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SYSTEMATICS AND PHYLOGENY

Cutting up the climbers: Evidence for extensive polyphyly in *Friesodielsia* (Annonaceae) necessitates generic realignment across the tribe Uvarieae

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Abstract *Friesodielsia* and the closely related genera *Dasymaschalon*, *Desmos*, *Exellia*, *Gilbertiella* and *Monanthotaxis* (Annonaceae subfamily Annonoideae tribe Uvarieae) are taxonomically problematic, with obscure generic delimitations and poorly known phylogenetic relationships. The present study addresses the polyphyletic status of *Friesodielsia*, using two nuclear and five chloroplast DNA regions to resolve this taxonomic confusion by circumscribing strictly monophyletic genera across the tribe. Bayesian, maximum likelihood and maximum parsimony analyses using a broad taxon sampling (101 taxa) reveal that *Friesodielsia* species form five robust and morphologically distinct clades. In order to ensure strict monophyly of genera, we restrict the generic name *Friesodielsia* to an exclusively Asian clade, and the African species that were formerly included in the genus are transferred to *Afroguatteria*, *Monanthotaxis* and *Sphaerocoryne*, necessitating ten new nomenclatural combinations. *Schefferomitra*, a monospecific genus from New Guinea, is shown to be congeneric with Asian *Friesodielsia*, and the nomenclatural implications of this are discussed. Two monospecific genera, *Exellia* and *Gilbertiella*, are furthermore synonymised with *Monanthotaxis*, necessitating two additional nomenclatural changes. New generic descriptions are provided for *Dasymaschalon* (ca. 27 species), *Desmos* (ca. 22 species), *Friesodielsia* (ca. 38 species) and *Monanthotaxis* (ca. 94 species) to reflect these revised circumscriptions.

Keywords Annonaceae; *Friesodielsia*; *Monanthotaxis*; nomenclature; polyphyly; taxonomy

Supplementary Material Electronic Supplement (Figs. S1 & S2) and DNA sequence alignment are available in the Supplementary Data section of the online version of this article at http://www.ingentaconnect.com/content/iapt/tax

■ INTRODUCTION

Although the climbing growth habit has evolved several times within the early-divergent angiosperm family Annonaceae, it only occurs with a phylogenetic bias in subfam. Annonoideae. Apart from the palaeotropical genus *Artabotrys* R.Br. (tribe Xylopieae), in which the climbing habit is achieved by persistent inflorescence hooks (Posluszny & Fisher, 2000), and four species in two genera in the tribe Duguetieae (Chatrou & al., 2000), the other lianescent genera in the subfamily are restricted to the tribe Uvarieae (17 genera and ca. 400 species: Chatrou & al., 2012; Rainer & Chatrou, 2016), including *Desmos* Lour., *Fissistigma* Griff., *Friesodielsia* Steenis, *Monanthotaxis* Baill., and *Uvaria* L. In rain forests of the Paleotropics, Annonaceae are amongst the most dominant plant families in the liana community (Appanah & al., 1993; Ewango & al., 2015). The tribe Uvarieae offers an excellent opportunity to investigate ecologically significant shifts in growth habit, although evolutionary research on the tribe is currently impeded by the obscure phylogenetic relationships of several constituent genera (particularly *Dasymaschalon* (Hook.f. & Thomson) Dalla Torre & Harms and *Friesodielsia*) and, in some cases, probable non-monophyly.

Phylogenetic studies (Bygrave, 2000; Richardson & al., 2004; Couvreur & al., 2011; Chatrou & al., 2012; Wang & al., 2012) have consistently placed *Dasymaschalon* and *Friesodielsia* in a well-supported subclade of tribe Uvarieae (referred to here as the "*Dasymaschalon* alliance"), together

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with two other genera, *Desmos* and *Monanthotaxis*. This close relationship is corroborated by several diagnostic characters, including the glaucous abaxial surface of the leaves (Wang & al., 2012), inaperturate pollen with echinate-microbaculate ornamentation (Walker, 1971a; Le Thomas, 1980, 1981; Bygrave, 2000; Doyle & Le Thomas, 2012), and monocarps (when multi-seeded) with distinct constrictions between neighbouring seeds (Wang & al., 2012). As is generally the case in Annonaceae, however, these characters show homoplasies or reversals and therefore are not found in all species in the *Dasymaschalon* alliance. The constituent species in the *Dasymaschalon* alliance are nevertheless highly diverse morphologically, with different types of pollination chambers, stamens and monocarps (Fig. 1).

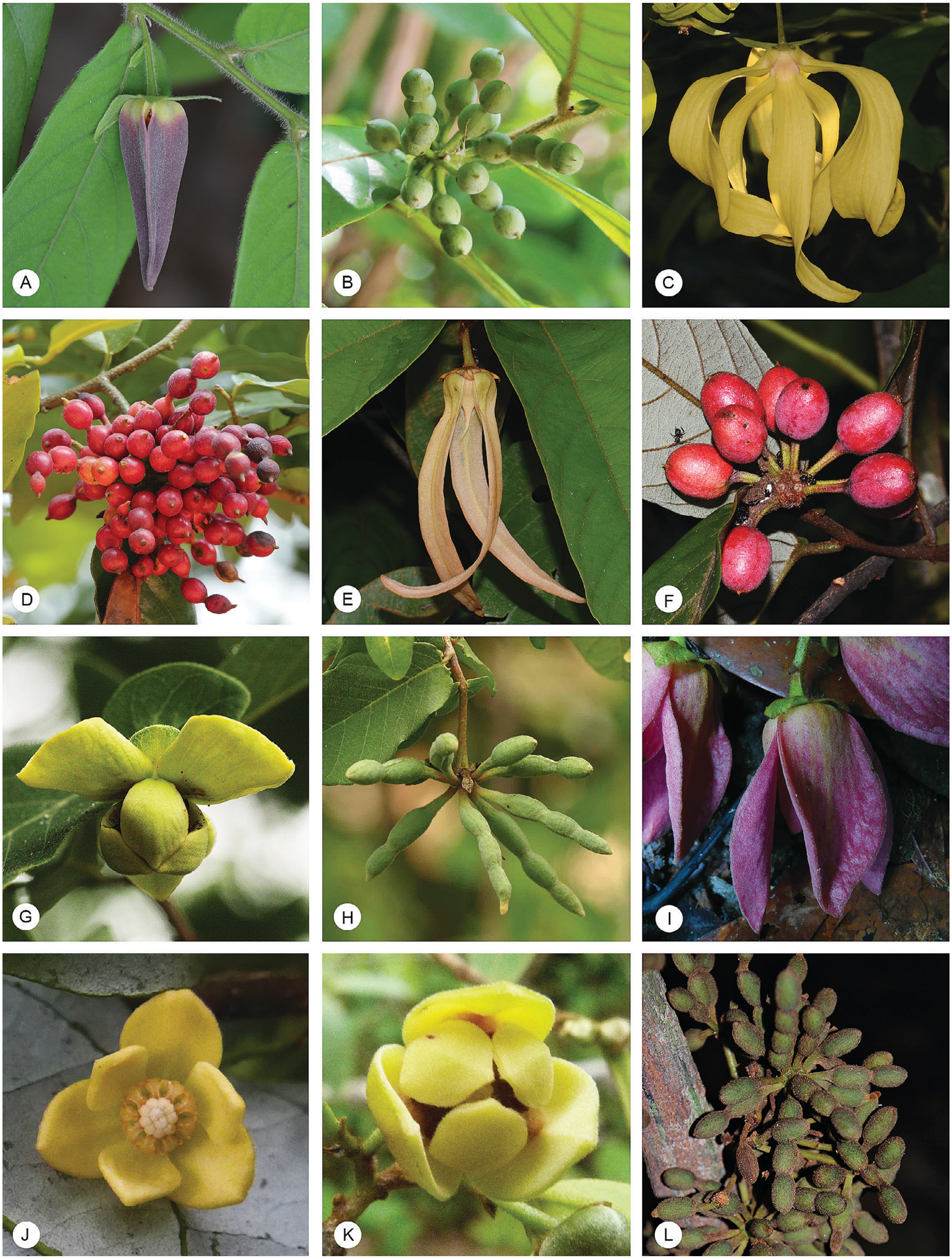
Friesodielsia currently comprises 49 species of woody climbers (Rainer & Chatrou, 2016), distributed in tropical Asia and Africa. The original generic circumscription was challenged by Sprague & Hutchinson (1916), who provisionally regarded the African and Asian species as congeneric, although they recognized that the species belong to different natural groups, and more recently by Verdcourt (1971) and Van Heusden (1992), who suggested that the Asian species may not be congeneric with those from Africa. The Asian species have elongate flowers with three inner petals that are apically connivent, forming a mitriform dome over the reproductive organs (Fig. 1E), and with subglobose monocarps containing only one or rarely two seeds (Fig. 1F); the African species, in contrast, have broader flowers with loosely coherent inner petals (Fig. 1G, I), and moniliform monocarps containing up to five seeds (Fig. 1H). Palynological data also indicate that *Friesodielsia* is heterogeneous, with Asian species possessing pollen with an echinate exine, whereas some African species (*F. gracilipes* (Benth.) Steenis and *F. discostigma* (Diels) Steenis) have coarsely verrucate pollen (Walker, 1971a). Verdcourt (1971) classified *Friesodielsia* into three subgenera: subg. *Amblymitra* Verdc., with only one species, *F. obovata* (Benth.) Verdc.; subg. *Oxymitropsis* Verdc., with three species (*F. enghiana* (Diels) Verdc. ex Le Thomas, *F. hirsuta* (Benth.) Steenis, *F. velutina* (Sprague & Hutch.) Steenis); and subg. *Friesodielsia*, comprising the remaining African and Asian species. Verdcourt (1971) also noted that the two small African subgenera (subg. *Amblymitra*, subg. *Oxymitropsis*) were strikingly different from subg. *Friesodielsia* and possibly deserved recognition as distinct genera, although he refrained from formalizing this.

The hypotheses of a distant relationship between the African and Asian species of the genus were later corroborated by molecular phylogenetic studies (Richardson & al., 2004; Couvreur & al., 2011; Chatrou & al., 2012), which consistently demonstrated that Asian species of *Friesodielsia* are closely related to *Dasymaschalon* and *Desmos*, whilst African *Friesodielsia* species were inferred to be more closely related to the African genus *Monanthotaxis*. These studies did not result in nomenclatural changes, however, because of limited taxon sampling (less than 5% of the ca. 180 species in the *Dasymaschalon* alliance). Wang & al. (2012) recently conducted a phylogenetic analysis of the *Dasymaschalon* alliance based on a more extensive taxon sampling (42 taxa, accounting for ca. 23% of species) and a concatenated dataset from five chloroplast regions (*matK*, *ndhF*, *psbA-trnH*, *rbcL*, *trnL-F*). Their results confirmed the close relationships of constituent genera within the alliance and the polyphyletic status of *Friesodielsia*, although intergeneric relationships between *Dasymaschalon*, *Desmos* and *Friesodielsia* remained unresolved due to inadequate resolution based on the chloroplast regions used, highlighting the need for further molecular phylogenetic studies based on more informative nuclear DNA markers.

Monanthotaxis currently consists of 67 species from tropical Africa and Madagascar (Hoekstra & al., 2016). In addition to the African species of *Friesodielsia*, the monospecific genera *Exellia* Boutique and *Gilbertiella* Boutique also appear to be closely related to *Monanthotaxis*. The taxonomic status of these two genera has been unclear, although they have been grouped with *Monanthotaxis* based on flower and pollen morphology (Walker, 1971a; Le Thomas, 1981; Van Heusden, 1992). *Gilbertiella* has also been classified in the same group as *Monanthotaxis* based on fruit and seed morphology (Van Setten & Koek-Noorman, 1992), while *Exellia* has very distinct fruits, comprising sessile biseriate monocarps, in contrast to the stipitate uniseriate monocarps in *Monanthotaxis* and *Gilbertiella*. In a previous phylogenetic study based on *rbcL* and *trnL-F*, *Exellia* was shown to be nested within *Monanthotaxis* (Bygrave, 2000). Thus far, no studies have included DNA sequences of *Gilbertiella*.

In this study, molecular phylogenetic analyses are based on an expanded taxon sampling, including representatives of almost all constituent genera in the tribe Uvarieae, and based on a combined chloroplast and nuclear DNA dataset, with three main objectives: (1) to clarify intergeneric relationships within the *Dasymaschalon* alliance; (2) to investigate the phylogenetic affinities of different segregates of *Friesodielsia*, enabling validation of nomenclatural changes as necessary; and (3) to assess the phylogenetic positions of some *Friesodielsia* segregates, *Exellia* and *Gilbertiella*, allowing an assessment of the generic circumscription of *Monanthotaxis*.

Fig. 1. Flower and fruit morphology in the *Dasymaschalon* alliance. **A,** *Dasymaschalon trichophorum* flower, with three connivent petals forming a pollination chamber; **B,** *Dasymaschalon trichophorum* fruit, composed of several multiseeded, moniliform monocarps; **C,** *Desmos chinensis* flower, with basally constricted petals forming a pollination chamber; **D,** *Desmos chinensis* fruit, with numerous multiseeded, moniliform monocarps; **E,** *Friesodielsia borneensis* flower, with long outer petals and short inner petals, three inner petals apically connivent forming a pollination chamber; **F,** *Friesodielsia borneensis* fruit, composed of single-seeded monocarps; **G,** *Friesodielsia obovata* flower, with subequal inner and outer petals; **H,** *Friesodielsia obovata* fruit, with multiseeded monocarps; **I,** *Friesodielsia hirsuta* flower, which is much wider, with subequal outer and inner petals; **J,** *Monanthotaxis mannii* flower, showing a ring of obconical stamens; **K,** *Monanthotaxis buchananii* flower, with loosely coherent petals forming a pollination chamber; **L,** *Monanthotaxis diclina* fruit, with multiseeded monocarps. — Photographs: A–C, E & F, Xing Guo; D, Yuen Yung Lau; G & H, Bart T. Wursten; I & J, Carel C.H. Jongkind; K, Warren McCleland; L, Jan J. Wieringa.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■ MATERIALS AND METHODS

Taxon and DNA region sampling. — The 42-taxon dataset generated by Wang & al. (2012) was used as the basis for an expanded taxon sampling, including additional species from the *Dasymaschalon* alliance, with a focus on *Friesodielsia* and *Monanthotaxis*, which were inadequately sampled previously (6 out of 49 *Friesodielsia* species, and 7 out of 66 *Monanthotaxis* species). A total of 101 accessions (96 species) were included in the extended dataset, with the ingroup consisting of 18 *Dasymaschalon* species, 9 *Desmos* species, 25 *Friesodielsia* species, and 27 *Monanthotaxis* species. The outgroups were selected on the basis of previous studies (Couvreur & al., 2011; Chatrou & al., 2012; Wang & al., 2012) and included 14 closely related taxa representing 11 genera from the tribe Uvarieae (*Afroguatteria* Boutique, *Cleistochlamys* Oliv., *Dielsiothamnus* R.E.Fr., *Exellia*, *Fissistigma*, *Mitrella* Miq., *Pyramidanthe* Miq., *Schefferomitra* Diels, *Sphaerocoryne* Scheff. ex Ridl., *Toussaintia* Boutique, *Uvaria*), and representative species from four more distantly related genera in the tribe Monodoreae (*Hexalobus* A.DC., *Isolona* Engl., *Sanrafaelia* Verdc., *Uvariodendron* (Engl. & Diels) R.E.Fr.).

An initial round of analyses indicated that the three *Dasymaschalon* species (*D. filipes* (Ridl.) Bân, *D. longiflorum* Finet & Gagnep., *D. tibetense* X.L.Hou) that were previously shown to be more closely related to Asian *Friesodielsia* species in the chloroplast phylogeny (Wang & al., 2012) belong to the same clade as the majority of *Dasymaschalon* species in the ribosomal DNA (rDNA) tree (Electr. Suppl.: Figs. S1 & S2). This topological discordance was strongly supported (Bayesian analysis posterior probability ≥0.95, and/or maximum parsimony or maximum likelihood analysis bootstrap/jackknife ≥ 75%) and hence was considered as hard incongruence, suggesting potential hybridization, incomplete lineage sorting or gene duplication (Wendel & Doyle, 1998; Slowinski & Page, 1999; Linder & Rieseberg, 2004). Distinguishing different causes for gene tree incongruence requires more than two unlinked genomic datasets (Buckley & al., 2006; Joly & al., 2009); this is beyond the scope of the present study, however, and consequently *D. filipes*, *D. longiflorum* and *D. tibetense* were excluded from later analyses.

DNA sequences of five chloroplast regions (*matK*, *ndhF*, *psbA-trnH*, *rbcL*, *trnL-F*) which are commonly used in Annonaceae phylogenetics were downloaded from the nucleotide database of the National Center for Biotechnology Information (http://www.ncbi.nlm.nih.gov) or generated for the newly added samples in this study. In order to improve resolution of the phylogeny two additional nuclear ribosomal regions, the internal transcribed spacer region (ITS-5.8S-ITS2) and the external transcribed spacer (ETS), which have previously been shown to be highly variable at the species level (reviewed by: Álvarez & Wendel, 2003; Feliner & Rosselló, 2007; Poczai & Hyvönen, 2010), were generated for all accessions, including the newly added species as well as the 42 taxa used in the chloroplast phylogeny by Wang & al. (2012). Voucher information and GenBank accession numbers for all samples included in the dataset are given in Appendix 1.

DNA extraction, amplification and sequencing. — DNA was extracted, amplified and sequenced using the same procedures as previously described (Thomas & al., 2012; Guo & al., 2014). For ITS and ETS, amplification reactions were performed with primers listed in Table 1 and the thermal cycling profile included template denaturation at 94°C for 2 min followed by 38 cycles of denaturation at 95°C for 1 min, primer annealing at 55°C for 1 min, and primer extension at 72°C for 1 min 30 s; followed by a final extension step at 72°C for 10 min.

Sequence assembly, alignment and phylogenetic analyses. — Sequence fragments were edited and assembled using GeneiousPro v.7.1.9 (Biomatters; http://www.geneious.com). Sequences of individual regions were subsequently aligned automatically using the MAFFT (Katoh & al., 2002) plugin in Geneious with default settings, and then manually edited and optimised. A total of 260 ambiguously aligned positions were excluded from the analyses because of difficult homology assessment: 24 positions from 1 block of the *ndhF* region; 91 positions from 2 blocks of the *psbA-trnH* region; 35 positions from 5 blocks of the *trnL-F* region; 99 positions from 11 blocks of the ITS region; and 11 positions from 1 block of the ETS region (Table 2). An inversion of 15 positions in the *psbA-trnH* spacer of some species was identified and reverse-complemented in the alignment, following a strategy previously applied by Pirie & al. (2006) to retain substitution information in the fragments.

Phylogenetic reconstruction was performed using maximum parsimony (MP), maximum likelihood (ML), and Bayesian inference (BI) methods. DNA sequences for the five chloroplast loci and the two rDNA gene regions were concatenated and analyzed independently of one another to resolve their respective gene trees. A simultaneous analysis (Kluge, 1989; Nixon & Carpenter, 1996) of all characters was then performed, which was the primary basis for phylogenetic inference.

Table 1. Primers used for amplification and sequencing of two nuclear DNA regions.

DNA region	Primer name	Sequence (5′–3′)	Source
ITS	ITS2	GCTGCGTTCTTCATCGATGC	White & al., 1990
	ITS3	GCATCGATGAAGAACGCAGC	White & al., 1990
	P17	CTACCGATTGAATGGTCCGGTGAA	Popp & Oxelman, 2001
	26S-82R	TCCCGGTTCGCTCGCCGTTACTA	Popp & Oxelman, 2001
ETS	ETS_092F	CCCATGACGGAGCGGGATGC	This study
	ETS_502R	CTGGCGGGCTCCCTGTAGGA	This study

For the MP analyses, all characters were treated as independent and of equal weight, with gaps treated as missing data. A heuristic search was performed in PAUP* v.4.0b10 (Swofford, 2002) with 2000 random addition sequence replicates with TBR branch-swapping, saving 10 trees per replicate. The most parsimonious trees were summarised using a strict consensus tree. Clade support was evaluated using the jackknife (JK) method (Farris & al., 1996) with the removal probability set to approximately e^{-1} (36.7879%), and "jac" resampling emulated. One thousand JK replicates were performed with 100 random addition tree bisection-reconnection searches (each with a maximum of 10 trees held) per replicate.

Maximum likelihood analyses were performed in RAxML v.8.2.6 (Stamatakis, 2006) provided by the CIPRES Science Gateway (Miller & al., 2010). The dataset was divided into seven partitions based on DNA region identity and run under the general time-reversible model with rate heterogeneity modeled by a gamma distribution (GTR+Γ). Fifty inferences were run from distinct random stepwise addition sequence MP starting trees. Branch support was subsequently estimated with 1000 non-parametric bootstraps under the partition data model.

Bayesian analysis was undertaken using MrBayes v.3.2.6 (Ronquist & al., 2012) with both partitioned (partitions based on DNA region identity) and non-partitioned (regions concatenated without partitioning) strategies. For the partitioned dataset, the parameter values for each locus were allowed to evolve independently using the unlinked setting. The appropriate DNA substitution model for each locus and the concatenated matrix (Table 2) was determined in MrModeltest v.2.3 (Nylander, 2004) using the Akaike information criterion. For analyses of both the partitioned and the non-partitioned datasets, four independent Metropolis-coupled Markov chain Monte Carlo analyses were run. Each search used three incrementally heated and one cold Markov chain, and was run for 10 million generations and sampled every 1000th generation. The temperature parameter was set to 0.08. The mean branch length prior was reset from the default mean (0.1) to 0.01 (brlenspr=unconstrained: exponential (100.0)) to reduce the likelihood of stochastic entrapment in local tree length optima (Brown & al., 2010; Marshall, 2010). Convergence was assessed using the standard deviation of split frequencies, with values <0.01 interpreted as indicating good convergence. The first 25% of samples (2500 trees) were discarded as burn-in, and the post-burn-in samples summarized as a 50% majority-rule consensus tree. Overall performance of analyses was assessed in Tracer v.1.5 (Rambaut & Drummond, 2009) to determine whether the parameter samples were drawn from a stationary, unimodal distribution, and whether adequate effective sample sizes (ESS) for each parameter (ESS >200) had been reached. Stationarity of posterior probabilities of splits within runs, and convergence of posterior probabilities of splits between different runs were visually checked using the Cumulative and Compare functions in AWTY (Nylander & al., 2008). Inference of non-partitioned and partitioned nucleotide datasets was assessed with Bayes factor comparison. The standard criterion of 2 ln Bayes factor >10 was used as a benchmark, indicating very strong evidence against an alternative strategy (Kass & Raftery, 1995; Nylander & al., 2004).

Bootstrap/jackknife values of 50%–74% were considered as weak support by the data, 75%–84% as moderate support, and 85%–100% as strong support. In BI, the estimation of branch support accompanies the tree estimation and is reflected by posterior clade probability (Larget & Simon, 1999); branches with values ≥0.95 are considered well supported, and <0.95 not supported (Yang & Rannala, 1997).

Table 2. Descriptive statistics and best-fitting substitution models for each of the five chloroplast and two nuclear DNA regions and the concatenated datasets.

			% missing data		Variable characters (%)		Parsimony-informative characters (%)		
DNA region	Alignment length	Excluded sites	Entire dataset	Ingroup	Entire dataset	Ingroup	Entire dataset	Ingroup	AIC model selection
Chloroplast DNA data									
matK	729	0	7.3	6.5	150 (20.6)	91 (12.5)	71 (9.7)	43 (5.9)	GTR+Γ
ndhF	2044	24	30.7	30.8	597 (29.6)	342 (16.9)	301 (14.9)	169 (8.4)	GTR+I+Γ
rbcL	1327	0	22.6	22.5	131 (9.9)	77 (5.8)	63(4.7)	35 (2.6)	GTR+I+Γ
psbA-trnH	477	91	9.9	9.2	144 (37.3)	104 (26.9)	84 (21.8)	58 (15)	GTR+Γ
trnL-F	922	35	11.2	12.4	155 (17.5)	95 (10.7)	72 (8.1)	47 (5.3)	GTR+Γ
Combined data	5499	150	21.9	22.1	1177 (22)	709 (13.3)	591 (11)	352 (6.6)	GTR+I+Γ
Nuclear DNA data									
ITS	959	99	51.4	44.4	187 (21.7)	160 (18.6)	97 (11.3)	70 (8.1)	GTR+I+Γ
ETS	430	11	35.7	22.5	–	150 (35.8)	–	98 (23.4)	HKY+I+Γ
Combined data	1389	110	46.2	37.3	337 (26.3)	310 (24.2)	195 (15.2)	168 (13.1)	HKY+I+Γ
Combined chloroplast and nuclear data									
	6888	260	26.4	24.9	1514 (22.8)	1019 (15.4)	786 (11.9)	520 (7.8)	GTR+I+Γ

■ RESULTS

The concatenated alignment of five chloroplast regions and two nuclear ribosomal regions consisted of 6628 aligned positions. Characteristics and the best-fitting nucleotide substitution model of each data matrix are presented in Table 2. The chloroplast and rDNA analyses with all available accessions are presented in Figs. S1 & S2 to exhibit the mutually well-supported topological incongruence within the clade comprising three *Dasymaschalon* species (*D. filipes*, *D. longiflorum*, *D. tibetense*). Apart from the exclusion of the observed topological discordance, the simultaneous analysis (Fig. 2) was shown to be the best resolved amongst all three data matrices. For this reason, it was considered to be the best estimate of the phylogeny and selected as the basis for further discussion of relationships and systematic inferences.

For the BI analysis, partitioning considerably improved mean $-\ln L$ value (mean $-\ln L_{\text{non-partitioned}} = 27{,}529$, mean $-\ln L_{\text{partitioned}} = 26{,}755$). Bayes factor comparison indicated that the partitioned analyses based on region identity provided distinctly better explanations of the data than the analyses of the non-partitioned model: $2 \ln \mathrm{B}$ (partitioned over non-partitioned) = 1540, significantly above the threshold value of 10. The 50% majority-rule consensus tree derived from the analyses using the partitioned strategy was therefore selected to present the results of the Bayesian analyses.

The MP, ML, and Bayesian analyses yielded similar topologies, differing mainly in the relative posterior probability (PP), MP jackknife (JK) and ML bootstrap (BS) values for particular groups (Fig. 2). The *Dasymaschalon* alliance (except *Friesodielsia discostigma* and *F. gracilipes*, which are distantly related to the majority of this genus) is unambiguously supported as monophyletic, with two sister clades (I and II) retrieved, showing a clear geographic pattern corresponding with African and Asian distributions, respectively.

Within the African Clade I (PP = 1; JK = 96; BS = 96), *Friesodielsia obovata* is shown to be sister to a clade comprising two weakly to strongly supported subclades, IA (PP = 1; JK = 93; BS = 75, consisting of 27 species of *Monanthotaxis* and *Exellia scamnopetala* (Exell) Boutique), and IB (PP = 1; JK = 57; BS = 76, comprising 8 species of African *Friesodielsia*).

Clade II (PP = 1; JK = 94; BS = 90) consists of the Asian species sampled, with the 10 accessions of *Desmos* forming an early-divergent branch, Clade IIA (PP = 1; JK = 95; BS = 95). The sister lineage to Clade IIA is strongly supported (PP = 1; JK = 93; BS = 93), and comprises two sister clades: Clade IIB (PP = 1; JK = 99; BS = 97), consisting of the Asian *Friesodielsia* taxa sampled and *Schefferomitra subaequalis* Diels; and Clade IIC (PP = 1; JK = 100; BS = 100), comprising the *Dasymaschalon* species sampled.

The results suggest that *Dasymaschalon* and *Desmos* are both monophyletic. *Friesodielsia* is highly polyphyletic, however, with the sampled species scattered across five different lineages, viz.: (1) the Asian Clade IIB, which includes the type, *F. cuneiformis* (Blume) Steenis; (2) *F. obovata* (the early-divergent branch within Clade I); (3) Clade IB, which is the sister to the *Monanthotaxis* clade; (4) *F. gracilipes*, which is sister to a clade comprising four accessions of *Sphaerocoryne*; and (5) *F. discostigma*, which is sister to *Afroguatteria bequaertii* (De Wild.) Boutique. The Asian *Friesodielsia* group and the African genus *Monanthotaxis* are furthermore paraphyletic, with *Schefferomitra subaequalis* and *Exellia scamnopetala* deeply nested within Clades IIB and IA, respectively.

■ DISCUSSION

Phylogenetic relationships within the *Dasymaschalon* alliance. — The present study corroborates and expands the results of previous phylogenetic analyses, which have suggested a close relationship between the genera within the *Dasymaschalon* alliance and the polyphyletic status of *Friesodielsia* (Couvreur & al., 2011; Chatrou & al., 2012; Wang & al., 2012). The *Dasymaschalon* alliance is shown to be collectively monophyletic and can easily be distinguished morphologically from other lineages in the tribe Uvarieae by its inaperturate pollen with a thin exine, the glaucous abaxial surface of the leaves with parallel tertiary venation (Wang & al., 2012, and references therein; pers. obs.), and often by basal leaf glands (Turner, 2012). The sister relationship retrieved between the African Clade I (comprising *Exellia*, *Monanthotaxis* and some *Friesodielsia* species) and the Asian Clade II (including *Desmos*, *Dasymaschalon*, *Schefferomitra* and some *Friesodielsia* species) is consistent with floral, pollen and fruit morphology: species belonging to Clade I have open or loosely coherent floral chambers (Fig. 1G, I–K), petals that are wide and short and pollen with a microbaculate exine; whereas species in Clade II have flowers with partially enclosed floral chambers, petals that are narrow and elongate (Fig. 1A, C, E) and echinate-scabrate pollen (Verdcourt, 1971; Walker, 1971a; Wang & al., 2009, 2012; Saunders, 2010; pers. obs.).

Relationships within the African clade (Clade I) are well resolved (Fig. 2). After the early-divergent species *Friesodielsia obovata*, the 27 species of *Monanthotaxis* form a well-supported lineage (Clade IA, PP = 1; JK = 93; BS = 75), as do the 7 other *Friesodielsia* species (Clade IB), although the MP analysis provides only weak support (PP = 1; JK = 57; BS = 76). *Exellia scamnopetala* is deeply nested within Clade IA, rendering *Monanthotaxis* paraphyletic. A subclade (Clade IAi) comprising all sampled Madagascan species (*M. ambrensis* (Cavaco & Keraudren) Verdc., *M. boivinii* (Baill.) Verdc., *M. komorensis* P.H.Hoekstra, *M. heterantha* (Baill.) Verdc., *M. micrantha* (Baker) Verdc., *M. sororia* (Diels) Verdc.) was retrieved, with one species (*M. filipes* P.H.Hoekstra) from East Africa as sister to the remaining species. The latter species and some Madagascar representatives of this subclade possess filiform pedicels, in contrast with all other members of *Monanthotaxis*, which have thicker pedicels. All continental African species with leaf-opposed or extra-axillary inflorescences formed another strongly supported subclade (Clade IAii) comprising seven species, whilst both (supra-)axillary and extra-axillary inflorescences are present in the Madagascar clade and all other species in Clade IA have (supra-)axillary inflorescences. The presence of staminodes seems to be restricted

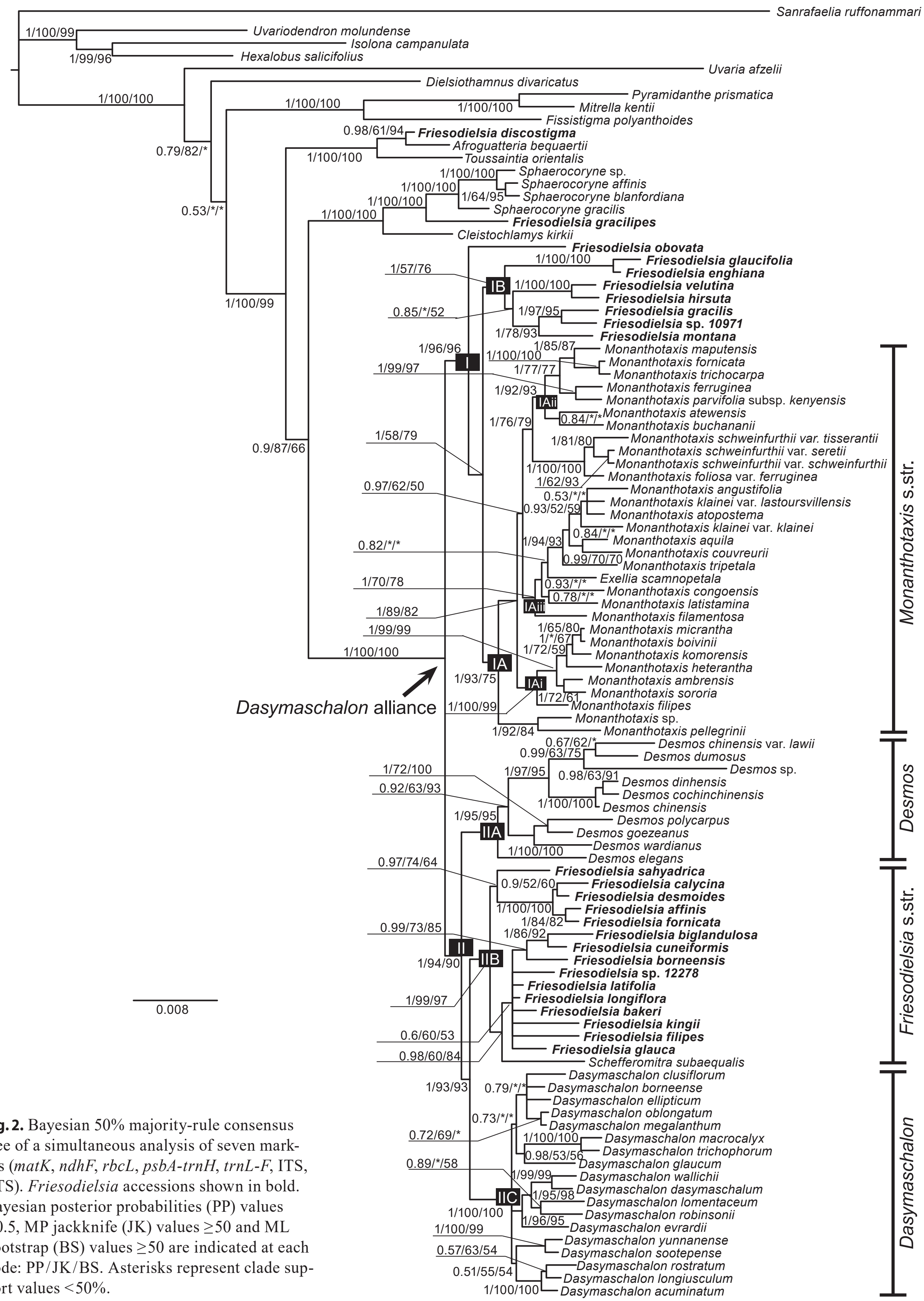

Fig. 2. Bayesian 50% majority-rule consensus tree of a simultaneous analysis of seven markers (*matK*, *ndhF*, *rbcL*, *psbA-trnH*, *trnL-F*, ITS, ETS). *Friesodielsia* accessions shown in bold. Bayesian posterior probabilities (PP) values ≥0.5, MP jackknife (JK) values ≥50 and ML bootstrap (BS) values ≥50 are indicated at each node: PP/JK/BS. Asterisks represent clade support values <50%.

to the Madagascan clade and to more than half of the species of a moderately supported subclade (Clade IAiii) comprising nine *Monanthotaxis* species (including its type) and *Exellia scamnopetala*. The sections *Popowiopsis* Verdc. and *Enneastemon* (Exell) Verdc., defined by Verdcourt (1971) based on petal aestivation, are revealed to be highly polyphyletic, with the species of the former (sampled species including *M. ambrensis*, *M. boivinii*, *M. buchananii* (Engl.) Verdc., *M. ferruginea* (Oliv.) Verdc., *M. heterantha*, *M. micrantha*, *M. parvifolia* (Oliv.) Verdc., *M. pellegrinii* Verdc., *M. sororia*, and *M. trichocarpa* (Engl. & Diels) Verdc.) retrieved in four different clades and the latter (sampled species including *M. angustifolia* (Exell) Verdc., *M. foliosa* (Engl. & Diels) Verdc., *M. fornicata* (Baill.) Verdc., and *M. schweinfurthii* (Engl. & Diels) Verdc.) in three clades. Furthermore, the species *M. klainei* (Engl.) Verdc., with multiple accessions that represent different varieties, is not monophyletic, with *M. angustifolia* and *M. atopostema* P.H.Hoekstra nested within the clade (Fig. 2). These phylogenetic relationships suggest that the delimitations of *M. klainei* and the previously defined sections are problematic: on-going research involving detailed morphological examination and increased phylogenetic sampling of specimens will lead to a new subgeneric classification and will show whether the varieties described in some species should be elevated to species rank.

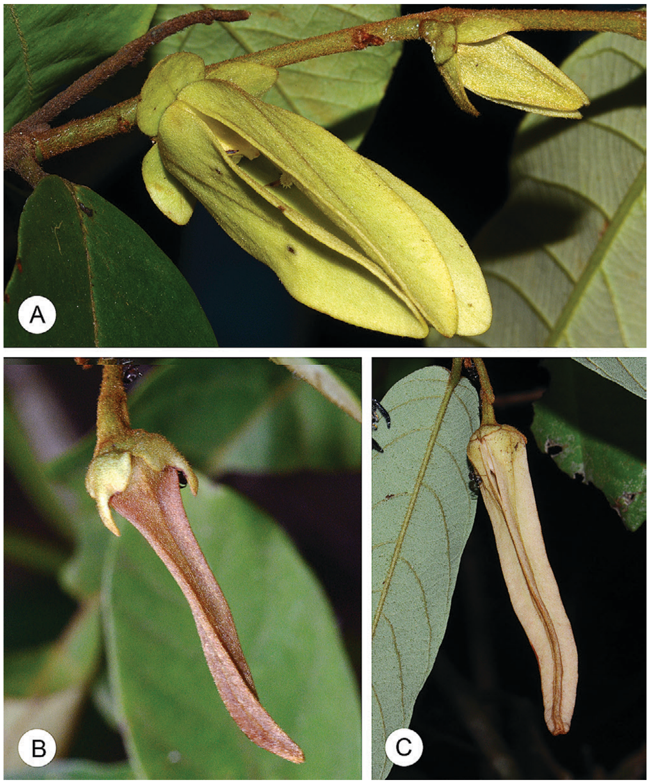

Fig. 3. Flower morphology of selected species of *Friesodielsia*. **A,** Flower bud of *Friesodielsia desmoides*, showing free-spreading outer petals; **B,** Flower bud of *Friesodielsia borneensis*, showing firmly connivent outer petals; **C,** Mature flower of *Friesodielsia borneensis*, showing three outer petals separating at base. — Photographs: Xing Guo.

The intergeneric relationships within the Asian Clade II have historically proven difficult to resolve despite the fact that the three constituent genera are morphologically very distinct, with different pollination chambers and monocarp shapes (Fig. 1). *Dasymaschalon*, *Desmos* and *Friesodielsia* s.str. repeatedly formed a polytomy in previous analyses (Bygrave, 2000; Couvreur & al., 2011; Chatrou & al., 2012; Wang & al., 2012). The resolution of the deeper nodes is significantly improved in the present study (Fig. 2) following the incorporation of two nuclear regions. *Dasymaschalon* is strongly supported as sister to *Friesodielsia* s.str., and these two genera are collectively sister to *Desmos*. The inferred relationships within this clade are consistent with floral morphology and pollination chamber types: *Friesodielsia* flowers have an enclosed floral chamber formed by the apical connivence of the three inner petals (Fig. 1E); *Dasymaschalon* flowers have a superficially similar floral chamber (Fig. 1A), although the petals that are apically connivent are inferred to be homologous with the outer petals of other Annonaceae; and *Desmos* flowers (Fig. 1C) possess a partially enclosed floral chamber formed by basally constricted petals, with the apical parts spreading outwards.

Whereas the subclades differentiated within *Dasymaschalon* (Clade IIC) received only weak support, several strongly supported subclades are retrieved in *Desmos* (Clade IIA) and the Asian *Friesodielsia* lineage (Clade IIB). Relationships within Clade IIA are well resolved and show a clear geographic pattern: the Sri Lankan species *Desmos elegans* Saff. is well supported as sister to the other *Desmos* species sampled, which form two subclades consisting of species from Australia (*D. goezeanus* (F.Muell.) Jessup, *D. polycarpus* Jessup, *D. wardianus* (F.M.Bailey) Jessup) and continental Asia (*D. chinensis* Lour., *D. chinensis* var. *lawii* (Hook.f. & Thomson) Bân, *D. cochinchinensis* Lour., *D. dinhensis* (Pierre ex Finet & Gagnep.) Merr., *D. dumosus* Saff.). Within Clade IIB, two main subclades with moderate to strong support can be distinguished. One subclade (comprising *F. affinis* (Hook.f. & Thomson) D.Das, *F. calycina* (King) Steenis, *F. desmoides* (Craib) Steenis, *F. fornicata* (Roxb.) D.Das, *F. sahyadrica* N.V.Page & Survesw.) is characterised by flowers with three outer petals that are freely spreading (Fig. 3A) and have a flat petal base, whereas the other subclade (including the remaining Asian *Friesodielsia* representatives sampled) has flowers with outer petals that are connivent before anthesis (Fig. 3B, C) and possess a distinctly concave petal base.

Polyphyly and classification of *Friesodielsia*. — The polyphyletic status of *Friesodielsia*, in which the African species are not congeneric with the Asian species, was previously indicated by palynological data (Walker, 1971a) and molecular phylogenetic analyses (Couvreur & al., 2011; Chatrou & al., 2012; Wang & al., 2012). Our increased sampling of both taxa and DNA markers reveals more extensive polyphyly: the African species of *Friesodielsia* are not only phylogenetically distinct from the Asian species, but are themselves not monophyletic, with the sampled species scattered across several different clades.

All Asian representatives of *Friesodielsia* sampled form a strongly supported clade, including the type, *F. cuneiformis*.

This Asian group can be distinguished from the African species by their elongate flowers (Fig. 1E) with partially closed floral chambers (Wang & al., 2012), and unequal outer and inner petals (Verdcourt, 1971). We therefore recommend that a narrower circumscription of *Friesodielsia* should be adopted, restricting the generic name to Asian species only; the African species should accordingly be transferred to other genera.

Among the 10 species (inclusive of a currently undescribed species) of African *Friesodielsia* sampled (out of a total of 11 species), eight form a basal grade within Clade I and are phylogenetically associated with the African genus *Monanthotaxis*, whereas two species (*F. gracilipes*, *F. discostigma*) are retrieved outside the accepted circumscription of the *Dasymaschalon* alliance (Fig. 2). Within Clade I, *F. obovata* is sister to all other African species, and seven species within Clade IB are retrieved as sister to Clade IA, which includes all the *Monanthotaxis* species sampled. These phylogenetic results suggest that *F. obovata* and the seven *Friesodielsia* species in Clade IB should be transferred to *Monanthotaxis*, or alternatively treated as new genera; the diagnostic morphological characters of each clade will be discussed in detail below (see "Delimitation of *Monanthotaxis*") to assess these two alternative classifications.

Friesodielsia gracilipes is sister to the palaeotropical genus *Sphaerocoryne*, corroborating the results of previous phylogenetic analyses based on *rbcL* and *trnL-F* sequences (Bygrave, 2000), which indicated that *F. gracilipes* was located in the *Cleistochlamys-Sphaerocoryne-Toussaintia* clade (Clade 13 in Bygrave, 2000: fig. 6.3b). The inferred close relationship between these two groups is consistent with their morphological similarities, as they both have reticulate tertiary leaf venation and axillary flowers. In contrast, the African species of *Friesodielsia* in Clade IB and *Monanthotaxis* have parallel tertiary leaf venation and extra-axillary flowers. Based on our assessment of the morphological affinities and phylogenetic relationships of these two groups, we believe that *F. gracilipes* is best considered congeneric with *Sphaerocoryne*, necessitating a new nomenclatural combination.

Friesodielsia discostigma, which differs from the *Friesodielsia* species in Clade IB in having reticulate tertiary leaf venation and axillary flowers, is shown to be closely related to the African genus *Afroguatteria* rather than the other four segregates of *Friesodielsia*. Great care was taken with older leaf material of *F. discostigma* (over 100 years) to avoid technical errors, including repeated DNA extraction, PCR and sequencing. Sequence similarity of *matK*, *psbA-trnH* and *trnL-F* (assessed by blast searching data in GenBank) support its relationship in the concatenated analysis (Fig. 2), indicating that our finding is not an artifact resulting from missing data. This inferred relationship between *F. discostigma* and *Afroguatteria* is consistent with their similarity in morphological characters, including subequal inner and outer petals, and numerous stipitate monocarps with one or two seeds. Van Heusden (1992: 73) recognized their similarity in secondary and tertiary leaf venation, stating that the "leaves of *F. discostigma* closely resemble those of *Afroguatteria*." Species of the *Dasymaschalon* alliance share eucamptodromous leaf venation (sensu Hickey, 1979) (Fig. 4A), with parallel secondary veins lacking prominent marginal arches, and parallel tertiary veins connecting adjacent secondaries (Klucking, 1986). In contrast, *Friesodielsia discostigma* and *Afroguatteria* have "festooned brochidodromous" leaf venation (Fig. 4B) with reticulate tertiary veins (sensu Hickey & Wolfe, 1975), in which the secondary veins anastomose and link to form prominent loops, with secondary arches outside the prominent loops that gradually diminish towards the margin (Klucking, 1986; Xue & al., 2012; Guo & al., 2014). Based on their close phylogenetic relationships and similar morphological characters, we propose that *F. discostigma* should be transferred to the genus *Afroguatteria*.

Congeneric status of *Friesodielsia* s.str. and *Schefferomitra*. — The phylogenetic analyses presented here (Fig. 2) suggest that the Asian *Friesodielsia* lineage is not monophyletic due to the inclusion of *Schefferomitra subaequalis* (sole representative of this monospecific genus) in Clade IIB (PP = 1; JK = 99; BS = 97). *Schefferomitra* is currently placed in tribe Uvarieae based on morphology (Chatrou & al., 2012), although its phylogenetic position was previously unknown due to the unavailability of DNA sequences.

Detailed examination of the morphological characters of *S. subaequalis* failed to reveal any character that supports the continued recognition of *Schefferomitra* as a genus distinct from *Friesodielsia* s.str.: the only consistent difference is the shape of the staminal connective, which is tongue-shaped in *Schefferomitra* (Keßler, 1993; Couvreur & al., 2012), whereas the staminal connectives of Asian *Friesodielsia* species have a truncate discoid apex.

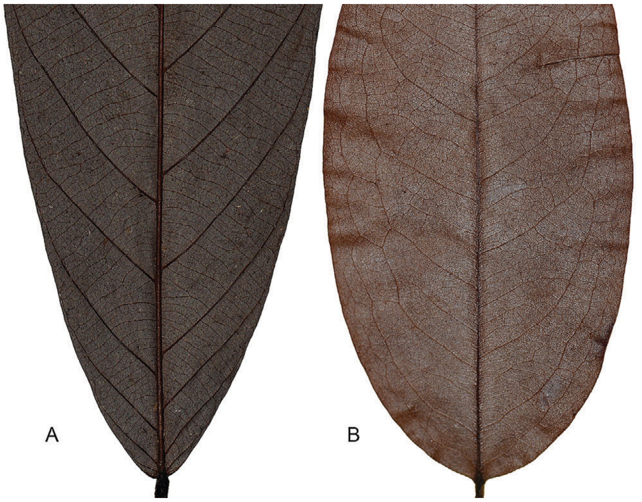

Fig. 4. Leaf venation patterns of selected species of *Friesodielsia*. **A,** *Friesodielsia cuneiformis* (abaxial view), showing eucamptodromous venation with parallel and upturned secondary veins, and parallel tertiary veins (type, *C.L. Blume s.n.*, P barcode P00732380); **B,** *Friesodielsia discostigma* (adaxial view), showing brochidodromous venation with curved anastomosing secondary veins and reticulate tertiary veins (isotype, *G.A. Zenker 2980*, P barcode P00363341).

The phylogenetic position of *S. subaequalis* within the Asian *Friesodielsia* clade and their considerable morphological similarity therefore provide convincing evidence that *Friesodielsia* s.str. and *Schefferomitra* are congeneric. Since the name *Schefferomitra* (first published by Diels, 1912) antedates that of *Friesodielsia* (first published by Van Steenis, 1948), strict application of the principle of priority would therefore require adoption of the former, necessitating the transfer of about 38 species names to *Schefferomitra* (excluding the African *Friesodielsia* species, which, as described elsewhere in this study, need to be transferred for taxonomic reasons). This change would create unnecessary confusion because *Friesodielsia* is firmly rooted in the Annonaceae literature owing to its species richness in tropical Asia. In an effort to promote nomenclatural stability we therefore propose conservation of the name *Friesodielsia* against *Schefferomitra* (Guo & al., 2017). The formal transfer of the name *S. subaequalis* to *Friesodielsia* is accordingly postponed pending a ruling by the Nomenclature Committee for Vascular Plants.

Delimitation of *Monanthotaxis*. — The MP, ML, and BI phylogenetic analyses consistently retrieved Clades I, IA and IB as well-supported lineages. This is consistent with two alternative interpretations of generic circumscription: either a broad delimitation of *Monanthotaxis* s.l. with the inclusion of *F. obovata* and species within Clade IB; or retaining the current delimitation of *Monanthotaxis* (equivalent to clade IA) and the segregation of *F. obovata* and the species within Clade IB as two new genera.

Friesodielsia obovata is sister to all other species of Clade I and can be readily distinguished from the remaining taxa in the alliance by the combination of peduncles that bear a conspicuous leafy bract (Verdcourt, 1971) and stellate hairs (Couvreur & al., 2012). Verdcourt (1971) noted the remarkable differences between *F. obovata* and the other species of *Friesodielsia* (including African and Asian species), and placed it in a new monospecific subgenus, *Friesodielsia* subg. *Amblymitra* Verdc. Clade IB is retrieved as sister to Clade IA, which comprises *Exellia* and *Monanthotaxis* species. There are no obvious synapomorphies for the seven species in Clade IB, although diagnostic plesiomorphic character states in stamens can distinguish this lineage from Clade IA: the species in Clade IB have numerous (up to 125) stamens in three to six whorls, compared to only a few (3–15[–40]) stamens in one or two, rarely three, whorls in Clade IA (Verdcourt, 1971; Van Heusden, 1992; pers. obs.). The narrower delimitation of *Monanthotaxis*, in which case *F. obovata* and the species in Clade IB would be treated as two distinct genera, would clearly be undesirable due to the lack of morphological synapomorphies. We therefore adopt a broader delimitation of *Monanthotaxis*, which possesses three characters that are likely to be synapomorphic, viz.: the climbing growth habit, loosely coherent floral chambers and moniliform monocarps. This broad *Monanthotaxis* shows very wide variation in several characters (e.g., inflorescence characters, see Hoekstra & al., 2014), but a more narrow approach would not have reduced most of this variation for core *Monanthotaxis*.

Phylogenetic results in all MP, ML, and BI analyses suggest that *Exellia scamnopetala* is deeply nested within Clade IA, rendering *Monanthotaxis* paraphyletic. The monospecific genus *Exellia* is characterized by globose and sessile monocarps (Boutique, 1951a) and differs from *Monanthotaxis* that possess moniliform monocarps with an obvious stipe (Keßler, 1993; Couvreur & al., 2012). *Exellia* and *Monanthotaxis* are nevertheless very similar in several characters, including: small flowers (petals generally 2–13 mm long, with the exception of *M. bokoli*, which has petals up to 27 mm) and few stamens (3–15[–40]) that are mostly obconical with a broad connective and a narrow filament. These character states are very different in *Dasymaschalon*, *Desmos* and *Friesodielsia* (including African and Asian species): these genera have large flowers (petals 15–145 mm long) and numerous (up to 200) oblong stamens (Van Heusden, 1992). On the basis of these floral morphological similarities, Van Heusden (1992) placed *Exellia* in the "*Monanthotaxis* group". Furthermore, both genera have microbaculate pollen exines (Walker, 1971a, b). Given the close affinity of *Exellia* and *Monanthotaxis*, supported by both molecular and morphological data, we consider *Exellia* congeneric with *Monanthotaxis*, thereby rendering the genus monophyletic.

Another monospecific genus, *Gilbertiella*, was placed in the "*Monanthotaxis* group" by Van Heusden (1992). The genus was described by Boutique (1951a) based on linear stamens, the outer petals that cover the slightly smaller inner petals only at the top and that have a curved hook of the petals towards the centre of the flower. All of these characters occur in at least some species of *Monanthotaxis*. Furthermore, it is highly similar to van Heusden's "*Monanthotaxis* group", in having small flowers (petals ca. 2–4 mm long), few (12) stamens, and multi-seeded monocarps (ca. 6 seeds) and the pollen are similar in having microbaculate exine (Walker, 1971a, b). We were unable to successfully sequence DNA from herbarium samples of the only described species in the genus, *Gilbertiella congolana* Boutique, due to the poor quality of leaf materials. Fortunately, a recently described new species (*Monanthotaxis latistamina* P.H.Hoekstra; Hoekstra & al., 2016) closely resembles *G. congolana*, and this species is shown here to be nested within the *Monanthotaxis* clade (Fig. 2). We therefore propose that the generic name *Gilbertiella* should be reduced to synonymy with *Monanthotaxis*, necessitating a new nomenclatural combination.

■ GENERIC DESCRIPTIONS

Dasymaschalon (Hook.f. & Thomson) Dalla Torre & Harms, Gen. Siphon.: 174. 1901, nom. cons. ≡ *Unona* sect. *Dasymaschalon* Hook.f. & Thomson, Fl. Ind., 1: 134. 1855 ≡ *Desmos* sect. *Dasymaschalon* (Hook.f. & Thomson) Saff. in Bull. Torr. Bot. Club 39: 507. 1912 – Type: *Dasymaschalon dasymaschalum* (Blume) I.M.Turner.

Small trees (rarely climbers), indument of simple hairs. Leaves elliptic to ovate-oblong, 8–18 pairs of secondary veins, abaxial surface glaucous. Inflorescences axillary, 1-flowered.

Flowers bisexual. Sepals 3, valvate, ovate-triangular. Petals 3 (rarely 2), ovate-triangular, in 1 whorl alternate with sepals, valvate, apically connivent to form a mitriform dome (floral chamber) over reproductive organs and often with very small basal apertures between petals; inner petal whorl absent. Stamens numerous; connectives apically truncate or apiculate; pollen inaperturate, in monads. Carpels numerous, free; ovaries densely hairy; ovules 1–7 per carpel, uniseriate. Fruit apocarpous; monocarps stipitate, globose or ellipsoid (1-seeded) or moniliform (multi-seeded); seeds 1–7 per monocarp, globose to ellipsoid, ruminations lamelliform.

Circa 27 species in tropical and subtropical Asia.

Desmos Lour., Fl. Cochinch.: 329, 352. 1790 – Type (designated by Safford in Bull. Torrey Bot. Club 39: 505. 1912): *Desmos cochinchinensis* Lour.

Woody climbers, indument of simple hairs. Leaves ovate-oblong, 7–16 pairs of secondary veins, abaxial surface glaucous. Inflorescences axillary, supra-axillary, or leaf-opposed, 1- or 2-flowered. Flowers bisexual. Sepals 3, valvate, ovate-triangular. Petals 6, in 2 whorls; each whorl valvate, subequal or outer whorl slightly longer than inner whorl; inner whorl basally constricted around reproductive organs to form enclosed floral chamber. Stamens numerous; connectives apically truncate or rounded; pollen inaperturate, in monads. Carpels numerous, free; ovary densely hairy; ovules 1–8 per carpel, uniseriate. Fruit apocarpous; monocarps stipitate, moniliform (rarely globose); seeds 1–8 per monocarp, subglobose to ellipsoid, ruminations lamelliform.

Circa 22 species in tropical and subtropical Asia and Australia.

Friesodielsia Steenis in Bull. Jard. Bot. Buitenzorg, sér. 3, 17: 458. 1948 ≡ *Polyalthia* sect. *Oxymitra* Blume in Blume & Fischer, Fl. Javae, Anonaceae: 71, pl. 34–37. 1830 ≡ *Oxymitra* (Blume) Hook.f. & Thomson, Fl. Ind.: 145. 1855, nom. illeg., non Bisch. ex Lindenb. in Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 14, Suppl. 1: 124. 1829 – Type: *Friesodielsia cuneiformis* (Blume) Steenis (≡ *Polyalthia cuneiformis* Blume).

= *Schefferomitra* Diels in Bot. Jahrb. Syst. 49: 152. 1912 [proposed as rejected against *Friesodielsia*: Guo & al., 2017].

Woody climbers, indument of simple hairs. Leaves oblong-lanceolate, 8–13 pairs of secondary veins, abaxial surface glaucous. Inflorescences axillary, supra-axillary or extra-axillary, 1-flowered. Flowers bisexual. Sepals 3, valvate, ovate-triangular. Petals 6, in 2 whorls; each whorl valvate, outer whorl much longer than inner whorl; inner whorl apically connivent, forming enclosed floral chamber. Stamens numerous; connectives apically truncate or rounded; pollen inaperturate, in monads. Carpels numerous, free; ovary densely hairy; ovules 1 (rarely 2) per carpel. Fruit apocarpous; monocarps stipitate, globose or ellipsoid (rarely cylindrical), seeds 1 (rarely 2) per monocarp, subglobose, ruminations lamelliform.

Circa 38 species in tropical and subtropical Asia.

Monanthotaxis Baill. in Bull. Mens. Soc. Linn. Paris 2: 878. 1890 – Type: *Monanthotaxis congoensis* Baill.

= *Clathrospermum* Planch. ex Benth. in Bentham & Hooker, Gen. Pl. 1: 29. 1862, nom. rej. against *Enneastemon* Exell – Type: *Clathrospermum vogelii* (Hook.f.) Benth. (≡ *Uvaria vogelii* Hook.f.).

= *Enneastemon* Exell in J. Bot. 70(Suppl. 1): 209. 1932, nom. cons. – Type: *Enneastemon angolensis* Exell.

= *Atopostema* Boutique in Bull. Jard. Bot. État Bruxelles 21: 121. 1951 – Type: *Atopostema klainei* (Engl.) Boutique.

= *Exellia* Boutique in Bull. Jard. Bot. État Bruxelles 21: 117. 1951 – Type: *Exellia scamnopetala* (Exell) Boutique (≡ *Popowia scamnopetala* Exell), **syn. nov.**

= *Gilbertiella* Boutique in Bull. Jard. Bot. État Bruxelles 21: 124. 1951 – Type: *Gilbertiella congolana* Boutique, **syn. nov.**

Shrubs or woody climbers, indument of simple hairs (stellate in a few species). Leaves lanceolate, elliptic, ovate, oblong-lanceolate or obovate, 6–23 pairs of secondary veins, abaxial surface glaucous. Inflorescences axillary, supra-axillary, extra-axillary, leaf-opposed or cauline, 1 to many-flowered. Flowers unisexual or bisexual. Sepals 3, valvate, broadly ovate to lanceolate. Petals 6 (rarely 3, 4, or 5), in 2 whorls (rarely 1), each whorl valvate, subequal or in some species outer whorl significantly longer than inner whorl; inner whorl freely spreading or loosely coherent. Stamens 3 to numerous; connectives apically truncate or apiculate; pollen inaperturate, in monads. Carpels 3 to numerous, free; ovary densely hairy or glabrous; ovules 1–7 per carpel, uniseriate (rarely biseriate). Fruit apocarpous; monocarps stipitate (rarely sessile), globose, ellipsoid or subcylindrical, seeds 1–7 per monocarp, subglobose or ellipsoid to subcylindrical, ruminations lamelliform.

Circa 94 species in tropical and subtropical Africa and Madagascar.

■ NOMENCLATURAL CHANGES

The present study reveals that the traditional circumscription of *Friesodielsia* is highly polyphyletic, with currently accepted species in this genus belonging to four different genera, viz. *Afroguatteria*, *Friesodielsia* s.str., *Monanthotaxis* and *Sphaerocoryne*. The two monospecific genera *Exellia* and *Gilbertiella* are furthermore shown to be congeneric with *Monanthotaxis*. A total of 12 nomenclatural changes are accordingly validated here, with types and synonymy provided.

Afroguatteria discostigma (Diels) X.Guo & R.M.K.Saunders, **comb. nov.** ≡ *Cleistopholis discostigma* Diels in Bot. Jahrb. Syst. 39: 474. 1907 ≡ *Oxymitra discostigma* (Diels) Ghesq. ex Pellegr. in Bull. Soc. Bot. France 1949: 66. 1950 (“1949”) ≡ *Richella discostigma* (Diels) R.E.Fr. in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 17a(2): 139. 1959 ≡ *Friesodielsia discostigma* (Diels) Steenis in Blumea 12: 359. 1964 – Holotype: Cameroon, Bipinde, 1904, *G.A. Zenker 2980* (B barcode B 10 0153055!; isotypes: BM barcode BM001125042!, BR barcode 000008800398!, G barcode

G00308361!, GOET barcode GOET005676 [photo!], HBG barcode HBG-502538 [photo!], K barcode K000198949!, L barcode L.1754813!, M barcode M-0107910 [photo!], MA [photo!], P barcode P00363341!, S No. S03-2239!, WAG barcode WAG0053550 [photo!]).

Monanthotaxis congolana (Boutique) P.H.Hoekstra, **comb. nov.** ≡ *Gilbertiella congolana* Boutique in Bull. Jard. Bot. État Bruxelles 21: 124. 1951 – Holotype: Democratic Republic of the Congo, Orientale, Yangambi, rive gauche, Litulombo, 8 Dec 1939, *R.G.A. Germain 17* (BR [on 2 sheets] barcodes 000008799586! & 000008799913!; isotypes: B barcode B 10 0153067!, K barcode K000198957!, NY [photo!], P!).

Monanthotaxis dielsiana (Engl.) P.H.Hoekstra, **comb. nov.** ≡ *Unona dielsiana* Engl. in Bot. Jahrb. Syst. 39: 476. 1907 ≡ *Oxymitra dielsiana* (Engl.) Sprague & Hutch in Bull. Misc. Inform. Kew 1916: 156. 1916 ≡ *Richella dielsiana* (Engl.) R.E.Fr. in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 17a(2): 139. 1959 ≡ *Friesodielsia dielsiana* (Engl.) Steenis in Blumea 12: 359. 1964 – Holotype: Cameroon, South Province, Bipinde, Dec 1901, *G.A. Zenker 2473* (B [on 4 sheets] barcodes B 10 0154098!, B 10 0154096!, B 10 0154097! & B 10 0154099!; isotypes: BM barcode BM001125043!, BR barcode 000008801388!, COI barcode COI00071518 [photo!], E [photo!], G barcode G00308364!, GOET [on 2 sheets] barcodes GOET005688 & GOET005689 [photos!], HBG [photo!], K barcode K000198948!, L barcode L 0182291!, M barcode M-0240178, [photo!], P [on 3 sheets] barcodes P00363342!, P00363343! & P01988326!, S [photo!], WAG barcode WAG0057970!, WU [photo!]).

Monanthotaxis enghiana (Diels) P.H.Hoekstra, **comb. nov.** ≡ *Popowia enghiana* Diels in Mildbraed, Wiss. Erg. Deut. Zentr.-Afr. Exped., Bot.: 213. 1911 ≡ *Friesodielsia enghiana* (Diels) Verdc. ex Le Thomas, Fl. Gabon 16: 240. 1969 – Holotype: Democratic Republic of the Congo, Nord-Kivu, Fort Beni a Semliki, 1907–1908, *G.W.J. Mildbraed 2213* (B barcode B 10 0153056!).

= *Unona obanensis* Baker f. in Rendle & al., Cat. Pl. Oban: 4. 1913 ≡ *Oxymitra obanensis* (Baker f.) Sprague & Hutch. in Bull. Misc. Inform. Kew 1916: 154. 1916 ≡ *Richella obanensis* (Baker f.) R.E.Fr. in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 17a(2): 139. 1959 ≡ *Friesodielsia obanensis* (Baker f.) Steenis in Blumea 12: 359. 1964 – Holotype: Nigeria, Cross River State, Oban, 1911, *P.A. Talbot 1246* (BM barcode BM000547069!).

= *Oxymitra grandiflora* Boutique in Bull. Jard. Bot. État Bruxelles 21: 116. 1951 ≡ *Richella grandiflora* (Boutique) R.E.Fr. in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 17a(2): 139. 1959 ≡ *Friesodielsia grandiflora* (Boutique) Steenis in Blumea 12: 359. 1964 – Holotype: Democratic Republic of the Congo, Orientale, Yalibutu, 45 km NW of Yangambi, 22 Jan 1948, *R.G.A. Germain 883* (BR!; isotypes: K [on 2 sheets] barcodes K000913652! & K000913653!, MO!).

= *Popowia mangenotii* Sillans in Bull. Mus. Natl. Hist. Nat., sér. 2, 24: 578. 1953 – Holotype: Central African Republic, Lobaye, Station de Boukoko, Boukoko, 14 Dec 1948, *C. Tisserant (Équipe) 1285* (P barcode P00363339!; isotypes: BR!, K barcode K000913654!, P barcode P00363338!).

= *Popowia mangenotii* f. *concolor* Sillans in Bull. Mus. Natl. Hist. Nat., sér. 2, 24: 580. 1953 – Holotype: Central African Republic, Lobaye, Station de Boukoko, Boukoko, 5 Apr 1951, *C. Tisserant (Équipe) 2062* (P barcode P00363336!; isotypes: BM barcode BM000547068!, BR!, P [on 2 sheets] barcodes P00363335! & P01985781!).

Monanthotaxis glaucifolia (Hutch. & Dalziel) P.H.Hoekstra, **comb. nov.** ≡ *Oxymitra glaucifolia* Hutch. & Dalziel in Bull. Misc. Inform. Kew 1927: 153. 1927 ≡ *Richella glaucifolia* (Hutch. & Dalziel) R.E.Fr. in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 17a(2): 139. 1959 ≡ *Friesodielsia glaucifolia* (Hutch. & Dalziel) Steenis in Blumea 12: 359. 1964 – Holotype: Nigeria, Cross River State, Oban, 1911, *P.A. Talbot 403* (BM barcode BM000843988!).

Monanthotaxis gracilis (Hook.f.) P.H.Hoekstra, **comb. nov.** ≡ *Uvaria gracilis* Hook.f., Niger Fl.: 210. 1849 ≡ *Oxymitra gracilis* (Hook.f.) Sprague & Hutch. in Bull. Misc. Inform. Kew 1916: 154. 1916 ≡ *Richella gracilis* (Hook.f.) R.E.Fr. in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 17a(2): 139. 1959 ≡ *Friesodielsia gracilis* (Hook.f.) Steenis in Blumea 12: 359. 1964 – Holoype: Sierra Leone, *G. Don s.n.* (BM barcode BM000547066!).

= *Oxymitra platypetala* Benth. in Trans. Linn. Soc. London 23: 472. 1862 ≡ *Cleistopholis platypetala* (Benth.) Engl. & Diels, Monogr. Afrik. Pflanzen-Fam. 6: 34. 1901 – Holotype: Sierra Leone, Southern Province, Bagroo river, Apr 1861, *G. Mann 857* (K barcode K00198952!).

= *Unona millenii* Engl. & Diels, Monogr. Afrik. Pflanzen-Fam. 6: 40. 1901 – Holotype: Nigeria, Lagos, Mar 1896, *H. Millen 149* (K n.v.).

= *Oxymitra rosea* Sprague & Hutch. in Bull. Misc. Inform. Kew 1916: 154. 1916 ≡ *Richella rosea* (Sprague & Hutch.) R.E.Fr. in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 17a(2): 139. 1959 ≡ *Friesodielsia rosea* (Sprague & Hutch.) Steenis in Blumea 12: 361. 1964, **syn. nov.** – Holotype: Nigeria, Cross River State, Oban, 1911, *P.A. Talbot 199* (BM barcode BM000547067!).

Note. – Sprague & Hutchinson (1916) described *Friesodielsia rosea* as distinct from *F. gracilis* based on leaf and petal form. These characters are highly variable, however, and all intermediate sizes and shapes are found in *Monanthotaxis gracilis*. We therefore synonymize the former name with the latter.

Monanthotaxis hirsuta (Benth.) P.H.Hoekstra, **comb. nov.** ≡ *Unona hirsuta* Benth. in Trans. Linn. Soc. London 23: 469. 1862 ≡ *Oxymitra hirsuta* (Benth.) Sprague & Hutch. in Bull. Misc. Inf. Kew 1916: 155. 1916 ≡ *Richella hirsuta* (Benth.) R.E.Fr. in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 17a(2): 139. 1959 ≡ *Friesodielsia hirsuta* (Benth.)

Steenis in Blumea 12: 360. 1964 – Holotype: Equatorial Guinea, Bioco, Fernando Poo, 1860, *G. Mann 559* (P barcode P00363313!; isotypes: K barcode K000198950!, P barcode P00363314!).

= *Uvaria caillei* A.Chev. ex Hutch. & Dalziel, Fl. W. Trop. Afr. 1: 50. 1927 – Holotype: Guinea, Mamou, Timbou, Kouria, 28 Nov 1905, *A.J.B. Chevalier 14817* (P barcode P00363329!; G barcode G00308375!, L barcode L.1765233!, P [on 3 sheets] barcodes P00363319!, P00363320! & P01954813!).

Monanthotaxis montana (Engl. & Diels) P.H.Hoekstra, **comb. nov.** ≡ *Unona montana* Engl. & Diels in Notizbl. Königl. Bot. Gart. Berlin 2: 296. 1899 ≡ *Oxymitra montana* (Engl. & Diels) Sprague & Hutch. in Bull. Misc. Inform. Kew 1916: 155. 1916 ≡ *Richella montana* (Engl. & Diels) R.E.Fr. in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 17a(2): 139. 1959 ≡ *Friesodielsia montana* (Engl. & Diels) Steenis in Blumea 12: 360. 1964 – Holotype: Cameroon, Central Province, Yaúnde-station, 11 Jan 1894, *G.A. Zenker 431* (B barcode B 10 0153061!).

= *Unona glauca* Engl. & Diels in Notizbl. Königl. Bot. Gart. Berlin 2: 296. 1899, pro parte ≡ *Oxymitra soyauxii* Sprague & Hutch. in Bull. Misc. Inform. Kew 1916: 155. 1916 ≡ *Richella soyauxii* (Sprague & Hutch.) R.E.Fr. in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 17a(2): 139. 1959 ≡ *Friesodielsia soyauxii* (Sprague & Hutch.) Steenis in Blumea 12: 361. 1964 – **Lectotype (designated here):** Gabon, Estuaire, Sibange farm, 6 Feb 1881, *H. Soyaux 203* (B barcode B 10 0153059!; isolectotype: K barcode K000198946!).

= *Oxymitra mortehanii* De Wild., Pl. Bequaert. 1: 472. 1922 – Holotype: Democratic Republic of the Congo, Equateur, Dundusana, Sep 1913, *M.G. Mortehan 512* (BR [on 3 sheets] barcodes 000008800459!, 000008800060! & 000008800787!).

Note. – *Unona glauca* was described based on two types, *H. Soyaux 203* and *Dupuis s.n.* Boutique (1951b) assigned the latter specimen to *Monanthotaxis oligandra* Exell., and we therefore designate *Soyaux 203* as the lectotype here to avoid confusion.

Monanthotaxis obovata (Benth.) P.H.Hoekstra, **comb. nov.** ≡ *Unona obovata* Benth. in Trans. Linn. Soc. London 23: 469. 1862 = *Popowia obovata* (Benth.) Engl. & Diels, Monogr. Afrik. Pflanzen-Fam. 6: 44. 1901 ≡ *Friesodielsia obovata* (Benth.) Verdc. in Kew Bull. 25: 18. 1971 – Holotype: Mozambique, Zambezia, foot of Mt. Morambala, 31 Dec 1858, *J. Kirk s.n.* (K [2 sheets] barcodes K000199033! & K000199034!; isotype: B barcode B 10 0153064!).

= *Popowia stormsii* De Wild. in Ann. Mus. Congo Belge, Bot., sér. 5, 1: 242. 1906 – Holotype: Tanzania, Rukwa, Karema, *E.P.J. Storms s.n.* (BR barcode 000008799258!).

Monanthotaxis scamnopetala (Exell) P.H.Hoekstra, **comb. nov.** ≡ *Popowia scamnopetala* Exell in J. Bot. 70(Suppl. 1): 207–208. 1932 ≡ *Exellia scamnopetala* (Exell) Boutique in Bull. Jard. Bot. État Bruxelles 21: 118. 1951 – Holotype: Buco-Zau, Cabinda, Angola, 1873, *J. Gossweiler 6884* (BM barcode BM000547053!; isotypes: COI [photo!], K barcode K000198958!, LISC [on 2 sheets] barcodes LISC 000082 & LISC 000084 [photos!], LISU!).

Monanthotaxis velutina (Sprague & Hutch.) P.H.Hoekstra, **comb. nov.** ≡ *Oxymitra velutina* Sprague & Hutch. in Bull. Misc. Inform. Kew 1916: 156. 1916 ≡ *Richella velutina* (Sprague & Hutch.) R.E.Fr. in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 17a(2): 139. 1959 ≡ *Friesodielsia velutina* (Sprague & Hutch.) Steenis in Blumea 12: 361. 1964 – **Lectotype (designated here):** Sierra Leone, Northern Province, Tonkolili, Makump, 18 Jul 1914, *N.W. Thomas 968* (K barcode K000041195!).

Note. – Sprague & Hutchinson (1916) described this species based on three specimens, *N.W. Thomas 968*, *4701* and *5005*. We did not see the specimen *Thomas 4701*, and *Thomas 968* is better preserved than *5005*.

Sphaerocoryne gracilipes (Benth.) X.Guo & R.M.K.Saunders, **comb. nov.** ≡ *Oxymitra gracilipes* Benth. in Trans. Linn. Soc. London 23: 471–472. 1862 ≡ *Cleistopholis gracilipes* (Benth.) Engl. & Diels in Engler, Monogr. Afrik. Pflanzen-Fam. 6: 34. 1901 ≡ *Richella gracilipes* (Benth.) R.E.Fr. in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 17a(2): 139. 1959 ≡ *Friesodielsia gracilipes* (Benth.) Steenis in Blumea 12: 359. 1964 – Holotype: Equatorial Guinea, Fernando Po, 1860, *G. Mann 251* (K barcode K000198951!).

= *Unona albida* Engl. in Notizbl. Königl. Bot. Gart. Berlin 2: 297. 1899 ≡ *Cleistopholis albida* (Engl.) Engl. & Diels in Engler, Monogr. Afrik. Pflanzen-Fam. 6: 34, t. 12 fig. Aa–h. 1901 ≡ *Oxymitra albida* (Engl.) Sprague & Hutch. in Bull. Misc. Inform. Kew 1916: 153–154. 1916 ≡ *Richella albida* (Engl.) R.E.Fr. in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 17a(2): 139. 1959 ≡ *Friesodielsia albida* (Engl.) Steenis in Blumea 12: 358. 1964 – **Lectotype (designated here):** Cameroon, Bipinde, 1898, *G.A. Zenker 1715* (B barcode B 10 0153057!; isolectotypes: B barcode B 10 0153058!, BM [on 2 sheets] barcodes BM000547065! & BM000843987!, BR barcode 000008800121!, E barcode E00181435 [photo!], G barcode G00308362!, HBG barcode HBG-502539 [photo!], K barcode K000198947!, L barcode L 0187107!, M barcode M-0107909!, NY barcode 0026308 [photo!], P [on 2 sheets] barcodes P00363331! & P00363333!, S!, U barcode U 0269929 [wood sample] n.v., US n.v, WAG barcode WAG0061084!, WU No. 025877 [photo!]).

= *Cleistopholis albida* var. *longipedicellata* Baker f. in Rendle & al., Cat. Pl. Oban: 3–4. 1913 ≡ *Oxymitra longipedicellata* (Baker f.) Sprague & Hutch. in Bull. Misc. Inform. Kew 1916: 154. 1916 ≡ *Richella longipedicellata* (Baker f.) R.E.Fr. in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 17a(2): 139. 1959 ≡ *Friesodielsia longipedicellata* (Baker f.) Steenis in Blumea 12: 360. 1964 – **Lectotype (designated here):** Nigeria, Oban, 1912, *P.A. Talbot 1677* (BM!; isolectotype: BM!).

■ KEY TO *FRIESODIELSIA* AND CLOSELY RELATED GENERA

1 Receptacle columnar; pollen released as tetrads .... ***Toussaintia***
1 Receptacle convex or flat; pollen released as monads .. **2**
2 Sepals connate and enclosing petals in bud .... ***Cleistochlamys***
2 Sepals free, not enclosing petals in bud **3**
3 Leaf venation brochidodromous, with secondary veins anastomosing and linking to form prominent loops **4**
3 Leaf venation eucamptodromous, with parallel secondary veins lacking prominent marginal arches **5**
4 Inflorescences axillary; inner petals coherent above reproductive organs .... ***Sphaerocoryne***
4 Inflorescences leaf-opposed; inner petals not coherent above reproductive organs .... ***Afroguatteria***
5 Petals loosely coherent or free spreading; tropical Africa and Madagascar .... ***Monanthotaxis***
5 Petals (partially) enclosing the reproductive organs; tropical Australasia **6**
6 Petals three per flower, in one whorl ... ***Dasymaschalon***
6 Petals six per flower, in two whorls **7**
7 Monocarps globose or ellipsoid; seeds 1 (rarely 2) per monocarp .... ***Friesodielsia***
7 Monocarps moniliform; seeds >1 per monocarp .... ***Desmos***

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Appendix 1. Species names and GenBank accession numbers of DNA sequences used in this study. Voucher data is given for accessions, for which DNA sequences were newly obtained, using the following format: Taxon name, *collector(s)* and *collector number*, herbarium code, country, largest political subdivision, GenBank accession numbers (*matK*, *ndhF*, *psbA-trnH*, *trnL-F*, *rbcL*, ITS, ETS). –: missing data; *: newly generated sequences.

Afroguatteria bequaertii (De Wild.) Boutique, *J. Lejoly 4865* (BR), Congo, KX786588*, –, –, KX786629*, KX786627*,–, –; ***Cleistochlamys kirkii*** (Benth.) Oliv., *Couvreur & Mbago 58* (WAG), Tanzania, Pwani, –, KM924880, KM924981, KM924948, –, –, –; ***Dasymaschalon acuminatum*** Jing Wang & R.M.K.Saunders, *Chalermglin 490520* (HKU), Thailand, cultivated in the private collection of P. Chalermglin (Bangkok), JQ768546, JQ768587, JQ768625, JQ768706, JQ768666, KX786542*, KX786585*; ***Dasymaschalon borneense*** Nurmawati, *Ambriansyah & Arifin 1687* (L), Indonesia, Kalimantan Timur, JQ768547, –, JQ768626, JQ768707, JQ768667, –, –; ***Dasymaschalon clusiflorum*** (Merr.) Merr., *Ramos & Edaño 45293* (NY), Philippines, Luzon, JQ768548, –, JQ768627, JQ768708, JQ768668, –, –; ***Dasymaschalon dasymaschalum*** (Blume) I.M.Turner, *Saunders 04/26* (HKU), Thailand, cultivated in the private collection of P. Chalermglin (Bangkok), JQ768549, JQ768588, JQ768628, JQ768709, JQ768669, KX786537*, KX786578*; ***Dasymaschalon ellipticum*** Nurmawati, *Kalat & al. 15734* (L), Brunei, JQ768550, JQ768589, JQ768629, JQ768710, JQ768670, KX786540*, KX786581*; ***Dasymaschalon evrardii*** Ast, *Poilane 9615* (P), Vietnam, Annam, JQ768551, JQ768590, JQ768630, JQ768711, JQ768671, KX786536*, KX786577*; ***Dasymaschalon glaucum*** Merr. & Chun, *Chalermglin 510521* (HKU), Thailand, Ratchaburi, JQ768553, JQ768592, JQ768632, JQ768713, JQ768673, KX786533*, KX786574*; ***Dasymaschalon lomentaceum*** Finet & Gagnep., *Saunders 04/5* (HKU), Thailand, cultivated in the private collection of P. Chalermglin (Bangkok), JQ768554, JQ768593, JQ768633, JQ768714, JQ768674, KX786538*, KX786579*; ***Dasymaschalon longiusculum*** (Bân) Jing Wang & R.M.K.Saunders, *Van der Werff & Nguyen 14292* (L), Vietnam, Tonkin, JQ768556, –, JQ768635, JQ768716, JQ768676, KX786543*, KX786586*; ***Dasymaschalon macrocalyx*** Finet & Gagnep., *Saunders 04/6* (HKU), Thailand, cultivated in the private collection of P. Chalermglin (Bangkok), JQ768557, JQ768595, JQ768636, JQ768717, JQ768677, –, KX786573*; ***Dasymaschalon megalanthum*** (Merr.) Jing Wang & R.M.K.Saunders, *Ramos & Edaño 46641* (UC), Philippines, Luzon, JQ768596, JQ768596, JQ768637, JQ768718, JQ768678, –, KX786583*; ***Dasymaschalon oblongatum*** Merr., *Merrill 9703* (NY), Philippines, Luzon, JQ768559, JQ768597, JQ768638, JQ768719, JQ768679, KX786541*, KX786582*; ***Dasymaschalon robinsonii*** Ast, *Poilane 6132* (P), Vietnam, Annam, JQ768561, –, JQ768640, JQ768721, JQ768681, KX786539*, KX786580*; ***Dasymaschalon rostratum*** Merr. & Chun, *Wang 0626* (HKU), China, Guangdong, JQ768562, JQ768599, JQ768641, JQ768722, JQ768682, –, KX786584*; ***Dasymaschalon sootepense*** Craib, *Kerr 1364* (L), Thailand, Chiang Mai, JQ768563, JQ768600, JQ768642, JQ768723, JQ768683, KX786544*, KX786587*; ***Dasymaschalon trichophorum*** Merr., *Wang 63* (HKU), China, Guangdong, JQ768565, JQ768602, JQ768644, JQ768725, JQ768685, KX786535*, KX786576*; ***Dasymaschalon wallichii*** (Hook.f. & Thomson) Jing Wang & R.M.K.Saunders, *David 257* (P), Malaysia, Johore, JQ768566, –, JQ768645, JQ768726, JQ768686, –, KX786572*; ***Dasymaschalon yunnanense*** (Hu) Bân, *Keßler 3271* (L), Thailand, Chiang Rai, JQ768560, JQ768598, JQ768639, JQ768720, JQ768680, KX786534*, KX786575*; ***Desmos chinensis*** Lour., *Pang N2* (HKU), China, Hong Kong, JQ768567, JQ768603, JQ768646, JQ768727, JQ768687, KX786520*, KX786556*; ***Desmos chinensis*** var. ***lawii*** (Hook.f. & Thomson) Bân, *N.V. Page s.n.* (CAL), India, Western Ghats, KC933937, KC933943, KC933941, KC933939, KC933935, –, –; ***Desmos cochinchinensis*** Lour., *Wang 0612* (HKU), China, Yunnan, JQ768568, JQ768604, JQ768647, JQ768728, JQ768688, KX786519*, KX786555*; ***Desmos dinhensis*** (Finet & Gagnep.) Merr., *Meinke & Chalermglin MEI013* (L), Vietnam, JQ768569, JQ768605, JQ768648, JQ768729, –, –, –; ***Desmos dumosus*** (Roxb.) Saff., *Wang 068* (HKU), China, Yunnan, JQ768570, JQ768606, JQ768649, JQ768730, JQ768689, KX786517*, KX786553*; ***Desmos elegans*** (Thwaites) Saff., *Kostermans 24761* (L), Sri Lanka, Galle, JQ768571, –, JQ768650, JQ768731, JQ768690, –, –; ***Desmos goezeanus*** (F.Muell.) Jessup, *Ford & Cinelli 04780* (BRI), Australia, Queensland, JQ768572, JQ768607, JQ768651, JQ768732, JQ768691, KX786518*, KX786554*; ***Desmos polycarpus*** Jessup, *Sankowsky 3167* (HKU), Australia, cultivated in the private collection of G. Sankowsky, KX786589*, KX786607*, KX786613*, KX786630*, –, –, –; ***Desmos* sp.,** *Sasidharan 3132* (L), India, JQ768573, –, JQ768652, JQ768733, JQ768692, –, –; ***Desmos wardianus*** (Bailey) Jessup, *Sankowsky 2664* (BRI), Australia, Queensland, JQ768574, JQ768608, JQ768653, JQ768734, JQ768693, KX786521*, KX786557*; ***Dielsiothamnus divaricatus*** (Diels) R.E.Fr., *D. Johnson 1903* (OWU), Tanzania, EU169692, –, EU169736, EU169781, EU169759, –, –; ***Exellia scamnopetala*** (Exell) Boutique, *Sosef & al. 2220* (WAG), Gabon, Ogooué-Ivindo, KX761286*, KX787006*, KX786945*, KX786975*, KX761317*, KX761261*, KX761234*; ***Fissistigma polyanthoides*** (A.DC.) Merr., *Keßler 3232* (WAG), Thailand, cultivated in Khao Hin Son Botanical Garden, JQ768575, JQ768609, JQ768654, JQ768735, JQ768694, KX786505*, –; ***Friesodielsia affinis*** (Hook.f. & Thomson) D.Das, *Guo & Pang 20130629-1* (HKU), Thailand, Chanthaburi, KX786590*, –, KX786614*, KX786631*, –, KX786524*, KX786561*; ***Friesodielsia bakeri*** (Merr.) Steenis, *Ng 2015-184* (SING), Singapore, Cultivated in the "Gardens by the Bay" (originally from Philippines), KX786591*, –, KX786615*, KX786632*,–, –, –; ***Friesodielsia biglandulosa*** (Blume) Steenis, *Slik 3809* (L), Indonesia, KX786592*, JQ768610, JQ768655, JQ768736, –, KX786526*, KX786563*; ***Friesodielsia borneensis*** (Miq.) Steenis, *Keßler 2018* (A), Indonesia, ITCI Kenangan, KX786593*, KX786608*, KX786616*, KX786633*, –, KX786529*, KX786566*; ***Friesodielsia calycina*** (King) Steenis, *Latiff 4029* (L), Malaysia, Temenggor Forest Reserve, KX786594*, –, KX786617*, KX786634*, –, KX786522*, KX786559*; ***Friesodielsia cuneiformis*** (Blume) Steenis, *Ardi 54* (HKU), Indonesia, cultivated at Kebun Raya, Bogor, JQ768576, JQ768611, –, JQ768737, JQ768695, KX786528*, KX786565*; ***Friesodielsia desmoides*** (Craib) Steenis, *Keßler 3189* (WAG), Thailand, cultivated in Khao Hin Son Botanical Garden, JQ768577, JQ768612, JQ768656, JQ768738, JQ768696, KX786523*, KX786560*; ***Friesodielsia discostigma*** (Diels) Steenis, *G. Zenker 3023* (P), Cameroon, Bipinde, KX786595*, –, KX786623*, KX786635*, –, –, –; ***Friesodielsia enghiana*** (Diels) Verdc. ex Le Thomas, *Harris & al. 8708* (E), Gabon, Ogooué-Maritime, JQ768578, JQ768613, JQ768657, JQ768739, JQ768697, KX786510*, KX786546*; ***Friesodielsia filipes*** (Hook.f. & Thomson) Steenis, *Sinclair 40762* (L), Malaysia, Besut, KX786596*, –, –, KX786636*, –, KX786531*, KX786569*; ***Friesodielsia fornicata*** (Roxb.) D.Das, *Tagane & al. 4331* (HKU), Cambodia, Kampot, KX786597*, –, KX786618*, KX786637*, –, KX786525*, KX786562*; ***Friesodielsia glauca*** (Hook.f. &Thomson) Steenis, *Guo & Chen GX074* (SING), Singapore, KX786598*, –, KX786619*, KX786638*, –, KX786532*, KX786570*; ***Friesodielsia glaucifolia*** (Hutch. & Dalziel) Steenis, *Ghogue & al. 500* (WAG), Cameroon, Kupe-Muanenguba, KX761298*, KX787018*, KX786957*, KX786987*, KX761329*, KX761273*, KX761245*; ***Friesodielsia gracilipes*** (Benth.) Steenis, *Tchouto Mbatchou & al. 0202853* (WAG), Cameroon, South Province, KX786599*, KX786609*, KX786620*, KX786639*, –, KX786507*, –; ***Friesodielsia gracilis*** (Hook.f.) Steenis, *Linder 794* (A), Liberia, Bong, KX786600*, KX786610*, KX786621*, KX786640*, –, KX786511*, KX786547*; ***Friesodielsia hirsuta*** (Benth.) Steenis, *Jongkind & Sambolah 12704* (WAG), Liberia, Grand Cape Mount, KX761293*, KX787013*, KX786952*, KX786982*, KX761324*, KX761268*, KX761240*; ***Friesodielsia kingii*** (J.Sinclair) Steenis, *Gardette & al. 2086* (L), Malaysia, Serting, KX786601*, –, –, KX786641*, –, –, KX786568*; ***Friesodielsia latifolia*** (Hook.f. & Thomson) Steenis, *Guo & Chen GX073* (SING), Singapore, KX786602*, –, KX786622*, KX786642*, –, KX786530*, –; ***Friesodielsia longiflora*** (Merr.) Steenis, *Barbon & al. 5701* (L), Philippines, KX786603*, –, –, –, –, –, KX786567*; ***Friesodielsia montana*** (Engl. & Diels) Steenis, *De Wilde & Van der Maesen 10959* (WAG), Gabon, Ogooué-Maritime, KX786604*, KX786611*, KX786624*, KX786643*, –, KX786512*, KX786548*; ***Friesodielsia obovata*** (Benth.) Verdc., *Chase 40526* (K), U.K., cultivated at the Royal Botanic Gardens, Kew, JQ768579, JQ768614,

Appendix 1. Continued.

JQ768658, JQ768740, JQ768698, KX786509*, KX786545*; ***Friesodielsia sahyadrica*** N.V.Page & S.Surveswaran, *Page 110949* (CAL), India, Western Ghats, KC933936, KC933942, KC933940, KC933938, KC933934, –, KX786558*; ***Friesodielsia* sp.,** *De Wilde & Van der Maesen 10971* (WAG), Gabon, Ogooué-Maritime, KX761305*, KX787025*, KX786964*, KX786994*, KX761336*, KX761279*, KX761251*; ***Friesodielsia* sp.,** *Thomas 12278* (A), New Guinea, KX786605*, KX786612*, KX786625*, KX786644*, –, KX786527*, KX786564*; ***Friesodielsia velutina*** (Sprague & Hutch.) Steenis, *Jongkind & al. 11824* (WAG), Liberia, Lofa, KX761292*, KX787012*, KX786951*, KX786981*, KX761323*, KX761267*, KX761239*; ***Hexalobus salicifolius*** Engl., *Sosef & al. 2376* (WAG), Gabon, Ogooué-Maritime, EU169694, EU169714, EU169738, EU169783, EU169761, –, –; ***Isolona campanulata*** Engl. & Diels, *UUBG 86GR00240*, cultivated in University of Utrecht Botanical Garden (origin in tropical Africa), AY238963, EU169715, DQ125127, AY231287 and AY238947, AY238954, –, –; ***Mitrella kentii*** (Blume) Miq., *Gardette 2239* (L), Malaysia, Pasoh Forest Reserve, FJ743751, JQ768616, FJ743789, AY841711, AY841633, KX786506*, –; ***Monanthotaxis ambrensis*** (Cavaco & Keraudren) Verdc., *Hong-Wa & al. 221* (WAG), Madagascar, Antsiranana, KX761295*, KX787015*, KX786954*, KX786984*, KX761326*, KX761270*, KX761242*; ***Monanthotaxis angustifolia*** (Exell) Verdc., *Sinsin 3380* (WAG), Benin, Zou, KX761303*, KX787023*, KX786962*, KX786992*, KX761334*, KX761277*, –; ***Monanthotaxis aquila*** P.H.Hoekstra, *Geerling & Bokdam 2327* (WAG), Ivory Coast, Sassandra, KX761309*, KX787029*, KX786968*, KX786998*, KX761340*, –, KX761254*; ***Monanthotaxis atewensis*** P.H.Hoekstra, *Hall & Lock GC43672* (WAG), Ghana, Eastern Region, KX761307*, KX787027*, KX786966*, KX786996*, KX761338*, –, KX761253*; ***Monanthotaxis atopostema*** P.H.Hoekstra, *Louis 3434* (BR), DR Congo, Orientale, KX761310*, KX787030*, KX786969*, KX786999*, KX761341*, –, KX761255*; ***Monanthotaxis boivinii*** (Baill.) Verdc., *Wohlhauser & Andriamalaza 60232* (WAG), Madagascar, Antsiranana, KX761299*, KX787019*, KX786958*, KX786988*, KX761330*, KX761274*, KX761246*; ***Monanthotaxis buchananii*** (Engl.) Verdc., *Robertson 7544* (WAG), Kenya, coast, JQ768581, JQ768617, JQ768660, JQ768742, JQ768700, KX786514*, KX786550*; ***Monanthotaxis congoensis*** Baill., *Wieringa & al. 7686* (WAG), Gabon, Estuaire, KX761287*, KX787007*, KX786946*, KX786976*, KX761318*, KX761262*, KX761235*; ***Monanthotaxis couvreurii*** P.H.Hoekstra, *Couvreur 762* (WAG), Cameroon, Central Province, KX761311*, KX787031*, KX786970*, KX787000*, KX761342*, KX761281*, KX761256*; ***Monanthotaxis ferruginea*** (Oliv.) Verdc., *Bidgood & al. 2870* (WAG), Tanzania, Kigoma, KX761306*, KX787026*, KX786965*, KX786995*, KX761337*, KX761280*, KX761252*; ***Monanthotaxis filamentosa*** (Diels) Verdc., *Couvreur & al. 417* (WAG), Cameroon, Central Province, KX761291*, KX787011*, KX786950*, KX786980*, KX761322*, KX761266*, KX761238*; ***Monanthotaxis filipes*** P.H.Hoekstra, *Bidgood & al. 1402* (WAG), Tanzania, Southern, KX761315*, KX787035*, KX786973*, KX787004*, KX761346*, KX761284*, KX761259*; ***Monanthotaxis foliosa*** var. ***ferruginea*** (Robyns & Ghesq.) Verdc., *Couvreur & al. 601* (WAG), Gabon, Estuaire, KX761290*, KX787010*, KX786949*, KX786979*, KX761321*, KX761265*, KX761237*; ***Monanthotaxis fornicata*** (Baill.) Verdc., *Couvreur & Mbago 89* (WAG),Tanzania, Morogoro, JQ768583, JQ768619, JQ768662, JQ768744, JQ768702, KX786515*, KX786551*; ***Monanthotaxis heterantha*** (Baill.) Verdc., *Callmander & Phillipson 684* (MO), Madagascar, Mahajanga, KX761297*, KX787017*, KX786956*, KX786986*, KX761328*, KX761272*, KX761244*; ***Monanthotaxis klainei*** (Engl.) Verdc. var. ***klainei*,** *Fruth 03/1231/c* (M), D.R. Congo, Bandundu, KX761304*, KX787024*, KX786963*, KX786993*, KX761335*, KX761278*, KX761250*; ***Monanthotaxis klainei*** var. ***lastoursvillensis*** (Pellegr.) Verdc., *Couvreur & al. 599* (WAG), Gabon, Estuaire, KX761289*, KX787009*, KX786948*, KX786978*, KX761320*, KX761264*, –; ***Monanthotaxis komorensis*** P.H.Hoekstra, *Barthelat & al.* 671 (MO), Mayotte, Grande Terre, KX761296*, KX787016*, KX786955*, KX786985*, KX761327*, KX761271*, KX761243*; ***Monanthotaxis latistamina*** P.H.Hoekstra, *Couvreur & al. 565* (WAG), Gabon, Ogooué-Ivindo, KX761288*, KX787008*, KX786947*, KX786977*, KX761319*, KX761263*, KX761236*; ***Monanthotaxis maputensis*** P.H.Hoekstra, *Koning 7766* (WAG), Mozambique, Maputo, KX761308*, KX787028*, KX786967*, KX786997*, KX761339*, –, –; ***Monanthotaxis micrantha*** (Baker) Verdc., *Madiomanana & al. 184* (WAG), Madagascar, Antsiranana, KX761300*, KX787020*, KX786959*, KX786989*, KX761331*, KX761275*, KX761247*; ***Monanthotaxis parvifolia*** subsp. ***kenyensis*** Verdc., *Luke & Luke 7299* (EA), Kenya, Eastern, KX761312*, KX787032*, KX786971*, KX787001*, KX761343*, –, KX761257*; ***Monanthotaxis pellegrinii*** Verdc., *Breteler & al. 14014* (WAG), Gabon, Ngounié, KX761302*, KX787022*, KX786961*, KX786991*, KX761333*, –, KX761249*; ***Monanthotaxis schweinfurthii*** (Engl. & Diels) Verdc. var. ***schweinfurthii*,** *Madidi 453* (MO), D.R. Congo, Orientale, KX761313*, KX787033*, –, KX787002*, KX761344*, KX761282*, KX761258*; ***Monanthotaxis schweinfurthii*** var. ***seretii*** (De Wild.) Verdc., *Fay 6534* (WAG), Central African Republic, Bamingui-Bangoran, KX761294*, KX787014*, KX786953*, KX786983*, KX761325*, KX761269*, KX761241*; ***Monanthotaxis schweinfurthii*** var. ***tisserantii*** (Le Thomas) Verdc., *Sosef & al. 2238* (WAG), Gabon, Ogooué-Ivindo, JQ768585, JQ768621, JQ768664, JQ768746, JQ768704, KX786513*, KX786549*; ***Monanthotaxis sororia*** (Diels) Verdc., *Schatz & Lowry 1439* (WAG), Madagascar, Mahajanga, KX761301*, KX787021*, KX786960*, KX786990*, KX761332*, KX761276*, KX761248*; ***Monanthotaxis* sp.,** *Couvreur & al. 869* (WAG), Gabon, Woleu-Ntem, KX761314*, KX787034*, KX786972*, KX787003*, KX761345*, KX761283*, –; ***Monanthotaxis trichocarpa*** (Engl. & Diels) Verdc., *Couvreur & al. 14* (WAG), Tanzania, Tanga, JQ768586, JQ768622, JQ768665, JQ768747, JQ768705, KX786516*, KX786552*; ***Monanthotaxis tripetala*** P.H.Hoekstra, *Leeuwenberg 5828* (WAG), Cameroon, East Province, KX761316*, KX787036*, KX786974*, KX787005*, KX761347*, KX761285*, KX761260*; ***Pyramidanthe prismatica*** (Hook.f. & Thomson) J.Sinclair, *Keßler 2773* (L), Indonesia, JN175163, –, JN175178, JN175208, JN175193, –, –; ***Sanrafaelia ruffonammari*** Verdc., *Kayombo & Ntemi Sallu 3027* (MO), Tanzania, Tanga, EU169703, EU169724, EU169746, EU169790, EU169768, –, –; ***Schefferomitra subaequalis*** (Scheff.) Diels, *R.D. Hoogland 10431* (WAG), Papua New Guinea, KX786606*, –, KX786626*, KX786645*, KX786628*, –, KX786571*; ***Sphaerocoryne affinis*** (Teijsm. & Binn.) Ridl., *Ardi 96* (KRB), cultivated in Kebun Raya, Bogor, KM924852, KM924886, KM924990, KM924953, –, –, –; ***Sphaerocoryne blanfordiana*** C.E.C.Fisch., *Chaowasku 36* (L), Myanmar, KM924853, KM924887, KM924991, KM924954, –, –, –; ***Sphaerocoryne gracilis*** (Oliv. ex Engl. & Diels) Verdc., *Robertson 7554* (WAG), Kenya, coast, EU169688, JQ768623, EU169732, EU169777, EU169755, KX786508*, –; ***Sphaerocoryne* sp.,** *Saunders 07/4* (HKU), Thailand, cultivated in the private collection of P. Chalermglin (Bangkok), AY518878, JQ768624, FJ743788, AY319185, AY319071, –, –; ***Toussaintia orientalis*** Verdc., *Johnson 1957* (OWU), Tanzania, Bagamoyo, EU169689, EU169710, EU169733, EU169778, EU169756, –, –; ***Uvaria afzelii*** G.Elliot, *UUBG 84GR00334*, cultivated in University of Utrecht Botanical Garden (origin in West Africa), AY238966, EF179310, AY841440, EF179319, AY238957, –, –; ***Uvariodendron molundense*** (Diels) R.E.Fr., *Sosef & al. 2219* (WAG), Gabon, Ogooué-Ivindo, EU169707, EU169727, EU169750, EU169794, EU169772, –, –.