

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

Authors: Bangkomnate, Rattikarn, Damthongdee, Anissara, Baka,  
Abdulromea, Aongyong, Kithisak, and Chaowasku, Tanawat

Source: Willdenowia, 51(3) : 383-394

Published By: Botanic Garden and Botanical Museum Berlin (BGBM)

URL: <https://doi.org/10.3372/wi.51.51306>

---

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/terms-of-use](http://www.bioone.org/terms-of-use).

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

---

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

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

Rattikarn Bangkomnate<sup>1,2</sup>, Anissara Damthongdee<sup>1</sup>, Abdulromea Baka<sup>3</sup>, Kithisak Aongyong<sup>4</sup> & Tanawat Chaowasku<sup>1</sup>

Version of record first published online on 23 December 2021 ahead of inclusion in December 2021 issue.

**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 lectotyped. *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*

**Article history:** Received 2 September 2021; peer-review completed 15 October 2021; received in revised form 29 November 2021; accepted for publication 7 December 2021.

**Citation:** Bangkomnate R., Damthongdee A., Baka A., Aongyong K. & Chaowasku T. 2021: *Pyramidanthe* and *Mitrella* (*Annonaceae*, *Uvarieae*) unified: molecular phylogenetic and morphological congruence, with new combinations in *Pyramidanthe*. – Willdenowia 51: 383–394. <https://doi.org/10.3372/wi.51.51306>

### 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

1 Herbarium, Department of Biology, Faculty of Science, Chiang Mai University, 239 Huay Kaew Rd., Chiang Mai 50200, Thailand.

2 M.Sc. Program in Biology, Graduate School and Faculty of Science, Chiang Mai University, 239 Huay Kaew Rd., Chiang Mai 50200, Thailand.

3 Chanae, Narathiwat 96220, Thailand.

4 Sichon, Nakhon Si Thammarat 80120, Thailand.

Author for correspondence: Tanawat Chaowasku, [tanawat.chaowasku@cmu.ac.th](mailto:tanawat.chaowasku@cmu.ac.th)

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 1000<sup>th</sup> 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)  $\geq 0.95$ , 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*

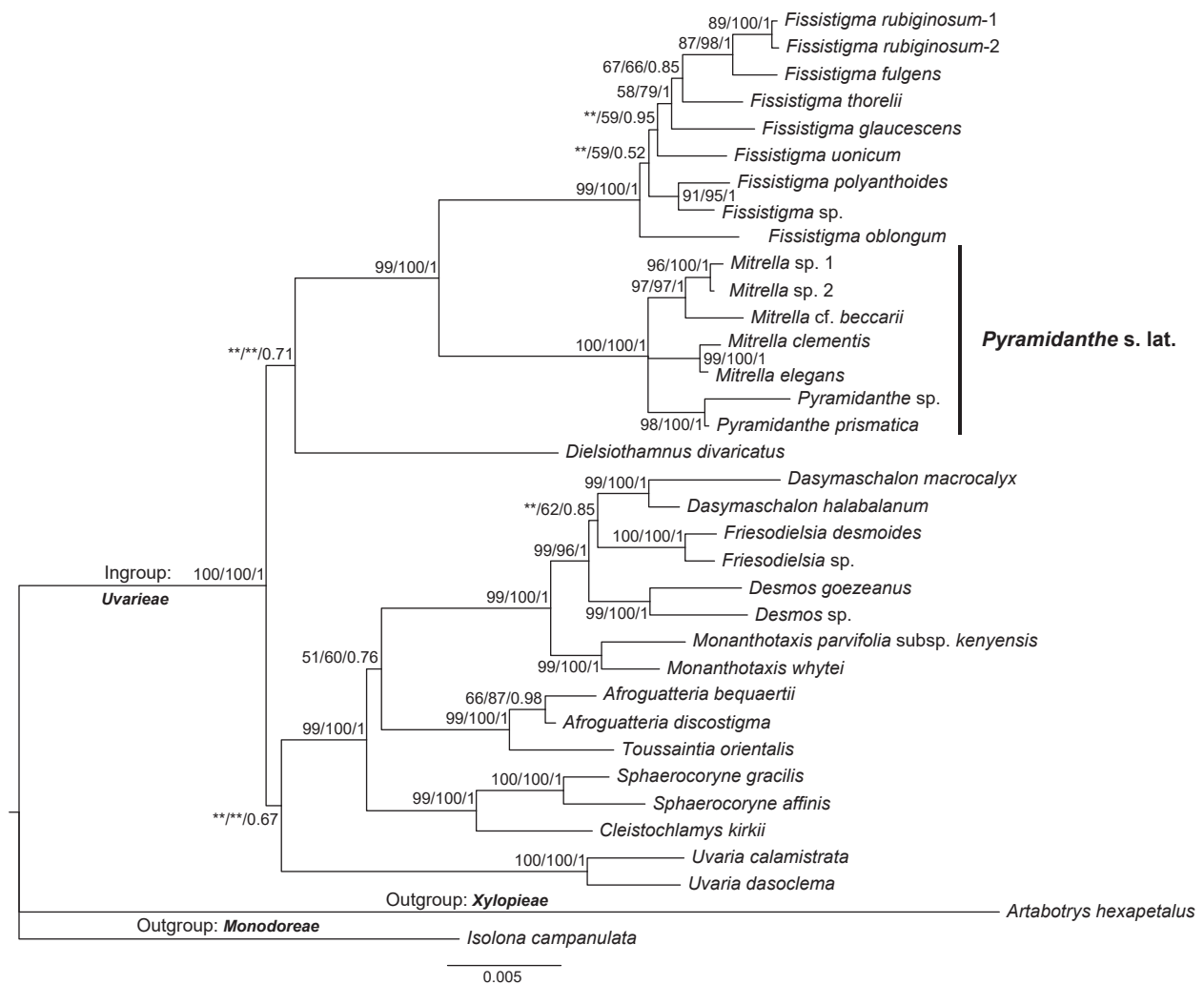


Fig. 1. Phylogram from Bayesian inference, showing relationships within *Uvarieae*. Parsimony symmetric resampling values (SR), maximum likelihood bootstrap values (BS) and Bayesian posterior probabilities (PP) are indicated: SR/BS/PP. \*\* = BS and/or SR < 50%. Scale bar unit = substitutions per site.

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

**Description** — Woody climbers; indumentum of simple hairs. *Leaves* petiolate; petiole often  $\geq$  10 mm long; abaxial leaf surface somewhat glaucous, secondary leaf veins usually indistinct, brochidodromous to brochidodromous-eucamptodromous, tertiary venation reticulate. *In-florescences* axillary (including in axils of fallen leaves), 1-flowered, rarely few-flowered. *Flowers* bisexual, buds  $\pm$  (ob)ovoid-triangular pyramidal to  $\pm$  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,

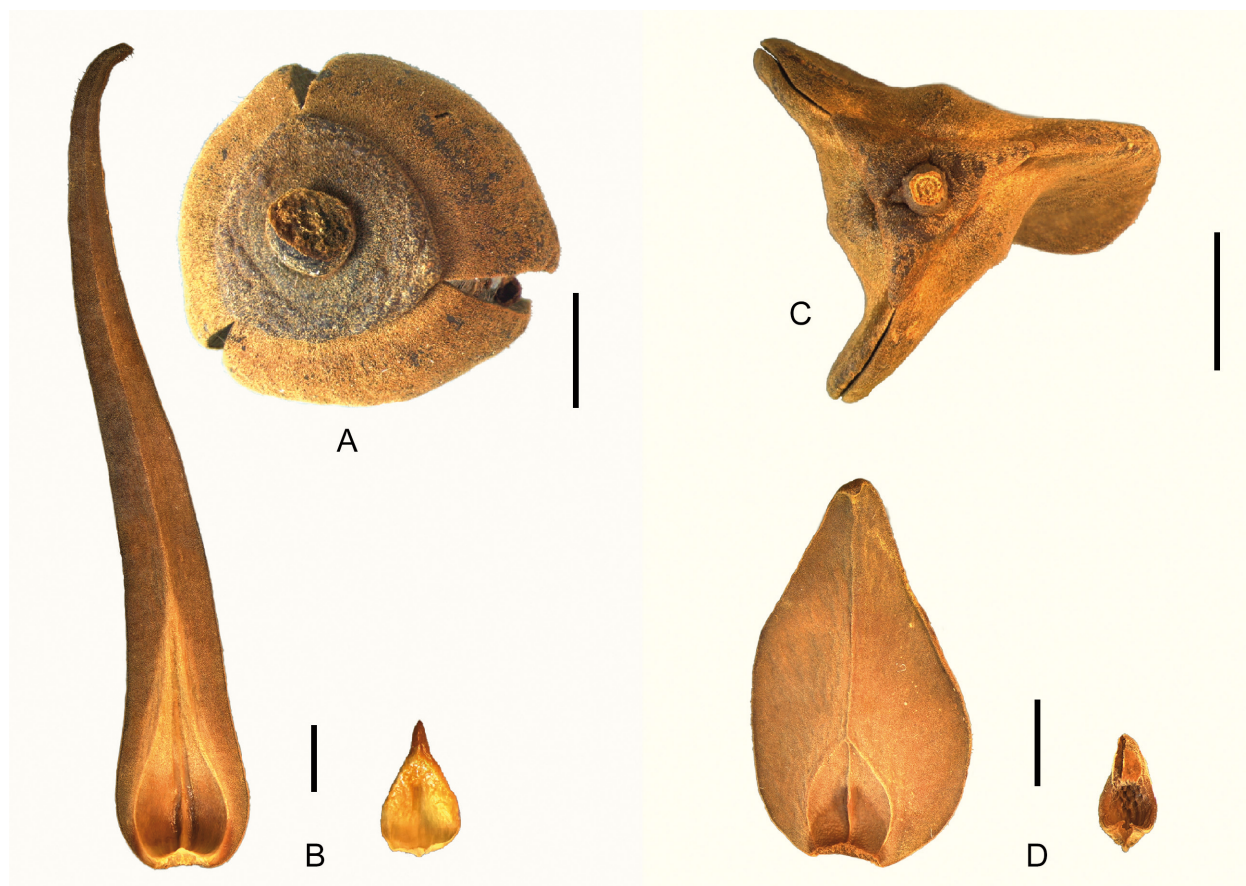


Fig. 2. Sepal and petal morphology of *Pyramidanthe prismatica* (A, B) and *Mitrella elegans* (C, D). – A: back view of flower, showing nearly completely connate sepals with indistinct apex; B: inner side of outer petal (left) with basal excavation and inner side of inner petal (right); C: back view 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

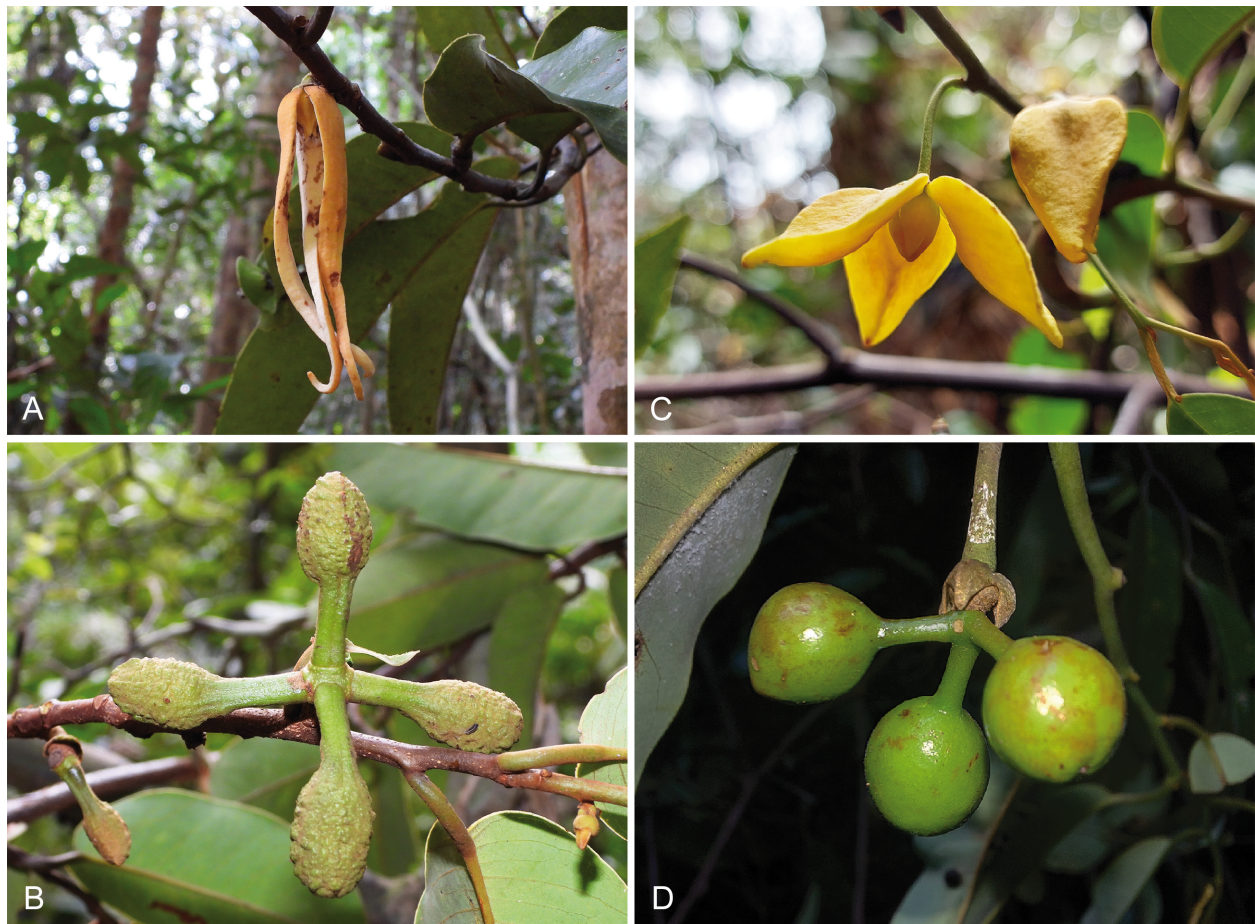


Fig. 3. Flower and fruit morphology of *Pyramidanthe prismatica* (A, B) and *Mitrella elegans* (C, D). – A: mature flower; B: immature fruit with more or less warty monocarps; C: flower bud and mature flower; D: nearly ripe fruit with smooth monocarps. – Photographs by Abdulromea Baka; A, B from Aongyong & 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.** ≡ *Unona kentii* Blume, Bijdr. Fl. Ned. Ind.: 16. 1825 ≡ *Polyalthia kentii* (Blume) Blume, Fl. Javae Anonac. 77. 1830 ≡ *Melodorum kentii* (Blume) Hook. f. & Thomson, Fl. Ind.: 116. 1855 ≡ *Mitrella kentii* (Blume) Miq. in Ann. Mus. Bot. Lugduno-Batavi 2: 39. 1865 ≡ *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.** ≡ *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!]; isolectotypes: K [× 2] [images!]).

**8. *Pyramidanthe mabiformis*** (Griff.) Bangkomnate & Chaowasku, **comb. nov.** ≡ *Uvaria mabiformis* Griff., Not. Pl. Asiat. 4: 709. 1854 ≡ *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-ovate 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 ≡ *Melodorum prismaticum* Hook. f. & Thomson, Fl. Ind.: 121. 1855 ≡ *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!]; isolectotype: 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 ≡ *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.** ≡ *Mitrella schlechteri* Diels in Bot. Jahrb. Syst. 49: 150. 1912 ≡ *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.** ≡ *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!]; isolectotypes: E [image!], K [image!], SING [image!]).

**12. *Pyramidanthe tiwiensis*** (Jessup & Bygrave) Bangkomnate & Chaowasku, **comb. nov.** ≡ *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 ≡ *Polyalthia aberrans* Maingay ex Hook. f. & Thomson in Hooker, Fl. Brit. India 1: 67. 1872 ≡ ***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. ≡ *Unona mesnyi* Pierre, Fl. Forest. Cochinch.: t. 17. 1881, nom. illeg. superfl. ≡ *Melodorum clavipes* Hance in J. Bot. 15: 328. 1877.

= *Melodorum lefevrei* Baill. in Adansonia 10: 108. 1871, as '*lefevrii*' ≡ ***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 ≡ ***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.

## Acknowledgements

We would like to kindly thank the herbaria A, B, BM, BRI, C, CMUB, DNA, E, FI, K, L, NY, P, SING, U and US for the material studied. Geerawit Sichaikhan, Maxim Nuraliev and Pitchayapa Damrongwuttitum provided useful material for molecular phylogenetic analyses. Support from the Graduate School, Chiang Mai University is appreciated. The last author would like to acknowledge the Thailand Science Research and Innovation (TSRI), as well as the National Research Council of Thailand (NRCT) and Office of the Permanent Secretary, Ministry of Higher Education, Science, Research and Innovation for the financial support. Thomas L. P. Couvreur (Pontificia Universidad Católica del Ecuador) and an anonymous reviewer improved an earlier draft of this article.

## References

- Akaike H. 1974: A new look at the statistical model identification. – *IEEE Trans. Automat. Contr.* **19**: 716–723. Crossref.
- Applequist W. L. 2014: Report of the nomenclature committee for vascular plants: 66. – *Taxon* **63**: 1358–1371. Crossref.
- Chaowasku T. 2013: (7) Request for a binding decision on whether *Huberia* DC. (*Melastomataceae*) and *Hubera* Chaowasku (*Annonaceae*) are sufficiently alike to be confused. – *Taxon* **62**: 412–412. Crossref.
- Chaowasku T. 2020: Toward a phylogenetic reclassification of the subfamily *Ambavioideae* (*Annonaceae*): establishment of a new subfamily and a new tribe. – *Acta Bot. Bras.* **34**: 522–529. Crossref.
- Chaowasku T., Aongyong K., Damthongdee A., Jongsook H. & Johnson D. M. 2020: Generic status of *Winitia* (*Annonaceae*, *Miliuseae*) reaffirmed by molecular phylogenetic analysis, including a new species and a new combination from Thailand. – *Eur. J. Taxon.* **659**: 1–23. Crossref.
- Chaowasku T., Damthongdee A., Jongsook H., Ngo D. T., Le H. T., Tran D. M. & Suddee S. 2018a: Enlarging the monotypic *Monocarpieae* (*Annonaceae*, *Malmioideae*): recognition of a second genus from Vietnam informed by morphology and molecular phylogenetics. – *Candollea* **73**: 261–275. Crossref.
- Chaowasku T., Damthongdee A., Jongsook H., Nuraliev M. S., Ngo D. T., Le H. T., Lithanatudom P., Osathanukul M., Deroin T., Xue B. & Wipasa J. 2018b: Genus *Huberanthe* (*Annonaceae*) revisited: erection of *Polyalthiopsis*, a new genus for *H. floribunda*, with a new combination *H. luensis*. – *Ann. Bot. Fenn.* **55**: 121–136. Crossref.
- Chaowasku T., Johnson D. M., van der Ham R. W. J. M. & Chatrou L. W. 2012: Characterization of *Hubera* (*Annonaceae*), a new genus segregated from *Polyalthia* and allied to *Miliusa*. – *Phytotaxa* **69**: 33–56. Crossref.
- Chaowasku T., Johnson D. M., van der Ham R. W. J. M. & Chatrou L. W. 2015: *Huberanthe*, a replacement name for *Hubera* (*Annonaceae*: *Malmioideae*: *Miliuseae*). – *Kew Bull.* **70**: article 23. Crossref.
- Chaowasku T., van der Ham R. W. J. M. & Chatrou L. W. 2013: Integrative systematics supports the establishment of *Winitia*, a new genus of *Annonaceae* (*Malmioideae*, *Miliuseae*) allied to *Stelechocarpus* and *Sageraea*. – *Syst. Biodivers.* **11**: 195–207. Crossref.
- Chatrou L. W., Pirie M. D., Erkens R. H. J., Couvreur T. L. P., Neubig K. M., Abbott J. R., Mols J. B., Maas J. W., Saunders R. M. K & Chase M. W. 2012: A new subfamilial and tribal classification of the pantropical flowering plant family *Annonaceae* informed by molecular phylogenetics. – *Bot. J. Linn. Soc.* **169**: 5–40. Crossref.
- Chatrou L. W., Turner I. M., Klitgaard B. B., Maas P. J. M. & Utteridge T. M. A. 2018: A linear sequence to facilitate curation of herbarium specimens of *Annonaceae*. – *Kew Bull.* **73**: article 39. Crossref.
- Chernomor O., von Haeseler A. & Minh B. Q. 2016: Terrace aware data structure for phylogenomic inference from supermatrices. – *Syst. Biol.* **65**: 997–1008. Crossref.
- Couvreur T. L. P., Helmstetter A. J., Koenen E. J. M., Bethune K., Brandão R. D., Little S. A., Sauquet H. & Erkens R. H. J. 2019: Phylogenomics of the major tropical plant family *Annonaceae* using targeted enrichment of nuclear genes. – *Frontiers Pl. Sci.* **9**: article 1941. Crossref.
- Couvreur T. L. P., Niangadouma R., Sonké B. & Sauquet H. 2015: *Sirdavidia*, an extraordinary new genus of *Annonaceae* from Gabon. – *PhytoKeys*. **46**: 1–19. Crossref.
- Couvreur T. L. P., van der Ham R. W. J. M., Mbele Y. M., Mbago F. M. & Johnson D. M. 2009: Molecular and morphological characterization of a new monotypic genus of *Annonaceae*, *Mwasumbia* from Tanzania. – *Syst. Bot.* **34**: 266–276. Crossref.
- Damthongdee A., Aongyong K. & Chaowasku T. 2021: *Orophea sichaikhani* (*Annonaceae*), a new species from southern Thailand, with a key to the species of *Orophea* in Thailand and notes on some species. – *Pl. Ecol. Evol.* **154**: 307–315. Crossref.
- Diels L. 1912: Beiträge zur Flora von Papuasien. Serie I. 8. Die Anonaceen von Papuasien. – *Bot. Jahrb. Syst.* **49**: 113–167.
- Doyle J. A., Sauquet H., Scharaschkin T. & Le Thomas A. 2004: Phylogeny, molecular and fossil dating, and biogeographic history of *Annonaceae* and *Myristi-*

- caceae* (*Magnoliales*). – *Int. J. Plant Sci.* **165**: S55–S67. Crossref.
- Felsenstein J. 1985: Confidence limits on phylogenies: an approach using the bootstrap. – *Evolution* **39**: 783–791. Crossref.
- Goloboff P. A. & Catalano S. A. 2016: TNT version 1.5, including a full implementation of phylogenetic morphometrics. – *Cladistics* **32**: 221–238. Crossref.
- Goloboff P. A., Farris J. S., Källersjö M., Oxelman B., Ramírez M. J. & Szumik C. A. 2003: Improvements to resampling measures of group support. – *Cladistics* **19**: 324–332. Crossref.
- Guo X., Hoekstra P. H., Tang C. C., Thomas D. C., Wieringa J. J., Chatrou L. W. & Saunders R. M. K. 2017a: Cutting up the climbers: evidence for extensive polyphyly in *Friesodielsia* (*Annonaceae*) necessitates generic realignment across the tribe *Uvarieae*. – *Taxon* **66**: 3–19. Crossref.
- Guo X., Tang C. C., Thomas D. C., Couvreur T. L. P. & Saunders R. M. K. 2017b: A mega-phylogeny of the *Annonaceae*: taxonomic placement of five enigmatic genera and support for a new tribe, *Phoenicantheae*. – *Sci. Rep.* **7**: article 7323. Crossref.
- Guo X., Wang J., Xue B., Thomas D. C., Su Y. C. F., Tan Y. H. & Saunders R. M. K. 2014: Reassessing the taxonomic status of two enigmatic *Desmos* species (*Annonaceae*): morphological and molecular phylogenetic support for a new genus, *Wangia*. – *J. Syst. Evol.* **52**: 1–15. Crossref.
- Hasegawa M., Kishino H. & Yano T. 1985: Dating of the human-ape splitting by a molecular clock of mitochondrial DNA. – *J. Molec. Evol.* **22**: 160–174. Crossref.
- Johnson D. M., Bunchalee P., Chalermglin P., Chantaranonthai P., Leeratiwong C., Murray N. A., Saunders R. M. K., Sirichamorn Y., Su Y. C. F. & Sutthisaksothon P. 2021: Additions to *Annonaceae* in the Flora of Thailand. – *Thai Forest Bull., Bot.* **49**: 163–172. Crossref.
- Katoh K., Misawa K., Kuma K. & Miyata T. 2002: MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. – *Nucl. Acids Res.* **30**: 3059–3066. Crossref.
- Katoh K., Rozewicki J. & Yamada K. D. 2019: MAFFT online service: multiple sequence alignment, interactive sequence choice and visualization. – *Briefings Bioinformatics* **20**: 1160–1166. Crossref.
- Kessler P. J. A., Jessup L. W. & Kruijer J. D. 1995: Provisional checklist of the Asiatic-Australian species of *Annonaceae*. – Serdang: The Herbarium, Universiti Pertanian Malaysia.
- Merrill E. D. 1919: On the application of the generic name *Melodorum* of Loureiro. – *Philipp. J. Sci.* **15**: 125–137.
- Miller M. A., Pfeiffer W. & Schwartz T. 2010: Creating the CIPRES Science Gateway for inference of large phylogenetic trees. – Pp. 45–52 in: Gateway Computing Environments Workshop (GCE). – Piscataway: IEEE. Crossref.
- Minh B. Q., Schmidt H. A., Chernomor O., Schrempf D., Woodhams M. D., von Haeseler A. & Lanfear R. 2020: IQ-TREE 2: new models and efficient methods for phylogenetic inference in the genomic era. – *Molec. Biol. Evol.* **37**: 1530–1534. Crossref.
- Miquel F. A. W. 1865: *Anonaceae* Archipelagi indici. – *Ann. Mus. Bot. Lugduno-Batavi* **2**: 1–45.
- Mols J. B., Kessler P. J. A., Rogstad S. H. & Saunders R. M. K. 2008: Reassignment of six *Polyalthia* species to the new genus *Maasia* (*Annonaceae*): molecular and morphological congruence. – *Syst. Bot.* **33**: 490–494. Crossref.
- Photikwan E., Damthongdee A., Jongsook H. & Chaowasku T. 2021: *Artabotrys angustipetalus* (*Annonaceae*), a new species from Thailand, including a plastid phylogeny and character evolutionary analyses of thorn occurrence in *Artabotrys*. – *Willdenowia* **51**: 69–82. Crossref.
- Pirie M. D., Chatrou L. W., Mols J. B., Erkens R. H. J. & Oosterhof J. 2006: ‘Andean-centred’ genera in the short-branch clade of *Annonaceae*: testing biogeographical hypotheses using phylogeny reconstruction and molecular dating. – *J. Biogeogr.* **33**: 31–46. Crossref.
- Posada D. & Crandall K. A. 1998: MODELTEST: testing the model of DNA substitution. – *Bioinformatics* **14**: 817–818. Crossref.
- Quattrocchi U. 2000: CRC world dictionary of plant names: common names, scientific names, eponyms, synonyms, and etymology **3** (M–Q). – Boca Raton, London, New York, Washington D.C.: CRC Press.
- Rambaut A., Suchard M. & Drummond A. 2013: Tracer, version 1.6. – Published at <http://tree.bio.ed.ac.uk/software/tracer/> [accessed 18 May 2017].
- 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. Crossref.
- Simmons M. P. 2004: Independence of alignment and tree search. – *Molec. Phylogen. Evol.* **31**: 874–879. Crossref.
- Simmons M. P. & Ochoterena H. 2000: Gaps as characters in sequence-based phylogenetic analyses. – *Syst. Biol.* **49**: 369–381. Crossref.
- Sinclair J. 1955: A revision of the Malayan *Annonaceae*. – *Gard. Bull. Singapore.* **14**: 149–516.
- Sinclair J. 1956: Miscellaneous notes on *Annonaceae*. – *Gard. Bull. Singapore* **15**: 14–17.
- Staden R., Beal K. F. & Bonfield J. K. 2000: The Staden Package, 1998. – Pp. 115–130 in: Misener S. & Krawetz S. A. (ed.), *Bioinformatics methods and protocols*. – Totowa: Humana Press. [= *Meth. Molec. Biol.* **132**]. Crossref.

- Surveswaran S., Wang R. J., Su Y. C. F. & Saunders R. M. K. 2010: Generic delimitation and historical biogeography in the early-divergent 'ambavioid' lineage of *Annonaceae*: *Cananga*, *Cyathocalyx* and *Drepananthis*. – *Taxon* **59**: 1721–1734. Crossref.
- Tavaré S. 1986: Some probabilistic and statistical problems in the analysis of DNA sequences. – *Lectures Math. Life Sci.* **17**: 57–86.
- Turland N. J., Wiersema J. H., Barrie F. R., Greuter W., Hawksworth D. L., Herendeen P. S., Knapp S., Kuster W.-H., Li D.-Z., Marhold K., May T. W., McNeill J., Monro A. M., Prado J., Price M. J. & Smith G. F. (ed.) 2018: International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. – Glashütten: Koeltz Botanical Books. [= *Regnum Veg.* **159**]. Crossref.
- Turner I. M. 2009: New species and nomenclatural combinations in *Polyalthia*, *Meiogyne* and *Mitrella* (*Annonaceae*) from Borneo. – *Malayan Nat. J.* **61**: 267–276. Crossref.
- Turner I. M. 2011: A catalogue of the *Annonaceae* of Borneo. – *Phytotaxa* **36**: 1–120. Crossref.
- Turner I. M. 2012: *Annonaceae* of Borneo: a review of the climbing species. – *Gard. Bull. Singapore.* **64**: 371–479.
- Turner I. M. 2018: *Annonaceae* of the Asia-Pacific region: names, types and distributions. – *Gard. Bull. Singapore* **70**: 409–744. Crossref.
- van Heusden E. C. H. 1992: Flowers of *Annonaceae*: morphology, classification, and evolution. – *Blumea, Suppl.* **7**: 1–218.
- van Setten A. K. & Koek-Noorman J. 1992: Fruits and seeds of *Annonaceae*: morphology and its significance for classification and identification. – *Biblioth. Bot.* **142**: 1–101.
- Wiens J. J. 1998: Combining data sets with different phylogenetic histories. – *Syst. Biol.* **47**: 568–581. Crossref.
- Xue B., Su Y. C. F., Mols J. B., Kessler P. J. A. & Saunders R. M. K. 2011: Further fragmentation of the polyphyletic genus *Polyalthia* (*Annonaceae*): molecular phylogenetic support for a broader delimitation of *Marsypopetalum*. – *Syst. Biodivers.* **9**: 17–26. Crossref.
- Xue B., Su Y. C. F., Thomas D. C. & Saunders R. M. K. 2012: Pruning the polyphyletic genus *Polyalthia* (*Annonaceae*) and resurrecting the genus *Monoon*. – *Taxon* **61**: 1021–1039. Crossref.
- Xue B., Tan Y. H., Thomas D. C., Chaowasku T., Hou X. L. & Saunders R. M. K. 2018: A new *Annonaceae* genus, *Wuodendron*, provides support for a post-boreotropical origin of the Asian-neotropical disjunction in the tribe *Miliuseae*. – *Taxon* **67**: 250–266. Crossref.
- Xue B., Thomas D. C., Chaowasku T., Johnson D. M. & Saunders R. M. K. 2014: Molecular phylogenetic support for the taxonomic merger of *Fitzalania* and *Meiogyne* (*Annonaceae*): new nomenclatural combinations under the conserved name *Meiogyne*. – *Syst. Bot.* **39**: 396–404. Crossref.
- Yang Z. & Rannala B. 1997: Bayesian phylogenetic inference using DNA sequences: a Markov Chain Monte Carlo method. – *Molec. Biol. Evol.* **14**: 717–724. Crossref.
- Zhou L., Su Y. C. F., Chalermglin P. & Saunders R. M. K. 2010: Molecular phylogenetics of *Uvaria* (*Annonaceae*): relationships with *Balonga*, *Dasoclema* and Australian species of *Melodorum*. – *Bot. J. Linn. Soc.* **163**: 33–43. Crossref.
- Zhou L., Su Y. C. F. & Saunders R. M. K. 2009: Molecular phylogenetic support for a broader delimitation of *Uvaria* (*Annonaceae*), inclusive of *Anomianthus*, *Cyathostemma*, *Ellipeia*, *Ellipeiopsis* and *Rauwenhoffia*. – *Syst. Biodivers.* **7**: 249–258. Crossref.

### Supplemental content online

See <https://doi.org/10.3372/wi.51.51306>

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

### Willdenowia

Open-access online edition [bioone.org/journals/willdenowia](http://bioone.org/journals/willdenowia)



Online ISSN 1868-6397 · Print ISSN 0511-9618 · 2020 Journal Impact Factor 0.985

Published by the Botanic Garden and Botanical Museum Berlin, Freie Universität Berlin

© 2021 The Authors · This open-access article is distributed under the CC BY 4.0 licence

## 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>Cleistocharmays kirkii</i> (Benth.) Oliv.	Mozambique	Maurin & al. OM 2339 (no herbarium indicated)	JX517486	—	—	JX572412	—
<i>Cleistocharmays kirkii</i>	Tanzania	Couvreur 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>Dielsiothamus 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>Monanithotaxis parvifolia</i> subsp. <i>kenyensis</i> Verdc.	Kenya	Luke 7299 (EA)	KX761312	KX787032	KX786971	KX761343	KX787001
<i>Monanithotaxis 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**