

Dissolution of Convolvulaceae tribe Merremieae and a new classification of the constituent genera

A. R. SIMÕES^{1*} and G. STAPLES²

¹*Instituto de Botânica, Herbário, Av. Miguel Stéfano, 3687, Água Funda, São Paulo, SP, CEP 04301-902, Brazil*

²*HRA, Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AE, UK*

Received 21 March 2016; revised 5 December 2016; accepted for publication 31 January 2017

The classification of Convolvulaceae tribe Merremieae has remained a challenge. *Merremia*, the largest genus, encompasses a wide range of morphological variation, particularly in characters such as fruit dehiscence and pollen apertures, which are usually diagnostic at the generic and even tribal level in the family. The taxonomy of the tribe and the included genera has been difficult, especially in assigning species to genera. Recent molecular phylogenetic studies did not find support for the monophyly of Merremieae and demonstrated that *Merremia* is polyphyletic. However, strongly supported monophyletic groups were discovered and diagnosable synapomorphies were identified for these. The present study addresses the taxonomic issues with ‘Merremieae’, highlighted by previous molecular results. The tribal rank for ‘Merremieae’ is abandoned due to lack of morphological and molecular evidence and the constituent genera are re-assessed. Morphological, palynological and molecular data are synthesized to propose a new generic classification for the group. The delimitation of *Merremia* is drastically narrowed. Three new genera are circumscribed and names previously published are here applied to these. New combinations are published for all taxa that can confidently be placed in this new generic scheme based on existing molecular and/or morphological data.

ADDITIONAL KEYWORDS: *Camonea* – *Daustinia* – *Decalobanthus* – *Distimake* – *Merremia* – molecular systematics – new combination – nomenclature – *Operculina* – *Remirema* – tribal classification

INTRODUCTION

Convolvulaceae are a family of climbers, herbs and shrubs (rarely trees), with 59 genera and *c.* 1900 species, occurring throughout tropical and warm temperate regions. They are usually recognized by their alternate leaves lacking tendrils and sympetalous corollas with five conspicuous mid-petaline bands. The inflorescence is fundamentally cymose and the fruit is often a dehiscent four-seeded capsule, although several other types of fruits also occur (Staples & Brummitt, 2007); they are the only asterid family to have seeds showing physical dormancy (Baskin *et al.*, 2000). A molecular synapomorphy of Convolvulaceae is the absence of the *rpl2* intron; they are the only asterid family with this deletion (Stefanovic *et al.*, 2002).

Pollen is a major character that divides the family into two taxonomically unranked groupings: Psiloconieae (non-spiny) and Echinoconieae (spiny). The currently

established classification of Convolvulaceae (Staples & Brummitt, 2007; Stevens, 2001) is based on a comprehensive molecular phylogenetic analysis of the family (Stefanovic *et al.*, 2002), in which 12 tribes are recognized and morphologically characterized (Aniseieae, Cardiochlamyaeae, Convolvuleae, Cresseae, Cuscutaeae, Dichondreae, Erycibeae, Humbertieae, Ipomoeaeae, Jacquemontieae, Maripeae and ‘Merremieae’).

Of these, ‘Merremieae’ has remained, to date, the least well-defined in Convolvulaceae. Austin (1982) was the first to formally recognize Merremieae, a grouping in which he included *Aniseia* Choisy, *Hewittia* Wight. & Arn., *Merremia* Dennst. ex Endl., *Operculina* Silva Manso and *Tetralocularia* O’Donell. The tribe was described as similar to Convolvuleae, but differing in the form of the sepals, in the glabrous corollas and the capsule (‘affinis Convolvuleae, sed sepalis, corolla glabra et capsula differt’), a weak tribal definition with several evident exceptions. Stefanovic *et al.* (2003) then applied major changes to the delimitation of Merremieae,

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

including in it *Merremia*, *Hewittia*, *Hyalocystis* Hallier f., *Decalobanthus* Ooststr., *Xenostegia* D.F.Austin & Staples and *Operculina* and transferring *Aniseia*, *Iseia* O'Donell, *Odonellia* K.R.Robertson and *Tetralocularia* to a newly formed tribe, Aniseieae. Unlike Aniseieae, Merremieae were not strongly supported, but molecular sampling of the group was limited at the species level and not all genera were included so no firm conclusions could be taken. The tribe was treated more as an informal group (addressed as 'Merremieae') and highlighted for future re-assessment. Recent molecular phylogenetic studies (Simões *et al.*, 2015) expanded the molecular sampling of Merremieae in relation to Stefanovic's work, but also could not unequivocally prove its monophyly. As Stefanovic *et al.* (2003) put it, Merremieae have mostly been 'defined as lacking some characters used to circumscribe other tribes [...] rather than their own putative synapomorphies'. We agree with this statement and have also not encountered synapomorphies to sustain this tribe, after years of thorough morphological and anatomical studies that both authors have developed on *Merremia* and allied genera. In addition, the recent discovery of *Daustinia* Buriel & Simões (Buriel *et al.*, 2013, 2015), previously included in *Jacquemontia* Choisy and resolved by Simões *et al.* (2015) as closely related to Ipomoeae and members of Merremieae, raises further questions about the circumscription of this group. The lack of success in proving the monophyly of 'Merremieae' in phylogenetic analyses (Stefanovic *et al.*, 2002; Simões *et al.*, 2015) and the ambiguous morphological delimitation lacking synapomorphic characters have led us to conclude that continuing to recognize Merremieae is unjustifiable. We propose in this paper to dissolve Merremieae and to consider the formerly included genera (Stefanovic *et al.*, 2003) and the genera circumscribed in the current paper to be *incertae sedis* in terms of tribal placement in accordance with Article 3.1 of the ICN (McNeill *et al.*, 2012).

Simões *et al.* (2015) further demonstrated that *Merremia* is not monophyletic. The lack of morphological synapomorphies for this genus has made *Merremia* extremely hard to separate unambiguously from *Ipomoea* L. and from other genera formerly included in 'Merremieae' (Staples, 1979). The molecular phylogenetic results (Stefanovic *et al.*, 2002; Simões *et al.*, 2015) confirmed what morphology has said all along: *Merremia* is not a good genus. The broadened molecular phylogenetic analysis of 'Merremieae' (Simões *et al.*, 2015) resolved monophyletic groups of species that do not entirely correspond to any of the currently accepted genera in the family (Staples & Brummitt, 2007). This urges a meticulous re-assessment of morphological characters thus far believed to be taxonomically informative at generic level, in the family and particularly in this group,

and a careful re-drawing of generic boundaries that reflects the newly resolved phylogenetic relationships between species and provides more morphologically intuitive genera (Table 1).

The aims of the present study are to (1) assess the generic status of the currently described genera in the dissolved 'Merremieae', in light of recent molecular phylogenetic results; (2) propose morphological synapomorphies which support the newly suggested monophyletic groups of species and (3) provide new hypotheses of generic entities which resolve in the best possible way the intricate taxonomy of the genera, in particular *Merremia*.

MATERIAL AND METHODS

For discovery of morphological synapomorphies, a thorough morphological survey was conducted. The survey aimed to sample as widely across the tribe as possible, with 116 taxa out of 126 being analysed. Despite the missing taxa, sampling still successfully covered the entire geographical distribution range occupied by Merremieae; all genera were included and all the main morphological groups of *Merremia* were represented (Staples, 2010). The morphological survey was based on herbarium specimens from A, BCU, BK, BKF, BM, BO, BR, COI, E, G, GH, K, KEP, L, LISC, M, MEXU, MICH, MO, NY, PNH, SAN, SAR and SING, complemented with observations of living plants from fieldwork in Singapore, Thailand and Cambodia (2009), Ethiopia (2011) and Sumatra, Indonesia (2012) and information abstracted from a wide range of taxonomic accounts. A data matrix of 43 vegetative and floral characters was compiled to record the

Table 1. Summary of the main taxonomic changes in Merremieae at the generic level, in comparison to the standing classification (Staples & Brummitt, 2007).

Staples & Brummitt (2007)	Present study
<i>Davenportia</i> (added by Johnson, 2010)	<i>Distimake</i>
<i>Decalobanthus</i>	<i>Decalobanthus</i> expanded
<i>Hewittia</i>	<i>Hewittia</i>
<i>Hyalocystis</i>	<i>Hyalocystis</i>
<i>Merremia s.l.</i>	<i>Merremia s.s.</i>
	<i>Distimake</i> expanded
	<i>Camonea</i> expanded
	<i>Decalobanthus</i> expanded
<i>Operculina</i>	<i>Operculina</i>
<i>Remirema</i>	<i>Remirema</i>
<i>Xenostegia</i>	<i>Xenostegia</i>
<i>Jacquemontia p.p.</i>	<i>Daustinia</i> (newly added)

morphological variation, with particular attention given to characters that are traditionally important for generic delimitation in Convolvulaceae, namely pistil morphology, calyx characters and fruit dehiscence mode (Staples & Brummitt, 2007). Seed images were obtained at the Sackler Imaging Lab (Natural History Museum of London) using a Leica Z16APO microscope (Objective 5x), in collaboration with the AntWeb Project (California Academy of Sciences, www.antweb.org). Images were flattened using Helicon Focus (Helicon Soft Ltd.) software and treated with Adobe Photoshop CS6.

The phylogenetic tree used as reference for taxonomic interpretation (Fig. 1) is based on the summary tree in Simões *et al.* (2015). Criteria for generic recognition follow those explicitly defined by Linder *et al.* (2010). In particular, genera are delimited so that they constitute monophyletic units, as inclusive as possible, with strong support [>0.85 posterior probability (PP) in BI analysis], there is morphological and geographical congruence and diagnostic characters are easily recognized, possible to organize in identification keys and readily observed in herbarium specimens.

In general, our working principle for deciding species placements is modelled on a triage concept. This admits three tiers of placement ability, depending on what kind of data and how many data we have available for each species: tier 1 (molecular sampling and some morphological sampling; e.g. all or some stages in life cycle present and analysed: leaves, flowers, fruit, seeds, pollen); tier 2 (no molecular sampling but reasonably complete morphological sampling) and tier 3 [no molecular sampling and no morphological sampling (no material available) or incomplete sampling (some stages of life cycle were not available for study)].

Typically, this means we have confidently assigned the species included in the molecular phylogenetic analysis (tier 1) as the core elements of each genus. To that core, we added tier 2 species for which adequate morphological evidence is in hand to assure the species possess the characters matching those of the tier 1 species. Tier 3 species are not included in the new classification at this time because we lack adequate data to confidently place them and we want to avoid repeating the pattern of 'agglomerative taxonomy' that has been so prevalent in Convolvulaceae in the past. Tier 3 species will be dealt with in full in the taxonomic revisions now under preparation for the genera circumscribed here; a series of taxonomic revisions will follow the publication of the present classification.

One further point to mention is that this new classification does not place all currently accepted species of *Merremia* or Merremieae. Firstly, several species names will be reduced to synonymy, so no new combinations are proposed for them in this paper. Secondly,

further study is required to place tier 3 species confidently in the new genera and those species will be placed only after the generic revisions, now under preparation, are completed.

DISCUSSION

MONOPHYLY AND NEWLY DISCOVERED GROUPS

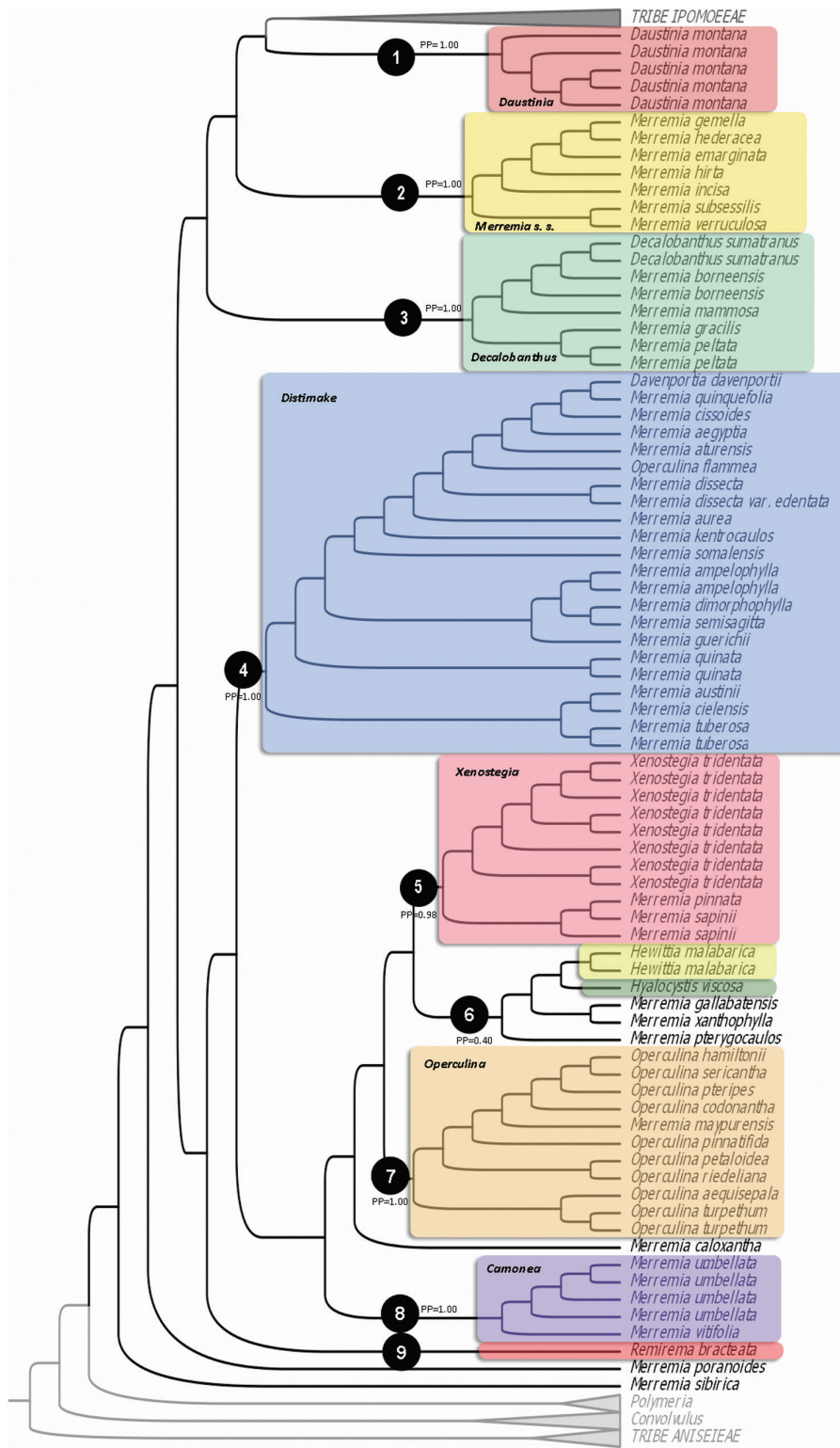
In light of the recently discovered phylogenetic relationships (Simões *et al.*, 2015), all genera in Merremieae have been re-assessed and several monophyletic groups resolved are here discussed as new generic entities (Fig. 1). They are presented in numerical sequence, the numbers corresponding to the clades in Figure 1; percent support values in maximum likelihood (ML) and Bayesian (PP) obtained for each clade (from Simões *et al.*, 2015) are indicated.

(1) *Daustinia* (ML = 100; PP = 1.00)

This new genus is a strongly supported separate lineage (Simões *et al.*, 2015). The single polymorphic species is not closely related to any *Merremia* spp. and was until recently included in *Jacquemontia*. Morphological studies (Buriel *et al.*, 2013) demonstrated that, despite sharing a few morphological characters with *Merremia s.l.*, this species has significant morphological differences, namely capitate inflorescences with an evident involucre, which do not occur in *Merremia s.l.* The recently described *Daustinia* (Buriel *et al.*, 2013, 2015) was recognized to accommodate this monospecific lineage.

(2) *Merremia* (ML = 100; PP = 1.00)

Considering the species richness in *Merremia* of just over 100 recognized species (Staples, 2010), the initial molecular sampling for this genus was rather limited, with only five taxa being included (Stefanovic *et al.*, 2002). Based on this initial sampling, *Merremia* was suggested to be paraphyletic in the resulting molecular phylogenetic trees (Stefanovic *et al.*, 2002). Simões *et al.* (2015) improved the sampling of the genus to 37 species, with a targeted approach so that all recognized sections (O'Donnell, 1941; Ooststroom & Hoogland, 1953) and the distinctive morphotypes that had been identified were represented (Staples, 2010). These results now confirm that *Merremia* as currently circumscribed is polyphyletic. One of the monophyletic lineages recovered (Clade 2) includes the type species of *Merremia* (*M. hederacea*); this clade therefore retains the generic name *Merremia*, although with a much narrowed circumscription. Hereafter *Merremia s.s.* refers to this narrowed circumscription.



Downloaded from https://academic.oup.com/bol/advance-article/doi/10.1093/bol/obz013/5373973 by guest on 20 April 2024

Figure 1. Cladogram depicting the phylogenetic relationships of tribes Ipomoeae, ‘Merremieae’, Convolvuleae (*Convolvulus* spp. and *Polymeria* spp.) and Aniseieae, based on four loci (*trnL–trnF*, *rps16*, *matK* and ITS) and reconstructed using Bayesian inference, modified from Simões *et al.* (2015). Nine clades (1–9) are indicated by numbers and discussed in the text.

(3) *Decalobanthus* (ML = 84; PP = 1.00)

Described as a monotypic genus from Sumatra (Ooststroom, 1936), *Decalobanthus* was found to be nested in a clade (clade 3) of several species of lianescent, tropical Asian *Merremia*. Several morphological traits were found to be shared between the species in this clade, further supporting this newly discovered group. The geographical distribution is centred on Southeast Asia and Malesia, with the exception of the widespread Indo-Pacific species, *Merremia peltata* (L.) Merr., the distribution of which may have been enhanced by human dispersal. This clade incorporates two sections of *Merremia* accepted by Ooststroom & Hoogland (1953): section *Hailale*, which included *M. boisi* (Gagnep.) Ooststr., *M. borneensis* Merr., *M. clemensiana* Ooststr., *M. crassinervia* Ooststr., *M. elmeri* Merr., *M. korthalsiana* Ooststr., *M. mammosa* (Lour.) Hallier f., *M. peltata* and *M. pulchra* Ooststr. and section *Wavula*, which included *M. calyculata* Ooststr., *M. pacifica* Ooststr. and *M. similis* Elmer.

(4) 'Tropical America/Africa' *Merremia* (ML = 89, PP = 1.00)

Clade 4 comprises a strongly supported clade of *Merremia* that includes more species than any other clade (Fig. 1). The constituent species share some morphological features despite a few exceptions, possibly due to adaptation to local extreme conditions. The species mostly occur in Central and South America and tropical Africa, with disjunct species found in western India and northern Australia. Because *Merremia* has never been comprehensively revised and floristic accounts have been conducted at a local scale, this is the first time the close relationship between these American and Old World species is suggested, with significant support from the analysis of molecular data. We conclude that there is enough evidence (molecular, morphological, palynological) to warrant the recognition of generic rank for this group of species, under the name *Distimake* Raf. Among the rarer species of *Merremia s.l.* that have not yet been sampled, many of them have morphological characters that suggest they will be placed here. Further sampling and analysis are ongoing to test this hypothesis.

(5) *Xenostegia* (ML = 78, PP = 0.98)

This strongly supported clade (Fig. 1) is congruent with the diagnostic characters used to circumscribe the genus (Austin & Staples, 1980), such as the pantoporate, non-spinulose pollen, a distinctive leaf shape, seed morphology and germination behaviour. Nonetheless, several floras rejected *Xenostegia* as a genus and kept the two species [*X. tridentata* (L.)

D.F.Austin & Staples and *X. medium* (L.) D.F.Austin & Staples] in *Merremia s.l.* (Gonçalves, 1987, 1992; Deroin, 2001); this taxonomic position is no longer tenable in light of the molecular analysis. Two more *Merremia* spp. were resolved in the molecular analysis (Simões *et al.*, 2015) in the same clade with strong support [– *M. pinnata* (Hochst. ex Choisy) Hallier f. and *M. sapinii* De Wild.]. These two species also fit the morphological characters of the genus and share the pantocolpate pollen; therefore, they are here transferred to *Xenostegia*.

(6) Unresolved African Group (PP = 0.40)

This clade is doubtful, and we suggest that it will require more investigation before any conclusions can be drawn. The support is low for the most inclusive clade and it encompasses great morphological variation, so much so that we could not recover any morphological synapomorphies for this group. It is speculative at best to try to circumscribe a new genus that would include all the taxa in this clade. *Hewittia* and *Hyalocystis* are resolved as monophyletic in a strict sense, and morphologically they are easily distinguishable by leaf, sepal and fruit characters. The remaining species are difficult to reconcile morphologically with either of these genera or with each other. The sampling of African taxa was limited, however, so the issue with this clade is probably data deficiency as we do not have enough evidence to resolve the relationships in this group at this time; research is underway to address this unresolved group.

(7) *Operculina* (ML = 100; PP = 1.00)

This genus, characterized by the distinctive operculate fruit, which is unique in the family, is resolved as monophyletic with the strongest possible support. Recognition of *Operculina* as a genus gained acceptance only in the second half of the 20th century; prior to that, the constituent species were dispersed among *Merremia* and *Ipomoea*. The molecular analysis supports recognizing *Operculina* and points out one additional species that must be transferred there from *Merremia s.l.* (*M. maypurensis* Hallier f.). A sample identified as *Operculina flammea* (Nees) Meisn. was resolved in the molecular phylogenetic analysis (Simões *et al.*, 2015) in Clade 4, inferring that this species had been placed in the wrong genus. Aside from the distinctive fruit dehiscence mode, *Operculina* is morphologically diverse and its geographical distribution is pantropical. A taxonomic revision (Staples & Simões, in preparation) will elucidate further the morphological diversity among the constituent species and identify additional characters to diagnose the genus.

(8) '*Merremia umbellata* and allies' (ML = 100; PP = 100)

Merremia umbellata is resolved in its own clade (Clade 7); this species has a number of autapomorphies in relation to the remainder of *Merremia s.l.*, strongly suggesting that it constitutes a separate genus. The main diagnostic characters are the presence of a pair of stipule-like outgrowths from the stem beside the petiole insertion and consistently hexazonocolpate pollen. A group of Asian species has been identified as morphologically close to *M. umbellata*, corresponding broadly to *Merremia s.l.* section *Xanthips* (Griseb.) Hallier f. (O'Donell, 1941). We here circumscribe a new genus to accommodate *M. umbellata* and the allied species, taking up the name *Camonea* Raf., and we anticipate that further species will be added after revisionary study clarifies species relationships among Asian taxa.

(9) *Remirema*

The enigmatic, monotypic genus *Remirema* is resolved as a single-species lineage, sister to all the other 'merremioid' genera (Fig. 1). It had not been sampled in a molecular phylogenetic study before Simões *et al.* (2015). It was recognized as a distinct, monospecific genus on the basis of its floral morphology (gynobasic style insertion, suprastaminal scales on the corolla) (Kerr, 1943). In 2009, we collected fruits of *Remirema* for the first time and these were later described (Staples & Traiperm, 2010): four free nutlets attached to a thickened woody receptacle, resembling a lamiaecous fruit only much larger. This suite of uncommon characters is unique in Convolvulaceae, and for now we maintain *Remirema* as a genus, pending further study.

NOMENCLATURE MATTERS

In deciding which names to apply to the new genera recovered in the molecular phylogeny, we first thought to create new names for them. However, there are already many names published by Rafinesque (1825, 1836, 1838), who seems to have had a particular affinity for Convolvulaceae and named many genera of them. Rafinesque's legacy is a profusion of names at all ranks, frequently proposed based on what others published in the literature, without study of specimens or critical analysis of what he read. This led him, for example, to create multiple generic names based on the same species, with each genus of Rafinesque based on a different synonym for that same species. These practices, eccentric even in his own time, combined with self-funded prolific and rapid publication, left a nomenclatural morass which many later authors preferred to ignore. Nonetheless, the names that Rafinesque published must be taken up if they are valid and legitimate, as required by the ICN (McNeill *et al.*, 2012). A significant

literature is devoted to solving the nomenclatural mess created by Rafinesque's unorthodox naming practices; in a comprehensive examination of his names, Merrill (1949) reduced many generic names to synonymy, but others were too cryptic to be resolved. Manitz (1974, 1976) typified some generic names of Rafinesque in Convolvulaceae and this allowed further reductions to synonymy. Our own study showed that there are several Rafinesque generic names that could, depending on how they are typified now, refer to *Merremia s.l.* Two of Rafinesque's names are applied here to clades recognized in the molecular study (Simões *et al.*, 2015) and a suitable morphological diagnosis has been prepared for them. Rafinesque's own diagnoses, often comprising only a few words and quite vague, technically meet the requirements of the ICN (McNeill *et al.*, 2012), but are not infrequently completely inadequate for recognizing the plants involved.

HOMOPLASY AND DIAGNOSTIC CHARACTERS

The high levels of homoplasy present in Convolvulaceae have long been a source of debate among taxonomists working on the family. Characters selected as diagnostic for generic or sectional rank often present exceptions at the species level, due to what has been called a mosaic pattern of evolution (Austin, 1998), in which a given character state shows reversal or is exceptionally derived, for example as an adaptation to extreme habitat conditions. *Merremia s.l.*, in particular, has been the subject of different sectional classifications (Hallier, 1893; O'Donell, 1941; Ooststroom, 1939; Ooststroom & Hoogland, 1953), themselves not in complete agreement, depending on which characters were selected to be diagnostic and which species were considered to have the 'exceptions'. It has been found that such sections agree to some extent with the monophyletic groups recovered by Simões *et al.* (2015), but it is evident that relying on morphology alone for classifying *Merremia* and its allied genera has not been enough to identify diagnostic characters for the taxonomic groups (genera or sections) unequivocally.

Molecular phylogenetic data (Simões *et al.*, 2015) have provided robust hypotheses of evolutionary relationships between species and helped tease apart synapomorphic characters from autapomorphies. The present classification focuses on synapomorphies as diagnostic characters for the genera and accommodates autapomorphies as 'exceptions'. Thus, the evolutionary perspective on the classification of the group allows a much less equivocal and more stable generic delimitation than has been achieved before, due to the mosaic nature of morphological evolution in this family. An effort has here been made to simplify the characterization of each genus, basing it on the main synapomorphies discovered, and where autapomorphies are present in the genus, they are noted and discussed.

TAXONOMIC TREATMENT

The following key has been prepared to aid in recognition of the several genera formerly included in tribe Merremieae.

Key to the genera

- 1a. Inflorescence capitate, with involucre of bracts; corolla vivid yellow; anthers spirally twisted at dehiscence.....1. *Daustinia*
- 1b. Without this combination of characters.....2.
- 2a. Leaves simple, entire.....3.
- 2b. Leaves lobed, parted, divided or compound.....9.
- 3a. Style gynobasic; ovary deeply four-lobed; fruits four (or fewer) free nutlets on woody receptacle.....10. *Remirema*
- 3b. Style terminal; ovary entire, unlobed; fruits capsules, utricles or berry-like.....4.
- 4a. Inflorescence peduncle with two (or more) persistent foliose bracts; ovary and fruit hairy.....5. *Hewittia*
- 4b. Without this combination of characters.....5.
- 5a. Fruit an operculate capsule: a leathery exocarp that falls off like a lid and a brittle endocarp that shatters irregularly.....8. *Operculina p.p.*
- 5b. Fruits valvate capsules or indehiscent, berry-like.....6.
- 6a. Stems with two firm outgrowths (paired auricles) at nodes.....9. *Camonea*
- 6b. Stems lacking outgrowths.....7.
- 7a. Lianas or large herbaceous twiners; anthers strongly spiralling at dehiscence; capsules delaminating above middle so lower half is dark brown, upper half is straw-yellow, or indehiscent, berry-like, blackish3. *Decalobanthus*
- 7b. Herbaceous creepers or small twiners; anthers slightly curving at the apex or not at all twisting in dehiscence; capsules not delaminating, unicolourous.....8
- 8a. Corolla campanulate, often gibbous on one side, without a maroon throat. Sepals obtuse, rounded, emarginate, never sharp-pointed. Pollen tricolpate.....2. *Merremia s.s.*
- 8b. Corolla funnelform, often with a maroon centre. Sepals attenuate-acuminate, forming a sharp point. Pollen pantoporate.....7. *Xenostegia p.p.*
- 9a. Sepal margins serrate or spinose-dentate; fruit indehiscent, a one-seeded utricle.....6. *Hyalocystis*
- 9b. Sepal margins entire; fruit a dehiscent capsule with four (or fewer) seeds.....10.
- 10a. Fruit an operculate capsule: a leathery exocarp that falls off like a lid and a brittle endocarp that shatters irregularly.....8. *Operculina p.p.*
- 10b. Fruit a four-valved capsule.11.

- 11a. Leaves shallowly three-lobed or three-angled (often with entire leaves on same plant); seeds hairy.....2. *Merremia s.s.*
- 11b. Leaves pinnately divided or palmately compound or five- or seven-lobed, -parted or -divided; seeds glabrous.....12.
- 12a. Leaves palmately compound or five- to seven-lobed, -parted or -divided. Anthers spirally twisting at dehiscence. Calyx greatly accrescent in fruit. Pollen tricolpate or 12-colpate.....4. *Distimake*
- 12b. Leaves pinnately divided. Anthers not spirally twisted at dehiscence. Calyx not or only slightly accrescent in fruit. Pollen pantoporate.....7. *Xenostegia p.p.*

1. *Daustinia* Buril & Simões, *Phytotaxa* 197: 60. 2015. Type: *D. montana* (Moric.) Buril & Simões.

Diagnostic characters: Climbing or rarely prostrate shrubs; the entire plant pubescent to velutinous, with simple trichomes; leaf margins often strongly serrate to dentate, more rarely serrulate or entire; inflorescences capitate, with involucre of overlapping bracts; corolla bright yellow, glabrous; stigma biglobular; anthers spirally twisting at dehiscence; pollen tricolpate; fruit four-valved chartaceous capsule; seeds glabrous.

Distribution. Endemic to Brazil (Fig. 10A).

Species included. *Daustinia montana* (Moric.) Buril & Simões.

2. *Merremia* Dennst. ex Endl., *Gen. Pl. Suppl.* 1: 1403. 1841. nom. cons., *sensu stricto*. Type: *Merremia hederacea* (Burm. f.) Hallier f.
= *Skinneria* Choisy, *Mém. Soc. Phys. Genève* 6: 487 [Conv. Or. 105]. 1834.
= *Merremia* section *Skinneria* (Choisy) Hallier f., *Bot. Jahrb. Syst.* 16: 552. 1893.

Diagnostic characters: Prostrate or twining herbs; leaves simple, entire or shallowly three-lobed or three-angled, often variable in shape; flowers small, corolla campanulate, often gibbous on one side, glabrous outside, drying with dark veins in the mid-petaline bands; anthers longitudinally dehiscing with the apex slightly curving or spirally dehiscing; ovary glabrous (in some species pubescent); fruit a chartaceous four-valved capsule, calyx not accrescent in fruit, exocarp not delaminating; seeds trigonous, pollen tricolpate, glabrous or puberulent (Fig. 2).

Distribution: Widespread in the Old World Tropics with the greatest number of species in Asia (Fig. 3); ten species.

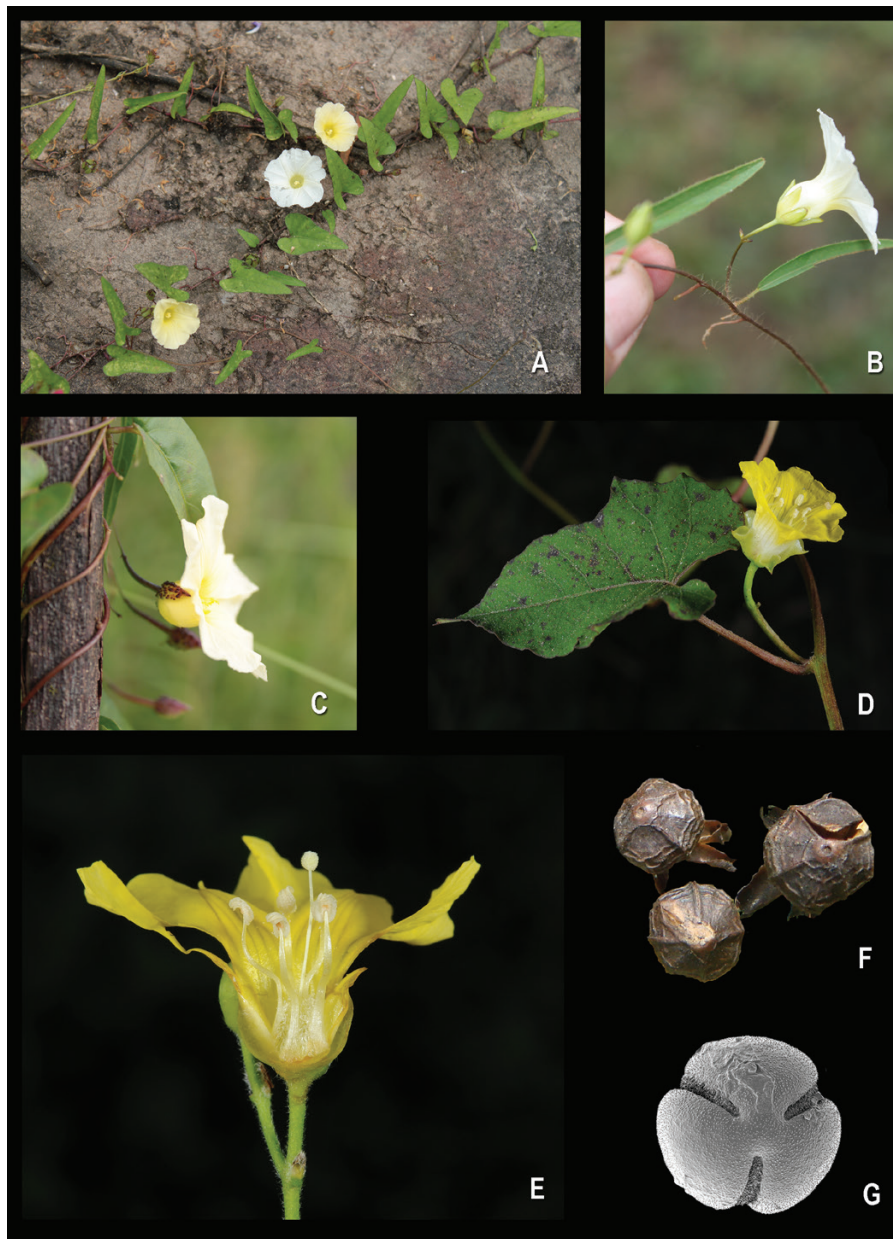


Figure 2. Main morphological characters of *Merremia*. (A) *Merremia hirta*, herbaceous creeper; leaf blades simple, entire; corolla colour polymorphism from white to pale yellow (Photograph: A. R. Simões); (B) *M. hirta*, small-sized flower, side view, showing radially symmetrical corolla (Photograph: A. R. Simões); (C) *M. verruculosa*, side view, showing a gibbous corolla (Photograph: A. R. Simões); (D) *M. hederacea*, showing anthers longitudinally dehiscent with slightly curved apex (Photograph: P. Karaket); (E) *M. hederacea*, dissected corolla showing androecium and gynoecium (Photograph: P. Karaket); (F) *M. hederacea*, fruits four-valved capsules with entire, not delaminating, fruit wall and persistent, reflexed calyx (Photograph: P. Traiperm); (G) *M. verruculosa*, tricolpate pollen. Voucher information: (A) not vouchered; (B) Cambodia, Simões *et al.* 34 (BM); (D, E) Thailand, Staples *et al.* 1319 (BKF); (F) Laos, Staples *et al.* 1513 (HNL); (C, G) Cambodia, Simões *et al.* 30 (BM).

Species included: *Merremia aniseiifolia* Ooststr.; *M. dichotoma* Ooststr.; *M. gemella* (Burm. f.) Hallier f.; *M. hainanensis* H.S.Kiu, *Merremia hederacea* (Burm. f.) Hallier f.; *M. hirta* (L.) Merr.; *M. incisa* (R.Br.) Hallier f.; *M. subsessilis* (Courchet & Gagnep.) T.N.Nguyen; *M. thorelii* (Gagnep.) Staples; *M. verruculosa* S.Y.Liu.

3. *Decalobanthus* Ooststr., *Blumea* 2: 99. 1936, **here expanded** – Type: *D. sumatranus* Ooststr. = *Merremia* section *Wavula* Ooststr., *Blumea* 3: 266. 1939. = *Merremia* section *Hailale* Hallier f., *Bot. Jahrb.* 49: 379. 1913.

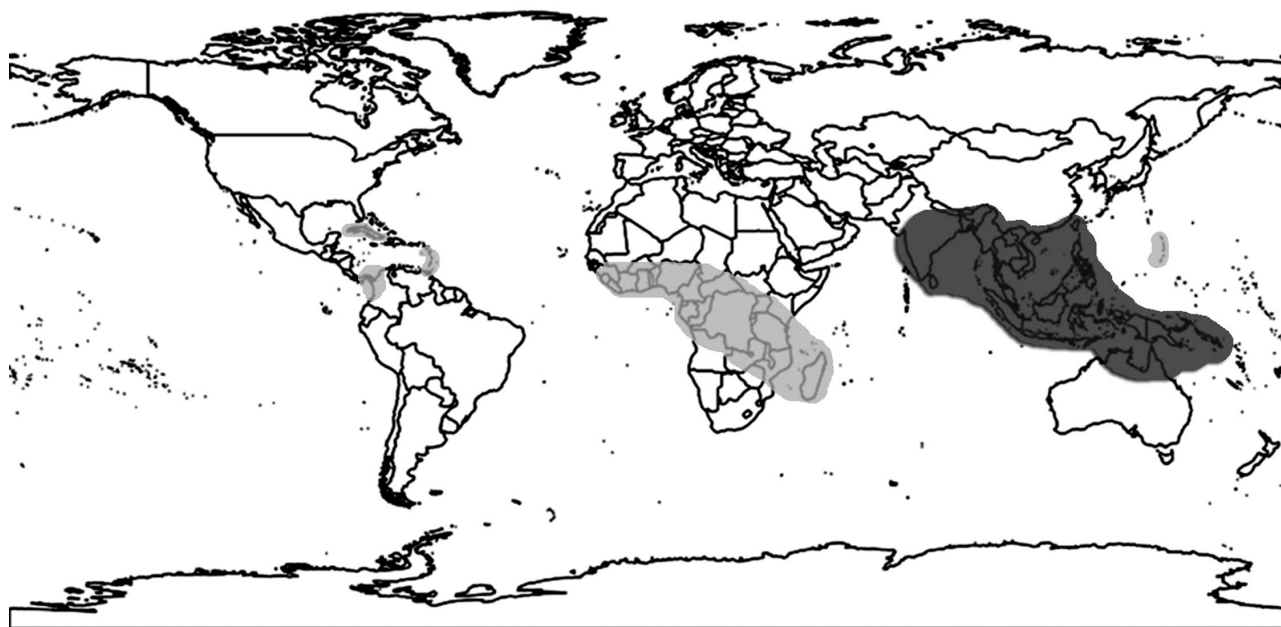


Figure 3. Distribution of *Merremia* s.s. Dark colour indicates the core distribution of the genus; distribution of its most widespread species, *M. hederacea*, is highlighted in grey colour.

Diagnostic characters: Woody lianas or large herbaceous climbers, stems twining; leaves simple, entire; inflorescences paniculate or corymbiform, the lowermost bract often foliaceous; sepals strongly convex (boat-shaped); corolla usually glabrous outside on mid-petaline bands (rarely sparsely sericeous or completely sericeous); anthers spirally twisted at dehiscence; pollen tricolpate, fruits usually valvate capsules with the exocarp delaminating above the middle (lower half is dark brown, upper half is straw-coloured), rarely dry indehiscent berries; seeds always pubescent, often with long golden hairs either covering the entire surface or concentrated along the edges of the seeds (Fig. 4).

Distribution: In Southeast Asia, throughout Malesia and extending eastward into the tropical Pacific; one species, *D. peltatus*, is distributed from Zanzibar and Madagascar throughout the Indo-Pacific to the Pacific Islands (Fig. 5); 12 species.

Species included: *Decalobanthus sumatranus* Ooststr.

New combinations

Decalobanthus bimbim (Gagnep.) Simões & Staples, **comb. nov.** \equiv *Merremia bimbim* (Gagnep.) Ooststr. \equiv *Ipomoea bimbim* Gagnep., Notul. Syst., Paris 3: 140. 1915. – Type: [Vietnam] Tonkin, ‘prov. de Hanoi, vers Vo-xa’, *Abbé Bon 2700* (holotype P!; isotype P!).

Decalobanthus boisianus (Gagnep.) Simões & Staples, **comb. nov.** \equiv *Merremia boisiana* (Gagnep.) Ooststr. \equiv *Ipomoea boisiana* Gagnep., Notul. Syst. (Paris) 3: 141. 1915. Type: Laos, near ‘Ken-trap’ [Cahn trap], *Spire 1049* (syntype P!); [Vietnam] Tonkin, ‘montagnes du Caï Kinh, route de Than Mai à Van Linh’, *Bois 138* (syntype P!); Country unknown. ‘du Mékong à Hué’ *Harmand 1827* (syntype P!).

var. ***fulvopilosus*** (Gagnep.) Simões & Staples, **comb. nov.** \equiv *Merremia boisiana* (Gagnep.) Ooststr. var. *fulvopilosa* (Gagnep.) Ooststr. \equiv *Ipomoea boisiana* Gagnep. var. *fulvopilosa* Gagnep., Notul. Syst. (Paris) 3: 142. 1915. Type: Vietnam, Tonkin méridional, in regione Lac Thô, *Bon 4801* (holotype P!; isotype P!).

var. ***sumatranus*** (Ooststr.) Simões & Staples, **comb. nov.** \equiv *Merremia boisiana* (Gagnep.) Ooststr. var. *sumatrana* Ooststr., Blumea 3: 344. 1939. Type: Indonesia, Sumatera, East coast, Sibolangit, in nature reserve, Feb. 1917, *Lörzing 4723* [holotype L; isotype BO ($\times 3$)!].

Decalobanthus borneensis (Merr.) Simões & Staples, **comb. nov.** \equiv *Merremia borneensis* Merr., Univ. Calif. Publ. Bot. 15: 260. 1929. Type: Malaysia, Sabah, Tawau district, *Elmer 20990* (syntypes A!, BISH!, F!, G!, GH!, K!, L!, M!, MO!, NY!, P!, SING!, U!).

Decalobanthus bracteatus (P.S.Bacon) Simões & Staples, **comb. nov.** \equiv *Merremia bracteata* P.S.Bacon, Bot. J. Linn. Soc. 84(3): 259 1982. Type:

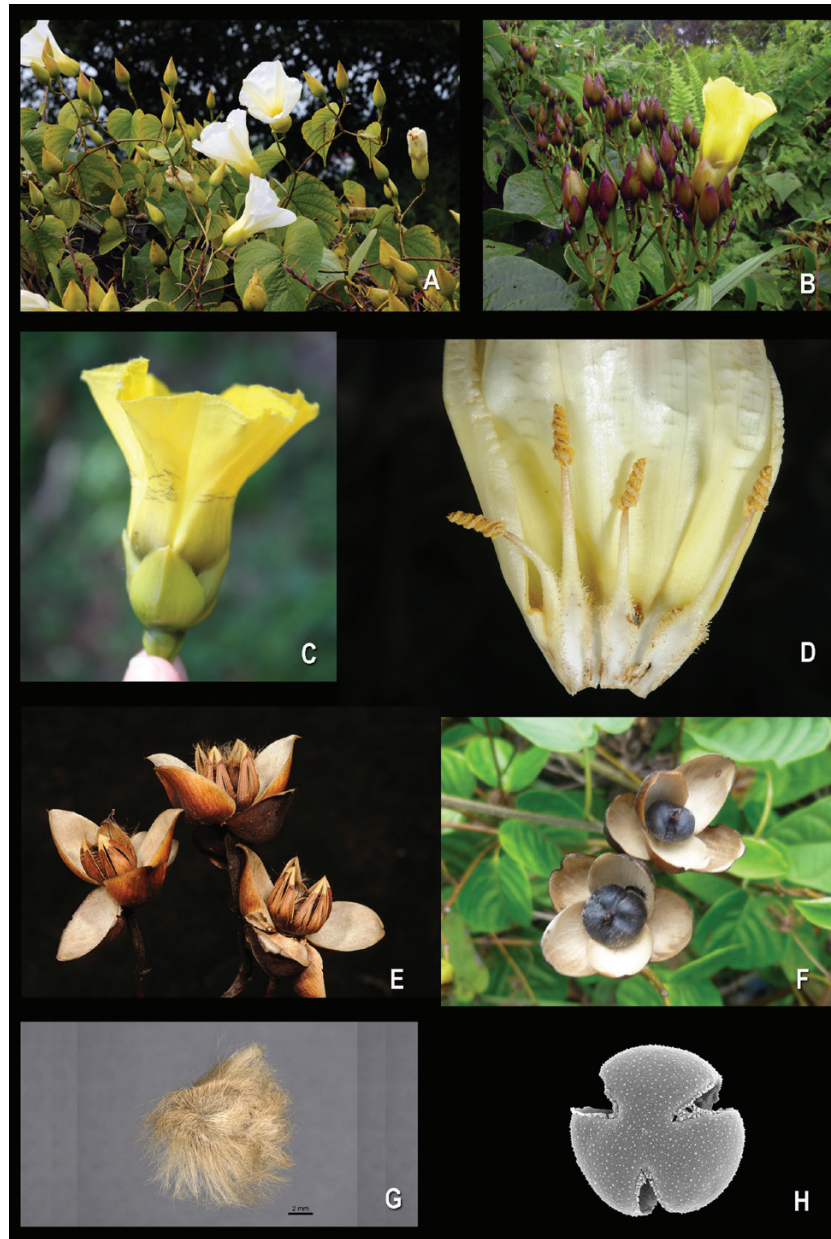


Figure 4. Main morphological characters of *Decalobanthus*. (A) *Decalobanthus mammosus*, lianoid habit; simple, entire leaves; large flowers (Photograph: P. Karaket); (B) *D. borneensis*, inflorescence corymbiform, many-flowered (Photograph: G. Staples); (C) *D. peltatus*, calyx strongly convex, sepals boat-shaped (Photograph: A. R. Simões); (D) *D. mammosus*, dissected corolla showing strongly spirally twisted anther dehiscence (Photograph: P. Karaket); (E) *D. mammosus*, fruit showing apical delamination of epicarp resulting in bicoloured fruit wall; persistent, accrescent calyx; secondary tears in capsule valves (Photograph: P. Karaket); (F) *D. borneensis*, indehiscent fruit with more than four seeds and persistent, accrescent calyx (Photograph: G. Staples); (G) *D. korthalsianus*, seed densely pubescent with long golden hairs covering the entire surface (Photograph: A. R. Simões); (H) *D. mammosus*, tricolpate pollen. Voucher information: (A, D, H) Thailand, *Staples et al. 1336* (BM); (B) Malaysia, Sabah, *Sugau et al. SAN-152887* (SAN); (C) not vouchered; (E) Thailand, *Staples et al. 1322* (BKF); (F) Malaysia, Sabah, *Sugau et al. SAN-152865* (SAN); (G) Indonesia, Kalimantan, *Arifin Z. BRF 1812* (L).

Solomon Islands. Kolombangara, roadside brush near Poitete forestry camp, *Bacon 2* (holotype K!; isotype BSIP, L!).

Decalobanthus eberhardtii (Gagnep.) Simões & Staples, **comb. nov.** \equiv *Merremia eberhardtii* (Gagnep.) T.N.Nguyen \equiv *Ipomoea eberhardtii*

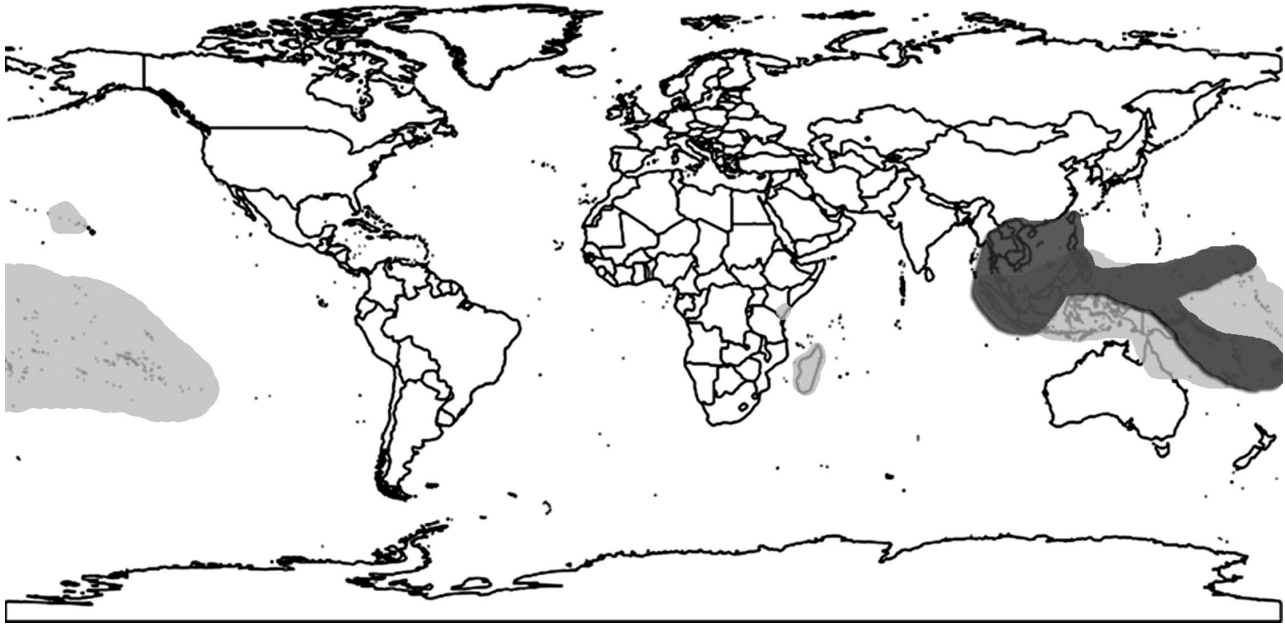


Figure 5. Distribution of *Decalobanthus*. Dark colour indicates the core distribution of the genus; distribution of its most widespread species, *D. peltatus*, is highlighted in grey colour.

Gagnep., Notul. Syst. (Paris) 3: 145. 1915. Type: [Vietnam.] Annam, Thua-thien, à Lang Cò, Eberhardt 1708 (holotype P!; isotype P!).

Decalobanthus elmeri (Merr.) Simões & Staples, **comb. nov.** \equiv *Merremia elmeri* Merr., Univ. Calif. Publ. Bot. 15: 261. 1929. Type: Malaysia. Sabah, Tawau district, A.D.E. Elmer 20396 (syntypes A[\times 2]!, B!, BISH!, BO!, F!, G!, L!, M!, MO!, NY!, PNH!, SING!, U!).

var. *glaberrimus* (Ooststr.) Simões & Staples, **comb. nov.** \equiv *Merremia elmeri* Merr. var. *glaberrima* Ooststr., Blumea 3: 359. 1939. Type: Indonesia. [Kalimantan, Kalimantan Barat] 'W. Division, Sungai Saniai' [actually Sungai Kenepai], 1893–94, Hallier 3370 (holotype L!; isotypes BO!, K!, L!, P!, SAR!).

Decalobanthus korthalsianus (Ooststr.) Simões & Staples, **comb. nov.** \equiv *Merremia korthalsiana* Ooststr., Bull. Misc. Inform. Kew 175. 1938. Type: [Indonesia. Kalimantan Selatan] 'Borneo, S. & E. Divisions, Doesoen', Korthals 237 (holotype, on two sheets, L!).

Decalobanthus mammosus (Lour.) Simões & Staples, **comb. nov.** \equiv *Merremia mammosa* (Lour.) Hallier f. \equiv *Convolvulus mammosus* Lour., Fl. Cochinchin. 108. 1790. Type: [icon] Rumphius, Herb. Amboin. 5: 370. t. 131. 1747 (lectotype, designated here).

Decalobanthus pacificus (Ooststr.) Simões & Staples, **comb. nov.** \equiv *Merremia pacifica* Ooststr., Blumea 3: 263. 1939. Type: Fiji. Vanua Levu, Mbua, Mt. Seatura, A.C. Smith 1690 (holotype BISH!; isotypes GH!, K!, L!, NY!, P!).

Decalobanthus peltatus (L.) Simões & Staples, **comb. nov.** \equiv *Merremia peltata* (L.) Merr. \equiv *Convolvulus peltatus* L., Sp. Pl. 1194. 1753. Type: [icon] 'Convolvulus laevis Indicus major' in Rumphius, Herb. Amboin. 5: 428, t. 157. 1747 (lectotype).

Decalobanthus pulchrus (Ooststr.) Simões & Staples, **comb. nov.** \equiv *Merremia pulchra* Ooststr., Blumea 3: 348. 1939. Type: [Brunei. Brunei Muara district] Brunei Bay, G.K. Gns 14 (holotype SING!).

Decalobanthus similis (Elmer) Simões & Staples, **comb. nov.** \equiv *Merremia similis* Elmer, Leaflet. Philipp. Bot. 1: 335. 1908. Type: Philippines. Leyte, Palo, A.D.E. Elmer 7341 (holotype PNH!; isotypes E!, G!, K!, NY!).

4. ***Distimake*** Raf., Fl. Tellur. 4: 82. 1838, **here expanded.** Type: *D. glaber* Raf. (lectotype, designated here) [= *Merremia macrocalyx* (Ruiz & Pavon) O'Donnell]

= *Astromerremia* Pilg., Notizbl. Bot. Gart. Berlin-Dahlem 13: 107. 1936.

= *Davenportia* R.W. Johnson, Austrobaileya 8(2): 171–176. 2010.

Diagnostic characters: Robust herbaceous climbers (rarely lianas or erect shrubs); leaves usually five- to seven-palmately lobed or compound (rarely simple or reduced to scales); calyx mostly with flat sepals (not convex) appressed to the corolla tube base, accrescent in fruit; corolla often white or pale yellowish, with or without a dark red centre, entirely glabrous, drying

with dark lines in mid-petaline bands; anthers spirally dehiscent; pollen trizonocolpate (12-zonocolpate in *D. tuberosus* and *D. quinatus*) fruit usually a four-valved capsule, calyx greatly accrescent in fruit, later the sepals reflexing; seeds glabrous (less commonly shortly velvety puberulent with dehiscent hairs) (Fig. 6).

Distribution: Widespread in tropical America and tropical Africa with disjunct species in Asia and northern Australia (Fig. 7); 35 species, with more possibly to be described.

Discussion: Molecular sampling did not include *M. macrocalyx*, which is conspecific with *Distimake*



Figure 6. Main morphological characters of *Distimake*. (A) *Distimake macrocalyx*, corolla white, calyx with sepals appressed to the base of the corolla tube (Photograph: F. Petrongari); (B) *D. aff. cissoides*, pale yellow corollas with a dark centre (Photograph: G. Staples); (C) *D. tuberosus*, leaf seven-palmately lobed (Photograph: G. Staples); (D) *D. aegyptius*, leaf five-palmately compound (Photograph: G. Staples); (E) *D. macrocalyx*, anthers strongly spirally dehiscent (Photograph: J. Lourenço); (F) *D. macrocalyx*, anthers strongly spirally dehiscent and biglobose stigma, view from above (Photograph: J. Lourenço); (G) *D. dissectus*, four-valved dehiscent capsule with entire (not delaminating) fruit wall and accrescent, persistent calyx, seeds glabrous (Photograph: S. Knees); (H) *D. tuberosus*, tardily dehiscent capsule with entire fruit wall and accrescent, persistent calyx (Photograph: G. Staples); (I) *D. aureus*, tricolpate pollen. Voucher information: (A) not vouchered; (B) Brazil, Pernambuco, Delgado *et al.* 807 (PEUFR, SP); (C) not vouchered; (D) USA, Hawaii, Staples 1565 (BISH); (E, F) Brazil, Pernambuco, Staples *et al.* 1710 (PEUFR); (G) not vouchered; (H) USA, Hawaii, Staples 1398 (SING); (I) Mexico, Brandegee 392 (GH).

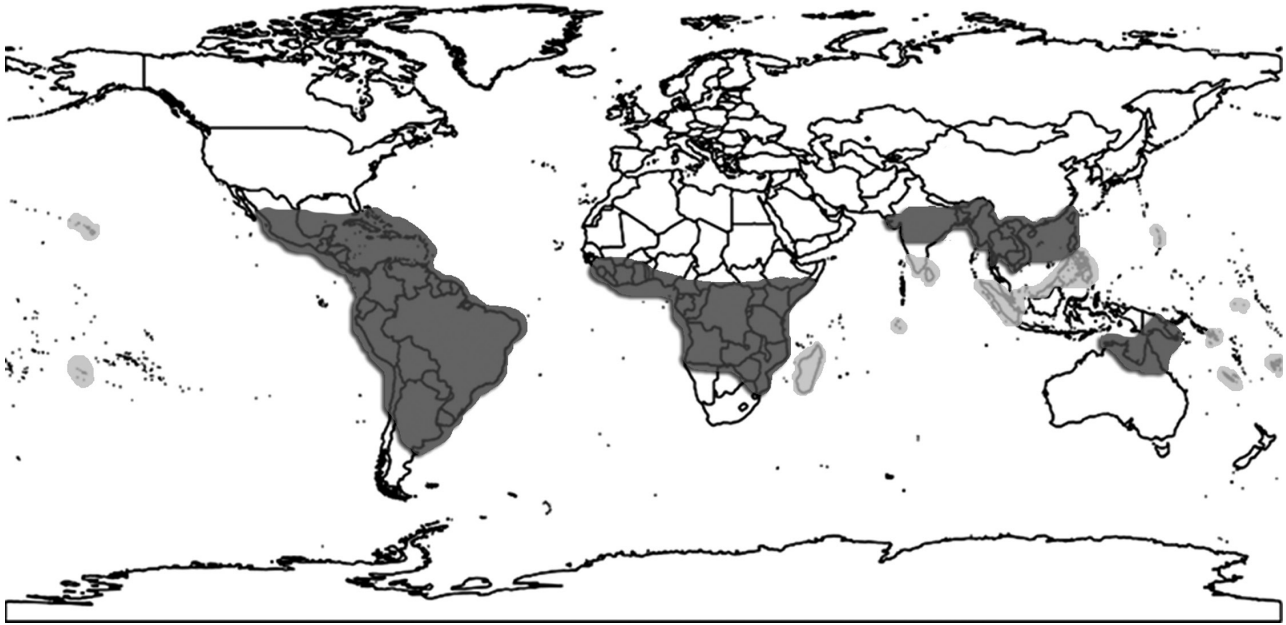


Figure 7. Distribution of *Distimake*. Dark colour indicates the core distribution of the genus; distribution of the widespread species, *D. cissoides*, *D. dissectus*, *D. quinquefolius* and *D. tuberosus*, is highlighted in grey colour.

glaber, the type species for Rafinesque's genus. We can confidently place *M. macrocalyx* in *Distimake* based on our own morphological study of this species and the last revision of tropical American *Merremia* (O'Donell, 1941). Rafinesque's (1838: 82) etymology '(2 ac. stig.)' for this genus name is too cryptic for a clear interpretation, but the name seems to refer to the biglobose stigma. Concerning the formation of epithets, the gender of Rafinesque's genus name *Distimake* is not stated and the single name combined in it (*D. glaber*) is in the masculine form. According to Article 62 of the ICN (McNeill *et al.*, 2012), new names or combinations should take the same gender that the original author adopted and therefore a masculine gender is appropriate. Accordingly, all new combinations below have been formed with masculine endings.

New combinations

Distimake aegyptius (L.) Simões & Staples, **comb. nov.** ≡ *Merremia aegyptia* (L.) Urb. ≡ *Ipomoea aegyptia* L., Sp. Pl. 162. 1753. Type: 'America calidiore', *Herbar. Linn.* No. 218.35 (lectotype, LINN!).

Distimake ampelophyllus Simões & Staples, **comb. nov.** ≡ *Merremia ampelophylla* Hallier f., Bot. Jahrb. Syst. 18: 115. 1893. Type: Kenya. Machakos district, Ulu, *Fischer 412* (holotype B[†], no duplicates found). Kenya. Machakos district, Kiambere, *Kirrika 152* (neotype EA; isoneotype K!).

Distimake aturensis (Kunth) Simões & Staples, **comb. nov.** ≡ *Merremia aturensis* (Kunth) Hallier

f. ≡ *Convolvulus aturensis* Kunth in H.B.K., Nov. Gen. Sp. 3: 96. 1819. Type: Venezuela. Amazonas, Atures Rapids, *Humboldt & Bonpland 852* (holotype B-W, image!).

Distimake aureus (Kellogg) Simões & Staples, **comb. nov.** ≡ *Merremia aurea* (Kellogg) O'Donell ≡ *Aniseia aurea* Kellogg, Proc. Calif. Acad. Sci. 5: 83. 1873. Type: [Mexico. Baja California Sur,] San Juan del Cabo, *Davidson s.n.* (holotype GH!).

Distimake austinii (J.A.McDonald) Simões & Staples, **comb. nov.** ≡ *Merremia austinii* J.A.McDonald, Brittonia 39: 106. 1987. Type: Mexico. Tamaulipas, c. 8 km W of Chamal Viejo on paved road between Limón and Ocampo, *J.A. McDonald 1832* (holotype MEXU; isotypes GH, K, NY!, TEX, US, WIS, XAL).

Distimake bipinnatipartitus (Engl.) Simões & Staples, **comb. nov.** ≡ *Merremia bipinnatipartita* (Engl.) Hallier f. ≡ *Ipomoea bipinnatipartita* Engl., Bot. Jahrb. Syst. 10: 246. 1889. Type: South Africa. 'Hereroland, Usakos', May 1886, *Marloth 1289* [holotype B[†]; isotypes K (×2)!, PRE, SAM].

Distimake cielensis (J.A.McDonald) Simões & Staples, **comb. nov.** ≡ *Merremia cielensis* J.A.McDonald, Syst. Bot. 33: 552. 2008. Type: Mexico. Tamaulipas, Municipio Gómez Farías, 2 km N of Ejido Alta Cima along road to San José, *Hernández 2991* (holotype TEX; isotypes ENCB, MEXU!).

Distimake cissoides (Lam.) Simões & Staples, **comb. nov.** ≡ *Merremia cissoides* (Lam.) Hallier f. ≡ *Convolvulus cissoides* Lam., Tabl. Encycl. 1: 462.

1793. Type: [French Guiana.] Cayenne, *Leblond s.n.* (holotype P-Lam, image!).
- Distimake contorquens*** (Choisy) Simões & Staples, **comb. nov.** ≡ *Merremia contorquens* (Choisy) Hallier f. ≡ *Ipomoea contorquens* Choisy in DC., Prodr. 9: 385. 1845. Type: Brazil. Minas Gerais, Serra do Cacarsa, *Martius s.n. sub Obs. 1007* (holotype M!; isotype M!).
- Distimake davenportii*** (F.Muell.) Simões & Staples, **comb. nov.** ≡ *Davenportia davenportii* (F.Muell.) R.W.Johnson ≡ *Merremia davenportii* (F.Muell.) Hallier f. ≡ *Ipomoea davenportii* F.Muell., Fragm. 6: 97. 1867. Type: Australia. [Northern Territory] Davenport Range, *D. Stuart s.n.* (holotype MEL; isotype K!).
- Distimake digitatus*** (Spreng.) Simões & Staples, **comb. nov.** ≡ *Merremia digitata* (Spreng.) Hallier f. ≡ *Gerardia digitata* Spreng., Syst. Veg. 2: 808. 1825. Type: Brazil, *Sello s.n.* (holotype B†; photograph F!, photograph GH!).
- Distimake dimorphophyllus*** (Verdc.) Simões & Staples, **comb. nov.** ≡ *Merremia dimorphophylla* (Verdc.) Sebsebe ≡ *Merremia semisagitta* subsp. *dimorphophylla* Verdc., Kew Bull. 24: 175. 1970. Type: Somali Republic. about 24 km SW of Burao, Arorih Plain, *Glover & Gilliland 531* (holotype K!; isotype EA).
- Distimake dissectus*** (Jacq.) Simões & Staples, **comb. nov.** ≡ *Merremia dissecta* (Jacq.) Hallier f. ≡ *Convolvulus dissectus* Jacq., Observ. Bot. 2: 4. tab. 28. 1767. Type: [icon] Jacquin's plate 28 (lectotype!).
- Distimake flagellaris*** (Choisy) Simões & Staples, **comb. nov.** ≡ *Merremia flagellaris* (Choisy) O'Donell ≡ *Ipomoea flagellaris* Choisy, Mém. Soc. Phys. Genève 8: 60 [Conv. Rar. 138] 1837. Type: Brazil. Bahia, *collector unknown s.n.* 'herb. Douville' (holotype G!).
- Distimake grandiflorus*** (Ooststr.) Simões & Staples, **comb. nov.** ≡ *Merremia grandiflora* Ooststr., Recueil Trav. Bot. Néerl. 30: 203. 1933. Type: Peru. Lima, railroad between San Bartolomé and Oroya, *Weberbauer 5218* [holotype B†; isotypes F (×2)!, GH!, U, US!].
- Distimake guerichii*** (A.Meeuse) Simões & Staples, **comb. nov.** ≡ *Merremia guerichii* A.Meeuse, Bothalia 7: 415. 1960. Type: Namibia. Kaokoveld, between Orupembe Waterhole and Kunene River, *De Winter & Leistner 5741* (holotype PRE; isotypes EA, K!, L, M, SRGH).
- Distimake hasslerianus*** (Chodat) Simões & Staples, **comb. nov.** ≡ *Merremia hassleriana* (Chodat) Hassler ≡ *Ipomoea hassleriana* Chodat, Bull. Herb. Boissier ser. II, 5: 693. 1905. Type: Paraguay. prope Igatimi, *Hassler 4692* [lectotype G, bar code G00175613!; isolectotypes BM!, G (×2)!].
- Distimake igneus*** (Schrad.) Simões & Staples, **comb. nov.** ≡ *Convolvulus igneus* Schrad., Gött. Gel. Anz. 1: 716. 5 May 1821. Type: Brazil, Bahia: caatinga Fazenda da Ladeira, Caxoeira, *Prince Maximilian von Wied 36* (syntypes BR!, GOET!). [The sample identified in Simões *et al.* (2015) as *Operculina flammea* belongs here. The nomenclature is complex and outside the scope of this paper; the relevant synonymy will be explicated fully in the revision of *Distimake*, now in preparation.]
- Distimake kentrocaulos*** (C.B.Clarke) Simões & Staples, **comb. nov.** ≡ *Merremia kentrocaulos* (C.B.Clarke) Hallier f. ≡ *Ipomoea kentrocaulos* C.B.Clarke, Fl. Brit. India 4: 213. 1883. Type: India, without locality, *Rottler s.n.* (syntype K!); *R. Wight Herbar. propr. 2279* [syntypes K (×2)!]; 'N.W. India' *Royle s.n.* (syntype K!).
- Distimake kimberleyensis*** (R.W.Johnson) Simões & Staples, **comb. nov.** ≡ *Merremia kimberleyensis* R.W.Johnson, Austrobaileya 8: 60. 2009. Type: Australia. Western Australia, Kachana Station, c. 40 km SE of Kununurra, *T. Handaside TH.95 KAC1* (holotype BRI!; isotypes BRI, PERTH).
- Distimake macdonaldii*** (S.Valencia & Mart. Gord.) Simões & Staples, **comb. nov.** ≡ *Merremia macdonaldii* S.Valencia & Mart. Gord., Anales Inst. Biol. Univ. Nac. Autón. México, Bot. 66: 108. 1995. Type: Mexico. Guerrero, Municipio Eduardo Neri, La Yesera, *M.R. Monroy de la Rosa 545* (holotype FCME; isotypes FCME, MEXU!, TEX).
- Distimake macrocalyx*** (Ruiz & Pav.) Simões & Staples, **comb. nov.** ≡ *Merremia macrocalyx* (Ruiz & Pav.) O'Donell ≡ *Convolvulus macrocalyx* Ruiz & Pav., Fl. Peruv. 2: 10. 1799. Type: Peru. Cuchero y Chinchao, *Ruiz & Pavon s.n.* (holotype MA; isotypes F, US).
- Distimake multisectus*** (Hallier f.) Simões & Staples, **comb. nov.** ≡ *Merremia multisecta* Hallier f., Bot. Jahrb. Syst. 18: 115. 1893. Type: Angola. Without locality, *Welwitsch 6112* (syntypes B†, COI, G, K!, LISU!, PRE).
- Distimake nervosus*** (Pittier) Simões & Staples, **comb. nov.** ≡ *Merremia nervosa* Pittier, J. Wash. Acad. Sci. 17: 286. 1927. Type: Venezuela. Lara, Cerro Gordo, circa de Barquisemeto, *J. Saer d'Hegeurt 294* (holotype VEN, image!).
- Distimake palmeri*** (S.Watson) Simões & Staples, **comb. nov.** ≡ *Merremia palmeri* (S.Watson) Hallier f. ≡ *Ipomoea palmeri* S.Watson, Proc. Amer. Acad. Arts 24: 63. 1889. Type: Mexico. Sonora, Guaymas, *E. Palmer 75* (holotype GH!; isotypes C!, US!).
- Distimake quercifolius*** (Hallier f.) Simões & Staples, **comb. nov.** ≡ *Merremia quercifolia* Hallier f., Bot. Jahrb. Syst. 18: 114. 1893. Type: Angola. Without locality, *Welwitsch 6172* (holotype G; isotypes COI, BM!, K!, LISU!).
- Distimake quinatus*** (R.Br.) Simões & Staples, **comb. nov.** ≡ *Merremia quinata* (R.Br.) Ooststr. ≡ *Ipomoea quinata* R.Br., Prodr. 486. 1810. Type: Australia, [Northern Territory] Arnheim N Bay, *R. Brown s.n.* [Iter Australiensis 2755] (lectotype BM!; isolectotypes E, K!, LINN-HS!, P).

Distimake quinquefolius (L.) Simões & Staples, **comb. nov.** \equiv *Merremia quinquefolia* (L.) Hallier f. \equiv *Ipomoea quinquefolia* L., Sp. Pl. 162. 1753. Type: [icon] '*Convolvulus quinquefolius glaber Americanus*' in Plukenet, Phytographia: t. 167, f. 6. 1692; Almag. Bot.: 116. 1696 (lectotype).

Distimake rhynchorrhizus (Dalzell) Simões & Staples, **comb. nov.** \equiv *Merremia rhynchorrhiza* (Dalzell) Hallier f. \equiv *Ipomoea rhynchorrhiza* Dalzell, Hooker's J. Bot. Kew Gard. Misc. 3: 179. 1851. Type: India. 'in montibus Syhadree, prope Tulkut-ghat' Dalzell s.n. [syntypes K ($\times 3$)!].

Distimake semisagittus (Griseb. ex Peter) Simões & Staples, **comb. nov.** \equiv *Merremia semisagitta* (Griseb. ex Peter) Dandy \equiv *Ipomoea semisagitta* Griseb. ex Peter in Engler & Prantl, Nat. Pflanzenfam. 4(3a): 31. 1891. Type: 'Arabia, in planitie deserti prope Djeddah [Jiddah]', Schimper [Unio Itinerare] 948 [proposed conserved type G-DC!; isotypes HBG!, K ($\times 2$)!, L, M, MO!, P ($\times 4$)!, WAG; Staples *et al.*, 2012].

Distimake somalensis (Hallier f.) Simões & Staples, **comb. nov.** \equiv *Merremia somalensis* Hallier f., Annuario Reale Ist. Bot. Roma 7: 226. 1898. \equiv *Convolvulus somalensis* Vatke, Linnaea 43: 517.

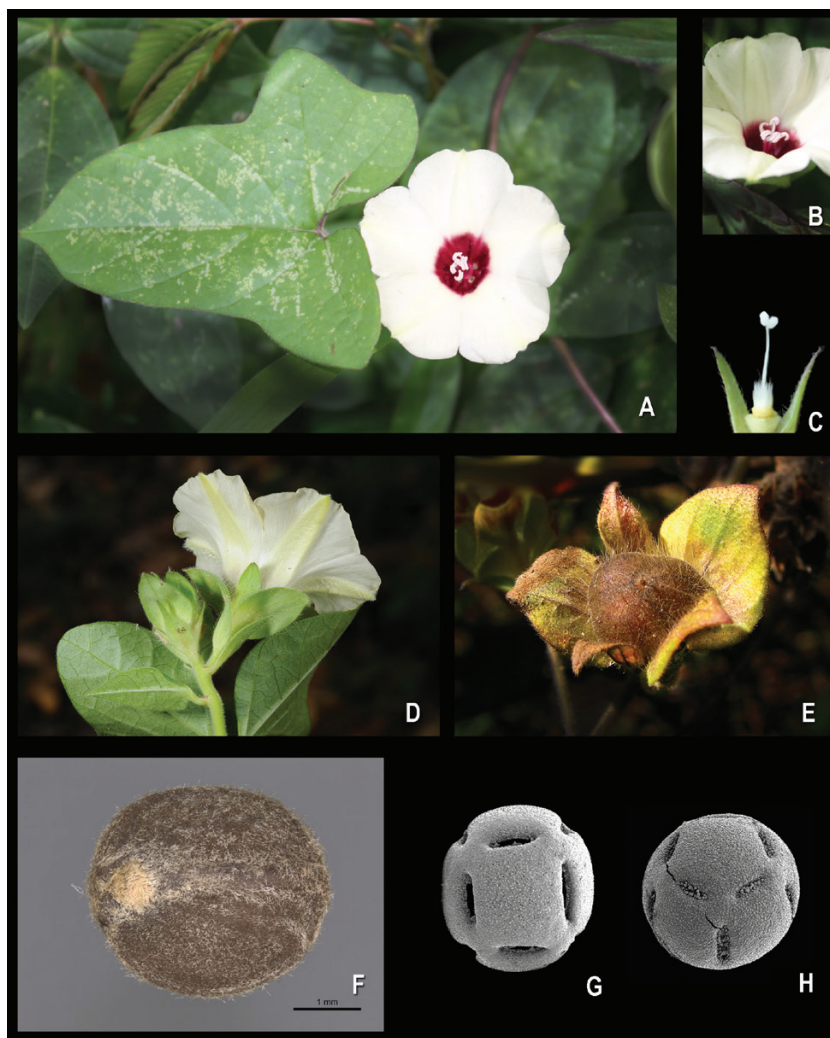


Figure 8. Main morphological characters of *Hewittia*. *H. malabarica*: (A) herbaceous habit, leaf shallowly trilobed, corolla pale yellow with distinct maroon centre (Photograph: A. R. Simões); (B) anthers longitudinally dehiscing with a curving apex (Photograph: A. R. Simões); (C) detail of gynoecium, showing stigmas ovoid-oblong and ovary densely pubescent (Photograph: A. R. Simões); (D) inflorescence peduncle with persistent foliaceous bracteoles inserted below the calyx, corolla with pilose mid-petaline bands (Photograph: P. Karaket); (E) fruit, showing densely pubescent fruit wall (Photograph: P. Suksathan); (F) seed scurfy with pubescent hilum; (G) 12-pantocolpate pollen; *H. puccioniana*: (H) 15-pantocolpate pollen. Voucher information: (A–D) Thailand, Staples *et al.* 1334 (BKF); (E) Thailand, Staples *et al.* 1393 (QBG); (F) not vouchered; (G) Jamaica, Gentry 28282 (K); (H) Somalia, Gillett, Hemming, Watson & Julin 25341 (K).

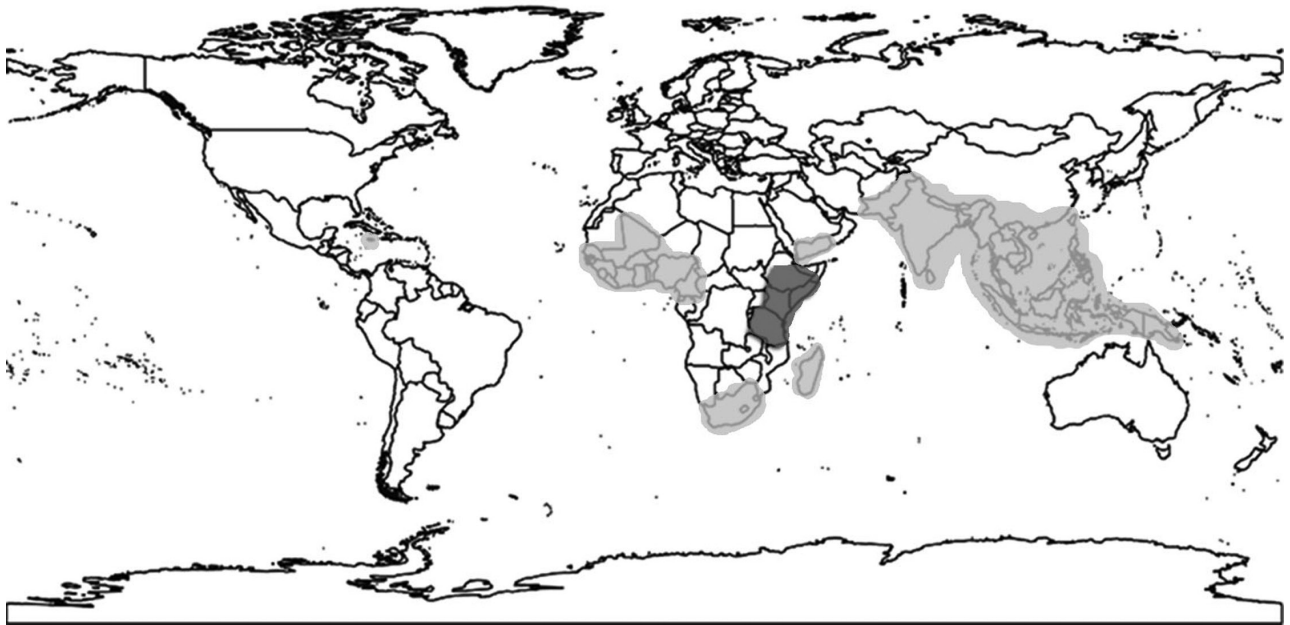


Figure 9. Distribution of *Hewittia*. Dark colour indicates the core distribution of the genus; distribution of its most widespread species, *H. malabarica*, is highlighted in grey colour.

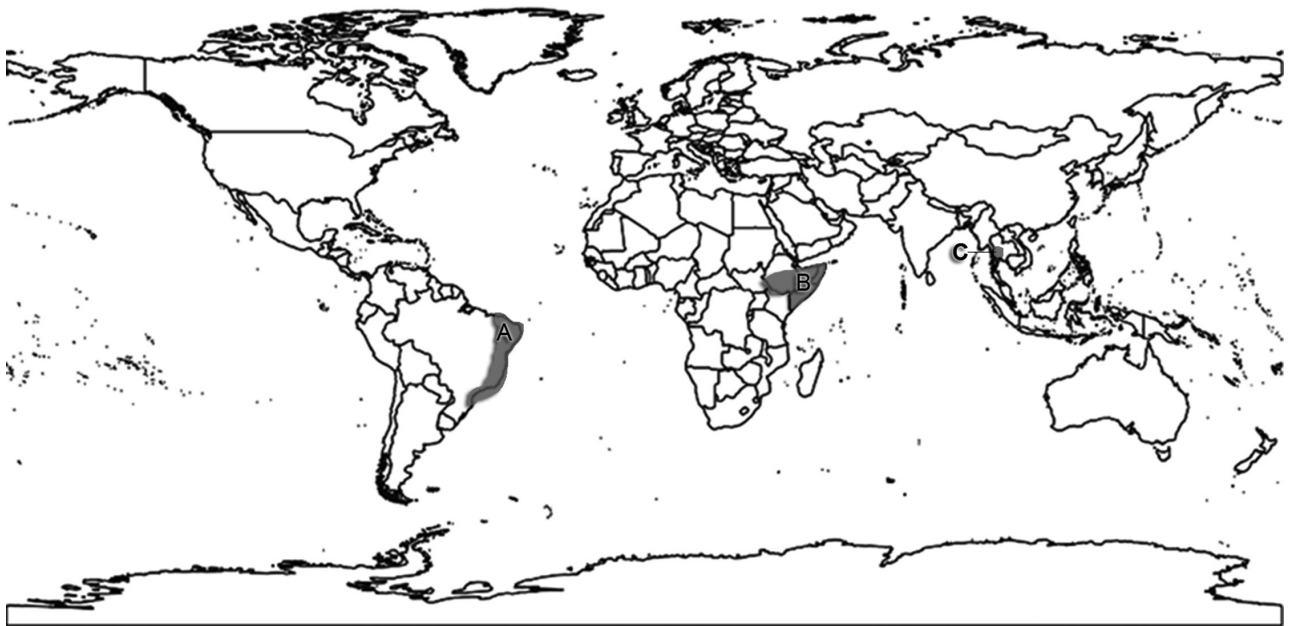


Figure 10. Distribution of (A) *Daustinia*, (B) *Hyalocystis* and (C) *Remirema*.

1881, *nom. illeg.* Type: Somali Republic, Wodderi, *Hildebrandt 883b* (holotype B[†]).

Distimake stellatus (Rendle) Simões & Staples, **comb. nov.** \equiv *Merremia stellata* Rendle, *J. Bot.* 46: 179. 1908. Type: Angola. SE at Kului, *Gossweiler 2906* (holotype BM!).

Distimake subpalmatus (Verdc.) Simões & Staples, **comb. nov.** \equiv *Merremia subpalmata* Verdc., *Kew Bull.* 13: 188. 1958. Type: Kenya. Northern Frontier Province, Wajir, *C.F. Hemming 451* (holotype EA; isotypes K!, PRE).

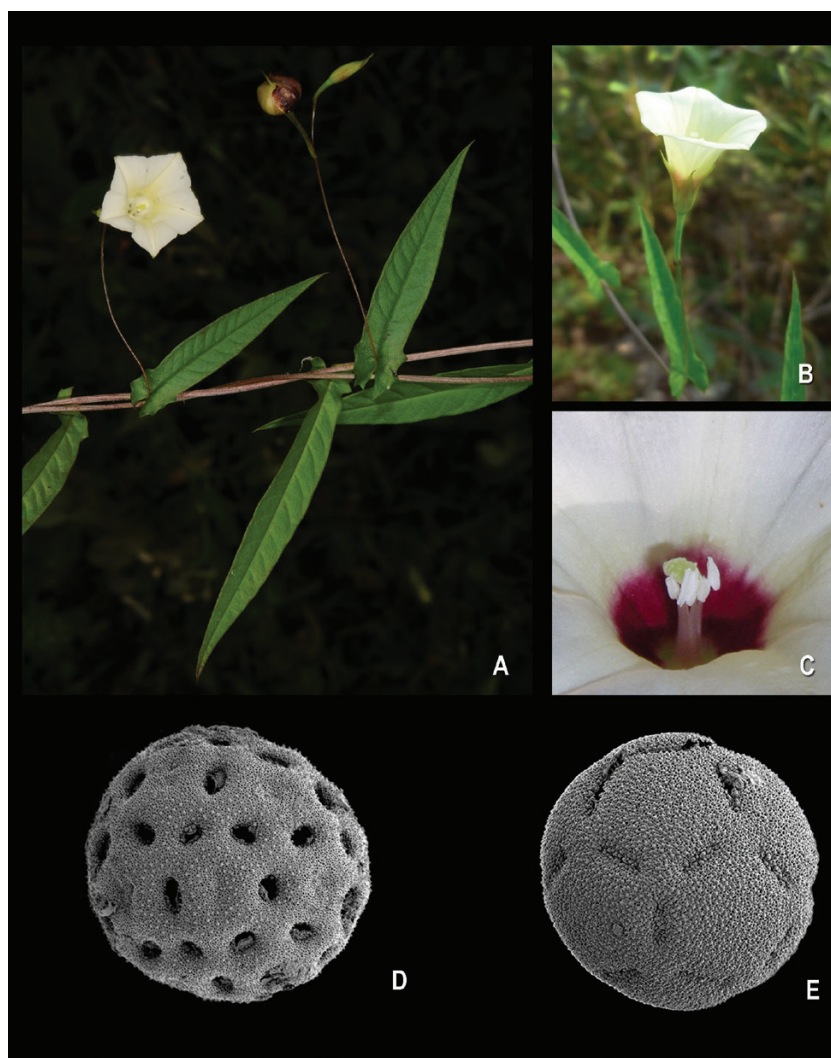


Figure 11. Main morphological characters of *Xenostegia*. *X. tridentata*: (A) twining, herbaceous habit; simple leaves with bases clasping stem and concolourous corolla (Photograph: P. Karaket); (B) calyx with slender attenuate sepal apices (Photograph: S. Syahida-Emiza); (C) bicolourous corolla; anthers longitudinally dehiscing (Photograph: M. Nuraliev); (D) pantoporate pollen (> 90 apertures). *X. pinnata*: (E) pantoporate pollen (c. 30 apertures). Voucher information: (A) Thailand, Staples *et al.* 1328 (BKF); (B) Malaysia, Syahida-Emiza *et al.* FRI-66072 (KEP); (C) Vietnam, not vouchered; (D) Thailand, Simões 41 (BM); (E) Moçambique, Torre 4997 (LISC).

Distimake ternifoliolus (Pittier) Simões & Staples, **comb. nov.** \equiv *Merremia ternifoliola* Pittier, Bol. Soc. Venez. Ci. Nat. 8: 142. 1943. Type: Venezuela. Guarico, Sabaneta de Santa Maria de Ipire, H. Pittier 14728 (holotype VEN, image!; isotype US).

Distimake tuberosus (L.) Simões & Staples, **comb. nov.** \equiv *Merremia tuberosa* (L.) Rendle \equiv *Ipomoea tuberosa* L., Sp. Pl. 160. 1753. Type: Jamaica, *Herb. Linn.* 219.4 (lectotype LINN!).

5. *Hewittia* Wight & Arnott, *Madras J. Lit. Sci.*, ser 1, 5: 22. 1837, nom. cons. Type: *Hewittia malabarica* (L.) Suresh.

= *Shutereia* Choisy *Mém. Soc. Phys. Genève* 6: 485 [Conv. Or. 103]. 1834, nom. rej.

Diagnostic characters: Twining or prostrate herbs; leaves simple, entire to angulate; inflorescence peduncle with two to many persistent foliaceous bracteoles inserted below the calyx; corolla yellow with a maroon centre and pilose mid-petaline bands; anthers longitudinally dehiscent, apex curved; pollen 12- or 15-pantoporate; stigmas biglobose or ovate-oblong, flattened; ovary densely pubescent; fruit a four-valved chartaceous capsule, pubescent, valves tardily splitting into

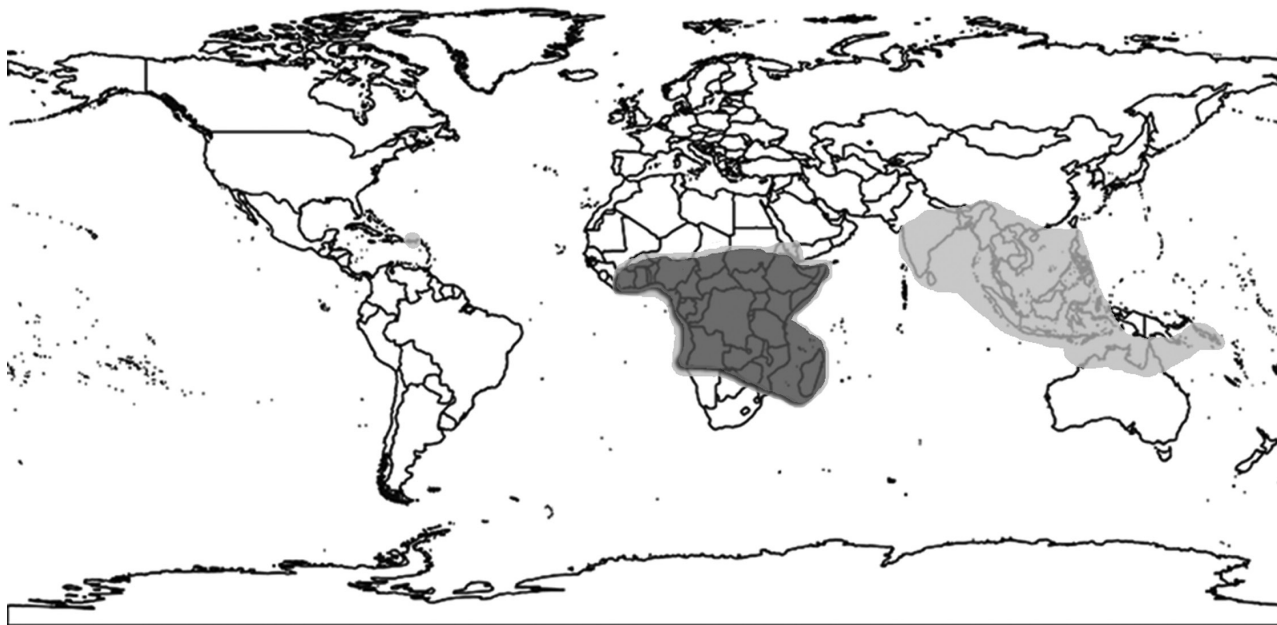


Figure 12. Distribution of *Xenostegia*. Dark colour indicates the core distribution of the genus; distribution of its most widespread species, *X. tridentata*, is highlighted in lighter colour.

multiple segments that remain coherent apically; seeds scurfy, hilum pubescent (Fig. 8).

Distribution: Widespread in Tropical Africa and Tropical Asia; also introduced in the Caribbean islands (Fig. 9); two species.

Species included: *Hewittia malabarica* (L.) Suresh; *H. puccioniana* (Chiov.) Verde.

6. *Hyalocystis* Hallier f., Ann. Ist. Bot. Roma 7: 227. 1898. Type: *Hyalocystis viscosa* Hallier f.

Diagnostic characters: Prostrate herbs; leaves entire to palmately seven-lobed, margins entire to spinose-dentate; sepal margins distinctly serrate or spinose-dentate; corolla with pilose mid-petaline bands; stigmas biglobular; ovary densely pubescent; anthers longitudinally dehiscent, apex curved; pollen 15-pantocolpate; fruit a papery, indehiscent, one-seeded utricle; seed glabrous.

Distribution: Ethiopia, Somalia (Fig. 10B); two species.

Species included: *Hyalocystis viscosa* Hallier f., *H. popovii* Verdc.

7. *Xenostegia* D.F.Austin & Staples, Brittonia 32: 533. 1980 (publ. 1981), **here expanded**. Type: *X. tridentata* (L.) D.F.Austin & Staples.
= *Merremia* section *Streptandra* (Griseb.) Hallier f., Bot. Jahrb. Syst. 18: 114. 1893.

Diagnostic characters: Slender twiners or prostrate herbs; stems angulate to narrowly winged; leaves simple, basally dentate or hastate to pinnately lobed; sepals long acuminate or emarginate and mucronate, entire, undulate or pinnately incised; corolla yellow to white, glabrous; anthers longitudinally dehiscent; pollen pantoporate; ovary densely pubescent (less often glabrous); fruit a four-valved chartaceous capsule; seeds completely glabrous (Fig. 11).

Distribution: Widespread in Eastern Africa, Madagascar, Tropical Asia and Australia (Fig. 12); five species.

Discussion: A revision of *Xenostegia* is currently in preparation (Simões *et al.*, in preparation), which addresses in greater detail the taxonomic intricacies of the specific and infraspecific delimitation in the genus.

Species included: *Xenostegia tridentata* (L.) D.F.Austin & Staples; *X. medium* (L.) D.F.Austin & Staples.

New combinations

Xenostegia alatipes (Dammer) Simões & Staples, **comb. nov.** = *Merremia alatipes* Dammer in Engler, Pflanzenw. Ost-Afrikas, C: 330. 1895. Type: [Tanzania.] Zanzibar, Amboni, *Holst* 2828

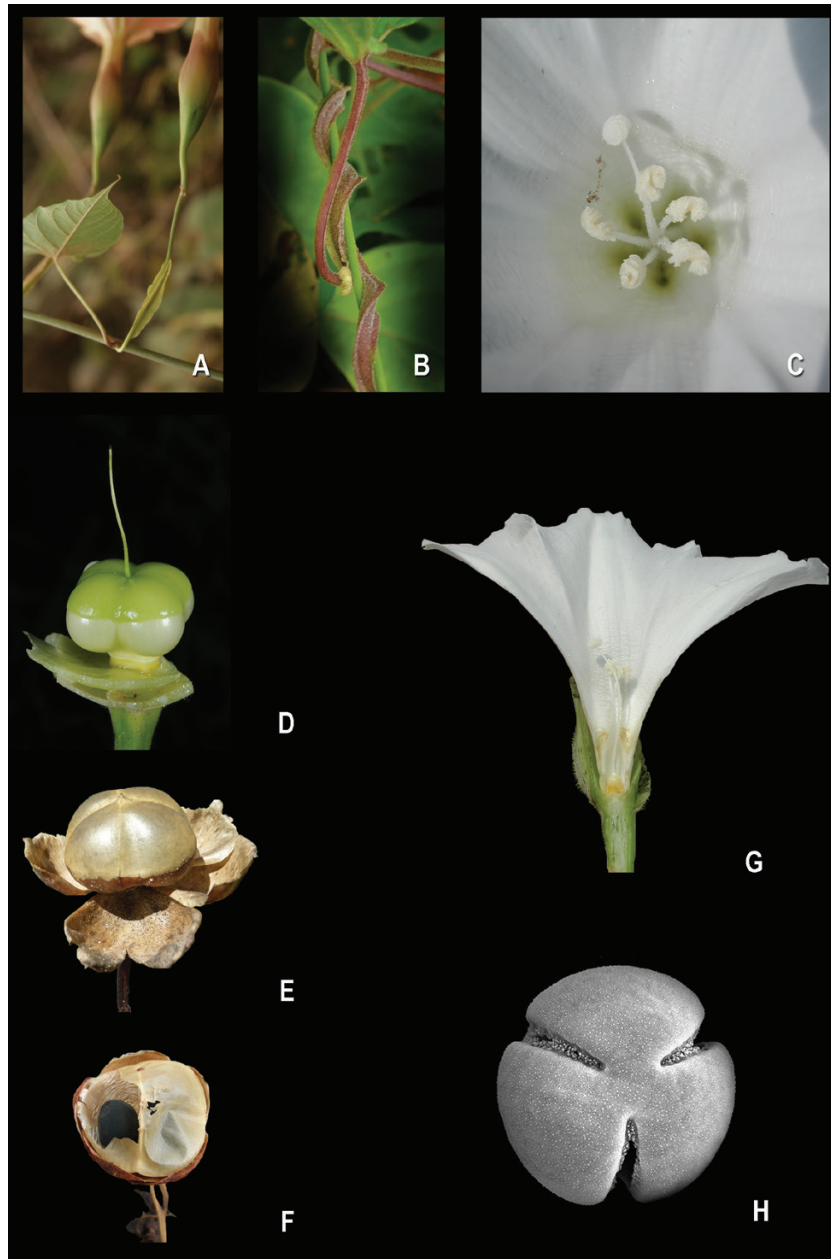


Figure 13. Main morphological characters of *Operculina*. (A) *Operculina pteripes*, winged peduncle (Photograph: André Moreira); (B) *O. turpethum*, herbaceous twiner with angled, winged stem (Photograph: P. Karaket); (C) *O. turpethum*, anthers spirally dehiscing and biglobose stigma (Photograph: M. Nuraliev); (D–F) fruit in developmental stages: (D) *O. turpethum*, immature fruit with operculum (exocarp) in place (Photograph: P. Karaket); (E) *O. macrocarpa*, mature fruit with operculum (exocarp) detached, brittle endocarp intact (Photograph: G. Staples); (F) *O. brownii*, mature fruit with brittle endocarp shattered, seeds exposed (Photograph: J.-F. Butaud); (G) *O. turpethum*, opened flower showing androecium, gynoecium with glabrous ovary and nectary disc (Photograph: M. Nuraliev); (H) *O. pteripes*, tricolpate pollen. Voucher information: (A) Brazil, MRV Zanatta & JEQ Faria 2005 (UB); (B, D) Thailand, Staples *et al.* 1332 (BKF); (C, G) not vouchered; (E) Brazil, Staples *et al.* 1656 (PEUFR); (F) French Polynesia, Nuku Hiva, Butaud & Jacq 1582 (PAP); (H) Venezuela, Williams & Alston 341 (BM).

(holotype B†, no duplicates found). Tanzania. Tanga district, H.G. Faulkner 2161 (neotype K!, designated here).

Xenostegia pinnata (Hochst. ex Choisy) Simões & Staples, **comb. nov.** ≡ *Ipomoea pinnata* Hochst. ex Choisy in DC., Prodr. 9: 353. 1845. ≡ *Merremia*

pinnata (Hochst. ex Choisy) Hallier f. Type: [Sudan. Northern Darfur] Kordofan, Tejara, *Kotschy 262* (lectotype, here designated, G-DC! bar code G00135552; isolectotypes GOET!, TCD!, WAG).

Xenostegia sapinii (De Wild.) Simões & Staples, **comb. nov.** \equiv *Merremia sapinii* De Wild., Bull. Jard. Bot. État 3: 260. 1911. Type: Democratic Republic of Congo. Kasai-Occidental, Bienge, *Sapin s.n.* (syntype BR!); Lula Lumene, *Hendrickx 3083* (syntype BR).

8. *Operculina* Silva Manso, Enum. Subst. Braz. 16. 1836. Type: *O. turpethum* (L.) Silva Manso.

Diagnostic characters: Slender twiners to lianas; axial parts (stems, petioles, peduncles, pedicels) often winged, angled or ribbed; leaves usually entire (divided or compound in *O. pinnatifida* and *O. macrocarpa*); corolla with pubescent mid-petaline bands (glabrous in *O. aequisepala* and *O. turpethum*); anthers spirally dehiscent; fruit an operculate capsule, cupped by the greatly accrescent calyx; seeds glabrous or covered in reddish glandular hairs that easily rub off; pollen trizonocolpate to sometimes hexapantocolpate (*O. hamiltonii* and *O. petaloidea*) (Fig. 13).

Distribution: Widely distributed in the tropics of the Americas, Africa, Asia, Malesia, Australia and the Pacific islands (Fig. 14); 14 species.

Discussion: The two characters that can be relied on to recognize *Operculina* are the strongly spirally twisted

anthers and the fruit type: an operculate capsule with a leathery exocarp that drops off, leaving a thin, brittle endocarp underneath, the endocarp eventually shatters, releasing the seeds. The operculate capsule is enclosed within an accrescent calyx. Other characters that are useful for recognizing the genus, but not found in all species, are the tendency for winged axial parts (stems, petioles, peduncles and pedicels), the hairy mid-petaline bands outside and the usually tricolpate pollen.

Species included: *Operculina aequisepala* (Domin) R.W.Johnson; *O. brownii* Ooststr.; *O. codonantha* (Benth.) Hallier f.; *O. hamiltonii* (G.Don) D.F.Austin & Staples; *O. macrocarpa* (L.) Urb.; *O. petaloidea* (Choisy) Ooststr.; *O. pinnatifida* (Kunth) O'Donnell; *O. polynesica* Staples; *O. pteripes* (G.Don) O'Donnell; *O. riedeliana* (Oliver) Ooststr.; *O. sericantha* (Miquel) Ooststr.; *O. tansaensis* Santapau & Patel; *O. turpethum* (L.) Silva Manso; *O. ventricosa* (Bertero) Peter.

Note. The fruit of *Operculina flammea* Meisn. has been unknown and the placement of this species in *Operculina* has been doubtful. Given strong molecular and morphological evidence, it has been transferred to *Distimake*, where it fits the generic circumscription perfectly.

New combination

Operculina maypurensis (Hallier f.) Simões & Staples, **comb. nov.** \equiv *Merremia maypurensis* Hallier f., Jahrb. Hamburg. Wiss. Anst. 16(Beih. 3): 36. 1898 [publ. 1899].



Figure 14. Distribution of *Operculina*. Dark colour indicates the core distribution of the genus; distribution of its most widespread species, *O. turpethum*, is highlighted in lighter colour.

Type: Venezuela. 'Amazonas, near Maypures on the Orinoco', Spruce 3593 (holotype W; isotype K!).

9. *Camonea* Raf., Fl. Tellur. 4: 81. 1838, here expanded.

Type: *C. bifida* (Vahl) Raf. [= *Merremia umbellata* (L.) Hallier f.]

= *Merremia* section *Xanthips* (Griseb.) Hallier f., Bot. Jahrb. Syst. 16: 552. 1893.

Diagnostic characters: Herbaceous twiners or prostrate creepers; leaves entire or angulate-lobed; with two firm outgrowths (paired auricles) at petiole base (absent in *C. vitifolia*); corolla with a tuft of hairs at the apex of the mid-petaline bands, otherwise glabrous; anthers longitudinally dehiscing and curved at the apex or spirally dehiscing; pollen hexazonocolpate; fruit a chartaceous four-valved capsule, exocarp not

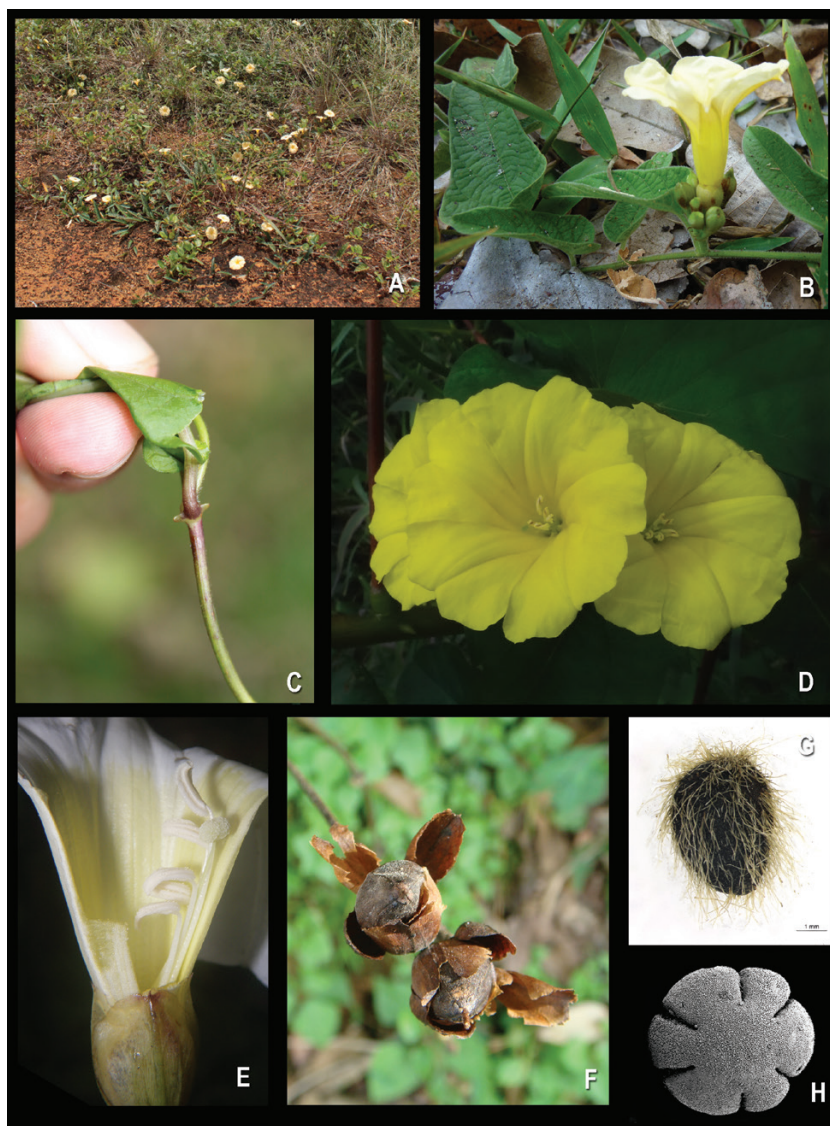


Figure 15. Main morphological characters of *Camonea*. (A) *Camonea pilosa*, creeping habit (Photograph: A. R. Simões); (B) *C. pilosa*, simple, entire leaves; umbelliform inflorescence architecture and convex sepals clasping corolla tube base (Photograph: Imin K.); (C) *C. pilosa*, paired auricles at the base of the petiole (Photograph: A. R. Simões); (D) *C. umbellata*, anthers longitudinally dehiscing with curved apex (Photograph: R. Simão-Bianchini); (E) *C. kingii*, calyx convex, biglobose stigma and anthers longitudinally dehiscing with curved apex (Photograph: M. Nuraliev); (F) *C. kingii*, four-valved capsular fruits. (Photograph: P. Traiperm); (G) *C. pilosa*, seed covered with long golden hairs (Photograph: A. R. Simões); (H) *C. umbellata*, hexazonocolpate pollen. Voucher information: (A) Cambodia, Simões 39 (BM); (B) Malaysia, Imin K. et al. FRI-70028 (KEP); (C) not vouchered; (D) Brazil, Bianchini 1915 (SP); (E) Vietnam, not vouchered; (F) Laos, Staples et al. 1514 (HNL); (G) Thailand, Staples & Wongprasert 394 (BM); (H) Australia, Mitchell 6377 (BRI).

delaminating during dehiscence; seeds pubescent, with long golden hairs either covering the entire surface or concentrated along the edges (except completely glabrous in *C. vitifolia*) (Fig. 15).

Distribution: *Camonea* is centred in tropical Asia with one species (*C. umbellata*) widespread in tropical America and Africa (Fig. 16); five species.

Discussion: Rafinesque's etymology for the name *Camonea* is cryptic: he stated (1838: 81) only '(nymph)', which may be an obscure allusion to the Roman minor goddesses, the Camoenae. The phylogenetic tree places *C. vitifolia* with *C. umbellata*. However, it differs in diagnostic characters: the leaves are five-palmately angled or lobed; the paired auricles are absent from the nodes/petiole base; the calyx is flat, with sepals appressed to the corolla; the corolla is completely glabrous; glands are present on the outer surface of the corolla; anthers spirally dehisce and the fruit is a chartaceous, four-valved capsule. Despite these morphological disparities, *Camonea vitifolia* shares with *C. umbellata* the hexazonocolpate pollen, which is unique in the family. Further molecular and morphological studies are needed to confirm the placement of *C. vitifolia* in the classification. *Camonea umbellata*, as historically conceived, is widely distributed in the tropics and is a highly variable species. The type is based on American plants (*M. umbellata* subsp. *umbellata*) and the Asian plants have been treated

grosso modo as subsp. *orientalis*. The Asian plants display considerable morphological diversity, whereas the American and West African plants are more uniform in appearance. Numerous names are already available and additional morphological and molecular evidence will need to be gathered and analysed to elucidate how these names are best applied to the range of variation observed. For the moment, we are convinced that Asian plants, which have been lumped together with the American plants called '*M. umbellata*' *sensu latissimo*, are certainly specifically distinct from them, and we have taken up a species epithet for them: *C. pilosa*. Further studies are needed to better understand taxonomic delimitation within this polymorphic Asian species complex, and such studies may disclose multiple species occurring in Asia.

New combinations

Camonea bambusetorum (Kerr) Simões & Staples, **comb. nov.** = *Merremia bambusetorum* Kerr, Bull. Misc. Inform. Kew 1941: 18. 1941. Type: Thailand, Chanthaburi, Khao Kuap, A.F.G. Kerr 17704 (holotype K!; isotype BK!).

Camonea kingii (Prain) Simões & Staples, **comb. nov.** = *Merremia kingii* (Prain) Kerr = *Ipomoea kingii* Prain, J. Asiatic Soc. Bengal, Pt. 2, Nat. Hist. 63(2): 110. 1895. Type: India. West Bengal, Darjiling district, Rishap, October 1872, J.S. Gamble 3408A (lectotype K, here designated K000830861!).



Figure 16. Distribution of *Camonea*. Dark colour indicates the core distribution of the genus; distribution of its most widespread species, *C. umbellata*, is highlighted in lighter colour.



Figure 17. Main morphological characters of *Remirema*. *Remirema bracteata*: (A) herbaceous climbing habit; simple, entire leaves; pendant flowers with large calyx (Photograph: G. Staples); (B) anthers spirally dehiscent; deeply four-lobed glabrous ovary with gynobasic style insertion; biglobose stigma (Photograph: G. Staples); (C) mature fruit showing four free nutlets with translucent apex and single seed visible inside each one; gynobasic style insertion (Photograph: P. Karaket); (D) 15-pantocolpate pollen; (E) immature fruit with two locules aborted and two locules developed, showing attachment on receptacle and gynobasic style insertion (Photograph: P. Karaket). Voucher information: (A) Thailand, *Staples et al.* 1557 (BKF); (B) Thailand, *Staples et al.* 1559 (BKF); (C, E) Thailand, *Staples et al.* 1338 (BKF); (D) Thailand, *Put* 1796 (K).

Camonea pilosa (Houttuyn) Simões & Staples, **comb. nov.** ≡ *Ipomoea pilosa* Houttuyn, Nat. Hist. 2(7): 573. 1777. Type: country and collector unknown (holotype G!).

Camonea umbellata (L.) Simões & Staples, **comb. nov.** ≡ *Merremia umbellata* (L.) Hallier f. ≡ *Convolvulus umbellatus* L., Sp. Pl. 155. 1753. Type: [icon] '*Convolvulus Americanus vulgaris folio, capsulis triquetris, numerosis, ex uno puncto longis*

petiolis propendentibus, semine lanugine ferruginea villosa' in Plukenet, Phytographia: t. 167, f. 1. 1692 (lectotype).

Camonea vitifolia (Burm. f.) Simões & Staples, **comb. nov.** ≡ *Merremia vitifolia* (Burm. f.) Hallier f. ≡ *Convolvulus vitifolius* Burm. f., Fl. Indica 45. 1768. Type: [Indonesia.] Java, *Garzin s.n.* (lectotype, G-PREL).

10. *Remirema* Kerr, in Hooker's Icon. Pl. 35: 1–2, pl. 3435 (1943). Type: *R. bracteata* Kerr.

Diagnostic characters: Herbaceous climber; leaves simple, cordiform, entire; corolla tube with a scale above the insertion of each stamen filament; anther dehiscence spirally twisted; ovary deeply four-lobed, style insertion gynobasic; fruit tightly enclosed in accrescent calyx, composed of four free nutlets attached on a woody receptacle; seed one per nutlet, glabrous; pollen 15-pantocolpate (Fig. 17).

Distribution: Western Thailand (only known from Kanchanaburi Province) (Fig. 10C).

Species included: *Remirema bracteata* Kerr.

UNRESOLVED AFRICAN GROUP

With the exception of *Hewittia*, which also occurs in Asia, all of the species in clade 6 are restricted to Africa, a region where clade 5, its putative but unsupported sister clade, is also most diverse. *Hewittia* can be easily distinguished by enlarged foliaceous bracts surrounding the calyx and *Hyalocystis* possesses a distinctive indehiscent fruit type; furthermore *Hewittia* and *Hyalocystis* share a unique 15-colpate pollen type that is unlike the pollen in other members of clade 6. The clade 6 group is morphologically heterogeneous and no diagnostic characters could otherwise be found to characterize it. *Hewittia* and *Hyalocystis*, both being strictly monophyletic and morphologically easily identifiable, have been maintained as genera to stabilize nomenclature.

Merremia pterygocaulos (Choisy) Hallier f. and *M. xanthophylla* Hallier f. (= *M. gallabatensis* Hallier f.) were resolved in the clade that includes *Hewittia* and *Hyalocystis* (Fig. 1). These species plus a number of other African species of *Merremia s.l.* (not included in the molecular phylogenetic study) were found to share a set of morphological characters including angular to shallowly winged stems; palmately lobed leaves (shallowly to more deeply so); corollas with pilose mid-petaline bands; spirally dehiscing anthers and tricolpate pollen. At this time their placement in the classification remains uncertain because we lack crucial information about character states for their pollen and fruit characters for some of the species. The African *Merremia* spp. in clade 6 differ most strikingly from *Distimake* for their pilose mid-petaline bands (completely glabrous in *Distimake*) and the calyx proportionality (sepals longer than wide in *Distimake*, and sepals almost isodiametric in these unresolved African species).

It would be premature and ill-advised to propose any new genera based on such incomplete information. Hence, these species are not transferred out

of *Merremia* for the time being. Further molecular and morphological studies in this African group are urgently needed before they can confidently be placed at the generic rank.

Doubtful species: *Merremia hornbyi* Verdc., *M. malvifolia* Rendle, *M. palmata* Hallier f., *M. pterygocaulos* (Choisy) Hallier f., *M. truncata* Verdc., *M. xanthophylla* Hallier f.

UNRESOLVED SINGLE-SPECIES LINEAGES

Three single-species lineages were recovered near the base of the tree for little-known Asian species, including *M. poranoides* (C.B. Clarke) Hallier f., *M. sibirica* (L.) Hallier f. and *M. caloxantha* (Diels) Staples & R.C. Fang. The three are poorly represented in herbaria and thus material could not be adequately studied for morphological observations. They do not fit any of the genera (newly described or extant) and it is not safe to assume they represent new monospecific genera, despite their position as single-species lineages in the recovered tree. There are still several taxa from remote areas of China which were not possible to include in this study: for example *Merremia cordata* R.C. Fang, *Merremia martinii* (H. Lévl.) Staples & Simões [= *M. hungaiensis* (Lingelsh. & Borza) R.C. Fang] and *M. yunnanensis* (Courchet & Gagnep.) R.C. Fang. Once these missing taxa are included it seems likely, based on the available morphological evidence, that the topology of these lower branches in the tree will change and a different grouping of these six species could emerge. Therefore no taxonomic decisions are implemented for the single-species lineages at this time.

ACKNOWLEDGEMENTS

The authors acknowledge the collaboration of staff at molecular facilities at the Natural History Museum of London and curators at A, AIGH, ANDA, BCU, BK, BKF, BM, BO, BR, COI, E, G, GH, K, KEP, L, LISC, M, MEXU, MICH, MO, NY, PNH, SAN, SAR and most especially SING (Singapore Botanic Gardens) for facilitating specimen study and collection of samples. We thank all the photographers who gave permission for their images to be used in this paper; they are acknowledged individually in the figure legends. We further appreciate Dr. Somran Suddee and Preecha Karaket (BKF) for collaboration in fieldwork in Thailand, Mathieu Leti, Bruno David and Fondation Pierre Fabre for kindly supporting fieldwork in Cambodia, Nurainas and Syamsuardi (ANDA) for enabling our fieldwork in Sumatra and Prof. Sebsebe Demissew (ETH) and Dr. Mark Carine (BM) for accommodating ARS in an

expedition in Ethiopia. We also thank Nelly Bouilhac (Collection Nationale des Convolvulacées) for providing fresh material of several taxa for DNA extraction and allowing visits to the CNC living collections for the purpose of morphological observations, José Grande Allende (VEN) for photographing fruits of *O. maypurensis*, Jefferson Guedes de Carvalho Sobrinho (UEFS) for sending material of *D. igneus* for molecular analysis and Rosângela Simão-Bianchini from Instituto de Botânica (SP) for unconditional support and scientific advice during the writing of this manuscript.

FUNDING

The authors would like to thank Fundação Ciência e Tecnologia for fully funding Ana Simões' PhD project (Grant SFRH/BD/45924/2008), of which this study was part; also the Royal Forest Herbarium in Bangkok for support with fieldwork in Thailand and Laboratoires/Fondation Pierre Fabre for partially funding fieldwork in Cambodia; the study was concluded with support in Brazil from CAPES – BJT 88881.067993/2014-01. The Singapore National Parks Board funded GS' research from 2007 to 2013 and also funded ARS' research project on *Decalobanthus* in 2013 through the H. M. Burkill Research Fellowship.

REFERENCES

- Austin DF. 1982.** Convolvulaceae. In: Febres ZL, Steyermark JA, eds. *Flora da Venezuela*, Vol. 8(3). Caracas: Fundación Educación Ambiental, 15–239.
- Austin DF. 1998.** Parallel and convergent evolution in the Convolvulaceae. In: Mathew P, Sivadasan M, eds. *Biodiversity and taxonomy of tropical flowering plants*, Calicut: Mentor Books, 201–234.
- Austin DF, Staples GW. 1980.** *Xenostegia*, a new genus of Convolvulaceae. *Brittonia* **32**: 533–536.
- Baskin JM, Baskin CC, Li X. 2000.** Taxonomy, anatomy and evolution of physical dormancy in seeds. *Plant Species Biology* **15**: 139–152.
- Buril MT, Simões AR, Carine M, Alves M. 2013.** *Austinia*, a new genus of Convolvulaceae from Brazil. *Phytotaxa* **186**: 254–260.
- Buril MT, Simões AR, Carine M, Alves M. 2015.** *Daustinia*, a replacement name for *Austinia* (Convolvulaceae). *Phytotaxa* **197**: 60.
- Deroin T. 2001.** Convolvulaceae. In: Morat P, ed. *Flore de Madagascar et des Comores*, Vol. 117. Paris: Muséum National d'Histoire Naturelle, 11–287.
- Gonçalves ML. 1987.** Convolvulaceae. In: Launert E, ed. *Flora Zambesiaca*, Vol. 8. Suffolk: Managing Committee on behalf of the contributors to the Flora Zambesiaca, 9–142.
- Gonçalves ML. 1992.** *Convolvulaceae. Flora de Moçambique*, Vol. 113. Lisbon: Instituto de Investigação Científica Tropical.
- Hallier HG. 1893.** Versuch einer natürlichen Gliederung der Convolvulaceen auf morphologischer und anatomischer Grundlage. *Botanische Jahrbücher für Systematik* **16**: 453–591.
- Johnson RW. 2010.** *Davenportia* R.W.Johnson, a new genus of Convolvulaceae (Merremieae) from central Australia. *Austrobaileya* **8**: 171–175.
- Kerr AFG. 1943.** *Remirema bracteata* A.F.G. Kerr (Convolvulaceae). *Hooker's Icones Plantarum* **35**: 3435.
- Linder HP, Baeza M, Barker NP, Galley C, Humphreys AM, Lloyd K, Orlovich D, Pirie MD, Simon BK, Walsh N, Verboom GA. 2010.** A classification of the Danthonioideae (Poaceae). *Annals of the Missouri Botanical Garden* **97**: 306–364.
- Manitz H. 1974.** Zur Lectotypisierung der Namen einiger Convolvulaceen-Gattungen. *Feddes Repertorium* **85**: 629–640.
- Manitz H. 1976.** Zur Lectotypisierung der Namen einiger Convolvulaceen- und Cuscutaceen-Gattungen. *Feddes Repertorium* **87**: 311–317.
- McNeill J, Barrie FR, Buck WR, Demoulin V, Greuter W, Hawsworth DL, Herendeen PS, Knapp S, Marhold K, Prado J, Prud'homme Van Reine WF, Smith GF, Wiersema JH, Turland NL. 2012.** International Code of Nomenclature for algae, fungi and plants (Melbourne Code). *Regnum Vegetabile*, Vol. 154. Königstein: Koeltz Scientific Books.
- Merrill ED. 1949.** Convolvulaceae. In: *Index Rafinesquianus*, Vol. 22. Privately published, 196–201.
- O'Donnell CA. 1941.** Revisión de las especies americanas de *Merremia* (Convolvulaceae). *Lilloa* **6**: 467–541.
- Ooststroom SJ van. 1936.** On *Decalobanthus*, a new genus of Convolvulaceae from Sumatra. *Blumea* **2**: 98–100.
- Ooststroom SJ van. 1939.** The Convolvulaceae of Malaysia, II. The genera *Jacquemontia*, *Aniseia*, *Convolvulus*, *Calystegia*, *Shutereia*, *Merremia*, *Operculina* and *Decalobanthus*. *Blumea* **3**: 267–371.
- Ooststroom SJ van, Hoogland RD. 1953.** Convolvulaceae. In: Van Steenis CGJ, ed. *Flora Malesiana*, Vol. 4. Jakarta: Noordhoff-Kolff N.V., 388–512.
- Rafinesque CS. 1825.** *Neogenyton*, or indication of sixty-six new genera of plants of North America. Privately published.
- Rafinesque CS. 1836.** Remarques sur les Convolvulacées. *Annales Générales des Sciences Physiques* **8**: 268–272.
- Rafinesque CS. 1838** [title page 1836]. *Flora Telluriana* 4. *Convolvulaceae*. 69–87.
- Simões AR, Culham A, Carine M. 2015.** Resolving the unresolved tribe: a molecular phylogenetic framework for Merremieae (Convolvulaceae). *Botanical Journal of the Linnenn Society* **179**: 374–387.
- Staples GW. 1979.** *Generic relationships of Ipomoea, Merremia, and Operculina (Convolvulaceae)*. MS thesis, Florida Atlantic University, Boca Raton.
- Staples GW. 2010.** A checklist of *Merremia* (Convolvulaceae) in Australasia and the Pacific. *The Gardens' Bulletin Singapore* **61**: 483–522.
- Staples GW, Austin DF, Simão-Bianchini R. 2012.** (2076) Proposal to conserve the name *Ipomoea semisagitta* (*Merremia semisagitta*) (Convolvulaceae) with a conserved type. *Taxon* **61**: 687–688.

- Staples GW, Brummitt RK. 2007.** Convolvulaceae. In: Heywood VH, Brummitt RK, Culham A, Seberg O, eds. *Flowering plant families of the World*. Kew: Royal Botanic Gardens, 108–110.
- Staples G, Traiperm P. 2010.** *Remirema*. In: Santisuk T, Larsen K, eds. *Flora of Thailand* **10**: 455–458, Fig. 38 & plate LIV, figs. 4.1–4.3.
- Stefanovic S, Austin DF, Olmstead RG. 2003.** Classification of Convolvulaceae: a phylogenetic approach. *Systematic Botany* **28**: 791–806.
- Stefanovic S, Krueger L, Olmstead RG. 2002.** Monophyly of the Convolvulaceae and circumscription of their major lineages based on DNA sequences of multiple chloroplast loci. *American Journal of Botany* **89**: 1510–1522.
- Stevens PF. (2001 onwards).** *Angiosperm Phylogeny Website*. Version 12, July 2012 [and more or less continuously updated since]. Available at: <http://www.mobot.org/MOBOT/research/APweb/>