Resolving the unresolved tribe: a molecular phylogenetic framework for the Merremieae (Convolvulaceae)

ANA RITA SIMOES[1,2]*, ALASTAIR CULHAM[2] and MARK CARINE[1]

[1]*The Natural History Museum of London, Department of Life Sciences, Cromwell Road, SW7 5BD London, UK*
[2]*University of Reading, 101 Harbourne Building, Whiteknights, RG6 6AH Reading, Berkshire, UK*

Tribe Merremieae, as currently circumscribed, comprise *c*. 120 species classified in seven genera, the largest of which (*Merremia*) is morphologically heterogeneous. Previous studies, with limited sampling, have suggested that neither Merremieae nor *Merremia* are monophyletic. In the present study, the monophyly of *Merremia* and its allied genera was re-assessed, sampling 57 species of Merremieae for the plastid *matK*, *trnL–trnF* and *rps16* regions and the nuclear internal transcribed spacer (ITS) region. All genera of Merremieae and all major morphotypes in *Merremia were represented*. Phylogenetic analyses resolve Merremieae in a clade with Ipomoeae, Convolvuleae and *Daustinia montana*. *Merremia* is confirmed as polyphyletic and a number of well-supported and morphologically distinct clades in Merremieae are recognized which accommodate most of the species in the tribe. These provide a framework for a generic revision of the assemblage. © 2015 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2015, **179**, 374–387.

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INTRODUCTION

Convolvulaceae are species of climbers, herbs and shrubs (occasionally trees), with 58 genera and *c*. 1840 species, occurring in tropical and temperate regions (Brummit & Staples, 2007). They are usually recognized by their bell- to funnel- or salver-shaped sympetalous corollas with five conspicuous midpetaline bands. The inflorescence is often an axillary cyme and the fruit is typically a dehiscent four-seeded capsule, although other types of fruits may occur (Brummit & Staples, 2007); it is the only asterid family to have seeds showing physical dormancy (Jayasuriya *et al*., 2009).

Molecular phylogenetic techniques have provided a means to clarify and stabilize tribal and generic classification in Convolvulaceae (e.g. Manos, Miller & Wilkin, 2001; Miller, Buckley & Manos, 2002, Stefanovic, Austin & Olmstead, 2003; Stefanovic &

Olmstead, 2004). Stefanovic, Krueger & Olmstead (2002) used evidence from four plastid regions (*rbcL*, *atpB*, *psbE-J* operon and *trnL–trnF*) to test the monophyly of the family, circumscribe the major lineages and, in a subsequent study (Stefanovic *et al*., 2003), establish hypotheses for tribal and generic delimitation based on the criterion of monophyly. Convolvulaceae were found to be monophyletic and taxa which had previously been suggested as distinct from the family (e.g. *Humbertia* Lam. and *Cuscuta* L.) were included in it. Two major lineages were identified and the family was consequently divided into two subfamilies: Convolvuloideae and Humbertioideae.

In the most recent tribal classification of the family (Brummit & Staples, 2007), Merremieae were one of 12 tribes recognized in subfamily Convolvuloideae. Brummit & Staples (2007) included seven genera in the tribe: the pantropical genera *Merremia* Dennst. ex. Endl. (*c*. 100 species), *Operculina* Silva Manso (14 species) and *Xenostegia* D.F. Austin & Staples (two species), the East African endemic *Hyalocystis* Hallier f. (two species), *Hewittia* Wight & Arn. (distributed in

*Corresponding author. E-mail: simoes.ana.convolv@gmail.com

East Africa and Asia, two species) and the monotypic genera *Decalobanthus* Ooststr. (endemic to Sumatra) and *Remirema* Kerr (endemic to Thailand). A further genus in Merremieae was more recently described by Johnson (2010) who separated *Davenportia* Johnson from *Merremia* as a monotypic Australian endemic genus.

Of the tribes in Convolvulaceae, Merremieae remain the least well defined. The tribe was first recognized informally by Austin (1982), as the 'merremioids', a group in which he included *Aniseia* Choisy, *Hewittia*, *Merremia*, *Operculina* and *Tetralocularia* O'Donell. The tribe was described as similar to tribe Convolvuleae, but differing in the form of the sepals, the glabrous corollas and the capsule, though exceptions to these morphological traits were known to exist in *Hewittia*, which has a pubescent capsule, and some species of *Operculina* and *Merremia*, which have pubescent corollas. Austin (1998) subsequently broadened the concept of the group to include *Decalobanthus*, *Hyalocystis* and *Xenostegia* and *Iseia* O'Donell and *Odonellia* K.R.Robertson, although the results of the morphological cladistics analysis he presented suggested that Merremieae were not monophyletic.

The tribe was first recognized formally (albeit tentatively) in the molecular-based classification of the family by Stefanovic *et al*. (2003). The molecular phylogenetic study of Stefanovic *et al*. (2002) suggested that the 'merremioids' of Austin (1982) were polyphyletic. As a consequence four genera (*Aniseia*, *Iseia*, *Odonellia*, *Tetralocularia*) were placed in a newly defined monophyletic tribe Aniseieae. The relationships between the remaining genera of Merremieae were largely unresolved. Moreover, deeper nodes in the phylogenetic tree of Stefanovic *et al*. (2002) were weakly supported, only half of the genera in Merremieae as currently circumscribed were included and no defining characters for the tribe were found. The tribal concept was maintained as it was in the morphology-based classification of the family (Austin, 1998), possibly for lack of evidence to make significant changes, but the group was flagged as problematic and in need of further work.

At the generic level, the circumscription of the largest genus, *Merremia*, has long been problematic. Stefanović (2002) included only five of the 101 *Merremia* spp., but found it to be polyphyletic, albeit with weak support at deeper nodes. Sampling of other genera to date has been extremely limited. Thus, only two of the 14 *Operculina* spp. were sampled by Stefanovic *et al*. (2002), *Xenostegia* and *Hewittia* were each represented by a single species (out of two in each case) and *Hyalocystis* two species), *Decalobanthus* and *Remirema* were not sampled. The relationships of *Davenportia* have also yet not been investigated.

A recent revision of *Jacquemontia* Choisy provided evidence that *J. montana* Meisn., a Brazilian endemic, did not fit the traditional circumscription of the genus but was instead morphologically close to *Merremia s.l.* with which it shared simple trichomes, tricolpate non-spiny pollen, a biglobular stigma and yellow flowers (Buril, 2013). However, the entire simple serrate leaves and capitate inflorescences make it distinct from the *Merremia* spp. occurring in Brazil and it has been recognized as a distinct genus *Daustinia* Buril & A.R. Simões (Buril, 2013; Buril *et al*., 2014, 2015).

In summary, the current members of Merremieae show a range of conflicting morphological evidence, some supporting, and some refuting, the group. In addition, the molecular evidence produced to date has been limited in taxon sampling and resolution.

The aim of this paper is to establish a molecular phylogenetic framework that will serve as a basis for a revised classification of Merremieae. Sampling broadly across the tribe and utilizing data from the plastid *matK*, *trnL–trnF* and *rps16* regions and the nuclear ribosomal internal transcribed spacer (ITS) region, we aim to: (1) test the monophyly of *Merremia*; (2) test the monophyly and resolve the relationships of its allied genera; and (3) resolve the placement of *Daustinia*.

MATERIAL AND METHODS

MORPHOLOGICAL OBSERVATIONS

A working list of accepted species names to be considered in the molecular phylogenetic analyses was first produced, based on a thorough literature review of taxonomic accounts, namely: Van Ooststroom & Hoogland (1953; Malesian region), Fang & Staples (1995, China), Austin & Staples (unpublished, Neotropics), Heine (1963, *Flora of West Tropical Africa*), Gonçalves (1987, south-central Africa), Verdcourt (1963, *Flora of Tropical East Africa*), Meeuse & Welman (2000, South Africa), Thulin (2006, Somalia), Staples (2010, Thailand), Staples (2010, Asia, Pacific and Australia), Johnson (2009, Australia), Demissew, 2001 (Horn of Africa) and O'Donell (1941, tropical America). Thorough morphological observations were conducted, based on herbarium specimens from the following herbaria: A, AIGH, BCU, BK, BKF, BM, BR, E, COI, K, KEP, G, L, LISC, M, MICH, MEXU, MO, NY, PNH, SAN, SING and SAR, complemented with observations from fieldwork in Singapore, Thailand and Cambodia (2009), Ethiopia (2011) and Sumatra (2012), and information from the abovementioned taxonomic accounts. A wide range of characters was observed, from general vegetative and floral morphology to palynology. These data (Table 2) were taken

into account when interpreting the obtained phylogenetic relationships.

TAXON SAMPLING

Samples were obtained from silica gel-dried material collected in Thailand, Cambodia, West Sumatra and Singapore and herbarium specimens from BM, BRI, ETH, L, MO, SAN and SING. Also, samples were collected from plants in cultivation at the Collection Nationale des Convolvulacées (Hauts-de-Seine, France), the largest living collection of Convolvulaceae in the world. For voucher information see Appendix. Fifty-seven taxa of Merremieae were sampled, corresponding to 74 accessions covering all eight genera and the main morphological groups in *Merremia* as proposed by Staples (2010). A further 56 samples were included as outgroup taxa representative of tribes Ipomoeae, Aniseieae and Convolvuleae and four species from three genera in the more distantly related 'bifid-style' clade: *Cladostigma* Radlk., *Hildebrandtia* Vatke and *Seddera* Hochst.

DNA EXTRACTION, AMPLIFICATION AND SEQUENCING

Total genomic DNA was extracted from approximately 0.1 g of dried leaf material (silica gel-dried or herbarium specimens) using a modification of the CTAB micro-extraction method (Doyle & Doyle, 1987), in which the aqueous phase from the chloroform precipitation was cleaned using Qiagen DNeasy kit and protocol (Carine *et al*., 2004). Plastid DNA barcoding region *matK* (matk390f-matK1326r) was amplified using PCR conditions as described in Hollingsworth *et al*. (2009). The plastid *rps16* [rps16x2F2-trnK(UUU)] and *trnL–trnF* (c and f) regions were amplified using PCR cycling conditions described in Shaw *et al*. (2007). The ITS region of nuclear ribosomal DNA (AB101-AB102) was amplified with betaine (1.2 mol L^{-1}) added to prevent the formation of secondary structures, following the protocol of Carine *et al*. (2004). Sequencing followed the Sanger dideoxy sequencing method, and was conducted by the Wellcome Trust sequencing laboratories at the Natural History Museum of London. Complimentary strands were assembled in Lasergene SeqMan (DNASTAR, Madison, Wisconsin, USA) and successfully assembled sequences were aligned by loci, finally concatenated, in BioEdit v7.1.3. (Hall, 1999).

Some sequences of *Convolvulus* (accession numbers KC528819, KC529015, KC528906, KC529150, KC528870, KC529131, KC528899, KC529121, KC528902, KC529133, KC528951, KC529028, Appendix) were generated by Miss Bethany Williams (University of Oxford). Sequences of *Daustinia montana*

(Moric.) Buril & A.R.Simões were generated by Dr Buril for her Doctoral thesis (Buril, 2013) and are as yet unpublished.

PHYLOGENETIC ANALYSES

Parsimony analyses were carried out using PAUP* 4.0b10 software (Swofford, 2001). Conflict between plastid and nrDNA data sets was initially evaluated by running an ILD test (Farris *et al*., 1994) which showed no significant incongruence between the data sets (*P* = 0.010000). For further reassurance that there were no major conflicts, a quick heuristic search was conducted for each region and the topologies of the best trees compared. For this, parsimony analyses of individual matrices were run with 10 000 heuristic search replicates, saving two trees per replicate, random sequence addition and tree bisection reconnection (TBR) branch swapping. Support for clades was estimated by bootstrapping (Felsenstein, 1985) with 100 bootstrap replicates, each comprising 1000 heuristic search replicates using the setting detailed above. The resulting trees were compared by visual inspection, looking for the presence of strongly supported yet conflicting topologies. No major conflicts were encountered, hence the datasets were combined. The matrices were concatenated using WinClada v.1.00.08 (Nixon, 2002) and the combined matrix was analysed using the same protocol. Maximum likelihood and Bayesian inference analyses were also performed on the concatenated dataset.

Maximum likelihood analyses (ML) were performed using RaxML-HPC2 on XSEDE via CIPRES portal (Miller, Pfeiffer & Schwartz, 2010). A random topology was used as a starting tree and general-time reversible (GTR) (Yang, 1994) mix model was applied (GTRCAT followed by GTRGAMMA) as recommended by Miller *et al*. (2010). Bootstrap support values were obtained with the rapid bootstrap algorithm, with 10 000 bootstrap replicates.

Bayesian phylogenetic inferences were performed using parallel (MPI) version of MrBayes version 3.1.2 (Ronquist & Huelsenbeck, 2003) compiled with the Intel C/C++ Compiler (ICC) and BEAGLE-lib (Ayres *et al*., 2012). The GTR model (Yang, 1994) of DNA substitution, with rate variation among nucleotides following a discrete gamma distribution and assuming a portion of invariant sites (GTR + I + G), was selected as the best-fit by Akaike information criterion (AIC; Akaike, 1974) in modelgenerator v0.85 (Keane *et al*., 2006). Two independent runs starting from random trees were carried out. The Metropolis-coupled Markov chain Monte Carlo algorithm was used with four simultaneous chains (one heated, three cold), set at 6×10^6 generations and sampled every 250 generations. The analysis was run until the

two MCMC runs converged to stationary distribution, with the first 10% of trees being discarded as burn-in, as assessed by inspection of lnL trace using Tracer v.1.5 (Rambaut & Drummond, 2009). An *allcompat* consensus of all postburn-in trees obtained in Bayesian inference was computed.

Levels of support obtained from the three different methodologies were mapped on the Bayesian Inference (BI) allcompat consensus tree, using the FigTree v.1.4 program (Rambaut, 2012).

RESULTS

SEQUENCE CHARACTERISTICS AND VARIATION

All accessions in the final combined matrix had data for at least two of the four markers sequenced (ITS, *rps16*, *matK*, *trnL–trnF*), except for *Hyalocystis viscosa* Hallier f. for which only the ITS region was successfully amplified and sequenced. A summary of the variation found and taxa represented in the final dataset are presented in Table 1. The combined data matrix comprised 1702 constant characters and 1100 variable characters of which 712 were potentially parsimony informative. GenBank accession numbers are provided in the Appendix.

TREE TOPOLOGY

The MP analysis resulted in 1686 trees 3692 steps long. All three optimality criteria (MP, ML and BI) support the monophyly of a clade comprising Convolvuleae, Ipomoeae, Merremieae and *Daustinia montana* [Fig. 1; MP bootstrap (hereafter MP) = 98%; ML bootstrap (hereafter ML) = 97%; Bayesian posterior probability (hereafter PP) = 1.00]. Accessions of *D. montana* (Fig. 1, clade 1) were resolved as a monophyletic group, though with relatively weak support in MP, (MP = 91; ML = 100; PP = 1.00) that is sister to the tribe Ipomoeae (MP = 51; ML = 64; PP = 99).

DISCUSSION

LEVELS OF SUPPORT

In general, the three phylogenetic methods have presented concordant levels of support for the different nodes. However, particular nodes showed high levels of support in ML and BI, with lower values for MP (Figs 1, 2). This is possibly due to the fact that the genes were analysed as a concatenated dataset and the possible discordance between the gene trees (plastid and nuclear) was not accounted for. Although in the overall phylogenetic tree obtained this is not a widespread issue, we acknowledge that further analyses could be conducted to improve this situation. New methods are being discussed to optimize phylogenetic methodologies which account, e.g. for incomplete lineage sorting and coalescence (Maddison & Knowles, 2006; Degnan & Rosenberg, 2009; Edwards, 2009); re-exploring the data in this light would probably help resolve the encountered discordance.

MAIN RELATIONSHIPS

The two clades comprising taxa of Merremieae [Fig. 1, clade 2 (MP = 100; ML = 100; PP = 1.00) and clade 3 (MP = 89; ML = 84; PP = 1.00)] form a monophyletic group with Ipomoeae and *D. montana* (clade 1) (MP = 52; ML = 74, PP = 1.00). Clade 2 comprises twining or prostrate herbs, with entire shallowly lobed leaves, glabrous corollas, spirally dehiscing anthers and chartaceous four-valved capsules (Table 2). The taxa included in this clade are widespread in the Old World tropics, among which is the type species of *Merremia* [*M. hederacea* (Burm.f.) Hallier f.]. Clade 3 comprises the monotypic *Decalobanthus sumatranus* Oostst. in a late branching position with four *Merremia* spp. All are large woody lianas with broad cordate leaves, corymbiform inflorescences, clavate pedicels, glabrous corollas, spirally dehiscing anthers and chartaceous four-valved capsules. *Decalobanthus sumatranus* was separated as a monotypic genus by Van Oostsroom on the basis of the ten-lobed corollas, but the results indicate that its distinction from other Southeast Asian species with similar morphology is unwarranted. The taxa in this clade occur in Southeast Asia and the Pacific (Table 2) and correspond broadly to *Merremia* section *Hailale* Hallier f. as described by Van Oostsroom & Hoogland (1953), in which they included *M. clemensiana* Oostst., *M. korthalsiana*

Table 1. Taxon sampling and variation for each of the molecular markers used

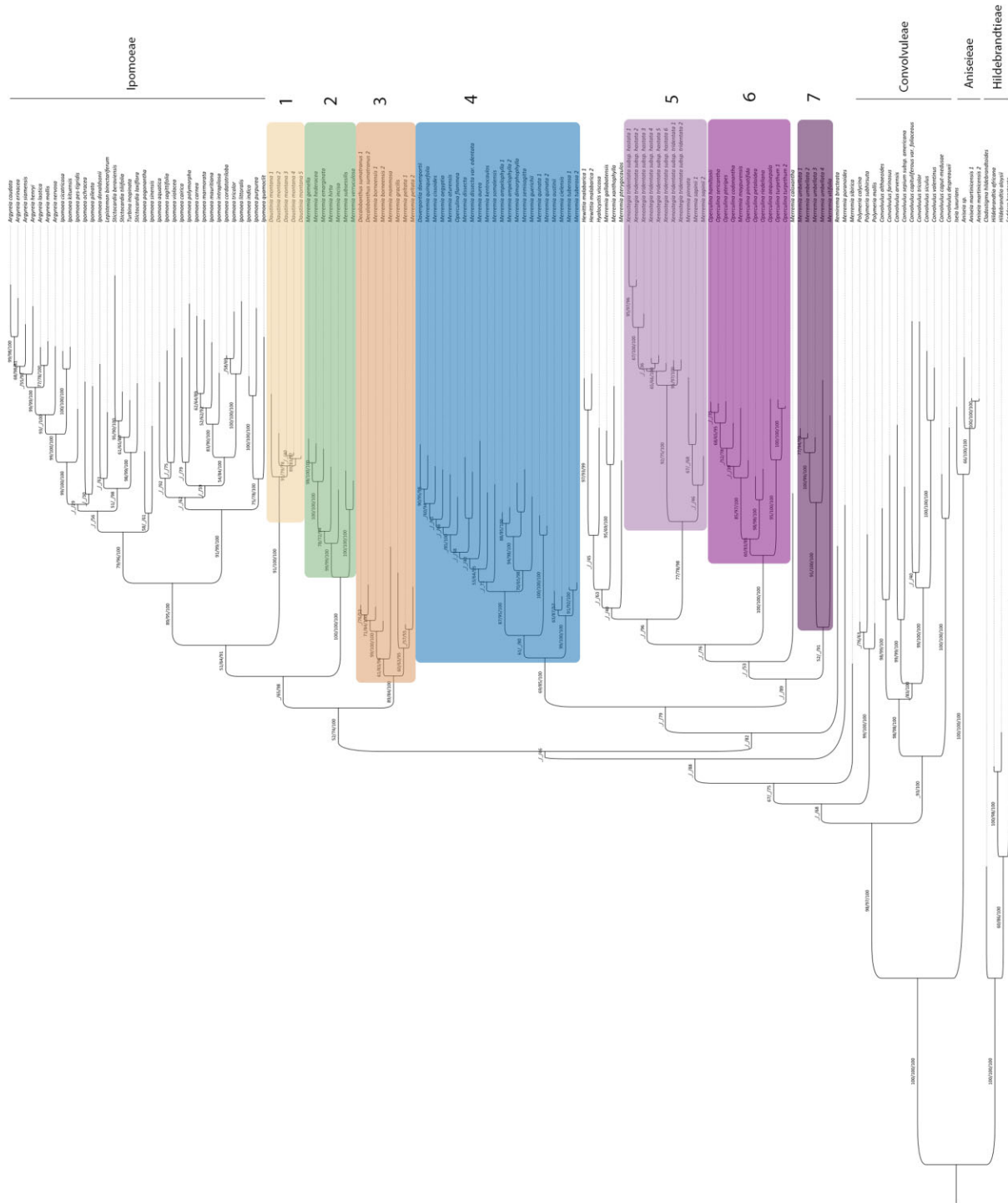|	*trnL–trnF*	*rps16*	*matK*	ITS	Combined dataset
Aligned length	412	1006	773	611	2802
Number of taxa	155	100	149	111	113
Variable sites	159	375	358	374	1100
Number of potentially parsimony informative sites	77	212	246	303	712

Figure 1. Cladogram depicting the phylogenetic relationships of tribes Ipomoeae, Merremieae, Convolvululeae and Aniseieae, based on four loci (*trnL–trnF*, *rps16*, *matK* and ITS) and reconstructed using Bayesian inference. Branch labels represent bootstrap per cent support in MP/per cent support in ML/Bayesian posterior probabilities. Nodes not present or with low support (< 50% bootstrap) in MP or ML analyses are indicated by the absence of support values. The tree is rooted on four taxa belonging to the bifid-style clade of Convolvulaceae (tribe Hildebrandtieae). Seven clades (1–7) are delimited by boxes and are discussed in the text.

Figure 2. Phylogram depicting the phylogenetic relationships of tribes Ipomoeae, Merremieae, Convolvuleae and Aniseieae, based on four loci (*trnL–trnF*, *rps16*, *matK* and ITS) and reconstructed using Bayesian inference. Branch labels represent bootstrap per cent support in MP/ percent support in ML/Bayesian posterior probabilities. Nodes not present or with low support (< 50% bootstrap) in MP or ML analyses are indicated by the absence of support values. The tree is rooted on four taxa belonging to the bifid-style clade of Convolvulaceae (tribe Hildebrandtieae). Seven clades (1–7) are delimited by boxes and are discussed in the text.

Table 2. Composition, morphological characterization and distribution of clades supported under at least two of the three optimality criteria (Bayesian > 0.95, maximum likelihood and parsimony > 70%) in the combined analyses of *trnL–trnF*, *rps16*, *matK* and *ITS* (Fig. 1)

Clade	Species included	Morphological characteristics	Distribution
Clade 1	*Daustinia montana* (Moric.) Buril & Simōes	Erect subshrub, with subsessile leaves, bright yellow flowers, anthers spirally dehiscing and four-valved capsules; pollen tricolpate, non-spiny	Endemic to Brazil
Clade 2	*Merremia emarginata* Hallier f.; *Merremia hederacea* Hallier f.; *Merremia gemella* (Choisy) Hallier f.; *Merremia hirta* (L.) Merrill; *Merremia incisa* (R.Br.) Hallier f.; *Merremia subsessilis* (Courchet & Gagnep.) T.N.Nguyen; *Merremia verruculosa* S.Y.Liu	Twining or prostrate herbs, leaves entire to shallowly lobed; corolla completely glabrous; dark veins along the midpetaline bands; corolla lacking a maroon centre; anthers spirally dehiscing; fruit a chartaceous four-valved capsule, not delaminating when dehisced	Widespread in the Old World tropics
Clade 3	*Decalobanthus sumatranus* Ooststr., *Merremia borneensis* Merrill, *Merremia mammosa* (Lour.) Hallier f.; *Merremia gracilis* E.J.F.Campbell & Argent; *Merremia peltata* (L.) Merrill	Large climbing woody lianas with broad cordate leaves; inflorescence corymbiform; pedicel clavate; corolla glabrous; corolla without maroon centre; anthers spirally dehiscing; fruit a chartaceous four-valved capsule, delaminating when dehiscing; pollen trizonocolpate	Widespread in SE Asia; also in the Pacific
Clade 4	*Davenportia davenportii* Johnson; *Merremia aegyptia* Urban; *Merremia ampelophylla* Hallier f.; *Merremia aturensis* Hallier f.; *Merremia aurea* (Kellogg) O'Donell; *Merremia austinii* J.A.McDonald; *Merremia cielensis* J.A.McDonald; *Merremia cissoides* Hallier f.; *Merremia dissecta* Hallier f.; *Merremia dissecta* var. *edentata* (Meisn.) O'Donell; *Merremia dimorphophylla* (Verdc.) Sebsebe; *Merremia guerichii* A.Meeuse; *Merremia kentrocaulos* Rendle; *Merremia quinata* (R.Br.) Ooststr.; *Merremia quinquefolia* (L.) Hallier f.; *Merremia semisagitta* (Griseb. ex Peter) Dandy; *Merremia somalensis* Hallier f.; *Merremia tuberosa* Rendle; *Operculina flammea* (Nees) Meisner	Twiners, robust climbers or rarely erect shrubs, with lobed or compound leaves (mostly five to seven lobes or leaflets), or rarely highly reduced leaves; flat calyx, with sepals adnate to the corolla; corolla with dark maroon centre, glabrous; anthers spirally twisting; fruit a chartaceous four-valved capsule; pollen trizonocolpate or 12-zono-colpate	Central and South America, Tropical Africa and Northern Australia
Clade 5	*Merremia pinnata* Hallier f., *Merremia sapinii* De Wild., *Xenostegia tridentata* (L.) D.F. Austin & Staples	Slender twiners or prostrate herbs; stems angulate to narrowly winged; leaves basally dentate or hastate to pinnately lobed; sepals long acuminate or emarginate and mucronate, entire or pinnately incised; corolla yellow to white, glabrous; anthers longitudinally dehiscing; ovary densely pubescent; fruit four-valved chartaceous capsule; pollen pantoporate; seeds glabrous	Tropical Africa, South East Asia and Northern Australia
Clade 6	*Operculina aequisepala* (Domin) R.W.Johnson; *Operculina codonantha* Hallier f.; *Operculina hamiltonii* (G.Don) D.F. Austin & Staples; *Operculina petaloidea* (Choisy) Ooststr.; *Operculina pinnatifida* (Kunth) O'Donell; *Operculina pteripes* (G. Don) O'Donell; *Operculina riedeliana* (Oliver) Ooststr.; *Operculina sericantha* (Miq.) Ooststr.; *Operculina turpethum* (L.) Silva Manso, *Merremia maypurensis* Hallier f.	Slender twiners, with an operculate fruit, leaves entire or lobed; corolla with pubescent midpetaline bands and lacking a maroon centre; pollen trizonocolpate	
Clade 7	*Merremia umbellata* (L.) Hallier f.	Herbaceous twiners or prostrate creepers; leaves entire; paired auricles below the leaf; corolla with a tuft of hairs at the apex of the midpetaline bands; anthers longitudinally dehiscing; fruit a chartaceous four-valved capsule, not delaminating when dehisced; pollen hexazonocolpate	Widespread in the tropics

Taxa not assigned to one of the clades above (see text for discussion): *Merremia vitifolia*; *Hewittia malabarica*, *Hyaloyistis viscosa*, *M. gallabatensis*, *M. xanthophylla*; *M. pterygocaulos*; *M. caloxantha*, *M. sibirica*, *M. poranoides*, *Remirema bracteata*

Ooststr., *M. crassinervia* Ooststr., *M. borneensis* Merr., *M. elmeri* Merr., *M. peltata* Merr., *M. mammosa* (Lour.) Hallier f. and *M. boisiana* (Gagnep.) Ooststr.

Among the remaining taxa of Merremieae, four further well supported clades can be identified that, collectively, account for the majority of Merremieae sampled. Clade 4 (MP = 69, ML = 89, PP = 1.00) comprises the Australian endemic *Davenportia davenportii* (F.Muell) R.W.Johnson, *Operculina flammea* Meisn. and 17 *Merremia* spp. The members of this group occur in Central and South America, tropical Africa and northern Australia. They typically possess lobed or compound leaves (mostly five to seven lobes or leaflets), except *M. somalensis* Hallier f. and *M. aturensis* Hallier f., both of which have reduced leaves (Table 2). These species also share an erect habit and they are restricted to arid habitats. Their highly reduced leaves are likely an adaptation to these extreme conditions. *Davenportia davenportii* was separated as a monotypic genus by Johnson (2010) based on the presence of stellate hairs and hexazonocolpate and tricolpate pollen, but it is readily accommodated here as it shares the characters that define the group. *Operculina flammea* is included in this group and is the only *Operculina* sp. not resolved in clade 6. The operculate capsule is the defining character of *Operculina* and, significantly, the fruits of *O. flammea* are not known. All other members of this clade possess four-valved capsules and we hypothesize that this is also the case for *O. flammea*.

Clade 5 (MP = 77, ML = 78, PP = 0.98) comprises *Xenostegia* and the East African endemics *M. pinnata* Hallier f. and *M. sapinii* De Wild. *Xenostegia* has lobed to palmately divided leaves, whereas *M. sapinii* and *M. pinnata* have distinctly pinnately lobed leaves; nevertheless, they all possess panto-aperturate pollen and share a number of other significant characters (Table 2).

The strongly supported clade 6 (MP = 100, ML = 100, PP = 1.00) broadly corresponds to the traditional circumscription of *Operculina*. The fruit of *Merremia maypurensis* Hallier f., which was also resolved in this clade, is unknown and based on this result is likely to be an operculate capsule which is otherwise diagnostic of the clade (Table 2).

Finally, clade 7 (MP = 91, ML = 100, PP = 1.00) comprises *M. bambusetorum* Kerr and *M. umbellata* (L.) Hallier f. *Merremia vitifolia* Hallier f. is resolved as sister to this clade although with limited support (MP = 52, ML < 50, PP = 0.91). *Merremia bambusetorum*, *M. umbellata* and *M. vitifolia* all possess hexazonocolpate pollen (Simões, unpublished data). In other respects however, notably its five-lobed palmate leaves, flat calyx with sepals adnate to the completely glabrous corolla, spirally dehiscing anthers and papery, almost four-valved capsule, *M. vitifolia* is

morphologically closer to species in clade 4 (Table 2). The documented high levels of homoplasy in morphology of Convolvulaceae (Austin, 1998; Wilkin, 1999) could explain its morphological similarity with others in a distinct clade, although it should be noted that its placement is only weakly supported in the analysis and further data are necessary to resolve its relationships robustly.

Of the taxa of Merremieae not resolved in these clades, *Hewittia*, *Hyalocystis*, *M. gallabatensis* Hallier f., *M. xanthophylla* Hallier f. and *M. pterygocaulos* Hallier f. are resolved as a group in the Bayesian analysis that is sister to clade 5. It is notable that, with the exception of *Hewittia* that also occurs in Asia, all of these species are restricted to Africa, where clade 5, its putative but unsupported sister clade, is also most diverse. Although *Hewittia* can be easily distinguished by enlarged foliaceous bracts surrounding the calyx and *Hyalocystis* possesses a distinctive indehiscent fruit type, the group is morphologically heterogeneous and no diagnostic characters could otherwise be found to characterize it.

The placement of *M. caloxantha* (Diels) Staples & R.C.Fang, *M. sibirica* Hallier f., *M. poranoides* (C.B.Clarke) Hallier f. and *Remirema bracteata* Kerr is not clear. The Thai endemic *Remirema bracteata* has a gynobasic style and four-nutlet fruit type, otherwise unknown in the family. The remaining taxa are little-known species from China and Thailand, for which key morphological characters such as fruit and pollen types are still undocumented.

IMPLICATIONS FOR TRIBAL DELIMITATION

Stefanovic *et al.* (2002) found that Ipomoeae were nested in Merremieae, although their results lacked support and they were unable to reject the monophyly of Merremieae confidently. Given the lack of clarity regarding its status, they tentatively recognized the tribe in their phylogenetic classification of the family (Stefanovic *et al.*, 2003) pending further research. Significantly, they noted that the morphological characterization of the tribe was also problematic (Stefanovic *et al.*, 2003).

The present study, with expanded taxon sampling and additional markers, supports the paraphyly of Merremieae *sensu* Stefanovic *et al.* (2003) relative to Ipomoeae (Fig. 1) whereas the relationship of Merremieae with Convolvuleae remains less clear.

Merremieae is resolved in the Convolvuloideae clade of Stefanovic *et al.* (2003), which also comprises Ipomoeae, Convolvuleae and Aniseae (Fig. 1). The clade comprises about two thirds of the species in Convolvulaceae, but lacks a single unifying morphological character (Stefanovic *et al.*, 2003). In this clade, we have not been able to identify morphologi-

cal characters that would allow morphological characterization of Ipomoeae expanded to include *D. montana* (resolved as sister to Ipomoeae) or to also include clades 2 and 3 of Merremieae (resolved as successive sister clades to Ipomoeae + *D. montana*; Fig. 1). Difficulties with the morphological characterization of larger clades suggest that tribal classification may be problematic. At the generic level, however, a re-classification of Merremieae, recognizing monophyletic, morphologically diagnosable groups may be achievable.

IMPLICATIONS FOR GENERIC DELIMITATION

In contrast with earlier studies, we sampled representatives of all currently accepted genera of Merremieae. The potential non-monophyly of *Merremia* supported further by this analysis, combined with strong support for certain groups, highlights the need for a re-circumscription of the genus. The relationships of the monotypic *Remirema* are investigated for the first time but it ultimately remains unresolved in our analysis (Fig. 1). This taxon is morphologically quite distinct, possessing a gynobasic style and an uncommon four-nutlet fruit; on the basis of our results, there are no grounds to change the taxonomic status of this monotypic Thai endemic genus.

In the case of *Operculina*, the second largest genus in Merremieae, monophyly may be achieved if *M. maypurensis* is included and *O. flammea* excluded. The operculate fruit is the characteristic that most readily defines *Operculina* and, significantly, this trait is unknown in these two taxa. In light of their placement we predict that *M. maypurensis* possesses an operculate fruit and *O. flammea* does not.

Of the remaining genera, our results indicate that the monotypic genera *Decalobanthus* and *Davenportia* are nested in late branching positions in clades 3 and 4, respectively (Fig. 1), in which they are readily accommodated morphologically. *Xenostegia* is resolved as sister to a clade comprising *M. pinnata* and *M. sapinii* and given the features shared by these taxa, including a distinctive panto-aperturate pollen type (Simões, 2013), a broader circumscription of *Xenostegia* appears to be warranted.

The placement of *Hewittia* and *Hyalocystis*, both of which occur in the Horn of Africa (although *Hewittia* is more widespread), is not well supported, but they appear to be closely related and in a clade with other East African taxa. Although these genera are morphologically distinct, their recognition would leave the problem of how to deal with the other taxa that are resolved in the same clade albeit without support. The clade is centred on East Africa and a more broadly circumscribed genus of East African taxa may be appropriate, even if the monophyly of the clade is equivocal.

Daustinia montana (Fig. 1, clade 1) is resolved as sister to *Ipomoea*, albeit with weak support. However, this species is clearly morphologically distinct from *Jacquemontia* (Buril et al., 2014) and is justifiably recognized as the distinct genus *Daustinia* (Buril *et al.*, 2014, 2015).

The well supported groups identified in Figure 1 provide the basis for a revised generic classification since they are monophyletic and morphologically diagnosable (Table 2). We have sampled approximately half of taxa in Merremieae and are confident that the majority of the remainder could be accommodated in one of the six groups recognized. However, some taxa are clearly not referable to the six groups we have recognized; thus, our data are equivocal with regards the status of *Hyalocystis* and *Hewittia*. As already noted, the monotypic status of the unresolved *Remirema* appears justified given its distinctive gynoecium structure. Our results provide no indication of the placement of *M. caloxantha*, *M. poranoides* or *M. sibirica*. *Merremia caloxantha* is an East Asian endemic that is morphologically similar to a number of other species from East Asia [*M. hungaiensis* (Lingelsh. & Borza) R.C.Fang, *M. yunnanensis* (Courchet & Gagnep.) R.C.Fang, *M. cordata* C.Y.Wu & R.C.Fang]; we were unable to sample those taxa but hypothesize that they would constitute a monophyletic group. *Merremia poranoides* and *M. sibirica* are poorly known and further morphological and molecular data would be desirable for more solid hypotheses of their relationships with the remaining taxa examined.

CONCLUSIONS

This study provides the most extensive analysis of Merremieae to date, sampling all recognized genera and approximately half of the *c.* 120 currently recognized species. Our results fail to ascertain the monophyly of the tribe and we suggest that attempts at tribal delimitation in the Convolvuloideae clade to which it belongs are likely to be problematic. At the generic level, we have identified several morphologically diagnosable monophyletic groups in Merremieae that provide a clear framework for a new generic classification based on the criteria of monophyly and diagnosability. Some of these groups broadly correspond to currently recognized genera with minor modifications (e.g. clade 5 – *Xenostegia*; clade 6 – *Operculina)*. Basal relationships remain poorly resolved and a number of taxa are not readily accommodated by these groups because they are unresolved in the analysis. In some cases these represent morphologically divergent lineages (e.g. *Remirema*) that warrant recognition.

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APPENDIX

VOUCHER INFORMATION AND GENBANK ACCESSION NUMBERS FOR TAXA USED IN THIS STUDY

Species	Locality	Voucher specimen	ITS	trnL-trnF	matK	rps16
Aniseia martinicensis (Jacq.) Choisy	Malaysia	*FRI 70036* (KEP)	KP261943	KP236600	KR024890	KR025033
Aniseia martinicensis (Jacq.) Choisy	C.N.C. (cultivation)	*Simões 65* (BM)	KP261944	KP236601	KR024891	KR025034
Argyreia caudata Ooststr.	Malaysia	*SAN 152877* (SAN)	KP261908	KP236602	KR024892	KR025035
Argyreia erinacea Ooststr.	Malaysia	*SAN 152883* (SAN)	–	KP236603	KR024893	KR025036
Argyreia henryi Craib	Thailand	*Staples 1424* (SAN)	KP261910	KP236605	KR024895	KR025038
Argyreia laotica Gagnep.	Thailand	*Staples 1390* (SING)	KP261911	KP236606	KR024896	KR025039
Argyreia mollis (Burm.f.) Choisy	Thailand	*Staples 1391* (SING)	KP261912	KP236607	KR024897	KR025040
Argyreia nervosa (Burm.f.) Bojer	SBG (cultivation)	*SBG 20031385* (SING)	KP261913	KP236608	KR024898	KR025041
Argyreia siamensis (Craib) Staples	Thailand	*Staples 1412* (SING)	KP261914	KP236609	KR024899	KR025042
Convolvulus althaeoides L.	Spain	*Carine 164* (BM)	KC528819	–	KC529015	–
Convolvulus arvensis L.	Turkey	*Davis & Hedge 30675* (BM)	KC528906	–	KC529020	–
Convolvulus sepium L. var. *americanus* Sims	Portugal	*Carine 50* (BM)	KC528910	–	KC529150	–
Convolvulus tricolor L.	Morocco	*Carine 250* (BM)	KC528870	–	KC529131	–
Convolvulus siculus L.	Spain	*Carine 231* (BM)	KC528899	–	KC529121	–
Convolvulus valentinus Cav.	Morocco	*Carine 327* (BM)	KC528902	–	KC529133	–
Convolvulus caput-medusae Lowe	Spain	*Carine & Duraes 158* (BM)	KC528951	–	KC529028	–
Convolvulus capituliferus Franch. var. *foliaceus* Verdc.	Ethiopia	*Ensermu et al. 3679* (ETH)	KP261946	–	–	–
Convolvulus × despreauxii A.Santos & Carine	CNC (cultivation)	*Simoes 5* (BM)	KP261947	–	KR024902	KR025043
Convolvulus farinosus L.	Ethiopia	*Sebsebe, D. 2967* (ETH)	KP261948	–	KR024903	KR025044
Davenportia davenportii (F.Muell.) R.W.Johnson	Australia	*Bean, A. R. 23827* (BRI)	KP261966	KP236610		KR025045
Decalobanthus sumatranus Ooststr.	Malaysia	*Amb. & Arifin 1682* (L)	KP261986	KP236611	KR024904	KR025045
Hewittia malabarica (L.) Suresh (1)	Thailand	*Staples 1334* (BM)	KP261950	KP236613	KR024909	KR025047
Hewittia malabarica (L.) Suresh (2)	CNC (cultivation; Tanzania)	*Simoes 2* (BM)	KP261951	KP236615	KR024910	KR025048
Hyalocystis viscosa Hallier f.	Somalia	*Bally & Melville 15536* (MO)	–	–	KR024911	
Ipomoea aquatica Forssk.	Malaysia	*FRI 70037* (FRIM)	KP261915	KP236616	KR024912	KR025049
Ipomoea cairica (L.) Sweet	USA, Hawaii	*Staples 1399* (SING)	KP261916	KP236618		KR025051
Ipomoea carnea Jacq.	Singapore (cultivation)	*SBG 19971190* (SING)	KP261917	KP236619	KR024914	KR025052
Ipomoea cicatricosa Baker	Ethiopia	*Sebsebe D, M, Carine, A, Simoes, Wege A. & Ermias G. 6967* (BM)	KP261918	KP236620	KR024915	KR025053
Ipomoea cordatotriloba Dennst.	USA, Florida	*Staples 1465* (SING)	KP261919	KP236621	KR024916	KR025054
Ipomoea donaldsonii Rendle	Ethiopia	*Sebsebe D, M, Carine, A, Simoes, Wege A. & Ermias G. 6942* (BM)	KP261920	KP236622	KR024917	KR025055
Ipomoea indica Merr.	USA, Hawaii	*Staples 1397* (SING)	KP261921	KP236625	KR024921	KR025058
Ipomoea intrapilosa Rose	CNC (cultivation, Mexico)	*Simoes 52* (BM)	KP261922	KP236626	KR024922	KR025059
Ipomoea kituiensis Vatke var. *kituiensis*	Ethiopia	*Sebsebe D, M, Carine, A, Simoes, Wege A. & Ermias G. 6958* (BM)	KP261923	KP236627	KR024923	KR025060
Ipomoea littoralis Blume	Malaysia	*SAN 152892* (SAN)	KP261924	KP236628	KR024924	KR025061
Ipomoea marmorata Britten & Rendle subsp. *marmorata*	Ethiopia	*Sebsebe D, M, Carine, A, Simoes, Wege A. & Ermias G. 6939* (BM)	KP261925	–	KR024925	KR025062
Ipomoea mauritiana Jacq.	CNC (cultivation, France)	*Simoes 48* (BM)	KP261926	KP236629	KR024926	KR025063
Ipomoea ochracea (Lindl.) G.Don	Thailand	*Staples 1396* (SING)	KP261927	KP236631	KR024928	KR025065
Ipomoea pes-tigridis L.	Singapore (cultivation)	*SBG 20100015* (SING)	KP261928	KP236632	KR024929	KR025066
Ipomoea pileata Roxb.	Thailand	*Staples 1449* (SING)	KP261929	KP236633	KR024930	KR025067
Ipomoea pogonantha Thulin	Ethiopia	*Sebsebe D, M, Carine, A, Simoes, Wege A. & Ermias G. 6937* (BM)	KP261930	KP236634	KR024931	KR025068
Ipomoea polymorpha Schult.	Ethiopia	*Sebsebe D, M, Carine, A, Simoes, Wege A. & Ermias G. 6961* (BM)	KP261931	KP236635	KR024932	–
Ipomoea purpurea (L.) Roth	CNC (cultivation, Madagascar)	*Simoes 50* (BM)	KP261932	KP236636	KR024933	KR025070
Ipomoea quamoclit L.	Singapore (cultivation)	*SBG 20080990* (SING)	KP261933	KP236637	KR024934	KR025071
Ipomoea sagittifolia Burm.f.	Malaysia	*FRI 7036* (FRIM)	KP261934	KP236638	KR024935	KR025072
Ipomoea sinensis (Desr.) Choisy	Ethiopia	*Sebsebe D, M, Carine, A, Simoes, Wege A. & Ermias G. 6920* (BM)	KP261935	KP236639	KR024936	KR025073
Ipomoea tricolor Cav.	Singapore	*Simoes 19* (BM)	KP261936	KP236640	KR024937	KR025074
Ipomoea violacea L.	Malaysia	*FRI 70039* (FRIM)	KP261937	KP236641	KR024938	KR025075

APPENDIX *Continued*

Species	Locality	Voucher specimen	ITS	*trnL-trnF*	*matK*	*rps16*
Iseia luxurians (Moric.) O'Donell	CNC (cultivation, Madagascar)	*Simoes 66* (BM)	KP261945	KP236642	KR024939	KR025076
Lepistemon binectariferum (Wall.) Kuntze	Malaysia	*FRI 66675* (FRIM)	KP261938	–	KR024940	KR025077
Merremia aegyptia (L.) Urb.	CNC (cultivation, Senegal)	*Simoes 17* (BM)	KP261965	KP236643	KR024941	KR025078
Merremia ampelophylla Hallier f. (1)	Kenya	*Festo et al. 2645* (K)	KP261972	KP236645	KR024943	KR025079
Merrmia ampelophylla Hallier f. (2)	Ethiopia	*Sebsebe D, M, Carine, A, Simoes, Wege A. & Ermias G. 6971* (BM)	KP261969	KP236644	KR024942	–
Merremia aturensis Hallier f.	Brazil	*Whitefoord 2330* (BM)	KP261974	KP236646	–	–
Merremia aurea (Kellogg) O'Donell	Mexico	*Wiggins 5591* (A)	KP261975	–	KR024944	–
Merremia austinii J.A.McDonald	Mexico	*McDonald s.n.* (BM)	KP261983	–	KR024945	KR025080
Merremia borneensis Merr. (1)	Malaysia	*FRI s.n.* (FRIM)	KP261984	KP236648	KR024948	KR025082
Merremia borneensis Merr. (2)	Malaysia	*SAN 152852* (SAN)	KP261985	KP236650	KR024950	–
Merremia caloxantha (Diels) Staples & R.C.Fang	China	*G. Goligong Shan Exp. (GSE97) 9928*	KP262006	KP236649	KR024949	–
Merremia cielensis J.A.McDonald	Mexico	*McDonald s.n.* (BM)	KP261976	KP236651	–	KR025085
Merremia cissoides Hallier f.	Thailand	*Staples 1318* (BM)	KP261977	KP236652	KR024951	KR025086
Merremia dimorphophylla (Verdc.) Sebsebe subsp. *ogadenensis* Sebsebse	Ethiopia	*Ensermu & Wondafrash 2816* (ETH)	KP261978	KP236654	KR024953	KR025087
Merremia dissecta (Jacq.) Hallier f.	CNC (cultivation, Guyane)	*Simoes 6* (BM)	KP261981	KP236656	KR024956	KR025090
Merremia dissecta Hallier f. *var. edentata* (Meisn.) O'Donell	Brazil	*Nee & Chavez 48899* (MO)	KP261982	KP236657	KR024957	KR025091
Merremia emarginata Hallier f.	Thailand	*Staples 1335* (BM)	KP261993	KP236659	KR024958	KR025092
Merremia gallabatensis Hallier f.	Ethiopia	*Demissew, Wondafrash, Awas & Kagnew 6091* (ETH)	KP261949	KP236660	KR024959	KR025093
Merremia gemella (Choisy) *Hallier f.*	Thailand	Staples 1333 (BM)	KP261994	KP236661	KR024960	KR025094
Merremia guerichii A.Meeuse	CNC (cultivation, Namibia)	*Simoes 44* (BM)	KP261979	KP236662	KR024962	KR025096
Merremia hederacea Hallier f.	Thailand	*Simoes 26* (BM)	KP261995	KP236664	KR024964	KR025098
Merremia hirta Merr.	Cambodia	*Simoes 44* (BM)	KP261996	KP236665	KR024965	KR025099
Merremia incisa (R.Br.) Hallier f.	Australia	*Courie, 1234b* (BRI)	KP261997	KP236667	KR024967	KR025101
Merremia kentrocaulos Rendle	CNC (cultivation, South Africa)	*Simoes 9* (BM)	KP261998	KP236668	KR024968	KR025102
Merremia mammosa (Lour.) Hallier f.	Thailand	*Staples 1351* (BM)	KP261987	–	KR024972	KR025104
Merremia maypurensis Hallier f.	Venezuela	*Groger & Llamozas 1145* (MO)	–	KP236673	KR024973	KR025105
Merremia peltata (L.) Merr. (1)	Malaysia	*SAN 152853* (SAN)	KP261988	KP236676	KR024976	KR025107
Merremia peltata (L.) Merr. (2)	Malaysia	*SAN 152851* (SAN)	KP261989	KP236677	KR024977	KR025108
Merremia pinnata Hallier f.	CNC (cultivation)	*Simoes 15* (BM)	KP261959	KP236678	KR024978	KR025109
Merremia poranoides (C.B.Clarke) Hallier f.	Malaysia	*Staples 1441* (SING)	KP262005	KP236680	KR024979	KR025110
Merremia pterygocaulos Hallier f.	CNC (cultivation, Madagascar)	*Simoes 64* (BM)	KP261999	KP236681	KR024980	KR025111
Merremia quinata (R.Br.) Ooststr. (1)	Thailand	*Staples 1347* (BM)	KP262001	KP236682	KR024982	KR025112
Merremia quinata (R.Br.) Ooststr. (2)	Australia	*K. R. McDonald KRM 3270* (BRI)	KP262002	KP236683	KR024983	KR025113
Merremia quinquefolia Hallier f.	CNC (cultivation)	*Simoes 10* (BM)	KP262003	KP236684	KR024984	KR025114
Merremia sapinii De Wild. (1)	Congo, D. R. C.	*Breyne 3197* (BR)	–	KP236685	–	–
Merremia sapinii De Wild. (2)	Congo, D. R. C.	*Pauwels 2991* (BR)	–	–	KR024985	–
Merremia semisagitta (Griseb. ex Peter) Dandy	s. l.	*Popov 69154* (BM)	KP261970	KP236687	KR024986	–
Merremia sibirica Hallier f.	China	*Forrest 11314* (BM)	KP262004	KP236688	KR024987	–
Merremia somalensis Hallier f.	Ethiopia	*Thesiger s.n.* (BM)	KP261971	KP236689	KR024988	–
Merremia subsessilis (Courchet & Gagnep.) P.H.Hô	Malaysia	*Staples 1456* (SING)	KP261990	–	KR024990	–
Merremia thorelii (Gagnep.) Staples	Thailand	*Staples 1324* (BM)	–	KP236691	KR024991	KR025117
Merremia tuberosa Rendle (1)	CNC (cultivation, Guadeloupe)	*Simoes 4* (BM)	KP261967	KP236692	–	KR025118
Merremia tuberosa Rendle (2)	Australia	*Waterhouse et al. BMW 5044* (BRI)	KP261968	KP236693	KR024992	KR025119
Merremia umbellata (L.) Hallier f. (1)	Thailand	*Staples 1329* (BM)	KP261960	KP236696	KR024946	KR025081

APPENDIX *Continued*

Species	Locality	Voucher specimen	ITS	*trnL-trnF*	*matK*	*rps16*
Merremia umbellata (L.) Hallier f. (2)	Thailand	*Staples 1369* (BM)	KP261963	KP236696	KR024995	KR025122
Merremia umbellata (L.) Hallier f. (3)	Malaysia	*FRI 70028* (FRIM)	KP261962	KP236694	KR024993	KR025120
Merremia umbellata (L.) Hallier f. (4)	Cambodia	*Simoes 28* (BM)	KP261961	–	KR024947	–
Merremia verruculosa S.Y.Liu	Thailand	*Staples 1320* (BM)	KP261991	KP236700	KR024999	KR025125
Merremia vitifolia Hallier f.	Thailand	*Staples 1330* (BM)	KP261964	KP236701	KR0245000	–
Merremia xanthophylla Hallier f.	s. l.	*Smith 437* (MO)	KP261973	KP236702	KR0245001	KR025126
Operculina aequisepala (Domin) R.W.Johnson	CNC (cultivation, Australia)	*Simoes 14* (BM)	KP262008	KP236703	KR0245003	KR025127
Operculina codonantha Hallier f.	CNC (cultivation, Ecuador)	*Simoes 8* (BM)	KP262009	KP236705	KR0245005	–
Operculina flammea Meisn.	Brasil	*Carvalho-Sobrinho, J. G. 3017* (HUEFS)	KP262010	KP236706	KR0245006	–
Operculina hamiltonii (G.Don.) D.F. Austin & Staples	CNC (cultivation, Panama)	*Simoes 59* (BM)	KP262011	KP236707	KR0245007	KR025129
Operculina petaloidea (Choisy) Ooststr.	Thailand	*Staples 1372* (BM)	KP262012	KP236708	KR0245009	–
Operculina pinnatifida (Kunth) O'Donell	–	*Dwyer 1455* (BM)	KP262013	KP236709	KR0245010	KR025130
Operculina pteripes (G.Don) O'Donell	–	*Wiggins & Rollins 398* (A)	–	KP236710	KR0245011	–
Operculina riedeliana (Oliver) Ooststr.	Singapore (cultivation)	*Staples 1469* (SING)	KP262014	KP236712	KR0245012	KR025131
Operculina sericantha (Miq.) Ooststr.	–	*Evans et al. 2695* (MO)	–	KP236713	KR0245014	–
Operculina turpethum (L.) Silva Manso (1)	CNC (cultivation)	*Simoes 18* (BM)	KP262015	KP236714	KR0245015	KR025133
Operculina turpethum (L.) Silva Manso (2)	Malaysia	*SAN 152888* (SAN)	KP262016	KP236715	KR0245016	KR025134
Remirema bracteata Kerr	Thailand	*Staples 1338* (BM)	KP262007	KP236716	KR0245018	KR025135
Stictocardia beraviensis Hallier f.	CNC (cultivation, Madagascar)	*Simoes 62* (BM)	KP261939	KP236717	KR0245019	KR025136
Stictocardia laxiflora (Baker) Hallier f.	CNC (cultivation, Uganda)	*Simoes 49* (BM)	KP261940	KP236718	KR0245020	KR025137
Stictocardia tiliifolia (Desr.) Hallier f.	USA, Hawaii	*Staples 1400* (SING)	KP261941	KP236719	KR0245021	KR025138
Turbina inopinata Heine	CNC (cultivation, France)	*Simoes 57* (BM)	KP261942	KP236720	KR0245022	KR025139
Xenostegia tridentata (L.) D.F. Austin & Staples subsp. *tridentata* (1)	Ghana	*Merello et al. 1581* (BM)	KP261952	KP236723	KR0245024	KR025140
Xenostegia tridentata (L.) D.F. Austin & Staples subsp. *tridentata* (2)	CNC (cultivation, Senegal)	*Simoes 16* (BM)	KP261958	–	KR0245031	KR025150
Xenostegia tridentata (L.) D.F. Austin & Staples subsp. *hastata* (Desr.) P.H.Hô (1)	Malaysia	*FRI 70040* (FRIM)	KP261953	KP236725	–	KR025142
Xenostegia tridentata (L.) D.F. Austin & Staples subsp. *hastata* (Desr.) P.H.Hô (2)	Malaysia	*FRI 70029* (FRIM)	–	KP236729	KR0245028	KR025146
Xenostegia tridentata (L.) D. F. Austin & Staples subsp. hastata (3)	Singapore	*Simoes 22* (BM)	KP261955	KP236730	KR0245029	KR025147
Xenostegia tridentata (L.) D.F. Austin & Staples subsp. *hastata* (Desr.) P.H.Hô (4)	Malaysia	*FRI 74576a* (FRIM)	KP261956	KP236721	KR0245030	KR025148
Xenostegia tridentata (L.) D.F. Austin & Staples subsp. *hastata* (Desr.) P.H.Hô (5)	Malaysia	*FRI 74576b* (FRIM)	KP261956	KP236731	KR0245030	KR025148
Xenostegia tridentata (L.) D.F. Austin & Staples subsp. *hastata* (Desr.) P.H.Hô (6)	Thailand	*Staples 1328* (BM)	–	KP236728	KR0245027	KR025145