

# Untangling a vine and its parasite: Host specificity of Philippine *Rafflesia* (Rafflesiaceae)

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**Abstract** *Rafflesia* species are endo-holoparasites of *Tetrastigma* (Vitaceae) vines. Despite receiving considerable attention because of their rarity, enormous flowers, and fascinating parasitic life style, surprisingly little is known about their host specificity and host preference. This lack of information prevents a better understanding of the evolution of the host-parasite associations and host-focused conservation management of these threatened plants. This study is the first comprehensive analysis of host specificity and preference in *Rafflesia*. A total of 180 host plants of 11 out of 13 species of Philippine *Rafflesia* as well as non-parasitized *Tetrastigma* plants from most areas where *Rafflesia* species have been found were included in our study. Morphological data and nuclear and plastid DNA sequence phylogenies were used to identify and distinguish *Tetrastigma* lineages. Our studies provide support for previous claims that *Tetrastigma* species are the exclusive hosts of *Rafflesia*. A total of eight lineages of Philippine *Tetrastigma* were identified of which six are hosts of *Rafflesia*. Most of these *Tetrastigma* lineages are hosts of multiple *Rafflesia* species. In addition, four *Rafflesia* species parasitize multiple *Tetrastigma* lineages. The finding that *Tetrastigma* lineages and *Rafflesia* species that are relatively common are involved in multiple host-parasite associations suggests that these *Rafflesia* species are less host-specific than previous studies indicated. However, because some sympatric *Tetrastigma* species are not among the observed host species, we tentatively conclude that Philippine *Rafflesia* show at least some degree of host specificity. Host phylogenies suggest that cospeciation might not have occurred in the diversification of Philippine *Rafflesia* and *Tetrastigma*.

**Keywords** co-evolution; host preference; parasitic plants; taxonomy; *Tetrastigma*; Vitaceae

**Supplementary Material** Electronic Supplement (Appendix S1) and DNA sequence alignment are available in the Supplementary Data section of the online version of this article at <http://ingentaconnect.com/content/iapt/tax>

## ■ INTRODUCTION

Parasites are paradigm breakers: they challenge basic concepts in biology, for example, in molecular evolution, speciation, physiology, conservation, and ecology (e.g., Nickrent & al., 2004; Davis & al., 2005; Press & Phoenix, 2005; Barbrook & al., 2006; Vega & al., 2008; Bromham & al., 2013; Molina & al., 2014). Parasites are therefore valuable subjects for studying the mechanisms of evolution and the origin of biodiversity (Westwood & al., 2010). However, whereas the evolution of parasitic animals has been comparatively well studied, relatively little is known about parasitic plant evolution (Norton & Carpenter, 1998; Vega & al., 2008; Irving & Cameron, 2009).

One of the outstanding questions regarding the diversification of parasitic plants is the role of co-evolution with their hosts (Vega & al., 2008). Although rare, the association between parasites and their hosts can be very specific, with parasites restricted to a single host species. This relationship can be so intimate that speciation of the host can trigger speciation of the parasite (Page, 2003). Cospeciation can be an

important process in the diversification of parasitic and mutualistic animals, fungi and bacteria (e.g., Hafner & Page, 1995; Paterson & Banks, 2001; Hommla & al., 2009; Mikheyev & al., 2010; Maneesakorn & al., 2011), although there are only a few taxa for which cospeciation has been convincingly demonstrated (Vienne & al., 2013). Cospeciation has thus far not been demonstrated in parasitic plants. Host-switching is perhaps a more common driver of diversification. It occurs when parasites evolve preferences for species other than their primary host. This can result in the formation of host races (Vega & al., 2008; Norton & Carpenter, 1998; Román & al., 2007): genetically distinct groups (races) within a parasite species that have different host species. These races may ultimately evolve into different species (Amico & Nickrent, 2009). Cospeciation and host-switching are most likely to be detected in the most specialized of parasites (Vega & al., 2008; Mikheyev & al., 2010) for which high host specificity is observed (Norton & Carpenter, 1998).

Endo-holoparasitic plants live within their host plants and are completely dependent on them for their reduced carbon.

As a result, they have extremely intimate and specialized associations with their hosts. There are only nine genera of endo-holoparasitic plants (i.e., *Apodanthes* Poit., *Bdallophytum* Eichler, *Berlinianche* (Harms) Vattimo-Gil, *Cytinus* L., *Mitrastemon* Makino, *Pilostyles* Guill., *Rafflesia* R.Br., *Rhizanthus* Dumort., *Sapria* Griff.), of which the Malesian genus *Rafflesia* (Rafflesiaceae) has the highest number of species (ca. 30; Sofiyanti & al., 2016). *Rafflesia* species are parasites of the subtropical and tropical Asian and Australasian vine genus *Tetrastigma* (Miq.) Planch. (Vitaceae). They only emerge from their hosts to produce their spectacular flowers, which are the largest of all flowering plants, reaching up to 1.5 m in diameter in *R. arnoldii* R.Br. (Nais, 2001). *Rafflesia* has recently been the focus of several research projects in which new species were discovered and described (e.g., Barcelona & al., 2009b, 2014; Balet & al., 2010; Mat-Salleh & al., 2010; Galindon & al., 2016). Molecular phylogenetic studies further revealed that *Rafflesia* mitochondria contain DNA regions that were obtained from *Tetrastigma* through horizontal gene transfer (Davis & Wurdack, 2004) and that some of these genes are expressed by the parasite (Xi & al., 2012). These findings suggest an intimate evolutionary interaction between the parasite and its host. Thus far, however, this relationship has been mainly studied with an emphasis on the parasitic partner in the interaction. Just like in many other genera of non-aerial parasitic plants (Marvier & Smith, 1997), comparatively little is known about the identity of the hosts of individual *Rafflesia* species, their host specificity (the number of species in their host range), host-preference (which species are most frequently parasitized), and other aspects of the interaction between *Rafflesia* and *Tetrastigma* (Bänziger, 1991). Such information could be used to improve our understanding of the evolutionary origin of host-parasite relationships by providing data needed for co-evolutionary studies.

The paucity of host specificity and preference information for *Rafflesia* can largely be attributed to the absence of a comprehensive taxonomic treatment of *Tetrastigma*. This is by itself a daunting task, because of the large number of *Tetrastigma* species (ca. 95) and their wide distribution (Wen, 2007; Chen & al., 2011a). In combination, three life history and morphological characteristics of *Tetrastigma* plants further complicate taxonomic studies and species identification. Firstly, *Tetrastigma* is dioecious and flowering and fruiting occurs at different times. As a result, original species descriptions (protologues) often lack information about staminate, pistillate or fruiting plants (e.g., for Philippine *Tetrastigma* species, Merrill, 1914, 1916; Wen & al., 2013). Secondly, the majority of *Tetrastigma* collections lack flowers or fruits. This is probably because it is often difficult to see the reproductive parts among the dense canopy of the trees upon which *Tetrastigma* plants climb. Moreover, parasitized *Tetrastigma* vines rarely produce reproductive structures, possibly because of diverted nutrients or direct interference by the parasite (Nais, 2001). Thirdly, *Tetrastigma* species display considerable diversity in leaf morphology, making the identification of sterile specimens very difficult. Even on the same plant, leaves can vary in number of leaflets, their size, shape of the leaflet margin, and texture.

Host specificity studies of *Rafflesia* are also complicated by their endo-holoparasitic nature: *Rafflesia* plants are cryptic in the absence of flowers or fruits. Although scars left by *Rafflesia* flowers on *Tetrastigma* vines or roots can indicate the presence of *Rafflesia*, these scars can be easily overlooked. It is therefore not possible to conclude with certainty that a *Tetrastigma* plant is not infected with *Rafflesia*.

Most *Rafflesia* species are rare and endangered (Nais, 2001) and the tropical rainforests in which they live are decreasing in size owing to development, logging, and “slash-and-burn” agriculture (Nais, 2001; Barcelona & al., 2009b). These species are thus in desperate need of effective conservation strategies. Knowing the identities of the host species of each *Rafflesia* species is essential for this, because holoparasitic plants cannot survive without their hosts (Marvier & Smith, 1997; Norton & Carpenter, 1998). Host-preference information at the population level is also important for conservation management (Marvier & Smith, 1997), because parasite seedlings might develop better on their maternal host species (i.e., the host species of the maternal parent of the seedling) than on a different host species. Examples include mistletoes such as *Phoradendron* Nutt. (Clay & al., 1985; Lichter & Berry, 1991), *Arceuthobium* M.Bieb. (Parmeter & Scharpf, 1963) and *Psittacanthus* Mart. (Buen & Ornelas, 2002) as well as Orobanchaceae (Thorogood & al., 2009).

In this study, we aim to contribute to knowledge of the evolution of the host-parasite associations between *Tetrastigma* and *Rafflesia* and the conservation of *Rafflesia* in the Philippines by determining patterns of host specificity and preference. The Philippine archipelago is home to 13 currently recognized *Rafflesia* species (Barcelona & al., 2014; Galindon & al., 2016), all of which are endemic to the country. A total of 11 *Rafflesia* species were included in our studies and their hosts were collected throughout their distribution range and in most areas from which *Rafflesia* is presently known. Morphological and DNA sequence data were used to assign parasitized and non-parasitized *Tetrastigma* plants to putative species (lineages) and to assess the phylogenetic relationships among them and plants included in a previous phylogenetic study of *Tetrastigma* (Chen & al., 2011a). We use these data (1) to identify the hosts of Philippine *Rafflesia* species, (2) to determine if individual *Tetrastigma* lineages are hosts of more than a single *Rafflesia* species, and (3) to find out if individual *Rafflesia* species parasitize more than a single *Tetrastigma* lineage. In addition, we discuss the implications of our results for determining the role of co-evolution and host-switching in the diversification of Philippine *Rafflesia*.

## ■ MATERIALS AND METHODS

**Specimen sampling.** — Tissue samples on silica gel and voucher specimens were collected from hosts of all but two currently recognized species of Philippine *Rafflesia* as well as from *Tetrastigma* plants that did not show visible signs of infection. The host plants of *R. aurantia* Barcelona & al. (Barcelona & al., 2009a) were not included in our studies. This species is

only known from one area, which is remote and was not accessible to us at the time of our study. *Rafflesia consueloae* Galindon & al. (Galindon & al., 2016) was described after our fieldwork was completed and was therefore also not sampled. A total of 234 host plants from 39 out of the ca. 46 areas from which the 11 selected species of *Rafflesia* are currently known (Appendix 1) and 91 *Tetrastigma* plants that did not show signs of infection were included in our study. The number of sampled areas ranged from 11 for *R. lagascae* Blanco and *R. speciosa* Barcelona & Fernando, which are the most abundant and widespread species of Philippine *Rafflesia*, to one for *R. leonardi* Barcelona & Pelser, *R. manillana* Teschem., *R. mira* Fernando & Ong, and *R. philippensis* Blanco, which are rarer and only known from one to three areas (Barcelona & al., 2009b; David & al., 2011; Table 2; Appendix 1). During sampling, we confirmed that the host plants of individual *Rafflesia* plants were correctly determined by tracing the roots and vines of the host plant on which *Rafflesia* flowers or flower buds were attached to where tissue and a voucher specimen of the host were collected. Voucher specimens of the *Rafflesia* and *Tetrastigma* plants that were included in our study are deposited in CAHUP, CANU, CHR, PNH and SIU (Appendix 2).

**DNA sequencing.** — Because of the difficulties regarding the taxonomic identification of *Tetrastigma* species outlined in the Introduction, DNA sequence data were generated to enable the identification of lineages of *Tetrastigma* plants that have morphological as well as genetic similarities and could be considered putative species. For this purpose, we sequenced the *atpB-rbcL*, *psbA-trnH*, and *trnL-F* intergenic spacers and the *rps16* and *trnL* introns of the plastid genome. These plastid regions were selected because they were used in the most comprehensive phylogenetic study of *Tetrastigma* to date (Chen & al., 2011a) and therefore enabled us to use the Chen & al. (2011a) dataset as phylogenetic context for our study. In addition, the internal transcribed spacer (ITS) region of the 18S-5.8S-26S nuclear ribosomal cistron was sequenced to increase phylogenetic resolution below the species level.

Total genomic DNA was extracted from *Tetrastigma* leaf tissue using the DNeasy Plant Mini Kit (Qiagen, Valencia, California, U.S.A.) and following the manufacturer's protocol. The *atpB-rbcL*, *psbA-trnH*, *rps16*, *trnL*, and *trnL-F* regions were amplified using the same primers as used by Chen & al. (2011a) in 10 µl reactions that included 1 µl of template DNA, 4 pmol of each primer and either 2× KappaTaq ReadyMix DNA Polymerase (Kappa Biosystems, Wilmington, Massachusetts, U.S.A.) or GoTaq Flexi DNA Polymerase (Promega, Madison, Wisconsin, U.S.A.) using the supplied 5× Green GoTaq Flexi buffer, 3.75 nmol of each dNTP, 25 nmol of MgCl<sub>2</sub>, and 0.4 U of polymerase. PCR conditions for *atpB-rbcL*, *rps16*, *trnL*, and *trnL-F* were as follows: an initial denaturation of 3 min at 95°C followed by 20 s at 94°C, 30 s at 50°C, 40 s at 72°C for 37 cycles, and a final extension of 5 min at 72°C. The *psbA-trnH* region was amplified under the following conditions: an initial denaturation of 5 min at 94°C followed by 40 s at 94°C, 30 s at 58°C, 50 s at 72°C for 35 cycles, and a final extension of 5 min at 72°C. PCR amplification of the ITS region (ITS1-5.8S-ITS2) was performed with primers ITSA, B, C and E

developed by Blattner (1999) in 15 µl reactions that included 1 µl of template DNA, 6 pmol of each primer, 5× Green GoTaq Flexi buffer, 3 nmol of each dNTP, 37.5 nmol of MgCl<sub>2</sub>, and 0.6 U of polymerase. The ITS region was amplified under the following conditions: an initial denaturation of 5 min at 94°C followed by 30 s at 94°C, 30 s at 58°C, 50 s at 72°C for 35 cycles, and a final extension of 5 min at 72°C. PCR products were purified with the Wizard SV Gel and PCR Clean-Up System (Promega). Cycle sequencing was carried out with BigDye Terminator 3.1 (Applied Biosystems, Foster City, California, U.S.A.) using the same primers as for the PCR amplification. The sequenced samples were run on an ABI 3130xL Genetic Analyzer at the University of Canterbury. Geneious v.6.1.7 (Biomatters, Auckland, New Zealand) was used for trace file editing. Edited sequences are deposited in GenBank (accession numbers KT597084–KT597520). Sequences were manually aligned using the program Se-AL v.2.0a11 (Rambaut, 1996). Gapcode.py v.2.1 (distributed by Richard Ree, Field Museum, Chicago, Illinois, U.S.A.) was used to code indels as binary characters using the simple indel coding method of Simmons & Ochoterena (2000). Some indels in alignment regions that were associated with strings of mononucleotides (e.g., poly-A strings) were coded as missing data for accessions obtained from GenBank, because repeat numbers were highly variable and could not be confirmed in the absence of trace files.

**Phylogenetic analyses.** — Three datasets were compiled for phylogenetic analyses. The first dataset (“plastid”) concatenates *atpB-rbcL*, *psbA-trnH*, *rps16*, *trnL*, and *trnL-F* and contains a wide selection of *Tetrastigma* accessions used by Chen & al. (2011a) as well as several other accessions available from GenBank (106 specimens in total), 2 newly sequenced extra-Philippine *Tetrastigma* species, and newly generated sequences from a subset (53) of *Tetrastigma* specimens from the Philippines. The latter specimens were selected to represent the diversity in morphology and geographic origin encountered in this genus in the Philippines. The results of phylogenetic analyses of an ITS dataset (see below) were also used to inform specimen selection for the plastid dataset. Phylogenetic analyses of the plastid data were performed to identify lineages of Philippine *Tetrastigma* and to determine their phylogenetic affinities.

The second dataset (“ITS”) is composed of ITS sequences. It contains sequences of 129 Philippine *Tetrastigma* plants, data of 2 newly sequenced extra-Philippine *Tetrastigma* species and 9 accessions obtained from GenBank. The study by Chen & al. (2011a) did not include ITS data and therefore there are only a limited number of *Tetrastigma* sequences available in GenBank that can be used to provide phylogenetic context in the present study. Because the ITS region provides more DNA sequence variation than the plastid regions utilized here, this dataset was instead used to provide greater phylogenetic resolution within the Philippine *Tetrastigma* lineages that were identified from phylogenetic analyses of the plastid dataset.

The third dataset (“combined”) contains data of the same specimens as the plastid dataset. It is composed of all plastid data as well as ITS sequences for specimens for which these data were available. This dataset was compiled after separate phylogenetic analyses of the plastid and ITS datasets indicated



the absence of well-supported (>70% bootstrap support or >0.95 posterior probability) phylogenetic incongruence. This was done with the aim of using all available data for resolving relationships among *Tetrastigma* accessions.

Sequences of *Ampelocissus* Planch., *Causonis* Raf., and *Cayratia* Juss. (all Vitaceae) were used to root the *Tetrastigma* phylogenies obtained from the plastid and combined datasets. *Causonis* is the genus that is most closely related to *Tetrastigma* (Lu & al., 2013; Wen & al., 2013). *Ampelocissus* was assigned as outgroup, because it is the most distantly related to *Tetrastigma* of the three genera. ITS sequences of *Ampelocissus* and *Cayratia* could not be unambiguously aligned with *Tetrastigma* sequences. Therefore, only an accession of *Causonis trifolia* Raf. ex B.D.Jacks. was used as outgroup for analyses of the ITS dataset.

Maximum parsimony (MP) analyses were carried out in TNT v.1.1 (Goloboff & al., 2008) using the Driven Search option with the default settings for Sectorial Searches (RSS, CSS, XSS), Ratchet, Tree Drifting and Tree Fusing; using 100 initial random addition sequences, and terminating the search after minimum length trees were found ten times. Bootstrap support was calculated with Poisson independent reweighting using 1000 replicates. Bayesian inference (BI) analyses were performed using MrBayes v.3.2.5 (Ronquist & al., 2012). Prior to the BI analyses, the Akaike information criterion in jModel-Test v.2.1.7 (Guindon & Gascuel, 2003; Darriba & al., 2012) was employed to choose nucleotide substitution models for each DNA region. The GTR+G model was used for analyses of the ITS data and the GTR+I+G model was employed for the plastid data. Indel characters were included as “restriction type” data in the BI analyses. These analyses were performed using two independent, simultaneous runs. The Markov chain Monte Carlo analyses (Geyer, 1991) were run with four chains per analysis, temperature settings of 0.001, and one tree saved per 100 generations. BI analyses were run until the average deviation of split frequencies between both simultaneous analyses reached a value below 0.01, indicating convergence. The burn-in values were determined empirically from the likelihood values. Trees were visualized using FigTree v.1.4.2 (Rambaut, 2014).

## RESULTS

**Plant collecting.** — Of the 234 *Tetrastigma* host plants that were encountered during our fieldwork, we were not able to make herbarium collections and leaf tissue samples of 54 hosts. The leaves of these plants were positioned too high in the forest canopy to be accessed or observed. Of the 180 remaining host plants, only one was flowering and two were fruiting when collected. Also for apparently non-parasitized plants, flowering and fruiting specimens were infrequently encountered.

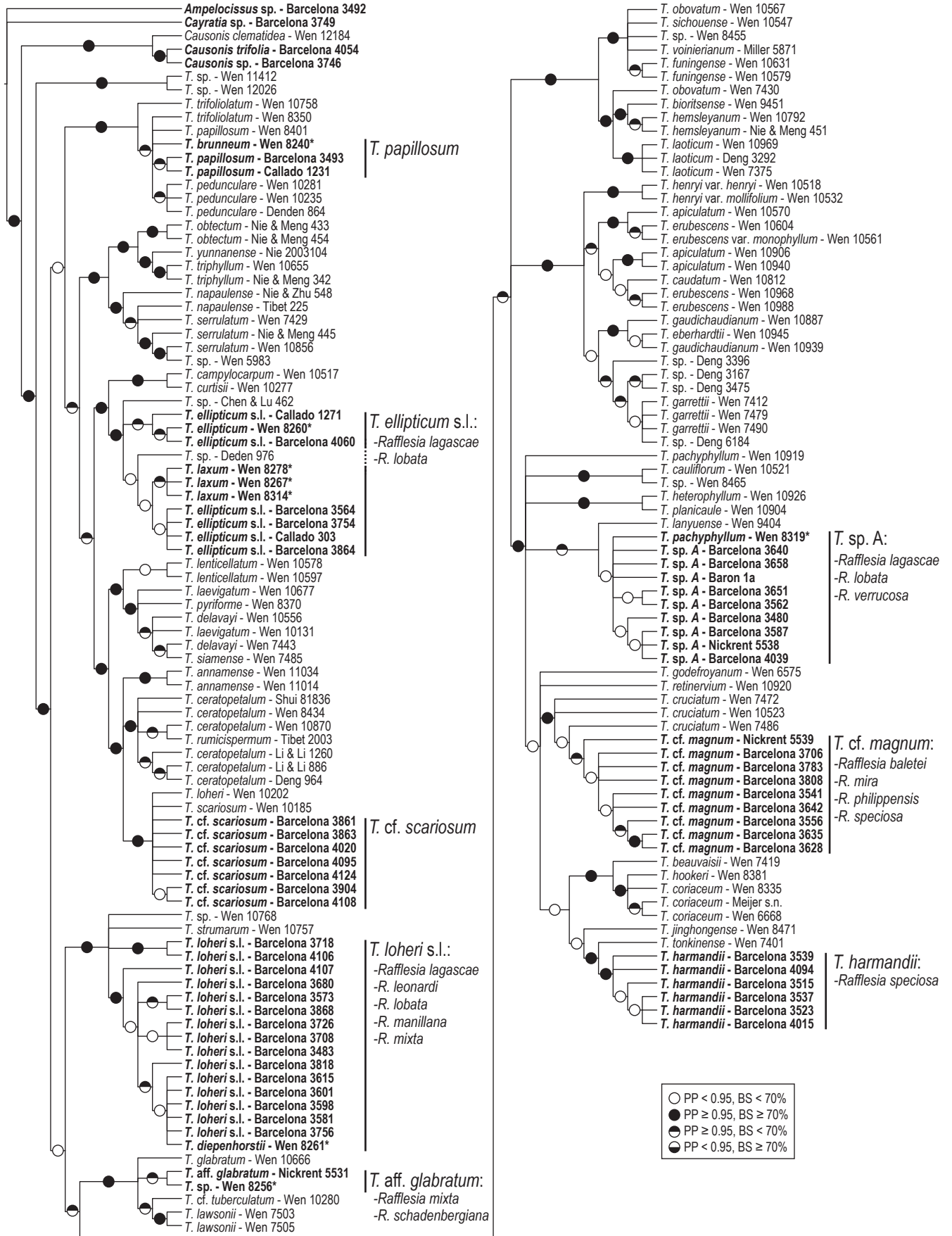
**Identification of Philippine *Tetrastigma* lineages.** — MP and BI analyses of a plastid DNA sequence dataset were performed to identify lineages of Philippine *Tetrastigma* that could be considered putative species and to determine the phylogenetic affinities among them and *Tetrastigma* species included in a previous phylogenetic study of this genus (Chen & al., 2011a). These analyses resulted in phylogenies in which specimens of Philippine *Tetrastigma* form eight phylogenetic lineages (Fig. 1) that can be morphologically distinguished from each other (Table 1). Four of these lineages are monophyletic and the members of the remaining four are placed in polytomies with non-Philippine specimens or with non-Philippine specimens nested among them. Nearly identical phylogenetic patterns were obtained from the phylogenetic analyses of a combined plastid/ITS dataset (not shown) that contains the sequences of the same specimens that are included in the plastid dataset and any phylogenetic differences between both datasets were not well supported.

Phylogenetic analyses of an ITS dataset that contains very few non-Philippine specimens, but a much larger number of Philippine specimens than the plastid and combined plastid/ITS datasets (Fig. 2), were used to provide greater phylogenetic resolution within the eight Philippine *Tetrastigma* lineages that were identified in the plastid cladograms (Fig. 1). Some of the lineages could be tentatively identified to species using morphological descriptions in protologues, other taxonomic literature, and online images of type specimens. Other lineages, however, could not be assigned to species with certainty. This was either because of a lack of information in the literature about the diagnostic characters of morphologically similar species or because these characters could not be observed in our specimens (e.g., specimens without staminate or pistillate flowers, or fruits). These lineages were assigned provisional names or tag names. Photos of representative specimens of each lineage can be viewed on the PhytoImages website (Nickrent & al., 2006).

Philippine *Tetrastigma* specimens collected by others and included in previous studies (Chen & al., 2011a, b; Lu & al., 2013; Wen & al., 2013) grouped together with the specimens that were collected for the present study, although some were assigned different species names by the authors of those studies. Unfortunately, herbarium voucher collections of some of these specimens could not be located in US or in herbaria in the Philippines. It was therefore not possible for us to verify their identifications. The *Tetrastigma* identifications are further discussed in the Electr. Suppl.: Appendix S1.

**General distribution of Philippine *Tetrastigma*.** — Of the eight Philippine *Tetrastigma* lineages that were encountered during our studies, seven were widespread and found in all three main regions of the Philippines: Luzon, Visayas, Mindanao (Table 1). *Tetrastigma* aff. *glabratum* (Blume) Planch.,

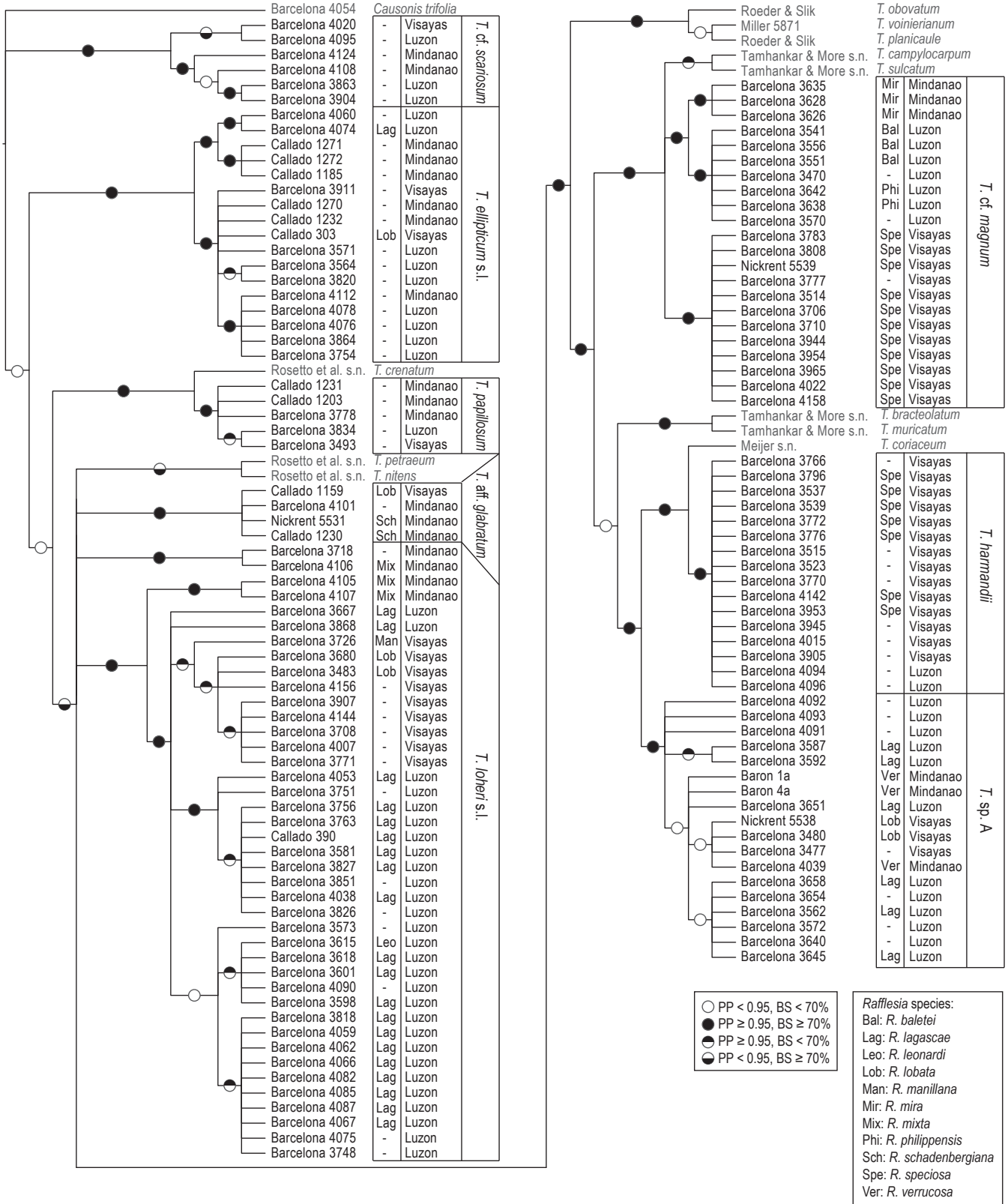
**Fig. 1.** Bayesian inference phylogeny of *atpB-rbcL*, *psbA-trnH*, *rps16*, *trnL*, and *trnL-F* DNA sequence data. Posterior probabilities (PP) and bootstrap support values (BS) obtained from maximum parsimony analyses are presented on the branches. Accessions in bold are of plants collected in the Philippines. Accessions with an asterisk are of Philippine plants included in Chen & al. (2011a). *Rafflesia* species that parasitize *Tetrastigma* lineages are indicated for each lineage.



**Table 1.** Distribution and key morphological features of all Philippine *Tetrastigma* lineages identified in this study.

<i>Tetrastigma</i> lineage	Parasitized by Philippine <i>Rafflesia</i>	Distribution in the Philippines	Tendrils	# Leaflets	Leaf morphology	Key morphological features			
						Secondary venation on adaxial leaf surface	Fruit color	Fruit shape	Epidermis of internodes
<i>T. ellipticum</i> Merr. s.l.	Yes	Luzon, Visayas (Panay), Mindanao (Dinagat, Mindanao Isl.)	Forked	1, 3, 5	Palmate	Obscure and flat, or clear and sunken	Yellow turning orange (mature fruits not observed)	Longer than wide	Lenticels relatively inconspicuous
<i>T. aff. glabratum</i> (Blume) Planch.	Yes	Luzon,* Mindanao	Simple	(4)5(6, 7)	Pedate	Clear and sunken	Fruits not observed	Fruits not observed	Lenticels often conspicuous and raised
<i>T. harmandii</i> Planch.	Yes	Luzon, Visayas (Mindoro, Negros, Panay), Mindanao	Simple	(3)5(6)	Pedate	Obscure, flat	Rusty brown	Globose or wider than long	Lenticels often conspicuous and raised
<i>T. loheri</i> Gagnep. s.l.	Yes	Luzon, Visayas (Negros, Panay, Samar), Mindanao	Simple (except for <i>Barcelona 4007</i> )	(1)3	–	Obscure and flat, or clear and sunken	Red turning dark purple turning black	Globose or longer than wide	Lenticels often conspicuous and raised
<i>T. cf. magnum</i> Merr.	Yes	Luzon, Visayas (Negros, Panay), Mindanao	Simple	(5)7	Pedate	Usually clear and sunken	White	Globose or wider than long	Lenticels often conspicuous and raised
<i>T. papillosum</i> (Blume) Planch.	No	Luzon, Visayas (Panay), Mindanao	Forked	3(4)	Pedate	Usually clear and slightly sunken	Red turning dark purple	Globose or wider than long	Very conspicuous tubercle-like epidermal outgrowths or lenticels
<i>T. cf. scariosum</i> (Blume) Planch.	No	Luzon, Visayas (Negros), Mindanao (Dinagat, Mindanao Isl.)	Forked	(3)5, 7	Pedate	Usually clear and sunken	Fruits not observed	Fruits not observed	Lenticels often conspicuous and raised
<i>Tetrastigma</i> sp. A	Yes	Luzon, Visayas (Panay), Mindanao	Simple	(1)3, 5	Pedate	Usually clear and sunken	Fruits not observed	Fruits not observed	Lenticels often conspicuous and raised

\* Specimen included in previous *Tetrastigma* research (*J. Wen 8256*, US; Chen & al., 2011a), identification not confirmed.



**Fig. 2.** Bayesian inference phylogeny of ITS1-5.8S-ITS2 DNA sequence data. Posterior probabilities (PP) and bootstrap support values (BS) obtained from maximum parsimony analyses are presented on the branches. The identities of *Rafflesia* species that parasitize individual *Tetrastigma* specimens are indicated using three-letter codes. Hyphens indicate *Tetrastigma* specimens without visible signs of infection. Accessions in grey print are of the outgroup (*Causonis trifolia*) or indicate sequences obtained from GenBank.

**Table 2.** *Tetrastigma-Rafflesia* interaction matrix.

	<i>R. baletae</i> Barcelona & Cajano (2/2)	<i>R. lagascae</i> Blanco (11/ca. 14)	<i>R. leonardi</i> Barcelona & Pelser (1/3)	<i>R. lobata</i> R. Galang & Madulid (5/ca. 5)	<i>R. manillana</i> Teschem. (1/1)	<i>R. mira</i> Fernando & Ong (1/1)	<i>R. mixta</i> Barcelona & al. (2/2)	<i>R. philip- pensis</i> Blanco (1/1)	<i>R. schaden- bergiana</i> Göpp. ex Hieron. (2/2)	<i>R. speciosa</i> Barcelona & Fernando (11/ca. 12)	<i>R. verrucosa</i> Baleta & al. (2/3)
<i>T. ellipticum</i> Merr. s.l.		1 parasitized plant (2%)		1 parasitized plant (4%)				Sympatric	Sympatric in 1 area	Sympatric in 2 areas	
<i>T. aff. glabratum</i> (Blume) Planch.		Possibly sympatric in 1 area*					1 parasitized plant (33%)		2 parasitized plants (100%)		
<i>T. harmandii</i> Planch.		Sympatric in 1 area		Sympatric in 1 area						21 parasitized plants (30%) in 8 areas (73%)	
<i>T. loheri</i> Gagnep. s.l.	Sympatric in 1 area	37 parasitized plants (77%) in 9 areas (82%)	6 parasitized plants (100%)	19 parasitized plants (83%) in 3 areas (60%)	1 parasitized plant (100%)	Sympatric	2 parasitized plants (67%) in 1 area (50%)	Sympatric		Sympatric in 6 areas	
<i>T. cf. magnum</i> Merr.	8 parasitized plants (100%)	Sympatric in 2 areas		Sympatric in 2 areas		4 parasitized plants (100%)		10 parasitized plants (100%)		48 parasitized plants (70%) in 11 areas (100%)	
<i>T. papillosum</i> (Blume) Planch.		Sympatric in 1 (or 2*) areas		Sympatric in 1 area			Sympatric in 1 area		Sympatric in 2 areas		
<i>T. cf. scariosum</i> (Blume) Planch.		Sympatric in 1 area					Sympatric in 1 area			Sympatric in 1 area	
<i>T. sp. A</i>		10 parasitized plants (21%) in 4 areas (36%)	Sympatric	3 parasitized plants (13%) in 3 areas (60%)				Sympatric		Sympatric in 1 area	6 parasitized plants (100%)

Dark grey cells: *Tetrastigma-Rafflesia* species pairs for which host-parasite relationships were observed. For each *Rafflesia* species the number of observed parasitized host plant individuals of each *Tetrastigma* host species is presented. This number is divided by the total number of observed parasitized host plant individuals for each *Rafflesia* species and presented as a percentage as a measure of relative host preference. For *Tetrastigma-Rafflesia* host-parasite interactions that were observed in more than one area, the number and percentage of areas in which this interaction was found is presented. Light grey cells: sympatric *Tetrastigma* and *Rafflesia* species for which host-parasite relationships were not observed. Numbers in parentheses following *Rafflesia* species names indicate the number of sampled areas out of the total number of areas from which each species is currently known. \*: Specimens included in previous *Tetrastigma* research (*J. Wen 8240* and *J. Wen 8256*, US; Chen & al., 2011a), not seen.



however, was only found in Mindanao and possibly in Luzon (*Wen 8256*, not located in US).

**Host specificity and preference.** — Six of the eight *Tetrastigma* lineages were identified as hosts of Philippine *Rafflesia* (Table 1). Only *T. papillosum* (Blume) Planch. and *T. cf. scariosum* (Blume) Planch. were never found to be parasitized. Except for *T. harmandii* Planch. (only parasitized by *R. speciosa*), all host lineages are host to more than one *Rafflesia* species and this number ranges from two (*T. ellipticum* Merr. s.l. and *T. aff. glabratum*) to five (*T. loheri* Gagnep. s.l.; Table 2). Seven of the 11 *Rafflesia* species included in our study were only found to parasitize a single *Tetrastigma* lineage. These were all relatively uncommon *Rafflesia* species that are currently only known from one to three areas (*R. baletii* Barcelona & Cajano, *R. leonardi*, *R. manillana*, *R. mira*, *R. philippensis*, *R. schadenbergiana* Göpp. ex Hieron., *R. verrucosa* Balet & al.). Four *Rafflesia* species were collected from two or three host lineages. These are the three most common Philippine *Rafflesia* species (*R. lagascae*, *R. lobata* R. Galang & Madulid, *R. speciosa*) and *R. mixta* Barcelona & al. Between 67% and 83% of the plants parasitized by each of these *Rafflesia* species belonged to the primary host lineage (i.e., the most commonly parasitized host lineage of an individual *Rafflesia* species) and between 2% and 33% of the individual host plants of these four *Rafflesia* species were of secondary host lineages (i.e., host lineages of individual *Rafflesia* species that are less frequently parasitized than the primary host lineage; Table 2).

**Sympatry.** — Parasitized primary and secondary host lineages co-occur in 36% (*R. lagascae*) to 82% (*R. speciosa*) of the areas in which the four *Rafflesia* species that parasitize multiple *Tetrastigma* lineages are found (Appendix 1). In up to 36% (*R. lagascae*) of the areas, primary and secondary host lineages were sympatric, but only one of these host lineages was found to be parasitized. *Rafflesia* species were also commonly found to be sympatric with *Tetrastigma* lineages that were never found to be parasitized by them (Table 2; Appendix 1). This is best illustrated by *R. lagascae*, which is sympatric with all eight *Tetrastigma* lineages that are documented in this study (Table 2), although it was only observed to parasitize three of them.

Sympatric *Rafflesia* species were only found in four of the areas that we visited. *Rafflesia lagascae* and *R. leonardi* both grow in Bolos Point (Cagayan Prov.), *R. lagascae* and *R. philippensis* are found in close vicinity at Mt. Banahaw (Quezon Prov.), and *R. lobata* and *R. speciosa* co-occur in the Aningalan/Cabladan (Antique Prov.) and Camandag/Alimodian (Iloilo Prov.) areas. In one of these areas (Bolos Point), both *Rafflesia* species parasitize the same host lineage (*T. loheri* s.l.), whereas in the three other areas the host ranges of the sympatric *Rafflesia* species are not overlapping.

**Phylogenetic host specificity patterns.** — Most main clades of the plastid DNA phylogenies contain specimens of Philippine *Tetrastigma* and those parasitized by *Rafflesia* do not form a monophyletic group (Fig. 1). In addition, *Tetrastigma* lineages that are parasitized by the same *Rafflesia* species do not form monophyletic groups to the exclusion of

species that were not observed to be parasitized. For example, the three host lineages of *R. lagascae* (*T. ellipticum* s.l., *T. loheri* s.l., *T. sp. A*) are each more closely related to *Tetrastigma* lineages that were not identified as hosts of *R. lagascae* than to each other (Fig. 1).

Some of the parasitized *Tetrastigma* lineages are composed of clades that are formed by accessions from the same region. For example, one of the three main clades of *T. cf. magnum* Merr. contains all specimens from the Visayas (Panay and Negros) that were included in our analyses, whereas a second clade is composed of all specimens from Luzon, and a third clade is made up of specimens from Mindanao (Fig. 2). Although less well resolved, similar biogeographical patterns can be observed in *T. loheri* s.l. and *Tetrastigma* sp. A. In some of these lineages, clades also appear to align with different *Rafflesia* species. For example, the Visayan *T. cf. magnum* clade contains all specimens of this lineage that are parasitized by *R. speciosa*, the Luzon clade is parasitized by *R. baletii* and *R. philippensis*, and the Mindanao clade contains the hosts of *R. mira*.

## ■ DISCUSSION

Parasitic plants show large differences in host specificity (Norton & Carpenter, 1998). For example, *Mitrastemon* (Mitrastemonaceae) shows little host specificity and parasitizes hosts belonging to various plant orders (Meijer & Veldkamp, 1993; Nickrent & al., 2004), *Alepis flavida* Tiegh. (Loranthaceae) primarily parasitizes Nothofagaceae species (Norton & Carpenter, 1998), *Cytinus* (Cytinaceae) show host specificity at the level of infrageneric sections of their host species (Vega & al., 2008), and *Epifagus virginiana* (L.) W.P.C. Barton (Orobanchaceae) is only known from *Fagus grandifolia* Ehrh. (Musselman & Press, 1995). Most parasitic plants, however, have more than a single host. Those with a relatively narrow host range often have a single “preferred” host species (i.e., primary host) in addition to a few host species that are less commonly parasitized (i.e., secondary hosts), and even generalist parasites usually prefer some host species to others (Marvier & Smith, 1997; Norton & Carpenter, 1998). Host-preference can, however, be different in different parts of the distribution area of a parasite (Clay & al., 1985) and some taxa that are host generalists at the species level can be specialists at the population or regional level (Norton & Carpenter, 1998 and references therein).

Studies of host specificity of Philippine *Rafflesia* species are complicated by widespread habitat destruction. Only an estimated 7% of natural forest cover of the Philippines remains (Ong & al., 2002) and this means that with the local extinction of *Rafflesia* populations due to the destruction of their habitat also particular host-associations might have been lost. This is exacerbated by the fact that 8 out of the 11 Philippine *Rafflesia* species that were included in our study are rare and known from only one to three areas (sometimes from very few host plants), consequently resulting in low sample sizes for those species (Appendix 1).

**Host specificity of Philippine *Rafflesia* at the genus level.**

— In line with the results of other research (Meijer, 1997; Nais, 2001; Barcelona & al., 2009b), although never before studied with a dataset as large as that used in the present study (i.e., from 180 host plants), our findings suggest that *Rafflesia* exclusively parasitizes species of *Tetrastigma*. Members of other Vitaceae genera were found to be sympatric with Philippine *Rafflesia* (particularly *Ampelocissus*, *Causonis*, and *Cayratia*), but were never observed to be parasitized. Therefore, at the genus level, *Rafflesia* appears to be very host-specific.

**Host specificity and preference at the species level.** — Our study resulted in a better characterization of the host lineages of each species of Philippine *Rafflesia* than previously available. However, pending a comprehensive taxonomic revision of *Tetrastigma*, our identifications should only be considered preliminary. Even though our approach allowed us to identify *Tetrastigma* lineages that can be morphologically and genetically distinguished from each other (Table 1; Figs. 1, 2), future research might show that these lineages are actually species complexes that can be further resolved. Because of considerable morphological variation among plants of *T. loheri* s.l. in, amongst others, the size, shape, length/width ratio, margin, and venation of their leaflets, this lineage is a prime candidate for such studies. This lineage, as well as *T. ellipticum* s.l., contains sympatric plants that are placed in different well-supported clades and thus have different phylogenetic affinities (Figs. 1, 2). Future studies might therefore prove that these lineages consist of more than a single species.

Our findings indicate that Philippine *Rafflesia* species are less host-specific than what could be concluded from previous, largely incidental, reports (as summarized in Barcelona & al., 2009b). In fact, we did not find any exclusive *Rafflesia*-*Tetrastigma* associations. Four *Rafflesia* species (*R. lagascae*, *R. lobata*, *R. mixta*, *R. speciosa*) parasitize multiple host lineages. Likewise, six out of the eight *Tetrastigma* lineages encountered are host to *Rafflesia* and five of these are host to more than one *Rafflesia* species (Table 2). Although the relative abundance of Philippine *Tetrastigma* lineages was not quantified in our study, it appears that most *Tetrastigma* lineages that are not known to be parasitized by *Rafflesia* and those that are only parasitized by a single species are relatively rare in the Philippines (Appendix 1). Similarly, *Rafflesia* species that are only known from a single host lineage are also the rarest species of this genus in the Philippines (Table 2). This might suggest that the potential host ranges of some Philippine *Rafflesia* species could be larger than what is determined in the present study. Alternatively, this could mean that rare *Rafflesia* species are rare because they are very host specific and their hosts are rare. The latter seems unlikely, however, because all of the rarest Philippine *Rafflesia* species are known from host species that are common and found throughout the Philippines (Tables 1, 2).

*Rafflesia* species are typically sympatric with *Tetrastigma* lineages that are not within their observed host range. In addition, Philippine *Rafflesia* species that infect multiple hosts are more commonly found on some *Tetrastigma* lineages than others (Table 2; Appendix 1). This might suggest that *Rafflesia*

species have some degree of host specificity and preference. Overall, *T. loheri* s.l. is the most common host of *R. lagascae* and *R. lobata*. This species was identified as the host of these *Rafflesia* species in 77% and 83% of all observed host-parasite interactions (Table 2). The other host lineages (*T. sp. A*, *T. ellipticum* s.l.) were much less frequently recorded as hosts of *R. lagascae* and *R. lobata* (21% and 2%, 13% and 4%, resp.; Table 2). Similarly, most *R. speciosa* parasitize *T. cf. magnum* (70%), but this species has also been found on *T. harmandii* (30%). At the local level, host-preference appears to depend on the local abundance of individual *Tetrastigma* lineages and the primary and secondary hosts of a *Rafflesia* species might vary between areas. *Rafflesia* species typically parasitize the most common *Tetrastigma* lineages in their vicinity. For example, although not quantified in the present study, we noted that *T. cf. magnum* is much more common in the Igaras area than *T. harmandii* and is also more frequently parasitized by *R. speciosa*. The reverse pattern was found in nearby Miag-ao, where *T. harmandii* is more common than *T. cf. magnum* (Appendix 1). This pattern has also been observed in other plant parasites and might indicate that their populations adapt to host species that are locally abundant (Atsatt, 1983). In this context, although secondary hosts may be important in maintaining genetic variation within parasite populations, common primary hosts are needed to sustain these populations (Norton & Carpenter, 1998).

An alternative hypothesis to explain the observed differences in how often individual *Tetrastigma* lineages are parasitized by particular *Rafflesia* species should also be considered. Most *Tetrastigma* plants in an area do not appear to be parasitized by *Rafflesia* even if they belong to the locally most common host lineage. The observation that *Rafflesia* species are usually found on locally more common *Tetrastigma* lineages and are not observed to parasitize lineages that are relatively rare might therefore even be expected if *Rafflesia* species could not discriminate between *Tetrastigma* lineages. In other words, because parasite abundance is relatively low compared to host abundance, the probability that a parasite is observed on a rare host might be extremely small and this association might therefore have remained undetected during our studies. Although our present data do not allow us to conclusively reject this hypothesis, we think that it is more likely that *Rafflesia* species have at least some degree of host specificity and preference. Perhaps this is best observed in the three areas where two *Rafflesia* species with non-overlapping host ranges are sympatric (Mt. Banahaw, Camandag/Alimodian, Aningalan/Cabladan). In these areas, one *Rafflesia* species and its potential host lineages are much less common than the other species and its host lineages. For example, *R. philippensis* is common in the Mt. Banahaw area and so is its exclusive host, *T. cf. magnum* (Appendix 1). In contrast, *R. lagascae* is only known from a single *T. loheri* s.l. host plant in the Mt. Banahaw area and this lineage is much less common (Appendix 1). This might suggest that *R. lagascae* has adapted to *T. loheri* s.l. and the other lineages in its host range, perhaps in an area where these lineages are more common, and that the low abundance of these hosts in the Mt. Banahaw area prevents *R. lagascae* from being as abundant as it is in other areas.

In summary, although we tentatively conclude from our data that Philippine *Rafflesia* show a degree of host specificity and host preference at the species level, quantitative surveys are needed to determine if sympatric *Tetrastigma* species are statistically less frequently or more frequently parasitized than can be expected in the absence of host specificity and preference.

**Evolution of host-parasite associations in Philippine *Rafflesia*.** — Cospeciation of parasites and their hosts has thus far not been demonstrated in plants. Because it requires high host specificity, cospeciation would be most likely detected in highly specialized parasites (Norton & Carpenter, 1998; Vega & al., 2008; Mikheyev & al., 2010) and endo-holoparasitic plants such as *Rafflesia* are therefore suitable study systems. Our results, however, show that Philippine *Rafflesia* are not highly host-specific. Although *Rafflesia* species have only been observed to parasitize *Tetrastigma*, the most common species of Philippine *Rafflesia* are parasites of two or three *Tetrastigma* lineages and these are relatively distantly related to each other (Figs. 1, 2). Cospeciation in these lineages therefore seems unlikely, because a speciation event in one of the hosts would not likely result in speciation in a parasite that already has the ability to infect several other hosts (Norton & Carpenter, 1998). In addition, the phylogenetic relationships between host-lineages do not show patterns that suggest cospeciation. Such a pattern would show sister-group relationships between *Tetrastigma* lineages that are each parasitized by different species of *Rafflesia*. If these *Rafflesia* species were also sister, and if the timing of the speciation events in the most recent common ancestors of both species for the hosts and parasites coincided, then this pattern would be compatible with cospeciation. However, we did not identify in our study sister-group relationships between parasitized Philippine *Tetrastigma* lineages. Our findings therefore suggest that cospeciation might not have occurred in the diversification of Philippine *Rafflesia* and *Tetrastigma*.

That being said, some of the lineages of Philippine *Tetrastigma* are composed of clades that align well with different *Rafflesia* species (e.g., *T. cf. magnum*, Fig. 2). If future studies would show that these clades represent different *Tetrastigma* species, then these patterns might be compatible with cospeciation. However, considering that these clades also align with different regions in the Philippines and *Rafflesia* species are endemic to these regions, they might instead be biogeographic in origin. As well as further studies aimed at clarifying species delimitation in *Tetrastigma*, phylogenetic studies of Philippine *Rafflesia* need to be carried out to then allow cophylogenetic analyses to be conducted. Such studies are needed to more conclusively determine if *Rafflesia* and *Tetrastigma* species have cospeciated. Thus far, only four species of Philippine *Rafflesia* have been included in phylogenetic analyses and the relationships between them are poorly resolved and supported (Bendiksby & al., 2010).

Host-switching might have been an alternative driver of diversification of Philippine *Rafflesia*. This mode of speciation would, however, also require high host specificity, because it relies on reproductive isolation between parasites that have colonized a new host species and those that are growing on the ancestral host species. Because the most common Philippine

*Rafflesia* species parasitize multiple hosts, host-switching would not appear to have resulted in parasite speciation in these lineages. Future work aimed at studying genetic differentiation between conspecific *Rafflesia* plants that have parasitized different host lineages might reveal if these host-related *Rafflesia* groups are genetically distinct from each other and therefore might be incipient species.

**Conservation of Philippine *Rafflesia*.** — Ten of the 13 species of Philippine *Rafflesia* have only been found in one to three locations (Table 2) and some of them are only known from a handful of host plants. In addition, their habitats are under continuous threat by illegal logging and slash-and-burn agriculture, although some species are found within Protected Areas (Barcelona & al., 2009b). As far as we are aware, host-focused conservation management of Philippine *Rafflesia* has only taken place for *R. schadenbergiana*, a species that is currently only known from two host plant individuals. As part of the conservation strategy for this species, rooted cuttings of *Tetrastigma* were planted in the vicinity of one of the host plants in an attempt to increase host availability. Our host specificity and preference data can contribute to this and other host-based conservation efforts by providing site-specific host-range information. These data are important, because parasite seedlings might develop better on the same host species that their maternal parent grew on than on a different host species (Parmeter & Scharpf, 1963; Clay & al., 1985; Lichter & Berry, 1991; Buen & Ornelas, 2002; Thorogood & al., 2009). Similarly, host specificity and preference data can be used to assess local host-availability in areas where *Rafflesia* species are under threat. Finally, because *Rafflesia* plants are very difficult to find when their flower buds, flowers or fruits are absent, information about the identity of potential host plants might allow conservationists to identify potentially infected host plants more easily.

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## Appendix 1. Continued.

<i>Rafflesia</i> species	Collection areas	Parasitized <i>Tetrastigma</i> species (# parasitized plants recorded)	Non-parasitized <i>Tetrastigma</i> species
<i>R. philippensis</i> Blanco	-Mt. Banahaw, Quezon	<i>T. cf. magnum</i> (10)	<i>T. ellipticum</i> s.l. <i>T. loheri</i> s.l. <i>T. sp. A</i>
<i>R. schadenbergiana</i> Göpp. ex. Hieron.	-Baungon, Bukidnon	<i>T. aff. glabratum</i> (1)	<i>T. papillosum</i>
	-Lantapan, Bukidnon	<i>T. aff. glabratum</i> (1)	<i>T. ellipticum</i> s.l. <i>T. papillosum</i>
<i>R. speciosa</i> Barcelona & Fernando	-Culasi, Antique	<i>T. cf. magnum</i> (3)	
	-Barbaza, Antique	<i>T. harmandii</i> Planch. (1)	
		<i>T. cf. magnum</i> (3)	
	-Valderrama, Antique	<i>T. harmandii</i> (2)	<i>T. loheri</i> s.l.
		<i>T. cf. magnum</i> (9)	
	-Villa Valderrama, Antique	<i>T. harmandii</i> (3)	<i>T. loheri</i> s.l.
		<i>T. cf. magnum</i> (2)	
	-Camandag/Alimodian, Iloilo	<i>T. cf. magnum</i> (2)	<i>T. loheri</i> s.l.
	-Igaras, Iloilo	<i>T. cf. magnum</i> (9)	<i>T. harmandii</i> <i>T. loheri</i> s.l.
		<i>T. harmandii</i> (3)	<i>T. ellipticum</i> s.l.
		<i>T. cf. magnum</i> (3)	<i>T. sp. A</i>
		Unknown (1)	
	-Imparayan, Antique	<i>T. harmandii</i> (1)	
		<i>T. cf. magnum</i> (2)	
-Miag-ao, Iloilo	<i>T. harmandii</i> (8)	<i>T. loheri</i> s.l.	
	<i>T. cf. magnum</i> (2)		
	Unknown (1)		
	<i>T. harmandii</i> (2)		
	<i>T. cf. magnum</i> (5)		
	<i>T. harmandii</i> (1)	<i>T. loheri</i> s.l.	
	<i>T. cf. magnum</i> (5)		
<i>R. verrucosa</i> Balete & al.	-Mt. Balatukan, Misamis Oriental	<i>T. sp. A</i> (1)	
	-Mt. Kampalili, Davao Oriental	<i>T. sp. A</i> (5)	

## Appendix 2. Species names and GenBank accession numbers (where appropriate) of specimens studied.

Voucher data follows the following format: Taxon name, geographic origin, collector and collection number (herbarium code), ITS, *atpB-rbcL*, *psbA-trnH*, *rps16*, *trnL* & *trnL-F* GenBank accession number. \*, new sequence; –, missing data.

*Ampelocissus* sp., Philippines, Antique Prov., Pandan, *J.F. Barcelona 3492* with *P.B. Pelser* (CAHUP/CANU), –, KT597333\*, KT597460\*, KT597280\*, KT597216\*; *Causonis clematidea* (F.Muell.) Domin, Australia, cult., *Wen 12184*, –, KC166297, KC166552, KC166388, KC166625; *Causonis* sp., Philippines, Camarines Sur Prov., Buhí, *J.F. Barcelona 3746* with *P.B. Pelser* & *N. Gapas* (CANU), –, –, –, KT597283\*, KT597219\*; *Causonis trifolia* (L.) Raf., Philippines, Antique Prov., Sibalom, Egaña, *J.F. Barcelona 3767* with *P.B. Pelser* (CANU); *C. trifolia*, Philippines, Palawan Prov., cult., *J.F. Barcelona 4054* (No voucher), KT597084\*, KT597334\*, KT597461\*, KT597281\*, KT597217\*; *Cayratia* sp., Philippines, Camarines Sur/Albay Prov., Mt. Malinao, *J.F. Barcelona 3749* with *P.B. Pelser* (CANU), –, KT597335\*, KT597462\*, KT597282\*, KT597218\*; *Cayratia* sp., Philippines, Iloilo Prov., Iloilo, *J.F. Barcelona 3765* with *P.B. Pelser* (CANU), –, KT597337\*, –, –, –, *Cayratia* sp., Philippines, Quezon Prov., Mt. Banahaw, *J.F. Barcelona 3825* with *P.B. Pelser* (CANU), –, KT597338\*, –, –, –, *Cayratia* sp., Philippines, Surigao del Norte Prov., Mainit, *J.F. Barcelona 4041* (CANU); *Rafflesia baletei* Barcelona & Cajano, Philippines, Camarines Sur Prov., Mt. Isarog, *J.F. Barcelona 3542* with *D.L. Nickrent* & *P.B. Pelser* (CAHUP/SIU); *R. baletei*, Philippines, Camarines Sur Prov., Mt. Asog, *J.F. Barcelona 3550* with *D.L. Nickrent*, *P.B. Pelser* & *D. Bagacina* (CAHUP/SIU); *R. lagascae*, Philippines, Bataan Prov., Mt. Natib, *J.F. Barcelona 3563* with *L.L. Co* (CAHUP/SIU); *R. lagascae*, Philippines, Cagayan Prov., Bolos Point, *J.F. Barcelona 3600* with *J. Payba*, *R. Echnique* & *Tabuc* (CAHUP/SIU); *R. lagascae*, Philippines, Laguna Prov., Mt. Makiling, *J.F. Barcelona 3648* with *D.L. Nickrent*, *E. Malinao* & *R. Brevia* (CAHUP/SIU); *R. lagascae*, Philippines, Quezon Prov., Mt. Irid, *J.F. Barcelona 3657* with *Joel Sarmiento* (CAHUP/SIU); *R. lagascae*, Philippines, Aurora Prov., Aurora Memorial National Park, *J.F. Barcelona 3758* et al. (CANU); *R. lagascae*, Philippines, Quezon Prov., Mt. Banahaw, *J.F. Barcelona 3819* with *P.B. Pelser* (CANU); *R. lagascae*, Philippines, Camarines Norte/Camarines Sur Prov., Mt. Labo, *J.F. Barcelona 3849* with *P.B. Pelser* (CANU/PNH); *R. lagascae*, Philippines, Aurora Prov., Mt. Mingan, *J.F. Barcelona 3867* with *P.B. Pelser* (PNH); *R. lagascae*, Philippines, Aurora Prov., Maria Aurora, *J.F. Barcelona 4033* (PNH); *R. lagascae*, Philippines, Camarines Sur/Albay Prov., Mt. Malinao, *J.F. Barcelona 4046* (CANU); *R. lagascae*, Philippines, Nueva Ecija Prov., Carranglan, *J.F. Barcelona 4055* (PNH); *R. leonardi* Barcelona & Pelser, Philippines, Cagayan Prov., Bolos Point, *J.F. Barcelona 3603*

## Appendix 2. Continued.

with *J. Payba*, *R. Echanique & Tabuc* (CAHUP/SIU); **R. lobata** R.Galang & Madulid, Philippines, Antique Prov., Pandan, *J.F. Barcelona 3475* with *P.B. Pelsner* (CAHUP/SIU); **R. lobata**, Philippines, Antique Prov., Sebaste, *J.F. Barcelona 3692* with *P.B. Pelsner* (CAHUP/SIU); **R. lobata**, Philippines, Antique Prov., San Remigio, Aningalan, *J.F. Barcelona 3698* with *P.B. Pelsner* (CAHUP/SIU); **R. lobata**, Philippines, Iloilo Prov., Alimodian, *J.F. Barcelona 3717* with *P.B. Pelsner* (CAHUP/SIU); **R. lobata**, Philippines, Iloilo Prov., Calinog, *J.R. Callado 301* (PNH); **R. manillana** Teschem., Philippines, Samar Prov., Basesy, *J.F. Barcelona 3734* et al. (CANU/PNH); **R. mira** Fernando & Ong, Philippines, Compostella Valley Prov., Mt. Candalaga, *J.F. Barcelona 3634* with *D.L. Nickrent & N. Badilla* (CAHUP/SIU); **R. mixta** Barcelona, Manting, Arbolonio, R.B.Caball. & Pelsner, Philippines, Surigao del Norte Prov., Mainit, *J.F. Barcelona 4042* (PNH); **R. mixta**, Philippines, Surigao del Sur Prov., Lanuza, *J.F. Barcelona 4100* with *P.B. Pelsner* (PNH); **R. philippensis** Blanco, Philippines, Quezon Prov., Mt. Banahaw, *J.F. Barcelona 3823* with *P.B. Pelsner* (CANU/PNH); **R. schadenbergiana** Göpp. ex Hieron., Philippines, Bukidnon Prov., Baungon, *J.F. Barcelona 3357* (SIU); **R. speciosa** Barcelona & Fernando, Philippines, Antique Prov., San Remigio, Aningalan, *J.F. Barcelona 3701* with *P.B. Pelsner* (SIU); **R. speciosa**, Philippines, Antique Prov., Villa Valderrama, *J.F. Barcelona 3769* with *P.B. Pelsner* (CANU/PNH); **R. speciosa**, Philippines, Antique Prov., Barbaza, *J.F. Barcelona 3782* (CANU/PNH); **R. speciosa**, Philippines, Antique Prov., Culasi, *J.F. Barcelona 3797* (CANU/PNH); **R. speciosa**, Philippines, Antique Prov., Sibalom, Cabladan, *J.F. Barcelona 3931* with *P.B. Pelsner* (PNH); **R. speciosa**, Philippines, Antique Prov., Sibalom, Imparayan, *J.F. Barcelona 3955* with *P.B. Pelsner* (PNH); **R. speciosa**, Philippines, Antique Prov., Sibalom, Bululacao, *J.F. Barcelona 3980* with *P.B. Pelsner* (PNH); **R. speciosa**, Philippines, Antique Prov., Sibalom, Bad-as, *J.F. Barcelona 3991* with *P.B. Pelsner* (PNH); **R. speciosa**, Philippines, Negros Occidental Prov., Mt. Kanlaon, *J.F. Barcelona 3997* with *P.B. Pelsner* (PNH); **R. speciosa**, Philippines, Iloilo Prov., Miag-a, *J.F. Barcelona 4131* with *P.B. Pelsner* (PNH); **R. speciosa**, Philippines, Iloilo Prov., Igaras, *J.F. Barcelona 4154* with *P.B. Pelsner* (PNH); **R. verrucosa** Balete, Pelsner, Nickrent & Barcelona, Philippines, Misamis Oriental Prov., Mt. Balatukan, *J.F. Barcelona 4040* (PNH); **Tetrastigma annamense** Gagnep., Vietnam, *Wen 11014*, –, HM585542, HM585682, HM585818, HM585958; **T. annamense**, Vietnam, *Wen 11034*, –, HM585543, HM585683, HM585819, HM585959; **T. apiculatum** Gagnep., China, *Wen 10570*, –, HM585544, HM585684, HM585820, HM585960; **T. apiculatum**, Vietnam, *Wen 10906*, –, HM585545, HM585685, HM585821, HM585961; **T. apiculatum**, Vietnam, *Wen 10940*, –, HM585546, HM585686, HM585822, HM585962; **T. beauvaisii** Gagnep., Thailand, *Wen 7419*, –, HM585547, HM585687, HM585823, HM585963; **T. bioritsense** (Hayata) Hsu & Kuoh, Taiwan, *Wen 9451*, –, HM585548, HM585688, HM585824, HM585964; **T. bracteolatum** Planch., India, *Tamhankar & More s.n.*, KF544878, –, –, –, **T. brunneum** Merr., Philippines, Laguna Prov., Mt. Makiling, *Wen 8240*, –, HM585549, HM585689, HM585825, HM585965; **T. campylocarpum** Planch., India, *Tamhankar & More s.n.*, KF544880, –, –, –, **T. campylocarpum**, China, *Wen 10517*, –, HM585550, HM585690, HM585826, HM585966; **T. caudatum** Merr. & Chun, Vietnam, *Wen 10812*, –, HM585551, HM585691, HM585827, HM585967; **T. cauliflorum** Merr., China, *Wen 10521*, –, HM585552, HM585692, HM585828, HM585968; **T. ceratopetalum** C.Y.Wu, Myanmar, *Deng 964*, –, HM585554, HM585694, HM585830, HM585970; **T. ceratopetalum**, China, *Li & Li 1260*, –, HM585555, HM585695, HM585831, HM585971; **T. ceratopetalum**, China, *Li & Li 886*, –, HM585556, HM585696, HM585832, HM585972; **T. ceratopetalum**, China, *Shui 81836*, –, HM585557, HM585697, HM585833, HM585973; **T. ceratopetalum**, Vietnam, *Wen 10870*, –, HM585558, HM585698, HM585834, HM585974; **T. ceratopetalum**, China, *Wen 8434*, –, HM585553, HM585693, HM585829, HM585969; **T. coriaceum** (DC.) Gagnep., Indonesia, West Sumatra. Cultivated at Missouri Botanic Garden, *W. Meijer s.n. Living plant, accession no. 930071* (MOBOT), KT597120\*, KT597367\*, KT597476\*, KT597296\*, KT597234\*; **T. coriaceum**, USA, cult., *Wen 6668*, –, HM585649, HM585784, HM585927, HM586064; **T. coriaceum**, Malaysia, *Wen 8335*, –, HM585651, HM585785, HM585922, HM586066; **T. crenatum** Jackes, Australia, *Rosetto et al. s.n.*, AY037909, –, –, –, **T. cruciatum** Craib & Gagnep., China, *Wen 10523*, –, HM585560, HM585700, HM585836, HM585976; **T. cruciatum**, Thailand, *Wen 7472*, –, HM585561, HM585701, HM585837, HM585977; **T. cruciatum**, Thailand, *Wen 7486*, –, HM585562, HM585702, HM585838, HM585978; **T. curtisii** (Ridl.) Suess., Indonesia, *Wen 10277*, –, HM585563, HM585703, HM585839, HM585979; **T. delavayi** Gagnep., China, *Wen 10556*, –, HM585564, HM585704, HM585840, HM585980; **T. delavayi**, Thailand, *Wen 7443*, –, HM585565, HM585705, HM585841, HM585981; **T. diepenhorstii** (Miq.) Latiff, Philippines, Laguna Prov., Mt. Makiling, *Wen 8261*, –, HM585567, –, HM585843, HM585983; **T. eberhardtii** Gagnep., Vietnam, *Wen 10945*, –, HM585568, HM585708, HM585844, HM585984; **T. ellipticum** Merr., Philippines, Laguna Prov., Mt. Makiling, *Wen 8260*, –, HM585569, HM585709, HM585845, HM585985; **T. ellipticum** Merr. s.l., Philippines, Bataan Prov., Mt. Natib, *J.F. Barcelona 3564* with *L.L. Co* (CAHUP/CANU), KT597145\*, KT597392\*, KT597489\*, –, KT597247\*; **T. ellipticum** s.l., Philippines, Bataan Prov., Mt. Natib, *J.F. Barcelona 3571* with *L.L. Co* (CAHUP/CANU), KT597144\*, KT597391\*, –, –, –, **T. ellipticum** s.l., Philippines, Aurora Prov., Baler, *J.F. Barcelona 3754* with *P.B. Pelsner* (No voucher), KT597154\*, KT597401\*, KT597495\*, KT597310\*, KT597253\*; **T. ellipticum** s.l., Philippines, Quezon Prov., Mt. Banahaw, *J.F. Barcelona 3820* with *P.B. Pelsner* (CANU), KT597183\*, KT597428\*, –, –, –, **T. ellipticum** s.l., Philippines, Aurora Prov., Mt. Mingan, *J.F. Barcelona 3864* with *P.B. Pelsner* (CANU), KT597186\*, KT597431\*, KT597511\*, KT597323\*, KT597269\*; **T. ellipticum** s.l., Philippines, Antique Prov., San Remigio, Aningalan, *J.F. Barcelona 3910* with *P.B. Pelsner* (CANU); **T. ellipticum** s.l., Philippines, Antique Prov., San Remigio, Aningalan, *J.F. Barcelona 3911* with *P.B. Pelsner* (CANU), KT597189\*, KT597434\*, –, –, –, **T. ellipticum** s.l., Philippines, Nueva Ecija Prov., Carranglan, *J.F. Barcelona 4060* (CANU/PNH), KT597199\*, KT597444\*, –, KT597328\*, KT597274\*; **T. ellipticum** s.l., Philippines, Nueva Ecija Prov., Carranglan, *J.F. Barcelona 4074* (CANU/PNH), KT597200\*, –, –, –, **T. ellipticum** s.l., Philippines, Nueva Ecija Prov., Carranglan, *J.F. Barcelona 4076* (CANU/PNH), KT597201\*, KT597445\*, –, –, –, **T. ellipticum** s.l., Philippines, Nueva Ecija Prov., Carranglan, *J.F. Barcelona 4078* (CANU/PNH), KT597202\*, KT597446\*, –, –, –, **T. ellipticum** s.l., Philippines, Dinagat Prov., Loreto, *J.F. Barcelona 4112* with *P.B. Pelsner* (CANU/PNH), KT597211\*, KT597455\*, –, –, –, **T. ellipticum** s.l., Philippines, Bukidnon Prov., Lantapan, *J.R. Callado 1185* (PNH), KT597172\*, –, KT597503\*, –, KT597261\*; **T. ellipticum** s.l., Philippines, Bukidnon Prov., Lantapan, *J.R. Callado 1232* (PNH), KT597176\*, KT597422\*, –, –, –, **T. ellipticum** s.l., Philippines, North Cotabato Prov., Mt. Apo, *J.R. Callado 1270* (CANU/PNH), KT597177\*, KT597423\*, –, –, –, **T. ellipticum** s.l., Philippines, North Cotabato Prov., Mt. Apo, *J.R. Callado 1271* (CANU/PNH), KT597178\*, KT597424\*, KT597505\*, KT597319\*, KT597263\*; **T. ellipticum** s.l., Philippines, North Cotabato Prov., Mt. Apo, *J.R. Callado 1272* (CANU/PNH), KT597179\*, –, KT597506\*, –, KT597264\*; **T. ellipticum** s.l., Philippines, Iloilo Prov., Calinog, *J.R. Callado 303* (PNH), KT597155\*, KT597402\*, KT597496\*, KT597311\*, KT597254\*; **T. erubescens** Planch., China, *Wen 10604*, –, HM585570, HM585710, HM585846, HM585986; **T. erubescens**, Vietnam, *Wen 10968*, –, HM585571, HM585711, HM585847, HM585987; **T. erubescens**, Vietnam, *Wen 10988*, –, HM585572, HM585712, HM585848, HM585988; **T. erubescens** Planch. var. *monophyllum* Gagnep., China, *Wen 10561*, –, HM585573, HM585713, HM585849, HM585989; **T. funingense** C.L.Li, China, *Wen 10579*, –, HM585574, HM585714, HM585850, HM585990; **T. funingense**, China, *Wen 10631*, –, HM585575, HM585715, HM585851, HM585991; **T. garrettii** Gagnep., Thailand, *Wen 7412*, –, HM585576, HM585716, HM585852, HM585992; **T. garrettii**, Thailand, *Wen 7479*, –, HM585577, –, HM585853, HM585993; **T. garrettii**, Thailand, *Wen 7490*, –, HM585578, HM585718, HM585854, HM585994; **T. gaudichaudianum** Planch., Vietnam, *Wen 10887*, –, HM585582, HM585720, HM585858, HM585998; **T. gaudichaudianum**, Vietnam, *Wen 10939*, –, HM585583, HM585721, HM585859, HM585999; **T. glabratum** (Blume) Planch., Indonesia, *Wen 10666*, –, HM585579, –, HM585855, HM585995; **T. aff. glabratum** (Blume) Planch., Philippines, Bukidnon Prov., Baungon, *D.L. Nickrent 5531* with *B. Van Ee & J.F. Barcelona* (No voucher), KT597151\*, KT597398\*, KT597492\*, KT597307\*, KT597250\*; **T. aff. glabratum**, Philippines, Bukidnon Prov., Baungon, *J.F. Barcelona 3360* (No voucher), –, KT597336\*, –, –, –, **T. aff. glabratum**, Philippines, Surigao del Sur Prov., Lanuza, *J.F. Barcelona 4101* with *P.B. Pelsner* (CANU/PNH), KT597209\*, KT597453\*, –, –, –, **T. aff. glabratum**, Philippines, Bukidnon Prov., Lantapan, *J.R. Callado 1159* (PNH), KT597171\*, KT597418\*, –, –, –, **T. aff. glabratum**, Philippines, Bukidnon Prov., Lantapan, *J.R. Callado 1230* (PNH), KT597174\*, KT597420\*, –, –, –, **T. godefroyanum** Planch., China, *Wen 6575*, –, HM585581, HM585719, HM585857, HM585997; **T. harmandii** Planch., Philippines, Antique Prov., Valderrama, *J.F. Barcelona 3515* with *D.L. Nickrent & P.B. Pelsner* (CAHUP/CANU), KT597131\*, KT597378\*, KT597483\*, –, KT597241\*; **T. harmandii**, Philippines, Antique Prov., Valderrama, *J.F. Barcelona 3523* with *D.L. Nickrent & P.B. Pelsner* (CAHUP/CANU), KT597130\*, KT597377\*, KT597482\*, –, KT597240\*; **T. harmandii**, Philippines, Antique Prov., Valderrama, *J.F. Barcelona 3537* with *D.L. Nickrent & P.B. Pelsner* (CAHUP/CANU), KT597129\*, KT597376\*, KT597481\*, KT597300\*, –, **T. harmandii**, Philippines, Antique Prov., Valderrama, *J.F. Barcelona 3539* with *D.L. Nickrent & P.B. Pelsner* (CAHUP/CANU), KT597128\*, KT597375\*, KT597480\*, –, KT597238\*; **T. harmandii**, Philippines, Antique Prov., Sibalom, Egaña, *J.F. Barcelona 3766* with *P.B. Pelsner* (CANU), KT597165\*, KT597412\*, –, –, –;



## Appendix 2. Continued.

*T. harmandii*, Philippines, Antique Prov., Villa Valderrama, *J.F. Barcelona 3770 with P.B. Pelser* (CANU), KT597166\*, KT597413\*, –, –, –; *T. harmandii*, Philippines, Antique Prov., Villa Valderrama, *J.F. Barcelona 3772 with P.B. Pelser* (CANU), KT597167\*, KT597414\*, –, –, –; *T. harmandii*, Philippines, Antique Prov., Villa Valderrama, *J.F. Barcelona 3776 with P.B. Pelser* (CANU), KT597168\*, KT597415\*, –, –, –; *T. harmandii*, Philippines, Antique Prov., Barbaza, *J.F. Barcelona 3796* (CANU), KT597181\*, KT597426\*, –, –, –; *T. harmandii*, Philippines, Aurora Prov., Mt. Mingan, *J.F. Barcelona 3905 with P.B. Pelser* (CANU), KT597188\*, KT597433\*, –, –, –; *T. harmandii*, Philippines, Antique Prov., Sibalom, Cabladan, *J.F. Barcelona 3932 with P.B. Pelser* (CANU); *T. harmandii*, Philippines, Antique Prov., Sibalom, Cabladan, *J.F. Barcelona 3941 with P.B. Pelser* (CANU); *T. harmandii*, Philippines, Antique Prov., Sibalom, Cabladan, *J.F. Barcelona 3943 with P.B. Pelser* (PNH); *T. harmandii*, Philippines, Antique Prov., Sibalom, Imparayan, *J.F. Barcelona 3945 with P.B. Pelser* (PNH), KT597191\*, KT597436\*, –, –, –; *T. harmandii*, Philippines, Antique Prov., Sibalom, Imparayan, *J.F. Barcelona 3953 with P.B. Pelser* (CANU), KT597192\*, KT597437\*, –, –, –; *T. harmandii*, Philippines, Antique Prov., Sibalom, Bululacao, *J.F. Barcelona 3971 with P.B. Pelser* (CANU); *T. harmandii*, Philippines, Antique Prov., Sibalom, Bululacao, *J.F. Barcelona 3977 with P.B. Pelser* (CANU); *T. harmandii*, Philippines, Antique Prov., Sibalom, Bululacao, *J.F. Barcelona 3977 with P.B. Pelser* (No voucher); *T. harmandii*, Philippines, Antique Prov., Sibalom, Bululacao, *J.F. Barcelona 3981 with P.B. Pelser* (CANU); *T. harmandii*, Philippines, Negros Occidental Prov., Mt. Kanlaon, *J.F. Barcelona 3992 with P.B. Pelser* (No voucher); *T. harmandii*, Philippines, Negros Occidental Prov., Mt. Kanlaon, *J.F. Barcelona 4015 with P.B. Pelser* (CANU), KT597195\*, KT597440\*, KT597513\*, KT597325\*, KT597271\*; *T. harmandii*, Philippines, Ilocos Norte Prov., Pagudpud, *J.F. Barcelona 4094 with P.B. Pelser* (CANU/PNH), KT597206\*, KT597450\*, KT597516\*, –, –, –; *T. harmandii*, Philippines, Ilocos Norte Prov., Burgos, *J.F. Barcelona 4096 with P.B. Pelser* (CANU/PNH), KT597208\*, KT597452\*, –, –, –; *T. harmandii*, Philippines, Iloilo Prov., Miag-ao, *J.F. Barcelona 4130 with P.B. Pelser* (CANU/PNH); *T. harmandii*, Philippines, Iloilo Prov., Miag-ao, *J.F. Barcelona 4132 with P.B. Pelser* (CANU/PNH); *T. harmandii*, Philippines, Iloilo Prov., Miag-ao, *J.F. Barcelona 4136 with P.B. Pelser* (CANU/PNH); *T. harmandii*, Philippines, Iloilo Prov., Miag-ao, *J.F. Barcelona 4138 with P.B. Pelser* (CANU/PNH); *T. harmandii*, Philippines, Iloilo Prov., Miag-ao, *J.F. Barcelona 4140 with P.B. Pelser* (CANU/PNH); *T. harmandii*, Philippines, Iloilo Prov., Miag-ao, *J.F. Barcelona 4142 with P.B. Pelser* (CANU/PNH), KT597213\*, KT597457\*, –, –, –; *T. harmandii*, Philippines, Iloilo Prov., Igaras, *J.F. Barcelona 4157 with P.B. Pelser* (CANU/PNH); *T. hemsleyana* Diels et Gilg, China, *Nie & Meng 451*, –, HM585584, HM585722, HM585860, HM586000; *T. hemsleyana*, Vietnam, *Wen 10792*, –, HM585585, HM585723, HM585861, HM586001; *T. henryi* Gagnep. var. *henryi*, China, *Wen 10518*, –, HM585586, HM585724, HM585862, HM586002; *T. henryi* Gagnep. var. *mollifolium* W.T.Wang, China, *Wen 10532*, –, HM585587, HM585725, HM585863, HM586003; *T. heterophyllum* Gagnep., Vietnam, *Wen 10926*, –, HM585588, HM585726, HM585864, HM586004; *T. hookeri* Planch., Malaysia, *Wen 8381*, –, HM585589, HM585727, HM585865, HM586005; *T. jinghongense* C.L.Li, China, *Wen 8471*, –, HM585590, HM585728, HM585866, HM586006; *T. laevigatum* (Blume) Gagnep., Indonesia, *Wen 10131*, –, HM585591, HM585729, HM585867, HM586007; *T. laevigatum*, Indonesia, *Wen 10677*, –, HM585592, HM585730, HM585868, HM586008; *T. lanyuense* C.E.Chang, Taiwan, *Wen 9404*, –, HM585593, HM586016; *T. laxum*, Philippines, Benguet Prov., *Wen 8278*, –, HM585601, HM585739, HM585876, HM586017; *T. laxum*, Philippines, Ifugao/Mountain Prov., Mt. Polis, *Wen 8314*, –, HM585602, HM585740, HM585877, HM586018; *T. lenticellatum* C.Y.Wu, China, *Wen 10578*, –, HM585603, HM585741, HM585878, HM586019; *T. lenticellatum*, China, *Wen 10597*, –, HM585604, HM585742, HM585879, HM586020; *T. loheri* Gagnep., Indonesia, *Wen 10202*, –, HM585605, HM585743, HM585880, HM586021; *T. loheri* Gagnep. s.l., Philippines, Camarines Sur Prov., Mt. Asog, *J.F. Barcelona 3471 with N.P. Gapas* (PNH); *T. loheri* s.l., Philippines, Camarines Sur Prov., Mt. Asog, *J.F. Barcelona 3472 with N.P. Gapas* (PNH); *T. loheri* s.l., Philippines, Antique Prov., Pandan, *J.F. Barcelona 3476 with P.B. Pelser* (CAHUP/CANU); *T. loheri* s.l., Philippines, Antique Prov., Pandan, *J.F. Barcelona 3478 with P.B. Pelser* (CAHUP/CANU); *T. loheri* s.l., Philippines, Antique Prov., Pandan, *J.F. Barcelona 3483 with P.B. Pelser* (CAHUP/CANU), KT597101\*, KT597353\*, –, KT597293\*, KT597231\*; *T. loheri* s.l., Philippines, Antique Prov., Pandan, *J.F. Barcelona 3487 with P.B. Pelser* (CAHUP/CANU); *T. loheri* s.l., Philippines, Antique Prov., Pandan, *J.F. Barcelona 3491 with P.B. Pelser* (CAHUP/CANU); *T. loheri* s.l., Philippines, Antique Prov., Pandan, *J.F. Barcelona 3495 with P.B. Pelser* (CAHUP/CANU); *T. loheri* s.l., Philippines, Antique Prov., Pandan, *J.F. Barcelona 3498 with P.B. Pelser* (CAHUP/CANU); *T. loheri* s.l., Philippines, Antique Prov., Pandan, *J.F. Barcelona 3501 with P.B. Pelser* (CAHUP/CANU); *T. loheri* s.l., Philippines, Antique Prov., Pandan, *J.F. Barcelona 3503 with P.B. Pelser* (CAHUP/CANU); *T. loheri* s.l., Philippines, Antique Prov., Pandan, *J.F. Barcelona 3505 with P.B. Pelser* (CAHUP/CANU); *T. loheri* s.l., Philippines, Antique Prov., Pandan, *J.F. Barcelona 3507 with P.B. Pelser* (CAHUP/CANU); *T. loheri* s.l., Philippines, Antique Prov., Pandan, *J.F. Barcelona 3509 with P.B. Pelser* (CAHUP/CANU); *T. loheri* s.l., Philippines, Antique Prov., Valderrama, *J.F. Barcelona 3518 with D.L. Nickrent & P.B. Pelser* (CAHUP/CANU); *T. loheri* s.l., Philippines, Camarines Sur Prov., Mt. Asog, *J.F. Barcelona 3552 with D.L. Nickrent, P.B. Pelser & D. Bagacina* (CAHUP/CANU); *T. loheri* s.l., Philippines, Camarines Sur Prov., Mt. Asog, *J.F. Barcelona 3554 with D.L. Nickrent, P.B. Pelser & D. Bagacina* (CAHUP/CANU); *T. loheri* s.l., Philippines, Bataan Prov., Mt. Natib, *J.F. Barcelona 3565 with L.L. Co* (CAHUP/CANU); *T. loheri* s.l., Philippines, Bataan Prov., Mt. Natib, *J.F. Barcelona 3569 with L.L. Co* (CAHUP/CANU); *T. loheri* s.l., Philippines, Bataan Prov., Mt. Natib, *J.F. Barcelona 3573 with L.L. Co* (CAHUP/CANU), KT597090\*, –, KT597467\*, KT597287\*, KT597224\*; *T. loheri* s.l., Philippines, Camarines Norte/Camarines Sur Prov., Mt. Labo, *J.F. Barcelona 3579 with L.L. Co* (CAHUP/CANU); *T. loheri* s.l., Philippines, Camarines Norte/Camarines Sur Prov., Mt. Labo, *J.F. Barcelona 3581 with L.L. Co* (CAHUP/CANU), KT597089\*, KT597344\*, KT597466\*, –, KT597223\*; *T. loheri* s.l., Philippines, Cagayan Prov., Bolos Point, *J.F. Barcelona 3598 with J. Payba, R. Echanique & Tabuc* (CAHUP/CANU), KT597088\*, KT597343\*, KT597465\*, KT597286\*, KT597222\*; *T. loheri* s.l., Philippines, Cagayan Prov., Bolos Point, *J.F. Barcelona 3601 with J. Payba, R. Echanique & Tabuc* (CAHUP/CANU), KT597087\*, KT597342\*, KT597464\*, KT597285\*, KT597221\*; *T. loheri* s.l., Philippines, Cagayan Prov., Bolos Point, *J.F. Barcelona 3604 with J. Payba, R. Echanique & Tabuc* (CAHUP/CANU); *T. loheri* s.l., Philippines, Cagayan Prov., Bolos Point, *J.F. Barcelona 3606 with J. Payba, R. Echanique & Tabuc* (CAHUP/CANU); *T. loheri* s.l., Philippines, Cagayan Prov., Bolos Point, *J.F. Barcelona 3608 with J. Payba, R. Echanique & Tabuc* (CAHUP/CANU); *T. loheri* s.l., Philippines, Cagayan Prov., Bolos Point, *J.F. Barcelona 3612 with J. Payba, R. Echanique & Tabuc* (CAHUP/CANU); *T. loheri* s.l., Philippines, Cagayan Prov., Bolos Point, *J.F. Barcelona 3613 with J. Payba, R. Echanique & Tabuc* (CAHUP/CANU); *T. loheri* s.l., Philippines, Cagayan Prov., Bolos Point, *J.F. Barcelona 3615 with J. Payba, R. Echanique & Tabuc* (CAHUP/CANU), KT597086\*, KT597341\*, KT597463\*, KT597284\*, KT597220\*; *T. loheri* s.l., Philippines, Cagayan Prov., Bolos Point, *J.F. Barcelona 3618 with J. Payba, A. Gabriel & S. Aresta* (CAHUP/CANU), KT597085\*, KT597340\*, –, –, –; *T. loheri* s.l., Philippines, Cagayan Prov., Bolos Point, *J.F. Barcelona 3622 with J. Payba, O. Ocampo & J. Vidar* (CAHUP/CANU); *T. loheri* s.l., Philippines, Compostella Valley Prov., Mt. Candalaga, *J.F. Barcelona 3636 with D.L. Nickrent & N. Badilla* (CAHUP/CANU), –, KT597339\*, –, –, –; *T. loheri* s.l., Philippines, Quezon Prov., Mt. Irid, *J.F. Barcelona 3660 with Joel Sarmiento* (CAHUP/CANU); *T. loheri* s.l., Philippines, Quezon Prov., Mt. Irid, *J.F. Barcelona 3667 with Joel Sarmiento* (CAHUP/CANU), KT597097\*, –, KT597470\*, –, KT597227\*; *T. loheri* s.l., Philippines, Antique Prov., Sebaste, *J.F. Barcelona 3676 with P.B. Pelser* (CANU); *T. loheri* s.l., Philippines, Antique Prov., Sebaste, *J.F. Barcelona 3678 with P.B. Pelser* (CANU); *T. loheri* s.l., Philippines, Antique Prov., Sebaste, *J.F. Barcelona 3680 with P.B. Pelser* (CANU), KT597100\*, KT597352\*, KT597473\*, KT597292\*, KT597230\*; *T. loheri* s.l., Philippines, Antique Prov., Sebaste, *J.F. Barcelona 3684 with P.B. Pelser* (CANU); *T. loheri* s.l., Philippines, Antique Prov., Sebaste, *J.F. Barcelona 3686 with P.B. Pelser* (CANU); *T. loheri* s.l., Philippines, Antique Prov., Sebaste, *J.F. Barcelona 3688 with P.B. Pelser* (CANU); *T. loheri* s.l., Philippines, Antique Prov., Sebaste, *J.F. Barcelona 3690 with P.B. Pelser* (CANU); *T. loheri* s.l., Philippines, Antique Prov., Sebaste, *J.F. Barcelona 3694 with P.B. Pelser* (CANU); *T. loheri* s.l., Philippines, Iloilo Prov., Leon, Camandag, *J.F. Barcelona 3707 with P.B. Pelser* (CANU); *T. loheri* s.l., Philippines, Iloilo Prov., Leon, Camandag, *J.F. Barcelona 3708 with P.B. Pelser* (CANU), KT597099\*, KT597351\*, KT597472\*, KT597291\*, KT597229\*; *T. loheri* s.l., Philippines, Iloilo Prov., Alimodian,

## Appendix 2. Continued.

*J.F. Barcelona 3718 with P.B. Pelsler* (CANU), KT597098\*, KT597350\*, KT597471\*, KT597290\*, KT597228\*; **T. loheri** s.l., Philippines, Iloilo Prov., Ali-modian, *J.F. Barcelona 3720 with P.B. Pelsler* (CANU); **T. loheri** s.l., Philippines, Samar Prov., Basey, *J.F. Barcelona 3726 et al.* (CANU), KT597092\*, KT597346\*, KT597468\*, KT597288\*, KT597225\*; **T. loheri** s.l., Philippines, Camarines Sur Prov., Buhi, *J.F. Barcelona 3747 with P.B. Pelsler & N. Gapas* (CANU); **T. loheri** s.l., Philippines, Camarines Sur Prov., Buhi, *J.F. Barcelona 3748 with P.B. Pelsler & N. Gapas* (CANU), KT597093\*, –, –, –; **T. loheri** s.l., Philippines, Camarines Sur/Albay Prov., Mt. Malinao, *J.F. Barcelona 3750 with P.B. Pelsler* (CANU); **T. loheri** s.l., Philippines, Camarines Sur/Albay Prov., Mt. Malinao, *J.F. Barcelona 3751 with P.B. Pelsler* (CANU), KT597091\*, KT597345\*, –, –, –; **T. loheri** s.l., Philippines, Aurora Prov., Aurora Memorial National Park, *J.F. Barcelona 3756 et al.* (CANU/PNH), KT597094\*, KT597347\*, –, KT597289\*, KT597226\*; **T. loheri** s.l., Philippines, Aurora Prov., Aurora Memorial National Park, *J.F. Barcelona 3763 et al.* (CANU/PNH), KT597096\*, KT597349\*, –, –, –; **T. loheri** s.l., Philippines, Antique Prov., Villa Valderrama, *J.F. Barcelona 3771 with P.B. Pelsler* (CANU), KT597102\*, KT597354\*, –, –, –; **T. loheri** s.l., Philippines, Quezon Prov., Mt. Banahaw, *J.F. Barcelona 3818 with P.B. Pelsler* (CANU), KT597121\*, KT597368\*, KT597477\*, KT597297\*, KT597235\*; **T. loheri** s.l., Philippines, Quezon Prov., Mt. Banahaw, *J.F. Barcelona 3826 with P.B. Pelsler* (CANU), KT597103\*, KT597355\*, –, –, –; **T. loheri** s.l., Philippines, Camarines Norte/Camarines Sur Prov., Mt. Labo, *J.F. Barcelona 3827 with P.B. Pelsler* (CANU), KT597122\*, KT597369\*, –, –, –; **T. loheri** s.l., Philippines, Camarines Norte/Camarines Sur Prov., Mt. Labo, *J.F. Barcelona 3831 with P.B. Pelsler* (CANU); **T. loheri** s.l., Philippines, Camarines Norte/Camarines Sur Prov., Mt. Labo, *J.F. Barcelona 3836 with P.B. Pelsler* (CANU); **T. loheri** s.l., Philippines, Camarines Norte/Camarines Sur Prov., Mt. Labo, *J.F. Barcelona 3840 with P.B. Pelsler* (CANU); **T. loheri** s.l., Philippines, Camarines Norte/Camarines Sur Prov., Mt. Labo, *J.F. Barcelona 3845 with P.B. Pelsler* (CANU); **T. loheri** s.l., Philippines, Camarines Norte/Camarines Sur Prov., Mt. Labo, *J.F. Barcelona 3848 with P.B. Pelsler* (CANU); **T. loheri** s.l., Philippines, Camarines Norte/Camarines Sur Prov., Mt. Labo, *J.F. Barcelona 3850 with P.B. Pelsler* (CANU); **T. loheri** s.l., Philippines, Camarines Norte/Camarines Sur Prov., Mt. Labo, *J.F. Barcelona 3851 with P.B. Pelsler* (No voucher), KT597123\*, KT597370\*, –, –, –; **T. loheri** s.l., Philippines, Aurora Prov., Mt. Mingan, *J.F. Barcelona 3862 with P.B. Pelsler* (CANU); **T. loheri** s.l., Philippines, Aurora Prov., Mt. Mingan, *J.F. Barcelona 3868 with P.B. Pelsler* (CANU), KT597124\*, KT597371\*, KT597478\*, KT597298\*, KT597236\*; **T. loheri** s.l., Philippines, Antique Prov., Sibolom, Egaña, *J.F. Barcelona 3907 with P.B. Pelsler* (CANU), KT597125\*, KT597372\*, –, –, –; **T. loheri** s.l., Philippines, Negros Occidental Prov., Mt. Kanlaon, *J.F. Barcelona 4007 with P.B. Pelsler* (CANU), KT597104\*, –, –, –; **T. loheri** s.l., Philippines, Aurora Prov., Maria Aurora, *J.F. Barcelona 4038* (CANU), KT597105\*, –, –, –; **T. loheri** s.l., Philippines, Camarines Sur/Albay Prov., Mt. Malinao, *J.F. Barcelona 4050* (CANU); **T. loheri** s.l., Philippines, Camarines Sur/Albay Prov., Mt. Malinao, *J.F. Barcelona 4053* (PNH), KT597126\*, KT597373\*, –, –, –; **T. loheri** s.l., Philippines, Nueva Ecija Prov., Carranglan, *J.F. Barcelona 4056* (CANU/PNH); **T. loheri** s.l., Philippines, Nueva Ecija Prov., Carranglan, *J.F. Barcelona 4059* (CANU/PNH), KT597106\*, –, –, –; **T. loheri** s.l., Philippines, Nueva Ecija Prov., Carranglan, *J.F. Barcelona 4062* (CANU/PNH), KT597107\*, KT597356\*, –, –, –; **T. loheri** s.l., Philippines, Nueva Ecija Prov., Carranglan, *J.F. Barcelona 4066* (CANU/PNH), KT597108\*, –, –, –; **T. loheri** s.l., Philippines, Nueva Ecija Prov., Carranglan, *J.F. Barcelona 4067* (CANU/PNH), KT597109\*, KT597357\*, –, –, –; **T. loheri** s.l., Philippines, Nueva Ecija Prov., Carranglan, *J.F. Barcelona 4077* (CANU/PNH); **T. loheri** s.l., Philippines, Nueva Ecija Prov., Carranglan, *J.F. Barcelona 4079* (CANU/PNH); **T. loheri** s.l., Philippines, Nueva Ecija Prov., Carranglan, *J.F. Barcelona 4082* (CANU/PNH), KT597111\*, KT597358\*, –, –, –; **T. loheri** s.l., Philippines, Nueva Ecija Prov., Carranglan, *J.F. Barcelona 4085* (CANU/PNH), KT597112\*, KT597359\*, –, –, –; **T. loheri** s.l., Philippines, Nueva Ecija Prov., Carranglan, *J.F. Barcelona 4087* (CANU/PNH), KT597113\*, KT597360\*, –, –, –; **T. loheri** s.l., Philippines, Ilocos Norte Prov., Pagudpud, *J.F. Barcelona 4090 with P.B. Pelsler* (CANU/PNH), KT597114\*, KT597361\*, –, –, –; **T. loheri** s.l., Philippines, Surigao del Sur Prov., Lanuza, *J.F. Barcelona 4105 with P.B. Pelsler* (CANU/PNH), KT597115\*, KT597362\*, –, –, –; **T. loheri** s.l., Philippines, Surigao del Sur Prov., Lanuza, *J.F. Barcelona 4106 with P.B. Pelsler* (CANU/PNH), KT597116\*, KT597363\*, KT597474\*, KT597294\*, KT597232\*; **T. loheri** s.l., Philippines, Surigao del Sur Prov., Lanuza, *J.F. Barcelona 4107 with P.B. Pelsler* (CANU/PNH), KT597117\*, KT597364\*, KT597475\*, KT597295\*, KT597233\*; **T. loheri** s.l., Philippines, Iloilo Prov., Miag-ao, *J.F. Barcelona 4144 with P.B. Pelsler* (CANU/PNH), KT597118\*, KT597365\*, –, –, –; **T. loheri** s.l., Philippines, Iloilo Prov., Igbaras, *J.F. Barcelona 4156 with P.B. Pelsler* (CANU/PNH), KT597119\*, KT597366\*, –, –, –; **T. loheri** s.l., Philippines, Aurora Prov., Aurora Memorial National Park, *J.R. Callado 381* (CANU/PNH); **T. loheri** s.l., Philippines, Aurora Prov., Aurora Memorial National Park, *J.R. Callado 383* (CANU/PNH); **T. loheri** s.l., Philippines, Aurora Prov., Aurora Memorial National Park, *J.R. Callado 386* (CANU/PNH); **T. loheri** s.l., Philippines, Aurora Prov., Aurora Memorial National Park, *J.R. Callado 390* (CANU/PNH), KT597095\*, KT597348\*, KT597469\*, –, –, –; **T. loheri** s.l., Philippines, Aurora Prov., Aurora Memorial National Park, *J.R. Callado 392* (CANU/PNH); **T. loheri** s.l., Philippines, Aurora Prov., Aurora Memorial National Park, *J.R. Callado 394* (CANU/PNH); **T. cf. magnum** Merr., Philippines, Antique Prov., Villa Valderrama, *D.L. Nickrent 5539 with B. Van Ee & J.F. Barcelona* (SIU), KT597152\*, KT597399\*, KT597493\*, KT597308\*, KT597251\*; **T. cf. magnum**, Philippines, Quezon Prov., Mt. Banahaw, *J.F. Barcelona 3346 with M.A.O. Cajano & J. Mendua* (PNH); **T. cf. magnum**, Philippines, Quezon Prov., Mt. Banahaw, *J.F. Barcelona 3347 with M.A.O. Cajano & J. Mendua* (PNH); **T. cf. magnum**, Philippines, Camarines Sur Prov., Mt. Asog, *J.F. Barcelona 3470 with N.P. Gapas* (PNH), KT597150\*, KT597397\*, –, –, –; **T. cf. magnum**, Philippines, Camarines Sur Prov., Mt. Asog, *J.F. Barcelona 3473 with N.P. Gapas* (PNH); **T. cf. magnum**, Philippines, Antique Prov., Valderrama, *J.F. Barcelona 3514 with D.L. Nickrent & P.B. Pelsler* (CAHUP/CANU), KT597132\*, KT597379\*, –, –, –; **T. cf. magnum**, Philippines, Antique Prov., Valderrama, *J.F. Barcelona 3517 with D.L. Nickrent & P.B. Pelsler* (CAHUP/CANU); **T. cf. magnum**, Philippines, Antique Prov., Valderrama, *J.F. Barcelona 3520 with D.L. Nickrent & P.B. Pelsler* (CAHUP/CANU); **T. cf. magnum**, Philippines, Antique Prov., Valderrama, *J.F. Barcelona 3522 with D.L. Nickrent & P.B. Pelsler* (CAHUP/CANU); **T. cf. magnum**, Philippines, Antique Prov., Valderrama, *J.F. Barcelona 3525 with D.L. Nickrent & P.B. Pelsler* (CAHUP/CANU); **T. cf. magnum**, Philippines, Antique Prov., Valderrama, *J.F. Barcelona 3528 with D.L. Nickrent & P.B. Pelsler* (CAHUP/CANU); **T. cf. magnum**, Philippines, Antique Prov., Valderrama, *J.F. Barcelona 3530 with D.L. Nickrent & P.B. Pelsler* (CAHUP/CANU); **T. cf. magnum**, Philippines, Antique Prov., Valderrama, *J.F. Barcelona 3532 with D.L. Nickrent & P.B. Pelsler* (CAHUP/CANU); **T. cf. magnum**, Philippines, Antique Prov., Valderrama, *J.F. Barcelona 3534 with D.L. Nickrent & P.B. Pelsler* (CAHUP/CANU); **T. cf. magnum**, Philippines, Camarines Sur Prov., Mt. Isarog, *J.F. Barcelona 3541 with D.L. Nickrent & P.B. Pelsler* (CAHUP/CANU), KT597127\*, KT597374\*, KT597479\*, KT597299\*, KT597237\*; **T. cf. magnum**, Philippines, Camarines Sur Prov., Mt. Isarog, *J.F. Barcelona 3547 with D.L. Nickrent & P.B. Pelsler* (CAHUP/CANU); **T. cf. magnum**, Philippines, Camarines Sur Prov., Mt. Isarog, *J.F. Barcelona 3549 with P.B. Pelsler* (CAHUP/CANU); **T. cf. magnum**, Philippines, Camarines Sur Prov., Mt. Asog, *J.F. Barcelona 3551 with D.L. Nickrent, P.B. Pelsler & D. Bagacina* (CAHUP/CANU), KT597149\*, KT597396\*, –, –, –; **T. cf. magnum**, Philippines, Camarines Sur Prov., Mt. Asog, *J.F. Barcelona 3556 with D.L. Nickrent, P.B. Pelsler, D. Bagacina & F. Peñones* (CAHUP/CANU), KT597164\*, KT597411\*, KT597502\*, KT597317\*, KT597260\*; **T. cf. magnum**, Philippines, Camarines Sur Prov., Mt. Asog, *J.F. Barcelona 3557 with D.L. Nickrent, P.B. Pelsler, D. Bagacina & F. Peñones* (CAHUP/CANU); **T. cf. magnum**, Philippines, Bataan Prov., Mt. Natib, *J.F. Barcelona 3570 with L.L. Co* (CAHUP/CANU), KT597143\*, KT597390\*, –, –, –; **T. cf. magnum**, Philippines, Compostella Valley Prov., Mt. Candalaga, *J.F. Barcelona 3626 with D.L. Nickrent & N. Badilla* (CAHUP/CANU), KT597138\*, KT597385\*, –, –, –; **T. cf. magnum**, Philippines, Compostella Valley Prov., Mt. Candalaga, *J.F. Barcelona 3628 with D.L. Nickrent & N. Badilla* (CAHUP/CANU), KT597137\*, KT597384\*, KT597487\*, KT597304\*, KT597245\*; **T. cf. magnum**, Philippines, Compostella Valley Prov., Mt. Candalaga, *J.F. Barcelona 3631 with D.L. Nickrent & N. Badilla* (CAHUP/CANU); **T. cf. magnum**, Philippines, Compostella Valley Prov., Mt. Candalaga, *J.F. Barcelona 3635 with D.L. Nickrent & N. Badilla* (CAHUP/CANU), KT597136\*, KT597383\*, KT597486\*, KT597303\*, KT597244\*; **T. cf. magnum**, Philippines, Quezon Prov., Mt. Banahaw, *J.F. Barcelona 3638 with D.L. Nickrent & J. Mendua* (CAHUP/CANU), KT597133\*, KT597380\*, –, –, –; **T. cf. magnum**, Philippines, Quezon Prov., Mt. Banahaw, *J.F. Barcelona 3642 with D.L. Nickrent & J. Mendua* (CAHUP/CANU), KT597135\*, KT597382\*, KT597485\*, KT597302\*, KT597243\*; **T. cf. magnum**, Philippines, Antique Prov., San Remigio, Aningalan, *J.F. Barcelona 3704 with P.B. Pelsler* (CANU); **T. cf. magnum**, Philippines, Iloilo Prov., Leon, Camandag, *J.F. Barcelona 3706 with P.B. Pelsler* (CANU), KT597159\*, KT597406\*, KT597498\*, KT597313\*, KT597256\*; **T. cf. magnum**, Philippines, Iloilo Prov., Leon, Camandag, *J.F. Barcelona 3710 with P.B. Pelsler* (CANU), KT597158\*, KT597405\*, –, –, –; **T. cf. magnum**, Philippines, Antique Prov., Villa Valderrama, *J.F. Barcelona 3777 with P.B.*



## Appendix 2. Continued.

Pelser (CANU), KT597169\*, KT597416\*, –, –, –; **T. cf. magnum**, Philippines, Antique Prov., Barbaza, *J.F. Barcelona 3783* (CANU), KT597180\*, KT597425\*, KT597507, –, –, KT597265\*; **T. cf. magnum**, Philippines, Antique Prov., Barbaza, *J.F. Barcelona 3785* (CANU); **T. cf. magnum**, Philippines, Antique Prov., Barbaza, *J.F. Barcelona 3787* (CANU); **T. cf. magnum**, Philippines, Antique Prov., Barbaza, *J.F. Barcelona 3790* (CANU); **T. cf. magnum**, Philippines, Antique Prov., Barbaza, *J.F. Barcelona 3793* (CANU); **T. cf. magnum**, Philippines, Antique Prov., Culasi, *J.F. Barcelona 3800* (CANU); **T. cf. magnum**, Philippines, Antique Prov., Culasi, *J.F. Barcelona 3804* (CANU); **T. cf. magnum**, Philippines, Antique Prov., Culasi, *J.F. Barcelona 3808* (CANU), KT597182\*, KT597427\*, KT597508\*, KT597320\*, KT597266\*; **T. cf. magnum**, Philippines, Quezon Prov., Mt. Banahaw, *J.F. Barcelona 3810 with P.B. Pelser* (CANU); **T. cf. magnum**, Philippines, Quezon Prov., Mt. Banahaw, *J.F. Barcelona 3813 with P.B. Pelser* (CANU); **T. cf. magnum**, Philippines, Quezon Prov., Mt. Banahaw, *J.F. Barcelona 3815 with P.B. Pelser* (CANU); **T. cf. magnum**, Philippines, Quezon Prov., Mt. Banahaw, *J.F. Barcelona 3821 with P.B. Pelser* (CANU); **T. cf. magnum**, Philippines, Quezon Prov., Mt. Banahaw, *J.F. Barcelona 3824 with P.B. Pelser* (CANU); **T. cf. magnum**, Philippines, Antique Prov., Sibalom, Cabladan, *J.F. Barcelona 3936 with P.B. Pelser* (CANU); **T. cf. magnum**, Philippines, Antique Prov., Sibalom, Cabladan, *J.F. Barcelona 3939 with P.B. Pelser* (CANU); **T. cf. magnum**, Philippines, Antique Prov., San Remigio, Aningalan, *J.F. Barcelona 3944 with P.B. Pelser* (PNH), KT597190\*, KT597435\*, –, –, –; **T. cf. magnum**, Philippines, Antique Prov., Sibalom, Imparayan, *J.F. Barcelona 3954 with P.B. Pelser* (CANU), KT597193\*, KT597438\*, –, –, –; **T. cf. magnum**, Philippines, Antique Prov., Sibalom, Imparayan, *J.F. Barcelona 3962 with P.B. Pelser* (CANU); **T. cf. magnum**, Philippines, Antique Prov., Sibalom, Bululacao, *J.F. Barcelona 3965 with P.B. Pelser* (CANU), KT597194\*, KT597439\*, –, –, –; **T. cf. magnum**, Philippines, Antique Prov., Sibalom, Bululacao, *J.F. Barcelona 3970 with P.B. Pelser* (CANU); **T. cf. magnum**, Philippines, Antique Prov., Sibalom, Bululacao, *J.F. Barcelona 3982 with P.B. Pelser* (CANU); **T. cf. magnum**, Philippines, Antique Prov., Sibalom, Bad-as, *J.F. Barcelona 3984 with P.B. Pelser* (CANU); **T. cf. magnum**, Philippines, Antique Prov., Sibalom, Bad-as, *J.F. Barcelona 3986 with P.B. Pelser* (CANU); **T. cf. magnum**, Philippines, Antique Prov., Sibalom, Bad-as, *J.F. Barcelona 3989 with P.B. Pelser* (CANU); **T. cf. magnum**, Philippines, Negros Occidental Prov., Mt. Kanlaon, *J.F. Barcelona 4000 with P.B. Pelser* (CANU); **T. cf. magnum**, Philippines, Negros Occidental Prov., Mt. Kanlaon, *J.F. Barcelona 4004 with P.B. Pelser* (CANU); **T. cf. magnum**, Philippines, Negros Occidental Prov., Mt. Kanlaon, *J.F. Barcelona 4011 with P.B. Pelser* (No voucher); **T. cf. magnum**, Philippines, Negros Occidental Prov., Mt. Kanlaon, *J.F. Barcelona 4014 with P.B. Pelser* (CANU); **T. cf. magnum**, Philippines, Negros Occidental Prov., Mt. Kanlaon, *J.F. Barcelona 4014 with P.B. Pelser* (No voucher); **T. cf. magnum**, Philippines, Negros Occidental Prov., Mt. Kanlaon, *J.F. Barcelona 4022 with P.B. Pelser* (CANU), KT597197\*, KT597442\*, –, –, –; **T. cf. magnum**, Philippines, Iloilo Prov., Miag-ao, *J.F. Barcelona 4145 with P.B. Pelser* (CANU/PNH); **T. cf. magnum**, Philippines, Iloilo Prov., Miag-ao, *J.F. Barcelona 4147 with P.B. Pelser* (CANU/PNH); **T. cf. magnum**, Philippines, Iloilo Prov., Igaras, *J.F. Barcelona 4155 with P.B. Pelser* (CANU/PNH); **T. cf. magnum**, Philippines, Iloilo Prov., Igaras, *J.F. Barcelona 4158 with P.B. Pelser* (CANU/PNH), KT597214\*, KT597458\*, –, –, –; **T. cf. magnum**, Philippines, Camarines Sur Prov., Mt. Asog, *N. Gapas s.n.* (CANU); **T. muricatum** Gamble, India, *Tamhankar & More s.n.*, KF544881, –, –, –; **T. napaulense** (DC.) C.L.Li, Nepal, *Nie & Zhu 548*, –, HM585606, HM585744, HM585881, HM586022; **T. napaulense**, Tibet, *Tibet 225*, –, HM585607, HM585745, HM585882, HM586023; **T. nitens** (F.Muell.) Planch., Australia, *Rosetto et al. s.n.*, AF365984, –, –, –; **T. obovatum** (M.A.Lawson) Gagnep., China, *Roeder & Slik*, HG004824, –, –, –; **T. obovatum**, China, *Wen 10567*, –, HM585608, HM585746, HM585883, HM586024; **T. obovatum**, Thailand, *Wen 7430*, –, HM585609, HM585747, HM585884, HM586025; **T. obtectum** Planch. ex Franch., China, *Nie & Meng 433*, –, HM585612, HM585750, HM585886, HM586027; **T. obtectum**, China, *Nie & Meng 454*, –, HM585614, HM585751, HM585888, HM586029; **T. pachyphyllum** (Hemsl.) Chun, Vietnam, *Wen 10919*, –, HM585615, HM585752, HM585890, HM586031; **T. pachyphyllum**, Philippines, Ifugao/Mountain Prov., Mt. Polis, *Wen 8319*, –, HM585616, HM585753, HM585891, HM586032; **T. papillosum** (Blume) Planch., Philippines, Antique Prov., Pandan, *J.F. Barcelona 3493 with P.B. Pelser* (CAHUP/CANU), KT597162\*, KT597409\*, KT597500\*, KT597315\*, KT597258\*; **T. papillosum**, Philippines, Bukidnon Prov., Baungon, *J.F. Barcelona 3778 with P.B. Pelser* (No voucher), KT597170\*, KT597417\*, –, –, –; **T. papillosum**, Philippines, Camarines Norte/Camarines Sur Prov., Mt. Labo, *J.F. Barcelona 3834 with P.B. Pelser* (CANU), KT597184\*, KT597429\*, –, –, –; **T. papillosum**, Philippines, Bukidnon Prov., Lantapan, *J.R. Callado 1203* (PNH), KT597173\*, KT597419\*, –, –, –; **T. papillosum**, Philippines, Bukidnon Prov., Lantapan, *J.R. Callado 1231* (PNH), KT597175\*, KT597421\*, KT597504\*, KT597318\*, KT597262\*; **T. papillosum**, Malaysia, *Wen 8401*, –, HM585617, –, HM585892, HM586033; **T. pedunculare** Planch., Indonesia, *Denden 864*, –, HM585618, HM585755, HM585893, HM586034; **T. pedunculare**, Indonesia, *Wen 10235*, –, HM585619, HM585756, HM585894, HM586035; **T. pedunculare**, Indonesia, *Wen 10281*, –, HM585620, HM585757, HM585895, HM586036; **T. petraeum** Jackes, Australia, *Rosetto et al. s.n.*, AY037910, –, –, –; **T. planicaule** (Hook.f.) Gagnep., China, *Roeder & Slik*, HG004820, –, –, –; **T. planicaule**, Vietnam, *Wen 10904*, –, HM585622, HM585759, HM585897, HM586037; **T. pyriforme** Gagnep., Malaysia, *Wen 8370*, –, HM585624, HM585761, HM585898, HM586039; **T. retinerium** Planch., Vietnam, *Wen 10920*, –, HM585625, HM585762, HM585899, HM586040; **T. rumicisperrum** (M.A.Lawson) Planch., Tibet, *Tibet 2003*, –, HM585626, –, HM585900, HM586041; **T. scariosum** (Blume) Planch., Indonesia, *Wen 10185*, –, HM585621, HM585758, HM585896, –, –; **T. cf. scariosum** (Blume) Planch., Philippines, Aurora Prov., Casiguran, *J.F. Barcelona 3861 with P.B. Pelser* (CANU), –, KT597430\*, KT597509\*, KT597321\*, KT597267\*; **T. cf. scariosum**, Philippines, Aurora Prov., Mt. Mingan, *J.F. Barcelona 3863 with P.B. Pelser* (CANU), KT597185\*, –, KT597510\*, KT597322\*, –, –; **T. cf. scariosum**, Philippines, Aurora Prov., Mt. Mingan, *J.F. Barcelona 3904 with P.B. Pelser* (CANU), KT597187\*, KT597432\*, KT597512\*, KT597324\*, KT597270\*; **T. cf. scariosum**, Philippines, Negros Occidental Prov., Mt. Kanlaon, *J.F. Barcelona 4020 with P.B. Pelser* (CANU), KT597196\*, KT597441\*, KT597514\*, KT597326\*, KT597272\*; **T. cf. scariosum**, Philippines, Ilocos Norte Prov., Adams, *J.F. Barcelona 4095 with P.B. Pelser* (CANU/PNH), KT597207\*, KT597451\*, KT597517\*, KT597329\*, KT597276\*; **T. cf. scariosum**, Philippines, Surigao del Sur Prov., Lanuza, *J.F. Barcelona 4108 with P.B. Pelser* (CANU/PNH), KT597210\*, KT597454\*, KT597518\*, KT597330\*, KT597277\*; **T. cf. scariosum**, Philippines, Dinagat Prov., San Jose, *J.F. Barcelona 4124 with P.B. Pelser* (CANU/PNH), KT597212\*, KT597456\*, KT597519\*, KT597331\*, KT597278\*; **T. serrulatum** Planch., China, *Nie & Meng 445*, –, HM585627, HM585764, HM585901, HM586042; **T. serrulatum**, Vietnam, *Wen 10856*, –, HM585628, HM585765, HM585902, HM586043; **T. serrulatum**, Thailand, *Wen 7429*, –, HM585629, HM585766, HM585903, HM586044; **T. siamense** Gagnep. & Craib, Thailand, *Wen 7485*, –, HM585630, HM585767, HM585904, HM586045; **T. sichouense** C.L.Li, China, *Wen 10547*, –, HM585631, HM585768, HM585905, HM586046; **T. sp.**, Indonesia, *Chen & Lu 462*, –, KC428768, KC428814, HM585913, –, **T. sp.**, Indonesia, *Deden 976*, –, HM585640, HM585777, HM585906, HM586055; **T. sp.**, Myanmar, *Deng 3167*, –, HM585633, HM585770, HM585907, HM586048; **T. sp.**, Myanmar, *Deng 3396*, –, HM585634, HM585771, HM585908, HM586049; **T. sp.**, Myanmar, *Deng 3475*, –, HM585635, HM585772, HM585909, HM586050; **T. sp.**, Myanmar, *Deng 6184*, –, HM585636, HM585773, HM585910, HM586051; **T. sp.**, Indonesia, *Wen 10768*, –, HM585637, HM585774, KC166463, HM586052; **T. sp.**, China, *Wen 11412*, –, KC166376, KC166615, KC166646, KC166681; **T. sp.**, China, *Wen 12026*, –, KC166377, KC166616, KC166465, KC166682; **T. sp.**, Vietnam, *Wen 5983*, –, KC166378, JF437073, HM585911, JF437294; **T. sp.**, Philippines, Laguna Prov., Mt. Makiling, *Wen 8256*, –, HM585638, HM585775, HM585926, HM586053; **T. sp.**, China, *Wen 8455*, –, HM585653, HM585787, HM585912, HM586068; **T. sp.**, China, *Wen 8465*, –, HM585639, HM585776, HM585914, HM586054; **T. sp. A**, Philippines, Antique Prov., San Remigio, Aningalan, *D.L. Nickrent 5538 with B. Van Ee & J.F. Barcelona* (SIU), KT597153\*, KT597400\*, KT597494\*, KT597309\*, KT597252\*; **T. sp. A**, Philippines, Davao Oriental Prov., Mt. Kampilili, *J. Baron 1a* (CANU), KT597160\*, KT597407\*, KT597499\*, KT597314\*, KT597257\*; **T. sp. A**, Philippines, Davao Oriental Prov., Mt. Kampilili, *J. Baron 2a* (CANU); **T. sp. A**, Philippines, Davao Oriental Prov., Mt. Kampilili, *J. Baron 3a* (CANU); **T. sp. A**, Philippines, Davao Oriental Prov., Mt. Kampilili, *J. Baron 4a* (CANU), KT597161\*, KT597408\*, –, –, –; **T. sp. A**, Philippines, Davao Oriental Prov., Mt. Kampilili, *J. Baron 5a* (CANU); **T. sp. A**, Philippines, Antique Prov., Pandan, *J.F. Barcelona 3477 with P.B. Pelser* (CAHUP/CANU), KT597148\*, KT597395\*, –, –, –; **T. sp. A**, Philippines, Antique Prov., Pandan, *J.F. Barcelona 3480 with P.B. Pelser* (CAHUP/CANU), KT597163\*, KT597410\*, KT597501\*, KT597316\*, KT597259\*; **T. sp. A**, Philippines, Bataan Prov., Mt. Natib, *J.F. Barcelona 3558 with L.L. Co* (CAHUP/CANU); **T. sp. A**, Philippines, Bataan Prov., Mt. Natib, *J.F. Barcelona 3562 with L.L. Co* (CAHUP/CANU), KT597147\*, KT597394\*, KT597491\*, KT597306\*, KT597249\*; **T. sp. A**, Philippines, Bataan Prov., Mt. Natib, *J.F. Barcelona 3567 with L.L. Co* (CAHUP/CANU); **T. sp. A**, Philippines, Bataan Prov., Mt. Natib, *J.F. Barcelona 3572 with L.L. Co* (CAHUP/CANU), KT597142\*, KT597389\*, –, –, –; **T. sp. A**, Philippines, Cagayan Prov., Bolos Point, *J.F. Barcelona 3587 with J. Payba, R. Echanique & Tabuc*

## Appendix 2. Continued.

(CAHUP/CANU), KT597141\*, KT597388\*, KT597488\*, KT597305\*, KT597246\*; *T. sp. A*, Philippines, Cagayan Prov., Bolos Point, *J.F. Barcelona 3589* with *J. Payba, R. Echanique & Tabuc* (CAHUP/CANU); *T. sp. A*, Philippines, Cagayan Prov., Bolos Point, *J.F. Barcelona 3592* with *J. Payba, R. Echanique & Tabuc* (CAHUP/CANU), KT597139\*, KT597386\*, –, –, –; *T. sp. A*, Philippines, Quezon Prov., Mt. Banahaw, *J.F. Barcelona 3640* with *D.L. Nickrent & J. Mendua* (CAHUP/CANU), KT597146\*, KT597393\*, KT597490\*, –, KT597248\*; *T. sp. A*, Philippines, Laguna Prov., Mt. Makiling, *J.F. Barcelona 3645* with *D.L. Nickrent, E. Malinao & R. Brevia* (CAHUP/CANU), KT597140\*, KT597387\*, –, –, –; *T. sp. A*, Philippines, Laguna Prov., Mt. Makiling, *J.F. Barcelona 3651* with *D.L. Nickrent, E. Malinao & R. Brevia* (CAHUP/CANU), KT597134\*, KT597381\*, KT597484\*, KT597301\*, KT597242\*; *T. sp. A*, Philippines, Quezon Prov., Mt. Irid, *J.F. Barcelona 3654* with *Joel Sarmiento* (CAHUP/CANU), KT597157\*, KT597404\*, –, –, –; *T. sp. A*, Philippines, Quezon Prov., Mt. Irid, *J.F. Barcelona 3658* with *Joel Sarmiento* (CAHUP/CANU), KT597156\*, KT597403\*, KT597497\*, KT597312\*, KT597255\*; *T. sp. A*, Philippines, Antique Prov., Sebaste, *J.F. Barcelona 3682* with *P.B. Pelsler* (CANU); *T. sp. A*, Philippines, Antique Prov., San Remigio, Aningalan, *J.F. Barcelona 3700* with *P.B. Pelsler* (CANU); *T. sp. A*, Philippines, Quezon Prov., Mt. Banahaw, *J.F. Barcelona 3812* with *P.B. Pelsler* (CANU); *T. sp. A*, Philippines, Misamis Oriental Prov., Mt. Balatukan, *J.F. Barcelona 4039* (CANU), KT597198\*, KT597443\*, KT597515\*, KT597327\*, KT597273\*; *T. sp. A*, Philippines, Ilocos Norte Prov., Pagudpud, *J.F. Barcelona 4091* with *P.B. Pelsler* (CANU/PNH), KT597203\*, KT597447\*, –, –, –; *T. sp. A*, Philippines, Ilocos Norte Prov., Pagudpud, *J.F. Barcelona 4092* with *P.B. Pelsler* (CANU/PNH), KT597204\*, KT597448\*, –, –, –; *T. sp. A*, Philippines, Ilocos Norte Prov., Pagudpud, *J.F. Barcelona 4093* with *P.B. Pelsler* (CANU), KT597205\*, KT597449\*, –, –, –; *T. strumarum* (Planch.) Gagnep., Indonesia, *Wen 10757*, –, HM585641, HM585778, HM585915, HM586056; *T. sulcatum* Gamble, India, *Tamhankar & More s.n.*, KF544883, –, –, –, –; *T. tonkinense* Gagnep., Thailand, *Wen 7401*, –, HM585642, HM585779, HM585916, HM586057; *T. trifoliolatum* Merr., Indonesia, *Wen 10758*, –, HM585643, HM585780, HM585917, HM586058; *T. trifoliolatum*, Malaysia, *Wen 8350*, –, HM585644, HM585781, HM585921, HM586059; *T. triphyllum* (Gagnep.) W.T. Wang, China, *Nie & Meng 342*, –, HM585646, HM585782, HM585924, HM586061; *T. triphyllum*, China, *Wen 10655*, –, HM585648, HM585783, HM585919, HM586063; *T. cf. tuberculatum* (Blume) Latiff., Indonesia, *Wen 10280*, –, HM585559, HM585699, HM585835, HM585975; *T. voinierianum* (Baltet) Gagnep., Laos? Source unknown. Cultivated at Missouri Botanic Garden, *Miller 5871* (MO), KT597215\*, KT597459\*, KT597520\*, KT597332\*, KT597279\*; *T. yunnanense* Gagnep., China, cult., *Nie 2003104*, –, HM585654, –, –, HM586069