

RESEARCH ARTICLE

Phylogeny of Marsdenieae (Apocynaceae, Asclepiadoideae) based on chloroplast and nuclear loci, with a conspectus of the genera

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Abstract A densely sampled molecular phylogeny of the pantropical, predominantly forest-dwelling tribe Marsdenieae (Apocynaceae) is presented, including almost a quarter of the ca. 740 species. Sampling focused on resolving the circumscription of *Marsdenia*, which ranges from *Marsdenia* sensu Bullock with less than 10 Asian species closely related to the type, *M. tinctoria*, to *Marsdenia* sensu Forster, with ca. 300 species distributed throughout the range of the tribe, encompassing the genera *Cionura*, *Dregea*, *Gongronema*, *Gymnema*, *Leichhardtia*, *Stephanotis*, and *Wattakaka* as synonyms. All analyses resolve two well-supported clades: an Asia-Pacific Clade that includes the large epiphytic *Dischidia-Hoya* alliance and a number of *Marsdenia* species, among them the type *M. tinctoria*, and a Cosmopolitan Clade that includes most of the rest of Marsdenieae with several moderately to well-supported subclades that span the entire geographic range of Marsdenieae. The position of two small genera, *Rhysolobium* (southern Africa) and *Sicyocarpus* (Madagascar), is ambiguous. Given this topology, a monophyletic *Marsdenia* s.l. would subsume all species of Marsdenieae. Instead, we propose a classification that maintains *Dischidia* and *Hoya* as distinct genera. We revise generic circumscriptions, reducing *Marsdenia* s.str. to a small clade of Asian species. Two new genera, *Gongreos* gen. nov. and *Gongronemopsis* gen. nov., are described, with two and nine species, respectively. A total of twenty-six new combinations, one new name, and six new synonyms are proposed. Three neotypes and eleven lectotypes are selected, and one 2nd step lectotypification is carried out. Diagnostic morphological characters for identified clades are discussed. Biogeographic analysis retrieves tropical Asia as most likely ancestral area for Marsdenieae, with widespread tropical Asia-Africa almost equally likely. The first-branching lineages in both major clades are tropical Asian; the Asia-Pacific Clade comprises a sizeable radiation in the Pacific area, with two dispersals from Australia to New Caledonia. The Cosmopolitan Clade comprises several genera (*Gongronemopsis*, *Gymnema*, *Stephanotis*, *Telosma*) widespread in Africa and tropical Asia, and some also in Madagascar, and the New World genus *Ruehssia*.

Keywords biogeography; classification; evolution; genus circumscription; *Marsdenia*; systematics; taxonomy; typification

Supporting Information may be found online in the Supporting Information section at the end of the article.

INTRODUCTION

The Apocynaceae has been transformed from one of the least-studied angiosperm groups to a model family for research in evolution, biogeography, and pollination biology (e.g., Fishbein & al., 2018; Ollerton & al., 2018; Weitemier & al., 2019; Bitencourt & al., 2021). Subfamily Asclepiadoideae, characterized by pollen united in pollinia and one pollinium per locule, comprises 183 genera (Endress & al., 2018; Keller & Liede-Schumann, 2020; Rodda & al., 2020). Of its

five tribes, Marsdenieae with 27 genera and roughly 740 species is the third-largest, after Asclepiadeae (106 genera, ca. 1820 species) and Ceropegieae (46 genera, ca. 790 species), while Fockeeae (2 genera, 9 species) and Eustegieae (2 genera, 4 species) constitute small lineages (Endress & al., 2018; Bitencourt & al., 2021). Fockeeae, with pollinaria lacking well-developed caudiculae, is sister to the other four tribes, Eustegieae-Asclepiadeae with pendent pollinia and Marsdenieae-Ceropegieae with erect pollinia (e.g., Surveswaran & al., 2014). However, while the phylogenetic structures of Asclepiadeae (e.g., Rapini

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& al., 2003; 2007) and Ceropegieae (e.g., Meve & Liede, 2004; Meve & al., 2017) have been studied intensively in the last 20 years, Marsdenieae have remained understudied, except for the horticulturally important genus *Hoya* R.Br. and its relatives (e.g., Wanntorp & al., 2014; Rodda & al., 2020).

Marsdenieae comprise mostly woody twiners, lianas, and succulent epiphytic vines, more rarely erect shrubs, with a high diversity in floral structure (Fig. 1). The tribe is characterized by pollinaria with a well-developed translator apparatus and an erect orientation of pollinia (Endress & al., 2018) (Fig. 2G,I,J). However, insertion crests are usually absent from the pollinia, or, if present (e.g., in *Hoya*, or *Telosma* Coville, Fig. 2K,L), they are located on the outer side of the pollinium, versus consistently present on the inner side of the pollinium in its sister tribe Ceropegieae (Bruyns & Forster, 1991). The corolla is highly variable in size, shape, color and degree of indument on the lobes (Fig. 1). A corona is almost always present, and is usually of gynostegial origin (Fig. 2A,C,D,F,G), more rarely of corolline origin (e.g., in *Gymnema* R.Br., Fig. 2E). The style-head can be flat (Fig. 2A), conical (Fig. 2B,C,E,G), or rostrate (Fig. 2D); the follicles can be thin-walled and fusiform or thick-walled, obclavate, and often with ornamentation; the seeds are often winged, and usually comose.

The monophyly of Marsdenieae has been well supported in all molecular phylogenetic analyses to date (e.g., Meve & Liede, 2004; Surveswaran & al., 2014; Fishbein & al., 2018), but infratribal classification remains ambiguous. Marsdenieae as understood by Endress & al. (2018) comprises 26 genera, of which two are species-rich, *Hoya* with 350–450 spp. and *Marsdenia* R.Br. with c. 150 spp. Twelve genera are monotypic, and of these, four are poorly known because the original material was destroyed during World War II in Berlin. Of the remaining 12 genera, only one exceeds 50 species (*Dischidia* R.Br.), and five exceed 10 species (Table 1). Twenty genera were found in Asia, thirteen of them exclusively there. One genus (*Cionura* Griseb.) was found in Europe, six in Australia, one (*Gunnessia* P.I.Forst.) exclusively there. Africa (incl. Madagascar) was home to eight genera, of which three were found exclusively there. In a few cases genera were distributed in Africa and Asia, but with only one of the species in Africa (e.g., *Gymnema* with *G. sylvestre* (Retz.) R.Br. ex Schult. and *Telosma* with *T. africana* (N.E.Br.) N.E.Br.). In the New World, only species attributed to *Marsdenia* by Endress & al. (2018) were found.

Of the two large genera, *Hoya* has been studied extensively in recent years (see Wanntorp & al., 2014 and Rodda & al., 2020 and references therein), and has been found monophyletic after the inclusion of several monotypic genera. The closely related *Oreosparte* Schltr. and newly described *Papua-hoya* Rodda & Simonsson are maintained as distinct, with the status of *Dischidia* still debated (Rodda & al., 2020). *Marsdenia*, on the other hand, has seen little study. The only recent molecular phylogeny (Espírito Santo & al., 2019) focused on New World taxa and supported Omlor's (1998) hypothesis

that the genus is polyphyletic. Espírito Santo & al. (2019) recognized the New World *Ruehssia* H.Karst. as distinct from the Old World *Marsdenia* and revised the 42 Brazilian *Ruehssia* species. Keller & al. (2020) confirmed monophyly of *Ruehssia* and its separation from *Marsdenia*. Nomenclatural transfer of New World species to *Ruehssia* is ongoing (for details see under “2.11 *Ruehssia*”). Most recently, Rodda (2020) resurrected the monotypic *Harmandiella* Costantin as distinct from *Marsdenia*, with which it had been synonymized by Omlor (1998).

The purpose of the present study is to clarify relationships in Marsdenieae and to improve the circumscription of the genera recognized. Recent taxonomic practice in Asclepiadoideae has trended toward recognition of large, broadly circumscribed, polymorphic genera, e.g., *Cynanchum* L. (Khanum & al., 2016), *Vincetoxicum* Wolf (Liede-Schumann & al., 2016) and the still disputed *Ceropegia* L. (Bruyns & al., 2017 vs. Endress & al., 2018). The main question is therefore whether *Marsdenia*, as presently circumscribed, with the exclusion of *Ruehssia*, is monophyletic, and if not, how the phylogeny of Marsdenieae can best be translated into a classification. To address this larger question, it is necessary to determine whether continued taxonomic recognition of numerous mono- or bitypic genera in Marsdenieae renders larger genera paraphyletic. Secondly, we investigate biogeographic structure in the tribe.

■ MATERIALS AND METHODS

Taxon sampling. — Our sampling comprises 219 ingroup (Marsdenieae) samples, representing 171 species and 1 subspecies, and 36 outgroup taxa. Outgroup sampling was comprehensive to include at least one representative of each recognized tribe and subtribe of Asclepiadoideae (Endress & al., 2018), using the sister subfamily Secamonoideae as the most distant outgroup. For the ingroup, as many genera of Marsdenieae as possible were sampled; however, of some described genera, no material could be obtained (Table 1). For larger, widespread, and/or potentially nonmonophyletic genera, in particular *Marsdenia* and *Hoya*, sampling covers the whole taxonomic, morphological and geographical diversity in the genus, as far as available.

DNA isolation, PCR amplification, and sequencing. — DNA was extracted from silica-dried leaves (vouchers held at UBT) or from leaf fragments taken from herbarium specimens held at A, ABD, B, BH, BKF, BR, BRI, CNS, E, GH, HUEFS, IBSC, K, L, M, MO, MSUN, NOU, NY, OMA, P, PMNH, QBG, S, SING, UBT, ULM, and USTH. Total DNA was extracted using the DNeasy Plant Mini Kit (Qiagen, Hilden, Germany) following the manufacturer's instructions. PCR primers and protocols for the plastid *trnT-L* and *trnL-F* spacers and the *trnL* intron corresponded to Taberlet & al. (1991). The *trnL* intron and *trnL-F* intergenic spacer were amplified either as one fragment using primers c and f or as two separate fragments using primers c and d, and e and f, respectively. The

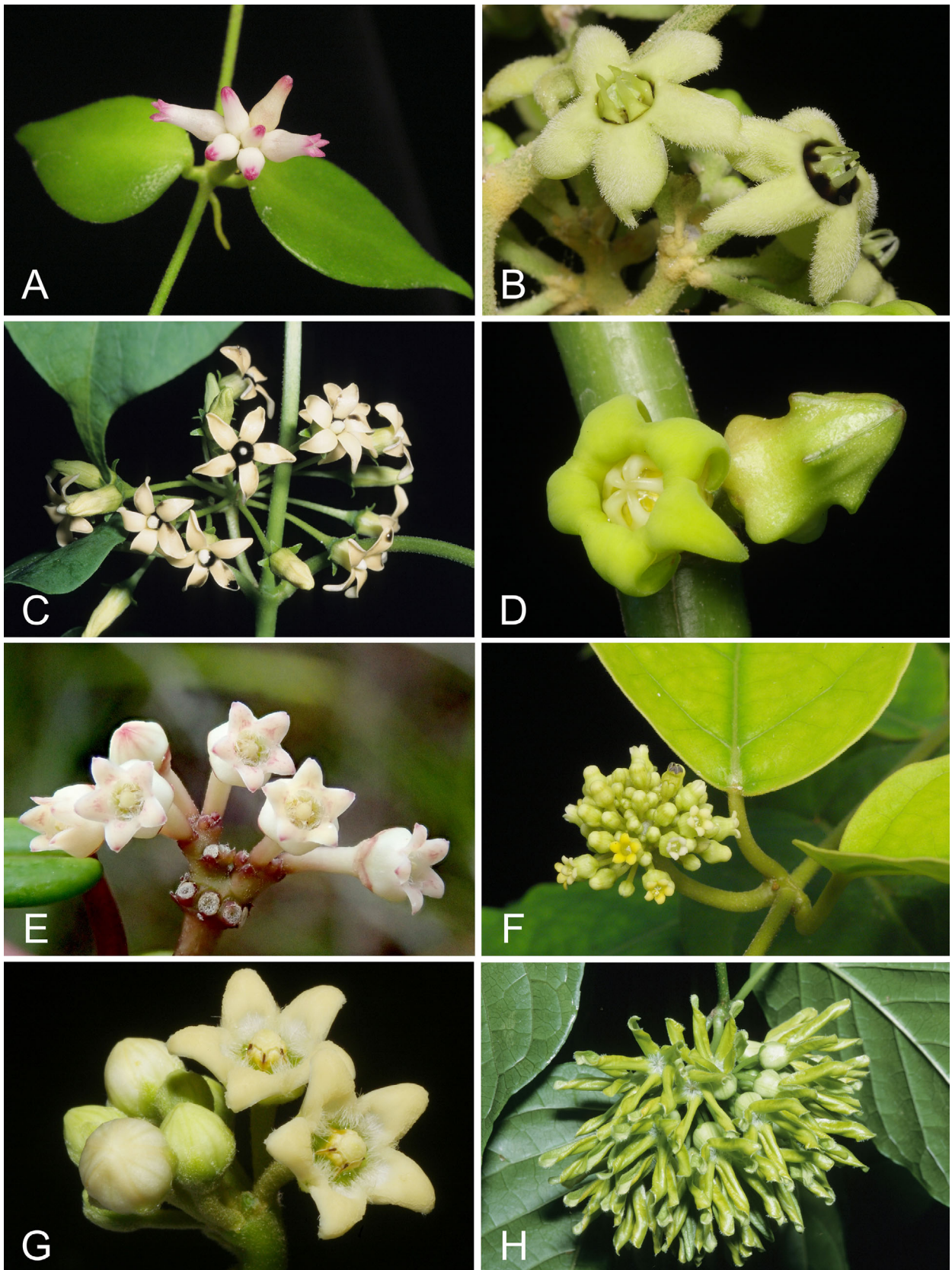


Fig. 1. Floral diversity in Marsdenieae. **A**, *Dischidia truncata* (ex hort.); **B**, *Stephanotis rubicunda* (Kenya; with nectar turned blackish with age); **C**, *Gymnema inodorum* (Philippines; with nectar turned blackish with age); **D**, *Hoya omlorii* (Malaysia); **E**, *Leichhardtia mackeeorum* (New Caledonia); **F**, *Marsdenia tinctoria* (China); **G**, *Ruehssia cundurango* (Ecuador); **H**, *Telosma procumbens* (Philippines). — All photographs by U. Meve.

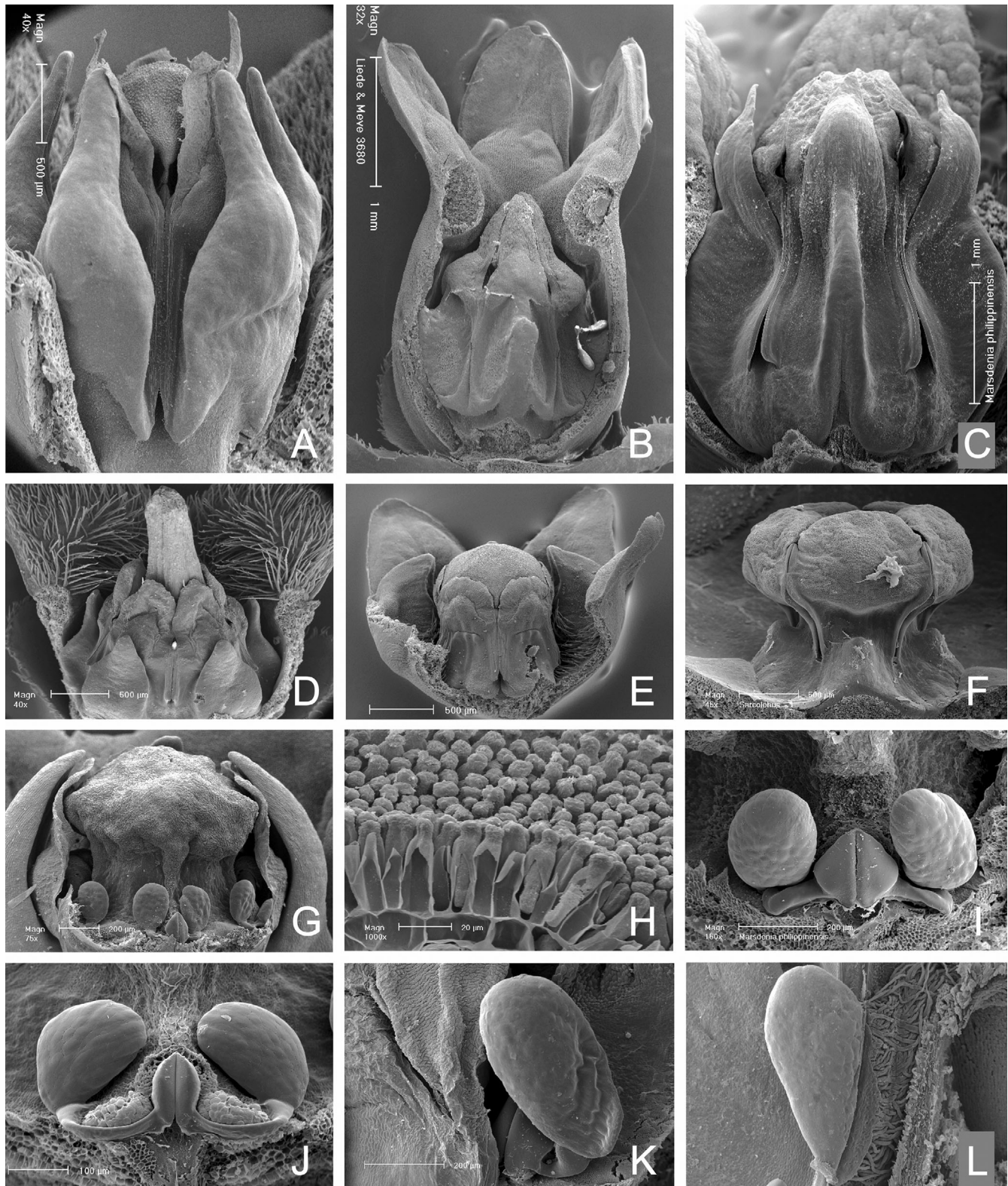


Fig. 2. SEM studies of Marsdenieae flowers and flower details. **A**, *Anisopus efulensis*; **B**, *Dischidanthus urceolatus*; **C**, *Gongronemopsis philippinensis*; **D**, *Marsdenia coulteri* (*Ruehssia*); **E**, *Gymnema pachyglossum*; **F**, *Sarcobolus globosus* subsp. *peregrinus*; **G**, *Gongronemopsis angolensis*; **H**, *Gongronemopsis angolensis* (corolla lobe in transverse section, with bottle-shaped papillae); **I**, *Gongronemopsis philippinensis*; **J**, *Marsdenia coulteri* (*Ruehssia*); **K**, *Telosma procumbens* (pollinium with pellucid margin); **L**, *Telosma procumbens* (pollinium inserted in guide-rail, pollen tubes germinated; one anther wing removed). — All photographs by U. Meve.

Table 1. Accepted genera of Marsdenieae.

Genus	Species number in					Accessions (species) included in present study	Distribution (Endress & al., 2018)	Distribution (present study)
	Endress & al., 2018	Espírito Santo & al., 2019	Rodda, 2020; Rodda & al., 2020; Kidyoo, 2020	POWO, 2021	Present study			
<i>Anatropanthus</i> Schltr.	1	1	→ <i>Hoya</i>	–	–	[1 (1)]	Asia	–
<i>Anisopus</i> N.E.Br.	2	2	<i>n.a.</i>	2	4	4 (4)	Africa	Africa
<i>Asterostemma</i> Decne.	1	1	<i>n.a.</i>	1	1	–	Asia	Asia
<i>Campestigma</i> Pierre ex Costantin	1	3	<i>n.a.</i>	1	1	1 (1)	Asia	Asia
<i>Cathetostemma</i> Blume	1	1	<i>n.a.</i>	–	1	–	Asia	Asia
<i>Cionura</i> Griseb.	1	1	<i>n.a.</i>	1	1	1 (1)	Europe	Europe
<i>Cosmostigma</i> Wight	3	3	<i>n.a.</i>	3	3	1 (1)	Asia	Asia
<i>Dalzielia</i> Turrill	–	–	–	–	1	–	–	Africa
<i>Dischidanthus</i> Tsiang	–	–	<i>n.a.</i>	1	2	2 (2)	–	Asia (China)
<i>Dischidia</i> R.Br.	c. 80	c. 80	c. 80	126	c. 80	11 (9)	Asia Australia	Asia Australia
<i>Dolichopetalum</i> Tsiang	1	1	<i>n.a.</i>	1	1	–	Asia (China)	Asia (China)
<i>Dregea</i> E.Mey.	c. 12	c. 12	<i>n.a.</i>	7	→ <i>Stephanotis</i>	[11 (8)]	Asia	–
<i>Gongreos</i> Rodda, Liede & Meve	–	–	–	–	2	2 (2)	–	Asia
<i>Gongronema</i> (Endl.) Decne.	c. 12	c. 12	<i>n.a.</i>	9	4	[9 (6)] 2 (2)	Asia Africa	Asia
<i>Gongronemopsis</i> Rodda, Liede & Meve	–	–	–	–	9	9 (5)	–	Asia Africa
<i>Gunnessia</i> P.I.Forst.	1	1	<i>n.a.</i>	1	→ <i>Sarcolobus</i>	[2 (1)]	Australia	–
<i>Gymnema</i> R.Br.	c. 30	c. 30	<i>n.a.</i>	34	c. 40	24 (15)	Asia Australia Africa (incl. Madagascar)	Asia Australia Africa (incl. Madagascar)
<i>Gymnemopsis</i> Costantin	–	–	3	–	3	–	–	Asia
<i>Harmandiella</i> Costantin	–	–	1	–	1	1 (1)	–	Asia
<i>Heynella</i> Backer	1 (poorly known)	1	<i>n.a.</i>	1	1	–	Asia (Java)	Asia (Java)
<i>Hoya</i> R.Br.	350–450	350–450	350–450	542	350–450	29 (24)	Asia Australia	Asia Australia
<i>Jasminanthes</i> Blume	7	6	<i>n.a.</i>	13	→ <i>Gymnema</i>	[5 (2)]	Asia	Asia
<i>Leichhardtia</i> R.Br.	–	–	<i>n.a.</i>	–	85	45 (37)	–	Australia Oceania
<i>Lygisma</i> Hook.f.	c. 5	6	<i>n.a.</i>	4	c. 5	2 (2)	Asia	Asia

(Continues)

Table 1. Continued.

Genus	Species number in					Accessions (species) included in present study	Distribution (Endress & al., 2018)	Distribution (present study)
	Endress & al., 2018	Espírito Santo & al., 2019	Rodda, 2020; Rodda & al., 2020; Kidyoo, 2020	POWO, 2021	Present study			
<i>Marsdenia</i> R.Br.	c. 150	c. 100	<i>n.a.</i>	294	7–8	9 (5)	Africa America Asia Australia	Asia
<i>Oreosparte</i> Schltr.	1 (poorly known)	1	3	3	3	3 (3)	Asia	Asia
<i>Papuahoya</i> Rodda & Simonsson	–	–	3	3	3	3 (3)	–	New Guinea
<i>Pseudosarcolobus</i> Costantin	–	–	–	–	1	–	–	Asia
<i>Pycnorhachis</i> Benth.	1 (poorly known)	1	<i>n.a.</i>	1	1	–	Asia	Asia
<i>Rhyssolobium</i> E.Mey.	1	1	<i>n.a.</i>	1	1	2 (1)	Africa	Africa
<i>Ruehssia</i> H.Karst.	–	>42	<i>n.a.</i>	56	c. 130	35 (31)	–	America
<i>Sarcolobus</i> R.Br.	c. 12	c. 12	<i>n.a.</i>	20	c. 12	6 (5)	Asia Australia	Asia Australia
<i>Sicyocarpus</i> Bojer	–	–	–	–	2	3 (2)	–	Madagascar
<i>Sinomarsdenia</i> P.T.Li & J.J.Chen	–	–	–	–	1	–	–	Asia
<i>Stephanotis</i> Thouars	c. 5	c. 5	<i>n.a.</i>	4	c. 20	14 (10)	Madagascar	Africa (incl. Madagascar) Asia
<i>Stigmatorhynchus</i> Schltr.	2–3	2–3	<i>n.a.</i>	2	2	2 (1)	Africa	Africa
<i>Telosma</i> Coville	12	6	<i>n.a.</i>	9	12	7 (4)	Africa (incl. Madagascar) Asia	Africa (incl. Madagascar) Asia
<i>Tetragonocarpus</i> Hassk.	–	–	–	–	1 (poorly known)	–	–	Asia (Java, Bali)
<i>Treutlera</i> Hook.	1 (poorly known)	1	<i>n.a.</i>	1	1	–	Asia	Asia

According to Endress & al. (2018), Espírito Santo & al. (2019), Rodda (2020), Rodda & al. (2020), Kidyoo (2020), and POWO (2021).

– indicates genera listed in synonymy; *n.a.* indicates genera not treated in the publication; → indicates “transferred to synonymy of” in the publication.

Sample and species numbers in square brackets belong to genera no longer recognized and have been counted again under the accepted genus

psbA-trnH intergenic spacer was amplified with the primers designed by Sang & al. (1997), and for the *rps16* intron, the procedures described in Liede-Schumann & al. (2005) were followed. The entire internal transcribed spacer region (ITS) including 5.8S of ribosomal DNA (rDNA) was amplified using the flanking primers ITS4 and ITS5 following a modified protocol based on Baldwin (1992) described in Meve & Liede (2001). Two additional nuclear markers, At2g06530a and At2g34620b, were sequenced using the primers and protocol given by Straub & al. (2011). The same primers were used for

both PCR and Sanger sequencing. Both strands were sequenced for all PCR products. In total, 790 partial sequences were newly created for the present study. For all nuclear markers, and *psbA-trnH*, no outgroup sequences were included, even if they were available, because they were too variable for an unambiguous alignment. All vouchers and sequence information are provided in Appendix 1.

Phylogenetic analysis. — For all regions, forward and reverse sequences were aligned with CodonCode Aligner, v.3.0.3 (CodonCode Corp., Dedham, Massachusetts, U.S.A.),

and the consensus was exported in fasta format. Sequences previously published in GenBank were added, provided the taxon identification was reliable, sequences of at least two loci were available for the specimen, and the sequence covered more than half of the locus. The fasta files of each locus were aligned with the MAFFT package (Kato & Standley, 2013) inside Mesquite v.3.5 (Maddison & Maddison, 2018), using standard settings, and the resulting alignments were corrected manually to fix gap and alignment mistakes. The *psbA-trnH* spacer contained a considerable amount of ambiguously aligned positions, therefore regions of ambiguous alignment were removed with GBLOCKS v.0.91.1 (Talavera & Castresana, 2007) run on the NGPhylogeny.fr Server (<https://ngphylogeny.fr>; Lemoine & al., 2019). Because a run under default settings retrieved no alignment, the less stringent settings, allowing smaller final blocks, gap positions within final blocks, and less strict flanking positions were chosen, reducing the alignment from 1946 bp to 352 bp; alignment details are listed in Table 2. Alignments have been uploaded to TreeBase (Study Number S27302, <http://purl.org/phylo/treebase/phyloids/study/TB2:S27302>). Congruence between the nuclear and the plastid partition of the dataset was assessed by conducting separate Bayesian and maximum likelihood (ML) bootstrap analyses of each partition. For the nuclear dataset, no outgroup could be assembled due to alignment problems, and both datasets (plastid and nuclear) were analyzed without outgroups. The resulting phylograms were visualized using the option “draw radial phylogram” in Dendroscope (v.3.7.6; Huson & Scornavacca, 2012). Because sample names and support values are hard to read in this format, rectangular phylograms are additionally presented. Conflict between datasets was assumed when different positions were well supported (i.e., maximum likelihood bootstrap support [BS_{ML}] > 75%

and Bayesian posterior probability [PP] > 0.95) in each dataset (Schliep & al., 2017). Because discordance between nuclear and plastid datasets was restricted to members of one small clade only and not well supported (see below under “Position of the Afro-Malagasy Clade”), nuclear and plastid data were united in a combined dataset, with only cpDNA data (without *psbA-trnH*) available for the outgroups

For ML, RAxML (Stamatakis, 2014) was used to search for the tree with the greatest likelihood and to conduct bootstrap search. All partitions (Table 2) were allowed to evolve independently under the GTR+ Γ substitution model. RAxML analyses were conducted using the CIPRES Gateway (<https://www.phylo.org>, Miller & al., 2010) with number of bootstrap replicates set automatically (Pattengale & al., 2010).

For Bayesian inference (BI), two simultaneous independent runs with four chains each (one cold and three heated) were conducted, using MrBayes v.3.2.2 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003; Ronquist & al., 2012). They were initiated with random trees, saving one tree every 1000 generations, and branch lengths saved. The nucleotide substitution models (Table 2) found by Model-Test-NG v.1.0.0 (Darriba & al., 2020) under the Akaike information criterion (AIC; Akaike, 1974), run on the CIPRES gateway (<https://www.phylo.org>, Miller & al., 2010) were implemented for each partition; the parameters statefreq, revmat, shape, and pinvar were all unlinked between the partitions. Ten million generations were performed for analyses of the combined dataset, with a final deviation of split frequencies of 0.007. Parameters from the independent runs were inspected with Tracer v.1.6 (Rambaut & al., 2014) to find where the chains converged. The first 5000 trees (50%) of each run were discarded as burn-in and the remaining 10,000 trees summarized in a 50% majority-rule consensus tree, with

Table 2. Alignment characteristics.

	<i>trnT-L</i>	<i>trnLLF</i>	<i>rps16</i>	<i>psbA-trnH</i>	ITS1	5.8S	ITS2	At2g06530a	At2g34620b	Σ
Number of aligned positions	1416	1162	1050	352 (1951 uncured)	323	166	315	508	487	5779
Number of variable characters	529	347	354	210 (1103 uncured)	237	74	232	264	207	2244
Number of parsimony-informative characters	281	194	194	141 (634 uncured)	184	34	164	153	111	1315
Number of missing accessions (ingroup)	26	6	38	80	41	41	41	80	109	
Number of undetermined positions (missing characters and gaps; ingroup, in percent)	50.7	30.1	35.7	44.9 (84.2 uncured)	38.5	20.9	40.3	46.3	50.9	41.0
Model of evolution (AIC)	TVM+ Γ	TVM+ Γ	GTR+I+ Γ	TIM3+ Γ	TIM3+ Γ	SYM+I	GTR+ Γ	TIM3+ Γ	TVM+ Γ	
Maximum proportional sequence difference (ingroup)	0.07	0.05	0.03	0.32 (uncured) 0.28 (cured)	0.27	0.16	0.3	0.1	0.07	

posterior probabilities as an estimate of support for nodes of the tree.

For a first exploratory approach to the biogeographical history of Marsdenieae, 10 areas were defined using the *World geographical scheme for recording plant distributions* (Brummitt, 2001) as guideline, but attributing the Arabian Peninsula to Africa, and southern China to tropical Asia: A, Africa, incl. the Arabian Peninsula; B, Madagascar; C, Europe + temperate Asia; D, tropical Asia (including southern China, Taiwan and Hainan); E, New Guinea; F, Australia; G, New Caledonia; H, North and Central America; I, Caribbean; J, South America. Cultivated samples and samples of neophytic plants were coded according to the known native area of the species. Coding was restricted to the origin of the sample in order not to blur the picture by possible cryptic species; an assumed wider species distribution is indicated in brackets (Appendix 1).

An ultrametric tree was constructed from a subsample of 1000 trees of both MrBayes runs, using penalized likelihood (Sanderson, 2002) as implemented in *ape::chronos* v.5.5 (Paradis, 2013). The root node (split between Secamoideae and Asclepiadoideae) was set to 44.5 Ma (stem age of Asclepiadoideae according to Fishbein & al., 2018), and an uncorrelated relaxed clock was applied. The resulting trees were imported in *TreeAnnotator* v.1.10 (Drummond & Rambaut, 2007) to calculate the maximum clade credibility tree, using the option “-heights ca” (“common ancestor trees”, aiming at summarizing clade ages across all posterior trees, avoiding negative branch lengths, Heled & Bouckaert, 2013).

The resulting tree was used as input for BioGeoBEARS v.1.1 (Matzke, 2013), a likelihood framework for the three common biogeographic models: dispersal and vicariance analysis (DIVA; Ronquist, 1997), dispersal-extinction-cladogenesis (DEC; Ree & al., 2005; Ree & Smith, 2008), and BayArea models (Landis & al., 2013), implemented in R (v.4.1.1; R Core Team, 2021). BioGeoBEARS (Matzke, 2013) can also add the founder event (+J) parameter to all models, allowing speciation and dispersal to occur simultaneously. It has been argued that likelihoods under the classical models and their +J variants cannot be compared because +J models are biased toward having higher likelihoods (see discussion in Matzke, 2021). Since only minor differences in ancestral area estimates under the +J models compared to estimates without this parameter were found (besides that model fit was generally much better for the +J models), only the classical models were considered here. For model comparison, we relied on log likelihoods and the sample size corrected Akaike information criterion (AICc).

■ RESULTS

General tree structure. — The phylogenetic trees derived from combined plastid and nuclear data (Fig. 3A,B; suppl. Figs. S1, S2) show Marsdenieae as a strongly ($BS_{ML} = 100\%$, $PP = 1$) supported tribe in sister group position ($BS_{ML} = 93\%$, $PP = 1$) to Ceropegieae ($BS_{ML} = 98\%$, $PP = 1$). Most taxa fall in two well-supported species-rich clades, one

strongly supported ($BS_{ML} = 100\%$, $PP = 1$) clade exclusively comprising taxa of Southeast Asia, Australia and the Pacific area (A in Fig. 3A; henceforth termed Asia-Pacific Clade), the other one ($BS_{ML} = 98\%$, $PP = 1$) ranging over the whole distribution area of Marsdenieae (B in Fig. 3B; henceforth termed Cosmopolitan Clade). A poorly supported ($BS_{ML} = 63\%$, $PP = 0.77$) small clade of two Malagasy species (*Sicyocarpus* Bojer) and the African *Rhysolobium dumosum* E.Mey. (C in Fig. 3B; henceforth termed Afro-Malagasy Clade) forms a polytomy with these two clades but is retrieved as unsupported sister to the Cosmopolitan Clade in the completely resolved tree constructed for input in BioGeoBEARS.

Inside the Asia-Pacific Clade (A in Fig. 3A) and the Cosmopolitan Clade (B in Fig. 3B), five main subclades each (I–V) with varying support were retrieved, while there are two well-supported subclades in the Afro-Malagasy Clade (C in Fig. 3B). The clades identified in Marsdenieae correspond in some cases to currently accepted genera, e.g., *Sarcolobus* R.Br., *Telosma* (Endress & al., 2018), but also to genera that were placed in synonymy in recent classifications but had been recognized by nineteenth century taxonomists, such as Wenceslas Bojer (*Sicyocarpus* in the Afro-Malagasy Clade, C in Fig. 3B) or Robert Brown (*Gymnema* in subclade BIV of the Cosmopolitan Clade, Fig. 3B; *Leichhardtia* R.Br. in subclade AIV of the Asia-Pacific Clade, Fig. 3A).

Position of the Afro-Malagasy Clade. — The Afro-Malagasy Clade ($BS_{ML} = 63\%$, $PP = 0.77$; C in Fig. 3B) is poorly supported. Analyses of the plastid dataset (with outgroups) show the same polytomy among the three main clades as the combined dataset, with higher support than the combined dataset for monophyly of the Afro-Malagasy clade ($BS_{ML} = 93.2\%$, $PP = 1$; suppl. Figs. S3, S4). Analyses of the plastid and the nuclear datasets without outgroups reveal the same basic structure for both datasets (Fig. 4). Both topologies can be rooted to render the two large clades A (Asia-Pacific Clade) and B (Cosmopolitan Clade) monophyletic, while the two genera of the Afro-Malagasy clade are almost equidistant to both. The main difference lies in strong support for the Afro-Malagasy clade in the plastid dataset ($BS_{ML} = 96\%$, Fig. 4A), while no rooting can render the two genera of the Afro-Malagasy clade into a monophyletic group in the nuclear dataset (Fig. 4B, suppl. Fig. S7–S9). This might, however, reflect either the lack of an outgroup for the nuclear dataset or the poor sampling of this clade in the nuclear dataset, in which two of the five included samples have no nuclear data, and there is no At2g06530a sequence for *Marsdenia cordifolia* Choux (*Sicyocarpus*), and no ITS2 sequence for *Rhysolobium* E.Mey.

ML analyses of the individual nuclear datasets ITS1, ITS2, At2g06530a, At2g34620b and 5.8S (suppl. Figs. S10–S14) are less resolved and supported than the combined dataset (suppl. Fig. S8), but there are no well-supported incongruences among them. Only the At2g06530a tree can be rooted to render clades A and B monophyletic (suppl. Fig. S12). In the ITS1 (suppl. Fig. S10) and ITS2 (suppl. Fig. S11) topologies, *Marsdenia cordifolia* of the Afro-Malagasy clade (clade C) is

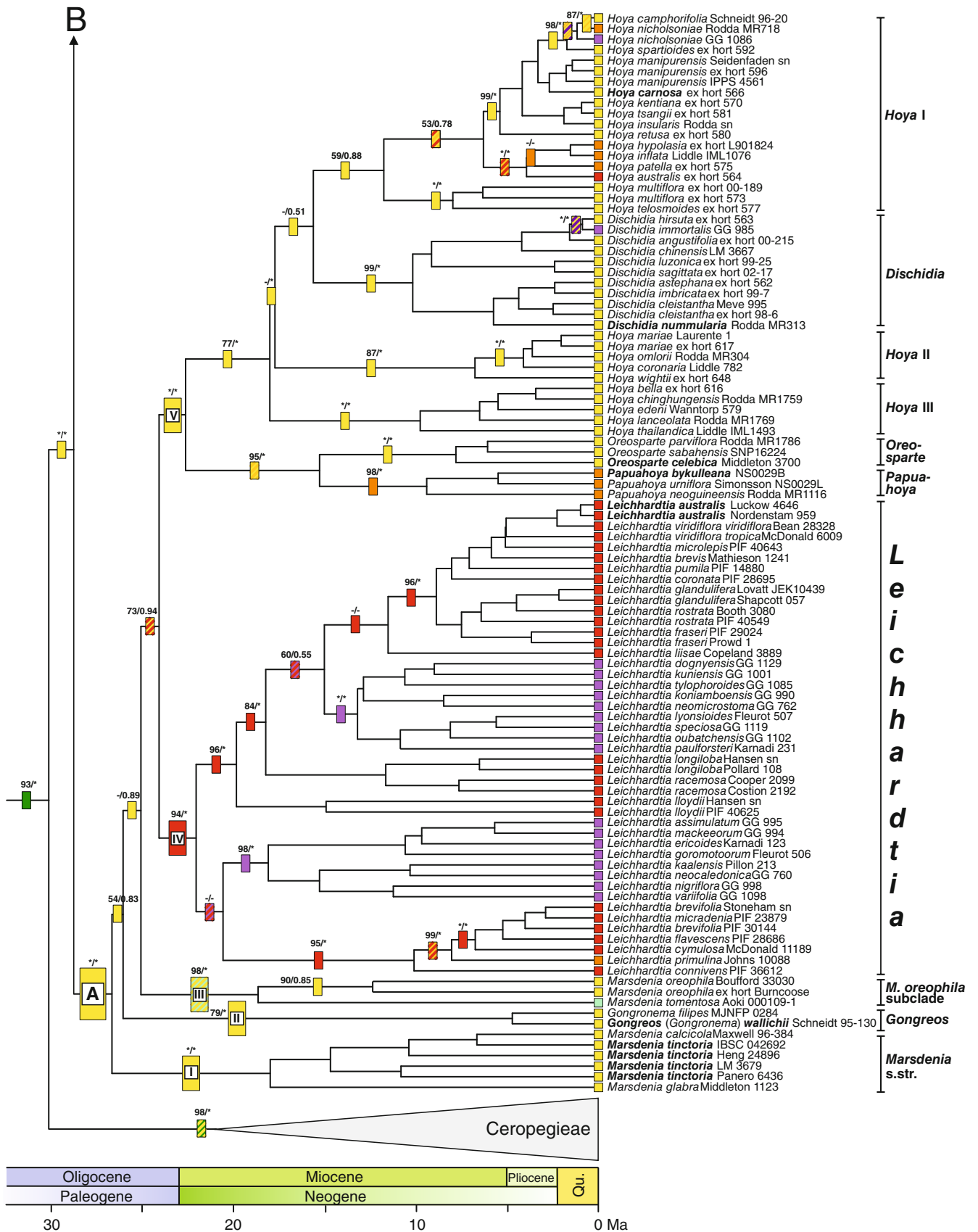


Fig. 3. For caption, see p. 843. (Continues)

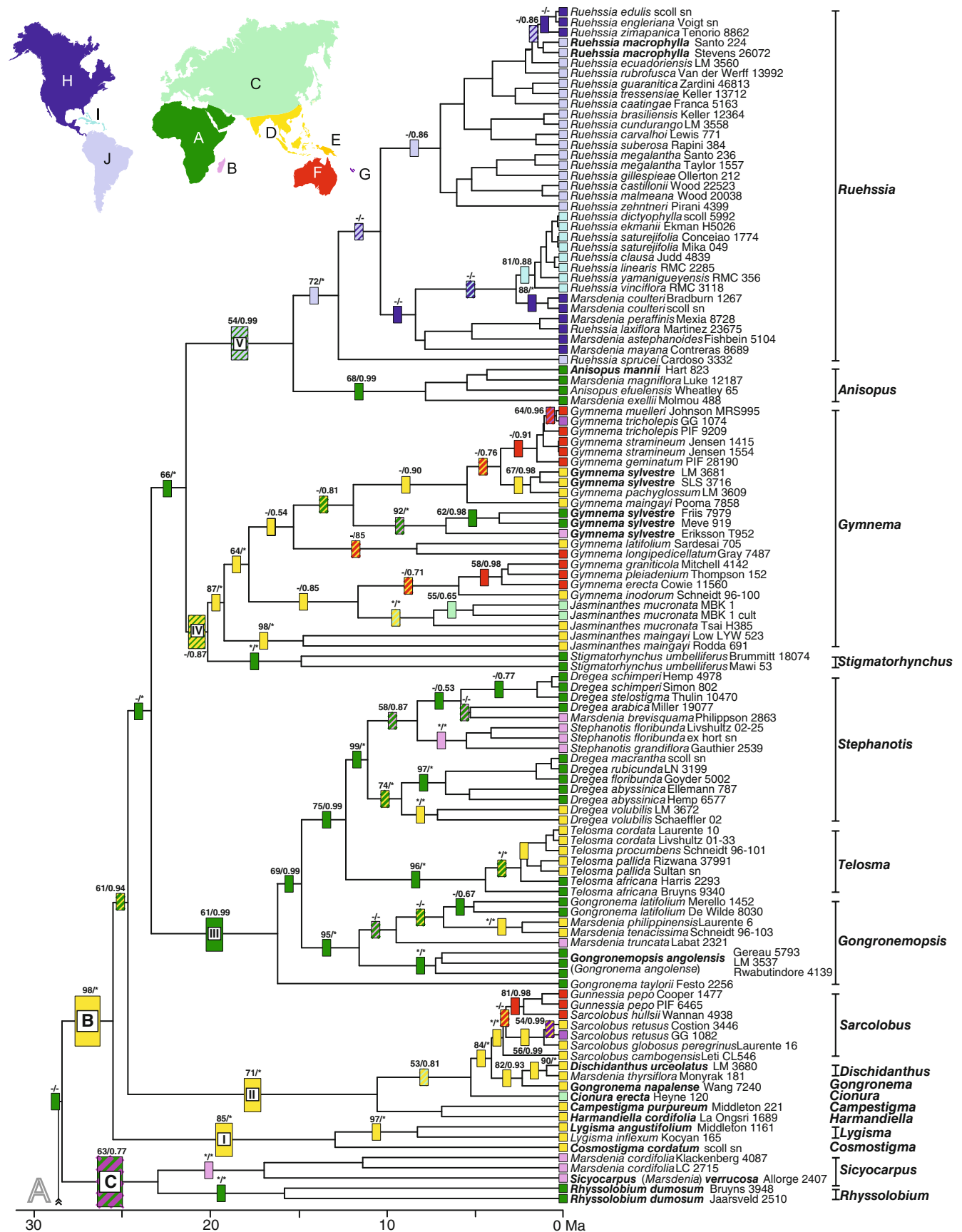


Fig. 3. Continued. For caption, see p. 843.

nested among the sublineages of the Asia-Pacific Clade (clade A). Adding an ITS1-only sequence of *Rhysolobium dumosum* to the ITS1 dataset (GenBank accession AM233378; only complete ITS sequences have been included in the total analyses) also retrieves it among the sublineages of the Asia-Pacific Clade, but not monophyletic with *Marsdenia cordifolia* (suppl. Fig. S10). In the At2g34620b topology, in contrast, *Rhysolobium dumosum* is nested among the sublineages of the Cosmopolitan Clade (clade B; suppl. Fig. S13). In the 5.8S topology (suppl. Fig. S14), no rooting can render the Asia-Pacific Clade (A) and the Cosmopolitan Clade (B) monophyletic relative to each other. However, none of these topologies is well-supported, and there is no compelling evidence that these incongruences indicate a hybrid origin for any lineage rather than insufficient phylogenetic signal in these short sequence alignments.

Asia-Pacific Clade. — The Asia-Pacific Clade (BS_{ML} = 100%, PP = 1; A in Fig. 3A) comprises five moderately to strongly supported subclades. Subclade AI (BS_{ML} = 100%, PP = 1) includes the type of *Marsdenia*, *M. tinctoria* R.Br., and is weakly supported as sister to the remainder of the Asia-Pacific Clade (BS_{ML} = 54%, PP = 0.83). Subclade AII, *Gongronema wallichii* (Wight) Decne.–*G. filipes* Kerr (*Gongreos*) (BS_{ML} = 79%, PP = 1), and subclade AIII, a strongly supported (BS_{ML} = 98%, PP = 1) subclade of the Far Eastern *M. tomentosa* C.Morren & Decne. and *M. oreophila* W.W. Sm., are successive sister groups to two large, well-supported clades, subclade AIV, *Leichhardtia* (BS_{ML} = 94%, PP = 1) and subclade AV, the *Hoya* alliance (BS_{ML} = 100%, PP = 1). However, the relationships among the five subclades have poor support (BS_{ML} < 50%–70%, PP = 0.83–0.94).

The well-supported *Leichhardtia* clade (AIV; BS_{ML} = 94%, PP = 1), a species-rich radiation in Australia, New Guinea and New Caledonia, includes two well-supported (BS_{ML} = 98%–100%, PP = 1) subclades of New Caledonian species. One of these is unsupported as sister to a well-supported (BS_{ML} = 95%, PP = 1) Australian subclade that also includes the only *Leichhardtia* species sampled from New Guinea (*L. primulina* (P.I.Forst.) P.I.Forst.). The other New Caledonian *Leichhardtia* clade is nested in a well-supported (BS_{ML} = 96%, PP = 1) clade of Australian species, among them the type of *Leichhardtia*, *L. australis*.

The strongly supported *Hoya* alliance (AV; BS_{ML} = 100%, PP = 1) includes *Hoya* s.l., *Dischidia*, *Oreosparte* Schltr., and *Papuahoya* Rodda & Simonsson (Fig. 3A). Within the *Hoya* alliance, a well-supported clade (BS_{ML} = 95%, PP = 1) of the two

strongly supported genera *Papuahoya* (BS_{ML} = 98%, PP = 1) and *Oreosparte* (BS_{ML} = 100%, PP = 1), is sister to the only moderately supported clade of *Hoya* s.l. and *Dischidia* (BS_{ML} = 77%, PP = 1). *Hoya* s.l. falls in three clades (designated as *Hoya* I, II, and III). The most species-rich clade, *Hoya* I, which includes the type *H. carnosa* (L.f.) R.Br., is poorly supported (BS_{ML} = 59%, PP = 0.88). *Hoya* II (BS_{ML} = 87%, PP = 1) includes *H. wightii* Hook.f., *H. coronaria* Blume and two species traditionally treated under *Clemensiella* Schltr. (*H. mariae* (Schltr.) L.Wanntorp & Meve, and *H. omlorii* (Livsh. & Meve) L.Wanntorp & Meve). *Hoya* III (corresponding to *Hoya* sect. *Ancistrostemma* Hook.f.) comprises *H. chinghungensis* (Y.Tsiang & P.T.Li) M.G.Gilbert & al., *H. edeni* King ex Hook.f., *H. lanceolata* Wall. ex D.Don and *H. thailandica* Thaithong and is strongly supported (BS_{ML} = 100%, PP = 1). The relationships of these three subclades to each other and to the strongly supported *Dischidia* (BS_{ML} = 99%, PP = 1) are unsupported or weakly supported.

Cosmopolitan Clade. — The well-supported Cosmopolitan Clade (BS_{ML} = 98%, PP = 1; B in Fig. 3B) comprises five, mostly poorly supported subclades. Subclade BI (BS_{ML} = 85%, PP = 1) comprises the Asian *Lygisma* Hook.f. (BS_{ML} = 97%, PP = 1) and *Cosmostigma* Wight, in poorly supported sister-group position to all other genera of the Cosmopolitan Clade (BS_{ML} = 61%, PP = 0.94). Subclade BII is moderately supported (BS_{ML} = 71%, PP = 1) and includes the tropical Asian monotypic genera *Campestigma* Pierre ex Costantin and *Harmandiella*, the Eurasian *Cionura*, and a moderately supported clade of tropical Asian genera (*Gongronema* (Endl.) Decne. s.str. + *Dischidanthus* Tsiang + *Sarcolobus* (BS_{ML} = 84%, PP = 1). The monotypic Chinese genus *Dischidanthus* is sister to *Marsdenia thyrsoflora* Hook.f. (BS_{ML} = 90%, PP = 1). *Sarcolobus* is strongly supported (BS_{ML} = 100%, PP = 1) and the monotypic Australian genus *Gunnessia* is nested in it.

Subclade BIII (BS_{ML} = 61%, PP = 0.99) includes both Asian and African taxa. *Gongronema taylorii* (Schltr. & Rendle) Bullock is poorly supported as sister to a clade (BS_{ML} = 69%, PP = 0.99) that includes (1) a well-supported group of African species hitherto placed in *Gongronema* along with two Asian and one Malagasy *Marsdenia* species (BS_{ML} = 95%, PP = 1); (2) the well-supported *Telosma* (BS_{ML} = 96%, PP = 1); and (3) the likewise well-supported wider *Stephanotis* alliance (BS_{ML} = 99%, PP = 1), comprising, besides the Malagasy *Stephanotis* s.str., *Marsdenia brevisquama* Jum. & H.Perrier from Madagascar and species of *Dregea* from Africa, Arabia (Socotra), and Asia.

Fig. 3. Phylogeny and biogeography of Marsdenieae. Result from DIVALIKE analysis in BioGeoBEARS based on 1000 trees retrieved from Bayesian analysis of 255 samples, and combined plastid and nuclear datasets; maxareas set to 4 (d = 0.0023; e = 0; j = 0; LnL = -314.48; see suppl. Fig. S15). Of the outgroups, only Ceropegieae are shown (summarized as triangle). Numbers at important nodes indicate bootstrap percentages / posterior probability from the trees shown in suppl. Figs. S1 and S2. * indicates 100% bootstrap support / PP = 1. Taxa in **bold** indicate samples attributed to the type of the genus. Area designations: A, Africa, incl. the Arabian Peninsula; B, Madagascar; C, Europe + temperate Asia; D, tropical Asia (including southern China, Taiwan and Hainan); E, New Guinea; F, Australia; G, New Caledonia; H, North and Central America; I, Caribbean; J, South America. Clade designations: A, Asia-Pacific Clade; B, Cosmopolitan Clade; C, Afro-Malagasy Clade. Both the Asia-Pacific and the Cosmopolitan Clade fall in five major subclades, denoted with I–V.

Monophyly of the clade formed by subclades BIV and BV is ambiguous (strongly supported in Bayesian analysis, weakly supported by ML; $BS_{ML} = 66\%$, $PP = 1$). Subclade BIV ($BS_{ML} < 50$, $PP = 0.87$) consists of the small African *Stigmatorhynchus* Schltr. and the larger *Gymnema* (incl. *Jasminanthes* Blume) alliance ($BS_{ML} = 87\%$, $PP = 1$). Subclade BV is ambiguously supported ($BS_{ML} = 54\%$, $PP = 0.99$) and includes the small, tropical African alliance of *Anisopus* N.E.Br. and two *Marsdenia* species (weakly supported, $BS_{ML} = 68\%$, $PP = 0.99$) as sister to the moderately supported ($BS_{ML} = 72\%$, $PP = 1$), exclusively American *Ruehssia* clade. While all American Marsdenieae species studied so far are retrieved in *Ruehssia*, nomenclatural transfers are not yet

complete for the Central American and Caribbean species that have combinations only in *Marsdenia*.

Biogeography. — Of the three models implemented in BioGeoBEARS, the DIVALIKE model performed best, with the DEC model performing only a little worse, whereas the BAYAREALIKE model performed much worse (suppl. Table S1, suppl. Figs. S15–S20). The main difference between the results of the DIVALIKE and the DEC model concerns the ancestral area of Marsdenieae, reconstructed as tropical Asia in DIVALIKE (Fig. 3, suppl. Fig. S15); and as widespread (tropical Asia+Africa) in DEC (suppl. Fig. S17). The first branching lineages in the Asia-Pacific Clade are distributed in tropical Asia, one of them (*M. oreophila* subclade,

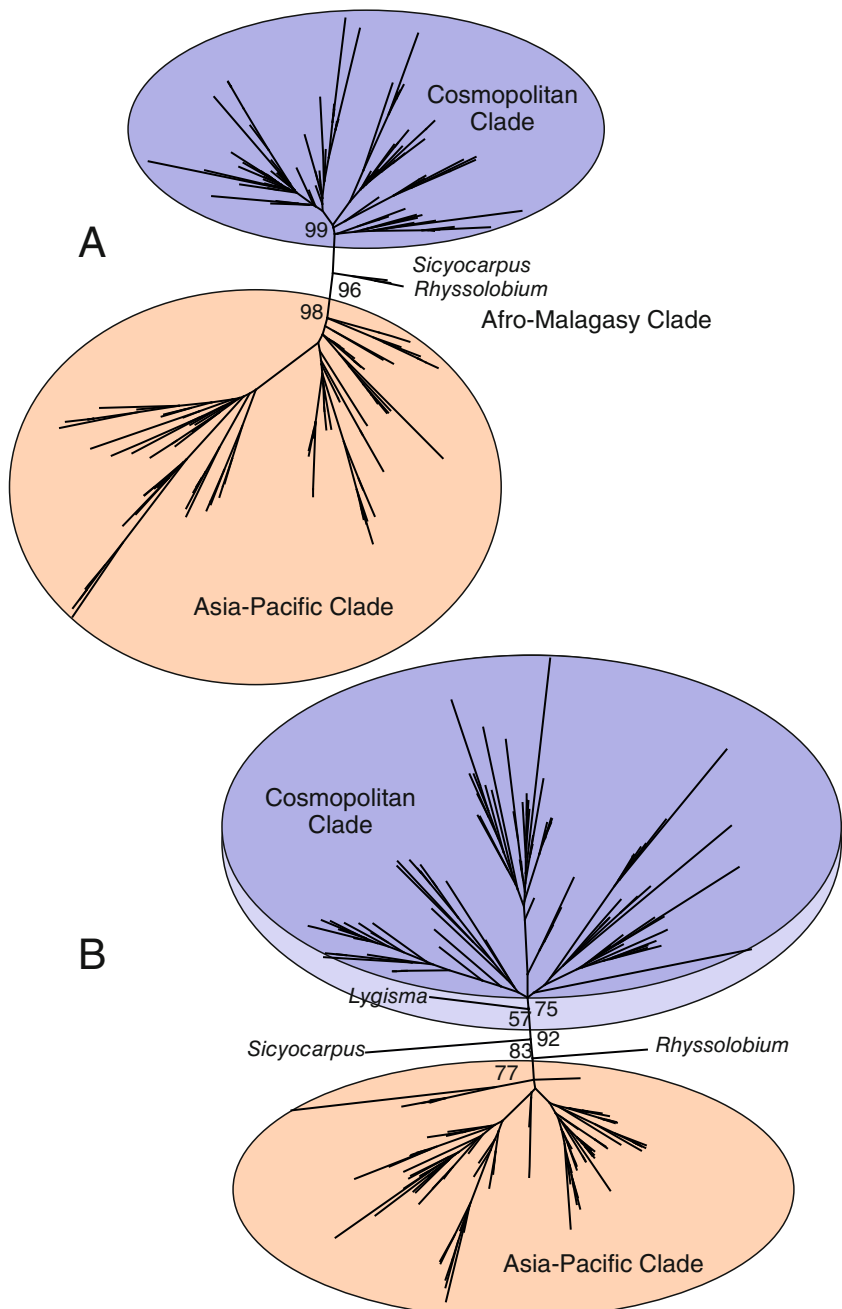


Fig. 4. Data congruence, depicted in unrooted phylograms. **A**, ML phylogram of the plastid dataset (219 terminals), drawn from suppl. Fig. S5; **B**, Nuclear dataset (199 terminals). Numbers indicate bootstrap percentages (BS_{ML}).

subclade AIII) expanding into temperate Asia. *Leichhardtia* (subclade AIV), sister to the predominantly tropical Asian *Hoya* alliance (subclade AV), radiated in Australia and the Pacific, reaching New Caledonia independently twice (Fig. 3A). In the *Hoya* alliance (subclade AV), *Papuahoya* constitutes an early expansion into New Guinea; other area expansions in the *Hoya* alliance to Australia, New Caledonia, and New Guinea are of more recent origin (Fig. 3A).

The two first-branching lineages of the Cosmopolitan Clade (BI and BII in Fig. 3B) are also tropical Asian, expanding into temperate Eurasia with *Cionura*, and to the Pacific area with *Sarcobolus* (Australia, New Caledonia, and possibly also to New Guinea, from where no sample was available). The first branching lineages of subclades BIII–BV are always African (*Gongronema taylorii*, *Stigmatorhynchus*, *Anisopus*). Subclades BIII and BIV are both widely distributed in the Paleotropics, including Africa, Madagascar, and tropical Asia, but only subclade BIV has expanded into the Pacific area (Australia, New Caledonia, and possibly also to New Guinea with *Gymnema*, from where no sample was available). In subclade BV, *Ruehssia* expands the area of Marsdenieae to the Neotropics, first to South America followed by two dispersals to Central America. One of the two Central American radiations gave rise to the Caribbean radiation.

The two genera of the Afro-Malagasy Clade (*Rhyssolobium*, *Sicyocarpus*) make biogeographic reconstruction difficult due to their almost equidistant position to the two larger clades with support for the clade only derived from the plastid dataset (suppl. Figs. S5–S13), but suggest an African and also Malagasy element early in the history of Marsdenieae.

Divergence time analysis reconstructs stem age of Marsdenieae in the Oligocene at 30.2 Ma (suppl. Table S2, suppl. Fig. S21), followed rapidly by the divergence of the three main clades (Asia-Pacific Clade, Cosmopolitan Clade, Afro-Malagasy Clade) between 28.8 Ma and 26.5 Ma. Stem-age of the *Hoya* alliance and of *Leichhardtia* is estimated at 24.1 Ma, and stem-ages of the two *Leichhardtia*-clades in New Caledonia at 20.6 Ma and 15 Ma, respectively. Stem ages of the widespread African-Asian genera *Gongronemopsis*, *Telosma*, *Stephanotis*, and *Gymnema* are estimated in the Mid-Miocene, at 14.9 Ma, 12.4 Ma, 12.4 Ma, and 20.1 Ma, respectively. Stem-age of *Ruehssia* is estimated at 15.4 Ma, the two Central American subclades at 12.1 Ma and 1.45 Ma, respectively, and the Caribbean subclade at 2.69 Ma.

DISCUSSION

Prior to the present study, the largest molecular phylogeny of Marsdenieae included 93 species (Espírito Santo & al., 2019) and showed that the large genus *Marsdenia* was probably polyphyletic. However, their analysis was focused on the New World, with most species now transferred to *Ruehssia* (for references, see under “2.11 *Ruehssia*”). The present work includes 171 Marsdenieae species from all areas of its distribution and presents the most comprehensive analysis of Marsdenieae to

date, further supporting the polyphyly of *Marsdenia* s.l. As in the topology of Espírito Santo & al. (2019), most Marsdenieae species fall in two large clades, the Asia-Pacific Clade (clade A) and the Cosmopolitan Clade (clade B). The small Afro-Malagasy Clade (Clade C) was represented only by *Rhyssolobium dumosum* and *Marsdenia verrucosa* in the topology of Espírito Santo & al. (2019). Of the three species with incongruent positions between nuclear (ITS, ETS) and plastid (*trnL-F*, *psbD-trnT*) datasets in Espírito Santo & al. (2019: fig. 2), two, *M. tinctoria* and *M. oreophila*, were firmly embedded in the Asia-Pacific Clade by both the plastid and the nuclear datasets in our analysis (suppl. Figs. S3–S13). The third incongruent species of Espírito Santo & al. (2019) is *Rhyssolobium dumosum*, which is sister to *Marsdenia verrucosa* (*Sicyocarpus*) in the analysis of the plastid dataset of Espírito Santo & al. (2019), forming a clade corresponding to our Afro-Malagasy Clade (the third species of the Afro-Malagasy clade, *Marsdenia cordifolia*, was not included in the dataset of Espírito Santo & al., 2019). Both in Espírito Santo & al. (2019) and in our analysis, the monophyly of the Afro-Malagasy Clade is supported only by the plastid topology (Fig. 4, suppl. Figs. S3–S14). Analyses of more slowly evolving nuclear loci are necessary to test the monophyly of the Afro-Malagasy Clade with outgroup rooting.

Relationships among the three main clades are unresolved in the present analysis, and the uncertain position of the two genera of the Afro-Malagasy Clade does affect the reconstruction of the ancestral area of Marsdenieae and needs further study. While the DIVALIKE model reconstructs tropical Asia as ancestral area for the tribe (though with a rather high probability for Africa or Africa-tropical Asia, suppl. Fig. S16), the DEC model gives widespread Africa-tropical Asia as ancestral area, a result also obtained by Bitencourt & al. (2021). In our analysis, stem age of Marsdenieae is estimated to be somewhat younger (30.2 Ma) than in Fishbein & al. (2018) with 39.5 Ma, and crown age somewhat older (28.8 Ma vs. 22.8 Ma) than in Fishbein & al. (2018).

The Asia-Pacific Clade has undergone extensive radiation in tropical Asia, while the Cosmopolitan Clade has spread throughout the tropics, most likely also starting from Asia (Fig. 3A,B). Early diversification in the Asia-Pacific Clade, resulting in five major subclades AI–AV took place in the late Oligocene (stem ages 26.7–24.1 Ma, suppl. Table S2), while diversification within subclades AI–AV started in the Miocene (crown ages 22.6–18 Ma); except for subclade AII (*Gongreos*), for which a crown age in the Pliocene (4.75 Ma) is reconstructed. From tropical Asia, the ancestors of *Leichhardtia* colonized Australia as early as the Oligocene-Miocene boundary, possibly in connection with the initial phase of the collision of the Australian Plate with the Philippine Plate close to the Oligocene-Miocene boundary (Morley, 2003). From Australia, *Leichhardtia* successfully dispersed to New Caledonia twice in the Miocene and today constitutes the second most species-rich Apocynaceae genus in the island with 19 species (Liede-Schumann & al., 2020). Both long-distance colonization events of the two New Caledonian *Leichhardtia*

lineages (stem ages 20.6 Ma and 15.1 Ma; crown ages 18.2 Ma and 13.3 Ma, respectively) occurred after presumed land re-emergence in the region (dated ca. 25 Ma, Maurizot & Campbell, 2020), like most other plant lineages studied (Barrabé & al., 2019). *Leichhardtia* also reached New Guinea from Australia at least once (with *L. primulina* and several species not included in the present study, see Forster, 2021). In the *Hoya* alliance, New Guinea has been colonized early from tropical Asia by *Papuahoya* (stem age 17.6 Ma). For a detailed phylogeography of *Hoya* s.l. itself, see Wanntorp & al. (2014).

In the Cosmopolitan Clade, early diversification also resulted in five major subclades BI–BV and occurred from the late Oligocene to the early Miocene (stem ages 25.6–21.4 Ma). Diversification within these five subclades occurred considerably later (20.1–10.6 Ma) than in all subclades of the Asia-Pacific Clade (22.6–18 Ma) except for subclade AII (*Gongreos*). Subclade BII is notable for its morphologically distinct, monotypic or very small genera (*Harmandiella*, *Campestigma*, *Cionura*, *Gongronema* s.str., *Dischidanthus*) in tropical Asia and Eurasia. Also in subclade BII, a Pliocene stem age (4.1 Ma) is reconstructed for the littoral and rheophytic *Sarcolobus*. The recently described Asian species *S. cambogensis* (McHone & al., 2015) is sister to the remaining species that have apparently spread rapidly along the Asian and Pacific coasts. Subclades BIII–BV expanded over a much larger area than the earlier diversifying subclades of the Asia-Pacific Clade. Subclade BIII is widespread over Africa, Madagascar and Asia, subclade BIV expanded additionally to Australia and New Guinea (see Forster, 2021) and New Caledonia, and subclade BV enlarged the area of Marsdenieae to the Neotropics in the mid-Miocene with *Ruehssia*, in agreement with the results of Rapini & al. (2007). The small, predominantly West African genus *Anisopus* is sister to the large *Ruehssia* (Table 1), supporting the idea that the progenitors of *Ruehssia* (and thus of all New World Marsdenieae) probably reached the American continent from West Africa, another example of Miocene transatlantic dispersal (see Renner, 2005, and references therein). As in Espirito Santo & al. (2019) and Keller & al. (2020), the Amazonian species *R. sprucei* (W.Rothe) F.Esp. Santo & Rapini is sister to all remaining species in the genus (albeit here without support), suggesting a South American origin for *Ruehssia*. Central America was reached twice, the first time soon after the arrival of the genus in the Neotropics (12.1 Ma), corresponding to the well-supported (PP = 0.98) clade B in Espirito Santo & al. (2019), and a second time as late as the Pleistocene (1.5 Ma). These dates correspond to the closure of the Central American Seaway (12–10 Ma) and the establishment of a continuous terrestrial landscape across the Isthmus of Panama (from 3.5 Ma onwards; Jaramillo, 2018). The older Central American lineage gave rise to a Caribbean lineage in the late Pliocene (2.7 Ma), coinciding with a presumed terrestrial connection between the islands at the Plio-Pleistocene transition (Iturralde-Vinent, 2006).

While all New World taxa so far studied fall into a coherent monophyletic group, there has been considerable

exchange between Africa and Asia in several lineages of subclades BIII and BIV. The Pacific area has been only marginally involved in this exchange (with *Gymnema*), an observation also confirmed for subclade BII of the Cosmopolitan Clade with *Sarcolobus* and for the *Hoya* alliance (subclade AV). The bulk of Marsdenieae species in the Pacific area (Australia, New Guinea, New Caledonia) belongs to a single lineage, *Leichhardtia*. Madagascar, in contrast, harbors representatives of several genera of subclades BIII and BIV of the Cosmopolitan Clade (*Gongronemopsis*, *Telosma* [not sampled here], *Stephanotis*, *Gymnema*), along with the endemic *Sicyocarpus*, and seems to have played an important role in the biogeographic history of these genera.

A better sampled analysis will be necessary to resolve the biogeographic history of the larger lineages identified here, in particular for subclades BIII and BIV of the Cosmopolitan Clade and in the *Hoya* alliance (subclade AV). Our calibration point, the stem age of Asclepiadoideae at 44.5 Ma (Fishbein & al., 2018), corresponds roughly to the oldest known Asclepiadoideae fossils, seed impressions from the central Qinghai-Tibetan Plateau (Del Rio & al., 2020). No fossils of Marsdenieae are known yet. In addition, we coded sample origin and not presumed species distribution for widespread species, which might have influenced reconstruction of ancestral areas. However, this is justified by the observation that only nine ingroup species are reported from more than one area (Appendix 1). Four of these were sampled from multiple areas and in three cases, these samples were not monophyletic (*Gymnema sylvestre*, *G. tricholepis* Schltr., *Hoya nicholsoniae* F.Muell.), while they were monophyletic only in one case (*Jasminanthes mucronata* (Blanco) W.D.Stevens & P.T.Li). This is indicative that more work is necessary to test species circumscriptions within widespread species complexes.

While our analysis throws a first light on the biogeographical history of a so far neglected tribe in Asclepiadoideae, the focus of the present paper lies on an understanding of the lineages constituting Marsdenieae and on providing a framework for a stable classification in the tribe. Several roads could be pursued to arrive at a taxonomy based on monophyletic groups in Marsdenieae. First, the whole tribe could be united in a single genus, *Marsdenia*. However, this would mean that large and horticulturally important genera, such as *Hoya* and *Dischidia*, would be sunk into obscurity. Additionally, tremendous renaming would be necessary. Second, the two main, well-supported clades could be circumscribed as two genera. In this case, the Asia-Pacific Clade, comprising the type of *Marsdenia*, *M. tinctoria*, would also comprise *Hoya* and *Dischidia*, meaning, that all *Hoya* species would need to be renamed to *Marsdenia*. In addition, the monophyletic and morphologically well-defined *Hoya* alliance would need to be included in a morphologically diverse, hard to circumscribe and thus diffuse group. The Cosmopolitan Clade is hardly less problematic, albeit it does not contain charismatic taxa such as *Hoya*. However, it includes all American species of the

tribe, also asking for large-scale renaming, in this case to *Stephanotis* Thouars. Lastly, and this is the solution preferred here, monophyletic, well-supported and morphologically at least rather coherent groups are considered as genera. While this solution also requires new names for well-known taxa, it creates the least havoc with the existing system of classification in Marsdenieae. Furthermore, future evidence will be easier to incorporate if not so many taxa are affected. For most of the groups recognized here, historical names are available, which need to be reinstated, indicating that these plants have been considered for a long time by workers using what are now construed as morphological synapomorphies.

This phylogeny also highlights the extreme variability of certain morphological characters in Asclepiadoideae and, in particular, Marsdenieae. Almost every clade has at least one taxon with long-tubed salverform corollas apparently adapted to Lepidopteran pollination (e.g., *Jasminanthes*, *Stephanotis* s.str., *Leichhardtia speciosa* (Baill.) Liede, Gâteblé & Meve, *Ruehssia caatingae* (Morillo) F.Esp.Santo & Rapini). Likewise, color of latex, shape of leaves, indumentum, inflorescence structure, corolla trichomes, style-head or follicle characters are at best indicative of relationships, but cannot diagnose clades unambiguously. For example, in *Marsdenia glabra* Costantin, the typical blue coloration of dried stems and leaves characteristic for *Marsdenia* s.str. is usually not observed; *M. brevisquama* has white latex, while the other members of the *Stephanotis* clade have colorless latex. This is particularly true for traits of the larger radiations of *Stephanotis*, *Leichhardtia*, and *Ruehssia*, for which geographical distribution is often the better indicator of relationship than morphology.

From the nomenclatural point of view, we here take the conservative approach and suggest only transfers for which we consider the evidence presented here as sufficient. This includes the African species of *Gongronema*, which form a lineage distinct from *Gongronema* s.str., and a new genus, *Gongronemopsis* (within subclade BIII of the Cosmopolitan clade, Fig. 3B) is described to accommodate these species. This new genus also includes some Asian members hitherto known under “*Marsdenia*”. Two Asian species, *Gongronema wallichii* and *G. filipes*, are neither monophyletic with *G. napalense* (Wall.) Decne., the type of *Gongronema*, nor with *Gongronemopsis*, but form the small, probably undersampled, subclade AII in the Asia-Pacific Clade (Fig. 3A) and are accommodated in another new genus, *Gongreos*.

Marsdenia oreophila + *M. tomentosa* constitute another independent clade. However, considering present morphological evidence, a relationship with the aberrant *M. jenkinsii* Hook.f. (*M. incisa* P.T.Li & Y.H.Li, see Rodda, 2019), the only species of *Sinomarsdenia* P.T.Li & J.J.Chen, cannot be excluded. As long as no sequenceable material of *M. jenkinsii* can be obtained, it is considered premature to effect nomenclatural changes for *M. oreophila* and *M. tomentosa*.

Jasminanthes mucronata (Blanco) W.D.Stevens & P.T.Li and *J. maingayi* (Hook.f.) Rodda are embedded in the

Gymnema clade, but the type of *Jasminanthes* (*J. suaveolens* Blume) has not been sequenced so far, so formal transfer of *Jasminanthes* species is postponed for now.

Hoya species are separated in three clades; however, the type of the genus, *H. carnosa*, is member of the only poorly supported clade *Hoya* I (BS_{ML} = 59%, PP = 0.88). *Hoya* II (BS_{ML} = 87% PP = 1) corresponds to the genus *Clemensiella*, which could be resurrected, while a new genus name could be coined for the strongly supported *Hoya* III (BS_{ML} = 100%, PP = 1). However, the relationships between these and other clades in the *Hoya* alliance are not supported. Other analyses (Rodda & al., 2020; Rodda & Niissalo, 2021) whilst supporting the separation of *Hoya* III (clade I of Rodda & al., 2020), do not support the recognition of *Clemensiella* as a separate genus unless *Hoya* is further divided into several smaller genera. In the present analysis, *Hoya* is paraphyletic without *Dischidia*, in agreement with, e.g., Wanntorp & al. (2014), while plastome analysis (Rodda & Niissalo, 2021) retrieved *Dischidia* as sister genus to *Hoya*. Because the relationships between the *Hoya* clades and between *Hoya* and *Dischidia* vary considerably between different datasets analyzed (compare, e.g., Rodda & al., 2020; Rodda & Niissalo, 2021 and the present study) and are mostly poorly supported, no nomenclatural changes in the *Hoya* alliance are suggested here.

In Madagascar, *Sicyocarpus* is available as a name for the small Malagasy *Marsdenia* species group in the Afro-Malagasy Clade, and evidence is sufficient to transfer the two species involved (*M. cordifolia*, *M. verrucosa*). However, not all Malagasy “*Marsdenia*” species belong to *Sicyocarpus*. *Marsdenia brevisquama*, together with the traditional *Stephanotis* species, is embedded in *Stephanotis* (in subclade BIII of the Cosmopolitan Clade). *Marsdenia truncata* Jum. & H.Perrier, however, is retrieved in the new genus *Gongronemopsis* comprising African and Asian *Gongronema* species (in subclade BIII of the Cosmopolitan Clade). With a species of *Gymnema* (*G. sylvestre*) and of *Telosma* (*T. madagascariensis* W.D.Stevens, not included in the present study) also present on the island, Madagascar harbors at least five lineages of Marsdenieae.

In Africa, *Marsdenia exellii* C.Norman and *M. magniflora* P.T.Li (= *M. normaniana* Omlor) can be transferred to *Anisopus* safely, raising the number of species of the latter to four. The bulk of species in Africa belong to the genera *Stephanotis* and *Gongronemopsis*. *Stigmatorhynchus* (subclade BIII of the Cosmopolitan Clade) and *Rhyssolobium* (Afro-Malagasy Clade) are endemic to arid areas of continental Africa and possibly constitute relict genera. *Telosma* possibly evolved in Africa, but diversified later in Asia. *Gymnema*, by contrast, reached Africa only relatively late in its history with one species.

In Australasia, the single species of *Gunnessia*, *G. pepo* P.I.Forst., can be transferred safely to *Sarcolobus*. All species of “*Marsdenia*” hitherto sequenced from Australasia either fall in the *Leichhardtia* or in the *Gymnema* clade.

The transfer of the New Caledonian species to *Leichhardtia* is complete (Liede-Schumann & al., 2020); for Australia, many species have been originally published under *Gymnema* or *Leichhardtia*, for the remainder, the necessary transfers were recently proposed by Forster (2021). Establishing the phylogenetic positions of Marsdenieae species from New Guinea presents a particular problem because of the paucity of recently collected voucher material. Thus, the affinities of morphologically unusual New Guinean species presently remain largely unclear. Finally, there is a considerable number of Chinese, Indian and Southeast Asian *Marsdenia* or Marsdenieae taxa that are still unsequenced and thus await reconsideration of their generic affiliation in future. In addition, we will refrain from extensive transfers of species to the large genera *Gymnema* and *Ruehssia* because several such projects are presently under way.

■ CONCLUSIONS

The present paper presents the first densely sampled phylogeny of Marsdenieae, confirming the polyphyly of *Marsdenia* s.l. and establishing polyphyly for *Gongronema* s.l. Furthermore, it establishes two lineages (Asia-Pacific Clade, Cosmopolitan Clade) with entirely different phylogeographic histories, comprising almost all species studied. While both lineages started in tropical Asia, one (the Asia-Pacific Clade) expanded to Australia and the Pacific area producing two species-rich (>50 species) radiations (*Leichhardtia* and the *Hoya* alliance), while the other one (the Cosmopolitan Clade) became widespread over the tropics worldwide, generating one species-rich radiation (*Ruehssia*). Our analysis also identifies two species-poor “oddballs”, *Sicyocarpus* and *Rhyssolobium*, of which the position needs further study.

Even though almost a quarter of Marsdenieae species was studied here, and sampling included the morphological and geographic range within the tribe, it cannot be excluded that additional material will reveal additional lineages not retrieved here. Future studies should particularly focus on the small Asian genera not included here (*Asterostemma* Decne., *Cathetostemma* Blume, *Dolichopetalum* Tsiang, *Gymnemopsis* Costantin, *Heynella* Backer, *Pseudosarcolobus* Costantin, *Pycnorhachis* Benth., *Sinomarsdenia* P.T.Li & J.J.Chen, *Tetragonocarpus* Hassk., *Treutlera* Hook.), but also on a denser sampling particularly in subclades BIII and BIV of the Cosmopolitan Clade, of which the biogeographic history is anything but understood. Intensified study of *Gongreos* (subclade AII) and the *Marsdenia oreophila* subclade (subclade AIII) will possibly shed light on the early biogeographical history of the Asia-Pacific Clade.

Assignment of any Marsdenieae species to one of the genera recognized here by morphological characters only is difficult, because many characters previously used to

delimit genera, such as rostrate style-heads and long-tubular corollas, have evolved several times. Nevertheless, in many cases combinations of characters can be used to assign species that have not yet been sequenced to the correct genus outside “*Marsdenia* s.l.” in order to arrive at a classification based on monophyletic genera.

■ KEY TO THE GENERA

1. Neotropical species**Ruehssia**
1. Palaeotropical species2
2. Plants usually epiphytic; corolla lobes valvate in bud; seeds spindle-shaped3
2. Plants terrestrial; corolla lobes contorted to the right in bud; seeds usually dorsiventrally flattened.....6
3. Plants usually without adventitious roots4
3. Plants usually with adventitious roots5
4. Corona lobe apices bifid, plants from W Malesia and Sulawesi **Oreosparte**
4. Corona lobe apices entire, plants from New Guinea.....
..... **Papuahoya**
5. Flowers usually rotate, staminal corona lobes well developed, divided in distal, erect, apically toothed lobule with lateral keels for nectar and proximal, introrse, tooth-shaped lobule; pollinia usually with pellucid margin.....
..... **Hoya**
5. Flowers usually urn-shaped, staminal corona consisting of five stalked, apically bifid lobes or absent; pollinia without pellucid margin **Dischidia**
6. Plants often with conspicuous adventitious roots; leaves coriaceous or succulent, usually waxy or shiny7
6. Plants normally without adventitious roots; if leaves coriaceous, then not waxy or shiny8
7. Flowers large, of various shapes, but staminal corona and gynostegium usually visible; staminal corona lobes three-dimensional, usually conspicuously horizontally widened; pollinia with pellucid margin.....**Hoya**
7. Flowers small, usually urn-shaped; concealing corona (when present) and gynostegium; staminal corona lobes (when present) usually consisting of stalked, apically entire or bifid lobes with two recurved arms; pollinia without pellucid margin **Dischidia**
8. Staminal corona differentiated in distal, erect lobule and proximal, inflexed lobule; pollinia often with a flattened germination crest..... **Telosma**
8. Staminal corona simple or absent; pollinia without a flattened germination crest9
9. Shoots usually hollow; corolla almost without tube, flatly radiate; corpuscle narrowly oblong; caudicles geniculate, usually much longer than the corpuscle (except *S. cambogensis*); style-head often apically papillose; often growing between mangrove and adjacent vegetation, or rheophytic (Asia-Pacific area)..... **Sarcolobus**
9. Shoots not hollow; corolla usually with distinct tube; caudicles not ribbon-shaped; style-head usually not

- papillose (except for *Lygisma*); not growing close to the sea..... 10
10. Rigid shrubs; leaves and inflorescences sessile; follicles with 1–2 seeds only; plants of Africa..... 11
10. Plants suffrutescent twiners or lianas, if erect or shrubby, then not rigid and not both leaves and inflorescences sessile; follicles with more than 2 seeds; plants Palearctic..... 12
11. Leaves marginally strongly convolute; style-head conical; follicles solitary, ellipsoid, with thick pericarp; latex clear..... **Rhysolobium**
11. Leaves marginally not strongly convolute; style-head long, rostrate; follicles occasionally paired, obclavate, pericarp not particularly thick, latex white.....
..... **Stigmatorhynchus**
12. Stems and leaves usually turning blackish-blue when dried; inflorescences many-flowered, condensed; flowers short-pedicellate; corolla urceolate; follicles pubescent to pilose; plants of Asia..... **Marsdenia**
12. Stems and leaves not turning blackish-blue when dried; combination of characters not as above; plants widespread in the Palearctic..... 13
13. Inflorescences paired, axillary, corolla carinate, densely covered with trichomes; style head conical to rostrate; plants of West Africa, one species extending to southern Tanzania, northern Mozambique and Malawi
..... **Anisopus**
13. Inflorescences not paired, usually extra-axillary; corolla usually not carinate and not densely covered with trichomes, style-head usually not rostrate; widespread in the Palearctic 14
14. Corolline corona annular, bulged, with trichomes; follicles paired, adnate basally and apically; plants of Asia ...
..... **Campestigma**
14. Corolline corona absent or present, but not annular; follicles solitary or paired, but not basally and apically adnate; plants widespread in the Palearctic 15
15. Corolline corona present, staminal corona absent or only as small scales 16
15. Corolline corona usually absent, if present, then staminal corona prominent 17
16. Inflorescences basally dichotomously bifurcated, branches racemose; many-flowered; flowers small (<2 mm diam.), almost sessile; corolline corolla of 5 longitudinal, erect, triangular segments in the tube along the sutures; staminal corona reduced to small horn-shaped extensions at the base of the anthers; plants of Asia..... **Harmandiella**
16. Inflorescences not bifurcated, less than 12-flowered; flowers larger (>2 mm diam.), short-tubed or long-tubed and showy, pedicellate; corolline corona as 5 [10] longitudinal ridges below the sinus of the corolla lobes, densely pubescent with trichomes; staminal corona usually absent; plants widespread in the Palearctic
..... **Gymnema**
17. Inflorescences pedunculate racemes, sciadoid, branching upon peduncle, or in shortly pedunculate sciadoids along unbranched rachis, then rachis up to 15 cm long; corolla urceolate; staminal corona hook-shaped; plants of Asia..... **Dischidanthus**
17. Inflorescences of different structure; corolla of various shapes; staminal corona not hook-shaped; plants widespread in the Palearctic..... 18
18. Plants erect, herbaceous; inflorescences terminal and lateral; connective appendages twice as long as anthers; plants of Europe and Asia Minor **Cionura**
18. Plants usually twining, if erect, then inflorescences not terminal; connective appendages less than twice as long as the anthers; plants widespread in the Palearctic 19
19. Corolla lobes oblong, strongly infolded in bud; plants of Asia **Lygisma**
19. Corolla lobes of various shapes, never infolded in bud; plants widespread in the Palearctic 20
20. Corolla yellow, conspicuously spotted with red dots; gynostegium exposed; staminal corona deeply bifurcate or irregularly toothed; plants of Asia..... **Cosmostigma**
20. Corolla of various colors, but never spotted with red dots; gynostegium usually enclosed in corolla; corona of various shapes, but not deeply bifurcate; plants widespread in the Palearctic 21
21. Follicles thick-walled, often ornamented, often in pairs with follicles forming an angle of (almost) 180°, latex usually clear; corolla highly variable..... **Stephanotis**
21. Follicles usually thinner walled; if thick-walled and ornamented, then latex white; if in pairs, then follicles forming a much smaller angle..... 22
22. Corolla lobes densely pubescent; follicles verrucose, latex white; plants of Madagascar..... **Sicyocarpus**
22. Corolla lobes not densely pubescent (but often with trichomes); follicles usually smooth 23
23. Plants distributed in Australia and the Pacific, latex clear or whitish to yellow-cream, other characters highly variable **Leichhardtia**
23. Plants distributed in Asia or Africa; inflorescences sciadoid; corolla usually urceolate or campanulate; latex white..... 24
24. Corolla urceolate with distinctly swollen tube; staminal corona of oblong lobes with a globose spreading basal process; follicles slenderly elliptical, glabrous, plants of Asia **Gongreos**
24. Corolla tube not distinctly swollen; staminal corona different; follicles ovate, clavate or elliptical; plants of Africa or Asia..... 25
25. Style-head long, rostrate; plants of Asia
..... **M. oreophila**-group
25. Style-head not long and rostrate; plants of Africa or Asia 26
26. Staminal corona basally attached to the anther; plants of Asia **Gongronema**
26. Staminal corona attached below the filament tube, apically adnate to the anther, shorter than the gynostegium; plants of Africa or Asia..... **Gongronemopsis**

■ CONSPECTUS OF THE GENERA RECOGNIZED

1. Asia-Pacific Clade

1.1 *Marsdenia* R.Br., Prodr.: 460. 1810 – Type: *Marsdenia tinctoria* R.Br.

Illustrated in Fig. 1F.

Description. – Plants suffrutescent twiners, glabrescent, occasionally slightly pubescent (yellowish golden), older parts with cork ridges; latex white. *Leaves* slenderly ovate, basally cordate or rounded, apically acuminate. *Inflorescences* solitary, extra-axillary, sciadioid or bostryoid, many-flowered, crowded, flowers short-pedicellate. *Corolla* yellowish white, urceolate, inside densely covered with trichomes; lobes erect, short, ovate. *Corolline corona* absent, but corolla lobes adaxially with downward-pointing trichomes between the anthers. *Staminal corona* erect, lanceolate, not exceeding connective appendages. *Pollinaria*: Pollinia oblongoid, caudicles long, curved upward, corpuscles much smaller than pollinia. *Style-head* conical, not exceeding connective appendages. *Follicles* solitary, ovate to lanceolate, 5–7 cm long, pericarp pilose to pubescent. *Seeds* flattened, coma up to 2.5 cm long.

Notes. – The *Marsdenia* s.str. clade (subclade AI, BS_{ML} = 100%, PP = 1) comprises *M. tinctoria*, the type of *Marsdenia*, *M. calcicola* and *M. glabra*. It is weakly (BS_{ML} = 54%, PP = 0.83) supported as sister group to the remainder of the Asia-Pacific clade.

Diagnostic for most members of *Marsdenia* s.str. is in particular the blackish-blue color of stems and leaves when drying, due to their content of indigo-like substances, often used for dyeing (e.g., Teron & Borthakur, 2012). Morphologically, the genus is characterized by a combination of sciadioid to bostrychoid, many-flowered, condensed inflorescences, short-pedicellate flowers, small and urceolate corollas and pubescent to pilose follicles.

Omlor (1998) additionally attributed *Marsdenia eriocaulis* Kerr, *M. glomerata* Tsiang, *M. lachnostoma* Benth., *M. schneideri* Tsiang (incl. *M. balansae* Costantin), and *M. tonkinensis* Costantin to *Marsdenia* s.str., raising the species number to eight. However, in our phylogeny, a sample of *M. calcicola* is nested in the four samples of *M. tinctoria*, raising the need for more careful species delimitation in *Marsdenia* s.str. *Marsdenia* s.str. is distributed in NE India, Nepal, China, Thailand, Laos, Vietnam, Myanmar, Malaysia, Indonesia and the Philippines.

1.2 *Gongreos* Rodda, Liede & Meve, **gen. nov.** – Type: *Gongreos wallichii* (Wight) Rodda, Liede & Meve (≡ *Gymnema wallichii* Wight).

Diagnosis. – Plants terrestrial climbers; latex clear or whitish. *Stems* glabrous or pubescent along two longitudinal lines only, twining. *Leaves* petiolate; petiole bases connected by a line across the node; lamina herbaceous, entire, elliptic to lanceolate. *Inflorescences* simple or bifid racemes. *Corolla* urceolate; tube present, swollen. *Corolline corona* absent. *Staminal corona* of oblong lobes with a globose spreading

basal process. *Stamens* inserted at the base of the corolla tube, included within the tube. *Pollinarium* with erect pollinia lacking pellucid margins. *Style head* conical. *Follicles* solitary or paired, divaricate, slenderly elliptical, glabrous. *Seeds* ovate, winged, comose.

Etymology. – *Gongronema* means swollen-thread (i.e., swollen filaments). For reminiscence of the original placement of the species, the new name is combined with “eos” (Greek: dawn) to indicate its eastern distribution.

Notes. – After *Gongronema* has been shown to be polyphyletic, we propose the name *Gongreos* for two species in China and Southeast Asia that form subclade AII of the Asia-Pacific Clade. Upon examination of the type specimen, *Marsdenia longipes* is here considered a new synonym of *Gongreos filipes*. Chinese material appears to have slightly longer peduncles (to 7 cm long vs. to 4 cm long) and pedicels (to 1.5 cm long vs. to 1 cm long), but is otherwise indistinguishable from *G. filipes* in vegetative and floral morphology.

Gongreos filipes (Kerr) Rodda, Liede & Meve, **comb. nov.** ≡ *Gongronema filipes* Kerr in Bull. Misc. Inform. Kew 1939: 456. 1939 – Holotype: Thailand, Doi Lang Ka, Chiangmai, 24 Apr 1931, *N. Put* 3768 (K barcode K000872884!; isotypes: BK barcode 257728!, BKF barcode 005518!, BM barcode BM001014169!).

= *Marsdenia longipes* W.T. Wang in Acta Phytotax. Sin. 12(1): 117. 1974 – **Lectotype (designated here)**: China, Yunnan, Jiangdong, 27 Mar 1940, *M.K. Li* 1937 (KUN barcode 1209048!; isolectotype: KUN barcode 1263143!), **syn. nov.**

Gongreos wallichii (Wight) Rodda, Liede & Meve, **comb. nov.** ≡ *Gymnema wallichii* Wight, Contr. Bot. India: 46. 1834 ≡ *Gongronema wallichii* (Wight) Decne. in Candolle, Prodr. 8: 624. 1844 – Lectotype (designated by Rodda in Gard. Bull. Singapore 71: 77. 2019): Singapore, *N. Wallich s.n.* [EIC 8195B, Asclep. 135a] (K barcode K001129202!; isolectotype: E barcode E00288666!).

1.3 *Leichhardtia* R.Br., Bot. Sturt’s Exped. Australia: 18. 1848 – Type: *Leichhardtia australis* R.Br. = *Thozetia* F.Muell. ex Benth., Fl. Austral. 4: 347. 1868 – Type: *Thozetia racemosa* F.Muell. ex Benth. (≡ *Leichhardtia racemosa* (F.Muell. ex Benth.) P.I.Forst.). Illustrated in Fig. 1E.

Description. – Plants suffrutescent twiners or lianas, glabrescent or pubescent; latex whitish or clear. *Leaves* oblong to linear. *Corolla* rotate, campanulate or urceolate, occasionally with trichomes; lobes valvate or contorted. *Corolline corona* (when present) as five ridges opposite the anthers, occasionally with trichomes. *Staminal corona* attached at the filament tube, carnos, erect, rather short, occasionally absent (*L. goromotoorum*). *Pollinaria*: Pollinia oblongoid to clavate, corpuscle smaller than pollinia. *Style-head* rostrate, occasionally semi-globose. *Follicles* occasionally winged, occasionally with thick pericarp. *Seeds* winged, coma occasionally absent.

Notes. – Brown (1848) instated the new genus *Leichhardtia* for a new species in Australia, *L. australis*, to commemorate Ludwig Leichhardt, a German explorer that went missing in 1848 in the Australian outback. Several authors, such as Bullock (1956) and Smith (1975), classified four more species in the genus, all distributed in Oceania (Australia, Fiji). Our analysis shows that *Leichhardtia* forms an independent lineage from *Marsdenia* s.str., comprising species currently known under “*Marsdenia*” in Oceania (Australia, New Guinea, New Caledonia, and the Solomon Islands, see Forster, 2021). The Fiji species, *L. stenophylla* (A.Gray) A.C.Sm., has been transferred to *Sarcolobus* (*S. stenophyllus* (A.Gray) P.I.Forst.) by Forster (1992).

Forster (1995: 721) synonymized the only species of *Thozetia*, *T. racemosa*, with *Marsdenia hemiptera* Rchb.f. Because *M. hemiptera* was retrieved in *Leichhardtia*, *Thozetia* constitutes a synonym of *Leichhardtia*.

Leichhardtia (subclade AIV) falls into several well-supported ($BS_{ML} > 90\%$) clades in our analysis but includes broad variation in almost all morphological characters both within the subclades and between them. As in the parallel case of *Diplolepis* R.Br. in South America (Hechem & al., 2011) and *Cynanchum* L. in Africa (Liede & Täuber, 2002), distribution is the most reliable identifier for *Leichhardtia*.

The New Caledonian species of *Leichhardtia* fall in two well-supported clades, each in sister-group position to Australian clades. Their full taxonomic treatment is presented in Liede-Schumann & al. (2020). Because recognition of *Leichhardtia* also results in a considerable number of new combinations in Australia and Papuasia, this task has been undertaken separately (Forster, 2021).

1.4 *Marsdenia oreophila* subclade

Description. – Plants suffrutescent twiners or lianas, pubescent to shortly tomentose; latex white. Leaves coriaceous, broadly ovate, basally obtuse to rounded, apically acuminate, abaxially pubescent on the veins, adaxially glabrescent; petiole adaxially caniculate. Inflorescences solitary, extra-axillary, sciadioidal, short-pedunculate. Flowers short-pedicellate, drooping, pedicels and sepals shortly tomentose. Corolla urceolate, greenish white, throat bearded with trichomes; lobes white, valvate, ovate, apically mucronate, glabrescent. Corolline corona absent. Staminal corona simple, lobes adjacent to the anthers, slightly carnosose and compressed, without further appendages. Gynostegium sessile, concealed in corolla. Style-head conical to rostrate. Follicles solitary, ovoid.

Notes. – *Marsdenia tomentosa* and *M. oreophila* form the well-supported subclade AIII ($BS_{ML} = 98\%$, PP = 1) in poorly supported sister-group position ($BS_{ML} < 50\%$, PP = 0.98) to the wider *Hoya* alliance + *Leichhardtia* clade (subclades AIV, AV). Omlor (1998) has discussed these species in his “*Marsdenia lucida*” group, a small group of Chinese and Himalayan species, characterized in particular by a long, rostrate style-head. Omlor (1998) considered *M. formosana*

Masam., *M. griffithii* Hook.f., *M. lucida* Edgew. ex Madden, *M. officinalis* Tsiang & P.T.Li, and *M. yunnanensis* (H.Lév.) Woodson as further species in this group. However, Omlor (1998) did not discuss the inclusion of *M. jenkinsii* in the “*Marsdenia lucida*” group, the only known Marsdenieae species with an inflorescence enveloped in showy bracts. For *M. jenkinsii*, the genus *Sinomarsdenia* P.T.Li & J.J.Chen was coined, but because no sequenceable material of this species could be obtained, we cannot be certain that our *M. oreophila* clade does not represent *Sinomarsdenia*. Therefore, we refrain here from describing a new genus for this distinctive group of species.

For *Marsdenia formosana*, Sakagami & al. (2019) have observed nocturnal moths as potential pollinators, a group of pollinators possibly associated with long, rostrate style-heads (see also Sugiura & Yamazaki, 2005).

Hoya alliance

The following genera of the Asia-Pacific Clade are all members of the morphologically and phylogenetically well-supported *Hoya* alliance (subclade AV), which will be treated in detail in another place.

- 1.5 *Dischidia* R.Br., Prodr.: 461. 1810 – Type: *Dischidia nummularia* R.Br.
 = *Collyris* Vahl in Skr. Naturhist.-Selsk. 6: 109. 1810 – Lectotype (designated by Panigrahi in Bangladesh J. Bot. 15: 195. 1986): *Collyris major* Vahl (\equiv *Dischidia major* (Vahl) Merr.).
 = *Conchophyllum* Blume, Bijdr. Fl. Ned. Ind.: 1060. 1826 – Type: *Conchophyllum imbricatum* Blume (\equiv *Dischidia imbricata* (Blume) Steud.).
 = *Leptostemma* Blume, Bijdr. Fl. Ned. Ind.: 1057. 1826 – Lectotype designated by Rodda in Gard. Bull. Singapore 71: 77. 2019): *Leptostemma hirsutum* Blume (\equiv *Dischidia hirsuta* (Blume) Decne.).
 = *Dischidiopsis* Schltr. in Perkins, Fragm. Fl. Philipp.: 128. 1904 – Type: *Dischidiopsis philippinensis* Schltr. (\equiv *Dischidia parasita* (Blanco) Arshed, Agoo & Rodda).
 = *Spathidolepis* Schltr. in Schumann & Lauterbach, Fl. Schutzgeb. Südsee, Nachtr.: 356. 1905 – Type: *Spathidolepis torricellensis* Schltr. (\equiv *Dischidia torricellensis* (Schltr.) P.I.Forst.).
 = *Oistonema* Schltr. in Bot. Jahrb. Syst. 40, Beibl. 92: 12. 1908 – Type: *Oistonema dischidioides* Schltr. – Holotype: Indonesia. Borneo, Samarinda, Jul 1901, R. Schlechter 13517 (B \dagger). **Lectotype (designated here):** [illustration] “*Oistonema dischidioides* Schltr. n. sp.” in Bot. Jahrb. Syst. 40, Beibl. 92: t. 1. 1908 (\equiv *Dischidia latifolia* (Blume) Decne.), **syn. nov.**
 = *Dolichostegia* Schltr. in Repert. Spec. Nov. Regni Veg. 13: 554. 1915 – Type: *Dolichostegia boholensis* Schltr. (\equiv *Dischidia boholensis* (Schltr.) Livsh.).
 = *Hoyella* Ridl. in J. Fed. Malay States Mus. 8(4): 62. 1917 – Type: *Hoyella rosea* Ridl. (\equiv *Dischidia hoyella* Omlor). Illustrated in Fig. 1A.

Description. – *Plants* usually epiphytic, rarely epilithic twiners, usually forming adventitious roots at the nodes. *Leaves* white. *Leaves* often succulent, occasionally shell- or urn-shaped and inhabited by ants. *Inflorescences* long-lived, extra-axillary, usually pedunculated (rarely sessile), producing flowers over a long time along one (rarely) to several (usually 2–6) elongating rachises. *Corolla* fleshy, (rarely) tubular to urn-shaped to (rarely) campanulate, lobes valvate in bud, often adaxially pubescent with various patterns of trichomes (on the lobes, a ring below the lobes, a distinct band in the tube, etc.). *Corolline corona* sometimes present, typically of lobes below the petal sinuses. *Staminal corona* occasionally absent, when present usually consisting of stalked, apically entire or bifid lobes with two recurved arms, sessile and saddle-shaped in species assigned to the segregate *Dischidiopsis* and related species. *Pollinaria*: Pollinia ovate, caudicles usually between 1× and 2× length of corpuscle, apically flattened, shovel-shaped, corpuscle ovate. *Follicles* small, linear to fusiform, apically obtuse to acute. *Seeds* spindle-shaped, margins wingless, comose.

Notes. – *Dischidia* and *Hoya*, together with the recently resurrected *Oreosparte* and the newly described *Papuahoya* (Rodda & al., 2020), form the always strongly supported *Hoya* alliance (subclade AV; BS_{ML} = 100%, PP = 1). As in previous studies (Rodda & al., 2020), *Dischidia* is well supported as monophyletic, including the analyzed species of *Dischidiopsis* (*D. luzonica*). In our study, *Dischidia* is unsupported sister to *Hoya* I (see below), while the plastome study of Rodda & Niissalo (2021) retrieved the genus in fully supported sister-group position to *Hoya*. Because of these contradictory results, we refrain here from including *Dischidia* in *Hoya*.

Oistonema is considered a synonym of *Dischidia* (Endress & al., 2018). Its type (*Schlechter 13517*) was lost in Berlin and no duplicate has been found. Therefore, the illustration associated with the protologue is the only available material for lectotypification. A new combination in *Dischidia* is not necessary as we consider *Oistonema dischidioides* a synonym of the earlier *Dischidia latifolia* (Blume) Decne.

The only species of *Spathidolepis*, *S. torricellensis*, was refound in Papua New Guinea and transferred to *Dischidia* by Forster (2000). Morphologically, however, it is reminiscent of *Leichhardtia*, judging from the shape of the corona and the pollinaria. In the absence of sequenceable material, we refrain from a formal transfer here.

1.6 *Hoya* R.Br., Prodr.: 459. 1810 – Type: *Hoya carnosa* (L.f.) R.Br. (= *Asclepias carnosa* L.f.).

= *Sperlingia* Vahl in Skr. Naturhist.-Selsk. 6: 112. 1810 – Type: *Sperlingia verticillata* Vahl. (= *Hoya verticillata* (Vahl) G.Don).

= *Schollia* J.Jacq., Ecl. Pl. Rar. 1: 5, t. 2. 1811 – Type: *Schollia crassifolia* J.Jacq., nom. illeg. (= *Hoya carnosa* (L.f.) R.Br.).

= *Hoya* [unranked] *Acanthostemma* Blume, Bijdr. Fl. Ned. Ind.: 1065. 1826 = *Acanthostemma* (Blume) Blume in Rumphia 4: 29. 1849 – Type: not designated.

= *Pterostelma* Wight, Contr. Bot. India: 39. 1834 – Type: *Pterostelma acuminata* Wight (= *Hoya acuminata* (Wight) Benth. ex Hook.f.).

= *Physostelma* Wight, Contr. Bot. India: 39. 1834 – Type: *Physostelma wallichii* Wight (= *Hoya wallichii* (Wight) C.M.Burton).

= *Triplosperma* G.Don, Gen. Hist. 4: 107, 134. 1837 – Type: *Triplosperma cochinchinense* (Lour.) G.Don (= *Stapelia cochinchinensis* Lour.) (= *Hoya verticillata* (Vahl) G.Don).

= *Centrostemma* Decne. in Ann. Sci. Nat., Bot., ser. 2, 9: 271. 1838 – Type: *Centrostemma multiflorum* (Blume) Decne. (= *Hoya multiflora* Blume).

= *Cyrtoceras* Benn., Pl. Jav. Rar. 1: 90, t. 21. 1838 – Type: *Cyrtoceras reflexum* Benn. (= *Hoya multiflora* Blume).

= *Cystidianthus* Hassk., Cat. Hort. Bot. Bogor.: 126. 1844 – Type: *Cystidianthus campanulatus* (Blume) Hassk. (= *Hoya campanulata* Blume).

= *Otostemma* Blume, Mus. Bot. 1: 59. 1849 – Type: *Otostemma lacunosum* (Blume) Blume (= *Hoya lacunosa* Blume).

= *Plocostemma* Blume, Mus. Bot. 1: 59. 1849 – Type: not designated.

= *Absolmsia* Kuntze, Revis. Gen. Pl. 2: 417. 1891 = *Asterostemma* Benth. in Hooker's Icon. Pl. 14: t. 1311. 1880, nom. illeg., non *Asterostemma* Decne. in Ann. Sci. Nat. Bot., sér. 2, 9: 371, t. 10. 1838 – Type: *Absolmsia spartioides* (Benth.) Kuntze (= *Hoya spartioides* (Benth.) Kloppenb.).

= *Anatropanthus* Schltr. in Bot. Jahrb. Syst. 40, Beibl. 92: 18. 1908 – Type: *Anatropanthus borneensis* Schltr. (= *Hoya insularis* Rodda & S.Rahayu, non *Hoya borneensis* Kloppenb. in *Hoya New* 8(3): 10. 2018).

= *Micholitzia* N.E.Br. in Bull. Misc. Inform. Kew 1909: 358. 1909 – Type: *Micholitzia obcordata* N.E.Br. (= *Hoya manipurensis* Deb.).

= *Clemensiella* Schltr. in Repert. Spec. Nov. Regni Veg. 13: 566. 1915 = *Clemensia* Schltr. in Repert. Spec. Nov. Regni Veg. 13: 542. 1915, nom. illeg., non *Clemensia* Merr. 1908 – Type: *Clemensiella mariae* (Schltr.) Schltr. (= *Hoya mariae* (Schltr.) L.Wanntorp & Meve).

= *Hoya* sect. *Antiostelma* Tsiang & P.T.Li in Acta Phytotax. Sin. 12(1): 126. 1974 = *Antiostelma* (Tsiang & P.T.Li) P.T.Li in Novon 2(3): 218. 1992 – Type: *Antiostelma lantsangense* (Tsiang & P.T.Li) P.T.Li (= *Hoya lantsangensis* Tsiang & P.T.Li) (= *Hoya manipurensis* Deb.).

= *Madangia* P.I.Forst., D.J.Liddle & I.M.Liddle in Austrobaileya 5: 53. 1997 – Type: *Madangia inflata* P.I.Forst., D.J.Liddle & I.M.Liddle. (= *Hoya inflata* (P.I.Forst., D.J.Liddle & I.M.Liddle) L.Wanntorp & P.I.Forst.).

= *Hoya* sect. *Eriostemma* Schltr. in Bot. Jahrb. Syst. 50: 106. 1914 = *Eriostemma* (Schltr.) Kloppenb. & Gilding in Fraterna 14(2): 1. 2001 – Type: *Eriostemma coronarium* (Blume) Kloppenb. & Gilding (= *Hoya coronaria* Blume).

= *Hiepia* V.T.Pham & Aver. in Turczaninowia 14: 6. 2011 – Type: *Hiepia corymbosa* V.T.Pham & Aver. (= *Hoya ignorata* T.B.Tran, Rodda, Simonsson & Joongku Lee). Illustrated in Fig. 1D.

Description. – *Plants* suffrutescent lianas, occasionally (hemi-)epiphytes or terrestrial, occasionally small epiphytic shrubs, often with conspicuous adventive roots; latex white but also clear occasionally. *Leaves* coriaceous, succulent or waxy, often caducous. *Inflorescences* solitary, extra-axillary, many-flowered, sessile to long-pedunculate (up to 25 cm), sciadioidal or with durable, thickened rachis. *Corolla* valvate, urceolate, campanulate or rotate, often pilose or pubescent, membranous to carnose; lobes ovate or triangular, occasionally cucullate. *Corolline corona* occasionally as glabrescent or pubescent ring or five ridges. *Staminal corona* very variable in shape, generally bisected, horizontally widened, distal lobule erect or spreading, apically toothed, with lateral keels (nectar pit), proximal lobule introrse, acute. *Gynostegium* sessile or stalked, occasionally concealed in corolla. *Pollinaria*: Pollinia ellipsoid to oblongoid, generally with pellucid margin, caudicles generally very short, corpuscle ellipsoid, occasionally small or basally with protuberances. *Style-head* conical to ovoid. *Follicles* solitary or paired, 4–10 (–30) cm long, linear to small ellipsoid, pericarp thin to occasionally fleshy. *Seeds* apically winged, with coma surrounding the seed.

Notes. – It can be debated that *Eriostemma* (Schltr.) Klop-penb. & Gilding constitutes a valid name, because the elements of a valid new combination (ICN Art. 41.5, Turland & al., 2018), while all present in the new description, are not found in the expected places. Because *Eriostemma* is quite frequently cited in *Hoya* literature, it is kept as a synonym here.

First described by Robert Brown (1810), the genus *Hoya* comprises 350–450 species. *Hoya* (incl. *Dischidia*) forms a very well-supported and easy to recognize group. Rodda & al. (2020) suggested the inclusion of the monotypic genus *Anatropanthus*, characterized by pedicels turned by 180°, in *Hoya*, a result supported by the present results for *A. borneensis* (≡ *Hoya insularis*).

However, retaining the well-supported, morphologically distinctive genus *Dischidia* would lead to a *Hoya* whose monophyly is unsupported by this or most previous analyses (e.g., Rodda & al., 2020). Alternatively, *Hoya* could be split in several monophyletic groups, but morphologically, splitting of *Hoya* would be extremely difficult. Shared characters of *Hoya* and *Dischidia* include distribution and habitat choice (Kleijn & Van Donkelaar, 2001), epiphytic growth, adventitious roots, leaf succulence, adaptations of seeds and leaves for ant mutualisms (Kaufmann & al., 2001; Kaufmann & Maschwitz, 2006), fleshy and nectariferous flowers with valvate lobes in bud, more or less linear follicles with generally thin pericarp and spindle-shaped seeds without lateral wings. Inclusion of *Dischidia* in *Hoya* might be the solution for long term nomenclatural stability in this group, but until the data for a final decision are at hand, accepting a paraphyletic *Hoya* seems the least nomenclaturally upsetting solution.

Hoya, as understood here (i.e., paraphyletic with regards to *Dischidia*), is distributed in tropical and subtropical Asia, Australia and Oceania and is commonly recognized by its usually epiphytic habit, producing conspicuous adventitious roots, its succulent, occasionally coriaceous leaves, its usually showy flower with complex staminal corona, with the lobes often divided in distal and proximal lobule, and pollinia often with pellucid margin.

1.7 *Oreosparte* Schltr. in Beih. Bot. Centralbl., Abt. 2, 34(2): 16. 1916 – Type: *Oreosparte celebica* Schltr.

Description. – *Plants* epiphytic climbers, pubescent; latex white. *Leaves* ovate to elliptic, leathery to fleshy. *Inflorescences* long-pedunculate, long-lived, extra-axillary, producing a small number of flowers over a long time along a thickened rachis. *Corolla* basally campanulate, with a contracted throat and free, lanceolate, spreading lobes. *Staminal corona* stalked, exceeding the corolla, lobes lanceolate, flattened, apices bifid. *Pollinaria*: pollinia clavate, without pellucid margin, corpuscle rhomboid. *Style-head* gibbous. *Follicles* narrowly fusiform. *Seeds* small, unwinged, long-comose.

Notes. – *Oreosparte* has been considered an insufficiently known genus for a long time because its type was lost in Berlin. A collection from the type locality enabled Rodda & Omlor (2013) to resurrect the genus, and molecular studies (Rodda & al., 2020) identified two further species, *O. parviflora* (Ridl.) Rodda & Simonsson and *O. sabahensis* Rodda & Simonsson. The known distribution of the genus is restricted to Malaysia, Borneo and Sulawesi.

1.8 *Papuahoya* Rodda & Simonsson in Willdenowia 50(1): 130. 2020 – Type: *Papuahoya bykulleana* Simonsson & Rodda.

Description. – *Plants* epiphytic climbers, pubescent; latex white. *Leaves* lanceolate to ovate, stiff and chartaceous. *Inflorescences* solitary, extra-axillary (1–)2–10-flowered. *Corolla* campanulate to urceolate; lobes triangular-lanceolate. *Staminal corona* shortly stipitate, lobes erect, almost completely fused to the back of the anthers, inner processes acute with a round tip, outer processes round. *Style-head* conical, hidden by anther appendages. *Pollinaria*: Pollinia oblong, without pellucid margin, corpuscle ovoid. *Style-head* conical. *Follicles* and *seeds* unknown.

Notes. – The *Papuahoya* clade is sister to the *Oreosparte* clade, and both are sister to the remainder of *Hoya-Dischidia* in subclade AV; all relationships are well supported. The known distribution of *Papuahoya* is restricted to New Guinea.

2. Cosmopolitan Clade

2.1 *Anisopus* N.E.Br in Bull. Misc. Inform. Kew 1895: 259. 1895 – Type: *Anisopus mannii* N.E.Br.

Illustrated in Fig. 2A.

Description. – *Plants* suffrutescent twiners or lianas, glabrescent, older parts occasionally corky; latex white. *Leaves* ovate to oblong, 4–15 cm long, basally cordate, truncate or

rounded. *Inflorescences* subsessile to short-pedunculate, axillary if paired (usually one of the two is stronger), extra-axillary if solitary. *Corolla* carnosae, rotate to campanulate, white or yellowish to reddish purple, pubescent to pilose; lobes ovate to oblong. *Corolline corona* present in some species as free oblong lobes opposite the anthers, with trichomes. *Staminal corona* attached at the filament tube, obovate, erect, occasionally winged, more or less adnate to the anther, carnosae, apically toothed, connective appendages broadly ovate. *Pollinaria*: Pollinia ovoid, caudicles curved convex, corpuscle slenderly ovoid. *Style-head* conical to rostrate, occasionally exceeding the corolla, then apically bifurcate. *Follicles* usually paired, slenderly fusiform, 8–16 cm long. *Seeds* with undulate wing.

Notes. – In subclade BV of the Cosmopolitan clade, *Anisopus* (BS_{ML} = 68%, PP = 0.99) is sister to *Ruehssia*, but support for this position is ambiguous (BS_{ML} = 54%, PP = 0.99). This ambiguous support may be due to the incomplete set of partial sequences for the two *Anisopus* s.str. species (see, e.g., Simmons & Randle, 2014).

Anisopus species are large lianas of tropical forests with white latex, often with paired inflorescences, paired follicles and seeds with undulate wings. *Anisopus mannii* has a conspicuously rostrate style-head far exceeding the gynostegium, while the style-heads of the other species hardly exceed the gynostegium.

Anisopus is mainly distributed in the rainforests of tropical West (and East) Africa with presently four species; *A. exellii* is also found in southern Tanzania, northern Mozambique and Malawi. Apart from *A. efulensis* and *A. mannii*, two of the four species of Omlor's (1998) *Marsdenia* sect. *Pterygocarpus* (Hochst.) Omlor (*M. exellii*, *M. magniflora*), both also from West Africa, have to be included in *Anisopus*. *Marsdenia abyssinica* Schltr., however, also considered a member of *Pterygocarpus* by Omlor (1998), is here retrieved as a member of the *Stephanotis* clade, while for the fourth species, the West African *M. oblanceolata* (Turrill) Omlor, type of *Dalzielia* Turrill, no material was available for analysis.

Anisopus exellii (C.Norman) S.Reuss, Liede & Meve, **comb. nov.** ≡ *Marsdenia exellii* C.Norman, Cat. Vasc. Pl. S. Tome: 244. 1944 – Holotype: São Tomé, Vanhulst (Macambrará), 1067–1220 m, 29 Oct 1932, *A.W. Exell* 138 (BM barcode BM000017073!).

Anisopus magniflorus (P.T.Li) S.Reuss, Liede & Meve, **comb. nov.** ≡ *Marsdenia magniflora* P.T.Li in J. S. China Agric. Univ. 15(1): 64. 1994 ≡ *Marsdenia grandiflora* C.Norman in J. Bot. 67(Suppl. 2): 97. 1929, nom. illeg., non *Marsdenia grandiflora* (Decne.) Choux in Ann. Mus. Colon. Marseille, sér. 4, 1(2): 44. 1923, ≡ *Marsdenia normaniana* Omlor, Gen. Revis. Marsdenieae: 81. 1998, nom. illeg. – Holotype: Angola. Near Mboka – Belise – Maiombe, 07 Mar 1917, *J. Gossweiler* 7024 (BM barcode BM000017075!; isotype: COI barcode COI00070592!).

2.2 *Campestigma* Pierre ex Costantin in Lecomte, Fl. Indo-Chine 4: 117. 1912 – Type: *Campestigma purpureum* Pierre ex Costantin.

Description. – *Plants* large suffrutescent twiners, basally woody, shoots glabrescent, distichously winged (3 mm wide); latex white. *Leaves* long-petiolate, broadly ovate, basally cordate or rounded. *Inflorescences* extra-axillary, solitary, basally branched, thyrsoïdal, up to 7 cm long. *Flowers* long-pedicellate; sepals basally adaxially with 5 glandular scales in a row. *Corolla* rotate, up to 6.5 mm long, throat pubescent; lobes up to 5 mm long, contorted oblong to ovate, adaxially with trichomes. *Corolline corona* annular, bulged, with trichomes. *Staminal corona* lobes dolabriform. *Pollinaria*: Pollinia pyriform, caudicles S-shaped, corpuscle slenderly clavate. *Style-head* rostrate, exceeding connective appendages. *Follicles* paired, widely divergent, adnate basally and apically, 20–25 cm long, slenderly oblong. *Seeds* winged.

Notes. – The position of *Campestigma purpureum* in the moderately supported subclade BII of the Cosmopolitan Clade (BS_{ML} = 71%, PP = 1), either as unsupported sister to the remainder of the subclade (suppl. Figs. S1, S2) or as unsupported sister of *Harmandiella* (Fig. 3B) suggests that a monotypic genus is probably best reflecting the isolation of this species.

The monotypic *Campestigma* constitutes large suffrutescent twiners in tropical Asian forest with distichously winged shoots, basally branched thyrsoïdal inflorescences, and characteristic sepal bases that adaxially bear 5 large glandular scales (colleters) each, and paired, basally and apically adnate follicles. It was found in Thailand, Laos and Vietnam.

2.3 *Cionura* Griseb., Spic. Fl. Rumel. 2: 69. 1844 – Type: *Cionura erecta* (L.) Griseb. (≡ *Cynanchum erectum* L.).

Description. – *Plants* suffrutescent shrubs, occasionally apically twining, glabrescent; latex white. *Leaves* 4–10 cm long, broadly ovate, basally cordate. *Inflorescences* terminal or solitary, extra-axillary, sciadioid, with 15–20 flowers. *Corolla* rotate, yellowish white, deeply divided, glabrescent; lobes oblong, apically rounded, glabrescent. *Corolline corona* absent. *Staminal corona* shorter than gynostegium, erect, slenderly lanceolate, slightly introrse. *Connective appendages* oblong, twice as long as anthers. *Pollinaria*: Pollinia clavate, apically papillate, caudicles S-shaped, tubular, corpuscle bone-shaped. *Style-head* rostrate, apically bifurcate, exceeding connective appendages. *Follicles* solitary, 6.5–8 cm long, obclavate, glabrescent. *Seeds* winged.

Notes. – *Cionura* is a monotypic genus, and its only species, *C. erecta*, is the only Marsdenieae species occurring in southeastern Europe and Asia Minor, where it grows on sandy, rocky soils in oak forests, and in littoral shrub. It is retrieved in subclade BII of the Cosmopolitan Clade in poorly supported (BS_{ML} = 53%, PP = 0.81) sister-group position to (*Gongronema* s.str. + *Dischidanthus*) + *Sarcolobus*.

Cionura plants often form huge, dense mats, as the shrubs often twine or sprawl. Florally, *Cionura* is characterized by

connective appendages twice as long as the anthers, and style-heads that are rostrate and apically bifurcate.

2.4 *Cosmostigma* Wight, Contr. Bot. India: 41. 1834 – Type: *Cosmostigma racemosum* Wight.

Description. – *Plants* suffrutescent twiners or lianas, pubescent (occasionally yellow); latex clear. *Leaves* papery, 5–11 cm long, long-petiolate, ovate, basally cordate. *Inflorescences* long-pedunculate, solitary, extra-axillary, with 6–15 flowers, sciadioidal, getting racemiform with time. *Corolla* 4–6 mm long, rotate to campanulate, yellowish green, spotted dark red, throat occasionally with trichomes; lobes valvate or contorted, ovate to oblong. *Staminal corona* shorter than gynostegium, erect, ovate to rectangular, deeply bifurcate or irregularly toothed. *Gynostegium* sessile, protruding from corolla. *Pollinaria*: Pollinia clavate, caudicles horizontal to declinate, tubular, long, corpuscle ovoid to oblongoid, exceeding pollinia. *Style-head* umbonate. *Follicles* solitary, 12–20 cm long, with thick pericarp, obclavate. *Seeds* broadly winged.

Notes. – *Cosmostigma* is retrieved in a moderately supported (BS_{ML} = 85%, PP = 1) sister-group position to *Lygisma*, with which it shares the pubescent shoots and the membranous leaves, but differs widely in flower structure. These two genera form the first-branching subclade (subclade BI) of the Cosmopolitan Clade.

Cosmostigma, with three accepted species, comprises suffrutescent twiners or lianas with pubescent, occasionally yellowish, shoots, clear latex and flowers with a deeply bifurcate or irregularly toothed staminal corona, and long (to 20 cm), obclavate, single follicles. *Cosmostigma* is reportedly pollinated by flies (Mitra, 2010). *Cosmostigma* is distributed in Bangladesh, India, Sri Lanka, China, Thailand, Vietnam, Indonesia and the Philippines.

The type, *Cosmostigma racemosum*, was based on *Asclepias racemosa* Roxburgh (Fl. Ind., ed. 1832, 2: 32. 1832). However, *Asclepias racemosa* Jacq. (Enum. Syst. Pl.: 17. 1760; ≡ *Cynanchum racemosum* (Jacq.) Jacq.) has priority. Therefore, *Cosmostigma racemosum* constitutes the correct name of the species.

2.5 *Dischidanthus* Tsiang in Sunyatsenia 3(2–3): 185–187, pl. 20. 1936 – Type: *Dischidanthus urceolatus* (Decne.) Tsiang (≡ *Marsdenia urceolata* Decne.). Illustrated in Fig. 2B.

Description. – *Plants* suffrutescent twiners, shoots bifariously (occasionally unifariously) indumented, otherwise glabrescent; latex white. *Leaves* up to 10 cm long, ovate to lanceolate, cordate (*M. thyrsoiflora*), apically acuminate. *Inflorescences* solitary, extra-axillary, flowers in shortly pedunculate racemes, sciadioidal, branching upon peduncle, or in shortly pedunculate sciadioids along unbranched rachis, then rachis up to 15 cm long. *Corolla* urceolate, glabrous on both sides, or papillate on right half of adaxial surface; lobes erect, triangular to ovoid. *Staminal corona* short, erect, slightly carnose, horn-shaped, protruding. *Pollinaria*: Pollinia obovate to

oblong, flattened, caudicles long, curved upwards, corpuscle slenderly ovoid. *Style-head* shortly rostrate, not exceeding long, triangular connective appendages. *Follicles* 1 or 2 per flower, to 7 cm long, thin-walled, fusiform. *Seeds* c. 5 × 2 mm, dorsiventrally flattened, samaroid.

Notes. – The only species of hitherto monotypic *Dischidanthus*, *D. urceolatus*, was separated from *Marsdenia* by Tsiang (1936) because it superficially resembles the genus *Dischidia*. Omlor (1998), however, saw no reason to maintain generic status for the species and included it in *Marsdenia* s.l. The present analysis adds a second species, *M. thyrsoiflora*, to the clade (BS_{ML} = 90%, PP = 1). *Dischidanthus* is moderately supported as sister to *Gongronema* s.str. (BS_{ML} = 82%, PP = 0.93) in subclade BII of the Cosmopolitan Clade.

Both species are suffrutescent twiners with (uni- or) bifarious stem indument, shortly pedunculate inflorescences, urn-shaped, glabrous, or (right-side) papillate corollas, and carnose, projecting and somewhat horn-shaped staminal corona lobes. Because of the unambiguous position and shared significant morphological characters, *Marsdenia thyrsoiflora* is transferred to *Dischidanthus* here.

Dischidanthus in this circumscription is distributed in northeast India, Bangladesh, southern China, Thailand, Cambodia, Vietnam and Malaysia.

Dischidanthus thyrsoiflorus (Hook.f.) S.Reuss, Liede & Meve, **comb. nov.** ≡ *Marsdenia thyrsoiflora* Hook.f., Fl. Brit. India 4: 37. 1883 – Lectotype (designated by Rahman & Wilcock in Bangladesh J. Bot. 22: 10. 1993): India, Assam, banks of Saobtum, *J.W. Masters s.n.* (K barcode K000872963!).

2.6 *Gongronema* (Endl.) Decne. in Candolle, Prodr. 8: 624. 1844 ≡ *Gymnema* subg. *Gongronema* Endl., Gen. Pl.: 595. 1838 – Type: *Gongronema napalense* (Wall.) Decne. (≡ *Gymnema napalense* Wall.).

Description. – *Plants* suffrutescent twiners or lianas; latex white. *Leaves* papery to coriaceous, broadly ovate to elliptical, basally slightly cordate, nervature brochidodromous. *Inflorescences* solitary, extra-axillary, long-pedunculate, sciadioidal or split in several branches with terminal inflorescences, occasionally short-pedunculate or flowers along thickened rachis. *Corolla* urceolate to campanulate, occasionally inflated. *Corolline corona* absent. *Staminal corona* attached basally to the gynostegium, upwardly curved, carnose, spreading, free tip absent. *Pollinaria*: Pollinia clavate, caudicles straight, corpuscle smaller than pollinia, ovoid. *Style-head* conical, obtuse, shorter than connective appendages. *Follicles* usually paired, thin-walled, fusiform to slenderly obclavate.

Notes. – *Gongronema* in its current circumscription is polyphyletic. The type, *G. napalense*, is retrieved in moderately supported (BS_{ML} = 82%, PP = 0.93) sister-group position to the two species of *Dischidanthus* in subclade BII of the Cosmopolitan Clade. The other two Asian species included in the present analysis (*G. filipes*, *G. wallichii*) form the moderately supported subclade AII of the Asia-Pacific

Clade (BS_{ML} = 79%, PP = 1). The African species of *Gongronema* are retrieved in a well-supported (BS_{ML} = 95%, PP = 1) clade inside subclade BIII of the Cosmopolitan Clade. Both clades are separated here as independent genera, *Gongreos* and *Gongronemopsis*.

Gongronema s.str. is thus most likely restricted to the four species enumerated by Omlor (1998) for India, Nepal and China, namely *G. napalense*, *G. multibracteolatum* P.T.Li & X.M.Wang, *G. thomsonii* (Hook.f.) K.M.Matthew and *G. ventricosum* Hook.f. They constitute woody climbers with white latex, papery to coriaceous, broadly ovate, basally slightly cordate leaves, long-pedunculate, sciadioidal inflorescences and a staminal corona basally attached to the gynostegium.

For the type of the genus, *Gongronema napalense*, the spellings ‘*G. nepalense*’ and ‘*G. napalense*’ are used (compare IPNI, TROPICOS). This Nepalese taxon was originally published by Wallich (1826) as *Gymnema napalense* and the change occurred when Decaisne (1844) transferred the taxon to *Gongronema*, as ‘*G. nepalense*’. The *International Code of Nomenclature for algae, fungi, and plants* does not encourage the change of “a” to “e” (Art. 60, Turland & al., 2018), therefore, the correct name of the species is *G. napalense*. The spelling ‘*napalense*’ should not be considered a typographical error, because this spelling is also used in 12 more names published by Wallich and seven names published by other authors (IPNI, 2021).

2.7 *Gongronemopsis* S.Reuss, Liede & Meve, **gen. nov.** –

Type: *Gongronemopsis angolensis* (N.E.Br.) S.Reuss, Liede & Meve (≡ *Gongronema angolense* (N.E.Br.) Bullock ≡ *Marsdenia angolensis* N.E.Br.).

Illustrated in Figs. 2C,G–I, 5.

Diagnosis. – *Plants* suffrutescent twiners or lianas, 5–8 m high, glabrescent or pubescent; latex white. *Leaves* occasionally papery, 5–14 cm long, elliptic to oblong, or cordate. *Inflorescences* short-pedunculate, solitary, extra-axillary, sciadioidal, occasionally branched, many-flowered. *Corolla* 4–8 mm long, campanulate or urceolate, cream yellow, abaxially pubescent to shortly pilose, adaxially densely covered with bottle-shaped papillae ca. 40 μm long; lobes contorted, ovate, occasionally ciliate. *Corolline corona* absent. *Staminal corona* attached below the filament tube, shorter than the gynostegium, ovate, lingulate or unguiculate, apically reaching about the half of the connective appendages, more or less adnate to the anthers. *Gynostegium* concealed in corolla. *Pollinaria*: Pollinia ovoid. *Style-head* conical. *Follicles* usually solitary, 4.5–8 cm long, fusiform to obclavate.

Notes. – The African species of *Gongronema* were separated from *Marsdenia* by Bullock (1961), but Omlor (1998) doubted their attribution to *Gongronema* and placed them in *Marsdenia* sect. *Obscurae* Omlor. Of these five species (*G. angolense* (N.E.Br.) Bullock, *G. gazenze* (S.Moore) Bullock, *G. latifolium* Benth., *G. obscurum* Bullock, and *G. taylorii* (Schltr. & Rendle) Bullock), three were included in the present phylogeny. Of these, *G. angolense* and *G. latifolium* were retrieved in a well-supported (BS_{ML} = 95%, PP =

1) clade in subclade BIII of the Cosmopolitan Clade, together with some *Marsdenia* s.l. species from Madagascar, and Asia, that is separated here as independent genus, *Gongronemopsis*.

Gongronema gazenze is closely related to *G. latifolium* (Bullock, 1961: 199), differing only in larger flowers and less deeply cordate leaves, while *G. obscurum* is closely related to *G. angolense*, but with erect (nontwining) habit, apiculate leaf apices, and fewer-flowered inflorescences (Bullock, 1961: 200). Because these differences are considered minor, they are also transferred to *Gongronemopsis* here. *Gongronema taylorii*, however, not only takes an isolated position at the base of subclade BIII of the Cosmopolitan Clade, but is also morphologically fairly distinct, in particular with respect to its acute to cuneate leaf bases (in contrast to cordate to truncate ones in the other four species), so that it is not transferred to *Gongronemopsis* here. As in other Asclepiad genera (e.g., *Cynanchum*, Liede & Täuber, 2002; *Philibertia*, Goyder, 2004), a vegetative character such as leaf shape seems a better indicator for generic affinity than the often highly variable and convergent floral characters. Besides the African species, the *Gongronemopsis* clade also comprises two Asian species formerly classified in *Marsdenia*: *M. tenacissima* (Roxb.) Wight & Arn. from India, China and Indochina, and *M. philippinensis* Schltr. from the Philippines. Omlor (1998) has pointed out the close relationship between these two species and *M. cavaleri* (H.Lév.) Hand.-Mazz. ex Woodson from China, all characterized as lianas with large, heart-shaped leaves, branched, loose inflorescences and campanulate corollas with trichomes on the abaxial side, a feature otherwise rare in Asian Marsdenieae (Omlor, 1998: 114). In addition, Omlor (1998) associated *M. calesiana* Wight from India, *M. crocea* (Zipp. ex Span.) Hook.f. ex Boerl. and *M. stenocentra* Bakh.f., both from Java, with this group of species. For both, *M. cavaleri* and *M. calesiana*, the type specimens, E00275191 and K000872964, respectively, bear excellent flower drawings that allow verification of Omlor’s (1998) assessment enabling transfer of these species to *Gongronemopsis*. However, material available for the two Javanese species is not sufficient to advocate transfer without further study.

Diagnostic for *Gongronemopsis* is a combination of lianescent growth form, a more or less papery leaf lamina, short-pedunculate, branched inflorescences, bottle-shaped papillae covering the adaxial corolla lobes surface (Fig. 2H), and a staminal corona attached below the filament tube, apically adnate to the anther, shorter than the gynostegium.

Gongronemopsis angolensis (N.E.Br.) S.Reuss, Liede & Meve, **comb. nov.** ≡ *Marsdenia angolensis* N.E.Br. in Bull. Misc. Inform. Kew 1895: 258. 1895 ≡ *Gongronema angolense* (N.E.Br.) Bullock in Kew Bull. 15: 199. 1961 – Lectotype (designated by Bullock in Kew Bull. 9: 367. 1954): Angola, Pungo Andongo; in thickets in the Praesidium at Cabombo, Mar 1857, F.M.J. Welwitsch 4245 (K barcode K000305265!).

= *Marsdenia gondarensis* Chiov. in Ann. Bot. (Rome) 9: 80. 1911 – Holotype: Ethiopia, Amhara-Dembia: Gondar, macchie tra i ruderi, 31 Aug 1909, *E. Chiovenda 1741* (FT barcode FT002701!).

Gongronemopsis calesiana (Wight) S.Reuss, Liede & Meve, **comb. nov.** ≡ *Marsdenia calesiana* Wight, Contr. Bot. India: 41. 1834 ≡ *Pergularia calesiana* (Wight) Buch.-Ham. ex D.Dietr., Syn. Pl. 2: 895. 1840 ≡ *Pergularia calesiana* (Wight) Buch.-Ham. ex Hook.f., Fl. Brit. India 4: 37. 1883, nom. superfl. – Lectotype (designated by Jagtap & Singh, Fasc. Fl. India 24, Asclepiad., Periploc.: 125. 1999): Nepal, Morang, *F. Buchanan-Hamilton 57* (K barcode K000872964!).

Gongronemopsis cavalieri (H.Lév.) S.Reuss, Liede & Meve, **comb. nov.** ≡ *Metaplexis cavalieri* H.Lév., Fl. Kouy-Tchéou 42. 1914 ≡ *Marsdenia cavalieri* (H.Lév.) Hand.-Mazz. ex Woodson in J. Arnold Arbor. 15(4): 318. 1934 – Holotype: China, Guizhou: Houa-Liang, 01 Jun 1904, *J. Cavalerie 2155* (E barcode E00275191!; isotype: P barcode P03873684!).

Gongronemopsis gazensis (S.Moore) S.Reuss, Liede & Meve, **comb. nov.** ≡ *Marsdenia gazensis* S.Moore in J. Bot. 46: 306. 1908 ≡ *Gongronema gazense* (S.Moore) Bullock in Kew Bull. 15: 199. 1961 – Holotype: Mozambique, Gazaland, Kurumadji, Jichu river, 600 m, 04 Jan 1906, *C.F.M. Swynnerton 224* (BM barcode BM000925984!; isotype: K barcode K000305261!).

Gongronemopsis latifolia (Benth.) S.Reuss, Liede & Meve, **comb. nov.** ≡ *Gongronema latifolium* Benth. in Hooker, Niger Fl.: 456. 1849 ≡ *Marsdenia latifolia* (Benth.) K.Schum. in Bot. Jahresber. (Just) 26(1): 372. 1900 – Holotype: São Tomé and Príncipe, St. Thomas, *D. Don s.n.* (K barcode K000305284!; isotype: BM barcode BM000925986!).

= *Marsdenia leonensis* Benth. in Hooker, Niger Fl.: 61. 1849 – **Lectotype (designated here)**: Sierra Leone, *J.R.T. Vogel s.n.* (K barcode K000305290!; isolectotype: K barcode K000305291!).

= *Marsdenia glabriflora* Benth. in Hooker, Niger Fl.: 61. 1849, non *Gongronema glabriflorum* Warb. in Bot. Jahrb. Syst. 13: 411. 1891 (≡ *Tylophora glabriflora* (Warb.) Schltr. in Schumann & Lauterbach, Fl. Schutzgeb. Südsee, Nachtr.: 354. 1905) – Holotype: Sierra Leone, *J.R.T. Vogel s.n.* (K barcode K000305289!).

= *Marsdenia racemosa* K.Schum. in Bot. Jahrb. Syst. 17: 147. 1893 – **Lectotype (designated here)**: Angola, Am Lulua River, *P. Pogge 1249* (K barcode K000305263!).

= *Marsdenia glabriflora* var. *orbicularis* N.E.Br. in Thiselton-Dyer, Fl. Trop. Afr. [Oliver] 4(1): 424. 1903 – Holotype: Nigeria, Bonny River, Oct 1860, *G. Mann s.n.* (K barcode K000305288!).

Notes. – Of the two specimens of *Vogel s.n.*, the richer one, provided with a pollinarium drawing, is selected as the lectotype of *Marsdenia leonensis*.

Even though Schumann (1893) did not indicate the location of his types, it is likely that the original material of *Marsdenia racemosa* has been destroyed in B. The K specimen (K000305328) is poor, consisting of a leaf and an incomplete inflorescence, but bears a pollinarium drawing and the note “Ex Museo botanico Berolinensi”, so it was apparently taken from original material and is, therefore, designated as the lectotype of *Marsdenia racemosa*.

Gongronemopsis obscura (Bullock) S.Reuss, Liede & Meve, **comb. nov.** ≡ *Gongronema obscurum* Bullock in Kew Bull. 15: 200. 1961 ≡ *Marsdenia obscura* (Bullock) Omlor, Gen. Revis. Marsdenieae: 75. 1998 – Holotype: Ghana, Navrongo Northern Territories, Navrongo, Sedoza Tankara F.R., Jun 1954, *J.E. Andoh 5905* (K barcode K000042536!).

Gongronemopsis philippinensis (Schltr.) S.Reuss, Liede & Meve, **comb. nov.** ≡ *Marsdenia philippinensis* Schltr. in Perkins, Fragm. Fl. Philipp. 1: 133. 1904 – Holotype: Philippines, Luzon Isl., Mariveles, *O. Warburg 13548* (B†). **Neotype (designated here)**: Philippines, Luzon, Bataan Province, Lamao River, Mt. Mariveles, Oct 1903, *E.D. Merrill 3315* (K barcode K000872988!). Illustrated in Fig. 5.

Notes. – No material of *Warburg 13548*, type of *Marsdenia philippinensis*, could be traced. *Merrill 3315*, of which a reasonably well-preserved specimen is extant in K, was collected at the same locality as given for *Warburg 13548* and is, therefore, selected as the neotype of *M. philippinensis*.

Gongronemopsis tenacissima (Roxb.) S.Reuss, Liede & Meve, **comb. nov.** ≡ *Asclepias tenacissima* Roxb., Pl. Coromandel 3: 35–36, t. 240. 1815 ≡ *Gymnema tenacissimum* (Roxb.) Spreng., Syst. Veg. 1: 844. 1824 ≡ *Marsdenia tenacissima* (Roxb.) Moon, Cat. Pl. Ceylon: 21. 1824 ≡ *Marsdenia tenacissima* (Roxb.) Wight & Arn. in Wight, Contr. Bot. India: 41. 1834, nom. illeg. ≡ *Pergularia tenacissima* (Roxb.) D.Dietr., Syn. Pl. 2: 895. 1840 – Lectotype (designated by Jagtap & Singh, Fasc. Fl. India 24, Asclepiad., Periploc.: 132: 1999): [illustration] “*Asclepias tenacissima*” in Roxburgh, Pl. Coromandel 3: t. 240. 1815.

Gongronemopsis truncata (Jum. & H.Perrier) S.Reuss, Liede & Meve, **comb. nov.** ≡ *Marsdenia truncata* Jum. & H.Perrier in Ann. Inst. Bot.-Géol. Colon. Marseille, ser. 3, 6: 233. 1908 – **Lectotype (designated here)**: Madagascar, Mahajanga, Bois sablonneux, Ankirihitra, près du M. Tsitondraina (Boïna), Nov 1902, *H. Perrier de la Bâthie 8992* (P barcode P04023545!; isolectotypes: P barcodes P04023546!, P04023547!).

Notes. – Of the two syntypes (*Perrier de la Bâthie 8992* and *8993*) cited by Jumelle & Perrier (1908), the richest

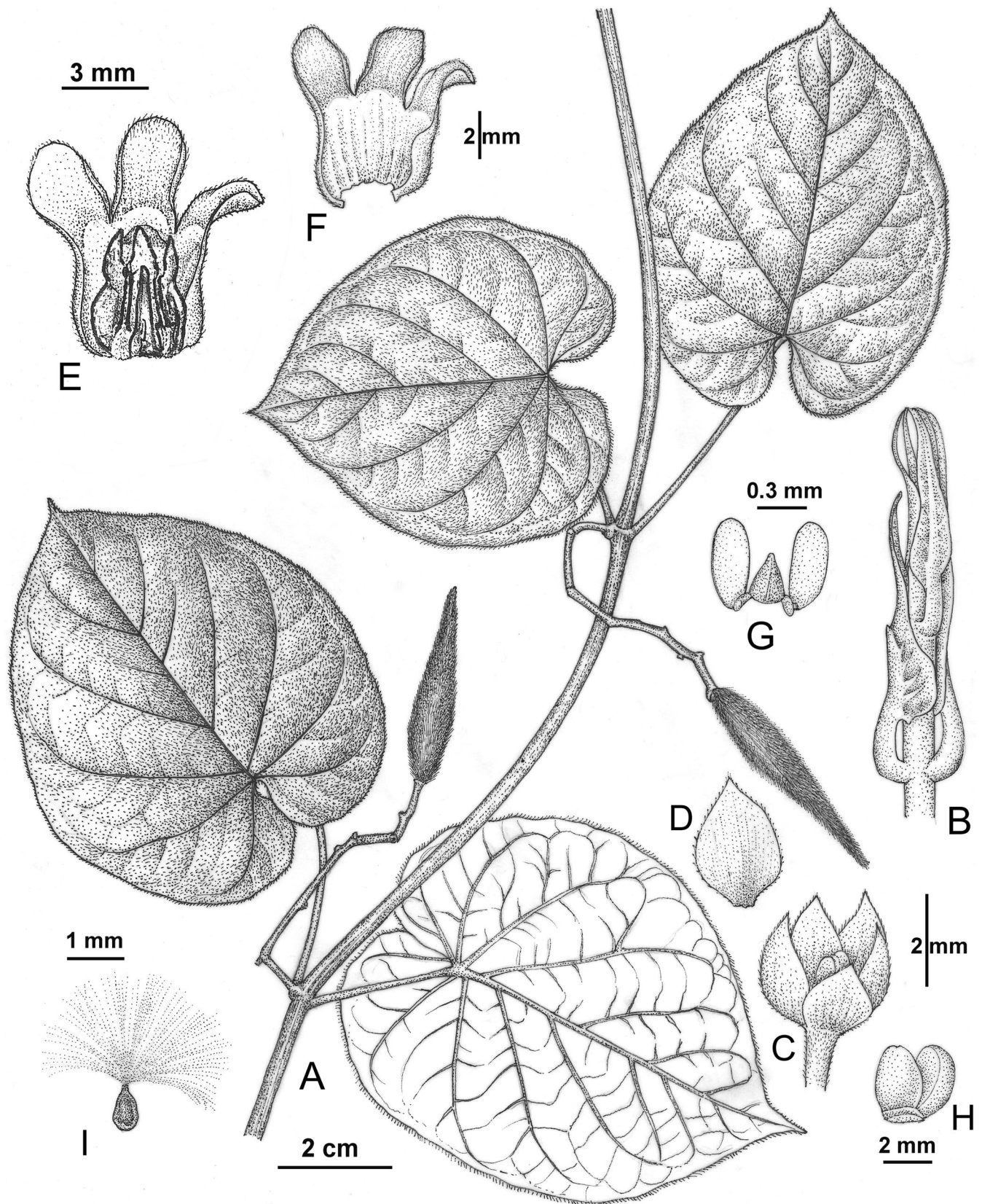


Fig. 5. *Gongronemopsis philippinensis*. **A**, Fruiting section of stem; **B**, Stem tip; **C**, Calyx; **D**, Calyx lobe; **E**, Opened corolla with gynostegium; **F**, Opened corolla; **G**, Pollinarium; **H**, Ovaries; **I**, Seed. — Drawn from *Laurente & Vasquez 6* (USTH) by N. Diego.

specimen of *Perrier de la Bâthie 8992* was annotated by Stevens (in schedis) as lectotype, with two isolectotypes, and his choice is followed here.

- 2.8 *Gymnema* R.Br., Prodr.: 461. 1810 – Type: *Gymnema sylvestre* (Retz.) R.Br. ex Sm. (\equiv *Periploca sylvestris* Retz.). = *Gymnema* [unranked] *Bidaria* Endl., Gen. Pl.: 595. 1838 \equiv *Bidaria* (Endl.) Decne. in Candolle, Prodr. 8: 623. 1844 \equiv *Gymnema* sect. *Bidaria* (Endl.) Benth., Fl. Austral. 4: 342. 1868 – Type: *Bidaria tingens* (Roxb.) Decne. (\equiv *Asclepias tingens* Roxb.) (\equiv *Gymnema inodorum* (Lour.) Decne.). = *Jasminanthes* Blume, Mus. Bot. 1: 148. 1850 – Type: *Jasminanthes suaveolens* Blume, **syn. nov.** = *Huthamnus* Tsiang in Bull. Fan Mem. Inst. Biol. 8(3): 9. 1939 – Type: *Huthamnus sinicus* Tsiang. Illustrated in Figs. 1C, 2E.

Description. – Plants suffrutescent twiners or lianas, up to 12 m high, occasionally pubescent, lenticellate; latex white, occasionally clear. *Leaves* 1–13(–19) cm long, ovate to oblong, basally occasionally cordate, occasionally slightly pubescent. *Inflorescences* rarely in pairs, extra-axillary, with up to 12 flowers. Flowers occasionally sweetly fragrant. *Corolla* 2–8(–50) mm long, campanulate to urceolate, rarely salverform, creamish or yellowish green, inside occasionally with trichomes, tube occasionally inflated; lobes valvate to contorted, oblong to ovate, occasionally twisted. *Corolline corona* as five (ten) longitudinal ridges below the sinus of the corolla lobes, densely pubescent with trichomes. *Staminal corona* absent or occasionally reduced to a scale (e.g., *G. pachyglossum*). *Gynostegium* sessile, concealed in corolla. *Pollinaria*: Pollinia ovoid to oblongoid, caudicles horizontal, short. *Style-head* conical, rostrate, rarely semi-globose. *Follicles* solitary, (3.5–) 9–16(–21) cm long, obclavate, occasionally ellipsoid. *Seeds* winged.

Notes. – *Jasminanthes* is retrieved inside the larger *Gymnema* clade in subclade BIV of the Cosmopolitan Clade. This clade comprises ca. 40 species and is widespread in the Paleotropics with a center of diversity in Australasia.

Members of the *Gymnema* clade are morphologically fairly easily recognized by a complete absence or strong reduction of a staminal corona, and the presence of a corolline corona in the form of five (or ten) longitudinal ridges below the corolla sinuses. However, *Jasminanthes maingayi*, supported ($BS_{ML} = 87\%$, $PP = 1$) as sister-group to the remainder of the species, does not conform to this pattern. This showy species from Peninsular Malaysia, Singapore and Borneo, that has been illustrated recently after its rediscovery in Singapore (Yeoh & al., 2013), lacks a corolline corona, as does the second *Jasminanthes* species studied, *J. mucronata* from Japan and China. For this reason, these two species had been transferred to *Stephanotis* by Hooker (1885: 39). The two *Jasminanthes* species are not monophyletic in the *Gymnema* clade (subclade BIV of the Cosmopolitan Clade). Members of the *Gymnema* clade are usually large suffrutescent twiners or lianas and possess winged seeds. Shape of corolla, in contrast, is highly variable, ranging

from small, short-tubed and inconspicuous (e.g., *G. sylvestre*) to large, long-tubed and showy (*Jasminanthes* species).

Because recognition of *Gymnema* as separate from *Marsdenia* (in contrast to, e.g., Forster, 1995), but including *Jasminanthes*, will result in a considerable number of new combinations, this task is postponed to a thorough re-analysis of this clade at a later point in time; only the Australian and New Guinean species hitherto attributed to *Marsdenia* have so far been transferred (Forster, 2021). Therefore, the types of *Jasminanthes* (*J. suaveolens* Blume) and *Huthamnus* (*H. sinicus* Tsiang) have not yet been transferred to *Gymnema*.

The type, *Gymnema sylvestre* (Retz.) R.Br. ex Sm. has been described from Indian material (see Forster, 1989: 126), but is thought to be widespread in tropical Africa (incl. Madagascar), the western parts of India, and southern China and Taiwan. In our analysis, the Malagasy and the mainland African samples (from Cameroon and Ethiopia) of this species were well supported as monophyletic ($BS_{ML} = 92\%$, $PP = 1$). The position of this clade, however, is only poorly supported ($BS_{ML} < 50\%$, $PP = 0.81$). In addition, the Malagasy and African accessions were not monophyletic with our two accessions from China, which took a supported ($BS_{ML} = 67\%$, $PP = 0.98$) sister-group position to the Asian *G. pachyglossum*. Because we were not able to secure Indian material, it is not yet clear which of the two clades, if any, represents the typical *G. sylvestre* and which one has to be described newly as a cryptic species.

- 2.9 *Harmandiella* Costantin in Lecomte, Fl. Indo-Chine 4: 89. 1912 – Type: *Harmandiella cordifolia* Costantin.

Description. – Plants large woody twiners, entirely glabrous. *Leaves* long-pedunculate, large ($>11 \times 9$ cm), ovate, basally cordate, apically long-acuminate, discolourous. *Inflorescences* solitary, extra-axillary, with petioles shorter than peduncles, basal dichasia carrying cymose partial inflorescences. *Flowers* almost sessile, small, rotate with short tube, lobes dextrorse in bud. *Corolline corolla* of five longitudinal, erect, triangular segments in the tube along the sutures. *Staminal corona* reduced to small horn-shaped extensions at the base of the anthers. *Pollinaria*: pollinia elongatedly obovate, caudicles straight, horizontal, vaguely geniculate, corpuscle ellipsoid, with a broad flat rim on the ventral side. *Style-head* slightly umbonate. *Follicles* ellipsoid, thick-walled; *seeds* ovate, smooth, winged.

Notes. – Even though Omlor (1998) noted the unusual morphology of *Harmandiella cordifolia*, he (Omlor, 1998: 118) decided to include this monotypic genus in *Marsdenia*. Its rediscovery in Laos (Rodda, 2020) allowed its inclusion in the present study. The position of *H. cordifolia* in subclade BII of the Cosmopolitan Clade (see discussion under “2.2 *Campestigma*”) justifies retaining *Harmandiella* as a monotypic genus.

- 2.10 *Lygisma* Hook.f. in Hooker’s Icon. Pl. 15: t. 1423. 1883 – Type: *Lygisma angustifolium* (Wight) Hook.f. (\equiv *Marsdenia angustifolia* Wight).

- = *Costantina* Bullock in Kew Bull. 19(2): 199. 1965 ≡ *Pilostigma* Costantin in Lecomte, Fl. Indo-Chine 4: 73. 1912, nom. illeg., non *Pilostigma* Tiegh. in Bull. Soc. Bot. France 41: 483. 1894 (Loranthaceae) – Type: *Costantina inflexa* (Costantin) Bullock (≡ *Pilostigma inflexum* Costantin ≡ *Lygisma inflexum* (Costantin) Kerr).
- = *Vietnamia* P.T.Li in J. S. China Agric. Univ. 15(4): 72. 1994 – Type: *Vietnamia inflexa* P.T.Li (= *Lygisma inflexum* (Costantin) Kerr), **syn. nov.**

Description. – Plants suffrutescent twiners, up to 3 m high, pubescent; latex white. *Leaves* papery, ovate to lanceolate, 3–6.5 cm long. *Inflorescences* solitary, extra-axillary, occasionally paired, axillary or terminal, long-pedunculate, loose, with up to eight flowers. *Corolla* 3–4 mm long, campanulate, white, tube inside pilose; lobes (apically) inwardly bent, oblong. *Corolline corona* absent. *Staminal corona* not exceeding gynostegium, erect, slightly carnosely, ovate. Gynostegium concealed in corolla. *Pollinaria*: Pollinia oblongoid, one species with pellucid margin, caudicles short, S-shaped. *Style-head* flattened, papillose. *Follicles* solitary, 5–7 cm long, obclavate. *Seeds* winged.

Notes. – *Lygisma* is with moderate support (BS_{ML} = 85%, PP = 1) retrieved in sister-group position to *Cosmostigma*, forming the first-branching subclade BI of the Cosmopolitan Clade. Presently, the genus comprises four species in China, continental Southeast Asia and Malaysia.

Lygisma comprises suffrutescent twiners with pubescent shoots and papery leaves. It is most easily distinguished by the oblong corolla lobes apically bent inwardly in bud in combination with a flattened, papillose style-head.

Vietnamia has been synonymized with *Pentasachme* (Ceropegieae) by Endress & al. (2018). However, the papery leaves, the loose, long-pedunculate inflorescences and pollinaria structure are indicative of *Lygisma*. Even though *Vietnamia inflexa* has been identified as a synonym of *Lygisma inflexum*, with the epithet ‘*inflexum*’ referring to the apically conspicuously inflexed corolla lobes (Costantin, 1912: fig. 12), the two species have been described from different types; *Lygisma* (*Pilostigma*) *inflexum* from *M. Thorel 1031* (P00645887, P00645888) and *Vietnamia inflexa* from *P.A. Pételot 8935* (MO-423438). The latter specimen, however, bears a label by W.D. Stevens (2004), identifying it as *Lygisma inflexum*, the view adopted here. Thus, the type of *Vietnamia* was also included in our analysis and is sister to *Lygisma angustifolia*, the type of *Lygisma* with strong support (BS_{ML} = 97%, PP = 1).

- 2.11 *Ruehssia* H.Karst. in Verh. Vereins Beförd. Gartenbaues Königl. Preuss. Staaten 19: 304. 1849 – Lectotype (designated by Espírito Santo & al. in Kew Bull. 74, no. 30: 4. 2019): *Ruehssia macrophylla* (Humb. & Bonpl. ex Schult.) H.Karst. (≡ *Asclepias macrophylla* Humb. & Bonpl. ex Schult.).
- = *Pseudomagnettus* Ruschenb., Rep. Cundurango: 15. 1873 – Type: *Pseudomagnettus equatoriensis* Ruschenb. (= *Ruehssia cundurango* (Triana) Liede & H.A.Keller).

- = *Verlotia* E.Fourn. in Martius, Fl. Bras. 6(4): 324. 1885 – Lectotype (designated by Espírito Santo & al. in Kew Bull. 74, no. 30: 5. 2019): *Verlotia suberosa* E.Fourn. (≡ *Ruehssia suberosa* (E.Fourn.) F.Esp.Santo & Rapini).
- = *Pseudomarsdenia* Baill., Hist. Pl. 10: 268. 1890 – Type: *Pseudomarsdenia bourgeana* Baill. (≡ *Marsdenia bourgeana* (Baill.) W.Rothe).
- = *Elcomarhiza* Barb.Rodr., Vellosia, ed. 2: 44. 1892 – Type: *Elcomarhiza amylacea* Barb.Rodr. (≡ *Ruehssia amylacea* (Barb.Rodr.) F.Esp.Santo & Rapini).
- = *Ecliptostelma* Brandege in Univ. Calif. Publ. Bot. 6: 371. 1917 – Type: *Ecliptostelma molle* Brandege (≡ *Marsdenia purpusiana* W.D.Stevens).
- = *Baxtera* Rchb., Conspect. Regn. Veg.: 131. 1828, nom. rej. ≡ *Harrisonia* Hook. in Bot. Mag. 53: 2699. 1826, nom. illeg., non *Harrisonia* R.Br. ex A.Juss. in Mém. Mus. Hist. Nat. 12: 517. 1825 (Simaroubaceae) ≡ *Loniceroides* Bullock in Kew Bull. 17: 487. 1964 – Type: *Loniceroides harrisoniae* Bullock (≡ *Harrisonia loniceroides* Hook. ≡ *Ruehssia loniceroides* (Hook.) F.Esp.Santo & Rapini).
- “*Sphinctostoma* Benth.” in Bentham & Hooker, Gen. Pl. 2: 772. 1876, not validly published.
- Illustrated in Figs. 1G, 2D,J.

Description. – *Lianas*, twining or climbing plants, shrubs or subshrubs, erect or prostrate; latex white. *Leaves* opposite, distichous or decussate, less often up to 4 leaves irregularly arranged at the nodes or in brachyblasts, sessile or petiolate, of various shapes, membranous to coriaceous, glabrous or with trichomes. *Inflorescences* axillary or sub-axillary, umbelliform, glomeruliform or racemiform, rarely scorpioid, fasciculate or paniculiform, multi-flowered, rarely with solitary flowers, usually congested, sessile to longly pedunculate. *Flowers* sessile to pedicellate, tiny and discrete or large and showy; corolla urceolate, campanulate, tubular, hypocrateriform or rotate, generally vinaceous, greenish, white or yellowish, glabrous or with trichomes. *Staminal corona* with 5 lobes of different shapes, completely fused to the dorsal side of anthers or segmented with an upper free portion, occasionally exceeding the style-head. *Gynostegium* inserted to exserted, sessile or stipitate. *Style-head* of various shapes. *Pollinaria*: pollinia erect, oblong, obovoid, elliptic, rarely reniform, attached to the caudicle by the base; corpuscle ovoid, oblong, lanceolate or linear. *Follicles* solitary, fusiform, ellipsoid, ovoid or oblongoid, glabrous or with trichomes. *Seeds* comose, rarely without coma.

Notes. – All Neotropical Marsdenieae species group in a single clade in subclade BV of the Cosmopolitan Clade, unrelated to the type of *Marsdenia*, *M. tinctoria*. While this clade was strongly supported in the phylogeny of Espírito Santo & al. (2019), it is only moderately (BS_{ML} = 72%, PP = 1) supported in our phylogeny that uses a different set of markers. As in previous analyses (Espírito Santo & al., 2019; Keller & al., 2020), *Ruehssia sprucei* from northern South America is sister to all other species (PP = 1 in Espírito Santo & al., 2019; BS_{ML} = 73%, PP = 0.93 in Keller & al., 2020; no support in the present analysis), which fall in two main subclades, one mainly

South American, the other Central American-Caribbean. However, three Central American species (*Marsdenia edulis*, *M. engleriana*, *M. zimapanica*) are nested in the South American subclade, indicating that at least some of the Central American species are more recent immigrants from South America. The Caribbean species form a moderately supported ($BS_{ML} = 81\%$, $PP = 0.88$) clade nested in the unsupported Central American species. The weak support within the *Ruehssia* clade might be due to a very incomplete set of partial sequences for most Central American species.

Espirito Santo & al. (2019) reinstated the genus *Ruehssia* and provided new combinations for the 42 Brazilian species. Former *Marsdenia* s.l. species of Cuba have recently been transferred to *Ruehssia* (Reuss & al., 2020), some species of Puerto Rico (Bárrios & al., 2020) and Mexico (Lozada-Pérez & al., 2020), as well as all species occurring in South America (Keller & al., 2020; Liede-Schumann & Keller, 2020) and the Caribbean (Acevedo-Rodríguez, 2021) have also been transferred to date. Transfer is still pending for the Central American species. Therefore, no new combinations for the type of *Ecliptostelma* (*E. molle* Brandege) and *Pseudomarsdenia* (*P. bourgeana* Baill.) are yet available.

Comprising all Neotropical species, *Ruehssia* is a monophyletic, but morphologically heterogeneous clade with ca. 130 species. As in *Leichhardtia* for the Pacific region, no clear-cut morphological differences between *Ruehssia* and some Paleotropical Marsdenieae lineages can be named at present.

2.12 ***Sarcolobus*** R.Br., Asclepiadeae: 23. 1810 – Type: *Sarcolobus banksii* Schult.

= *Dorystephania* Warb. in Perkins, Fragm. Fl. Philipp.: 123. 1904 – Type: *Dorystephania luzonensis* Warb. (≡ *Sarcolobus luzonensis* (Warb.) P.I.Forst.).

= *Petalonema* Schltr. in Repert. Spec. Nov. Regni. Veg. 13: 543. 1915, nom. illeg., non *Petalonema* Berk. ex Correns in Flora 72: 321. 1889 (Cyanophyceae: Scytonemataceae) ≡ *Schlechterianthus* Quisumb. in Philipp. J. Sci. 41: 342. 1930, nom. illeg., non *Schlechterianthus* Schwantes in Monatsschr. Deutsch. Kakteen-Ges. 1: 16. 1929 (Aizoaceae), ≡ *Quisumbingia* Merr. in Philipp. J. Sci. 60: 33. 1936 – Type: *Quisumbingia merrillii* (Schltr.) Merr. (≡ *Petalonema merrillii* Schltr. ≡ *Sarcolobus merrillii* (Schltr.) Omlor).

= *Papuastelma* Bullock in Kew Bull. 19: 202. 1965 ≡ *Astelma* Schltr. in Bot. Jahrb. Syst. 50: 138. fig. 7. 1913, nom. illeg., non *Astelma* R.Br. ex Ker Gawl. in Bot. Reg. 7: ad t. 532. 1821 (Asteraceae) – Type: *Papuastelma secamonoides* (Schltr.) Bullock (≡ *Astelma secamonoides* Schltr. ≡ *Sarcolobus secamonoides* (Schltr.) P.I.Forst.).

= *Gunnessia* P.I.Forst. in Austrobaileya 3(2): 282. 1990 – Type: *Gunnessia pepo* P.I.Forst. (≡ *Sarcolobus pepo* (P.I.Forst.) S.Reuss, Liede & Meve), **syn. nov.** Illustrated in Fig. 2F.

Description. – Plants suffrutescent lianas or rheophytic shrubs, 0.5–5 m high, shoots hollow, glabrescent (*Sarcolobus*

pepo pubescent), occasionally with papery bark; latex white to yellow. *Leaves* oblong to ovate, occasionally cordate, obtuse or retuse, lamina 7–13(–15) cm long, basally adaxially with up to 6 colleters. *Inflorescences* extra-axillary, solitary, sciadoidal, (sub)sessile, with up to 6(8) flowers. *Corolla* up to 20 mm in diam., often reticulated, broadly urceolate, campanulate or rotate; lobes contorted, ovate to triangular, occasionally papillose to pilose. *Corolline corona* (when present) as ridges opposite the anthers, or as small annulus (*S. pepo*). *Gynostegial corona* absent, or staminal corona ovoid (hump-like) to rectangular, occasionally bent back along the central axis (*S. cambogensis*), or fused to a tube (*S. pepo*), not exceeding the gynostegium. *Gynostegium* usually stipitate (occasionally sessile), filament tube occasionally basally expanding disc-like, adnate to the corolla tube. *Pollinaria*: Pollinia ovoid, oblongoid or globose, caudicles (mostly) geniculate, flattened (band-like), corpuscle slenderly ellipsoid, in size similar to pollinia. *Style-head* often papillose, umbonate to semi-globose. *Follicles* solitary, 4–10 cm long, ovoid, occasionally inflated. *Seeds* ovate, broadly winged, coma short or absent.

Notes. – *Sarcolobus*, including *Gunnessia* with a single, morphologically aberrant species from northern Queensland, forms a strongly ($BS_{ML} = 100\%$, $PP = 1$) supported clade in moderately supported sister-group position ($BS_{ML} = 84\%$, $PP = 1$) to the *Gongronema-Dischidanthus* clade in subclade BII of the Cosmopolitan Clade. *Sarcolobus* is distributed from India to Australia with ca. 13 species.

Sarcolobus has always been recognized as a genus independent of *Marsdenia* s.l. because it is easily recognized by its subsessile inflorescences, broadly urceolate or rotate corollas, usually geniculate, flattened (band-like) caudicles, and often papillate style-heads. Furthermore, it is one of the few genera typically growing close to the sea, mainly in the narrow band between mangrove and the adjacent vegetation or as rheophytes (Forster, 1991), and species growing there often have hollow shoots, an unusual character in Marsdenieae. However, with *S. pepo*, and the recently described *S. cambogensis* (McHone & al., 2015), the morphological and ecological heterogeneity of the genus has increased.

Sarcolobus pepo (P.I.Forst.) S.Reuss, Liede & Meve, **comb.**

nov. ≡ *Gunnessia pepo* P.I.Forst. in Austrobaileya 3(2): 282. 1990 – Holotype: Australia, 1 km S of Cape York, 11 Feb 1986, B. Gray 4268 (CNS barcodes QRS081323! & QRS081324!; isotypes: BRI barcode BRI-AQ0194594!, CANB barcode CANB422186!).

Notes. – The two specimens at CNS are labeled as parts of the same gathering according to ICN Art. 8.3., so that no lectotypification is necessary.

2.13 ***Stephanotis*** Thouars, Gen. Nov. Madagasc.: 11. 1806 – Type: *Stephanotis thouarsii* Brongn.

= *Dregea* E.Mey., Comm. Pl. Afr. Austr.: 199. 1838, nom. cons. against *Dregea* Eckl. & Zeyher, Enum. Pl. Afric. Austral.: 350. 1837 (Apiaceae), nom. rej., ≡ *Pterophora* Harv., Gen. S. Afr. Pl.: 223. 1838, nom. illeg., non

- Pterophora* L., Pl. Rar. Afr.: 17. 1760 (Asteraceae), nom. rej. – Type: *Dregea floribunda* E.Mey. (= *Stephanotis ernstmeyeri* S.Reuss, Liede & Meve).
- = *Pterygocarpus* Hochst. in Flora 26: 78. 1843 – Type: *Pterygocarpus abyssinicus* Hochst. (= *Stephanotis abyssinica* (Hochst.) S.Reuss, Liede & Meve).
- = *Hoya* [unranked] *Wattakaka* Endl., Gen. Pl.: 596. 1838 ('*Wattakaka*') = *Hoya* sect. *Wattakaka* (Endl.) Decne. in Candolle, Prodr. 8: 639. 1844 = *Wattakaka* (Endl.) Hassk. in Flora 40: 99. 1857 – Type: *Wattakaka volubilis* (L.f.) Stapf (= *Asclepias volubilis* L.f.).
- = *Chlorochlamys* Miq. in Ann. Mus. Bot. Lugduno-Batavi 4: 142. 1869 – Type: *Chlorochlamys celebica* Miq. (= *Stephanotis volubilis* (L.f.) S.Reuss, Liede & Meve), **syn. nov.**
- = *Traunia* K.Schum. in Notizbl. Königl. Bot. Gart. Berlin 1: 22. 1895 = *Dregea* subg. *Traunia* (K.Schum.) Bullock in Kew Bull. 11: 518. 1956 – Type: *Traunia albiflora* K.Schum. (= *Stephanotis schimperi* (Decne.) S.Reuss, Liede & Meve).
- "*Isaura* Comm. ex Poir." in Lamarck, Encycl., Suppl. 3: 185. 1813, not validly published.
Illustrated in Fig. 1B.

Description. – Plants suffrutescent twiners or lianas; latex clear (white in *Stephanotis brevisquama*). Leaves subcoriaceous to carnose, broadly ovate to elliptical, occasionally cordate. Inflorescences solitary, extra-axillary, distinctly pedunculate (except *S. brevisquama*, *S. stelostigma*), spreading or pendulous. Flowers long-pedicellate, often sweetly fragrant; sepals mostly foliaceous. Corolla broadly rotate to campanulate or salverform. Staminal corona not longer than gynostegium (except *S. rubicunda*). Style-head usually conical. Pollinaria: Pollinia ellipsoid to rectangular, caudicles short, horizontal, or geniculate, rectangular to trapezoidal, corpuscle ovate to oblongoid. Follicles solitary or paired, then in an angle of almost 180°, broadly fusiform, ovoid or obclavate, with thick pericarp, occasionally inflated or with four wings, many-seeded. Seeds ovate, broadly winged, comose.

Notes. – The strongly supported *Stephanotis* clade (BS_{ML} = 99%, PP = 1) is the largest clade in subclade BIII of the Cosmopolitan Clade and moderately supported (BS_{ML} = 75%, PP = 0.99) as sister to the *Telosma* clade. It comprises two moderately supported subclades, but it would not ease circumscription problems to recognize these subclades as different genera. One subclade comprises *Dregea volubilis* from Asia as sister (BS_{ML} = 74%, PP = 1) to *Dregea* species from central East Africa. Thus, the view of Omlor (1998) that the Asian taxa are fundamentally different and should be separated from *Dregea* as *Wattakaka* is contradicted by molecular results at least for *D. volubilis*. The other subclade (BS_{ML} = 58%, PP = 0.87) comprises two species of *Stephanotis* s.str. from Madagascar, the short-tubed *Marsdenia brevisquama*, also from Madagascar, and three *Dregea* species from northeast Africa. The retrieval of *M. brevisquama* in the same subclade as the three samples of *Stephanotis* s.str. suggests that in this

clade, the differentiation of the typical long-tubed *Stephanotis* flower probably took place in Madagascar.

Stephanotis was originally restricted to four Malagasy species with long tubular corollas, that are undoubtedly very closely related, sharing several unusual characters, such as fleshy leaves, clear latex and thick-walled, broadly ovoid follicles, so that failure to obtain sequenceable material of the type *S. thoursii* does not give reason to doubt the results presented here. Long-tubed flowers, on the other hand, are also found in *Gymnema* (former *Jasminanthes*), *Ruehssia* and *Leichhardtia*, indicating that this conspicuous character has apparently evolved several times, probably as adaptation to the pollinators available. Our phylogeny retrieves *Stephanotis* embedded in a larger, predominantly African alliance, of which many species had been known under the name of *Dregea*. Because the type, *D. floribunda* E.Mey., is also among the species sequenced, *Dregea* is transferred in the synonymy of *Stephanotis* here, which constitutes the older name. Because of *Stephanotis floribunda* Brongn. (1837), the transfer of *Dregea floribunda* E.Mey. (1838) to *Stephanotis* requires a new name for the species. *Stephanotis* has been rejected against *Marsdenia* (Forster, 1990) but not against *Dregea*, so that the name is available for the clade circumscribed here. Presently, *Dregea* comprises 12 accepted species (Endress & al., 2018) distributed in Africa and Arabia, of which five are included in the present analysis. *Wattakaka* with eight Asian species (The Plant List <http://www.theplantlist.org>, accessed 23 Oct 2019) has often been included in the synonymy of *Dregea*, a view supported by the present analysis. The only species of *Chlorochlamys*, *C. celebica*, has been described by Miquel (1869: 142) to replace *Wattakaka pubescens* Miq. and is thus superfluous. *Wattakaka pubescens* is a synonym of *Stephanotis volubilis*. Thus, *Chlorochlamys* represents a synonym of *Stephanotis*.

The type of *Pterygocarpus*, *P. abyssinicus*, is also retrieved here, so that the genus is also placed in synonymy of *Stephanotis*. Following Bullock (1957), *Traunia albiflora* is synonymous with *Marsdenia schimperi*, so that *Traunia* also constitutes a synonym of *Stephanotis*. Furthermore, the aberrant *Marsdenia brevisquama* from Madagascar and *M. robusta* H.Balf. from Socotra (presently included in the more widespread *M. arabica* (Decne.) Omlor) are retrieved inside this clade.

Stephanotis as circumscribed here comprises large, twining plants, usually with clear latex, flowers borne on long pedicels, and thick-walled, often winged follicles, which form an angle of 180° if borne in pairs.

Stephanotis is widespread throughout Africa to Arabia, including Madagascar and Socotra. With the former *Wattakaka* species, it reaches Pakistan, India, Sri Lanka, Nepal, China, Taiwan, Cambodia, Laos, Myanmar, Thailand, Vietnam, Indonesia and the Philippines. While there is no doubt that *Wattakaka* is an Asian taxon, the exact limits of its distribution are hard to assess because its attractive flowers in rich inflorescences have contributed to its popularity as horticultural, often introduced plants. While the African species of

Dregea are fairly uniform and can be transferred safely to *Stephanotis* even based on morphological evidence only, the Asian taxa are much more heterogeneous and are only transferred here if molecular evidence is available.

Stephanotis abyssinica (Hochst.) S.Reuss, Liede & Meve, **comb. nov.** ≡ *Pterygocarpus abyssinicus* Hochst. in Flora 26: 78. 1843 ≡ *Hoya africana* Decne. in Candolle, Prodr. 8: 639. 1844, nom. superfl. ≡ *Dregea africana* Martelli, Fl. Bogos.: 55. 1886 ≡ *Dregea abyssinica* (Hochst.) K.Schum. in Engler, Pflanzenw. Ost Afr. C: 326. 1895 ≡ *Marsdenia abyssinica* (Hochst.) Schltr. in Bot. Jahrb. Syst. 51: 143. 1913 – **Lectotype (first step designated by Bullock in Kew Bull. 11: 517. 1957; second step designated here)**: Ethiopia, in dumetis arbores scandens in vallibus regionis Medschara, 19 Apr 1841, *G.W. Schimper 1573* (TUB barcode TUB-003597!; isolectotype: BR barcode 000008358202!).

= *Marsdenia spissa* S.Moore in J. Bot. 39: 260. 1901 – Holotype: Kenya, near Lake Marsabit, 1898, *Lord H. Delamere s.n.* (BM barcode BM000925985!; isotype: K barcode K000305266).

= *Marsdenia abyssinica* f. *complicata* Bullock in Kew Bull. 7: 423. 1952 – Holotype: Tanzania, Ufipa Distr., Kate, 1530 m, 21 Oct 1949, *L. Silungwe 24* (K barcode K000305267!; isotype: S No. 12-12299!).

Stephanotis arabica (Decne.) S.Reuss, Liede & Meve, **comb. nov.** ≡ *Dregea arabica* Decne. in Candolle, Prodr. 8: 618. 1844 ≡ *Marsdenia arabica* (Decne.) Omlor, Gen. Revis. Marsdenieae: 79. 1998 – Holotype: Yemen. s. loc., *P.E. Botta s.n.* (P barcode P00645996!).

= *Marsdenia robusta* Balf.f. in Proc. Roy. Soc. Edinburgh 12: 79. 1884 – Lectotype (designated by Bruyns & Miller in Edinburgh J. Bot. 66: 100. 2009): Yemen, Socotra, Feb 1880, *I.B. Balfour, C. Cockburn & A. Scott 522* (E barcode E00199373!).

Stephanotis brevisquama (Jum. & H.Perrier) S.Reuss, Liede & Meve, **comb. nov.** ≡ *Marsdenia brevisquama* Jum. & H.Perrier in Ann. Mus. Colon. Marseille, sér. 2, 6: 235–236. 1908 – **Lectotype (designated here)**: Madagascar, bords du Jabohazo, a Ankirihitra près du mont Tsitondraina, Dec 1900, *Perrier de la Bâthie 8991* (P barcode P032540!).

Notes. – The lectotype of *Stephanotis brevisquama* has been selected by Stevens (*in schedis*) in accordance with the data given in the protologue, and his choice is followed here.

Stephanotis crinita (Oliv.) S.Reuss, Liede & Meve, **comb. nov.** ≡ *Marsdenia crinita* Oliv. in Hooker's, Icon. Pl. 20: t. 1993. 1891 ≡ *Dregea crinita* (Oliv.) Bullock in Kew Bull. 11: 519. 1957 – Lectotype (designated by Bullock in Kew Bull. 9: 367. 1954): Nigeria, expedition to the interior of Yoruba, Oyo, 2 May 1890, *A. Millson s.n.* (K barcode K000305286!).

Stephanotis ernstmeyeri S.Reuss, Liede & Meve, **nom. nov.** ≡ *Dregea floribunda* E.Mey., Comm. Pl. Afr. Austr.: 199. 1837 ≡ *Pterophora dregea* Harvey, Gen. S. Afr. Pl.: 223. 1838, nom. illeg. ≡ *Marsdenia floribunda* (E.Mey.) N.E.Br. in Thiselton-Dyer, Fl. Trop. Afr. [Oliver] 4(1): 422. 1903 ≡ *Marsdenia dregea* Schltr. in Bot. Jahrb. Syst. 51: 143. 1914 – **Lectotype (designated here)**: South Africa, im Wald im Gebüsch windend, 2500–3000', *J.F. Drège s.n.* (P barcode P04212510!).

Notes. – Of the syntypes cited by Decaisne (1844: 618) for *Dregea floribunda* [Port Natal; Zunrebergen, in sylvia prope Stroebels, alt. 2500–3000 pds, *Drège s.n.*; Hoffmanns Kloof prope Enon, alt. 400 pds, *Drège s.n.*; in collib. prope Katrivier, alt. 200 ft., *Drège s.n.*; all in P “(v.s.h. Mus. par.)”] numerous specimens have been located. Of these, the flower-bearing specimen (P04212510) is selected as the lectotype for the species.

Stephanotis faulknerae (Bullock) S.Reuss, Liede & Meve, **comb. nov.** ≡ *Dregea faulknerae* Bullock in Kew Bull. 11: 520. 1957 ≡ *Marsdenia faulknerae* (Bullock) Omlor, Gen. Revis. Marsdenieae: 79. 1998 – **Lectotype (designated here)**: Tanzania, Tanga Distr. Korogwe, Magunga, 1500 ft., 30 Apr 1953, *H.G. Faulkner 1189* (K barcode K000305270!; isolectotypes: B barcode B 10 0153227!, BR barcode 000008862488!, EA barcode EA000001841!, K barcodes K000305271!, K000305272!).

Notes. – Of the three specimens *Stephanotis faulknerae* labeled as “holotype”, the best preserved one, K000305270, is selected to serve as lectotype. Because the name commemorates the collector of the type, the botanical artist *Helen G. Faulkner*, the original spelling “faulknerae” is the correct form of the epithet, and correction to “faulkneri” (Goyder & al., 2012) was not necessary (*ICN Art. 60.8*, Turland & al., 2018).

Stephanotis macrantha (Klotzsch) S.Reuss, Liede & Meve, **comb. nov.** ≡ *Dregea macrantha* Klotzsch in Peters, Naturw. Reise Mossambique: 272. 1861 ≡ *Periploca petersiana* Vatke in Österr. Bot. Z. 26: 147. 1876, nom. superfl. ≡ *Marsdenia macrantha* (Klotzsch) Schltr. in Bot. Jahrb. Syst. 51: 143. 1913 – Syntypes: Mocambique, an den Ufern der Bäche von Rios de Sena, *W. Peters s.n.* (B†); In der Umgebung von Tette, *W. Peters s.n.* (B†). **Neotype (designated here)**: Mozambique, Tette, Feb 1859, *J. Kirk s.n.* (K barcode K000305448!).

= *Marsdenia zambesiaca* Schltr. in J. Bot. 33: 338. 1895 – Holotype: Malawi, Chiromo, Jan 1893, *G.F. Scott-Elliott 2791* (BM, not traced; isotype: K barcode K000305449!).

Notes. – Because the original material of *Dregea macrantha*, *Peters s.n.*, was destroyed in B, a neotype needs to be selected. We chose the specimen collected by *J. Kirk* and housed in K (K000305448) that has been collected at the type locality, Tette (Mozambique).

Stephanotis rubicunda (K.Schum.) S.Reuss, Liede & Meve, **comb. nov.** ≡ *Dregea rubicunda* K.Schum. in Bot. Jahrb. Syst. 17: 147. 1893 ≡ *Marsdenia rubicunda* (K.Schum.) N.E.Br. in Thiselton-Dyer, Fl. Trop. Afr. [Oliver] 4(1): 421. 1903 – Lectotype (designated by Bullock in Kew Bull. 11: 515. 1957): Kenya, Sansibar-Küste, Insel Mom-bassa, Jul 1876, *J.M. Hildebrandt 2024* (K barcode K000305274!).

Stephanotis schimperi (Decne.) S.Reuss, Liede & Meve, **comb. nov.** ≡ *Marsdenia schimperi* Decne. in Candolle, Prodr. 8: 616. 1844 – Holotype: Ethiopia. In fruticetis prop Genniam regionis Mensach, 26 Jun 1937, *G.H.W. Schimper 260* (P not traced; isotypes: BR barcode 000008358059!, HBG barcode HBG502929, K barcode K000305280!, LG barcode LG0000090024511!, M barcode M-0110242!, S No. 12-12294!, TUB barcode TUB003593!).

= *Gymnema macrocarpum* A.Rich., Tent. Fl. Abyss. 2: 43. 1851 – Syntypes: Ethiopia, Tigray, Beless, *R. Quartin Dillon s.n.* (P, not traced); Ethiopia, Shoa, *A. Petit s.n.* (P, not traced).

= *Traunia albiflora* K.Schum. in Notizbl. Bot. Gart. Berlin 1: 23. 1895 – Holotype Tanzania, Kilimanjaro, Marangu, 1500 m, Apr 1894 (fl.), *G.L.A. Volkens 2110* (B⁺). **Lectotype (designated here)**: Tanzania, Kilimanjaro, Marangu, 1500 m, Apr 1894 (fl.), *G.L.A. Volkens 2110* (BR barcode 000008862198!; isolectotype: HBG barcode HBG-502821!).

Notes. – The two syntypes of *Gymnema macrocarpum* could not be traced, therefore, no typification is carried out here.

Likewise, the original material of *Traunia albiflora* was most likely destroyed in B, but the existence of two isotypes allows selection of a lectotype, for which BR barcode 000008862198, the richer of the two specimens, was chosen.

Stephanotis stelostigma (K.Schum.) S.Reuss, Liede & Meve, **comb. nov.** ≡ *Marsdenia stelostigma* K.Schum. in Bot. Jahrb. Syst. 33: 330. 1903 ≡ *Stigmatorhynchus stelostigma* (K.Schum.) Schltr. in Bot. Jahrb. Syst. 51: 141. 1913 ≡ *Dregea stelostigma* (K.Schum.) Bullock in Kew Bull. 1956: 516. 1957 – Syntypes: Somalia, Tarro Gumbi, Boran, 22 Apr 1901, *H. Ellenbeck 2080* and *2082* (B⁺). **Neotype (designated here)**: Somalia: Boscaglia di Ischia Baidoa, 19 Oct 1913, *G. Paoli 1216* (FT barcode FT002702).

= *Marsdenia stefaninii* Chiov. in Res. Sci. Somalia Ital.: 116. 1916 – Holotype: Somalia. Boscaglia di Ischia Baidoa, 19 Oct 1913, *G. Paoli 1216* (FT barcode FT002702!).

Notes. – The two syntypes of *Marsdenia stelostigma* have been destroyed in B. Because synonymy of this species with *M. stefaninii* Chiov. is well established, and both have been described from plants of Somalia, it seems most prudent to neotypify *M. stelostigma* with the type of *M. stefaninii*. The attribution of this species to *Stigmatorhynchus* by Schlechter (1913) is erroneous, because the similarities of *S. stelostigma* to *Stigmatorhynchus* restrict themselves to the growth form of

rigid shrubs with very shortly stalked leaves, and a sizeable style-head. However, short shoots (brachyblasts), and a four-winged fruit with a woody pericarp clearly attribute this species to *Stephanotis* (see also Albers & Guldenberg, 2003: 152).

Stephanotis volubilis (L.f.) S.Reuss, Liede & Meve, **comb. nov.** ≡ *Asclepias volubilis* L.f., Suppl. Pl.: 170. 1781 ≡ *Hoya viridiflora* R.Br. in Mem. Wern. Nat. Hist. Soc. 1: 27. 1810, nom. superfl. ≡ *Schollia volubilis* (L.f.) Jacq. ex Steud., Nomencl. Bot.: 414, 746. 1821 ≡ *Dregea volubilis* (L.f.) Benth. ex Hook.f., Fl. Brit. India 4: 46. 1883 ≡ *Wattakaka viridiflora* Hassk. in Flora 40: 99. 1887, nom. superfl. ≡ *Dregea volubilis* var. *viridiflora* Kuntze, Revis. Gen. Pl. 2: 419. 1891 ≡ *Marsdenia volubilis* (L.f.) Cooke, Fl. Bombay 2: 166. 1904 ≡ *Wattakaka volubilis* (L.f.) Stapf in Bot. Mag. 148: sub t. 8976. 1923 – Holotype: Sri Lanka. *J.G. König s.n.* in Herb. Linnaeus 310.6 (LINN!).

= *Wattakaka pubescens* Miq., Fl. Ned. Ind. 2: 496. 1857 ≡ *Chlorochlamys celebica* Miq. in Ann. Mus. Bot. Lugduno-Batavi 4: 142. 1869, nom. illeg. & superfl. ≡ *Dregea pubescens* (Miq.) Boerl., Handl. Fl. Ned. Ind. 2: 438. 1899 – **Lectotype (designated here)**: Indonesia, Java, *T. Horsfield s.n.* (K barcode K000872991!; isolectotype: K barcode K000872990!).

= *Tylophora macrantha* Hance in J. Bot. 20(231): 79. 1882 – Holotype: China, Hongkong, May 1881, *C. Ford s.n.*, Herb. no. 21728 (BM barcode BM001014273!; isotype: MO barcode MO-078235!).

= *Dregea formosana* T.Yamaz. in J. Jap. Bot. 43(7): 219, fig. 1(1–3). 1968 – Holotype: Taiwan. Kuraru-Oluanpi, 12 May 1932, *K. Kimura s.n.* (TI n.v.).

= *Hoya formosana* T.Yamaz. in J. Jap. Bot. 43(7): 223, fig. 4. 1968 – Type: Taiwan. Hengchun, *M. Yanagawa s.n.* (TI n.v.).

Notes. – Of *Wattakaka pubescens*, two *Horsfield s.n.* specimens from Java are extant at K. The richer one of these two specimens, K000872991, is selected as the lectotype.

In India, type material pertaining to further names probably belonging into the synonymy of *Stephanotis volubilis* (see, e.g., Karthikeyan & al., 2009), in particular *Dregea lanceolata* (Cooke) Santapau & Wagh., *D. volubilis* var. *angustifolia* Hook.f., var. *glabra* Costantin, and var. *lacuna* (Buch.-Ham. ex Wight) Hook.f. could not be assessed and these names are therefore not listed here.

2.14 ***Stigmatorhynchus*** Schltr. in Bot. Jahrb. Syst. 51: 141. 1913 – Type: *Stigmatorhynchus hereroensis* Schltr.

Description. – Plants rigid shrubs, 0.5–2 m high, glabrescent or shortly pubescent, older parts lenticellate; latex white. *Leaves* (sub)sessile, lamina up to 3 cm long, ovate, basally cuneate, apically obtuse. *Inflorescences* few-flowered, solitary, extra-axillary, subsessile, flowers short-pedicellate. *Corolla* white, ca. 5 mm long, campanulate, inside bearded opposite the anthers; lobes contorted, oblong, apex obtuse. *Staminal corona* lobes basally adnate to each other, attached along

filament tube, erect, lanceolate, basally widened, exceeding the gynostegium (except for style-head). *Gynostegium* concealed in corolla tube. *Pollinaria*: Pollinia ovoid, caudicles geniculate, connection to pollinia widened, corpuscle slenderly elliptical. *Style-head* long, rostrate, exceeding the corolla. *Follicles* obclavate, 3.5–5 cm long, occasionally paired, slightly pubescent, 1(–2) seeds per follicle. *Seeds* narrowly ovate, 10–12 mm long, with long coma.

Notes. – The African *Stigmatorhynchus* is retrieved in subclade BIV of the Cosmopolitan Clade in poorly supported sister-group position ($BS_{ML} > 50\%$, $PP = 0.87$) to the *Gymnema* clade. *Stigmatorhynchus* has a disjunct distribution in Africa with one species in Namibia, and a second one in Tanzania.

Stigmatorhynchus is easily recognized by its habit as a rigid shrub up to 2 m high exuding white latex, shortly stalked to sessile leaves, inflorescences and flowers, a campanulate corolla exceeded by the long, rostrate style-head, and obclavate follicles with a transverse ridge in the lower half only containing one or two comose seeds.

The third published *Stigmatorhynchus* species (*S. stelostigma* (K.Schum.) Schltr. from Somalia), has been attributed to *Dregea* by Bullock (1957: 516), a view followed by Albers & Guldenberg (2003: 152) and confirmed here. Thus, this species, together with the other African *Dregea* species, is transferred to *Stephanotis* here (see above).

2.15 *Telosma* Coville in Contr. U.S. Natl. Herb. 9: 384. 1905, nom. cons. prop. – Type: *Telosma odoratissima* (Lour.) Coville (= *Telosma cordata* (Burm.f.) Merr.).
= *Stephanotella* E.Fourn. in Martius, Fl. Bras. 6: 326. 1885, nom. rej. prop. – Type: *Stephanotella glaziovii* E.Fourn. (= *Telosma cordata* (Burm.f.) Merr.).
= *Prageluria* N.E.Br. in Bull. Misc. Inform. Kew 1907: 325. 1907, nom. superfl.
Illustrated in Figs. 1H, 2K, I.

Description. – *Plants* suffrutescent twiners or lianas, up to 8 m high; latex white or clear. *Leaves* long-petiolate, lamina membranous, often undulate, 4–13 cm long, ovate, cordate. *Inflorescences* solitary, extra-axillary, sciadioidal, pendulous, with 15–30 flowers. *Flowers* fragrant. *Corolla* 10–20 mm long, salverform, basally urceolate, yellowish, throat bearded; lobes contorted, lanceolate or ovate, occasionally ciliate. *Staminal corona* adnate along the filament tube, often differentiated into a distal, erect, oblong to triangular lobule and a longer, proximal, inflexed, oblong to linear lobule. *Gynostegium* concealed in corolla tube, sessile, conical, guide-rails extending along half to whole length of gynostegium. *Pollinaria*: Pollinia obovoid, basally with pellucid margin in distal position, caudicles shortly rectangular. *Style-head* conical to semi-globose. *Follicles* 4.5–16 cm long, obclavate to fusiform, occasionally winged, with thick pericarp. *Seeds* broadly ovate, winged, coma yellowish.

Notes. – *Telosma*, a genus that has always been recognized as distinct from *Marsdenia*, but was involved in a rather complex nomenclatural mix-up with *Pergularia* (Liede, 1990), forms a strongly ($BS_{ML} = 96\%$, $PP = 1$) supported clade in

subclade BIII of the Cosmopolitan Clade, with less than 100% support probably due to missing partial sequences for both accessions of *T. africana*. It comprises six species, one in Africa, one in Madagascar (not sampled here), and the remaining ones in Asia. The South African accession of *T. africana* (*Bruyns 9340*) branches off first, followed by the second accession of *T. africana* from the Central African Republic (*Harris 2293*), which is sister to the Pakistani accessions of *T. pallida* and the three Philippine accessions (*T. procumbens*, *T. cordata*), suggesting an African origin for the genus. The nonmonophyly of the two samples of *T. africana* is probably not only due to a rather incomplete coverage of markers in both, but might indicate the possibility of more than one species of *Telosma* in continental Africa.

Telosma species prefer open bushland and riverine thickets as habitat. *Telosma cordata* is widely cultivated for its fragrant flowers and has been introduced in Brazil, where it was described as *Stephanotella* E.Fourn., which has priority. Because *Stephanotella* is based on an introduced plant and renaming all *Telosma* species to *Stephanotella* would cause considerable nomenclatural instability, Rapini & al. (2018) have proposed to conserve *Telosma* against *Stephanotella*.

Telosma is easily recognized by its staminal corona differentiated in a distal, erect, oblong to triangular lobule and a longer, proximal, inflexed, oblong to linear lobule, pollinia with pellucid margin (Fig. 2K), and a yellowish coma of its seeds.

2.16 *Gongronema taylorii* (Schltr. & Rendle) Bullock in Kew Bull. 15: 201. 1961 ≡ *Marsdenia taylorii* Schltr. & Rendle in J. Bot. 34: 100. 1896 – Holotype: Kenya, K7, Rabai Hills near Mombasa, *W.E. Taylor s.n.* (BM barcode BM000925987!; isotype: K barcode K000305275!, fragment).

Description. – *Plants* suffrutescent twiners, slightly pubescent; latex white. *Leaves* lanceolate. *Inflorescences* short-pedunculate, solitary, extra-axillary, sciadioidal, occasionally branched; flowers short-pedicellate. *Corolla* campanulate, deeply divided, throat with long, retrorse trichomes; lobes ovate, apex obtuse. *Staminal corona* completely adnate to the anther except for small tip. *Pollinaria*: Pollinia broadly ellipsoid, caudicles long, retrorse, corpuscle slender. *Style-head* semi-globose.

Notes. – Occurring in eastern Africa from Zimbabwe to Kenya, this species is retrieved as first branching taxon of subclade BIII of the Cosmopolitan Clade with little support ($BS_{ML} = 69\%$, $PP = 0.99$). Bullock (1961) transferred the species to *Gongronema*, together with the four West African species here transferred to *Gongronemopsis* (for justification, see under “2.7 *Gongronemopsis*”). While floral morphology would not contradict its inclusion in *Gongronemopsis*, the molecular position of this species is too ambiguous to execute the transfer here and the differences in leaf shape and texture also support its independence. Following Goyder & al. (2012: 197), *Marsdenia cyanchooides* Schltr., cited by Bullock (1961: 202) as synonym of *Gongronema taylorii*, is considered an independent species. More sequenceable material of both species would be needed,

however, to justify the creation of a new genus for these two species, as here suggested by the position of *G. taylorii* in the phylogeny. For the time being, the name ‘*Gongronema taylorii*’ should be applied to refer to this species.

Gongronema taylorii is easily recognizable by its acute to cuneate leaf bases, a gynostegium included in the corolla tube (except for the semi-globose style-head), a staminal corona attached to the filament tube and completely adnate to the anther, except for the tip, and ellipsoidal pollinia.

3. Afro-Malagasy Clade

3.1 *Rhyssolobium* E.Mey., Comm. Pl. Afr. Austr.: 217. 1838 – Type: *Rhyssolobium dumosum* E.Mey.

Description. – Plants rigid, heavily branched dwarf shrubs, up to 40 cm high, younger parts densely pubescent; latex clear. *Leaves* sessile, coriaceous, 1 cm long, elliptic, obtuse, marginally heavily convolute, adaxially glabrescent, abaxially densely pubescent. *Inflorescences* solitary, extra-axillary, sessile, sciadioidal, with 1–3 flowers. *Corolla* 4–5 mm long, campanulate, adaxially with long, erect trichomes on lobes and sinuses; lobes oblong. *Corolline* and *staminal corona* absent. *Anthers* conspicuously winged, with long, lanceolate connective appendages, apex obtuse. *Pollinaria*: Pollinia oblongoid to obovoid, caudicles straight, horizontal, short, corpuscle slenderly ellipsoid. *Style-head* conical. *Follicles* 4–5 cm long, broadly ellipsoid, with thick pericarp; 1–2 seeds per follicle, rounded, broadly winged.

Notes. – The monotypic genus *Rhyssolobium* E.Mey. is distributed in the winter rainfall area of Namibia and South Africa where it prefers rocky, arid coasts.

The sister-group relationship of *Rhyssolobium* with the Malagasy *Sicyocarpus* Bojer is poorly supported (BS_{ML} = 63%, PP = 0.77), with support derived exclusively from the plastid dataset (suppl. Figs. S3, S4). *Rhyssolobium* is retrieved outside of the Asia-Pacific and Cosmopolitan Clades for the plastid dataset and the nuclear At2g06530a dataset (suppl. Figs. S3–S6, S12), while it constitutes a weakly supported member of the Asia-Pacific Clade for ITS1 (suppl. Fig. S10) or the Cosmopolitan Clade for the nuclear At2g34620b dataset (suppl. Fig. S13).

Rhyssolobium is easily recognized by its stunted shrubby growth, the small, marginally heavily convolute, abaxially densely pubescent leaves, the complete lack of coronal structures and broadly ovoid, slightly winged follicles with only 1–2 seeds per follicle. *Rhyssolobium* shares both the shrubby habit and the strongly reduced number of seeds per follicle with the unrelated *Stigmatorhynchus*, with which it also shares the distribution in Namibia. However, latex is clear in *Rhyssolobium* (white in *Stigmatorhynchus*), the thick follicles lack a transverse ridge in the lower half (with transverse ridge in *Stigmatorhynchus*), and the seeds in *Rhyssolobium* are broadly ovate and slightly winged (narrowly ovate and unwinged in *Stigmatorhynchus*).

3.2 *Sicyocarpus* Bojer, Hortus Mauriti.: 214. 1837 – Type: *Sicyocarpus verrucosus* Bojer (≡ *Marsdenia verrucosa* (Bojer) Decne.).

Augmented description. – Plants suffrutescent twiners, glabrescent; latex white. *Leaves* long-petiolate, ovate to broadly cordate, basally cordate or rounded. *Inflorescences* unilaterally paired, occasionally solitary, extra-axillary, long-pedunculate, many-flowered, sciadioidal. *Corolla* campanulate, small, tube slightly longer than the erect lobes, adaxially densely pubescent. *Staminal corona* ovate, carnosely, completely adnate to the anther except for the short tip, shorter than gynostegium. *Pollinaria*: Pollinia strongly flattened, caudicles geniculate, long, corpuscle very small, ovate. *Style-head* rostrate. *Follicles* obclavate-ovoid with thick, verrucose pericarp.

Notes. – The description of *Sicyocarpus*, instated by Bojer (1837: 214), and included in *Marsdenia* by Decaisne (1844: 615), is limited to “Arbuste liane” for the only species, *S. verrucosus* Bojer. However, the ICN (Art. 38.5, Turland & al., 2018) provides the means of a “descriptio generico-specifica”, that a monotypic genus is validly published provided its only species is validly published. Thus, accepting “arbuste liane” as description for *S. verrucosus* also validates the genus *Sicyocarpus* Bojer. Nevertheless, we here provide an augmented description for *Sicyocarpus*.

Sicyocarpus verrucosus and *Marsdenia cordifolia* form a strongly supported clade (BS_{ML} = 100%, PP = 1) positioned outside of the Asia-Pacific and Cosmopolitan Clades for the plastid dataset and the nuclear At2g34620b dataset (suppl. Figs. S3–S6, S13), but constitute weakly supported members of the Asia-Pacific Clade for ITS1 and ITS2 (suppl. Figs. S10, S11).

Presently, *Sicyocarpus* seems endemic to Madagascar, but only two of the Malagasy *Marsdenia* s.l. species have been identified as members of *Sicyocarpus*. Other Malagasy *Marsdenia* s.l. species have been retrieved as members of different subclades in the Cosmopolitan Clade and several species cannot be assigned at present to any of these clades due to lack of sequenceable material and aberrant morphological characters.

Sicyocarpus comprises suffrutescent twiners or lianas with white latex, unilaterally paired inflorescences, adaxially densely pubescent corolla lobes, a carnosely staminal corona completely adnate to the anther except for the short tip, and follicles with a conspicuously thick, verrucose pericarp.

Sicyocarpus cordifolius (Choux) S.Reuss, Liede & Meve, **comb. nov.** ≡ *Marsdenia cordifolia* Choux in Ann. Inst. Colon. Marseille, ser. 3, 2: 428, t. 46. 1914 – **Lectotype (designated here)**: Madagascar, Toliara, sur les dunes boisées qui se trouvent entre le Fiherenana et le Manombo, May 1910, *Perrier de la Bâthie 11745* (P barcode P00442713!).

Note. – The lectotype of *Sicyocarpus cordifolius* has been selected by Stevens (*in schedis*) in accordance with the data given in the protologue, and his choice is followed here.

4. Genera of doubtful status

Under this heading, a number of small (1–3 species) genera are assembled of which no material for sequencing was available.

Several of them (*Dalzielia*, *Gymnemopsis*, *Pseudosarcolobus*, *Sinomarsdenia*, and *Tetragonocarpus*, see Omlor, 1998; Endress & al., 2018) have hitherto been hidden in the synonymy of *Marsdenia* s.l., but cannot be considered synonyms of *Marsdenia* as circumscribed here. Others have always been considered distinct from *Marsdenia*, but are apparently rare and have not been recollected lately (*Asterostemma*, *Cathetostemma*, *Dolichopetalum*, *Heynella*, *Pycnorhachis*, *Treutlera*).

Asterostemma Decne. in Ann. Sci. Nat., Bot., sér. 2, 9: 271, t. 10D. 1838 – Type: *Asterostemma repandum* Decne.

The only species of this genus, *Asterostemma repandum* (not sampled here), is a suffrutescent twiner from Java. The most unusual feature of this plant is the annular corona, formed by basally fused, two to three-partite staminal corona lobes. Omlor (1998) mentioned similarly shaped, but unfused staminal corona lobes for *Campestigma*, so that *Asterostemma* likely constitutes one of the Asian species-poor lineages here retrieved in subclade BII of the Cosmopolitan Clade.

Cathetostemma Blume in Rumphia 4: 30. 1849 – Type: *Cathetostemma laurifolium* (Decne.) Blume (≡ *Hoya laurifolia* Decne.).

While most workers include *Cathetostemma* in *Hoya* (e.g., Baltazar & Buot, 2019), Omlor (1998) stated that *Cathetostemma* constitutes a taxon independent of *Hoya* because of its unique staminal corona. However, no sequenceable material of this genus has yet been secured to ascertain the position of this rare genus from Timor and the southern Philippines, so that its affinities remain doubtful.

Dalzielia Turrill in Hooker's Icon. Pl. 31: t. 3061. 1922 – Type: *Dalzielia oblanceolata* Turrill.

The only species of this genus, *Dalzielia oblanceolata* (not sampled here) is a rheophytic shrub distributed from Guinea (Conakry) to the Ivory Coast and was attributed by Omlor (1998) to *Marsdenia* sect. *Pterygocarpus*. Because the three species of *M.* sect. *Pterygocarpus* included in this phylogeny are retrieved in two clades, the *Anisopus* clade and the *Stephanotis* clade, attribution of this morphologically aberrant species is not possible without molecular evidence. However, because the present phylogeny restricts *Marsdenia* s.str. to a small group of East Asian plants, the transfer of *Dalzielia* to *Marsdenia* by Omlor (1998: 81) should not be followed and the name *Dalzielia oblanceolata* should be applied for the species.

Dolichopetalum Tsiang in Acta Bot. Sin. 15(1): 137. 1973 – Type: *Dolichopetalum kwangsiense* Tsiang.

Omlor (1998: 104) described the peculiarities of the only species, *Dolichopetalum kwangsiense* (not sampled here), concluding that its status as a monotypic genus is probably justified. The parallels Omlor (1998: 105) drew with *Campestigma* inspire speculations that *Dolichopetalum* might constitute one of the Asian species-poor lineages of subclade BII of the Cosmopolitan Clade. Based on

similarities in inflorescence, corolla, corona and pollinarium morphology it might also be related to the monotypic *Pycnorhachis* Benth.

Gymnemopsis Costantin in Lecomte, Fl. Indo-Chine 4: 88. 1912 – Type: *Gymnemopsis pierrei* Costantin.

The Southeast Asian genus *Gymnemopsis* has been resurrected lately by Kidyoo (2020), who accepts three species. Kidyoo (2020) based his decision on the narrowly oblong corpuscle that is at least five times longer than wide and larger than the pollinia, ribbon-shaped translator arms, and the inconspicuous to missing staminal corona. Instead, the entrance of the corolla tube is narrowed by barbate corolline scales. Omlor (1998: 116) suggested a close relationship of *Gymnemopsis* with *Pseudosarcolobus* and *Harmandiella*, but in absence of molecular evidence it seems prudent to keep these genera separate.

Heynella Backer in Blumea 6: 381. 1950 – Type: *Heynella lactea* Backer.

Heynella lactea (not sampled here), only species of *Heynella*, is an epiphytic dwarf shrub from Java. The only known collection is housed in BO (BO-110496), but was not available for study. Omlor (1998: 152) suggested a relationship to *Hoya*, and most likely this plant will be retrieved in the *Hoya* alliance, but whether it constitutes an independent lineage or whether it can be included in one of the existing genera, cannot be ascertained at present.

Pseudosarcolobus Costantin in Lecomte, Fl. Indo-Chine 4: 77. 1912 – Type: *Pseudosarcolobus villosus* Costantin.

This monotypic Southeast Asian genus (*Pseudosarcolobus villosus* not sampled here) lacks a staminal corona and possesses barbate corolline scales. It differs from *Gymnemopsis* and *Harmandiella* by a stalked gynostegium. Omlor (1998: 116) pointed out that *P. villosus* is conspecific with *Gymnema barbatum* (Collett & Hemsley) Kerr. Omlor (1998: 116), however, also indicated that the plants only superficially resemble *Gymnema* with their fleshy corolline corona scales with trichomes, but differ in their racemiform inflorescences, the shape of the corona scales, the indument of the corolla tube, the flat style-head, and pollinarium morphology. Nevertheless, Thaithong & al. (2018: 156) treat the plant under *Gymnema barbatum*. They add the observation that the plants produce clear latex in contrast to the other Thai species of *Gymnema*, which exude white latex.

In the view of these discrepancies, and in the absence of molecular evidence, we prefer to presently keep the genus separate and consider it as one of the Asian species-poor lineages, probably closely related to *Gymnemopsis*, as Omlor (1998: 116) assumed based on structure of the corolline corona scales and the pollinarium.

Pycnorhachis Benth. in Bentham & Hooker, Gen. Pl. 2(2): 737, 776. 1876 – Type: *Pycnorhachis maingayi* Hook.f.

Pycnorhachis maingayi (not sampled here) is a rare species from Peninsular Malaysia, characterized by small, deep

purple flowers standing singly or in pairs along an elongated, occasionally branched rachis. It might constitute yet another species-poor lineage in subclade BII of the Cosmopolitan Clade, possibly related to *Dolichopetalum*. A second species, *P. benthamiana*, was described by Baillon (1890: 278), but the description and the absence of type material support the conclusion by Govaerts (2019) that *P. benthamiana* only constitutes an illegitimate new name for *P. maingayi*.

Sinomarsdenia P.T.Li & J.J.Chen in J. S. China Agric. Univ. 18(1): 39. 1997 – Type: *Sinomarsdenia incisa* (P.T.Li & Y.H.Li) P.T.Li & J.J.Chen (= *Marsdenia jenkinsii* Hook.f.).

See discussion under “1.4 *Marsdenia oreophila* subclade”.

Tetragonocarpus Hassk. in Flora 40: 99. 1857 – Type: *Tetragonocarpus teysmannii* Hassk.

Tetragonocarpus teysmannii (not sampled here), only species of *Tetragonocarpus*, is a suffrutescent climber reported from Bali and the eastern province of Java (Banjuwangi), with petiolate, ovate to ovate-oblong, basally subcordate, apically shortly acuminate leaves, a yellowish-green, urceolate corolla, with trichomes in the sinus, oblong-lanceolate, acute lobes that are longer than the tube, and a staminal corona of fleshy, greenish erect lobes, linear-lanceolate, connivent anther appendages, and paired, tetragonal follicles containing narrowly winged comose seeds.

The type specimen of *Tetragonocarpus teysmannii* was supposedly collected by J.E. Teysmann and given to Bogor, but could not be traced. No other specimen fitting the above description was encountered.

Treutlera Hook.f. in Hooker’s Icon. Pl. 15: t. 1425. 1883 – Type: *Treutlera insignis* Hook.f.

Omlor (1998: 131) pointed to the large, dark colored radiate flowers of the only species, *Treutlera insignis* Hook.f. (not sampled here), as the single character separating the species from other Marsdenieae of the area. Because the plants are unlikely to conform to the circumscription of *Marsdenia* s.str., the generic status of *Treutlera* should be maintained until material for molecular analysis becomes available.

■ AUTHOR CONTRIBUTIONS

TL, SLS, and LW designed the study and carried out initial analyses. PIF, GG, and MR provided additional material. SJR and UM carried out morphological studies. SLS and MR wrote the bulk of the manuscript, PIF, TL, and UM contributed to the writing. — SLS, <https://orcid.org/0000-0003-2707-0335>; UM, <https://orcid.org/0000-0001-7395-5199>; GG, <https://orcid.org/0000-0003-2831-6384>; MR, <https://orcid.org/0000-0002-4130-6685>

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Appendix 1. Sampling for the molecular phylogenetic and biogeographic analyses of Marsdeniaceae. Biogeographical coding (if species area is larger, it is indicated in brackets), voucher information (including country origins, collectors, collection numbers and herbaria) and GenBank DNA accession numbers of *trnT-L*, *trnL-F*, *rps16*, *psbA-trnH*, ITS, At2g06530a and At2g34620b. * indicates new sequences; “-” indicates missing sequences.

INGROUP: *Anisopus efulensis* (N.E.Br.) Goyder, A, Cameroon, *Wheatley 65* (MO), -, LR794709, LR794736, -, -, LR794805, -, *Anisopus mannii* N.E.Br., A, Democratic Republic of the Congo, *Hart 823* (BR), -, LR794710, LR794737, -, -, LR794826; *Campestigma purpureum* Pierre ex Costantin, D, Thailand, *Middleton 221* (A), MW226189*, MW226398*, MW226052*, -, -, MW226777*, MW226809*; *Cionura erecta* Griseb., C, Turkey, *Heyne 120* (UBT), AJ410172, AJ410173 & AJ410174, LT595597, MW226307*, MW226536*, MW226629*, MW226716*; *Cosmostigma cordatum* (Poir.) M.R.Almeida, D, India: Maharashtra, *s.coll. s.n.* (SUK), -, HG530574, HG530599, -, -, -, *Dischidanthus urceolatus* (Decne.) Tsiang, D, China: Hainan, *Liede & Meve 3680* (UBT), MW226215*, MW226424*, MW226082*, MW226308*, MW226537*, MW226630*, -, *Dischidia angustifolia* Miq., D, ex hort., *Livshultz 00_215* (BH), MW226190*, MW226399*, MW226053*, -, -, MW226778*, -, *Dischidia astephana* Scortechini ex King & Gamble, D, ex hort., *Wanntorp 562* (S), HE794723, DQ334534, MW226043*, HQ327682, DQ334459, -, -, *Dischidia chinensis* Champ. ex Benth., D, China: Hainan, *Liede & Meve 3667* (UBT), MW226216*, MW226425*, MW226083*, MW226309*, MW226538*, MW226631*, -, *Dischidia cleistantha* Livsh., D, ex hort., *Livshultz 98_6* (BH), MW226191*, MW226400*, MW226054*, -, -, MW226810*, *Dischidia cleistantha* Livsh., D, Philippines, *Meve 995* (UBT), MW226217*, MW226426*, MW226084*, MW226310*, MW226539*, MW226632*, MW226717*; *Dischidia hirsuta* (Blume) Decne., D (E), Dept. Bot., ex hort., *Wanntorp 563* (S), HE794724, DQ334531, -, HQ327669, DQ334452, -, -, *Dischidia imbricata* (Blume) Steud., D, ex hort., *Livshultz 99_7* (BH), MW226192*, MW226401*, MW226055*, -, -, -, *Dischidia immortalis* Guillaumin, G, New Caledonia, *Gâteblé 985* (NOU), MW226218*, MW226427*, MW226085*, MW226311*, MW226540*, MW226633*, -, *Dischidia nummularia* R.Br., D, Singapore, *Rodda MR313* (SING), MF197987, MF198032, -, MF198065, MF198099, -, -, *Dischidia sagittata* Decne., D, ex hort., *Livshultz 02_17* (BH), MW226193*, MW226402*, MW226056*, -, MW226525*, MW226779*, -, *Dischidiopsis luzonica* Schltr., D, ex hort., *Livshultz 99_25* (BH), MW226194*, MW226403*, MW226057*, -, -, MW226780*, -, *Dregea abyssinica* (Hochst.) K.Schum., A, Tanzania, *Ellemann 787* (NY), MW226187*, MK214587, MW226086*, -, MK214515, -, MW226808*; *Dregea abyssinica* (Hochst.) K.Schum., A, Tanzania, *Hemp 6577* (UBT), MW226219*, MW226428*, MW226051*, MW226312*, MW226541*, -, -, *Dregea arabica* Decne., A, Yemen, *Miller & Talib 19077* (E), MW226220*, MW226429*, MW226087*, MW226313*, MW226542*, -, -, *Dregea floribunda* E.Mey., A, Mozambique, *Goyder 5002* (K), MW226221*, MW226430*, MW226088*, MW226314*, MW226543*, MW226634*, -, *Dregea macrantha* Klotzsch, A, ex hort., *Wanntorp 489* (S), MW226185*, MW226395*, MW226044*, -, MW226521*, MW226766*, MW226796*; *Dregea rubicunda* K.Schum., A, Kenya, *Liede & Newton 3199* (ULM), AJ574838, AJ574839 & AJ574840, MW226089*, -, MW226544*, MW226635*, MW226718*; *Dregea schimperi* (Decne.) Bullock, A, Tanzania, *Hemp 4978* (UBT), MW226222*, MW226431*, MW226090*, MW226315*, MW226545*, MW226636*, MW226719*; *Dregea schimperi* (Decne.) Bullock, A, Tanzania, *Simon & Mlwanga 802* (MO), MW226195*, MW226404*, MW226058*, -, MW226526*, MW226781*, MW226811*; *Dregea stelostigma* (K.Schum.) Bullock, A, Somalia, *Thulin & al. 10470* (UPS), MW226223*, MW226432*, MW226091*, MW226316*, MW226546*, MW226637*, MW226720*; *Dregea volubilis* (L.f.) Benth. ex Hook.f., D, China: Hainan, *Liede & Meve 3672* (UBT), MW226224*, MW226433*, MW226092*, MW226317*, MW226547*, MW226638*, -, *Dregea volubilis* (L.f.) Benth. ex Hook.f., D, India, *Schäffler 2* (UBT), MW226225*, HG530577, MW226093*, MW226318*, MW226548*, MW226639*, MW226721*; *Gongronema angolense* (N.E.Br.) Bullock, A, Tanzania, *Gereau & al. 5793* (MO: MO-5034900), MW226196*, -, MW226059*, -, MW226527*, MW226782*, MW226812*; *Gongronema angolense* (N.E.Br.) Bullock, A, Ethiopia, *Liede & Meve 3537* (UBT), MW226226*, MW226434*, MW226094*, -, MW226549*, MW226640*, MW226722*; *Gongronema angolense* (N.E.Br.) Bullock, A, Uganda, *Rwabutindore 4139* (S), HE799696, HQ327495, -, -, -, *Gongronema filipes* Kerr, D, China: Yunnan, *MJNFP-0284* (SING), MW226227*, MW226435*, MW226095*, MW226319*, MW226550*, MW226641*, -, *Gongronema latifolium* Benth., A, Cameroon, *de Wilde 8030* (MO), -, MW226405*, -, -, -, *Gongronema latifolium* Benth., A, Ghana, *Merello & al. 1452* (MO), -, -, MW226060*, -, MW226528*, -, -, *Gongronema napalense* (Wall.) Decne., D, China: Yunnan, *Wang 7240* (IBSC: IBSC-742585), MW226228*, MW226436*, MW226096*, MW226320*, -, -, *Gongronema taylorii* (Schltr. & Rendle) Bullock, A, Tanzania, *Festo & al. 2256* (MO), MW226197*, MW226406*, MW226061*, -, MW226529*, -, MW226813*; *Gongronema wallichii* Decne., D, Malaysia, *Schneid 95-130* (ABD), AJ431746, AJ431747 & AJ431748, LT595598, MW226321*, MW226551*, MW226642*, MW226723*; *Gunnessia pepo* P.I.Forst., F, Australia, *Cooper & Jensen 1477* (BRI: AQ0669779), MW226198*, MW226407*, MW226062*, -, -, MW226814*; *Gunnessia pepo* P.I.Forst., F, Australia, *Forster & Reilly PIF6465* (BRI: AQ0470541), MW226186*, DQ334528, -, -, DQ334446, -, -, *Gynnema erecta* (F.Muell.) P.I.Forst. (*Marsdenia angustata* P.I.Forst.), F, Australia, *Cowie 11560* (MO: MO-6076576), MW226202*, MW226413*, MW226068*, -, -, -, *Gynnema geminatum* R.Br., F (E), Australia, *Forster & al. PIF28190* (L), MW226229*, MW226437*, MW226097*, MW226322*, MW226552*, MW226643*, MW226724*; *Gynnema graniticola* (P.I.Forst.) P.I.Forst., F, Australia, *Mitchell 4142* (BRI), -, MW226483*, MW226146*, MW226369*, -, -, *Gynnema inodorum* (Lour.) Decne., D, Philippines, *Schneid 96-100* (B, UBT), AJ431749, AJ431750 & AJ431751, MW226098*, MW226323*, MW226553*, MW226644*, MW226725*; *Gynnema latifolium* Wall. ex Wight, D, India, *Sardesai 705* (UBT), MW226230*, HG530575, HG530601, MW226324*, MW226554*, MW226645*, MW226726*; *Gynnema longipedicellatum* (P.I. Forst.) P.I.Forst., F, Australia, *Gray 7487* (A), MW226279*, MW226490*, MW226154*, MW226377*, -, -, *Gynnema maingayi* Hook.f., D, Thailand, *Pooma & al. 7858* (BKF), MW226231*, MW226438*, MW226099*, MW226325*, MW226555*, MW226646*, -, *Gynnema muelleri* Benth., F, Australia, *Johnson & Thomas MRS995* (BRI: AQ0489416), MW226232*, MW226439*, MW226100*, MW226326*, MW226556*, MW226647*, -, *Gynnema pachyglossum* Schltr., D, Philippines, *Liede & Meve 3609* (UBT), MW226233*, MW226640*, MW226101*, MW226327*, MW226557*, MW226648*, MW226727*; *Gynnema pleiadenium* F.Muell., F, Australia, *Thompson & Sharpe CHA152* (L), MW226234*, MW226441*, MW226102*, MW226328*, MW226558*, MW226649*, -, *Gynnema stramineum* (P.I.Forst.) P.I.Forst., F, Australia, *Jensen 1415* (BRI: AQ0613464), MW226286*, MW226498*, MW226162*, MW226383*, MW226614*, MW226699*, MW226756*; *Gynnema stramineum* (P.I.Forst.) P.I.Forst., F, Australia, *Jensen & Curran 1554* (BRI: AQ0862164), MW226287*, MW226499*, MW226163*, MW226384*, MW226615*, MW226700*, MW226757*; *Gynnema sylvestre* (Retz.) Schult., B (A,D), Madagascar, *Eriksson & al. T952* (S), MW226235*, MW226442*, MW226138*, MW226330*, MW226559*, MW226650*, MW226728*; *Gynnema sylvestre* (Retz.) Schult., A (B,D), Ethiopia, *Friis & al. 7979* (BR), -, MW226408*, MW226063*, -, -, MW226815*; *Gynnema sylvestre* (Retz.) Schult., A (B,D), Cameroon, *Meve 919* (UBT), AJ402118, AJ402137 & AJ402142, LT595599, MW226329*, FM178492, MW226651*, MW226729*; *Gynnema sylvestre* (Retz.) Schult., D (A,B), China: Guangdong, *Liede 3716* (UBT), MW226237*, MW226444*, MW226104*, MW226332*, MW226561*, -, -, *Gynnema sylvestre* (Retz.) Schult., D (A,B), China: Hainan, *Liede & Meve 3681* (UBT), MW226236*, MW226443*, MW226103*, MW226331*, MW226560*, -, MW226730*; *Gynnema tricholepis* Schltr., F (E,G), Australia, *Forster PIF9209* (L), MW226238*, MW226445*, MW226105*, -, MW226562*, -, -, *Gynnema tricholepis* Schltr., G (E,F), New Caledonia, *Gâteblé & al. 1074* (NOU: NOU-106115), MW226239*, MW226446*, MW226106*, MW226333*, MW226563*, MW226652*, MW226731*, *Harmandiella cordifolia* Costantin, D, Vietnam, *La Ongri 1689* (QBG), MW226240*, MW226447*, MW226107*, MW226334*, MW226564*, MW226653*, MW226732*; *Hoya australis* R.Br. ex J.Traill, F (D,E), ex hort., *Wanntorp 564* (S), HE794784, DQ334527, -, HE794474, DQ334428, MW226768*, -, *Hoya bella* Hook., D, ex hort., *Wanntorp 616* (S), HE794725, MW226448*, MW226108*, HQ327660, MW226565*, MW226654*, MW226733*; *Hoya camphorifolia* Warb., D, Philippines, *Schneid & Liede 96-20* (UBT), AJ431752, AJ431753 & AJ431754, MW226109*, -, -, MW226734*; *Hoya carnosa* (L.f.) R.Br., D, ex hort., *Wanntorp 566* (S), HE794837, DQ334535, -, HQ327665, DQ334460-DQ334464 clone consensus, MW226769*, MW226798*; *Hoya chinglungensis* (Tsiang & P.T.Li) M.G.Gilbert, D, Thailand, *Rodda MR1759* (SING), MF197996, MF198039, -, MF198072, MF198106, -, -, *Hoya coronaria* Blume, D (E,F), Sarawak, *Liddle 782* (BRI), HE794735, -, -, HE794447, HE794389, MW226770*, MW226799*; *Hoya edeni* King ex Hook.f., D, ex hort., *Wanntorp 579* (S), HE794726, MF350512, -, HQ327661, DQ334476, -, -, *Hoya hypolasia* Schltr., E, ex hort., *Wanntorp L901824* (S), HE794780, DQ334538, -, HQ327627, DQ334470, -, MW226800*; *Hoya inflata* (P.I.Forst., Liddle & I.M.Liddle) L.Wanntorp & P.I.Forst., E, Papua New Guinea, *Liddle IML1076* (BRI), HE794781, DQ334541, MW226045*, HQ327618, DQ334508-DQ334510 clone consensus, MW226767*, MW226797*; *Hoya insularis* Rodda & S.Rahayu

Appendix 1. Continued.

(*Anatropanthus borneensis* Schltr.), D, Borneo, *Rodda s.n.* (SING), MN931594, MN931597, MW226110*, MN931595, MN931599, MW226655*, –, *Hoya kentiana* C.M.Burton, D, ex hort., *Wanntorp 570* (S), HE794815, DQ334522, –, HQ327677, DQ334424, MW226771*, MW226801*, *Hoya lanceolata* Wall. ex D.Don, D, Nepal (ex hort.), *Rodda MR1769* (SING), MF198003, MF198044, –, MF198078, MF198118, –, –, *Hoya manipurensis* Deb, D, ex hort., *Wanntorp 596* (S), HE794829, –, MW226046*, –, MW226522*, MW226772*, MW226802*; *Hoya manipurensis* Deb, D, Thailand, *Seidenfaden s.n.* (K: MWC 733), AJ431764, AJ431765 & AJ431766, HG530602, HQ327628, MW226566*, –, –, *Hoya manipurensis* Deb, D, ex hort., *Van Donkelaar s.n.* (IPPS 4561) (L), –, MW226409*, MW226064*, –, –, –, *Hoya mariae* Schltr., D, Philippines, *Laurente 1* (USTH), MW226241*, MW226449*, MW226111*, MW226335*, MW226567*, MW226656*, MW226735*; *Hoya mariae* Schltr., D, Philippines (ex hort.), *Wanntorp 617* (S), HE794731, HQ332596, –, HQ327613, HQ327500, –, –, *Hoya multiflora* Blume, D, ex hort., *Livshultz 00_189* (BH), MW226199*, MW226410*, MW226065*, –, –, –, *Hoya multiflora* Blume, D, ex hort., *Wanntorp 573* (S), HE794750, DQ334552, –, HQ327629, DQ334487, –, MW226803*; *Hoya nicholsoniae* F.Muell., G (E,F), New Caledonia, *Gâteblé & al. 1086* (NOU: NOU-106132), MW226242*, MW226450*, MW226112*, MW226336*, MW226568*, MW226657*, MW226736*; *Hoya nicholsoniae* F.Muell., E (F,G), Papua New Guinea, *Rodda MR718* (SING), MF198005, MF198048, –, MF198080, MF198123, –, –, *Hoya omlorii* (Livsh. & Meve) L.Wanntorp & Meve, D, Malaysia, *Rodda MR304* (SING), MF198006, MF198056, –, MF198084, MF198124, –, –, *Hoya patella* Schltr., E, ex hort., *Wanntorp 575* (S), HE794767, DQ334556, –, HQ327633, DQ334498, –, MW226804*; *Hoya retusa* Dalzell, D, ex hort., *Wanntorp 580* (S), HE794881, DQ334532, –, HQ327632, DQ334457, MW226773*, –, *Hoya spartioides* (Benth.) Kloppenb., D, Malaysia: Sabah, *Wanntorp 592* (S), HE794830, DQ334549, MW226047*, HQ327619, DQ334484, MW226774*, –, *Hoya telosmoides* Omlor, D, ex hort., *Wanntorp 577* (S), HE794752, DQ334551, –, HQ327671, DQ334486, –, –, *Hoya thailandica* Thaithong, D, Thailand, *Liddle IML1493* (SING), HE794729, MF350520, –, –, *Hoya cf. tsangii* C.M.Burton, D, ex hort., *Wanntorp 581* (S), HE794821, DQ334523, –, HQ327679, DQ334425–DQ334427 clone consensus, –, MW226805*; *Hoya wightii* Hook.f., D, ex hort., *Wanntorp 648* (S), HE794889, MW226451*, MW226113*, MW226337*, HE794392, MW226658*, –, *Jasminanthes maingayi* (Hook.f.) Rodda, D, Singapore, *Low & al. LYW523* (SING), MW226243*, MW226452*, MW226114*, MW226338*, MW226569*, MW226659*, –, *Jasminanthes maingayi* (Hook.f.) Rodda, D, Singapore, *Rodda MR691* (SING), MF350522, MF198024, –, MF198057, MF198091, –, –, *Jasminanthes mucronata* (Blanco) W.D.Stevens & P.T.Li, C (D), Japan: Shikoku Kochi Pref., *MBK 1* (SING), MW226244*, MW226453*, MW226115*, MW226339*, MW226570*, MW226660*, –, *Jasminanthes mucronata* (Blanco) W.D.Stevens & P.T.Li, C (D), ex hort., *MBK 1_cult* (SING), MW226245*, MW226454*, MW226116*, MW226340*, MW226571*, –, –, *Jasminanthes mucronata* (Blanco) W.D.Stevens & P.T.Li, D (C), Taiwan, *Tsai H395* (TCB), –, MF400823*, –, –, MG818142, –, –, *Leichhardtia assimulata* (S.Moore) Liede, Gâteblé & Meve, G, New Caledonia, *Gâteblé 995* (NOU: NOU-105476), MW226246*, MW226455*, MW226117*, MW226341*, MW226572*, MW226661*, MW226737*; *Leichhardtia australis* R.Br., F, Australia, *Luckow 4646* (BH), MW226200*, MW226411*, MW226066*, –, –, MW226783*, MW226816*; *Leichhardtia australis* R.Br., F, Australia, *Nordenstam & Anderberg 959* (S), –, MW226396*, MW226048*, –, MW226523*, MW226775*, MW226806*; *Leichhardtia brevifolia* (Benth.) P.I.Forst., F, Australia, *Forster & Halford PIF30144* (BRI: AQ0767560), MW226264*, MW226473*, MW226135*, MW226359*, MW226590*, MW226678*, –, *Leichhardtia brevifolia* (Benth.) P.I.Forst., F, Australia, *Stoneham s.n.* (BRI: AQ0852307), MW226265*, MW226474*, MW226136*, MW226360*, MW226591*, MW226679*, –, *Leichhardtia brevis* (P.I.Forst.) P.I.Forst., F, Australia, *Mathieson MTM1241* (BRI: AQ0798290), –, MW226475*, MW226137*, MW226361*, MW226592*, MW226680*, –, *Leichhardtia connivens* (P.I.Forst.) P.I.Forst., F, Australia, *Forster & Thomas PIF36612* (BRI: AQ0815284), MW226267*, MW226477*, MW226140*, MW226363*, MW226594*, MW226682*, –, *Leichhardtia coronata* (Benth.) P.I.Forst., F, Australia, *Forster & Endress PIF28695* (BRI: AQ0555518), MW226205*, MW226415*, MW226071*, –, MW226531*, MW226786*, MW226820*; *Leichhardtia cymulosa* (Benth.) P.I.Forst., F, Australia, *McDonald KRM11189* (BRI: AQ0830520), MW226268*, MW226478*, MW226141*, MW226364*, MW226595*, MW226683*, MW226750*; *Leichhardtia dognyensis* (Guillaumin) Liede, Gâteblé & Meve, G, New Caledonia, *Gâteblé & al. 1129* (NOU: NOU-106168), MW226247*, MW226456*, MW226118*, MW226342*, MW226573*, MW226662*, –, *Leichhardtia ericoides* (Schltr.) Bullock, G, New Caledonia, *Karnadi & al. 123* (NOU: NOU-052083), MW226248*, MW226457*, MW226119*, MW226343*, MW226574*, MW226663*, MW226738*; *Leichhardtia flavescens* (A.Cunn. ex Hook.) P.I.Forst., F, Australia, *Forster & Endress PIF28686* (BRI: AQ0555521), MF198011, MF198025, MW226072*, MF198058, MF198092, –, MW226821*; *Leichhardtia fraseri* (Benth.) P.I.Forst., F, Australia, *Forster PIF29024* (BRI: AQ0770448), MW226269*, MW226479*, MW226142*, MW226365*, MW226596*, MW226684*, –, *Leichhardtia fraseri* (Benth.) P.I.Forst., F, Australia, *Prowd 1* (BRI: AQ0915100), MW226270*, MW226480*, MW226143*, MW226366*, MW226597*, MW226685*, –, *Leichhardtia glandulifera* (C.T.White) P.I.Forst., F, Australia, *Lovatt & Brushe JEK10439* (BRI: AQ0841661), MW226271*, MW226481*, MW226144*, MW226367*, MW226598*, MW226686*, –, *Leichhardtia glandulifera* (C.T.White) P.I.Forst., F, Australia, *Shapcott & Howard MGH057* (BRI: AQ0906971), MW226272*, MW226482*, MW226145*, MW226368*, MW226599*, MW226687*, –, *Leichhardtia goramotoorum* (Gâteblé, Fleuret, Meve & Liede) Gâteblé, Fleuret, Meve & Liede, G, New Caledonia, *Fleuret 506* (NOU: NOU-089979), MW226249*, MW226458*, MW226120*, MW226344*, MW226575*, –, *Leichhardtia kaalensis* (Meve, Gâteblé & Liede) Liede, Gâteblé & Meve, G, New Caledonia, *Pillon & al. 213* (NOU: NOU-009225), MW226250*, MW226459*, MW226121*, MW226345*, MW226576*, MW226664*, MW226739*; *Leichhardtia koniamboensis* (Guillaumin) Liede, Gâteblé & Meve, G, New Caledonia, *Gâteblé 990* (NOU: NOU-105499), MW226251*, MW226460*, MW226122*, MW226346*, MW226577*, MW226665*, MW226740*; *Leichhardtia kuniensis* (Meve, Gâteblé & Liede) Liede, Gâteblé & Meve, G, New Caledonia, *Gâteblé & Ounémoa 1001* (NOU: NOU-089970), MW226252*, MW226461*, MW226123*, MW226347*, MW226578*, MW226666*, –, *Leichhardtia liusae* (J.B.Williams) P.I.Forst., F, Australia, *Copeland 3889* (BRI), –, MW226519* & MW226520*, MW226149*, MW226372*, MW226602*, –, –, *Leichhardtia lloydii* (P.I.Forst.) P.I.Forst., F, Australia, *Forster & al. PIF40625* (BRI: AQ0836351), MW226276*, MW226487*, MW226151*, MW226374*, MW226603*, MW226690*, MW226751*; *Leichhardtia lloydii* (P.I.Forst.) P.I.Forst., F, Australia, *Hansen & al. s.n.* (BRI: AQ0576285), MW226275*, MW226486*, MW226150*, MW226373*, MW226604*, –, –, *Leichhardtia longiloba* (Benth.) P.I.Forst., F, Australia, *Hansen S6b* (BRI: AQ0858279), MW226277*, MW226488*, MW226152*, MW226375*, MW226605*, MW226691*, –, *Leichhardtia longiloba* (Benth.) P.I.Forst., F, Australia, *Pollard 108* (BRI: AQ0759213), MW226278*, MW226489*, MW226153*, MW226376*, MW226606*, MW226692*, –, *Leichhardtia lyonsioides* (Schltr.) Liede, Gâteblé & Meve, G, New Caledonia, *Fleuret 507* (NOU: NOU-106616), MW226253*, MW226462*, MW226124*, MW226348*, MW226579*, MW226667*, MW226741*; *Leichhardtia mackeeorum* (Meve, Gâteblé & Liede) Liede, Gâteblé & Meve, G, New Caledonia, *Gâteblé & al. 994* (NOU: NOU-105475), MW226254*, MW226463*, MW226125*, MW226349*, MW226580*, MW226668*, MW226742*; *Leichhardtia micradenia* (Benth.) P.I.Forst., F, Australia, *Forster & Booth PIF23879* (L), MW226280*, MW226491*, MW226155*, MW226378*, MW226607*, MW226693*, –, *Leichhardtia microlepis* (Benth.) P.I.Forst., F, Australia, *Forster & al. PIF40643* (BRI: AQ0836359), MW226281*, MW226492*, MW226156*, MW226379*, MW226608*, MW226694*, MW226752*; *Leichhardtia neocaledonia* Meve, Liede & Gâteblé, G, New Caledonia, *Gâteblé 760* (NOU), MW226255*, MW226464*, MW226126*, MW226350*, MW226581*, MW226669*, MW226743*; *Leichhardtia neomicrostoma* (Meve, Gâteblé & Liede) Liede, Gâteblé & Meve, G, New Caledonia, *Gâteblé 762* (NOU), MW226256*, MW226465*, MW226127*, MW226351*, MW226582*, MW226670*, MW226744*; *Leichhardtia nigriflora* (Guillaumin) Liede, Gâteblé & Meve, G, New Caledonia, *Gâteblé 998* (NOU: NOU-105479), MW226257*, MW226466*, MW226128*, MW226352*, MW226583*, MW226745*; *Leichhardtia oubatchensis* (Schltr.) Liede, Gâteblé & Meve, G, New Caledonia, *Gâteblé & al. 1102* (NOU: NOU-106153), MW226258*, MW226467*, MW226129*, MW226353*, MW226584*, MW226672*, MW226746*; *Leichhardtia paulforsteri* (Meve, Gâteblé & Liede) Liede, Gâteblé & Meve, G, New Caledonia, *Karnadi 231* (NOU: NOU-052046), MW226259*, MW226468*, MW226130*, MW226354*, MW226585*, MW226673*, MW226747*; *Leichhardtia primulina* (P.I.Forst.) P.I.Forst., E, Papua New Guinea, *Johns 10088* (L, dup. at A), MW226284*, MW226495*, MW226159*, MW226381*, MW226611*, MW226697*, –, *Leichhardtia pumila* (P.I.Forst.) P.I.Forst., F, Australia, *Forster & Bean PIF14880* (BRI: AQ0520806), –, MW226496*, MW226160*, –, MW226612*, –, –, *Leichhardtia racemosa* (F.Muell. ex Benth.) P.I.Forst. (*Marsdenia hemiptera* Rchb.f.), F, Australia, *Cooper 2099* (BRI: AQ0849858), MW226273*, MW226484*, MW226147*, MW226370*, MW226600*, MW226688*, –, *Leichhardtia racemosa* (F.Muell. ex Benth.) P.I.Forst. (*Marsdenia hemiptera*

Appendix 1. Continued.

Rchb.f.), F, Australia, *Costion 2192* (BRI: AQ0849389), MW226274*, MW226485*, MW226148*, MW226371*, MW226601*, MW226689* –; *Leichhardtia rostrata* (R.Br.) P.I.Forst., F, Australia, *Booth & Jensen 3080* (BRI: AQ0557343), MF350523, MF198026, MW226050*, MF198059, MF198093, MW226776* –; *Leichhardtia rostrata* (R.Br.) P.I.Forst., F, Australia, *Forster & Leiper PIF40549* (BRI: AQ0836047), MW226285*, MW226497*, MW226161*, MW226382*, MW226613*, MW226698*, MW226755*; *Leichhardtia speciosa* (Baill.) Liede, Gâteblé & Meve, G, New Caledonia, *Gâteblé & al. 1119* (NOU: NOU-106162), MW226260*, MW226469*, MW226131*, MW226355*, MW226586*, MW226674* –; *Leichhardtia tylophoroides* (Schltr.) Liede, Gâteblé & Meve, G, New Caledonia, *Gâteblé & al. 1085* (NOU: NOU-106131), MW226261*, MW226470*, MW226132*, MW226356*, MW226587*, MW226675* –; *Leichhardtia variifolia* (Guillaumin) Liede, Gâteblé & Meve, G, New Caledonia, *Gâteblé & al. 1098* (NOU: NOU-106151), MW226262*, MW226471*, MW226133*, MW226357*, MW226588*, MW226676*, MW226748*; *Leichhardtia viridiflora* (R.Br.) P.I.Forst. subsp. *tropica* (P.Forst.) P.I.Forst., F (E), Australia, *McDonald KRM6009* (BRI: AQ0742308), MW226291*, MW226503*, MW226168*, MW226388*, MW226618*, MW226705* –; *Leichhardtia viridiflora* (R.Br.) P.I.Forst. subsp. *viridiflora*, F, Australia, *Bean & Grimshaw 28328* (BRI: AQ0820303), MW226292*, MW226504*, MW226169*, MW226389*, MW226619*, MW226706* –; *Lygisma angustifolium* (Wight) Hook.f., D, Thailand, *Middleton & al. 1161* (A), MW226201*, MW226412*, MW226607* –; –; MW226784*, MW226817*; *Lygisma inflexum* (Costantin) Kerr, D, Thailand, *Kocyan 165* (M), MW226263*, MW226472*, MW226134*, MW226358*, MW226589*, MW226677* –; *Marsdenia astephanoides* (A.Gray) Woodson, H, Mexico: Michoacán, *Fishbein 5104* (OKLA), KF539849, KF539849, KF539849, –; –; –; *Marsdenia brevisquama* Jum. & H.Perrier, B, Madagascar, *Phillipson 2863* (MO: MO-3767748), MW226203* –; MW226609* –; –; MW226785*, MW226818*; *Marsdenia calcicola* Kerr, D, Thailand, *Maxwell 96-384* (L), MW226266*, MW226476*, MW226139*, MW226362*, MW226593*, MW226681*, MW226749*; *Marsdenia cordifolia* Choux, B, Madagascar, *Klackenberg 4087* (S), –; MW226397*, MW226049* –; MW226524* –; MW226807*; *Marsdenia cordifolia* Choux, B, Madagascar, *Liede & al. 2715* (MO: MO-4027788), MW226204*, MW226414*, MW226070* –; MW226530* –; MW226819*; *Marsdenia coulteri* Hemsl., H, Mexico, *s.coll. s.n. "Corralejo"* (UBT), LR794689, LR794714, LR794741, LR794790, LR794769, LR794808, LR794829; *Marsdenia coulteri* Hemsl., H, Mexico: Yucatan, *Bradburn & Darwin 1267* (S), HE799698, HQ327496, LR794742, LR794791, HQ327498, –; –; *Marsdenia edulis* Watson, H, Mexico, *Wanntorp s.n.* (S), –; LR794717, LR794745, –; LR794772, –; –; *Marsdenia engleriana* W.Rothe, H, Costa Rica, *Voigt s.n.* (UBT), AJ574820, AJ574821 & AJ574822, LT595600, LR794794, LR794774, LR794811, LR794832; *Marsdenia exellii* Norman, A, Guinea, *Molmou & al. 488* (K), LR794686, LR794711, LR794738, LR794788, LR794766, LR794806, LR794827; *Marsdenia glabra* Costantin, D, Thailand, *Middleton & al. 1123* (A), MW226206*, EF456114, EF456652, –; MW226532*, MW226787*, MW226822*; *Marsdenia magniflora* P.T.Li, A, Equatorial Guinea, *Luke 12187* (EA, UBT), LR794687, LR794712, LR794739, LR794788, LR794767, –; LR794828; *Marsdenia mayana* Lundell, H, Guatemala, *Contreras 8689* (S), –; LR794721, LR794750, –; –; –; *Marsdenia oreophila* W.W.Sm., D, China, *Boufford 33030* (HUH), –; MK214614, –; –; MK214534, –; –; *Marsdenia oreophila* W.W.Sm., D, ex hort., ex hort. *Burncoose s.n.* (UBT), MW226282*, MW226493*, MW226157*, MW226380*, MW226609*, MW226695*, MW226753*; *Marsdenia peraffinis* S.F.Blake, H, Mexico: Oaxaca, *Mexia 8728* (S), LR794695, LR794722, LR794751, –; –; –; *Marsdenia philippinensis* Schltr., D, Philippines, *Laurent & Vasquez 6* (UBT, USTH), MW226283*, MW226494*, MW226158* –; MW226610*, MW226696*, MW226754*; *Marsdenia tenacissima* Wight & Arn., D, Philippines, *Schneid & Liede 96-103* (ABD), AJ431758, AJ431759 & AJ431760, HG530604, MW226385*, FM178493, MW226701*, MW226758*; *Marsdenia thyriflora* Hook.f., D, Cambodia, *Monyrak 181* (L, dup. A), MW226288*, MW226500*, MW226164* –; –; MW226702* –; *Marsdenia tinctoria* R.Br., D, China, *Li Heng & al. Gaolingshan Biodiversity Survey 24896* (MO), MW226207*, MW226416*, MW226073* –; –; MW226788*, MW226823*; *Marsdenia tinctoria* R.Br., D, China: Hainan, *Liede & Meve 3679* (UBT), MW226289*, MW226502*, MW226166*, MW226387*, MW226617*, MW226704* –; *Marsdenia tinctoria* R.Br., D, Taiwan, *Panero 6436* (NY), –; MK214626, –; –; MK214545, –; –; *Marsdenia tinctoria* R.Br., D, China, *South China Bot. Garden 042692* (UBT), MW226290*, MW226501*, MW226165*, MW226386*, MW226616*, MW226703*, MW226759*; *Marsdenia tomentosa* C.Morren & Decne., C, Japan, *Aoki & al. 000109-1* (KYO), –; AB178638 (only *trnL-F*), AB178639, –; –; –; *Marsdenia truncata* Jum. & H.Perrier, B, Madagascar, *Labat & Deroin 2321* (MO), MW226208*, MW226417*, MW226074* –; –; MW226533*, MW226789*, MW226824*; *Marsdenia verrucosa* Decne., B, Madagascar, *Allorge 2407* (UBT, P), AJ431761, AJ431762 & AJ431763, MW226167* –; –; –; *Marsdenia zimapanica* Hemsl., H, Mexico, *Tenorio L. 8862* (BH), MW226209*, MW226418*, MW226075* –; –; –; MW226825*; *Oreosparte celebica* Schltr., D, Indonesia, *Middleton 3700* (E), MF198013, MF198051, –; MF198087, MF198133, –; –; *Oreosparte parviflora* (Ridl.) Rodda & Simonsson, D, ex hort. (Malaysia), *Rodda MR1786* (SING), MF198015, MF198054, –; MF198089, MF198136, –; –; *Oreosparte sabahensis* Rodda & Simonsson, D, Malaysia, *SNP16224* (SNP), MF198016, MF198055, –; MF198090, MF198137, –; –; *Papuahoya bykulleana* Simonsson & Rodda, E, Papua New Guinea, *Simonsson Juhonewe & Juhonewe NS0029B* (LAE, SING), MF198014, MF198052, MW226170*, MF198088, MF198134, MW226707* –; *Papuahoya neoguineensis* Simonsson & Rodda, E, Papua New Guinea, *Rodda MR1116* (SING), MF197992, MF198053, –; MF198086, MF198135, –; –; *Papuahoya urniflora* (P.I.Forst.) Rodda & Simonsson, E, Papua New Guinea, *Simonsson Juhonewe & Juhonewe NS0069L* (LAE, SING), MF198009, MF198049, –; MF198081, MF198131, –; –; *Rhysosolobium dumosum* E.Mey., A, South Africa, *Bruyns 3948* (K: MWC 3857), AJ431773, AJ431774 & AJ431775, MW226171*, AM231771, –; –; *Rhysosolobium dumosum* E.Mey., A, South Africa, *Van Jaarsveld 2510* (MO), MW226210*, MW226419*, MW226076* –; –; MW226790*, MW226826*; *Ruehssia brasiliensis* (Decne.) F.Esp.Santo & Rapini, J, Argentina, *Keller 12364* (CTES), LR794697, LR794724, LR794753, LR794796, LR794778, LR794815, LR794837; *Ruehssia caatingae* (Morillo) F.Esp.Santo & Rapini, J, Brazil: Bahia, *França & al. 5163* (K), LR794698, LR794725, LR794754, –; –; LR794779, LR794816, LR794838; *Ruehssia carvalhoi* (Morillo & Carnevali) F.Esp.Santo & Rapini, J, Brazil: Bahia, *Lewis & Carvalho 771* (K), LR794699, LR794726, LR794755, LR794797, LR794780, –; LR794839; *Ruehssia castillonii* (Lillo ex T.Mey.) H.A.Keller & Liede, J, Bolivia, *Wood & Taylor 22523* (K), LR794688, LR794713, LR794740, –; LR794768, LR794807, –; *Ruehssia clausa* (R.Br.) Liede, S.Reuss & Meve, I, Haiti, *Judd 4839* (S), LR794700, LR794727, LR794756, –; –; LR794817, LR794840; *Ruehssia cundurango* (Rchb.) Liede & H.A.Keller, J, Ecuador, *Liede & Meve 3558* (UBT), LR794690, LR794715, LR794743, LR794792, LR794770, LR794809, LR794830; *Ruehssia dictyophylla* (Urb.) Acev.-Rodr., I, Puerto Rico, *Wanntorp 5992* (S), LR861637, LR861638, LR861678, –; LR861690, –; –; *Ruehssia ecuadorensis* (Morillo & Spellman) Liede & H.A.Keller, J, Ecuador, *Liede & Meve 3560* (UBT), LR794691, LR794716, LR794744, LR794793, LR794771, LR794810, LR794831; *Ruehssia ekmanii* (Alain) Acev.-Rodr., I, Haiti, *Ekman H5026* (S), LR794692, LR794718, LR794746, –; LR794773, –; –; *Ruehssia gillespieae* (Morillo) Liede & H.A.Keller, J, Guyanas, *Ollerton & al. 212* (UBT), AJ431755, AJ431756 & AJ431757, LR794747, –; LR794775, LR794812, LR794833; *Ruehssia guaranitica* (Malme) Liede & H.A.Keller, J, Paraguay, *Zardini 46813* (MO), LR794693, LR794719, LR794748, –; –; LR794834; *Ruehssia laxiflora* (Donn.Sm.) Gonz.-Martínez & Lozada-Pérez, H, Guatemala, *Martínez 23675* (MO), LR794694, LR794720, LR794749, –; LR794776, LR794813, LR794835; *Ruehssia linearis* (Decne.) Liede, S.Reuss & Meve, I, Cuba, *Mangelsdorff RMC 2285* (UBT), LR794701, LR794728, LR794798, LR794781, LR794818, LR794841; *Ruehssia macrophylla* (Humb. & Bonpl. ex Schult.) H.Karst., J, Brazil, *Santo 224* (HUEFS), –; MK214609, –; –; MK214529, –; –; *Ruehssia macrophylla* (Humb. & Bonpl. ex Schult.) H.Karst., J, Paraguay, *Stevens 26072* (MO), LR794702, LR794729, LR794758, –; –; LR794819, LR794842; *Ruehssia malmeana* (W.Rothe) F.Esp.Santo & Rapini, J, Bolivia, *Wood & al. 20038* (K), LR794703, LR794730, LR794759, LR794799, LR794782, LR794820, LR794843; *Ruehssia megalantha* (Goyder & Morillo) F.Esp.Santo & Rapini, J, Brazil, *Santo 236* (HUEFS), –; MK214611, –; –; MK214530, –; –; *Ruehssia megalantha* (Goyder & Morillo) F.Esp.Santo & Rapini, J, Brazil, *Taylor & al. 1557* (K, MO, MSUN), AJ574837, AJ574836 & AJ574835, LR794760, LR794800, LR794783, LR794821, LR794844; *Ruehssia rubrofusca* (E.Fourn.) F.Esp.Santo & Rapini, J, Peru, *Van der Werff 13992* (MO), LR794704, LR794731, LR794761, –; LR798073, LR794822, LR794845; *Ruehssia satirejifolia* (A.Rich.) Liede, S.Reuss & Meve, I, Dominican Republic: Pedernales, *Conceicao 1774* (HUEFS), LR794705, LR794732, LR794762, LR794801, LR794784, –; –; *Ruehssia satirejifolia* (A.Rich.) Liede, S.Reuss & Meve, I, Dominican Republic, *Mika 49* (UBT), LR794706, LR794733, LR794763, LR794802, LR794785, LR794823, LR794846; *Ruehssia sprucei* (W.Rothe) F.Esp.Santo & Rapini, J, Brazil: Amazonas, *Cardoso 3332* (HUEFS), –; MK214625, –; –; MK214543, –; –; *Ruehssia suberosa* Malme, J, Brazil, *Rapini 384/2004* (HUEFS), AJ704456, AY163697, AJ704457, –; MK214544, –; –; *Ruehssia tresseniae* (S.Cáceres & Morillo) H.A.Keller & Liede, J, Argentina, *Keller 13712* (CTES), LR794696, LR794723, LR794752, LR794795,

Appendix 1. Continued.

LR794777, LR794814, LR794836; *Ruehssia vinciflora* (Griseb.) Liede, S.Reuss & Meve, I, Cuba, *Mangelsdorff RMC 3118* (FR), LR794707, LR794734, LR794764, LR794803, LR794786, LR794824, LR794847; *Ruehssia yamanigueyensis* Mangelsdorff, I, Cuba, *Mangelsdorff RMC 356* (FR), LR794708, LR794735, LR794765, LR794804, LR794787, LR794825, LR794848; *Ruehssia zehntneri* (Fontella) F.Esp.Santo & Rapini, J, Brazil, *Pirani 4399/Espirito Santo 195* (HUEFS), –, AY163698, –, –, MK214548, –, –, *Sarcobolus cambogensis* McHone & Livsh., D, Cambodia, *Leti CL546* (P), –, MW226420*, MW226077*, –, –, –, *Sarcobolus globosus* Wall. subsp. *peregrinus* (Blanco) Rintz, D, Philippines, *Laurente & al. 16* (USTH), MW226296*, MW226508*, MW226175*, –, MW226623*, MW226711*, MW226762*; *Sarcobolus hullsii* (F.Muell. ex Benth.) P.I.Forst., F, Australia, *Wannan 4938* (BRI: AQ0853949), MW226293*, MW226505*, MW226172*, –, MW226620*, MW226708*, –, *Sarcobolus retusus* K.Schum., D, Palau, *Coston 3446* (BRI), MW226294*, MW226506*, MW226173*, MW226390*, MW226621*, MW226709*, MW226760*; *Sarcobolus retusus* K.Schum., G, New Caledonia, *Gâteblé & al. 1082* (NOU: NOU-106129), MW226295*, MW226507*, MW226174*, MW226391*, MW226622*, MW226710*, MW226761*; *Stephanotis floribunda* Brongn., B, ex hort., *Livshultz 02_25* (OMA), MW226211*, MW226421*, MW226078*, –, –, MW226791*, MW226827*; *Stephanotis floribunda* Brongn., B, ex hort., *ex hort. s.n.* (UBT), MW226302*, MW226514*, MW226181*, –, –, MW226624*, MW226712*, MW226763*; *Stephanotis grandiflora* Decne., B, Madagascar, *Gauthier & Derleth 2539* (S), HE799699, HQ327494, –, –, –, –, *Stigmatorhynchus umbelliferus* (K.Schum.) Schltr., A, Tanzania, *Brunnmitt & al. 18074* (MO), MW226212*, MW226422*, MW226079*, –, –, MW226792*, MW226828*; *Stigmatorhynchus umbelliferus* (K.Schum.) Schltr., A, Tanzania, *Mawi & Kadeketa 53* (MO), MW226213*, MW226423*, MW226608*, –, MW226534*, MW226793*, MW226829*; *Telosma africana* N.E.Br., A, South Africa, *Bruyns 9340* (BOL), –, AM233380, –, AM231773, –, –, *Telosma africana* N.E.Br., A, Central African Republic, *Harris 2293* (MO), –, –, MW226081*, –, MW226535*, MW226794*, MW226830*; *Telosma cordata* (Burm.f.) Merr., D, Philippines, *Laurente & Pesito 10* (USTH), MW226303*, MW226515*, –, –, MW226626*, –, –, *Telosma cordata* (Burm.f.) Merr., D, cult. U.S.A., Cornell University, *Livshultz 01_33* (BH), MW226214*, EF456112, DQ660620, –, –, MW226795*, MW226831*; *Telosma pallida* Wight, D, Pakistan, *Ritzwana 37988-89* (PMNH), MW226304*, MW226516*, MW226182*, MW226393*, MW226627*, MW226714*, –, *Telosma pallida* Wight, D, Pakistan, *Sultan s.n.* (UBT), MW226305*, MW226517*, MW226183*, MW226394*, MW226628*, MW226715*, MW226765*; *Telosma procumbens* (Blanco) Merr., D, Philippines, *Schneid 96-101* (UBT), AJ431782, AJ431783 & AJ431784, LT595601, MW226392*, MW226625*, MW226713*, MW226764*. — **OUTGROUP:** *Araujia sericifera* Brot., Argentina, J, *Liede & Conrad 3007* (ULM), AJ428792, AJ428793 & AJ428794, AJ699352, –, –, –, *Asclepias syriaca* L., United States, H, *Livshultz 03_33* (GH, BH), MW226188*, EF456111, DQ660564, –, –, –, *Astephanus triflorus* (L.f.) Schult., South Africa, A, *Williams 659* (MO), AJ410187, AJ410188 & AJ410189, AJ699324, –, –, –, *Caralluma arachnoidea* (P.R.O.Bally) M.G.Gilbert, Kenya, A, *Meve 934* (UBT), AJ410037, AJ410038 & AJ410039, AJ699321, –, –, –, *Ceropegia juncea* Roxb., India, D, *Hanáček 92* (UBT), AJ428798, AJ428799 & AJ428800, AJ699322, –, –, –, *Cibirhiza dhofarensis* Bruyns, Oman, A, *Butler 834* (UBT), AJ431737, AJ431738 & AJ431739, LT595595, –, –, –, *Cynanchum altiscandens* K.Schum., Kenya: Kiambu, A, *Liede & Newton 2873* (UBT), AJ428591, AJ428592 & AJ428593, LN896888, –, –, –, *Diplolepis nummulariifolia* (Hook. & Arn.) Liede & Rapini, Argentina, J, *Liede & Conrad 3050* (MO, MSUN, ULM), AJ290853, AJ290852 & AJ290851, AJ699334, –, –, –, *Emplectanthus gerrardii* N.E.Br., South Africa: KwaZulu-Natal, A, *Jürgens 1454* (UBT), LT595687, LT595700, LT595617, –, –, –, *Eustegia minuta* (L.f.) N.E.Br., South Africa, A, *Bruyns 4357* (K: MWC 3291), AJ410205, AJ410206 & AJ410207, HG530587, –, –, –, *Fockea multiflora* K.Schum., Tanzania: Dodoma, A, *Specks 248* (UBT), AJ431743, AJ431744 & AJ431745, LT595596, –, –, –, *Funastrum clausum* (Jacq.) Schult., Mexico, H, *Liede & Conrad 2599* (MO, MSUN), AJ290860, AJ290861 & AJ290862, AJ699355, –, –, –, *Heterostemma piperifolium* King & Gamble, Thailand, D, *Middleton 194* (A), –, EF456110, EF456610, –, –, –, *Leptadenia lanceolata* (Poir.) Goyder, Gambia, A, *Huber s.n.* (UBT), AJ410055, AJ410056 & AJ410057, HG530591, –, –, –, *Macrocepis diademata* (Ker Gawl.) W.D.Stevens, Guatemala, H, *Heyne s.n.* (UBT), AJ704266, AJ704268 & AJ704267, AJ704265, –, –, –, *Matelea cyclophylla* (Standl.) Woodson, Mexico, H, *Barad s.n.* (UBT), AJ704271, AJ704269 & AJ704272, AJ704273, –, –, –, *Metastelma* aff. *parviflora* R.Br., Venezuela, J, *Liede & Meve 3328* (UBT), AJ428777, AJ428778 & AJ428779, –, –, –, *Microloma tenuifolium* (L.) K.Schum., South Africa, A, *Albers s.n.* (MSUN), AJ410220, AJ410221 & AJ410222, AJ699325, –, –, –, *Neoschumannia kamerunensis* Schltr., Cameroon, A, *Meve & Etuge 910* (B, K, UBT), AJ410052, AJ410053 & AJ410054, LT595608, –, –, –, *Orthosia ellemannii* (Morillo) Meve & Liede, Ecuador, J, *Liede & Meve 3457* (UBT), AJ428780, AJ428781 & AJ428782, AJ699350, –, –, –, *Oxypetalum balansae* Malme, Argentina, J, *Liede & Conrad 3015* (ULM), AJ704347, AJ704346 & AJ704348, AJ704349, –, –, –, *Pentacypus andinus* (Ball.) Liede, Peru, J, *Liede & Meve 3451* (UBT), AJ492149, AJ492150 & AJ492151, AJ699335, –, –, –, *Pentacypus nivalis* (J.F.Gmel.) D.V.Field & J.R.I.Wood, Cameroon, A, *Meve 949* (B, MSUN, UBT), AJ410238, AJ410239 & AJ410240, AJ699329, –, –, –, *Pergularia daemia* (Forssk.) Chiov., Kenya, A, *Masinde 888* (UBT), AJ290891, AJ290892 & AJ290893, AJ699323, –, –, –, *Pervillaea tomentosa* Decne., Madagascar, B, ex hort. Palmengarten s.n. (UBT), AJ431767, AJ431768 & AJ431769, AJ699319, –, –, –, *Schizostephanus alatus* Hochst. ex. K.Schum., Kenya, A, *Nolte s.n.* (IPPS 8111) (UBT), AJ410247, AJ410248 & AJ410249, HF547220, –, –, –, *Secamone afzelii* (Roem. & Schult.) K.Schum., Cameroon, A, *Meve 922* (UBT), MW226297*, MW226509*, MW226176*, –, –, –, *Secamone alpinii* Schult., South Africa, A, *Liede 2931* (UBT), AJ428828, AJ428829 & AJ428830, AJ699320, –, –, –, *Secamone elliptica* R.Br., New Caledonia, G (D,E,F), *Gâteblé 761* (NOU), MW226298*, MW226510*, MW226177*, –, –, –, *Secamone elliptica* R.Br., China: Hainan, D (E,F,G), *Liede & Meve 3678* (UBT), MW226299*, MW226511*, MW226178*, –, –, –, *Secamone letouzeana* (H.Huber) Klack., Angola, A, *Goyder & al. 7116* (K), MW226300*, MW226512*, MW226179*, –, –, –, *Secamone parvifolia* (Oliv.) Bullock, Tanzania: Manyara, A, *Liede & Meve 3728* (UBT), MW226301*, MW226513*, MW226180*, –, –, –, *Sisyranchium compactum* N.E.Br., South Africa, A, *Nicholas 2825* (UDW), AJ410067, AJ410068 & AJ410069, LT595612, –, –, –, *Tassadia berteriana* (Spreng.) W.D.Stevens, Bolivia, J, *Nee & Williams 36256* (NY), AJ428789, AJ428790 & AJ428791, AJ699336, –, –, –, *Topoa patens* (H.A.Keller) H.A.Keller, Argentina, J, *H.A. Keller & L.J. Rojas 13539* (CTES), LT960582, LT960580, LT960578, –, –, –, *Vincetoxicum nigrum* Moench, Canada, C, *Murray s.n.* (GH, BH), MW226306*, MW226518*, MW226184*, –, –, –.