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Pyramidanthe and *Mitrella* (Annonaceae, Uvarieae) unified: molecular phylogenetic and morphological congruence, with new combinations in *Pyramidanthe*

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Abstract: The delimitation of the genera *Pyramidanthe* and *Mitrella* in the tribe *Uvarieae* of the family *Annonaceae* is assessed by molecular phylogenetic analyses and morphological re-evaluation. Using up to six plastid DNA regions (*matK*, *ndhF*, *rbcL* exons; *trnL* intron; *psbA-trnH*, *trnL-trnF* intergenic spacers) and including, among others, two accessions of *Pyramidanthe* and five accessions of *Mitrella*, the resulting phylogeny shows that *Pyramidanthe* and *Mitrella* are recovered in a clade sister to the *Fissistigma* clade. The *Pyramidanthe*-*Mitrella* clade is composed of a trichotomy: a clade consisting of *Pyramidanthe* accessions and two clades containing *Mitrella* accessions. In combination with negligible morphological distinctions between the two genera, they are consequently merged, with 11 new combinations under the chosen name *Pyramidanthe*: *P. beccarii*, *P. clementis*, *P. cylindrica*, *P. dielsii*, *P. elegans*, *P. kentii*, *P. ledermannii*, *P. mabiformis*, *P. schlechteri*, *P. sylvatica* and *P. tiwiensis*. The names *M. dielsii* (the basionym of *P. dielsii*) and *P. rufa* (a heterotypic synonym of *P. prismatica*) are lectotypified. *Pyramidanthe* s. lat. possesses the following diagnostic traits: usually indistinct secondary leaf veins with a brochidodromous to brochidodromous-eucamptodromous venation, a reticulate tertiary leaf venation, axillary inflorescences, presence of a basal excavation on an inner side of each outer petal, and inner petals that are much smaller than the outer petals and cohering marginally at anthesis.

Keywords: *Annonaceae*, *Annonoideae*, *Mitrella*, nomenclatural combinations, plastid phylogeny, *Pyramidanthe*, taxonomy, typification, *Uvarieae*

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Introduction

Annonaceae, a pantropical angiosperm family prominent in lowland rain forests, are the largest family in the order *Magnoliales* (Doyle & al. 2004), with five subfamilies, 18 tribes, 108 genera and c. 2430 species (Chatrou & al. 2018; Couvreur & al. 2019; Chaowasku 2020; Damthongdee & al. 2021; Photikwan & al. 2021). The generic delimitation in various clades of *Annonaceae* has been intensely realigned in the past two decades based on molecular phylogenetic analyses; for example, the tribes *Canangeae* (*Ambavioideae*; Surveswaran & al. 2010), *Miliuseae* (*Malmeoideae*; e.g. Xue & al. 2011, 2012, 2014, 2018; Chaowasku & al. 2012, 2013, 2015, 2018b; Guo & al. 2014) and *Uvarieae* (*Annonoideae*; Zhou & al. 2009, 2010; Guo & al. 2017a). Additionally,

molecular phylogenetics also assisted the establishment of new genera (Mols & al. 2008; Couvreur & al. 2009, 2015; Chaowasku & al. 2018a). Nevertheless, there are still some genera that lack adequate phylogenetic data for assessing their delimitation. This can be well exemplified in the *Pyramidanthe*-*Mitrella* clade. *Pyramidanthe* Miq. is a monotypic genus distributed in S Thailand, Peninsular Malaysia, Singapore, Sumatra and Borneo, whereas *Mitrella* Miq. is a small genus consisting of nine species distributed in S Thailand, Peninsular Malaysia, Singapore, Java, Borneo, New Guinea and the Australian Tiwi Islands (Turner 2018; Johnson & al. 2021). The phylogenetic relationships hitherto reported indicate that these two genera constitute a strongly supported clade sister to *Fissistigma* Griff., but only one species of *Mitrella* was included; the three genera form a strongly supported

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clade within the tribe *Uvarieae* of the subfamily *Annonoideae* (Guo & al. 2017a, 2017b). It is worthwhile noting that most members of *Uvarieae* are lianas (Chatrou & al. 2012), including the only species of *Pyramidanthe* and nine of *Mitrella* (Turner 2012).

Morphologically, the genera *Pyramidanthe* and *Mitrella* are quite similar; they possess, for example, leaf blades with a reticulate tertiary venation, a basal excavation on an inner side of each outer petal, and inner petals that are much smaller than the outer petals (Turner 2012). As presented in the key in Turner (2012), the two genera differ from each other only in the sepal appearance, and this weak differentiation prompted him to reluctantly consider *Pyramidanthe* and *Mitrella* as distinct from each other. In this study, we reassess the generic delimitation of *Pyramidanthe* and *Mitrella* by molecular phylogenetic inferences (with additions of one new accession of *Pyramidanthe*, five new accessions of *Mitrella* and six new accessions of the closely related *Fissistigma*) and morphological reappraisal.

Material and methods

Molecular phylogenetic analyses

Thirty-three accessions constituted the ingroup, covering all accepted genera of *Uvarieae*, including two accessions of *Pyramidanthe* and five accessions of *Mitrella*. The tribe *Uvarieae* has been demonstrated to form a strongly supported clade (e.g. Guo & al. 2017b). Outgroups were an accession of *Xylopieae* [*Artabotrys hexapetalus* (L. f.) Bhandari] and an accession of *Mono-doreae* [*Isolona campanulata* Engl. & Diels]. The information of voucher specimens and GenBank accession numbers used in this study is shown in Appendix 1. Up to six plastome regions (*psbA-trnH*, *trnL-trnF* intergenic spacers; *trnL* intron; *matK*, *ndhF*, *rbcL* exons) were included. Regarding the DNA extraction, amplification and sequencing used in the present study, their methods, including primer information, followed Chaowasku & al. (2018a, 2018b, 2020). Sequences were edited using the Staden package (Staden & al. 2000) and the data matrix was aligned by Multiple Alignment using Fast Fourier Transform (MAFFT; Katoh & al. 2002) via an online platform (Katoh & al. 2019), with default settings. The aligned data matrix was subsequently manually checked and realigned where necessary using the similarity criterion (Simmons 2004). In some accessions, an inversion of a 15-nucleotide stretch in the *psbA-trnH* intergenic spacer was present and, following Pirie & al. (2006), this was complement-reversed to be homologically alignable to the remaining accessions. In total, there were 5500 nucleotide plus 19 binary-coded indel characters. Indel coding followed the simple method of Simmons & Ochoterena (2000).

Parsimony analysis was carried out in TNT version 1.5 (Goloboff & Catalano 2016). All characters were

equally weighted and unordered. Incongruence among plastome regions was measured by analysing each region individually to see if there was any significant topological conflict (e.g. Wiens 1998). Most parsimonious trees were produced by a heuristic search of the combined data, with 9000 replicates of random sequence addition, saving 10 trees per replicate and using the tree bisection and reconnection (TBR) branch-swapping algorithm. Clade support was assessed by symmetric resampling (SR; Goloboff & al. 2003), with default change probability. Two hundred thousand replicates were run, each with four replicates of random sequence addition, saving four trees per replicate. A clade with SR $\geq$ 85%, 70–84% or 50–69% was considered strongly, moderately or weakly supported, respectively.

Maximum likelihood analysis was performed in IQ-TREE version 2.1.2 (Minh & al. 2020) under partition models (Chernomor & al. 2016) implemented with the “-p” command, whereas Bayesian Markov chain Monte Carlo (MCMC; Yang & Rannala 1997) phylogenetic analysis was performed in MrBayes version 3.2.7a (Ronquist & al. 2012) via the CIPRES Science Gateway version 3.3 (Miller & al. 2010). The aligned data matrix was divided into five partitions based on identity of DNA regions (the *trnL* intron and adjacent *trnL-trnF* intergenic spacer were united into a single partition). The most suitable model of sequence evolution for each DNA partition was chosen by the Akaike Information Criterion (AIC; Akaike 1974) scores, using FindModel (<http://www.hiv.lanl.gov/content/sequence/findmodel/findmodel.html>; Posada & Crandall 1998). The General Time Reversible (GTR; Tavaré 1986) nucleotide substitution model with a gamma distribution for among-site rate variation was selected for *matK*, *ndhF* and *rbcL* partitions, while the Hasegawa-Kishino-Yano (HKY; Hasegawa & al. 1985) substitution model with a gamma distribution for among-site rate variation was chosen for the remaining partitions (*psbA-trnH* and *trnL-F* [= *trnL* intron + *trnL-trnF* intergenic spacer]). In the maximum likelihood analysis, the model “JC2+FQ+ASC” was chosen by corrected AIC scores for the binary indel partition. Clade support was measured by a non-parametric bootstrap resampling (BS; Felsenstein 1985) with 2000 replicates. A clade with BS $\geq$ 85%, 70–84% or 50–69% was considered strongly, moderately or weakly supported, respectively. In the Bayesian analysis, the “coding=variable” command was assigned to the binary indel partition, which was implemented under a simple F81-like model without a gamma distribution for among-site rate variation. Four independent runs, each using four MCMC chains, were simultaneously carried out; each run was set for 10 million generations. The default prior settings were used except for the prior parameter of rate multiplier (“ratepr” [=variable]). The temperature parameter was set to 0.08. Trees and all parameter values were sampled every 1000th generation. Convergence was evaluated by checking the standard deviation of split frequencies of

the runs with values < 0.01 interpreted as indicative of a good convergence and by checking for adequate effective sample sizes ($ESS > 200$) using Tracer version 1.6 (Rambaut & al. 2013). The first 25% of all trees sampled were removed as burn-in and the 50% majority-rule consensus tree was generated from the remaining trees. A clade with posterior probabilities (PP) ≥ 0.95 , 0.9–0.94 or 0.5–0.89 was considered strongly supported, weakly supported or unsupported, respectively.

Morphology

Morphological data were derived from literature (Sinclair 1955, 1956; van Heusden 1992; van Setten & Koek-Noorman 1992; Turner 2012), as well as observations on type specimens of relevant names, voucher specimens for molecular phylogenetic analyses listed in Appendix 1, a specimen of *Fissistigma uonicum* (Dunn) Merr. [Tutcher 494 (K)] and additional specimens of *Mitrella kentii* (Blume) Miq. [Anon. s.n. (L [L.1757631]); Anon. s.n. (U [U.1073759]); Janse 1697 (L)].

Results and Discussion

The parsimony analysis resulted in 36 most parsimonious trees with 1256 steps. The consistency and retention indices (CI and RI) were 0.8 and 0.87, respectively. There was no strong topological conflict ($SR \geq 85\%$) among the analyses of each plastome region. Fig. 1 shows the Bayesian 50% majority-rule consensus phylogram, with support values from the other two methods of phylogenetic analysis indicated. The ingroup (*Uvarieae*) was recovered with maximum support. In *Uvarieae*, there was a strongly supported (SR 99%, BS 100%, PP 1) clade composed of a strongly supported (SR 99%, BS 100%, PP 1) *Fissistigma* clade and a maximally supported *Pyramidanthe-Mitrella* clade. In the latter clade, there was a trichotomy consisting of (1) a strongly supported (SR 98%, BS 100%, PP 1) clade comprising *P. prismatica* (Hook. f. & Thomson) Merr. and *P. sp.*, (2) a strongly supported (SR 99%, BS 100%, PP 1) clade consisting of *M. clementis* (Merr.) I. M. Turner and *M. elegans* (Hook. f. & Thomson) D. M. Johnson & N. A. Murray and (3) a strongly supported clade (SR 97%, BS 97%, PP 1) composed of *M. cf. beccarii* (Scheff.) Diels, *M. sp. 1* and *M. sp. 2.*, with the last two accessions forming a strongly supported (SR 96%, BS 100%, PP 1) clade.

Similar to the previously reported phylogenetic hypotheses (Guo & al. 2017a, 2017b), the relationships in the tribe *Uvarieae* herein depicted (Fig. 1) are still considerably unresolved, especially in the uncertain position of *Dielsiothamnus* R. E. Fr. and *Uvaria* L. In the maximally supported *Pyramidanthe-Mitrella* clade (Fig. 1), the relationships of the three strongly supported major clades (one of which contains *Pyramidanthe* accessions,

whereas the other two consist of *Mitrella* accessions) are unresolved. However, when more data become available, especially from next-generation sequencing approaches, the monophyly of *Mitrella* could be demonstrated. The two genetically close genera, *Pyramidanthe* and *Mitrella*, are morphologically alike, i.e. they share usually indistinct secondary leaf veins with a brochidodromous to brochidodromous-eucamptodromous venation, a reticulate tertiary leaf venation, axillary inflorescences, adaxially basally excavated outer petals (Fig. 2B [left], D [left]), and inner petals that are much smaller than the outer petals (Fig. 2B, D, Fig. 3A, C) and marginally adjoining at anthesis (Fig. 3A, C) (Turner 2012; personal observations). *Pyramidanthe* differs from *Mitrella* only in sepal appearance (Turner 2012), i.e. nearly completely connate sepals with an indistinct apex (Fig. 2A) in the former genus vs partially connate sepals with a distinct apex (Fig. 2C) in the latter genus. In addition, the monocarps of *Pyramidanthe* are more or less warty (Fig. 3B), whereas they are smooth in *Mitrella* (Fig. 3D) except in *M. dielsii* J. Sinclair, which has the same monocarp appearance as that of *Pyramidanthe* (Sinclair 1955, 1956; Turner 2012). Based primarily on the negligible morphological distinctions between the two genera, unifying them is appropriate. The two genera are of equal nomenclatural priority because they were established on the same date (Miquel 1865); therefore, a choice must be made (see Art. 11.5 of the *International Code of Nomenclature for algae, fungi, and plants*; Turland & al. 2018). Although the name *Mitrella* contains several more species, strikingly similar generic names pre-exist: *Mitella* Tourn. ex L. (*Saxifragaceae*) and *Mitreola* L. (*Loganiaceae*); the three generic names (*Mitella*, *Mitrella* and *Mitreola*) have the same etymology, i.e. they are diminutive forms of the Greek-derived Latin noun *mitra* (= mitre, cap; Quattrocchi 2000). It is worth mentioning that the recent case of near-identical generic names of *Hubera* Chaowasku (*Annonaceae*) vs *Huberia* DC. (*Melastomataceae*) has resulted in homonymy (Chaowasku 2013; Applequist 2014). Consequently, to avoid possible nomenclatural confusion, we select *Pyramidanthe*, with 11 new combinations under the selected name. It is noteworthy that *Pyramidanthe* and *Mitrella* were once considered as congeneric with *Fissistigma*, the sister group of the *Pyramidanthe* inclusive of *Mitrella* (= *Pyramidanthe* s. lat.) clade (Fig. 1), by Merrill (1919). Our molecular phylogenetic results reveal that *Fissistigma* and *Pyramidanthe* s. lat. are better kept apart. The former principally differs from the latter by having distinct secondary leaf veins with a eucamptodromous venation, a usually percurrent tertiary leaf venation, and inner petals that are usually more or less two-thirds to more or less half the size of the outer petals (Turner 2012; personal observations). Furthermore, *Fissistigma* usually does not show a basal excavation on an inner side of each outer petal (Turner 2012; the excavation, when present, e.g. in *F. uonicum*, is shallow and broad [personal observations]) and generally possesses multi-flowered inflorescences (vs usually 1-flowered or rarely few-flowered in *Pyramidanthe*

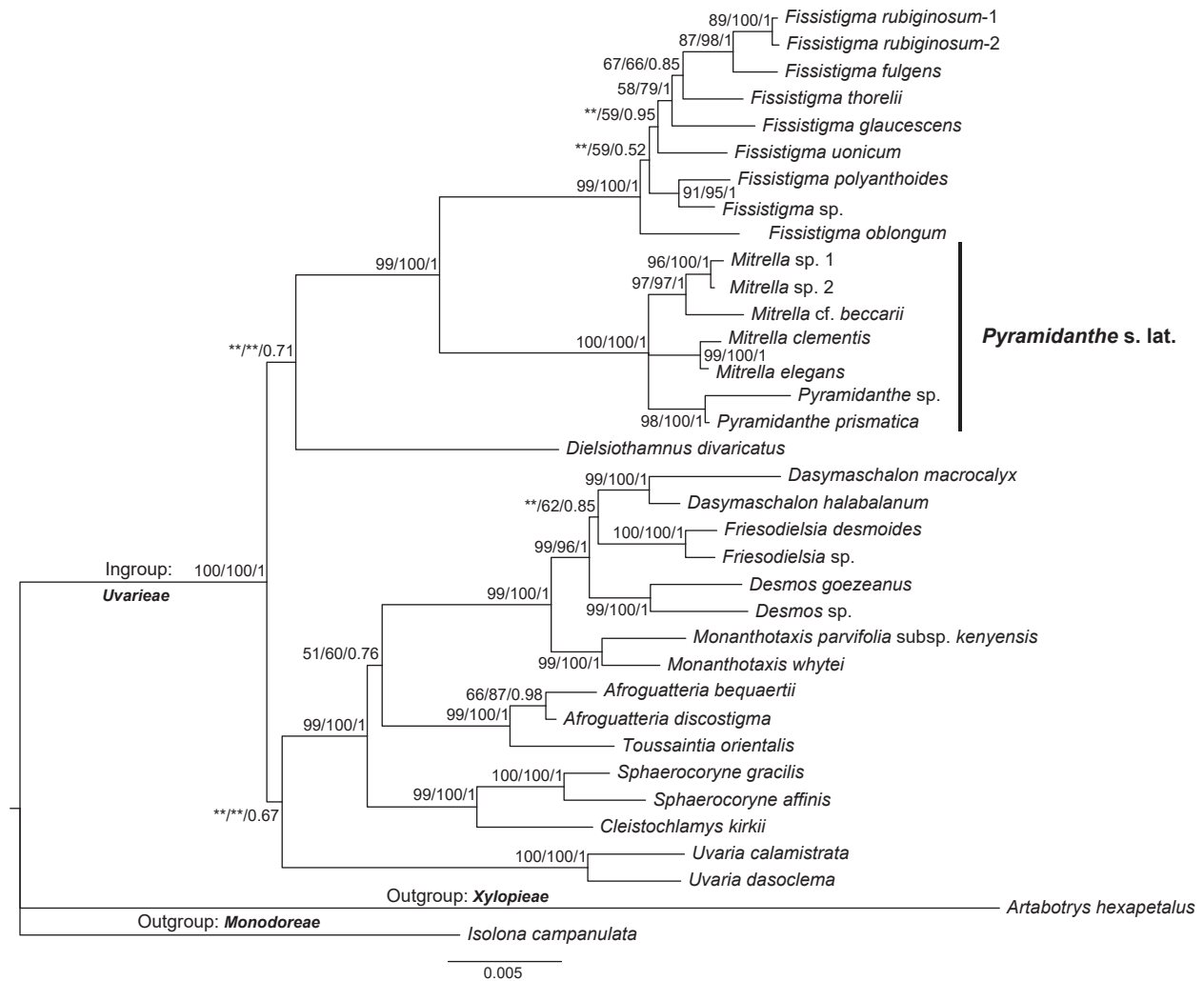


Fig. 1. Phylogram from Bayesian inference, showing relationships within *Uvarieae*. Parsimony symmetric resampling values (SR), maximum likelihood bootstrap values (BS) and Bayesian posterior probabilities (PP) are indicated: SR/BS/PP. ** = BS and/or SR < 50%. Scale bar unit = substitutions per site.

s. lat.; Turner 2012). The present study will facilitate a future revision of *Pyramidanthe* s. lat. Based on preliminary observations, several new species are anticipated, including *M. sp. 1* (from Papua New Guinea) and *M. sp. 2* (from Indonesian New Guinea). Regarding *Pyramidanthe* sp., it was identified as *P. prismatica* in e.g. Guo & al. (2017a, 2017b), but its outer petals are shorter (personal observations) and there are high amounts of nucleotide substitutions (Fig. 1). We believe that a revisionary study, combined with extensive phylogenetic inferences, can finally shed light on its identity.

Taxonomic treatment

Pyramidanthe Miq. in Ann. Mus. Bot. Lugduno-Batavi 2: 39. 1865 ≡ *Unona* sect. *Pyramidanthe* (Miq.) Baill., Hist. Pl. 1: 213. 1868 ≡ *Melodorum* sect. *Pyramidanthe* (Miq.) Kurz in J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 43: 56. 1870. – Type: *Pyramidanthe rufa* Miq. [= *Pyramidanthe prismatica* (Hook. f. & Thomson) Merr.].

= *Mitrella* Miq. in Ann. Mus. Bot. Lugduno-Batavi 2: 38. 1865 ≡ *Polyalthia* sect. *Kentia* Blume, Fl. Javae Anonac. 71. 1830 ≡ *Polyalthia* sect. *Schnittspahnia* Rchb., Deut. Bot. Herb.-Buch: 236. 1841, nom. illeg. superfl. ≡ *Melodorum* sect. *Kentia* (Blume) Hook. f. & Thomson, Fl. Ind.: 122. 1855 ≡ *Unona* sect. *Kentia* (Blume) Baill., Hist. Pl. 1: 213. 1868, **syn. nov.** – Type: *Polyalthia kentii* (Blume) Blume [= *Unona kentii* Blume ≡ *Mitrella kentii* (Blume) Miq.].

Description — Woody climbers; indumentum of simple hairs. *Leaves* petiolate; petiole often ≥ 10 mm long; abaxial leaf surface somewhat glaucous, secondary leaf veins usually indistinct, brochidodromous to brochidodromous-eucamptodromous, tertiary venation reticulate. *Inflorescences* axillary (including in axils of fallen leaves), 1-flowered, rarely few-flowered. *Flowers* bisexual, buds ± (ob)ovoid-triangular pyramidal to ± narrowly ovoid-triangular pyramidal. *Sepals* 3, valvate, nearly completely connate with indistinct apex or partially connate with distinct apex, persistent in fruit. *Petals* 6, in 2 whorls,

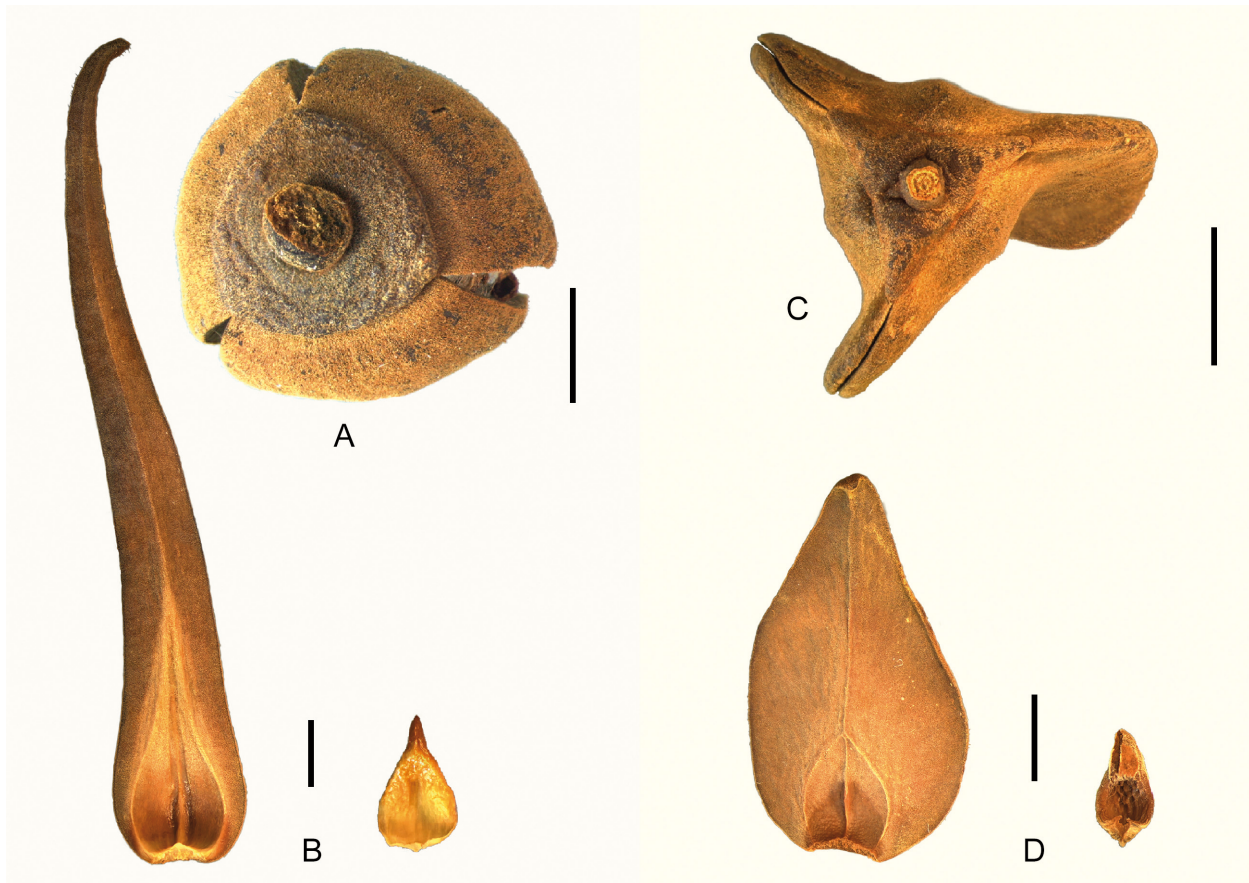


Fig. 2. Sepal and petal morphology of *Pyramidanthe prismatica* (A, B) and *Mitrella elegans* (C, D). – A: back view of flower, showing nearly completely connate sepals with indistinct apex; B: inner side of outer petal (left) with basal excavation and inner side of inner petal (right); C: back view of flower, showing partially connate sepals with distinct apex; D: inner side of outer petal (left) with basal excavation and inner side of inner petal (right). – Scale bars = 5 mm. – A, B from Aongyong & Baka 38 (CMUB); C, D from Aongyong & Baka 37 (CMUB).

each whorl valvate; outer whorl much larger than inner whorl, elliptic-obovate, ovate, ovate-triangular to narrowly ovate-triangular; inner whorl marginally cohering at anthesis, base of each inner petal excavated adaxially. *Stamens* numerous; connective apex discoid to $\pm$ tongue-shaped. *Carpels* (5)–6–15; stigmas $\pm$ ellipsoid-cylindric or irregularly shaped; ovaries glabrous or sparsely hairy; ovules (2)–4–18 per ovary, lateral. *Fruits* each consisting of globose, ellipsoid to cylindric monocarps; each monocarp stipitate, smooth or $\pm$ warty. *Seeds* sometimes pitted; endosperm ruminations $\pm$ flattened pegs and often $\pm$ lamellate toward raphe, sometimes spiniform.

Diversity and distribution — Twelve species, distributed in S Thailand, Peninsular Malaysia, Singapore, Sumatra, Java, Borneo, New Guinea and the Australian Tiwi Islands.

Accepted names in *Pyramidanthe*

1. *Pyramidanthe beccarii* (Scheff.) Bangkomnate & Chaowasku, **comb. nov.** $\equiv$ *Melodorum beccarii* Scheff. in Ann. Jard. Bot. Buitenzorg 2: 24. 1881 $\equiv$ *Mitrella bec-*

carii (Scheff.) Diels in Bot. Jahrb. Syst. 49: 149. 1912 $\equiv$ *Fissistigma beccarii* (Scheff.) Merr. in Philipp. J. Sci. 15: 131. 1919. – Lectotype (designated by Diels 1912: 150): Indonesia, Papua, Andai, 1872, *Beccari P.P.* 795 (FI-B barcode FI007574 [Erb. Coll. Becc. No. 497] [image!]; isolectotypes: A [image!], B [$\times$ 2] [images!], FI-B [Erb. Coll. Becc. No. 497A] not seen, K [image!]).

2. *Pyramidanthe clementis* (Merr.) Bangkomnate & Chaowasku, **comb. nov.** $\equiv$ *Fissistigma clementis* Merr. in J. Straits Branch Roy. Asiat. Soc. 85: 178. 1922 $\equiv$ *Mitrella clementis* (Merr.) I. M. Turner in Malayan Nat. J. 61: 273. 2009. – Lectotype (designated by Turner 2009: 273): Borneo, Sabah, Sandakan and vicinity, Sep–Dec 1920, *Ramos 1474* (K barcode K000574737 [image!]; isolectotypes: A [$\times$ 2] [images!], BM [image!], L [image!], US [image!]).

3. *Pyramidanthe cylindrica* (Maingay ex Hook. f. & Thomson) Bangkomnate & Chaowasku, **comb. nov.** $\equiv$ *Melodorum cylindricum* Maingay ex Hook. f. & Thomson in Hooker, Fl. Brit. India 1: 80. 1872 $\equiv$ *Fissistigma cylindricum* (Maingay ex Hook. f. & Thomson) Merr. in

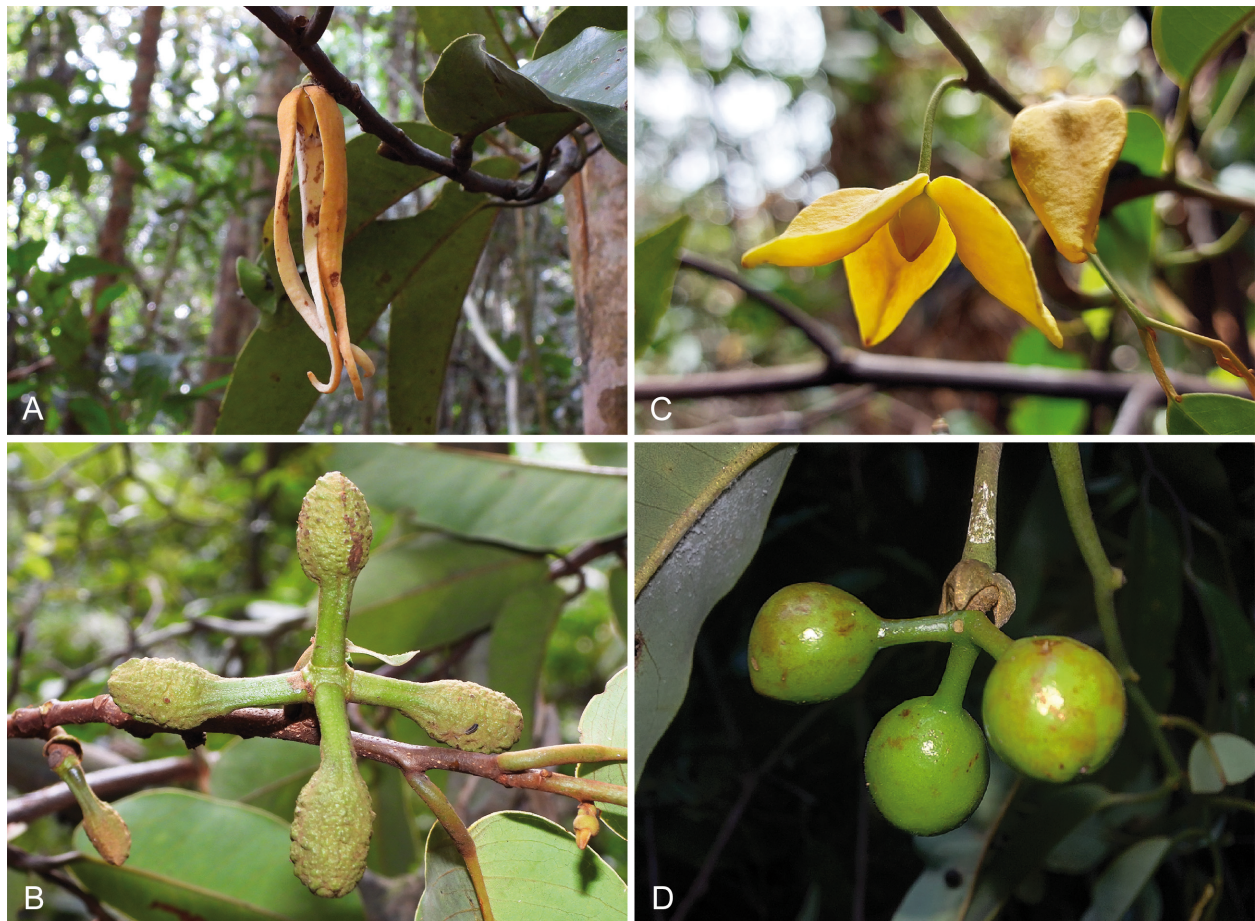


Fig. 3. Flower and fruit morphology of *Pyramidanthe prismatica* (A, B) and *Mitrella elegans* (C, D). – A: mature flower; B: immature fruit with more or less warty monocarps; C: flower bud and mature flower; D: nearly ripe fruit with smooth monocarps. – Photographs by Abdulromea Baka; A, B from Aongyong & Baka 38 (CMUB); C, D from Aongyong & Baka 37 (CMUB).

Philipp. J. Sci. 15: 131. 1919. – Holotype: Peninsular Malaysia, Malacca, 1865–1866, *Maingay 1507* [Kew Distrib. No. 78] (K barcode K000574661 [image!]; isotype: CAL not seen).

Remarks — This species was regarded as a heterotypic synonym of *Pyramidanthe prismatica* by Sinclair (1955) and Turner (2012, 2018). After a careful examination on the holotype, some features are different from those of *P. prismatica*, e.g. leaf base (broadly acute, obtuse to rounded [never subcordate or truncate] vs subcordate, more or less truncate to rounded [never broadly acute or obtuse] in *P. prismatica*), outer petal shape and length (ovate-triangular and c. 1 cm long vs narrowly ovate-triangular and (3.8–)5–8 cm long in *P. prismatica*) and monocarp shape (shortly cylindric to cylindric, more or less curved vs ellipsoid to shortly cylindric, never curved in *P. prismatica*). Consequently, *P. cylindrica* deserves recognition as a distinct species.

4. *Pyramidanthe dielsii* (J. Sinclair) Bangkomnate & Chaowasku, **comb. nov.** ≡ *Mitrella dielsii* J. Sinclair in Gard. Bull. Singapore 15: 14. 1956 ≡ *Melodorum beccarii* Diels in Notizbl. Bot. Gart. Berlin-Dahlem 11:

85. 1931, nom. illeg., non *Melodorum beccarii* Scheff. in Ann. Jard. Bot. Buitenzorg 2: 24. 1881. – **Lectotype (designated here)**: Borneo, Sarawak, near Sungai Igan, Oct 1867, *Beccari P.B. 3899* (FI-B [FI007576, FI007577, 1 specimen on 1 sheet with 2 barcodes] [Erb. Coll. Becc. No. 509] [image!]; isolectotypes: B [image!], FI-B [Erb. Coll. Becc. No. 509A] not seen, K [image!]).

5. *Pyramidanthe elegans* (Hook. f. & Thomson) Bangkomnate & Chaowasku, **comb. nov.** ≡ *Melodorum elegans* Hook. f. & Thomson, Fl. Ind.: 122. 1855 ≡ *Fissistigma elegans* (Hook. f. & Thomson) Merr. in Philipp. J. Sci. 15: 131. 1919 ≡ *Mitrella elegans* (Hook. f. & Thomson) D. M. Johnson & N. A. Murray in Thai Forest Bull., Bot. 49: 167. 2021. – Lectotype (designated by Turner 2011: 55): Peninsular Malaysia, Penang, 1822, *Anon. s.n.* [EIC 6474A] (K barcode K000574739 [image!]; isolectotypes: C [image!], CAL not seen, E [image!], GZU not seen, K not seen, K-W [image!], L [image!], NY [image!], PH not seen). – Fig. 2C, D, Fig. 3C, D.

Remarks — We follow the reasons given in Johnson & al. (2021) for the recognition of this species.

6. *Pyramidanthe kentii* (Blume) Bangkomnate & Chaowasku, **comb. nov.** $\equiv$ *Unona kentii* Blume, Bijdr. Fl. Ned. Ind.: 16. 1825 $\equiv$ *Polyalthia kentii* (Blume) Blume, Fl. Javae Anonac. 77. 1830 $\equiv$ *Melodorum kentii* (Blume) Hook. f. & Thomson, Fl. Ind.: 116. 1855 $\equiv$ *Mitrella kentii* (Blume) Miq. in Ann. Mus. Bot. Lugduno-Batavi 2: 39. 1865 $\equiv$ *Fissistigma kentii* (Blume) Merr. in Philipp. J. Sci. 15: 132. 1919. – Lectotype (designated by Turner 2011: 54): Java, *Anon. s.n.* (L [L.1757643] [image!]).

7. *Pyramidanthe ledermannii* (Diels) Bangkomnate & Chaowasku, **comb. nov.** $\equiv$ *Mitrella ledermannii* Diels in Bot. Jahrb. Syst. 52: 183. 1915. – Lectotype (designated by Kessler & al. 1995: 39): Papua New Guinea, Hauptlager Malu, am Sepik, 19 Mar 1912, *Ledermann 6672* (B barcode B 10 0325315 [image!]; isoelectotypes: K [x 2] [images!]).

8. *Pyramidanthe mabiformis* (Griff.) Bangkomnate & Chaowasku, **comb. nov.** $\equiv$ *Uvaria mabiformis* Griff., Not. Pl. Asiat. 4: 709. 1854 $\equiv$ *Fissistigma mabiforme* (Griff.) Merr. in Philipp. J. Sci. 15: 133. 1919. – Lectotype (designated by Sinclair 1955: 367): Peninsular Malaysia, Malacca, Aloor Gajah, *Verupha s.n.* [Kew Distrib. No. 389] (K barcode K000574743 [image!]).

Remarks — This species was considered as a heterotypic synonym of *Mitrella kentii* (now *Pyramidanthe kentii*) by Sinclair (1955) and Turner (2012, 2018). After a careful examination on the lectotype, some traits differ from those of *P. kentii*, e.g. leaf base (obtuse to rounded vs usually cuneate in *P. kentii*), pedicel length (6–8 mm long vs 12–19 mm long in *P. kentii*), outer petal shape (elliptic-obovate vs ovate in *P. kentii*) and outer petal apex (obtuse-rounded vs acute to obtuse-acute in *P. kentii*). Therefore, *P. mabiformis* deserves recognition as a distinct species.

9. *Pyramidanthe prismatica* (Hook. f. & Thomson) Merr. in J. Straits Branch Roy. Asiat. Soc., Spec. No.: 262. 1921 $\equiv$ *Melodorum prismaticum* Hook. f. & Thomson, Fl. Ind.: 121. 1855 $\equiv$ *Fissistigma prismaticum* (Hook. f. & Thomson) Merr. in Philipp. J. Sci. 15: 135. 1919. – Lectotype (designated by Turner 2011: 87): Peninsular Malaysia, Penang, Aug 1822, *Wallich s.n.* [EIC 6455] (K-W barcode K001123944 [image!]; isoelectotype: BM not seen). – Fig. 2A, B, Fig. 3A, B.

= *Pyramidanthe rufa* Miq. in Ann. Mus. Bot. Lugduno-Batavi 2: 39. 1865. – **Lectotype (designated here)**: Borneo, Martapoera, *Korthals s.n.* (L [L.1775037] [image!]).

= *Pyramidanthe rufa* var. *parvifolia* Boerl., Icon. Bogor. 1: 131. 1899 $\equiv$ *Pyramidanthe prismatica* var. *parvifolia* (Boerl.) Merr. in J. Straits Branch Roy. Asiat. Soc., Spec. No.: 263. 1921. – Lectotype (designated by Turner 2011: 88): Borneo, Sarawak, nr Kuching, 1892, *Haviland 421* (BO [sheet no. BO-134059] not seen).

10. *Pyramidanthe schlechteri* (Diels) Bangkomnate & Chaowasku, **comb. nov.** $\equiv$ *Mitrella schlechteri* Diels in Bot. Jahrb. Syst. 49: 150. 1912 $\equiv$ *Fissistigma schlechteri* (Diels) Merr. in Philipp. J. Sci. 15: 136. 1919. – Holotype: Papua New Guinea, Kaiser Wilhelmsland, in den Wäldern des Kani-Gebirges, 23 Dec 1907, *Schlechter 17025* (B barcode B 10 0325314 [image!]; isotype: P [image!]).

11. *Pyramidanthe silvatica* (Diels) Bangkomnate & Chaowasku, **comb. nov.** $\equiv$ *Mitrella silvatica* Diels in Bot. Jahrb. Syst. 52: 183. 1915. – Lectotype (designated by Turner 2018: 577): Papua New Guinea, Etappenberg, 6 Oct 1912, *Ledermann 9058* (B barcode B 10 0325311 [image!]; isoelectotypes: E [image!], K [image!], SING [image!]).

12. *Pyramidanthe tiwiensis* (Jessup & Bygrave) Bangkomnate & Chaowasku, **comb. nov.** $\equiv$ *Mitrella tiwiensis* Jessup & Bygrave, Fl. Australia 2: 447. 2007. – Holotype: Australia, Northern Territory, Bathurst Island, 23 km E Rocky Point, 11 Dec 1991, *Russell-Smith & Brock 8573* (BRI barcode BRI-AQ0621374 [image!]; isotypes: DNA [image!], K [image!], L [image!], MO not seen).

Excluded names

Currently accepted names are indicated in bold italics.

Mitrella aberrans (Maingay ex Hook. f. & Thomson) Bân in Bot. Zhurn. (Moscow & Leningrad) 59: 244. 1974 $\equiv$ *Polyalthia aberrans* Maingay ex Hook. f. & Thomson in Hooker, Fl. Brit. India 1: 67. 1872 $\equiv$ *Sphaerocoryne aberrans* (Maingay ex Hook. f. & Thomson) Ridl. in J. Straits Branch Roy. Asiat. Soc. 75: 8. 1917.

Mitrella mesnyi Bân in Bot. Zhurn. (Moscow & Leningrad) 59: 244. 1974, nom. illeg. superfl. $\equiv$ *Unona mesnyi* Pierre, Fl. Forest. Cochinch.: t. 17. 1881, nom. illeg. superfl. $\equiv$ *Melodorum clavipes* Hance in J. Bot. 15: 328. 1877.

= *Melodorum lefevrei* Baill. in Adansonia 10: 108. 1871, as '*lefevrii*' $\equiv$ *Sphaerocoryne lefevrei* (Baill.) D. M. Johnson & N. A. Murray in Thai Forest Bull., Bot. 49: 170. 2021.

Mitrella touranensis Bân, Fl. Vietnam 1: 190. 2000 $\equiv$ *Sphaerocoryne touranensis* (Bân) I. M. Turner in Gard. Bull. Singapore 70: 685. 2018.

Author contributions

T. C. conceived and coordinated the study and obtained the research grant; A. B. and K. A provided crucial plant specimens; R. B. and A. D performed morphological

examinations; R. B. and T. C. performed molecular phylogenetic analyses; all authors drafted every version of the manuscript.

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Supplemental content online

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Original alignments and alignments for phylogenetic analyses, including binary-coded indels.

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Appendix 1

Specimens for molecular phylogenetic analyses and their GenBank accession numbers. Unavailable sequences are denoted with —; newly generated sequences are denoted with **.

Taxon	Location	Collector and number (herbarium)	matK	ndhF	psbA-trnH	rbcL	trnL-F
<i>Afroguatteria bequaertii</i> (De Wild.) Boutique	Congo	Lejoly 4865 (BR)	KX786588	—	—	KX786627	KX786629
<i>Afroguatteria discostigma</i> (Diels) X. Guo & R. M. K. Saunders	Cameroon	Zenker 3023 (P)	KX786595	—	KX786623	—	KX786635
<i>Artabotrys hexapetalus</i> (L. f.) Bhandari	India	Chatrou 470 (U)	—	EF179284	AY841429	—	EF179317
<i>Artabotrys hexapetalus</i>	cultivated (Utrecht Univ. Bot. Gard., 94GR01614)	Anon. s.n. (U)	AY238962	—	—	AY238953	—
<i>Cleistoclamys kirkii</i> (Benth.) Oliv.	Mozambique	Maurin & al. OM 2339 (no herbarium indicated)	JX517486	—	—	JX572412	—
<i>Cleistoclamys kirkii</i>	Tanzania	Couvreux 58 (WAG)	—	KM924880	KM924981	—	KM924948
<i>Dasymaschalon halabalanum</i> Jongsook & Chaowasku	Thailand	Chaowasku 180 (CMUB)	MT264033	MT264001	MT264009	MT264017	MT264025
<i>Dasymaschalon macrocalyx</i> Finet & Gagnep.	Thailand	Kessler 3199 (L)	FJ743748	EF179290	EF179313	AY841610	AY841688
<i>Desmos goezeanus</i> (F. Muell.) Jessup	Australia	Ford & Cinelli 04780 (BRI)	JQ768572	JQ768607	JQ768651	JQ768691	JQ768732
<i>Desmos</i> sp.	Thailand	Aongyong 33 (CMUB)	OL546467**	OL546483**	OL546494**	OL546510**	OL546526**
<i>Dielsiothamnus divaricatus</i> (Diels) R. E. Fr.	Tanzania	Johnson 1903 (OWU)	EU169692	—	EU169736	EU169759	EU169781
<i>Fissistigma fulgens</i> (Hook. f. & Thomson) Merr.	Thailand	Aongyong & Baka 34 (CMUB)	OL546473**	OL546486**	OL546500**	OL546516**	OL546532**
<i>Fissistigma glaucescens</i> (Hance) Merr.	China	Anon. s.n. [isolate SCBGP353_1] (no herbarium indicated)	AY743482	—	—	AY743444	—
<i>Fissistigma glaucescens</i>	Hong Kong	Law 00/07b (L)	—	—	KP095606	—	AY743463
<i>Fissistigma oblongum</i> (Craib) Merr.	Thailand	Chaowasku 214 (CMUB)	OL546469**	—	OL546496**	OL546512**	OL546528**
<i>Fissistigma polyanthoides</i> (Aug. DC.) Merr.	Thailand	Kessler 3232 (WAG)	JQ768575	JQ768609	JQ768654	JQ768694	JQ768735
<i>Fissistigma rubiginosum</i> (A. DC.) Merr. [accession F. rubiginosum-1]	Thailand	Aongyong & Damrong- wuttitum 35 (CMUB)	OL546470**	—	OL546497**	OL546513**	OL546529**
<i>Fissistigma rubiginosum</i> [accession F. rubiginosum-2]	Thailand	Chaowasku 215 (CMUB)	OL546474**	OL546487**	OL546501**	OL546517**	OL546533**

continued on next page

Taxon	Location	Collector and number (herbarium)	matK	ndhF	psbA-trnH	rbcL	trnL-F
<i>Fissistigma thorelii</i> (Pierre ex Finet & Gagnep.) Merr.	Thailand	Sichaikhan 2 (CMUB)	OL546472**	OL546485**	OL546499**	OL546515**	OL546531**
<i>Fissistigma uonicum</i> (Dunn) Merr.	China	Anon. s.n. [isolate SCBGP360_2] (no herbarium indicated)	KP093872	—	KP095611	—	—
<i>Fissistigma uonicum</i>	Hong Kong	Law & Kendrick 00/05 (L)	—	—	—	AY841617	AY841695
<i>Fissistigma</i> sp.	Vietnam	Nuraliev 2125 (CMUB)	OL546471**	—	OL546498**	OL546514**	OL546530**
<i>Friesodielsia desmoides</i> (Craib) Steenis	Thailand	Kessler 3189 (WAG)	JQ768577	JQ768612	JQ768656	JQ768696	AY841696
<i>Friesodielsia</i> sp.	Thailand	Aongyong 36 (CMUB)	OL546468**	OL546484**	OL546495**	OL546511**	OL546527**
<i>Isolona campanulata</i> Engl. & Diels	cultivated (Utrecht Univ. Bot. Gard., 86GR00240)	Anon. s.n. (U)	AY238963	—	—	AY238954	—
<i>Isolona campanulata</i>	unknown	Chatrou 472 (U)	—	EF179301	DQ125127	—	EF179318
<i>Mitrella</i> cf. <i>beccarii</i> (Scheff.) Diels	Indonesian New Guinea	Utteridge 330 (L)	OL546476**	OL546488**	OL546503**	OL546519**	OL546535**
<i>Mitrella clementis</i> (Merr.) I. M. Turner	Borneo	Ambriansyah & Arifin AA 338 (L)	OL546475**	—	OL546502**	OL546518**	OL546534**
<i>Mitrella elegans</i> (Hook. f. & Thomson) D. M. Johnson & N. A. Murray	Thailand	Aongyong & Baka 37 (CMUB)	OL546479**	OL546490**	OL546506**	OL546522**	OL546538**
<i>Mitrella</i> sp. 1	Papua New Guinea	Takeuchi & al. 14912 (L)	OL546477**	—	OL546504**	OL546520**	OL546536**
<i>Mitrella</i> sp. 2	Indonesian New Guinea	Coode 8031 (L)	OL546478**	OL546489**	OL546505**	OL546521**	OL546537**
<i>Monanthotaxis parvifolia</i> subsp. <i>kenyensis</i> Verdc.	Kenya	Luke 7299 (EA)	KX761312	KX787032	KX786971	KX761343	KX787001
<i>Monanthotaxis whytei</i> (Stapf) Verdc.	cultivated (Utrecht Univ. Bot. Gard.)	Chatrou 475 (U)	EF179278	EF179304	EF179315	AY841635	AY841713
<i>Pyramidanthe prismatica</i> (Hook. f. & Thomson) Merr.	Thailand	Aongyong & Baka 38 (CMUB)	OL546480**	OL546491**	OL546507**	OL546523**	OL546539**
<i>Pyramidanthe</i> sp.	Borneo	Kessler & Arifin PK 2773 (L)	JN175163	—	JN175178	JN175193	JN175208
<i>Sphaerocoryne affinis</i> (Teijsm. & Binn.) Ridl.	cultivated (Bogor Bot. Gard.)	Chaowaska 216 (CMUB)	OL546466**	OL546482**	OL546493**	OL546509**	OL546525**
<i>Sphaerocoryne gracilis</i> (Oliv. ex Engl. & Diels) Verdc.	Kenya	Robertson 7554 (WAG)	EU169688	KM924888	EU169732	EU169755	EU169777
<i>Toussaintia orientalis</i> Verdc.	Tanzania	Johnson 1957 (OWU)	EU169689	EU169710	EU169733	EU169756	EU169778
<i>Uvaria calamistrata</i> Hance	Hong Kong	Law & al. 00/11 (HKU)	FJ743759	KM924889	FJ743797	FJ743831	FJ743866
<i>Uvaria dasoclema</i> L. L. Zhou & al.	Thailand	Damthongdee AD 1 (BKF)	OL546465**	OL546481**	OL546492**	OL546508**	OL546524**