussaendeae and Sabiceae, (Bremer & Thulin, 1998), Alberteae and *Scyphiphora* C.F.Gaertn. (Bremer *et al.*, 1999), Condamineae and many genera formerly placed in Cinchoneae or Rondeletiae (e.g. Bremer *et al.*, 1999; Rova *et al.*, 2002; Delprete & Cortés-B., 2004; Kainulainen *et al.*, 2010). *Crossoteryx* Fenzl, part of Ixoroideae *sensu* Bremekamp (included in Coptosapelteae), but considered part of Cinchoneae by Robbrecht (1988), has also been found to be nested in Ixoroideae (Razafimandimbison & Bremer, 2001), as have *Mussendopsis* (Razafimandimbison & Bremer, 2001), *Hekistocarpa* Hook.f. (Dessein *et al.*, 2001), *Gleasonia* Standl., *Retiniphyllum* Humb. & Bonpl. and Sipaneeae (Rova *et al.*, 2002; Delprete & Cortés-B., 2004), *Boholia* Merr. and *Steenisia* Bakh.f. (Bremer & Eriksson, 2009), *Airosperma* K.Schum. & Lauterb. (Kainulainen *et al.*, 2009), *Greeniopsis* Merr. (Alejandro *et al.*, 2010), *Glionnetia* Tirveng., *Jackiopsis* Ridsdale and *Trailliaedoxa* W.W.Sm. & Forrest (Razafimandimbison *et al.*, 2011). Although the expanded Ixoroideae is well supported by molecular data, internal resolution and clade support, especially among the early divergent clades, have generally been low.

Ixoroideae, as widely delimited according to recent molecular phylogenetic studies, includes all tribes of Robbrecht's (1988) narrow circumscription of the subfamily, whereas tribes Acranthereae, Chiococceae and Coptosapelteae are not part of Ixoroideae as suggested by Bremekamp (1966). Chiococceae has been shown to be part of Cinchonoideae (Bremer *et al.*, 1995), and *Acranthera* Arn. ex Meisn. and *Coptosapelta* Korth. appear to represent a separate, early divergent clade in the family (Rydin *et al.*, 2009). The expanded Ixoroideae is morphologically diverse and can no longer be easily characterized morphologically. Molecular phylogenetic studies have also shown that some tribes of the subfamily are not monophyletic (i.e. Gardenieae including Aulacocalyceae, and Pavetteae; Andreasen & Bremer, 2000; Persson, 2000; Bremer & Eriksson, 2009) and that several genera found to be nested in Ixoroideae do not appear to be associated with any described tribe, i.e. *Airosperma*, *Aleisanthia* Ridl., *Aleisanthiopsis* Tange, *Augusta* Pohl, *Boholia*, *Glionnetia*, *Greenea* Wight & Arn., *Scyphiphora*, *Steenisia*, *Trailliaedoxa* and *Wendlandia* Bartl. ex DC. (Rova *et al.*, 2002; Bremer & Eriksson, 2009;

Kainulainen *et al.*, 2009; Razafimandimbison *et al.*, 2011). Subsequent tribal recognition of the lineages represented by these genera has so far only been performed for *Aleisanthia* and *Aleisanthiopsis* and *Greenea* (Aleisanthieae and Greeneeae, respectively; Mouly *et al.*, 2009a).

In this study, we analyse data from six combined plastid DNA regions (*matK*, *ndhF*, *rbcL*, the *rps16* intron, *trnS-G* and *trnT-F*) using Bayesian and parsimony methods of phylogenetic reconstruction to resolve the tribal relationships of the expanded Ixoroideae and, in particular, the relationships of the genera which, in previous studies, have not been associated with any previously described tribes. Following the inferred phylogenetic hypothesis, we also provide a revised tribal classification of the subfamily.

## MATERIAL AND METHODS

### TAXON SAMPLING

This study includes genera representing all tribes associated with Ixoroideae in previous molecular phylogenetic studies. The ingroup included 110 species from 87 genera. An effort was made to sample primarily material representing the types of genera. *Gelsemium sempervirens* (L.) J.St.-Hil. (Gelsemiaceae), *Logania vaginalis* (Labill.) F.Muell. (Loganiaceae), *Luculia gratissima* (Wall.) Sweet, *Coltoecema dewevrei* (De Wild.) E.M.A.Petit, *Ophiorrhiza mungos* L. and six species of Cinchonoideae were utilized as outgroup. Because the focus of the study is primarily concerned with the phylogeny of the early divergent lineages of the subfamily, sampling was limited in the large and problematic Gardenieae and associated tribes (Octotropideae and Pavetteae), the phylogeny of which will be investigated further in an upcoming study (A. Mouly *et al.*, Université de Franche-Comté, Besançon, unpubl. data). Sampling was increased for *Airosperma*, *Augusta* and *Wendlandia*, all of which have widely disjunct distributions and in previous molecular phylogenetic studies have been resolved in Ixoroideae, but not in association with any previously recognized tribes (Rova *et al.*, 2002; Kainulainen *et al.*, 2009). We were able to obtain sequences of *Airosperma* taxa from New Guinea and Fiji, including *A. trichotomum* (Gillespie) A.C.Sm., originally described as *Abramsia trichotoma* Gillespie. The *Augusta* sample comprised specimens of the type *A. longifolia* (Spreng.) Rehder from Brazil, *A. austrocaledonica* (Brongn.) J.H.Kirkbr. from New Caledonia and *A. rivalis* (Benth.) J.H.Kirkbr. from Central America, the last two species of which were previously recognized as *Lindenia* Benth. The *Wendlandia* sample included *W. arabica* Deflers and *W. ligustroides* (Boiss. & Hohen.) Blakelock, the inclusion of

which in *Wendlandia* was considered to be doubtful in the last comprehensive revision of the genus by Cowan (1932). We were unsuccessful in obtaining DNA sequences from any *Steenisia* spp. other than *S. pleurocarpa* (Airy Shaw) Bakh.f. An overview of the sampling and voucher specimens is given in the Appendix, and a few species representing the different tribes of Ixoroideae are shown in Figure 1.

#### DNA EXTRACTION, AMPLIFICATION AND SEQUENCING

Three protein coding genes (*matK*, *ndhF* and *rbcL*) and three noncoding regions [the *rps16* intron, the *trnS-G* spacer including the *trnG* intron (*trnS<sup>GCU</sup>-trnG<sup>UUC</sup>-trnG<sup>UUC</sup>*) and the *trnT-F* region (*trnT<sup>UGU</sup>-trnL<sup>UAA</sup>-trnL<sup>UAA</sup>-trnF<sup>GAA</sup>*)] of the plastid DNA, previously shown to be phylogenetically informative in Rubiaceae (Andersson & Rova, 1999; Bremer *et al.*, 1999; Razafimandimbison & Bremer, 2002; Rova *et al.*, 2002; Andersson & Antonelli, 2005; Kainulainen *et al.*, 2009), were used in this study. DNA was extracted from leaf material using a Mini-Beadbeater 3110BX (BioSpec), following the protocol of Doyle & Dickson (1987), and was subsequently purified using the QIAquick® PCR purification kit according to the manufacturer's instructions (Qiagen). PCR amplifications were performed using standard PCR settings and the following primers: *matK*1198F and *matK*2053R (Andersson & Antonelli, 2005) for *matK*; 2F, 1000R, 720F, 1700R, 1320F and 2280R (Rydin, Razafimandimbison & Bremer, 2008) for *ndhF*; *rbcL*5'F, *rbcL*\_Z895F, *rbcL*\_Z895R and *rbcL*3'R (Bremer *et al.*, 2002) for *rbcL*; *rsp16*\_2F (Bremer *et al.*, 2002) and *rpsR*2 (Oxelman, Lidén & Berglund, 1997) for the *rps16* intron; and cF, eF, dR, fR (Taberlet *et al.*, 1991), A1F, IR (Bremer *et al.*, 2002), 820R, 940F, 1250F, 1880F and 2670R (Rydin *et al.*, 2008) for *trnT-F*. The *trnS-G* region was amplified using the primers and protocols of Shaw *et al.* (2005). Sequences were assembled using the Staden package v1.5.3 (Staden, 1996). Sequences new to this study (324) were deposited in GenBank (Appendix). Additional sequences (361) were obtained from GenBank (for references, see Appendix).

#### DATA ANALYSES

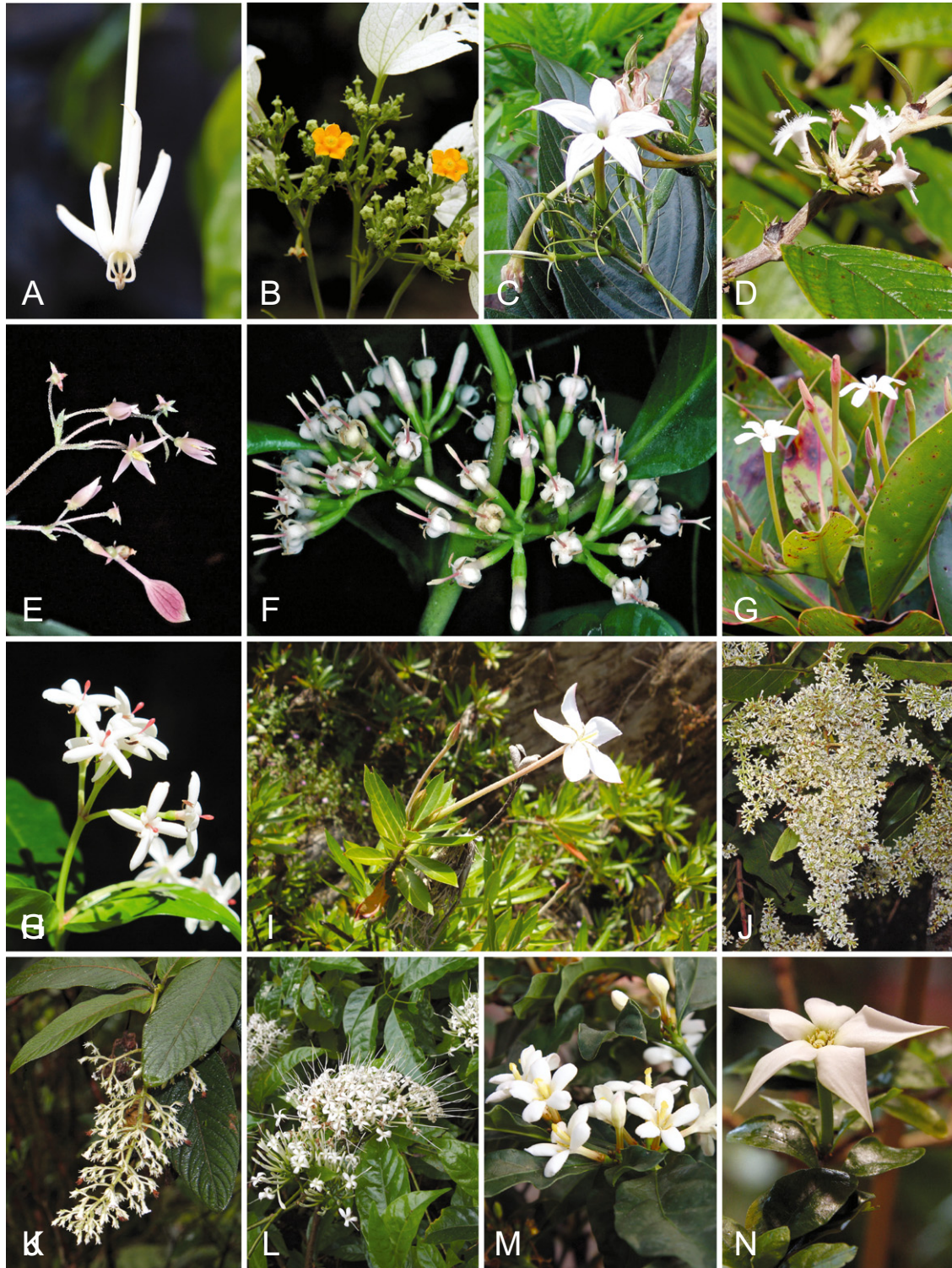
The sequences were preliminarily aligned using Clustal W (default settings; Thompson, Higgins & Gibson, 1994), as implemented in BioEdit (Hall, 1999), and then adjusted manually. Sequence inversions were dealt with by separating the alternative sequence versions in the alignment. Inversions in the included sequences occurred in regions corresponding to positions 5417–5430 (*rps16*), 9082–9113, 9164–9169, 9330–9335 and 9714–9723 (*trnS-G*) of the

*Coffea arabica* L. plastid genome (GenBank accession number, EF044213; Samson *et al.*, 2007). An AT-rich region in the *trnS-G* spacer, corresponding to positions 9184–9203 of the *C. arabica* plastid genome, was excluded from the analyses because of difficulties in finding an unambiguous alignment. The combined dataset consisted of 10 165 characters, 10 003 of which were included in the analyses. Methods of phylogenetic reconstruction included maximum parsimony (MP) and Bayesian inference (BI; Yang & Rannala, 1997), using the programs PAUP\* v4.0b10 (Swofford, 2002) and MrBayes v3.1.2 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003), respectively. Gaps were treated as missing data. MP analyses were performed using heuristic searches with the tree bisection–reconnection (TBR) branch swapping algorithm, Multrees on, 1000 random sequence addition replicates and a maximum of 10 trees saved per replicate. Clade support was estimated using 1000 bootstrap replicates, with three random addition replicates per replicate. For the BI analyses, the protein coding and noncoding data were analysed as separate partitions with unlinked model parameter estimates (except topology). Substitution models suggested as best fit to the data under the corrected Akaike information criterion (AICc), as implemented in MrAIC v1.4.4 (Nylander, 2004; a script dependent on the program PHYML v3.0; Guindon & Gascuel, 2003), were used for each partition (the GTR + G + I model for both datasets). The analysis comprised two runs of four chains each and was monitored for 10<sup>7</sup> generations, with every 1000th generation being sampled. The chain heating parameter was 0.10. The initial 25% of the sampled trees were considered as burn-in and excluded from the consensus. The effective sample sizes (ESSs) of the model parameters were checked using the program Tracer v1.5 (Rambaut & Drummond, 2007), in order to ensure an ESS > 200, as recommended by Drummond *et al.* (2007) for the adequate representation of the posterior probability (PP).

#### RESULTS

The combined dataset contained 10 003 DNA characters, 2410 of which were potentially phylogenetically informative in the MP analysis. Analyses of the coding and noncoding datasets separately (data not shown) showed no incongruences with bootstrap support (BS) values ≥ 70% or PPs ≥ 0.95, with the exception of the position of *Randia* L., which formed a sister group to *Euclinia* Salisb. (PP, 0.99; BS, 73%) in the coding dataset, but was resolved as sister group to a clade comprising *Rosenbergiodendron* Fagerl. and *Tocoyena* Aubl. in the noncoding dataset (PP, 0.95; BS, 84%). The inferred phylogenetic hypotheses of the MP and BI





**Figure 1.** Selected taxa of Ixoroideae: A, *Posoqueria longiflora*; B, *Schizomussaenda henryi*; C, *Bremeria pervillei*; D, *Sabicea diversifolia*; E, *Steenisia pleurocarpa*; F, *Scyphiphora hydrophylacea*; G, *Glionnetia sericea*; H, *Ixora borboniae*; I, *Augusta rivalis*; J, *Wendlandia tinctoria*; K, *Bertiera rufa*; L, *Pavetta* sp.; M, *Mitriostigma axillare*; N, *Rosenbergiodendron densiflorum* (image credits: A–D, G, H, K–N, by Kent Kainulainen; E, F, J, © Christian Puff, Faculty Centre of Biodiversity, University of Vienna; used with permission; I, by Indiana Coronado, Tropicos, botanical information system at the Missouri Botanical Garden – <http://www.tropicos.org>, © MBG, licensed under a Creative Commons by-nc-nd 3.0 licence).

analyses were overall mostly congruent, well resolved and strongly supported. Figure 2 shows the majority rule consensus tree from the BI analyses of the combined data, including the PPs of the clades and the clade BS values of the MP analysis.

The clades corresponding to the Coffeae and Vanguerieae alliances, respectively (cf. Razafimanambison *et al.*, 2011), were resolved as sister groups ('the core Ixoroideae'; PP, 1.00; BS, 100%). The Coffeae alliance comprised the tribes Alberteae, Bertiereae, Coffeae, Gardenieae, Octotropideae and Pavetteae and the genera *Airosperma*, *Augusta*, *Boholia* and *Wendlandia*. Gardenieae did not appear to be monophyletic, because *Burchellia* R.Br. was resolved as sister group to Octotropideae (PP, 1.00; BS, 64%), and *Mitriostigma* Hochst. and *Oxyanthus* DC. formed a sister group to Pavetteae, although with weak support (PP, 0.80; BS, 54%). The Gardenieae–Pavetteae clade was resolved as sister group to the *Burchellia*–Octotropideae clade (PP, 1.00; BS, 65%), and a clade comprising Bertiereae and Coffeae (PP, 1.00; BS, 98%), in turn, formed a sister group to this clade (PP, 1.00; BS, 100%). Strongly supported successive sister groups were Alberteae (PP, 1.00; BS, 85%), an *Augusta*–*Wendlandia* clade (PP, 1.00; BS, 100%) and an *Airosperma*–*Boholia* clade (PP, 1.00; BS 100%).

In the Vanguerieae alliance, Aleisanthiae formed a sister group to Ixoreae (PP, 1.00; BS, 100%) and this clade was, in turn, sister to Greeneae (PP, 1.00; BS, 100%). Relationships between the Aleisanthiae–Greeneae–Ixoreae clade, Vanguerieae and *Glionnetia* were unresolved. Although strongly supported by the BI analyses (PP, 1.00), the support for this trichotomy was low in the MP analysis (<50%). *Trailiaedoxa* was resolved as sister to the clade formed by this trichotomy. However, this clade also had low support (PP, 0.83; BS, 54%). Successive sister groups were *Scyphiphora* (PP, 1.00; BS, 87%), *Jackiopsis* (PP, 1.00; BS, 97%) and *Crossopteryx* (PP, 1.00; BS, 91%).

A grade of successive sister clades to core Ixoroideae comprised, in turn, Retiniphyllae (PP, 1.00; BS, 100%), *Steenisia* (PP, 1.00; BS, 100%) and a clade comprising the sister tribes Mussaendeae and Sabiceae (PP, 0.98; BS, 54%). The Mussaendeae–Sabiceae clade was well supported (PP, 1.00; BS, 96%). A Condamineae–Henriquezieae–Posoquerieae–Sipaneae clade was resolved as the earliest diverging clade in relation to the rest of the subfamily. However, the support for this clade was low (PP, 0.79; BS, 72%). Subfamily Ixoroideae received strong support (PP, 1.00; BS, 100%).

## DISCUSSION

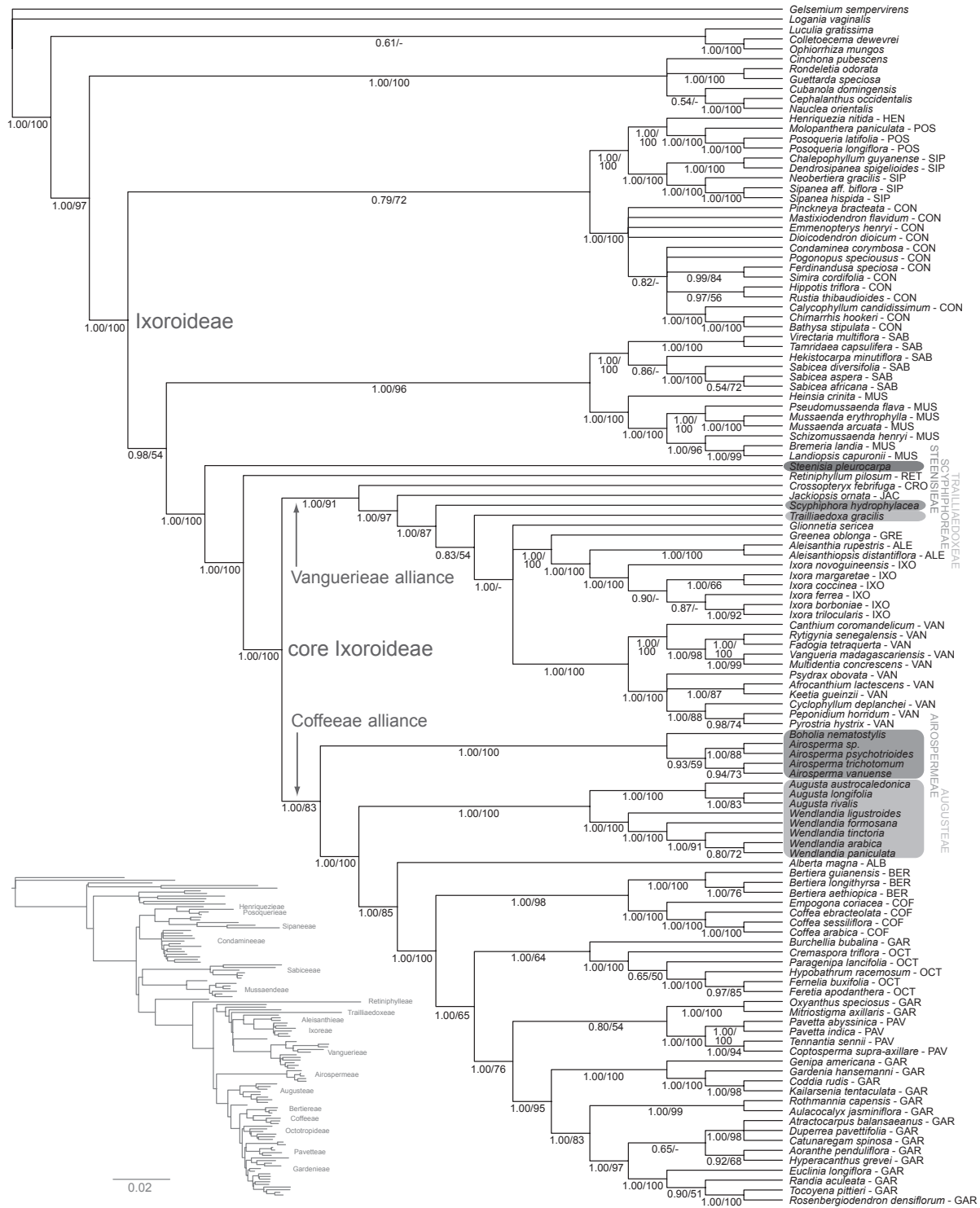
In this study, we infer the tribal relationships in Ixoroideae by the phylogenetic reconstruction of

six combined plastid regions. The phylogenetic hypotheses indicate that Ixoroideae can be considered as comprising the Coffeae alliance, the Vanguerieae alliance and a grade consisting of Retiniphyllae, *Steenisia*, Mussaendeae with Sabiceae and a Condamineae–Henriquezieae–Posoquerieae–Sipaneae clade (Fig. 2). Henriquezieae, Posoquerieae and Sipaneae form a clade, as in the study by Rova *et al.* (2002). This clade forms a weakly supported sister group to Condamineae, and the Condamineae–Henriquezieae–Posoquerieae–Sipaneae clade is, in turn, sister group to the remainder of the subfamily. This is congruent with the results of Rydin *et al.* (2009). However, in the phylogenetic hypotheses of Kainulainen *et al.* (2009), Condamineae appeared closer to core Ixoroideae. Further research is needed in order to better understand the relationships of these early divergent lineages. As in previous studies (Rova *et al.*, 2002; Bremer & Eriksson, 2009; Kainulainen *et al.*, 2010), the resolution in Condamineae was low.

In the phylogenetic tree presented, Mussaendeae is resolved as sister group to Sabiceae with strong support, in agreement with the results of Alejandro, Razafimanambison & Liede-Schumann (2005). As, in their study, *Heinsia* DC. forms a sister group to the remaining genera of the tribe, and *Mussaenda* L. forms a clade with *Pseudomussaenda* Wernham., *Schizomussaenda* H.L.Li (Fig. 1B) from South-East Asia is here further resolved as sister group to a clade comprising the Malagasy–Mascarene genera *Bremeria* Razafim. & Alejandro (Fig. 1C) and *Landiopsis* Capuron ex Bosser. In Sabiceae, *Virectaria* Bremek. is resolved as sister group to *Tamridaea* Thulin & B. Bremer, as in previous studies by Bremer & Thulin (1998) and Khan *et al.* (2008). These genera, together with *Hekistocarpa*, have been suggested as constituting a clade recognized at tribal level (Virectarieae *s.l.*, based on molecular data) by Dessein *et al.* (2001), and the three genera also formed a well-supported clade in the study by Bremer & Eriksson (2009). These relationships are not supported in our study, in which *Hekistocarpa* instead forms a poorly supported sister group to *Sabicea* Aubl. However, previously, *Hekistocarpa* has also been resolved as sister group to the remaining Sabiceae (Khan *et al.*, 2008; based on nrDNA data). Phylogenetic relationships in this tribe should be investigated further. The position of *Retiniphyllum* indicated in this study conforms with that first found in the study by Rova *et al.* (2002). Cortés-B., Delprete & Motley (2009) have subsequently demonstrated the monophyly of the monogeneric Retiniphyllae.

The South-East Asian genus *Steenisia* (Fig. 1E) was segregated from *Neurocalyx* Hook. (subfamily Rubioideae) by Bakhuizen van den Brink (1952). In a





**Figure 2.** The majority-rule consensus tree from the Bayesian inference analysis of the combined plastid data (*ndhF*, *matK*, *rbcL*, *rps16* intron, *trnS-G* and *trnT-F*). Posterior probabilities and bootstrap support values from the parsimony analysis are indicated below the clades (a dash indicates bootstrap support of <50%). Phylogram of the tree with the highest marginal likelihood in inset. New tribal names presented in this article are highlighted. ALB, Alberteae; ALE, Alesanthieae; BER, Bertiereae; COF, Coffeae; CON, Condamineae; CRO, Crossopterygeae; GAR, Gardenieae; GRE, Greeneae; HEN, Henriquezieae; IXO, Ixoreae; JAC, Jackieae; MUS, Mussaendeae; OCT, Octotropideae; PAV, Pavetteae; POS, Posoquerieae; RET, Retiniphyllae; SAB, Sabiceae; SIP, Sipaneeae; VAN, Vanguerieae.

revision of the genus, Bremer (1984) proposed that it should be transferred from Argostemmatae to Rondeletieae (subfamily Cinchonoideae). However, in the molecular phylogenetic study of Bremer & Eriksson (2009), *Steenisia* was found nested in Ixoroideae. *Steenisia* can be readily characterized by a suffrutescent unicaulous habit, rotate corolla and anthers with apical appendages fused to form a hollow cone around the style (in a manner reminiscent of the flowers of *Solanum* L.), characters which are all unusual (the latter unique) in Ixoroideae. A region of the style covered with hairs that probably catch released pollen is usually found level with the pollen sacs (Bremer, 1984; Puff *et al.*, 1995). However, as this region does not appear to extend above the surrounding staminal tube, pollen is not presented in a secondary manner. Instead, the mode of pollination is most likely by buzz pollination (Puff *et al.*, 1995). *Steenisia* is not associated with any previously described tribe in our analyses and, consequently, the recognition of the *Steenisia* clade at the tribal level is proposed in the Taxonomic synopsis section.

#### THE VANGUERIEAE ALLIANCE

The Vanguerieae alliance comprises Aleisanthieae, Crossopterygeae, *Glionnetia*, Greeneae, Ixoreae, Jackieae, *Scyphiphora*, *Trailliaedoxa* and Vanguerieae. The clades resolved in Vanguerieae in this study are congruent with the results of Lantz & Bremer (2004). However, the position of *Psydrax* Gaertn. is here further resolved in a clade consisting of *Afrocanthium* (Bridson) Lantz & B. Bremer, *Keetia* E. Phillips and a clade comprising *Cyclophyllum* Hook. f., *Peponidium* (Baill.) Arènes and *Pyrostria* Comm. ex Juss., representing the 'dioecious group' of Razafimandimbison *et al.* (2009). In agreement with the results of Rova *et al.* (2002) and Mouly *et al.* (2009a), Ixoreae forms a sister group to Aleisanthieae, and these are, in turn, sister to Greeneae. *Aleisanthia* and *Greenea* both have traditionally been considered part of Rondeletieae (Hooker, 1873), a tribe characterized by contorted or imbricate corolla aestivation and capsular fruits. Molecular phylogenetic studies have indicated that this is an unnatural group, and Rondeletieae has since been much reduced (see Rova *et al.*, 2002; Manns & Bremer, 2010; Rova, Delprete & Bremer, 2009).

*Glionnetia* (Fig. 1G), an endemic of the Seychelles, has also been suggested as part of Rondeletieae by its author (Tirvengadam, 1984). However, in a recent study by Razafimandimbison *et al.* (2011), *Glionnetia* was found nested in the Vanguerieae alliance, although with an unresolved position relative to Vanguerieae and the Aleisanthieae–Greeneae–Ixoreae clade (Rondeletieae s.s. can consequently be consid-

ered as restricted to the New World; cf. Manns & Bremer, 2010). Despite the inclusion of more sequence data in this study, the phylogenetic position of *Glionnetia* is still unresolved.

As in the study by Razafimandimbison *et al.* (2011), successive sister groups to the Aleisanthieae–*Glionnetia*–Greeneae–Ixoreae clade are *Trailliaedoxa*, *Scyphiphora*, Jackieae and Crossopterygeae. The little-studied *Trailliaedoxa* has hitherto remained without taxonomic placement in Rubiaceae. It occurs in the highlands of southern China, although it has rarely been collected. *Trailliaedoxa* is an erect shrublet with minute schizocarpic fruits with solitary pendulous ovules. The corolla aestivation is left-contort. Whether or not secondary pollen presentation occurs is not known. Our results support the recognition of a monogeneric tribe, Trailliaedoxeae (see Taxonomic synopsis section).

The mangrove plant *Scyphiphora* (Fig. 1F) occurs in coastal areas of tropical Asia and the western Pacific (Puff & Rohrhofer, 1993). *Scyphiphora* has a complex taxonomic history (see Puff & Rohrhofer, 1993; Mouly *et al.*, 2009a), as the highly modified fruits, in particular, which are adapted for sea dispersal, have caused difficulties in assessing its systematic placement. The fruits are indehiscent and corky, with one ascending and one descending ovule per locule (Puff & Rohrhofer, 1993). However, the flowers have secondary pollen presentation and left-contort corolla aestivation, characteristics shared by most of the core Ixoroideae. Andreasen & Bremer (2000) tentatively included the genus in Ixoreae. However, in the studies by Bremer *et al.* (1999), Bremer & Eriksson (2009) and Cortés-B. *et al.* (2009), *Scyphiphora* was resolved as sister to the Ixoreae–Vanguerieae clade, a position congruent with this study, in which *Scyphiphora* is resolved as sister to the Aleisanthieae–*Glionnetia*–Greeneae–Ixoreae–*Trailliaedoxa*–Vanguerieae clade. Consequently, we propose the recognition of tribe Scyphiphoreae (see Taxonomic synopsis section).

#### THE COFFEEAE ALLIANCE

The Coffeeae alliance comprises *Airosperma*, *Augusta*, *Boholia*, *Wendlandia* and tribes Alberteae, Coffeae, Gardenieae, Octotropideae and Pavetteae. As in previous molecular studies (Andreasen & Bremer, 1996; Bremer & Eriksson, 2009), Gardenieae is not monophyletic. *Mitriostigma* (Fig. 1M) and *Oxyanthus* form a poorly supported sister group to Pavetteae, and *Burchellia* forms a sister group to Octotropideae. Further research is needed to better understand the phylogenetic relationships in the Gardenieae–Octotropideae–Pavetteae complex. Successive sister groups to this complex are the Bertiereae–Coffeae

clade, Alberteae, the *Augusta*–*Wendlandia* clade and the *Airosperma*–*Boholia* clade. The included representatives of *Bertiera* form a monophyletic group sister to Coffeae, a relationship also inferred in other studies (e.g. Bremer *et al.*, 1995; Persson, 2000; Davis *et al.*, 2007; see the latter for a discussion on the delimitation and morphological differentiation of these tribes, which some authors have treated as one, i.e. Andreasen & Bremer, 2000; Robbrecht & Manen, 2006).

*Augusta* and *Wendlandia* have traditionally (Hooker, 1873) been considered as part of Rondeletieae. However, in the molecular phylogenetic study of Rova *et al.* (2002), they were resolved as a clade in Ixoroideae. Both genera have widely disjunct distributions. In *Augusta*, *A. longifolia* occurs in north-eastern and central Brazil (Delprete, 1997), *A. rivalis* (Fig. 1I) in Central America, *A. austrocaledonica* in New Caledonia and *A. vitiensis* (Seem.) J.H. Kirkbr. in Fiji. The last three species have previously been recognized as *Lindenia*, a name that was reduced to synonymy by Kirkbride (1997). This is supported by our results, because *A. rivalis* and *A. austrocaledonica* are paraphyletic with respect to *A. longifolia* (Fig. 2). *Wendlandia* (Fig. 1J) has a wide distribution in East Asia and Australasia (centre of diversity in China), with one species, *W. ligustroides*, in south-eastern Turkey–northern Iraq and one species, *W. arabica*, in Ethiopia, Somalia and Yemen (see Puff, 1990). Cowan (1932), who provided the last comprehensive revision of the genus, considered the last two species as exceptional, and their inclusion in *Wendlandia* as doubtful. However, *Wendlandia* appears to be monophyletic in our phylogenetic analyses, in which *W. ligustroides* forms a sister group to the remaining included species, whereas *W. arabica* is nested in the East Asian clade. Secondary pollen presentation appears to be absent in *Wendlandia* (D. Zhang, South China Botanical Garden, Guangzhou, Guangdong, China, pers. comm.). The status of this character in *Augusta* is not known. Both genera have left-contorted corolla aestivation. In the Coffeae alliance, the *Augusta*–*Wendlandia* clade is distinguished by capsular fruits. This clade is not associated with any previously described tribe; consequently, we propose that it should be recognized at tribal level (see Taxonomic synopsis section).

*Airosperma* and *Boholia* were placed in Alberteae by their respective authors (Schumann & Lauterbach, 1900; Merrill, 1926) based on the presence of solitary pendulous ovules and contorted corolla aestivation. *Boholia* occurs in the Philippines, but has also been collected on the island of Flores in Indonesia (Schmutz 2691; P; image seen). *Airosperma* has a disjunct distribution, occurring in New Guinea and the Fiji islands (in the phylogenetic hypothesis, the

included species from the respective areas form sister groups). One of the Fijian species, *A. trichotomum*, was originally described by Gillespie (1932) as *Abramsia trichotoma*. Smith (1945: 108) considered the generic concepts as ‘essentially identical’ and subsumed *Abramsia*. This synonymization is supported by the molecular data, because *A. trichotomum* is nested in *Airosperma*, forming a sister group to *A. vanuense* S.P. Darwin (Fig. 2). Secondary pollen presentation is not present in *Airosperma* (Darwin, 1979) and at least some of the New Guinean species of the genus appear to be functionally dioecious (Darwin, 1980). The status of this character in *Boholia* is not known. Although having been described as right-contorted or imbricate, the corolla aestivation is left-contorted in both genera (K. Kainulainen, pers. observ.). The fruits are fleshy and contain pyrenes, and were interpreted by Robbrecht (1988) as adapted for dispersal by sea currents. However, animal dispersal also seems a possibility considering the vivid colour of the fruits (blue–purple, white or yellow; Darwin, 1980). In this study, as in that of Kainulainen *et al.* (2009), they form a clade separate from Alberteae; consequently, we propose that this clade should be recognized at the tribal level (see Taxonomic synopsis section).

## TAXONOMIC SYNOPSIS

Following the results of the molecular phylogenetic analyses, we present here a revised tribal classification of Ixoroideae, although we do not address the tribal delimitation in the problematic Gardenieae complex, i.e. Gardenieae, Octotropideae (including Cremasporeae) and Pavetteae, which will be discussed further by A. Mouly *et al.* (Université de Franche-Comté, Besançon; unpubl. data). Including these three tribes, Ixoroideae comprises 24 tribes, five of which are newly and formally described below. Although the molecular support for Ixoroideae is strong, morphologically the members are diverse and not easily characterized; no potential morphological synapomorphies for the subfamily are known at this point. In particular, Condamineae and Henriquezieae contain morphologically aberrant genera (Rogers, 1984; Kainulainen *et al.*, 2010), some of which, at times, have been classified outside Rubiaceae [e.g. *Dialypetalanthus* Kuhl. in Dialypetalanthaceae (Rizzini & Occhioni, 1949) and *Henriquezia* Spruce ex Benth. and *Platycarpum* Humb. & Bonpl. in Henriqueziaceae (Bremekamp, 1957)].

### SUBFAMILY IXOROIDEAE RAF.

Trees, shrubs, monocaulous treelets, subshrubs or rarely herbs. Raphides absent. Stipules entire, bifid



or rarely fimbriate; interpetiolar or rarely intrapetiolar. Flowers usually actinomorphic, protandrous, often with secondary pollen presentation; rarely zygomorphic, heterostylous, dioecious, monoecious or protogynous. Calyces mostly persistent, in several taxa with one or several lobes expanded and showy. Corolla aestivation contorted to left, rarely to right, imbricate, valvate or rarely open. Fruits fleshy and indehiscent, dry and indehiscent or capsular, with numerous, few or solitary ovules per locule.

*Tribe Airospermeae Kainul. & B.Bremer, trib. nov.*

*Type: Airosperma K.Schum. & Lauterb., Fl. Schutzgeb. Südsee: 565 (1900)*

Suffrutices, frutices vel arbusculae unicaules. Flores 5-meri in paniculis terminalibus. Calyx persistens. Corolla brevi- vel longi-tubularis, lobis in aestivatione sinistrorsum contortis. Ovarium biloculare, ovulo uno pendulo in quoque loculo. Stylus inclusus vel (longi-) exsertus. Fructus carnosus, pyrenis duabus, in maturitate azureo-purpurei, albidi vel lutescentes.

Unicaulous subshrubs, shrubs or small trees. Flowers 5-merous in terminal panicles. Calyx persistent. Corolla short- to long-tubular, with left-contorted aestivation. Ovary bilocular, with one pendulous ovule in each locule. Style included to (long-)exserted. Fruits fleshy, with two pyrenes, becoming blue-purple, whitish or yellowish in maturity.

*Included genera: Airosperma* with six species in Fiji and New Guinea, and the monotypic *Boholia* from the Philippines and the island of Flores, Indonesia.

*Tribe Alberteae Hook.f.*

For descriptions, see Puff *et al.* (1984), Robbrecht (1988) and Kainulainen *et al.* (2009).

*Distribution:* South-east Africa and Madagascar.

*Included genera (here investigated): Alberta.*

Included based on Kainulainen *et al.* (2009): *Nematostylis* Hook.f and *Razafimandimbisonia* Kainul. & B.Bremer.

*Tribe Aleisanthieae Mouly, J.Florence & B.Bremer*

For descriptions, see Mouly *et al.* (2009a) and Alejandro *et al.* (2010).

*Distribution:* South-East Asia.

*Included genera (here investigated): Aleisanthia* and *Aleisanthiopsis*.

Inclusion based on Alejandro *et al.* (2010): *Greeniopsis*, occurring in South-East Asia.

*Tribe Augusteae Kainul. & B.Bremer, trib. nov.*

*Type: Augusta Pohl, Pl. Bras. Icon. Descr. 2: 1 (1828)*

Frutices vel arbusculae. Inflorescentiae cymae terminales compositae aut raro corymbi. Flores 5-meri. Calyx persistens. Corolla tubulari-infundibuliformis, lobis in aestivatione sinistrorsum contortis. Ovarium biloculare, ovulis numerosis horizontaliter insertis. Stylus exsertus. Fructus capsulares, dehiscentia septicida (*Augusta*) aut loculicida (*Wendlandia*). Semina minuta, complanata, testa reticulata.

Shrubs to small trees. Inflorescences terminal compound cymes or rarely corymbs. Flowers 5-merous. Calyx persistent. Corolla tubular-funnel-shaped, with left-contorted aestivation. Ovary bilocular, with numerous ovules horizontally inserted. Style exserted. Fruits capsular, with septicidal (*Augusta*) or loculicidal (*Wendlandia*) dehiscence. Seeds minute, compressed, with reticulate testa.

*Included genera: Augusta*, with four species occurring in Mexico, north-eastern and central Brazil, the Fiji islands and New Caledonia, and *Wendlandia* (c. 80 spp.), occurring in north-eastern Africa, west Asia, South-East Asia and northern Australia.

*Tribe Bertiereae Bridson*

For a description, see Bridson & Verdcourt (2003). Bertiereae as currently defined is monogeneric.

*Distribution:* Tropical South America to southern Mexico, tropical Africa, Madagascar and Mascarenes.

*Included genus: Bertiera.*

*Tribe Coffeae DC.*

For a description, see Davis *et al.* (2007). Recent taxonomic changes have been made by Tosh *et al.* (2009; resurrection of *Empogona* Hook.f.) and Davis *et al.* (2011; inclusion of *Psilanthus* Hook.f. in *Coffea*).

*Distribution:* Tropical Africa, Madagascar, Comores, Mascarenes, Seychelles and tropical Asia to Australia.

*Included genera (here investigated): Coffea* and *Empogona*.

Inclusion based on Davis *et al.* (2007): *Argocoffeopsis* Lebrun, *Belonophora* Hook.f., *Calycosiphonia* Pierre ex Robbr., *Diplospora* DC., *Discospermum*

Dalzell, *Nostolachma* T.Durand, *Sericanthe* Robbr., *Tricalysia* A.Rich. ex DC. and *Xantonnea* Pierre ex Pit.

*Tribe Condamineae Hook.f.*

For a description, see Kainulainen *et al.* (2010).

*Distribution:* Neotropics, south-eastern USA (*Pinckneya* Michx.), South-East Asia (*Emmenopterys* Oliv.) and the Malesia-Pacific region (*Dolicholobium* A.Gray, *Mastixiodendron* Melch. and *Mussaendopsis* Baill.).

*Included genera (here investigated):* *Bathysa* C.Presl, *Calycophyllum* DC., *Chimarrhis* Jacq., *Condaminea* DC., *Dioicodendron* Steyerl., *Emmenopterys*, *Ferdinandusa* Pohl, *Hippotis* Ruiz & Pav., *Mastixiodendron*, *Pinckneya*, *Pogonopus* Klotzsch, *Rustia* Klotzsch and *Simira* Aubl.

Inclusion based on Kainulainen *et al.* (2010): *Alseis* Schott, *Bothriospora* Hook.f., *Capirona* Spruce, *Dialypetalanthus*, *Dolichodelphys* K.Schum. & K.Krause, *Dolicholobium*, *Elaeagia* Wedd., *Holtonia* Standl., *Macbrideina* Standl., *Macrocnemum* P.Browne, *Mussaendopsis*, *Parachimarrhis* Ducke, *Pentagonia* Benth., *Picardaea* Urb., *Schizocalyx* Wedd., *Semaphyllanthe* L.Andersson, *Sommerera* Schltldl., *Tammsia* H.Karst., *Warszewiczia* Klotzsch and *Wittmackanthus* Kuntze.

*Tribe Crossopterygeae F.White ex Bridson*

For a description, see Bridson & Verdcourt (2003). Crossopterygeae as currently defined is monogeneric.

*Distribution:* Tropical Africa.

*Included genus: Crossopteryx.*

*Tribe Greeneae Mouly, J.Florence & B.Bremer*

For a description, see Mouly *et al.* (2009a).

*Distribution:* South-East Asia.

*Included genera (here investigated): Greenea.*

Inclusion based on Mouly *et al.* (2009a): *Spathichlamys* R.Parker.

*Tribe Henriquezieae Hook.f.*

For a description, see Rogers (1984).

*Distribution:* Tropical South America.

*Included genera (here investigated): Henriquezia.*

Inclusion based on Rogers (1984) and Delprete & Cortés-B. (2004): *Gleasonia* Standl. and *Platycarpum*.

*Tribe Ixoreae A.Gray.*

For descriptions, see Mouly *et al.* (2009a, b). Ixoreae as currently defined is monogeneric.

*Distribution:* Neotropics, tropical Africa, Madagascar, Comores, Mascarenes, Seychelles, tropical Asia to the Pacific.

*Included genus: Ixora.*

*Tribe Jackieae Korthals*

For descriptions, see Ridsdale (1979) and Razafimandimbison *et al.* (2011). Jackieae as currently defined is monogeneric.

*Distribution:* South-East Asia.

*Included genus: Jackiopsis.*

*Tribe Mussaendeae Hook.f.*

For descriptions, see Alejandro *et al.* (2005).

*Distribution:* Tropical Africa, Madagascar, Mascarenes, South-East Asia to the Pacific.

*Included genera (here investigated): Bremeria, Heinsia, Landiopsis, Mussaenda, Pseudomussaenda and Schizomussaenda.*

Inclusion based on Tange (1994): *Neomussaenda* Tange.

*Tribe Posoquerieae Delprete*

For a description, see Delprete (2009).

*Distribution:* Neotropics.

*Included genera: Molopanthera* Turcz. and *Posoqueria* Aubl.

*Tribe Retiniphyllae Hook.f.*

For a description, see Robbrecht (1988). Retiniphyllae as currently defined is monogeneric.

*Distribution:* Tropical South America.

*Included genus: Retiniphyllum.*

*Tribe Sabiceae Bremek.*

For a description, see Khan *et al.* (2008).

*Distribution:* Neotropics, Tropical Africa, Madagascar, São Tomé, Socotra, and Sri Lanka.

*Included genera:* *Hekistocarpa*, *Sabicea*, *Tamridaea* and *Virectaria*.

*Tribe Scyphiphoreae Kainul. & B. Bremer, trib. nov.*  
*Type:* *Scyphiphora* C.F. Gaertn., *Suppl. Carp.*: 91 (1806)

Frutices vel arbusculae. Flores 4(–5)-meri, in thyrsis axillaribus. Calyx tubularis, brevis, persistens, lobis indistinctis. Corolla tubularis, lobis in aestivatione sinistrorsum contortis. Ovarium biloculare, ovulo uno ascendenti et uno descendenti in quoque loculo. Stylus exsertus. Fructus sicci, indehiscentes, porcati, mesocarpio extenso.

Shrubs or small trees. Flowers 4(–5)-merous, in axillary thyrses. Calyx tubular, short, persistent, with indistinct lobes. Corolla tubular, with left-contorted aestivation. Ovary bilocular, with one ascending and one descending ovule in each locule. Style exserted. Fruits dry, indehiscent, ridged, with extensive mesocarp.

*Included genus:* The monotypic *Scyphiphora*, occurring in tropical Asia and the western Pacific.

*Tribe Sipaneeae Bremek.*

For a description, see Delprete & Cortés-B. (2004).

*Distribution:* Central America and tropical South America.

*Included genera (here investigated):* *Chalepophyllum* Hook.f., *Dendrosipanea* Ducke, *Neobertiera* Wernham and *Sipanea* Aubl.

Inclusion based on Delprete & Cortés-B. (2004): *Limnosipanea* Hook.f., *Maguireothamnus* Steyerf., *Neblinathamnus* Steyerf., *Pteridocalyx* Wernham, *Sipaneopsis* Steyerf. and *Steyermarkia* Standl.

*Tribe Steenisiae Kainul. & B. Bremer, trib. nov.*

*Type:* *Steenisia* Bakh.f., *Webbia* 8: 381 (1952)

Suffrutices unicaules. Flores 4–5-meri, in thyrsis axillaribus. Calyx persistens, interdum uno lobo post anthesin expanso. Corolla rotata, lobis in aestivatione sinistrorsum contortis. Ovarium biloculare, ovulis numerosis horizontaliter insertis. Stylus curvatus. Antherae appendicibus apicalibus prolongatis, connatis tubumque stamineum stylum cingentem facientibus. Fructus capsulares septicales. Semina minuta, complanata, testa reticulata granulata.

Unicaulous subshrubs. Flowers 4–5-merous, in axillary thyrses. Calyx persistent, sometimes with one lobe expanding after anthesis. Corolla rotate, with left-contorted aestivation. Ovary bilocular, with numerous ovules horizontally inserted. Style curved. Anthers with extended apical appendages, united and

forming a tube surrounding the style. Fruits septical capsules. Seeds minute, flattened, with a reticulate, granulate testa.

*Included genus:* *Steenisia*, with five species in Sundaland (Borneo, Natuna Islands and Peninsular Malaysia).

*Tribe Trailliaedoxae Kainul. & B. Bremer, trib. nov.*  
*Type:* *Trailliaedoxa* W.W. Sm. & Forrest, *Notes Roy. Bot. Gard. Edinburgh* 10: 74 (1917)

Fruticuli erecti. Flores minuti, 5-meri, in cymis terminalibus. Calyx persistens. Corolla infundibuliformis, lobis in aestivatione sinistrorsum contortis. Ovarium biloculare, ovulo uno pendulo in quoque loculo. Stylus exsertus. Fructus schizocarpi.

Erect shrublets. Flowers minute, 5-merous, in terminal cymes. Calyx persistent. Corolla funnel-shaped, with left-contorted aestivation. Ovary bilocular, with one pendulous ovule in each locule. Style exserted. Fruits schizocarpous.

*Included genus:* The monotypic *Trailliaedoxa*, occurring in south-western China (Sichuan, Yunnan).

*Tribe Vanguerieae A. Rich. ex Dum.*

For descriptions, see Robbrecht (1988) and Lantz & Bremer (2004).

*Distribution:* Southern Africa, tropical Africa, Madagascar, Comores, Mascarenes, Seychelles, (sub-) tropical Asia to Australia and the Pacific.

*Included genera (here investigated):* *Afrocanthium*, *Canthium* Lam., *Cyclophyllum*, *Fadogia* Schweinf., *Keetia*, *Multidentia* Gilli, *Peponidium*, *Psydrax*, *Pyrostria*, *Rytigynia* Blume and *Vangueria* Juss.

Inclusion based on Robbrecht (1988), Lantz & Bremer (2004) and Razafimandimbison *et al.* (2009): *Bullockia* (Bridson) Razafim., Lantz & B. Bremer, *Cuviera* DC., *Eriosemopsis* Robyns, *Everistia* S.T. Reynolds & R.J.F. Hend., *Fadogiella* Robyns, *Hutchinsonia* Robyns, *Perakanthus* Robyns ex Ridl., *Plectroniella* Robyns, *Pygmaeoathamnus* Robyns, *Robynsia* Hutch., *Temnocalyx* Robyns ex Ridl., *Vangueriella* Verdc. and *Vangueriopsis* Robyns.

## CONCLUSIONS

Here, we analysed the tribal relationships and delimitation in Ixoroideae using six plastid DNA regions and Bayesian and parsimony methods of phylogenetic reconstruction. Following the results of this study, Ixoroideae can be considered as being composed of two well-supported lineages, the Coffeae alliance and the Vanguerieae alliance, and a grade consisting of the



tribes Condamineae, Henriquezieae, Mussaendeae, Posoquerieae, Retiniphylleae, Sabiceae, Sipaneeae and Steenisieae. The Vanguerieae alliance comprises *Glionnetia* (with unplaced tribal position) and the tribes Aleisanthieae, Crossopterygeae, Greeneae, Ixoreae, Jackieae, Scyphiphoreae, Trailliaedoxeae and Vanguerieae. The Coffeae alliance contains Airospermeae, Alberteae, Augusteae, Bertiereae, Coffeae, Gardenieae, Octotropideae and Pavetteae. Molecular data furthermore support the transfer of *Abramsia* to *Airosperma* and *Lindenia* to *Augusta*. Future studies should further investigate the phylogenetic positions of *Glionnetia* and *Hekistocarpa* and the relationships of the early divergent Condamineae and Henriquezieae–Posoquerieae–Sipaneeae clades with respect to the rest of the subfamily.

#### ACKNOWLEDGEMENTS

We thank the curators of the herbaria AAU, BR, GB, HUH, L, MO, S and UPS for providing loans and/or access to collections. We also thank Anbar Khodabandeh for laboratory assistance, Claes Persson for DNA samples, Christian Puff and the Missouri Botanical Garden for photographs and Dianxiang Zhang for sharing unpublished information on *Wendlandia*. Per Ola Karis and Philip Oswald checked the Latin diagnoses. Piero Delprete and two anonymous reviewers provided helpful comments on the manuscript. The Knut and Alice Wallenberg Foundation and the Swedish Research Council provided financial support to BB.

#### REFERENCES

- Alejandro GD, Meve U, Uy M, Mouly A, Thiev M, Liede-Schumann S. 2010. Molecular support of the classification of *Greeniopsis* Merr. in Aleisanthieae (Rubiaceae), with a revision of the genus. *Taxon* **59**: 1547–1564.
- Alejandro GD, Razafimandimbison SG, Liede-Schumann S. 2005. Polyphyly of *Mussaenda* inferred from ITS and *trnT-F* data and its implication for generic limits in Mussaendeae (Rubiaceae). *American Journal of Botany* **92**: 544–557.
- Andersson L, Antonelli A. 2005. Phylogeny of the tribe Cinchoneae (Rubiaceae), its position in Cinchonoideae, and description of a new genus, *Ciliosemina*. *Taxon* **54**: 17–28.
- Andersson L, Rova JHE. 1999. The *rps16* intron and the phylogeny of the Rubioideae (Rubiaceae). *Plant Systematics and Evolution* **214**: 161–186.
- Andreasen K, Baldwin BG, Bremer B. 1999. Phylogenetic utility of the nuclear rDNA ITS region in subfamily Ixoroideae (Rubiaceae): comparisons with cpDNA *rbcL* sequence data. *Plant Systematics and Evolution* **217**: 119–135.
- Andreasen K, Bremer B. 1996. Phylogeny of the subfamily Ixoroideae (Rubiaceae). *Opera Botanica Belgica* **7**: 119–138.
- Andreasen K, Bremer B. 2000. Combined phylogenetic analysis in the Rubiaceae–Ixoroideae: morphology, nuclear and chloroplast DNA data. *American Journal of Botany* **87**: 1731–1748.
- Backlund M, Bremer B, Thulin M. 2007. Paraphyly of Paederieae, recognition of Putorieae and expansion of *Plocama* (Rubiaceae–Rubioideae). *Taxon* **56**: 315–328.
- Backlund M, Oxelman B, Bremer B. 2000. Phylogenetic relationships within the Gentianales based on *ndhF* and *rbcL* sequences, with particular reference to the Loganiaceae. *American Journal of Botany* **87**: 1029–1043.
- Bakhuizen van den Brink RC Jr. 1952. ‘*Steenisia*’ a new genus of Malaysian Rubiaceae. *Webbia* **8**: 381–382.
- Bremekamp CEB. 1952. The African species of *Oldenlandia* L *sensu* Hiern et K. Schumann. *Verhandelingen der Koninklijke Nederlandsche Akademie van Wetenschappen, Afdeling Natuurkunde, Tweede sectie* **18**: 1–297.
- Bremekamp CEB. 1957. On the position of *Platycarpum* Humb. et Bonpl., *Henriquezia* Spruce and *Gleasonia* Standl. *Acta Botanica Neerlandica* **6**: 351–377.
- Bremekamp CEB. 1966. Remarks on the position, the delimitation and the subdivision of the Rubiaceae. *Acta Botanica Neerlandica* **15**: 1–33.
- Bremer B. 1984. The genus *Steenisia* (Rubiaceae) and its taxonomic position. *Nordic Journal of Botany* **4**: 333–345.
- Bremer B, Andreasen K, Olsson D. 1995. Subfamilial and tribal relationships in the Rubiaceae based on *rbcL* sequence data. *Annals of the Missouri Botanical Garden* **82**: 383–397.
- Bremer B, Bremer K, Heidari N, Erixon P, Olmstead RG, Anderberg AA, Källersjö M, Barkhordarian E. 2002. Phylogenetics of asterids based on 3 coding and 3 non-coding chloroplast DNA markers and the utility of non-coding DNA at higher taxonomic levels. *Molecular Phylogenetics and Evolution* **24**: 274–301.
- Bremer B, Eriksson T. 2009. Time tree of Rubiaceae: phylogeny and dating the family, subfamilies, and tribes. *International Journal of Plant Sciences* **170**: 766–793.
- Bremer B, Jansen RK, Oxelman B, Backlund M, Lantz H, Kim KJ. 1999. More characters or more taxa for a robust phylogeny – case study from the coffee family (Rubiaceae). *Systematic Biology* **48**: 413–435.
- Bremer B, Thulin M. 1998. Collapse of Isertieae, re-establishment of Mussaendeae, and a new genus of Sabiceae (Rubiaceae); phylogenetic relationships based on *rbcL* data. *Plant Systematics and Evolution* **211**: 71–92.
- Bridson DM, Verdcourt B. 2003. Rubiaceae. In: Pope GV, ed. *Flora Zambesiaca, vol. 5, part 3*. London: Royal Botanic Gardens, Kew, 379–720.
- Cortés-B. R, Delprete PG, Motley TJ. 2009. Phylogenetic placement of the tribe Retiniphylleae among the subfamily Ixoroideae (Rubiaceae). *Annals of the Missouri Botanical Garden* **96**: 61–67.
- Cowan JM. 1932. The genus *Wendlandia*. *Notes from the Royal Botanic Garden, Edinburgh* **16**: 233–314.
- Darwin SP. 1976. Subfamilial, tribal and sub-tribal nomenclature of Rubiaceae. *Taxon* **25**: 595–610.
- Darwin SP. 1979. A synopsis of the indigenous genera of the Pacific Rubiaceae. *Allertonia* **2**: 1–44.

- Darwin SP. 1980.** Notes on *Airosperma* (Rubiaceae), with a new species from Fiji. *Journal of the Arnold Arboretum* **61**: 95–105.
- Davis AP, Chester M, Maurin O, Fay MF. 2007.** Searching for the relatives of *Coffea* (Rubiaceae, Ixoroideae): the circumscription and phylogeny of Coffeae based on plastid sequence data and morphology. *American Journal of Botany* **94**: 313–329.
- Davis AP, Govaerts R, Bridson DM, Ruhsam M, Moat J, Brummitt NA. 2009.** A global assessment of distribution, diversity, endemism, and taxonomic effort in the Rubiaceae. *Annals of the Missouri Botanical Garden* **96**: 68–78.
- Davis AP, Tosh J, Ruch N, Fay MF. 2011.** Growing coffee: *Psilanthus* (Rubiaceae) subsumed on the basis of molecular and morphological data; implications for the size, morphology, distribution and evolutionary history of *Coffea*. *Botanical Journal of the Linnean Society* **167**: 357–377.
- Delprete PG. 1997.** Revision and typification of Brazilian *Augusta* (Rubiaceae, Rondeletieae), with ecological observation on riverine vegetation of cerrado and Atlantic forest. *Brittonia* **49**: 487–497.
- Delprete PG. 2009.** Taxonomic history, morphology, and reproductive biology of the tribe Posoquerieae (Rubiaceae, Ixoroideae). *Annals of the Missouri Botanical Garden* **96**: 79–89.
- Delprete PG, Cortés-B. R. 2004.** A phylogenetic study of the tribe Sipaneeae (Rubiaceae, Ixoroideae), using *trnL-F* and ITS sequence data. *Taxon* **53**: 347–356.
- Dessein S, Andersson L, Robbrecht E, Smets E. 2001.** *Hekistocarpa* (Rubiaceae): a member of an emended tribe Virectariae. *Plant Systematics and Evolution* **229**: 59–78.
- Doyle JJ, Dickson EE. 1987.** Preservation of plant-samples for DNA restriction endonuclease analysis. *Taxon* **36**: 715–722.
- Drummond AJ, Ho SY, Rawlence WN, Rambaut A. 2007.** *A rough guide to BEAST 1.4*. Auckland: University of Auckland.
- Endress ME, Sennblad B, Nilsson S, Civeyrel L, Chase MW, Huysmans S, Grafström E, Bremer B. 1996.** A phylogenetic analysis of Apocynaceae *s.str.* and some related taxa in Gentianales – a multidisciplinary approach. *Opera Botanica Belgica* **7**: 59–102.
- Gillespie JW. 1932.** New plants from Fiji—III. *Bernice P. Bishop Museum Bulletin* **91**: 1–81.
- Guindon S, Gascuel T. 2003.** A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. *Systematic Biology* **52**: 696–704.
- Hall TA. 1999.** BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* **41**: 95–98.
- Hooker JD. 1873.** Ordo LXXXIV: Rubiaceae. In: Bentham G, Hooker JD, eds. *Genera plantarum* 2. London: Lovell Reeve & Co., 7–151.
- Huelsenbeck JP, Ronquist F. 2001.** MrBayes: Bayesian inference of phylogeny. *Bioinformatics* **17**: 754–755.
- Kainulainen K, Mouly A, Khodabandeh A, Bremer B. 2009.** Molecular phylogenetic analysis of the tribe Alberteae (Rubiaceae), with description of a new genus, *Razafimandimbisonia*. *Taxon* **58**: 757–768.
- Kainulainen K, Persson C, Eriksson T, Bremer B. 2010.** Molecular systematics and morphological character evolution of the Condamineae (Rubiaceae). *American Journal of Botany* **97**: 1961–1981.
- Khan SA, Razafimandimbison SG, Bremer B, Liedes-Schumann S. 2008.** Sabiceae and Virectariae (Rubiaceae, Ixoroideae): one or two tribes? New tribal and generic circumscriptions of Sabiceae and biogeography of *Sabicea s.l.* *Taxon* **57**: 7–23.
- Kirkbride JH. 1997.** Manipulus rubiacearum VI. *Brittonia* **49**: 354–379.
- Lantz H, Bremer B. 2004.** Phylogeny inferred from morphology and DNA data: characterizing well-supported groups in Vanguerieae (Rubiaceae). *Botanical Journal of the Linnean Society* **146**: 257–283.
- Manns U, Bremer B. 2010.** Towards a better understanding of intertribal relationships and stable tribal delimitations within Cinchonoideae *s.s.* (Rubiaceae). *Molecular Phylogenetics and Evolution* **56**: 21–39.
- Merrill ED. 1926.** Additions to our knowledge of the Philippine flora, II. *Philippine Journal of Science* **29**: 475–496.
- Mouly A, Razafimandimbison SG, Achille F, Haevermans T, Bremer B. 2007.** Phylogenetic placement of *Rhopalobrachium fragrans* (Rubiaceae): evidence from molecular (*rps16* and *trnT-F*) and morphological data. *Systematic Botany* **32**: 872–882.
- Mouly A, Razafimandimbison SG, Florence J, Jérémie J, Bremer B. 2009a.** Paraphyly of *Ixora* and new tribal delimitation of Ixoreae (Rubiaceae): inference from combined chloroplast (*rps16*, *rbcL*, and *trnT-F*) sequence data. *Annals of the Missouri Botanical Garden* **96**: 146–160.
- Mouly A, Razafimandimbison SG, Khodabandeh A, Bremer B. 2009b.** Phylogeny and classification of the species-rich pantropical showy genus *Ixora* (Rubiaceae–Ixoreae) with indications of geographical monophyletic units and hybrids. *American Journal of Botany* **96**: 686–706.
- Novotny V, Basset Y, Miller SE, Weiblen GD, Bremer B, Cizek L, Drozd P. 2002.** Low host specificity of herbivorous insects in a tropical forest. *Nature* **416**: 841–844.
- Nylander JAA. 2004.** MrAIC.pl. Version 1.4.4. Program distributed by the author, Evolutionary Biology Centre, Uppsala University. Software. Available at: <http://www.abc.se/~nylander/> (Accessed on 12 April 2010).
- Olmstead RG, Bremer B, Scott K, Palmer JD. 1993.** A parsimony analysis of the Asteridae *sensu lato* based on *rbcL* sequences. *Annals of the Missouri Botanical Garden* **80**: 700–722.
- Oxelman B, Backlund M, Bremer B. 1999.** Relationships of the Buddlejaceae *s.l.* investigated using parsimony jackknife and branch support analysis of chloroplast *ndhF* and *rbcL* sequence data. *Systematic Botany* **24**: 164–182.
- Oxelman B, Lidén M, Berglund D. 1997.** Chloroplast *rps16* intron phylogeny of the tribe Sileneae (Caryophyllaceae). *Plant Systematics and Evolution* **206**: 393–410.
- Persson C. 2000.** Phylogeny of Gardenieae (Rubiaceae) based on chloroplast DNA sequences from the *rps16* intron and

- trnL*(UAA)–*F*(GAA) intergenic spacer. *Nordic Journal of Botany* **20**: 257–269.
- Piesschaert F, Andersson L, Jansen S, Dessein S, Robbrecht E, Smets E. 2000.** Searching for the taxonomic position of the African genus *Colletoeceema* (Rubiaceae): morphology and anatomy compared to an *rps16*-intron analysis of the Rubioideae. *Canadian Journal of Botany* **78**: 288–304.
- Puff C. 1990.** Comments on the Rubiaceae of N. E. Africa (*Flora of Ethiopia* and *Flora of Somalia* area). *Mitteilungen aus dem Institut für allgemeine Botanik in Hamburg* **23b**: 803–822.
- Puff C, Robbrecht E, Randrianasolo V. 1984.** Observations on the SE African-Madagascan genus *Alberta* and its ally *Nematostylis* (Rubiaceae, Alberteae), with a survey of the species and a discussion of the taxonomic position. *Bulletin du Jardin botanique national de Belgique / Bulletin van de National Plantentuin van België* **54**: 367–391.
- Puff C, Igersheim A, Buchner R, Rohrhofer U. 1995.** The united stamens of Rubiaceae. Morphology, anatomy; their role in pollination ecology. *Annals of the Missouri Botanical Garden* **82**: 357–382.
- Puff C, Rohrhofer U. 1993.** The character states and taxonomic position of the monotypic mangrove genus *Scyphiphora* (Rubiaceae). *Opera Botanica Belgica* **6**: 143–172.
- Rambaut A, Drummond AJ. 2007.** Tracer v. 1.4. Available at: <http://beast.bio.ed.ac.uk/Tracer> (Accessed on 25 November 2010).
- Razafimandimbison SG, Bremer B. 2001 [publ. 2002].** Tribal delimitation of Naucleaeae (Cinchonoideae, Rubiaceae): inference from molecular and morphological data. *Systematics and Geography of Plants* **71**: 515–538.
- Razafimandimbison SG, Bremer B. 2002.** Phylogeny and classification of Naucleaeae *s.l.* (Rubiaceae) inferred from molecular (ITS, *rbcl*, and *trnT-F*) and morphological data. *American Journal of Botany* **89**: 1027–1041.
- Razafimandimbison SG, Kainulainen K, Khoon KM, Beaver K, Bremer B. 2011.** Molecular support for a basal grade of morphologically distinct, monotypic genera in the species-rich Vanguerieae alliance (Rubiaceae, Ixoroideae): its systematic and conservation implications. *Taxon* **60**: 941–952.
- Razafimandimbison SG, Lantz H, Mouly A, Bremer B. 2009.** Evolutionary trends, major lineages, and new generic limits in the dioecious group of the tribe Vanguerieae (Rubiaceae): insights into the evolution of functional dioecy. *Annals of the Missouri Botanical Garden* **96**: 161–181.
- Ridsdale CE. 1979.** *Jackiopsis*, a new name for *Jackia* Wall. (Rubiaceae–Jackieae). *Blumea* **25**: 295–296.
- Rizzini CT, Occhioni P. 1949.** Dialypetalanthaceae. *Lilloa* **17**: 243–288.
- Robbrecht E. 1988.** Tropical woody Rubiaceae. *Opera Botanica Belgica* **1**: 1–272.
- Robbrecht E, Manen J-F. 2006.** The major evolutionary lineages of the coffee family (Rubiaceae, angiosperms). Combined analysis (nDNA and cpDNA) to infer the position of *Coptosapelta* and *Luculia*, and supertree construction based on *rbcl*, *rps16*, *trnL-F* and *atpB-rbcL* data. A new classification in two subfamilies, Cinchonoideae and Rubioideae. *Systematics and Geography of Plants* **76**: 85–146.
- Rogers GK. 1984.** *Gleasonia*, *Henriquezia*, and *Platycarpum* (Rubiaceae). *Flora Neotropica*, vol. 39. New York: New York Botanical Garden Press.
- Ronquist F, Huelsenbeck JP. 2003.** MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* **19**: 1572–1574.
- Rova JHE, Delprete PG, Andersson L, Albert VA. 2002.** A *trnL-F* cpDNA sequence study of the Condamineae–Rondeletiae–Sipaneae complex with implications on the phylogeny of the Rubiaceae. *American Journal of Botany* **89**: 145–159.
- Rova JHE, Delprete PG, Bremer B. 2009.** The *Rondeletia* complex (Rubiaceae): an attempt to use ITS, *rps16*, and *trnL-F* sequence data to delimit Guettardeae, Rondeletiae, and sections within *Rondeletia*. *Annals of the Missouri Botanical Garden* **96**: 182–193.
- Rydin C, Kainulainen K, Razafimandimbison SG, Smedmark J, Bremer B. 2009.** Deep divergences in the coffee family and the systematic position of *Acranthera*. *Plant Systematics and Evolution* **278**: 101–123.
- Rydin C, Razafimandimbison SG, Bremer B. 2008.** Rare and enigmatic genera (*Dunnia*, *Schizocolea*, *Colletoeceema*), sisters to species-rich clades: phylogeny and aspects of conservation biology in the coffee family. *Molecular Phylogenetics and Evolution* **48**: 74–83.
- Samson N, Bausher MG, Lee S-B, Jansen RK, Daniell H. 2007.** The complete nucleotide sequence of the coffee (*Coffea arabica* L.) chloroplast genome: organization and implications for biotechnology and phylogenetic relationships among angiosperms. *Plant Biotechnology Journal* **5**: 339–353.
- Schumann K, Lauterbach K. 1900 (1901).** *Die Flora der Deutschen Schutzgebiete in der Südsee XVI*. Leipzig: Gebrüder Borntraeger.
- Shaw J, Lickey EB, Beck JT, Farmer SB, Liu W, Miller J, Siripun KC, Winder CT, Schilling EE, Small RL. 2005.** The tortoise and the hare II: relative utility of 21 noncoding chloroplast DNA sequences for phylogenetic analysis. *American Journal of Botany* **92**: 142–166.
- Smith AC. 1945.** Studies of Pacific Island plants, IV Notes on Fijian flowering plants. *Journal of the Arnold Arboretum* **26**: 97–110.
- Staden R. 1996.** The Staden sequence analysis package. *Molecular Biotechnology* **5**: 233–241.
- Swofford DL. 2002.** *PAUP: phylogenetic analysis using parsimony (and other methods)*. Sunderland, MA: Sinauer Associates.
- Taberlet P, Gielly L, Pautou G, Bouvet J. 1991.** Universal primers for amplification of 3 noncoding regions of chloroplast DNA. *Plant Molecular Biology* **17**: 1105–1109.
- Tange C. 1994.** *Neomussaenda* (Rubiaceae), a new genus from Borneo. *Nordic Journal of Botany* **14**: 495–500.
- Thompson JD, Higgins DG, Gibson TJ. 1994.** CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, positions-specific gap penalties and weight matrix choice. *Nucleic Acids Research* **22**: 4673–4680.



**Tirvengadam DD. 1984.** *Glionnetia*, un nouveau genre de Rubiacées (Rondéletiales) des Seychelles. *Bulletin du Muséum National d'Histoire Naturelle, Section B, Adansonia* **2**: 197–205.

**Tosh J, Davis AP, Dessein S, De Block P, Huysmans S, Fay MF, Smets E, Robbrecht E. 2009.** Phylogeny of *Tricalysia* (Rubiaceae) and its relationships with allied genera based on plastid DNA data: resurrection of the genus

*Empogona*. *Annals of the Missouri Botanical Garden* **96**: 194–213.

**Verdcourt B. 1958.** Remarks on the classification of the Rubiaceae. *Bulletin du Jardin Botanique de l'État à Bruxelles* **28**: 209–281.

**Yang Z, Rannala B. 1997.** Bayesian phylogenetic inference using DNA sequences: a Markov chain Monte Carlo method. *Molecular Biology and Evolution* **14**: 717–724.

## APPENDIX

Overview of taxon sampling, including GenBank sequence accession numbers and voucher specimens for previously unpublished sequences (indicated with \*). Italic sequences originate from a different specimen from that indicated

Species	Voucher	<i>matK</i>	<i>ndhF</i>	<i>rbcL</i>	<i>rps16</i>	<i>trnS-G</i>	<i>trnT-L-F</i>
<i>Afrocanthium lactescens</i> (Hiern) Lantz	Luke & Luke 9045 (UPS)	HM119502*	HM164346*	HM164152*	HM164189*	HM164234*	AJ620127 <sup>1</sup>
<i>Airosperma psychotrioides</i> K.Schum. & Lauterb.	Nyman 569 (UPS)	–	HM164347*	–	–	–	HM164302*
<i>Airosperma</i> sp.	Sands 6819 (L)	HM119503*	HM164348*	–	–	HM164235*	HM164303*
<i>Airosperma trichotomum</i> (Gillespie) A.C.Sm.	Degener & Ordonez 15542 (S)	–	HM164349*	–	HM164190*	–	HM164304*
<i>Airosperma vanuense</i> S.P.Darwin	Smith 8214 (P)	HM119504*	AM949845 <sup>2</sup>	–	FM204700 <sup>2</sup>	FM204740 <sup>2</sup>	FM207108 <sup>2</sup>
<i>Alberta magna</i> E.Mey.	Tonkin 200 (UPS)	HM119505*	AJ236282 <sup>3</sup>	Y18708 <sup>3</sup>	FM204701 <sup>2</sup>	FM204741 <sup>2</sup>	AJ620118 <sup>1</sup>
<i>Aleisanthia rupestris</i> (Ridl.) Ridl.	Tange 45171 (AAU)	HM119506*	–	HM164153*	AF242902 <sup>4</sup>	HM164236*	HM164305*
<i>Aleisanthiopsis distantiflora</i> (Merr.) Tange	Tange 46977 (AAU)	HM119507*	HM16435028	HM164154*	AF2429034	HM164237*	HM164306*
<i>Aoranthie penduliflora</i> (K.Schum.) Somers	Iverson & Steiner 86776 (UPS)	HM119508*	–	Y11845 <sup>5</sup>	HM164191*	HM164238*	HM164307*
<i>Atractocarpus balansaeanus</i> Guillaumin	Munzinger & McPherson 635 (MO)	HM119509*	HM164351*	HM164155*	HM164192*	HM164239*	HM164308*
<i>Augusta austrocaledonica</i> (Brongn.) J.H.Kirkbr.	Mouly & Innocente 237 (P)	HM119510*	HM164352*	EU817412 <sup>6</sup>	HM164193*	HM164240*	EU817454 <sup>6</sup>
<i>Augusta longifolia</i> (Spreng.) Rehder	Kirkbride 5295 (BR)	HM119511*	HM164353*	–	–	HM164241*	HM164309*
<i>Augusta rivalis</i> (Benth.) J.H.Kirkbr.	McDowell 5017 (ETSU)	HM119512*	AM949846 <sup>2</sup>	AM949842 <sup>2</sup>	HM164194*	FM204752 <sup>2</sup>	FM207118 <sup>2</sup>
<i>Aulacocalyx jasminiflora</i> Hook.f.	Schmidt et al. 1672 (MO)	HM119513*	HM164354*	EU817413 <sup>6</sup>	EF205639 <sup>7</sup>	FM204753 <sup>2</sup>	EU817455 <sup>6</sup>
<i>Bathysa stipulata</i> (Vell.) C.Presl	Pirani & Bremer 4901 (SPF)	FJ905337 <sup>8</sup>	FJ871947 <sup>8</sup>	HM164156*	FJ884637 <sup>8</sup>	FJ948302 <sup>8</sup>	FJ948371 <sup>8</sup>
<i>Bertiara aethiopica</i> Hiern	Dessein s.n. (BR)	HM119514*	HM164355*	HM164157*	HM164195*	HM164242*	HM164310*

APPENDIX *Continued*

Species	Voucher	<i>matK</i>	<i>ndhF</i>	<i>rbcL</i>	<i>rps16</i>	<i>trnS-G</i>	<i>trnT-L-F</i>
<i>Bertiera guianensis</i> Aubl.	Andersson <i>et al.</i> 2029 (GB)	HM119515*	AM949847 <sup>2</sup>	AJ224845 <sup>9</sup>	AF200983 <sup>10</sup>	FM204754 <sup>2</sup>	FM207119 <sup>2,33</sup>
<i>Bertiera longithyrsa</i> Baker	Kårehed <i>et al.</i> 256 (UPS)	HM119516*	HM164356*	HM164158*	HM164196*	HM164243*	HM164311*
<i>Boholia</i> <i>nematostylis</i> Merr.	Bicknell 1561A (SUNIV)	HM119517*	AM949848 <sup>2</sup>	AM117210 <sup>11</sup>	AM117286 <sup>11</sup>	FM204755 <sup>2</sup>	HM164312*
<i>Bremeria landia</i> (Poir.) Razafim. & Alejandro	Andriambololonera 37 (MAU)	HM119518*	HM164357*	–	HM164197*	HM164244*	HM164313*
<i>Burchellia</i> <i>bubalina</i> (L.f.) Sims	Bremer 3129 (UPS)	HM119519*	HM164358*	Z68833 <sup>12</sup>	HM164198*	HM164245*	HM164314*
<i>Calycophyllum</i> <i>candidissimum</i> (Vahl) DC.	Sanders 1805 (FTG)	FJ905340 <sup>8</sup>	AJ236285 <sup>3</sup>	X83627 <sup>13</sup>	FM204712 <sup>2</sup>	FM204756 <sup>2</sup>	AJ847398 <sup>14</sup>
<i>Canthium</i> <i>coromandelicum</i> (Burm.f.) Alston	Andreasen 36 (UPS)	HM119520*	HM164359*	Z68851 <sup>12</sup>	HM164199*	HM164246*	AJ847401 <sup>14</sup>
<i>Catunaregam</i> <i>spinosa</i> (Thunb.) Tirveng.	Luke 8332A (UPS)	HM119522*	–	AM117214 <sup>11</sup>	HM164200*	HM164248*	HM164315*
<i>Cephalanthus</i> <i>occidentalis</i> L.	Forbes <i>s.n.</i> (S)	AY538377 <sup>15</sup>	AJ236288 <sup>3</sup>	X83629 <sup>13</sup>	AF004033 <sup>16</sup>	–	AJ346955 <sup>17</sup>
<i>Chalepophyllum</i> <i>guyanense</i> Hook.f.	Sandwith 1346 (S)	HM119523*	–	HM164159*	HM164201*	HM164249*	HM164316*
<i>Chimarrhis hookeri</i> K.Schum.	Delprete & Verduga 6421 (UPS)	FJ905344 <sup>8</sup>	AJ236289 <sup>3</sup>	Y18712 <sup>3</sup>	FJ884643 <sup>8</sup>	FJ948309 <sup>8</sup>	FJ948378 <sup>8</sup>
<i>Cinchona</i> <i>pubescens</i> Vahl.	McDowell 4613 (DUKE)	Z70197 <sup>18</sup>	AJ235843 <sup>19</sup>	X83630 <sup>13</sup>	FM204714 <sup>2</sup>	FM204758 <sup>2</sup>	AJ346963 <sup>17</sup>
<i>Coddia rudis</i> (E.Mey. ex Harv.) Verdc.	Bremer 3764 (UPS)	HM119524*	HM164361*	AJ286695 <sup>20</sup>	HM164202*	HM164250*	HM164317*
<i>Coffea arabica</i> L.		EF044213 <sup>21</sup>	EF044213 <sup>21</sup>	EF044213 <sup>21</sup>	EF044213 <sup>21</sup>	EF044213 <sup>21</sup>	EF044213 <sup>21</sup>
<i>Coffea ebracteolata</i> (Hiern) Brenan	Andreasen 223 (UPS)	HM119560*	HM164387*	AJ286692 <sup>20</sup>	HM164219*	HM164283*	HM164333*
<i>Coffea sessiliflora</i> Bridson	Luke 9024 (UPS)	HM119525*	HM164362*	HM164160*	HM164203*	HM164251*	HM164318*
<i>Colletocema</i> <i>dewevrei</i> (De Wild.) E.M.A.Petit	Lisowski 47195 (K)	HM119526*	EU145409 <sup>22</sup>	EU145457 <sup>22</sup>	AF129272 <sup>23</sup>	HM164252*	EU145532 <sup>22</sup>
<i>Condaminea</i> <i>corymbosa</i> (Ruiz & Pav.) DC.	Pennington & Daza 17436 (MOL)	FJ905347 <sup>8</sup>	FJ871950 <sup>8</sup>	HM164161*	FJ884645 <sup>8</sup>	FJ948312 <sup>8</sup>	FJ948381 <sup>8</sup>
<i>Coptosperma</i> <i>supra-axillare</i> (Hemsl.) Degreef	Bremer 3810 (UPS)	HM119527*	HM164363*	AJ286711 <sup>20</sup>	HM164204*	HM164253*	HM164319*
<i>Cremaspora triflora</i> <i>ssp. confluens</i> (K.Schum.) Verdc.	Andreasen 51 (UPS)	HM119528*	AM949850 <sup>2</sup>	Z68856 <sup>12</sup>	FM204716 <sup>2</sup>	FM204759 <sup>2</sup>	FM207121 <sup>2</sup>
<i>Crossopteryx</i> <i>febrifuga</i> (Afzel. ex G.Don) Benth.	Bremer 3097 (UPS)	FJ905329 <sup>8</sup>	AM949851 <sup>2</sup>	AM117223 <sup>11</sup>	FM204717 <sup>2</sup>	FM204760 <sup>2</sup>	FM207123 <sup>2</sup>
<i>Cubanola</i> <i>domingensis</i> (Britton) Aiello	McDowell 4427 (DUKE)	AY538386 <sup>15</sup>	AM117345 <sup>11</sup>	X83632 <sup>13</sup>	FM204718 <sup>2</sup>	FM204761 <sup>2</sup>	FM207124 <sup>2</sup>

APPENDIX *Continued*

Species	Voucher	<i>matK</i>	<i>ndhF</i>	<i>rbcL</i>	<i>rps16</i>	<i>trnS-G</i>	<i>trnT-L-F</i>
<i>Cyclophyllum deplanchei</i> Hook.f.	Mouly & Innocente 228 (P)	HM119529*	–	EU817416 <sup>6</sup>	EF205640 <sup>7</sup>	HM164254*	EF205631 <sup>7</sup>
<i>Dendrosipanea spigelioides</i> Ducke	Prance et al. 16199 (S)	FJ905324 <sup>8</sup>	FJ871943 <sup>8</sup>	HM164162*	FJ884627 <sup>8</sup>	FJ948291 <sup>8</sup>	FJ948360 <sup>8</sup>
<i>Dioicodendron dioicum</i> (K.Schum. & Krause) Steyerm.	Zarucchi & Echeverry 4780 (MO)	FJ905349 <sup>8</sup>	FJ871952 <sup>8</sup>	HM164163*	FJ884647 <sup>8</sup>	FJ948314 <sup>8</sup>	FJ948383 <sup>8</sup>
<i>Duperrea pavettifolia</i> (Kurz) Pit.	cult. Bergius Botanic Garden	HM119531*	HM164365*	AJ286709 <sup>20</sup>	HM164205*	HM164256*	HM164320*
<i>Emmenopterys henryi</i> Oliv.	Robbrecht s.n. (UPS)	FJ905360 <sup>8</sup>	AJ236294 <sup>3</sup>	Y18715 <sup>3</sup>	FM204719 <sup>2</sup>	FM204762 <sup>2</sup>	FM207125 <sup>2</sup>
<i>Empogona coriacea</i> (Sond.) Tosh & Robbr.	Bremer et al. 4302 (UPS)	HM119574*	HM164401*	HM164184*	HM164228*	HM164295*	HM164340*
<i>Euclinia longiflora</i> Salisb.	De Block 27 (BR)	HM119532*	HM164366*	Z68835 <sup>12</sup>	HM164206*	HM164257*	AJ847399 <sup>14</sup>
<i>Fadogia tetraquetra</i> K.Schum. & Krause	Bremer & Bremer 3799 (UPS)	HM119533*	HM164367*	AM117225 <sup>11</sup>	HM164207*	HM164258*	AJ620139 <sup>1</sup>
<i>Ferdinandusa speciosa</i> Pohl	Malme 2442 (UPS)	HM119534*	EU145412 <sup>22</sup>	AM117226 <sup>11</sup>	FJ884657 <sup>8</sup>	FJ948327 <sup>8</sup>	EU145534 <sup>22</sup>
<i>Feretia apodanthera</i> Delile	Luke 8385 (UPS)	HM119535*	HM164368*	HM164164*	HM164208*	HM164259*	HM164321*
<i>Fernelia buxifolia</i> Lam.	Nat. Bot. Gard. Meise, no. 19940025-26	HM119536*	HM164369*	AJ286704 <sup>20</sup>	AF244892 <sup>4</sup>	HM164260*	EU145540 <sup>22</sup>
<i>Gardenia hansemannii</i> K.Schum.	Drozdz & Molem 1998-11-13	HM119537*	AM949852 <sup>2</sup>	AJ318446 <sup>24</sup>	AJ320077 <sup>24</sup>	FM204763 <sup>2</sup>	FM207126 <sup>2</sup>
<i>Gelsemium sempervirens</i> (L.) J.St.-Hil.	Bremer 3026 (UPS)	AJ429322 <sup>25</sup>	AJ011984 <sup>26</sup>	L14397 <sup>27</sup>	AJ431033 <sup>25</sup>	–	AJ430908 <sup>25</sup>
<i>Genipa americana</i> L.	Kiehn, HBVsub RR-420 (WU, UPS)	HM119538*	HM164370*	Z68839 <sup>12</sup>	HM164209*	HM164261*	HM164322*
<i>Glionnetia sericea</i> (Baker) Tirveng.	Beaver 17 (S)	HM569720*	HM536217 <sup>28</sup>	HM536223 <sup>28</sup>	HM536229 <sup>28</sup>	HM569721*	HM536235 <sup>28</sup>
<i>Greenea oblonga</i> Craib	Larsen & Larsen 33451 (P)	HM119539*	HM164371	–	EU817439 <sup>6</sup>	HM164262*	EU817459 <sup>6</sup>
<i>Guettarda speciosa</i> L.	Persson 141 (GB)	AY538389 <sup>15</sup>	FJ871942 <sup>8</sup>	AY538485 <sup>15</sup>	AF242964 <sup>4</sup>	FJ948289 <sup>8</sup>	FJ948358 <sup>8,34</sup>
<i>Heinsia crinita</i> (Afzel.) G.Taylor	McPherson 16188A (MO)	HM119540*	HM164372*	Y11849 <sup>5</sup>	HM164210*	HM164263*	HM164323*
<i>Hekistocarpa minutiflora</i> Hook.f.	Leuvenberg 6393 (BR, K, WAG)	HM119541*	HM164373*	AF332366 <sup>29</sup>	AF332367 <sup>29</sup>	HM164264*	HM164324*
<i>Henriquezia nitida</i> var. <i>macrophylla</i> (Ducke) Steyerm.	Liesner 8531 (MO)	–	HM164374*	–	HM164211*	–	HM164325*
<i>Hippotis triflora</i> Ruiz & Pav.	Ståhl 2660 (GB)	FJ905365 <sup>8</sup>	FJ871956 <sup>8</sup>	HM164165*	FJ884659 <sup>8</sup>	FJ948329 <sup>8</sup>	FJ948397 <sup>8</sup>
<i>Hyperacanthus grevei</i> Rakotonas. & A.P.Davis	Razafimandimbison 547 (UPS)	HM119542*	HM164375*	HM164166*	HM164212*	HM164265*	HM164326*



APPENDIX *Continued*

Species	Voucher	<i>matK</i>	<i>ndhF</i>	<i>rbcL</i>	<i>rps16</i>	<i>trnS-G</i>	<i>trnT-L-F</i>
<i>Hypobathrum racemosum</i> (Roxb.) Kurz	Ridsdale 81	HM119543*	AM949853 <sup>2</sup>	AJ286705 <sup>20</sup>	AM117318 <sup>11</sup>	HM164266*	FM207127 <sup>2</sup>
<i>Ixora borboniae</i> Mouly & B.Bremer	Friedmann 3049 (P)	HM119552*	HM164383*	HM164173*	FJ150685 <sup>6</sup>	HM164275*	FJ150609 <sup>6</sup>
<i>Ixora coccinea</i> L.	Bremer 2719 (UPS)	HM119544*	HM164376*	HM164167*	EF205641 <sup>7</sup>	FM204764 <sup>2</sup>	EU817464 <sup>6</sup>
<i>Ixora ferrea</i> (Jacq.) Benth.	Taylor 11693 (MO)	HM119545*	HM164377*	EU817422 <sup>6</sup>	EF205642 <sup>7</sup>	HM164267*	EU817465 <sup>6</sup>
<i>Ixora margaretae</i> (N.Hallé) Mouly & B.Bremer	Mouly & Innocente 222 (P)	HM119521*	HM164360*	EU817415 <sup>6</sup>	EU817436 <sup>6</sup>	HM164247*	EU817456 <sup>6</sup>
<i>Ixora novoguineensis</i> Mouly & B.Bremer	Drozd & Molem 1998-11-13	HM119581*	HM164406*	AJ318459 <sup>24</sup>	AJ320090 <sup>24</sup>	HM164300*	EU817476 <sup>6</sup>
<i>Ixora trilocularis</i> (Balf.f.) Mouly & B.Bremer	Lesouef 31 (TAN)	HM119530*	HM164364*	EU817417 <sup>6</sup>	EU817437 <sup>6</sup>	HM164255*	EU817457 <sup>6</sup>
<i>Jackiopsis ornata</i> (Wall.) Ridsdale	K. S. Tan s.n.	HM119546*	HM536213 <sup>28</sup>	HM536219 <sup>28</sup>	HM536225 <sup>28</sup>	HM164268*	HM536231 <sup>28</sup>
<i>Kailarsenia tentaculata</i> (Hook.f.) Tirveng.	Larsen 41627 (AAU)	HM119547*	HM164378*	HM164168*	HM164213*	HM164269*	HM164327*
<i>Keetia gueinzii</i> (Sond.) Bridson	Bremer et al. 4349 (UPS)	HM119548*	HM164379*	HM164169*	HM164214*	HM164270*	AJ620143 <sup>1</sup>
<i>Landiopsis capuronii</i> Capuron ex Bosser	Gautier 4533 (MO)	HM119549*	HM164380*	HM164170*	HM164215*	HM164271*	HM164328*
<i>Logania vaginalis</i> (Labill.) F.Muell.	Bremer 3013 (UPS)	AJ429324 <sup>25</sup>	AJ235837 <sup>19</sup>	Z68826 <sup>12</sup>	AJ431035 <sup>25</sup>	HM164272*	AJ430910 <sup>25</sup>
<i>Luculia gratissima</i> (Wall.) Sweet	CT 870064	AJ429325 <sup>25</sup>	AJ011987 <sup>26</sup>	AM117243 <sup>11</sup>	AJ431036 <sup>25</sup>	FM204765 <sup>2</sup>	AJ430911 <sup>25</sup>
<i>Mastixiodendron flavidum</i> (Seem.) A.C.Sm.	Rova & Gustavsson 2429 (GB)	FJ905369 <sup>8</sup>	FJ871959 <sup>8</sup>	HM164171*	AF242979 <sup>4</sup>	FJ948332 <sup>8</sup>	FJ948401 <sup>8</sup>
<i>Mitriostigma axillare</i> Hochst.	Bremer 2705 (UPS)	HM119550*	HM164381*	X83650 <sup>13</sup>	HM164216*	HM164273*	HM164329*
<i>Molopantha paniculata</i> Turcz.	Williams 6861 (S)	–	HM164382*	HM164172*	AF242981 <sup>4</sup>	–	FJ948361*
<i>Multidentia conrescens</i> (Bullock) Bridson & Verdc.	Bidgood et al. 845 (K)	–	–	–	–	HM164274*	AJ620150 <sup>1</sup>
<i>Mussaenda arcuata</i> Poir.	McPherson 16213 (MO)	HM119551*	AJ236301 <sup>3</sup>	Y11854 <sup>5</sup>	FM204721 <sup>2</sup>	FM204767 <sup>2</sup>	FM207128 <sup>2</sup>
<i>Mussaenda erythrophylla</i> Schumach. & Thonn.	Gillis 10838 (FTG)	FJ905326 <sup>8</sup>	AJ130836 <sup>3</sup>	X83652 <sup>13</sup>	FJ884628 <sup>8</sup>	FJ948292 <sup>8</sup>	AJ620116 <sup>1</sup>
<i>Nauclea orientalis</i> (L.) L.	Bremer 3001 (UPS)	AY538407 <sup>15</sup>	EU145410 <sup>22</sup>	X83653 <sup>13</sup>	AJ320080 <sup>24</sup>	HM164276*	AJ346958 <sup>17</sup>
<i>Neobertiera gracilis</i> Wernh.	de Granville 2888 (NY)	–	–	–	AF242984 <sup>4</sup>	–	AF152679 <sup>30</sup>
<i>Ophiorrhiza mungos</i> L.	Bremer 3301 (UPS)	AY538408 <sup>15</sup>	AJ130838 <sup>3</sup>	X83656 <sup>13</sup>	AF004064 <sup>16</sup>	HM164277*	DQ662151 <sup>31</sup>

APPENDIX *Continued*

Species	Voucher	<i>matK</i>	<i>ndhF</i>	<i>rbcL</i>	<i>rps16</i>	<i>trnS-G</i>	<i>trnT:L-F</i>
<i>Oxyanthus speciosus</i> DC.	Bremer 4348 (S)	HM119554*	HM164384*	AM117252 <sup>11</sup>	AM117330 <sup>11</sup>	HM164278*	AM117375 <sup>11</sup>
<i>Paragenipa lancifolia</i> (Bojer ex Baker) Tirveng. & Robbr	Persson 156 (GB)	HM119555*	HM164385*	AJ286707 <sup>20</sup>	AF004066 <sup>16</sup>	HM164279*	HM164330* <sup>35</sup>
<i>Pavetta abyssinica</i> Fresen.	De Block 6 (BR)	HM119556*	AM949854 <sup>2</sup>	Z68863 <sup>12</sup>	FM204726 <sup>2</sup>	FM204772 <sup>2</sup>	FM207133 <sup>2</sup>
<i>Pavetta indica</i> L.	Andreasen 202 (UPS)	HM119557*	–	–	HM164217*	HM164280*	HM164331*
<i>Peponidium horridum</i> Arènes	Labat et al. 2236 (K)	–	–	–	–	HM164281*	AJ620153 <sup>1</sup>
<i>Pinckneya bracteata</i> (Bartram) Raf.	Massey s.n. 15F	FJ905377 <sup>8</sup>	AJ130839 <sup>3</sup>	X83661 <sup>13</sup>	FJ884668 <sup>8</sup>	FJ948339 <sup>8</sup>	FJ948408 <sup>8</sup>
<i>Pogonopus speciosus</i> (Jacq.) K.Schum.	Meier 2548 (GB)	FJ905378 <sup>8</sup>	FJ871964 <sup>8</sup>	HM164174*	FJ884670 <sup>8</sup>	FJ948341 <sup>8</sup>	FJ948410 <sup>8</sup>
<i>Posoqueria latifolia</i> (Rudge) Roem. & Schult.	Andreasen 90 (UPS)	FJ905325 <sup>8</sup>	AM949855 <sup>2</sup>	Z68850 <sup>12</sup>	FM204728 <sup>2</sup>	FM204774 <sup>2</sup>	FM207135 <sup>2</sup>
<i>Posoqueria longiflora</i> Aubl.	cult. Bergius Botanic Garden	HM119558*	HM164386*	HM164175*	HM164218*	HM164282*	HM164332*
<i>Pseudomussaenda flava</i> Verdc.	Nissen s.n. (UPS)	HM119559*	AM949856 <sup>2</sup>	Y11855 <sup>5</sup>	FM204729 <sup>2</sup>	FM204775 <sup>2</sup>	FM207136 <sup>2</sup>
<i>Psydrax obovata</i> (Klotzsch ex Eckl. & Zeyh.) Bridson	Bremer & Bremer 3762 (UPS)	HM119561*	HM164388*	HM164176*	HM164220*	HM164284*	AJ620161 <sup>1</sup>
<i>Pyrostria hystrix</i> (Bremek.) Bridson	Bremer & Bremer 3791 (UPS)	HM119562*	HM164389*	AM117262 <sup>11</sup>	AM117338 <sup>11</sup>	HM164285*	AJ620168 <sup>1</sup>
<i>Randia aculeata</i> L.	F.G.x.1–145	HM119563*	HM164390*	Z68832 <sup>12</sup>	HM164221*	HM164286*	HM164334*
<i>Retiniphyllum pilosum</i> (Spruce ex Benth.) Müll. Arg.	Wurdack & Adderley 43270 (S)	–	HM164392*	AF331654 <sup>32</sup>	AF004076 <sup>16</sup>	FM204776 <sup>2</sup>	FM207137 <sup>2</sup>
<i>Rondeletia odorata</i> Jacq.	Bremer & Andreasen 3504 (UPS)	–	AJ235845 <sup>19</sup>	Y11857 <sup>5</sup>	AF243010 <sup>4</sup>	FJ948290 <sup>8</sup>	FJ948359 <sup>8,36</sup>
<i>Rosenbergiodendron densiflorum</i> (K. Schum.) Fagerl.	Jansen-Jacobs 3977 (GB)	HM119566*	HM164393*	HM164177*	HM164222*	HM164287*	HM164335*
<i>Rothmannia capensis</i> Thunb.	Bremer et al. 4346 (S)	HM119567*	HM164394*	AM117266 <sup>11</sup>	AM117340 <sup>11</sup>	HM164288*	AM117384 <sup>11</sup>
<i>Rustia thibaudioides</i> (H.Karst.) Delprete	Delprete 6378 (UPS)	FJ905385 <sup>8</sup>	AJ236310 <sup>3</sup>	Y18716 <sup>3</sup>	FM204731 <sup>2</sup>	FM204777 <sup>2</sup>	FM207138 <sup>2</sup>
<i>Rytigynia senegalensis</i> Blume	van den Berghen 8746 (BR)	–	–	HM164178*	HM164223*	HM164289*	AJ620175 <sup>1</sup>
<i>Sabicea africana</i> (P. Beauv.) Hepper	Wieringa 3591 (WAG)	–	HM164397*	HM164180*	HM164225*	HM164292*	HM164337*
<i>Sabicea aspera</i> Aubl.	Andersson et al. 1941 (GB)	AY538420 <sup>15</sup>	EU145416 <sup>22</sup>	AY538508 <sup>15</sup>	AF004079 <sup>16</sup>	FJ948293 <sup>8</sup>	FJ948362 <sup>8,37</sup>
<i>Sabicea diversifolia</i> Pers.	Bremer et al. 4018-B18 (UPS)	HM119568*	EU145415 <sup>22</sup>	EU145459 <sup>22</sup>	EU145494 <sup>22</sup>	HM164290*	AJ847396 <sup>14</sup>
<i>Schizomussaenda henryi</i> (Hutch.) X.F.Deng & D.X.Zhang	Puff 961116-1/1 (WU)	HM119569*	HM164395*	AM117273 <sup>11</sup>	HM164224*	HM164291*	AJ847383 <sup>14</sup>

APPENDIX *Continued*

Species	Voucher	<i>matK</i>	<i>ndhF</i>	<i>rbcL</i>	<i>rps16</i>	<i>trnS-G</i>	<i>trnT-L-F</i>
<i>Scyphiphora hydrophyllacea</i> C.F.Gaertn.	Bremer <i>et al.</i> 99 (S)	FJ905327 <sup>8</sup>	AJ236311 <sup>3</sup>	Y18717 <sup>3</sup>	EU817450 <sup>6</sup>	FM204779 <sup>2</sup>	EU817475 <sup>6</sup>
<i>Simira cordifolia</i> (Hook.f.) Steyererm.	Bremer 3361 (UPS)	FJ905388 <sup>8</sup>	FJ871970 <sup>8</sup>	HM164179*	FJ884677 <sup>8</sup>	FJ948350 <sup>8</sup>	FJ948419 <sup>8</sup>
<i>Sipanea aff. biflora</i> (L.f.) Cham. & Schltld.	Rova <i>et al.</i> 2005 (GB)	AY538421 <sup>15</sup>	EU145413 <sup>22</sup>	AY538509 <sup>15</sup>	AF004085 <sup>16</sup>	FM204780 <sup>2</sup>	FM207141 <sup>2,38</sup>
<i>Sipanea hispida</i> Benth. ex Wernham	Irwin <i>et al.</i> 34756 (UPS)	–	EU145414 <sup>22</sup>	EU145458 <sup>22</sup>	EU145492 <sup>22</sup>	–	HM164336*
<i>Steenisia pleurocarpa</i> (Airy Shaw) Bakh.f.	Puff BF 990619-1/4 (WU)	FJ905328 <sup>8</sup>	HM164396*	AM117279 <sup>11</sup>	FM204735 <sup>2</sup>	FM204781 <sup>2</sup>	FM207142 <sup>2</sup>
<i>Tamriddaea capsulifera</i> (Balf. f.) Thulin & B. Bremer	Thulin & Gifri 8663 (UPS)	–	HM164398*	Y11860 <sup>5</sup>	FM204736 <sup>2</sup>	FM204782 <sup>2</sup>	FM207143 <sup>2</sup>
<i>Tennantia sennii</i> (Chiov.) Verdc. & Bridson	Abdalla <i>et al.</i> 96/166 (P)	HM119570*	AM949858 <sup>2</sup>	AM949843 <sup>2</sup>	FM204737 <sup>2</sup>	FM204783 <sup>2</sup>	FM207144 <sup>2</sup>
<i>Tocoyena pittieri</i> (Standl.) Standl.	Rova <i>et al.</i> 2369 (GB)	HM119571*	AM949859 <sup>2</sup>	HM164181*	FM204738 <sup>2</sup>	FM204784 <sup>2</sup>	FM207145 <sup>2</sup>
<i>Trailliaedoxa gracilis</i> W.W.Sm. & Forrest	Boufford <i>et al.</i> 35041 (MO)	HM119573*	HM164400 <sup>28</sup>	HM164183 <sup>28</sup>	HM164227 <sup>28</sup>	HM164294*	HM164339 <sup>28</sup>
<i>Vangueria madagascariensis</i> J.F.Gmel.	Sanders 1798, #62146 (FTG)	HM119575*	AJ130840 <sup>3</sup>	X83670 <sup>13</sup>	HM164229*	FM204785 <sup>2</sup>	AJ620184 <sup>1</sup>
<i>Wendlandia arabica</i> Deflers	Thulin <i>et al.</i> 10192 (UPS)	HM119576*	HM164402*	HM164185*	HM164230*	HM164296*	HM164341*
<i>Wendlandia formosana</i> Cowan	Chung 1403 (S)	HM119577*	HM164403*	HM164186*	HM164231*	HM164297*	HM164342*
<i>Wendlandia ligustroides</i> (Boiss. & Hohen.) Blakelock	Rechinger 183 (S)	HM119578*	HM164404*	HM164187*	AF243036 <sup>4</sup>	HM164298*	HM164343* <sup>39</sup>
<i>Wendlandia paniculata</i> (Roxb.) DC.	Ridsdale 2179	HM119579*	HM164405*	HM164188*	HM164232*	HM164299*	HM164344*
<i>Wendlandia tinctoria</i> (Roxb.) DC.	Parker 3227 (S)	HM119580*	AM949860 <sup>2</sup>	FM207649 <sup>2</sup>	FM204739 <sup>2</sup>	FM204786 <sup>2</sup>	FM207147 <sup>2</sup>
<i>Virectaria multiflora</i> (Sm.) Bremek.	Adames 606 (UPS)	HM119582*	HM164407*	Y11861 <sup>5</sup>	HM164233*	HM164301*	HM164345*

Published sequences: <sup>1</sup>Lantz & Bremer (2004); <sup>2</sup>Kainulainen *et al.* (2009); <sup>3</sup>Bremer *et al.* (1999); <sup>4</sup>J. H. E. Rova (unpubl. data); <sup>5</sup>Bremer & Thulin (1998); <sup>6</sup>Mouly *et al.* (2009a); <sup>7</sup>Mouly *et al.* (2007); <sup>8</sup>Kainulainen *et al.* (2010); <sup>9</sup>Andreasen, Baldwin & Bremer (1999); <sup>10</sup>Persson (2000); <sup>11</sup>Bremer & Eriksson (2009); <sup>12</sup>Andreasen & Bremer (1996); <sup>13</sup>Bremer *et al.* (1995); <sup>14</sup>Alejandro *et al.* (2005); <sup>15</sup>Andersson & Antonelli (2005); <sup>16</sup>Andersson & Rova (1999); <sup>17</sup>Razafimandimbison & Bremer (2002); <sup>18</sup>Endress *et al.* (1996); <sup>19</sup>Backlund, Oxelman & Bremer (2000); <sup>20</sup>Andreasen & Bremer (2000); <sup>21</sup>Samson *et al.* (2007); <sup>22</sup>Rydin *et al.* (2008); <sup>23</sup>Piesschaert *et al.* (2000); <sup>24</sup>Novotny *et al.* (2002); <sup>25</sup>Bremer *et al.* (2002); <sup>26</sup>Oxelman, Backlund & Bremer (1999); <sup>27</sup>Olmstead *et al.* (1993); <sup>28</sup>Razafimandimbison *et al.* (2011); <sup>29</sup>Dessein *et al.* (2001); <sup>30</sup>Rova *et al.* (2002); <sup>31</sup>Backlund, Bremer & Thulin (2007); <sup>32</sup>L. Andersson (unpubl. data).

Combined sequences: <sup>33</sup>with AF152670; <sup>34</sup>with AF152725; <sup>35</sup>with AF152672; <sup>36</sup>with AF152741; <sup>37</sup>with AY538475; <sup>38</sup>with AF152675; <sup>39</sup>with AF152661.