



## Two new species of *Artocarpus* (Moraceae) from Thailand and Vietnam

ELLIOT M. GARDNER<sup>1,2,3,8</sup>, ARUNRAT CHAVEERACH<sup>4,9</sup>, RUNGLAWAN SUDMOON<sup>5,10</sup>  
& NYREE J.C. ZEREGA<sup>6,7,11</sup>

<sup>1</sup> The Morton Arboretum, 4100 IL-53, Lisle, Illinois 60532, USA.

<sup>2</sup> Singapore Botanic Gardens, National Parks Board, 1 Cluny Road, 259569, Singapore.

<sup>3</sup> Case Western Reserve University, Department of Biology, 2080 Adelbert Road, Cleveland, Ohio 44106, USA.

<sup>4</sup> Department of Biology, Faculty of Science, Khon Kaen University, Thailand.

<sup>5</sup> Faculty of Law, Khon Kaen University, Thailand.

<sup>6</sup> Northwestern University, Program in Plant Biology and Conservation, Hogan Hall, 2205 Tech Drive, Evanston, Illinois 60028, USA.

<sup>7</sup> Chicago Botanic Garden, Negaunee Institute for Plant Conservation Science and Action, 1000 Lake Cook Road, Glencoe, IL, 60022, USA.

<sup>8</sup> [egardner@mortonarb.org](mailto:egardner@mortonarb.org); <https://orcid.org/0000-0003-1133-5167>

<sup>9</sup> [raccha@kku.ac.th](mailto:raccha@kku.ac.th); <https://orcid.org/0000-0002-7466-4243>

<sup>10</sup> [rsudmoon@yahoo.com](mailto:rsudmoon@yahoo.com); <https://orcid.org/0000-0003-4878-2964>

<sup>11</sup> [n-zerega@northwestern.edu](mailto:n-zerega@northwestern.edu); <https://orcid.org/0000-0003-1132-4943>

### Abstract

Recent taxonomic work on *Artocarpus* has revealed two undescribed species from Thailand and Vietnam. *Artocarpus rubrosoccatatus*, endemic to peninsular Thailand, resembles *A. lacucha* but is distinguished by its deep red clavate staminate inflorescences. *Artocarpus montanus* is found in the montane regions of southern and central Vietnam, and perhaps also in Thailand. This species resembles the vegetative parts of *A. lowii* and *A. excelsus*, but *A. montanus* differs in its longer syncarp processes and its geographic distribution. The vast majority of *Artocarpus* species are found in tropical lowlands, and *A. montanus*, along with *A. excelsus*, represent the only known members of the genus that are restricted to montane habitats. The provisional conservation assessment of both new species is Near Threatened, because although their known areas of occupancy are restricted, both occur in protected areas.

**Keywords:** Moraceae, *Artocarpus*, Thailand, Vietnam, crop wild relatives

*Artocarpus* J.R. Forster and G. Forster (1776: 102) (Moraceae) contains about 70 species of trees, distributed in tropical to subtropical regions from India in the west to the Solomon Islands in the east, with a center of diversity in Borneo (Williams *et al.* 2017). Among its species are several high-yield but underutilized crops that may help improve food security in tropical regions, in particular breadfruit (*A. altilis* (Parkinson 1773: 45) Fosberg (1941: 95)) and jackfruit (*A. heterophyllus* Lamarck 1789: 209) (Zerega *et al.* 2010; Jones *et al.* 2011). While the greatest diversity of *Artocarpus* is in Borneo, a secondary center of diversity lies to the north in Thailand and Vietnam (Williams *et al.* 2017). We present two new species of *Artocarpus* from this region—one from Thailand, and the other from the mountain forests of Vietnam. The Thai species represents material previously assigned to *A. lacucha* Roxburgh ex Buchanan-Hamilton (1826: 333) but noted as distinct due to its red clavate staminate inflorescences (Berg *et al.* 2011). Although the Vietnamese species was collected by Poilane over 70 years ago, his collection was assigned to *A. lowii* King in Hooker (1888: 542), a species with similar vegetative parts but whose distribution does not extend further north than the Malay Peninsula (Berg *et al.* 2006). Examination of specimens as well as phylogenomic analyses have confirmed that both entities are in fact distinct species.

*Artocarpus rubrosoccatatus* E.M. Gardner, A. Chaveerach, and N.J.C. Zerega, sp. nov.

Differt ab *A. lacucha* Roxb. ex Buch.-Ham. inflorescentiis masculis clavatis rubris profundis.—Differs from *Artocarpus lacucha* Buch.-Ham. ex Roxb. in the deep red clavate staminate inflorescences.



**FIGURE 1.** Drawing of *Artocarpus rubrosocatus* showing (A) leafy shoot with staminate inflorescences; (B) staminate flower and peltate bract; (C) pistillate inflorescence and flower; and (D) syncarp. Drawn by EMG from *S. Gardner et al. ST1738* (A, D), *S. Phusomsaeng 196* (B), and *S. Gardner & P. Sidisunthorn ST2740* (C).

Type:—THAILAND, Surat Thani Province. Phanom Distr., Khao Sok National Park, headquarters, edge of partially disturbed lowland evergreen forest, 8°54' N, 98° 31' E, 80m elev., 24 March 2005, *S. Gardner et al. ST1738* (holotype: BKF, ♂; isotypes: K, QBG—not seen).

Trees, height to 40 m. Outer bark pale brown to cream, rough, slightly fissured, inner bark pink; latex white. **Twigs** 3.5–5 mm thick, smooth, becoming fissured, densely rufous pubescent with an underlayer of shorter hairs; non-amplexicaul stipular scars ca. 1 x 3 mm, prominent; lenticels scattered. **Stipules** ca. 5–10 x 3–5 mm, triangular, (sub)appressed rufous pubescent. **Leaves** broadly ovate to elliptical, often inequilateral, 16–33 x 9–22 cm, apex acute to obtuse or nearly rounded and shortly acuminate, base acute to subcordate, attachment, inequilateral, adaxially densely rufous pubescent on the main veins and otherwise sparsely pubescent with scattered whitish straight to uncinuate hairs, abaxially densely rufous to fulvous pubescent, soft, the hairs generally not on the lamina itself but originating from the reticulum and appressed over the lamina, margin denticulate in the upper half of the leaf with dense tufts of pubescence around the teeth; main veins nearly flat above, raised beneath; secondary veins 10–14 curved and ascending except crowded and nearly horizontal at the base, occasionally forked and usually noticeably looping back at the margin; tertiary venation scalariform, indistinct above, prominent below; lamina dark green above, pale brownish green

beneath due to pubescence, drying greenish to reddish brown; venation concolorous above, yellowish below and drying medium brown; petiole 14–30 x 2–5 mm, epidermis persistent to exfoliating. Leaves on juvenile trees not seen. **Inflorescences** solitary or paired in leaf axils. **Staminate inflorescences** clavate, 3–5 x 0.5–1 cm when dry, dark red, drying dark red, smooth, covered by bracts with the stamens exerted between them; fertile flowers with perianths deeply 3–4-lobed with nearly separate tepals, ca. 0.5 mm long, rufous pubescent; stamen ca. 1 mm long, filament conical, anther-cells globose, ca. 0.15 mm long; bracts numerous, heads peltate, dark red and densely ciliate around the edges, to ca. 0.3 mm across, the larger bracts occasionally more densely pubescent, giving the surface a spotted look; stout, clavate, densely rufous pubescent processes (bracts or sterile flowers) clustered irregularly at the base of the inflorescence; peduncle 8–12 x 1.5 mm, densely rufous pubescent;  **pistillate inflorescences** cylindrical, ca. 1.8–2.2 x 1–1.5 cm, reddish brown, densely rufous pubescent, perianth apices umbonate, simple styles exerted to c. 0.15 mm through ciliate papillae; peltate, ciliate interfloral bracts numerous, persistent between the perianth apices, peduncle 10–12 x 2.5–3 mm, indumentum as on males.  **Syncarp** subglobose, to ca. 4.5 cm across, irregularly lobed, green with raised brown bumps (pubescent perianth apices and persistent bracts), drying brown, flesh cream to light pink but drying dark reddish brown; with numerous persistent peltate bracts; core (receptacle upon which fruiting perianths are attached) ca. 5 to 10 mm across; fruiting perianths at least several, proximal region free, “seeds” (endocarps) ellipsoid, ca. 7 mm long, style attachment (sub?)apical; peduncle 20–30 mm x 2–4 mm, indumentum as on inflorescences. Figures 1–3.



**FIGURE 2.** The holotype of *Artocarpus rubrosoccatus*, S. Gardner et al. ST1738 (BKF), showing (A) main sheet and (B) close up of immature male inflorescences. Photographs by EMG.

**Vernacular name:**—Ma-hat khang-khok.

**Distribution:**—Peninsular Thailand (Fig. 4)

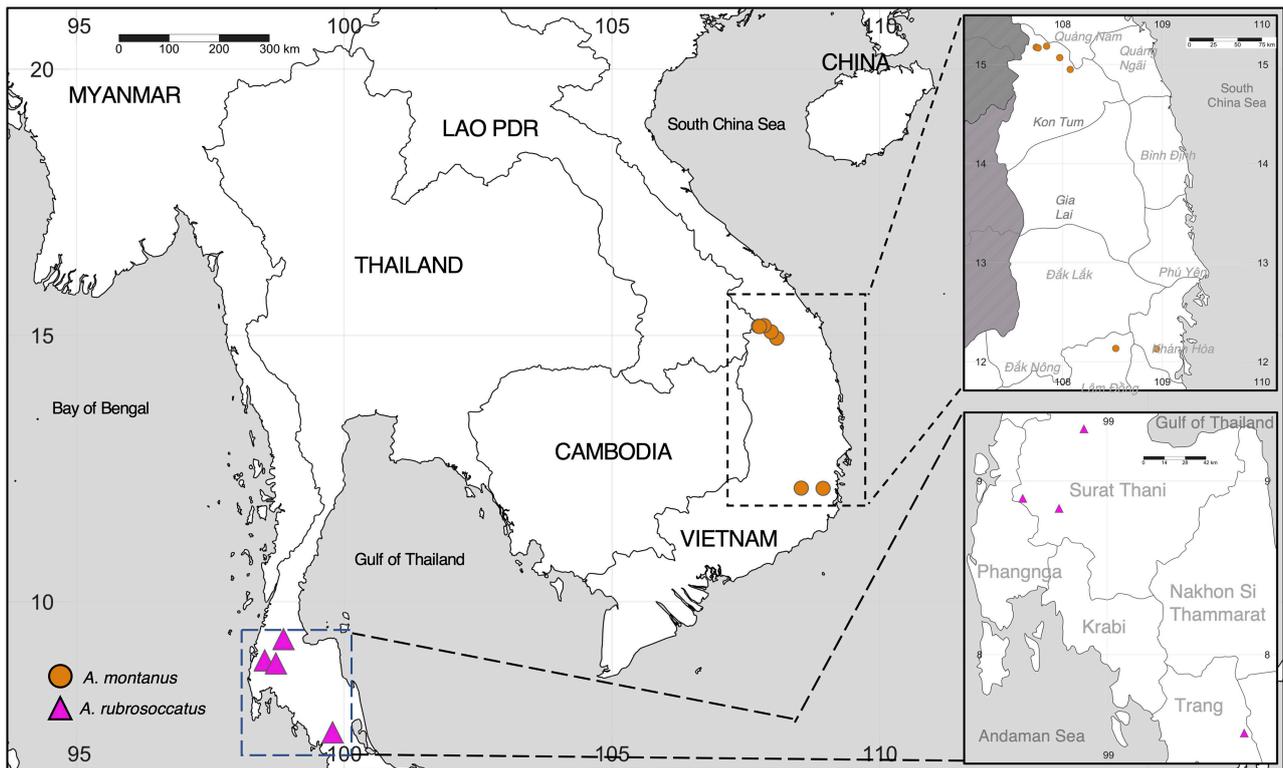
**Habitat:**—Lowland evergreen forest.

**Provisional conservation assessment:**—Although there are few identified collections, *Artocarpus rubrosoccatus* exists within the protected area of Kae Krung National Park, as well in other localities further north. Any threat would therefore arise primarily from its rarity. Our provisional designation is therefore Near Threatened.

**Etymology:**—The epithet comes from the Latin *rubro*- (red) and *soccus* (slipper, antecedent of the English “sock”) and may be loosely translated “red-socked”, referring to the staminate inflorescences that resemble a pair of feet in red socks.



**FIGURE 3.** *Artocarpus rubrosoccatu*, showing (A) habit, (B) leafy shoot with young pubescent leaves, (C) immature staminate inflorescences, (D) bark slash with exudate, (E) leaf margin, (F–G) syncarps, and (H) syncarp on leafy shoot. Photographs by NJCZ; voucher *N. Zerega 517* deposited at CHIC and KKU.

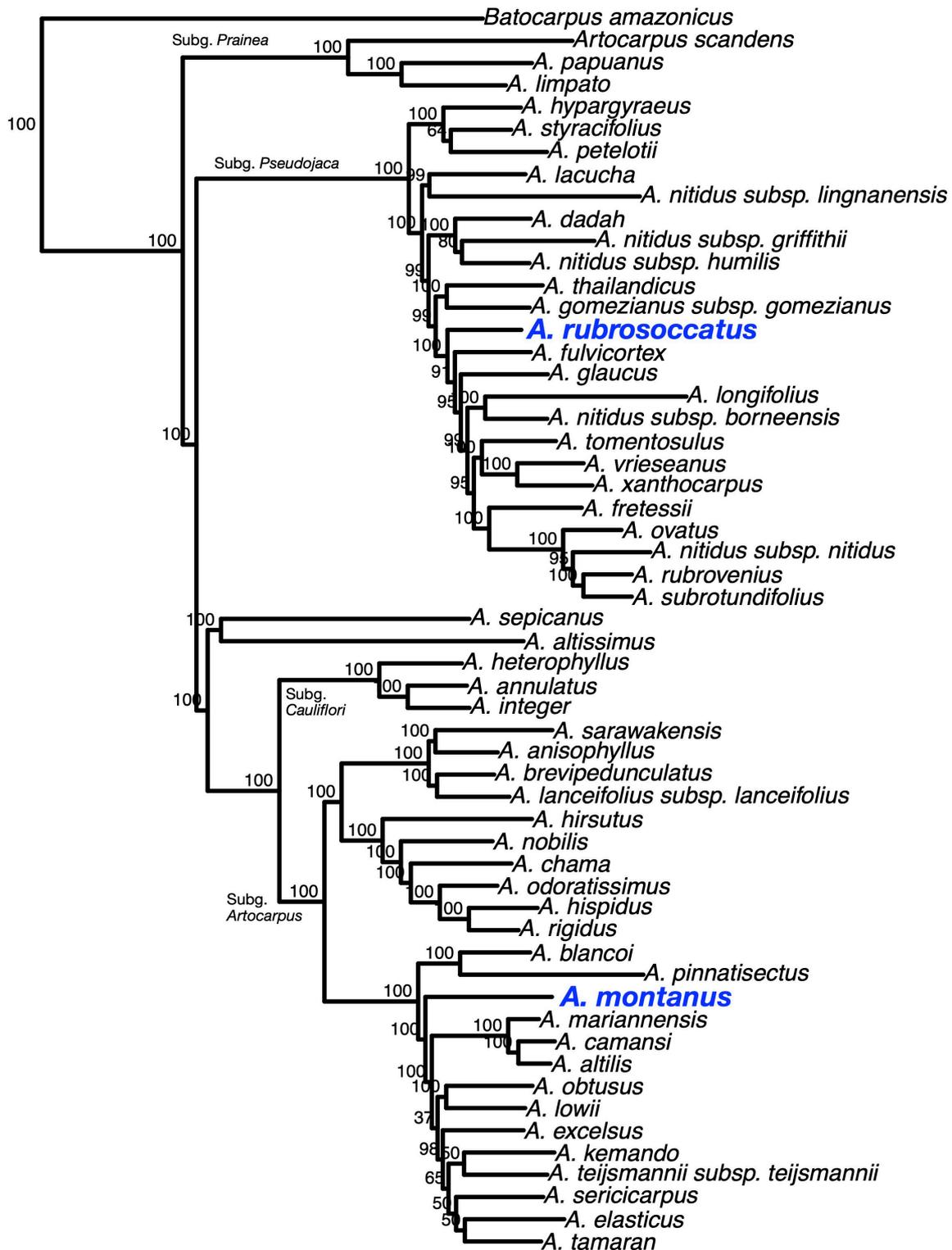


**FIGURE 4.** Map showing the distribution of *Artocarpus rubrosoccatu* (triangles) and *A. montanus* (circles). Insets show Vietnamese and Thai provinces.

**Notes:**—*Artocarpus rubrosoccatu* was previously treated as an uncommon variant of *A. lacucha*. In the *Flora of Thailand*, Berg *et al.* (2011) noted that some material treated under *A. lacucha* had clavate to spicate inflorescences, citing two collections here assigned to *A. rubrosoccatu* (*S. Gardner ST1738* and *S. Phusomsang 196*). The deep red inflorescences, which maintain some of their color even when dry, clearly distinguish this species from *A. lacucha*. Whether the red coloration is suited to particular pollinators or represents some other adaptation remains unknown.

In a phylogenetic analysis of 517 nuclear loci, *A. rubrosoccatu* was sister to a clade containing *A. fulvicortex*

Jarrett (1960: 116) and was not a close ally of *A. lacucha* (Gardner 2017; Gardner *et al.* 2020) (Fig. 5). However, in an 8-gene phylogeny consisting of mostly chloroplast loci, it was sister to the *A. lacucha* clade (containing samples from Thailand, Bangladesh, and China) (Williams *et al.* 2017), suggesting that although it is clearly distinct, its chloroplast may share close ancestry with that of *A. lacucha*.



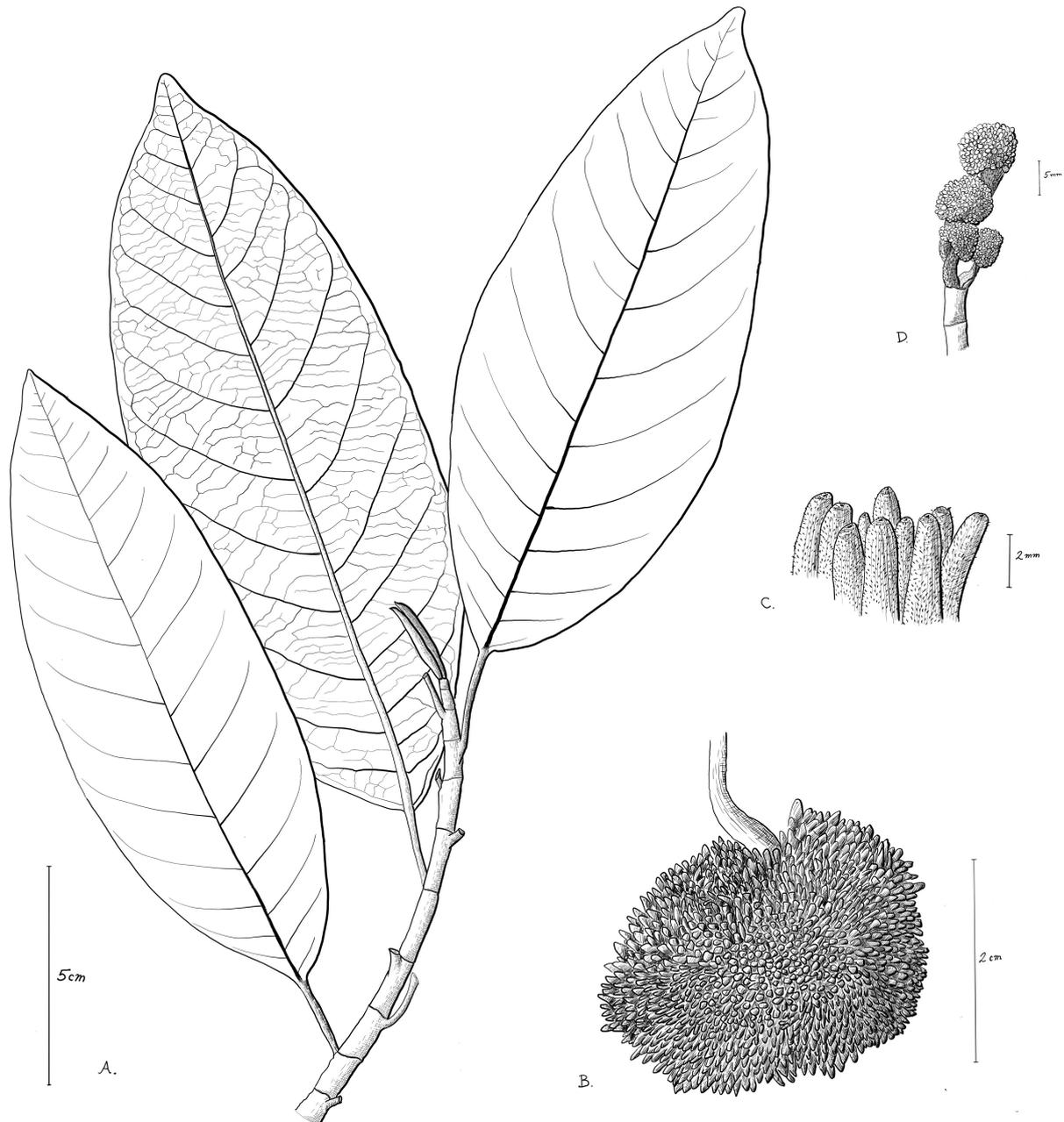
**FIGURE 5** Maximum-likelihood phylogenetic tree based on a supermatrix of 517 nuclear loci showing the positions of *Artocarpus rubrosoccatus* and *A. montanus* (adapted from Gardner 2017 and Gardner *et al.* 2020). Node labels denote bootstrap support.

**Additional specimens examined.**

**THAILAND, Peninsula. Trang Province.** Khao Chong, evergreen forest: *S. Phusomsaeng* 196, 17 April 1969 (BKF!, K!, L!, ♂). **Surat Thani Province.** Wipawadi Distr., Kae Krung N.P., headquarters close to office, in disturbed lowland evergreen/bamboo forest, 9° 18' N, 98° 52' E, 110m: *S. Gardner & P. Sidisunthorn* ST2740, 14 May 2006 (K!, L!, ♀); Phanom Distr., 8° 50' 52.3" N 98° 43' 47.6" E, 45m: *N. Zerega et al.* 517, 15 March 2012 (CHIC!, KCU, ♀).

***Artocarpus montanus* E.M. Gardner and N.J.C. Zerega, sp. nov. (Figs. 6–8)**

Differt ab *A. lowii* King et *A. excelso* F.M. Jarrett syncarpii processis longiis.—Differs from *Artocarpus lowii* King and *A. excelsus* F.M. Jarrett in the longer syncarp processes.



*Elliot Gardner 2019*

**FIGURE 6.** Drawing of *Artocarpus montanus* showing (A) leafy shoot, (B) syncarp (immature), (C) detail of syncarp, and (D) immature inflorescences (malformed). Drawn by EMG from *Averyanov et al. VH 1819* (A–C) and *Poilane 35982* (D).

Type:—VIETNAM. Kon Tum Province, Dak Gley District, between Dak Nen & Mang Khen villages, secondary evergreen mountain forest, 800–900m evel., 19 November 1995, *L. Averyanov et al. VH 1819* (holotype: P; isotypes: HN—not seen, LE, MO).

Evergreen trees, monoecious, height to 30 m; outer bark (on twigs) greyish brown, inner bark reddish; latex white. **Young twigs** 3–6 mm thick, smooth, green, drying wrinkled and dark brown, minutely whitish to yellowish appressed-puberulous, hairs longer on very young growth; amplexicaul stipular scars ca. 0.5 mm broad, prominent; lenticels few, scattered. **Stipules** 12–57 x 3–8 mm, ovate-lanceolate, minutely whitish appressed puberulous, hairs longer and dense on very young growth. **Leaves** spirally arranged, elliptical, 10–21 x 3.5–7.5 cm, apex acute to nearly obtuse, not or only slightly acuminate and rather blunt, base (subcuneate to) acute to obtuse, attachment sometimes slightly inequilateral, lamina coriaceous, upper surface dark green, drying grey-green to reddish brown, (sub)-glabrous except for rare whitish hairs on or near the midrib and the scattered heads of immersed gland hairs; lower surface pale green, drying pale brown, glabrous except for rare whitish hairs on or near the midrib, sometimes uncinata; margin entire; main veins flat above, prominent beneath; lateral veins 9–13, ascending, nearly straight, only occasionally forked or looping back at the margin, pale yellow-green, drying pale to reddish brown; tertiary venation sub-scalariform, indistinct above and barely prominent below; petiole 1.4–5 cm x 2–3 mm, pale green and smooth, drying dark brown and striate, epidermis persistent, subglabrous to minutely whitish appressed-puberulous. Leaves on juvenile trees sometimes pinnately lobed. **Inflorescences** paired in leaf axils. **Staminate inflorescences** not seen. **Pistillate inflorescences** (post-receptive) subglobose, ca. 2 cm across, minutely rufous hispidulous, drying brown, perianth apices tapering, fluted, ca. 0.7 mm wide, styles simple; interfloral bracts absent, peduncle not seen. **Syncarp** (decayed) sub-globose, to at least 4 cm across, surface covered with tapering fluted processes, ca. 3 x 1 mm, minutely rufous hispidulous; interfloral bracts mostly caducous; wall ca. 2 mm thick; core ca. 1–2 cm across; fruiting perianths 20–25 per syncarp (fide *Averyanov et al. VH 1819*), proximal and apical regions free, “seeds” (endocarps) ellipsoid, ca. 1.5 x 1 cm, style attachment sub-apical(?); peduncle ca. 60 mm, indumentum as on twigs. Figures 6–8.



**FIGURE 7.** The holotype of *Artocarpus montanus*, *L. Averyanov et al. VH 1819* (P), showing (A) main sheet, (B) syncarps, and (C) detail of syncarp processes. Photographed by Project Renobota (A) and Germinal Rouhan (B, C).

**Distribution:**—Vietnam: Kon Tum, Khánh Hòa, and Lâm Đồng provinces; perhaps also Thailand, Udun Thani Prov., Pan Don Pa Ko National Reserve Park, Phu Foi Lom (Fig. 4).

**Habitat:**—Primary and secondary forest from 800–1600 m in elevation.

**Provisional conservation assessment:**—Because *Artocarpus montanus* exists within protected areas in Kon Tum and is apparently locally common there (fide *Averyanov et al. VH 1819*), any threat would arise primarily from its rather restricted area of occupancy. Our provisional designation is therefore Near Threatened.

**Etymology:**—The epithet reflects the montane habitat of *Artocarpus montanus*.

**Notes:**—In her notes on *A. lowii*, Jarrett mentioned an as-yet unnamed new entity, allied to the former, in Borneo and Indochina, citing among other specimens *Poilane 35982*—which we assign here to *A. montanus*. It thus seems nearly certain that *A. montanus* represents the unspecified Indo-Chinese material later referred to in the protologue of *A. excelsus* Jarrett (1975: 409). However, despite the striking similarities of its vegetative parts to those of *A. excelsus*, and to a lesser extent *A. lowii*, the tapering fluted syncarp processes of *A. montanus* (not seen by Jarrett) differ substantially from the flat, nearly sessile processes of *A. excelsus* or the low areolate processes of *A. lowii*. The leaves of *A. montanus* also tend to be smaller than those of *A. lowii*. Phylogenetic analyses have placed *A. montanus* as sister to a clade consisting of all of section *Artocarpus* except for the Philippine clade of series *Incisifolii* Jarrett (1959: 327) (Gardner 2017; Gardner *et al.* 2020) (Fig. 5).

Because the distribution of *A. montanus* does not overlap with any of its close morphological allies, it is not likely to be confused with them. Within its native range, it might be mistaken only for *A. chama* Buchanan-Hamilton (1826: 331) (the form corresponding to *A. melinoxylus* Gagnepain (1926: 88)), however the narrower leaves, almost completely glabrous mature parts (compared to appressed, subhispid pubescence on the main veins beneath in *A. chama/melinoxylus*), and longer synarp processes of *A. montanus* would soon dispel any confusion.



**FIGURE 8.** *Artocarpus montanus* at Ngoc Linh, Vietnam, showing (A) leafy shoots (B) stipule, and (C) leaf underside from *S. Tagane et al.* V6772 and (D) juvenile shoot from *S. Tagane et al.* V6169. Scale bars approximate. Photographs by S. Tagane.

Available material has not permitted the proper description of the male inflorescence. *Poilane 35982* has curious malformed inflorescences (Fig. 6(D)) that may relate to the general plan of the male heads: sub-globose, to ca. 1 cm wide, perianths deeply 2–4 lobed, minutely puberulous, interspersed with larger sterile  $\pm$ conical processes (sterile pistillate flowers?), without interfloral bracts. Recent collections (noted above) in plots established by Tagane and collaborators and the observation by *Averyanov et al.* (VH 1819) that *A. montanus* is locally common at the type locality raise the possibility that additional fertile material may be collected soon.

To date, all verified specimens have been collected in southern Vietnam. However, *A. montanus* (or a close ally) has been observed but so far not collected in Don Pa Ko National Reserve Park in Thailand, Udon Thani Province (AC pers. obs.).

### Additional specimens examined

**VIETNAM. Kon Tum Province:** Near Dak Bro village, on red volcanic soil, 1500m: *Poilane* 35982, 21 Dec. 1946 (P♀!); northwest slopes of Ngoc Linh mountain system, evergreen primary forest along mountain stream, 1600m. *L. Averyanov et al. VH 445*, 5 March 1995 (LE!, MO!); Ngoc Linh, hill evergreen forest, 15°11'11.8"N 107°50'36.3"E, 833m: *S. Tagane et al. V6772*, 16 Feb. 2017 (FU!, DLU, TAI); 15°10'05.7"N, 107°45'23.6"E, 1067m, *S. Tagane et al. V6169*, 11 Feb. 2017 (FU!, DLU, TAI). **Khánh Hòa Province.** Mt. Hon Ba, 12°07'8.64"N 108°56'51.99"E, 1498m: *S. Tagane et al. V177*, 17 July 2013 (FU!). **Lâm Đồng Province.** Lạc Dýỡng District, Bi Doup Nui Ba National Park, 12 09'27.6"N, 108 32'06.6"E, 1602m, *T. Yahara et al. V7684* 23 March 2018 (FU!, DLU).

### Acknowledgements.

We thank Germinal Rouhan of the Muséum National D'Histoire Naturelle (Paris) for providing numerous high-resolution images of fertile specimens from P herbarium; MO herbarium (M. Merello) for loans of specimens and permission to sample DNA; LE herbarium (L. Averyanov) herbaria for sharing high-resolution images of specimens; S. Tagane and T. Yahara (FU herbarium) for sharing field and herbarium images of *Artocarpus montanus*; and BKF (N. Pattharahirantricin) and K (A. Monro, A. Moore) herbaria for access to specimens. This research received support from the United States National Science Foundation (DEB awards 0919119 and 1501373, and DBI award 1711391) and the SYNTHESYS Project <http://www.synthesys.info/> which is financed by European Community Research Infrastructure Action under the FP7 "Capacities Program".

### Literature Cited

- Berg, C.C., Corner, E.J.H. & Jarrett, F.M. (2006) *Moraceae (genera other than Ficus)*. *Flora Malesiana*, ser. 1, vol. 17, pt. 1. Nationaal Herbarium Nederland, Leiden, vi + 154 pp.
- Berg, C.C., Pattharahirantricin, N., Chantarasuwan, B., Santisuk, T. & Larsen, K. (2011) *Flora of Thailand*, Vol. 10, Pt. 4: Cecropiaceae and Moraceae. Forest Herbarium, Bangkok, 240 pp.
- Buchanan-Hamilton, F. (1826) Commentary on the *Herbarium Amboinense*. *Memoirs of the Wernerian Natural History Society*. Edinburgh 5 (2): 307–383.
- Forster, Johann Reinhold, White, B., Elmsly, P. & Cadell, T. (1776) *Characteres generum plantarum, quas in itinere ad insulas maris Australis: collegerunt, descripserunt, delinearunt, annis 1772–1775*. Prostant apud B. White, T. Cadell, & P. Elmsly, Londini, 247 pp.  
<https://doi.org/10.5962/bhl.title.4448>
- Fosberg, F.R. (1941) Names in *Amaranthus*, *Artocarpus*, and *Inocarpus*. *Journal of the Washington Academy of Sciences* 31 (30): 93–96.
- Gagnepain, F. (1926) Quelques *Artoacarpus* nouveaux d'Indo-Chine. *Bulletin de la Société botanique de France* 73: 86–91.  
<https://doi.org/10.1080/00378941.1926.10833584>
- Gardner, E.M. (2017) *Dissertation: Evolutionary Transitions: Phylogenomics and pollination of Artocarpus* (Moraceae). Northwestern University, Evanston, Illinois, USA, 192 pp.  
<https://doi.org/10.21985/N2CF59>
- Gardner, E.M., Johnson, M.G., Pereira, J.T., Ahmad Puad, A.S., Arifiani, D., Sahromi, Wickett, N.J. & Zerega, N.J.C. (2020) Paralogs and off-target sequences improve phylogenetic resolution in a densely-sampled study of the breadfruit genus (*Artocarpus*, Moraceae). *bioRxiv*: 854232.  
<https://doi.org/10.1101/854232>
- Hooker, J.D. (1888) *The Flora of British India*, vol. 5. L. Reeve, London, 910 pp.
- Jarrett, F.M. (1959) Studies in *Artocarpus* and allied genera III. A revision of *Artocarpus* subgenus *Artocarpus* [continued]. *Journal of the Arnold Arboretum* 40: 327–368.
- Jarrett, F.M. (1960) Studies in *Artocarpus* and allied genera IV. A revision of *Artocarpus* subgenus *Pseudojaca* [continued]. *Journal of the*

*Arnold Arboretum* 41: 111–140.

Jarrett, F.M. (1975) Four new *Artocarpus* species from Indo-Malesia (Moraceae). *Blumea* 22: 409–410.

Jones, A.M.P., Ragone, D., Tavana, N.G., Bernotas, D.W. & Murch, S.J. (2011) Beyond the Bounty: Breadfruit (*Artocarpus altilis*) for food security and novel foods in the 21st Century. *Ethnobotany Research and Applications* 9: 129–149.  
<https://doi.org/10.17348/era.9.0.129-149>

Lamarck, J.-B. & Poiret, J.-L.-M. (1789) *Encyclopédie méthodique. Botanique*. Tom. 3. Paris, Liège: Panckoucke, Plomteux. viii+759 pp.

Parkinson, S. (1773) *A journal of a voyage to the South Seas, in His Majesty's ship, The Endeavour*. Stanfield Parkinson, London, 212 pp.

Williams, E.W., Gardner, E.M., Harris, R., Chaveerach, A., Pereira, J.T. & Zerega, N.J.C. (2017) Out of Borneo: Biogeography, phylogeny, and divergence date estimates of *Artocarpus* (Moraceae). *Annals of Botany* 119: 611–627.  
<https://doi.org/10.1093/aob/mew249>

Zerega, N.J.C., Nur Supardi, M.N. & Motley, T.J. (2010) Phylogeny and Recircumscription of Artocarpeae (Moraceae) with a Focus on *Artocarpus*. *Systematic Botany* 35: 766–782.  
<https://doi.org/10.1600/036364410X539853>