SYSTEMATICS AND PHYLOGENY

Phylogenetic reconstruction of *Ficus* subg. *Synoecia* and its allies (Moraceae), with implications on the origin of the climbing habit

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Abstract The infrageneric classification of *Ficus* (Moraceae) has raised concerns since Berg put forward his six subgenera system. Molecular analyses have revealed some unnatural groups within this system. The status of *F.* subg. *Synoecia* and the relationships between this subgenus and its allies are among the major challenges facing classification within the genus. To resolve these problems, we reconstructed the phylogenetic trees with three nuclear markers from 147 ingroup taxa (including approximately half of *F.* subg. *Synoecia* species and three-fifths of *F.* subg. *Ficus*) and implemented ancestral area and life-form reconstructions to trace the evolutionary history. Results showed that *F.* subg. *Synoecia* and *F.* subg. *Ficus* (except *F.* subsect. *Ficus*) constituted a well-supported monophylum, which is sister to *F.* subg. *Terega*. This monophylum comprises two clades: one clade covers *F.* subsect. *Frutescentiae* of *F.* sect. *Ficus* and *F.* subsect. *Plagiostigma* of *F.* sect. *Pogonotrophe*, and the other covers *F.* sect. *Eriosycea*, *F.* sect. *Apiosycea* and the rest of *F.* sect. *Pogonotrophe.* Ancestral area reconstruction revealed that the first clade has a distinct origin in East Asia, but the second one shows fewer obvious signs. Ancestral life-form reconstruction suggested that the climbing habit, a key trait used to divide *F.* subg. *Ficus* and *F.* subg. *Synoecia*, has evolved independently more than four times, rendering it an unsuitable characteristic to circumscribe the subgenera. Thus, we merged *F.* subg. *Synoecia* and *F.* subg. *Ficus* (excluding *F.* subsect. *Ficus*) into one subgenus, containing two newly delimited sections and six new synonyms.

Keywords climbing shrubs; *Ficus*; phylogeny; *Synoecia*; taxonomy

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

■ INTRODUCTION

Ficus L., a key component of tropical ecosystems (Janzen, 1979; Shanahan & al., 2001; Harrison, 2005), comprises ca. 735 species and is widely distributed in tropical and subtropical regions (Berg & Corner, 2005). Various life-forms exist within *Ficus*, such as terrestrial shrubs and trees, hemi-epiphytes, holo-epiphytes, lithophytes, climbers, creeping shrubs, and rheophytic shrubs. Therefore, fig trees occupy a multitude of different substrates such as rocks, soil, river beds, and tree trunks (Berg & Corner, 2005). As one of the largest woody genera in angiosperms, subdivisions of *Ficus* have attracted the attention of taxonomists for a long time. It was divided into four subgenera by Corner (1960a,b, 1965), in which *F.* subg. *Ficus* encompassed all the gynodioecious fig trees and was broken into eight subsections. Later, Berg (2003a) divided the genus into six subgenera based on morphology, molecular phylogenetic results (Herre & al., 1996; Weiblen, 2000), and pollinating fig wasp classification (Berg & Wiebes, 1992; Wiebes, 1994, 1995). The main improvement in Berg's system was the disintegration of *F.* subg. *Ficus* established by Corner (Berg, 2003a,b; Berg & Corner, 2005) (Fig. 1). However, some unnatural groups remained in *F.* subg. *Ficus*, subg. *Pharmacosycea* (Miq.) Miq. and subg. *Urostigma* (Endl.) Miq. (updated as subg. *Spherosuke* Raf.; Pederneiras & al., 2015). These subgenera were not recognized as monophyletic based on the phylogeny of nuclear genes (Xu & al., 2011; Cruaud & al., 2012; Pederneiras & al., 2018). Furthermore, none of the six subgenera could be characterized as monophyletic when assessed by chloroplast phylogenomic analysis (Bruun-Lund & al., 2017).

Ficus subg. *Synoecia* (Miq.) Miq. is a distinct group consisting of ca. 75 climbing species, which are distributed from Nepal to East Asia and southward to Australia and the Solomon Islands (Berg, 2003c). Molecular phylogenetic analysis revealed that *F. pumila* L., a species of *F.* subg. *Synoecia*, is embedded within *F.* subsect. *Frutescentiae* Sata in *F.* subg. *Ficus* (Rønsted & al., 2008; Xu & al., 2011; Cruaud & al., 2012; Pederneiras & al., 2018). Additionally, the pollinator *Wiebesia pumilae* (Hill) of *F. pumila* is sister to the pollinators of *F. oleifolia* King and *F. deltoidea* Jack in *F.* subsect. *Frutescentiae* (Cruaud & al., 2012). *Ficus pumila* was also reported to form a monophyletic group together with *F. chartacea* (Will. ex Kurz) King, *F. glandulifera* (Wall. ex Miq.) King (*F.* subg. *Ficus* sect. *Eriosycea* (Miq.) Miq.), and *F. albert-smithii* Standl. (*F.* subg. *Spherosuke* sect. *Americana* (Miq.) Corner) based on results from a chloroplast phylogenomic analysis (Bruun-Lund & al., 2017). These results

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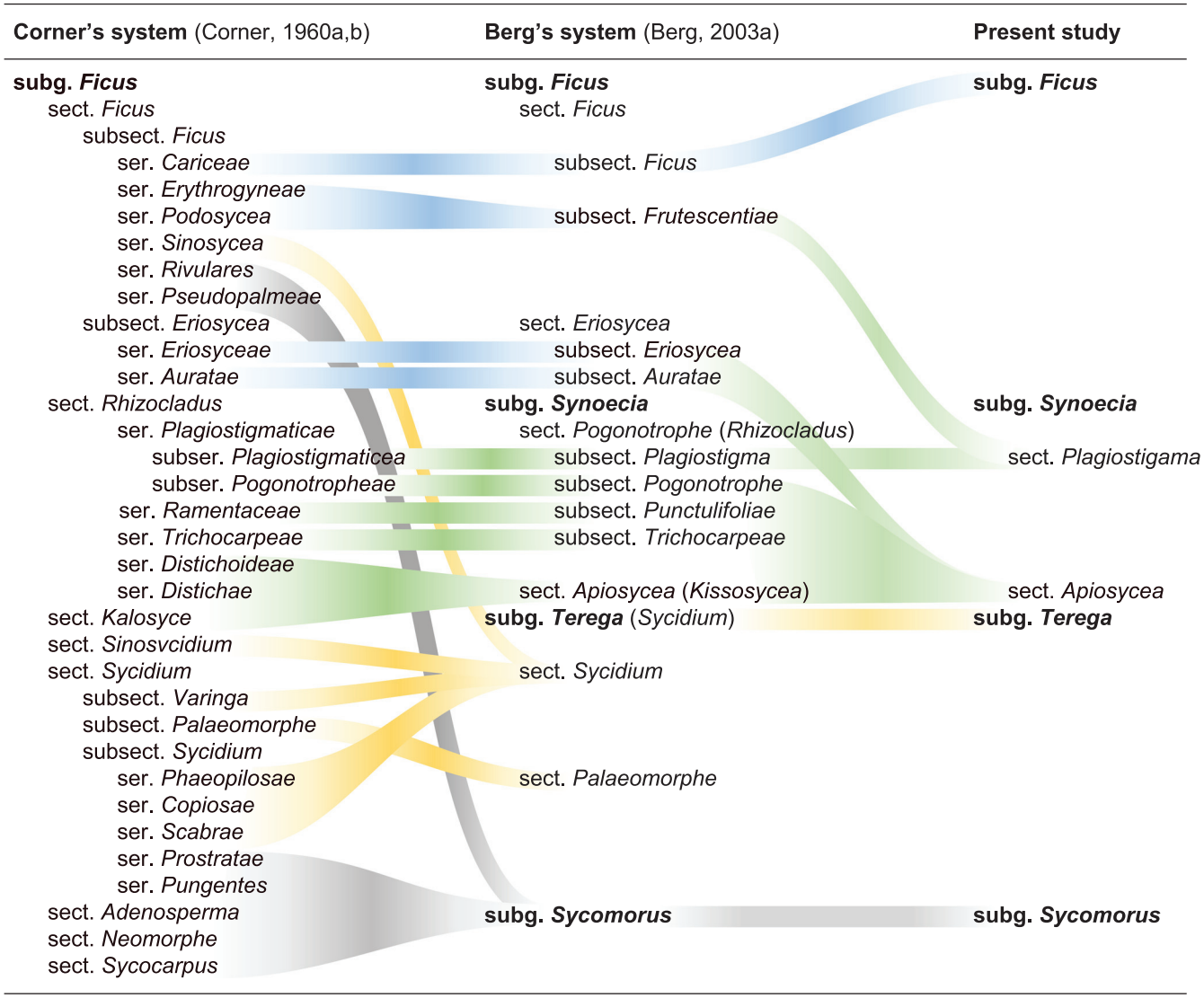


Fig. 1. Subdivision of gynodioecious figs in systems of Corner, Berg and the present study.

indicated that *F.* subg. *Synoecia* may not be monophyletic. However, other studies reported that *F. pumila*, together with *F. sarmentosa* Buch.-Ham. ex Sm. and *F. pubigera* (Wall. ex Miq.) Brandis of the same *F.* subsect. *Plagiostigma* (Sieb. & Zucc. ex Miq.) C.C.Berg, forms a reliable monophyletic group (Azuma & al., 2010; Kusumi & al., 2012; Li & al., 2012a,b), rather than being aggregated with *F.* subsect. *Frutescentiae*. In addition, *F. laevis* Blume was assigned to *F.* subg. *Synoecia* subsect. *Pogonotrophe* (Miq.) C.C.Berg. based on its climbing habit and systematic position of its pollinator (Berg, 2003c). However, *F. laevis* has abundant bristles on the internal surface of the syconia and lacks leaf dimorphism, which suggests this species might be an intermediate taxon between *F.* subg. *Ficus* and *F.* subg. *Synoecia* and possibly an ally to *F.* subg. *Ficus* (Rønsted & al., 2008). Based on phylogenetic studies by Li & al. (2012a,b), *F. laevis* may be a member of subsect. *Eriosycea* (*F.* subg. *Ficus*). These studies also indicated that *F. pedunculosa* Miq., as a member of subsect. *Frutescentiae* (*F.* subg. *Ficus*), though having a creeping habit, unexpectedly revealed a close affiliation to *F.* subg. *Synoecia*, albeit based on a limited number of samples (Li & al., 2012a,b). Morphologically, traits such as gynodioecy, figs axillary, basal bracts three, verticillate, and the absence of lateral bracts are shared by both *F.* subg. *Ficus* and subg. *Synoecia* (Berg, 2003a), indicating a potentially close relationship between the two subgenera. However, due to the lack of comprehensive sampling and in-depth exploration, the status of *F.* subg. *Synoecia* and subg. *Ficus* and the relationship between them remains unclear.

Although all members of *F.* subg. *Synoecia* are climbers, both climbing and procumbent habits are also present in *F.* subg. *Ficus* subsect. *Frutescentiae*, *F.* subg. *Terega* Raf. (formerly *F.* subg. *Sycidium* (Miq.) Mildbr. & Burret) sect. *Palaeomorphe* King, and *F.* subg. *Spherosuke* sect. *Cordifoliae* G.Don and sect. *Americana* (Corner, 1976; Zhou & Gilbert, 2003). These observations indicate that the climbing habit

may be homoplasious. Moreover, a few taxa of *F*. subg. *Synoecia*, which exhibit the climbing habit when they are juvenile, such as *F. sagittata* Vahl (Chang & al., 1998) and *F. anserina* (Corner) C.C.Berg (Berg, 2007), can form an erect tree when mature. The same pattern also occurs in *F. tannoensis* Hayata (*F*. subg. *Ficus*) and *F. subulata* Blume (*F*. subg. *Terega*) (Chang & al., 1998; Berg & Corner, 2005). The origin of the climbing habit was preliminarily discussed by Corner (1976) based on morphological characteristics. He suggested that the climbing habit in *F*. subg. *Spherosuke* and subg. *Terega* has originated from the strangling habit, while the origin of the climbing habit in *F*. sect. *Pogonotrophe* (Miq.) Miq. and *F*. sect. *Apiosycea* (Miq.) Pedern. & Romaniuc remains unclarified (Corner, 1976). Based on its various life-forms, *Ficus* represents a good case for exploring the origin(s) of the climbing habit.

Here, based on three nuclear loci and ancestral area and life-form reconstructions of corresponding fig trees, we aim to (1) detect whether *F*. subg. *Synoecia* is a monophyletic group, (2) trace the origin of climbing habit in *Ficus*, and (3) reveal the phylogeny and revise the taxonomy of *F*. subg. *Synoecia* and its allies.

■ MATERIALS AND METHODS

Taxon sampling, DNA extraction, and sequencing. — Twenty-one accessions representing eight out of ten recorded species in *F*. subsect. *Plagiostigma* of subg. *Synoecia*, together with ten new additional species of this subgenus and two Mediterranean field samples of the common fig (*F. carica* L., type of the genus) were collected and included in this study. The rest of the taxa were selected from works of Jousselin & al. (2003), Rønsted & al. (2005, 2008), Azuma & al. (2010), Xu & al. (2011), Cruaud & al. (2012), Kusumi & al. (2012), J. Lu & al. (2016) and Z.L. Lu & al. (2017). In total, 165 individuals representing 147 taxa were sampled as the ingroup, including 112 gynodioecious fig trees and major monoecious clades (detailed list provided in Appendix 1). These gynodioecious fig trees included 37 taxa in *F*. subg. *Synoecia* and 38 taxa in *F*. subg. *Ficus*, covering about one-half and three-fifths of the species, respectively. Because it is under debate which taxon should be regarded as the basal group within *Ficus*, *Antiaropsis decipiens* K.Schum., *Castilla elastica* Sessé ex Cerv., *Poulsenia armata* (Miq.) Standl., and *Sparattosyce dioica* Bureau were chosen as outgroups according to the methods delineated by Cruaud & al. (2012).

Leaf materials were sealed in silica gel immediately after collection in the field. All voucher specimens were deposited in the herbarium of East China Normal University (HSNU). Genomic DNA was extracted using the CTAB method (Doyle & Doyle, 1987). Internal and external transcribed spacers (ITS, ETS) were amplified following protocols established by Z.L. Lu & al. (2017), and the single-copy nuclear gene encoding glyceraldehyde 3-phosphate dehydrogenase (*G3pdh*) was amplified according to the protocol established by Rønsted & al. (2008). Polymerase chain reaction (PCR) was performed on a TaKaRa TP6000 thermocycler (TaKaRa Bio, Kusatsu, Shiga, Japan), and products were inspected in 1% TAE agarose gel, and then sequenced bidirectionally by HuaGene Biotech (Shanghai, China). Sequences were assembled and edited using SeqManII v.5.00 software (DNASTAR package; Madison, Wisconsin, U.S.A.) (Burland, 2000), aligned using MUSCLE (Edgar, 2004) from the MEGA5 package (Tamura & al., 2011). Finally, uneven ends with missing data were trimmed for downstream analyses (alignment dataset shown in suppl. Appendix S1).

Phylogenetic analysis. — Considering topologies of the single-locus trees were universally consistent except low-resolution clades (shown in suppl. Fig. S1), we concatenated the three loci for further analyses.

Bayesian inference (BI) and maximum likelihood (ML) analyses were implemented to reconstruct phylogenetic trees. ML analysis was conducted using rapid bootstrap analysis (-f a) via RAxML v.8.2.0 (Stamatakis, 2014) with 1000 replications and a GTRGAMMA model. Sequence matrices were specified for three partitions (-q) based on loci to apply respective substitution parameters. To avoid possible locally optimal solutions, we ran two independent analyses and chose the tree with the higher likelihood value (ln*L*).

Before implementing the BI, the optimal substitution models were identified for each locus with MrModelTest v.2 (Nylander, 2004) in conjunction with PAUP* v.4.0b10 (Swofford, 2003) under the Akaike information criterion (AIC) (Posada & Buckley, 2004). The optimal models are GTR+I+Γ for ITS, GTR+Γ for ETS, and GTR+I+Γ for *G3pdh*. MrBayes v.3.2.6 (Ronquist & al., 2012) on the CIPRES platform (Miller & al., 2010) was used to complete Bayesian tree reconstruction. Four parallel independent runs, each consisting of three heated Monte Carlo Markov chains and one cold chain, were iterated for 15 million generations with sampling every 1000 generations. Lastly, the average deviation of split frequencies was below 0.01, and the effective sample sizes (ESS) were over 200 in Tracer v.1.5 (Rambaut & Drummond, 2009). Sequence matrices were also divided into three parts, as in the ML analysis, for the respective substitution models. The first 25% of the samples were treated as burn-in, and the remaining samples were used to summarize the majority-rule consensus tree and posterior probabilities with the "sumt" and "sump" commands.

Trees were visualized in the Interactive Tree of Life (iTOL v.5) (Letunic & Bork, 2016). The Bayesian tree was selected to show the topology with Bayesian posterior probabilities (PP) and ML bootstrap values (MLBS). Phylogenetic topologies were considered strongly supported when PP ≥ 0.95 or MLBS ≥ 85, moderate when 0.95 > PP ≥ 0.80 or 85 > MLBS ≥ 70, and weak when PP < 0.80 or MLBS < 70.

Assessing the confidence of the phylogenetic tree. — To evaluate the relationships among the major clades (i.e., *F*. subg. *Ficus*, subg. *Synoecia*, subg. *Terega*, and part of sect. *Oreosycea* (Miq.) Corner of *F*. subg. *Pharmacosycea*), three alternative topologies (shown in suppl. Fig. S2) were tested against our best ML tree, which were mapped to the key phylogenetic results in *Ficus* (Rønsted & al., 2008;

Xu & al., 2011; Cruaud & al., 2012). Herein, our best ML tree was reconstructed based on a resampled matrix including the aforementioned major clades with *F*. sect. *Pharmacosycea* (Miq.) Griseb. as the outgroup. Per-site log-likelihoods for each topology were calculated in RAxML with GTRGAMMA (Stamatakis, 2014). The approximately unbiased (AU) test, bootstrap probability of the selection (NP), approximate Bayesian posterior probability (PP) test, bootstrap probability (BP) test, Kishino-Hasegawa (KH) test, weighted Kishino-Hasegawa (WKH) test, Shimodaira-Hasegawa (SH) test, and weighted Shimodaira-Hasegawa (WSH) test were performed using Consel v.0.1j (Shimodaira & Hasegawa, 2001).

Ancestral area reconstruction. — To check the geographical distribution and migration history, ancestral area reconstruction was implemented based on three methods: a statistical dispersal-vicariance analysis (S-DIVA) (Ronquist, 1997), a dispersal-extinction-cladogenesis (DEC) model of Lagrange (Ree & Smith, 2008), and a statistical DEC model (S-DEC; Yu & al., 2015) in RASP v.3.2b (Yu & al., 2015). The distribution area ranges of extant *Ficus* spp. used in this study were obtained from related Floras (Berg & al., 1984; Berg & Wiebes, 1992; Zhou & Gilbert, 2003; Berg & Corner, 2005) and listed in Appendix 1. According to Chantarasuwan & al. (2016), 12 distribution areas with an additional Mediterranean region were discriminated. All parameters were set with a default value. Fifteen thousand trees generated by MrBayes were used as the input file, and the first 20% of the trees were used as burn-in. Since a polytomous tree was not available for S-DIVA analysis, we employed a re-summary of the Bayesian strict consensus tree as the input consensus tree for the three analyses.

Ancestral state reconstruction of life-forms. — We considered four independent life-forms, including terrestrial shrubs and trees, hemi-epiphytes, climbers, and holo-epiphytic shrubs, based on the description from Berg & Corner (2005) (life-forms for the species used in this study listed in Appendix 1). Ancestral state reconstruction was conducted using Mesquite v.3.10 (Maddison & Maddison, 2016) based on two complementary approaches, parsimony ancestral states and likelihood ancestral states. For the likelihood ancestral states method, the current probability model was selected. The Bayesian strict consensus tree mentioned above was used as the input tree.

■ RESULTS

Phylogenetic analysis of *F.* subg. *Synoecia* and *F.* subg. *Ficus*. — Based on three concatenated loci, the phylogenetic tree demonstrated that neither *F*. subg. *Ficus* nor subg. *Synoecia* can be characterized as monophyletic and none of their sections (*F*. sect. *Pogonotrophe*, sect. *Apiosycea*, sect. *Ficus*, sect. *Eriosycea*) are monophyletic. In contrast, the two subgenera together comprise a well-supported lineage (PP = 1, MLBS = 86; Fig. 2, clade I), excluding *F*. subsect. *Ficus*, which is distant from this clade. This lineage consists of two highly supported clades: (1) *F*. subsect. *Frutescentiae* + subsect. *Plagiostigma* (PP = 1, MLBS = 97; Fig. 2, clade II), and (2) *F*. sect. *Eriosycea* + the remaining of *F*. subg. *Synoecia* (PP = 0.97, MLBS = 62; Fig. 2, clade III). In clade II, members of the two subsections are divided into seven subclades, in which subclade *a* is exclusively composed of members of *F*. subsect. *Plagiostigma*, and subclade *b* is exclusively composed of members of *F*. subsect. *Frutescentiae*. None of the seven subclades support the current circumscription of the subsections (*a*–*g* in Fig. 2). All *F. pumila* samples were imbedded in *F*. subsect. *Plagiostigma* (subclade *a*), which is sister to the subclade (*b*) that includes *F. deltoidea*. Additionally, *Ficus* sp. 1 (subclade *c*) from Yunnan, China, might be a new species. However, confirmation of this deduction requires additional information. In clade III, three highly supported subclades are identified. Subclade *h* consists of all members of *F*. subsect. *Punctulifoliae* Sata and *F*. subsect. *Trichocarpeae* (Corner) C.C.Berg of *F*. sect. *Pogonotrophe*, and *F*. sect. *Apiosycea*. Subclade *i* includes two groups, *F*. sect. *Eriosycea* (except *F. langkokensis* Drake) and *F*. subsect. *Pogonotrophe* (namely, *F. laevis*). Subclade *j* includes a single species, *F. langkokensis*. Both *F*. subsect. *Eriosycea* and subsect. *Auratae* (Corner) C.C.Berg are not monophyletic. *Ficus* subsect. *Ficus*, including the type of *Ficus*, is sister to sect. *Oreosycea* (*F*. subg. *Pharmacosycea*) with weak support rather than ally to the remaining of *F*. subg. *Ficus*. Additionally, *F*. subg. *Terega* is recognized as monophyletic and sister to clade I, with moderate to high support (PP = 1, MLBS = 79).

Assessing phylogenetic trees. — The topology of the resampled phylogenetic tree (shown in suppl. Fig. S3) was consistent with the fully sampled tree (Fig. 2). We have demonstrated that the test of dependability for different patterns among major clades confirmed the credibility of our tree and disagreed with those of Rønsted & al. (2008) (suppl. Fig. S2A) and Cruaud & al. (2012) (suppl. Fig. S2C), except that the SH and WSH tests are slightly over 0.05 (Table 1). The phylogenetic topology from Xu & al. (2011) (suppl. Fig. S2B) cannot be significantly rejected based on most *p*-values. However, the AU, BP, KH, and WKH tests all generated relatively small values, and the PP test provided a much smaller value (much less than 0.05). In fact, the phylogenetic topology from Xu & al. (2011) is similar to our study, except for the relationships among *F*. subsect. *Frutescentiae*, subg. *Synoecia*, and sect. *Eriosycea*. We noted that the topology among these three groups was well resolved in our paper, in comparison to the unsupported results (<0.5 for posterior probability) reported by Xu & al. (2011).

Ancestral area reconstruction. — The ancestral area reconstruction based on DEC model was chosen to show the dispersal and vicariance events of *Ficus* (Fig. 3), and the results of S-DIVA and S-DEC are shown in supplementary Figs. S4 & S5. The three different methods were generally consistent in shallow nodes, but incongruent in deep nodes, especially for the ancestral node of the whole genus. S-DIVA discovered African mainland and America (AL) were most likely the ancestral area of *Ficus*. However, according to

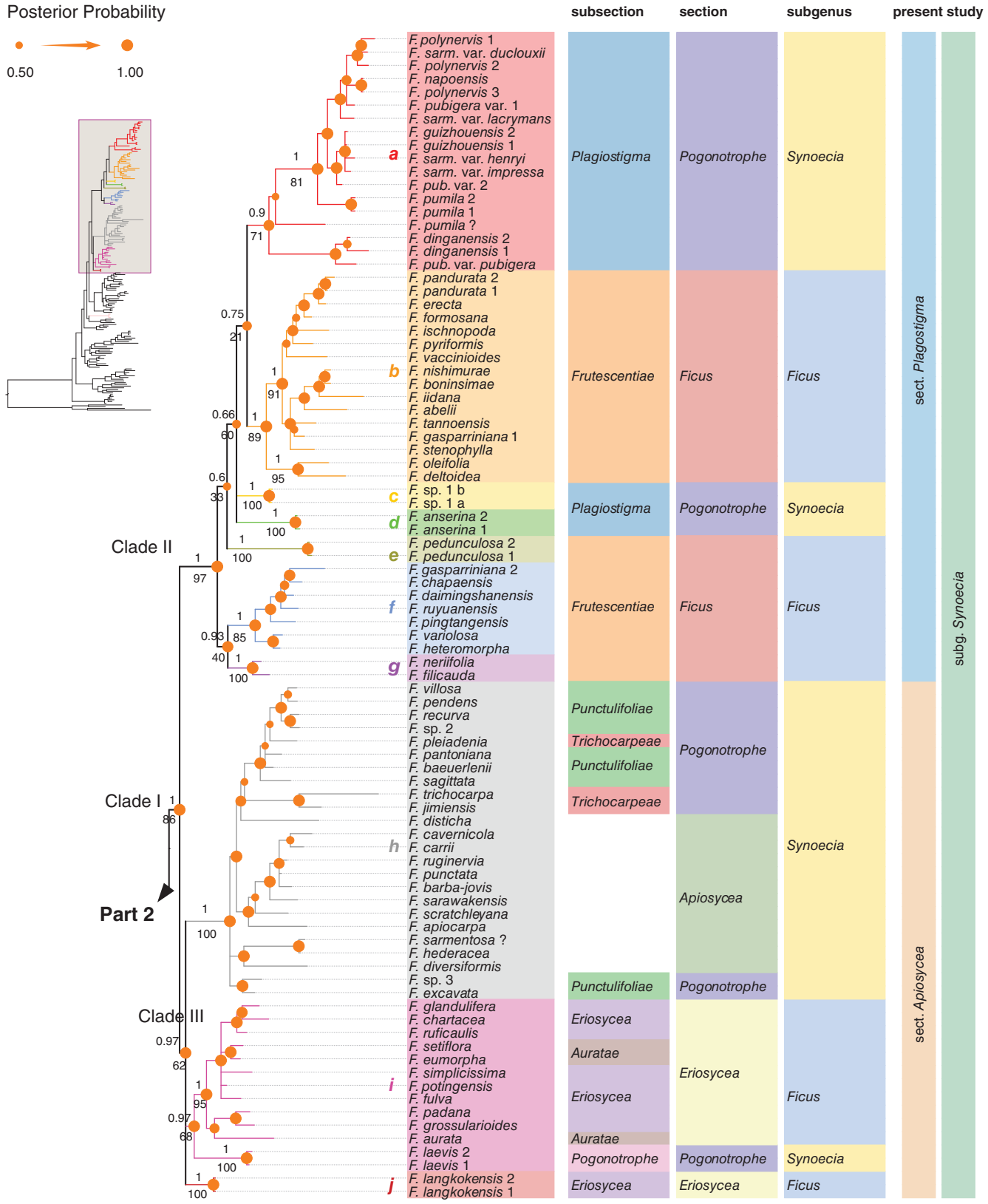


Fig. 2. Bayesian majority consensus tree based on ITS, ETS, and *G3pdh* concatenated markers. The posterior probability (PP) values are listed above the branches and the maximum likelihood bootstrap supports (MLBS) are below the branches. Disks at nodes correspond to the PP values (see legend). Taxonomic assignments according to Berg (2003a,b,c) and the present study are provided to the right of the sample names. A dash (-) indicates a branch not supported.

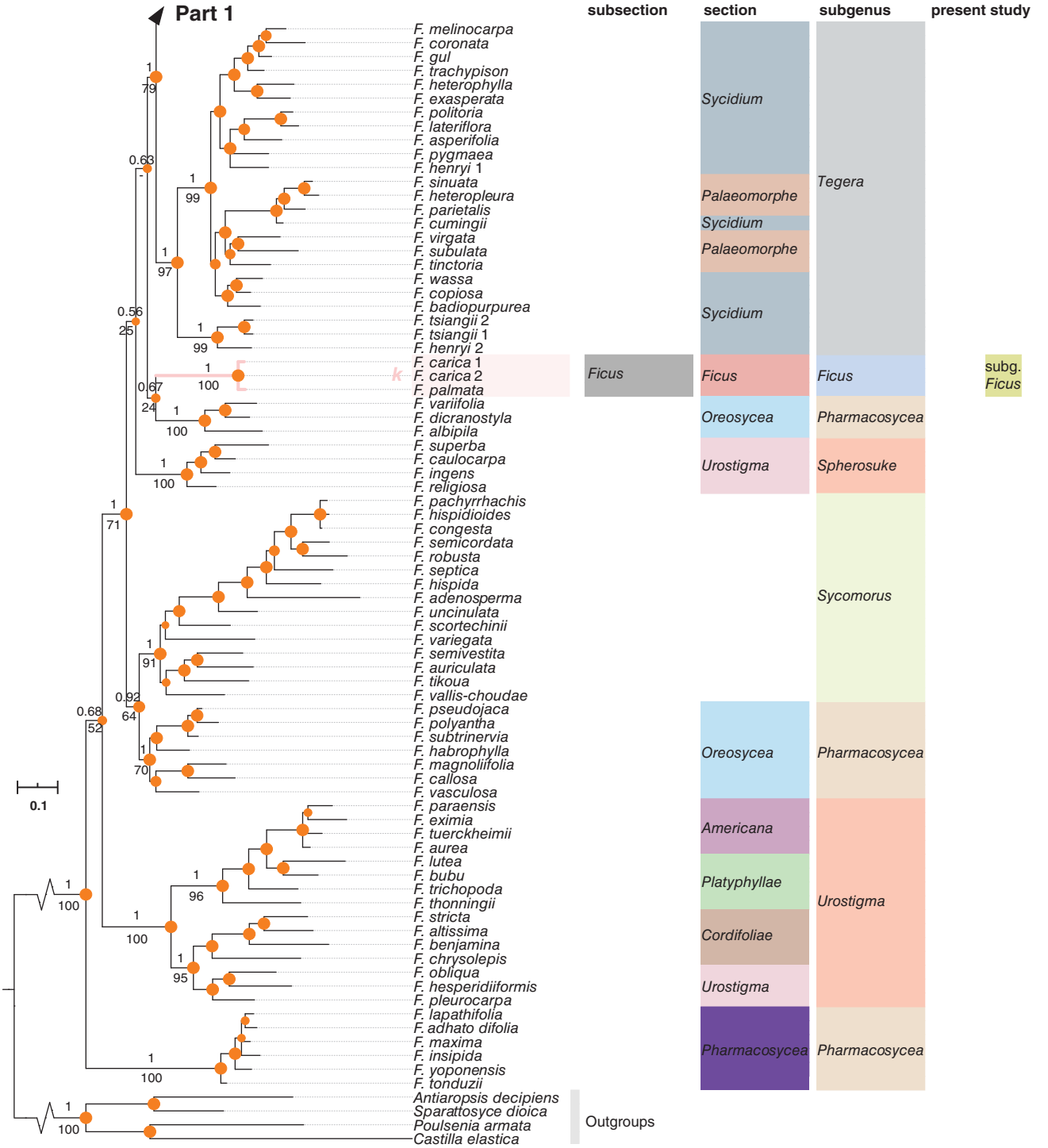


Fig. 2. Continued.

DEC and S-DEC methods, east Malesia (H) was most likely the ancestral area, with the latter being in line with previous studies (Cruaud & al., 2012; Pederneiras & al., 2018). Because of the sparse sampling in *F.* subg. *Urostigma*, subg. *Pharmacosycea* and subg. *Spherosuke*, the area of the origin of *Ficus* is still not clear. We noticed that node 217 (Fig. 3, corresponding to clade II in Fig. 2) showed an East Asian origin (D) in all the three methods (S-DIVA: 0.93; DEC: 0.72; S-DEC: 0.57), but nodes 255 (corresponding to clade III in Fig. 2, the sister clade of clade II) and 256 (clade I in Fig. 2) did not have a clear origin (Fig. 3, suppl. Figs. S4, S5).

Ancestral life-form state reconstruction. — The results of the life-form reconstruction based on MP and ML were largely consistent, and the MP analysis is displayed (Fig. 4).

Table 1. Assessing the confidence of the phylogenetic relationship between the major clades using Consel v.0.1j.

Rank	References	Obs.	AU	NP	BP	PP	KH	SH	WKH	WSH
1	present study	suppl. Fig. S3; (((((Fru,(Eri,Syn)),Ter),Fic),Ore),outgroups)								
		−11.2	0.942	0.894	0.895	1.00	0.896	0.954	0.896	0.975
2	Xu & al., 2011	suppl. Fig. S2B; (((((Fru,Syn),Eri),Ter),(Fic,Ore)),outgroups)								
		11.2	0.147	0.076	0.076	1.00E-05	0.104	0.250	0.104	0.250
3	Cruaud & al., 2012	suppl. Fig. S2C; (((((Fru,Syn),Eri),Ore),(Fic,Ter)),outgroups)								
		20.2	0.040	0.026	0.026	2.00E-09	0.050	0.096	0.050	0.098
4	Rønsted & al., 2008	suppl. Fig. S2A; ((((Fru,Syn),(Eri,Ter)),(Fic,Ore)),outgroups)								
		26.2	0.007	0.004	0.004	4.00E-12	0.025	0.044	0.025	0.052

Topologies from the present and previous studies are shown. Obs., observation value. Hypothesis testing methods: AU, approximately unbiased test; BP, bootstrap probability test; NP, bootstrap probability of the selection; PP, approximate Bayesian posterior probability test; KH, Kishino-Hasegawa test; SH, Shimodaira-Hasegawa test; WKH, weighted Kishino-Hasegawa test; WSH, weighted Shimodaira-Hasegawa test. Names of related groups are abbreviated: Fru, subsect. *Frutescentiae* and subsect. *Plagiostigma*; Eri, sect. *Eriosycea*; Syn, subg. *Synoecia* excluding subsect. *Plagiostigma*; Ter, subg. *Terega*; Fic, subsect. *Ficus*; Ore, subsect. *Oreosycea*. Given that samples of subsect. *Plagiostigma* were newly added in this study, we treated this subsection and subsect. *Frutescentiae* as a whole to map subsect. *Frutescentiae* that appeared in previous studies.

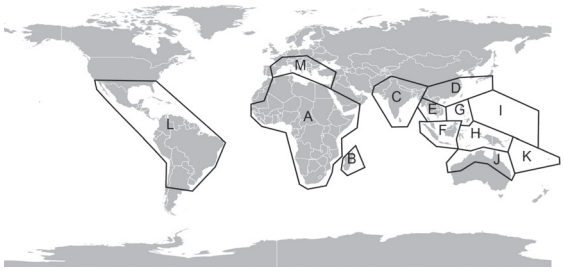
They revealed that terrestrial shrubs/trees represent the ancestral state of figs. Climbing, the trait that differentiates *F*. subg. *Synoecia* from subg. *Ficus* according to Berg (2003a), appears to have evolved independently at least four times. Holo-epiphytic shrubs (only two species) might derive from the climbing species. Note that hemi-epiphytes, which often grow ultimately into trees or shrubs, do not show a clear evolutionary pattern.

■ DISCUSSION

Robustness of phylogenetic reconstruction and cyto-nuclear discordance. — Sufficient sampling coverage can prevent stochastic bias in phylogenetic analysis (Tëmkin, 2010). Therefore, we sampled over 80% of the species in *F*. subsect. *Plagiostigma* and subsect. *Frutescentiae* (Fig. 2, clade II). Though only half of the species were sampled from *F*. sect. *Eriosycea*, sect. *Apiosycea*, and sect. *Pogonotrophe* (except subsect. *Plagiostigma*), typical representatives of all the related species groups designated by Berg & Corner (2005) were included (Fig. 2, clade III). As a result, those unsampled species will not impact the credibility of the basic topology of clade I in Fig. 2. In this context, the assessment of the phylogenetic tree resulted in the rejection of topologies presented in previous studies (suppl. Fig. S1, Table 1), such as a sister relationship between *F*. subsect. *Frutescentiae* + *F*. subg. *Synoecia* and *F*. sect. *Eriosycea* (Xu & al., 2011). Moreover, the relationships among major clades (subclades *a–j* and *F*. subg. *Terega* in Fig. 2) remain invariable when setting up different outgroups (such as outgroup from *F*. sect. *Pharmacosycea* or subg. *Spherosuke*, data not shown), as well as when resampling in the assessment of phylogenetic trees (shown in suppl. Fig. S3). Taken together, these results confirm the robustness of our topology.

However, there is an obvious incongruity between the present nuclear phylogenetic analysis (Fig. 2) and the previous plastome topology (Bruun-Lund & al., 2017), except a lack of resolution in a few situations (soft incongruity). In general, cyto-nuclear discordance could be caused by hybridization, introgression, or incomplete lineage sorting. Inconsistent evolutionary histories among different genes might also play an important role in the obvious incongruity (Van der Niet & Linder, 2008; Ruiz-Sanchez & Sosa, 2010; Scheunert & Heubl, 2017). Owing to the enormous quantity and biparentally inherited features, the phylogenetic results of nuclear loci may be more accordant with morphology than those of the plastome (Zeng & al., 2014). Renoult & al. (2009) studied the phylogeny of *F*. sect. *Galoglychia* (Gasp.) Endl. and found that, compared to the chloroplast phylogeny, the nuclear one is more coinciding with morphology-based taxonomy at the subsection level. At the genus level, the nuclear phylogeny of *Ficus* is more in accordance with the classic subdivision (Bruun-Lund & al., 2017). This phenomenon was also reported in Cyperaceae, Rosaceae, and Poaceae (Massatti & al., 2016; Xiang & al., 2016; Wang & al., 2017). These observations imply that the nuclear phylogeny of *Ficus* may be a suitable model for the investigation of evolutionary history.

Origin and evolution of climbing. — Ancestral state reconstruction revealed that the climbing habit in different clades originated from terrestrial shrubs/trees (Fig. 4). This is consistent with the opinion of Bruun-Lund & al. (2018) that the climbing habit stems from shrubs, rather than partially from hemi-epiphytic stranglers (Corner, 1976). Additionally, ancestral state reconstruction found that some members of *F*. subsect. *Frutescentiae* reinstated the shrub habit from climbing ancestors (Fig. 4), revealing its distinct evolutionary history. However, given the lack of resolution among



Code	Region
A	Africa mainland
B	Madagascar and surrounding islands
C	Indian subcontinent and Pan-Himalaya region
D	south China, Japan, Korean peninsula
E	Indo-China peninsula
F	west Malesia Islands
G	Philippine and South China Sea Islands
H	east Malesia Islands
I	Micronesia Islands
J	Australia
K	west Pacific Islands
L	America
M	Mediterranean

Node	most possible ancestral states		
217	D, 0.74	DH, 0.26	
255	FH, 0.32	H, 0.27	F, 0.22
256	DH, 0.38	D, 0.28	H, 0.27
279	DH, 0.73	H, 0.27	
286	H, 0.76	DH, 0.12	A, 0.12
312	H, 0.86	A, 0.14	
326	AH, 1		
327	H, 0.85	A, 0.15	
333	H, 0.55	HL, 0.25	

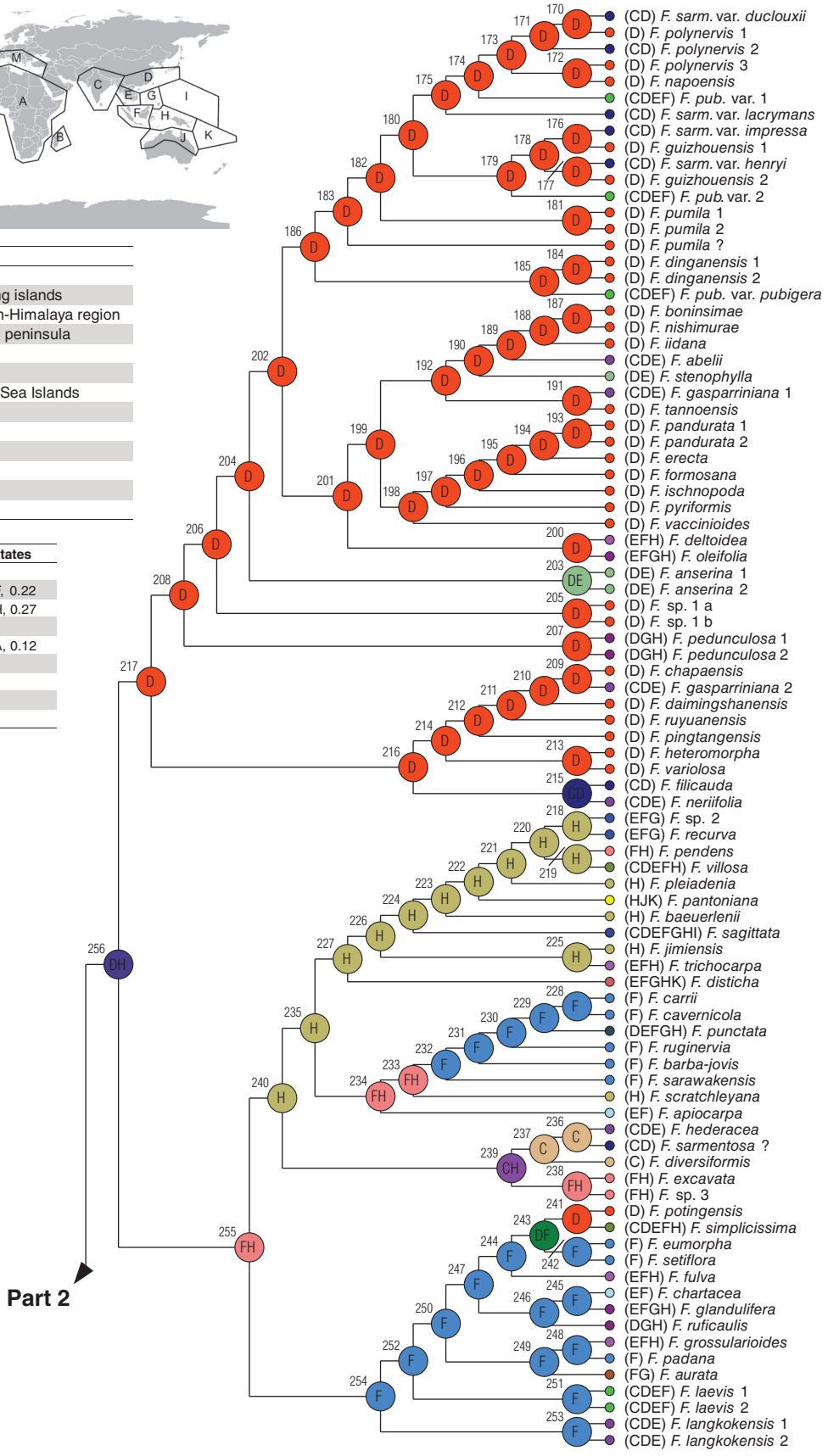


Fig. 3. For caption, see second part.

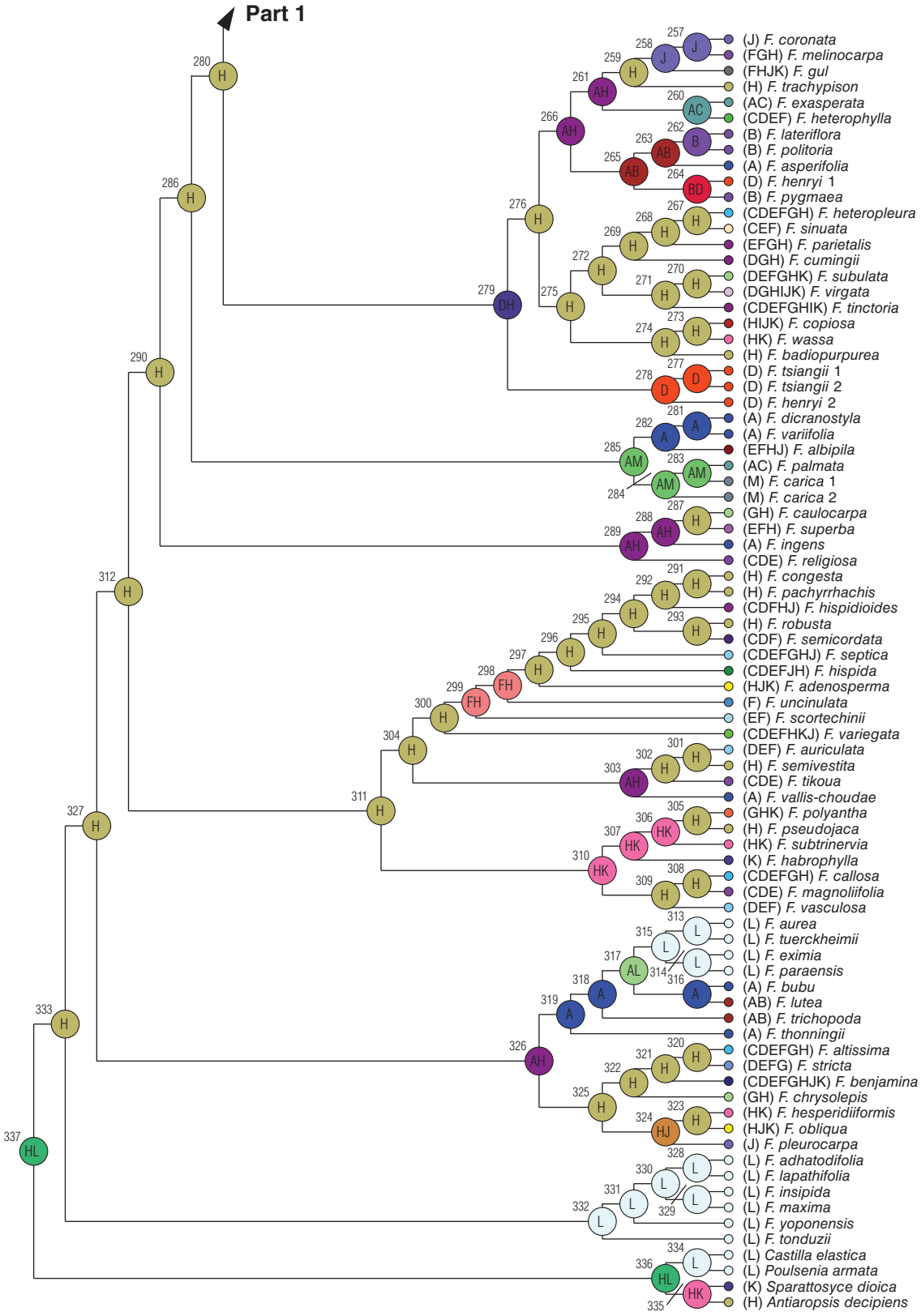


Fig. 3. Ancestral area reconstruction based on DEC analysis in RASP v.3.2b. Most likely states are shown in each node disk and node numbers are shown in the upper left corner of the nodes. Distribution region of every species is provided as code in the bracket before the sample name. Corresponding region of every code and ancestral states of partial key nodes are shown in the legend.

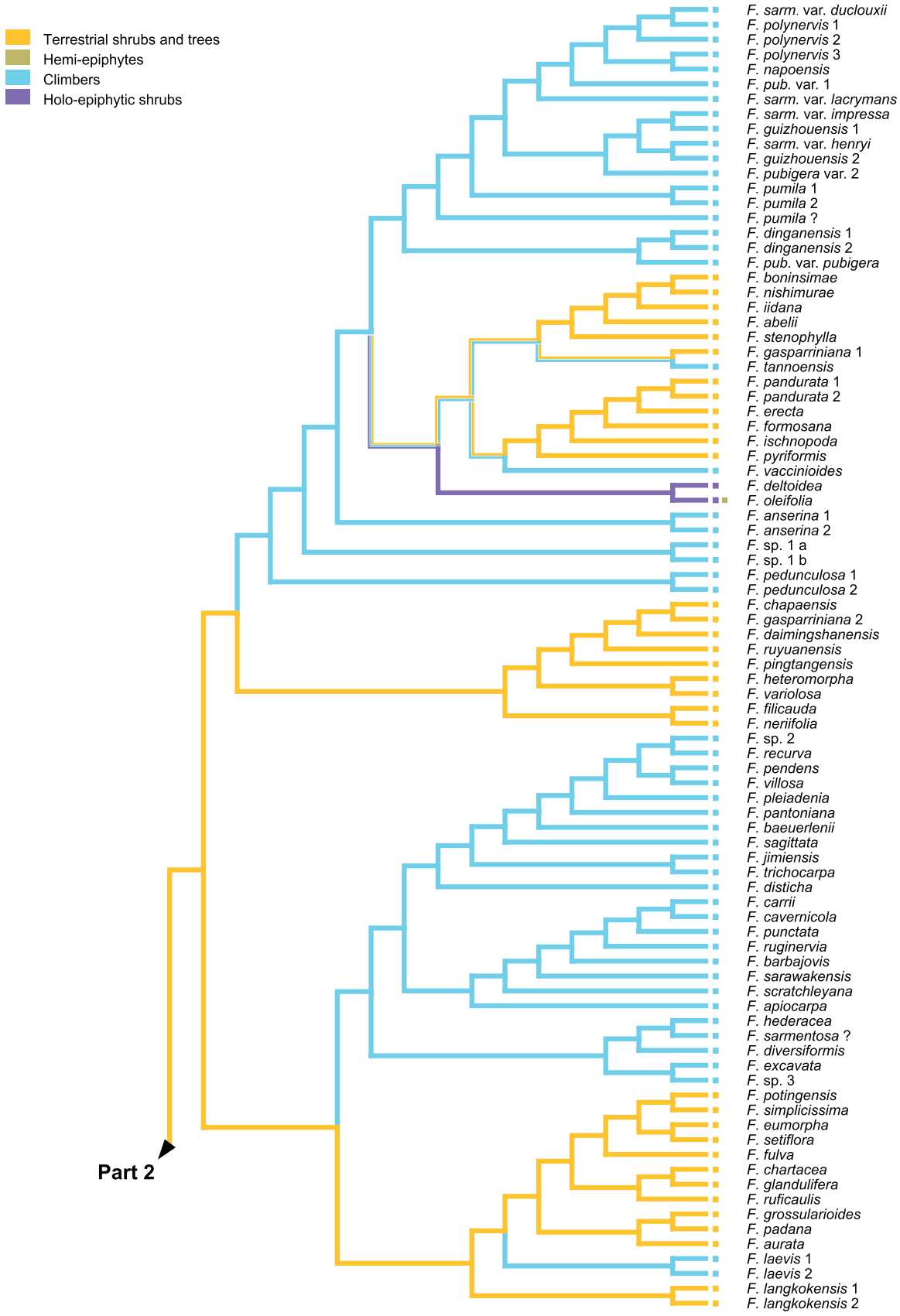


Fig. 4. Maximum parsimony ancestral state reconstruction using Mesquite v.3.10. Ancestral states are shown as the colors of the branches (see legend). Actual states of samples are represented by colored squares and multiple states by multiple squares.

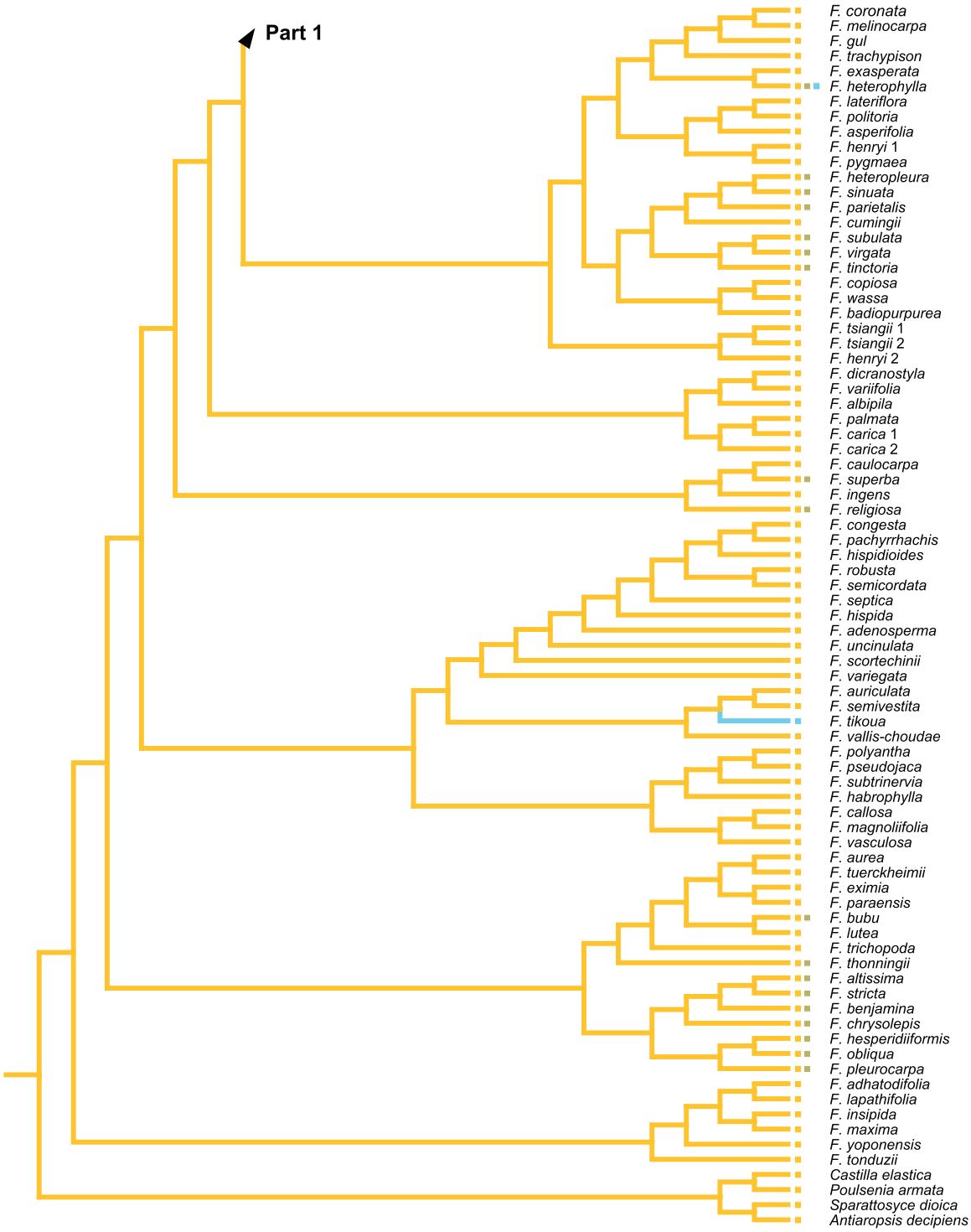


Fig. 4. Continued.

subclades *a*–*g* in clade II (Fig. 2), the life-form state of its ancestor node requires further verification.

It has also been reported that the climbing habit originated from the terrestrial shrub/tree habit in some other taxa. For example, Dubuisson & al. (2003) explored the evolutionary history of life-forms in *Trichomanes* L., a rare genus of ferns with diverse habits, and found that the liana life-form derives from the erect habit repeatedly. In our study, the climbing *F.* subg. *Synoecia* was divided and assigned to several clades. Climbing habit also evolved independently at least four times

in *Ficus* (Fig. 4). Therefore, climbing habit here can not be treated as an effective trait for delimiting the taxa, as it is autapomorphic rather than symplesiomorphic or synapomorphic (Page & Holmes, 2009). A similar situation occurred in Madiinae (Asteraceae) in Hawaii, which comprises 28 species with extreme life-form diversity. Carr (1985) summarized their life-form variation and realized that it would create several unnatural groups when classifying members of this taxa based on habit. These studies confirm that the climbing habit is not a reasonable trait to divide groups, though it is convenient in practice (Berg, 2003a).

Disintegration of Berg's subg. *Synoecia* and subg. *Ficus*, and some related taxonomic notes. — In this study, 48 accessions representing 32 out of 75 species in *F*. subg. *Synoecia* and 43 accessions representing 38 out of 50 species in *F*. subg. *Ficus* were used, and all the subsections were included. The results suggest that *F*. subg. *Synoecia* and its subdivisions, i.e., *F*. sect. *Pogonotrophe*, sect. *Apiosycea*, subsect. *Plagiostigma*, subsect. *Punctulifoliae*, and subsect. *Trichocarpeae*, and *F*. subg. *Ficus* and its subdivisions, i.e., *F*. sect. *Ficus*, sect. *Eriosycea*, subsect. *Frutescentiae*, subsect. *Auratae*, and subsect. *Eriosycea*, cannot be considered as monophyletic groups (Fig. 2). Based on the robustness of our phylogenetic tree and its congruence to lineage relationships established by previous studies (Li & al., 2012b; Z.L. Lu & al., 2017), it is reasonable to deduce that Berg's system of *F*. subg. *Synoecia* and subg. *Ficus* is untenable and must be re-evaluated, and that the life-form, distribution of cystoliths, and the length and shape of stamen are unreliable to define phylogenetic subdivisions of the genus. Obviously, molecular data could contradict with morphological characteristics in phylogenetic analyses. Such conflicts could be a result of artificial incongruence, such as sampling strategy and algorithms used for tree reconstruction, unequal rates of morphological evolution, convergence of morphological characteristics, hybridization and/or introgression, and polyploidy (Sytsma, 1990). Another important factor that can drive such conflicts is the weight assigned to each trait. For example, traditionally, Fabaceae was divided into three subfamilies according to corolla pattern and shape. However, it has now been divided into six subfamilies based on molecular phylogenetic analysis, and it was found that seed surface and leaf shape traits play a more important role (LPWG, 2017).

Subclade *a* (Fig. 2) is a well-supported lineage comprising *F. pumila*, *F. sarmentosa*, *F. pubigera*, and a number of Chinese endemic species described by Chang (1982, 1983, 1984). These species bear branchlets without waxy glands and dimorphic leaves differentiated as bathyphylls and acrophylls. They are distributed in subtropical regions such as South China and the Ryukyu Islands (Fig. 3). Subclades *c* and *d* both belong to *F*. subsect. *Plagiostigma*, but they are distant from subclade *a*, likely indicating a distinct evolutionary event. Their well-developed indumentum and sparse teeth on the apex of the juvenile lamina can be used to distinguish species of subclades *c* and *d* from those of subclade *a*. The existence of such sparse teeth in subclades *b* and *f* indicates a close relationship between subclades *c* and *d* as well as *b* and *e*. Considering the lack of resolution in clade II, we need more data to explore its phylogenetic history. Additionally, a displaced sample of "*F. sarmentosa*?" (quoted from Cruaud & al., 2012) indicates a close relationship with *F. hederacea* Roxb. (Fig. 2, subclade *h*) rather than species in *F*. subsect. *Plagiostigma* (subclade *a*). As it is difficult to distinguish young plantlets of *F. sarmentosa* from those of *F. hederacea* due to their morphological similarity, this displaced sample might be a misidentified member of *F. hederacea* or an ally of that species.

The systematic position of *F. pumila* has always been a focus of discussions. Based on the cultivated material (here named as "*F. pumila*?" in Fig. 2, subclade *a*, voucher number: *JYR 3*, stored in Centre de Biologie pours la Gestion des Populations, Montpellier, France) from Jousselin & al. (2003), a series of studies showed that the climber *F. pumila* had the closest relationship with the holo-epiphytic shrub *F. deltoidea* and may be a member of *F*. subsect. *Frutescentiae* (Rønsted & al., 2008; Xu & al., 2011; Cruaud & al., 2012). To examine this problem, we chose two additional field samples of *F. pumila* in this study. The result was congruent with the traditional classification (Corner, 1965; Berg, 2003c) and supported by Azuma & al. (2010), Kusumi & al. (2012), and Li & al. (2012a,b). Therefore, *F. pumila* is still a member of *F*. subsect. *Plagiostigma*. After investigating the sequences of "*F. pumila*?" from Jousselin & al. (2003), we discovered that its ITS sequence was inherited from *F. pumila* and its ETS sequence possibly inherited from *F. deltoidea* (Fig. 5). Though it is reported that the phenomenon of multiple copies and pseudogenes exist within ITS and ETS makers (Álvarez & Wendel, 2003), both fast concerted evolution (Hillis & al., 1991) and the relatively distant relationship between *F. pumila* and *F. deltoidea* make hybridization the most likely acceptable mechanism. Therefore, "*F. pumila*?" should be a hybrid, unless these data are the result of contamination. However, *F. pumila* and *F. deltoidea* are allopatric, and therefore it is unclear how a hybrid would form. Though the collection location of "*F. pumila*?" (voucher number: *JYR 3*) was not provided in the original paper, the co-author Jean-Yves Rasplus (JYR) gathered specimens mainly from the Malesia (Jousselin & al., 2003). As *F. deltoidea* is extensively distributed in Malesia, it is possible that these two species are sympatric when cultivated. Environmental stress and the lack of obligate pollinators during cultivation can lead to host shift or invasion of non-pollinator wasps, followed by hybridization. At B phase, syconia of *F. pumila* can reach 3 cm or longer in diameter, and its ostiole bracts are slightly open. This structure allows access by other fig wasps with similar shape to pollinate or oviposit. Tsai & al. (2015) reported hybridization between *F. pumila* and *F. thunbergii* Maxim. under the environmental conditions with small populations of an island habitat. Bruun-Lund & al. (2017) stated that hybridization during cultivation might give rise to displaced systematic position of some species, such as *F. pumila*, *F. albert-smithii*, and *F. ischnopoda* Miq.. For pollinators, it was also shown that host shifts of *Wiebesia pumilae* ex *F. pumila*, *Blastophaga*

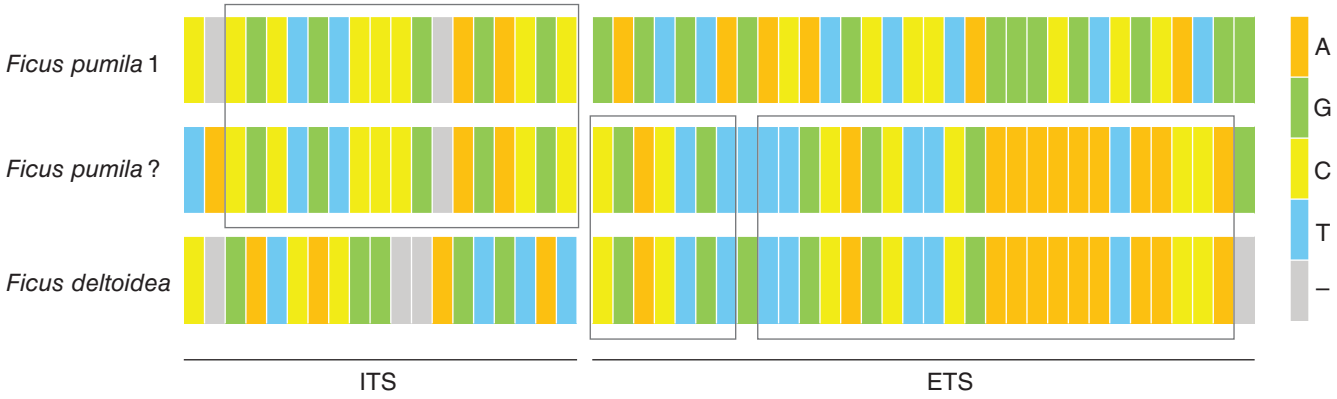


Fig. 5. Comparison of variable sites among three samples, wild "*F. pumila* 1" and "*F. deltoidea*" and cultivated "*F. pumila*?", based on ITS and ETS sequences. Data suggests that "*F. pumila*?" is a hybrid. All variable sites and indels are shown, invariable sites are omitted. Each column represents a variable site and each color indicates a kind of nucleotide base or a gap. Empty rectangles indicate bases that were unchanged between the two selected sequences.

quadrupes Mayr ex *F. deltoidea*, and *Blastophaga* sp. ex *F. oleifolia* indicated the possibility of hybridization between their hosts (Cruaud & al., 2012). Compared with other taxa that naturally hybridize (Parrish & al., 2003; Kusumi & al., 2012; Ghana & al., 2015; Tsai & al., 2015), *F. pumila* and *F. deltoidea* would be a relatively distant species pair. As early as 1950, artificial hybridization between *F. pumila* and *F. carica* has been reported (Condit, 1950), and it has been shown that the systematic relationship of these two species is fairly distant (Fig. 2) (Xu & al., 2011; Cruaud & al., 2012), which supports the possibility of hybridization between *F. pumila* and *F. deltoidea*. These studies also suggested that one-to-one mutualistic symbiosis between figs and pollinators is less strict than previously recognized.

Ficus subsect. *Frutescentiae* comprises 25 species and is primarily restricted to East Asia (Berg & Corner, 2005). The *F. erecta* Thunb. complex of this subsection (Fig. 2, subclade *b*) is clearly distinct from *F. heteromorpha* Hemsl. and its allies (subclade *f*), which was uncovered in the research of Z.L. Lu & al. (2017). However, the variation patterns of the two groups are almost identical. For example, they share extreme morphological plasticity of lamina shape and length-to-width ratio. This makes morphological identification difficult. Consequently, it would be a promising area to investigate the genetic background of related taxa and to discover the mechanism of such plasticity.

Subclade *h* in clade III (Fig. 2) consists of species (*F.* subg. *Synoecia*) distributed in Malesia and forms a well-supported clade. However, within this subclade, branch length is usually rather short and the lineages are not reliable, suggesting that species of subclade *h* experienced rapid evolutionary radiation in Southeast Asia, with Malesia as the center of divergence (Fig. 3). However, the included species revealed insufficient genetic differentiation of this species-rich subclade. As a result, more samples and molecular data are essential for a comprehensive phylogenetic history.

Ficus laevis was assigned to *F.* sect. *Pogonotrophe* subsect. *Pogonotrophe* according to its climbing habit and the systematic position of the corresponding fig wasp (Berg, 2003c). However, the lack of differentiation between bathyphylls and acrophylls, leaves spiral in arrangement, and the presence of abundant, long, and stiff internal bristles, make this species similar to *F.* subsect. *Eriosycea*. This relationship is also apparent in the phylogenetic trees (Fig. 2, subclade *i*) (Li & al., 2012a,b).

Ficus langkokensis was treated as a member of *F.* sect. *Ficus* (Corner, 1965), but was moved to *F.* subsect. *Frutescentiae* based on number of tepals and characteristics of the seed surface (Berg & Corner, 2005). The present study revealed that samples of *F. langkokensis* form a distinct clade within clade III (Fig. 2, subclade *j*), differing from both *F.* subsect. *Frutescentiae* and most species of *F.* sect. *Eriosycea* (as preliminarily shown in J. Lu & al., 2016 and Z.L. Lu & al., 2017). Anatomically, *F. langkokensis* bears cystoliths on the lamina, which are absent in other species of *F.* sect. *Eriosycea*, which is consistent with the unique systematic position of *F. langkokensis* in clade III, sister to subclades *h* and *i*.

Ficus subsect. *Ficus* (Fig. 2, subclade *k*), which includes the type of *Ficus*, has been frequently reported to be far from the remaining taxa of *F.* subg. *Ficus* (sensu Berg) (Rønsted & al., 2008; Xu & al., 2011; Cruaud & al., 2012; Pederneiras & al., 2018). Our study also clarified its distinct genetic background based on field samples (Fig. 2). This subsection traditionally includes three species, *F. carica*, *F. palmata* Forssk., and *F. iidana* Rehder & E.H.Wilson (Berg & Corner, 2005). They all share some distinct characteristics, such as lenticular and smooth fruits, staminate flowers mostly near the ostiole, and lamina with cystoliths only beneath (Corner, 1965; Berg & Corner, 2005). *Ficus carica* is similar to *F. palmata* morphologically. The former is native to the Mediterranean region while the latter is distributed from Nepal to Northeast Africa. This is far away from the divergence center of *F.* subg. *Ficus*, namely, regions from the Pan-Himalaya to Southeast Asia. Furthermore, palmate lamina, glabrous tepal, and big and smooth syconium clearly distinguish *F. carica* and *F. palmata* from the remaining species of *F.* subg. *Ficus*. As for *F. iidana* (named after Mr. S. Iida, but incorrectly derived as "*Ficus iidaiana*" in the

protologue), it bears an undivided lamina and long peduncle, and is only distributed on Ogasawara Island. This reveals the particularity of *F. iidana* compared with *F. carica* and *F. palmata*, and the species was moved to *F*. subsect. *Frutescentiae* based on molecular data (Kusumi & al., 2012). Apparently, *F*. subsect. *Ficus* (including *F. carica* and *F. palmata* only) is a morphologically, genetically, and geographically distinct group (Fig. 2) (Rønsted & al., 2008; Xu & al., 2011; Cruaud & al., 2012; Pederneiras & al., 2018), and its systematic position should be upgraded to the subgenus rank (*F*. subg. *Ficus* s. str.). Meanwhile, the remaining subsections of *F*. subg. *Ficus* (sensu Berg) should be recombined.

Establishment of a recircumscribed subg. *Synoecia* and its sections. — Based on results of this study, a well-supported subdivision of *F*. subg. *Synoecia* and subg. *Ficus*, differing from what was proposed by Berg (2003a), has been obtained (Fig. 2, clade I). *Ficus* subsect. *Frutescentiae* and subsect. *Plagiostigma* (Fig. 2, clade II) are mainly distributed in subtropical regions of China and Japan, and their ancestral distribution pattern obviously agreed with the current distribution based on ancestral area reconstruction. Meanwhile, clade II possesses numerous endemic species in south China and Japan (Zhou & Gilbert, 2003). These data indicate that clade II is a group originated from subtropical Asia (Pederneiras & al., 2018) and occupying the northernmost distribution area of *Ficus* in Asia (Fig. 3). *Ficus pumila* (Chen & al., 2012), *F. sarmentosa*, *F. erecta*, and *F. heteromorpha* of this clade spread to the northern margin (adjacent middle and lower Yangtze River) of this genus. Clade III, consisting of the remaining species of *F*. subg. *Ficus* (except *F. carica* and *F. palmata*) and *F*. subg. *Synoecia*, is distributed mainly in western Malesia, ranging from the Malay Peninsula to the Solomon Islands (Fig. 3). Clade III is geographically close to clade II except for a few sympatric, widely distributed species such as *F. punctata* Thunb., *F. sagittata* Vahl, and *F. simplicissima* Lour. (s.l.). Pollinators of these two clades (II and III) are *Wiebesia* Bouček or *Blastophaga* Gravenhorst, two closely related genera of Agaonidae Walker. However, some critical traits that distinguish them, such as the longitudinal median suture on the mesonotum, are shared in certain taxa (Jousselin & al., 2003), blurring the circumscription of these two genera.

In conclusion, considering that the systematic position and taxonomic level of *F*. subg. *Terega* is clear (Fig. 2) (Rønsted & al., 2008; Xu & al., 2011; Cruaud & al., 2012; Pederneiras & al., 2018), we propose that clade I should be treated as a subgenus sister to *F*. subg. *Terega*. Furthermore, both clade II and clade III should be treated as sections (Figs. 1, 2). Given that the phylogenetic relationships within clades II and III (subclades *a–j*) are unclear, the subdivision of these sections is not provided.

■ TAXONOMIC TREATMENT

Ficus subg. ***Ficus*** L., Sp. Pl.: 1059. 1753 ≡ *F*. subsect. *Eucarica* Miq. in Ann. Sci. Nat., Bot., sér. 3, 1: 32. 1844 ≡ *F*. ser. *Cariceae* Corner in Gard. Bull. Singapore 17: 418. 1960 ≡ *F*. subsect. *Ficus* sensu C.C. Berg in Blumea 48: 530. 2003 – Type: *F. carica* L.

Description. – Shrubs up to 10 m tall, with milky white sap, gynodioecious. Leaves spirally arranged; lamina cordiform to ovate, often palmately 3–7-lobed, chartaceous to thickly papery, margin dentate to crenate or subentire; cystoliths only beneath. Figs axillary or also below the leaves on previous season's growth, solitary; receptacle (sub)pyriform to subglobose, 1.5–4 cm diam., puberulous, smooth at maturity; basal bracts 3; staminate flowers mostly near the ostiole; Stamens (1–)3–6; internal hairs abundant, short; Stigmas 2-branched, linear. Fruits lenticular, smooth.

Distribution. – Ranging from the Mediterranean region to Ethiopia and North India. Widely cultivated (*F. carica*) under subtropical and temperate conditions throughout the world.

Note. – This subgenus only comprises two species currently, *F. carica* and *F. palmata*, corresponding to *F*. subsect. *Ficus* following Berg (2003b) excluding *F. iidana*.

Ficus subg. ***Synoecia*** (Miq.) Miq. in Ann. Mus. Bot. Lugduno-Batavi 3: 289. 1867 ≡ *Synoecia* Miq. in London J. Bot. 7: 469. 1848 ≡ *F*. sect. *Synoecia* (Miq.) Benth. & Hook.f., Gen. Pl. 3: 369. 1880 – Type: *F. falcata* Thunb. (≡ *Synoecia falcata* (Thunb.) Miq.).

Description. – Root-climbers, shrubs, and small to medium-sized trees with milky white (sometimes watery or pink) sap, gynodioecious. Leaves alternate, spirally arranged, subdistichous or distichous; lamina chartaceous to thick papery and even to coriaceous, usually with indumentum; stipules often fully amplexicaul. Figs usually axillary or just below the leaves, in pairs to solitary, or ramiflorous with short spurs, or cauliflorous with long spurs; lateral bracts absent; basal bracts 3, verticillate; staminate flowers scattered among the pistillate ones or near the ostiole; stamens 1–3; stigmas of the galls and pistillate flowers often clearly different, stigmas of pistillate 2 (often unequally long) or 1. Fruits compressed, keeled all around, or with tuberculate.

Distribution. – Mainly in Malesia and East Asia with extension into Sri Lanka and the Solomon Islands.

Note. – The extended *F*. subg. *Synoecia* includes all the taxa of Berg's *F*. subg. *Synoecia* and *F*. subg. *Ficus* (except *F. carica* and *F. palmata*). Two sections can be obviously distinguished.

1. ***Ficus*** sect. ***Plagiostigma*** (Zucc. ex Miq.) Miq. in Ann. Mus. Bot. Lugduno-Batavi 3: 280, 294. 1867 ≡ *Plagiostigma* Zucc. in Abh. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. 4: 154. 1846, non C.Presl 1845 ≡ *F*. [unranked] *Plagiostigma* Zucc. ex Miq. in London J. Bot. 7: 436. 1848 ≡ *F*. ser. *Plagiostigmaticae* Corner in Gard. Bull. Singapore 18: 3. 1960 ≡ *F*. subsect. *Plagiostigma* (Zucc. ex Miq.) C.C.Berg in Blumea 48(3): 553. 2003 – Type (designated for *Plagiostigma* by Corner in Gard. Bull. Singapore 18: 3. 1960): *F. pumila* L. (≡ *P. pumila* (L.) Zucc.; *Varinga repens* Raf., nom. superfl. et illeg.).

= *Ficus* subsect. *Frutescentiae* Sata in Contr. Hort. Inst. Taihoku Imp. Univ. 32: 332, 385. 1944 – **Type (designated here):** *F. pedunculosa* Miq., **syn. nov.**

Description. – Shrubs or climbers. Lamina relatively small, often with indumentum, chartaceous to subcoriaceous, ovate to elliptic to obovate, and usually variable but never palmate, margin entire or apex with some teeth; cystoliths only beneath. Figs axillary, often pedunculate, rather small in diameter, often no more than 3 cm; basal bracts 3, persistent; internal hairs rather sparse or absent; staminate flowers near the ostiole or scattered; stamens 2 or 3, filaments free; tepals of the pistillate flowers dark red (only red in *F. pumila* and *F. pubigera*), glabrous or sparse hairs at the apex. Fruits usually lenticular and compressed without obvious keel, smooth.

Distribution. – Sino-Himalayan region, ranging from Northeast India through China and the northern Malay Peninsula to the Philippines, Japan, and Korea. Only four species, *F. deltiodea*, *F. kofmaniae* C.C.Berg, *F. oleifolia*, and *F. pedunculosa*, extend into Malesia.

Note. – This section includes the *F. erecta* group (Z.L. Lu & al., 2017), *F. sarmentosa* group, *F. heteromorpha* group, and several other well-defined species, with about 29–39 species in total. As there is only low support for most of its descendant nodes, the subdivision of *F.* sect. *Plagiostigma* is not proposed.

2. ***Ficus*** sect. ***Apiosycea*** (Miq.) Pedern. & Romaniuc in Taxon 64(3): 591. 2015 ≡ *Urostigma* sect. *Apiosycea* Miq., Fl. Ned. Ind., Eerste Bijv.: 440. 1861 – Type: *F. apiocarpa* (Miq.) Miq. (≡ *U. apiocarpum* Miq.).

= *Pogonotrophe* Miq. in London J. Bot 6: 525. 1847 ≡ *F.* subg. *Pogonotrophe* (Miq.) Miq. in Ann. Mus. Bot. Lugduno-Batavi 3: 293. 1867 ≡ *F.* subser. *Pogonotrophe* (Miq.) Corner in Gard. Bull. Singapore 18: 4. 1960 ≡ *F.* subsect. *Pogonotrophe* (Miq.) C.C. Berg in Blumea 48(3): 553. 2003 – Type: *F. emodi* (Miq.) Wall. ex Miq., **syn. nov.**

= *Ficus* [unranked] *Eriosycea* Miq. in London J. Bot. 7: 455. 1848 ≡ *Ficus* sect. *Eriosycea* (Miq.) Miq. in Ann. Mus. Bot. Lugduno-Batavi 3: 269, 290. 1867 ≡ *F.* subsect. *Eriosycea* (Miq.) Corner in Gard. Bull. Singapore 17: 419. 1960 ≡ *F.* ser. *Eriosycea* (Miq.) Corner in Gard. Bull. Singapore 17: 419. 1960 ('*Eriosyceae*') ≡ *F.* subser. *Eriosycea* (Miq.) Corner in Gard. Bull. Singapore 17: 419. 1960 ('*Eriosyceae*') – Type (designated by Pederneiras & al. in Taxon 64: 591. 2015): *F. gossypina* Wall. ex Miq., **syn. nov.**

= *Ficus* subsect. *Punctulifoliae* Sata in Contr. Hort. Inst. Taihoku Imp. Univ. 32: 329, 384. 1944 ('*Punctuliifoliae*') – Type (designated by Corner in Gard. Bull. Singapore 18: 4. 1960): *F. villosa* Blume, **syn. nov.**

= *Ficus* ser. *Auratae* Corner in Gard. Bull. Singapore 17: 420. 1960 ≡ *F.* subser. *Auratae* Corner in Gard. Bull. Singapore 17: 420. 1960 ≡ *Ficus* subsect. *Auratae* (Corner) C.C.Berg in Blumea 48: 531. 2003 – Type: *F. aurata* Miq., **syn. nov.**

= *Ficus* ser. *Trichocarpeae* Corner in Gard. Bull. Singapore 18: 5. 1960 ≡ *F.* subsect. *Trichocarpeae* (Corner) C.C. Berg in Blumea 48(3): 554. 2003 – Type: *F. trichocarpa* Blume, **syn. nov.**

Description. – Climbers and in part shrubs to medium-sized trees. Lamina relatively small in climbers or big but with tufted fairs in shrubs and trees; chartaceous to subcoriaceous to coriaceous, often asymmetric in climbers and palmately lobed in shrubs and trees, margin entire or undulate or serrate; cystoliths absent or above or on both sides, rare beneath. Figs axillary and partly cauliflorous, rather big to 10 cm in diameter when cauliflorous; internal hairs rather abundant or sometimes sparse (*F.* subsect. *Apiosycea*); staminate flowers ostiolar or mostly scattered; stamens 1 or 2 (3); tepals of the pistillate flowers red or yellow. Fruits slightly or hardly compressed, usually with tuberculate or with a distinct keel.

Distribution. – Mainly in Malesia. Some species are present in Sri Lanka, Malay Peninsula, and the Solomon Islands, and a few species extend to south China and Taiwan island.

Note. – This section includes ca. 90 species. Three obviously well-supported subclades were detected in the phylogenetic tree but subsections should not be assigned until the group has been more comprehensively sampled. This section differs from *F.* sect. *Plagiostigma* in the cystoliths being absent or present on both surfaces of the lamina, or rarely only beneath, in male flower bearing only 1 or 2 stamens, and in the fruit usually with an obvious tuberculate or clear keel.

Key to *Ficus* subg. *Synoecia* and allied groups

1. Stipules often not fully amplexicaul; lamina often asymmetric; bracts mostly scattered on the peduncle and not 3 in a whorl as basal bracts; pistillode (or pistil) always present in the staminate flower ..... subg. ***Terega***
1. Stipules (nearly always) fully amplexicaul; lamina symmetric or asymmetric; basal bracts 3, in a whorl, sometimes basal and lateral bracts not distinguishable; pistillode rarely present **2**
2. Lamina often palmate, with cystoliths only beneath; syconium puberulous, smooth when mature; staminate flowers mostly near the ostiole, stamens (1–)3–6; fruits smooth ..... subg. ***Ficus***
2. Lamina undivided (if palmate, syconium hirsute), with cystoliths absent, on both surfaces, or only beneath; syconium glabrous to hirsute; staminate flowers mostly near the ostiole or scattered, stamens 2–3; fruits tuberculate or smooth ..... **3** (subg. *Synoecia*)
3. Lamina with cystoliths absent or on both surfaces, rarely only beneath (*Ficus trichocarpa* allies); stamens 1 or 2; fruits slightly or hardly compressed, usually with tuberculate or obvious keel ..... sect. ***Apiosycea***
3. Lamina with cystoliths only beneath; stamens 2 or 3; Fruits usually lenticular and compressed without obvious keel, smooth ..... sect. ***Plagiostigma***

■ AUTHOR CONTRIBUTIONS

HQL conceived and designed the study; ZZ performed experiments and analyzed the data; ZZ, XMW, and JHZ carried out fieldwork; SL finished the nomenclature part of this paper. All authors

contributed to manuscript writing and correction. — SL, https://orcid.org/0000-0002-3876-8002

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■ LITERATURE CITED

Álvarez, I. & Wendel, J.F. 2003. Ribosomal ITS sequences and plant phylogenetic inference. *Molec. Phylogen. Evol.* 29: 417–434. https://doi.org/10.1016/S1055-7903(03)00208-2

Azuma, H., Harrison, R.D., Nakamura, K. & Su, Z.H. 2010. Molecular phylogenies of figs and fig-pollinating wasps in the Ryukyu and Bonin (Ogasawara) islands, Japan. *Genes Genet. Systems* 85: 177–192. https://doi.org/10.1266/ggs.85.177

Berg, C.C. 2003a. Flora Malesiana precursor for the treatment of Moraceae 1: The main subdivision of *Ficus*: the subgenera. *Blumea* 48: 166–177. https://doi.org/10.3767/000651903X686132

Berg, C.C. 2003b. Flora Malesiana precursor for the treatment of Moraceae 3: *Ficus* subgenus *Ficus*. *Blumea* 48: 529–550. https://doi.org/10.3767/000651903X489537

Berg, C.C. 2003c. Flora Malesiana precursor for the treatment of Moraceae 4: *Ficus* subgenus *Synoecia*. *Blumea* 48: 551–571. https://doi.org/10.3767/000651903X489546

Berg, C.C. 2007. Precursory taxonomic studies on *Ficus* (Moraceae) for the Flora of Thailand. *Thai Forest Bull., Bot.* 35: 4–28.

Berg, C.C. & Corner, E.J.H. 2005. Moraceae (*Ficus*). Pp. 1–730 in: Santisuk, T. & Larsen, K. (eds.), *Flora Malesiana*, ser. I, vol. 17 (2). Leiden: National Herbarium of the Netherlands.

Berg, C.C. & Wiebes, J.T. 1992. African fig trees and fig wasps. *Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Sect. 2*, 89: 1–298.

Berg, C.C., Avila, M.V. & Kooy, F. 1984. *Ficus* species of Brazilian Amazonia and the Guianas. *Acta Amazon.* 14, Suppl. 1–2: 159–194. https://doi.org/10.1590/1809-43921984145194

Bruun-Lund, S., Clement, W.L., Kjellberg, F. & Rønsted, N. 2017. First plastid phylogenomic study reveals potential cytonuclear discordance in the evolutionary history of *Ficus* L. (Moraceae). *Molec. Phylogen. Evol.* 109: 93–104. https://doi.org/10.1016/j.ympev.2016.12.031

Bruun-Lund, S., Verstrae, B., Kjellberg, F. & Rønsted, N. 2018. Rush hour at the Museum – Diversification patterns provide new clues for the success of figs (*Ficus* L., Moraceae). *Acta Oecol.* 90: 4–11. https://doi.org/10.1016/j.actao.2017.11.001

Burland, T.G. 2000. DNASTAR's Lasergene sequence analysis software. *Meth. Molec. Biol.* 132: 71–91. https://doi.org/10.1385/1-59259-192-2:71

Carr, G.D. 1985. Habital variation in the Hawaiian Madiinae (Heliantheae) and its relevance to generic concepts in the Compositae. *Taxon* 34: 22–25. https://doi.org/10.2307/1221559

Chang, S.S. 1982. Three new species of the Moraceae from China. *Acta Phytotax. Sin.* 20: 95–98.

Chang, S.S. 1983. New taxa of Moraceae from China (I). *Guihaia* 3: 295–306.

Chang, S.S. 1984. New taxa of Moraceae from China (II). *Guihaia* 4: 113–122.

Chang, S.S., Wu, C.Y. & Cao, Z.Y. 1998. Moraceae. Pp. 1–245 in: Chang, S.S. & Wu, C.Y. (eds.), *Flora Reipublicae Popularis Sinicae*, vol. 23(1). Beijing: Science Press.

Chantarasuwan, B., Rønsted, N., Kjellberg, F., Sungkaew, S. & Welzen, P.C. 2016. Palaeotropical intercontinental disjunctions revisited using a dated phylogenetic hypothesis with nearly complete species level sampling of *Ficus* subsect. *Urostigma* (Moraceae). *J. Biogeogr.* 43: 384–397. https://doi.org/10.1111/jbi.12637

Chen, Y., Compton, S.G., Liu, M. & Chen, X.Y. 2012. Fig trees at the northern limit of their range: The distributions of cryptic pollinators indicate multiple glacial refugia. *Molec. Ecol.* 21: 1687–1701. https://doi.org/10.1111/j.1365-294X.2012.05491.x

Condit, I.J. 1950. An interspecific hybrid in *Ficus*. *J. Heredity* 41: 165–168. https://doi.org/10.1093/oxfordjournals.jhered.a106120

Corner, E.J.H. 1960a. Taxonomic notes on *Ficus* Linn., Asia and Australasia. III. Subgen. *Ficus* and sect. *Ficus*. IV. Subgen. *Ficus* sect. *Sycidium* Miq. *Gard. Bull. Singapore* 17: 417–485.

Corner, E.J.H. 1960b. Taxonomic notes on *Ficus* Linn., Asia and Australasia. V. Subgen. *Ficus* Sect. *Rhizocladus*, *Kalosyce*, *Sinosycidium*, *Adenosperma*, and *Neomorphe*. VI Subgen. *Ficus* sect. *Sycocarpus* Miq. *Gard. Bull. Singapore* 18: 1–69.

Corner, E.J.H. 1965. Check-list of *Ficus* in Asia and Australasia with keys to identification. *Gard. Bull. Singapore* 21: 1–186.

Corner, E.J.H. 1976. The climbing species of *Ficus*: Derivation and evolution. *Philos. Trans., Ser. B* 273: 359–386. https://doi.org/10.1098/rstb.1976.0021

Cruaud, A., Rønsted, N., Chantarasuwan, B., Chou, L.S., Clement, W.L., Couloux, A., Cousins, B., Genson, G., Harrison, R.D., Hanson, P.E., Hossaert-McKey, M., Jabbourzahab, R., Jousselin, E., Kerdelhue, C., Kjellberg, F., Lopez-Vaamonde, C., Peebles, J., Peng, Y.Q., Pereira, R.A.S., Schramm, T., Ubaidillah, R., Vvan Noort, S., Weiblen, W.D., Yang, D.R., Yodpinyanee, A., Libeskind-Hadas, R., Cook, J.M., Rasplus, J.Y. & Savolainen, V. 2012. An extreme case of plant–insect codiversification: Figs and fig-pollinating wasps. *Syst. Biol.* 61: 1029–1047. https://doi.org/10.1093/sysbio/sys068

Doyle, J.J. & Doyle, J.L. 1987. A rapid DNA isolation procedure for small quantities of fresh leaf tissue. *Phytochem. Bull. Bot. Soc. Amer.* 19: 11–15.

Dubuisson, J.Y., Hennequin, S., Rakotondrainibe, F. & Schneider, H. 2003. Ecological diversity and adaptive tendencies in the tropical fern *Trichomanes* L. (Hymenophyllaceae) with special reference to climbing and epiphytic habits. *Bot. J. Linn. Soc.* 142: 41–63. https://doi.org/10.1046/j.1095-8339.2003.00165.x

Edgar, R.C. 2004. MUSCLE: Multiple sequence alignment with high accuracy and high throughput. *Nucl. Acids Res.* 32(5): 1792–1797. https://doi.org/10.1093/nar/gkh340

Ghana, S., Suleman, N. & Compton, S.G. 2015. A comparison of pollinator fig wasp development in figs of *Ficus montana* and its hybrids with *Ficus asperifolia*. *Entomol. Exp. Appl.* 156: 225–237. https://doi.org/10.1111/eea.12338

Harrison, D.R. 2005. Figs and the diversity of tropical rainforests. *Bioscience* 55: 1053–1064. https://doi.org/10.1641/0006-3568(2005)055[1053:FATDOT]2.0.CO;2

Herre, E.A., Machado, C.A., Bermingham, E., Nason, J.D., Windsor, D.M., McCafferty, S., Houten, W.V. & Bachmann, K. 1996. Molecular phylogenies of figs and their pollinator wasps. *J. Biogeogr.* 23: 521–530. https://doi.org/10.1111/j.1365-2699.1996.tb00014.x

Hillis, D.M., Moritz, C., Porter, C.A. & Baker, R.J. 1991. Evidence for biased gene conversion in concerted evolution of ribosomal DNA. *Science* 251: 308–310. https://doi.org/10.1126/science.1987647

Janzen, D.H. 1979. How to be a fig. *Annual Rev. Ecol. Syst.* 10: 13–51. https://doi.org/10.1146/annurev.es.10.110179.000305

Jousselin, E., Rasplus, J.Y., Kjellberg, F. & May, G. 2003. Convergence and coevolution in a mutualism: Evidence from a molecular

phylogeny of *Ficus*. *Evolution* 57: 1255–1269. https://doi.org/10.1554/02-445

Kusumi, J., Azuma, H., Tzeng, H.Y., Chou, L.S., Peng, Y.Q., Nakamura, K. & Su, Z.H. 2012. Phylogenetic analyses suggest a hybrid origin of the figs (Moraceae: *Ficus*) that are endemic to the Ogasawara (Bonin) Islands, Japan. *Molec. Phylogen. Evol.* 63: 168–179. https://doi.org/10.1016/j.ympev.2012.01.004

Letunic, I. & Bork, P. 2016. Interactive tree of life (iTOL) v3: An online tool for the display and annotation of phylogenetic and other trees. *Nucl. Acids Res.* 44: W242–W245. https://doi.org/10.1093/nar/gkw290

Li, H.Q., Chen, J.Y., Wang, S. & Xiong, S.Z. 2012a. Evaluation of six candidate DNA barcoding loci in *Ficus* (Moraceae) of China. *Molec. Ecol. Resources* 12: 783–790. https://doi.org/10.1111/j.1755-0998.2012.03147.x

Li, H.Q., Wang, S., Chen, J.Y. & Gui, P. 2012b. Molecular phylogeny of *Ficus* section *Ficus* in China based on four DNA regions. *J. Syst. Evol.* 50: 422–432. https://doi.org/10.1111/j.1759-6831.2012.00221.x

LPWG 2017. A new subfamily classification of the Leguminosae based on a taxonomically comprehensive phylogeny. *Taxon* 66: 44–77. https://doi.org/10.12705/661.3

Lu, J., Gui, P., Lu, Z.L., Zhang, L.F., Tian, H.Z., Gilbert, M.G. & Li, H.Q. 2016. Phylogenetic analysis and taxonomic delimitation of the "Hairy-Fig" complex of *Ficus* sect. *Eriosycea* (Moraceae) in China. *Phytotaxa* 261: 121–136. https://doi.org/10.11646/phytotaxa.261.2.2

Lu, Z.L., Zhang, Z., Zhou, Q.M., Lu, J., Tian, H.Z. & Li, H.Q. 2017. Molecular analyses of *Ficus erecta* and its allies within the subsection *Frutescentiae* (Moraceae). *Pl. Syst. Evol.* 303: 603–614. https://doi.org/10.1007/s00606-017-1393-z

Maddison, W.P. & Maddison, D.R. 2016. Mesquite: A modular system for evolutionary analysis, version 3.10, Available from: http://mesquiteproject.wikispaces.com/

Massatti, R., Reznicek, A.A. & Knowles, L.L. 2016. Utilizing RAD-seq data for phylogenetic analysis of challenging taxonomic groups: A case study in *Carex* sect. *Racemosae*. *Amer. J. Bot.* 103: 337–347. https://doi.org/10.3732/ajb.1500315

Miller, M.A., Pfeiffer, W. & Schwartz, T. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. Pp. 45–52 in: *Proceedings of the Gateway Computing Environments Workshop (GCE)*, New Orleans, Louisiana, 14 Nov 2010. Piscataway: IEEE. https://doi.org/10.1109/GCE.2010.5676129

Nylander, J.A.A. 2004. MrModeltest, version 2. Program distributed by the author. Evolutionary Biology Centre, Uppsala University. Available from: https://github.com/nylander/MrModeltest2

Page, R.D. & Holmes, E.C. 2009. *Molecular evolution: A phylogenetic approach*. London: Blackwell.

Parrish, T.L., Koelewijn, H.P., Van Dijk, P.J. & Kruijt, M. 2003. Genetic evidence for natural hybridization between species of dioecious *Ficus* on island populations. *Biotropica* 35: 333–343. https://doi.org/10.1646/02051

Pederneiras, L.C., Carauta, J.P.P., Neto, S.R. & Mansano, V.D.F. 2015. An overview of the infrageneric nomenclature of *Ficus* (Moraceae). *Taxon* 64: 589–594. https://doi.org/10.12705/643.12

Pederneiras, L.C., Gaglioti, A.L., Romaniuc-Neto, S. & Mansano, V.D.F. 2018. The role of biogeographical barriers and bridges in determining divergent lineages in *Ficus* (Moraceae). *Bot. J. Linn. Soc.* 187: 594–613. https://doi.org/10.1093/botlinnean/boy036

Posada, D. & Buckley, T.R. 2004. Model selection and model averaging in phylogenetics: Advantages of Akaike information criterion and Bayesian approaches over likelihood ratio tests. *Syst. Biol.* 53: 793–808. https://doi.org/10.1080/10635150490522304

Rambaut, A. & Drummond, A. 2009. Tracer: MCMC trace analysis tool, version 1.5. Oxford: University of Oxford. Available from: http://beast.community/tracer

Ree, R.H. & Smith, S.A. 2008. Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. *Syst. Biol.* 57: 4–14. https://doi.org/10.1080/10635150701883881

Renoult, J.P., Kjellberg, F., Grout, C., Santoni, S. & Khadari, B. 2009. Cyto-nuclear discordance in the phylogeny of *Ficus* section *Galoglychia* and host shifts in plant-pollinator associations. *B. M. C. Evol. Biol.* 9(248): 1–18. https://doi.org/10.1186/1471-2148-9-248

Ronquist, F. 1997. Dispersal-vicariance analysis: a new approach to the quantification of historical biogeography. *Syst. Bio.* 46: 195–203. https://doi.org/10.1093/sysbio/46.1.195

Ronquist, F., Teslenko, M., Van der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A. & Huelsenbeck, J.P. 2012. MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Syst. Biol.* 61: 539–542. https://doi.org/10.1093/sysbio/sys029

Rønsted, N., Weiblen, G.D., Cook, J.M., Salamin, N., Machado, C.A. & Savolainen, V. 2005. 60 million years of co-divergence in the fig-wasp symbiosis. *Proc. Roy. Soc. London, Ser. B, Biol. Sci.* 272: 2593–2599. https://doi.org/10.1098/rspb.2005.3249

Rønsted, N., Weiblen, G.D., Clement, W., Zerega, N. & Savolainen, V. 2008. Reconstructing the phylogeny of figs (*Ficus*, Moraceae) to reveal the history of the fig pollination mutualism. *Symbiosis* 45(1–3): 45–55.

Ruiz-Sanchez, E. & Sosa, V. 2010. Delimiting species boundaries within the Neotropical bamboo *Otatea* (Poaceae: Bambusoideae) using molecular, morphological and ecological data. *Molec. Phylogen. Evol.* 54: 344–356. https://doi.org/10.1016/j.ympev.2009.10.035

Scheunert, A. & Heubl, G. 2017. Against all odds: Reconstructing the evolutionary history of *Scrophularia* (Scrophulariaceae) despite high levels of incongruence and reticulate evolution. *Organisms Diversity Evol.* 17: 323–349. https://doi.org/10.1007/s13127-016-0316-0

Shanahan, M., So, S., Compton, S.G. & Corlett, R. 2001. Fig-eating by vertebrate frugivores: A global review. *Biol. Rev. (Cambridge)* 76: 529–572. https://doi.org/10.1017/S1464793101005760

Shimodaira, H. & Hasegawa, M. 2001. CONSEL: For assessing the confidence of phylogenetic tree selection. *Bioinformatics* 17: 1246–1247. https://doi.org/10.1093/bioinformatics/17.12.1246

Stamatakis, A. 2014. RAxML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30: 1312–1313. https://doi.org/10.1093/bioinformatics/btu033

Swofford, D. 2003. PAUP*: Phylogenetic analysis using parsimony (*and other methods), version 4.0b10. Sunderland, Massachusetts: Sinauer.

Sytsma, K.J. 1990. DNA and morphology: Inference of plant phylogeny. *Tree* 5: 104–110. https://doi.org/10.1016/0169-5347(90)90163-8

Tamura, K., Peterson, D., Peterson, N., Stecher, G., Nei, M. & Kumar, S. 2011. MEGA5: Molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Molec. Biol. Evol.* 28: 2731–2739. https://doi.org/10.1093/molbev/msr121

Tëmkin, I. 2010. Molecular phylogeny of pearl oysters and their relatives (Mollusca, Bivalvia, Pterioidea). *B. M. C. Evol. Biol.* 10: 342. https://doi.org/10.1186/1471-2148-10-342

Tsai, L., Hayakawa, H., Fukuda, T. & Yokoyama, J. 2015. A Breakdown of obligate mutualism on a small island: An interspecific hybridization between closely related fig species (*Ficus pumila* and *Ficus thunbergii*) in western Japan. *Amer. J. Pl. Sci.* 6: 126–131. https://doi.org/10.4236/ajps.2015.61014

Van der Niet, T. & Linder, H.P. 2008. Dealing with incongruence in the quest for the species tree: A case study from the orchid genus *Satyrium*. *Molec. Phylogen. Evol.* 47: 154–174. https://doi.org/10.1016/j.ympev.2007.12.008

Wang, X.Q., Ye, X.Y., Zhao, L., Li, D.Z., Guo, Z.H. & Zhuang, H.F. 2017. Genome-wide RAD sequencing data provide unprecedented resolution of the phylogeny of temperate bamboos (Poaceae: Bambusoideae). *Sci. Rep.* 7: 11546. https://doi.org/10.1038/s41598-017-11367-x

Weiblen, G.D. 2000. Phylogenetic relationships of functionally dioecious *Ficus* (Moraceae) based on ribosomal DNA sequences and morphology. *Amer. J. Bot.* 87: 1342–1357. https://doi.org/10.2307/2656726

Wiebes, J.T. 1994. The Indo-Australian Agaoninae (pollinators of figs). *Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Sect. 2*, 92: 1–208.

Wiebes, J.T. 1995. The New World Agaoninae (pollinators of figs). *Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Sect. 2*, 94: 1–60.

Xiang, Y.Z., Huang, C.H., Hu, Y., Wen, J., Li, S.S., Yi, T.S., Chen, H.Y., Xiang, J. & Ma, H. 2016. Evolution of Rosaceae fruit types based on nuclear phylogeny in the context of geological times and genome duplication. *Molec. Biol. Evol.* 34: 262–281. https://doi.org/10.1093/molbev/msw242

Xu, L., Harrison, R.D., Yang, P. & Yang, D.R. 2011. New insight into the phylogenetic and biogeographic history of genus *Ficus*: Vicariance played a relatively minor role compared with ecological opportunity and dispersal. *J. Syst. Evol.* 49: 546–557. https://doi.org/10.1111/j.1759-6831.2011.00155.x

Yu, Y., Harris, A.J., Blair, C. & He, X.J. 2015. RASP (Reconstruct Ancestral State in Phylogenies): A tool for historical biogeography. *Molec. Phylogen. Evol.* 87: 46–49. https://doi.org/10.1016/j.ympev.2015.03.008

Zeng, L.P., Zhang, Q., Sun, R.R., Kong, H.Z., Zhang, N. & Ma, H. 2014. Resolution of deep angiosperm phylogeny using conserved nuclear genes and estimates of early divergence times. *Nature, Commun.* 5: 4596 https://doi.org/10.1038/ncomms5956

Zhou, Z.K. & Gilbert, M.G. 2003. Moraceae. Pp. 21–73 in: Wu, Z.Y., Raven, P.H. & Hong, D.Y. (eds.), *Flora of China*, vol. 5. Beijing: Science Press; St. Louis: Missouri Botanical Garden Press.

Appendix. 1. Voucher information and GenBank accession numbers.

Taxon, GenBank accession number of ITS, ETS, *G3pdh*, distribution region code (A, Africa mainland; B, Madagascar and surrounding islands; C, Indian subcontinent and Pan-Himalaya region; D, south China, Japan, Korean peninsula; E, Indo-China peninsula; F, west Malesia Islands; G, Philippine and South China Sea Islands; H, east Malesia Islands; I, Micronesia Islands; J, Australia; K, west Pacific Islands; L, America; M, Mediterranean), life form code (A, Terrestrial shrubs and trees; B, Hemi-epiphytes; C, Climbers; D, Holo-epiphytic shrubs). For the newly added materials, collecting location, collector, voucher number, and herbarium were listed. Accession numbers that begin with MN9 (MN9*****) obtained in this study; a dash (–) indicates missing GenBank accession number.

Ficus*, subg. *Ficus*, sect. *Eriosycea*, subsect. *Auratae*, *F. aurata (Miq.) Miq., EU091642, EU084469, –, FG, A; ***F. eumorpha*** Corner, EU091644, EU084471, EU087674, F, A; ***F. setiflora*** Stapf, EU091648, KP407002, –, F, A; **subsect. *Eriosycea*, *F. chartacea*** (Kurz) Wall. ex King, AY730126, EU084470, EF092384, EF, A; ***F. fulva*** Elmer, KX055695, KX055664, –, EFH, A; ***F. glandulifera*** (Miq.) King, EU091646, EU084472, –, EFGH, A; ***F. grossularioides*** Burm.f., AY063591, AY063548, EF092385, EFH, A; ***F. langkokensis*** Drake **1**, KX055736, KX055661, –, CDE, A; ***F. langkokensis*** Drake **2**, JN117638, JN117663, JN117703, CDE, A; ***F. padana*** Burm.f., AF165398, –, EF092387, F, A; ***F. pingtangensis*** S.S.Chang, China, Guangxi, Napo, Nasang, *Hongqing Li & Zhen Zhang 2013242* (HSNU), KY388609, KY388756, MN988563, D, A; ***F. potingensis*** Merr. & Chun, China, Hainan, Changjiang, Bawangling, *Hongqing Li & al. 2014026* (HSNU), KY388589, KY388720, MN988564, D, A; ***F. ruficaulis*** Merr., KX055740, KP407001, –, DGH, A; ***F. simplicissima*** Lour., China, Hainan, Lingshui, Diaoluoshan, *Hongqing Li & al. 2014116* (HSNU), KX055714, KX055629, MN988565, CDEFH, A; **sect. *Ficus*, subsect. *Ficus*, *F. carica*** L. **1**, France, Montpellier, *Hongqing Li FM11* (HSNU), MN960122, –, MN988566, M, A; ***F. carica*** L. **2**, France, Montpellier, *Hongqing Li FM7* (HSNU), MN960123, –, MN988567, M, A; ***F. palmata*** Forssk., AY730125, AY730214, EF092383, AC, A; **subsect. *Frutescentiae*, *F. abelii*** Miq., China, Guangxi, Yangshuo, Lijiang, *Hongqing Li 2010035* (HSNU), JQ773829, KY388623, MN988568, CDE, A; ***F. boninsimae*** Koidz., AB485918, –, HQ890580, D, A; ***F. chapaensis*** Gagnep., China, Yunnan, Fengqing, Xiaowan, *Hongqing Li & al. 2013033* (HSNU), KY388525, KY388634, MN988569, D, A; ***F. daiminshangensis*** S.S.Chang, China, Guangxi, Wuming, Damingshan, *Hongqing Li 2010354* (HSNU), JQ773860, KY388640, MN988570, D, A; ***F. deltoidea*** Jack, AY063579, AY063540, EF092378, EFH, D; ***F. erecta*** Thunb., KY388532, KY388647, –, D, A; ***F. filicauda*** Hand.-Mazz., China, Xizang, Motuo, Renqingben, *Hongqing Li & al. 2014554* (HSNU), KY388539, KY388654, MN988571, CD, A; ***F. formosana*** Maxim., China, Taiwan, Nantou, Huisun, *Hongqing Li 2011440* (HSNU), KY388542, KY388656, MN988572, D, A; ***F. gasparriniana*** Miq. **1**, China, Chongqing, Beibei, North hotspring, *Zhongling Lu 2104003* (HSNU), KY388553, KY388670, MN988573, CDE, A; ***F. gasparriniana*** Miq. **2**, China, Yunnan, Xichou, Fadou, *Hongqing Li & Zhen Zhang 2013223* (HSNU), KY388552, KY388665, MN988574, CDE, A; ***F. heteromorpha*** Hemsl., China, Guangdong, Ruyuan, Nanling, *Hongqing Li & al. 2012064* (HSNU), KY388559, KY388678, MN988575, D, A; ***F. iidana*** Rehder & E.H.Wilson, HQ890766, –, HQ890581, D, A; ***F. neriifolia*** Sm., China, Yunnan, Lushui, Pianma, *Hongqing Li & al. 2013011* (HSNU), KY388572, KY388692, MN988576, CDE, A; ***F. nishimurae*** Koidz., AB485915, –, HQ890579, D, A; ***F. oleifolia*** King, AY730124, EF092322, EF092382, EFGH, B/D; ***F. pandurata*** Hance **1**, China, Guangdong, Xingning, Luofu, *Hongqing Li & al. 2012013* (HSNU), KY388575, KY388700, MN988577, D, A; ***F. pandurata*** Hance **2**, China, Guangdong, Ruyuan, Shuiyuan'gong, *Hongqing Li & al. 2012052* (HSNU), KY388579, KY388704, MN988578, D, A; ***F. pedunculosa*** Miq. **1**, China, Taiwan, Pingdong, Eluanbi, *Hongqing Li 2010235* (HSNU), JQ773947, KY388715, MN988579, DGH, C; ***F. pedunculosa*** Miq. **2**, China, Taiwan, Lanyu, *Hongqing Li 2011426* (HSNU), KY388588, KY388716, MN988580, DGH, C; ***F. periptera*** D.Fang & D.H.Qin, China, Guangxi, Napo, Nonghua, *Hongqing Li & Zhen Zhang 2013234* (HSNU), KY388568, KY388717, MN988581, D, A; ***F. pyriformis*** Hook. & Arn., China, Guangdong, Fengkai, Heishiding, *Hongqing Li & Shuang Wang 2010339* (HSNU), JQ773962, KY388724, MN988582, D, A; ***F. ruyuanensis*** S.S.Chang, KY388595, KY388728, –, D, A; ***F. stenophylla*** Hemsl., China, Guizhou, Libo, Maolan, *Shuang Wang & al. 2011061* (HSNU), KY388599, KY388736, MN988583, DE, A; ***F. tannoensis*** Hayata, China, Taiwan, Lanyu, *Hongqing Li 2011427* (HSNU), KY388601, KY388743, MN988584, D, A/C; ***F. vaccinioides*** Hemsl. & King ex King, China, Taiwan, Lanyu, *Hongqing Li 2011430* (HSNU), KY388610, KY388758, MN988585, D, C; ***F. variolosa*** Lindl. ex Benth., JQ773911, KY388762, –, D, A; **subg. *Pharmacosycea*, sect. *Oreosycea*, subsect. *Glandulosae*, *F. habrophylla*** G.Bennett & Seem., EU091567, EU084408, EU087612, K, A; ***F. magnoliifolia*** Blume, EU091569, EU084409, EU087614, CDE, A; ***F. polyantha*** Warb., EU091571, KP406971, EU087616, GHK, A; ***F. pseudojaca*** Corner, EF092317, EF092320, EF092370, H, A; ***F. subtrinervia*** K.Schum. & Lauterb., AF165389, EU084411, EU087617, HK, A; **subsect. *Pedunculata*, *F. albipila*** (Miq.) King, AF165375, EU084406, EF092366, EFHJ, A; ***F. callosa*** Willd., AY063565, AY063526, EF092367, CDEFGH, A; ***F. dicranostyla*** Mildbr., EU091566, EU084407, EF092368, A, A; ***F. variifolia*** Warb., EF092318, EF092319, EU087618, A, A; ***F. vasculosa*** Wall. ex Miq., China, Hainan, Ledong, Jianfengling, *Hongqing Li & Shuang Wang 2010285* (HSNU), JQ773887, EU084412, MN988586, DEF, A; **sect. *Pharmacosycea*, subsect. *Bergianae*, *F. insipida*** Willd., AY063592, AY063549, AY967961, L, A; ***F. yoponensis*** Desv., AY063594, AY063552, AY967959, L, A; ***F. adhatodifolia*** Schott ex Spreng., EU091563, EU084404, EU087608, L, A; **subsect. *Petenenses*, *F. maxima*** Mill., AY063595, AY063551, AY967958, L, A; ***F. tonduzii*** Standl., AY730140, AY730230, EU087611, L, A; ***F. lapathifolia*** Miq., EU091564, EU084405, EU087609, L, A; **subg. *Spherosuke*, sect. *Americana*, *F. aurea*** Nutt., EU091598, EU084431, EU087636, L, A; ***F. eximia*** Schott, AY730079, AY730167, EF092344, L, A; ***F. paraensis*** Miq., AY730086, AY730174, AY967954, L, A; ***F. tuerckheimii*** Standl., EU091608, EU084438,

Appendix. 1. Continued.

EU087640, L, A; **sect. *Cordifoliae*, subsect. *Conosycea*, *F. altissima*** Blume, AY730064, AY730152, EU087621, CDEFGH, A/B; ***F. benjamina*** L., AY063559, AY063520, EF092333, CDEFGHJK, A/B; ***F. chrysolepis*** Miq., EU091583, EU084420, EU087624, GH, A/B; ***F. stricta*** (Miq.) Miq., EU091595, EU084429, EU087632, DEFG, A/B; **subsect. *Urostigma*, *F. religiosa*** L., AY063582, AY063543, EF092331, CDE, A/B; ***F. superba*** (Miq.) Miq., AF165410, AY730149, EF092332, EFH, A/B; ***F. ingens*** Miq., AY730061, AY730147, EF092330, A, A; ***F. caulocarpa*** (Miq.) Miq., EU091573, EU084413, EU087619, GH, A; **sect. *Platyphyllae*, *F. bubu*** Warb., DQ455637, DQ455671, EU087642, A, A/B; ***F. lutea*** Warb., AY063564, AY063525, EF092347, AB, A; ***F. thonningii*** Blume, AY730102, AY730191, EF092353, A, A/B; ***F. trichopoda*** Baker, DQ455666, DQ455684, EU087648, AB, A; **sect. *Urostigma*, *F. hesperidiiformis*** King, AF165387, AY730203, EF092362, HK, A/B; ***F. obliqua*** Miq., EF545659, EF538774, EF538793, HJK, A/B; ***F. pleurocarpa*** F.Muell., AY063568, AY063529, EF538795, J, A/B; **subg. *Sycomorus*, *F. adenosperma*** Miq., AF165374, EF092321, EF092374, HJK, A; ***F. auriculata*** Lour., AF165376, FJ812281, EU087653, DEF, A; ***F. congesta*** Roxb., AY730136, AY730225, DQ367620, H, A; ***F. hispida*** L.f., EU091623, EU084454, EU087659, CDEFJH, A; ***F. hispidioides*** L.f., AF165388, AY730227, DQ367622, CDFHJ, A; ***F. pachyrrhachis*** S.Moore, EU091628, EU084456, DQ367626, H, A; ***F. robusta*** Corner, AF165406, EU084442, DQ367628, H, A; ***F. scortechinii*** King, AY730139, KP406996, EF092377, EF, A; ***F. semicordata*** Miq., EU091613, EU084441, EU087652, CDF, A; ***F. semivestita*** Corner, EU091616, EU084443, DQ367629, H, A; ***F. septica*** Burm.f., AF165409, AY730229, DQ367630, CDEFGHJ, A; ***F. tikoua*** Bur., JN117648, JN117679, JN117712, CDE, C; ***F. uncinulata*** Corner, AY063576, AY063537, EU087669, F, A; ***F. vallis-choudae*** Dugand, AY063574, AY063535, EF092373, A, A; ***F. variegata*** Blume, AF165415, AY063539, DQ367633, CDEFHKJ, A; **subg. *Synoecia*, sect. *Apiosycea*, *F. apiocarpa*** (Miq.) Miq., EU091655, EU084480, –, EF, C; ***F. barba-jovis*** Corner, Malaysia, Borneo, Sepilok, *Zhen Zhang & Pengcheng Yao 20160133* (HSNU), MN960124, MN966805, MN988587, F, C; ***F. carrii*** Corner, Malaysia, Borneo, Mt. Kinabalu, *Zhen Zhang & Pengcheng Yao 20160075* (HSNU), MN960125, –, –, F, C; ***F. cavernicola*** C.C.Berg, Malaysia, Borneo, Mt. Kinabalu, *Zhen Zhang & Pengcheng Yao 20160087* (HSNU), MN960126, –, MN988588, F, C; ***F. disticha*** Blume, EU091656, EU084481, –, EFGHK, C; ***F. diversiformis*** Miq., AY730128, AY730215, EF092392, C, C; ***F. hederacea*** Roxb., China, Yunnan, Jinghong, Xishuangbanna Garden, *Hongqing Li 2009377* (HSNU), MN960127, MN966806, MN988589, CDE, C; ***F. punctata*** Thunb., AF165403, AY063545, –, DEFGH, C; ***F. ruginervia*** Corner, –, EF092323, EF092393, F, C; ***F. sarawakensis*** Corner, EU091657, KP407003, –, F, C; ***F. scratchleyana*** King, EU091658, –, EU087680, H, C; ***F.* sp. 2**, Malaysia, Borneo, Mt. Kinabalu, *Zhen Zhang & Pengcheng Yao 20160059* (HSNU), MN960128, –, MN988590, F, C; ***F.* sp. 3**, Malaysia, Borneo, Mt. Kinabalu, *Zhen Zhang & Pengcheng Yao 20160103* (HSNU), MN960129, –, MN988591, F, C; **sect. *Pogonotrophe*, subsect. *Plagiostigma*, *F. anserina*** (Corner) C.C.Berg **1**, China, Yunnan, Jinghong, *Zhen Zhang & al. 20150863a* (HSNU), MN960130, MN966807, MN988592, DE, C; ***F. anserina*** (Corner) C.C.Berg **2**, China, Yunnan, Jinghong, *Zhen Zhang & al. 20150864a* (HSNU), MN960131, MN966808, MN988593, DE, C; ***F. dinganensis*** S.S.Chang **1**, China, Hainan, Lingshui, Diaoluoshan, *Hongqing Li & al. 2014098* (HSNU), MN960132, MN966809, MN988594, D, C; ***F. dinganensis*** S.S.Chang **2**, China, Hainan, Lingshui, Diaoluoshan, *Zhen Zhang DLP28* (HSNU), MN960133, –, MN988595, D, C; ***F. guizhouensis*** S.S.Chang **1**, China, Guandong, Ruyuan, Nanling, *Hongqing Li & al. 2014143* (HSNU), MN960134, MN966810, MN988596, D, C; ***F. guizhouensis*** S.S.Chang **2**, China, Guangdong, Xinyi, Dawuling, *Zhen Zhang DWP23* (HSNU), MN960135, –, MN988597, D, C; ***F. napoensis*** S.S.Chang, China, Guangxi, Bose, Nasang, *Hongqing Li & Zhen Zhang 2013239* (HSNU), MN960136, MN966811, MN988598, D, C; ***F. polynervis*** S.S.Chang **1**, China, Yunnan, *Hongqing Li GBOWS0029* (HSNU), MN960137, MN966812, MN988599, D, C; ***F. polynervis*** S.S.Chang **2**, China, Yunnan, Xichou, Fadou, *Hongqing Li & Zhen Zhang 2013226* (HSNU), MN960138, MN966813, MN988600, CD, C; ***F. polynervis*** S.S.Chang **3**, China, Guangxi, Bose, Nonghua, *Hongqing Li & Zhen Zhang 2013236* (HSNU), MN960139, MN966814, MN988601, D, C; ***F. pubigera*** (Wall. ex Miq.) Brandis **var. 1**, China, Guangxi, Jinxiu, Yinshan Garden, *Shuang Wang & al. 2011080* (HSNU), MN960140, MN966815, MN988602, CDEF, C; ***F. pubigera*** (Wall. ex Miq.) Brandis **var. 2**, China, Guangxi, Shangsi, Shiwandashan National Park, *Shuang Wang & al. 2011016* (HSNU), MN960141, MN966816, MN988603, CDEF, C; ***F. pubigera*** (Wall. ex Miq.) Brandis **var. *pubigera***, China, Linzhi, Motuo, Beibeng, *Hongqing Li & al. 2014536* (HSNU), MN960142, –, MN988604, CDEF, C; ***F. pumila*** L.**?**, AY063580, AY063541, EF092390, D, C; ***F. pumila*** L. **1**, China, Fujian, Ningde, Nanshan, *Hongqing Li & al. 2010053* (HSNU), MN960143, MN966817, MN988605, D, C; ***F. pumila*** L. **2**, China, Hainan, Danzhou, Nada, *Hongqing Li & al. 2014012* (HSNU), MN960144, MN966818, MN988606, D, C; ***F. sarmentosa*** Buch.-Ham. ex Sm.**?**, EU091653, EU084478, EU087679, CDE, C; ***F. sarmentosa*** var. ***duclouxii*** (Lévl. & Vant.) Corner, China, Linzhi, Motuo, *Hongqing Li & al. 2014564* (HSNU), MN960145, MN966819, MN988607, CD, C; ***F. sarmentosa*** var. ***henryi*** (King ex Oliv.) Corner, China, Zhejiang, Lin'an, Tianmushan, *Hongqing Li 2010080* (HSNU), MN960146, MN966820, MN988608, CD, C; ***F. sarmentosa*** var. ***impressa*** (Champ.) Corner, China, Fujian, Changtai, Tianzhushan, *Shenzhan Xiong 2009204* (HSNU), MN960147, MN966821, MN988609, CD, C; ***F. sarmentosa*** var. ***lacrymans*** (Lévl. & Vant.) Corner, China, Guizhou, Libo, Maolan, *Shuang Wang & al. 2011068* (HSNU), MN960148, MN966822, MN988610, CD, C; ***F.* sp. 1 a**, China, Yunnan, *Zhen Zhang & al. 20150908a* (HSNU), MN960149, –, MN988611, D, C; ***F.* sp. 1 b**, China, Yunnan, *Zhen Zhang & al. 20150909a* (HSNU), MN960150, –, MN988612, D, C; **subsect. *Pogonotrophe*, *F. laevis*** Blume **1**, China, Yunnan, Jinghong, Xishuangbanna Garden, *Hongqing Li 2009411* (HSNU), MN960151, MN966823, MN988613, CDEF, C; ***F. laevis*** Blume **2**, China, Guangxi, Jingxi, Tongling Canyon, *Shenzhan Xiong 2010149* (HSNU), MN960152, MN966824, –, CDEF, C; **subsect. *Punctulifoliae*, *F. baeuerlenii*** King, AF165377, EU084474, –, H, C; ***F. excavata*** King, Malaysia, Borneo, Mt. Kinabalu, *Zhen Zhang & Pengcheng Yao 20160060* (HSNU), MN960153, –, MN988614, F, C; ***F. pantoniana*** King, EU091649, KP407004, –, HJK, C; ***F. pendens*** Corner, Malaysia, Borneo, Mt. Kinabalu, *Zhen Zhang & Pengcheng Yao 20160093* (HSNU), MN960154, –, –, F, C; ***F. recurva*** Blume, Malaysia, Borneo, Sepilok, *Zhen Zhang & Pengcheng Yao 20160127* (HSNU), MN960155, –, MN988615, EFG, C; ***F. sagittata*** Vahl, China, Hainan, Changjiang, Bawangling, *Hongqing Li & al. 2014078* (HSNU), MN960156, MN966825, MN988616, CDEFGHI, C; ***F. villosa*** Blume, AY730130, AY730217, EF092391, CDEFH, C; **subsect. *Trichocarpeae*, *F. jimiensis*** C.C.Berg, AY730129, AY730216, EF092388, H, C; ***F. pleiadenia*** Diels, EU091650, EU084475, EU087676, H, C; ***F. trichocarpa*** Blume, EU091654, EU084479, –, EFH, C; **subg. *Terega*, sect. *Palaeomorphe*, *F. heteropleura*** Blume, JQ773895, AY730220, EF092400, CDEFGH, A/B; ***F. parietalis*** Blume, AY063583, AY063544, EF092401, EFGH, A/B; ***F. sinuata*** Thunb., AY730135, AY730222, EF092402, CEF, A/B; ***F. subulata*** Blume, EU091677, EU084495, EU087690, DEFGHK, A/B; ***F. tinctoria*** G.Forst., AF165413, AY730223, EF092403, CDEFGHIK, A/B; ***F. virgata*** Reinw. ex Blume, AB485897, AY730224, EF092404, DGHIJK, A/B; **sect. *Sycidium*, *F. asperifolia*** Miq., EU091661, EU084484, EF092394, A, A; ***F. badiopurpurea*** Diels, EU091662, EU084485, EU087681, H, A; ***F. copiosa*** Steud., AF165382, EF092324, EF092395, HIJK, A; ***F. coronata*** Spin, AY730131, AY730218, EF092396, J, A; ***F. cumingii*** Miq., EU091663, EU084487, EU087682, DGH, A; ***F. exasperata*** Vahl, EU091665, EU084489, EU087683, AC, A; ***F. gul*** K.Schum. & Lauterb., AY730132, AY730219, EF092397, FHJK, A; ***F. henryi*** Warb. ex Diels **1**, JN117633, JN117660, JN117699, D, A; ***F. henryi*** Warb. ex Diels **2**, EU091639, EU084466, EU087672, D, A; ***F. heterophylla*** L.f., EU091667, EU084491, EU087684, CDEF, A/B/C; ***F. lateriflora*** Vahl, AY063585, AY063546, EF092398, B, A; ***F. melinocarpa*** Blume, EU091669, KP407006, EU087685, FGH, A; ***F. politoria*** Lour., EU091671, KP407007, EU087687, B, A; ***F. pygmaea*** Welw. ex Hiern, AY730134, AY730221, EF092399, B, A; ***F. trachypison*** K.Schum., EU091674, EU084493, EU087688, H, A; ***F. tsiangii*** Merr. ex Corner **1**, EU091675, EU084494, –, D, A; ***F. tsiangii*** Merr. ex Corner **2**, JN117650, JN117676, JN117714, D, A; ***F. wassa*** Roxb., AF165418, EF092325, DQ367635, HK, A. **OUTGROUP:** ***Antiaropsis decipiens*** K.Schum., AY730142, EU084403, EF092326, H, A; ***Castilla elastica*** Sessé ex Cerv., AY730143, AY730232, EF092327, L, A; ***Poulsenia armata*** (Miq.) Standl., AY730144, AY730233, –, L, A; ***Sparattosyce dioica*** Bureau, AY730141, AY730231, EU087607, K, A.