R e s e a r c h   a r t i c l e

Generic status of *Winitia* (Annonaceae, Miliuseae) reaffirmed by molecular phylogenetic analysis, including a new species and a new combination from Thailand

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Abstract. The generic status of *Winitia* Chaowasku (Annonaceae Juss., Miliuseae Hook.f. & Thomson) is reaffirmed by an extensive phylogenetic reconstruction using seven plastome regions (*mat*K, *ndh*F, *rbc*L, *ycf*1 exons; *trn*L intron; *psb*A-*trn*H, *trn*L-*trn*F intergenic spacers) and including, among others, seven accessions of *Winitia* plus two accessions of its sister group, *Stelechocarpus* Hook.f. & Thomson. The results disclosed a maximally supported clade of *Winitia*, as well as of *Stelechocarpus*. The sister relationship of the two genera is still rather poorly supported and the branch uniting them is very short, whereas the branches leading to *Winitia* and to *Stelechocarpus* are relatively long, corresponding to their considerable morphological differences. Additionally, in Miliuseae there is a particular indel of eight continuous base pairs in the *trn*L-*trn*F intergenic spacer potentially diagnostic for generic discrimination, i.e., members in the same genus possess the same indel structure (absence or presence of a gap), and this indel differentiates *Winitia* from *Stelechocarpus*. *Winitia cauliflora* (Scheff.) Chaowasku appears polyphyletic and *Winitia longipes* (Craib) Chaowasku & Aongyong comb. nov. based on *Stelechocarpus longipes* Craib is consequently proposed. Furthermore, our phylogenetic data support a new species, *Winitia thailandana* Chaowasku & Aongyong sp. nov. from southern Thailand, which is described and illustrated. A key to genera in the sageraeoid clade (*Sageraea-Winitia-Stelechocarpus*) and a key to the four species of *Winitia* are provided.

Keywords. Identification key, Malmeoideae, phylogenetics, systematics, taxonomy.

Introduction

Annonaceae Juss. are a large pantropical family of flowering plants prominent in lowland rainforests and consisting of ca 2430 species (Couvreur *et al.* 2019) in 110 genera (Guo *et al.* 2017b; Chaowasku *et al.* 2018a, 2018b; Xue *et al.* 2018). Infrafamilial classifications and generic realignments of the family have been stabilized lately with the help of molecular phylogenetics (e.g., Zhou *et al.* 2009, 2010; Chatrou *et al.* 2012; Chaowasku *et al.* 2012; Xue *et al.* 2012; Guo *et al.* 2017a, 2017b). Additionally, in combination with thorough morphological examinations, a number of previously undescribed genera have been established in the past 12 years (Mols *et al.* 2008; Couvreur *et al.* 2009, 2015; Chaowasku *et al.* 2012, 2013, 2015, 2018a, 2018b; Guo *et al.* 2014; Xue *et al.* 2018). One of these is the genus *Winitia* Chaowasku (Chaowasku *et al.* 2013), which is closely allied to the monotypic genus *Stelechocarpus* Hook.f. & Thomson (Hooker & Thomson 1855) and the genus *Sageraea* Dalzell (Dalzell 1851) composed of nine species (van Heusden 1997). Despite a rather poor support for the sister relationship of *Winitia* and *Stelechocarpus* (Chaowasku *et al.* 2013), the former was reduced into synonymy of the latter by Turner (2016).

Winitia can be recognized by a suite of morphological traits, e.g., monoecious habit; conspicuously thick, fleshy, and ± rose-colored petals; multicolumellar stigmas, i.e., each stigma with multiple columnar lobes; rather massive, ± blackish brown, and multi-seeded monocarps as well as several palynological features (Chaowasku *et al.* 2013). The genus is distributed from southern Thailand and southern Vietnam through the Malay Peninsula to Sumatra and Borneo, and currently contains two species: the widespread *W. cauliflora* (Scheff.) Chaowasku (Chaowasku *et al.* 2013; basionym: Scheffer 1881) and the type species *W. expansa* Chaowasku (Chaowasku *et al.* 2013) endemic to Thailand; so far, only a single accession of each species has been included in phylogenetic analyses (Chaowasku *et al.* 2013: accession of *W. cauliflora* was from cultivation in Bogor Botanical Garden, Indonesia).

In Gardner *et al.* (2015: 174) there are photographs of *Winitia* sp., which occurs in Surat Thani Province of Thailand and superficially resembles *W. expansa*, especially in the inner petals spreading at anthesis, but some features are different. Further, *W. cauliflora* occurring in Thailand has never been included in any phylogenetic inferences. The aims of the present study are, therefore, to (1) elucidate the phylogenetic position of *Winitia* sp. from Surat Thani Province and *W. cauliflora* accessions from Thailand and (2) determine their taxonomic status. The additional accessions will also provide a test of the monophyly of the genus.

Material and methods

Taxon and character samplings

Fifty-six accessions comprised the ingroup with representatives of all currently recognized tribes of the Annonaceae subfamily Malmeoideae Chatrou, Pirie, Erkens & Couvreur except Piptostigmateae Chatrou & R.M.K.Saunders (*Mwasumbia alba* Couvreur & D.M.Johnson [Couvreur *et al.* 2009] and *Brieya fasciculata* De Wild. [De Wildeman 1914]), which were assigned as outgroups, and Annickieae Couvreur. The Malmeoideae minus Piptostigmateae and Annickieae have been previously shown to constitute a strongly supported clade (e.g., Guo *et al.* 2017b). For Miliuseae Hook.f. & Thomson, the largest tribe of Malmeoideae, representatives of all genera currently recognized were included. Seven accessions of *Winitia* were included: two accessions of *Winitia* sp. (= *Winitia* aff. *expansa*) from Surat Thani Prov., Thailand, one accession of *W. expansa* (endemic to Thailand) and four accessions of *W. cauliflora* (two from Nakhon Si Thammarat Prov., Thailand, another two from cultivation in Bogor Botanical Garden, Indonesia), together with two accessions of *Stelechocarpus burahol* (Blume) Hook.f. & Thomson (Hooker & Thomson 1855; basionym: Blume 1825), the sister group of *Winitia*, and two accessions of *Sageraea*, another genus closely allied to *Winitia*. Appendix 1 shows voucher information of the 58 accessions. Seven plastome regions were used in this study; they were composed of four exons

(*mat*K, *ndh*F, *rbc*L, and *ycf*1), one intron (*trn*L), and two intergenic spacers (*psb*A-*trn*H, *trn*L-*trn*F). The *ycf*1 sequences of the outgroups plus *Monocarpia euneura* Miq. (Miquel 1865) were not available.

DNA extraction, amplification and sequencing

All methods used for DNA extraction, amplification, and sequencing in the present study were the same as those described in Chaowasku *et al.* (2018a), with the same primer sequences as used in Chaowasku *et al.* (2012) except for the *psb*A-*trn*H intergenic spacer, which used Fw-GTTATGCATGAACGTAATGCTC (Sang *et al.* 1997) and Rv-CGCGCATGGTGGATTCACAATCC (Tate & Simpson 2003).

Phylogenetic analyses

Sequences were edited using the Staden package (Staden *et al.* 2000; available from http://staden.sourceforge.net/) and subsequently aligned by Multiple Sequence Comparison by Log-Expectation (MUSCLE; Edgar 2004) in MEGA7 (Kumar *et al.* 2016). The alignments were then manually optimized on the basis of homology assessment using the similarity criterion (Simmons 2004). A total of 7026 nucleotide plus nine non-autapomorphic indel characters were included. Indel coding followed the simple method of Simmons & Ochoterena (2000). An inversion of 15 continuous nucleotides in the *psb*A-*trn*H intergenic spacer was observed in some sequences and changed to its reverse complement to be homologically alignable to the remaining sequences, following Pirie *et al.* (2006). Parsimony analysis was carried out in TNT ver. 1.5 (Goloboff & Catalano 2016). All characters were equally weighted and unordered. Incongruence among regions was evaluated by individually analyzing each region to see if there was any significant conflict in clade support (e.g., Wiens 1998). Multiple 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 measured by symmetric resampling (SR; Goloboff *et al.* 2003). A default change probability was used. One hundred thousand replicates were run, each with four replicates of random sequence addition, saving four trees per replicate. A clade with SR ≥ 85%, 70–84% or 50–69% was regarded as strongly, moderately or weakly supported, respectively.

Maximum likelihood analysis was accomplished in IQ-TREE ver. 1.6.10 (Nguyen *et al.* 2015) using partition models (Chernomor *et al.* 2016) employed under the "-spp" command, whereas Bayesian Markov chain Monte Carlo (MCMC; Yang & Rannala 1997) phylogenetic analysis was implemented in MrBayes ver. 3.2.6 (Ronquist *et al.* 2012). Both analytical methods were performed via the CIPRES Science Gateway ver. 3.3 (Miller *et al.* 2010). The data matrix was divided into seven partitions based on DNA region identity (the *trn*L intron and the adjacent *trn*L-*trn*F intergenic spacer were united as a single partition) plus a binary indel-coded partition. The most suitable model of sequence evolution for each DNA partition was chosen by Akaike Information Criterion (AIC) 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 chosen for five partitions (*mat*K, *ndh*F, *rbc*L, *trn*LF [= *trn*L intron + *trn*L-*trn*F intergenic spacer] and *ycf*1) and the Hasegawa-Kishino-Yano (HKY; Hasegawa *et al.* 1985) substitution model with a gamma distribution for among-site rate variation was chosen for the remaining partition (*psb*A-*trn*H).

In the maximum likelihood analysis, the model "JC2+FQ+ASC" was selected by corrected AIC scores for the binary indel partition. Clade support was evaluated by non-parametric bootstrap resampling method (BS; Felsenstein 1985) with 2000 replicates. A clade with BS ≥ 85%, 70–84% or 50–69% was regarded as strongly, moderately or weakly supported, respectively. In the Bayesian analysis, the "coding=variable" setting was chosen for the binary indel partition, which was employed with a simple F81-like model without a gamma distribution for among-site rate variation. Three independent analyses, each using four MCMC chains, were simultaneously run; 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 assessed by checking the standard deviation of split frequencies of the runs with values < 0.01 interpreted as indicating a good convergence and by checking for adequate effective sample sizes (ESS > 200) using Tracer ver. 1.6 (Rambaut *et al.* 2013). The first 25% of all trees sampled were removed as burn-in, and the 50% majority-rule consensus tree was constructed from the remaining trees. A clade with posterior probabilities (PP) ≥ 0.95, 0.9–0.94 or 0.5–0.89 was regarded as strongly supported, weakly supported or unsupported, respectively.

Morphology

The indumentum terminology used followed Hewson (1988). When there was a single observation or measurement, the word 'circa' (ca) was added before. Appendix 2 indicates a list of ten specimens morphologically studied.

Fig. 1. Phylogram derived from maximum likelihood analysis, with support values shown: SR/BS/PP. Maximally supported clades are represented by thick branches without support values shown; strongly supported clades are represented by thick branches with support values shown; branches without support values shown signify SR < 50%, BS < 50%, and PP < 0.85. ** signifies SR/BS < 50%. Scale bar unit = substitutions per site. MAL. = Malmeeae; MON. = Monocarpieae.

Results

Phylogenetic analyses

There was no strong topological conflict (SR ≥ 85%) in the analysis of each plastome region. The parsimony analysis resulted in 188 most parsimonious trees with 2258 steps. The consistency and retention indices (CI and RI) were 0.74 and 0.71, respectively. As depicted in Fig. 1, the ingroup and tribe Miliuseae received maximum support. In Miliuseae, three genera (*Sageraea*, *Stelechocarpus*, and *Winitia*) constituted the sageraeoid clade, with each genus maximally supported for its monophyly. The sageraeoid clade received moderate to strong support (SR 91%, BS 84%, PP 1), with *Stelechocarpus* and *Winitia* being weakly to moderately supported (SR 79%, BS 75%, PP 0.9) as sister groups. In *Winitia*, there was a trichotomy consisting of (1) a strongly supported clade (SR 96%, BS 99%, PP 1) of two accessions of *Winitia* aff. *expansa* from Surat Thani Prov., Thailand, (2) a strongly supported clade (SR 98%, BS 98%, PP 1) comprising *W. cauliflora*-1 and *W. cauliflora*-2, each from a different individual cultivated in Bogor Botanical Garden, Indonesia, and (3) a weakly supported clade (SR 69%, BS 64%, PP 0.93) composed of *W. expansa* plus two accessions of *W. cauliflora* from Nakhon Si Thammarat Prov., Thailand (*W. cauliflora*-3 and *W. cauliflora*-4); these Thai accessions of *W. cauliflora* were retrieved as a strongly supported clade (SR 99%, BS 100%, PP 1).

Upon a closer observation at part of the multiple sequence alignment of the *trn*L-*trn*F intergenic spacer, it is clear that *Winitia* and *Stelechocarpus* differ from each other by having dissimilar indel structures: absence of a gap in *Winitia* vs presence of a gap in *Stelechocarpus* (Fig. 2). This eight-base-pair indel is one of the nine indel-coded characters included in the binary indel partition.
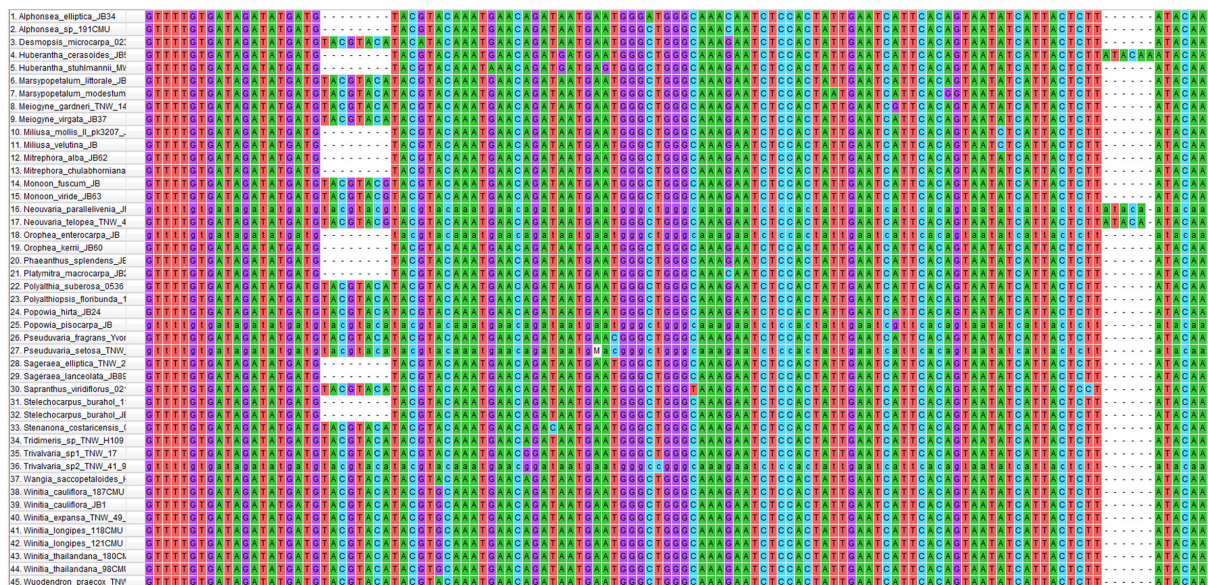

Fig. 2. Part of multiple sequence alignment of *trn*L-*trn*F intergenic spacer, showing an indel (arrow) potentially diagnostic for generic discrimination in Miliuseae.

Taxonomy

<div align="center">

Order Magnoliales Juss. ex Bercht. & J.Presl
Family Annonaceae Juss., nom. cons.
Tribe Miliuseae Hook.f. & Thomson
Genus *Winitia* Chaowasku

Winitia longipes (Craib) Chaowasku & Aongyong comb. nov.
urn:lsid:ipni.org:names:77209777-1
Fig. 3B, D, F, H

</div>

≡ *Stelechocarpus longipes* Craib, *The Journal of the Natural History Society of Siam* 6: 43 (Craib 1923).
  Type: THAILAND · Khao Rum [Nakhon Si Thammarat Prov.]; fl; *Native Collector s.n.* (Herb. Eryl
  Smith 643); holotype: K[K000382080]; isotype: BK.

Notes

From Fig. 1, it is apparent that the four accessions of *W. cauliflora* did not form a clade. There are two strongly supported clades of *W. cauliflora*: one consisting of *Winitia cauliflora*-1 and *Winitia cauliflora*-2, both cultivated in Bogor Botanical Garden, Indonesia, and another comprising *Winitia cauliflora*-3 and *Winitia cauliflora*-4, both from Nakhon Si Thammarat Prov., Thailand. The latter clade is the sister group of *W. expansa* endemic to Phatthalung Prov. of Thailand, though with only weak support. According to van Heusden (1995), the type of *Sageraea cauliflora* Scheff., which is the basionym of *W. cauliflora*, was from cultivation in Bogor Botanical Garden, Indonesia (Cult. Hort. Bog. IV-H-58, origin: Indonesia, Sumatra, Prov. Lampong). The samples *Winitia cauliflora*-1 and *Winitia cauliflora*-2 were collected from individual X-F-96 and individual XV-A-196, respectively, whereas the living individual IV-H-58 could not be found, probably this individual has died. The morphology of *Winitia cauliflora*-1 and *Winitia cauliflora*-2 is very much in agreement with that of the type specimens (Scheffer 1881; neotype: L [L 0038174] and possible isoneotype: L [L 0038175]), but is different from that of *Winitia cauliflora*-3 and *Winitia cauliflora*-4 in several respects, i.e., petal size and shape, and stamen and stigma morphology (Table 1, Fig. 3). On the basis of combined molecular phylogenetic and morphological evidence, *Winitia cauliflora*-3 and *Winitia cauliflora*-4 should be classified in a species distinct from *W. cauliflora*. The name *Stelechocarpus longipes* Craib (Craib 1923) is available and its type specimens, which were also collected in Nakhon Si Thammarat Prov., Thailand (holotype: http://specimens.kew.org/herbarium/K000382080), is morphologically similar to *Winitia cauliflora*-3 and *Winitia cauliflora*-4 regarding leaves, inflorescences, and flowers. Therefore, a new combination in *Winitia* for *Stelechocarpus longipes* is made. It should be noted that although the name *Stelechocarpus nitidus* King (King 1892) is older, its type specimens collected from Perak, Malay Peninsula (lectotype: http://specimens.kew.org/herbarium/K000382081) exhibit petals that are similar in size and shape to those of *Winitia cauliflora*-1 and *Winitia cauliflora*-2 (Table 1, Fig. 3A); hence, for now we still consider it as a junior synonym of *W. cauliflora* until more evidence is obtained.

On the basis of personal observations by the second author, *W. longipes* is generally found near streams. During monsoon seasons, the areas where this species occurs are shortly flooded, and it is possible that the ripe monocarps fallen on the ground are taken away by the water current. Sometimes the seeds are found germinated despite still being partially covered by the pericarp. *Winitia longipes* is widespread in Nakhon Si Thammarat and neighboring provinces where several protected areas are located, but many individuals do occur outside the protected areas; these unprotected forests diminish nearly every single day due mainly to agricultural expansion (pers. obs.). Therefore, we recommend that its conservation status based on IUCN (2012) be assessed as "Near Threatened (NT)".
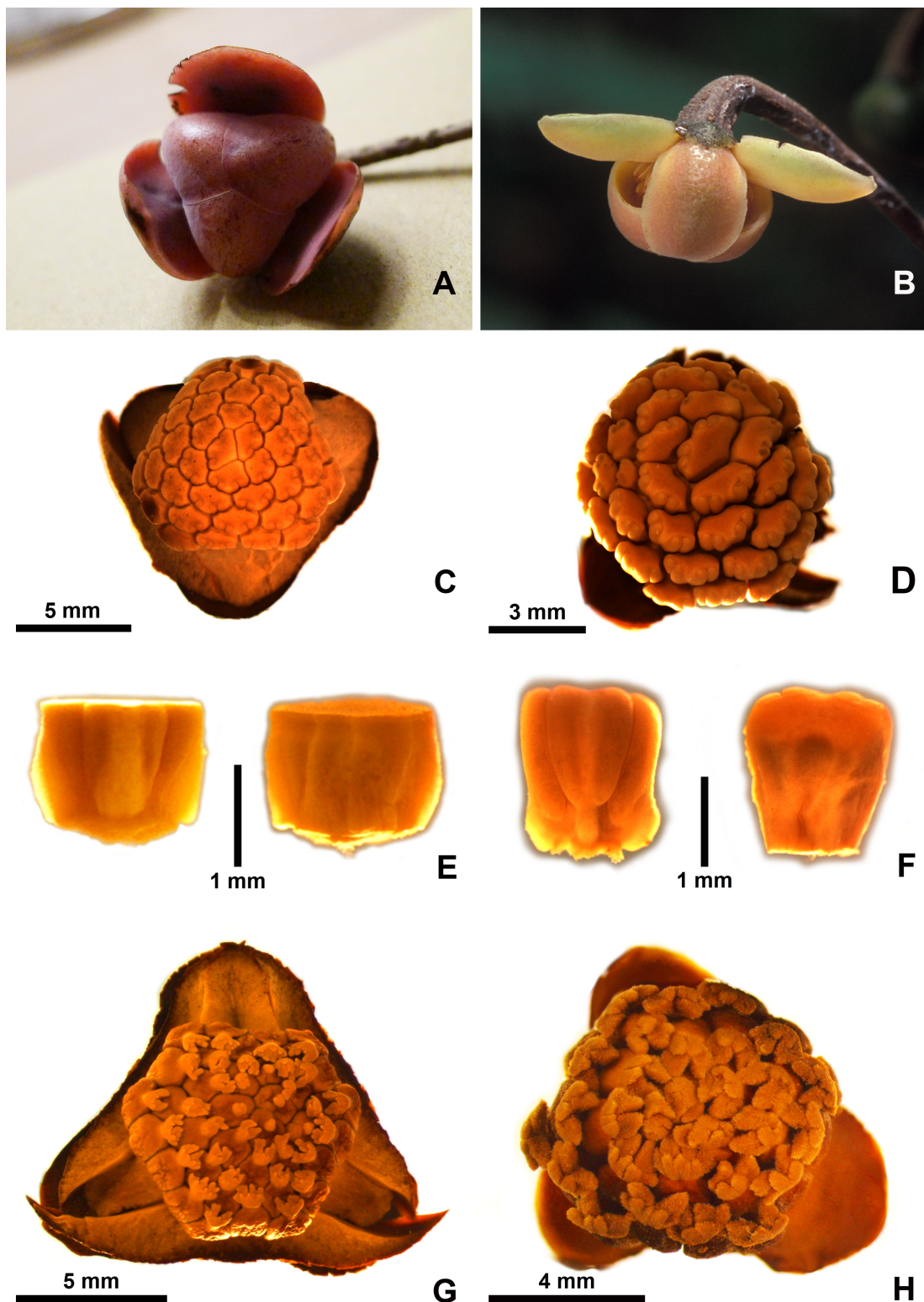
Fig. 3. Flowers and floral organs of *Winitia cauliflora* (Scheff.) Chaowasku (**A**, **C**, **E**, **G**) and *Winitia longipes* (Craib) Chaowasku & Aongyong comb. nov. (**B**, **D**, **F**, **H**). **A–B**. Flowers. **C–D**. Male flowers with petals removed. **E–F**. Stamens, abaxial (left) and adaxial (right) sides. **G–H**. Female flowers with petals removed. A, C, E, G from *Chaowasku 185* (CMUB); B from *Gardner et al. ST1665* (L); D, F, H from *Aongyong 8* (CMUB). Photographs by T. Chaowasku (A) and S. Gardner (B).

Table 1. Principal morphological differences between *Winitia cauliflora* (Scheff.) Chaowasku and *Winitia longipes* (Craib) Chaowasku & Aongyong comb. nov.

Features	*W. cauliflora*	*W. longipes* comb. nov.
Outer petal size (mm) and shape	9–12 × 13–14, broadly ovate	12.5 × 8.5–10, elliptic to slightly ovate
Inner petal size (mm) and shape	10.5–12 × 7.5–9, slightly obovate to obovate	8.5–9 × 8–8.5, elliptic to slightly ovate
Stamens	Tightly packed, not bending inward	More loosely packed, slightly bending inward (best observable in outer-whorl ones)
Stigmas	Generally with ≥ 10 columnar lobes per stigma; lobes not deeply divided	With 5–7 columnar lobes per stigma; lobes deeply divided

The phylogenetic results (Fig. 1) revealed that *Winitia* aff. *expansa*-1 and *Winitia* aff. *expansa*-2 formed a strongly supported clade, which is not the sister group of *W. expansa*. Although *W. expansa* as well as *Winitia* aff. *expansa*-1 and *Winitia* aff. *expansa*-2 exhibit inner petals that are spreading at anthesis (Fig. 4A–B), the latter two accessions differ from *W. expansa* by having a non-glaucous appearance on the petal adaxial surface (Fig. 4A–B; glaucous in *W. expansa*; Chaowasku *et al.* 2013) and shallow pits on the adaxial surface of the inner petals (Fig. 4B; no pitted structures in *W. expansa*; Chaowasku *et al.* 2013). In addition, the inflorescences of *Winitia* aff. *expansa*-1 and *Winitia* aff. *expansa*-2 are mostly clustered on large roots and at the unswollen base of trunks, while those of *W. expansa* are mostly clustered at the swollen base of trunks. Based on the above-mentioned differences, *Winitia* aff. *expansa* is described as new to science.

Winitia thailandana Chaowasku & Aongyong sp. nov.
urn:lsid:ipni.org:names:77209778-1
Figs 4–6

Diagnosis

Morphologically similar to *Winitia expansa*, differs by having a non-glaucous appearance on the petal adaxial surface (glaucous in *W. expansa*) and shallow pits on the adaxial surface of the inner petals (no pitted structures in *W. expansa*). Moreover, its inflorescences are mostly clustered on large roots and at the unswollen base of trunks, whereas the inflorescences of *W. expansa* are mostly clustered at the swollen base of trunks.

Etymology

Named after Thailand, a country where this species is endemic.

Type material

    Holotype
THAILAND • Surat Thani Prov., Phanom Distr.; 8 May 2017; fl; *Aongyong 9*; holotype: CMUB; isotypes: G, P.

    Paratypes
THAILAND • Surat Thani Province, Phanom District; fl; *Chaowasku 51*; CMUB • Khlong Phanom National Park; fl; *Gardner & Sidisunthorn ST0817*; L.

Description

Medium-sized trees 12–14 m tall, dbh ca 27 cm. Young twigs glabrous. Petiole 6–8 mm long, grooved on upper surface, glabrous on both surfaces; leaf blade elliptic to slightly ovate, 13–17.8 × 3.7–5.8 cm, glabrous on both surfaces, in young leaves numerous black dots present on lower surface, base broadly cuneate to obtuse, apex acute-acuminate to acuminate; midrib raised and glabrous on both surfaces, in young leaves numerous black dots present on lower surface; secondary veins 8–10 per side, rather prominent on lower surface and forming loops, angle with midrib 50°–60° (at middle part of leaf blade). Flowers fasciculate, mostly clustered on large roots and at unswollen base of trunks, up to 3 flowers per fascicle, possibly unisexual [only male flowers found]; peduncle when present inconspicuous; pedicel 7–15 mm long, appressed-puberulous, bracts 2(–3), triangular, placed at base, sometimes a bit higher for upper one. Sepals basally connate, triangular-ovate to broadly triangular-ovate, 4.5–5.1 × 3–5 mm, outside appressed-puberulous, inside and margin glabrous. Outer petals ovate to broadly ovate, 10–11 × 9–10 mm, indumentum similar to sepals, outside with scattered warts, inside non-glaucous, apex
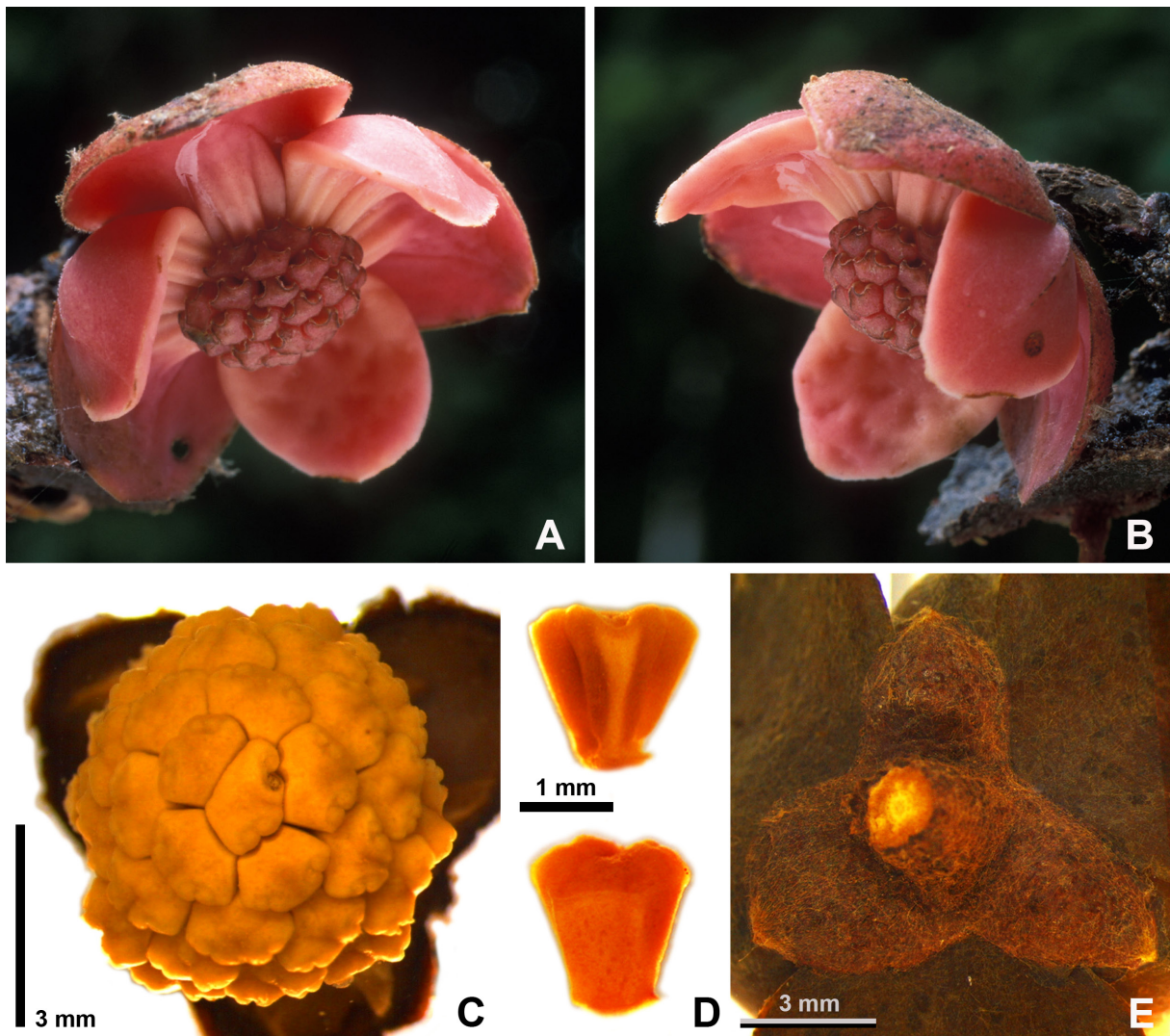

Fig. 4. Flowers and floral organs of *Winitia thailandana* Chaowasku & Aongyong sp. nov. **A–B**. Flower. **C**. Flower with petals removed. **D**. Stamen, abaxial (above) and adaxial (below) sides. **E**. Back side of flower, showing sepals (abaxial side). A, B from *Gardner & Sidisunthorn ST0817* (L), photographs by S. Gardner; C–E from *Aongyong 9* (CMUB).

Fig. 5. Holotype of *Winitia thailandana* Chaowasku & Aongyong sp. nov. at CMUB.

between acute and obtuse; inner petals elliptic, 9–10 × 6 mm, glabrous on both sides and margin, inside non-glaucous and with shallow pits, apex obtuse to rounded. Torus elongated hemispherical in male flowers, glabrous. Stamens 32–39 per male flower, 1.8–2 mm long, tightly packed, each not bending inward, connective apex ± truncate, not covering thecae; female flowers not found. Monocarps unknown.

Distribution, habitat, and phenology

Surat Thani Province, Phanom District (Fig. 6); occurs in evergreen forests among rugged limestone outcrops; at an elevation of ca 400 m; flowering material collected in May and June.

Field notes

Flowers orange-pink.

Notes

The new species is so far known only from Phanom District. We observed only three individuals, which occur among limestone outcrops beside a trail surrounded by a rubber tree plantation. In Khlong Phanom National Park where this species has also been reported (Gardner *et al.* 2015) less than ten individuals were found (pers. comm., S. Gardner). Based on our observations and estimations, we believe at least the category "endangered: EN D" (IUCN 2012) is applicable.
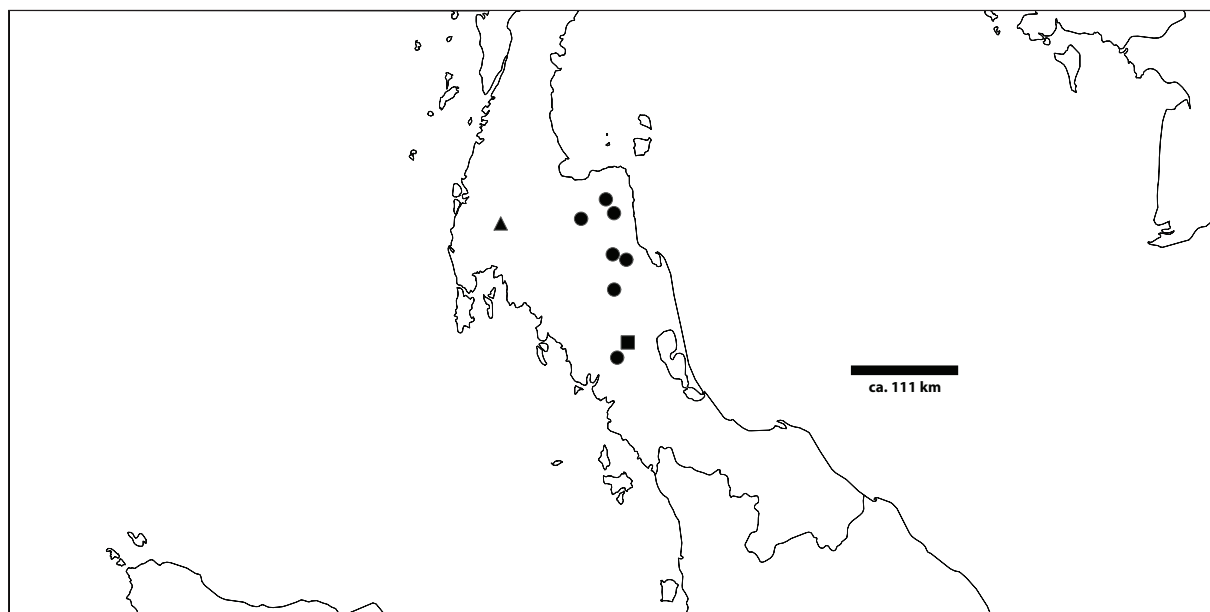

Fig. 6. Distribution of *Winitia* in Thailand. *Winitia expansa* Chaowasku (■), *Winitia longipes* (Craib) Chaowasku & Aongyong comb. nov. (●), and *Winitia thailandana* Chaowasku & Aongyong sp. nov. (▲).

Key to genera in the sageraeoid clade

1. Plants bisexual or monoecious. Leaf midrib sunken on adaxial side, leaf venation (especially secondary veins) generally indistinct .... ***Sageraea*** Dalzell (Dalzell 1851)
– Plants monoecious. Leaf midrib raised on adaxial side, leaf venation (especially secondary veins) distinct 2

2. Flowers dimorphic (in the same individual male flowers smaller with shorter pedicels, female flowers larger with longer pedicels); male and female flowers allocated spatially differently (male flowers ramiflorous, female flowers cauliflorous); petals greenish yellow to cream at maturity, each stigma bilobed (± heart-shaped), torus conical-cylindrical to cylindrical in male flowers; monocarps light brown at maturity .... ***Stelechocarpus*** Hook.f. & Thomson (Hooker & Thomson 1855)
– Flowers monomorphic; male and female flowers intermixed and clustered along trunks, at swollen or unswollen base of trunks, and/or on large roots; petals ± rose-colored at maturity, each stigma with multiple (≥ 5) columnar lobes, torus ± hemispherical in male flowers; monocarps ± blackish brown at maturity .... ***Winitia*** Chaowasku (Chaowasku *et al.* 2013)

Key to the species of *Winitia*

1. Inner petals spreading at maturity.. 2
– Inner petals tightly cohering at maturity.. 3

2. Flowers mostly clustered on large roots and at unswollen base of trunks; inner side of both petal whorls without a glaucous appearance, inner side of inner petals with shallow pits ....***Winitia thailandana*** Chaowasku & Aongyong sp. nov.
– Flowers mostly clustered at swollen base of trunks; inner side of both petal whorls with a glaucous appearance; inner side of inner petals without pitted structures ....***Winitia expansa*** Chaowasku (Chaowasku *et al.* 2013)

3. Outer petals broadly ovate, 9–12 × 13–14 mm; inner petals slightly obovate to obovate, 10.5–12 × 7.5–9 mm; stamens tightly packed, not bending inward; each stigma generally with ≥ 10 columnar lobes, lobes not deeply divided ....
.... ***Winitia cauliflora*** (Scheff.) Chaowasku (Chaowasku *et al.* 2013; basionym: Scheffer 1881)
– Outer petals elliptic to slightly ovate, 12.5 × 8.5–10 mm; inner petals elliptic to slightly ovate, 8.5–9 × 8–8.5 mm; stamens more loosely packed, slightly bending inward (best observable in outer-whorl ones); each stigma with 5–7 columnar lobes, lobes deeply divided ....***Winitia longipes*** (Craib) Chaowasku & Aongyong comb. nov.

Discussion

The monophyly of *Winitia*, when more accessions have been added, remains maximally supported (Fig. 1), as compared with previous studies that included only two accessions (Chaowasku *et al.* 2013, 2018b; Guo *et al.* 2017b). The genus, however, was subsumed under *Stelechocarpus* by Turner (2016), principally based on the arguments that (1) the erection of *Winitia* has caused *Stelechocarpus* to become a monotypic genus, which conveys little taxonomic information, and (2) *Stelechocarpus* inclusive of *Winitia* is identifiable by a raised leaf midrib adaxially. However, there are also clear morphological differences, including petal color and texture, floral dimorphism (absent vs present), locations of male and female flowers in individuals (mixed vs separate), and stamen and stigma morphology that warrants the recognition of two separate genera (Chaowasku *et al.* 2013). These differences are comparable to those of two sister monotypic genera, *Mwasumbia* Couvreur & D.M.Johnson (Couvreur *et al.* 2009) and *Sirdavidia* Couvreur & Sauquet (Couvreur *et al.* 2015), belonging to the African tribe Piptostigmateae of subfamily Malmeoideae and primarily differing from each other in petal color and configuration as well as stamen morphology. Furthermore, support for the sister relationship of *Mwasumbia* and *Sirdavidia* was already strong with only three plastid regions (*rbc*L exon, *trn*L intron, and *trn*L-*trn*F intergenic spacer; Couvreur *et al.* 2015) included, whereas support for the sister relationship of *Winitia* and *Stelechocarpus* is still rather poor and the branch uniting the two genera is very short (Fig. 1) despite using seven plastid regions and adding more accessions. In addition, the branches leading to *Winitia* and to *Stelechocarpus* are relatively long (Fig. 1) and comparable to those leading to *Monoon* Miq. (Miquel

1865) and to *Neo-uvaria* Airy Shaw (Airy Shaw 1939). Given the same amounts of nucleotide data, the support for the sister relationship of *Monoon* and *Neo-uvaria* is even much higher with a longer branch uniting them (Fig. 1).

It is worth noticing that there is an indel of eight continuous base pairs in the *trn*L-*trn*F intergeneric spacer potentially diagnostic for generic discrimination in the tribe Miliuseae (Fig. 2), i.e., all members in the same genus possess the same indel structure (absence or presence of an eight-base-pair gap; personal observations based on all GenBank accessions of the *trn*L-*trn*F intergeneric spacer indicated in Chaowasku *et al.* 2014, 2018a, 2018b; Guo *et al.* 2017b). This gap is present in *Stelechocarpus* and absent in *Winitia* (Fig. 2). Besides Miliuseae, members of other tribes of Malmeoideae and other subfamilies also possess this indel (pers. obs.), but its utility for generic discrimination is still unknown, awaiting detailed observations.

Regarding pollen morphology, the two genera do not possess the same infratectum type, i.e., ± columellate/coarsely granular in *Winitia* vs finely and densely granular in *Stelechocarpus* (Chaowasku *et al.* 2013); in Miliuseae, there have been no reports of different infratectal structures occurring in the same genus (Chaowasku *et al.* 2014). There are also other palynological traits (exine sculpturing, tectum, and basal layer) that are significantly different in the two genera (Chaowasku *et al.* 2013).

In recognizing the genus *Winitia*, we believe that the most important issue to consider is the support for monophyly, then the morphological distinctions as well as relative phylogenetic branch lengths. On the basis of the above-mentioned morphological and phylogenetic evidence reaffirming a clear-cut differentiation of *Winitia* and *Stelechocarpus*, we are therefore strongly convinced that the recognition of the genus *Winitia* is appropriate. Rather equivalent to the case of *Winitia* and *Stelechocarpus*, in Annonaceae acceptance of a non-monotypic genus being the sister group of a monotypic genus is not unprecedented, for example, *Fusaea* (Baill.) Saff. (Safford 1914; basionym: Baillon 1868) with a monotypic *Duckeanthus* R.E.Fr. (Fries 1934) as the sister group, *Letestudoxa* Pellegr. (Pellegrin 1920) with a monotypic *Pseudartabotrys* Pellegr. (Pellegrin 1920) as the sister group, and *Mitrella* Miq. (Miquel 1865) with a monotypic *Pyramidanthe* Miq. (Miquel 1865) as the sister group (see Guo *et al.* 2017b).

Acknowledgements

References

Airy Shaw H.K. 1939. Additions to the flora of Borneo and other Malay Islands: XII. The Annonaceae of the Oxford University expedition to Sarawak, 1932. *Bulletin of Miscellaneous Information, Royal Botanic Gardens, Kew* 1939: 275–290.

Baillon H. 1868. Mémoire sur la famille des Anonacées. *Adansonia* 8: 295–344.

Blume C.L. von 1825. *Bijdragen tot de Flora van Nederlandsch Indië*. Part 1. Lands Drukkerij, Batavia [Jakarta].

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. https://doi.org/10.11646/phytotaxa.69.1.6

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 (Malmeoideae, Miliuseae) allied to *Stelechocarpus* and *Sageraea*. *Systematics and Biodiversity* 11: 195–207. https://doi.org/10.1080/14772000.2013.806370

Chaowasku T., Thomas D.C., van der Ham R.W.J.M., Smets E.F., Mols J.B. & Chatrou L.W. 2014. A plastid DNA phylogeny of tribe Miliuseae: insights into relationships and character evolution in one of the most recalcitrant major clades of Annonaceae. *American Journal of Botany* 101: 691–709. https://doi.org/10.3732/ajb.1300403

Chaowasku T., Johnson D.M., van der Ham R.W.J.M. & Chatrou L.W. 2015. *Huberantha*, a replacement name for *Hubera* (Annonaceae: Malmeoideae: Miliuseae). *Kew Bulletin* 70: 23. https://doi.org/10.1007/S12225-015-9571-Z

Chaowasku T., Damthongdee A., Jongsook H., Ngo D.T., Le H.T., Tran D.M. & Suddee S. 2018a. Enlarging the monotypic Monocarpieae (Annonaceae, Malmeoideae): recognition of a second genus from Vietnam informed by morphology and molecular phylogenetics. *Candollea* 73: 261–275. https://doi.org/10.15553/c2018v732a11

Chaowasku T., Damthongdee A., Jongsook H., Nuraliev M.S., Ngo D.T., Le H.T., Lithanatudom P., Osathanunkul M., Deroin T., Xue B. & Wipasa J. 2018b. Genus *Huberantha* (Annonaceae) revisited: erection of *Polyalthiopsis*, a new genus for *H. floribunda*, with a new combination *H. luensis*. *Annales Botanici Fennici* 55: 121–137. https://doi.org/10.5735/085.055.0114

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. *Botanical Journal of the Linnean Society* 169: 5–40. https://doi.org/10.1111/j.1095-8339.2012.01235.x

Chernomor O., Haeseler A. von & Minh B.Q. 2016. Terrace aware data structure for phylogenomic inference from supermatrices. *Systematic Biology* 65: 997–1008. https://doi.org/10.1093/sysbio/syw037

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. *Systematic Botany* 34: 266–276. https://doi.org/10.1600/036364409788606398

Couvreur T.L.P., Niangadouma R., Sonké B. & Sauquet H. 2015. *Sirdavidia*, an extraordinary new genus of Annonaceae from Gabon. *PhytoKeys* 46: 1–19. https://doi.org/10.3897/phytokeys.46.8937

Couvreur T.L., Helmstetter A.J., Koenen E.J., Bethune K., Brandão R.D., Little S.A., Hervé Sauquet & Erkens R.H. 2019. Phylogenomics of the major tropical plant family Annonaceae using targeted enrichment of nuclear genes. *Frontiers in Plant Science* 9: 1941. https://doi.org/10.3389/fpls.2018.01941

Craib W.G. 1923. Six new flowering plants from Siam. *Journal of the Natural History Society of Siam* 6: 43–45.

Dalzell N.A. 1851. Contributions to the botany of western India [Anonaceae]. *Hooker's Journal of Botany and Kew Garden Miscellany* 3: 206–208.

de Wildeman E. 1914. Neue Arten aus Zentral-Afrika (Belgisch-Kongo) I. *Repertorium Specierum Novarum Regni Vegetabilis* 13: 369–384. https://doi.org/10.1002/fedr.19140132402

Edgar R.C. 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 32: 1792–1797. https://doi.org/10.1093/nar/gkh340

Felsenstein J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39: 783–791. https://doi.org/10.1111/j.1558-5646.1985.tb00420.x

Fries R.E. 1934. Revision der Arten einiger Anonaceen-Gattungen III. *Acta Horti Bergiani* 12: 1–220.

Gardner S., Sidisunthorn P. & Chayamarit K. 2015. *Forest Trees of southern Thailand*. Vol. 1: *Acanthaceae to Escalloniaceae*. Kobfai Printing Project, Bangkok.

Goloboff P.A. & Catalano S.A. 2016. TNT version 1.5, including a full implementation of phylogenetic morphometrics. *Cladistics* 32: 221–238. https://doi.org/10.1111/cla.12160

Goloboff P.A., Farris J.S., Källersjö M., Oxelman B., Ramirez M.J. & Szumik C.A. 2003. Improvements to resampling measures of group support. *Cladistics* 19: 324–332.
https://doi.org/10.1111/j.1096-0031.2003.tb00376.x

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*. *Journal of Systematics and Evolution* 52: 1–15.
https://doi.org/10.1111/jse.12064

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. https://doi.org/10.12705/661.1

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 recognition of a new tribe, Phoenicantheae. *Scientific Reports* 7: 7323. https://doi.org/10.1038/s41598-017-07252-2

Hasegawa M., Kishino H. & Yano T. 1985. Dating of the human-ape splitting by a molecular clock of mitochondrial DNA. *Journal of Molecular Evolution* 22: 160–174. https://doi.org/10.1007/BF02101694

Hewson H.J. 1988. *Plant Indumentum. A Handbook of Terminology*. Australian Flora and Fauna Series 9, Australian Government Publishing Service, Canberra.

Hooker J.D. & Thomson T. 1855. *Flora Indica: Being a Systematic Account of the Plants of British India, Together with Observations on the Structure and Affinities of their Natural Orders and Genera*. Pamplin, London. https://doi.org/10.5962/bhl.title.57706

IUCN 2012. *IUCN Red List categories and criteria*. Version 3.1. Second Edition. IUCN, Gland & Cambridge.

King G. 1892. Materials for a flora of the Malay Peninsula. *Journal of the Asiatic Society of Bengal* (part 2, Natural Science) 61: 1–130.

Kumar S., Stecher G. & Tamura K. 2016. MEGA7: molecular evolutionary genetics analysis version 7.0 for bigger datasets. *Molecular Biology and Evolution* 33: 1870–1874.
https://doi.org/10.1093/molbev/msw054

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

Miquel F.A.W. 1865. Anonaceae Archipelagi Indici. *Annales Musei Botanici 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. *Systematic Botany* 33: 490–494. https://doi.org/10.1600/036364408785679752

Nguyen L.T., Schmidt H.A., Haeseler A. von & Minh B.Q. 2015. IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution* 32: 268–274. https://doi.org/10.1093/molbev/msu300

Pellegrin F. 1920. Plantae Letestuanae novae ou Plantes nouvelles récoltées par M. Le Testu de 1907 à 1919 dans le Mayombe congolais. *Bulletin du Muséum national d'histoire naturelle* 26: 654–659.

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 biogeographic hypotheses using phylogeny reconstruction and molecular dating. *Journal of Biogeography* 33: 31–46. https://doi.org/10.1111/j.1365-2699.2005.01388.x

Posada D. & Crandall K.A. 1998. MODELTEST: testing the model of DNA substitution. *Bioinformatics* 14: 817–818. https://doi.org/10.1093/bioinformatics/14.9.817

Rambaut A., Suchard M. & Drummond A. 2013. Tracer. Version 1.6. Available from 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. *Systematic Biology* 61: 539–542. https://doi.org/10.1093/sysbio/sys029

Safford W.E. 1914. Classification of the genus *Annona*, with descriptions of new and imperfectly known species. *Contributions from the United States National Herbarium* 18: 1–68.

Sang T., Crawford D.J. & Stuessy T.F. 1997. Chloroplast DNA phylogeny, reticulate evolution and biogeography of *Paeonia* (Paeoniaceae). *American Journal of Botany* 84: 1120–1136. https://doi.org/10.2307/2446155

Scheffer R.H.C.C. 1881. Sur quelques plantes nouvelles ou peu connues de l'Archipel Indien. *Annales du Jardin botanique de Buitenzorg* 2: 1–31.

Simmons M.P. 2004. Independence of alignment and tree search. *Molecular Phylogenetics and Evolution* 31: 874–879. https://doi.org/10.1016/j.ympev.2003.10.008

Simmons M.P. & Ochoterena H. 2000. Gaps as characters in sequence-based phylogenetic analyses. *Systematic Biology* 49: 369–381. https://doi.org/10.1093/sysbio/49.2.369

Staden R., Beal K.F. & Bonfield J.K. 2000. The Staden package, 1998. *In*: Misener S. & Krawetz S.A. (eds) *Bioinformatics Methods and Protocols. Methods in Molecular Biology™*: 115–130. Humana Press, Totowa. https://doi.org/10.1385/1-59259-192-2:115

Tate J.A. & Simpson B.B. 2003. Paraphyly of *Tarasa* (Malvaceae) and diverse origins of the polyploid species. *Systematic Botany* 28: 723–737. https://doi.org/10.1043/02-64.1

Tavaré S. 1986. Some probabilistic and statistical problems in the analysis of DNA sequences. *Lectures on Mathematics in the Life Science* 17: 57–86.

Turner I.M. 2016. Notes on the Annonaceae of the Malay Peninsula. *Gardens' Bulletin Singapore* 68: 65–69.

van Heusden E.C.H. 1995. Revision of the Southeast Asian genus *Stelechocarpus* (Annonaceae). *Blumea* 40: 429–438.

van Heusden E.C.H. 1997. Revision of the southeast Asian genus *Sageraea* (Annonaceae). *Nordic Journal of Botany* 17: 39–54. https://doi.org/10.1111/j.1756-1051.1997.tb00289.x

Wiens J.J. 1998. Combining data sets with different phylogenetic histories. *Systematic Biology* 47: 568–581. https://doi.org/10.1080/106351598260581

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. https://doi.org/10.1002/tax.615009

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. https://doi.org/10.12705/672.2

Yang Z. & Rannala B. 1997. Bayesian phylogenetic inference using DNA sequences: a Markov Chain Monte Carlo method. *Molecular Biology and Evolution* 14: 717–724. https://doi.org/10.1093/oxfordjournals.molbev.a025811

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*. *Systematics and Biodiversity* 7: 249–258. https://doi.org/10.1017/S1477200009003028

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*. *Botanical Journal of the Linnean Society* 163: 33–43. https://doi.org/10.1111/j.1095-8339.2010.01045.x

Appendix 1. Voucher specimens for molecular phylogenetic analyses with GenBank accession numbers indicated. – signifies unavailable sequences; * signifies sequences newly produced in this study.

Species	Origin/voucher	*mat*K	*ndh*F	*psb*A-*trn*H	*rbc*L	*trn*LF	*ycf*1
Alphonsea elliptica	Bogor Bot. Gard., Indonesia/ van Balgooy 5141 (L)	AY519907	JQ690401	JQ690402	AY318966	AY319078	JQ690403
Alphonsea sp.	Bogor. Bot. Gard., Indonesia/*Chaowasku 186* (CMUB)	MT040200*	MT040210*	MT040222*	MT040233*	MT040245*	MT040256*
Bocageopsis canescens	Brazil/*Maas et al. 9243* (U)	JQ690409	JQ690410	JQ690411	JQ690407	JQ690408	JQ690412
Brieya fasciculata	Ghana/*Jongkind et al. 1862* (WAG)	MH585796	MH585822	AY841497	AY841647	AY841725	–
Dendrokingstonia gardneri	Malaysia [Peninsular]/ *Gardner & Sidisunthorn MY 067* (L)	MH585797	MH585823	MH585803	MH585807	MH585812	MH585816
Dendrokingstonia nervosa	Malaysia [Peninsular]/ *Rogstad 961* (L)	MH585798	KJ418386	KJ418400	KJ418382	KJ418407	MH585817
Desmopsis microcarpa	Costa Rica/*Chatrou et al. 85* (U)	AY518804	JX544771	AY841461	AY319059	AY319173	JX544758
Fenerivia chapelieri	Madagascar/*Rabevohitra et al. 4439* (MO)	KJ418393	KJ418387	KJ418397	MH585808	KJ418403, KJ418404	MG264598
Huberantha cerasoides	Thailand/*Chalermglin 440214-4* (L)	AY518854	JQ889985	JQ889980	AY319017	AY319131	JQ889975
Huberantha stuhlmannii	Kenya/*Luke & Robertson 1424* (K)	AY518853	JX544882	JX544862	AY319035	AY319149	JX544852
Leoheo domatiophorus	Vietnam/*Chaowasku 165* (CMUB)	MH585799	MH585824	MH585804	MH585809	MH585813	MH585818
Maasia glauca	Thailand/*Chaowasku 169* (CMUB)	MG264584	MG264589	MG264571	MG264581	MG264576	MG264594
Marsypopetalum littorale	Bogor Bot. Gard., Indonesia/*Rastini 153* (L)	AY518835	JX544827	JX544804	AY319026	AY319140	JX544813
Marsypopetalum modestum	Thailand/*Keßler PK 3192* (L)	AY518834	KC857561	KC857562	AY318980	AY319092	KC857563

Appendix 1 (continued). Voucher specimens for molecular phylogenetic analyses with GenBank accession numbers indicated. – signifies unavailable sequences; * signifies sequences newly produced in this study.

Species	Origin/voucher	*mat*K	*ndh*F	*psb*A-*trn*H	*rbc*L	*trn*LF	*ycf*1
Meiogyne gardneri	Thailand/Gardner et al. ST 2014 (L)	KC857566	KC857567	KC857568	KC857564	KC857565	KC857569
Meiogyne virgata	Indonesia [Borneo]/Keßler PK2751 (L)	AY518798	JX544769	JX544784	AY318982	AY319094	JX544756
Miliusa mollis	Thailand/Keßler PK 3207 (L)	AY518851	JQ690503	JQ690504	AY318990	AY319102	JQ690505
Miliusa velutina	Thailand/Pholsena & Koonkhunthod 2842 (L)	AY518847	JQ690536	JQ690537	AY318993	AY319105	JQ690538
Mitrephora alba	Thailand/Chalermglin 440304-1 (TISTR, Bangkok)	AY518855	JQ889983	JQ889978	AY318994	AY319106	JQ889973
Mitrephora chulabhorniana	Thailand/Aongyong 11 (CMUB)	MT040201*	MT040211*	MT040223*	MT040234*	MT040246*	MT040257*
Monocarpia euneura	Indonesia [Borneo]/Slik 2931 (L)	AY518865	AY841412	AY841477	AY318998	AY319111	–
Monocarpia maingayi	Thailand/Gardner & Sidisunthorn ST0541 (L)	MH585801	MH585826	MH585806	MH585811	MH585815	MH585819
Monoon fuscum	Thailand/Keßler PK 3222 (L)	AY518787	JX544779	JX544792	AY318973	AY319085	JX544767
Monoon viride	Thailand/Chalermglin 440214-3 (L)	AY518784	JX544780	JX544793	AY319040	AY319154	JX544768
Mwasumbia alba	Tanzania/Couvreur 85 (WAG)	MH585795	MH585821	MH585802	EU747680	EU747674	–
Neo-uvaria parallelivenia	Bogor Bot. Gard., Indonesia/Keßler sub IV-H-73 (L)	AY518794	KC857570	KC857571	AY319000	AY319113	KC857572
Neo-uvaria telopea	Thailand/Chaowasku 77 (L)	JX544751	JX544778	JX544791	JX544755	JX544783	JX544766
Orophea enterocarpa	Thailand/Chalermglin 440403 (TISTR, Bangkok)	AY518815	JQ690416	JQ690417	AY319006	AY319119	JQ690418

Appendix 1 (continued). Voucher specimens for molecular phylogenetic analyses with GenBank accession numbers indicated. – signifies unavailable sequences; * signifies sequences newly produced in this study.

Species	Origin/voucher	*mat*K	*ndh*F	*psb*A-*trn*H	*rbc*L	*trn*LF	*ycf*1
Orophea kerrii	Thailand/*Chalermglin 440416-1* (L)	AY518818	JQ690419	JQ690420	AY319008	AY319121	JQ690421
Oxandra espintana	Peru/*Chatrou et al. 133* (U)	DQ018260	MH585827	AY841487	AY319066	AY319180	MH585820
Oxandra venezuelana	Costa Rica/*Chatrou et al. 120* (U)	JQ690413	JQ690414	AY841495	AY841645	MT040247*	JQ690415
Phaeanthus splendens	Indonesia [Borneo]/*Keßler B 1564* (L)	AY518864	JX544777	JX544790	JX544754	AY319126	JX544765
Phoenicanthus obliquus	Sri Lanka/*Huber 518* (L)	MG264587	MG264592	MG264574	MG264582	MG264579	MG264597
Platymitra macrocarpa	Bogor Bot. Gard., Indonesia/*Okada 3457* (L)	AY518812	JQ690422	JQ690423	AY319013	AY319127	JQ690424
Polyalthia suberosa	Utrecht Univ. Bot. Gard., The Netherlands/*Chatrou 480* (U)	AY238965	AY841417	AY841502	AY238956	AY231289, AY238949	JX544817
Polyalthiopsis floribunda	Vietnam/*Chaowasku 128* (CMUB)	MG264583	MT040212*	MT040224*	MG264580	MG264575	MG264593
Popowia hirta	Indonesia [Borneo]/*Keßler B 1628* (L)	AY518860	JX544830	JX544806	AY319042	AY319156	JX544816
Popowia pisocarpa	Bogor Bot. Gard., Indonesia/*van Balgooy & van Setten 5683* (L)	AY518862	KC857578	KC857579	AY319044	AY319158	KC857580
Pseuduvaria fragrans	Thailand/*Chaowasku 27* (L)	EU522286	JX544829	EU522176	EU522341	EU522231	JX544815
Pseuduvaria setosa	Thailand/*Chaowasku 66* (L)	KC857582	KC857583	KC857584	MT040235*	KC857581	KC857585
Sageraea elliptica	Thailand/*Chaowasku 45* (L)	KC857587	KC857588	KC857589	MT040236*	KC857586	KC857590
Sageraea lanceolata	Malaysia [Borneo]/*Ridsdale DI-M2-1692* (L)	AY518799	JX544774	JX544787	AY319050	AY319164	JX544762
Sapranthus viridiflorus	Costa Rica/*Chatrou et al. 55* (U)	AY743493	AY841422	AY841515	AY319051	AY319165	JX544760

Appendix 1 (continued). Voucher specimens for molecular phylogenetic analyses with GenBank accession numbers indicated. – signifies unavailable sequences; * signifies sequences newly produced in this study.

Species	Origin/voucher	*mat*K	*ndh*F	*psb*A-*trn*H	*rbc*L	*trn*LF	*ycf*1
Stelechocarpus burahol [= *Stelechocarpus burahol*-1]	Thailand/*Chaowasku 187* (CMUB)	MT040202*	MT040213*	MT040225*	MT040237*	MT040248*	MT040258*
Stelechocarpus burahol [= *Stelechocarpus burahol*-2]	Bogor Bot. Gard., Indonesia/*Mols 13* (L)	AY518803	JX544775	JX544788	AY319053	AY319167	JX544763
Stenanona costaricensis	Costa Rica/*Chatrou et al. 67* (U)	AY518801	JX544772	AY841516	AY319069	AY319183	JX544759
Tridimeris sp.	Missouri Bot. Gard., USA/*Maas 8646* (U)	JX544750	JX544773	JX544786	JX544753	JX544782	JX544761
Trivalvaria sp. 1	Thailand/*Chaowasku 35* (L)	JX544824	JX544828	JX544805	JX544822	JX544794	JX544814
Trivalvaria sp. 2	Thailand/*Chaowasku 73* (CMUB)	MT040203*	MT040214*	MT040226*	MT040238*	MT040249*	MT040259*
Wangia saccopetaloides	China/*Li 752* (QBG)	MT040204*	MT040215*	MT040227*	MT040239*	MT040250*	MT040260*
Winitia cauliflora [= *Winitia cauliflora*-1]	Bogor Bot. Gard., Indonesia/*Chaowasku 178* (CMUB)	MT040205*	MT040216*	MT040228*	MT040240*	MT040251*	MT040261*
Winitia cauliflora [= *Winitia cauliflora*-2]	Bogor Bot. Gard., Indonesia/*Unknown s.n. sub XV-A-196* (L)	AY518800	JX544776	JX544789	AY319054	AY319168	JX544764
Winitia expansa	Thailand/*Chaowasku 93* (L)	KC857617	KC857618	KC857619	MT081401*	KC857616	KC857620
Winitia longipes [= *Winitia cauliflora*-3]	Thailand/*Aongyong 10* (CMUB)	MT040206*	MT040217*	MT040229*	MT040241*	MT040252*	MT040262*
Winitia longipes [= *Winitia cauliflora*-4]	Thailand/*Aongyong 8* (CMUB)	MT040207*	MT040218*	MT040230*	MT040242*	MT040253*	MT040263*

Appendix 1 (continued). Voucher specimens for molecular phylogenetic analyses with GenBank accession numbers indicated. – signifies unavailable sequences; * signifies sequences newly produced in this study.

Species	Origin/voucher	*mat*K	*ndh*F	*psb*A-*trn*H	*rbc*L	*trn*LF	*ycf*1
Winitia thailandana [= *Winitia* aff. expansa-1]	Thailand/*Aongyong 9* (CMUB)	MT040208*	MT040219*	MT040231*	MT040243*	MT040254*	MT040264*
Winitia thailandana [= *Winitia* aff. expansa-2]	Thailand/*Chaowasku 51* (CMUB)	MT040209*	MT040220*	MT040232*	MT040244*	MT040255*	MT040265*
Wuodendron praecox	Thailand/*Chaowasku 108* (L)	JX544749	MT040221*	JX544785	JX544752	JX544781	JX544757

Appendix 2. Specimens morphologically examined in this study.

Species	Origin/voucher	Remarks
Winitia cauliflora	Bogor Bot. Gard., Indonesia/*Chaowasku 178* (CMUB)	X-F-96
Winitia cauliflora	Bogor Bot. Gard., Indonesia/*Chaowasku 185* (CMUB)	XV-A-196
Winitia longipes	Thailand/*Aongyong 8* (CMUB)	-
Winitia longipes	Thailand/*Aongyong 10* (CMUB)	-
Winitia longipes	Thailand/*Gardner et al. ST1665* (BKF, L)	Newly identified
Winitia longipes	Thailand/*Plernchit 788* (BKF)	Newly identified
Winitia longipes	Thailand/*Smitinand 2340* (BKF)	Newly identified
Winitia longipes	Thailand/*van Beusekom & Phengkhlai 1032* (BKF, L)	Newly identified
Winitia thailandana	Thailand/*Aongyong 9* (CMUB)	Type specimens
Winitia thailandana	Thailand/*Chaowasku 51* (CMUB)	-