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Phylogeny and Generic Delimitations in the Sister Tribes Hymenodictyeae and Naucleeae (Rubiaceae)

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Abstract—The Hymenodicteae-Naucleeae clade is a predominantly Paleotropical group with 220 species in 28 genera. The phylogenetic relationships and generic limits within Naucleeae have previously been assessed using combined molecular-morphological data, however the status of some genera remains questionable. The evolutionary relationships within Hymenodictyeae have never been investigated before. We performed phylogenetic analyses of the Hymenodictyeae-Naucleeae clade using nuclear [nrETS; nrITS] and chloroplast [*ndhF*; *rbcL*; *rps16*; *trnT-F*] data and a large sampling of both tribes. Our study supports the monophyly of the tribes, all subtribes of Naucleeae (Adininae, Breoniinae, Cephalanthinae, Corynantheinae, Mitragyninae, Naucleinae, and Uncariinae), and the Hymenodictyeae genera *Hymenodictyon* and *Paracorynanthe*. In Naucleeae, the monotypic genera *Adinauclea*, *Metadina*, and *Pertusadina* are nested within *Adina*, *Mitragyna* within *Fleroya*, *Ludekia*, *Myrmeconauclea*, and *Ochreinauclea* within *Neonauclea*, and *Burttdavya* and *Sarcocephalus* within *Nauclea*. *Corynanthe* and *Pausinystalia* are mutually paraphyletic. We provisionally maintain the current generic status of *Neonauclea* and its allied genera, pending further study. In sum, we recognize 17 genera in Naucleeae: *Adina* s. l., *Breonadia*, *Breonia*, *Cephalanthus*, *Corynanthe* s. l., *Diyaminauclea*, *Gyrostipula*, *Janotia*, *Khasiaclunea*, *Ludekia*, *Mitragyna* s. l., *Myrmeconauclea*, *Nauclea* s. l., *Neolamarckia*, *Neonauclea*, *Ochreinauclea*, and *Uncaria*. Five new combinations were made: ***Adina euryncha***, ***Adina malaccensis***, ***Corynanthe lane-poolei* subsp. *iturense***, ***Corynanthe talbotii***, and ***Nauclea nyasica***.

Keywords—Bayesian analyses, chloroplast DNA, Cinchonoideae, nuclear DNA, parsimony, taxonomy.

The sister tribes Hymenodictyeae sensu Razafimandimbison and Bremer (2006) and Naucleeae sensu Razafimandimbison and Bremer (2001, 2002) are positioned as an early branch in the mostly Neotropical subfamily Cinchonoideae of the family Rubiaceae (Andersson and Antonelli 2005; Manns and Bremer 2010; Manns et al. 2012). This group has been circumscribed to include 220 species in 28 genera.

Hymenodictyeae includes two genera, *Hymenodictyon* Wall. with 24 species and *Paracorynanthe* Capuron with two species (Razafimandimbison and Bremer 2006). The tribe is restricted to the Paleotropics with the highest species diversity found in Madagascar. Hymenodictyeae species are typically medium-sized to tall trees, and often grow on rocky substrates; however, *Hymenodictyon epiphyticum* Razafim. & B. Bremer is an epiphyte, and *Hymenodictyon biafranum* Hiern and *Hymenodictyon flaccidum* Wall. are facultative epiphytes. The members of the tribe can easily be distinguished from those of Naucleeae by their spiciform to racemose inflorescences and lenticellate capsular fruits (Razafimandimbison and Bremer 2006). Hymenodictyeae is additionally characterized by its stipules bearing large, deciduous colleters on the margins, valvate corolla aestivation, and elongate, bilaterally flattened, and accrescent placentae. The generic status of *Hymenodictyon* and *Paracorynanthe* has never been questioned, but their monophyly and sister-group relationship have yet to be tested using molecular data.

Naucleeae includes 26 genera and 194 species (Govaerts et al. 2013) of trees, shrubs, and lianas mostly distributed in the Paleotropics, with a few species in the Neotropics and North America (Ridsdale 1975, 1978a, 1978b; 1989; Razafimandimbison and Bremer 2002). The tribe is a well-defined monophyletic group that can easily be recognized by its spherical inflorescences; an additional synapomorphy for the tribe is epigynous floral nectaries, deeply embedded in the hypanthia (see Razafimandimbison and Bremer (2001, 2002) and Verellen et al. (2007) for more information on the morphological characters in the tribe). Naucleeae has received much attention over the last 40 yr, and is known to have problematic intratribal classifications (e.g. Bremer et al. 1995; Razafimandimbison and Bremer 2001, 2002; Razafimandimbison et al. 2005; Ridsdale 1975, 1978a; Wikström et al. 2010).

The broad circumscription of Naucleeae, established by Razafimandimbison and Bremer (2002), subdivided the tribe in seven subtribes: Adininae, Breoniinae, Cephalanthinae, Corynantheinae, Mitragyninae, Naucleinae, and Uncariinae. However, the monophyly of Adininae and Cephalanthinae has been questioned, because the subtribes were not supported as monophyletic in their analyses and the inter-subtribal relationships were poorly supported. Razafimandimbison and Bremer (2002) proposed new generic limits within Naucleeae based on their combined molecular-morphological tree. In that study, genera that contain more than one species are maintained as a genus if they 1) are monophyletic, 2) maximize nomenclatural stability, and 3) are easy to recognize in the field, criteria as outlined by Backlund and Bremer (1998). For the assessment of the monotypic genera in Naucleeae, Razafimandimbison and Bremer (2002) utilized the following three criteria: 1) not nested within a well-defined genus, 2) with at least two autoapomorphic characters, and 3) with relationships to other genera that are strongly supported. Razafimandimbison and Bremer (2002) accepted a total of 24 genera based on their combined molecular-morphological tree. However, the monophyly of *Corynanthe* Welw., *Neonauclea* Merr., and *Pausinystalia* Pierre ex Beille, based on molecular data alone remains questionable, as the genera were shown to be non-monophyletic in the combined molecular (nrITS/*rbcL*/*trnT-F*) tree in Razafimandimbison and Bremer (2002). For example, *Ludekia* Ridsdale and *Myrmeconauclea* Merr., represented each by one species in their analyses, were nested within *Neonauclea* Merr, and the African genera *Corynanthe* and *Pausinystalia*, both sensu Stoffelen et al. (1996),

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were mutually paraphyletic. *Nauclea* L. received low support and *Pertusadina* Ridsdale and *Cephalanthus* L. respectively were not supported as monophyletic. *Hallea* J.-F. Leroy was recognized as illegitimate because it was previously described as a fossil genus, *Hallea* G.B.Matthews (Matthews 1948). Because this is inconsistent with the priority rule of the current nomenclature code, Deng (2007) formally provided a new name for the genus, *Fleroya* Y. F. Deng. More recently, Wikström et al. (2010) generated a resolved phylogeny of Naucleeae based on 31 taxa sampled from 17 genera. Inter-subtribal relationships received low support, and Adininae was potentially paraphyletic with respect to Corynantheinae. Although that study did not focus on tribe Naucleeae specifically, it raises doubts on the monophyly of *Adina* Salisb., *Breonia* A.Rich ex DC., *Neonauclea*, *Pausinystalia*, and *Pertusadina*.

The objective of the present study is to reconstruct a robust phylogeny of the Hymenodictyeae-Naucleeae clade using a large sampling of both tribes. This will allow us to: 1) test the monophyly of the subtribes of Naucleeae, 2) test the monophyly of genera in Naucleeae and revise the classification accordingly, and 3) test the monophyly of the two genera in Hymenodictyeae.

Materials and Methods

***Taxon Sampling*—**Taxa studied were predominantly those included in earlier phylogenetic studies of Naucleeae; 48 of the 50 taxa investigated by Razafimandimbison and Bremer (2002) were included in this study, with an addition of subsequently published nrETS, nrITS, *ndhF*, *rbcL*, *rps16*, and *trnT-F* sequences. A total of 77 species representing 24 of the 26 genera in Naucleeae and 20 taxa (18 species) representing both of the genera of Hymenodictyeae were analyzed (Table 1). The sampling included 30 species not previously investigated with molecular methods. Two genera from Naucleeae, *Diyaminauclea* Ridsdale and *Khasiaclunea* Ridsdale, were not included due to lack of material.

Five species from the subfamily Ixoroideae and one species from the subfamily Cinchonoideae were utilized as outgroup taxa based on Manns and Bremer (2010) and Manns et al. (2012). More information regarding the taxa investigated in this study (species names, voucher information, and sequence accession numbers) can be found in Appendix 1.

***Laboratory Procedures*—**DNA extraction, amplification, and sequencing followed the procedures outlined in Kårehed and Bremer (2007). The primers used for amplification are listed in Table 2. The raw sequencing data were assembled using the Staden package version 2.0 (Staden 1996).

***Alignment*—**The DNA sequences were aligned manually, using Se-Al version 2.0 (Rambaut 2002). Insertion/deletion events (indels) were visually inferred, following the alignment criteria outlined in Oxelman et al. (1997). One inversion of six base pairs was found in some of the *rps16* sequences in Naucleeae (position circa 585–591). The inversion was treated as a separate indel to prevent false sister group relationships forming. The aligned DNA matrices are available on TreeBASE (Study number TB2:S14215).

***Phylogenetic Analyses*—**Sequence data for each individual marker was analysed using Bayesian inference. The chloroplast [*ndhF*, *rbcL*, *rps16*, and *trnT-F*] datasets were combined in one partition (hereafter referred to as "cp"; Table 3), and the nuclear [ETS and ITS] datasets in another partition (hereafter referred to as "nr"; Table 3). We performed visual comparisons of the cp and nr trees to detect any taxa with conflicting positions. A combined Bayesian analysis, based on these two partitions (hereafter referred to as "cp/nr"; Table 3) was conducted. Gaps were treated as missing data.

For each single marker data set, as well as the cp and nr data sets, the best-performing evolutionary model was identified using MrAIC version 1.4.4 (Nylander 2004) under the AICc criterion (Posada and Buckley 2004). Bayesian analyses were performed in MrBayes version 3.2 (Ronquist et al. 2012). The cp and nr matrices were analysed unpartitioned, and the cp/nr analysis in two unlinked partitions, nr and cp. The following settings were applied in all Bayesian analyses: two parallel runs of 10,000,000 generations in four chains each, a sample frequency of 1,000 and the temperature set to 0.10. Convergence of the Monte Carlo Markov Chains was assumed when the standard deviation of split frequencies for the parallel runs was below 0.01 (Ronquist et al. 2011). In addition, the minimum Estimated Sample Size was well above 100

Table 1. Distribution of taxa included in the study. Genus and species counts retrieved from Govaerts et al. (2013). *Hymenodictyon parvifolium* is represented by three individual specimens. One undescribed new species of *Hymenodictyon* is included.

Tribe	Subtribe	Genus	No. spp. in genus	No. spp. in study
Hymenodictyeae		*Hymenodictyon*	25	16
		Paracorynanthe	2	2
		Total:	**27**	**18**
Naucleeae	Adininae	*Adina*	4	3
		Adinauclea	1	1
		Diyaminauclea	1	0
		Haldina	1	1
		Khasiaclunea	1	0
		Ludekia	2	2
		Metadina	1	1
		Myrmeconauclea	4	2
		Neonauclea	68	10
		Ochreinauclea	2	1
		Pertusadina	4	3
		Sinoadina	1	1
	Breoniinae	*Breonadia*	1	1
		Breonia	20	11
		Gyrostipula	3	2
		Janotia	1	1
	Cephalanthinae	*Cephalanthus*	6	5
	Corynantheinae	*Corynanthe*	3	3
		Pausinystalia	5	3
	Mitragyninae	*Fleroya*	3	2
		Mitragyna	7	6
	Naucleinae	*Burttdavya*	1	1
		Nauclea	10	6
		Neolamarckia	2	1
		Sarcocephalus	2	2
	Uncariinae	*Uncaria*	40	8
		Total:	**194**	**77**

Table 2. Primers used for PCR and sequencing. F = Forward; R = Reverse.

Region	Primer names	Reference
nrETS	Erit-F	Negròn-Ortiz and Watson (2002)
nrETS	18S-E (R)	Baldwin and Markos (1998)
nrITS	ITS4R; Leu1 (F)	White et al. (1990)
ndhF	2F; 720F; 1320F	Rydin et al. (2008)
ndhF	1000R; 1700R; 2280R	Rydin et al. (2008)
rbcL	5′F; bs427F; 3′R	Bremer et al. (2002)
rbcL	z895R	Zurawski et al. (1981)
rps16	F; 2R	Oxelman et al. (1997)
trnT-F	a1F; iR	Bremer et al. (2002)
trnT-F	820F; 940R; 1880F	Rydin et al. (2008)
trnT-F	cF; dR; fR	Taberlet et al. (1991)

Table 3. Parsimony data, percentage of characters scored as missing data, and evolutionary model selection results.

	cp	nr	cp/nr
Number of taxa	103	103	103
Length of aligned matrix (bp)	6,391	1,086	7,477
Parsimony informative characters	616	488	1,104
% informative characters of total	9.6%	44.9%	14.8%
% missing data	13.9%	10.9%	13.5%
Evolutionary models	GTRG	HKYG	

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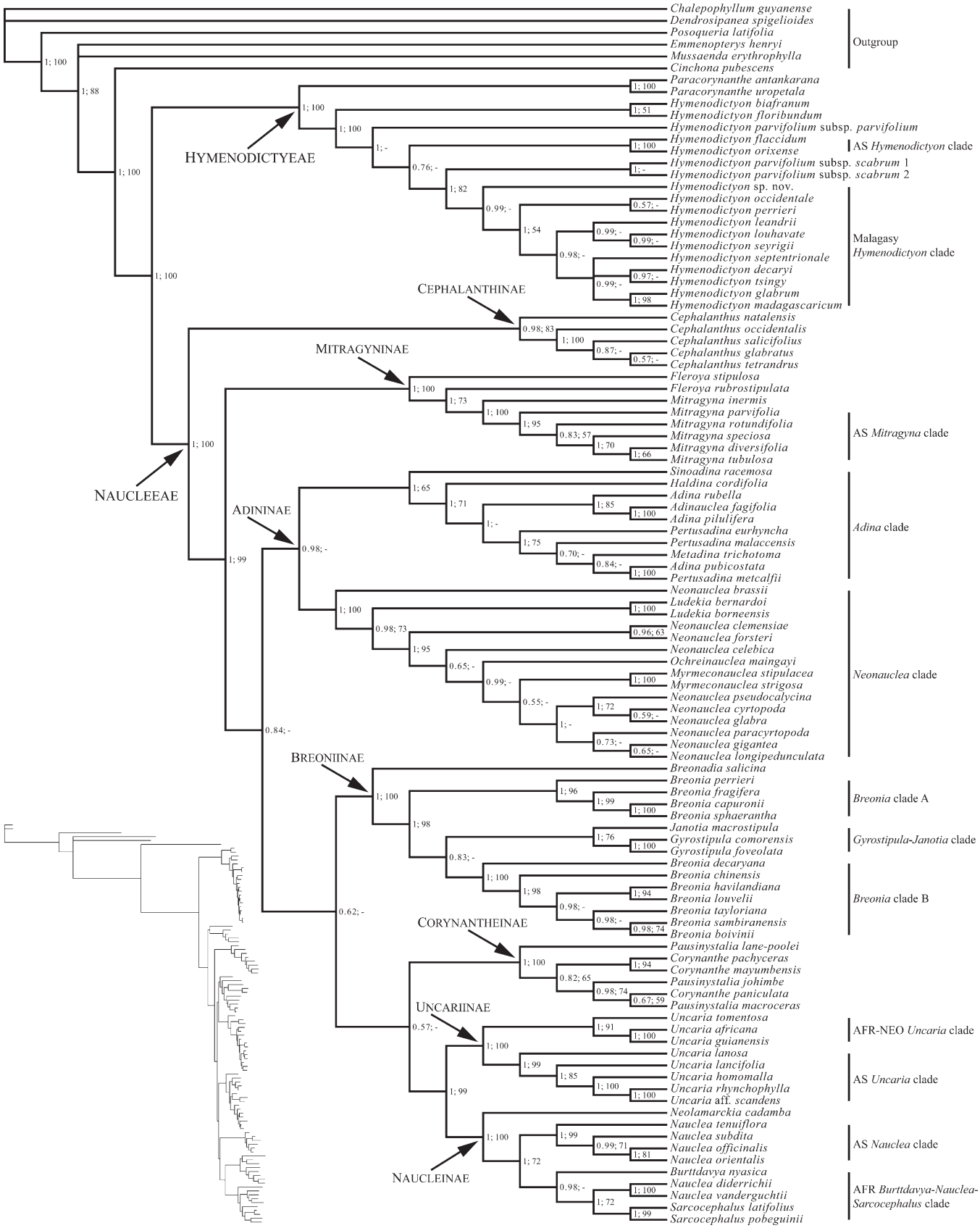


FIG. 1. Bayesian 50% Majority rule consensus cladogram of the combined chloroplast and nuclear data set. Bayesian posterior probablilities (PP) and parsimony bootstrap values (BS) are included to the right of the nodes, separated by a semi-colon (PP; BS). BS < 50 is indicated by a hyphen (-). Tribes and subtribes are marked with arrows and subclades discussed in the text are delimited with vertical bars. In the lower left corner of the figure a small phylogram is included to illustrate the branch lengths.

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(Ronquist et al. 2011) and the Potential Scale Reduction Factor was 1.00 (Gelman and Rubin 1992) for all parameters. The trees sampled from the first quarter of generations were discarded as burn-in. A 50% majority rule consensus tree was produced from the remaining trees (Fig. 1; TreeBASE study number TB2:Tr63481).

To support the Bayesian analysis, a parsimony analysis of the cp/nr data was performed in PAUP* version 4.0 beta 10 (Swofford 1998). Parsimony bootstrap support values were obtained by performing 1,000 bootstrap replicates with 10 random sequence additions, tree-bisection-reconnection branch swapping, and no topological constraints. A 50% majority rule consensus tree was produced from the resulting trees (Fig. 1; TreeBASE accession number TB2:Tr63482). The parsimony data, results of the evolutionary model selection, and number of characters scored as missing data are summarized in Table 3.

Results

In total, 276 new sequences were generated for this study: 44 nrETS, 39 nrITS, 59 *ndhF*, 42 *rbcL*, 61 *rps16,* and 31 *trnT-F*. There was no conflict between the phylogenies resulting from the Bayesian analyses of the individual chloroplast (*ndhF, rbcL, rps16,* and *trnT-F*) or nuclear (nrETS and nrITS) markers. Posterior probablitity (PP) values of nodes are further discussed as follows: nodes with PP between 0.98 and 1 are considered to be strongly supported, those with PP between 0.95 and 0.97 are supported, and those with PP below 0.95 are not supported.

The cp and nr trees (TreeBASE study numbers TB2: Tr63483 and TB2:Tr63484) both identify two major lineages (Hymenodictyeae and Naucleeae) and five of the seven subtribes of Naucleeae (Mitragyninae, Breoniinae, Corynantheinae, Uncariinae, and Naucleinae). Visual inspections of the cp and nr trees reveal that nine taxa, namely *Adina pilulifera* Franch. ex Drake, *Cephalanthus occidentalis* L., *Janotia macrostipula* (Capuron) J.-F. Leroy, *Mitragyna inermis* (Wild.) Kuntze, *Neonauclea celebica* (Havil.) Merr., *Neonauclea clemensiae*, *Neonauclea forsteri* (Seem. ex Havil.) Merr., *Neonauclea glabra* (Roxb.) Bakh.f. & Ridsdale, and *Neonauclea pseudocalycina* Ridsdale have strongly supported conflicting positions. However, the incongruent positions of these species do not affect our conclusions regarding generic delimitations, because they are nested within their respective strongly supported clades in all our analyses. We therefore combined the cp and nr data sets in accordance with a total evidence approach (Kluge 1989; de Queiroz et al. 1995; Wiens 1998).

The 50% majority rule consensus tree generated from the Bayesian cp/nr analysis is depicted in Fig. 1. The overall tree topology from the parsimony analysis (TreeBASE accession number TB2:Tr63482) was consistent with the result from the Bayesian analyses, and the parsimony bootstrap (BS) support values from the cp/nr analysis are presented in Fig. 1 but are not further discussed.

Hymenodictyeae and Naucleeae are both strongly supported as monophyletic (PP = 1) and as sisters in all performed analyses (Fig. 1).

Hymenodictyeae—*Paracorynanthe* is resolved as sister to *Hymenodictyon* (PP = 1). Within *Hymenodictyon* the two sampled Asian species (*Hymenodictyon orixense* (Roxb.) Mabb. and *H. flaccidum*) and the Malagasy species (Fig. 1), respectively, form two strongly supported monophyletic groups (PP = 1 and PP = 0.99 respectively; Fig. 1). The African *Hymenodictyon* species (*Hymenodictyon biafranum* Hiern and *Hymenodictyon floribundum* (Hochst. & Steud.) B.L.Rob. form an early diverging lineage of the genus, which is sister to the remaining *Hymenodictyon*. The African species form a grade together with the Asian clade, subtending with *Hymenodyction parvifolium* subsp. *scabrum* (Stapf.) Verdc. as sister to the Malagasy *Hymenodictyon* clade (represented by 11 of the 15 species, Fig. 1). Additionally, *Hymenodictyon parvifolium* subsp. *parvifolium* Oliv. does not form a monophyletic group with the two sampled specimens of *Hymenodyction parvifolium* subsp. *scabrum* (Fig. 1).

Naucleeae—Within the tribe, all seven subtribes as delimited by Razafimandimbison and Bremer (2002) are strongly supported in our analysis (Fig. 1), but the intersubtribal relationships remain unsupported with two exceptions: Cephalanthinae is a strongly supported sister to the remaining Naucleeae (PP = 1) and Naucleinae and Uncariinae form a strongly supported clade (PP = 1).

Subtribe Cephalanthinae (PP = 0.98) is strongly supported as monophyletic in our analysis (Fig. 1). The African and Asian species of *Mitragyna* Korth. form a monophyletic group (PP = 1) in our analysis (Fig. 1), while *Fleroya* is paraphyletic with respect to *Mitragyna* sensu Ridsdale (1978b). Within subtribe Adininae (PP = 0.98), two strongly supported clades are formed: the *Adina* clade (PP = 1), containing the genera *Adina*, *Adinauclea* Ridsdale, *Haldina* Ridsdale, *Metadina* Bakh.f., *Pertusadina,* and *Sinoadina* Ridsdale, and the *Neonauclea* clade (PP = 1), consisting of the genera *Ludekia*, *Myrmeconauclea*, *Neonauclea*, and *Ochreinauclea* Ridsdale & Bakh.f. (Fig. 1). *Adinauclea*, *Metadina* and *Pertusadina* nested within *Adina*, and *Ludekia*, *Myrmeconauclea*, and *Ochreinauclea* are nested within *Neonauclea*. Within subtribe Breoniinae (PP=1), *Breonadia* Ridsdale is resolved as sister (PP = 1) to a clade containing three strongly supported subclades (Fig. 1): the *Gyrostipula* J.-F. Leroy-*Janotia* J.-F. Leroy clade (PP = 1), the *Breonia* clade A (PP = 1) and the *Breonia* clade B (PP = 1). Within the subtribe Corynantheinae (PP = 1) *Pausinystalia* and *Corynanthe* are mutually paraphyletic (Fig. 1). Uncariinae (PP = 1) is resolved in two lineages (Fig. 1): one Asian clade (PP = 1) and one Afro-Neotropical clade (PP = 1). Within Naucleinae (PP = 1) *Neolamarckia* Bosser is resolved as sister to a clade resolved two distinct lineages: one subclade is formed by the African *Nauclea* species, *Sarcocephalus* Afzel. ex R.Br., and *Burttdavya* Hoyle (PP = 0.98) and the other subclade consists of the Asian *Nauclea* species (PP = 1). The monotypic *Burttdavya* and the monophyletic *Sarcocephalus* are both nested within *Nauclea* with strong support (Fig. 1).

Discussion

We discuss the phylogenetic relationships within the Hymenodictyeae-Naucleeae clade and re-evaluate the generic limits of Hymenodictyeae and Naucleeae based on the cp/nr tree (Fig. 1), as it is the best-supported hypothesis. The cp and nr partitions were utilized because the individual chloroplast and nuclear markers, respectively, resolved in congruent phylogenies, and the combination of genetic sequences in partitions is proved to increase the phylogenetic accuracy of the resulting species tree (e.g. Gadagkar et al. 2005; Nylander et al. 2004).

It is worth noting that the sampling in this study is considerably larger than that of earlier phylogenetic studies of Naucleeae (e.g. Razafimandimbison and Bremer 2001, 2002; Manns and Bremer 2010; Wikström et al. 2010).

Major Lineages of the Hymenodictyeae-Naucleeae Clade— The present study reinforces the monophyly of both

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Hymenodictyeae as defined by Razafimandimbison and Bremer (2006) and the broadly circumscribed Naucleeae as proposed by Razafimandimbison and Bremer (2001, 2002). The tribes are sisters, also consistent with the results of previous phylogenetic studies (e.g. Bremer and Eriksson 2009; Manns and Bremer 2010; Razafimandimbison and Bremer 2001; Robbrecht and Manen 2006). This sister group relationship is supported by the presence of fiber tracheids (Koek-Noorman 1970) and chromosome data (x = 11, 2x-4x-6x series of polyploids, Kiehn 1986) in both tribes. Moreover, the Hymenodictyeae-Naucleeae clade is a predominantly Paleotropical group in the otherwise mainly Neotropical Cinchonoideae.

Within Naucleeae, all seven subtribes (Adininae, Breoniinae, Cephalanthinae, Corynantheinae, Mitragyninae, Naucleinae, and Uncariinae) are strongly supported as monophyletic. The monophyly of Adininae was neither supported in Razafimandimbison and Bremer (2002), nor Wikström et al. (2010). The most likely explanation is our larger sampling size and data set. The inter-subtribal relationships in Naucleeae remain largely unsupported, with the exceptions previously mentioned (Fig. 1). The sister relationship between Naucleinae and Uncariinae was moderately supported by the combined molecular tree in Razafimandimbison and Bremer (2002), but not supported by their combined molecular-morphological tree. They postulated "a rapid early diversification of the subtribes" as the likely cause of the relatively low number of informative characters resolving the phylogeny of the tribe.

Phylogenetic Relationships Within Hymenodictyeae—This study supports the sister group relationship between the Malagasy genus *Paracorynanthe* and the Palaeotropical genus *Hymenodictyon*, as reported by Razafimandimbison and Bremer (2006). The monophyly of the genera is also supported, which is inconsistent with the results of Razafimandimbison and Bremer (2001) and Manns and Bremer (2010). The previously uncertain monophyly of Hymenodictyon with respect to Paracorynanthe could be explained by the low variability of the markers used in these two studies; the rbcL sequences of the genera are almost identical, and the rps16, ndhF, and nrETS sequences display very low variation.

Paracorynanthe is morphologically distinct from *Hymenodictyon* by its thin, plated bark, corolla lobes prolonged by conspicuous appendages, bilaterally flattened fruits, and oblanceolate, angular placentae, as opposed to thick, nonplated bark, corolla lobes without appendages, ellipsoid fruits, and fusiform, bilaterally flattened placentae in the latter genus (Razafimandimbison and Bremer 2006).

Hymenodictyon is resolved in an Asian clade, a Malagasy clade, and the African species, that do not group in one clade. The African species *Hymenodictyon parvifolium* appears to be non monophyletic, as the two subspecies do not form a monophyletic group in our analyses (Fig. 1). No taxonomic changes will be made, pending further study.

Phylogenetic Relationships and Generic Circumscriptions Within Naucleeae—For a historic overview of previous circumscriptions in Naucleeae, see Razafimandimbison and Bremer (2002).

Cephalanthinae—The subtribe, as defined by Razafimandimbison and Bremer (2002) contains a single genus, *Cephalanthus*, with six species (Ridsdale 1976). This study confirms Cephalanthinae to be the first-diverging lineage in Naucleeae and sister to the remaining members of the tribe (Fig. 1).

Cephalanthus has a disjunct geographic distribution; two species (*Cephalanthus angustifolius* Lour. and *Cephalanthus tetrandrus* (Roxb.) Ridsdale & Bakh.f.) are restricted to Asia, one species (*Cephalanthus natalensis* Oliv.) is found in southeastern Africa, and three species (*Cephalanthus glabratus* (Spreng.) K. Schum., *Cephalanthus occidentalis*, and *Cephalanthus salicifolius* Humb. & Bonpl.) are native to the New World. *Cephalanthus glabratus* is found in Brazil to Uruguay and northeastern Argentina, *C. occidentalis* has a wide distribution from eastern Canada to Honduras and Cuba, and *C. salicifolius* from Texas to Honduras (Govaerts et al. 2013; Tropicos.org 2013).

Cephalanthinae is characterized by a combination of the following characters: a single ovule per locule, infructescences formed by schizocarpous fruits splitting into two indehiscent mericarps, and the young inflorescences are not surrounded by calyptra-like bracts. Our analyses resolve *C. natalensis* as sister to the rest of *Cephalanthus*, in accordance with Manns and Bremer (2010). The other members of the genus differ from *C. natalensis* in having large colleters in the sinuses between the corolla lobes and arillate seeds. *Cephalanthus angustifolius* is not investigated in this study due to lack of material.

Mitragyninae—The subtribe, as defined by Razafimandimbison and Bremer (2002), comprises two genera, *Fleroya* and *Mitragyna*. Our analyses reaffirm the paraphyly of *Fleroya* (= *Hallea* sensu Leroy 1975), as shown by Razafimandimbison and Bremer (2002) and Manns and Bremer (2010). Accordingly, the generic status of *Fleroya* is untenable, and we formally put *Hallea* J.-F. Leroy and *Fleroya* Y. F. Deng as synonyms of *Mitragyna* (see Taxonomic Treatment). No new combinations are needed, because all three species of *Fleroya* were originally described as *Mitragyna* (Ridsdale 1978b). The broadly delimited *Mitragyna* is distinct in Naucleeae by having mitriform stigmas, and is additionally distinguished by three-zonocolporate pollen with H-shaped endoapertures (Huysmans et al. 1994) and numerous, basally attatched ovules per locule (Razafimandimbison and Bremer 2002).

Adininae—The subtribe is resolved in two strongly supported subclades: the *Adina* clade (PP = 1) and the *Neonauclea* clade (PP = 1). The *Adina* clade corresponds largely to *Adina* as defined by Haviland (1897), containing *Adina cordifolia* (Roxb.) Ridsdale (= *Haldina*, Ridsdale 1978a), *Adina multifolia* (Havil.) Ridsdale and *Adina rubescens* Hemsl. (= *Pertusadina*, Ridsdale 1978a), *Adina oligocephala* Havil. (= *Khasiaclunea* (Havil.) Ridsdale, Ridsdale 1978a), *Adina polycephala* Wall. (= *Metadina*, Bakhuizen van den Brink 1970), *Adina racemosa* (Siebold & Zucc.) Miq. (= *Sinoadina*, Ridsdale 1978a), *Adina pilulifera* (Lam.) Franch. ex Drake, and *Adina rubella* Hance (= *Adina* sensu Ridsdale 1978a). The only exception is Haviland's *Adina microcephala* (Delile) Hiern (= *Breonadia*, Ridsdale 1975), which belongs to Breoniinae. The *Adina* clade is restricted to tropical Asia and characterized by the presence of interfloral bracteoles, capsular fruits with the calyx remnants falling off together with the central axes, and winged seeds. *Breonadia* also has interfloral bracteoles and capsular fruits, but differs in having unwinged seeds. *Adinauclea*, *Haldina*, *Khasiaclunea*, *Metadina*, and *Sinoadina* are all monotypic. In our analyses (Fig. 1), *Sinoadina* and *Haldina* form a basal grade in the *Adina* clade

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and are distinct from the rest of the *Adina* clade by their cordate (sometimes obtuse in *Sinoadina*) leaves and capsular fruits dehiscing first septicidally, then loculicidally into two valves (in contrast to two or four valves in the other genera of the *Adina* clade). The two genera can easily be distinguished from eachother by their inflorescences: terminal in *Sinoadina* and axillary in *Haldina*. However, all other genera of Adininae bear terminal inflorescences so *Sinoadina* does not differ from the rest of the subtribe in this feature. Moreover, *Adinauclea* forms a clade with *Adina rubella* and *A. pililufera*, while *Pertusadina* is paraphyletic with respect to *Metadina* and *Adina pubicostata*. These genera are only separated by a few small characters (Ridsdale 1975), which is incongruent with our criterion 2. Based on these findings, we here accept a broad circumscription of *Adina*, including *Adinauclea*, *Haldina*, *Metadina*, *Pertusadina*, and *Sinoadina*. The monotypic *Khasiaclunea* is also a likely candidate for inclusion in our broadly delimited *Adina*, but it was not included in our analyses and thus, we refrain from making the taxonomic change, pending further study.

The *Neonauclea* clade comprises the four genera, *Ludekia, Neonauclea, Myrmeconauclea*, and *Ochreinauclea*. Based on morphology, *Diyaminauclea* Ridsdale (Ridsdale 1978a) probably also belongs to the clade. The lineage is characterized by well-developed, deciduous calyx lobes and the absence of interfloral bracteoles (although these are present in a few *Neonauclea* species). *Myrmeconauclea* and *Ochreinauclea* are distinct from *Ludekia* and *Neonauclea* in having pseudomultiple fruits. *Myrmeconauclea* additionally have seeds with long, ventral wings (Ridsdale 1978a) and *Ochreinauclea* has spindle-shaped stigmas; both characters are unique in the clade. *Ludekia* is unique in the clade in having globose stigmatic lobes with seven to nine prominent, longitudinal ridges. *Neonauclea* sensu Ridsdale (1989) is characterized by its unusually well-developed or appendaged calyx lobes. The four genera all have free (sometimes pseudomultiple), capsular fruits and winged seeds (Ridsdale 1978a). In our analyses (Fig. 1) both *Myrmeconauclea* and *Ludekia* are monophyletic, but the genera are nested in *Neonauclea*, along with *Ochreinauclea maingayi* (Hook.f.) Ridsdale; in other words, *Neonauclea* is paraphyletic with respect to *Ludekia*, *Myrmeconauclea*, and *Ochreinauclea*. Razafimandimbison et al. (2005) found *Neonauclea* as delimited by Ridsdale (1989) to be monophyletic, based on nrETS and nrITS datasets of 28 *Neonauclea* species, two *Myrmeconauclea* species, and one *Ludekia* species. It is worth noting that *Neonauclea brassii* S.Moore, the sister of the rest of the *Neonauclea* clade in this study was not investigated by Razafimandimbison et al. (2005). Therefore, a larger sampling of *Neonauclea* is needed to evaluate the monophyly of the genus. Additionally, the inclusion of *Ochreinauclea* within the *Neonauclea* clade is inconsistent with Ridsdale (1978a), who considered the genus to be closely related to *Nauclea*, based on its spindle-shaped stigmas. We provisionally maintain the genera *Diyaminauclea*, *Ludekia*, *Myrmeconauclea*, *Neonauclea*, and *Ochreinauclea,* pending further study.

Breoniinae—The subtribe, as defined by Razafimandimbison (2002) and Razafimandimbison and Bremer (2002) comprises four genera, the Afro-Malagasy *Breonadia*, the Malagasy *Breonia* and *Janotia*, and the Malagasy-Comorian *Gyrostipula*. Both *Breonadia* and *Janotia* are monotypic, while *Breonia* contains 20 species (Razafimandimbison 2002), and *Gyrostipula* contains three species (Emanuelsson and Razafimandimbison 2007). *Breonadia* is clearly distinct from the other genera by its verticillate leaves, intrapetiolar stipules, interfloral bracteoles, and wingless seeds. *Breonia* has multiple fruits, as opposed to capsular fruits in the other three genera. *Gyrostipula* is distinguished from the other genera by its long, red, and convolute stipules and long, filiform calyx lobes. *Janotia* is easily identified by its very large leaves and persistent, foliaceous stipules.

In our analyses (Fig. 1), Breoniinae is resolved in four lineages: *Breonadia*, sister to the rest of Breoniinae, the *Breonia* clades A and B, and the *Gyrostipula-Janotia* clade, making *Breonia* potentially non-monophyletic. These results are consistent with those of Wikström et al. (2010), but inconsistent with those of Razafimandimbison and Bremer (2002), which support a monophyletic *Breonia*. We suspect that the findings of Razafimandimbison and Bremer (2002) are due to a smaller sampling than in the present study; *Breonia* clade A (Fig. 1) was only represented by *Breonia perrieri* Homolle in their analysis, and it grouped with the members of our present *Breonia* clade B. In contrast, four species (*Breonia perrieri, Breonia fragifera* Capuron ex Razafim., *Breonia capuronii* Razafim., and *Breonia sphaerantha* (Baille.) Homolle ex Ridsdale) of the *Breonia* clade A were analyzed in this study. Additionally, we investigated seven species of the *Breonia* clade B in this study; only four were included in Razafimandimbison and Bremer (2002). Our analyses suggest that *Breonia* is potentially paraphyletic with respect to *Janotia* and *Gyrostipula*, but we refrain from making any taxonomic changes, pending further study.

Corynantheinae—The subtribe contains two African genera: *Corynanthe* and *Pausinystalia*. *Corynanthe* is distinct by its infundibular corolla tubes, exserted styles and anthers, spherical, undivided stigmas, and mainly loculicidal capsules. *Pausinystalia* is characterized by its corolla being differentiated into a basal narrow and cylindrical part, ending apically in a bladder-shaped part (resembling a wine glass), inserted styles and anthers, bilobed stigmas, and mainly septicidal capsules (Stoffelen et al. 1996). Chevalier (1909) described the genus *Pseudocinchona* A.Chev as morphologically distinct from *Corynanthe* by its four-merous flowers, exserted styles and anthers, and largely septicidal capsules, as opposed to five-merous flowers, exserted styles and anthers, and loculicidal capsules in *Corynanthe* s. s. In Razafimandimbison and Bremer (2002), *Corynanthe* and *Pausinystalia*, both sensu Stoffelen et al. (1996), were mutually paraphyletic in the combined molecular tree. In their combined molecular-morphological tree, *Pausinystalia* became monophyletic and *Corynanthe paniculata* Welw. (includes the type of the genus), was resolved as sister to the rest of Corynantheinae, but *Corynanthe* remained paraphyletic. Based on their combined molecular-morphological tree, Razafimandimbison and Bremer (2002) tentatively resurrected the genus *Pseudocinchona*, restricted *Corynanthe* to include only the type of the genus, and retained *Pausinystalia* as defined by Stoffelen et al. (1996).

The results of our analyses (Fig. 1) support the paraphyly of *Corynanthe* and *Pausinystalia*, as suggested by the combined molecular tree of Razafimandimbison and Bremer (2002). *Pseudocinchona* sensu Chevalier (1909), represented in our analyses by *Corynanthe mayumbensis* (R. D. Good) N. Hallé and *Corynanthe pachyceras* K.Schum, form a monophyletic group that is nested in a paraphyletic *Pausinystalia*. Accordingly, we merge both *Pausinystalia* sensu

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Stoffelen et al. (1996) and *Pseudocinchona* sensu Chevalier (1909) in *Corynanthe* in order to make the latter monophyletic. The broadly delimited *Corynanthe* is characterized by valvate corolla lobes, prolonged by glabrous, well-developed appendages, numerous basally attached and ascendingly imbricate ovules, and capsular fruits. This taxonomic adjustment requires two new combinations.

Uncariinae—The monogeneric subtribe has a pantropical distribution, most species rich in Asia (36 species), with only two species in the Neotropics and two species in Africa (Ridsdale 1978b). The subtribe is strongly supported as monophyletic and is resolved in two sister lineages: an Asian clade and an Afro-Neotropical clade. However, we cannot draw any major conclusions, because only five of the Asian *Uncaria* species are represented in this study. *Uncaria* is easily recognized by the lianescent growth habit and the presence of paired hooks (modified peduncles), both characters are unique in Naucleeae.

Naucleinae—The Palaeotropical subtribe Naucleinae is composed of four genera: the African *Burttdavya,* the Afro-Asian *Nauclea*, the Asian *Neolamarckia*, and the African *Sarcocephalus*. *Burttdavya*, *Nauclea*, and *Sarcocephalus*, all sensu Ridsdale (1975), can be distinguished based on their placentas, stipule shapes, and fruit type. The placentas in *Burttdavya* and *Sarcocephalus* are attached to the middle of the septum, while they are attached to the upper third in *Nauclea* (Ridsdale 1975, 1978a). *Burttdavya* has linear-oblong to slightly bilobed placentas, while they are discoidal in *Sarcocephalus*, and Y-shaped in *Nauclea*. Both *Nauclea* and *Sarcocephalus* have multiple fruits, but *Sarcocephalus* can be distinguished by the deltoid or short stipules, while *Nauclea* has ovate, elliptic, or obovate stipules. *Sarcocephalus* is also distinct by having obtuse to emarginate or shortly bilobed stipule apices and calyx lobes prolonged by small appendages rather than large stipules and corolla lobes without appendages as in *Nauclea*. *Burttdavya* bears infructescences composed of indehiscent, simple fruits without exocarps. *Neolamarckia* is distinct by its indehiscent, free fruits, the placentae are branched and attached to upper third of the septa, and the ovaries split into two locules by the false septa in their upper parts. The genus has previously been shown to be sister to the rest of Naucleinae (Razafimandimbison and Bremer 2002), consistent with our results. Both *Nauclea* and *Sarcocephalus* have previously been supported as monophyletic (Razafimandimbison and Bremer 2002; Wikström et al. 2010; Manns and Bremer 2010).

Our analyses resolve *Nauclea* as biphyletic, with one Asian clade and one African clade. The African *Nauclea* clade is more closely related to *Burttdavya* and *Sarcocephalus* than to the Asian *Nauclea* clade (Fig. 1). As a result, the current generic circumscription of *Nauclea* sensu Ridsdale (1975) cannot be maintained.

There are at least three different possibilities to make *Nauclea* monophyletic. One is to transfer the African *Nauclea* to *Sarcocephalus*, and restrict *Nauclea* to include only the Asian *Nauclea* species. This would require no new combinations, but we have not been able to find any diagnostic synapomorphies to distinguish this *Nauclea* s. s. from *Sarcocephalus* s. l. The second alternative is to restrict *Nauclea* to include only the Asian species, describe a new genus to accommodate the African *Nauclea* species, and retain the generic status of *Burttdavya* and *Sarcocephalus*. We have not been able to find any morphological characters to distinguish these two lineages. The third scenario is to merge *Sarcocephalus* and *Burttdavya* in *Nauclea*. This broadly delimited *Nauclea* in easily distinguished from *Neolamarckia* by flattened terminal buds, multiple fruits (this latter absent in *Burttdavya*), and the lack of the false septa in their locules. Accordingly we here include *Burttdavya* and *Sarcocephalus* in a broadly delimited *Nauclea*. This requires one new combination.

Taxonomic Treatment

Based on this study we propose new generic limits of Naucleeae, reducing the number of genera from 26 to 17. Accordingly, we make five new combinations, two lectotypifications, and formally put the genera *Fleroya* Y. F. Deng and *Hallea* J.-F. Leroy as synonyms of *Mitragyna* Korth. Only taxa affected by the taxonomic and nomenclatural changes are presented here; a complete list of species and synonymous taxon names can be seen in Ridsdale (1978a) for *Adina* and *Nauclea,* Ridsdale (1978a) and Deng (2007) for *Mitragyna,* and Stoffelen et al. (1996) for *Corynanthe.*

Adina Salisb., Parad. Lond. pl. 115. 1807.—TYPE: *Adina globiflora* Salisb. = *Adina pilulifera* Franch. ex Drake.

Metadina Bakh.f., Taxon 19: 472. 1970, syn. nov.—TYPE: *Metadina trichotoma* (Zoll. & Moritzi) Bakh.f. = *Adina trichotoma* (Zoll. & Moritzi) Benth & Hook. f. ex B. D. Jacks.

Adinauclea Ridsdale, Blumea 24: 349. 1978, syn. nov.—TYPE: *Adinauclea fagifolia* (Teijsm. & Binn. ex Havil.) Ridsdale = *Adina fagifolia* (Teijsm. & Binn. ex Havil.) Valeton ex Merr.

Haldina Ridsdale, Blumea 24: 360. 1978, syn. nov.—TYPE: *Haldina cordifolia* (Roxb.) Ridsdale = *Adina cordifolia* (Roxb.) Hook. f. ex B. D. Jacks.

Pertusadina Ridsdale, Blumea 24: 353. 1978, syn. nov.—TYPE: *Pertusadina eurhyncha* (Miq.) Ridsdale = *Adina eurhyncha* (Miq.) Å. Krüger & Löfstr.

1. Adina cordifolia (Roxb.) Brandis., Forest Fl. N. W. India 263. 1874. *Haldina cordifolia* (Roxb.) Ridsdale, Blumea 24: 361 (1978).—TYPE: INDIA. *Roxburgh s. n.* (holotype: Herb. Smith 316/5, LINN!).

2. **Adina eurhyncha** (Miq.) Å. Krüger & Löfstr. comb. nov. *Uncaria eurhyncha* Miq., Fl. Ned. Ind., Eerste Bijv. 3: 539. 1861. *Pertusadina eurhyncha* (Miq.) Ridsdale, Blumea 24: 354. 1978.—TYPE: INDONESIA. *Teijsmann s. n.* (syntypes: K, L *n.v.*).

Representative Specimens Examined—BORNEO. Teijsmann s. n. (K). SUMATRA. Teijsmann s. n. (K).

3. Adina fagifolia (Teijsm. & Binn. ex Havil.) Valeton ex Merr. Interpr. Herb. Amboin. 481. 1917. *Adinauclea fagifolia* (Teijsm. & Binn. ex Havil.) Ridsdale, Blumea 24: 350. 1978.—TYPE: INDONESIA. *Teijsmann s. n.* (holotype: L! digital image seen, isotype: BO).

4. **Adina malaccensis** (Ridsdale) Å. Krüger & Löfstr. comb. nov. *Pertusadina malaccensis* Ridsdale, Blumea 24: 356 1978.—TYPE: MALAYSIA. *SFN (Henderson) 23813* (lectotype: K! digital image seen, designated here, isotypes: A, BK, BO, K!).

Nomenclatural Notes—The holotype in L was lost at sea when it was sent on a loan (Ridsdale 2007). We select

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one of the isotypes currently housed at K as lectotype. A photocopy of the holotype is available at L but is inadequate as a holotype.

5. Adina metcalfii Merr. ex H. L. Li. J. Arnold Arbor. 24: 454. 1943.—TYPE: CHINA. *W. T. Tsang 27683* (holotype: A! digital image seen, isotype: IBSC).

Adina hainanensis F. C. How, Sunyatsenia 6: 240, f. 29. 1946. *Pertusadina hainanensis* (F. C. How) Ridsdale, Blumea 24: 354. 1978. *Pertusadina metcalfii* (Merr. ex H. L. Li) Y. F. Deng & C. M. Hu, Blumea 51: 559. 2006.—TYPE: CHINA. *How 73659* (holotype: IBSC *n. v.*).

6. Adina multifolia Havil., J. Linn. Soc. Bot. 33: 45. 1897. *Metadina multifolia* (Havil.) Ridsdale, Gard. Bull. Singapore 25: 250. 1970. *Pertusadina multifolia* (Havil.) Ridsdale, Blumea 24: 356. 1978.—TYPE: PHILIPPINES. *Vidal 2948* (holotype: K! digital image seen).

7. Adina racemosa (Sieb. & Zucc.) Miq. Ann. Mus. Bot. Lugduno-Batavi 4: 184. 1890. *Sinoadina racemosa* (Sieb. & Zucc.) Ridsdale syn. nov. Blumea 24: 351. 1978—TYPE: JAPAN. *Siebold 601* (holotype: L, isotype: K! digital image seen).

8. Adina trichotoma (Zoll. & Moritzi) Benth & Hook. f. ex B. D. Jacks., Index Kew. 1: 43. 1893. *Metadina trichotoma* (Zoll. & Moritzi) Bakh. f., Taxon 19: 472. 1970.—TYPE: INDONESIA. *Zollinger 613* (holotype: L!, isotype: K! digital images seen).

Corynanthe Welw. Trans. Linn. Soc. London 27: 37. 1869.—TYPE: *Corynanthe paniculata* Welw.

Pausinystalia Pierre, Actes Soc. Linn. Bordeaux 61: 130. 1906. syn. nov.—TYPE: *Pausinystalia johimbe* (K. Schum.) Pierre = *Corynanthe johimbe* K. Schum.

Pseudocinchona A. Chev. ex Perrot, Compt. Rend. Hebd. Séances Acad. Sci. 148: 1466; 1909. syn. nov.—TYPE: *Pseudocinchona africana* A. Chev. ex Perrot = *Corynanthe pachyceras* K. Schum.

1. Corynanthe brachythyrsus K. Schum., Notizbl. Bot. Gart. Berlin-Dalhem 3: 95. 1901. *Pausinystalia brachythyrsum* (K. Schum.) W. Brandt, Arch. Pharm. 260: 66. 1922. *Pausinystalia macroceras* f. *brachythyrsum* (K. Schum.) N. Hallé, Fl. Gabon 12: 71. 1966.—TYPE: CAMEROON. *Zenker 1746* (holotype: B†, lectotype: P! digital image seen, designated here, isotypes: BR!, WAG! digital image seen).

Nomenclatural Notes—The holotype at B was destroyed and we select the isotype at P as lectotype.

2. Corynanthe johimbe K. Schum., Notizbl. Bot. Gart. Berlin-Dalhem 3: 95. 1901. *Pausinystalia johimbe* (K. Schum.) Pierre, Act. Soc. Linn. Bordeaux 61: 130. 1906.—TYPE: CAMEROON. *Zenker 2883* (neotype: P, isotypes: WAG, BR! digital image seen).

Nomenclatural Notes—The neotype at P was designated by N. Hallé, Fl. Gabon 12: 68. 1966.

3. Corynanthe lane-poolei Hutch., Kew Bull., 98. 1912. *Pausinystalia lane-poolei* (Hutch.) Hutch ex Lane-Poole, Trees Shrubs, Herbs & Climbers of Sierra Leone 74 1916.—TYPE: SIERRA LEONE. *Lane-Poole 46* (holotype: K! digital image seen).

3A. **Corynanthe lane-poolei** Hutch. subsp. **ituriense** (De Wild.) Å. Krüger & Löfstr. comb. nov. *Pausinystalia lane-poolei* subsp. *ituriense* (De Wild.) Stoffelen & Robbr., Bot. J. Linn. Soc. 120: 310. 1996. *Pausinystalia ituriense* De Wild., Ann. Soc. Sci. Bruxelles 42: 176. 1922.—TYPE: ZAIRE (Democratic republic of the Congo). *Bequaert 2543* (holotype: BR! digital image seen).

4. Corynanthe macroceras K. Schum. Bot. Jahrb. Syst. 23: 424. 1896. *Pausinystalia macroceras* (K. Schum.) Pierre, Actes Soc. Linn. Bordeaux, 61: 130. 1906.—TYPE: CAMEROON. *Staudt 20* (syntypes: B†, K! digital image seen) and *Zenker & Staudt 650* (syntypes: B†, K).

5. Corynanthe mayumbensis (R. D. Good) N. Hallé, Fl. Gabon 12: 64. 1966. *Pausinystalia mayumbensis* R. D. Good, J. Bot. [London], 64, suppl. 2: 1. 1926. *Pseudocinchona mayumbensis* (R. D. Good) Raym.-Hamet, Compt. Rend. Hebd. Séances Acad. Sci. 212: 305. 1941.—TYPE: ANGOLA. *Gossweiler 6973* (holotype: BM, isotype: LISC! digital image seen).

6. **Corynanthe talbotii** (Wernham) Å. Krüger & Löfstr. comb. nov. *Pausinystalia talbotii* Wernham in A. B. Rendle et al. Cat. Pl. Oban [Cat. Talbots Nigerian pl.]*:* 40. 1913.—TYPE: NIGERIA. *Talbot 1493* (holotype: K!).

Pseudocinchona mobiusii (W. Brandt) A. Chev., Compt. Rend. Hebd. Séances Acad. Sci. 182: 1403. 1926.—TYPE: CAMEROON. *Zenker 2435* (holotype: B†, isotypes: BR!, K!, WU!).

Mitragyna Korth. Observ. Naucl. Indic. 19. 1839, nom. cons.—TYPE: *Mitragyna parvifolia* (Roxb.) Korth., typus cons.

Paradina Pierre ex Pit. Fl. Indo-Chine [P. H. Lecomte et al.] 3: 39. 1922.—TYPE: *Paradina hirsuta* (Havil.) Pit. = *Mitragyna hirsuta* Havil.

Hallea J.-F. Leroy, Adansonia n. s. 12: 66. 1975, nom. illeg., *Fleroya* Y. F. Deng, Taxon 56: 247. 2007, replacement name. syn. nov.—TYPE: *Hallea stipulosa* (DC.) J.-F. Leroy. = *Mitragyna stipulosa* (DC.) Kuntze.

1. Mitragyna ledermannii (K. Krause) Ridsdale, Blumea 24: 68. 1978. *Adina ledermannii* K. Krause, Bot. Jahrb. Syst. 57: 27. 1920. *Hallea ledermannii* (K. Krause) Verdc., Kew Bull. 40: 508. 1985. *Fleroya ledermanni* (K. Krause) Y. F. Deng., Taxon 56: 247. 2007.—TYPE: CAMEROON. *Zenker 1619* (neotype: BR! designated here). *Mitragyna ciliata* Aubrév. & Pellegr., Bull. Soc. Bot. France 83: 36. 1936. *Hallea ciliata* (Aubrév. & Pellegr.) J.-F. Leroy, Adansonia n. s., 15: 66. 1975.—TYPE: IVORY COAST. *Aubréville 877* (lectotype: P! digital image seen).

Nomenclatural Notes—The holotype for *Mitragyna ledermannii*, *Ledermann 2402* (B), was destroyed and a neotype is needed. No other specimen was cited in the original description and no duplicates of this collection have been located. The *Zenker, G. 1619* collection is a good representative of the species based on the description in the protologue. The lectotype for *Mitragyna ciliata* at P was designated by N. Hallé, Fl. Gabon 12: 37. 1966.

2. Mitragyna rubrostipulata (K. Schum.) Havil., J. Linn. Soc. Bot 33: 73. 1897. *Hallea rubrostipulata* (K. Schum.) J.-F. Leroy, Adansonia n.s., 15: 66. 1975. *Fleroya rubrostipulata* (K. Schum.) Y. F. Deng, Taxon 56: 247. 2007.—TYPE: CONGO. *Volkens 1583* (lectotype: K! digital image seen).

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Nomenclatural Notes—The lectotype at K was designated by Haviland, J. Linn. Soc. Bot 33: 73. 1897.

3. Mitragyna stipulosa (DC.) Kuntze, Revis. Gen. Pl. 1: 289. 1891. *Hallea stipulosa* (DC.) J.-F. Leroy, Adansonia n. s. 15: 66. 1975. *Fleroya stipulosa* (DC). Y. F. Deng, Taxon 56: 247. 2007.—TYPE: GAMBIA. *Leprieur s. n.* (1829) (holotype: P! digital image seen).

Nauclea L. Sp. Pl. ed. 2: 243. 1762.—TYPE: *Nauclea orientalis* (L.) L.

Sarcocephalus Afzel. ex R.Br. in J.H. Tuckey, Narr. Exped. Zaire. 5:467. 1818, syn. nov.—TYPE: *Sarcocephalus esculentus* Afzel. ex Sabine = *Nauclea latifolia* Sm.

Burttdavya Hoyle, Hooker's., Icon. Pl.: 3318. 1939, syn. nov.—TYPE: *Burttdavya nyasica* Hoyle. = *Nauclea nyasica* (Hoyle) Å. Krüger & Löfstr.

1. Nauclea latifolia Sm. in A. Rees, Cycl. 24: n.°5.'1813. *Sarcocephalus latifolius* (Sm.) E. A. Bruce, Kew Bull. 2: 31. 1947.—TYPE: SIERRA LEONE. *Smeathman s. n.* (lectotype: BM! digital image seen).

Nomenclatural Notes—The lectotype at BM is an illustration based on the Smeathman s. n. (BM) collection. We have not been able to determine who designated the lectotype.

2. **Nauclea nyasica** (Hoyle) Å. Krüger & Löfstr. comb. nov. *Burttdavya nyasica* Hoyle, Hooker's Icon. Pl. 34: t. 3318. 1936.—TYPE: MALAWI. *Townsend 23* (holotype: K!).

3. Nauclea pobeguinii (Hua ex Pobég.) Merr., J. Wash. Acad. Sci. 5: 536. 1915. *Sarcocephalus pobeguinii* Hua ex Pobég, Ess. Fl. Guin. Fr. 313. 1906.—TYPE: GUINEA. *Pobéguin 433* (holotype: P! digital image seen).

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Appendix 1. Specimens investigated. Taxon voucher information and Genbank accession numbers are given in the form [Taxon, voucher information, nrETS, nrITS, *ndhF*, *rbcL*, *rps16*, *trnT-F*;]. New sequences, generated for this study are indicated with asterisks (*), sequences missing from the dataset are marked with hyphens (-). When only previously published sequences were included for the taxon, voucher information is marked with a plus sign (+) and the original publication is given in superscript after the GenBank accession number: [1]Razafimandimbison and Bremer (2002); [2]Manns and Bremer (2010); [3]Wikström et al. (2010); [4]Razafimandimbison et al. (2005); [5]Bremer et al. (1999); [6]Bremer et al. (1995); [7]Andersson and Rova (1999); [8]Kainulainen et al. (2013); [9]Kainulainen et al. (2010); [10]Andreasen et al. (1999); [11]Bremer and Eriksson (2009); [12]Rydin et al. (2008); [13]Novotny et al. (2002); [14]Kainulainen et al. (2009); [15]Rova et al. (2002); [16]Aoki et al. (2004); [17]Delprete and Cortés (2004).

Adina pilulifera Franch. ex Drake. +, -, AJ346885[1], GQ852165[2], AJ346964[1], GQ852366[2], AJ414548[1]. ***Adina pubicostata*** Merr. *Liu Biao 186* (MO), KC737581*, KC737621*, KC737667*, KC737729*, KC737778*, KC737828*. ***Adina rubella*** Hance. *MacDougal 5082* (MO), KC737582*, AJ346856, KC737695*, AJ346965, KC737779*, AJ346910. ***Adinauclea fagifolia*** (Teijsm. & Binn ex Havil.) Ridsdale. +, FN376383[3], AJ346901[1], GQ852164[2], AJ346966[1], GQ852365[2], AJ346911[1]. ***Breonadia salicina*** (Vahl) Hepper & J.R.I.Wood. +, AJ812070[4], AJ346857[1], GQ852178[2], AJ346967[1], GQ852377[2], AJ346912[1]. ***Breonia boivinii*** Havil. *Razakamalala 6286* (S), -, KC737628*, KC737697*, KC737734*, KC737789*, KC737832*. ***Breonia capuronii*** Razafim. *Bremer et al. 5179* (S), KC737584*, KC737622*, KC737696*, KC737730*, KC737781*, KC737829*. ***Breonia chinensis*** (Lam.) Capuron. +, FN376384[3], AJ346858[1], GQ852291[2], AJ346968[1], GQ852375[2], AJ346913[1]. ***Breonia decaryana*** Homolle. +, AJ812072[4], AJ346859[1], GQ852177[2], AJ346969[1], GQ852376[2], AJ346914[1]. ***Breonia fragifera*** Capuron ex Razafim. *Ranirison 776* (G), FN376385, KC737623*, KC737670*, FN376373, KC737782*, FN376377. ***Breonia havilandiana*** Homolle. *Razafimandimbison 389* (MO), FN376386, AJ346860, KC737671*, AJ346970, KC737783*, AJ346915. ***Breonia louvelii*** Homolle. *Razafimandimbison 358* (MO), KC737585*, KC737624*, KC737672*, KC737731*, KC737784*, -.

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Breonia perrieri Homolle. *Razafimandimbison 273* (MO), FN376388, AJ346862, KC737673*, AJ346972, KC737785*, AJ346917. ***Breonia sambiranensis*** Razafim. *Razakamalala 6222* (S), -, KC737627*, KC737676*, KC737733*, KC737788*, KC737831*. ***Breonia sphaerantha*** (Baill.) Homolle ex Ridsdale. *Ranirison 532* (G), FN376389, KC737625*, KC737676*, FN376374, KC737786*, FN376378. ***Breonia tayloriana*** Razafim. *Razafimandimbison et al. 1176* (S), KC737586*, KC737626*, KC737675*, KC737732*, KC737787*, KC737830*. ***Burttdavya nyasica*** Hoyle. +, FN376390[3], AJ346863[1], GQ852179[2], AJ346973[1], GQ852378[2], AJ346918[1]. ***Cephalanthus glabratus*** (Spreng.) K. Schum. *Vanni et al. 1431* (GB), KC737571*, KC737615*, KC737654*, KC737716*, KC737762*, KC737822*. ***Cephalanthus natalensis*** Oliv. +, FN376391[3], AJ346906[1], GQ852182[2], Y18711[5], GQ852380[2], AJ414549[1]. ***Cephalanthus occidentalis*** L. +, AJ812074[4], AJ346883[1], AJ236288[5], X83629[6], AF004033[7], AJ346955[1]. ***Cephalanthus salicifolius*** Humb. & Bonpl. +, AJ812075[4], AJ346886[1], GQ852183[2], AJ346975[1], GQ852381[2], AJ346920[1]. ***Cephalanthus tetrandrus*** (Roxb.) Ridsdale & Bakh.f. *Ye 2485* (MO), KC737572*, KC737616*, KC737655*, KC737717*, KC737763*, - ***Chalepophyllum guyanense*** Hook. f. +, -, AY555120[17], -, HM164159[8], HM164201[8], HM164316[8]. ***Cinchona pubescens*** Vahl, +, AJ812031[4], AJ224838[10], AJ235843[10], X83630[6], AF004035[7], AJ346963[1]. ***Corynanthe mayumbensis*** (R. D. Good) N. Hallé. +, AJ812078[4], AJ346864[1], GQ852296[2], AJ346976[1], GQ852434[2], AJ346921[1]. ***Corynanthe pachyceras*** K. Schum. *Jongkind and Abbiw 1910* (UPS), FN376402, AJ346865, KC737677*, AJ346977, KC737790*, AJ346922. ***Corynanthe paniculata*** Welw. *Mukwimuvi 34* (BR), KC737587*, AJ346887, KC737678*, AJ346978, KC737791*, AJ346923. ***Dendrosipanea spigeloides*** Ducke. +, -, AY555121[17], FJ871943[9], HM164162[8], FJ884627[9], FJ948360[9]. ***Emmenopterys henryi*** Oliv. *Robbrecht s. n.* (UPS), KC878470*, FJ984985, AJ236294, Y18715, AM117302, AF152637. ***Fleroya rubrostipulata*** (K. Schum.) Y. F. Deng. *Razafimandimbison 289* (MO), KC737575*, AJ346895, GQ852239, X83640, AY538429, AJ346957. ***Fleroya stipulosa*** (DC.) Y. F. Deng. *Razafimandimbison 295* (MO), -, AJ346868, GQ852240, AJ346981, KC737767*, AJ346927. ***Gyrostipula comoriensis*** J.-F. Leroy, +, FN376392[3], AJ346866[1], GQ852215[2], AJ346979[1], AM117312, AJ346925. ***Gyrostipula foveolata*** (Capuron) J.-F. Leroy. +, FN376393[3], AJ346867[1], GQ852216[2], AJ346980[1], GQ852399[2], AJ346926[1]. ***Haldina cordifolia*** (Roxb.) Ridsdale +, FN376394[3], AJ346884[1], GQ852217[2], X83639[6], GQ852400[2], AJ346956[1]. ***Hymenodictyon biafranum*** Hiern. *van der Burgt 90* (WAG), KC737553*, KC737599*, KC737638*, KC737700*, KC737744*, KC737808*. ***Hymenodictyon decaryi*** Homolle. *Razafimandimbison 528* (UPS), KC737554*, KC737600*, KC737639*, KC737701*, KC737745*, KC737809*. ***Hymenodictyon flaccidum*** Wall. +, -, AJ346904[1], -, -, -, AJ347014[1], -, -. ***Hymenodictyon floribundum*** (Hochst. & Steud.) B.L. Rob. +, FN376405[3], AJ346905[1], EU145411[12], AJ347015[1], AF004058[7], GQ852517[2]. ***Hymenodictyon glabrum*** (Cavaco) Razafim. & B. Bremer. *Razafimandimbison and Bremer 500* (UPS), KC737556*, KC737601*, -, KC737702*, KC737747*, KC737810*. ***Hymenodictyon leandri*** Cavaco. *Krüger and Razafimandimbison 97* (S), KC737557*, KC737602*, KC737641*, KC737703*, KC737748*, KC737811*. ***Hymenodictyon louhavate*** Homolle. *Razafimandimbison and Bremer 502* (UPS), KC737558*, KC737603*, KC737642*, KC737704*, KC737749*, KC737812*. ***Hymenodictyon madagascaricum*** Baill. ex Razafim. & B. Bremer. *Kårehed et al. 245* (UPS), KC737559*, KC737604*, KC737643*, KC737705*, KC737750*, KC737813*. ***Hymenodictyon occidentale*** Homolle. *Razafimandimbison and Bremer 501* (UPS), KC737560*, KC737605*, KC737644*, KC737706*, KC737751*, KC737814*. ***Hymenodictyon orixense*** (Roxb.) Mabb. *Davis 4087* (P), KC737561*, KC737606*, KC737645*, KC737707*, KC737752*, KC737815*. ***Hymenodictyon parvifolium*** subsp. ***parvifolium*** Oliv. *Bremer 3809* (UPS), FN376407, -, KC737754*, AJ347016, KC737647*, FN376382. ***Hymenodictyon parvifolium*** subsp. ***scabrum*** (Stapf) Verdc. *Luke 8358* (UPS), KC737562*, KC737607*, KC737646*, KC737708*, KC737753*, KC737816*. ***Hymenodictyon parvifolium*** subsp. ***scabrum*** (Stapf) Verdc. *Pawek 13438* (MO), KC737563*, KC737608*, KC737648*, KC737709*, KC737755*, KC737817*. ***Hymenodictyon perrieri*** Drake. *Razafimandimbison and Ravelonaviro 663* (UPS), KC737564*, KC737609*, KC737649*, KC737710*, KC737756*, -. ***Hymenodictyon septentrionale*** Cavaco. *Kårehed et al. 229* (UPS), KC737565*, KC737610*, KC737650*, KC737711*, KC737757*, KC737818*. ***Hymenodictyon seyrigii*** Cavaco. *Razafimandimbison 536a* (S), KC737566*, KC737611*, KC737651*, KC737712*, KC737758*, KC737819*. ***Hymenodictyon*** sp. nov. *Bremer et al. 5172* (S), KC737568*, KC737613*, KC737691*, KC737714*, KC737760*, KC737819*. ***Hymenodictyon tsingy*** Razafim. & B. Bremer. *Kårehed et al. 249* (UPS), KC737567*, KC737612*, KC737652*, KC737713*, KC737659*, KC737820*. ***Janotia macrostipula*** (Capuron) J.-F. Leroy. +, AJ812071[4], AJ346869[1], GQ852229[2], AJ346982[1], AM117322[11], AJ346928[1]. ***Ludekia bernardoi*** (Merr.) Ridsdale. *Sulit 22889* (MO), KC737598*, KC737637*, KC737690*, KC737743*, KC737806*, -. ***Ludekia borneensis*** Ridsdale. +, AJ812069[4], AJ346870[1], GQ852230[2], AJ346983[1], GQ852407[2], AJ346962[1]. ***Metadina trichotoma*** (Zoll. & Moritzi) Bakh.f. + AJ812077[1], AJ346871[1], -, AJ346984[1], GQ852411[2], AJ346930[1]. ***Mitragyna diversifolia*** (Wall. ex G. Don) Havil. *Puff 990725-1/1* (WU), AJ812079, AJ346872, KC737656*, AJ346985, KC737764*, AJ346931. ***Mitragyna inermis*** (Wild.) Kuntze. *Lorence 8376* (PTBG), KC737573*, AJ346873, GQ852237, AJ346986, GQ852412, AJ346932. ***Mitragyna parvifolia*** (Roxb.) Korth. *Fagerlind and Klackenberg 400* (S), KC737574*, KC737617*, KC737657*, KC737718*, KC737765*, -. ***Mitragyna rotundifolia*** (Roxb.) Kuntze. +, FR731995[3], AJ346874[1], GQ852238[2], AJ346987[1], GQ852413[2], AJ346933[1]. ***Mitragyna speciosa*** (Korth.) Havil. *Löfstrand 1* (S), KC737576*, KC737618*, KC737658*, KC737719*, KC737766*, KC737823*. ***Mitragyna tubulosa*** (Arn.) Kuntze. *Fagerlind and Klackenberg 237* (S), KC737577*, KC737619*, KC737659*, KC737720*, KC737768*, -. ***Mussaenda erythrophylla*** Schumach. & Thonn. +, -, AJ224823[10], AJ130836[10], X83652[6], EU145493[12], EU145535[12]. ***Myrmeconauclea stipulacea*** Ridsdale. *Bearman 9770* (NY), AJ812066, AJ821879, KC737660*, KC737721*, KC737769*, KC737824*. ***Myrmeconauclea strigosa*** (Korth) Merr. +, AJ812067[4], AJ821881[4], GQ852242[2], AJ346989[1], GQ852415[2], AJ346934[1]. ***Nauclea diderichii*** (De Wild.) Merr. *Razafimandimbison 297* (MO), KC737588*, AJ346855, GQ852243, AJ346994, KC737793*, AJ346935. ***Nauclea officinalis*** (Pierre ex Pit.) Merr. & Chun. *Kessler et al. 1348* (L), KC737589*, KC737629*, KC737679*, KC737735*, KC737794*, -. ***Nauclea orientalis*** (L.) L. *Bremer 3001* (UPS), FN376396, AJ346897, KC737680*, X83653, -, AJ346958. ***Nauclea subdita*** (Korth.) Steud. +, -, AJ346876[1], -, AJ346996[1], -, AJ346936[1]. ***Nauclea tenuiflora*** (Havil.) Merr. *Takeuchi W. 7145* (MO), KC737591*, KC737630*, KC737698*, KC737736*, KC737796*, KC737833*. ***Nauclea vanderguchtii*** (De Wild.) E.M.A.Petit. *Razafimandimbison 296* (MO), AJ812083, KC737631*, KC737699*, KC737737*, KC737797*, -. ***Neolamarckia cadamba*** (Roxb.) Bosser. *Ridsdale 2247* (L), -, KC737632*, KC737682*, KC737738*, KC737798*, KC737834*. ***Neonauclea brassii*** S. Moore. +, FN376398[3], AJ346879[1], GQ852244[2], AJ346991[1], GQ852416[2], AJ346939[1]. ***Neonauclea celebica*** (Havil.) Merr. *Moog 128* (L), AJ812051, AJ821870, KC737661*, KC737722*, KC737770*, KC737825*. ***Neonauclea clemensiae*** Merr. & L.M.Perry. +, AJ812034[4], AJ346898[1], GQ852246, AJ318450[13], AJ320081[13], AJ346940[1]. ***Neonauclea cyrtopoda*** (Miq.) Merr. *Moog 101* (L), AJ812058, AJ821869, KC737692*, KC737723*, KC737771*, -. ***Neonauclea forsteri*** (Seem. ex Havil.) Merr. *Lorence 8668* (PTBG), AJ812033, AJ346880, KC737662*, AJ346992, KC737772*, AJ346941. ***Neonauclea gigantea*** (Valeton) Merr. *Moog 030* (L), AJ812048, AJ821867, KC737663*, KC737724*, KC737773*, KC737826*. ***Neonauclea glabra*** (Roxb.) Bakh.f. & Ridsdale. *Brass 25477* (S), AJ812045, AJ821863, KC737693*, KC737725*, KC737774*, -. ***Neonauclea longipedunculata*** Merr. *Ridsdale 2468* (L), AJ812052, AJ346881, KC737664*, AJ346993, KC737775*, AJ346942. ***Neonauclea paracyrtopoda*** Bakh.f. & Ridsdale. *Moog 071* (L), AJ812047, AJ821865, KC737665*, KC737726*, KC737776*, KC737827*. ***Neonauclea pseudocalycina*** Ridsdale. *Moog 067* (L), AJ812038, AJ821855, KC737694*, KC737727*, KC737777*, -. ***Ochreinauclea maingayi*** (Hook.f.) Ridsdale. *Puff 960424-1/2* (WU), KC737579*, KC737620*, GQ852249, AJ346997, GQ852419, AJ346943. ***Paracorynanthe antankarana*** Capuron ex J.-F. Leroy. *Gautier 4483* (G), KC737659*, GQ852148, GQ852253, AJ347017, GQ852423, GQ852517. ***Paracoryhnanthe uropetala*** Capuron. *Leandri et al. 2069* (TEF), KC737570*, KC737614*, KC737653*, KC737715*, KC737761*, -. ***Pausinystalia johimbe*** (K. Schum.) Pierre. +, FN376399[3], AJ346888[1], GQ852254[2], AJ346998[1], GQ852424[2], AJ346945[1]. ***Pausinystalia lane-poolei*** subsp. ***iturense*** (De Willd) Stoff. & Robbr. *Hart 1350* (BR), -, AJ346889, -, AJ346999, KC737792*, AJ346946. ***Pausinystalia macroceras*** (K. Schum.) Pierre. *Hart 573* (BR), AJ812076, AJ346890, GQ852255, AJ347000, GQ852425, AJ346944. ***Pertusadina eurhyncha*** (Miq.) Ridsdale. +, FN376400[3], AJ346891[1], GQ852256[2], AJ347001[1], GQ852426[2], AJ346947[1]. ***Pertusadina malaccensis*** Ridsdale. +, FN376401[3], AJ346893[1], GQ852257[2], AJ347003[1], GQ852427[2], AJ346949[1]. ***Pertusadina metcalfii*** (Merr. ex H. L. Li) Y. F. Deng & C.M.Hu. *Guizhou 2220* (NY), KC737583*, AJ346892, KC737669*, AJ347002, KC737780*, AJ346948. ***Posoqueria latifolia*** (Rudge) Schult. +, -, AJ224828[10], AM949855[14], GQ981837[2], AF242998[15], AF152680[15.] ***Sarcocephalus latifolius*** (Sm.) E.A.Bruce. +, FN376403[3], AJ346899[1], GQ852274[2], X83629[6], AF004080 (Andersson and Rova 1999), AJ346960[1]. ***Sarcocephalus pobeguinii*** Hua ex Pobég. *Razafimandimbison 303* (MO), KC737592*, AJ347005, KC737683*, AJ347005, KC737799*, AJ346950. ***Sinoadina racemosa*** (Siebold & Zucc.) Ridsdale. *Jer-Ming Hu and Wang 859* (MO), KC737578*, -, GQ852278, AJ347004, GQ852443, AJ346961. ***Uncaria africana*** G. Don. *Razafimandimbison 304* (MO), FN376404, AJ414545, KC737684*, AJ347006, KC737800*, AJ346951. ***Uncaria guianensis*** (Aubl.) J. F. Gmel. *Taylor 12075* (MO), AJ812081, AJ414546,

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KC737685*, AJ347007, KC737801*, AJ346952. ***Uncaria homomalla*** Miq. *Munzinger 177* (P), KC737593*, KC737633*, KC737686*, KC737739*, KC737802*, KC737835*. ***Uncaria lancifolia*** Hutch. *Razafimandimbison et al. 713* (S), KC737595*, KC737634*, KC737687*, KC737740*, KC737803*, KC737836*. ***Uncaria lanosa*** Wall. *Razafimandimbison et al. 766* (S), KC737596*, KC737635*, KC737688*, KC737741*, KC737804*, KC737837*. ***Uncaria rhynchophylla*** (Miq.) Miq. ex Havil. +, AJ812080[4], AJ346900[1], GQ852289[2], X83669[6], AB178637[16], AJ346959[1]. ***Uncaria*** aff. ***scandens*** (Sm.) Hutch. *Razafimandimbison et al. 768* (S), KC737597*, KC737636*, KC737689*, KC737742*, KC737805*, KC737838*. ***Uncaria tomentosa*** (Wild. ex Schult.) DC. *Andersson et al. 2038* (GB), KC737594*, GQ852159, GQ852290, GQ852363, GQ852450, GQ852564.

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