TAXON 67 (2) • April 2018: 250–266

A new Annonaceae genus, *Wuodendron*, provides support for a post-boreotropical origin of the Asian-Neotropical disjunction in the tribe Miliuseae

Bine Xue,[1] Yun-Hong Tan,[2,3] Daniel C. Thomas,[4] Tanawat Chaowasku,[5] Xue-Liang Hou[6] & Richard M.K. Saunders[7]

1 *Key Laboratory of Plant Resources Conservation and Sustainable Utilization, South China Botanical Garden, Chinese Academy of Sciences, Guangzhou 510650, China*
2 *Southeast Asia Biodiversity Research Institute, Chinese Academy of Sciences, Yezin, Nay Pyi Taw, Myanmar*
3 *Center for Integrative Conservation, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun 666303, Yunnan, China*
4 *National Parks Board, Singapore Botanic Gardens, 1 Cluny Road, Singapore 259569, Singapore*
5 *Herbarium, Division of Plant Science and Technology, Department of Biology, Faculty of Science, Chiang Mai University, Thailand*
6 *School of Life Sciences, Xiamen University, Xiamen 361005, Fujian, China*
7 *School of Biological Sciences, The University of Hong Kong, Pokfulam Road, Hong Kong, China*
Authors for correspondence: *Bine Xue, xuebine@scib.ac.cn; Yunhong Tan, tyh@xtbg.org.cn*

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

Abstract Recent molecular and morphological studies have clarified generic circumscriptions in Annonaceae tribe Miliuseae and resulted in the segregation of disparate elements from the previously highly polyphyletic genus *Polyalthia* s.l. Several names in *Polyalthia* nevertheless remain unresolved, awaiting assignment to specific genera, including *Polyalthia litseifolia*. Phylogenetic analyses of seven chloroplast regions (*atpB-rbcL*, *matK*, *ndhF*, *psbA-trnH*, *rbcL*, *trnL-F*, *ycf1*; ca. 8.3 kb, 116 accessions, including representatives of all currently accepted genera in subfamily Malmeoideae) unambiguously placed *Polyalthia litseifolia* in a clade with three accessions from Thailand, which have previously been shown to represent an undescribed genus sister to the Neotropical clade (*Desmopsis*, *Sapranthus*, *Stenanona*, *Tridimeris*) in the predominantly Asian tribe Miliuseae. The collective clade is sister to *Meiogyne*. *Polyalthia litseifolia* shares several diagnostic characters with most species in the Neotropical genera and *Meiogyne*, including: petals that are similar in shape and size in both whorls; multiple ovules per ovary in one or two rows; and lamelliform endosperm ruminations. It is distinct in being deciduous, bearing subpetiolar buds and having inflorescences growing from the leaf scar of the dropped leaves. Morphological comparisons and phylogenetic analyses corroborate its recognition as a new genus, which is formally described and illustrated here as *Wuodendron*. *Polyalthia litseifolia* is furthermore found to be conspecific with *Desmos praecox*, and the latter name is used as the basis for the name of the type. Molecular divergence time estimates under an uncorrelated lognormal relaxed clock place the *Wuodendron*-Neotropical clade split within the Miocene (ca. 14–12 Ma), highlighting the importance of post-boreotropical dispersal and vicariance in shaping intercontinental tropical disjunctions in Annonaceae.

Keywords Annonaceae; deciduous; *Desmos praecox*; intercontinental tropical disjunction; new genus; *Polyalthia litseifolia*

Supplementary Material The Electronic Supplement (Figs. S1, S2) and DNA sequence alignments are available from https://doi.org/10.12705/672.2.S1 and https://doi.org/10.12705/672.2.S2, respectively.

■ INTRODUCTION

The Annonaceae is a large pantropical family of flowering trees and lianas, with ca. 108 genera and ca. 2400 species in tropical and subtropical lowland forests (Rainer & Chatrou, 2006; Chatrou & al., 2012; Guo & al., 2017). The family often forms an important component of tropical lowland forest ecosystems due to its extraordinary species richness (Burnham & Johnson, 2004; Richardson & al., 2004). Annonaceae are classified into four subfamilies, Anaxagoreoideae, Ambavioideae, Annonoideae and Malmeoideae, based on phylogenetic reconstructions derived from a supermatrix containing up to eight plastid markers (Chatrou & al., 2012; Guo & al., 2017). The relationship among the subfamilies was further supported by a recent phylogenomic study based on chloroplast genomes and nuclear ribosomal DNA sequences (Hoekstra & al., 2017). The tribe Miliuseae is the largest tribe in subfam. Malmeoideae, with more than 550 species in 23 currently accepted genera. Phylogenetic relationships in the tribe remain poorly understood, however: although it is consistently retrieved as a well-supported clade in molecular phylogenetic analyses, the backbone of the phylogeny remains largely unresolved (Mols & al., 2004a, b; Couvreur & al., 2011; Chatrou & al., 2012; Thomas & al., 2012; Chaowasku & al., 2013a, 2014; Guo & al., 2014, 2017; Xue & al., 2014, 2016, 2017).

Article history: Received: 3 Jul 2017 | returned for (first) revision: 14 Sep 2017 | (last) revision received: 19 Dec 2017 | accepted: 20 Dec 2017 | published: online fast track, n/a; in print and online issues, 9 May 2018 || **Associate Editor:** Michael D. Pirie ||

Recent molecular phylogenetic studies have clarified generic circumscriptions in the Miliuseae and resulted in the segregation of disparate elements from the previously highly polyphyletic genus *Polyalthia* Blume s.l., including removal of species now placed in two new genera—*Maasia* Mols & al. (Mols & al., 2008) and *Huberantha* Chaowasku (Chaowasku & al., 2012a [as "*Hubera*"], 2015)—and the transfer of species to *Fenerivia* Diels (Saunders & al., 2011), *Marsypopetalum* Scheff. (Xue & al., 2011), *Monoon* Miq. (Xue & al., 2012), *Goniothalamus* (Blume) Hook.f. & Thomson (Tang & al., 2013), *Meiogyne* Miq. (Xue & al., 2014), and *Wangia* X.Guo & R.M.K.Saunders (Xue & al., 2016). The circumscription of *Polyalthia* s.str. was consequently redefined (Xue & al., 2012). Several names in *Polyalthia* nevertheless remain unresolved, awaiting assignment to specific genera (Xue & al., 2012; Xue 2013), including *P. litseifolia* C.Y.Wu ex P.T.Li. The protologue of this name was published in 1976 based on a collection (*Sino-Russia Exped. 9488*, KUN & PE) with very young fruits that are only 2–3 mm long from Jinghong, Yunnan Province, China, in 1957 (Li, 1976; Li & Gilbert, 2011). A specimen with mature fruits was subsequently collected in 1989 (*H. Zhu & H. Wang 2480*, KUN) and a flowering specimen was first collected in 1991 (*H. Zhu & H. Wang 3005*, KUN), both from Mengla County, Yunnan. Zhu & Wang (1993) were therefore able to supplement the previously inadequate description of the species. Sixty years after it was first collected, the species was only represented by five collections, with the type locality, Jinghong, and the second locality, Mengla, both dramatically deforested (Wang, 1992).

Based solely on the morphological information derived from the limited collections available, Xue & al. (2012) refrained from inferring its taxonomic placement when realigning *Polyalthia* species to different genera. In the protologue, the Latin diagnosis states "Affinis *P. thorelii* Finet et Gagnep. ex Indo-China, sed foliis membranaceis, nervis lateralibus 13–16-paribus differt." The leaf shape and venation of the type specimen of *P. litseifolia* resemble those of *P. thorelii*, although the latter species has thicker leaves and fewer secondary veins, and lacks foliar glands and subpetiolar buds (Pierre, 1881). *Polyalthia thorelii* furthermore has multiple flowers per inflorescence (Pierre, 1881), whereas *P. litseifolia* has inflorescences that are reduced to a solitary flower. *Polyalthia thorelii* has a single seed in each monocarp, and was accordingly transferred to *Monoon* (Xue & al., 2012). As Li (1976) described *P. litseifolia* based on specimens with young fruits that are only 2–3 mm long, the author failed to report information on seed number; based on additional collections, however, more than two seeds per monocarp are found in *P. litseifolia* (Zhu & Wang, 1993), indicating that it is unlikely to belong to *Monoon.* Although *Polyalthia* s.str. is characterized by having more than two seeds per monocarp, *P. litseifolia* differs from *Polyalthia* spp. in not having the characteristic asymmetrical leaf base, brochidodromous venation, and spiniform endosperm ruminations. Fortunately, the recent collection of additional material of *P. litseifolia* has enabled us to conduct a molecular phylogenetic study to assess the taxonomic affinities of this enigmatic species. The molecular results presented here reveal that it does not belong to *Polyalthia*, but falls within the same clade as a potentially undescribed genus that was previously demonstrated to be sister to the Neotropical clade in the tribe Miliuseae (Chaowasku & al., 2014). The only known material of this undescribed genus are three accessions from Thailand, including two sterile specimens (*T. Chaowasku 108*, L; *Nakorn-Thiemchan NTC16*, L) collected from a mountainous area of Chiang Mai Province, and one fruiting specimen (*T. Chaowasku 111*, L) from a cultivated plant in Thailand; the fruit of the latter specimen was represented by a single detached monocarp that was subglobose and multi-seeded (Chaowasku & al., 2014). Because of the lack of sufficient flowering and fruiting materials, the new species and genus have yet to be formally described.

While investigating the identity of *Polyalthia litseifolia*, we also assessed the enigmatic species *Desmos praecox* (Hook.f. & Thomson) Saff. *Desmos praecox*, which was transferred from *Unona praecox* Hook.f. & Thomson in 1912, is represented by only one specimen (*C.J. Simons s.n.*, K), collected from Assam in India (Hooker & Thomson, 1855, 1872; King 1893; Safford, 1912; Turner, 2015). In addition, two more collections from Thailand, *N. Morci 1323.0* (CMUB) and *Maxwell 96-468* (CMUB), were annotated as "*Desmos* aff. *praecox*" (Ng, 2010). The three collections all possess peculiar inflorescences that grow in the axils of the circular leaf scars where the old leaves have fallen, and comprise a solitary flower with long sub-equal linear petals; the species is furthermore obviously deciduous with only young leaves on the sheet. After comparing the three specimens with those flowering specimens of *P. litseifolia*—*H. Zhu & H. Wang 3005* (KUN), *H. Zhu, H. Wang & B.G. Li* 299 (HITBC) and *H. Wang 6301* (PE, HITBC)—we concluded that *D. praecox* is conspecific with *P. litseifolia* based on the same inflorescence position, flower morphology and the deciduous phenology. As a tree rather than a climber, this species is unequivocally not congeneric with *Desmos* and instead has affinities with tribe Miliuseae.

Members of tribe Miliuseae are predominantly distributed in tropical and subtropical Asia (from India, across continental Southeast Asia and Malesia), as well as in Australia and Oceania (Pacific islands such as New Caledonia and Fiji), although the tribe also includes an Afro-Malagasy clade within *Huberantha* (Chaowasku & al., 2012a, 2014; Thomas & al., 2015) as well as a clade comprising four genera distributed in Central America, viz. *Desmopsis* Saff., *Sapranthus* Seem., *Stenanona* Standl., and *Tridimeris* Baill. (Chaowasku & al., 2014; Ortiz-Rodriguez & al., 2016).

The Asian-Neotropical split in the Miliuseae is of considerable biogeographical interest, as it may provide additional insights into the processes underlying intercontinental tropical disjunctions in Annonaceae. Disjunctions between the Neotropics and tropical areas on the western border of the Pacific are a common biogeographic pattern in angiosperms: Van Steenis (1962) and Thorne (1972) identified more than 100 taxa, including 89 genera, showing such an amphi-Pacific tropical distribution. Amphi-Pacific tropical disjunctions in Annonaceae involving Asian and Neotropical taxa were previously identified within *Anaxagorea* A.St.-Hil. (Scharaschkin & Doyle, 2005), and between the Asian genus *Disepalum* Hook.f.

and the Neotropical genus *Asimina* Adans. (Li & al., 2017; Thomas & al., 2017), as well as the split of the Neotropical clade nested in predominantly Asian Miliuseae (Chaowasku & al., 2014). Numerous hypotheses have been proposed to explain amphi-Pacific tropical disjunctions (Van Damme & Sinev, 2013, and references therein), but most recent studies have invoked either the boreotropics hypothesis or transoceanic long-distance dispersal. The boreotropics hypothesis (Wolfe, 1975; Tiffney, 1985; Morley, 2000) explains tropical intercontinental disjunctions by vicariance of populations that were previously connected by suitable habitats and land bridges in the Paleocene and Eocene due to climate deterioration in the late Eocene and Oligocene. This hypothesis has been highlighted as the most plausible explanation for tropical intercontinental disjunctions based on the fossil record and/or temporal congruence of molecular divergence time estimates in studies of various plant groups (e.g., Davies & al., 2002, 2005; Baker & Couvreur, 2013) including several Annonaceae taxa (Erkens & al., 2009; Couvreur & al., 2011; Thomas & al., 2015, 2017; Li & al., 2017). However, temporal incongruence of molecular divergence time estimates with the boreotropical hypothesis have indicated that post-boreotropical dispersal and vicariance likely also had a major impact on the assembly of tropical floras and shaping tropical intercontinental disjunctions (e.g., Clayton & al., 2009; Michalak & al., 2010; Christenhusz & Chase, 2013; Nie & al., 2013; Thomas & al., 2015).

Based on the newly available material of *P. litseifolia*, detailed morphological comparison with related taxa, as well as newly generated DNA sequence data and molecular phylogenetic evidence, this study aims to: (i) formally describe the new monotypic genus, *Wuodendron* gen. nov.; and (ii) provide molecular divergence time estimates for the Neotropical-Asian split in Miliuseae and discuss processes potentially underlying Neotropical-Asian disjunctions in Annonaceae.

■ MATERIALS AND METHODS

Taxon and DNA region sampling. — Newly generated DNA sequence data of two accessions of *Polyalthia litseifolia* (*B. Xue 190*, IBSC and *B. Xue 256*, IBSC; voucher information and GenBank accession numbers given in Appendix 1), were integrated with data of seven cpDNA regions (*atpB-rbcL*, *matK*, *ndhF, psbA-trnH*, *rbcL*, *trnL-F*, *ycf1*) of 107 Annonaceae accessions selected from previous datasets (Chaowasku & al., 2014; Guo & al., 2017; Thomas & al., 2017). The final dataset comprised a total of 109 ingroup accessions, representing 105 species, all Annonaceae tribes and ca. 95% of genera including all currently accepted genera in subfamily Malmeoideae as well as tribe Miliuseae. Seven accessions from the other five Magnoliales families (Degeneriaceae, Eupomatiaceae, Himantandraceae, Magnoliaceae, Myristicaceae) were included as the outgroup.

DNA extraction, amplification and sequencing. — Genomic DNA was extracted from herbarium materials using a modified cetyl trimethyl ammonium bromide (CTAB) method (Doyle & Doyle, 1987). A single amplification protocol was used for amplification of the chloroplast regions: template denaturation at 94°C for 5 min, followed by 35 cycles of denaturation at 95°C for 30 s; primer annealing at 50°C for 1 min; and primer extension at 72°C for 1 min, followed by a final extension step at 72°C for 10 min. The primers used to amplify the *psbA-trnH* intergenic spacer were psbAF (Sang & al., 1997) and trnH2 (Tate & Simpson, 2003); other primers are the same as those used by Thomas & al. (2012). PCR products were visualized using agarose gel electrophoresis. Successful amplifications were purified, and sequenced on an Applied Biosystems 3730xl DNA Analyzer at Sangon Biotech (Shanghai), Guangzhou, China.

Alignment and phylogenetic analyses. — Sequences were assembled, edited and aligned using Geneious v.10 (Kearse & al., 2012; Biomatters, 2016). A total of 18 ambiguously aligned positions in the *trnL-F* matrix were excluded from the analyses. An inversion (15 positions) in the *psbA-trnH* matrix was reverse complemented to retain substitution information in the fragments (Pirie & al., 2006).

Maximum parsimony (MP) analyses of the seven combined regions were conducted using PAUP v.4.0b10 (Swofford, 2003). All characters were weighted equally and gaps treated as missing data. The most parsimonious trees were obtained with heuristic searches of 1000 replicates of random stepwise sequence addition, tree bisection-reconnection (TBR) branch swapping with no limit to the number of trees saved. Percentage bootstrap support (BS) was calculated following Müller (2005), with 10,000 simple stepwise addition replicates with TBR branch swapping and no more than 10 trees saved per replicate.

Maximum likelihood (ML) analyses were performed using the NSF Extreme Science & Engineering Discovery Environment (XSEDE) applications of RAxML v.8.2.10 (Stamatakis, 2006) provided by the CIPRES Science Gateway (Miller & al., 2010). The dataset was divided into partitions based on DNA region identity. Fifty inferences were run under the general time-reversible nucleotide substitution model with among-site rate variation modelled with a gamma distribution (GTR+Γ). One thousand non-parametric bootstraps were subsequently performed under the partitioned data mode.

Bayesian analysis was performed using the NSF Extreme Science & Engineering Discovery Environment (XSEDE) application of MrBayes v.3.2.6 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003) provided by the CIPRES Science Gateway (Miller & al., 2010). PartitionFinder2 was used to test the dataset for partitions (model of evolution: mrbayes; model of selection: AICc; scheme search: greedy) (Guindon & al., 2010; Lanfear & al., 2012, 2017). The best partition scheme suggested seven partitions based on DNA region identity with GTR+Γ chosen for *atpB-rbcL*, *matK*, *psbA-trnH*, and *trnL-F* regions and GTR+I+Γ selected for the *ndhF*, *rbcL*, and *ycf1* regions. A parallel Bayesian analysis under non-partitioned model was also undertaken, with GTR+I+Γ model selected for the concatenated matrix in jModelTest v.2.1.6 (Darriba & al., 2012). Two independent Metropolis-coupled Markov chain Monte Carlo (MCMC) analyses were run. Each search used three incrementally heated and one cold Markov chain, and was run for 10 million generations and sampled every 1000th generation. The temperature parameter was set to 0.08. The mean branch length prior was set from the default mean (0.1) to 0.01 (brlenspr = unconstrained: exponential (100.0)) to reduce the likelihood of stochastic entrapment in local tree length optima (Brown & al., 2010; Marshall, 2010). Convergence was assessed using the standard deviation of split frequencies, with values <0.01 interpreted as indicating good convergence. The first 25% of samples (2500 trees) were discarded as burn-in, and the post-burn-in samples summarized as a 50% majority-rule consensus tree.

Divergence time estimation. — Four of the five accessions of the undescribed genus and three accessions of *Meiogyne* were pruned from the original dataset so that all genera were represented by a single accession. The rationale of fossil calibrations and analysis settings follow Thomas & al. (2017): in short, two fossil calibrations (*Endressinia brasiliana* Mohr & Bernardes-de-Oliveira, late Aptian, ca. 112 Ma; and *Futabanthus asamigawaensis* Takahashi & al., Late Cretaceous, ca. 89 Ma) were used to constrain the Magnoliineae and Annonaceae crown nodes, respectively. Two calibration schemes (CS1 and 2) were implemented: CS1 provided minimum ages based on the fossil ages (Magnoliineae crown node fixed to 112.6 Ma; uniform calibration prior distribution from 89 Ma to 112.6 Ma assigned to the Annonaceae crown node); and CS2 biased results towards considerable older divergence times (Magnoliineae crown node fixed to 136.4 Ma; and a uniform calibration prior distribution from 89 Ma to 136.4 Ma assigned to the Annonaceae crown node). The latter scheme biases the estimates towards considerably older ages than the occurrence of the single fossilized structures of *Endressinia* and *Futabanthus*, and includes a provisional maximum age constraint (Thomas & al., 2015). Analyses were performed using BEAST v.1.8.4 (Drummond & Rambaut, 2007) under an uncorrelated lognormal relaxed clock (UCLD), the Yule process selected as tree prior, a starting tree which was random except for adhering to the hard calibration priors (initial values under CS1: Magnoliineae crown node 112, Annonaceae crown node 89; initial starting values under CS2: Magnoliineae crown node 136.4, Annonaceae crown node 89), eight Markov chain Monte Carlo (MCMC) analyses of 50 million generations each, sampled every 5000th generation. Tracer v.1.6 (Rambaut & al., 2014) was used to check parameter convergence, effective sample sizes, and sufficient burn-in selection, which was set to 20% of the initial samples. The results were summarized using the maximum clade credibility (MCC) tree option in TreeAnnotator v.1.8.4 (Drummond & Rambaut, 2007).

Morphological studies. — Comparative morphological data were obtained from specimens deposited in CANT, CMUB, HITBC, IBSC, K, KUN, L, and PE herbaria and from the literature (Li, 1976; Klucking, 1986; Schatz, 1987; Van Setten & Koek-Noorman, 1992; Van Heusden, 1992, 1994; Zhu & Wang 1993; Bakker, 2001; Mols & al., 2004a; Schatz & Maas, 2010; Chaowasku & al., 2014). Field surveys were carried out in Jinghong City, Jiangcheng County, Lincang County and Mengla County in Yunnan Province in China, as well as Kachin State in Myanmar, and Chiang Mai, Kanchanaburi and Uttaradit Provinces in Thailand.

Carpels, stamens and pollen of the new species were removed from air-dried herbarium specimens and were directly attached to metal stubs using adhesive carbon tabs, sputter-coated with gold/palladium, and viewed using a JSM-6360LV scanning electron microscope at 25 kV.

■ RESULTS

The concatenated alignment of the 116-terminal dataset consisted of 8280 characters. The MP heuristic search retrieved 240 most parsimonious trees of 8266 steps (consistency index, CI = 0.530; retention index, RI = 0.724).

The MP, ML and Bayesian analyses with partitioned and non-partitioned strategies resulted in similar topologies. The 50% majority-rule consensus tree resulting from the Bayesian analyses under the seven-partitioned model is shown in Figs. 1 & 2. The results of Bayesian analyses under non-partitioned model is shown in Figs. S1 & S2 (Electr. Suppl). The results are consistent with previous phylogenetic analyses of the family.

The two accessions of *Polyalthia litseifolia* were strongly supported (PP [posterior probability] = 1, MP BS = 100, ML BS = 100) as members of the same clade as the undescribed genus (sensu Chaowasku & al., 2014), and the whole clade was retrieved as sister to the Neotropical clade (comprising *Desmopsis*, *Sapranthus*, *Stenanona*, and *Tridimeris*) with strong support in Bayesian analyses (PP = 1) and weak support in MP analyses (BS = 65) and ML analyses (BS = 71). The broader clade comprising the undescribed genus and the Neotropical clade is collectively sister to *Meiogyne*, although only receiving support in the Bayesian analyses (PP = 0.96), consistent with the relationship revealed by Chaowasku & al. (2014) and Ortiz-Rodriguez & al. (2016). The relationship is also supported by a phylogenomic study of the subfamily Malmeoideae based on chloroplast sequences (D.C. Thomas & al., unpub. data). The collective clade, inclusive of the undescribed genus and representative species from the genera *Desmopsis*, *Meiogyne*, *Sapranthus*, *Stenanona* and *Tridimeris* are labeled as the "Meiogynoid" clade in Fig. 2, corresponding to clade D1 in Chaowasku & al. (2014). According to Chaowasku & al. (2014), the "Meiogynoid" clade is characterized by a suite of character states that are symplesiomorphic, e.g., petals that are more or less similar in shape and size in both whorls and the multi-ovuled ovaries.

Divergence times of selected nodes are provided in Table 1. Morphological observations are illustrated in Figs. 3 & 4 and evaluated in detail in the Discussion.

■ DISCUSSION

Morphological comparison. — Our molecular phylogenetic analyses strongly support the inference that *Polyalthia litseifolia* is a member of the same clade as the undescribed genus (sensu Chaowasku & al., 2014) which is sister to the Neotropical clade in the tribe Miliuseae. Morphological examination of the three collections sampled by Chaowasku & al. (2014) revealed that they all possess foliar glands and subpetiolar buds. Apart from *P. litseifolia*, foliar glands are also observed in *P. verrucipes* C.Y.Wu ex P.T.Li and *P. chinensis* S.K.Wu & P.T.Li. The combination of subpetiolar buds together with the peculiar inflorescences, growing from the axils of the circular leaf scars where old leaves have fallen, is rare in Annonaceae, only having been recorded previously in *Annona* L. (discussed below). The subglobose multi-seeded monocarp of the only fruiting specimen available (*T. Chaowasku 111*, L) and the lamelliform endosperm ruminations are furthermore consistent with *P. litseifolia*. *Polyalthia litseifolia* was furthermore recorded growing in the mountains of northwest Thailand, bordering Myanmar (Hong Wang, pers. comm.). After detailed examination of the three collections assigned to the undescribed genus by Chaowasku & al. (2014) and nine additional specimens collected in Thailand (Chiang Mai: *Chaowasku 114* and *Nakorn-Thiemchan NTC20*, CMUB, *Maxwell 92-297*, L; Kanchanaburi: *Chaowasku 167*, CMUB; Lampang: *N. Morci 1323.0* and *Maxwell 96-468* CMUB; Uttaradit: *Nakorn-Thiemchan NTC22* and *Nakorn-Thiemchan NTC23*, CMUB) and northern Vietnam (*N.M. Cuong 403*, L), it is clear that these specimens are conspecific with *P. litseifolia*,

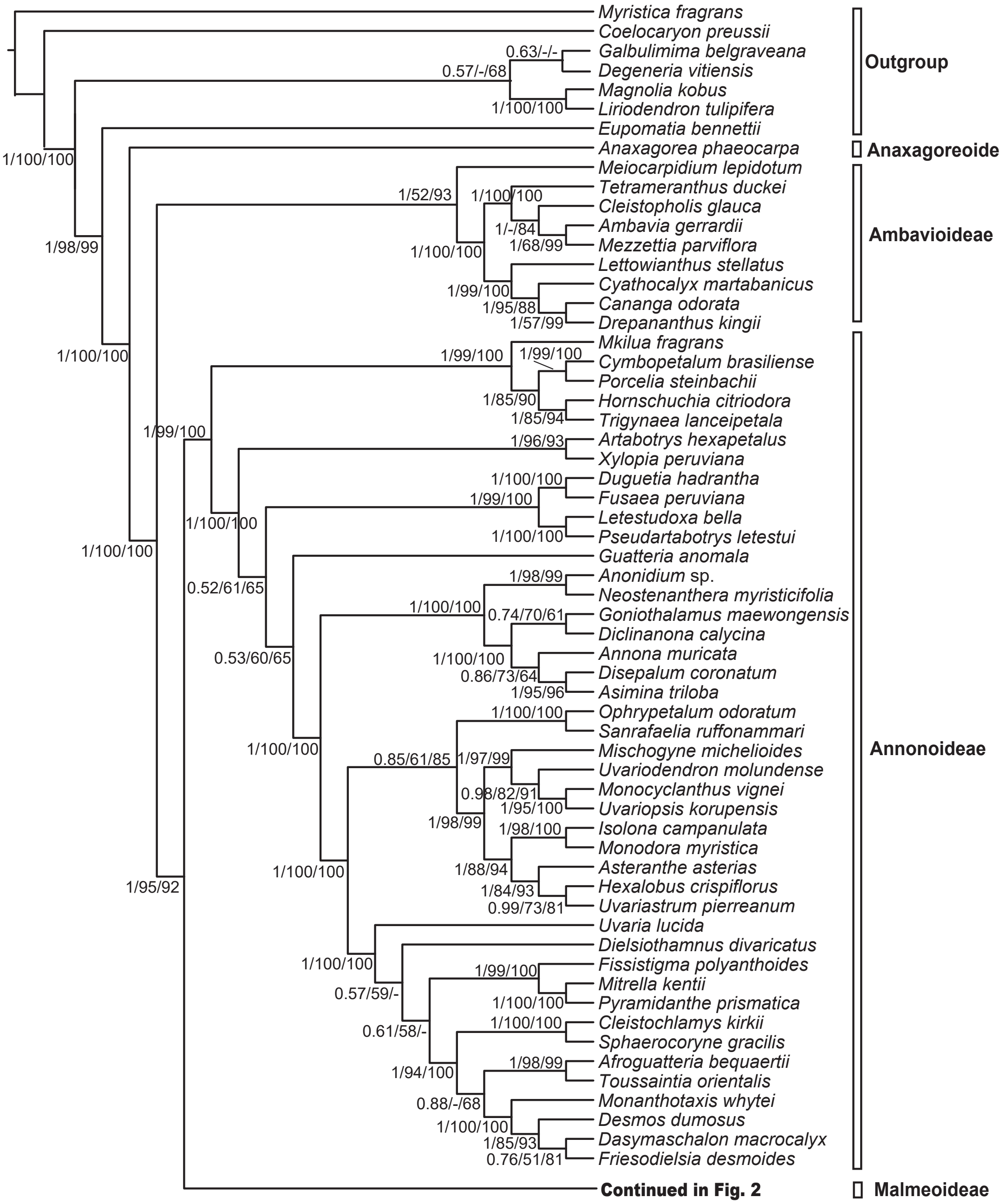

Fig. 1. Bayesian 50% majority-rule consensus tree under partitioned models (cpDNA data: *atpB-rbcL*, *matK*, *ndhF, psbA-trnH*, *rbcL*, *trnL-F*, and *ycf1*; 116 accessions), showing the outgroup and Annonaceae subfamilies Anaxagoreoideae, Ambavioideae, and Annonoideae. Numbers at the nodes indicate Bayesian posterior probabilities (≥0.5%), maximum parsimony bootstrap values (>50%), maximum likelihood bootstrap values (>50%) in that order.

Table 1. Divergence time estimates for selected nodes.

		CS1		CS2	
Node	Clade	Mean [Ma]	95% HPD [Ma]	Mean [Ma]	95% HPD [Ma]
1	Meiogynoid clade stem	14.3	18.0–11.1	16.9	21.8–12.8
2	Meiogynoid clade crown	13.4	17.1–10.1	15.8	20.4–11.5
3	*Wuodendron*–Neotropical clade split	12.1	15.8–8.8	14.3	18.7–10.1
4	Neotropical clade crown	10.6	14.3–7.4	12.5	16.7–8.4

CS: calibration scheme (see Material and Methods for details of CS1 and 2).
HPD, highest posterior density date range; Ma, million years ago.

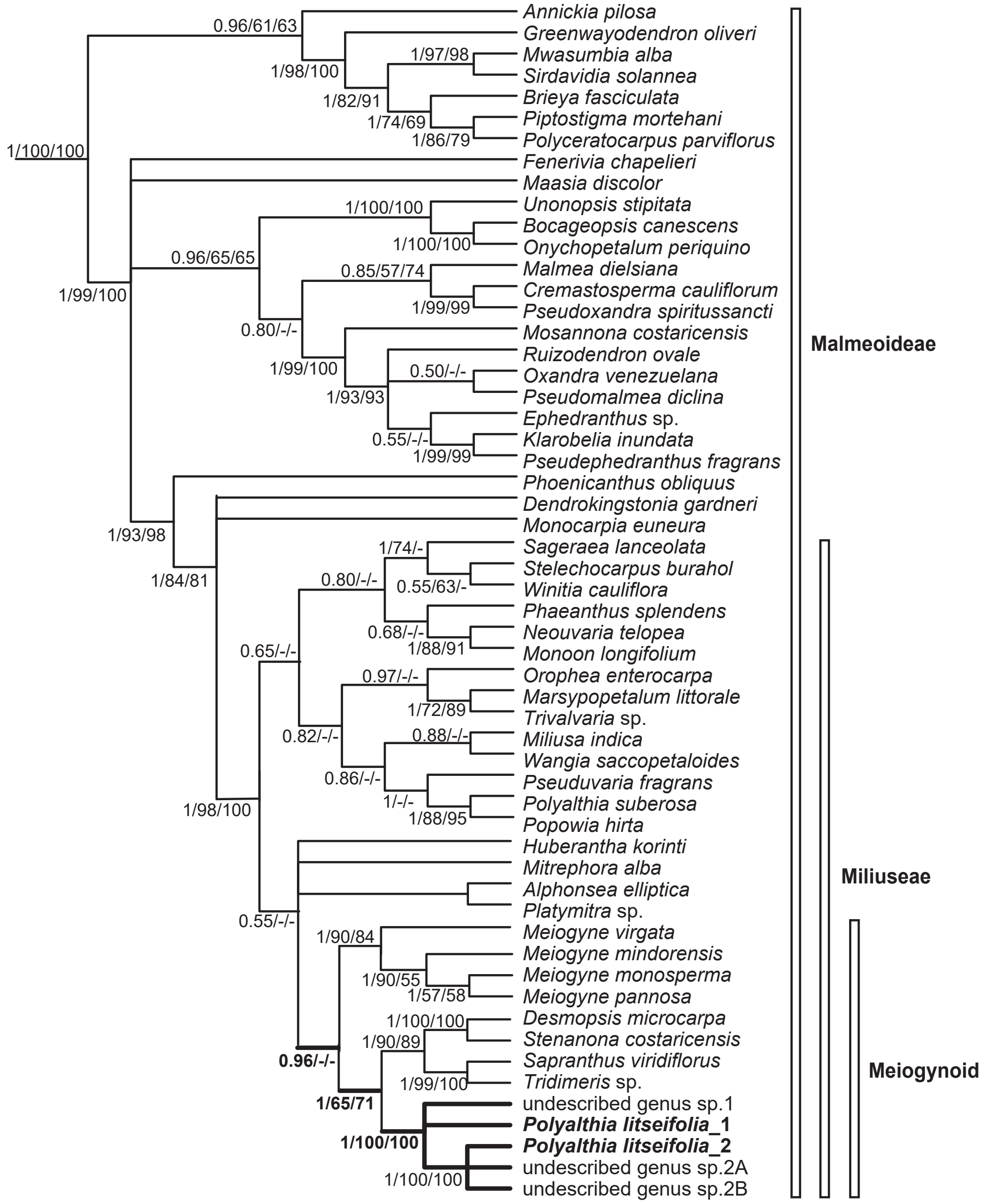

Fig. 2. (Continued from Fig. 1) Bayesian 50% majority-rule consensus tree under partitioned models (cpDNA data: *atpB-rbcL*, *matK*, *ndhF, psbA-trnH*, *rbcL*, *trnL-F*, and *ycf1*; 116 accessions), showing Annonaceae subfamily Malmeoideae. Numbers at the nodes indicate Bayesian posterior probabilities (≥0.5%), maximum parsimony bootstrap values (>50%), maximum likelihood bootstrap values (>50%) in that order.

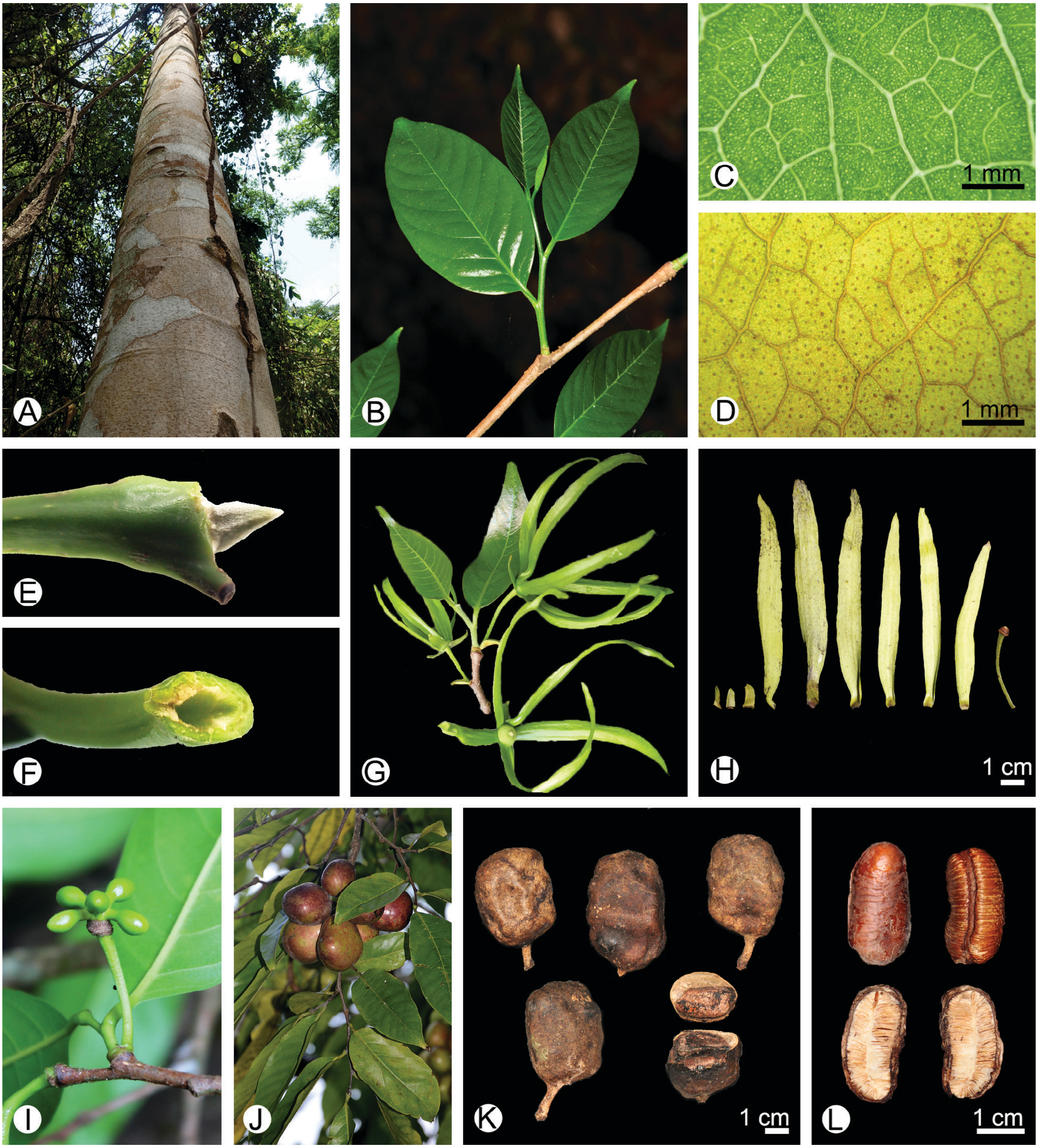

Fig. 3. Morphology of *Wuodendron praecox* comb. nov. (= *Polyalthia litseifolia*). **A,** Trunk, showing grayish bark with lenticels; **B,** Young leaves; **C,** Close-up of the adaxial surface of fresh leaf, showing glands; **D,** Close-up of the adaxial surface of dried leaf, showing glands; **E,** Subpetiolar bud; **F,** Swollen base of the petiole that encloses the bud; **G,** Inflorescence and new leaf growing from the axil of the dropped leaf; **H,** Dissected flower, showing three sepals, three outer petals, three inner petals and the pedicel (*Y.H. Tan 12258*, HITBC); **I,** Young fruit, showing the infructescence and the branchlet growing from the same axil (*Nakorn-Thiemchan NTC23*, CMUB); **J,** Mature fruit; **K,** Monocarps, showing slight constrictions between seeds, and multiple seeds in one row in one monocarp (*Y.H. Tan 10946*, HITBC); **L,** Cylindrical seeds, showing the distinct circumferential groove; and the longitudinal section of the seed, showing lamelliform endosperm rumination (*Y.H. Tan 10946*, HITBC).

because the specimens all share the subpetiolar buds and foliar glands, which is a unique character combination in the tribe Miliuseae. A collection with young fruits from Thailand (*Nakorn-Thiemchan NTC23*, CMUB) (Fig. 3I) matches the type specimens of *P. litseifolia*. Moreover, this conclusion is also supported by molecular data, as the accessions from Thailand and the samples of *P. litseifolia* from China are strongly supported as members of the same clade.

The morphological data also provide strong support for distinguishing *P. litseifolia* from closely related genera in the Meiogynoid clade. The clade accordingly warrants recognition as distinct genus, and is described below as *Wuodendron*. *Wuodendron* is closely related to the Neotropical clade (*Desmopsis*, *Sapranthus*, *Stenanona*, *Tridimeris*) and the Indo-Malayan and Australasian-Pacific genus *Meiogyne*. A recent phylogenetic study based on a more comprehensive taxon sampling suggested that *Desmopsis* and *Stenanona* are probably congeneric (Ortiz-Rodriguez & al., 2016), but taxonomic changes have yet to be made. Morphological comparisons were made between the new genus and the five closely related genera *Desmopsis*, *Meiogyne*, *Sapranthus*, *Stenanona* and *Tridimeris* (Table 2). *Wuodendron* is characterized by the following morphological features: (i) petioles with an enlarged base that encloses the subpetiolar bud (Fig. 3E, F); (ii) leaves with secondary veins that are upturned and gradually diminish towards the apex, connecting to super-adjacent secondaries by a series of cross veins without forming prominent marginal loops (i.e., eucamptodromous venation sensu Hickey, 1979) (Fig. 3B); (iii) flowers that are solitary and grow in the axils of pilose circular leaf scars where the old leaves have fallen, sometimes accompanied with the young branchlet (Fig. 3G); (iv) petals that are similar in shape and size in both whorls; (v) 3–5(–8) ovules per carpel (and hence seeds per monocarp), in one or two row(s) (Fig. 3K); (vi) seeds with a distinct circumferential groove and lamelliform ruminations (Fig. 3L); and (vii) disulculate pollen grains (Fig. 4C).

Subpetiolar buds are rare in Annonaceae, and this represents the first such observation in the tribe Miliuseae, although similar buds have previously been recorded in *Annona* (Soler & Cuevas, 2009; Liu & al., 2016). *Wuodendron* resembles

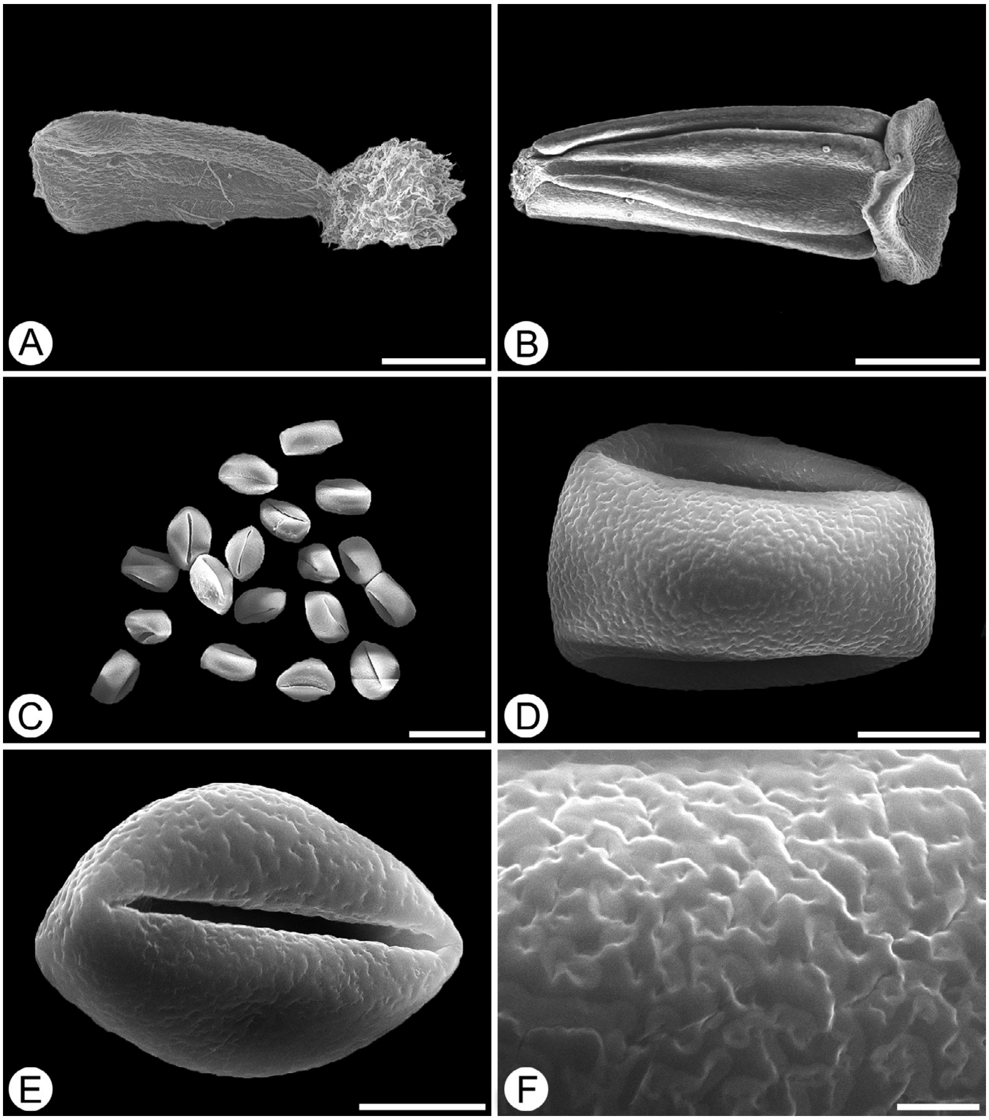

Fig. 4. Morphology of carpel, stamen, and pollen of *Wuodendron praecox* comb. nov. (= *Polyalthia litseifolia*) (scanning electron micrographs). **A,** Carpel; **B,** Stamen; **C,** Pollen grains; **D,** Pollen grain showing two germination zones; **E,** Lateral view of pollen grain, one germination zone showing on top, the other one beneath (not shown); **F,** Rugulate pollen exine ornamentation. — Scale bars: A & B = 500 µm; C = 50 µm; D & E = 10 µm; F = 2 µm. Voucher specimen: *B. Xue 256* (IBSC).

Meiogyne and *Sapranthus* in its eucamptodromous leaf venation; this feature is common in the tribe Miliuseae, as well as the closely related tribes Monocarpieae (Mols & Keßler, 2000) and Dendrokingstonieae (Chaowasku & al., 2012b). Eucamptodromous venation is therefore likely to be symplesiomorphic for all three genera, with brochidodromous venation the derived state in *Desmopsis*, *Stenanona* and *Tridimeris*.

Inflorescences within Annonaceae are either terminal or axillary (Fries, 1959), and although these two conditions rarely coexist within genera (Koek-Noorman & al., 1990); terminal inflorescences can appear leaf-opposed or become extra-axillary (Weberling & Hoppe, 1996). Inflorescences are axillary in *Meiogyne* p.p., *Tridimeris* and *Wuodendron*, in contrast with those of *Desmopsis*, *Sapranthus* and *Stenanona* (Schatz & Maas, 2010; Chaowasku & al., 2014). It could be hypothesized that axillary inflorescences are possibly symplesiomorphic for the Meiogynoid clade, with parallel shifts to the terminal position in *Desmopsis*, *Sapranthus* and *Stenanona*. The inflorescences of *Wuodendron* grow in the axils of circular leaf scars of leaves that have fallen, often accompanied with the young branchlet. Flowering and leaf flushing occur simultaneously in spring: when inflorescence growth is accompanied by a young branchlet (Fig. 3G), it is evident in the fruiting stage that the fruit and the emerging branch originate from the same axil (Fig. 3I).

The two petal whorls in Annonaceae flowers can be morphologically distinct or similar. The petals in the two whorls are similar throughout the Meiogynoid clade, although with some deviations occurring in *Meiogyne bidwillii* (Benth.) D.C.Thomas & al. which possesses sepaloid outer petals (Thomas & al., 2012; Xue & al., 2014). Morphologically similar petal whorls are likely to be symplesiomorphic for the Meiogynoid clade (Chaowasku & al., 2014). Nevertheless, inner petals with verrucose or corrugated base of the adaxial surface and innermost stamens with tongue-shaped apical prolongations are only found in *Meiogyne* in the Meiogynoid clade, and is synapomorphic for the genus. These two characters easily distinguish *Wuodendron* from *Meiogyne*.

Wuodendron bears multiple ovules in each ovary in one or two rows. This feature is observed in most other species in the Meiogynoid clade, and is also likely to be symplesiomorphic (Chaowasku & al., 2014). In addition to *Wuodendron*, lamelliform endosperm ruminations are also recorded in *Desmopsis* p.p., *Meiogyne* p.p., *Sapranthus*, and *Tridimeris* p.p. (Van Setten & Koek-Noorman, 1992). Chaowasku & al. (2014) interpreted this character state as synapomorphic for the Meiogynoid clade, although with some subsequent independent reversals

Table 2. Morphological comparisons between *Wuodendron* and closely related genera.

Character	*Wuodendron* gen. nov.	*Meiogyne* Miq.	*Sapranthus* Seem.	*Desmopsis* Saff.	*Tridimeri*s Baill.	*Stenanona* Standl.
Subpetiolar bud	+	–	–	–	–	–
Leaf venation	Eucamptodromous	Eucamptodromous	Eucamptodromous	Brochidodromous	Brochidodromous	Brochidodromous
Position of inflorescence	Growing from the axils of the circular leaf scars where old leaves have fallen	Axillary, sometimes terminal	Terminal, leaf-opposed, among leaves or cauliflorous	Terminal, leaf-opposed or internodal, among leaves, ramiflorous or cauliflorous	Axillary	Terminal, leaf-opposed to supra-axillary, on leafless branches, from the main trunk, basiflorous, or flagelliflorous
Shape of outer petals	Similar to inner petals	Similar to inner petals, sometimes sepaloid	Similar to inner petals	Similar to inner petals	Similar to inner petals	Similar to inner petals
Base of the adaxial surface of the inner petals	Smooth	Verrucose or corrugated	Smooth	Smooth	Smooth	Smooth
Tongue-shaped apical prolongations on innermost stamens	+	–	–	–	–	–
Seed number per monocarp	3–5(–8)	3–20	1–19	1–7(–14)	3–18	1–8
Seed arrangement	1- or 2-seriate	1- or 2-seriate	1- or 2-seriate	1- or 2-seriate	1- or 2-seriate	1- or 2-seriate
Endosperm ruminations	Lamelliform	Lamelliform or spiniform	Lamelliform	Spiniform to peg-shaped	Flattened pegs, becoming lamelliform towards raphe	Spiniform to peg-shaped
Pollen apertures	Disulculate	Disulculate or crytpoaperturate	Disulculate or cryptoaperturate	Disulculate or cryptoaperturate	Disulculate or cryptoaperturate	Disulculate or cryptoaperturate

Data sources: Hooker & Thomson (1855, 1872); King (1893); Li (1976); Klucking (1986); Schatz (1987); Van Setten & Koek-Noorman (1992); Van Heusden (1992, 1994); Zhu & Wang (1993); Bakker (2001); Mols & al. (2004a); Schatz & Maas (2010); Chaowasku & al. (2014).

to spiniform rumination. Disulculate or cryptoaperturate pollen grains are widespread in the tribe Miliuseae, and have been inferred as synapomorphic for the tribe (Chaowasku & al., 2014).

Origin of Asian-Neotropical disjunctions in Annonaceae. — Three Asian-Neotropical disjunctions have been identified in Annonaceae: (i) an infrageneric split in *Anaxagorea* dated at ca. 29 Ma (Scharaschkin & Doyle, 2005); (ii) the split of the Asian genus *Disepalum* and the Neotropical genus *Asimina* in tribe Annoneae estimated at 27.4–23.6 Ma (Thomas & al., 2017); and (iii) the split between the new genus *Wuodendron* and the Neotropical clade in tribe Miliuseae estimated at 14.3–12.1 Ma (this study).

The Oligocene disjunctions in *Anaxagorea* and tribe Annoneae can be interpreted as temporally congruent with the boreotropics hypothesis (see Introduction) and the result of the disruption of wider distributions in the boreotropics of N America and Asia due to climate deterioration in the late Eocene and Oligocene and subsequent vicariance. Based on molecular divergence time and ancestral range estimations this has been evaluated as a plausible scenario for the *Asimina*-*Disepalum* split (Thomas & al., 2017). For *Anaxagorea*, however, Scharaschkin & Doyle (2005) used parsimony-based ancestral area reconstructions that identified S America as the ancestral range. They emphasized that the results of their ancestral area reconstructions and divergence time estimates were not congruent with the hypothesis that the boreotropics facilitated dispersal via N America. In the case of *Wuodendron*, both minimum ages (analyses under the calibrations scheme 1) and divergence times estimates biased towards considerably older ages (calibration scheme 2) indicate that the disjunction originated in the Miocene, which is temporally incongruent with the boreotropics hypothesis.

The presence of fossilized Annonaceae seeds from Eocene deposits of the London Clay flora (Collinson, 1983) as well as Eocene deposits in northern America (Manchester, 1994) show that the boreotropics harbored a diverse Annonaceae flora and likely played an important role in facilitating intercontinental dispersal. However, while molecular divergence time estimates indicate temporal congruence with the boreotropical hypothesis for several older splits in Annonaceae (Erkens & al., 2009; Couvreur & al., 2011; Thomas & al., 2015, 2017), numerous other intercontinental splits across the family were inferred in a Miocene timeframe, considerably postdating Oligocene climate deterioration and the almost complete disappearance of tropical forest from the northern mid-latitudes (Collinson,1992; Wolfe, 1992; Morley, 2000). The *Wuodendron*-Neotropical clade divergence belongs to the latter category and highlights the fact that post-boreotropical dispersal likely also played a major role in shaping intercontinental disjunctions in the family (Thomas & al., 2015).

Deciduousness in Annonaceae. — Although most Annonaceae species are evergreen, a (semi-)deciduous habit is recorded in several species. Within the tribe Miliuseae, for example, a (semi-)deciduous habit is common in *Miliusa* Lesch. ex A.DC., not only in species distributed in Austro-Malesia where monsoonal climate is typical—e.g., *M. brahei* (F.Muell.) Jessup, *M. horsfieldii* (Benn.) Pierre, *M. koolsii* (Kosterm.) J.Sinclair, *M. novoguineensis* Mols & Kessler, *M. parviflora* Ridl., *M. traceyi* Jessup, and *M. vidalii* J.Sinclair (Mols & Keßler, 2003)—but also in species from mainland Asia such as *M. fragrans* Chaowasku & Kessler (Chaowasku & Keßler, 2013), *M. tomentosa* (Roxb.) Baill. ex Finet & Gagnep. and *M. velutina* (Dunal) Hook.f. & Thomson (Mols & Keßler, 2003). Chaowasku & al. (2013b) furthermore noted that there are associations between clades and habitat preferences in *Miliusa*: in two *Miliusa* clades most species occupy drier habitats (e.g., deciduous/dipterocarp forests), resulting in various degrees of the deciduous habit (Chaowasku & al., 2013b); it is therefore evident that habitat shifts occurred in *Miliusa* (Chaowasku & Keßler, 2013). Remarkably, the genus *Sapranthus* is predominantly distributed in tropical dry deciduous forest, and is often deciduous, e.g., *S. campechianus* (Kunth) Standl., *S. isae* J.G.Vélez & Cogollo, *S. palanga* R.E.Fr., and *S. violaceus* (Dunal) G.E.Schatz (Schatz, 1987; Vélez-Arango & Cogollo-Pacheco, 2007). Nevertheless, the above-mentioned species do not possess subpetiolar buds, although we observed some intermediates with canaliculate petioles in *S. palanga*.

Subpetiolar buds are typically found in plants from temperate regions, including *Actinidia* Lindl. p.p. (Li & al., 2007), *Calycanthus* L. (Chen & Ke, 2010), *Cladrastis* Rafin. (Li & Fan, 1994) and *Platanus* L. (Li & al., 2012). Such buds have been interpreted as an adaptation to protect the bud from low winter temperatures (Wang, 1992), and are accordingly rare in tropical plants (Wang, 1992). Leaf fall is a prerequisite for bud-break in species with subpetiolar buds, with natural leaf drop occurring after winter, resulting in a spring bud bursting and flowering. The deciduous phenology of *Wuodendron* is probably an adaptation to comparatively dry periods in seasonal rain forests. It is noteworthy that *Wuodendron* generally occurs at relatively high elevations, often exceeding 1000 m; the subpetiolar buds might therefore function in a similar way as those in temperate plants because sub-zero temperatures can be experienced in some mountainous areas.

■ TAXONOMY

Following detailed examination of protologues and specimens, we did not find any evidence to uphold both the poorly known *Desmos praecox* and *Polyalthia litseifolia* as distinct species. The basionym *Unona praecox* antedates *P. litseifolia* and hence its specific epithet has priority.

Wuodendron B.Xue, Y.H.Tan & Chaowasku, **gen. nov.** – Type: *W. praecox* (Hook.f. & Thomson) B.Xue, Y.H.Tan & X.L.Hou (≡ *Unona praecox* Hook.f. & Thomson).

Number of species. – One.

Diagnosis. – *Wuodendron* resembles the closely related genera *Desmopsis*, *Meiogyne*, *Sapranthus*, *Stenanona* and *Tridimeris*, with which it shares petals that are more or less similar in shape and size in both whorls and the multi-ovuled ovaries; *Wuodendron* differs, however, in having subpetiolar buds and inflorescences growing from the axils of the circular leaf scars where old leaves have fallen.

Description. – Large deciduous trees. Petioles with a furrow above, enlarged at base and enclosing the subpetiolar bud; leaf laminas elliptic, oblong, ovate or obovate, secondary veins parallel, upturned and gradually diminishing towards the apex, tertiary veins more or less percurrent to reticulate. Flowers solitary, growing from the axils of circular leaf scars where the old leaves have fallen, often accompanied by the young branchlet; sepals 3 per flower, triangular-lanceolate; petals 6 per flower in two whorls, sub-equal, linear; stamens numerous per flower, connective truncate; carpels 5–9 per flower, stigma broad and pubescent; ovules 3–5(–8) per carpel, 1- or 2-seriate. Fruits subglobose to oblong, slightly constricted between seeds. Seeds 3–5(–8) per monocarp, oblong, with a distinct circumferential groove; endosperm ruminations lamelliform.

Distribution. – A single species, known from China, India, Myanmar, Thailand, and Vietnam; as well as in Cambodia and Laos (Hong Wang, pers. comm.).

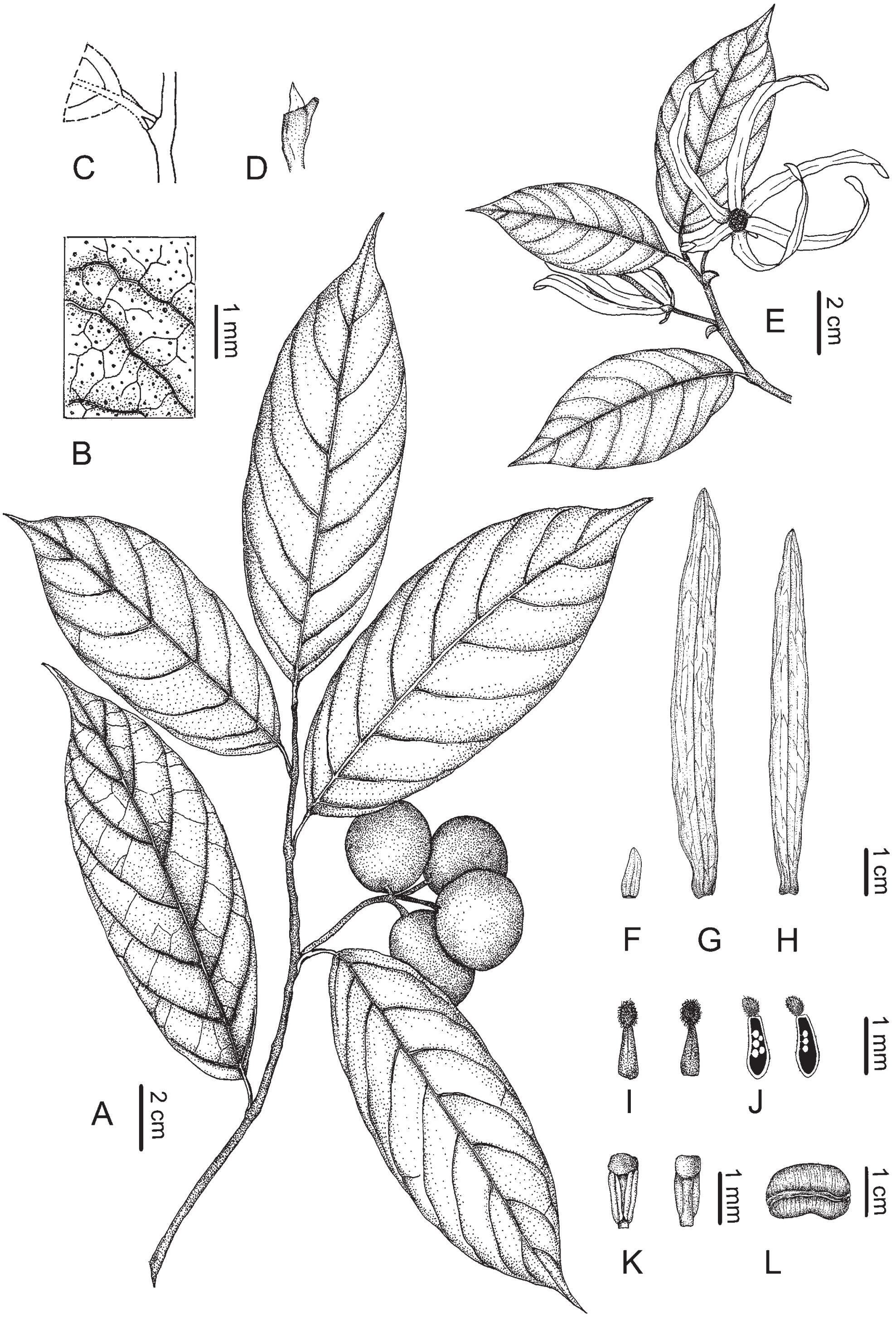

Fig. 5. *Wuodendron praecox* (= *Polyalthia litseifolia*). **A,** Fruiting branch; **B,** Close-up of adaxial surface of leaf, showing glands; **C,** Subpetiolar bud; **D,** Close-up of subpetiolar bud; **E,** Flowering branch; **F,** Sepal (adaxial view); **G,** Outer petal (adaxial view); **H,** Inner petal (adaxial view); **I,** Carpel; **J,** Carpel (ovules arranged in one row or two rows); **K,** Stamens (abaxial and adaxial view); **L,** Cylindrical seed. — A, *H. Zhu & H. Wang 2480* (KUN); B, *Sino-Russia Exped. 9488* (KUN, PE); C & D, *B. Xue 190* (IBSC); E, *Y.L. Li & B. Xue 300* (IBSC, KUN, PE, SING), F–H, *Y.H. Tan 12258* (HITBC); I–K, *B. Xue 256* (IBSC); L, *Y.H. Tan 10946* (HITBC). — Drawn by Zhengmeng Yang.

Etymology. – Named after Wu Zhengyi (= C.Y. Wu, of the Kunming Institute of Botany, Chinese Academy of Sciences), who proposed the name of *Polyalthia litseifolia*, in honor of his great contribution to plant taxonomy.

Wuodendron praecox (Hook.f. & Thomson) B.Xue, Y.H.Tan & X.L.Hou, **comb. nov.** ≡ *Unona praecox* Hook.f. & Thomson, Fl. Ind. 1: 136. 1855 ≡ *Desmos praecox* (Hook.f. & Thomson) Saff. in Bull. Torrey Bot. Club 1912: 39. 1912 – Lectotype (designated by Turner in Nordic J. Bot. 33: 265. 2015): INDIA. Assam: Mikir Hills, Feb, *C.J. Simons 156* (K barcode K000190045, digital image!).

= *Polyalthia litseifolia* C.Y.Wu ex P.T.Li in Acta Phytotax. Sin. 14: 110. 1976 – Holotype: CHINA. Yunnan: Jinghong, elevation 1100 m, 24 Apr 1957, *Sino-Russia Exped. 9488* (KUN barcode 0046659!; isotype: PE barcode 00934528!).

Chinese name. – mu jiang ye zheng yi mu (木姜叶征镒木).

Description. – Large trees 15–40 m tall, ca. 30–40(–80) cm dbh. Bark grayish with numerous conspicuous lenticels (Fig. 3A). Young twigs green, glabrous, becoming brownish with age. Petioles 6–10 mm long, ca. 2 mm in diameter, furrowed above (Fig. 3B), transversely striate when dry, base enlarged and enclosing the hairy subpetiolar bud (Figs. 3E, F, 5C, D); leaf laminas elliptic, oblong, ovate or obovate, 9–20 cm long, 4.5–8 cm wide, base broadly cuneate or rounded, apex shortly acute or obtuse, membranous to slightly coriaceous, both sides glabrous, with glands conspicuous below (Figs. 3C, D, 5B); secondary veins 10–13 on each side of the leaf, parallel, diverging at 45–60° from midrib, ascending to the margin, upturned and gradually diminishing towards the apex, distinctly raised below; tertiary veins percurrent to reticulate, raised on both sides. Flowers solitary, growing from the axils of circular leaf scars where the old leaves have fallen, often accompanied with the young branchlet (Figs. 3G, 5E); pedicel 20–35 mm long, glabrous (Figs. 3G, H, 5E); sepals 3 per flower, triangular-lanceolate, ca. 12 mm long, 4 mm wide, adaxially slightly pubescent, abaxially glabrous (Fig. 5F); petals 6 per flower in two whorls, sub-equal, linear, 6–10 cm long, 7–11 mm wide, margin slightly reflexed, glabrous, with 3–6 parallel primary veins with reticulations (Figs. 3G, H, 5G, H); stamens numerous (to ca. 100) per flower, ca. 1.5 mm long, connective truncate (Figs. 4B, 5K); pollen grains solitary, symmetrical, rectangular, disulculate, 28–37 μm long, 15–21 μm wide, 20–28 μm high, exine sculpturing rugulate (Fig. 4C–F); carpels 5–9 per flower, stigma broad and pubescent (Figs. 4A, 5I); ovules 3–5(–8) per carpel, 1- or 2-seriate (Fig. 5J). Fruits subglobose to oblong, slightly constricted between seeds, glabrous, 3–3.5 cm long, 2–2.5 cm in diameter; stipe 1–1.3 cm long (Figs. 3I–K, 5A). Seeds 3–5(–8) per monocarp, 1- or 2-seriate, oblong, ca. 2 cm long, 1 cm in diameter, with a distinct circumferential groove; endosperm ruminations lamelliform (Figs. 3L, 5L).

Distribution and habitat. – Growing in rainforests at medium elevations (750–1100 m). Known from Assam, India (Mikir Hills), Yunnan Province, China (Jiangcheng, Jinghong, Lincang, Maguan, Mengla), Thailand (Chiang

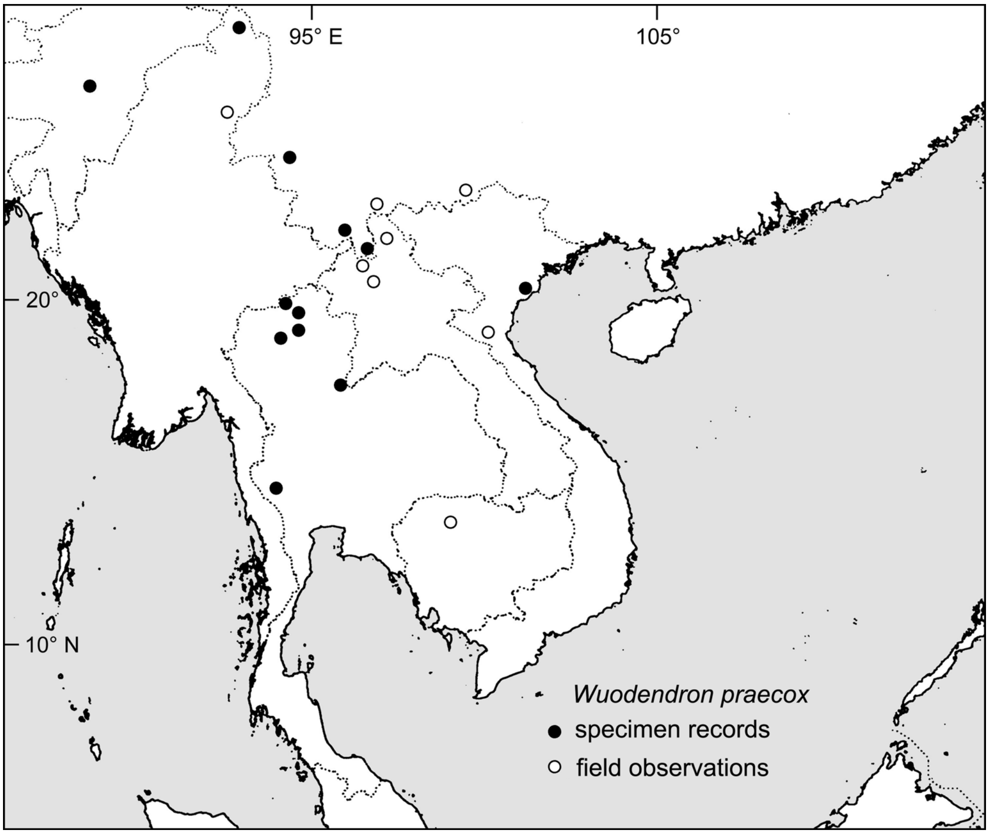

Fig. 6. Distribution of *Wuodendron praecox* (= *Polyalthia litseifolia*).

Mai, Kanchanaburi, Lampang, and Uttaradit Provinces), and Myanmar (Kachin State) (Fig. 6). In addition, extensive field surveys by Hong Wang (Xishuangbanna Tropical Botanical Gardens) in the 1980s and 1990s revealed several localities with young individuals of *W. praecox*: (i) Myitkyina, Kachin State, Myanmar, growing with *Pometia pinnata* J.R.Forst. & G.Forst. in forest valleys; (ii) Phnom Kulen National Park, Siem Reap Province, Cambodia, in dipterocarp forests, growing with *Diospyros hasseltii* Zoll.; (iii) Phongsaly, Luang Namtha, and Oudomxay Provinces, Laos, sparsely distributed in humid rain forest dominated by *Pterocarpus macrocarpus* Kurz and *Pometia pinnata*; (iv) in the Northwest mountainous areas of Thailand bordering Myammar, growing in humid forest valleys, with *Harpullia cupanioides* Roxb.; and (v) Pù Mát National Park in Nghệ An Province, Vietnam.

Phenology. – Deciduous, shedding leaves from mid-December or January to March; flowering and leaf flushing in March or April; fruiting from May to October.

Additional specimens examined. – CHINA. Yunnan: Mengla, 20 Sep 1989, *H. Zhu & H. Wang 2480* (CANT, KUN); 5 Apr 1991, *H. Zhu & H. Wang 3005* (KUN); 8 Apr 1991, *H. Zhu, H. Wang & B.G. Li* 299 (HITBC); 1995, *H. Wang 6301* (HITBC, PE); 28 Apr 2015, *B. Xue 190* (IBSC); 25 Apr 2016, *B. Xue 258* (IBSC); 26 Apr 2016, *B. Xue 263* (IBSC); 30 Apr 2016, *B. Xue 272* (IBSC); 2 May 2016, *B. Xue 277* (IBSC, KUN, PE, SING); 2 Aug 2016, *Y.H. Tan 10946* (HITBC); 4 Apr 2017, *Y.H. Tan 11258* (HITBC); Jinghong, 24 Apr 2016, *B. Xue 256* (IBSC); Lincang, 1 Apr 2017, *Y.L. Li & B. Xue 300* (IBSC, KUN, PE, SING). — THAILAND. Chiang Mai: Doi Ang Khang, Jun 2010, *Chaowasku 108* (L); Jul 2010, *Nakorn-Thiemchan NTC16* (L); 17 Aug 2013, *Chaowasku 114* (CMUB); Mar 2014, *Nakorn-Thiemchan NTC20* (CMUB); Doi Suthep-Pui National Park, 17 Jun 1992, *Maxwell 92-297* (L); Kanchanaburi: Thong Pha Phum, 9 Sep 2016, *Chaowasku 167* (CMUB); Lampang: Doi Luang National Park, 4 Apr 1998, *N. Morci 1323.0* (CMUB); Jae Sawn National Park, 29 Mar 1996, *Maxwell 96-468* (CMUB); Uttaradit: Phu Soi Dao, Mar 2014, *Nakorn-Thiemchan NTC22* and *Nakorn-Thiemchan NTC23* (CMUB); Aug 2010, cultivated, *Chaowasku 111* (L). — MYANMAR. Kachin State: Putao County, 16 May 2017, *Myanmar Exped. 1800* (HITBC). — VIETNAM. Ninh Binh: Cuc Phuong National Park, 8 Aug 1999, *N.M. Cuong 403* (L).

IUCN conservation status. – EN A2a, C2(a)(i) (IUCN, 2012). Prior to this study, *W. praecox* was only represented in herbaria by five collections from Yunnan, China (two localities, both of which have subsequently been severely deforested), one collection from India, and two collections from Thailand. Our field surveys in Yunnan identified only five large trees: two in Mengla County, one in Jiangcheng County, one in Jinghong City, and one in Lincang County. It is clear that deforestation is increasing in these regions: in Mengla County, in particular, lowland forests have been felled and converted to rubber plantations, and only two of the six large trees located by Hong Wang in the 1990s (Wang, 1992) remain. Populations in Thailand are similarly poorly represented in herbaria, and hence the species is also likely to be very rare. In the 1980s, Hong Wang observed several large trees in Phongsaly Province in Laos, although these trees were felled in the 1990s when the forests were logged to create rubber plantations. Although young trees were recorded in Cambodia, Laos, Myanmar, Thailand, and Vietnam in 1980s and 1990s, the fragmented habitat and continuous logging severely threaten survival of the species. The distribution range of this species is nevertheless broad, and in Thailand and China, more individuals have been found in new localities; it is therefore possible that additional undocumented subpopulations will be found throughout its range, and further field investigation is needed to better understand the current status of populations. At present, we recommend that this species be regarded as endangered (EN) based on current IUCN red list categories and criteria (IUCN, 2012).

■ AUTHOR CONTRIBUTIONS

Design of the research: BX, YHT; Performed research: BX, YHT, DCT, TC; Data analysis, collection: BX, YHT, DCT, TC, XLH; Writing the manuscript: BX, YHT, DCT, TC, RMKS. — ORCID: BX, http://orcid.org/0000-0002-4515-4316; YHT, http://orcid.or/0000-0001-6238-2743; DCT, http://orcid.org/0000-0002-1307-6042; TC, http://orcid.org/0000-0002-1602-8468; RMKS, http://orcid.org/0000-0002-8104-7761

■ ACKNOWLEDGEMENTS

This research was supported by a grant from National Natural Science Foundation of China (Grant no. 31400199) awarded to Bine Xue, by the Foundation of Southeast Asia Biodiversity Research Institute, Chinese Academy of Sciences (Y4ZK111B01), and two grants (the Thailand Research Fund TRG5880118 and Chiang Mai University New Researcher Fund-2015) awarded to Tanawat Chaowasku. We are grateful to the curators of CANT, CMUB, HITBC, K, KUN, L and PE herbaria for permission to access their collections; Shi-Shun Zhou and Yong-Liang Li for permission to use their photos; Chun-Fen Xiao and Yong-Liang Li for helping with field collections; Hong Wang and Hua Zhu for sharing information on *Polyalthia litseifolia*; Yun-Yun Shao for helping to repare Figs. 3 and 4; Zheng-Meng Yang for the line drawing of Fig. 5; Xiaoying Hu for technical assistance with SEM at South China Botanical Garden; and three anonymous reviewers and the editors for their constructive comments to improve the manuscript.

■ LITERATURE CITED

Baker, W.J. & Couvreur, T.L.P. 2013. Global biogeography and diversification of palms sheds light on the evolution of tropical lineages. II. Diversification history and origin of regional assemblages. *J. Biogeogr.* 40: 286–298. https://doi.org/10.1111/j.1365-2699.2012.02794.x

Bakker, M.E. 2001. *ETI CD – Annonaceae – genera worldwide*. Amsterdam: Springer.

Biomatters 2016. Geneious, version 10. Auckland: Biomatters. https://www.geneious.com/

Brown, J.M., Hedtke, S.M., Lemmon, A.R. & Lemmon, E.M. 2010. When trees grow too long: Investigating the causes of highly inaccurate Bayesian branch-length estimates. *Syst. Biol.* 59: 145–161. http://doi.org/10.1093/sysbio/syp081

Burnham, R.J. & Johnson, K.R. 2004. South American palaeobotany and the origins of Neotropical rainforests. *Philos. Trans., Ser. B* 359: 1595. http://doi.org/10.1098/rstb.2004.1531

Chaowasku, T. & Keßler, P.J.A. 2013. Seven new species of *Miliusa* (Annonaceae) from Thailand. *Nordic J. Bot.* 31: 680–699. https://doi.org/10.1111/j.1756-1051.2012.01785.x

Chaowasku, T., Johnson, D.M., Van der Ham, R.W.J.M. & Chatrou, L.W. 2012a. Characterization of *Hubera* (Annonaceae), a new genus segregated from *Polyalthia* and allied to *Miliusa*. *Phytotaxa* 69: 33–56. http://dx.doi.org/10.11646/phytotaxa.69.1.6

Chaowasku, T., Keßler, P.J.A. & Van Der Ham, R.W.J.M. 2012b. A taxonomic revision and pollen morphology of the genus *Dendrokingstonia* (Annonaceae). *Bot. J. Linn. Soc.* 168:76–90. https://doi.org/10.1111/j.1095-8339.2011.01187.x

Chaowasku, T., Van der Ham, R.W.J.M. & Chatrou, L.W. 2013a. Integrative systematics supports the establishment of *Winitia*, a new genus of Annonaceae (Malmeoideae, Miliuseae) allied to *Stelechocarpus* and *Sageraea*. *Syst. Biodivers.* 11: 195–207. http://doi.org/10.1080/14772000.2013.806370

Chaowasku, T., Keßler, P.J.A. & Chatrou, L.W. 2013b. Phylogeny of *Miliusa* (Magnoliales: Annonaceae: Malmeoideae: Miliuseae), with descriptions of two new species from Malesia. *Eur. J. Taxon.* 54: 1–21. https://doi.org/10.5852/ejt.2013.54

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. *Amer. J. Bot.* 101: 691–709. http://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 Bull.* 70: 1–4. http://doi.org/10.1007/s12225-015-9571-z

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. http://doi.org/10.1111/j.1095-8339.2012.01235.x

Chen, M.S. & Ke, S.S. 2010. Anatomical structure characteristics of vegetative organs of endangered plant *Calycanthus chinensis*. *J. Pl. Resources Environm.* 19: 37–41.

Christenhusz, M.J.M. & Chase, M.W. 2013. Biogeographical patterns of plants in the Neotropics – Dispersal rather than plate tectonics is most explanatory. *Bot. J. Linn. Soc.* 171: 277–286. http://doi.org/10.1111/j.1095-8339.2012.01301.x

Clayton, J.W., Soltis, P.S. & Soltis, D.E. 2009. Recent long-distance dispersal overshadows ancient biogeographical patterns in a pantropical angiosperm family (Simaroubaceae, Sapindales). *Syst. Biol.* 58: 395–410. https://doi.org/10.1093/sysbio/syp041

Collinson, M.E. 1983. *Fossil plants of the London Clay*. London: Palaeontological Association.

Collinson, M.E. 1992. Vegetational and floristic changes around the Eocene/Oligocene boundary in western and central Europe. Pp. 437–450 in: Prothero, D.R. & Berggren, W.A. (eds.), *Eocene-Oligocene climatic and biotic evolution*. Princeton: Princeton University Press.

Couvreur, T.L.P., Pirie, M.D., Chatrou, L.W., Saunders, R.M.K., Su, Y.C.F., Richardson, J.E. & Erkens, R.H.J. 2011. Early evolutionary history of the flowering plant family Annonaceae: Steady diversification and boreotropical geodispersal. *J. Biogeogr.* 38: 664–680. http://doi.org/10.1111/j.1365-2699.2010.02434.x

Darriba, D., Taboada, G.L., Doallo, R. & Posada, D. 2012. jModelTest 2: More models, new heuristics and parallel computing. *Nature, Meth.* 9: 772. http://dx.doi.org/10.1038/nmeth.2109

Davis, C.C., Bell, C.D., Mathews, S. & Donoghue, M.J. 2002. Laurasian migration explains Gondwanan disjunctions: Evidence from Malpighiaceae. *Proc. Natl. Acad. Sci. U.S.A.* 99: 6833–6837. https://doi.org/10.1073/pnas.102175899

Davis, C.C., Webb, C.O., Wurdack, K.J., Jaramillo, C.A. & Donoghue, M.J. 2005. Explosive radiation of Malpighiales supports a mid-cretaceous origin of modern tropical rain forests. *Amer. Naturalist* 165: E36–E65. https://doi.org/10.1086/428296

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

Drummond, A.J. & Rambaut, A. 2007. BEAST: Bayesian evolutionary analysis by sampling trees. *B. M. C. Evol. Biol.* 7: 214. http://dx.doi.org/10.1186/1471-2148-7-214

Erkens, R.H.J., Maas, J.W. & Couvreur, T.L.P. 2009. From Africa via Europe to South America: Migrational route of a species-rich genus of Neotropical lowland rain forest trees (*Guatteria*, Annonaceae). *J. Biogeogr.* 36: 2338–2352. http://doi.org/10.1111/j.1365-2699.2009.02162.x

Fries, R.E. 1959. Annonaceae. Pp. 1–171 in: Melchior, H. (ed.), *Die natürlichen Pflanzenfamilien*, vol. 17aII. Berlin: Duncker and Humblot.

Guindon, S., Dufayard, J.F., Lefort, V., Anisimova, M., Hordijk, W. & Gascuel, O. 2010. New algorithms and methods to estimate maximum-likelihood phylogenies: Assessing the performance of PhyML 3.0. *Syst. Biol.* 59: 307–321. https://doi.org/10.1093/sysbio/syq010

Guo, X., Wang, J., Xue, B., Thomas, D.C., Su, Y.C., 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. http://doi.org/10.1111/jse.12064

Guo, X., Tang, C.C., Thomas, D.C., Couvreur, T.L.P. & Saunders, R.M.K. 2017. A mega-phylogeny of the Annonaceae: Taxonomic placement of five enigmatic genera and recognition of a new tribe, Phoenicantheae. *Sci. Rep.* 7: 7323. http://doi.org/10.1038/s41598-017-07252-2

Hickey, L.J. 1979. A revised classification of the architecture of dicotyledonous leaves. Pp. 25–39 in: Metcalfe, C. & Chalk, L. (eds.), *Anatomy of the dicotyledons*, ed. 2, vol. 1, *Systematic anatomy of the leaf and stem*. Oxford: Clarendon Press.

Hoekstra, P.H., Wieringa, J.J., Smets, E., Brandão, R.D., Lopes, J. de C., Erkens, R.H.J. & Chatrou, L.W. 2017. Correlated evolutionary rates across genomic compartments in Annonaceae. *Molec. Phylogen. Evol.* 114: 63–72. http://dx.doi.org/10.1016/j.ympev.2017.05.026

Hooker, J.D. & Thomson, T. 1855. *Flora Indica*. London: printed for the authors, published by W. Pamplin. https://doi.org/10.5962/bhl.title.57706

Hooker, J.D. & Thomson, T. 1872. Anonaceae. Pp. 45–94. in: Hooker, J.D. (ed.), *The flora of British India*, vol. 1(1). Ashford, Kent: L. Reeve. https://doi.org/10.5962/bhl.title.678

Huelsenbeck, J.P. & Ronquist, F. 2001. MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* 17: 754–755. http://doi.org/10.1093/bioinformatics/17.8.754

IUCN 2012. *IUCN red list categories and criteria: version 3.1*, ed. 2. Gland & Cambridge (U.K.): IUCN.

Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., Buxton, S., Cooper, A., Markowitz, S., Duran, C., Thierer, T., Ashton, B., Mentjies, P. & Drummond, A. 2012. Geneious Basic: An integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics* 28: 1647–1649. https://doi.org/10.1093/bioinformatics/bts199

King, G. 1893. The Annonaceae of British India. *Ann. Roy. Bot. Gard., Calcutta* 4: 1–169+pl. 161–220.

Klucking, E.P. 1986. *Leaf venation patterns*, vol. 1. Berlin & Stuttgart: Cramer.

Koek-Noorman, J., Westra, L.Y.T. & Maas, P.J.M. 1990. Studies in Annonaceae XIII: The role of morphological characters in subsequent classifications of Annonaceae; A comparative study. *Taxon* 39: 16–32.

Lanfear, R., Calcott, B., Ho, S.Y. & Guindon, S. 2012. PartitionFinder: Combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molec. Biol. Evol.* 29: 1695–1701. https://doi.org/10.1093/molbev/mss020

Lanfear, R., Frandsen, P.B., Wright, A.M., Senfeld, T. & Calcott, B. 2017. PartitionFinder 2: New methods for selecting partitioned models of evolution formolecular and morphological phylogenetic analyses. *Molec. Biol. Evol.* 34: 772–773. https://doi.org/10.1093/molbev/msw260

Li, J.Q., Li, X.W. & Soejarto, D.D. 2007. Actinidiaceae. Pp. 334–360 in: Wu, Z.Y., Raven, P.H. & Hong, D.Y. (eds.), *Flora of China*, vol. 12. Beijing: Science Press; St. Louis: Missouri Botanical Garden Press.

Li, P.S., Thomas, D.C. & Saunders, R.M.K. 2017. Historical biogeography and ecological niche modelling of the *Asimina*-*Disepalum* clade (Annonaceae): Role of ecological differentiation in Neotropical-Asian disjunctions and diversification in Asia. *B. M. C. Evol. Biol.* 17: 188. https://doi.org/10.1186/s12862-017-1038-4

Li, P.T. 1976. Some notes on the Annonaceae of China. *Acta Phytotax. Sin.* 14: 96–113.

Li, P.T. & Gilbert, M.G. 2011. Annonaceae. Pp. 672–713 in: Wu, Z.Y., Raven, P.H. & Hong, D.Y. (eds.), *Flora of China*, vol. 19. Beijing: Science Press; St. Louis: Missouri Botanical Garden Press.

Li, X.W. & Fan, G.S. 1994. A new species of *Cladrastis* Raf. *Bull. Bot. Res., Harbin* 14: 347–348.

Li, Z.N., Zhang, J.Q., Liu, G.F., Li, X.M., Lu, C., Zhang, J.W. & Bao, M.Z. 2012. Phylogenetic and evolutionary analysis of A-, B-, C- and E-class MADS-box genes in the basal eudicot *Platanus acerifolia*. *J. Pl. Res.* 125: 381–393. https://doi.org/10.1007/s10265-011-0456-4

Liu, K., Feng, S., Pan, Y., Zhong, J., Chen, Y., Yuan, C. & Li, H. 2016. Transcriptome analysis and identification of genes associated with floral transition and flower development in sugar apple (*Annona squamosa* L.). *Frontiers Pl. Sci. (Lausanne)* 7: 1695.

Manchester, S.R. 1994. Fruits and seeds of the Middle Eocene nut beds flora, Clarno Formation, Oregon. *Palaeontogr. Amer.* 58: 1–205.

Marshall, D.C. 2010. Cryptic failure of partitioned Bayesian phylogenetic analyses: Lost in the land of long trees. *Syst. Biol.* 59: 108–117. http://doi.org/10.1093/sysbio/syp080

Michalak, I., Zhang, L.B. & Renner, S.S. 2010. Trans-Atlantic, trans-Pacific and trans-Indian Ocean dispersal in the small Gondwanan Laurales family Hernandiaceae. *J. Biogeogr.* 37: 1214–1226. http://doi.org/10.1111/j.1365-2699.2010.02306.x

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

Mols, J.B. & Keßler, P.J.A. 2000. The genus *Monocarpia* (Annonaceae) in Borneo including a new species *Monocarpia borneensis*. *Bot. Jahrb. Syst.* 122: 233–240.

Mols, J.B. & Keßler ["Kessler"], P.J.A. 2003. The genus *Miliusa* (Annonaceae) in the Austro-Malesian area. *Blumea* 48: 421–462. https://doi.org/10.3767/000651903X489384

Mols, J.B., Co, D.L.V., Gravendeel, B., Chatrou, L.W., Pirie, M.D., Van der Ham, R.W.J.M., Van Marle, E.J. & Keßler, P.J.A. 2004a. Morphological character evolution in the miliusoid clade (Annonaceae). Pp 37–75. in: Mols, J.B. (ed.), *From Miliusa to Miliuseae to miliusoid: Identifying clades in Asian Annonaceae.* Ph.D. thesis, Nationaal Herbarium Nederland, Universiteit Leiden branch, Leiden, Netherlands.

Mols, J.B., Gravendeel, B., Chatrou, L.W., Pirie, M.D., Bygrave, P.C., Chase, M.W. & Keßler, P.J.A. 2004b. Identifying clades in Asian Annonaceae: Monophyletic genera in the polyphyletic Miliuseae. *Amer. J. Bot.* 91: 590–600. http://doi.org/10.3732/ajb.91.4.590

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. http://doi.org/10.1600/036364408785679752

Morley, R.J. 2000. *Origin and evolution of tropical rain forests.* New York: Wiley.

Müller, K. 2005. The efficiency of different search strategies in estimating parsimony jackknife, bootstrap, and Bremer support. *B. M. C. Evol. Biol.* 5: 58. http://doi.org/10.1186/1471-2148-5-58

Nie, Z.L., Deng, T., Meng, Y., Sun, H. & Wen, J. 2013. Post-Boreotropical dispersals explain the pantropical disjunction in *Paederia* (Rubiaceae). *Ann. Bot. (Oxford)* 111: 873–886. https://doi.org/10.1093/aob/mct053

Ng, K.W. 2010. *Systematics of Desmos (Annonaceae) in Thailand, Peninsular Malaysia and Sumatra*. M.Phil. thesis, the University of Hong Kong, Hong Kong, China.

Ortiz-Rodriguez, A.E., Ruiz-Sanchez, E. & Ornelas, J.F. 2016. Phylogenetic relationships among members of the Neotropical clade of Miliuseae (Annonaceae): Generic non-monophyly of *Desmopsis* and *Stenanona*. *Syst. Bot.* 41: 815–822. http://doi.org/10.1600/036364416X693928

Pierre, J.B.L. 1881. *Flore forestière de la Cochinchine*, fasc. 2. Paris: Octave Doin. https://doi.org/10.5962/bhl.title.61558

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. http://doi.org/10.1111/j.1365-2699.2005.01388.x

Rainer, H. & Chatrou, L.W. 2006. AnnonBase: World species list of Annonaceae, version 1.1. Available at: http://www.annonaceae.org/frameset.html

Rambaut, A., Suchard, M.A., Xie, D. & Drummond, A.J. 2014. Tracer, version 1.6. Available from: http://beast.bio.ed.ac.uk/Tracer

Richardson, J.E., Chatrou, L.W., Mols, J.B., Erkens, R.H.J. & Pirie, M.D. 2004. Historical biogeography of two cosmopolitan families of flowering plants: Annonaceae and Rhamnaceae. *Philos. Trans., Ser. B* 359: 1495–1508. http://doi.org/10.1098/rstb.2004.1537

Ronquist, F. & Huelsenbeck, J.P. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1572–1574. http://doi.org/10.1093/bioinformatics/btg180

Safford, W.E. 1912. *Desmos* the proper generic name for the so-called *Unonas* of the Old World. *Bull. Torrey Bot. Club* 39: 501–508.

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

Saunders, R.M.K., Su, Y.C.F. & Xue, B. 2011. Phylogenetic affinities of *Polyalthia* species (Annonaceae) with columellar-sulcate pollen: Enlarging the Madagascan endemic genus *Fenerivia*. *Taxon* 60: 1407–1416.

Scharaschkin, T. & Doyle, J.A. 2005. Phylogeny and historical biogeography of *Anaxagorea* (Annonaceae) using morphology and non-coding chloroplast sequence data. *Syst. Bot.* 30: 712–735. https://doi.org/10.1600/0363644054223675

Schatz, G.E. 1987. *Systematic and ecological studies of Central American Annonaceae.* Ph.D. thesis, University of Wisconsin, Madison, U.S.A.

Schatz, G.E. & Maas, P.J.M. 2010. Synoptic revision of *Stenanona* (Annonaceae). *Blumea* 55: 205–223. https://doi.org/10.3767/000651910X535618

Soler, L. & Cuevas, J. 2009. Early flower initiation allows ample manipulation of flowering time in cherimoya (*Annona cherimola* Mill.). *Sci. Hort.* 121: 327–332. https://doi.org/10.1016/j.scienta.2009.02.005

Stamatakis, A. 2006. RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22: 2688–2690. https://doi.org/10.1093/bioinformatics/btl446

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

Tang, C., Xue, B. & Saunders, R.M.K. 2013. A new species of

Goniothalamus (Annonaceae) from Palawan, and a new nomenclatural combination in the genus from Fiji. *PhytoKeys* 32: 27–35. https://doi.org/10.3897/phytokeys.32.6663

Tate, J.A. & Simpson, B.B. 2003. Paraphyly of *Tarasa* (Malvaceae) and diverse origins of the polyploid species. *Syst. Bot.* 28: 723–737.

Thomas, D.C., Surveswaran, S., Xue, B., Sankowsky, G., Mols, J.B., Keßler, P.J.A. & Saunders, R.M.K. 2012. Molecular phylogenetics and historical biogeography of the *Meiogyne-Fitzalania* clade (Annonaceae): Generic paraphyly and late Miocene-Pliocene diversification in Australasia and the Pacific. *Taxon* 61: 559–575.

Thomas, D.C., Chatrou, L.W., Stull, G.W., Johnson, D.M., Harris, D.J., Thongpairoj, U.-S. & Saunders, R.M.K. 2015. The historical origins of palaeotropical intercontinental disjunctions in the pantropical flowering plant family Annonaceae. *Perspect. Pl. Ecol. Evol. Syst.* 17: 1–16. http://doi.org/10.1016/j.ppees.2014.11.001

Thomas, D.C., Tang, C.C. & Saunders, R.M.K. 2017. Historical biogeography of *Goniothalamus* and Annonaceae tribe Annoneae: Dispersal-vicariance patterns in tropical Asia and intercontinental tropical disjunctions revisited. *J. Biogeogr.* 44: 2862–2876. https://doi.org/10.1111/jbi.13086

Thorne, R.F. 1972. Major disjunctions in geographic ranges of seed plants. *Quart. Rev. Biol.* 47: 365–411. https://doi.org/10.1086/407399

Tiffney, B.H. 1985. Perspectives on the origin of the floristic similarity between eastern Asia and eastern North America. *J. Arnold Arbor.* 66: 73–94.

Turner, I.M. 2015. A conspectus of Indo-Burmese Annonaceae. *Nordic J. Bot.* 33: 257–299. https://doi.org/10.1111/njb.00689

Van Damme, K. & Sinev, A.Y. 2013. Tropical amphi-Pacific disjunctions in the Cladocera (Crustacea: Branchiopoda). *J. Limnol.* 72: 209–244. https://doi.org/10.4081/jlimnol.2013.s2.e11

Van Heusden, E.C.H. 1992. Flowers of Annonaceae: Morphology, classification, and evolution. *Blumea Suppl.* 7: 1–218. http://doi.org/10.1111/j.1756-1051.1993.tb00089.x

Van Heusden, E.C.H. 1994. Revision of *Meiogyne* (Annonaceae). *Blumea* 38: 487–511.

Van Setten, A.K. & Koek-Noorman, J. 1992. Fruits and seeds of Annonaceae: Morphology and its significance for classification. *Biblioth. Bot.* 142: 1–101 + pl. 1–50.

Van Steenis, C.G.G.J. 1962. The land-bridge theory in botany, with particular reference to tropical plants. *Blumea* 11: 235–542.

Vélez-Arango, J.G. & Cogollo-Pacheco, Á. 2007. First record of the genus *Sapranthus* (Annonaceae) and a new species for South America. *Caldasia* 29: 229–233.

Wang, H. 1992. Xi shuang ban na te you ye sheng zhi wu – mu jiang ye an luo [*Polyalthia litseifolia*, an endemic wild plant in Xishuangbanna]. *Chin. Wild Pl.* 1: 22–23. [in Chinese]

Weberling, F. & Hoppe, J.R. 1996. Comparative morphological evaluation of inflorescence characters in Annonaceae. Pp. 29–53 in: Morawetz, W. & Winkler, H. (eds.), *Reproductive morphology in Annonaceae*. Vienna: Öterreichische Akademie der Wissenschaften.

Wolfe, J.A. 1975. Some aspects of plant geography of the Northern Hemisphere during the late Cretaceous and Tertiary. *Ann. Missouri Bot. Gard* 62: 264–279.

Wolfe, J.A. 1992. Climatic, floristic, and vegetational changes near the Eocene/Oligocene boundary in North America. Pp. 421–436 in: Prothero, D.R. & Berggren, W.A. (eds.), *Eocene-Oligocene biotic and climatic evolution*. Princeton: Princeton University Press.

Xue, B. 2013. *Molecular phylogenetics of Polyalthia (Annonaceae): Identifying clades and morphological synapomorphies in a large polyphyletic genus.* Ph.D. thesis, the University of Hong Kong, Hong Kong, China.

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. http://doi.org/10.1080/14772000.2010.542497

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.

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. http://doi.org/10.1600/036364414X680825

Xue, B., Tan, Y.H. & Ye, X.E. 2016. The identity of *Polyalthia florulenta* (Annonaceae): A second species of *Wangia* in China. *Phytotaxa* 283: 163–171. http://doi.org/10.11646/phytotaxa.283.2.5

Xue, B., Shao, Y.Y., Saunders, R.M.K. & Tan, Y.H. 2017. *Alphonsea glandulosa* (Annonaceae), a new species from Yunnan, China. *PLoS ONE* 12: e0170107. https://doi.org/10.1371/journal.pone.0170107

Zhu, H. & Wang, H. 1993. An addendum to the species *Polyalthia litseifolia* (Annonaceae). *Acta Phytotax. Sin.* 31: 383–384.

Appendix 1. Species names and GenBank accession numbers of DNA sequences used in this study.

Voucher data is given for accessions, for which DNA sequences were newly obtained, using the following format: Taxon name, country, largest political subdivision, collector(s) and collector number, herbarium code, GenBank accession numbers (*atpB-rbcL*, *matK*, *ndhF*, *psbA-trnH*, *rbcL*, *trnL-F*, *ycf1*). –, missing data; *, newly generated sequences.

Afroguatteria bequaertii (De Wild.) Boutique, –, KX786588, –, –, KX786627, KX786629, –; ***Alphonsea elliptica*** Hook.f. & Thomson, –, AY518807, JQ690401, JQ690402, –, AY319078, JQ690403; ***Ambavia gerrardii*** (Baill.) Le Thomas, AY578118, AY220435, AY218168, –, JQ513886, JQ513889, –; ***Anaxagorea phaeocarpa*** Mart., EF179244, AY238960, EF179279, AY841426, AY238952, EF179316, –; ***Annickia pilosa*** (Exell) Setten & Maas, AY841371, AY743488, AY841402, AY841444, AY743450, AY743469, –; ***Annona muricata*** L., EF179247, AF543722, EF179282, AY743440, AY743459, EF179324, AY743440; ***Anonidium mannii*** (Oliv.) Engl. & Diels, EF179248, DQ125051, EF179283, AY841598, AY841675, EF179325, AY841598; ***Artabotrys hexapetalus*** (L.f.) Bhandari, EF179249, AY238962, EF179284, AY841429, AY238953, EF179317, –; ***Asimina triloba*** Dunal, EF179252, GQ139711, AY218171, AY743441, AY743460, EF179329, AY743441; ***Asteranthe asterias*** (S.Moore) Engl. & Diels, –, –, EU169711, EU169734, EU169757, EU169779, –; ***Bocageopsis canescens*** (Benth.) R.E.Fr., –, JQ690409, JQ690410, JQ690411, JQ690407, JQ690408, JQ690412; ***Brieya fasciculata*** De Wild., –, –, –, –, KU716142, KU716129, –; ***Cananga odorata*** (Lam.) Hook.f & Thomson, AY841372, AY220438, AY841403, AY841431, AY841602, AY841680, –; ***Cleistochlamys kirkii*** (Benth.) Oliv., –, –, KM924880, KM924981, –, KM924948, –; ***Cleistopholis glauca*** Engl. & Diels, AY841373, AY841395, AY841404, AY841432, AY841603, AY841681, –; ***Coelocaryon preussii*** Warb, –, AY743475, JQ437546, –, AY743437, AY743456, –; ***Cramatosperma cauliflorum*** R.E.Fr., AY841375, AY743542, AY841406, DQ018240, AY743519, AY743565, –; ***Cyathocalyx martabanicus*** Hook.f. & Thomson, EF179253, DQ125054, EF179288, DQ125120, AY841605, AY841683, –; ***Cymbopetalum brasiliense*** (Vell.) Benth. ex Baill., EF179254, DQ125055, EF179289, DQ125121, AY841608, AY841686, –; ***Dasymaschalon macrocalyx*** Finet & Gagnep., EF179255, EF179277, EF179290, EF179313, AY841610, AY841688, –; ***Degeneria vitiensis*** I.W.Bailey & A.C.Sm., AB332086, AB055549, AY394736, AB332084, L12643, –, –; ***Dendrokingstonia gardneri*** Chaowasku, –, KJ418391, KJ418385, KJ418399, KJ418381, KJ418406, KJ418378; ***Desmopsis microcarpa*** R.E.Fr., –, AY518804, JX544771, AY841461, –, AY319173, JX544758; ***Desmos dumosus*** (Roxb.) Saff., –, JQ768570, JQ768606, JQ768649, JQ768689, JQ768730, –; ***Diclinanona calycina*** Diels, –, KC196271, –, KC196269, KC196270, KC196272, –; ***Dielsiothamnus***

Appendix 1. Continued.

divaricatus (Diels) R.E.Fr., –, –, –, EU169736, EU169759, EU169781, –; ***Disepalum coronatum*** Becc., –, KT452820, KT452831, –, –, KT452842, KT452853; ***Drepananthus kingii*** (Boerl. ex Koord.) Surveswaran & R.M.K.Saunders, –, HM173728, –, HM173699, HM173785, HM173757, –; ***Duguetia hadrantha*** (Diels) R.E.Fr., EF179258, AY740541, EF179293, DQ125123, AY738161, AY740573, –; ***Ephedranthus*** **sp.**, AY841376, AY841396, AY841407, AY841463, AY841616, AY841694, –; ***Eupomatia bennettii*** F.Muell., –, JQ437547, –, –, DQ861790, DQ861842, –; ***Fenerivia chapelieri*** (Baill.) R.M.K.Saunders, –, JF810375, JQ723788, –, JF810387, JF810399, –; ***Fissistigma polyanthoides*** (A.DC.) Merr., –, JQ768575, JQ768609, JQ768654, JQ768694, JQ768735, –; ***Friesodielsia desmoides*** (Craib) Steenis, –, JQ768577, JQ768612, JQ768656, JQ768696, AY841696, –; ***Fusaea peruviana*** R.E.Fr., EF179260, AY743483, EF179295, AY841436, AY743445, AY743464, –; ***Galbulimima belgraveana*** (F.Muell.) Sprague, –, AY220441, AY218176, –, L12646, KC428524, –; ***Goniothalamus maewongensis*** R.M.K.Saunders & Chalermglin, KM818540, KM818597, KM818659, KM818725, KM818746, KM818838, KM818962; ***Greenwayodendron oliveri*** (Engl.) Verdc., AY841377, AY743489, AY841408, AY841465, AY743451, AY743470, –; ***Guatteria anomala*** R.E.Fr., EF179263, AY740913, EF179298, AY841437, AY740962, AY741011, –; ***Hexalobus crispiflorus*** A.Rich., –, –, EU169713, EU169737, EU169760, EU169782, –; ***Hornschuchia citriodora*** D.M.Johnson, –, –, –, –, AY841625, AY841703, –; ***Huberantha korinti*** (Dunal) Chaowasku, EU522345, EU522234, JX544877, EU522124, EU522289, EU522179, JX544847; ***Isolona campanulata*** Engl. & Diels, EF179266, AY238963, EF179301, DQ125127, AY238954, EF179318, –; ***Klarobelia inundata*** Chatrou, AY841378, AY743490, AY841409, AY841469, AY743452, AY743471, –; ***Letestudoxa bella*** Pellegr., EF179267, DQ125059, EF179302, DQ125128, AY841629, AY841707, –; ***Lettowianthus stellatus*** Diels, –, –, –, EU169730, EU169753, EU169775, –; ***Liriodendron chinense*** Sargent, –, –, –, AY841424, AY841593, AY841670, –; ***Maasia discolor*** (Diels) Mols, Kessler & Rogstad, AY841385, AY518872, AY841416, AY841500, –, AY319135, –; ***Magnolia kobus*** DC., –, AY743476, –, AY841425, AY743438, AY743457, –; ***Malmea dielsiana*** R.E.Fr., AY841379, AY238964, AY841410, AY841473, AY238955, AY319177, –; ***Marsypopetalum littorale*** (Blume) B.Xue & R.M.K.Saunders, –, AY518835, JX544827, JX544804, –, AY319140, JX544813; ***Meiocarpidium lepidotum*** Engl. & Diels, –, –, –, EU169731, EU169754, EU169776, –; ***Meiogyne mindorensis*** (Merr.) Heusden, –, JQ723776, JQ723800, –, JQ723863, JQ723916, JQ723939; ***Meiogyne monosperma*** (Hook.f. & Thomson) Heusden, –, JQ723777, –, –, JQ723864, JQ723917, JQ723940; ***Meiogyne pannosa*** (Dalzell) J.Sinclair, –, JQ723778, JQ723801, –, JQ723865, JQ723918, JQ723941; ***Meiogyne virgata*** (Blume) Miq. , –, AY518798, JQ723805, –, AY318982, AY319094, JQ723945; ***Mezzettia parviflora*** Becc., –, AY518881, –, –, –, AY319095, –; ***Miliusa indica*** Lesch. ex A.DC., –, JQ723781, JQ723806, –, JQ723868, JQ723921, JQ723946; ***Mischogyne michelioides*** Exell, –, –, EU169718, EU169741, EU169764, EU169786, –; ***Mitrella kentii*** (Blume) Miq., –, FJ743751, JQ768616, FJ743789, AY841633, AY841711, –; ***Mitrephora alba*** (Blume) Hook.f. & Thomson, –, AY518855, JQ723807, –, AY318994, AY319106, JQ723947; ***Mkilua fragrans*** Verdc., EF179268, –, EF179303, DQ861696, AY841634, AY841712, –; ***Monanthotaxis whytei*** (Stapf) Verdc., EF179269, EF179278, EF179304, EF179315, AY841635, AY841713, –; ***Monocarpia euneura*** Miq., AY841381, AY518865, AY841412, AY841477, –, AY319111, –; ***Monocyclanthus vignei*** Keay, –, –, EU169719, EU169742, EU169765, EU169787, –; ***Monodora myristica*** (Gaertn.) Dunal, EF179270, AY743485, EF179305, DQ125129, AY743447, EU216716, –; ***Monoon longifolium*** (Sonn.) B.Xue & R.M.K.Saunders, EU522346, AY518786, –, EU522125, EU522290, EU522180, –; ***Mosannona costaricensis*** R.E.Fr., AY841382, AY743503, AY841413, AY841479, AY743510, AY743496, –; ***Mwasumbia alba*** Couvreur & D.M.Johnson, –, –, –, –, EU747680, EU747674, –; ***Myristica fragrans*** Houtt., –, AJ966803, AY218188, –, AF206798, –, –; ***Neostenanthera myristicifolia*** (Oliv.) Exell, EF179271, AY743486, EF179306, AY743448, AY743467, EF179348, AY743448; ***Neo-uvaria telopea*** Chaowasku, –, JX544751, JX544778, JX544791, JX544755, JX544783, JX544766; ***Onychopetalum periquino*** (Rusby) D.M.Johnson & N.A.Murray, AY841383, AY518876, AY841414, AY841485, –, AY319179, –; ***Ophrypetalum odoratum*** Diels, –, –, EU169723, EU169745, EU169767, EU169789, –; ***Orophea enterocarpa*** Maingay ex Hook.f. & Thomson, –, AY518815, JQ690416, JQ690417, –, AY319119, JQ690418; ***Oxandra venezuelana*** R.E.Fr., –, JQ690413, JQ690414, AY841495, AY841645, AY841723, JQ690415; ***Phaeanthus splendens*** Miq., –, AY518864, JX544777, JX544790, JX544754, AY319126, JX544765; ***Phoenicanthus obliquus*** (Hook.f. & Thomson) Alston, –, MF322639, –, MF322658, MF322654, MF322667, –; ***Piptostigma mortehani*** De Wild., AY841384, AY743492, AY841415, AY841498, AY743454, AY743473, –; ***Platymitra*** **sp.**, –, JQ690426, JQ690427, JQ690428, –, JQ690425, JQ690429; ***Polyalthia suberosa*** (Roxb.) Thwait., AY841386, AY220439, AY841417, AY841502, AY238956, AY319152, JQ723952; ***Polyceratocarpus parviflorus*** (Baker f.) Ghesq., –, KC627837, –, KC688815, EU747682, EU747676, –; ***Popowia hirta*** Miq., –, AY518860, JX544830, JX544806, –, AY319156, JX544816; ***Porcelia steinbachii*** (Diels) R.E.Fr., –, –, –, –, AY841649, AY841727, –; ***Pseudartabotrys letestui*** Pellegr., EF179272, DQ125061, EF179307, DQ125131, AY841650, AY841728, –; ***Pseudephedranthus fragrans*** (R.E.Fr.) Aristeg., –, –, –, AY841504, AY841651, AY841729, –; ***Pseudomalmea diclina*** (R.E.Fr.) Chatrou, AY841388, AY841398, AY841419, AY841506, AY841530, AY319182, –; ***Pseudoxandra spiritus-sancti*** Maas, AY841390, AY841399, AY841421, AY841513, AY841533, AY841547, –; ***Pseuduvaria fragrans*** Y.C.F.Su, Chaowasku & R.M.K.Saunders, –, JQ723784, JX544829, –, JQ723871, JQ723924, JQ723954; ***Pyramidanthe prismatica*** (Hook.f. & Thomson) J.Sinclair, –, JN175163, –, JN175178, JN175193, JN175208, –; ***Ruizodendron ovale*** (Ruiz & Pav.) R.E.Fr., –, –, –, AY841514, AY841657, AY841735, –; ***Sageraea lanceolata*** Miq., –, AY518799, JX544774, JX544787, –, AY319164, JX544762; ***Sanrafaelia ruffonammari*** Verdc., –, –, EU169724, EU169746, EU169768, EU169790, –; ***Sapranthus viridiflorus*** G.E.Schatz, AY841391, AY743493, AY841422, AY841515, JQ590194, AY319165, JQ723955; ***Sirdavidia solannona*** Couvreur & Sauquet, –, –, –, –, KP144082, KP144080, –; ***Sphaerocoryne gracilis*** (Engl. & Diels) Verdc., –, –, JQ768623, EU169732, EU169755, EU169777, –; ***Stelechocarpus burahol*** (Blume) Hook.f. & Thomson, –, AY518803, JQ723814, –, AY319053, AY319167, JQ723956; ***Stenanona costaricensis*** R.E.Fr., –, AY518801, JX544772, AY841516, JQ590198, AY319183, JX544759; ***Tetrameranthus duckei*** R.E.Fr., –, –, –, AY841439, AY841658, AY841736, –; ***Toussaintia orientalis*** Verdc., –, –, EU169710, EU169733, EU169756, EU169778, –; ***Tridimeris*** **sp.**, –, JX544750, JX544773, JX544786, JX544753, JX544782, JX544761; ***Trigynaea lanceipetala*** D.M.Johnson & N.A.Murray, EF179274, AY743487, EF179309, –, AY743449, AY743468, –; ***Trivalvaria*** **sp.**, –, JX544824, JX544828, JX544805, JX544822, JX544794, JX544814; ***Unonopsis stipitata*** Diels, AY841392, AY841400, AY841423, AY841519, AY841662, DQ018202, –; ***Uvaria lucida*** subsp. ***virens*** (N.E.Br.) Verdc., EF179275, AY238966, EF179310, AY841440, AY238957, EF179319, –; ***Uvariastrum pierreanum*** Engl. & Diels, –, –, –, EU169748, EU169770, EU169792, –; ***Uvariodendron molundense*** (Diels) R.E.Fr., –, –, EU169727, EU169750, EU169772, EU169794, –; ***Uvariopsis korupensis*** Gereau & Kenfack, –, KC627757, EU169729, EU169752, EU169774, EU169796, –; ***Wangia saccopetaloides*** (W.T.Wang) X.Guo & R.M.K.Saunders, –, KF680921, –, KF680925, KF680927, KF680931, KF680932; ***Winitia cauliflora*** (Scheff.) Chaowasku, –, AY518800, JX544776, JX544789, AY319054, AY319168, JX544764; ***Wuodendron praecox*** (Hook.f. & Thomson) B.Xue, Y.H.Tan & X.L.Hou [= *Polyalthia litseifolia* C.Y.Wu ex P.T.Li, ***Polyalthia litseifolia*** **1**], China, Yunnan, *B. Xue 190* (IBSC), –, MF687367*, MF687369*, MF687371*, MF687373*, MF687375*, MF687377*; ***Wuodendron praecox*** (Hook.f. & Thomson) B.Xue, Y.H.Tan & X.L.Hou [= *Polyalthia litseifolia* C.Y.Wu ex P.T.Li, ***Polyalthia litseifolia*** **2**], China, Yunnan, *B. Xue 265* (IBSC), –, MF687368*, MF687370*, MF687372*, MF687374*, MF687376*, MF687378*; ***Wuodendron praecox*** (Hook.f. & Thomson) B.Xue, Y.H.Tan & X.L.Hou [= *Polyalthia litseifolia* C.Y.Wu ex P.T.Li, **undescribed genus sp. 1**], –, KC857612, KC857613, KC857614, –, KC857611, KC857615; ***Wuodendron praecox*** (Hook.f. & Thomson) B.Xue, Y.H.Tan & X.L.Hou [= *Polyalthia litseifolia* C.Y.Wu ex P.T.Li, **undescribed genus sp. 2A**], –, JX544749, JX544770, JX544785, JX544752, JX544781, JX544757; ***Wuodendron praecox*** (Hook.f. & Thomson) B.Xue, Y.H.Tan & X.L.Hou [= *Polyalthia litseifolia* C.Y.Wu ex P.T.Li, **undescribed genus sp. 2B**], –, KC857607, KC857608, KC857609, –, KC857606, KC857610; ***Xylopia peruviana*** R.E.Fr., EF179276, AY238967, EF179312, DQ125134, AY238958, EF179320, –.