

## **Artabotrys angustipetalus (Annonaceae), a new species from Thailand, including a plastid phylogeny and character evolutionary analyses of thorn occurrence in Artabotrys**

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## *Artabotrys angustipetalus* (*Annonaceae*), a new species from Thailand, including a plastid phylogeny and character evolutionary analyses of thorn occurrence in *Artabotrys*

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**Abstract:** *Artabotrys* R. Br. is one of the larger genera of *Annonaceae* with over 100 species distributed throughout the palaeotropics plus northern Australia. Although the genus is morphologically very well circumscribed, species delimitation is quite problematic owing to overlapping morphological characteristics. In Thailand, 20 species of *Artabotrys* have been reported, including *A. multiflorus* C. E. C. Fisch. Detailed comparisons with the type specimen from Myanmar revealed that *A. multiflorus* occurring in Kanchanaburi Province of Thailand represents a new species herein described as *A. angustipetalus* Photikwan & Chaowasku. The new species differs from *A. multiflorus* by having fewer flowers per hook, linear (vs oblong to oblong-lanceolate) petals, acute (vs obtuse) petal apex, longer and narrower petals and fewer carpels per flower. A multi-locus plastid phylogeny including an accession of *A. angustipetalus* and 30 accessions of other species of *Artabotrys* has been reconstructed. The results uncover a well-supported clade consisting of thorn-bearing species of *Artabotrys*, with *A. angustipetalus* recovered outside this clade. To understand the evolution of thorns in *Artabotrys*, ancestral character-state reconstructions were carried out; this trait is inferred to have evolved only once in *Artabotrys*. The benefits of thorns in *Artabotrys* species are discussed and hypothesized.

**Key words:** *Annonaceae*, *Artabotrys*, evolution, new species, systematics, taxonomy, Thailand, thorns, *Xylopieae*

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## Introduction

*Artabotrys* is one of the larger genera of *Annonaceae*, a pantropical family of flowering plants consisting of c. 2430 species (Couvreur & al. 2019) in 108 genera (Guo & al. 2017; Chaowasku & al. 2018a, 2018b; Xue & al. 2018; note that *Friesodielsia* Steenis and *Schefferomitra* Diels are synonymous, see Saunders & al. 2020;

and *Melodorum* Lour. has been synonymized with *Uvaria* L., see Turner 2018). *Artabotrys*, with over 100 species distributed in tropical forests of Africa-Madagascar, Asia, New Guinea and Australia, has been classified in the tribe *Xylopieae* of the subfamily *Annonoideae* (Charou & al. 2012). *Artabotrys* is mainly characterized by (1) hooked peduncles and inflorescence axes, (2) inner petals that are generally constricted over the reproductive

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organs, (3) biovulate carpels, with basal placentation and (4) sessile to shortly stipitate monocarps (Keßler 1993; Chen & al. 2018; Chen & Eiadthong 2020). Species of *Artabotrys* develop a climbing habit with the help of hooked peduncles and inflorescence axes, but sometimes appear as straggling shrubs (e.g. in *A. spinosus* Craib; Chalermglin 2001; personal observations). Moreover, some species even possess thorns, a rare character in *Annonaceae*; these thorns are generally observable on the lower part of plants (Posluszny & Fisher 2000; Chalermglin 2001; Fisher & al. 2002; personal observations). The genus has been inferred to have originated in Africa and subsequently dispersed to Madagascar and to Asia-Australasia (Chen & al. 2019). The latter dispersal event has been inferred to have occurred during the Middle Miocene via overland migration across Arabia. The majority of species diversity is in Asia-Australasia instead of Africa-Madagascar, with c. 75 species vs c. 30 species, respectively (Chen & al. 2018).

Although, as a genus, *Artabotrys* is easily recognizable, species delimitation and identification are somewhat problematic (e.g. Turner 2009; Turner & Utteridge 2015; Chen & al. 2018). In Thailand, there are 20 species of *Artabotrys* reported, two of which have recently been described (Chen & Eiadthong 2020). However, based on personal observations, identification of some specimens is still unsatisfactory due to the morphological heterogeneity of certain species, e.g. *A. harmandii* Finet & Gagnep., *A. siamensis* Miq. and *A. spinosus*. In the course of identifying specimens for the inclusion in a molecular phylogeny in order to solve some species complexes in Thai *Artabotrys* as part of the first author's M.Sc. study, we came across specimens from southwestern Thailand identified as *A. multiflorus* C. E. C. Fisch. These collections do not match the type specimen of *A. multiflorus* well. Therefore, in this study, we re-assess the taxonomic status of such specimens by detailed morphological comparisons. A multi-locus plastid phylogeny is also reconstructed, incorporating, among others, an accession of *A. cf. multiflorus* and multiple accessions of the above-mentioned three species. In addition, as mentioned earlier, certain species of *Artabotrys* exhibit thorns, a feature that is exceptional in the family. Several questions regarding this remarkable trait arise, e.g. did it evolve only once? Consequently, character evolutionary analyses are performed to shed light on the evolution of thorns in *Artabotrys*, with discussion on their putative advantages.

## Material and methods

### Phylogenetic reconstructions

The ingroup consisted of *Xylopieae*: 31 accessions of *Artabotrys* and two species of *Xylophia* L. On the basis of plastid DNA data, both genera have been consistently retrieved as sister genera with strong support (e.g. Charou & al. 2012; Guo & al. 2017), although this relation-

ship was not supported based on some nuclear DNA data (Couvreur & al. 2019). Outgroups were members of *Duguetieae* (a species of *Letestudoxa* Pellegr. plus a species of *Pseudartabotrys* Pellegr.). Six plastid DNA regions (*matK*, *ndhF* and *rbcL* exons; *trnL* intron; *psbA-trnH* and *trnL-trnF* intergenic spacers) were included. Sequences of 18 accessions were newly generated in the present study. Appendix 1 shows voucher information and GenBank accession numbers.

DNA extraction, amplification and sequencing, including primer sequences, used in the present study followed Chaowasku & al. (2018a, 2018b, 2020). Sequences obtained were edited using the Staden package (Staden & al. 2000) and then aligned using the Multiple Sequence Comparison by Log-Expectation (MUSCLE; Edgar 2004) implemented in MEGA7 (Kumar & al. 2016). The alignments were subsequently checked manually and adjusted where necessary based on the similarity criterion (Simmons 2004). In some accessions there was an inversion of 15-stretch nucleotides in the *psbA-trnH* intergenic spacer and this was complementarily reversed to be alignable to the remaining sequences, following Pirie & al. (2006). In total, 5484 nucleotide characters were included. Indel characters were not included because only a few non-autapomorphic indel structures were present. Alignments are available in the Supplemental content online (<https://doi.org/10.3372/wi.51.51106>).

Parsimony analysis was performed in TNT version 1.5 (Goloboff & Catalano 2016). All characters were equally weighted and unordered. Incongruence among regions was assessed by analysing each region individually to see if there was any significant topological conflict (e.g. Wiens 1998). Multiple most parsimonious trees were generated by a heuristic search of the combined data, with 9000 replicates of random sequence addition, saving 10 trees per replicate, and using the tree bisection and reconnection (TBR) branch-swapping algorithm. Clade support was assessed by symmetric resampling (SR; Goloboff & al. 2003). A default change probability was used. Two hundred thousand replicates were run, each with four replicates of random sequence addition, saving four trees per replicate. A clade with SR  $\geq 85\%$ , 70–84%, or 50–69% was considered strongly, moderately, or weakly supported, respectively. Maximum likelihood analysis was carried out in IQ-TREE version 1.6.10 (Nguyen & al. 2015) under partition models (Chernomor & al. 2016) implemented with the “-spp” command, whereas Bayesian Markov chain Monte Carlo (MCMC; Yang & Rannala 1997) phylogenetic analysis was accomplished in MrBayes version 3.2.6 (Ronquist & al. 2012). Both analyses were run via the CIPRES Science Gateway version 3.3 (Miller & al. 2010). The data matrix was divided into five partitions based on the identity of DNA regions (the *trnL* intron and the adjacent *trnL-trnF* intergenic spacer were combined as a single partition). The most appropriate model of sequence evolution for each DNA partition was chosen by the Akaike

Information Criterion (AIC; Akaike 1974) scores, using FindModel (<http://www.hiv.lanl.gov/content/sequence/findmodel/findmodel.html>; Posada & Crandall 1998). The General Time Reversible (GTR; Tavaré 1986) nucleotide substitution model was selected for one partition (*matK*), whereas GTR with a gamma distribution for among-site rate variation (G) was selected for two partitions (*ndhF* and *psbA-trnH*). The Hasegawa-Kishino-Yano (HKY; Hasegawa & al. 1985) substitution model was selected for one partition (*trnLF* [= *trnL* intron + *trnL-trnF* intergenic spacer]), while HKY with G was selected for the remaining partition (*rbcL*). Clade support in the maximum likelihood analysis was measured by a non-parametric bootstrap resampling (BS; Felsenstein 1985) with 2000 replicates. Similar to the differentiation of the SR values in the parsimony analysis, a clade with BS  $\geq 85\%$ , 70–84%, or 50–69% was considered strongly, moderately, or weakly supported, respectively. In the Bayesian analysis, four 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 1000<sup>th</sup> generation. Convergence was assessed by checking the standard deviation of split frequencies of the runs with values  $< 0.01$  interpreted as indicative of a good convergence and by checking for adequate effective sample sizes (ESS  $> 200$ ) using Tracer version 1.6 (Rambaut & al. 2013). The first 25% of all trees sampled were discarded as burn-in and the 50% majority-rule consensus tree was created from the remaining trees. A clade with posterior probabilities (PP)  $\geq 0.95$ , 0.9–0.94, or 0.5–0.89 was considered strongly supported, weakly supported, or unsupported, respectively.

#### **Ancestral character-state reconstructions of thorn occurrence in *Artabotrys***

The presence/absence of thorns in all accessions included was surveyed from literature (Blume 1830; Bentham 1861; Oliver 1868; Hooker & Thomson 1872; King 1892; Diels 1915, 1931; Pellegrin 1920; Craib 1925; Le Thomas 1969; Posluszny & Fisher 2000; Chalermglin 2001; Nurainas 2004; Jessup 2007; Li & al. 2011; Chen & Eiadthong 2020), from specimen labels and/or from personal observations in the field. Ten thousand post burn-in trees (2500 from each run) from the Bayesian analysis were used as input trees for parsimony and maximum likelihood ancestral character-state reconstructions in Mesquite version 3.6 (Maddison & Maddison 2018). Character state changes were treated as unordered. The “Mk1” model was adopted for the maximum likelihood ancestral character-state reconstructions, with default model settings. The “trace over trees” option was chosen and reconstructions across

the input trees were summarized at each node of the Bayesian 50% majority-rule consensus tree using the “uniquely best state” option.

#### **Morphology**

The morphological data of *Artabotrys multiflorus* for comparison were derived from Fischer (1937) and study of the type specimen. Two gatherings of *A. cf. multiflorus* from southwestern Thailand (*Keßler PK 3227* [B, BKF, CMUB, L] and *Aongyong 16* [CMUB]) were studied morphologically (herbarium codes according to Index herbariorum; <http://sweetgum.nybg.org/science/ih/>). *Aongyong 16* is a voucher for molecular phylogenetic analyses and, although sterile, can be identified as the same taxon as *Keßler PK 3227* because both gatherings have coriaceous leaves and both were collected  $\pm 3$  km apart at the same elevation. The indumentum terminology used followed Hewson (1988). The abbreviation “c.” (circa) was added when there was a single observation/measurement. The term “almost glabrous” means “with fewer than ten hairs”.

#### **Results**

The parsimony analysis resulted in 21 most parsimonious trees with 759 steps. The consistency and retention indices (CI and RI) were both 0.89. There was no strong topological conflict (SR  $\geq 85\%$ ) in the analyses of each plastid region. The ingroup monophyly was maximally supported as shown in Fig. 1. *Artabotrys* and *Xylopiopsis* were each recovered as a maximally supported sister clades. In the former genus, a maximally supported clade composed of two accessions of *A. thomsonii* Oliv., both from Africa, was retrieved as the sister group of a large maximally supported clade consisting of the remaining accessions of *Artabotrys*. In this large clade, there were two strongly supported sister clades: a clade of *A. pierreanus* Engl. & Diels and *A. stolzii* Diels (PP 1, BS 87%, SR 91%), both from Africa, and a clade containing the rest of the genus from Asia-Australasia (PP 1, BS 99%, SR 99%). The relationships in this Asian-Australasian clade were largely unresolved. There was a moderately to strongly supported clade (PP 1, BS 80%, SR 81%) comprising thorn-bearing species: *A. carnosipetalus* Jessup, *A. harmandii* (four accessions), *A. hexapetalus* (L. f.) Bhandari (two accessions), *A. oblanceolatus* Craib, *A. siamensis* (two accessions) and *A. spinosus* (four accessions). There were two strongly supported clades of *A. harmandii* (*A. harmandii*-1 + *A. harmandii*-2 [PP 1, BS 98%, SR 98%] and *A. harmandii*-3 + *A. harmandii*-4 [PP 1, BS 94%, SR 96%]) and of *A. spinosus* (*A. spinosus*-1 from Mun River + *A. spinosus*-2 from Chi River [PP 1, BS 99%, SR 99%] and *A. spinosus*-3 + *A. spinosus*-4 [PP 1, BS 100%, SR 99%], both from the Mekong River). The two



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

clades of *A. harmandii* did not show sister relationships, nor did the two clades of *A. spinosus*. Two accessions of *A. siamensis* also did not form a clade. Outside the thorn-bearing clade, *A. cf. multiflorus* was retrieved as the sister group of a strongly supported clade (PP 1, BS 100%, SR 99%) composed of *A. uniflorus* (Griff.) Craib

and *Artabotrys* sp. 1 THA with weak to strong support (PP 1, BS 60%, SR 59%).

In *Artabotrys*, the occurrence of thorns was inferred to have evolved once in the thorn-bearing clade (Fig. 2). The character state “thorns present” was reconstructed at the crown node of the thorn-bearing clade in all 10000



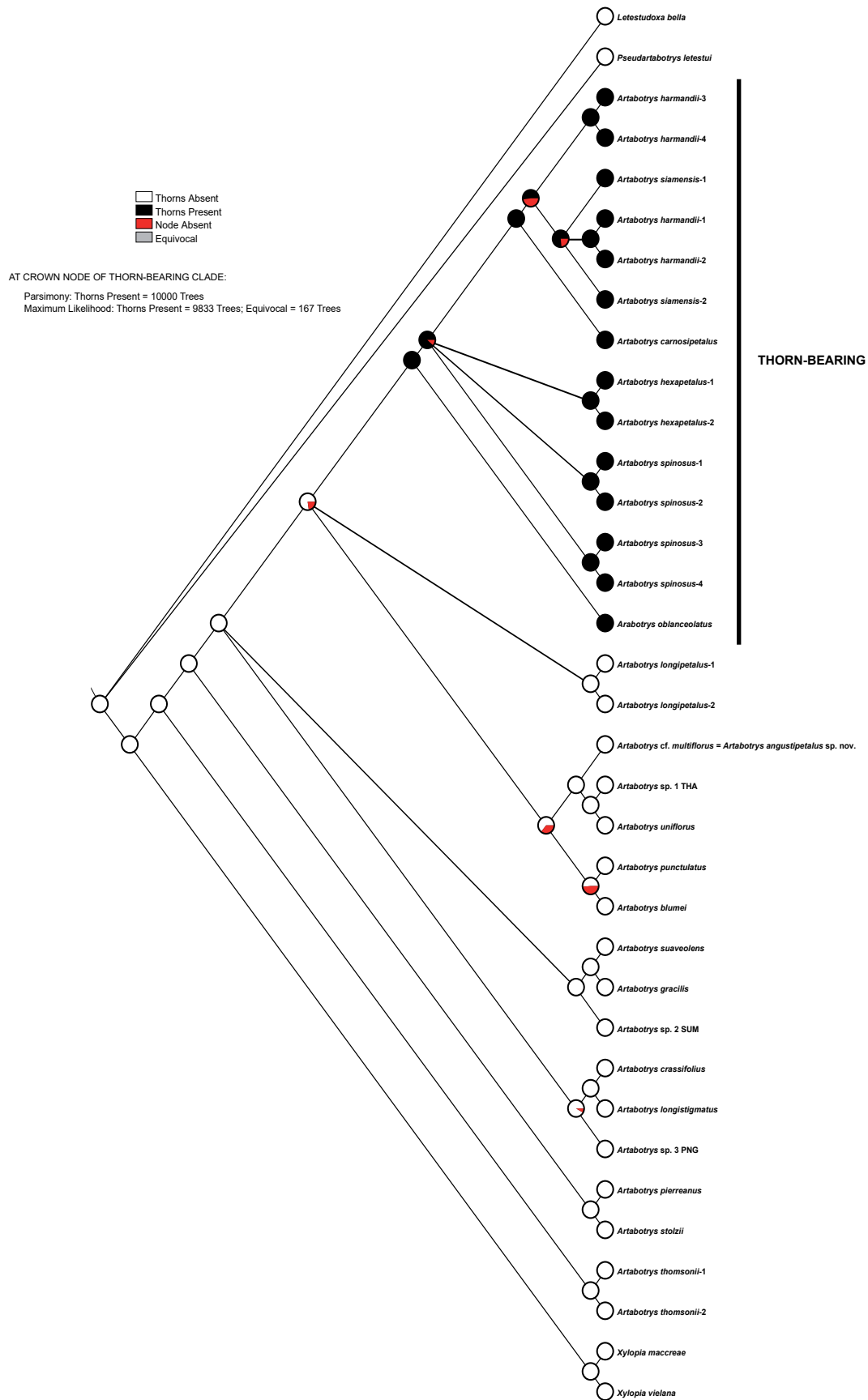


Fig. 2. Maximum likelihood and parsimony ancestral character-state reconstructions of thorn occurrence in *Artabotrys* across 10000 post burn-in trees from Bayesian phylogenetic inference shown on Bayesian 50% majority-rule consensus tree.

input trees under the parsimony criterion. Under the maximum likelihood approach it was reconstructed in 9833 trees, while the remaining 167 trees were equivocally reconstructed.

## Discussion

### *A new species of Artabotrys from Thailand*

*Artabotrys* cf. *multiflorus* is somewhat poorly supported as the sister species of a strongly supported clade composed of *A. uniflorus* and *Artabotrys* sp. 1 THA (Fig. 1). However, *A. uniflorus* and *Artabotrys* sp. 1 THA possess only one flower per hook with rather thick and fleshy petals (personal observations), whereas each hook of *A. cf. multiflorus* bears more or less five flowers exhibiting thin and rather chartaceous petals (Fig. 3). Upon a closer comparison with the type specimen (Fig. 4) and protologue (Fischer 1937) of *A. multiflorus*, *A. cf. multiflorus* differs in several respects (Table 1), i.e. number of flowers per hook (Fig. 3, 4), petal shape, length, width and apex (Fig. 4, 5A, 5B) and number of carpels per flower. In addition, the elevation where *A. cf. multiflorus* (c. 510 m) and *A. multiflorus* (c. 914 m) occur is also considerably different. The exact locality of *A. multiflorus* cannot be traced, but it is expected to be somewhere in the Burmese Dawna range (Fischer 1937 [as “Dawnas”]), northwest of the locality of *A. cf. multiflorus* (Kanchanaburi Province, Thailand). On the basis of these differences, *A. cf. multiflorus* is described here as new to science. As a consequence, *A. multiflorus* is most likely to be absent from the flora of Thailand.

***Artabotrys angustipetalus* Photikwan & Chaowasku, sp. nov.** – Fig. 3, 5.

Holotype: Thailand, Kanchanaburi Province, Thung Yai Naresuan Wildlife Sanctuary, 17 Feb 2002 [in flower], *Keßler* PK 3227 (BKF! [SN144809]); isotypes: B!, BKF!, CMUB!, L! [L.1749583, L.1749584]).

**Diagnosis** — *Artabotrys angustipetalus* is morphologically close to *A. multiflorus* C. E. C. Fisch. The former differs primarily from the latter by having more or less five flowers (vs > 12) per hook, linear (vs oblong to oblong-lanceolate) petals, acute (vs obtuse) petal apex, longer and narrower petals and fewer carpels per flower.

**Description** — Woody climbers to 30 m long, c. 10 cm in diam.; *young twigs* almost glabrous; *petiole* 4–7 mm long, grooved on upper surface, almost glabrous on both surfaces; *leaf blade* coriaceous, 10.7–14.2 × 4.8–7.7 cm, elliptic, sometimes ± obovate, glabrous on both surfaces including secondary veins, apex cuspidate-acute, base cuneate; *midrib* slightly raised and glabrous on upper surface, raised and glabrous on lower surface; *secondary veins* 10–12 per

side, angle with midrib 65°–80° (at middle part of leaf blade). *Inflorescences* terminal developing to ± leaf-opposed; *flowering peduncle and inflorescence axis* hook-shaped, first curve 17–27 mm long, 3–4 mm wide (at midpoint of curve), second curve 7–10 mm long, 2–2.3 mm wide (at midpoint of curve), both curves puberulous with appressed hairs, bearing ± 5 flowers per hook, divided into 1 or 2 fascicles, with several bracts at base of each fascicle, ± ovate; *flowering pedicel* 12–18 mm long, puberulous with appressed hairs. *Sepals* free, 2–2.5 × 2–2.5 mm, broadly ovate, apex acute-acuminate, sometimes slightly obtuse, outside and margin puberulous with appressed hairs, inside glabrous. *Outer petals* 29–30 × c. 3 mm, linear, apex acute, divided into a blade and a claw, claw c. 3.8 mm long, upper rim of claw slightly raised and curved, outside of outer petals puberulous with appressed hairs on blade, more densely so on claw, margin puberulous with appressed to erect hairs, inside puberulous with appressed hairs on blade, claw glabrous, but upper rim of claw tomentose with erect hairs; *inner petals* 30–31 × 2–2.5 mm, linear, apex acute, divided into a blade and a claw, claw c. 3.5 mm long, upper rim of claw distinctly raised and curved, covering stamens and carpels, outside of inner petals puberulous with appressed hairs on blade, but tomentose with erect hairs on claw (c. ⅓ of claw length from upper rim), remaining area of claw puberulous with appressed hairs, margin puberulous with appressed to erect hairs, inside puberulous with appressed hairs on blade, claw glabrous, but upper rim of claw tomentose with erect hairs. *Torus* c. 1 × 2 mm, slightly elevated, apex flat-topped, tomentose-villous with erect hairs on areas unoccupied by stamens and carpels. *Stamens* 25–32 per flower, 1.1–1.2 mm long, connective apex ± truncate, covering thecae. *Carpels* 7 or 8 per flower, 1.1–1.4 mm long; *stigmas* terete and curved; *ovaries* glabrous; *ovules* 2 per ovary, basal. *Fruit* unknown.

**Phenology** — Flowering material collected in February.

**Distribution and ecology** — Kanchanaburi Province, SW Thailand; occurring in primary evergreen forests at an elevation of c. 510 m.

**Field notes** — Bark blackish; flowers with very sweet fruity smell, petals greenish yellow.

Table 1. Main morphological differences between *Artabotrys angustipetalus* and *A. multiflorus*.

Feature	<i>A. angustipetalus</i>	<i>A. multiflorus</i>
Number of flowers per hook	± 5	> 12
Petal shape	linear	oblong to oblong-lanceolate
Petal apex	acute	obtuse
Petal length (mm)	29–31	18–25
Petal width (mm)	2–3	6–9
Number of carpels per flower	7 or 8	12–21



Nationaal Herbarium Nederland  
**FLORA OF THAILAND**  
 Leg.: Kessler, P.J.A. PK 3227  
 d.d.: 17 February 2002  
 With: Piya Chalermglin  
**Annonaceae**  
**Artabotrys multiflora**  
 Det.: Kessler, P.J.A. & Piya, 2/2002  
 Thailand, Thung Yai Naraeuan Wildlife S  
 Alt: 510 m 14.53 N, 98.50 E  
 Locality : Thailand, Kanchanaburi Province, Thung Yai Naraeuan Wildlife  
 Sanctuary (14.54°22.2'N; 98.50°11.1'E)  
 Habitat : Primary evergreen forest along forest trail.  
 Field notes: Large climber c. 30 m long, c. 10 cm in diameter, bark blackish,  
 flowers with very sweet fruity smell, 3–5 on the hooks, petals greenish-yellow.  
 DNA!

Forest Herbarium  
  
 SN 144809

Fig. 3. Holotype of *Artabotrys angustipetalus* Photikwan & Chaowasku – *Keßler* PK 3227 (BKF [SN144809]).





Fig. 4. Isotype of *Artabotrys multiflorus* C. E. C. Fisch. – Parkinson 5220 (E [E00393106]).





Fig. 5. Flowering organs of *Artabotrys angustipetalus*. – A: abaxial side of outer petal (left), adaxial side of outer petal (right); B: abaxial side of inner petal (left), adaxial side of inner petal (right); C: adaxial side of outer petal claw; D: adaxial side of inner petal claw; E: adaxial side of stamen (left), abaxial side of stamen (right); F: view from above showing sepals; G: carpel.

**Conservation status** — DD (Data Deficient) according to IUCN (2012) because this species is known from only two collections. Further explorations are required before an assessment can be made.

**Additional specimen examined** (paratype) — THAILAND: Kanchanaburi Province, Thongphaphum District, Phuye, without date [sterile], *Aongyong 16* (CMUB).

#### **Evolution of thorns in *Artabotrys***

The occurrence of thorns in *Annonaceae* is exceptional. Besides certain species of *Artabotrys*, thorns are also

present in a few species of *Annona* L. (H. Rainer, personal communication; e.g. *A. spinescens* Mart., personal observations on a specimen at P [P01984538]), which belongs to the tribe *Annoneae* of the subfamily *Anno-noideae* (Chatrou & al. 2012). Based on the ancestral character-state reconstructions of thorn occurrence in *Artabotrys*, this trait is inferred to have evolved only once as a synapomorphy of the thorn-bearing clade (Fig. 2), which is equivalent to clade D2 in Chen & al. (2019). Three species of *Artabotrys* that are absent in our analyses, *A. brevipes* Craib, *A. manoranjanii* M. V. Ramana & al. and *A. pleurocarpus* Maingay ex Hook. f. & Thomson, also possess thorns according to Insura (2009), Ramana & al. (2016) and personal observations. According to Insura (2009), at least one additional species, *A. vanprukii* Craib, endemic to Thailand, also exhibits thorns. The synapomorphic thorn occurrence is systematically powerful in elucidating coarse phylogenetic placements of Asian-Australasian species of *Artabotrys*, i.e. species with thorns are (or will be) members of the thorn-bearing clade, whereas those without thorns are (or will be) recovered outside the thorn-bearing clade. This is clearly exemplified in the new species *A. angustipetalus*, which does not possess thorns and has been recovered outside the thorn-bearing clade (Fig. 1, 2). Observations in living plants reveal that thorns

generally emerge in pairs and are generally found along the lower part of stems (Fig. 6A). In some species, e.g. *A. spinosus*, these thorns can appear on the upper part of stems as well, even on young orthotropic branches (personal observations). According to Posluszny & Fisher (2000), these thorns represent plagiotropic branches that do not develop further. We have observed the development of thorns in a sapling and noticed that a thorn emerged rather soon, i.e. as a second plagiotropic branch at a height of only c. 25 cm (Fig. 6B). One of the possible functions of thorns is herbivore protection, especially from larger vertebrate animals (Grubb 1992; Ronel & Lev-Yadun 2012; Nascimento & al. 2020). Addi-



Fig. 6. Thorns of *Artabotrys* species. – A: pairs of thorns at lower part of stems of *A. siamensis* [= *A. siamensis*-1]; B: thorn as a second plagiotropic branch of a sapling of *Artabotrys* sp.

tionally, as demonstrated by Fisher & al. (2002), light plays an important role for thorn development in *A. hexapetalus*, i.e. the more shaded the areas, the more thorns are developed. It seems that there is more driving force for plants in shaded areas to grow orthotropic branches up above to reach light and find support from other plants. Therefore, the growth of the less necessary plagiotropic branches is possibly minimized by developing more thorns instead. The orthotropic branches of the thorn-bearing species of *Artabotrys* can grow very fast and at some point after they reach other plants, fewer thorns but more plagiotropic branches with hooks are developed (personal observations). Regarding thorns in a few species of *Annona*, mentioned above, further ontogenetic study is indispensable to ascertain if they are homologous with thorns in *Artabotrys* species because the branching architecture of *Annona* is distichous, without the distinction between orthotropic and plagiotropic branches, whereas the branching architecture of *Artabotrys* is spiral, with the distinction between orthotropic and plagiotropic branches (Johnson 2003).

Three species in the thorn-bearing clade, *Artabotrys harmandii*, *A. siamensis* and *A. spinosus*, each appear to be non-monophyletic (Fig. 1). There are some morphological differences (e.g. leaf and/or petal shape) between two lineages/clades of each species; however, we believe that more resolved phylogenetic hypotheses incorporating more DNA sequences, particularly nuclear DNA markers via baiting (e.g. Couvreur & al. 2019; Brée & al. 2020), are required before any solid taxonomic conclusion on these species can be drawn.

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## Appendix 1

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

Taxon	Accession	Country	Collector and number (herbarium)	matK	ndhF	psbA-trnH	rbcL	trnLF
<i>Artabotrys angustipetalus</i>	<i>A. cf. multiflorus</i> = <i>A. angustipetalus</i> sp. nov.	Thailand	Aongyong 16 (CMUB)	MW057941**	MW057959**	MW057977**	MW057995**	MW058013**
Photikwan & Chaowasku & Thomson		Hong Kong	Thomas 11-544 (HKU)	KM924839	KM924869	KM924970	KM924909	KM924937
<i>Artabotrys blumei</i> Hook. f. & Thomson		Australia	Sankowsky 3196 (BRI)	KM924835	KM924865	KM924966	KM924905	KM924933
<i>Artabotrys carnosipetalus</i> Jessup		Malaysia	Teo 843 (L)	KM924836	KM924866	KM924967	KM924906	KM924934
<i>Artabotrys crassifolius</i> Hook. f. & Thomson		Indonesia	Puglisi 262 (HKU)	KM924837	KM924867	KM924968	KM924907	KM924935
<i>Artabotrys gracilis</i> King		Thailand	Redphitak 1 (CMUB)	MW057953**	MW057971**	MW057989**	MW058007**	MW058025**
<i>Artabotrys harmandii</i> Finet & Gagnep.	<i>A. harmandii</i> -1	Thailand						
<i>Artabotrys harmandii</i>	<i>A. harmandii</i> -2	Thailand	Keßler & al. 3213 (L)	KM924838	KM924868	KM924969	KM924908	KM924936
<i>Artabotrys harmandii</i>	<i>A. harmandii</i> -3	Thailand	Chaowasku 81 (CMUB)	MW057938**	MW057956**	MW057974**	MW057992**	MW058010**
<i>Artabotrys harmandii</i>	<i>A. harmandii</i> -4	Thailand	Chaowasku 193 (CMUB)	MW057946**	MW057964**	MW057982**	MW058000**	MW058018**
<i>Artabotrys hexapetalus</i> (L. f.) Bhandari	<i>A. hexapetalus</i> -1	Thailand	Chaowasku 194 (CMUB)	MW057939**	MW057957**	MW057975**	MW057993**	MW058011**
<i>Artabotrys hexapetalus</i>	<i>A. hexapetalus</i> -2	cultivated	Anon. s.n. [Utrecht Botanic Garden, 94GR01614] (U)	AY238962	—	—	AY238953	—
<i>Artabotrys hexapetalus</i>	<i>A. hexapetalus</i> -2	India	Chatrou 470 (U)	—	EF179284	AY841429	—	EF179317
<i>Artabotrys longipetalus</i> Junhao Chen & Eiadthong	<i>A. longipetalus</i> -1	Thailand	Aongyong 17 (CMUB)	MW057940**	MW057958**	MW057976**	MW057994**	MW058012**
<i>Artabotrys longipetalus</i>	<i>A. longipetalus</i> -2	Thailand	Aongyong 18 (CMUB)	MW057950**	MW057968**	MW057986**	MW058004**	MW058022**
<i>Artabotrys longistigmatus</i> Nuraenas		Indonesia	Puglisi 194 (HKU)	KM924840	KM924870	KM924971	KM924910	KM924938
<i>Artabotrys oblanceolatus</i> Craib		Thailand	Chaowasku 195 (CMUB)	MW057943**	MW057961**	MW057979**	MW057997**	MW058015**
<i>Artabotrys pierreanus</i> Engl. & Diels		Gabon	Wieringa 6132 (WAG)	KM924843	KM924874	KM924975	KM924913	KM924942
<i>Artabotrys punctulatus</i> C. Y. Wu		Thailand	Chaowasku 196 (CMUB)	MW057955**	MW057973**	MW057991**	MW058009**	MW058027**
<i>Artabotrys siamensis</i> Miq.	<i>A. siamensis</i> -1	Thailand	Damthongdee AD 3 (BKF)	MW057948**	MW057966**	MW057984**	MW058002**	MW058020**
<i>Artabotrys siamensis</i>	<i>A. siamensis</i> -2	Thailand	Kaitongsuk SK 226 (BKF)	MW057954**	MW057972**	MW057990**	MW058008**	MW058026**

(continued on next page)

Taxon	Accession	Country	Collector and number (herbarium)	matK	ndhF	psbA-trnH	rbcL	trnLF
<i>Artabotrys spinosus</i> Craib	<i>A. spinosus</i> -1 MUN RIV.	Thailand	<i>Chaowasku 197</i> (CMUB)	MW057947**	MW057965**	MW057983**	MW058001**	MW058019**
<i>Artabotrys spinosus</i>	<i>A. spinosus</i> -2 CHI RIV.	Thailand	<i>Chaowasku 198</i> (CMUB)	MW057945**	MW057963**	MW057981**	MW057999**	MW058017**
<i>Artabotrys spinosus</i>	<i>A. spinosus</i> -3 MEKONG RIV.	Thailand	<i>Chaowasku 199</i> (CMUB)	MW057944**	MW057962**	MW057980**	MW057998**	MW058016**
<i>Artabotrys spinosus</i>	<i>A. spinosus</i> -4 MEKONG RIV.	Thailand	<i>Chaowasku 200</i> (CMUB)	MW057952**	MW057970**	MW057988**	MW058006**	MW058024**
<i>Artabotrys stolzii</i> Diels		Tanzania	<i>Couvreur 72</i> (WAG)	KM924846	KM924877	KM924978	KM924916	KM924945
<i>Artabotrys suaveolens</i> (Blume) Blume		Thailand	<i>Chaowasku 201</i> (CMUB)	MW057942**	MW057960**	MW057978**	MW057996**	MW058014**
<i>Artabotrys thomsonii</i> Oliv.	<i>A. thomsonii</i> -1	Gabon	<i>Wieringa 4018</i> (WAG)	DQ125052	EF179285	DQ125118	AY841599	AY841676
<i>Artabotrys thomsonii</i>	<i>A. thomsonii</i> -2	Central African Republic	<i>Harris 4533</i> (E)	KM924847	KM924878	KM924979	KM924917	KM924946
<i>Artabotrys uniflorus</i> (Griff.) Craib		Thailand	<i>Kaewjaroy 1</i> (CMUB)	MW057951**	MW057969**	MW057987**	MW058005**	MW058023**
<i>Artabotrys</i> sp. 1	<i>A. sp.</i> 1 THA	Thailand	<i>Damthongdee AD 9</i> (BKF)	MW057949**	MW057967**	MW057985**	MW058003**	MW058021**
<i>Artabotrys</i> sp. 2	<i>A. sp.</i> 2 SUM	Indonesia	<i>Puglisi 164</i> (HKU)	KM924845	KM924876	KM924977	KM924915	KM924944
<i>Artabotrys</i> sp. 3	<i>A. sp.</i> 3 PNG	Papua New Guinea	<i>BRC &amp; Weiblen WP5B1081</i> (BRC)	KM924844	KM924875	KM924976	KM924914	KM924943
<i>Letestudoxa bella</i> Pellegr.		Gabon	<i>Wieringa 2797</i> (WAG)	DQ125059	EF179302	DQ125128	AY841629	AY841707
<i>Pseudartabotrys letestui</i> Pellegr.		Gabon	<i>Wieringa 3273</i> (WAG)	DQ125061	EF179307	DQ125131	AY841650	AY841728
<i>Xylopiya maccreae</i> (F. Muell.) L. S. Sm.		Australia	<i>Sankowsky 3148</i> (BRI)	KM924860	KM924900	KM924998	KM924928	KM924961
<i>Xylopiya vielana</i> Pierre		Thailand	<i>Chalermglin 530725</i> (HKU)	KM924863	KM924903	KM925001	KM924931	KM924964