Taxonomy, systematics, and biogeography of Ficus subsection Urostigma (Moraceae)

Chantarasuwan, B.

Chapter 5

A new classification of *Ficus* subsection *Urostigma* (Moraceae) based on four nuclear DNA markers (ITS, ETS, G3pdh, and ncpGS), morphology and leaf anatomy

Bhanumas Chantarasuwan, Cornelis C. Berg, Finn Kjellberg, Nina Rønsted, Marjorie Garcia, Claudia Baider and Peter C. van Welzen

Manuscript submitted to PLOS One.

Abstract

Ficus subsection *Urostigma* as currently circumscribed contains 27 species, distributed in Africa, Asia, Australia and the Pacific and is of key importance to understanding the origin and evolution of *Ficus* and the fig-wasp mutualism. The species of subsect. *Urostigma* are very variable in morphological characters and exhibit a wide range of often partly overlapping distributions, which makes identification often difficult. The systematic classification within and between this subsect. and others is problematic, e.g., it is still unclear where to classify *F. amplissima* and *F. rumphii*. To clarify the circumscription of subsection *Urostigma*, we present a phylogenetic reconstruction based on four nuclear DNA markers (ITS, ETS, G3pdh, and ncpGS) combined with morphology and leaf anatomy. The combined phylogenetic tree shows that *F. madagascariensis*, a Madagascan species, is sister to the remainder of subsect. *Urostigma*. *Ficus amplissima* and *F. rumphii*, formerly constituting sect. *Leucogyne*, appears to be imbedded in subsect. *Conosycea*. The result of the phylogenetic analysis necessitates nomenclatural adjustments. A new classification of *Ficus* subsect. *Urostigma* is presented along with morphological and leaf anatomical characters to recognise it. Two new species are described, one in subsect. *Urostigma*, the other in *Conosycea*. One variety is raised to species level.

Keywords classification; *Ficus* subsection *Urostigma; Ficus* subsection *Conosycea;* morphology; leaf anatomy.

Introduction

Despite substantial effort, the origin and evolution of *Ficus* L. and the fig-wasp mutualism remain unclear due to lack of resolution of the backbone of the phylogeny of *Ficus* (Cruaud et al., 2012; Rønsted et al., 2005; 2008). One of the key clades of uncertain placement is *Ficus* subsection *Urostigma* (Berg 2004; Chantarasuwan et al, 2013). *Ficus* subg. *Urostigma* sect. *Urostigma* subsect. *Urostigma* (Gasp.) C.C. Berg includes 27 species as currenly circumscribed with *Ficus religiosa* L. as the type. The distribution of the subsection ranges from West Africa and Madagascar via the Asian mainland to Japan and through (southern) Malesia to Australia and the Pacific. Typical characters of subsect. *Urostigma* are: Trees, many of which are hemi-epiphytic and some terrestrial, aerial roots not abundant, usually intermittent growth, leaves often deciduous, spirally arranged, and articulate or subarticulate (some African-Madagascan species lack the articulation), inflorescences often borne below the leaves and in some species they are borne on the spurs of the older branches, the colour of the syconium can change from whitish to pinkish, then to purplish, and finally blackish, although the final stage may never develop (Berg & Wiebes, 1992; Berg & Corner, 2005). *Urostigma*, was first described in 1844 when Gasparrini (1844) broke up the genus *Ficus* into several genera. Later Miquel (1867) abandoned this idea and reunited *Ficus*, but divided the genus into six subgenera. Subgen. *Urostigma* was further divided by him into series based on distribution, six series for species in Asia and Australia, three series for African species, and five series for species in America. The species presently included in subsect. *Urostigma* were mainly placed in series *Infectoriae* Miq. and *Religiosae* Miq. of Asia and Australia. The African representatives of the subsection were classified in series *Grandiores* Miq., *Oblongifoliae* Miq., and *Ellipticifoliae* Miq. Later, morphological characters were used to classify the genus, e.g. King (1887) divided *Ficus* into seven sections based on leaf morphology. Corner (1960) used the colour of the ovary and the position of the lythocists for his classification, an idea shared by Berg (2004). However, the concept of the sections varied between Corner's (1960) and Berg's (2004) classifications. Berg (2004) expanded Corner's section *Urostigma* by including former sections *Conosycea* and *Leucogyne* (Corner, 1959) and Corner's concept of section *Urostigma* was consequently reduced to the status of subsection. The relationship of the two species (*F. amplissima* J.E.Sm. and *F. rumphii* Blume) of former sect. *Leucogyne* was questioned when Rønsted et al. (2005) published a molecular phylogenetic hypothesis, which showed that *F. rumphii* belongs to subsect. *Conosycea* (Miq.) C.C.Berg (*F. amplissima* was not included in their study).

At present, molecular phylogenetic analyses have become the major basis for improving classifications. In an early molecular study of *Ficus* by Weiblen (2000) using the ITS marker together with morphological data, only three species of *Ficus* subsect. *Urostigma* (*F. prasinicarpa* Elmer ex C.C.Berg, *F. superba* (Miq.) Miq. and *F. virens* Aiton) were included. This study was the first to suggest that the monoecious subgenus *Urostigma* (Gasp.) Miq. is not

monophyletic, because section *Urostigma* (Gasp.) Endl. appeared to be the sister clade of a functionally dioecious clade, but support for this relationship was weak. Jousselin et al. (2003) combined ITS and ETS markers to construct the phylogenetic relationships of 41 species of *Ficus*, including three other species of subsection *Urostigma* (*F. prolixa* G. Forst., *F. religiosa* L., and *F. salicifolia* Vahl). Their results again suggested that subsection *Urostigma* forms a separate group from the remainder of subgenus *Urostigma*. Rønsted et al. (2005) also combined ITS and ETS in their work, which included nine species of subsect. *Urostigma* and *F. rumphii* of sect. *Leucogyne*. Their results indicated that *Ficus* subsect. *Urostigma* is monophyletic to the exclusion of *F. rumphii*, but subsect. *Urostigma* has to be excluded from the rest of subgenus *Urostigma*, and *F. rumphii* is embedded in sect. *Conosycea*. Addition of other nuclear markers and more species to the global analysis of *Ficus* have subsequently confirmed a narrow concept of subsection *Urostigma* excluding *F. rumphii* (Rønsted et al, 2008; Xu et al., 2011; Cruaud et al, 2013). However, more than half of the species of subsect. *Urostigma* and *F. amplissima* of (former) sect. *Leucogyne* are not included in any phylogenetic analysis yet, thus the monophyly and circumscription of the group is still far from clear.

To solve the problem of the classification of *Ficus* subsect. *Urostigma* and closely related subsections, we began a revision of *Ficus* subsect. *Urostigma* (Chantarasuwan et al., 2013) in its traditional classification, congruent with that of Berg (2004). However, we realised that morphology alone did not provide typical characters or a typical combination of characters to solve the classification problem. Leaf anatomy (Chantarasuwan et al., 2014) appeared to show more consistent characters and less variation within species than the morphological characters previously studied and, especially when combined with morphology, leaf anatomical characters provided a highly accurate tool for species recognition, enabling recognition of some of the morphologically highly variable species (e.g., *F. virens*). However, leaf anatomical evidence suggested that *F. amplissima* more closely resembles *F. arnottiana* (Miq.) Miq. (subsection *Urostigma*) than *F. rumphii* (former sect. *Leucogyne*). A result that upsets the present classification (Chantarasuwan et al, 2013).

Therefore, the main aim of this study is (1) to create a comprehensive and well supported phylogenetic hypothesis of subsection *Urostigma* by analysing several molecular markers (ITS, ETS, G3pdh, and ncpGS) for almost all known species of subsect. *Urostigma* and related groups and (2) to propose a new new classification of subsection *Urostigma* based on the resulting phylogenetic hypothesis.

Materials and methods

Taxon sampling

In total, 76 taxa were represented corresponding to thirty–six species out of c. 280 spp. of *Ficus* subgen. *Urostigma*, including 24 out of 27 species of subsect. *Urostigma*, and five (out of 60) species representating *Urostigma* subsect. *Conosycea* (*F. cf. rumphii*, *F. altissima* Blume, *F. benjamina* L., *F. glaberrima* Blume subsp. *siamensis* (Corner) C.C. Berg and *F. menabeensis* H. Perrier), as well as two species from each of sect. *Americana* (*F. americana* Aubl., *F. aurea* Nutt.; c. 100 species), sect. *Stilpnophyllum* subsect. *Malvanthera* (*F. pleurocarpa* F. Muell., *F. blachypoda* (Miq.) Miq.; c. 20 species), one species of sect. *Leucogyne* (*F. rumphii*), and one species of sect. *Galoghycia* (*F. bubu* Warb.; c. 72 species). Two species of subgenus *Pharmacosycea* (*F. maxima* Mill. and *F. tonduzii* Standl.) were included as outgroup representing the first diverging lineage of *Ficus* as currently understood (Cruaud et al, 2013).

Thirty–seven dried leaf samples from herbarium collections and 26 leaf samples dried on silica gel (collected in the field) were used for DNA extraction (for voucher information see Appendix 1). DNA sequence data were sampled for four nuclear DNA markers (ITS, ETS, G3pdh, ncpGS). In total, 233 sequences were used in the analysis, including 198 new sequences and 35 sequences downloaded from GenBank. All new sequences are available from GenBank (Appendix 1).

DNA extraction, amplification, and sequencing

About 20–50 mg of dried leaf tissue from each sample was used for extraction using the Qiagen DNeasy Plant Kit and following the manufacturers protocol. The ITS region was amplified using the primers 17SE_its and 26SE_its and ITS_5_F, ITS_4_R (Sun et al., 1994; Rønsted et al., 2008). The ETS region was amplified using primers ETS_Hel1_F, 18S_ETS_R and ETS_FIG1_F, 18S_ETS_R (Rønsted et al., 2008). The G3pdh gene was amplified using the primers GPDX7_F and GPDX9_R (Strand et al., 1997). The ncpGS region was amplified with the primers ncpGS_3_F and ncpGS_4_R (Rønsted et al., 2008). The primer sequences for all markers are shown in Table 5-1. The Polymerase chain reactions (PCR) were performed with 1µl of DNA product, 10 µl of Red-Sigma buffer (Qiagen Inc.), 2µl of each 10 µM primers (foreward and reverse), 0.4 µl of BSA (Promega, Madison, Wisconsin, USA) and 6.6 µl of H2O, in a total volume of 20 µl. The PCR programmes followed are summarised in Table 5-2. PCR fragments were checked for length and yield

Table 5-1. Sequences of primers used in this study.

Regions	Primer sequences
ITS	ITS_5F : 5´ - GGA AGT AAA AGT CGT AAC AAG G - 3´ ITS_4R : 5´ - TCC TCC GCT TAT TGA TAT GC - 3´ ITS_17SE : 5´ - ACG AAT TCA TGG TCC GGT GAA GTG TTC G - 3´ ITS_26SE : 5´ - TAG AAT TCC CCG GTT CGC TCG CCG TTA C - 3´
ETS	ETS_Hel1 : 5´ - GCT CTT TGC TTG CGC AAC AAC T - 3´ 18S_ETS : 5´ - GCA GGA TCA ACC AGG TAG CA- 3´
G3pdh	GPDX7F : 5´ - GAT AGA TTT GGA ATT GTT GAG G - 3´ GPDX9R : 5´ - AAG CAA TTC CAG CCT TGG - 3´
ncpGS	GS_3F : 5´ - GTT GTG ATT WAC CAT GCT - 3´ GS_4R : 5´ - AGA TTC AAA ATC GCC TTC - 3´

by gel electrophoresis on 2% agarose gels and cleaned using the Qiagen PCR clean-up kit before sequencing on an ABI 377 Genetic Analyzer according to the manufacturer's protocols (Applied Biosystems). Both strands were sequenced for each region for the majority of taxa.

DNA sequence alignments

Sequences were initially edited and improved by eye using CodonCode Aligner (CodonCode Corporation, Dedhem, USA) and MacClade 4.08 OSX (Maddison & Maddison, 2011), and forward and reverse sequences were assembled. All assembled sequences were blasted against the GenBank database to check for possible contamination with non-*Ficus* DNA. The alignment of whole sequences was done online with Phylogeny.fr (2008) and SeaView 3.2 (Galtier et al., 1996). Gaps were treated as missing data and indels were excluded from the alignments. Missing markers were also coded as missing data.

Morphological and leaf anatomical data

The morphological data matrix was constructed using the most recent taxonomic revision of *Ficus* subsection *Urostigma* (Chantarasuwan et al., 2013). The same specimens used in the revision were also the primary source for compiling the data matrix. In addition, specimens, stored in L, representing the species from other infrageneric taxa were also used to score data. In total, 43 qualitative morphological characters were coded for analysis (see Appendix 2 for characters, and Appendix 3 for the data matrix). The leaf anatomical data are based on recent work by Chantarasuwan et al. (2014), to which the character states of non-subsect. *Urostigma* species were added, either studied (*F. cf. rumphii*) or extracted from Berg and Corner (2005). In total 23 qualitative characters were coded for analysis (see Appendix 2 for characters,and Appendix 3 for the data matrix). All characters were treated as unordered and of equal weight, missing data were coded as unknown.

Table 5-2. PCR programs used for each molecular marker.

Regions	PCR program
ITS	2 min. at 94˚C followed by 35 cycles of 30 sec. denaturation (94˚C), 1 min. annealing (63˚C), and 1 min. extension (72˚C) and 10 cycles of 30 sec. denaturation (94˚C), 1 min. annealing (60˚C), and 1 min. extension (72˚C). After the last cycle, the temperature was kept at 72˚C for a final 5 min. extension and then lowered to 16˚C.
ETS	2 min. at 94˚C followed by 45 cycles of 30 sec. denaturation (94˚C), 1 min. annealing (60˚C), and 1 min. extension (72˚C). After the last cycle, the temperature was kept at 72˚C for a final 5 min. extension and then lowered to 16˚C.
G3pdh	2 min. at 94˚C followed by 40 cycles of 30 sec. denaturation (94˚C), 1 min. annealing (62˚C), and 1 min. extension (72˚C) and 10 cycles of 30 sec. denaturation (94˚C), 1 min. annealing (56˚C), and 1 min. extension (72˚C). After the last cycle, the temperature was kept at 72˚C for a final 5 min. extension and then lowered to 16˚C.
ncpGS	2 min. at 94˚C followed by 45 cycles of 30 sec. denaturation (94˚C), 1 min. annealing (57˚C), and 1 min. extension (72˚C) After the last cycle, the temperature was kept at 72˚C for a final 5 min. extension and then lowered to 16˚C.

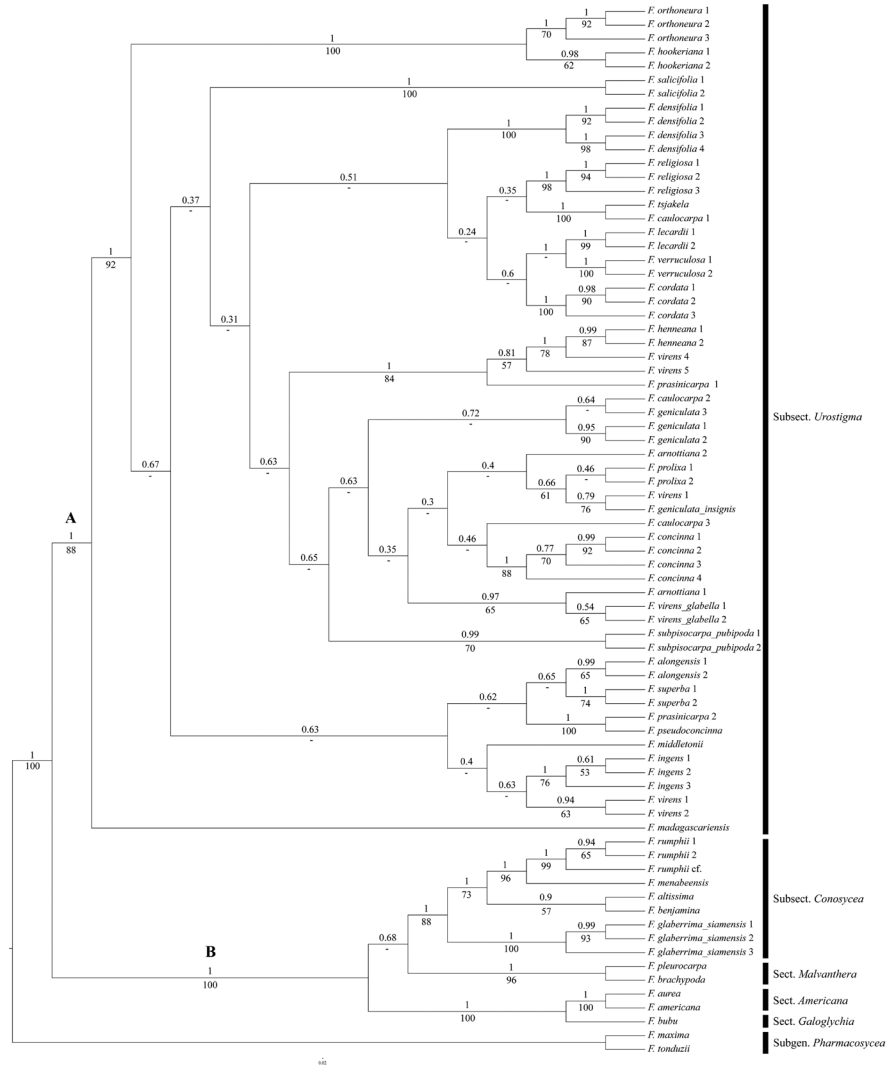

FIGURE 5-1: Majority rule consensus tree from Bayesian analysis of four combined DNA markers (ITS, ETS, G3pdh, and ncpGS) with posterior probabilities (PP) above and bootstrap supports (BS) below the branches.

Phylogenetic analysis

The analyses of the four combined molecular DNA markers were conducted under Maximum Parsimony (MP) and Bayesian Inference (BI). The morphology and leaf anatomy dataset was analysed under Maximum Parsimony (MP). Both datasets were subsequently combined and analysed under MP and BI.

The MP analyses were run using PAUP* v4.0b10 (Swofford, 2003) and heuristic searches with 3000 replicates, ten random taxon additions, tree-bisection-reconnection branch swapping (TBR), MulTrees option active, and no more than 10 trees saved per replicate. Branch support was performed in PAUP with bootstrap analyses (Felsenstein, 1995) with 1000 replicates and similar settings. Bootstrap percentages (BS) are defined as high (85–100%), moderate (75–84%), low (50–74%) or no support (<50%). Model selection for the Bayesian analysis was conducted using the model selection tool available through the online HIV sequence database site (http://www.hiv.lanl.gov/content/sequence/findmodel/findmodel.html). The chosen model was HKY+G for ITS, GTR+G for ETS, HrN+G for G3pdh, and HKY+G for ncpGS. The datasets were analysed online using MrBayes v.3.1.2 (Ronquist and Huelsenbeck, 2003) with 100,000,000 generations via the Cipres science gateway (http://www.phylo.org). Bayesian inference produces posterior probabilities that are relatively higher than the corresponding bootstrap frequencies (Erixon et al., 2003), thus we only used posterior probabilities (PP) above 0.9 as (high) support. A 10% burn-in was executed, after Tracer 1.6 (Rambaut et al., 2013) was used for each tree file to check whether or not the effective sampling sizes (ESS) of all parameters exceeded 200, indicating that they are a good representation of the posterior distributions. TreeAnnotator v.1.8.0 (part of BEAST v.1.8.0 package, Drummond & Rambaut, 2007, Drummond et al., 2012) was used to create a Maximum Clade Credibility (MCC) tree.

Mesquite v.2.7.5 (Maddison & Maddison, 2011) was used to map the morphological and anatomical characters on the MCC tree from the Bayesian analysis of the combined datasets.

Results

Analysis of four combined DNA markers

Seventy six taxa were included in the combined dataset, of which 74 taxa had ITS data, 68 taxa had ETS sequences, 53 taxa with G3pdh sequences, and 38 with ncpGS sequences. The combined aligned data matrix was 2674 bp long with 472 potentially informative characters. The MP analysis resulted in 1300 most parsimious trees (MPTs) with a length = 1636, consistency index (CI) = 0.68, and retention index (RI) = 0.78.

The strict consensus tree of 1300 most parsimonious trees (MPTs) (Fig. 5-1) splits into two clades. Clade A comprises all members of subsect. *Urostigma*

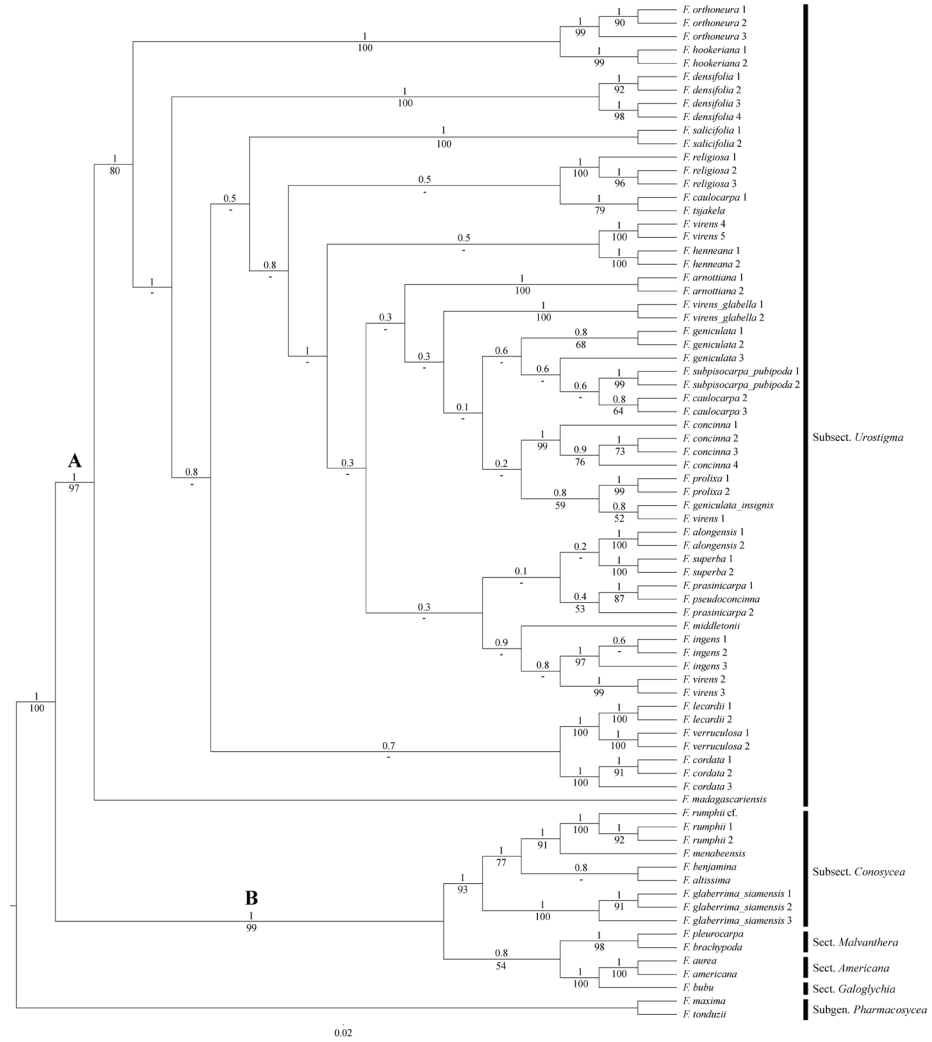

FIGURE 5-2. Total evidence majority rule consensus tree from Bayesian analysis of four DNA markers, morphology and leaf anatomy. Posterior probabilities (PP) above and bootstrap supports (BS) below the branches.

with a support of BS=88 and PP=1. *Ficus madagascariensis* is sister to the rest of this clade (high support, BS=92 and PP=1), but within clade A most internal nodes show low support, while the support for most nodes that unite the various specimens of a species is usually high. Clade B contains the members of sect. *Americana*, sect. *Galoghycia*, sect. *Malvanthera*, subsect. *Conosycea*, and *F. rumphii* of sect. *Leucogyne* with BS=100 and PP=1.

Analysis of morphological and leaf anatomical data

A total of 43 morphological and 23 leaf anatomical characters were used. The MP analysis resulted in 1368 most parsimonious trees with a length = 280, CI = 0.25, and RI = 0.77. The strict consensus tree is one large polytomy of all taxa (not shown here).

Analysis of DNA markers combined with morphology and leaf anatomy

A total of 2740 characters, 2674 DNA (ITS, ETS, G3pdh, and ncpGS) and 66 qualitative morphological and leaf anatomical characters were used; 538 characters were parsimony informative. The MP analysis resulted in 81 most parsimonious trees with a tree length = 1964, CI = 0.60, and RI = 0.76 (strict consensus not shown). Tracer(Rambaut et al., 2013) showed that all variables in the results of the BI analysis had an effective sampling size far above 200 (326–1851). The MCC tree, made of the cladograms in set 1 with TreeAnnotator, is shown in Fig. 5-2.

The cladogram (Fig. 5-2) shows the same two distinctive subclades as found in the analysis of the four combined DNA markers (Fig. 5-1). Clade A is composed of all species of subsect. *Urostigma* and it has high support, BS=97 and PP=1. *Ficus madagascariensis* is sister to the remainder of subsection *Urostigma* s.s. and the remaining clade is well supported, BS=80, and PP=1. Relationships within the remainder of clade A are not well supported in the combined analysis as was also the case in the 4-gene analysis alone (Fig. 5-1). The species that are represented by several samples usually form clades with high Bootstrap and Bayesian support except for *F. caulocarpa*, *F. geniculata*, *F. prasinicarpa* and *F. virens*. *Ficus prasinicarpa* is paraphyletic because of the inclusion of *F. pseudoconcinna*. The clade itself has low support (BS = 53, PP=0.4), but *F. prasinicarpa 2* and *F. pseudoconcinna* have high support (BS high= 87, PP high = 1). *Ficus geniculata 3* groups with *F. caulocarpa 2* and *3* and *F. subpisocarpa* Gagnep. subsp. *pubipoda*, but with very low support (BS<50, PP=0.6).

Two species, represented by several samples, appear to be polyphyletic, *F. caulocarpa* (Miq.) Miq. and *F. virens*. Of the three samples of *F. caulocarpa*, *F. caulocarpa 1* forms a clade with *F. tsjakela* Burm.f. (BS moderate =79, PP high = 1), while *F. caulocarpa 2* and *3* form a clade together as described above. Accessions of *F. virens* appears in four places; variety virens appears

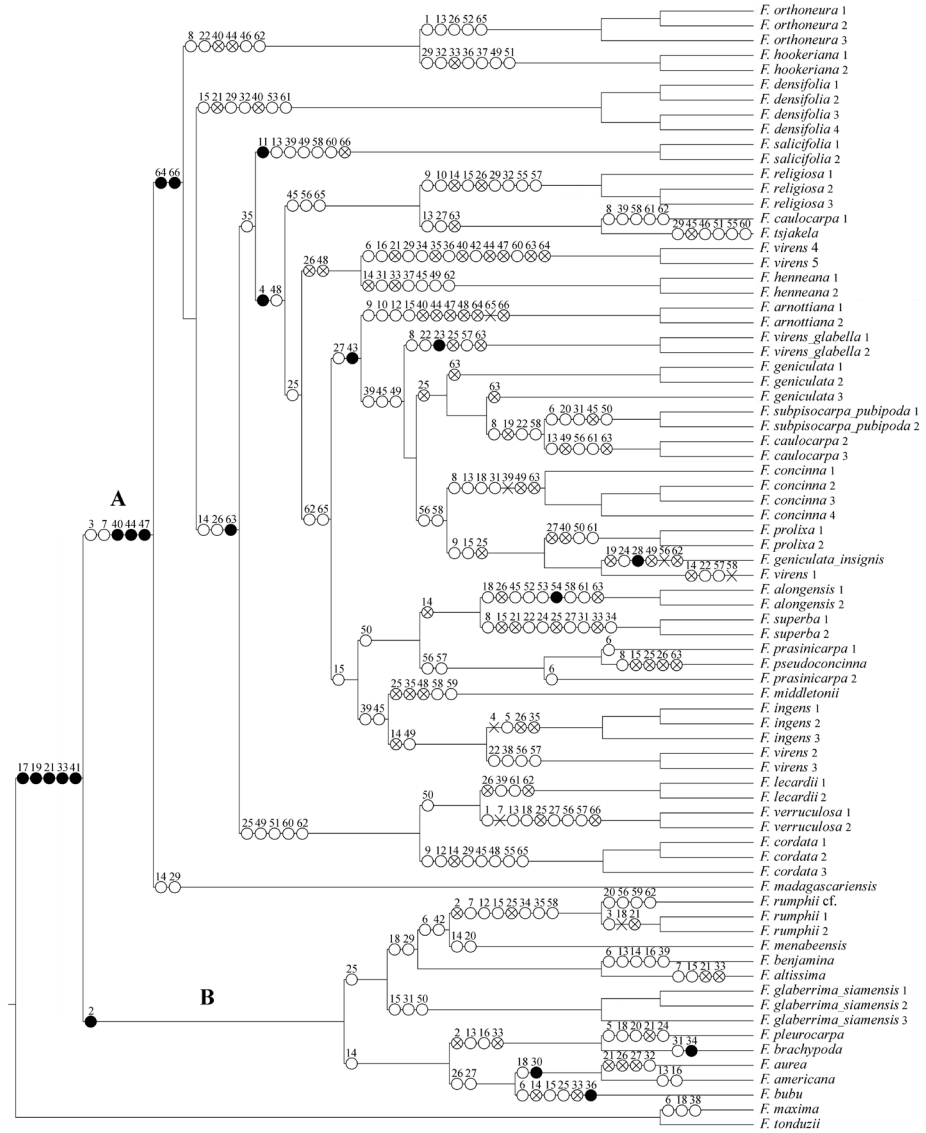

FIGURE 5-3. Character state changes of the morphological characters traced on the majority rule consensus Bayesian tree of the total evidence matrix (Fig. 5-2). ●= unique apomorphy; ○= parallelism; ✕ = reversal; ⊗= parallel reversal.

in three clades, *F. virens 1* groups with *F. geniculata_insignis* (low support, BS=52, PP=0.8), *F. virens 2* and *3* group together (strong support, BS=99 and PP = 1) and are further linked to the three specimens of *F. ingens* (Miq.) Miq., and *F. virens 4* and *5* group together (strong support, BS=100 and PP=1) and further group with two specimens of *F. henneana* Miq. The two specimens of *F. virens* var. *glabella* (*F. virens_glabella 1* and *F. virens_glabella 2*) also form a separate clade with high support (BS = 100 and PP = 1).

Clade B is composed of members of sect. *Americana*, sect. *Galoghycia*, subsect. *Malvanthera*, subsect. *Conosycea*, and *F. rumphii* of sect. *Leucogyne* and is well supported in this analysis. (BS=99, PP=1). Within this clade, subsect. *Conosycea* is well suppported (BS=93 and PP=1) and includes three accessions of *F. rumphii* (BS=100 and PP = 1).

Character mapping

The morphological and leaf anatomical character state changes are summarised in Fig. 5-3. Subsect. *Urostigma* (clade A in Fig. 5-3) is supported by the following apomorphies: intermittent growth (character 3, state 2; shared in parallel with *F. rumphii* of subsect. *Conosycea*, clade B), deciduous leaves (char. 7, state 1; reversal in *F. verruculosa*, parallel with some species of subsect. *Conosycea*: *F. altissima*, *F. rumphii* and *F. cf. rumphii*), staminate flowers near ostiole (char. 40, state 1; parallel reversals in *F. arnottiana*, *F. densifolia*, *F. hookeriana F. orthoneura*, *F. prolixa*, and *F. virens 4* and *5*), single-layered epidermis (char. 44, state 1; parallel reversals in *F. arnottiana*, *F. virens 4* and *5*, *F. orthoneura*, and *F. hookeriana*), abaxial enlarged lithocysts (char. 47, state 1; parallel reversals in *F. arnottiana* and *F. virens 4* and *5*).

Discussion

Phylogenetic circumscription of of *Ficus* subsect. *Urostigma*

Our results based on comprehensive sampling of subsection *Urostigma* are consistent with recent previous studies at the genus level supporting a narrow concept of subsection *Urostigma* s.s. excluding former section *Leucogyne* (Rønsted et al. 2005, 2008, Xu et al., 2011; Cruaud et al., 2012). Unfortunately the extraction of DNA from *Ficus amplissima*, the other species of sect. *Leucogyne*, was unsuccessful in our study, but a partial ITS sequence of *F. amplissima* (Rønsted unpublished; specimen Matthew 20582 (K)) forms a clade together with *F. rumphii* embedded in the *Conosycea* clade. This is supported by evidence from the pollinators, because *F. amplissima* (Wiebes, 1992) and *F. rumphii* (Berg and Corner, 2009) are pollinated by a wasp genus that is only known to be associated with subsect. *Conosycea*. Based on these two independent pieces of evidence we support the placement of *F. amplissima* in subsection *Conosycea*, which means that the complete sect. *Leucosyce* should now be synonymised with subsect. *Conosycea*. *Ficus madagascariensis* is the sister to all other members of subsect. *Urostigma*, which may imply that the origin of this subsection could be in Madagascar. Corner (1958) considered *F. prolixa*, a Polynesian species, to group with sect. *Americana*, because the

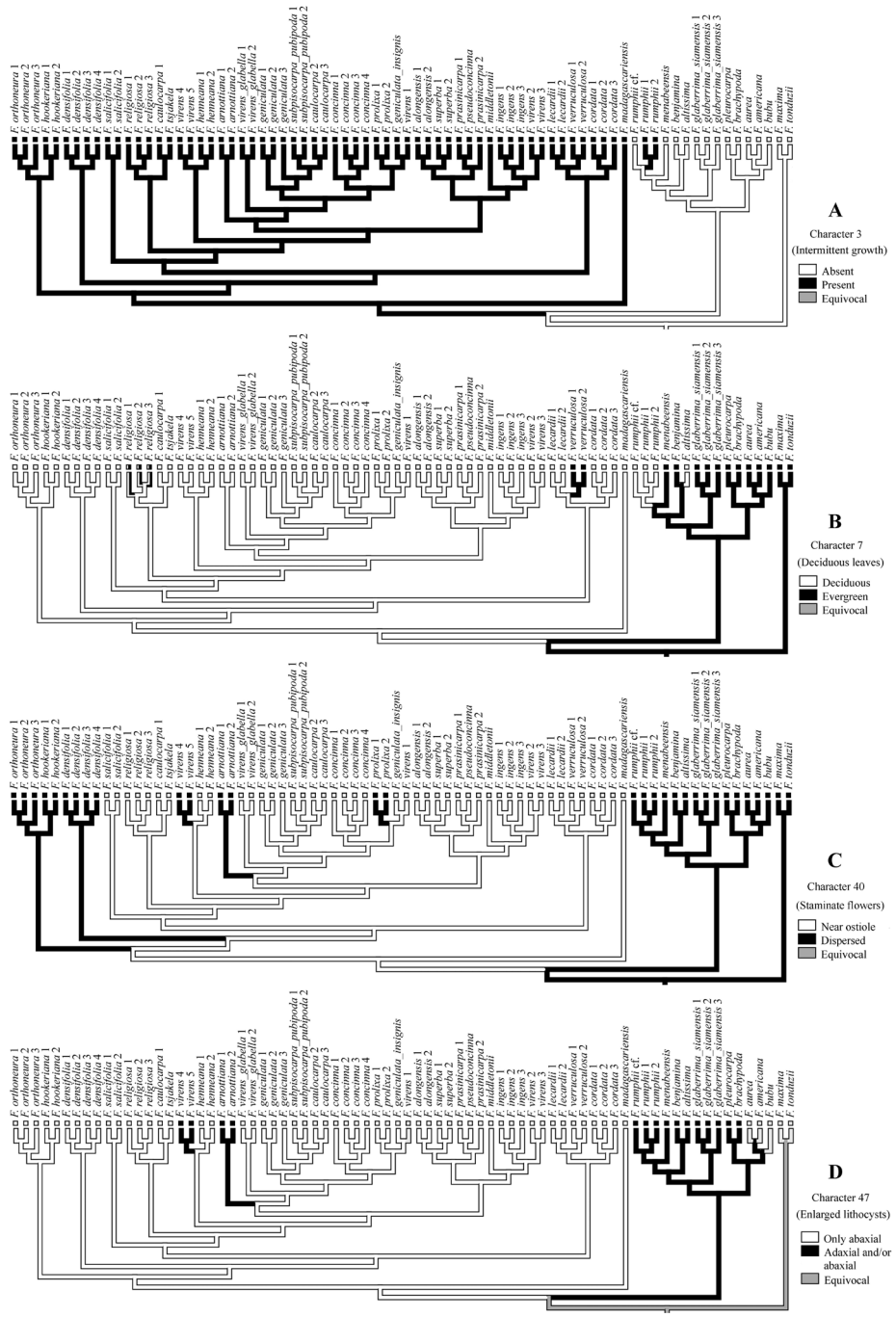

FIGURE 5-4. Evolution of some selected morphological and leaf anatomical characters optimized onto the phylogeny tree (Fig. 2) using Mesquite v.2.7.5. A: Intermittent growth (character 3), B: Deciduous leaves (character 7), C: Staminate flowers (character 40), and D: Enlarged lithocysts (character 47).

staminate flowers are scattered in the fig, which is similar to a large group of American hemi-epiphytic figs (over 100 species; section *Americana*). However, *F. prolixa* has three basal bracts and not two as in sect. *Americana*. Our phylogenetic results clearly show that there is no close relation between *F. prolixa* (clade A) and sect. *Americana* (clade B).

Relationships within subsection *Urostigma* s.s. are still not well supported based on four nuclear genes, morphology and leaf anatomy, and further work possibly using massive parallel sequencing is needed before subdivision of the subsection, and additional biogeographical analysis can meaningfully be conducted enabling our understanding of the evolution of this widespread group of *Ficus*. For example, *F. ingens*, an African species morphologically (Corner, 1958) and leaf anatomically close to *F. virens* (Chantarasuwan et al., 2014), forms a clade (Fig. 5-2) together with *F. virens 2* and *3* and *F. middletonii* from Asia constituting a biogeographical puzzle.

Molecular versus Total Evidence

The combination of all DNA and morphological data (total evidence analysis) resulted in a phylogenetic tree (Fig. 5-2) supporting the same major clades A and B and the position of *F. madagascariensis*, *F. orthoneura*, and *F. hookeriana* However, the tree (Fig. 5-2) resulting from analysis including morphological data differs in details from the tree solely based on molecular data (Fig. 5-1). Interestingly the total evidence tree groups within a clade all the Asian species presenting an leaf articulated on the petiole, supporting the idea of Wiens (2004) that morphology and leaf anatomy add valuable data to the phylogeny reconstruction when combined with molecular data. However, the support for relationships among species is low in both analyses precluding an infrageneric classification.

Comparing the phylogeny with traditional classifications

To some degree, our phylogenetic results support Miquel's classification (1867), with the taxa arranged per continent, e.g., a group of African species separate from Asian species, but with a few exceptions. In our results (Fig. 5-1) one African species, *F. ingens*, is placed among Asian species, and Sino-Himalayan *F. hookeriana* and *F. orthoneura* are among African species. Thus, a purely continental classification is not attainable. Corner (1959, 1965) divided section *Urostigma* (similar to subsection *Urostigma* here) of Asia and Australia into four series, *Religiosae* Miq., *Superbae* Corner, *Caulobotryae* (Miq.) Corner, and *Orthoneurae* Corner. However, species in the various series of Corner do not form monophyletic groups, but are mixed in our phylogenetic tree and the relationships among clades are not well supported. Moreover, Corner never included the African species, precluding direct comparison with his subdivision. Berg (2004) re-classified section *Urostigma* and included African species and recognized two subsections, *Urostigma* and *Conosycea*. He did not further subdivide subsect. *Urostigma* as Corner (1959, 1965) did. Berg's classification compares very well with ours and previous works (Rønsted et al, 2005, 2008, Xu et al, 2011; Cruaud et al, 2012) showing

two clades, which cannot easily be subdivided into recognisable subgroups (low support for most branches and no distinct character combinations in Fig. 5-3). *Ficus amplissima* and *F. rumphii* (formerly in *Leucosyce*) were united in subsect. *Urostigma* by Berg, which is now shown to be incorrect as they should instead by included in subsect. *Conosycea*.

Suitable characters for recognising subsection *Urostigma*

The character mapping showed three unique apomorphies for the subsect. *Urostigma* clade (Fig. 5-3), one morphological character (40.1: staminate flowers near ostiole), and two leaf anatomical characters (44.1: epidermis simple; 47.1: enlarged lythocysts only abaxially), of which especially the enlarged lythocysts are typical. Two morphological characters (3.1: intermittent growth present; 7.1: leaves deciduous) show parallel apomorphies in *Conosycea*, though the combination is unique. All characters were previously used for the recognition of subsection *Urostigma* by Berg (2004), Berg & Corner (2005), and Chantarasuwan et al. (2013). These results imply that morphology alone is not sufficient when trying to separate both subsections, whereas the combination with leaf anatomy allows a distinct subsectional recognition.

Intermittent growth (char. 3, Fig. 5-4A) was always the main character used to recognise subsection *Urostigma*, but also occurs in parallel in *F. amplissima* and *F. rumphii* (subsect. *Conosycea*). Thus this character has to be treated carefully and should be used in combination with others.

Deciduousness (char. 7, Fig. 5-4B) should also be used in combination with other characters, because subsection *Urostigma* has exceptions, *F. verruculosa* is evergreen and *F. religiosa* becomes evegreen when growing in wet areas. Moreover, many species of subsect. *Conosycea* are also deciduous. Thus, this is not a decisive character to be used for taxonomic recognition.

The character staminate flowers around the ostiole (char. 40, Fig. 5-4C) is the only typical morphological character, but also this character shows parallel reversals in *F. arnottiana*, *F. hookeriana*, *F. orthonera*, *F. prolixa*, and *F. virens 4* and *5*. The character was used to recognise the subsection by Berg (2004), Berg & Corner (2005), and Chantarasuwan et al. (2013).

Of the leaf anatomical characters, Corner (1959) and Berg & Corner (2005) used the enlarged lythocysts on only the abaxial surface (chr. 47, Fig. 5-4D) as typical for subsect. *Urostigma*. However, the leaf anatomical work of Chantarasuwan et al. (2014) revealed that *F. arnottiana* and *F. virens 4* and *5* show enlarged lithocysts on both the adaxial and abaxial sides, which is similar to subsect. *Conosycea*. Thus, this character also is not unique for subsection *Urostigma*.

The articulation of the leaf (char. 4) only occurs in Asian and Australian species, for which it is a unique apomorphy within the *Urostigma* clade, but again there

are reversals to absence in *F. hookeriana* and *F. orthoneura* (probably related to their non-deciduousness).

Circumscription of subsect. *Urostigma* and subsect. *Conosycea*

Ficus amplissima and *F. rumphii*, together constituting former section *Leucogyne*, were united because of the lythocysts at both sides of the leaf blade, staminate flowers dispersed, and whitish ovaries, while typical for subsect. *Urostigma* were the lythocysts at the abaxial side only, staminate flowers generally around the ostiole and red(-brown) ovaries. Both groups are pollinated by different fig wasps, *Eupristina* in section *Leucogyne* and *Platyscapa* in subsection *Urostigma* (Berg & Wiebes, 1992; Berg & Corner, 2005; Cruaud et al., 2009). However, section *Leucogyne* is not supported by phylogenetic evidence and both species have to be included in subsect. *Conosycea*. Section *Leucogyne* will then become a synonym of subsect. *Conosycea*.

Because of the reclassification of the species of former section *Leucogyne* the recognition of the subsection *Urostigma* and the subsection *Conosycea* changes compared to Berg (2004) Berg and Corner (2005).

Typical for subsect. *Urostigma* are: plants deciduous, intermittent growth present, leaf articulation present or not, petioles relatively long, enlarged lithocysts generally only abaxially to present at both sides, epidermis a single to multiple layers, staminate flowers near the ostiole or dispersed.

Typical for subsect. *Conosycea* are: plants evergreen or deciduous, without clear indication of intermittent growth, leaves without articulation, petioles relatively thick and short, enlarged lithocysts present at both sides, figs more frequently sessile than pedunculate, staminate flowers dispersed.

Paraphyletic species within subsect. *Urostigma*

The sampled specimens of two species show these to be paraphyletic:

Ficus geniculata var. *geniculata*

The two samples of *F. geniculata* var. *geniculata* (*1 & 2*) form a clade but with low support, while the other one (*F. geniculata 3*) forms a clade with *F. caulocarpa* and *F. subpisocarpa* subsp. *pubipoda*, also with low support. Consequently, *F. geniculata* is paraphyletic. However, the support at the internal nodes of the clades are low, therefore we refrain from changing the species concepts until more molecular information becomes available.

Ficus prasinicarpa

The sample *F. prasinicarpa 1* forms a clade with *F. pseudoconcinna* with high support. The two together are sister to *F. prasinicarpa 2*, but with low support.

Morphologically, the two specimens of *F. prasinicarpa* show a few differences, but because of the low support for the clade we do not make any decision about possible cryptic species.

Polyphyletic species within subsect. *Urostigma*

Besides the two paraphyletic species, three out of the 24 species included in our study appear to be polyphyletic:

Ficus caulocarpa

Three specimens of *F. caulocarpa* var. *caulocarpa* were included in this study. *F. caulocarpa 1* was separated from *F. caulocarpa 2* and *F. caulocarpa 3* and forms a clade with *F. tsjakela* with high PP support, while *F. caulocarpa 2* and *F. caulocarpa 3* form a separate clade. The three specimens share many morphological characters, but *F. caulocarpa 1* deviates in a few characters from *F. caulocarpa 2* and *F. caulocarpa 3* such as the stipule forming an ovoid terminal bud, the figs only on short spurs on the branches, and the figs solitary or in pairs. Based on these differences *F. caulocarpa 1* is described here as a separate species, *F. pseudocaulocarpa* (see below). However, in our phylogenetic analysis, the full genetic variation within *F. caulocarpa* is still not covered, because only samples with a narrow leaf form could be included.

Ficus geniculata

Four specimens of *F. geniculata* were analysed, three belong to *F. geniculata* var. *geniculata* and one to *F. geniculata* var. *insignis*. The three samples of var. *geniculata* show paraphyly, but the var. *insignis* specimen groups separately with *F. virens 1*, but with low support. Both varieties can be recognised at the species level, but because the support for the clades was low we refrain to make this decision until more molecular information becomes available.

Ficus virens

Chantarasuwan et al. (2013) recognised four varieties within the *F. virens* complex, var. *virens*, var. *glabella*, var. *matthewii*, and var. *dispersa*. Unfortunately, we only succeeded to amplify DNA sequences from two varieties (var. *virens* and var. *glabella*). Both varieties are separated in the resulting cladogram (Fig. 5-2), and the five samples of var. *virens* even proved to be polyphyletic. The clade of *F. virens* var. *glabella* is strongly supported, its morphology is clear, thus we will reinstate the species level for this taxon. We will maintain *F. virens* with three varieties, var. *virens*, var. *dispersa*, and var. *matthewii*. *F. virens* var. *virens* was represented by five samples in our analyses, which became divided into three groups (Figs. 5-1, 5-2), see above. *Ficus virens 1* shows some morphological differences with *F. virens 2–5*, but the support is low, thus we will not change the status of *F. virens 1*. The morphology and leaf anatomy of the united and highly supported *F. virens 4* and *F. virens 5* are distinctive rom *F. virens 1–3*. Both samples coincide with the previous name *F. wightiana* (Wall. ex Miq.) Benth., which King (1887) treated

as *F. infectoria* Roxb. var. *wightiana* (Wall. ex Miq.) King, and which Corner (1965) accepted as synonym of *F. virens*. Therefore, we will reinstate *F. wightiana*.

Taxonomic Treatment

In this part we will officially make the necessary changes in taxonomy on the basis of our phylogeny. Much of the nomenclature and descriptions can be found in Chantarasuwan et al. (2013) and these will not be repeated here.

Ficus L. subg. *Urostigma* (Gasp.) Miq. sect. *Urostigma* (Gasp.) Endl. subsect. *Urostigma* (Gasp.) C.C. Berg

For nomenclature and the subsection description, see Chantarasuwan et al. (2013)

The following species can be recognized in subsection *Urostigma*:
***Ficus virens* Aiton**, Hort. Kew. 3: 451. 1789 — TYPE: Introduced to Kew about 1762 by James Gordon (holotype: BM). For more nomenclature and description see Chantarasuwan et al. (2013: 679). Only three varieties will be recognised:
***Ficus virens* Aiton var. *virens* Corner** (Chantarasuwan et al., 2013: 679).
***Ficus virens* Aiton var. *dispersa* Chantaras.** (Chantarasuwan et al., 2013: 681).
***Ficus virens* Aiton var. *matthewii* Chantaras.** (Chantarasuwan et al., 2013: 683).

***Ficus glabella* Blume**, Bijdr.: 452. 1825 ≡ *Urostigma glabellum* (Blume) Miq., Fl. Ind. Bat. 1, 2: 340. 1859 ≡ *Ficus virens* Aiton var. *glabella* (Blume) Corner, Gard. Bull. Singapore 17: 377. 1960 — TYPE: INDONESIA. Java, Kiara beas, *Blume s.n.* (holotype: L; isotype: P).

= *Urostigma canaliculatum* Miq., London J. Bot. 6: 579. 1847 — TYPE: AUSTRALIA. Prince of Wales Island, *Hb. Hooker* (holotype: K; isotype: E).

The former variety is here reinstated as species again. For more nomenclature and description see Chantarasuwan et al. (2013: 681, under *F. virens* var. *glabella*).

Ficus wightiana (Wall. ex Miq.) Benth., Fl. Hongk.: 327. 1861 ≡ *Urostigma wightianum* Wall. ex Miq., London J. Bot. 6: 566. 1847 ≡ *Ficus infectoria* Roxb. var. *wightiana* (Wall. ex Miq.) King, Ann. Roy. Bot. Gard. (Culcutta) 1: 60, 63, t 75-77. 1887 — TYPE: INDIA. Bangaloor, *Wallich 4540* (Herb. Wight.) (holotype: K; isotype: E).

Tree. Branches drying brown or grey-brown. Leafy twigs 3–3.5 mm thick, glabrous. Leaves with (sub)articulation; lamina elliptic, 3.8–11.0 by 2.5–5.2 cm, (sub)coriaceous, apex acuminate, the acumen sharp, base attenuate, both

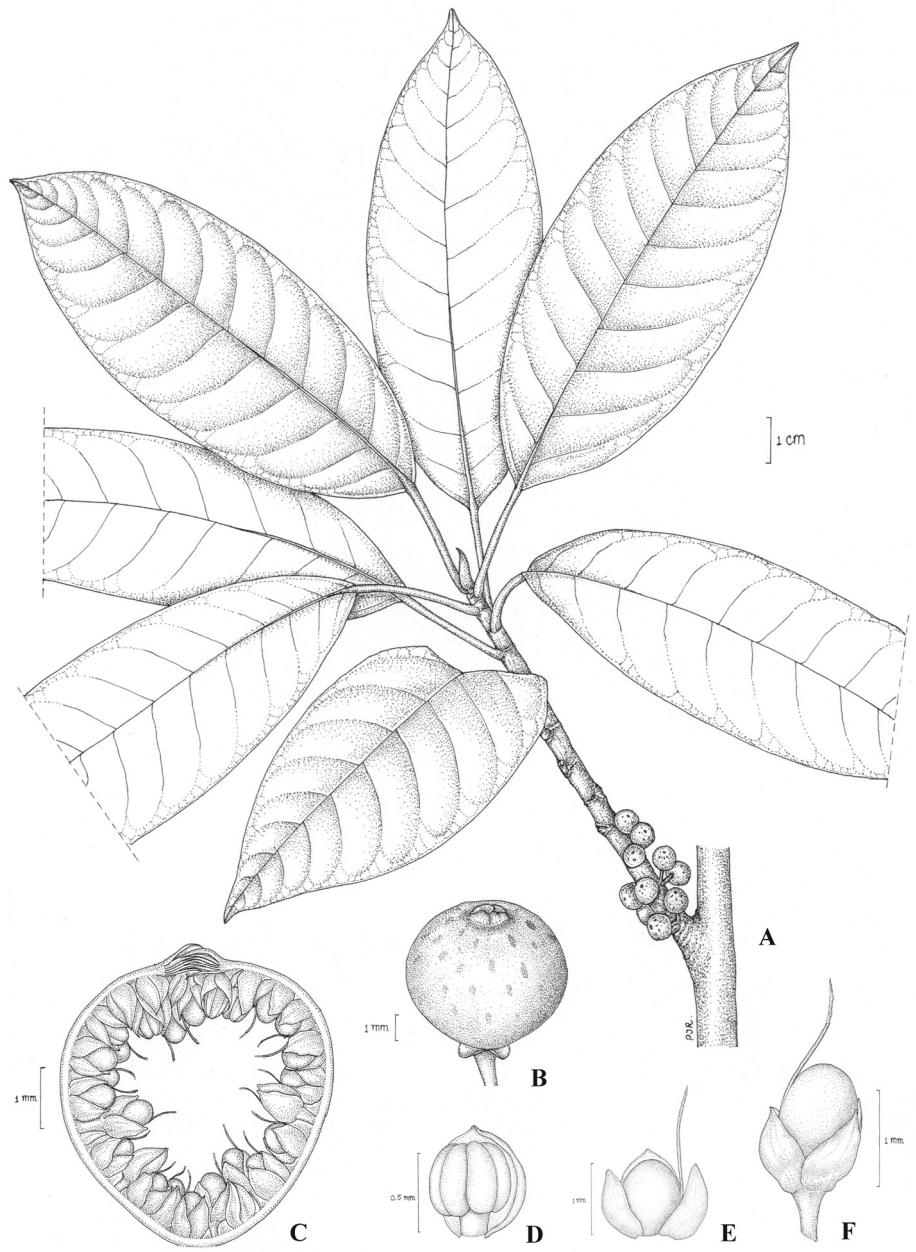

FIGURE 5-5. *Ficus pseudocaulocarpa* Chantaras. A: Twig with leaves and figs. B: Fig. C: Fig in longitudinal section. D: Staminate flower. E and F: Pistillate flowers.-Drawing: Pajaree Inthachup, 2014.

surfaces glabrous; lateral veins 6–10 pairs, the basal pair up to 1/5–1/3 the length of the lamina, unbranched, tertiary venation reticulate, partly parallel to lateral veins; petiole 2.0–6.5 cm long, glabrous, epidermis persistent; stipules 0.4–1.7 cm long, glabrous, persistent at the shoot apex, forming a terminal bud. Figs axillary or below the leaves, solitary or in pairs, sessile, basal bracts 1.5–3 mm long, glabrous, persistent; receptacle subglobose, 0.9–1.1 cm diam. when dry, glabrous, apex convex; ostiole 1–1.5 mm diam., the upper ostiolar bracts glabrous; internal hairs absent. Staminate flowers dispersed, mostely petiolate; tepals 2 – 3, reddish brown; stamen one. Pistillate flowers sessile or pedicellate; tepals 2–3, lanceolate or ovate, free or connate, reddish brown; ovary white to pale brown.

Note: Some samples of this species are very similar to *F. amplissima*. Distinctive are the elliptic leaves with an attenuate base and acuminate apex with sharp acumen. The samples *Gamble 16452* (K), *Preyadarsaman 5*(L), and *Worthington 4350*(K) were misidentified as *F. amplissima* by Chantarasuwan et al. (2013).

Ficus pseudocaulocarpa Chantaras., sp. nov. — TYPE : PHILIPPINES, Palawan, Tatay municipality, Lake Manguao(Danao), 5 April 1984, *C.E. Ridsdale SMHI 323* (holotype : L)

Resembling *Ficus caulocarpa* (Miq.) Miq. Lamina elliptic-ovate to oblong, 3.8–11.8 by 1.8–5.2 cm, subcoriaceous; stipules 0.7–1.1 cm long, puberulous, persistent at the shoot apex, forming an ovoid terminal bud. Figs on short spurs on the older wood, solitary or in pairs.

Tree. Branches drying brown or grey-brown. Leafy twigs 3–6 mm thick, puberulous. Leaves with articulation; lamina elliptic-ovate to oblong, 3.8–11.8 by 1.8–5.2 cm, subcoriaceous, apex acute to subacuminate, the acumen blunt, base cuneate, both surfaces glabrous; lateral veins 12–16 pairs, the basal pair up to 1/6–1/4 the length of the lamina, unbranched, tertiary venation reticulate, partly parallel to lateral veins; petiole 1.3–4.5 cm long, puberulous at base, epidermis flaking off; stipules 0.7–1.1 cm long, puberulous, persistent at the shoot apex, forming an ovoid terminal bud. Figs on short spurs on the older wood, solitary or in pairs, peduncle 0.1–0.2 cm long, glabrous or puberulous, basal bracts 1–1.5 mm long, glabrous or puberulous, persistent; receptacle subglobose, 0.4–0.5 cm diam. when dry, glabrous, apex convex; ostiole 1–1.5 mm diam., the upper ostiolar bracts glabrous; internal hairs present. Staminate flowers near ostiole, sessile; tepals connate, reddish brown; stamen one. Pistillate flowers sessile or pedicellate; tepals 3–4, lanceolate or ovate, free or connate, reddish brown; ovary dark red. Fig. 5-5.

Distribution and Habitat: Philippines. In lowland rain forest at altitude 60–80 m.

Other species in this subsection (see Chantarasuwan et al., 2013, 2014):

Ficus alongensis Gagnep. (Chantarasuwan et al., 2013: 658)
Ficus arnottiana (Miq.) Miq. (Chantarasuwan et al., 2013: 659)
Ficus caulocarpa (Miq.) Miq. (Chantarasuwan et al., 2013: 659)
  Ficus caulocarpa var. *caulocarpa* (Chantarasuwan et al., 2013: 660)
  Ficus caulocarpa var. *dasycarpa* Corner (Chantarasuwan et al., 2013: 660)
Ficus chiangraiensis Chantaras. (Chantarasuwan et al., 2013: 660)
Ficus concinna (Miq.) Miq. (Chantarasuwan et al., 2013: 662)
Ficus cordata Thunb. (Chantarasuwan et al., 2013: 663)
Ficus cornelisiana Chantaras. & Y.Q. Peng (Chantarasuwan et al., 2014: 6)
Ficus cupulata Haines (Chantarasuwan et al., 2013: 665)
Ficus densifolia Miq. (Chantarasuwan et al., 2013: 665)
Ficus geniculata Kurz (Chantarasuwan et al., 2013: 665)
  Ficus geniculata var. *geniculata* (Chantarasuwan et al., 2013: 666)
  Ficus geniculata var. *insignis* (Kurz) C.C.Berg (Chantarasuwan et al., 2013: 666)
Ficus henneana Miq. (Chantarasuwan et al., 2013: 666)
Ficus hookeriana Corner (Chantarasuwan et al., 2013: 667)
Ficus ingens (Miq.) Miq. (Chantarasuwan et al., 2013: 667)
Ficus lecardii Warb. (Chantarasuwan et al., 2013: 668)
Ficus madagascariensis C.C.Berg (Chantarasuwan et al., 2013: 669)
Ficus middletonii Chantaras. (Chantarasuwan et al., 2013: 669)
Ficus orthoneura H.Lév. & Vaniot (Chantarasuwan et al., 2013: 671)
Ficus prasinicarpa Elmer ex C.C.Berg (Chantarasuwan et al., 2013: 671)
Ficus prolixa G.Forst. (Chantarasuwan et al., 2013: 672)
Ficus pseudoconcinna Chantaras. (Chantarasuwan et al., 2013: 672)
Ficus religiosa L. (Chantarasuwan et al., 2013: 673)
Ficus salicifolia Vahl (Chantarasuwan et al., 2013: 673)
Ficus saxophila Blume (Chantarasuwan et al., 2013: 675)
  Ficus saxophila subsp. *saxophila* (Chantarasuwan et al., 2013: 675)
  Ficus saxophila subsp. *cardiophylla* (Merr.) C.C.Berg (Chantarasuwan et al., 2013: 676)
Ficus subpisocarpa Gagnep. (Chantarasuwan et al., 2013: 676)
  Ficus subpisocarpa subsp. *subpisocarpa* (Chantarasuwan et al., 2013: 676)
  Ficus subpisocarpa subsp. *pubipoda* C.C.Berg (Chantarasuwan et al., 2013: 676)
Ficus superba (Miq.) Miq. (Chantarasuwan et al., 2013: 677)
Ficus tjakela Burm.f. (Chantarasuwan et al., 2013: 677)
Ficus verruculosa Warb. (Chantarasuwan et al., 2013: 678)

***Ficus* L. subg. *Urostigma* (Gasp.) Miq. sect. *Urostigma* (Gasp.) Endl. subsect. *Conosycea* (Miq) C.C. Berg**, Blumea 49: 465. 2004 ≡ *Ficus* L. subg. *Urostigma* (Gasp.) Miq. sect. *Conosycea* (Miq.) Corner, Gard. Bull. Singapore 17: 371. 1960 ≡ *Urostigma* Gasp. subg. *Conosycea* Miq., Fl. Ind. Bat. 1,2: 349. 1859 — LECTOTYPE (designated by Corner, 1959): *Ficus annulata* Blume.

= *Urostigma* Gasp. sect. *Valida* Miq., Fl Ind. Bat. 1,2: 334. 1859 ≡ *Ficus* L. subg. *Urostigma* (Gasp.) Miq. ser. *Validae* (Miq.) Miq., Ann. Mus. Bot. Lugduno–Batavi 3: 285. 1867; Corner, Gard. Bull. Singapore 17: 272. 1960 — LECTOTYPE (designated by Corner, 1959): *Urostigma valida* (Blume) Miq. [= *Ficus annulata* Blume].

= *Ficus* L. sect. *Stilpnophyllum* Endl. subsect. *Sessiliflorae* Sata, Contr. Hort. Inst. Taihoku Imp. Univ. 32: 179, 190, 375, 376. 1944 — TYPE: unknown.

= *Ficus* L. subg. *Urostigma* (Gasp.) Miq. sect. *Conosycea* (Miq.) Corner subsect. *Conosycea* (Miq.) C.C. Berg ser. *Drupaceae* Corner, Gard. Bull. Singpore 17: 372. 1960 ≡ *Ficus* L. subg. *Urostigma* (Gasp.) Miq. sect. *Conosycea* (Miq.) Corner ser. *Drupaceae* Corner subser. *Drupaceae* Corner, Gard. Bull. Singapore 17: 372. 1960 — TYPE: *Ficus drupacea* Thunb.

= *Ficus* L. subg. *Urostigma* (Gasp.) Miq. sect. *Conosycea* (Miq.) Corner subsect. *Conosycea* (Miq.) C.C. Berg ser. *Drupaceae* Corner subser. *Indicae* Corner, Gard. Bull. Singapore 17: 372. 1960 ≡ Perula Raf., Sylv. Tellur.: 59.1838, non Schreb. 1791 — TYPE: *Ficus benghalensis* L.

= *Ficus* L. subg. *Urostigma* (Gasp.) Miq. sect. *Conosycea* (Miq.) Corner subsect. *Conosycea* (Miq.) C.C. Berg ser. *Drupaceae* Corner subser. *Zygotricheae* Corner, Gard. Bull. Singapore 17: 372. 1960 — TYPE: *Ficus consociata* Blume

= *Ficus* L. subg. *Urostigma* (Gasp.) Miq. sect. *Conosycea* (Miq.) Corner subsect. *Conosycea* (Miq.) C.C. Berg ser. *Drupaceae* Corner subser. *Crassirameae* Corner, Gard. Bull. Singapore 17: 373. 1960 — TYPE: *Ficus crassiramea* Miq.

= *Ficus* L. subg. *Urostigma* (Gasp.) Miq. sect. *Conosycea* (Miq.) Corner subsect. *Dictyoneuron* Corner, Gard. Bull. Singapore 17: 373. 1960 — TYPE: *Ficus sundaica* Blume

= *Ficus* L. subg. *Urostigma* (Gasp.) Miq. sect. *Conosycea* (Miq.) Corner subsect. *Dictyoneuron* Corner ser. *Dubiae* Corner, Gard. Bull. Singapore 17: 373. 1960 — TYPE: *Ficus dubia* Wall. ex King

= *Ficus* L. subg. *Urostigma* (Gasp.) Miq. sect. *Conosycea* (Miq.) Corner subsect. *Dictyoneuron* Corner ser. *Glaberrimae* Corner, Gard. Bull. Singapore 17: 373. 1960 — TYPE: *Ficus glaberrima* Blume

= *Ficus* L. subg. *Urostigma* (Gasp.) Miq. sect. *Conosycea* (Miq.) Corner subsect. *Dictyoneuron* Corner ser. *Subvalidae* (Miq.) Corner, Gard. Bull. Singapore 17: 373. 1960 ≡ *Urostigma* Gasp. sect. *Subvalida* Miq., Fl. Ind. Bat. 1,2: 339. 1859 — TYPE: *Ficus sundaica* Blume

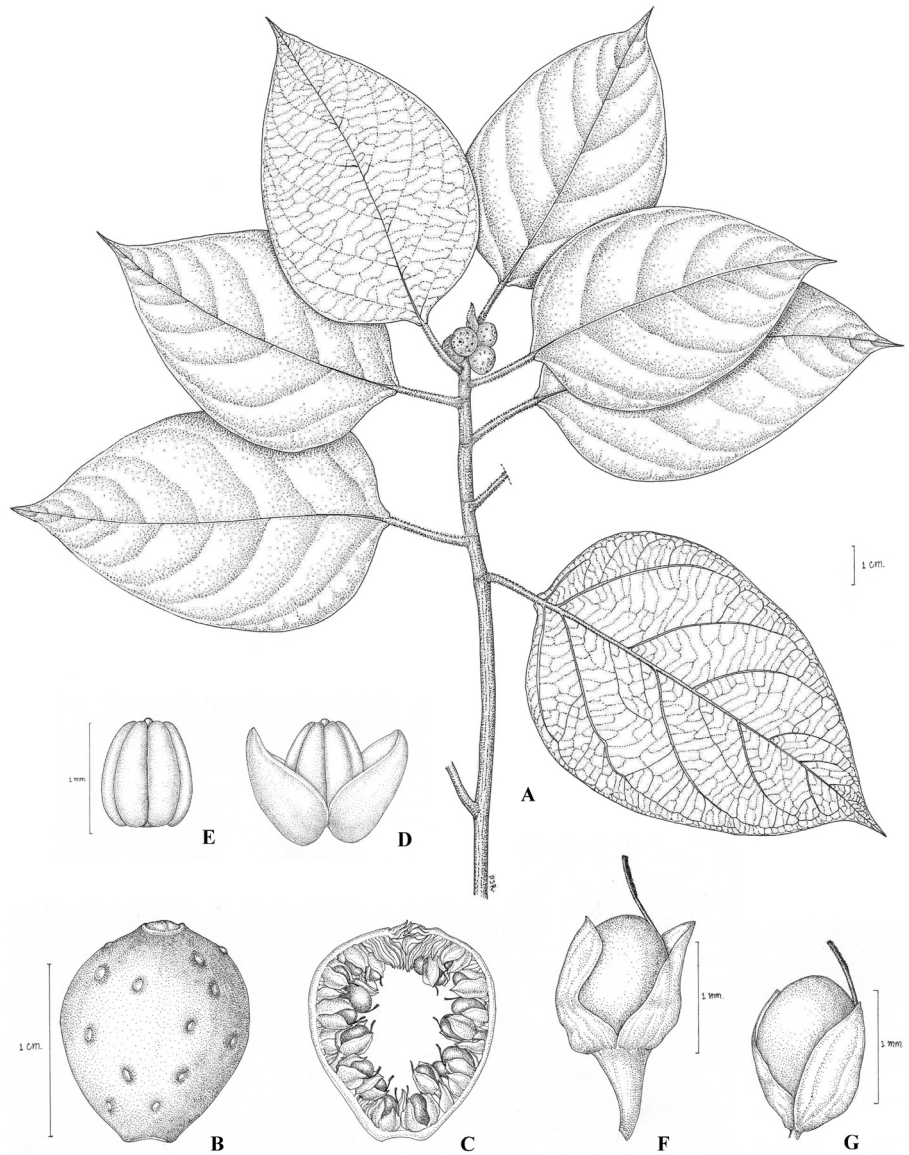

FIGURE 5-6. *Ficus pubipetiola* Chantaras. A: Twig with leaves and figs. B: Fig. C: Fig in longitudinal section. D: Staminate flower. E: Anther. F and G: Pistillate flowers.-Drawing: Pajaree Inthachup, 2014.

= *Ficus* L. subg. *Urostigma* (Gasp.) Miq. sect. *Conosycea* (Miq.) Corner subsect. *Dictyoneuron* Corner ser. *Perforatae* Corner, Gard. Bull. Singapore 17: 374. 1960 — TYPE: *Ficus pisocarpa* Blume

= *Ficus* L. subg. *Urostigma* (Gasp.) Miq. sect. *Conosycea* (Miq.) Corner subsect. *Benjamina* (Miq.) Corner, Gard. Bull. Singapore 17: 374. 1960 ≡ *Ficus* L. subg. *Urostigma* (Gasp.) Miq. ser. *Benjamineae* Miq. Ann. Mus Bot. Lugduno–Batavi 3: 287. 1867 — TYPE: *Ficus benjamina* L.

= *Ficus* L. subg. *Urostigma* (Gasp.) Miq. sect. *Conosycea* (Miq.) Corner subsect. *Benjamina* (Miq.) Corner ser. *Callophylleae* Corner, Gard. Bull. Singapore 17: 374. 1960 — TYPE: *Ficus callophylla* Blume

= *Ficus* L. subg. *Urostigma* (Gasp.) Miq. sect. *Leucogyne* Corner, Gard. Bull. Singapore 17: 371. 1960 — TYPE: *Ficus rumphii* Blume

Trees, mostly evergreen, without intermittent growth to rarely intermittent growth with 2 or 3 short internodes forming a transition zone. Leaves spirally arranged, not articulate; epidermis multiple, enlarged lithocysts at both sides of lamina; petiole relatively thick and short. Figs solitary or in pairs axillary, or just below the leaves, more frequently sessile than pedunculate; receptacle often longer than wide; basal bracts 3(2), small to large, often unequal in size or shape, mostly persistent; ostiole closed, with the upper ostiolar bracts overlapping, or open, with the upper ostiolar bracts not or partly imbricate, the 3 upper ostiolar bracts often unequal in size, sometimes only 2 clearly visible; internal hairs mostly absent; staminate flowers dispersed; tepals mostly red(dish) brown; ovary white or partly reddish, sometimes entirely reddish.

Ficus amplissima **J.E.Sm.** in Rees, Cycl. 14: n. 68. 1810, non Miq. 1867; Corner, Gard. Bull. Singapore 18: 84. 1961; 21: 11. 1965; K.M.Matthew, Fl. Tam. Carnatic 3: 1515. 1983 ≡ *Tsjela* Rheede, Hort. Mal. 3: 85, t. 63. 1682, nom. inval. ≡ *Ficus tsiela* Roxb., Hort. Bengal.: 66. 1826, nom. superfl.; Fl. Ind. 3: 549. 1832; King in Hook.f., Fl. Brit. India 5: 515. 1888. ≡ *Ficus tsjela* Roxb. ex Buch.–Ham., Tr. Linn. Soc. 15: 149. 1826, nom. superfl.; King, Ann. Roy. Bot. Gard. (Culcutta) 1: t.74. 1887 ≡ *Ficus indica* auct. non L.: L., Sp. Pl. 2: 1060. 1753; Vahl. Enum. Pl., ed. 2: 195. 1806; Willd., Sp. Pl., ed. 4, 4(2): 1146. 1806.—TYPE: Rheede (1682) t. 63, based on *Tsjela* Rheed.

= *Urostigma pseudobenjamineum* Miq., London J. Bot. 6: 566. 1847 ≡ *Ficus pseudobenjaminea* (Miq.) Miq., Ann. Mus. Bot. Lugduno–Batavi 3: 286. 1867—TYPE: INDIA. Luddaloor, *Wight s.n. in herb. Rupel* (holotype: K).

= *Urostigma pseudotsiela* Miq., London J. Bot. 6: 566. 1847. ≡ *Ficus pseudotsiela* (Miq.) King, Ann. Roy. Bot. Gard. (Culcutta) 1: t. 74. 1887—TYPE: *Wight*. in Herb. Hook. (not found yet, information based on Corner 1965).

Ficus rumphii **Blume**, Bijdr. Fl. Ned. Ind. 9: 437. 1825; Miq., Ann. Mus. Bot. Lugduno–Batavi 3: 287. 1867; King, Ann. Roy. Bot. Gard. (Calcutta) 1: 54, t. 67B. 1887; Gagnep. in Lecomte, Fl. Indo–Chine 5: 768. 1928; Corner, Wayside Trees 1: 687. 1940; Gard. Bull. Singapore 21: 11. 1965; C.C.Berg and Corner in Nooteb., Fl. Males. Ser. 1, 17 (2): 609. 2005 ≡ *Urostigma rumphii* (Blume) Miq. in Zoll., Syst. Verz. 2: 90. 1854; Fl. Ind. Bat. 1, 2: 322. 1859 — TYPE: INDONESIA. Java, *Reinwardt 1121* (holotype: L; isotype: P).

= [*Ficus populiformis* Schott ex Miq., Ann. Mus. Bot. Lugduno–Batavi 3: 287. 1867, nom.nud.]

= *Ficus religiosa* L. var. ß "*Arbor conciliorum* etc." Lam., Encycl. 2, 2: 493. 1788. nom. illig.–*Ficus cordifolia* Roxb., Fl. Ind. (Carey ed.) 3: 548. 1832 ≡*Urostigma cordifolium* (Roxb.) Miq., London J. Bot. 6: 564. 1847 ≡ *Ficus conciliorum* Oken, Allg. Naturgesch.3: 1561. 1841, nom. superfl. — TYPE: based on Rumphius: *Arbor conciliorum* Rumph., Herb. Amboin. 3: t.91, 92. 1743.

= *Ficus damit* Gagnep., Notul. Syst. (Paris) 4: 88. 1927; in Lecomte, Fl. Indo–Chine 5: 812, f.93. 1928 — TYPE: VIETNAM. Quang–tri, Lao–bao, *Poilane 1337* (holotype: P).

Ficus pubipetiola Chantaras., sp. nov. — TYPE : THAILAND, Lopburi, Tha Wung, Wat Khao Samorkhorn, 18 September 2010, *Chantarasuwan 180910–2*, (holotype : THNHM, isotype : L).

Leaf lamina ovate, 4–9 by 6.5–12 cm , subcoriaceous, apex (sub)acuminate, pubescent on midrib and primary veins on lower surface, petiole 1.1–2.5 cm long, pubescent. Figs axillary, sessile.

Small trees, up to 7 m tall. Branches drying grey-brown, without intermittent growth. Leafy twigs 2–4 mm thick, pubescent, epidermis flaking off. Leaves spirally arranged, not articulate; lamina ovate, 4–9 by 6.5–12 cm, subcoriaceous, apex (sub)acuminate, the acumen sharp, base broadly cuneate or sub-attenuate, rarely sub-cordate, upper surface glabrous except pubescent on midrib, lower surface glabrous except pubescent on midrib and primary veins; lateral veins 5–9 pairs, furcated away from margin, the basal pair up to ¼–2/5th the length of the lamina, branched, tertiary venation reticulate; petiole 1.1–2.5 cm long, pubescent, epidermis persistent. Stipules 0.8–1.7 cm long, brown pubescent, persistent at tip of twig. Figs axillary, solitary or in pairs, sessile; basal bracts 3, 1–2 mm long, glabrous, persistent, receptacle obovate, 0.8–1.1 cm diam. when dry, glabrous, apex convex, ostiole 2–2.5 mm diam., upper ostiolar bracts glabrous; internal hairs absent. Staminate flowers dispersed, sessile to pedicellate; tepals 3, ovate to broad-lanceolate, free, red-brown; stamen one. Pistillate flowers sessile to pedicellate, sometimes with a bract at base of pedicel; tepals 3, ovate or broadly lanceolate, free, red–brown; ovary white (or pale yellow). Fig. 5-6.

Distribution and Habitat: Thailand, on limestone in dwarf community, at elevation of c. 30 m. Figs in September–November.

Other species in this subsection are:

Ficus acamptophylla (Miq.) Miq. (Berg & Corner, 2005: 622)
Ficus altissima Blume (Berg & Corner, 2005: 625)
Ficus annulata Blume (Berg & Corner, 2005: 625)
Ficus archboldiana Summerh. (Berg & Corner, 2005: 627)
Ficus belete Merr. (Berg & Corner, 2005: 628)
Ficus benghalensis L. (Berg & Corner, 2005: 630)
Ficus benjamina L. (Berg & Corner, 2005: 631)
Ficus binnendijkii (Miq.) Miq. (Berg & Corner, 2005: 633)
Ficus borneensis Kochummen (Berg & Corner, 2005: 634)
Ficus bracteata (Wall. ex Miq.) Miq. (Berg & Corner, 2005: 635)
Ficus callophylla Blume (Berg & Corner, 2005: 637)
Ficus chrysolepis Miq. (Berg & Corner, 2005: 640)
Ficus chrysolepis subsp. *chrysolepis* (Berg & Corner, 2005: 626, 640)
Ficus chrysolepis subsp. *novoguineensis* (Corner) C.C. Berg (Berg & Corner, 2005: 626, 641)
Ficus consociata Blume (Berg & Corner, 2005: 641)
Ficus cordatula Merr. (Berg & Corner, 2005: 642)
Ficus corneri Kochummen (Berg & Corner, 2005: 643)
Ficus costata Aiton (Corner, 1981: 246)
Ficus crassiramea (Miq.) Miq. (Berg & Corner, 2005: 643)
Ficus crassiramea subsp. *crassiramea* (Berg & Corner, 2005: 644)
Ficus crassiramea subsp. *stupenda* (Miq.) C.C. Berg (Berg & Corner, 2005: 647)
Ficus cucurbitina King (Berg & Corner, 2005: 647)
Ficus curtipes Corner (Berg & Corner, 2005: 638, 648)
Ficus dalhousiae Miq. (Corner, 1965: 12)
Ficus delosyce Corner (Berg & Corner, 2005: 649)
Ficus depressa Blume (Berg & Corner, 2005: 650)
Ficus drupacea Thunb. (Berg & Corner, 2005: 651)
Ficus dubia Wall. ex King (Berg & Corner, 2005: 653)
Ficus fergusoni (King) Worthington (Corner, 1981: 253)
Ficus forstenii Miq. (Berg & Corner, 2005: 654)
Ficus glaberrima Blumea (Berg et al., 2011: 625)
Ficus glaberrima subsp. *glaberrima* (Berg et al., 2011: 625)
Ficus glaberrima subsp. *siamensis* (Corner) C.C. Berg (Berg et al., 2011: 625)
Ficus globosa Blume (Berge & Corner, 2005: 626, 657)
Ficus humbertii C.C. Berg (Berg & Wiebes, 1992)
Ficus involucrata Blume (Berg & Corner, 2005: 658)
Ficus juglandiformis King (Berg & Corner, 2005: 659)
Ficus kerkhovenii Valeton (Berg & Corner, 2005: 659)
Ficus kochummeniana C.C. Berg (Berg & Corner, 2005: 661)
Ficus kurzii King (Berg & Corner, 2005: 662)
Ficus lawesii King (Berg & Corner, 2005: 655, 663)
Ficus lowii King (Berg & Corner, 2005: 664)
Ficus maclellendii King (Berg & Corner, 2005: 665)
Ficus menabeensis Perrier (Berg & Wiebes, 1992: 95)
Ficus microcarpa L.f. (Berg & Corner, 2005: 624, 666)
Ficus microsyce Ridl. (Berg & Corner, 2005: 623, 670)
Ficus miqueliana C.C. Berg (Berg & Corner, 2005: 617)
Ficus mollis Vahl (Corner, 1981: 249)
Ficus pallescens (Weiblen) C.C. Berg (Berg & Corner, 2005: 671)
Ficus paracamptophylla Corner (Berg & Corner, 2005: 672)
Ficus patellata Corner (Berg & Corner, 2005: 673)
Ficus pellucidopunctata Griff. (Berg & Corner, 2005: 674)
Ficus pisocarpa Blume (Berg & Corner, 2005: 674)
Ficus pubilimba Merr. (Berg & Corner, 2005: 676)
Ficus retusa L. (Berg & Corner, 2005: 676)
Ficus rigo F.M. Bailey (Berg & Corner, 2005: 677)
Ficus soepadmoi Kochummen (Berg & Corner, 2005: 678)
Ficus spathulifolia Corner (Berg & Corner, 2005: 678)
Ficus stricta (Miq.) Miq. (Berg & Corner, 2005: 679)
Ficus subcordata Blume (Berg & Corner, 2005: 669, 680)
Ficus subgelderi Corner (Berg & Corner, 2005: 681)
Ficus sumatrana (Miq.) Miq. (Berg & Corner, 2005: 682)
Ficus sundaica Blume (Berg & Corner, 2005: 684)
Ficus talbotii King (= *F. calcicola* Corner) (Berg et al., 2011: 647)
Ficus tristaniifolia Corner (Berg & Corner, 2005: 669, 686)
Ficus xylophylla (Wall. ex Miq.) Miq. (Berg & Corner, 2005: 687)

Acknowledgements

The first author wishes to thank the Royal Thai Government for a scholarship and to acknowledge the support from the Thailand National Science Museum enabling him to study for a Ph.D. in Leiden, the Netherlands. We are grateful to L, P and WAG for herbarium material, Hortus Botanicus Leiden, Bob Harwood (BKF), S. Sirimongkol (BKF), K. Pruesapan (BK), and T. Vernimmen (L) for providing silica dried material for DNA extraction and J.F. Veldkamp for nomenclature suggestion. The staff of CEFE-CNRS and C is thanked for their assistence in the molecular laboratory and for their general help during visits of the first author. Special thanks for assistance to Y. Sirichamorn (L), staff of the Thailand Natural History Museum (A. Teerawatananon, C. Jaitrong, S. Makchai, and D. Prathumthong), and Y. Chuaykern (Khonkaen University) for support during a field trip in Thailand, and Pajaree Inthachup, Bangkok Herbarium (BK), for the beautiful drawings.

APPENDIX 1 Species, voucher specimen, and Gen Bank information for sequence data reported in the study: sequence per entry: Species; Taxon code; Voucher; Source and Geographic regions; GenBank accession (ITS, ETS, G3pdh, ncpGS)

Ficus alongensis Gagnep.; *alongensis* 1; Steward and Cheo 1187 (P); China, Shaanxi, Chang An; KJ845962, KJ845902, KJ846015, -
Ficus alongensis Gagnep.; *alongensis* 2; R.C. Ching 1917 (P); China; KJ845963, KJ845903, - , -
Ficus arnottiana (Miq.) Miq.; *arnottiana* 1; A.H.M. Jayasuriya 1293 (L); Sri Lanka, Anuradhapura, Ritigala Strict Natural reserve; - , KJ845879, - , -
Ficus arnottiana (Miq.) Miq.; *arnottiana* 2; 2038(no collector name) (L); India, Mangalor; - , KJ845880, - , -
Ficus caulocarpa (Miq.) Miq.; *caulocarpa* 1; C.E. Ridsdale SMHI 323 (L); Philippines, Taytay municipality, Lake Manguao; KJ845953, - , - , -
Ficus caulocarpa (Miq.) Miq.; *caulocarpa* 2; Chantarasuwan 261111-1 (L); Thailand, Trang, Nayong; KJ845954, KJ845894, KJ846009, -
Ficus caulocarpa (Miq.) Miq.; *caulocarpa* 3; Chantarasuwan 071010-2 (L); Thailand, Nakhon Si Thammarat, Noppitam; KJ845955, KJ845895, KJ846010, -
Ficus concinna (Miq.) Miq.; *concinna* 1; Chantarasuwan 071010-1 (L); Thailand, Nakhon Si Thammarat, Thasala; KJ845989, KJ845928, KJ846035, -
Ficus concinna (Miq.) Miq.; *concinna* 2; Chantarasuwan 140910-3 (L); Thailand, Ratchaburi, Chombung; KJ845990, KJ845929, KJ846036, -
Ficus concinna (Miq.) Miq.; *concinna* 3; Chantarasuwan 120910-5 (L); Thailand, Rayong, Pe; KJ845991, KJ845930, KJ846037, KJ846071
Ficus concinna (Miq.) Miq.; *concinna* 4; Chantarasuwan 051010-4 (L); Thailand, Prachuap Khiri Khan, Kuiburi; KJ845992, KJ845931, KJ846038, KJ846072
Ficus cordata Thunb.; *cordata* 1; Dinter 275 (WAG); Namibia;KJ845973, KJ845912, KJ846020, -
Ficus cordata Thunb.; *cordata* 2; Seydel 1555 (WAG); Namibia, Erongo, Okongawa; KJ845974, 845913, KJ846021, -
Ficus cordata Thunb.; *cordata* 3; Theson 3363 (WAG); Namibia; KJ845975, KJ845914, KJ846022, KJ846063
Ficus densifolia Miq.; *densifolia* 1; Baider CB2421 (L); Mauritius; KJ845983, KJ845922, KJ846030, KJ846068
Ficus densifolia Miq.; *densifolia* 2; Baider CB2422 (L); Mauritius; KJ845984, KJ845923, KJ846031, KJ846069
Ficus densifolia Miq.; *densifolia* 3; M02 (CEFE-CNRS); Mauritius; KJ845985, KJ845924, KJ846032, -
Ficus densifolia Miq.; *densifolia* 4; M01 (CEFE-CNRS); Mauritius; KJ845986, KJ845925, KJ846033, KJ846070
Ficus geniculata Kurz var. *geniculata; geniculata* 1; Chantarasuwan 150910-1 (L); Thailand, Kanchanaburi, Thong Pha Phum, Lintin; KJ845940, KJ845882, KJ845999, KJ846044
Ficus geniculata Kurz var. *geniculata; geniculata* 2; Chantarasuwan 210910-1 (L); Thailand, Lamphun, Muang; KJ845941, KJ845883, KJ846000, KJ846045

Ficus geniculata Kurz var. *geniculata; geniculata* 3; Chantarasuwan 301111-1 (L); Thailand, Chiang Rai, Muang, Pongsali; KJ845942, KJ845884, - , KJ846046
Ficus geniculata Kurz var. *insignis* (Kurz) C.C.Berg; geniculate-insignis; Parker 1144 (L); Australia, Northern Territory, Darwin; KJ845943, KJ845885, KJ846001, KJ846047
Ficus glaberrima Blume subsp. *siamensis* (Corner) C.C.Berg; *glaberrima-siamensis* 1; Chantarasuwan 110910-2 (L); Thailand, Sa Kaeo, Khao Chakan; KJ845996, KJ845935, KJ846041, KJ846076
Ficus glaberrima Blume subsp. *siamensis* (Corner) C.C.Berg; *glaberrima-siamensis* 2; Chantarasuwan 110910-3 (L); Thailand, Sa Kaeo, Khao Chakan; KJ845997, KJ845936, KJ846042, KJ846077
Ficus glaberrima Blume subsp. *siamensis* (Corner) C.C.Berg; *glaberrima-siamensis* 3; Chantarasuwan 180910-3 (L); Thailand, Lop Buri, Thawung; KJ845998, KJ845937, KJ846043, -
Ficus henneana Miq.; *henneana* 1; J.R. Maconochie 2208 (L); Australia, Arnhem Land, Elcho Isl.; KJ845967, - , KJ846016, KJ846058
Ficus henneana Miq.; *henneana* 2; B. Hyland 8086 (L); Australia, Queensland, Atherton; KJ845968, KJ845907, - , KJ846059
Ficus hookeriana Corner; *hookeriana*; Hooker & T.Thomson 120 (L); India, Sikkim; KJ845988, KJ845927, - , -
F*icus ingens* (Miq.) Miq.; *ingens* 1; BG 03 (L); Ivory Coast; KJ845964, KJ845904, - , KJ846056
Ficus ingens (Miq.) Miq.; *ingens* 2; Correia 3777 (WAG); Mozambique; KJ845965, KJ845905, - , -
Ficus ingens (Miq.) Miq.; *ingens* 3; Jongkind 4317 (WAG); Ivory Coast; KJ845966, KJ845906, - , KJ846057
Ficus lecardii Warb.; *lecardii* 1; Harris 2136 (WAG); Central African Republic; KJ845971, KJ845910, KJ846018, KJ846061
Ficus lecardii Warb.; *lecardii* 2; Letouzey 6949 (WAG); Cameroon; KJ845972, KJ845911, KJ846019, KJ846062
Ficus madagascariensis C.C.Berg; *madagascariensis* ; P.R. Montagnac 72 (WAG); Madagascar, without locality; KJ845956, KJ845896, - , KJ846053
Ficus middletonii Chantaras.; *middletonii* ; Chantarasuwan 051010-2 (L); Thailand, Prachuap Khiri Khan, Kuiburi; KJ845952, KJ845893, KJ846008, KJ846052
Ficus orthoneura H.Lév. & Vaniot; *orthoneura* 1; Chantarasuwan 231111-1 (L); Thailand, Tak, Phobpra; KJ845987, KJ845926, KJ846034, -
Ficus prasinicarpa Elmer ex C.C.Berg; *prasinicarpa* 1; Ridsdale 434 (L); Philippines; KJ845947, -, -, -
Ficus prasinicarpa Elmer ex C.C.Berg; *prasinicarpa* 2; Nagari 7309 (L); Papua New Guinea; KJ845948, KJ845889, - , -
Ficus prolixa G. Forst.; *prolixa* 1; Gillett 2206 (L); Marquesas; KJ845949, KJ845890, KJ846005, KJ846051
Ficus prolixa G. Forst.; *prolixa* 2; Fosberg 25302 (L); Guam; KJ845950, KJ845891, KJ846006, -
Ficus pseudoconcinna Chantaras.; *pseudoconcinna* ; Soenarko 355 (L); Indonesia,Sulawesi; KJ845946, KJ845888, KJ846004, KJ846050
Ficus religiosa L.; *religiosa* 1; BG 04(L); unknown; KJ845980, KJ845919, KJ846027, KJ846066
Ficus religiosa L.; *religiosa* 2; Chantarasuwan 110910-4 (L); Thailand, Sa Kaeo, Khao Chakan; KJ845981, KJ845920, KJ846028, -
Ficus religiosa L.; *religiosa* 3; Chantarasuwan 150910-2 (L); Thailand, Kanchanaburi, Thong Pha Phum, Lintin; KJ845982, KJ845921, KJ846029, KJ846067
Ficus cf. rumphii; rumphii cf.; Chantarasuwan 180910-2 (L); Thailand, Lop Buri, Thawung; KJ845995, KJ845934, - , KJ846075

Ficus rumphii Blume; *rumphii* 1; Chantarasuwan 120910-4 (L); Thailand, Rayong, Pe; KJ845993, KJ845932, KJ846039, KJ846073
Ficus rumphii Blume; *rumphii* 2; Chantarasuwan 140910-1 (L); Thailand, Ratchaburi, Chombung; KJ845994, KJ845933, KJ846040, KJ846074
Ficus salicifolia Vahl; *salicifolia* 1; Humbert s.n. (WAG); South Africa; KJ845976, KJ845915, KJ846023, KJ846064
Ficus salicifolia Vahl; *salicifolia* 2; Bornmüller 646 (WAG); Saudi Arabia; KJ845977, KJ845916, KJ846024, -
Ficus subpisocarpa Gagnep. subsp. *pubipoda* C.C. Berg; subpisocarpa- pubipoda 1; Chantarasuwan 110910-1 (L); Thailand, Chachoengsao, Panom Sarakham; KJ845969, KJ845908, - , -
Ficus subpisocarpa Gagnep. subsp. *pubipoda* C.C. Berg; subpisocarpa- pubipoda 2; Chantarasuwan 011211-1 (L); Thailand, Chachoengsao, Panom Sarakham; KJ845970, KJ845909, KJ846017, KJ846060
Ficus superba (Miq.) Miq.; *superba* 1; C. Friedberg 138 (L); Indonesia, Timor central; KJ845944, KJ845886, KJ846002, KJ846048
Ficus superba (Miq.) Miq.; *superba* 2; Chantarasuwan 120910-2 (L); Thailand, Rayong, Kleang; KJ845945, KJ845887, KJ846003, KJ846049
Ficus tsjakela Burm.f.; *tsjakela*; Kostermans 27682 (L); Sri Lanka, Botanics Garden Peradeniya; KJ845951, KJ845892, KJ846007, -
Ficus verruculosa Warb.; *verruculosa* 1; Radcliff-Smith 5982 (WAG); Malawi; KJ845978, KJ845917, KJ846025, -
Ficus verruculosa Warb.; *verruculosa* 2; Adjakidje 2779 (WAG); Benin; KJ845979, KJ845917, KJ846026, KJ846065
Ficus virens Aiton var. *glabella* (Blume) Corner; *virens-glabella 1*; Chantarasuwan 071010-3 (L); Thailand, Nakhon Si Thammarat, Noppitam; KJ845960, KJ845900, KJ846013, KJ846055
Ficus virens Aiton var. *glabella* (Blume) Corner; *virens-glabella 2*; Chantarasuwan 071010-4 (L); Thailand, Nakhon Si Thammarat, Noppitam; KJ845961, KJ845901, KJ846014, -
Ficus virens Aiton var. *virens; virens 1*; P. Martensz AE 257 (L); Australia, Northern Territory; KJ845957, KJ845897, KJ846011, KJ846054
Ficus virens Aiton var. *virens; virens 2*; E. Jacobson 2191 (L); Indonesia ,Sumatra; KJ845958, KJ845898, KJ846012, -
Ficus virens Aiton var. *virens; virens 3*; G. Leach UPNG 3747 (L); Papua New Guinea, Central Province; KJ845959, KJ845899, - , -
Ficus virens Aiton var. *virens; virens 4*; L.H. Cramer 4670 (L); Sri Lanka, North-Western province, Puttalam, Talawila; KJ845938, KJ845881, - , -
Ficus virens Aiton var. *virens; virens 5*; Preyadasaman 5 (L); India, Coimbatore; KJ845939, - , - , -

APPENDIX 2. List of morphological and leaf anatomical characters used in the phylogenetic analysis.

1. Habit: (1) shrub; (2) tree. 2. Aerial roots: (1) present; (2) absent. 3. Intermittent growth: (1) present; (2) absent. 4. Leaf articulation: (1) present; (2) absent. 5. Indumentum of leafy twig: (1) glabrous to puberulous; (2) tomentose to villous. 6. Periderm of leafy twig: (1) persistent; (2) flaking off. 7. Leaf persistence: (1) deciduous; (2) evergreen. 8. Position of broadest part of leaf: (1) base; (2) middle; (3) apex. 9. Relative presence of cordate leaves: (1) cordate leaves dominant (>50%) (2) cordate leaves not dominant (<50%). 10. Caudate leaf apex: (1) present; (2) absent. 11. Relative width of lamina compared to length: (1) broad (> ¼); (2) narrow (< ¼). 12. Relative length of basal pair of nerves: (1) ≤ 1/3 of lamina; (2) > 1/3 of lamina. 13. Number of lateral veins: (1) 4-9; (2) ≥10. 14. Branching of lateral veins: (1) present; (2) absent. 15. Branching of basal veins: (1) present; (2) absent. 16. Tertiary venation: (1) partly parallel with primary veins; (2) reticulate. 17. Waxy glands: (1) at base of midrib; (2) in axil of lateral veins. 18. Relative petiole length: (1) < ¼ of leaf length; (2) > ¼ of leaf length. 19. Epidermis of petiole: (1) persistent; (2) flaking off. 20. Indumentum of petiole: (1) glabrous; (2) puberulous. 21. Length of stipules: (1) < 1 cm long; (2) ≥ 1 cm long. 22. Stipular bracts: (1) forming broadly ovoid terminal bud; (2) forming ovoid terminal bud. 23. Epidermis of stipule: (1) persistent; (2) flaking off. 24. Indumentum of stipule: (1) glabrous to puberulous; (2) tomentose to villous. 25. Persistence of stipule: (1) persistent; (2) caducous. 26. Ramiflorous figs: (1) with spur; (2) without spur. 27. Grouping of figs: (1) 1 or 2; (2) 3 to 8. 28. Indumentum of figs: (1) glabrous to puberulous; (2) tomentose to villous. 29. Fig peduncle: (1) present; (2) absent. 30. Number of basal bracts: (1) 2; (2) 3. 31. Persistence of basal bracts: (1) persistent; (2) caducous. 32. Degree of covering of fig by basal bracts: (1) only base of fig; (2) up to middle of fig. 33. Fig size: (1) 0.4–1 cm diam. when dry; (2) > 1 cm diam. when dry. 34. Fig form: (1) ovate to subglobose; (2) obovate to subpyriform; (3) oblong. 35. Colour of fig at maturity: (1) orange-red; (2) black; (3) green. 36. Apex of fig: (1) convex; (2) flat; (3) concave. 37. Size of ostiole: (1) 1–3 mm diam.; (2) > 3 mm diam. 38. Indumentum of ostiolar bracts: (1) glabrous; (2) puberulous. 39. Internal hairs of fig: (1) present; (2) absent. 40. Position on staminate flowers: (1) near ostiole; (2) dispersed. 41. Number of stamens: (1) 1; (2) 2. 42. Colour of ovary: (1) white; (2) red-brown. 43. Tepal connectivity: (1) free; (2) connate. 44. Epidermis: (1) simple; (2) multiple. 45. Number of radiating epidermal cells around lithocysts: (1) 5–8; (2) 9–16. 46. Cuticular ridge abaxially: (1) present; (2) absent. 47. Occurrence of enlarged lithocysts: (1) only abaxially; (2) adaxially or abundantly adaxially and a few abaxially. 48. Crystarque cells: (1) present; (2) absent. 49. Epidermal lithocysts: (1) present; (2) absent. 50. Palisade layers: (1) single; (2) multiple (2 and more). 51. Marginal sclerenchyma: (1) present; (2) absent. 52. Vascular bundles in midrib; (1) separate bundles; (2) 2 opposing arcs to closed cylinder. 53. Pith bundles in midrib: (1) present; (2) absent. 54. Pith bundles in petiole: (1) present; (2) absent. 55. Bundle sheaths: (1) vertically transcurrent; (2) circular, not transcurrent. 56. Silicified cells in mesophyll: (1) present; (2) absent. 57. Silicified cells in epidermis: (1) present; (2) absent. 58. Glandular hairs at petiole: (1) present; (2) absent. 59. Glandular hairs at lamina: (1) present; (2) absent. 60. Stomata: (1) level to epidermis; (2) sunken. 61. Giant stomata: (1) present; (2) absent. 62. Inner stomatal ledge: (1) present; (2) absent. 63. Thickness of cuticle on adaxial lamina: (1) ≤ 1 μm; (2) > 1 μm 64. Ratio of prismatic and druse crystal in midrib: (1) prismatic > druse; (2) druse > prismatic. 65. Subepidermal sclerified layer in petiole: (1) present; (2) absent. 66. Subepidermal sclerified layer in midrib: (1) present; (2) absent.

APPENDIX 3. Data matrix of morphological(1-43) and leaf anatomical(44-66) characters scored for the phylogenetic analyses and character reconstruction. Polymorphisms are indicated by all states presented by a comma, and inapplicable or unknown characters by "-" . Details of characters and states are also listed below.

APPENDIX 3. Data matrix of morphological(1-43) and leaf anatomical(44-66) characters scored for the phylogenetic analyses and character reconstruction. Polymorphisms are indicated by all states presented by a comma, and inapplicable or unknown characters by "-" . Details of characters and states are also listed below.

Taxon/character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
F. alongensis 1	2	2	1	1	1	1	1	1	2	2	1	1,2	1	1	1	2	1	2	1	1	1	2
F. alongensis 2	2	2	1	1	1	1	1	1	2	2	1	1,2	1	1	1	2	1	2	1	1	1	2
F. altissima	2	1	2	2	1	1	1	1	2	2	1	1	1	1	1	2	1	2	1	1	2	2
F. americana	2	1	2	2	1	1	2	2,3	2	2	1	1	2	2	2	1	1	2	1	1	1	2
F. arnottiana 1	2	2	1	1	1	1,2	1	1	1	1	1	2	1	2	1	2	1	1	1	1,2	1	2
F. arnottiana 2	2	2	1	1	1	1,2	1	1	1	1	1	2	1	2	1	2	1	1	1	1,2	1	2
F. aurea	2	1	2	2	1	1	2	1	2	2	1	1,2	1	2	2	2	1	2	1	1	2	2
F. benjamina	2	1	2	2	1	2	2	1	2	2	1	1	2	2	2	1	1	2	1	1	1	2
F. brachypoda	2	2	2	2	1	1	2	1	2	2	1	1	2	2	2	1	1	1	1	1,2	1	2
F. bubu	2	1	2	2	1	2	2	1,2	2	2	1	1	1	1	1	2	1	1	1	1	1	2
F. caulocarpa 1	2	2	1	1	1	1	1	2	2	2	1,2	1	2	2	2	2	1	1	1	1	1	2
F. caulocarpa 2	2	2	1	1	1	1	1	2	2	2	1,2	1	2	2	2	2	1	1	1	1	1	2
F. caulocarpa 3	2	2	1	1	1	1	1	2	2	2	1,2	1	2	2	2	2	1	1	1	1	1	2
F. concinna 1	2	2	1	1	1	1	1	2	2	2	1	1	2	2	2	2	1	2	1	1	1	2
F. concinna 2	2	2	1	1	1	1	1	2	2	2	1	1	2	2	2	2	1	2	1	1	1	2
F. concinna 3	2	2	1	1	1	1	1	2	2	2	1	1	2	2	2	2	1	2	1	1	1	2
F. concinna 4	2	2	1	1	1	1	1	2	2	2	1	1	2	2	2	2	1	2	1	1	1	2
F. cordata 1	2	2	1	2	1	1	1	1	1	2	1	2	1	1	2	2	1	1	1	1	1	2
F. cordata 2	2	2	1	2	1	1	1	1	1	2	1	2	1	1	2	2	1	1	1	1	1	2
F. cordata 3	2	2	1	2	1	1	1	1	1	2	1	2	1	1	2	2	1	1	1	1	1	2
F. densifolia 1	2	2	1	2	1	1	1	1	2	2	1	1,2	1,2	1	1	2	1	1	1	1	2	2
F. densifolia 2	2	2	1	2	1	1	1	1	2	2	1	1,2	1,2	1	1	2	1	1	1	1	2	2
F. densifolia 3	2	2	1	2	1	1	1	1	2	2	1	1,2	1,2	1	1	2	1	1	1	1	2	2
F. densifolia 4	2	2	1	2	1	1	1	1	2	2	1	1,2	1,2	1	1	2	1	1	1	1	2	2
F. geniculata 1	2	2	1	1	1	1	1	1	2	2	1	1	1,2	2	2	2	1	1	1	1	1	2
F. geniculata 2	2	2	1	1	1	1	1	1	2	2	1	1	1,2	2	2	2	1	1	1	1	1	2
F. geniculata 3	2	2	1	1	1	1	1	1	2	2	1	1	1,2	2	2	2	1	1	1	1	1	2
F. geniculata_insignis	2	2	1	1	1	1	1	1	2	2	1	1	1,2	2	1	2	1	1	2	1,2	1	2
F. glaberrima_ siamensis 1	2	1	2	2	1	1	2	1	2	2	1	1	1	1	1	2	1	1	1	1	1	2
F. glaberrima_ siamensis 2	2	1	2	2	1	1	2	1	2	2	1	1	1	1	1	2	1	1	1	1	1	2
F. glaberrima_ siamensis 3	2	1	2	2	1	1	2	1	2	2	1	1	1	1	1	2	1	1	1	1	1	2
F. henneana 1	2	2	1	1	1	1	1	2	2	2	1	1	1,2	1	2	2	1	1	1	1	1	2
F. henneana 2	2	2	1	1	1	1	1	2	2	2	1	1	1,2	1	2	2	1	1	1	1	1	2
F. hookeriana 1	2	2	1	2	1	1	1	2	2	2	1	1	1	1	2	2	1	1	1	1	1	1
F. hookeriana 2	2	2	1	2	1	1	1	2	2	2	1	1	1	1	2	2	1	1	1	1	1	1
F. ingens 1	2	2	1	2	2	1	1	1	2	2	1	1,2	1	1	1	2	1	1	1	1	1	2
F. ingens 2	2	2	1	2	2	1	1	1	2	2	1	1,2	1	1	1	2	1	1	1	1	1	2
F. ingens 3	2	2	1	2	2	1	1	1	2	2	1	1,2	1	1	1	2	1	1	1	1	1	2
F. lecardii 1	2	2	1	2	1	1	1	1	2	2	1	1	1	2	2	2	1	1	1	1,2	1	2
F. lecardii 2	2	2	1	2	1	1	1	1	2	2	1	1	1	2	2	2	1	1	1	1,2	1	2
F. madagascariensis	1,2	2	1	2	1	1	1	1	2	2	1	1	1,2	2	2	2	1	1	1	1	1	2
F. maxima	2	2	2	2	1	2	2	1	2	2	1	1	1	1	2	2	2	2	2	1	2	2
F. menabeensis	2	1	2	2	1	2	2	1	2	2	1	1	1	2	2	2	1	2	1	2	1	2
F. middletonii	2	2	1	1	1	1	1	1	2	2	1	1	1	1	1	2	1	1	1	1,2	1	2
F. orthoneura 1	1	2	1	2	1	1	1	2	2	2	1	1	2	1	2	2	1	1	1	1	1	1
F. orthoneura 2	1	2	1	2	1	1	1	2	2	2	1	1	2	1	2	2	1	1	1	1	1	1
F. orthoneura 3	1	2	1	2	1	1	1	2	2	2	1	1	2	1	2	2	1	1	1	1	1	1
F. pleurocarpa	2	2	2	2	2	1	2	1	2	2	1	1	2	2	2	1	1	2	1	2	2	2
F. prasinicarpa 1	2	2	1	1	1	2	1	1	2	2	1	1,2	1	2	1	2	1	1	1	1	1	2
F. prasinicarpa 2	2	2	1	1	1	2	1	1	2	2	1	1,2	1	2	1	2	1	1	1	1	1	2
F. prolixa 1	2	2	1	1	1	1	1	2	2	1	1,2	1	2	1	2	1	1	1,2	1,2	1	2	
F. prolixa 2	2	2	1	1	1	1	1	2	2	1	1,2	1	2	1	2	1	1	1,2	1,2	1	2	
F. pseudoconcinna	2	2	1	1	1	1	1	2	2	2	1	1	1	2	2	2	1	1	1	1	1	2
F. religiosa 1	2	2	1	1	1	1	1,2	1	1	1	1	1,2	1	1	1	2	1	1	1	1	1	2
F. religiosa 2	2	2	1	1	1	1	1,2	1	1	1	1	1,2	1	1	1	2	1	1	1	1	1	2
F. religiosa 3	2	2	1	1	1	1	1,2	1	1	1	1	1,2	1	1	1	2	1	1	1	1	1	2
F. rumphii 1	2	2	1	2	1	2	1	1	2	2	1	2	1	1	1	2	1	1	1	1	2	2
F. rumphii 2	2	2	1	2	1	2	1	1	2	2	1	2	1	1	1	2	1	1	1	1	2	2
F. rumphii cf.	2	2	2	2	1	2	1	1	2	2	1	2	1	1	1	2	1	2	1	2	1	2
F. salicifolia 1	2	2	1	2	1	1	1	1	2	2	2	1	2	2	2	2	1	1	1	1,2	1	2
F. salicifolia 2	2	2	1	2	1	1	1	1	2	2	2	1	2	2	2	2	1	1	1	1,2	1	2
F. subpisocarpa_ pubipoda 1	2	2	1	1	1	2	1	2	2	2	1	1	1	2	2	2	1	1	2	2	1	1
F. subpisocarpa_ pubipoda 2	2	2	1	1	1	2	1	2	2	2	1	1	1	2	2	2	1	1	2	2	1	1
F. superba 1	2	2	1	1	1	1	1	2	2	2	1	1	1	1	2	2	1	1	1	1	2	1
F. superba 2	2	2	1	1	1	1	1	2	2	2	1	1	1	1	2	2	1	1	1	1	2	1
F. tonduzii	2	2	2	2	1	1	2	1	2	2	1	1	1	1	2	2	2	1	2	1	2	2
F. tsjakela	2	2	1	1	1	1	1	1	2	2	1	1	2	2	2	2	1	1	1	1	1	2
F. verruculosa 1	1	2	1	2	1,2	1	2	1,2	2	2	1	1,2	2	2	2	2	1	2	1	1,2	1	2
F. verruculosa 2	1	2	1	2	1,2	1	2	1,2	2	2	1	1,2	2	2	2	2	1	2	1	1,2	1	2
F. virens 1	2	2	1	1	1	1	1	1	1	2	1	1	1	1	2	1	1	1	1	1	1	1
F. virens 2	2	2	1	1	1	1	1	1	2	2	1	1	1,2	1	1	2	1	1	1	1	1	1
F. virens 3	2	2	1	1	1	1	1	1	2	2	1	1	1,2	1	1	2	1	1	1	1	1	1
F. virens 4	2	2	1	1	1	2	1	1	2	2	1	1	1,2	2	2	1	1	1	1	1	2	2
F. virens 5	2	2	1	1	1	2	1	1	2	2	1	1	1,2	2	2	1	1	1	1	1	2	2
F. virens_glabella 1	2	2	1	1	1	1	1	3	2	2	1	1	1,2	2	2	2	1	1	1	1	1	1
F. virens_glabella 2	2	2	1	1	1	1	1	3	2	2	1	1	1,2	2	2	2	1	1	1	1	1	1

Taxon/character	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
F. alongensis 1	1	1	2	2	1	1	1	2	1	1	1	1	-	1	1	1	2	1	1	2	1,2	1
F. alongensis 2	1	1	2	2	1	1	1	2	1	1	1	1	-	1	1	1	2	1	1	2	1,2	1
F. altissima	1	1	2	2	1	1	2	1,2	1	1	2	1	1	1	1	1	2	2	1	2	1	-
F. americana	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	2	2	1	-	1	-
F. arnottiana 1	1	1	2	1	2	1	1	2	1	1	1	1	-	1	1	1	2	2	1	2	2	2
F. arnottiana 2	1	1	2	1	2	1	1	2	1	1	1	1	-	1	1	1	2	2	1	2	2	2
F. aurea	1	1	1	2	1	1	1,2	1	1	2	1	1	1	1	1	1	-	2	1	2	1	-
F. benjamina	1	1	2	2	1	1	2	2	1	1	1	1	1	1	1	1	1	2	1	2	1	-

F. brachypoda	1	1	1,2	2	1	1	1	2	2	1	2	3	1	1	1	1	2	2	1	2	1	-
F. bubu	1	1	2	1	2	1	1	2	1	1	2	1	1	3	1	1	2	2	1	2	1	-
F. caulocarpa 1	1	1	1	1	2	1	1	2	1	1	1	1	2	1	1	1	1	1	1	2	1,2	1
F. caulocarpa 2	1	1	1	1	2	1	1	2	1	1	1	1	2	1	1	1	1	1	1	2	1,2	1
F. caulocarpa 3	1	1	1	1	2	1	1	2	1	1	1	1	2	1	1	1	1	1	1	2	1,2	1
F. concinna 1	1	1	2	1	2	1	1	2	2	1	1	1	2	1	1	1	2	1	1	2	2	1
F. concinna 2	1	1	2	1	2	1	1	2	2	1	1	1	2	1	1	1	2	1	1	2	2	1
F. concinna 3	1	1	2	1	2	1	1	2	2	1	1	1	2	1	1	1	2	1	1	2	2	1
F. concinna 4	1	1	2	1	2	1	1	2	2	1	1	1	2	1	1	1	2	1	1	2	2	1
F. cordata 1	1	1	2	1	1	1	2	2	1	1	1	1	1	1	1	1,2	2	1	1	2	1	1
F. cordata 2	1	1	2	1	1	1	2	2	1	1	1	1	1	1	1	1,2	2	1	1	2	1	1
F. cordata 3	1	1	2	1	1	1	2	2	1	1	1	1	1	1	1	1,2	2	1	1	2	1	1
F. densifolia 1	1	1	1	2	1	1	2	2	1	2	1	1	-	1	1	1	2	2	1	2	1	1
F. densifolia 2	1	1	1	2	1	1	2	2	1	2	1	1	-	1	1	1	2	2	1	2	1	1
F. densifolia 3	1	1	1	2	1	1	2	2	1	2	1	1	-	1	1	1	2	2	1	2	1	1
F. densifolia 4	1	1	1	2	1	1	2	2	1	2	1	1	-	1	1	1	2	2	1	2	1	1
F. geniculata 1	1	1	1	1	2	1	1,2	2	1	1	1	1	2	1	1	1	1	1	1	2	2	1
F. geniculata 2	2	2	1	1	1	1	1	2	1	1	1	2	2	2	2	1	2	2	2	1	1	1
F. geniculata 3	2	2	1	1	1	1	1	2	1	1	1	2	2	2	2	1	2	2	2	1	1	1
F. geniculata_insignis	1	2	1	1	2	2	1,2	2	1	1	1	1	2	1	1	1	1	1	1	2	2	1
F. glaberrima_ siamensis 1	1	1	2	2	1	1	1	2	2	1	1	1	1	1	1	1	2	2	1	2	1,2	2
F. glaberrima_ siamensis 2	1	1	2	2	1	1	1	2	2	1	1	1	1	1	1	1	2	2	1	2	1,2	2
F. glaberrima_ siamensis 3	1	1	2	2	1	1	1	2	2	1	1	1	1	1	1	1	2	2	1	2	1,2	2
F. henneana 1	1	1	2	2	1	1	1	2	2	1	2	1	2	1	2	1	2	1	1	2	1	1
F. henneana 2	1	1	2	2	1	1	1	2	2	1	2	1	2	1	2	1	2	1	1	2	1	1
F. hookeriana 1	1	1	1	2	1	1	2	-	1	2	2	1	-	2	2	1	2	2	1	2	1	2
F. hookeriana 2	1	1	1	2	1	1	2	-	1	2	2	1	-	2	2	1	2	2	1	2	1	2
F. ingens 1	1	1	2	2	1	1	1	2	1	1	1,2	1	1	1	1	1,2	1	1	1	2	1	1
F. ingens 2	1	1	2	2	1	1	1	2	1	1	1,2	1	1	1	1	1,2	1	1	1	2	1	1
F. ingens 3	1	1	2	2	1	1	1	2	1	1	1,2	1	1	1	1	1,2	1	1	1	2	1	1
F. lecardii 1	1	1	2	2	1	1	1	2	1	1	1	1	1	1	1	1,2	1	1	1	2	1	1
F. lecardii 2	1	1	2	2	1	1	1	2	1	1	1	1	1	1	1	1,2	1	1	1	2	1	1
F. madagascariensis	1	1	1	2	1	1	2	2	1	1	1	1	-	1	1	1	2	1	1	2	1	1
F. maxima	1	1	1	2	1	1	1	2	1	1	2	1	-	1	1	2	2	2	2	2	1	-
F. menabeensis	1	1	2	2	1	1	2	2	1	1	1	1	1	1	1	1	-	2	1	1	1	-
F. middletonii	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	2	1	1
F. orthoneura 1	1	1	1	1	1	1	1	2	1	1	1,2	1	-	1	1,2	1	2	2	1	2	1	2
F. orthoneura 2	1	1	1	1	1	1	1	2	1	1	1,2	1	-	1	1,2	1	2	2	1	2	1	2
F. orthoneura 3	1	1	1	1	1	1	1	2	1	1	1,2	1	-	1	1,2	1	2	2	1	2	1	2
F. pleurocarpa	1	2	1	2	1	1	1	2	1	1	2	1	1	1	1	1	2	2	1	2	1	-
F. prasinicarpa 1	1	1	2	1	1	1	1	2	1	1	1	1,2	2	1	1	1	2	1	1	2	1	1
F. prasinicarpa 2	1	1	2	1	1	1	1	2	1	1	1	1,2	2	1	1	1	2	1	1	2	1	1
F. prolixa 1	1	1	1	1	1	1	1	2	1	1	1	1,2	2	1	1	1	1	2	1	2	1,2	1
F. prolixa 2	1	1	1	1	1	1	1	2	1	1	1	1,2	2	1	1	1	1	2	1	2	1,2	1
F. pseudoconcinna	1	1	1	2	1	1	1	2	1	1	1	1	2	1	1	1	2	1	1	2	1	1
F. religiosa 1	1	1	1,2	2	1	1	2	2	1	2	1	1	2	1	1	1	2	1	1	2	1	1

F. religiosa 2	1	1	1,2	2	1	1	2	2	1	2	1	1	2	1	1	1	2	1	1	2	1	1
F. religiosa 3	1	1	1,2	2	1	1	2	2	1	2	1	1	2	1	1	1	2	1	1	2	1	1
F. rumphii 1	1	1	1	2	1	1	2	1,2	1	1	1	2	2	1	1	1	2	2	1	1	1	2
F. rumphii 2	1	1	1	2	1	1	2	1,2	1	1	1	2	2	1	1	1	2	2	1	1	1	2
F. rumphii cf.	1	1	1	2	1	1	2	2	1	1	1	2	2	1	1	1	2	2	1	1	1	2
F. salicifolia 1	1	1	1	1	1	1	1	2	1	1	1,2	1	2	1	1	1,2	1	1	1	2	1	1
F. salicifolia 2	1	1	1	1	1	1	1	2	1	1	1,2	1	2	1	1	1,2	1	1	1	2	1	1
F. subpisocarpa_ pubipoda 1	1	1	1	1	2	1	1	2	2	1	1,2	1,2	2	1	1	1	1	1	1	2	2	1
F. subpisocarpa_ pubipoda 2	1	1	1	1	2	1	1	2	2	1	1,2	1,2	2	1	1	1	1	1	1	2	2	1
F. superba 1	1	2	1	1	2	1	1	2	2	1	2	2	2	1	1	1	2	1	1	2	1,2	1
F. superba 2	1	2	1	1	2	1	1	2	2	1	2	2	2	1	1	1	2	1	1	2	1,2	1
F. tonduzii	1	1	1	2	1	1	1	2	1	1	2	1	-	1	1	1	2	2	2	2	1	-
F. tsjakela	1	1	1	1	2	1	2	2	1	1	1	1	-	1	1	1	2	1	1	2	1	1
F. verruculosa 1	1	1	1	1	2	1	1	2	1	1	1	1	1	1	1	1	2	1	1	2	1	1
F. verruculosa 2	1	1	1	1	2	1	1	2	1	1	1	1	1	1	1	1	2	1	1	2	1	1
F. virens 1	1	1	1	1	2	1	1	2	1	1	1	1	2	1	1	1	1	1	1	2	2	1
F. virens 2	1	1	2	1	1	1	1,2	2	1	1	1,2	1	2	1	1	2	1	1	1	2	1	1
F. virens 3	1	1	2	1	1	1	1,2	2	1	1	1,2	1	2	1	1	2	1	1	1	2	1	1
F. virens 4	1	1	2	2	1	1	2	2	1	1	1	2	1	2	1	1	2	2	1	1	1	2
F. virens 5	1	1	2	2	1	1	2	2	1	1	1	2	1	2	1	1	2	2	1	1	1	2
F. virens_glabella 1	2	1	1	1	2	1	1,2	2	1	1	1	1	2	1	1	1	1	1	1	2	2	1
F. virens_glabella 2	2	1	1	1	2	1	1,2	2	1	1	1	1	2	1	1	1	1	1	1	2	2	1

Taxon/character	**45**	**46**	**47**	**48**	**49**	**50**	**51**	**52**	**53**	**54**	**55**	**56**	**57**	**58**	**59**	**60**	**61**	**62**	**63**	**64**	**65**	**66**
F. alongensis 1	2	2	1	1	2	1	1	1	2	2	1	2	2	1	2	1	2	2	2	1	1	1
F. alongensis 2	2	2	1	1	2	1	1	1	2	2	1	2	2	1	2	1	2	2	2	1	1	1
F. altissima	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
F. americana	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
F. arnottiana 1	1	2	2	2	2	2	1,2	2	1	1	1	2	2	2	2	1	2	1	1	2	2	2
F. arnottiana 2	1	2	2	2	2	2	1,2	2	1	1	1	2	2	2	2	1	2	1	1	2	2	2
F. aurea	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
F. benjamina	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
F. brachypoda	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
F. bubu	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
F. caulocarpa 1	2	2	1	1,2	2	2	1	2	1	1	1	1	2	1	2	1	2	2	2	1	1	1
F. caulocarpa 2	2	2	1	1,2	2	2	1	2	1	1	1	1	2	1	2	1	2	2	2	1	1	1
F. caulocarpa 3	2	2	1	1,2	2	2	1	2	1	1	1	1	2	1	2	1	2	2	2	1	1	1
F. concinna 1	2	2	1	1	2	2	1	2	1	1	1	1	2	1	2	1	2	1	2	1	1	1
F. concinna 2	2	2	1	1	2	2	1	2	1	1	1	1	2	1	2	1	2	1	2	1	1	1
F. concinna 3	2	2	1	1	2	2	1	2	1	1	1	1	2	1	2	1	2	1	2	1	1	1
F. concinna 4	2	2	1	1	2	2	1	2	1	1	1	1	2	1	2	1	2	1	2	1	1	1
F. cordata 1	2	2	1	1	1,2	2	2	2	1	1	2	1,2	2	2	2	2	2	2	1	1	1	1
F. cordata 2	2	2	1	1	1,2	2	2	2	1	1	2	1,2	2	2	2	2	2	2	1	1	1	1
F. cordata 3	2	2	1	1	1,2	2	2	2	1	1	2	1,2	2	2	2	2	2	2	1	1	1	1
F. densifolia 1	1	2	1	2	2	2	1	2	2	1	1	2	2	2	2	1	1	2	2	1	2	1
F. densifolia 2	1	2	1	2	2	2	1	2	2	1	1	2	2	2	2	1	1	2	2	1	2	1
F. densifolia 3	1	2	1	2	2	2	1	2	2	1	1	2	2	2	2	1	1	2	2	1	2	1

F. densifolia 4	1	2	1	2	2	2	1	2	2	1	1	2	2	2	2	1	1	2	2	1	2	1
F. geniculata 1	2	2	1	1	1	2	1	2	1	1	1	2	2	2	2	1	2	2	2	1	1	1
F. geniculata 2	2	2	1	1	1	2	1	2	1	1	1	2	2	2	2	1	2	2	2	1	1	1
F. geniculata 3	2	2	1	1	1	2	1	2	1	1	1	2	2	2	2	1	2	2	2	1	1	1
F. geniculata_insignis	2	2	1	1	2	2	1	2	1	1	1	2	2	1	2	1	1	2	1	1	1	1
F. glaberrima_ siamensis 1	1	2	2	2	2	1	1	2	1	1	1	2	2	2	2	1	1	2	1,2	2	2	2
F. glaberrima_ siamensis 2	1	2	2	2	2	1	1	2	1	1	1	2	2	2	2	1	1	2	1,2	2	2	2
F. glaberrima_ siamensis 3	1	2	2	2	2	1	1	2	1	1	1	2	2	2	2	1	1	2	1,2	2	2	2
F. henneana 1	2	2	1	2	1	2	1	2	1	1	1	2	2	2	2	1	2	2	1	1	2	1
F. henneana 2	2	2	1	2	1	2	1	2	1	1	1	2	2	2	2	1	2	2	1	1	2	1
F. hookeriana 1	1	1	1	1,2	1	1,2	2	2	1	1	1	2	2	2	2	1	2	2	2	1	2	1
F. hookeriana 2	1	1	1	1,2	1	1,2	2	2	1	1	1	2	2	2	2	1	2	2	2	1	2	1
F. ingens 1	2	2	1	1	1	2	1	2	1	1	1	1,2	2	1,2	1,2	1	2	2	1	1	1	1
F. ingens 2	2	2	1	1	1	2	1	2	1	1	1	1,2	2	1,2	1,2	1	2	2	1	1	1	1
F. ingens 3	2	2	1	1	1	2	1	2	1	1	1	1,2	2	1,2	1,2	1	2	2	1	1	1	1
F. lecardii 1	1	2	1	2	1	1	2	2	1	1	1	2	2	2	2	2	1	2	1	1	2	1
F. lecardii 2	1	2	1	2	1	1	2	2	1	1	1	2	2	2	2	2	1	2	1	1	2	1
F. madagascariensis	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
F. maxima	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
F. menabeensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
F. middletonii	2	2	1	2	2	2	1	2	1	1	1	2	2	1	1	1	2	1,2	1	1	1	1
F. orthoneura 1	1	1	1	2	2	1,2	1	1	1	1	1	2	2	2	2	1	2	2	2	1	1	1
F. orthoneura 2	1	1	1	2	2	1,2	1	1	1	1	1	2	2	2	2	1	2	2	2	1	1	1
F. orthoneura 3	1	1	1	2	2	1,2	1	1	1	1	1	2	2	2	2	1	2	2	2	1	1	1
F. pleurocarpa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
F. prasinicarpa 1	1	2	1	1,2	1,2	1	1	2	1	1	1	1	1	2	2	1	2	2	1	1	1	1
F. prasinicarpa 2	1	2	1	1,2	1,2	1	1	2	1	1	1	1	1	2	2	1	2	2	1	1	1	1
F. prolixa 1	2	2	1	1,2	1,2	1	1	2	1	1	1	1	1,2	1	2	1	2	1,2	1	1	1	1
F. prolixa 2	2	2	1	1,2	1,2	1	1	2	1	1	1	1	1,2	1	2	1	2	1,2	1	1	1	1
F. pseudoconcinna	1	2	1	1	1,2	1	1	2	1	1	1	1	1	2	2	1	2	2	2	1	1	1
F. religiosa 1	2	2	1	1	1,2	2	1	2	1	1	2	1	1	2	2	1	1	2	1	1	1	1
F. religiosa 2	2	2	1	1	1,2	2	1	2	1	1	2	1	1	2	2	1	1	2	1	1	1	1
F. religiosa 3	2	2	1	1	1,2	2	1	2	1	1	2	1	1	2	2	1	1	2	1	1	1	1
F. rumphii 1	1	2	2	2	2	2	1	2	1	1	1	2	2	1	2	1	1	2	2	2	2	2
F. rumphii 2	1	2	2	2	2	2	1	2	1	1	1	2	2	1	2	1	1	2	2	2	2	2
F. rumphii cf.	1	2	2	2	2	2	1	2	1	1	1	1	2	1	1	1	2	2	2	2	2	2
F. salicifolia 1	1	2	1	2	1	2	1	2	1,2	1	1	2	2	1	2	2	1	1	1	1	2	2
F. salicifolia 2	1	2	1	2	1	2	1	2	1,2	1	1	2	2	1	2	2	1	1	1	1	2	2
F. subpisocarpa_ pubipoda 1	1	2	1	1	1	1	1	2	1	1	1	2	2	1	2	1	2	1	1	1	1	1
F. subpisocarpa_ pubipoda 2	1	2	1	1	1	1	1	2	1	1	1	2	2	1	2	1	2	1	1	1	1	1
F. superba 1	1	2	1	1	2	1	1	2	1	1	1	2	2	2	2	1	2	2	1	1	1	1
F. superba 2	1	2	1	1	2	1	1	2	1	1	1	2	2	2	2	1	2	2	1	1	1	1
F. tonduzii	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
F. tsjakela	1	1	1	1,2	1,2	2	2	2	1	1	2	1,2	2	2	2	2	1	2	2	1	1	1

F. verruculosa 1	1	2	1	1,2	1,2	1	2	2	1,2	1	1	1	1	2	2	1,2	2	2	1	1	2	2
F. verruculosa 2	1	2	1	1,2	1,2	1	2	2	1,2	1	1	1	1	2	2	1,2	2	2	1	1	2	2
F. virens 1	2	2	1	1	1	2	1	2	1	1	1	1	1	2	2	1	2	2	1	1	1	1
F. virens 2	2	2	1	1	1	2	1	2	1	1	1	1	1	2	2	1	2	2	1	1	1	1
F. virens 3	2	2	1	1	1	2	1	2	1	1	1	1	1	2	2	1	2	2	1	1	1	1
F. virens 4	1	2	2	2	2	2	1	2	1	1	1	1,2	1,2	2	2	2	1	2	2	2	2	1
F. virens 5	1	2	2	2	2	2	1	2	1	1	1	1,2	1,2	2	2	2	1	2	2	2	2	1
F. virens_glabella 1	2	2	1	1	1	2	1	2	1	1	1	2	1	2	2	1	2	2	2	1	1	1
F. virens_glabella 2	2	2	1	1	1	2	1	2	1	1	1	2	1	2	2	1	2	2	2	1	1	1