

SYSTEMATICS AND PHYLOGENY

Molecular-based assessments of tribal and generic limits and relationships in Rubiaceae (Gentianales): Polyphyly of Pomazoteae and paraphyly of Ophiorrhizeae and *Ophiorrhiza*

Sylvain G. Razafimandimbison¹  & Catarina Rydin^{2,3} 

¹ Department of Botany, Swedish Museum of Natural History, Box 50007, 10405 Stockholm, Sweden

² Department of Ecology, Environment and Plant Sciences, Stockholm University, 10691 Stockholm, Sweden

³ The Bergius Foundation, The Royal Swedish Academy of Sciences, 10405 Stockholm, Sweden

Address for correspondence: Sylvain G. Razafimandimbison, sylvain.razafimandimbison@nrm.se

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Abstract Circumscriptions of the Australasian tribes Ophiorrhizeae and Pomazoteae (Rubiaceae) as well as their generic relationships and limits have long remained unsettled. These tribes were originally delimited by Bremekamp based on the lack of raphides and testa cell patterns (thick- versus thin-walled testa cells, respectively). Some authors have synonymized the two or treated Pomazoteae as a synonym of other tribes despite the fact that the matter has never been sufficiently addressed. We performed molecular phylogenetic analyses of Ophiorrhizeae sensu Bremer & Manen (i.e., comprising *Coptophyllum*, *Lerchea*, *Neurocalyx*, *Ophiorrhiza*, *Spiradiclis* and *Xanthophyllum*) based on sequence data from four plastid and two nuclear markers. *Coptophyllum* (= *Pomazota*, type of Pomazoteae), *Lerchea* and *Xanthophyllum* together with seven other genera, were traditionally classified in Pomazoteae. We also investigated for the first time the two Pomazoteae genera *Keenania* and *Leptomischus*. Our analyses resolved *Leptomischus* as sister to the Rubioideae tribe Argostemmatae and we here formally classify this genus in that tribe. Ophiorrhizeae sensu Bremer and Manen is paraphyletic with respect to *Keenania*. Pomazoteae is polyphyletic, with most of its genera (including *Coptophyllum*) belonging in Ophiorrhizeae. Its tribal status cannot be held. Testa cell patterns are evolutionarily labile, and seem to have no phylogenetic value at tribal level. Our study strongly supports a broadly delimited Ophiorrhizeae that contains mostly suffrutescent herbs. Within Ophiorrhizeae as here defined, *Neurocalyx* is sister to the rest of the tribe, followed by *Xanthophyllum*. The *Coptophyllum-Lerchea* clade is sister to a large clade formed by *Keenania*, *Ophiorrhiza* and *Spiradiclis*. *Ophiorrhiza* is paraphyletic with respect to *Keenania* and *Spiradiclis*, and was resolved in two well-supported lineages, the *Ophiorrhiza-Keenania* and *Ophiorrhiza-Spiradiclis* lineages. Accordingly, we formally transferred all validly published names from *Keenania* and *Spiradiclis* to *Ophiorrhiza*, resulting in 40 new combinations and 15 new names.

Keywords *Keenania*; *Leptomischus*; Pomazoteae; *Spiradiclis*; systematics

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

■ INTRODUCTION

The pantropical, species-rich coffee family (Rubiaceae, Gentianales) contains about 13,000 species and 650 genera, which are currently classified in 65 tribes and 2 subfamilies (Robbrecht & Manen, 2006; Rydin & al., 2017). Circumscriptions of the majority of the tribes of Rubiaceae have been assessed using monophyly as a primary criterion (e.g., Backlund & Bremer, 1998) and molecular-based phylogenies (e.g., Andersson & Rova, 1999; Bremer & Manen, 2000; Robbrecht & Manen, 2006). Many of the traditionally recognized tribes were shown to be para- or polyphyletic and new circumscriptions were proposed to render them monophyletic (e.g., Bremer & Eriksson, 2009; Groeninckx & al., 2010; Razafimandimbison & al., 2014). New tribes have been described (e.g., Dunnieae C.Rydin & B.Bremer – Rydin & al., 2009a; Hymenodictyeae Razafim. & B.Bremer – Razafimandimbison

& Bremer, 2001; Palicoureeae Robbr. – Robbrecht & Manen, 2006). Few tribal names have been synonymized (e.g., Hedyotideae Cham. & Schldl. ex DC. merged into Spermaceae Cham. & Schldl. ex DC. – Bremer & Manen, 2000; Lathraeocarpeae Bremek. also merged into Spermaceae – Groeninckx & al., 2009) and some tribes have been resurrected (e.g., Mussaendeae Benth. & Hook.f. – Bremer & Thulin, 1998; Ixoreae A.Gray – Andreasen & Bremer, 2000). On the other hand, some tribes have never been assessed using molecular data and modern methods for phylogenetic inference. One such tribe is the Australasian Pomazoteae Bremek. ex S.P.Darwin (Bremekamp, 1952, 1966) whose type, *Coptophyllum* Ridl. (early synonym of *Pomazota* Korth.), was never included in any molecular phylogenetic study.

The present study addresses the circumscriptions and phylogenetic relationships in the poorly known, Australasian tribes Ophiorrhizeae Bremek. ex Verdc. and Pomazoteae, which

were originally proposed by Bremekamp (1952) to accommodate two groups of plants with peculiar testa cell patterns (see below) and without raphides. Bremekamp (1954) placed both tribes in his subfamily “Ophiorrhizoideae” Bremek. (not validly published) mainly based on the absence of raphides. The tribal names remained invalidly published until Verdcourt (1958) and Darwin (1976) provided their respective Latin diagnoses. Verdcourt (1958) and several other authors (e.g., Axelius, 1987; Robbrecht, 1988) correctly demonstrated the presence of raphides in members of Pomazoteae and Ophiorrhizeae (in particular *Ophiorrhiza* and *Spiradichlis*). Bremekamp (1966) changed his views on the subfamilial classification of Rubiaceae, giving the absence of raphides and testa cell patterns high taxonomic value for delimiting subfamilies. He viewed Ophiorrhizeae to be more closely related to the tribe Urophyllae Bremek. ex Verdc. than to Pomazoteae, as the two former tribes have thick-walled testa cells and were thought to lack raphides. As a result, Bremekamp (1966) transferred Ophiorrhizeae to his subfamily Urophyloideae Bremek. ex S.P. Darwin based on these two taxonomic characters. Ophiorrhizoideae became a synonym of Urophyloideae and remains invalidly published. The subfamily Pomazotoideae Bremekamp ex S.P. Darwin was proposed by Bremekamp (1966) to accommodate his Pomazoteae, which was characterized by the absence of raphides and thin-walled minutely dotted/granulate or coarsely tuberculate testa cells (Bremekamp, 1952). Pomazotoideae and Urophyloideae, all sensu Bremekamp (1954), were also invalid names because their author failed to provide Latin diagnoses. The names were later validly published by Darwin (1976). Robbrecht (1988, 1993) rejected Pomazotoideae and Urophyloideae as defined by Bremekamp (1966) and endorsed the inclusion of their respective members in subfamily Rubioideae based on the presence of raphides. This taxonomic decision has been supported by molecular data (e.g., Andersson & Rova, 1999; Bremer & Manen, 2000; Robbrecht & Manen, 2006) and is widely accepted by the Rubiaceae community.

Subsequent works have, however, repeatedly changed the circumscriptions of Pomazoteae and Ophiorrhizeae (see below) and some authors have even considered the names synonymous (e.g., Robbrecht, 1988; Bremer & Manen, 2000) or treated Pomazoteae as a synonym of other tribes. On the other hand, the phylogenetic value of testa cell patterns previously used for delimiting Ophiorrhizeae and Pomazoteae sensu Bremekamp (1952, 1966) has never been sufficiently addressed. Ophiorrhizeae as circumscribed by Bremekamp (1952, 1966) included the genera *Ophiorrhiza* L., *Spiradichlis* Blume and *Virectaria* Bremek. (Table 1) and was defined by thick-walled testa cells ornamented with warts and incorrectly by the lack of raphides. Bremekamp (1952) postulated a close relationship between *Ophiorrhiza* and *Spiradichlis* based on their habit (large-leaved herbs) and stipules (narrowly triangular or deeply bifid or fimbriate). This relationship was strongly supported by molecular data (Rydin & al., 2006, 2009a,b). However, the *rps16*-based phylogeny of Rubioideae resolved the type of *Spiradichlis*, *S. caespitosa* Blume, nested within

Ophiorrhiza (Rydin & al., 2006). This has raised questions on the monophyly of these two genera, which has not previously been tested. Verdcourt (1958) rejected Ophiorrhizeae sensu Bremekamp (1952, 1966) and excluded *Virectaria* from the tribe based on the lack of raphides and a number of distinct features such as capsular fruits with one of the valves attached to the rachis by a stiff pedicel and the other deciduous. The author classified the genus its own tribe, Virectarieae Verdc., which has recently been merged into the broadly delimited tribe Sabiceae (Khan & al., 2008; Zemagho & al., 2016) in subfamily Cinchonoideae Raf. sensu lato (s.l.). (Robbrecht & Manen, 2006; Rydin & al., 2017), based on molecular data.

Pomazoteae sensu Bremekamp (1952, 1966) originally contained about 52 species of erect herbs, subshrubs and shrubs, which are currently classified in five genera (see also Table 1): *Coptophyllum* (8 species, Bremekamp, 1947); *Lerchea* L. (10 species, Axelius, 1987); monospecific *Klossia* Ridl. and *Siderobombyx* Bremek.; and *Xanthophytum* Blume (32 species, Axelius, 1990). The author tentatively added the monospecific *Campanocalyx* Valetton and *Paedicalyx* Pit., *Keenania* Hook.f. (5 species, Govaerts & al., 2018), *Indopolysolenia* Bennet (as *Polysolenia* Hook.f., 1–2 species, Deb, 2001) and *Leptomischus* Drake (7–8 species, Govaerts & al., 2018). His circumscription was rejected by Verdcourt (1958) and many other authors (e.g., Axelius, 1987; Robbrecht, 1988), who correctly demonstrated the presence of raphides in members of Pomazoteae. As a result, all Pomazoteae genera were placed in the tribe Hedyotideae (now Spermaceae sensu Groeninckx & al., 2009) (Table 1), with the exceptions of *Klossia* and *Keenania*, which were transferred, respectively, to the tribes Ophiorrhizeae (subfamily Rubioideae; Robbrecht, 1988) and Isertieae A. Rich ex DC. (subfamily Cinchonoideae sensu Robbrecht, 1988). Tange (1995) proposed that *Keenania*, *Indopolysolenia*, *Leptomischus*, *Klossia*, and *Xanthophytum* should be placed in Hedyotideae or Ophiorrhizeae on the basis of their capsular fruits and the presence of raphides. Both *Paedicalyx* and *Siderobombyx* were synonymized with *Xanthophytum* (Tange, 1995) and *Indopolysolenia* with *Leptomischus* (Deb, 2001), all based on morphology (Table 1). This situation, coupled with the lack of molecular data from several genera originally classified in Pomazoteae, raises doubts on the monophyly of Pomazoteae and therefore its tribal status.

Phylogenetic analyses of Rubioideae based on molecular data (e.g., Bremer, 1996; Andersson & Rova, 1999; Bremer & Manen, 2000) revealed that *Lerchea* and *Xanthophytum*, traditionally associated with Pomazoteae and Spermaceae (Table 1), and *Neurocalyx* Hook.f. are closely related to *Ophiorrhiza* and *Spiradichlis*. As a result, Bremer & Manen (2000) adopted a broadly delimited Ophiorrhizeae to accommodate these five genera (Table 1). Bremekamp (1952) postulated a close relationship between *Coptophyllum* and *Lerchea* based on their thin-walled testa cells with numerous subglobose warts together with their large leaves and stipules. Axelius (1987) and Bremer & Manen (2000) agreed with this

Table 1. Tribal classifications of the genera traditionally or currently associated with the tribes Ophiorrhizeae and Pomazoteae investigated and/or only discussed in this study.

Genus	Number of species	Type of the genus	Bremekamp (1952)	Robbrecht (1988)	Tange (1995)	Bremer & Manen (2000)	This study
<i>Campanocalyx</i> Valetton	1	<i>C. winkleri</i> Valetton	Pomazoteae	Hedyotideae ^a	= <i>Lerchea</i>	Not mentioned	Isolated position in Rubioideae ^b
<i>Coptophyllum</i> Ridl.	8	<i>C. bracteatum</i> Korth.	Pomazoteae	Hedyotideae	Not mentioned	Ophiorrhizeae	Ophiorrhizeae ^c
<i>Indophsylenia</i> Bennet (as <i>Polysylenia</i> Hook.f.)	1–2	<i>I. wallichii</i> (Hook.f.) Bennet	Pomazoteae	Hedyotideae	Hedyotideae or Ophiorrhizeae	Not mentioned	= <i>Leptomischus</i> ^d
<i>Kajewskiella</i> Merrill & Perry	2	Not mentioned	Not mentioned	Condamineae	Hedyotideae	Not mentioned	Related to <i>Xanthophyllum</i> ^d
<i>Keenania</i> Hook.f.	5	<i>K. modesta</i> Hook.f.	Pomazoteae	Iserteae	Hedyotideae or Ophiorrhizeae	Not mentioned	= <i>Ophiorrhiza</i> ^c
<i>Klossia</i> Ridl.	1	<i>K. montana</i> Ridl.	Pomazoteae	Ophiorrhizeae	Hedyotideae or Ophiorrhizeae	Not mentioned	Related to <i>Coptophyllum</i> ^d
<i>Leptomischus</i> Drake	7–8	<i>L. primulooides</i> Drake	Pomazoteae	Hedyotideae	Hedyotideae or Ophiorrhizeae	Hedyotideae	Argostemmaeae ^c
<i>Lerchea</i> L.	10	<i>L. longicauda</i> L.	Pomazoteae	Hedyotideae	Not mentioned	Ophiorrhizeae	Ophiorrhizeae ^c
<i>Neurocalyx</i> Hook.f.	5	<i>N. zeylanicus</i> Hook.	Argostemmaeae	Argostemmaeae	Not mentioned	Ophiorrhizeae	Ophiorrhizeae ^c
<i>Ophiorrhiza</i> L.	Ca. 150	<i>O. mungos</i> L.	Ophiorrhizeae	Ophiorrhizeae	Not mentioned	Ophiorrhizeae	Ophiorrhizeae ^c
<i>Paedicalyx</i> Pit.	1	<i>P. attopewensis</i> Pierre ex Pit.	Pomazoteae	Hedyotideae	= <i>Xanthophyllum</i>	= <i>Xanthophyllum</i>	= <i>Xanthophyllum</i> ^d
<i>Siderobombyx</i> Bremek.	1	<i>S. kinabaluensis</i> Bremek.	Pomazoteae	Hedyotideae	= <i>Xanthophyllum</i>	Not mentioned	= <i>Xanthophyllum</i> ^d
<i>Spiradiclis</i> Blume	40	<i>S. caespitosa</i> Blume	Ophiorrhizeae	Ophiorrhizeae	Not mentioned	Ophiorrhizeae	= <i>Ophiorrhiza</i> ^c
<i>Virectaria</i> Bremek.	6	Not designated	Ophiorrhizeae	Iserteae	Not mentioned	Not mentioned	Sabiaceae s.l. ^c
<i>Xanthophytopsis</i> Pit.	2	<i>X. balansae</i> Pit.	Not mentioned	Hedyotideae	Not mentioned	= <i>Xanthophyllum</i>	= <i>Xanthophyllum</i> ^d
<i>Xanthophyllum</i> Blume	32	<i>X. fructiculosum</i> Reinw. ex Blume	Pomazoteae	Hedyotideae	Hedyotideae or Ophiorrhizeae	Ophiorrhizeae	Ophiorrhizeae ^c

^a Hedyotideae = Spermaceae

^b Conclusions based on morphological investigations

^c Conclusions based on analyses of molecular data

^d Tentative conclusions based on morphological data in the literature

assertion, although this relationship has never been tested with molecular data. The latter authors tentatively classified *Coptophyllum* in their broadly delimited Ophiorrhizeae (Table 1), a classification endorsed by Robbrecht & Manen (2006), who suggested that the circumscription of the tribe be further widened to include other genera of Pomazoteae (sensu Bremekamp, 1952, 1966) without specifying the names of the genera. The exact phylogenetic position of Ophiorrhizeae sensu Bremer & Manen (2000) within Rubioideae is currently unsettled (e.g., Wikström & al., 2015; Rydin & al., 2017). However, it is certain that the tribe is among the earliest diverging tribes within the subfamily.

In the light of these diverging opinions about the circumscriptions as well as generic relationships and limits in Ophiorrhizeae and Pomazoteae, we were compelled to conduct additional investigations. The main objectives of this study were therefore to produce a robust phylogeny of Ophiorrhizeae as delimited by Bremer & Manen (2000) and to investigate (for the first time) three genera of Pomazoteae (*Coptophyllum*, *Keenania*, *Leptomischus*). The resulting phylogeny was subsequently utilized: (1) to evaluate the phylogenetic value of testa cell patterns previously used for delimiting Ophiorrhizeae and Pomazoteae sensu Bremekamp (1952, 1966); (2) to assess the phylogenetic positions of *Coptophyllum*, *Keenania* and *Leptomischus* within subfamily Rubioideae; (3) to re-assess the circumscription as well as the generic relationships and limits within Ophiorrhizeae; and (4) to test the monophyly of the most species-rich genus of the tribe, *Ophiorrhiza*. We tentatively discuss the phylogenetic positions of relevant genera for which molecular data are currently unavailable, i.e., *Campanocalyx*, *Indopolysolenia*, *Klossia*, *Paedicalyx* and *Siderobombyx* of Pomazoteae and *Kajewskiella* Merrill & Perry, an endemic genus of the Solomon Islands of uncertain phylogenetic position. *Kajewskiella* was originally classified in the tribe Condamineae (Jansen, 1978; Robbrecht, 1993) but was later associated with *Xanthophytum* of Ophiorrhizeae (Tange, 1995).

■ MATERIALS AND METHODS

Sampling strategy and molecular markers. — Our main goal was to sample as many species as possible from all genera traditionally and currently associated with Ophiorrhizeae and Pomazoteae (including the Asian genera *Coptophyllum*, *Keenania* and *Leptomischus*). No material was available for DNA analyses of *Indopolysolenia*, *Klossia*, *Paedicalyx* and *Siderobombyx* (all Pomazoteae).

First, and in order to broadly assess the phylogenetic positions of *Leptomischus* (represented by the type of the genus *L. primuloides* Drake) and *Keenania*, we utilized the *rbcL* plastid sequence data from 139 samples, roughly covering the diversity of subfamily Rubioideae. Outgroup taxa from other families of the Gentianales, *Alstonia scholaris* (L.) R.Br. of Apocynaceae and *Mostuea brunonis* Didr. of Gelsemiaceae, were also included.

Second, sequence data from the nuclear (ETS, ITS) and plastid genome (*ndhF*, *rps16*, *trnT-F*) were used to assess whether or not these datasets were combinable. These were the same datasets utilized in the combined nuclear-plastid analysis (see below), except that taxa lacking sequences were excluded. These separate analyses were rooted with six species of Rubioideae (*Coccocypselum hirsutum* Bartl. ex DC., *Colletocema dewevrei* (De Wild.) E.M.A.Petit, *Faramea multiflora* A.Rich., *Pauridiantha paucinervis* (Hiern) Bremek., *Pravinaria leucocarpa* Bremek., *Trichostachys aurea* Hiern), as the ETS and ITS could not be unambiguously aligned across Gentianales or Rubiaceae. We had difficulty aligning the ETS data of Ophiorrhizeae with the ETS sequences from the six outgroup taxa. Therefore, these Rubioideae species were not included in the separate ETS analysis, which was rooted with *Neurocalyx*, based on the results from our separate *rbcL*, ITS, *ndhF*, *rps16* and *trnT-F* analyses (see supplemental Figs. S1–S5). In sum, the ETS, ITS, *ndhF*, *rps16* and *trnT-F* datasets, respectively, contained 58, 71, 60, 74 and 64 sequences. We failed to obtain ETS sequences from *Coptophyllum bracteatum* Korth. and *Lerchea bracteata* Valeton.

Third, based on results of the *rbcL*-based analysis we narrowed down our analyses, and conducted more in depth, combined analyses of Ophiorrhizeae. These analyses included 1 species each for *Coptophyllum* and *Lerchea*, 2 species of *Keenania*, 4 species of *Neurocalyx*, about 43 species of *Ophiorrhiza*, 3 species of *Spiradiclis* and about 13 species of *Xanthophytum*. The types of the genera *Coptophyllum*, *Neurocalyx*, *Ophiorrhiza* and *Spiradiclis* were included in our analyses. Two datasets were analyzed, one utilizing the plastid markers *ndhF*, *rps16* intron and *trnT-F* from 94 samples mainly from Ophiorrhizeae and the other using the same plastid markers and ETS and ITS from 84 samples. Outgroup taxa for the combined plastid analysis were the same two Gentianales taxa used for the *rbcL* analysis, while those for the combined nuclear-plastid analysis were the same Rubioideae taxa used to root the ITS, *ndhF*, *rps16* and *trnT-F* analyses. All taxa investigated are summarized in Appendix 1.

Molecular laboratory procedures. — DNA extraction and amplification were achieved following the protocols outlined in the following studies: Razafimandimbison & al. (2004) for ITS; Razafimandimbison & al. (2005) for ETS; Oxelman & al. (1997) for *rps16*; Bremer & al. (1999) for *ndhF*; and Razafimandimbison & Bremer (2002) for *trnT-F*. The same primers as for PCRs were utilized for sequencing reactions, which were sent to MacroGen Europe (Amsterdam, the Netherlands) for sequencing.

Phylogenetic analyses. — New sequence data were assembled using the Staden package v.2.0.09b (Staden, 1996). For each marker all sequences were aligned using MUSCLE v.3.8.31 (default settings; Edgar, 2004), as implemented in AliView v.1.18.1 (Larsson, 2014). Manual adjustments were subsequently done following the similarity criterion (Simmons, 2004) using AliView for the ETS, ITS, *rps16* and *trnT-F* datasets. The aligned matrices for the *rbcL*, combined plastid and combined nuclear-plastid datasets are

presented in supplemental Appendices S1–S3, respectively. In supplemental Appendices S2 and S3, 841 and 367 base pairs (bp) from the *rps16* and *trnT-F* datasets, respectively, were excluded, as they were ambiguously aligned. Phylogenetic reconstructions were achieved using the Bayesian Markov chain Monte Carlo (MCMC) method (Yang & Rannala, 1997) as implemented in the software MrBayes v.3.2.6 (Ronquist & al., 2012). Data partitioning was selected using the software PartitionFinder v.2 (Lanfear & al., 2017), which indicated the following best-fitting partitioning scheme for our data: ETS, ITS, coding plastid region (*ndhF*) and non-coding plastid regions (*rps16*, *trnT-F*). The general time reversible substitution model with rate variation across sites modelled as a gamma distribution (GTR+ Γ) was chosen for the ETS and the non-coding plastid regions (*rps16*+*trnT-F*). For ITS, *ndhF* and *rbcL* a proportion of invariable sites (GTR+ Γ +I) was implemented. Model selection was based on the corrected Akaike information criterion as calculated utilizing MrAIC v.1.4.6 (Nylander & al., 2004). All separate and combined Bayesian analyses were run on the CIPRES computing cluster (Miller & al., 2010) and each analysis comprised two runs of four chains each that were run for 30 million generations, sampling trees and parameters every 1000th generation.

■ RESULTS

This study investigated a total of 213 taxa and 504 sequences from the selected plastid (*ndhF*, *rbcL*, *rps16*, *trnT-F*) and nuclear (ETS, ITS) regions, of which 303 (ca. 61%) are newly published here. Voucher information and GenBank accession numbers of sequences of the studied taxa are summarized in Appendix 1. The Bayesian trees from the separate analyses of the plastid and nuclear sequence data were largely congruent (supplemental Figs. S1–S5). Visual inspection of the trees showed no strongly supported (Bayesian posterior probability [BPP] ≥ 0.95) conflicts regarding the phylogenetic relationships between the genera of Ophiorrhizeae, with the exception of the sister-group relationship of *Coptophyllum* and *Lerchea*, which collapsed in the *trnT-F* tree (supplemental Fig. S5). Within the *Ophiorrhiza* clade (including *Keenania* and *Spiradiclis*) phylogenetic relationships between species were largely unresolved, with some differences in support values of retained clades. Well-supported clades in some datasets received low support or partly or totally collapsed in the other datasets (e.g., the mostly Fijian *Ophiorrhiza* clade formed by *O. howii* H.S.Lo, *O. laxa* A.Gray, *O. peploides* A.Gray and *O. leptantha* A.Gray). Accordingly, we merged the sequence data from the five datasets for combined analyses. Figures 1–3 are the Bayesian majority-rule consensus trees from the *rbcL*, combined plastid and combined nuclear-plastid datasets, respectively.

Phylogenetic positions of *Coptophyllum*, *Leptomischus* and *Keenania* within subfamily Rubioideae. — Our *rbcL* analysis (Fig. 1) demonstrated that Pomazoteae as circumscribed

by Bremekamp (1952, 1966) is polyphyletic. *Leptomischus*, represented by the type of the genus (*L. primuloides*), was sister to the tribe Argostemmateae sensu Ginter & al. (2015) (BPP = 1) and *Keenania* (represented by *K. tonkinensis* Drake) was nested in Ophiorrhizeae. In the combined plastid (Fig. 2) and combined nuclear-plastid analyses (Fig. 3), *Keenania* (represented by *K. tonkinensis* and *K. ophiorrhizoides* Drake) was monophyletic (BPP = 0.99 & 1) and was nested within *Ophiorrhiza*. *Coptophyllum* (represented by two specimens of *C. bracteatum*, the type of the genus) was also resolved in Ophiorrhizeae as sister to *Lerchea* (represented by *L. bracteata*).

Generic limits and relationships within the tribe Ophiorrhizeae. — *Neurocalyx* and *Xanthophytum* were both strongly supported as monophyletic (BPP = 1, Figs. 2, 3), whereas *Ophiorrhiza* was resolved as paraphyletic with respect to *Keenania* and *Spiradiclis* (Figs. 2, 3). *Neurocalyx* was resolved (BPP = 1, Figs. 2, 3) as sister to a very large lineage formed by the rest of the sampled Ophiorrhizeae. Within this latter clade *Xanthophytum* was highly supported (BPP = 1) as sister to a lineage formed by the sampled members of *Coptophyllum*, *Lerchea*, *Ophiorrhiza* and *Spiradiclis* (BPP = 1). *Coptophyllum* and *Lerchea* were resolved as sisters with strong support (BPP = 0.99 and 0.96, Figs. 2, 3) and this *Coptophyllum-Lerchea* clade was sister to the *Ophiorrhiza* clade (including *Keenania* and *Spiradiclis*) (BPP = 1), which was in turn resolved in two mostly well-supported subclades: the *Ophiorrhiza-Keenania* clade (BPP = 0.80 and 0.99, Figs. 2, 3), and the *Ophiorrhiza-Spiradiclis* clade (BPP = 1 and 0.97, Figs. 2, 3).

■ DISCUSSION

This study demonstrates for the first time that *Coptophyllum*, the type of the tribe Pomazoteae as defined by Bremekamp (1952, 1966), is nested in Ophiorrhizeae. Pomazoteae is here shown to be polyphyletic, as four of its ten genera (*Coptophyllum*, *Keenania*, *Lerchea*, *Xanthophytum*) belong to Ophiorrhizeae and at least one, possibly three, genera are members of other tribes. The Asian genus *Leptomischus*, tentatively placed by Bremekamp (1952, 1966) in Pomazoteae, is sister to the tribe Argostemmateae sensu Ginter & al. (2015) (Fig. 1). Ophiorrhizeae sensu Bremer & Manen (2000), encompassing the six genera, *Coptophyllum*, *Lerchea*, *Neurocalyx*, *Ophiorrhiza*, *Spiradiclis* and *Xanthophytum*, is here demonstrated to also include *Keenania*, with *Coptophyllum* being sister to *Lerchea*. *Keenania* and *Spiradiclis* are nested in *Ophiorrhiza* and are formally transferred to *Ophiorrhiza* (Figs. 2, 3). Based on the results of our study, we present a total of 40 new combinations and 15 new names in *Ophiorrhiza*. Ophiorrhizeae as defined in this study encompass mostly suffrutescent, herbaceous plants, and include two genera of Ophiorrhizeae sensu Bremekamp (1952, 1966) with thick-walled testa cells (i.e., *Ophiorrhiza* and *Spiradiclis*; Figs. 2, 3) and four genera

of Pomazoteae sensu Bremekamp (1952, 1966) with thin-walled testa cells (i.e., *Coptophyllum*, *Keenania*, *Lerchea* and *Xanthophytum*; Figs. 2, 3). The latter four genera do not form

a monophyletic group and are distantly related to *Leptomischus* (Fig. 1). In sum, testa cell patterns, i.e., thick- versus thin-walled testa cells, traditionally used for circumscribing

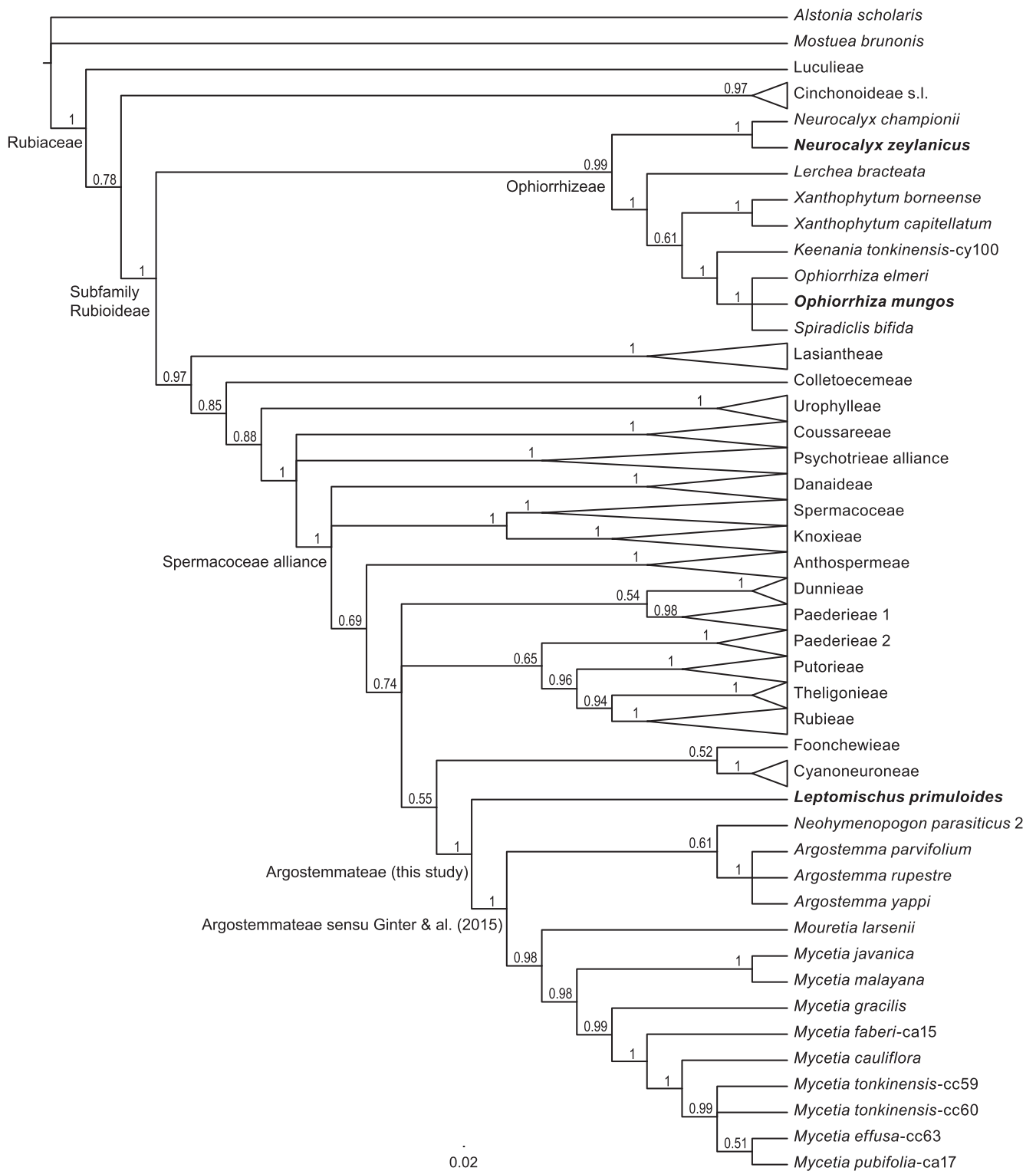


Fig. 1. Fifty-percent Bayesian majority-rule consensus tree of the Rubiaceae based on *rbcL* sequence data from 139 samples (mainly from the subfamily Rubioideae). Values above nodes are Bayesian posterior probabilities. Taxa in boldface are types of the Ophiorrhizeae genera. Part of taxon names are followed by DNA accession numbers or numerals.

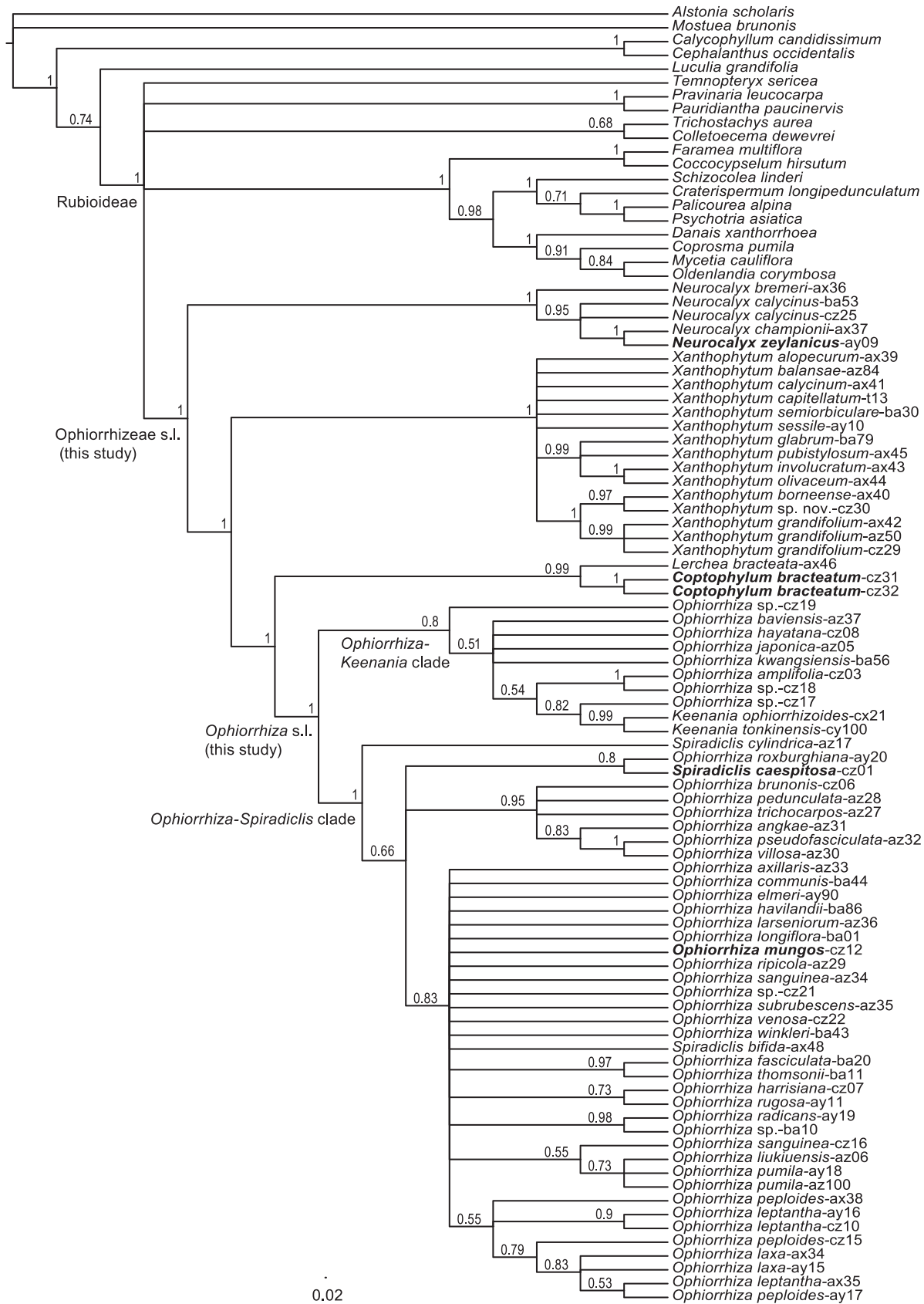


Fig. 2. Fifty-percent Bayesian majority-rule consensus tree of Rubioideae (with focus on the tribe Ophiorrhizeae) based on combined *ndhF-rps16-trnT-F* data from 94 samples. Values above nodes are Bayesian posterior probabilities. Taxa in boldface are types of the Ophiorrhizeae genera. Part of taxon names are followed by DNA accession numbers or numerals.

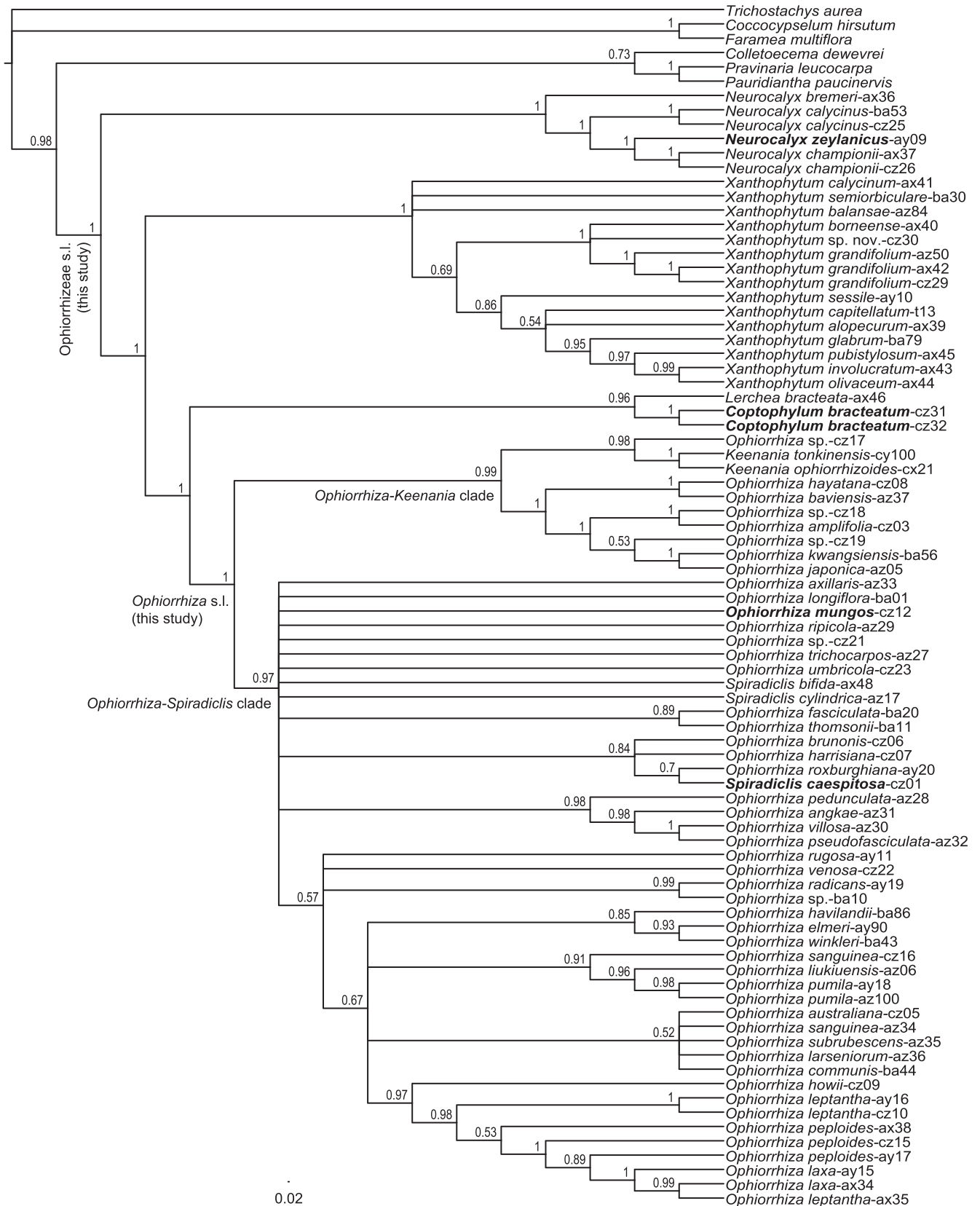


Fig. 3. Fifty-percent Bayesian majority-rule consensus tree of the tribe Ophiorrhizeae as delimited in this study based on combined ETS-ITS-*ndhF-rps16-trnT-F* data from 84 samples. Values above nodes are Bayesian posterior probabilities. Taxa in boldface are types of the Ophiorrhizeae genera. Part of taxon names are followed by DNA accession numbers or numerals.

Ophiorrhizeae and Pomazoteae sensu Bremekamp (1952, 1966), respectively, are evolutionarily labile, and have no phylogenetic value at tribal level.

Phylogenetic position of *Leptomischus*. — Bremekamp (1952, 1966) placed *Leptomischus* in Pomazoteae, but the genus is currently classified in the tribe Hedyotideae (= Spermacoceae) (e.g., Robbrecht, 1988, 1993; Groeninckx & al., 2009). Our *rbcL*-based phylogeny (Fig. 1) places *L. primuloides* as sister to Argostemmatae sensu Ginter & al. (2015). Therefore, *Leptomischus* does not seem to be closely related to the other genera of Pomazoteae sensu Bremekamp (1952, 1966) or to Spermacoceae as postulated by many authors (e.g., Verdcourt, 1958; Robbrecht, 1988; Groeninckx & al., 2009). *Leptomischus* is a small genus of six to seven species of herbaceous plants distributed in tropical Asia, from S China, NE India, and Myanmar, to Vietnam (Lo, 1993). This group of plants is characterized by a combination of the following characters: heterostylous, sessile flowers, numerous ovules attached to peltate placentae, dry capsular fruits dehiscing through an operculum, small and numerous seeds with reticulate testa cells. Argostemmatae are exclusively Asian, with the exception of a single African species of *Argostemma*. A broad delimitation of Argostemmatae has recently been proposed by Ginter & al. (2015), as the genera *Myrioneuron* R.Br. ex Benth. & Hook.f. and *Mycetia* Reinw. were shown to be mutually paraphyletic. We propose to further broaden the circumscription of Argostemmatae to accommodate *Leptomischus*. The features of the genus fit well with the characteristics of the tribe: hermaphroditic flowers, bilocular ovaries and numerous dust seeds. *Leptomischus* is, however, distinct from the other Argostemmatae genera by its ovules and seeds borne on stipitate placentae near the base of the septa, stamens inserted below the middle of the corolla tube in long-styled flowers and inserted in the corolla throat in short-styled flowers, and capsular fruits without calyx lobes, possibly reflecting its position as sister to the remaining Argostemmatae.

Generic relationships and limits within the tribe Ophiorrhizeae. — The phylogenetic relationships between the genera of Ophiorrhizeae as delimited in the present study are fully resolved (Figs. 2, 3). *Neurocalyx* is a small genus of five species of perennial and suffrutescent plants that are unbranched or rarely branched. This group of plants is restricted to Sri Lanka, with one species, *N. calycinus* (R.Br.) B.L.Rob, also found in South India (Bremer, 1984). The genus can easily be differentiated from the other genera of Ophiorrhizeae by its adnate anthers, and is sister to the rest of Ophiorrhizeae (Figs. 1–3), consistent with results in Bremer & Manen (2000).

The next lineage to diverge is *Xanthophytum*, which is sister to the large clade formed by *Coptophyllum*, *Lerchea* and *Ophiorrhiza* s.l. (including *Keenania* and *Spiradiclis*) (Figs. 2, 3). *Xanthophytum* is distinct by having ferruginous hairs on vegetative parts, axillary inflorescences, the presence of a ring of stiff hairs at the brim of the corolla tube, stamens with the main part of the filaments adnate to the corolla tube, mostly subglobose, indehiscent fruits with hard endocarps

and small brown seeds with tuberculate exotesta cell thickenings (Axelius, 1987; Tange, 1995). Our study strongly supports the transfer of the Vietnamese genus *Xanthophytopsis* Pit., represented by the type of the genus *X. balansae* Pit. (= *Xanthophytum balansae* (Pit.) H.S.Lo) to *Xanthophytum*. *Neurocalyx* and *Xanthophytum* are supported as monophyletic and are morphologically distinct. Therefore, their respective generic status is maintained.

The *Coptophyllum-Lerchea* clade is the next lineage to diverge (Figs. 2, 3). The sister-group relationship between *Coptophyllum* and *Lerchea* is supported by their comparatively thin-walled testa cells with basal walls decorated by a large number of subglobose warts (Bremekamp, 1952; S. Razafimandimbison, pers. obs.) coupled with their large leaves and stipules. On the contrary, this relationship is inconsistent with Axelius (1987), who postulated *Xanthophytum* as sister to *Lerchea* and *Coptophyllum* as sister to the *Lerchea-Xanthophytum* clade. Our present study demonstrates that Axelius's (1987) (*Coptophyllum (Lerchea-Xanthophytum)*) group is paraphyletic with respect to the broadly delimited *Ophiorrhiza* (including *Keenania* and *Spiradiclis*). Both *Coptophyllum* and *Lerchea* are here each represented by a single species; therefore we are unable to test their monophyly. Their current generic status is maintained, pending further study.

Coptophyllum (= *Pomazota*) is the type of Pomazoteae. In our analyses, *Coptophyllum* is represented by the type of the genus (*C. bracteatum*), which is strongly supported as member of Ophiorrhizeae. This is consistent with Bremer & Manen (2000), who tentatively placed the genus in that tribe based on morphology. The genus is distinct from the other Ophiorrhizeae genera by its terminal head-like inflorescences subtended by involucre bracts and globose capsules dehiscing apically through a lid or operculum (Bremekamp, 1947; S. Razafimandimbison, pers. obs.). It can additionally be characterized by stiff hairs on all young parts, presence of a hair-ring in the upper part and inside the corolla tube, stamens inserted at or below the middle of the corolla tubes and short and thick, rectangularly spreading stigmatic lobes always protruding beyond the anthers. Its sister genus, *Lerchea*, is distinct from *Coptophyllum* by its mostly terminal inflorescences bearing flowers with filaments nearly free from the corolla and indehiscent, bilocular fruits with hard endocarps (called bilocular nut by Axelius, 1987) as opposed to axillary inflorescences with flowers with the main part of filaments adnate to the corolla and capsular fruits dehiscing through an operculum or a lid in the latter genus (Axelius, 1987; S. Razafimandimbison, pers. obs.). The fruits and numerous, small seeds of *Lerchea* are comparable to those of the genus *Cyanoneuron* Tange (Tange, 1998) of the tribe Cyanoneuroneae Razafim. & B.Bremer in the Spermacoceae alliance. We, therefore, continue to recognize *Coptophyllum* and *Lerchea* at generic level, because they are morphologically distinct, and seem to represent distinct lineages within Ophiorrhizeae.

Phylogenetic position of *Keenania*: Bremekamp (1952) included *Keenania* in Pomazoteae based on the lack of raphides, but raphides are in fact present in this genus (e.g., Deb, 2001;

S. Razafimandimbison, pers. obs.). The genus was classified by Robbrecht (1988, 1993) in the tribe Isertieae in subfamily Cinchonoideae sensu stricto. Our analyses demonstrate that *K. ophiorrhizoides* and *K. tonkinensis* form a monophyletic group, which belongs to the *Ophiorrhiza-Keenania* clade of *Ophiorrhiza*. *Keenania* comprises six species of shrubby plants that are distributed from Vietnam, China, Malay Peninsula, and Indian Subcontinent. This group of plants is characterized by unbranched stems, terminal, head-like, involucre inflorescences, possibly being heterostylous, sessile flowers, numerous ovules attached to globose placentae, and capsular fruits crowned by persistent calyx lobes and numerous, small seeds. Some authors (e.g., Deb, 2001) have considered *Keenania* to be a synonym of *Leptomischus* and the type of the genus, *K. modesta* Hook.f., was transferred by Deb (2001) to the latter genus. We have not been able to find any morphological support for this transfer and argue that this taxonomic decision is erroneous and seems to be rejected by some other authors as well (e.g., Puff & al., 2005; Chen & al., 2011). Some authors (e.g., Puff & al., 2005) consider *Keenania* to be morphologically heterogeneous. We agree with Drake del Castillo (1895) that the salient characters (e.g., habit, inflorescence type, calyx and style shapes, ovule number and placenta shape) of *K. modesta* given by its author (Hooker, 1880) match that of *K. ophiorrhizoides* and *K. tonkinensis*, which, in addition, group together in our phylogeny (Figs. 2, 3); these two species are nested within the *Ophiorrhiza-Keenania* clade, rendering *Ophiorrhiza* paraphyletic. There seem to be differences in the attachment of stamens to the corolla tube. The stamens of *K. modesta* are inserted at the base of the corolla tube (Hooker, 1880), while they are inserted near the base in *K. tonkinensis* and near the corolla throat in *K. ophiorrhizoides*. These differences do, however, not necessarily indicate variation among species, but may indicate that these species have heterostylous flowers and that their original descriptions were based solely on either short- or long-styled flowers. Heterostylous flowers are reported from many *Ophiorrhiza* species (e.g., Schanzer, 2005). Based on the above-mentioned information, together with the phylogenetic positions of *K. ophiorrhizoides* and *K. tonkinensis* within *Ophiorrhiza*, we formally merge *Keenania* into *Ophiorrhiza* (see below). Another option would be to expand *Keenania* to accommodate all *Ophiorrhiza* species belonging to the *Ophiorrhiza-Keenania* lineage. We favor the first solution (i.e., merging *Keenania* in *Ophiorrhiza*), as we have not been able to find any obvious morphological character for characterizing the *Ophiorrhiza-Keenania* lineage.

Spiradiclis (here merged in *Ophiorrhiza*) contains about 40 species of annual or perennial herbs, with 35 species endemic to China (e.g., Chen & al., 2011; Wang, 2002). The genus has been considered distinct from *Ophiorrhiza* mainly by having linear-oblong or subglobose capsular fruits with two or four valves and dehiscing loculicidally and septically to the very base (e.g., Bremekamp, 1952; Darwin, 1976; S. Razafimandimbison, pers. obs.). In contrast, *Ophiorrhiza* species are reported to produce obovoid to oblate, mitriform,

or obcordate capsules that are strongly laterally compressed perpendicular to the septum and dehisce loculicidally across the top or along sides (e.g., Chen & al., 2011; Wang, 2002). However, *Ophiorrhiza* species with subglobose capsular fruits (e.g., *O. orofenensis* S.P. Darwin, *O. scorpioidea* Nadeaud, *O. subumbellata* G. Forst.) have also been reported from the Pacific (Darwin, 1976). We conclude that the present circumscriptions of *Ophiorrhiza* and *Spiradiclis* based on fruit shape and dehiscence are incongruent with our results. The sampled species of *Spiradiclis* (including the type of the genus, *S. caespitosa*) are all nested in the *Ophiorrhiza-Spiradiclis* clade (Figs. 2, 3), rendering *Ophiorrhiza* paraphyletic. *Ophiorrhiza* is thus supported as paraphyletic with respect to *Spiradiclis* (and *Keenania*) (Figs. 2, 3). As a result, we formally merge *Spiradiclis* into *Ophiorrhiza* (see below) and the adoption of this broadly delimited *Ophiorrhiza* requires the formal transfer of the species of *Keenania* and *Spiradiclis* to *Ophiorrhiza* (see the section on Taxonomic implications below). *Ophiorrhiza* as circumscribed here contains species that are mostly herbs or subshrubs, typically with membranaceous leaves that are dark green on upper surfaces and pale green on lower surfaces. The inflorescences are cymose to capitata, fasciculate, or paniculiform with axes varying from helicoid or scorpioid to dichasial. The fruits are typically capsules, whose shape varies from obovoid to oblate, mitriform or obcordate and laterally compressed to linear-oblong or subglobose. In contrast to Bremekamp (1952), our observations show that the stipules in *Ophiorrhiza* and *Spiradiclis* vary from narrowly triangular to deeply bifid or fimbriate.

This study allows us to comment on the current infrageneric classifications of *Ophiorrhiza* (Schumann, 1891) and *Spiradiclis* (Lo, 1998). Schumann (1891) proposed an informal infrageneric classification for *Ophiorrhiza* based on the presence or absence of conspicuous bracts on inflorescences: Bracteolatae (with conspicuous bracts) and Ebracteolatae (without conspicuous bracts). This classification is not supported by our results, as the sampled species with and without bracts are found in the *Ophiorrhiza-Keenania* clade as well as in the *Ophiorrhiza-Spiradiclis* clade. Lo (1998) subdivided *Spiradiclis* into two subgenera based on fruit shape and size and shape of valves of its capsular fruits: *S.* subg. *Sinospiradiclis* Lo with subglobose capsules that are as long as wide with twisted valves and *S.* subg. *Spiradiclis* with ellipsoid to linear-oblong capsules that are 2–4 times as long as wide with straight valves. We were unable to test the monophyly of these subgenera of *Spiradiclis* due to our limited sampling for the genus.

Key to the genera of the tribe Ophiorrhizeae as circumscribed in the present study

1. Flowers with adnate anthers; fruits dry indehiscent *Neurocalyx*
1. Flowers with free anthers; fruits dry dehiscent or indehiscent

2. Inflorescences/infructescences axillary; mostly flowers zygomorphic, rarely actinomorphic (in species with condensed heads) *Xanthophytum*
2. Inflorescences/infructescences terminal; flowers actinomorphic 3
3. Inflorescences involucrel; fruits capsular, dehiscent through an operculum *Coptophyllum*
3. Inflorescences non-involucrel; fruits dehiscent loculicidally or septicidally or both or indehiscent 4
4. Fruits capsular, varying from obovoid to obovate, mitriform or obcordate and laterally compressed to linear oblong or subglobose *Ophiorrhiza* s.l. (including *Keenania* and *Spiradiclis*)
4. Fruits indehiscent, subglobose *Lerchea*

Taxonomic positions of the genera traditionally associated with Pomazoteae, Ophiorrhizeae and Spermaceae. — We

were unable to include *Campanocalyx*, *Indopolysolenia*, *Kajewskiella*, *Klossia*, *Paedicalyx* and *Siderobombyx* in this study due to the lack of sequenceable material. Therefore, their respective positions within Rubiaceae are discussed here based solely on morphological grounds, i.e., on the basis of the information gathered from the literature (including protologues) and their scanned images that we could see. All of these genera are reported to contain raphides (Tange, 1995), suggesting that they belong to subfamily Rubioideae.

Campanocalyx is a monospecific genus restricted to Borneo, which is distinct by its calyx tubes completely ensheathing the corolla tubes. This trait differentiates the genus from the rest of Rubioideae (or even Rubiaceae). The genus was initially placed in Pomazoteae (Bremekamp, 1952), and was synonymized with *Keenania* (e.g., Robbrecht, 1988) and later with *Myrioneuron* (e.g., Robbrecht, 1993), which has recently been merged with the genus *Mycetia* of Argostemmatae sensu Ginter & al. (2015). Tange (1995) suspected *Campanocalyx* to be a Bornean species of *Lerchea*. We postulate that the genus may represent a distinct lineage that occupies an isolated position within Rubioideae.

Indopolysolenia is a small genus of one or two species, which was initially classified in Pomazoteae (Bremekamp, 1947) and later in Isertieae (Robbrecht, 1988). The genus was synonymized with *Leptomischus* (Lo, 1993), which is shown here to belong to Argostemmatae (Fig. 1). We have not seen any specimen of this genus and are therefore unable to comment on its taxonomic position. For now, we accept the taxonomic decision made by Lo (1993), pending further study.

Kajewskiella is a genus of two species from the Solomon Islands, which was tentatively placed by Merrill & Perry (1947), later endorsed by Jansen (1978) and Robbrecht (1993), in the tribe Condamineae based on the lack of raphides, valvate corolla aestivation and long linear placentae adnate to the septum. However, the presence of raphides is reported by Tange (1995), who postulated *Kajewskiella* to be closely related to *Xanthophytum* based on seed shape and exotesta thickenings. The former differs from the latter by the lack of hairs inside the corolla tube and its much larger flowers.

We agree with Tange (1995) that *Kajewskiella* may have a close affinity with *Xanthophytum* based on morphological grounds.

Klossia is a monotypic genus restricted to Malay Peninsula and resembles *Ophiorrhiza* by its habit and leaves. Bremekamp (1947) placed *Klossia* in his Pomazoteae, while Robbrecht (1988) tentatively placed it in Ophiorrhizeae. The genus is distinct from *Ophiorrhiza* as delimited in this study by its urn-shaped capsules that dehisce through an operculum. We agree with his assertion and postulate the genus to be closely related to *Coptophyllum*, which has the same type of fruit dehiscence.

Finally, Bakhuizen van den Brink (1953) merged the Vietnamese and Chinese *Paedicalyx* (and *Xanthophytopsis*) with *Xanthophytum* without presenting the reasons for his taxonomic change. This decision was endorsed by Axelius (1990), who included the two genera in her revision of *Xanthophytum*. We accept the inclusion of *Paedicalyx* in *Xanthophytum* because it presents the salient characteristics of this latter genus (axillary inflorescences, small brown seeds with tuberculate exotesta cell thickenings, and ferruginous hairs, Axelius, 1990; Tange, 1995). Further, we also endorse the transfer of *Siderobombyx* to *Xanthophytum* (Tange, 1995).

■ TAXONOMIC IMPLICATIONS

The results of the present study have taxonomic implications for the infratribal classification of Ophiorrhizeae. A total of 40 new combinations and 15 new names are presented below. It is worth noting that despite internet searches in digital herbaria and repeated inquiries to the herbaria where the type specimens are housed, we were unable to obtain barcodes for some types of the Chinese species of *Spiradiclis*.

Ophiorrhiza L., Sp. Pl.: 150. 1753 – Type (designated by Hitchcock in Sprague & al., Nom. Prop. Brit. Bot.: 129. 1929): *O. mungos* L.

= *Mitreola* Boehm. in Ludwig, Def. Gen. Pl., ed. 3: 31. 1760, nom. illeg., non L. 1758.

= *Mungos* Adans., Fam. Pl. 2: 225. 1763.

= *Spiradiclis* Blume, Bijdr.: 975. 1826–1827, **syn. nov.** – Type: *S. caespitosa* Blume (≡ *Ophiorrhiza caespitosa* (Blume) Razafim. & C.Rydin).

= *Keenania* Hook.f., Fl. Brit. India 3: 101. 1880, **syn. nov.** – Type: *K. modesta* Hook.f. (≡ *Leptomischus modestus* (Hook.f.) Deb ≡ *Ophiorrhiza modesta* (Hook.f.) Razafim. & C.Rydin).

= *Hayataella* Masam. in Trans. Nat. Hist. Soc. Taiwan 24: 206. 1934 – Type: *H. michelloides* Masam. (≡ *Ophiorrhiza michelloides* (Masam.) H.S.Lo).

= *Spiradiclis* subg. *Sinospiradiclis* H.S.Lo in Bull. Bot. Res., Harbin 18(3): 275–276. 1998, **syn. nov.** – Type: *S. microphylla* H.S.Lo (≡ *Ophiorrhiza microphylla* (H.S.Lo) Razafim. & C.Rydin).

1. *Ophiorrhiza arunachalensis* (Deb & Rout) Razafim. & C.Rydin, **comb. nov.** \equiv *Spiradiclis arunachalensis* Deb & Rout in *Candollea* 44(1): 225–227, fig. 1. 1989 – Holotype: India. Arunachal Pradesh, Subansiri District, Khru river banks, 17 Nov 1964, *A.R.K. Sastry 40721* (CAL).
2. *Ophiorrhiza baishaiensis* (X.X.Chen & W.L.Sha) Razafim. & C.Rydin, **comb. nov.** \equiv *Spiradiclis baishaiensis* X.X. Chen & W.L.Sha in *Bull. Bot. Res.*, Harbin 8(3): 107–108, pl. 1–6. 1988 – Holotype: China. Guangxi, Baishai Xian, Daleng Xiang, 9 May 1984, *X.X. Chen & G.X. Zhang 36951* (GXMI).
3. *Ophiorrhiza balansae* (Pit.) Razafim. & C.Rydin, **comb. nov.** \equiv *Notodontia balansae* Pit. in *Lecomte & al.*, *Fl. Indo-Chine* 3: 87. 1922 \equiv *Spiradiclis balansae* (Pit.) H.S.Lo in *Acta Bot. Austro. Sin.* 1: 32. 1983 – Holotype: Vietnam, forêt entre Than-Moï et Dong-son, 700 m alt., 5 Mar 1886, *B. Balansa 654* (P barcode P02273363!).
4. *Ophiorrhiza bifida* (Kurz) Razafim. & C.Rydin, **comb. nov.** \equiv *Spiradiclis bifida* Kurz in *J. Asiatic Soc. Bengal*, Pt. 2, *Nat. Hist.* 41(4): 310. 1872 – Holotype: Martaban, unknown.
Note. – Kurz (1872: 311) did not provide any information about the type of his *Spiradiclis bifida*. He wrote “Martaban”, which we consider to be the origin of the specimen(s) that he used for basing the description of his species.
5. *Ophiorrhiza bremeri* Razafim. & C.Rydin, **nom. nov.** \equiv *Spiradiclis howii* H.S.Lo in *Bull. Bot. Res.*, Harbin 6(4): 41–42. 1986, non H.S.Lo 1998 – Holotype: China. Yunnan, Xichu, Fadou, on rocks in forests, 1400–1500 m alt., 23 Sep 1947, *K.M. Feng 11593* (IBSC barcode 0510647; isotype: KUN barcode 483687).
Note. – This species is named after Prof. Birgitta Bremer for her important contribution to our knowledge of Rubiaceae.
6. *Ophiorrhiza caespitosa* (Blume) Razafim. & C.Rydin, **comb. nov.** \equiv *Spiradiclis caespitosa* Blume, *Bijdr.*: 975. 1826–1827 – Holotype: Java. *Blume s.n.* (L barcode L 0001355!).
7. *Ophiorrhiza capitata* (Ridl.) Razafim. & C.Rydin, **comb. nov.** \equiv *Myrioneuron capitatum* Ridl. in *J. Fed. Malay States Mus.* 10: 93. 1920 \equiv *Keenania capitata* (Ridl.) Craib, *Fl. Siam.* 2: 82. 1932 – Holotype: Thailand. Tasan, West Coast, 5 Nov 1919, *C.B. Kloss 7053* (K barcode K001067653!).
8. *Ophiorrhiza chenii* Razafim. & C.Rydin, **nom. nov.** \equiv *Spiradiclis fusca* H.S.Lo in *Guihaia* 11(2): 100–101. 1991, non Valetton 1925 – Holotype: China. Guangxi, Guilin, Liutang, on limestone hills, 29 Mar 1948, *Zh.N. Deng 13436* (IBSC barcode 0510636).
Note. – This species is named after Prof. Xiu Xiang Chen for his contribution to our knowledge of the *Spiradiclis* of China.
9. *Ophiorrhiza chuniana* (R.J.Wang) Razafim. & C.Rydin, **comb. nov.** \equiv *Spiradiclis chuniana* R.J.Wang in *Novon* 12(3): 423, fig. 2. 2002 – Holotype: China. Guangxi, Nonggang Nature Reserve, 390 m alt., 15 Aug 2000, *R.J. Wang 392* (IBSC barcode 0742210; isotypes: IBSC barcodes 0742211 & 0742212, MO barcode MO-2049204).
10. *Ophiorrhiza coccinea* (H.S.Lo) Razafim. & C.Rydin, **comb. nov.** \equiv *Spiradiclis coccinea* H.S.Lo in *Bull. Bot. Res.*, Harbin 6(4): 38–39. 1986 – Holotype: China, Guangxi, Longzhou, Wulian, Banbi, on rocks in dense forest, 4 Aug 1957, *S.H. Chun 13475* (IBSC barcode 0510628; isotypes: HITBC barcode 038296!, IBK barcode IBK00191517!, IBSC barcode 0510627).
Note. – According to the Chinese virtual herbarium (<http://www.cvh.ac.cn>), the type specimen of *Spiradiclis coccinea* is *S.H. Chu 13475*, instead of *S.H. Chu 13435* as stated in the protologue. The author of this species (H.S.Lo) annotated himself the holotype (barcode 0510628) and one isotype (barcode 0510627) housed at IBSC. The specimen *S.H. Chu 13435* (IBSC) is a paratype of *Jasminum guangxiense* B.M.Miao.
11. *Ophiorrhiza coriaceifolia* (R.J.Wang) Razafim. & C. Rydin, **comb. nov.** \equiv *Spiradiclis coriaceifolia* R.J.Wang in *Nordic J. Bot.* 32(5): 594–597. 2014 – Holotype: China. Guangxi Zhuang Autonomous Region, Baise City, Napo County, Mt. Kanalaoshan, on wet limestone cliffs under sparse forest, 10 Apr 2013, short-styled flower, pale purplish red, *R.J. Wang & S.J. Deng 2358* (IBSC; isotype: IBSC).
12. *Ophiorrhiza cylindrica* (Wall. ex Hook.f.) Razafim. & C.Rydin, **comb. nov.** \equiv *Spiradiclis cylindrica* Wall. ex Hook.f., *Fl. Brit. India* 3: 76. 1880 \equiv *Spiradiclis caespitosa* f. *cylindrica* (Wall. ex Hook.f.) H.S.Lo in *Acta Bot. Austro Sin.* 1: 31. 1983 – Syntypes: India. Khasia Mts., 2–4000 ft. alt., *De Silva & c. s.n.* (not located); Mishmi Hills, *W. Griffith s.n.* (not located).
Note. – Two syntypes (*De Silva & c.* and *Griffith*) were listed by Hooker (1880) when describing his *Spiradiclis cylindrica*. The author failed to indicate the names of the herbaria, where these collections were kept.
13. *Ophiorrhiza danxiashanensis* (R.J.Wang) Razafim. & C.Rydin, **comb. nov.** \equiv *Spiradiclis danxiashanensis* R.J.Wang in *Phytotaxa* 206: 31–34, fig. 1, 2A–E. 2015 – Holotype: China. Guangdong Province, Shaoguan City, Renhua County, Mt. Danxiashan, 25°01'N, 113°44'E, 145 m alt., 13 Apr 2011, short-styled flower, *R.J. Wang & H.Z. Wen 1548* (IBSC; isotype: IBSC).
14. *Ophiorrhiza darwinii* Razafim. & C.Rydin, **nom. nov.** \equiv *Keenania tonkinensis* Drake in *Bull. Mus. Hist. Nat.* (Paris)

- 1: 118. 1895, non Pit. 1923 – Holotype: Vietnam. Qui-Duc, Hoa-Binh Province, Vallée de Langkok, Mt. Bavi, *P.A. Eberhardt 4179* (P barcode P02273198!; isotype: P barcode P02273199!).
Note. – This species is named after Dr. Steven P. Darwin for his important contribution to our knowledge of the Pacific *Ophiorrhiza*.
15. *Ophiorrhiza emeiensis* (H.S.Lo) Razafim. & C. Rydin, **comb. nov.** ≡ *Spiradiclis emeiensis* H.S.Lo in Acta Bot. Austro Sin. 1: 31, 36. 1983 – Holotype: China. Sichuan, Emei Shan, 31 Aug 1957, *G.H. Yang 57031* (IBSC barcode 0005885!; isotype: PE barcode 00839003!).
16. *Ophiorrhiza fungiana* Razafim. & C.Rydin, **nom. nov.** ≡ *Spiradiclis ferruginea* D.Fang & D.H.Qin in Bull. Bot. Res., Harbin 13(4): 334–335, fig. 1, 5–10. 1993, non Valetton 1910 – Holotype: China. Guangxi, Napo, Baidu, Nunghua, in forests on volcanic rocks, 1200 m alt., 14 Mar 1986, *D. Fang & D.H. Qin 79849* (GXMI).
Note. – This species is named after Prof. Ding Fang for his contribution to our knowledge of the Chinese Rubiaceae.
17. *Ophiorrhiza flava* (H.S.Lo) Razafim. & C.Rydin, **comb. nov.** ≡ *Keenania flava* H.S.Lo in Wu & al., Fl. China 19: 183. 2011 – Holotype: China. Guangxi, Napo, Xiahua, Baikan, on slope, 21 Apr 1977, *C.X. Luo 3-5491 5491* (IBSC barcode 050450).
18. *Ophiorrhiza glabra* (L.Wu & Q.R.Liu) Razafim. & C. Rydin, **comb. nov.** ≡ *Spiradiclis glabra* L.Wu & Q.R. Liu in Nordic J. Bot. 34(6): 718–721. 2016 – Holotype: China. Guangdong, Yangchun County, Helang town, Yuxi village, Yuxisandong, at the throat of a cave from limestone karst, 23°35'N, 111°49'E, 132 m alt., 24 Mar 2013, *L. Wu 3121* (BNU).
19. *Ophiorrhiza glandulosa* (L.Wu & Q.R.Liu) Razafim. & C.Rydin, **comb. nov.** ≡ *Spiradiclis glandulosa* L.Wu & Q.R.Liu in Nordic J. Bot. 33(1): 79–82, figs. 1, 2A–F. 2014 – Holotype: China. Guangxi, Zhaoping County, Gongqiao town, under dense forests on limestone hill slopes, 150 m alt., 20 Mar 2013, *S.S. Mo MSS 0118* (BNU; isotype: PR).
20. *Ophiorrhiza guangdongensis* (H.S.Lo) Razafim. & C.Rydin, **comb. nov.** ≡ *Spiradiclis guangdongensis* H.S.Lo in Acta Bot. Yunnan. 9(3): 299–301, pl. 1. 1987 – Holotype: China. Guangdong, Longmen, Zengcheng, Nan-kun-shan, *Nan-kun-shan Exped. 71355* (IBSC barcode 0510638).
21. *Ophiorrhiza jingxiensis* (R.J.Wang) Razafim. & C.Rydin, **comb. nov.** ≡ *Spiradiclis jingxiensis* R.J.Wang in Nordic J. Bot. 34: 550–552, fig. 1. 2016 – Holotype: China. Guangxi, Zhuangzu Autonomous Region, Jingxi County, Ande town, Sanhe village, 23°12'N, 106°03'E, 1010 m alt., 6 Jun 2014, long-styled flowers, *R.J. Wang 2691* (IBSC barcode 0820972; isotype: IBSC barcode 0820973).
22. *Ophiorrhiza kainulainenii* Razafim. & C.Rydin, **nom. nov.** ≡ *Spiradiclis pauciflora* L.Wu & Q.R.Liu in Acta Bot. Fenn. 52(3–4): 257–260, figs. 1 & 2. 2015, non Hook.f. 1880 – Holotype: China. Guangxi, Leye County, Huaping town, Baiyantuo village, under dense forests on limestone hill slopes, 1070 m alt., 17 May 2013 (fl. & fr.), *L. Wu 3740* (BNU).
Note. – This species is named after Dr. Kent Kainulainen for his contribution to our knowledge of the Asian Rubiaceae.
23. *Ophiorrhiza laxiflora* (W.L.Sha & X.X.Chen) Razafim. & C.Rydin, **comb. nov.** ≡ *Spiradiclis laxiflora* W.L.Sha & X. X.Chen in Acta Bot. Austro Sin. 1: 31, 35. 1983 – Holotype: China, Guangxi, Longzhou Xian, 14 Jun 1979, *Guangxi Drug Pl. Exped. 0267* (GXMI).
24. *Ophiorrhiza lii* Razafim. & C.Rydin, **nom. nov.** ≡ *Spiradiclis longzhouensis* H.S.Lo in Guihaia 11(2) 99. 1991, non H.S.Lo 1990 – Holotype: China. Guangxi: Longzhou, Banbi, dense forest, on rocks, rare, 30 Apr 1956, *Y.K. Li 229* (IBSC barcode 0510633).
Note. – This species is named after Yong Kang Li who collected the type specimen.
25. *Ophiorrhiza loana* (R.J.Wang) Razafim. & C.Rydin, **comb. nov.** ≡ *Spiradiclis loana* R.J.Wang in Novon 12(3): 420–423, fig. 1. 2002 – Holotype: China. Guangxi, Nonggang Nature Reserve, 280 m alt., 15 Aug 2000, *R.J. Wang 390* (IBSC barcode 0742213; isotypes: IBSC barcodes 0742214, 0742215 & 0742216, MO barcode MO-2049205!).
26. *Ophiorrhiza longanensis* (R.J.Wang) Razafim. & C.Rydin, **comb. nov.** ≡ *Spiradiclis longanensis* J.R.Wang in PhytoKeys 55: 114–116, fig. 1. 2015 – Holotype: China. Guangxi Zhuangzu Autonomous Region, Nanning City, Longan County, Pingshan town, Tuanjie village, 22°57'N, 107°34'E, 219 m alt., 4 Jun 2014, long-styled flowers, *R.J. Wang 2682* (IBSC barcode 0820923; isotypes: IBSC barcodes 0820918, 0820919, 0820920, 0820921 & 0820922).
27. *Ophiorrhiza longibracteata* (S.Y.Liu & S.J.Wei) Razafim. & C.Rydin, **comb. nov.** ≡ *Spiradiclis longibracteata* S.Y. Liu & S.J.Wei in Acta Phytotax. Sin. 32(4): 362–364, pl. 1 & 2. 1994 – Holotype: China. Guangxi, Longan, Longhushan Nature Reserve, 21 Apr 1985, *S.J. Wei & S.Y. Liu 2530* (PE; isotypes: GXMI barcode 050494, IBK barcode IBK00191516).
28. *Ophiorrhiza lui* (Yan Liu & L.Wu) Razafim. & C.Rydin, **comb. nov.** ≡ *Spiradiclis lui* Yan Liu & L.Wu in Nordic

- J. Bot. 36(6)-e01786: 2. 2018 – Holotype: China. Guangxi Jingxi County, Sanhe town, Nongweng village, in a limestone cave, 23°08'N, 108°11'E, 1036 m alt., 11 May 2016, L. Wu & Z.-J. Wen 5920 (CSFI barcode 056401).
29. *Ophiorrhiza luochengensis* (H.S.Lo & W.L.Sha) Razafim. & C.Rydin, **comb. nov.** ≡ *Spiradiclis luochengensis* H.S.Lo & W.L.Sha in Acta Bot. Austro Sin. 1: 30, 34–35. 1983 – Holotype: China. Guangxi, Luo-cheng, Huai-qun, Jia-lin, Xian-guang, 1 Jun 1977, *Luo-cheng Exped. 4-1-1672* (GXMI).
30. *Ophiorrhiza malipoensis* (H.S.Lo) Razafim. & C.Rydin, **comb. nov.** ≡ *Spiradiclis malipoensis* H.S.Lo in Guihaia 11(2): 98–99. 1991 – Holotype: China. Yunnan, Malipo, Huangkingyin, under dense woods, 1100 m alt., 22 Jan 1940, C.W. Wang 86358 (IBSC barcode 0510657; isotypes: IBSC barcode 0510658, KUN barcode 483690).
31. *Ophiorrhiza microcephala* (Pit.) Razafim. & C.Rydin, **comb. nov.** ≡ *Keenania microcephala* Pit. in Lecomte & al., Fl. Indo-Chine 3: 169. 1923 – Holotype: Tonkin [= Vietnam]. Kien-khé et vallée de Đông Bàu, 19 May 1884, H.F. Bon 2609 (P barcode P02273197!).
32. *Ophiorrhiza microphylla* (H.S.Lo) Razafim. & C.Rydin, **comb. nov.** ≡ *Spiradiclis microphylla* H.S.Lo in Acta Bot. Austro. Sin. 1: 30, 34. 1983 – Holotype: China. Jiangxi, Cheng-Long, 9 Oct. 1942, *Mo Xi-mo 21172* (IBSC barcode 0005886; isotype: IBSC barcode 0510659).
33. *Ophiorrhiza modesta* (Hook.f.) Razafim. & C.Rydin, **comb. nov.** ≡ *Keenania modesta* Hook.f., Fl. Brit. India 3: 101. 1880 ≡ *Leptomischus modestus* (Hook.f.) Deb in Phytotaxonomy 1: 16. 2001 – Holotype: India. Assam, Cachar, at the Doarbund Pass, Jun 1874, R.L. Keenan s. n. (K barcode K000031981!; isotype: K barcode K000031982!).
34. *Ophiorrhiza oblanceolata* (W.L.Sha & X.X.Chen) Razafim. & C.Rydin, **comb. nov.** ≡ *Spiradiclis oblanceolata* W.L.Sha & X.X.Chen in Acta Bot. Austro Sin. 1: 30, 35. 1983 – Holotype: China. Guangxi, Chongzuo Xiau, 19 May 1974, J.Y. Luo 23196 (GXMI).
35. *Ophiorrhiza ophiorrhizoides* (Drake) Razafim. & C. Rydin, **comb. nov.** ≡ *Keenania ophiorrhizoides* Drake in Bull. Mus. Hist. Nat. (Paris) 1: 117. 1895 – Holotype: Vietnam. Vallée de Langkok (Mount-Bavi), 16 Apr 1888, B. Balansa 2623 (P barcode P03797793!; isotype: K barcode K000760593).
36. *Ophiorrhiza pengshuiensis* (B.Pan & R.J.Wang) Razafim. & C.Rydin, **comb. nov.** ≡ *Spiradiclis pengshuiensis* B.Pan. & R.J.Wang in PhytoKeys 63: 42–45, fig. 1. 2016 – Holotype: China. Chongqing Municipality, Pengshui County, Hanxia town, Baixiang village, 29°08'N, 108°06'E, 360 m alt., 29 Nov 2014, R.-J. Wang 2931 (IBSC; isotype: IBSC).
37. *Ophiorrhiza puffii* Razafim. & C.Rydin, **nom. nov.** ≡ *Spiradiclis villosa* X.X.Chen & W.L.Sha in Bull. Bot. Res, Harbin 11(3): 17–18. 1991, non Roxb. 1824 – Holotype: China, Guangxi, Gongzhou Xian, 7 Jun 1977, X.X. Chen & al. 2-0049 (GXMI).
Note. – This species is named after Dr. Christian Puff for his contribution to our knowledge of Rubiaceae.
38. *Ophiorrhiza purpureocaerulea* (H.S.Lo) Razafim. & C. Rydin, **comb. nov.** ≡ *Spiradiclis purpureocaerulea* H.S.Lo in Bull. Bot. Res., Harbin 6(4): 39–40. 1986 – Holotype: China. Guangxi: Longzhou, Shangjin, roadside, on limestone, 15 Aug 1935, S.P. Ko 55507 (IBSC barcode 0510671; isotypes: IBK barcode IBK00191520!, IBSC barcode 0510617).
39. *Ophiorrhiza qinii* Razafim. & C.Rydin, **nom. nov.** ≡ *Spiradiclis hainanensis* H.S.Lo in Acta Bot. Yunnan. 9(3): 301. 1987, non Y.Q.Tseng 1974 – Holotype: China. Hainan, Ya Xian, Si-feng-shan, 1933, C. Wang 34588 (IBSC barcode 0510646).
Note. – This species is named after Dr. De Hai Qin for his contribution to our knowledge of the Chinese *Spiradiclis*.
40. *Ophiorrhiza quanzhouensis* (J.Liu & W.B.Xu) Razafim. & C.Rydin, **comb. nov.** ≡ *Spiradiclis quanzhouensis* J.Liu & W.B.Xu in Nordic J. Bot. 36(3)-e01595: 2. 2017 – Holotype: China. Guangxi, Quanzhou County, Shitang town, in crevices of steep moist rock faces or cliffs of karst Tiankeng, 438 m alt., 25°40'N, 110°03'E, 4 Feb 2013, Y. Liu, B. Pan & J. Liu LJ013 (IBK barcode IBK00397295; isotype: PE barcode 02111927!).
41. *Ophiorrhiza ridsdalei* Razafim. & C.Rydin, **nom. nov.** ≡ *Spiradiclis petrophila* H.S.Lo in Acta Bot. Austro Sin. 1: 30, 33. 1983, non H.S.Lo 1990 – Holotype: China. Guangdong, Yangchun Xian, on limestone rocks, 10 Sep 1956, C. Wang 42113 (IBSC barcode 0005887; isotypes: IBK barcode IBK00103392, MO barcodes MO-2049224 & MO-2049225, PE barcode 02111927!).
Note. – This species is named after Dr. Colin Ridsdale for his important contribution to our knowledge of Asian Rubiaceae.
42. *Ophiorrhiza robbrechtii* Razafim. & C.Rydin, **nom. nov.** ≡ *Spiradiclis tomentosa* D.Fang & D.H.Qin in Bull. Bot. Res., Harbin 13(4): 330, fig. 1. 1993, non Roxb. 1824 – Holotype: China. Guangxi, Fengshan, Paoli, in cavern of calcareous rocks, 500 m alt., 20 Apr 1992, D.H. Qin 30574 (GXMI; isotype: PE barcode 00032245!).
Note. – This species is named after Prof. Elmar Robbrecht for his important contribution to our knowledge of Rubiaceae.

43. *Ophiorrhiza rubescens* (H.S.Lo) Razafim. & C.Rydin, **comb. nov.** \equiv *Spiradiclis rubescens* H.S.Lo in Guihaia 11(2): 101–102. 1991 – Holotype: China. Guangxi, Tiandong, under shade, on rocks, 15 Jun 1977, *M.L. Lo 3-1416* (Bose Institute for Drug Control).
44. *Ophiorrhiza scabrada* (D.Fang & D.H.Qin) Razafim. & C.Rydin, **comb. nov.** \equiv *Spiradiclis scabrada* D.Fang & D.H.Qin in Bull. Bot. Res., Harbin 13(4): 333, fig. 2. 1993 – Holotype: China. Guangxi, Napo, Baidu, Nunghua, in forests of calcareous rocks, 810 m alt., 8 Nov 1986, *D. H. Qin 79891* (GXMI).
45. *Ophiorrhiza seshagirii* (Deb & Rout) Razafim. & C. Rydin, **comb. nov.** \equiv *Spiradiclis seshagirii* Deb & Rout in Candollea 44: 227–229, fig. 2. 1989 – Holotype: India. Arunachal Pradesh, Siang Distr., Tutin, 690 m alt., 1 Nov 1958, *R.S. Rao 17354* (CAL; isotype: CAL).
46. *Ophiorrhiza shae* Razafim. & C.Rydin, **nom. nov.** \equiv *Spiradiclis longipedunculata* W.L.Sha & X.X.Chen in Acta Bot. Austro Sin. 1: 30, 35. 1983, non E.D.Merrill 1937 – Holotype: China, Guangxi, Daxin Xian, 11 Apr 1978, *C.G. Wei 2-435* (GXMI).
Note. – This species is named after Dr. Wen Lan Sha for her contribution on the flora of Rubiaceae of China.
47. *Ophiorrhiza spathulata* (X.X.Chen & C.C.Huang) Razafim. & C.Rydin, **comb. nov.** \equiv *Spiradiclis spathulata* X.X.Chen & C.C.Huang in Guihaia 13(1): 3–4, fig. 1–4. 1993 – Holotype: China. Guangxi, Ningming Xian, Duolong Xiang, shade, on rocks, 20 May 1991, *C.C. Huang 22986* (GXEM).
48. *Ophiorrhiza tonglingensis* (R.J.Wang) Razafim. & C. Rydin, **comb. nov.** \equiv *Spiradiclis tonglingensis* R.J.Wang in Nordic J. Bot. 32(5): 597–601, fig. 3, 4 & 5G–L. 2014 – Holotype: China. Guangxi Zhuang Autonomous Region, Baise City, Jingxi County, Hurun town, Tongling Gorge, on wet limestone cliffs, 23°01'08.6"N, 106°39'00.7"E, 497 m alt., 8 Apr 2013, short-styled flower, white, *R.J. Wang & S. J. Deng 2347* (IBSC; isotype: IBSC).
49. *Ophiorrhiza umbelliformis* (H.S.Lo) Razafim. & C.Rydin, **comb. nov.** \equiv *Spiradiclis umbelliformis* H.S.Lo in Bull. Bot. Res., Harbin 6(4): 36–37, pl. 1. 1986 – Holotype: China. Guangxi, Napo, Baidu, Longbu, Longhua, on limestone, 1200–1250 m alt., 22–28 Apr 1981, *D. Fang & al. 25041* (GXMI).
50. *Ophiorrhiza vietnamensis* Razafim. & C.Rydin, **nom. nov.** \equiv *Spiradiclis leptobotrya* Pit. in Lecomte & al., Fl. Indo. Chine 3: 85. 1922, non Drake 1895 – Holotype: Vietnam. Hoa Binh, Cho Bo, Tonkin Cho-bo, 12 Nov 1888, *B. Balansa 2635* (L barcode L 0001357!).
Note. – This species is named after Vietnam, to which its distribution is restricted.
51. *Ophiorrhiza wangii* Razafim. & C.Rydin, **nom. nov.** \equiv *Spiradiclis corymbosa* H.S.Lo in Wu & al., Fl. China 19: 334. 2011, non Wall. 1832 – Holotype: China. Guangxi, Daxin, Taiping, 4 Jun 1977, *D.L. Chao 2-64* (GXMI)
Note. – This species is named after Prof. Riu-Jiang Wang for his important contribution to the Chinese Rubiaceae.
52. *Ophiorrhiza wongiana* Razafim. & C.Rydin, **nom. nov.** \equiv *Spiradiclis cordata* H.S.Lo & W.L.Sha in Acta Bot. Austro Sin. 1: 30, 34, pl. 3, 4. 1983, non S.Y.Jin & Y.L. Chen 1999 – Holotype: China. Guangxi, Longzhou, on limestone, 14 Aug 1935, *S.P. Ko 55504* (IBSC barcode 00055884; isotypes: IBK barcode IBK00191518!, IBSC barcode 0510629, MO barcode MO-2049467)
Note. – This species is named after Prof. Khoon-Meng Wong for his important contribution to our knowledge of the Asian Rubiaceae.
53. *Ophiorrhiza xiei* Razafim. & C.Rydin, **nom. nov.** \equiv *Spiradiclis napoensis* D.Fang & Z.M.Xie in Acta Phytotax. Sin. 40(2): 154–155, pl. 1–3, fig. 1. 2002, non H.S.Lo 1990 – Holotype: China. Guangxi: Napo, Baidu, Nonghua, limestone hill, valley in forests, ca. 1000 m alt., 18 Apr 1991, *L. Zeng, L.S. Zhou & Z. M. Xie 1109* (GXMI)
Note. – This species is named after Dr. Zhi Ming Xie for his contribution to our knowledge of Chinese *Spiradiclis*.
54. *Ophiorrhiza xizangensis* (H.S.Lo) Razafim. & C.Rydin, **comb. nov.** \equiv *Spiradiclis xizangensis* H.S.Lo in Bull. Bot. Res., Harbin 6(4): 43. 1986 – Holotype: China. Xizang, Motuo [Medog], Beibeng, Gelin, under woods, 1800–2100 m alt., 20 May 1983, *B.S. Li & al. 3674* (PE barcode 01537457!).
55. *Ophiorrhiza yangchunensis* (R.J.Wang) Razafim. & C. Rydin, **comb. nov.** \equiv *Spiradiclis yangchunensis* R.J.Wang in Pl. Sci. J. 34(1): 14–17, fig. 1 & 2. 2016 – Holotype: China. Guangdong Prov., Yangchun County, Helang town, 22°37'N, 111°50'E, 40 m alt., 10 Nov 2014, *R.J. Wang 2917* (IBSC).

■ AUTHOR CONTRIBUTIONS

SGR and CR conceived this study. SGR assembled and analyzed the data, made all morphological observations and wrote the first draft, which was enhanced and complemented by CR. – SGR, <https://orcid.org/0000-0003-3618-4676>; CR, <https://orcid.org/0000-0002-3347-7820>

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Appendix 1. Voucher and sequence accession information.

Taxon names (sometimes followed by DNA accession numbers or numerals), voucher specimens (herbarium code), country, sequences (ETS, ITS, *ndhF*, *rbcL*, *rps16*, *trnT-F*). An asterisk (“*”) denotes new sequences; an n-dash (“-”) denotes missing sequences.

Alstonia scholaris (L.) R.Br.; *Fanning 212* (FTG); sine loco; –; –; AJ011982; X91760; AJ431032; AJ430907; *Amphidasya ambigua* (Standl.) Standl.; *J.L. Clark & C. Watt 736* (UPS); Ecuador; –; –; Y11844; –; –; *Anthospermum herbaceum* L.f.; *B. Bremer 3093* (UPS); Tanzania; –; –; X83623; –; –; *Appunia guatemalensis* Donn.Sm.; *C.L. Lundell 6675* (S); Belize; –; –; AJ288593; –; –; *Arcytophyllum aristatum* Standl.; *B. Bremer & al. 3371* (UPS); Ecuador; –; –; AJ288595; –; –; *Argostemma parvifolium* Bennet; *B. Bremer & K. Bremer 1811* (S); Malaysia; –; –; FJ695227; –; –; *Argostemma rupestre* Ridl.-bl46; *B. Bremer & K. Bremer 1609* (S); Borneo; –; –; FJ695229; –; –; *Argostemma yappii* King-bl47; *B. Bremer & K. Bremer 1675* (S); Peninsula Malaysia; –; –; FJ695239; –; –; *Batopedina pulvinellata* Robbr.; *Malaise 7695* (UPS); Democratic Republic of the Congo; –; –; AJ288596; –; –; *Bouvardia ternifolia* (Cav.) Schldl. (as *Bouvardia glaberrima* Engelm.); *H. Forbes 78.0400* (S); U.S.A.; –; –; X83626; –; –; *Calytophyllum candidissimum* (Vahl) DC.; *Sanders 1805* (FTG); unknown origin; –; –; AJ236285; X83627; AF004030; AJ847398; *Carpacoce* sp.; *B. Bremer & al. 4385* (UPS); South Africa; –; –; FJ695231; –; –; *Carphalea glaucescens* (Hiern) Verdc. (accepted name: *Dirichletia glaucescens* Hiern.); *Somali Medicinal Plant Project 215* (UPS); Somalia; –; –; Z68789; –; –; *Cephalanthus occidentalis* L.; *H. Forbes s.n.* (S); U.S.A.; –; –; AJ236288; X83629; AF004033; AJ346955; *Chassalia catatii* Drake ex Bremek.; *Razafimandimbison 480* (UPS); Madagascar; –; –; AM945305; –; –; *Coccocypselum condalia* Pers.; *Pirani & K. Bremer 4891* (SPF); Brazil; –; –; AM117217; –; –; *Coccocypselum hirsutum* Bartl. ex DC.; *B. Bremer 2700* (S); Cult at Univ. Connecticut (unknown origin); –; EU145359; U145421; X87145; EU145500; EU145548; *Coelospermum monticola* Baill. ex Guillaumin. (accepted name: *Coelospermum fragrans* (Montrouz.) Baill. ex Guillaumin.); *J.T. Johansson 87* (S); New Caledonia; –; –; AF331644; –; –; *Colletocema dewevrei* (De Wild.) E.M.A.Petit; *S. Lisowski 47195* (K); Congo; –; KJ804858; EU145409; EU145457; KF704874; EU145353; *Coprosma pumila* Hook.f.; *H. Forbes s.n.* (S); New Zealand; –; –; FJ695294; X87146; FJ695262; FJ695405; *Coptophyllum bracteatum* Korth.-cz31; *Axelius 161-S15-69583* (S); Sarawak, Malaysia; –; MH626791*; MH626856*; –; MH626910*; MH626978*; *Coptophyllum bracteatum* Korth.-cz32; *Axelius 161-S15-69590* (S); Sarawak, Malaysia; –; MH626792*; MH626857*; –; MH626911*; MH626979*; *Coussarea hydrangeifolia* (Benth.) Müll.Arg.; *Fuentes 5504* (GB); Bolivia; –; –; EU145460; –; –; *Craterispermum* sp. 1; *Eriksson & al. 999* (UPS); Madagascar; –; –;

Appendix 1. Continued.

AM945297; –; –; *Craterispermum* sp. 2; Razafimandimbison & Ravelonarivo 656 (S); Madagascar; –; –; AM945298; –; –; *Craterispermum longipedunculatum* Verdc.; *Q. Luke 9196* (UPS); Tanzania; –; –; LN680386; –; KJ805256; KJ805451; *Craterispermum motleyanum* De Block & Randriamb. (as *Craterispermum laurinum* (Poir.) Benth.); *J. Kårehed & al. 303* (UPS); Madagascar; –; –; AM945300; –; –; *Cruckshanksia hymenodon* Hook. & Arn.; *Rodriguez 10* (K); Chile; –; –; AJ288599; –; –; *Cyanoneuron cyaneum* (Hallier f.) Tange-bz85; *Beaman 10186* (L); Borneo, Indonesia; –; –; KP212813; –; –; *Cyanoneuron pubescens* (Valeton) Tange-bz86; *Ambriansyah 605* (L); Borneo, Indonesia; –; –; –; KP212817; –; –; *Damnacanthus indicus* C.F.Gaertn.; *Bremer 3107* (UPS); sine loco; –; –; Z68793; –; –; *Damnacanthus macrophyllus* Siebold ex Miq.; *Fukuoka 8792* (P); Japan; –; –; AM945285; –; –; *Danais comorensis* Drake; *Mouly 687* (P); Mayote, Comores; –; –; FJ695232; –; –; *Danais lyallii* Baker (as *Danais fragrans* (Lam.) Pers.); *Eriksson & al. 966* (S); Madagascar; –; –; FJ695233; –; –; *Danais xanthorrhoea* (K.Schum.) Bremek.; *Bremer 3079* (UPS); Tanzania; –; –; AJ236293; Z68794; AM117297; AM409329; *Declieuxia cordigera* Mart. & Zucc. ex Schult. & Schult.f.; *Pirani & Bremer 4893* (SPF); Brazil; –; –; AM117224; –; –; *Declieuxia fruticosa* (Willd. ex Roem. & Schult.) Kuntze; *B. Hammel 20875* (MO); Costa Rica; –; –; AJ002177; –; –; *Didymaea alsinoides* (Cham. & Schltdl.) Standl.; *Keller 1901* (CAS); Mexico; –; –; Z68795; –; –; *Dunnia sinensis* Tutcher 1; *Yangchun 10* (?); China; –; –; EU145467; –; –; *Dunnia sinensis* Tutcher 2; *Taishan 10* (?); China; –; –; EU145468; –; –; *Ernodea littoralis* Sw.; *M. Kiehn & al. s.n.* (WU); Cuba; –; –; AJ288601; –; –; *Fareamea multiflora* A.Rich.; *B. Bremer & al. 3331* (UPS); Ecuador; –; EU145363; EU145424; Z68796; AF004048; AF102422; *Foonchewia guangdongensis* R.J.Wang; *R. Wang 1557* (IBSC); China; –; –; JQ002641; –; –; *Gaertnera phyllosepala* Baker; *J. Kårehed & al. 274* (UPS); Madagascar; –; –; AM945288; –; –; *Gaertnera phyllostachya* Baker; *J. Kårehed & al. 272* (UPS); Madagascar; –; –; AM945289; –; –; *Galium album* Mill.; *JEA & NAT/4963* (G); sine loco; –; –; X81090; –; –; *Geophila obvallata* Didr.; *Q. Luke 9037* (UPS); Kenya; –; –; AM117228; –; –; *Gynochthodes coriacea* Blume; *C. Ridsdale XVII.C. 103* (L); Indonesia; –; –; AJ288603; –; –; *Gynochthodes* sp.; *Davis 4062* (K); Vietnam; –; –; AM945284; –; –; *Houstonia caerulea* L.; *Bremer s.n.* (UPS); Uppsala Bot. Gard. (unknown origin); –; –; AJ288604; –; –; *Keenania ophiorrhizoides* Pit.-cx21; *Puff 961125-1/2* (WU); Vietnam; MH626733*; MH626793*; MH626859*; MH626912*; MH626980*; *Keenania tonkinensis* Pit.-cy100 (as *Ophiorrhiza* sp.); *Swenson & al. 1411* (S); Vietnam; MH626734*; MH626794*; MH626860*; KP212836; MH626913*; MH626981*; *Kelloggia chinensis* Franch.; *Sun 8175* (KUN); Bhutan to China; –; –; AY570776; –; –; *Kelloggia galioides* Torr.; *Garyfield & al. 2437* (UPS); U.S.A.; –; –; DQ662179; –; –; *Knoxia platycarpa* Arn.; *Lundqvist 11302* (UPS); Sri Lanka; –; –; AJ288631; –; –; *Kohautia caespitosa* Schnizl.; *Pettersson & al. s.n.* (UPS); Tanzania; –; –; Z68800; –; –; *Lasianthus kilimandscharicus* K.Schum.; *H. Lantz 119* (UPS); Malawi; –; –; AM117237; –; –; *Lasianthus pedunculatus* E.A.Bruce; *Andreasen 71* (UPS); Tanzania; –; –; EU145368; EU145427; Z68802; EU145504; KF704936; *Leptodermis potaninii* Batalin; Cult. at Berkeley Bot. Gard. (no voucher); China; –; –; AM117241; –; –; *Leptomischus primuloides* Drake; CPG62354 (?); China; –; –; KX527450; –; –; *Lerchea bracteata* Valeton-ax46; *Axeliuss 343* (S); Sumatra, Indonesia; –; EU145537; MH626795*; MH626858*; MH626914*; MH626982*; *Luculia grandifolia* Ghose; *B. Bremer 2713* (S); Cult. at Univ. Stockholm (unknown origin); –; –; AM117346; –; –; DQ662205; AJ346929; *Luculia gratissima* (Wall.) Sweet; Cult. at Univ. Connecticut; *Storrs 870064* (?); sine loco; –; –; AM117243; –; –; *Manostachya ternifolia* E.S.Martins; *Bamps & Martins 4410* (UPS); Angola; –; –; AJ616213; –; –; *Margaritopsis acutifolia* C. Wright (accepted name); *Margaritopsis nudiflora* (Griseb.) K.Schum.; *Ekman 10248* (UPS); Cuba; –; –; AM117247; –; –; *Maschalocorymbus corymbosus* (Blume) Bremek.; *C. Ridsdale 2471* (L); Indonesia; –; –; AJ288611; –; –; *Mitchella repens* L.; *B. Bremer 2714* (UPS); U.S.A.; –; –; Z68805; –; –; *Mitrasacmopsis quadrivalvis* Jovet; *Richards 11069* (K); sine loco; –; –; AJ616214; –; –; *Morinda citrifolia* L.; *B. Bremer 3106* (UPS); Cult. Uppsala Bot. Gard. (unknown origin); –; –; X83651; –; –; *Mostuea brunonis* Didr.; *M. Thulin 7831* (UPS); Malawi; –; –; AJ235828; L14404; HQ385186; –; *Mouretia larsenii* Tange; *Beusekom & al. 4743* (P); Thailand; –; –; FJ695236; –; –; *Mycetia cauliflora* Reinw.-cv98; *Swenson & al. 1285* (S); Vietnam; –; –; KP212820; –; –; *Mycetia effusa* (Pit.) Razafim. & B.Bremer-cc63; *Nguyen Nghia Thin & al. 2353* (AAU); Vietnam; –; –; KP212823; –; –; *Mycetia fabri* (Hemsley) Razafim. & B.Bremer-ca15; *Boufford & Bartholomew 24308* (L); China; –; –; KP212824; –; –; *Mycetia gracilis* Craib; *Larsen & al. 46250* (AAU); Thailand; –; –; FJ695238; –; –; *Mycetia javanica* (Blume) Reinw. ex Korth.; *Larsen & al. 43970* (AAU); Thailand; –; –; FJ695239; –; –; *Mycetia malayana* (G.Don) Craib; *Larsen & al. 42486* (AAU); Thailand; –; –; Z68806; –; –; *Mycetia pubifolia* (Pit.) Razafim. & B.Bremer-ca17; *K. Kainulainen & al. 25* (S); Vietnam; –; –; KP212827; –; –; *Mycetia tonkinensis* (Pit.) Razafim. & B.Bremer-cc59; *Nguyen Nghia Thin & al. 3285* (AAU); Vietnam; –; –; KP212833; –; –; *Mycetia tonkinensis* (Pit.) Razafim. & B.Bremer-cc60; *Nguyen Nghia Thin & al. 3390* (AAU); Vietnam; –; –; KP212828; –; –; *Neohymenopogon parasiticus* (Wall.) Bennet 2; *B. Bremer 2743* (UPS); Cult. Univ. Stockholm (unknown origin); –; –; FJ695243; –; –; *Nertera granadensis* (Mutis ex L.f.) Druce; *CT 1348* (CONN); unknown origin; –; –; X83654; –; –; *Neurocalyx bremeri* M.B.Viswan-ax36; *J. Klackenberg & Lundin 539* (S); India; MH626735*; MH626796*; MH626861*; –; MH626915*; MH626983*; *Neurocalyx calycinus* (R.Br.) B.L.Rob.-ba53; *Thor 601* (S); Sri Lanka; MH626736*; MH626797*; MH626862*; –; MH626916*; MH626984*; *Neurocalyx calycinus* (R.Br.) B.L.Rob.-cz25; *Bremer & Bremer 1014* (S); Sri Lanka; MH626737*; MH626798*; MH626863*; –; MH626917*; MH626985*; *Neurocalyx championii* Benth. ex Thwaites-ax37; *Thor 601* (S); Sri Lanka; MH626738*; MH626799*; MH626864*; EU145463; MH626918*; MH626986*; *Neurocalyx championii* Benth. ex Thwaites-cz26; *Thor 558* (S); Sri Lanka; MH626739*; MH626800*; –; –; *Neurocalyx zeylanicus* Hook.-ay09; *B. Bremer & K. Bremer 937* (S); Sri Lanka; MH626740*; –; –; MH626919*; –; *Normandia neocaledonia* Hook.f.; *Munzinger 532* (MO); New Caledonia; –; –; AM117250; –; –; *Oldenlandia corymbosa* L.; *B. Bremer 3076* (UPS); Tanzania; –; –; X83655; –; –; *Opercularia vaginata* Juss.; *K. Bremer & Gustavsson 25* (UPS); Australia; –; –; Z68809; –; –; *Ophiorrhiza amplifolia* Drake-cz03; *K. Kainulainen & al. 20* (S); Vietnam; MH626741*; MH626801*; MH626870*; –; MH626920*; MH626987*; *Ophiorrhiza angkai* Craib-az31; *Hansen & Smitinand 12978* (AAU); Thailand; MH626742*; MH626802*; –; –; MH626921*; MH626988*; *Ophiorrhiza australiana* Benth.-cz05; *Mauritson s.n.* (S); Queensland, Australia; –; MH626803*; –; –; *Ophiorrhiza axillaris* Ridl.-az33; *Nielsen 52* (AAU); Sarawak, Malaysia; –; –; MH626865*; –; MH626922*; –; *Ophiorrhiza baviensis* Drake-az37; *Averyanov & al. VH940* (AAU); Vietnam; MH626743*; MH626804*; –; –; MH626923*; MH626989*; *Ophiorrhiza brunonis* Wight & Arn.-cz06; *J. Klackenberg & Lundin 222* (S); India; MH626744*; MH626805*; MH626866*; –; MH626924*; MH626990*; *Ophiorrhiza communis* Ridl.-ba44; *Puff & Sridith 930712-1/9* (AAU); Thailand; –; –; MH626806*; –; –; MH626925*; MH626991*; *Ophiorrhiza elmeri* Merr-ay90; *Kjeldsen & Poulsen 233* (AAU); Borneo, Indonesia; MH626745*; –; –; EU145464; MH626926*; –; –; *Ophiorrhiza fusciculata* D.Don-ba20; *Stainton 1556* (UPS); Central & E Himalaya to SE Tibet; MH626746*; MH626807*; MH626867*; –; MH626927*; MH626992*; *Ophiorrhiza harrisiana* H. Heyne-cz07; *Meebold 9933* (S); India; MH626747*; MH626808*; –; –; –; *Ophiorrhiza havilandii* Ridl.-ba86; *Erwin & Paul 27409* (K); Malaysia; MH626748*; MH626809*; MH626868*; –; MH626928*; MH626993*; *Ophiorrhiza hayatana* Ohwi-cz08; *K.-F. Chung & A. Anderberg 1273* (S); Taiwan; MH626749*; MH626810*; –; –; MH626929*; MH626994*; *Ophiorrhiza howii* H.S.Lo-cz09; *W. Kaudern 178* (S); Indonesia; MH626750*; MH626820*; –; –; –; *Ophiorrhiza japonica* Blume-az05; *Hsu 4319* (S); China; MH626750*; MH626811*; –; –; MH626930*; –; *Ophiorrhiza kwangsiensis* Merr. ex H.L.Li-ba56; *Tsang 22425* (S); China; MH626751*; MH626812*; MH626860*; –; MH626931*; –; *Ophiorrhiza larseniorum* Schanzer-az36; *Larsen & al. 40904* (AAU); Thailand; MH626752*; MH626813*; MH626873*; –; MH626932*; MH626995*; *Ophiorrhiza laxa* A.Gray-ax34; *Rova & Gustavsson 239* (GB); Fiji; MH626753*; MH626814*; MH626874*; –; –; MH626933*; MH626996*; *Ophiorrhiza laxa* A.Gray-ay15; *Smith 4418* (S); Fiji; MH626754*; MH626815*; MH626875*; –; –; MH626934*; MH626997*; *Ophiorrhiza leptantha* A.Gray-ax35; *Rova & Gustavsson 2457* (GP); Fiji; MH626755*; MH626816*; MH626876*; –; –; MH626935*; –; *Ophiorrhiza leptantha* A.Gray-ay16; *Smith 6762* (S); Fiji; MH626756*; MH626817*; MH626877*; –; –; MH626936*; MH626998*; *Ophiorrhiza leptantha* A.Gray-cz10; *Smith 785* (S); Fiji; MH626757*; MH626818*; MH626878*; –; MH626937*; MH626999*; *Ophiorrhiza liukiusens* Hayata-az06; *Furus 544* (S); Japan; MH626758*; –; MH626879*; –; MH626938*; MH627000*; *Ophiorrhiza longiflora* Blume-ba01; *Nyman 88* (UPS); Java, Indonesia; –; –; MH626819*; –; –; MH626939*; MH627001*; *Ophiorrhiza mungos* L.-cz12; *USA Typhus Commission 525* (S); sine loco; MH626761*; MH626822*; AJ130838; –; –; MH627003*; *Ophiorrhiza pedunculata* Schanzer-az28; *Larsen 46225* (AAU); Thailand; MH626762*; MH626823*; MH626896*; –; –; MH626941*; MH627004*; *Ophiorrhiza peplodes* A.Gray-

Appendix 1. Continued.

ax38; *Rova & Gustavsson 2493* (S); Fiji; MH626763*; MH626824*; MH626881*; –; MH626942*; MH627005*; *Ophiorrhiza peploides* A.Gray-ay17; *Smith 6354* (S); Fiji; MH626764*; MH626825*; MH626882*; –; MH626943*; MH627006*; *Ophiorrhiza peploides* A.Gray-cz15; *Smith 8333* (S); Fiji; MH626765*; MH626826*; MH626883*; –; MH626944*; MH627007*; *Ophiorrhiza pseudofusciculata* Schanzer-az32; *Larsen & al. 46164* (AAU); Thailand; MH626766*; MH626827*; MH626897*; –; MH626945*; MH627008*; *Ophiorrhiza pumila* Champ. ex Benth.-ay18; *Furuse 563* (S); Japan; MH626767*; MH626828*; MH626884*; –; MH626946*; MH627009*; *Ophiorrhiza pumila* Champ. ex Benth.-az100; *Tanaka & al. 13500* (UPS); Taiwan; MH626768*; MH626829*; MH626885*; –; MH626947*; MH627010*; *Ophiorrhiza radicans* Thwaites-ay19; *Fagerlind & J. Klackenberg 154b* (S); Sri Lanka; MH626769*; –; MH626886*; –; MH626948*; MH627011*; *Ophiorrhiza ripicola* Craib-az29; *Larsen & al. 44996* (AAU); Thailand; MH626770*; MH626830*; –; –; MH626949*; MH627012*; *Ophiorrhiza roxburghiana* Wight-ay20; *Meebold 13567* (S); India; MH626771*; –; MH626887*; –; MH626950*; MH627013*; *Ophiorrhiza rugosa* Wall.-ay11; *J. Klackenberg 255* (S); Sri Lanka; MH626772*; MH626831*; MH626888*; –; MH626951*; MH627014*; *Ophiorrhiza sanguinea* Blume-az34; *Averyanov & al. VHS37* (AAU); Vietnam; –; –; –; MH626952*; MH627015*; –; *Ophiorrhiza sanguinea* Blume-cz16; *Do Van Truong & al. VNMN 129* (S); Vietnam; MH626773*; MH626832*; MH626889*; –; MH626953*; –; *Ophiorrhiza sp.*-ba10; *Hepper & al. 4562* (UPS); Sri Lanka; MH626760*; MH626821*; MH626880*; –; MH626940*; MH627002*; *Ophiorrhiza sp.*-cz17; *Bremer & Bremer 1619* (S); Malaysia; MH626774*; MH626833*; –; –; MH626954*; MH627016*; *Ophiorrhiza sp.*-cz18; *Swenson & al. 1394* (S); Vietnam; MH626775*; MH626834*; MH626872*; –; MH626955*; MH627017*; *Ophiorrhiza sp.*-cz19; *Swenson & al. 1431* (S); Vietnam; MH626776*; MH626835*; –; –; MH627018*; *Ophiorrhiza sp.*-cz21; *Emanuelsson 4481* (S); Vietnam; MH626777*; MH626836*; MH626890*; –; MH626956*; MH627019*; *Ophiorrhiza subrubescens* Drake-az35; *Averyanov & al. VH1442* (AAU); Vietnam; MH626778*; MH626837*; MH626891*; –; –; MH627020*; *Ophiorrhiza thomsonii* Hook.f.-ba11; *Stainton & al. 3956* (UPS); Nepal; MH626779*; MH626838*; MH626892*; –; MH626957*; MH627021*; *Ophiorrhiza trichocarpos* Blume-az27; *Maxwell 90-817* (AAU); Thailand; MH626780*; –; MH626893*; –; MH626958*; –; *Ophiorrhiza umbricola* W.W.Sm.-cz23; *Forrest 26594* (S); Myanmar; –; MH626839*; –; –; –; *Ophiorrhiza venosa* Merr.-cz22; *Elmer 16176* (S); Philippines; MH626781*; MH626840*; MH626894*; –; MH626959*; MH627022*; *Ophiorrhiza villosa* Roxb.-az30; *Larsen & larsen 34163* (AAU); Thailand; MH626782*; MH626841*; MH626895*; –; MH626960*; MH627023*; *Ophiorrhiza winkleri* Valetton-ba43; *Sands 5798* (AAU); Borneo, Brunei; MH626783*; MH626842*; –; –; MH626961*; MH627024*; *Otiophora scabra* Zucc.; *S.T. Iversen & K. Martinson 89078* (UPS); Malawi; –; –; FJ695244; –; –; *Otomeria oculata* S.Moore; *C. Puff 821888-2/1* (K); Ethiopia; –; –; –; AJ288614; –; –; *Paederia bojeriana* (A.Rich. ex DC.) Drake; *Razafimandimbison & H. Bremer 483* (UPS); Madagascar; –; –; –; DQ662181; –; –; *Paederia majungensis* Homolle ex Puff; *Nilsson & al. D152* (UPS); Madagascar; –; –; –; DQ662184; –; –; *Paederia sambiranensis* Homolle ex Puff; *J. Kårehed & al. 238* (UPS); Madagascar; –; –; –; DQ662188; –; –; *Pagamea guianensis* Aubl.; *McDowell 5738* (ETSU); Guyana; –; –; –; AM945290; –; –; *Palicourea crocea* (Sw.) Schult; *Cordiero 2736* (SP); New World; –; –; AM945280; AM117253; AF147510; AM945259; *Parapentis silvatica* (K. Schum.) Bremek.; *B. Bremer 3091* (UPS); Tanzania; –; –; X83657; –; –; *Pauridiantha paucinervis* (Hiern) Bremek.; *Bremer 3090* (UPS); Tanzania; –; –; –; AJ236302; Z68811; AM900600; EU145578; *Pauridiantha symplocoides* (S.Moore) Bremek.; *H. Lantz 123* (UPS); Malawi; –; –; –; AY538502; –; –; *Pentanisia prunelloides* (Klotzsch) Walp.; *Bremer & al. 4316* (UPS); South Africa; –; –; –; AM117255; –; –; *Pentas lanceolata* (Forssk.) Deflers; *Bremer 2702* (UPS); Cult. Univ. Connecticut (unknown origin); –; –; –; X83659; –; –; *Pentodon pentandrus* Vatte; *B. Bremer 3082* (UPS); Tanzania; –; –; –; X83660; –; –; *Phyllis nobla* L.; *B. Bremer 3008* (UPS); Cult. Copenhagen Bot. Gard. (unknown origin); –; –; –; Z68814; –; –; *Placopoda virgata* Balf.f.; *M. Thulin & Giffri 8528* (UPS); Socotra; –; –; –; Z68815; –; –; *Plocama aucheri* (Guill.) M. Backlund & Thulin; *M. Thulin 9963* (UPS); United Arab Emirates; –; –; –; DQ662178; –; –; *Plocama calabrica* (L.f.) M. Backlund & Thulin; *Jonsell 4216* (UPS); Spain; –; –; –; AJ288620; –; –; *Plocama hymenostephana* (Jaub. & Spach) M. Backlund & Thulin; *M. Thulin 9993* (UPS); United Arab Emirates; –; –; –; DQ662190; –; –; *Plocama pendula* Aiton; *Andreasen 01* (UPS); Canary Islands; –; –; –; Z68816; –; –; *Pomax umbellata* (Gaertn.) Sol. ex A.Rich.; *B. Bremer & K. Bremer 3918* (UPS); Australia; –; –; –; AM117260; –; –; *Pravinaria leucocarpa* Bremek.; *J.H. Beaman & al. 7950* (S); Sabah, Malaysia; –; –; –; EU145441; –; –; AM900613; EU145580; *Prismatomeris albidiflora* Thwaites; *Marie 89* (P); Cambodia; –; –; –; AM945296; –; –; *Prismatomeris beccariana* (Baill. ex K.Schum.) J.T.Johanss.; *C. Ridsdale 2461* (L); Borneo, Indonesia; –; –; –; AJ288618; –; –; *Psychotria amboniana* K.Schum.; *Q. Luke 8344* (UPS); Kenya; –; –; –; AM945302; –; –; *Psychotria asiatica* L.; *K. Kainulainen & al. 38* (S); Vietnam; –; –; –; KJ805099; –; –; KJ805295; KJ805492; *Psychotria capensis* (Eckl.) Vatte; *B. Bremer & al. 4284* (UPS); South Africa; –; –; –; AM945301; –; –; *Psychotriaholtzii* (K.Schum.) E.M.A.Petit; *Q. Luke 8342* (UPS); Kenya; –; –; –; AM945304; –; –; *Psychotria kirki* Hiern.; *B. Bremer 3102* (UPS); Cult. Uppsala Bot. Gard. (unknown origin); –; –; –; X83663; –; –; *Psychotria poeppigiana* Müll.Arg. (accepted name: *Palicourea tomentosa* (Aubl.) Borhidi; *B. Bremer 3330* (UPS); Ecuador; –; –; –; Z68818; –; –; *Psychotria schliebenii* E.M.A.Petit; *Q. Luke 8348* (UPS); Kenya; –; –; –; AM945303; –; –; *Rubia tinctorum* L.; *B. Bremer 3300* (UPS); Sweden; –; –; –; X83666; –; –; *Saldinia* "sp. 1" A.Rich. ex DC.; *B. Bremer & al. 4038-BB38* (UPS); Madagascar; –; –; –; AM117269; –; –; *Saprosma foetens* (Wight) K.Schum.; *J. Klackenberg 325* (S); Sri Lanka; –; –; –; DQ662193; –; –; *Saprosma fruticosa* Blume; *C. Ridsdale IV.E.157* (L); Java, Indonesia; –; –; –; DQ662194; –; –; *Schismatoclada farahimpensis* Homolle; *J. Kårehed & al. 267* (UPS); Madagascar; –; –; –; FJ695245; –; –; *Schismatoclada psychotrioides* Baker; *T. Eriksson & al. 988* (S); Madagascar; –; –; –; FJ695247; –; –; *Schismatoclada sp. 1*; *Razafimandimbison 375* (UPS); Madagascar; –; –; –; AM117271; –; –; *Schismatoclada sp. 2*; *Razafimandimbison & Ravelonarivo 625* (S); Madagascar; –; –; –; FJ695246; –; –; *Schizocolea linderi* (Hutch. & Dalziel) Bremek.; *J.G. Adam 20116* (UPS); Liberia; –; –; –; FJ695334; AM117272; EU145498; EU145546; *Schradera sp. 2*; *C. Ridsdale 2152* (L); Indonesia; –; –; –; KP212838; –; –; *Schradera stellata* Benth.; *J.L. Clark & C. Watt 783* (QCNE); Ecuador; –; –; –; Y11859; –; –; *Serissa foetida* (L.f.) Lam. (accepted name: *Serissa japonica* (Thunb.) Thunb.); China; *B. Bremer 2717* (UPS); U.S.A.; –; –; –; Z68822; –; –; *Sherardia arvensis* L.; *K. Andreasen 345* (UPS); Cult. Bergius Bot. Gard. (unknown origin); –; –; –; X81106; –; –; *Spermacoce laevis* Lam.; *B. Bremer 3062* (UPS); Ecuador; –; –; –; Z68823; –; –; *Spermatidictyon suaveolens* Roxb.; *B. Bremer 3133* (UPS); Cult. Paris Bot. Gard. (unknown origin); –; –; –; Z68824; –; –; *Spiradictis bifida* Kurz-ax48; *J.B.H. 55* (S); India; –; –; MH626843*; –; –; EU145465; MH626962*; –; –; *Spiradictis caespitosa* Blume-cz01; *Hooker s.n.* (S [S14-34295]); India; –; –; –; MH626898*; –; –; *Spiradictis cylindrica* Wall. ex Hook.f.-az17; *Larsen & al. 2050* (AAU); Thailand; MH626784*; MH626844*; MH626899*; –; MH626963*; MH627025*; *Temnopteryx sericea* Hook.f.; *Tababe 99* (WAG); Gabon; –; –; –; AM900634; HM042590; *Thecorchus wauensis* (Schweinf. ex Hiern) Bremek. (accepted name: *Oldenlandia wauensis* Schweinf. ex Hiern); *Friis & al. 2550* (UPS); Ethiopia; –; –; –; AM117282; –; –; *Theligonum cynocrambe* L. 1; *L. Struwe 1004* (UPS); Cult. Uppsala Bot. Gard. (unknown origin); –; –; –; X83668; –; –; *Theligonum cynocrambe* L. 2; *Thor 654* (S); Greece; –; –; –; FJ695248; –; –; *Triainolepis mandraensis* Homolle ex Bremek.; *Razafimandimbison 521* (UPS); Madagascar; –; –; –; FJ695250; –; –; *Triainolepis xerophila* (Bremek.) Kårehed & B.Bremer; *T. Croat 30548* (MO); Madagascar; –; –; –; AJ288633; –; –; *Trichostachys aurea* Hiern.; *L. Andersson & Nilsson 2304* (GB); Gabon; –; –; –; EU145431; EU145462; EU145507; EU145559; *Trichostachys sp.*; *B. Sonké 1725* (UPS); Cameroon; –; –; –; AJ288626; –; –; *Urophyllum ellipticum* (Wight) Thwaites; *Lundqvist 11085* (UPS); Sri Lanka; –; –; –; AJ288627; –; –; *Valantia hispida* L.; *B. Bremer 3131* (UPS); Sweden; –; –; –; FJ695251; –; –; *Xanthophyllum alopurum* Axelius-ax39; *Axelius 85b* (S); Sarawak, Malaysia; –; MH626845*; MH626900*; –; MH626964*; –; *Xanthophyllum balansae* (Pit.) H.S.Lo-az84; *Tsang 30585* (UPS); China to Vietnam; –; –; MH626846*; –; –; MH626965*; MH627026*; *Xanthophyllum borneense* (Valeton) Axelius-ax40; *Axelius 316* (S); Sarawak, Malaysia; MH626785*; –; MH626901*; MH626966*; EU145513*; –; *Xanthophyllum calycinum* (A.Gray) Benth. & Hook.f. ex Drake-ax41; *Smith 4545* (S); Vanuatu, Fiji; –; –; MH626847*; –; –; MH626967*; MH627027*; *Xanthophyllum capitellatum* (Ridl.) Ridl.; *C. Ridsdale 2473* (L); Peninsula Malaysia; –; –; MH626848*; –; –; AJ288628*; MH626968*; –; *Xanthophyllum glabrum* Axelius-ba79; *Hansen 1590* (K); Sarawak, Malaysia; –; –; MH626849*; MH626902*; –; –; MH626969*; MH627028*; *Xanthophyllum grandifolium* Valetton ex Bakh.f.-ax42; *Axelius 216* (S); Sarawak, Malaysia; MH626786*; MH626850*; –; –; MH626970*; MH627029*; *Xanthophyllum grandifolium* Valetton ex Bakh.f.-az50; *Nielsen 36* (AAU); Sarawak, Malaysia; MH626787*; MH626851*; MH626903*; –; –; MH626971*; –; *Xanthophyllum grandifolium* Valetton ex Bakh.f.-cz29; *Axelius 297* (S); Sarawak, Malaysia; MH626788*; MH626852*; MH626904*; –; –; MH626972*;

Appendix 1. Continued.

MH627030*; *Xanthophytum involucreatum* Merr.-ax43; *Axelius 160* (S); Sarawak, Malaysia; –; MH626853*; MH626905*; –; MH626973*; MH627031*; *Xanthophytum olivaceum* Merr.-ax44; *Axelius 136* (S); Sarawak, Malaysia; –; –; MH626906*; –; MH626974*; MH627032*; *Xanthophytum pubistylousum* Axelius-ax45; *Axelius 154* (S); Sarawak, Malaysia; MH626789*; MH626854*; MH626907*; –; MH626975*; MH627033*; *Xanthophytum semiorbiculare* (Bakh.f.) Axelius-ba30; *Axelius 197* (S); Sarawak, Malaysia; –; –; –; MH626976*; –; *Xanthophytum sessile* Axelius-ay10; *Axelius 147* (S); Sarawak, Malaysia; –; –; MH626908*; –; MH626977*; MH627034*; *Xanthophytum* sp. nov.-cz30; *Axelius 292* (S); Sarawak, Malaysia; MH626790*; MH626855*; MH626909*; –; –; MH627035*.
