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Taxonomic updates to *Artocarpus* subgenus *Pseudojaca* (Moraceae), with a particular focus on the taxa in Singapore

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ABSTRACT. The breadfruit genus (*Artocarpus* J.R.Forst. & G.Forst., Moraceae) has 16 species in Singapore, 14 of them native. The following taxonomic changes in *Artocarpus* subgenus *Pseudojaca* Trécul, based on recent phylogenetic work, are presented with diagnostic characters. *Artocarpus griffithii* (King) Merr. is reinstated as distinct from *A. lamellosus* Blanco (which is called *A. nitidus* Trécul in the earlier literature), also requiring the reinstatement of the following taxa not found in Singapore: *A. borneensis* (Merr.) F.M.Jarrett, *A. humilis* Becc., *A. vrieseanus* Miq. var. *subsessilis* F.M.Jarrett and *A. xanthocarpus* Merr. *Artocarpus dadah* Miq. is reinstated as distinct from *A. lacucha* Roxb. ex Buch.-Ham., thereby necessitating the reinstatement of the following taxa not found in Singapore: *A. fretessii* Teijsm. & Binn. ex Hassk., *A. ovatus* Blanco, and *A. vrieseanus* var. *refractus* (Becc.) F.M.Jarrett. *Artocarpus gomezianus* Wall. ex Trécul is restricted to the type subspecies, and *A. zeylanicus* (F.M.Jarrett) E.M.Gardner & Zerega, formerly a subspecies, is elevated to species level. Thirteen lectotypes and two neotypes are designated.

Keywords. *Artocarpus gomezianus*, *Artocarpus lacucha*, *Artocarpus nitidus*

Introduction

The genus *Artocarpus* J.R.Forst. & G.Forst. (Moraceae) contains approximately 70 species of monecious trees. Its range extends from India to the Solomon Islands, with a centre of diversity in Borneo (Williams et al., 2017). Notable species include the widely-cultivated *Artocarpus altilis* (Parkinson) Fosberg (breadfruit) and *A. heterophyllus* Lam. (jackfruit), in addition to other species of more regional importance, such as *A. integer* (Thunb.) Merr. (cempedak) and *A. odoratissimus* Blanco (tarap). Sixteen

species of *Artocarpus* occur in Singapore, of which 14 are indigenous to the island (Table 1).

Artocarpus was revised by Jarrett (1959a, 1959b, 1960) with subsequent taxonomic work in regional floras (Kochummen, 2000; Berg et al., 2006, 2011). The subgenera were revised following a phylogenetic study by Zerega et al. (2010), and additional phylogenetic studies have provided a molecular framework for taxonomic revisions (Gardner, 2017; Williams et al., 2017; Gardner et al., in press). This taxonomic study focusing on *Artocarpus* subgenus *Pseudojaca* Trécul (c. 29 spp., four in Singapore) began as a precursor to the forthcoming *Artocarpus* treatment for the *Flora of Singapore* Moraceae but several of the taxonomic changes to taxa in Singapore have consequences in other taxa in Southeast Asia, and these are also discussed. In particular, we focus on the broadly-circumscribed *Artocarpus nitidus* Trécul and *A. lacucha* Roxb. ex Buch.-Ham. complexes. As detailed in the nomenclatural summary below, *Artocarpus nitidus* must be replaced by the earlier *A. lamellosus* Blanco. For the sake of clarity, however, we use *A. nitidus* s.l. to refer to the broad complex as done by the previous authors who accepted the broad circumscription (Jarrett, 1960; Kochummen, 2000; Berg et al., 2006).

The taxonomic changes proposed here generally follow Jarrett (1960) and Zerega et al. (2010), albeit with some differences in rank, and are based on extensive review of specimens at BKF, BM, F, IBSC, K, L, MO, SAN, SAR, SING, SNP and US, images of specimens from CAL, FI, KUN, P and PE, and recent phylogenetic work (Zerega et al., 2010; Gardner, 2017; Williams et al., 2017; Gardner et al., in press), including an updated phylogenetic reconstruction of *Artocarpus* subgenus *Pseudojaca* prepared for this study.

Phylogenetic methods and results

Following a target enrichment (HybSeq) strategy and using 493 nuclear genes, we reconstructed a phylogeny of *Artocarpus* subgenus *Pseudojaca* based on a subset of the samples from recent phylogenomic studies of *Artocarpus* (Johnson et al., 2016; Gardner, 2017; Gardner et al., in press) and also included some additional samples. The data set contained 73 samples (Appendix 1), including all currently-recognised taxa in *Artocarpus* subgenus *Pseudojaca* except *A. reticulatus* Miq. and *A. nigrifolius* C.Y.Wu. Outgroups included *Batocarpus costaricensis* Standl. & L.O.Williams and one member of each of the other subgenera of *Artocarpus* (*Artocarpus* subgen. *Artocarpus, Artocarpus* subgen. *Cauliflori* (F.M.Jarrett) Zerega, Supardi & Motley and *Artocarpus* subgen. *Prainea* (King) Renner). Methods for library preparation, hybridisation, sequencing, and assembly with HybPiper, followed the recent phylogenomic studies in *Artocarpus* (Gardner et al., 2016; Johnson et al., 2016; Gardner, 2017; Gardner et al., in press). The default ("exon") output from HybPiper was filtered by discarding sequences shorter than 100 bp or 20% of the average length

Table 1. *Artocarpus* species occurring in Singapore, with relevant taxonomic changes noted. Asterisks denote species found primarily in cultivation. Taxa in bold belong to *Artocarpus* subgenus *Pseudojaca*.

Species	**Differences from *Flora Malesiana***
Artocarpus altilis (Parkinson) Fosberg*	In the strict sense, following Zerega et al. (2005)
Artocarpus anisophyllus Miq.	
Artocarpus camansi Blanco*	Included by Berg et al. (2006) in *A. altilis* (Parkinson) Fosberg
Artocarpus dadah Miq.	Reinstated (prev. included in *A. lacucha* Roxb. ex Buch.-Ham.)
Artocarpus elasticus Reinw. ex Blume	In the strict sense, following Jarrett (1959b)
Artocarpus fulvicortex F.M.Jarrett	
Artocarpus gomezianus Wall. ex Trécul	
Artocarpus griffithii (King) Merr.	Included by Berg et al. (2006) in *A. nitidus* Trécul
Artocarpus heterophyllus Lam.*	
Artocarpus hispidus F.M.Jarrett	
Artocarpus integer (Thunb.) Merr.	
Artocarpus kemando Miq.	
Artocarpus lanceifolius Roxb.	
Artocarpus lowii King	
Artocarpus rigidus Blume	
Artocarpus scortechinii King	Included by Berg et al. (2006) in *A. elasticus* Reinw. ex Blume

for each locus. We then aligned each locus with MAFFT (Katoh & Standley, 2013), trimmed columns consisting of >75% gaps with TrimAl (Capella-Gutiérrez et al., 2009), and trimmed the sequence termini of some low-coverage herbarium samples with HerbChomper, which trims poorly-aligned ends from target sequences (https://github.com/artocarpus/HerbChomper). We inferred a maximum-likelihood tree for each locus separately using RAxML (Stamatakis, 2014) (GTRCAT model, 200 rapid bootstrap replicates), collapsed nodes with <30% bootstrap support using sumtrees.py (Sukumaran & Holder, 2010), and then used the collapsed trees to infer a species tree using ASTRAL-III (Zhang et al., 2018), calculating node support using n(-t 1),

which represents gene tree concordance at each node. We also reconstructed a single maximum-likelihood tree based on a partitioned supermatrix of all loci using RAxML (GTRCAT model, 200 rapid bootstrap replicates). Reads were deposited in GenBank (BioProject PRJNA322184).

The supermatrix phylogeny and the species tree were broadly concordant (Fig. 1). Neither supported the monophyly of *Artocarpus nitidus* s.l. or *A. lacucha* s.l.. However, both supported the monophyly of Jarrett's subspecies of *Artocarpus nitidus* as well as the monophyly of the species recognised by Jarrett (1960) that were later sunk into *A. lacucha* (Berg et al., 2006). In both analyses, *Artocarpus vrieseanus* sensu Jarrett (1960) was monophyletic, forming a clade encompassing all four varieties. The subspecies of *Artocarpus gomezianus* Wall. ex Trécul, represented by a single sample each, did not form a clade, with *A. gomezianus* subsp. *zeylanicus* F.M.Jarrett falling sister to *A. lacucha*. Disagreements between the supermatrix and species trees included whether the taxa hitherto called *Artocarpus nitidus* subsp. *griffithii* (King) F.M.Jarrett and *A. nitidus* subsp. *humilis* (Becc.) F.M.Jarrett form a clade (supermatrix) or a grade (species tree); the position of *A. rubrosoccatus* E.M.Gardner, Chaveer. & Zerega; whether *A. albobrunneus* C.C.Berg was sister to (supermatrix) or nested within (species tree) *A. fretessii* Teijsm. & Binn. ex Hassk.; the position of *A. lamellosus* (*A. nitidus* subsp. *nitidus*) as sister to *A. rubrovenius* Warb. (supermatrix) or *A. ovatus* Blanco (species tree); the positions of two samples of uncertain affinities (*E.G. et al. 410* and *A.A. 440*); and rearrangements within *A. lacucha* s.s., *A. dadah* Miq., and *A. vrieseanus* Miq. sensu Jarrett.

Taxonomic discussion

1. *Artocarpus nitidus* s.l.

Jarrett recognised a broadly circumscribed *Artocarpus nitidus* whose four subspecies united a disparate array of taxa previously recognised as species. They all have shiny, more or less glabrous leaves, smallish (under 5 cm) syncarps with short (under 5 mm) peduncles, and clavate staminate inflorescences, but they are morphologically distinct from one another in both vegetative and reproductive characters. The type subspecies (here treated as *Artocarpus lamellosus*) is restricted to the Philippines; it has few (5–7) lateral veins, consistently clavate staminate inflorescences, and small syncarps usually with no more than three seeds. *Artocarpus nitidus* subsp. *lingnanensis* (Merr.) F.M.Jarrett, found in Vietnam, Thailand, southern China, and in cultivation, also has few lateral veins, but its leaf apices are rather blunt, its velutinous synarps always larger, and its staminate inflorescences ranging from clavate to ellipsoid; its habit and dark rough bark are also distinctive. *Artocarpus nitidus* subsp. *humilis* is endemic to Borneo, has leaves with few (5–8) lateral veins that are often sharply ascending and pubescent syncarps. Also endemic to Borneo is *Artocarpus nitidus* subsp. *borneensis* (Merr.) F.M.Jarrett, with larger, often thickly coriaceous leaves bearing up to 15

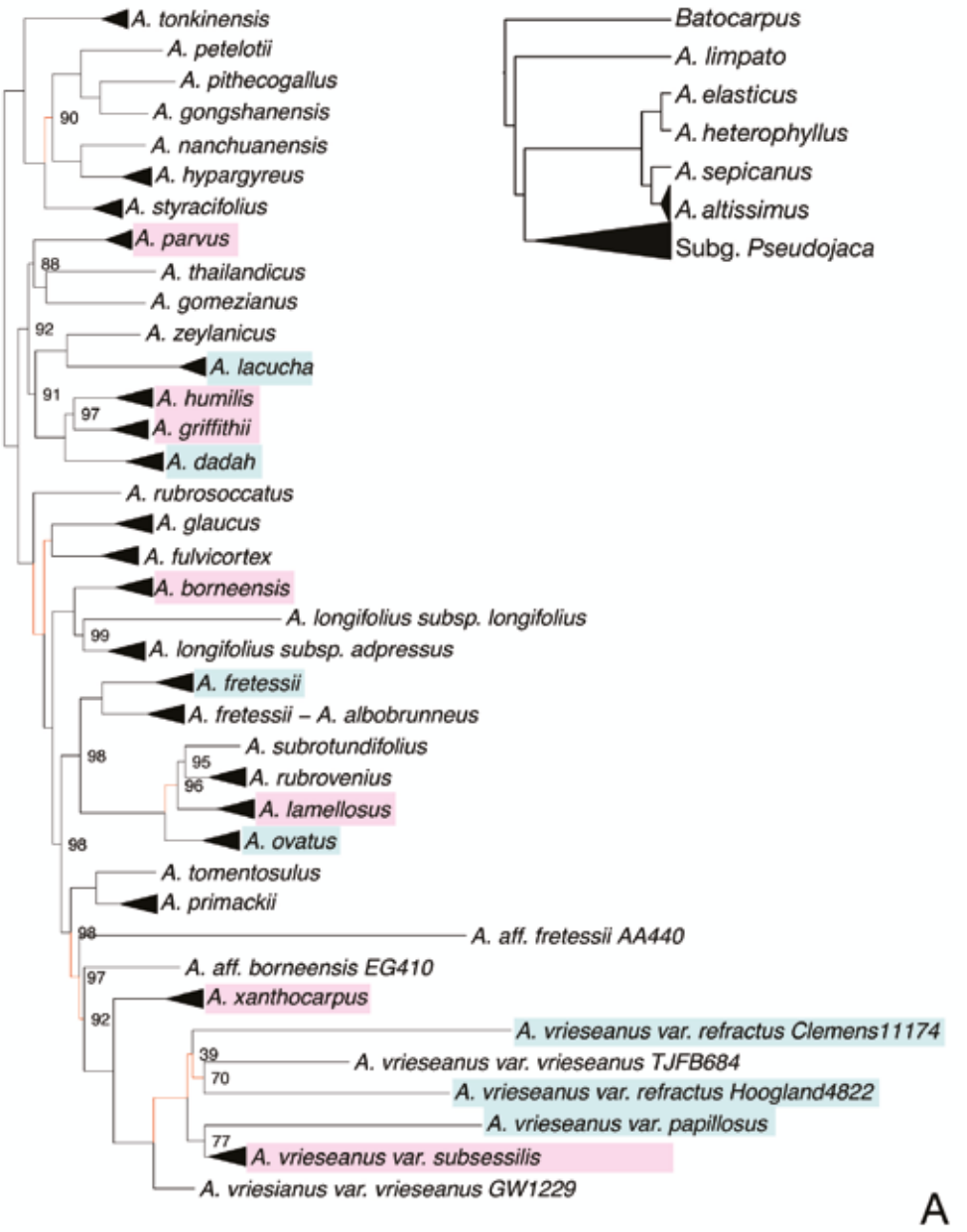

Fig. 1A. Phylogenetic tree based on a supermatrix of all loci, with branch lengths proportional to substitutions. Monophyletic taxa have been collapsed for clarity, indicated by black triangles. Branches disagreeing with the ASTRAL species tree (Fig. 1B) are coloured red. Taxa included in *Artocarpus lacucha* and *A. nitidus* by Berg et al. (2006) are shaded in blue and pink, respectively. Inset shows the placement of subgenus *Pseudojaca* within the Artocarpeae. Nodes without labels have 100% bootstrap support.

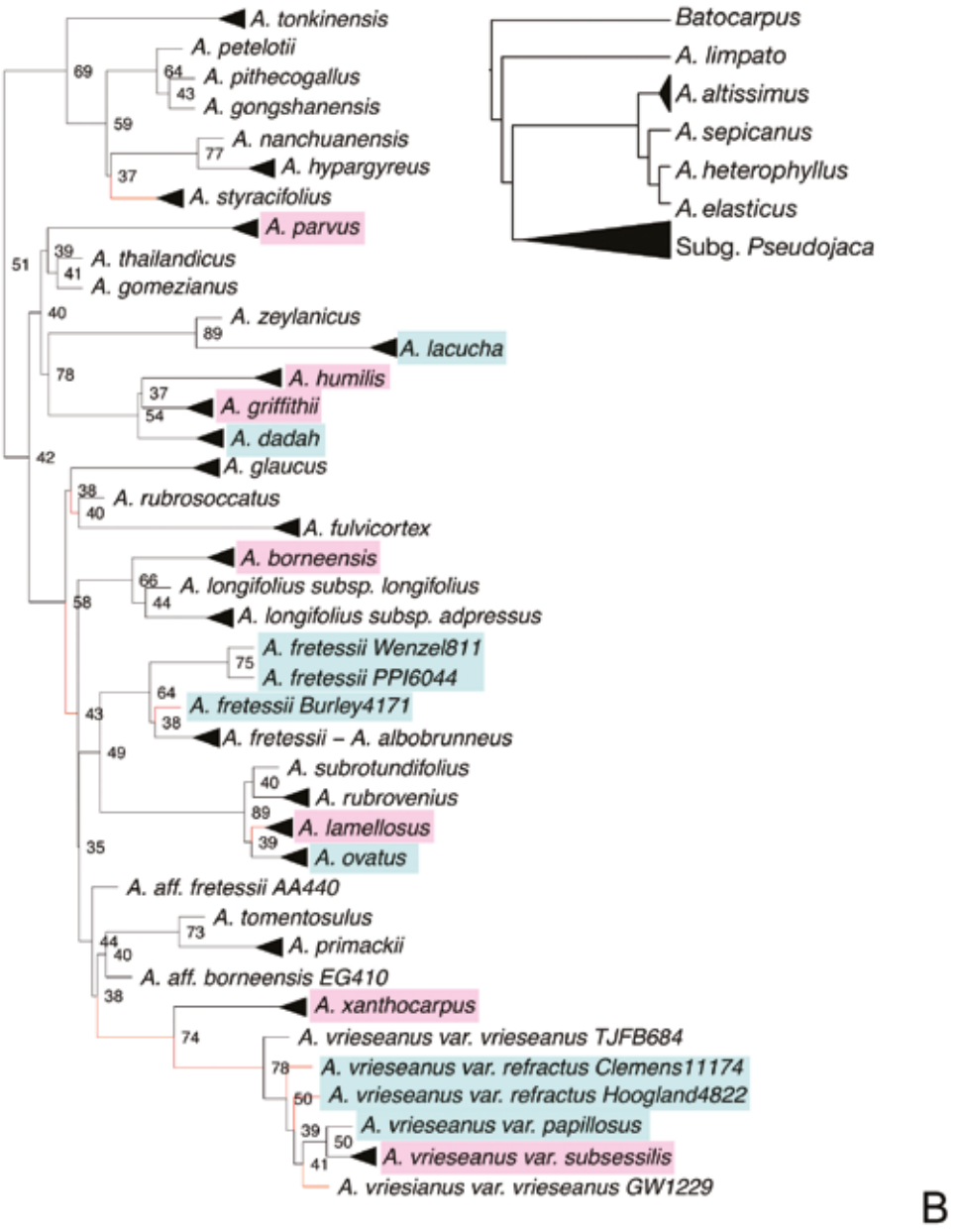

Fig. 1B. ASTRAL species tree based on gene trees for all loci, with branch lengths proportional to coalescent units. Monophyletic taxa have been collapsed for clarity, indicated by black triangles. Branches disagreeing with the supermatrix tree (Fig. 1A) are coloured red. Taxa included in *Artocarpus lacucha* and *A. nitidus* by Berg et al. (2006) are shaded in blue and pink, respectively. Inset shows the placement of subgenus *Pseudojaca* within the Artocarpeae. Nodes labels are normalized quartet scores.

lateral veins, syncarps covered in dense, deciduous rust-coloured hairs, and staminate inflorescences that are usually not clavate as in the other subspecies but more often ellipsoid to obovoid. *Artocarpus nitidus* subsp. *griffithii* (King) F.M.Jarrett occurs from Southern China to Borneo, including Singapore, overlapping the ranges of all of the other subspecies except for *A. nitidus* subsp. *nitidus* (= *A. lamellosus*). Originally described by King as a variety of *Artocarpus gomezianus*, Merrill raised it to species status before Jarrett combined it with *A. nitidus*; its leaves are variable in size, but the larger ones often have up to 15 lateral veins, and the abaxial venation often dries reddish. The syncarps are distinctive in being nearly glabrous, rather shiny, and drying black. Berg et al. (2006) broadened *Artocarpus nitidus* even further by subsuming all of the subspecies as well as *A. vrieseanus* Miq. var. *subsessilis* F.M.Jarrett and *A. xanthocarpus* Merr. within *A. nitidus*, recognising four informal forms: "nitidus," "griffithii," "borneensis," and "subsessilis," corresponding roughly to the subsumed taxa. The two added taxa differ most notably from *Artocarpus nitidus* sensu Jarrett in the complete fusion of adjacent pistillate perianths, without the proximal free portion typical in most species of *Artocarpus* subgen. *Pseudojaca*. Jarrett (1960) also distinguished *Artocarpus xanthocarpus* from *A. nitidus* by its often caudate leaf apices, subglobose staminate inflorescences, and its larger many-seeded syncarps. *Artocarpus vrieseanus* var. *subsessilis* may be distinguished from all of the other members of *A. nitidus* s.l. by the thinly coriaceous leaves and subglabrous unlobed syncarps with a reticulate or areolate surface.

The morphological differences between the components of *Artocarpus nitidus* s.l. are not less than those that exist between any number of species within *Artocarpus* subgen. *Pseudojaca*. For example, sterile specimens of *Artocarpus griffithii* are as likely to be confused with *A. gomezianus* as with any other subspecies of *A. nitidus*. Even the clavate staminate inflorescence is an inadequate distinguishing character as these are shared with *Artocarpus glaucus* Blume and *A. thailandicus* C.C.Berg but may be absent in *A. nitidus* subsp. *borneensis*. In addition, although some specimens may be difficult to identify due to poor preservation or the lack of fertile parts, an exhaustive review of specimens has not uncovered intermediate forms in any substantial numbers, unless the Bornean *Artocarpus nitidus* subsp. *griffithii*, discussed below, may be so considered.

Finally, phylogenetic work has revealed that this broad concept of *Artocarpus nitidus* is not monophyletic and that with the exception of an apparent affinity between *A. nitidus* subsp. *griffithii* and *A. nitidus* subsp. *humilis*, its components are not closely related (Fig. 1) (Zerega et al., 2010; Gardner, 2017; Williams et al., 2017). The phylogenetic reconstructions are also consistent with morphological patterns. For example, an apparently good synapomorphy for the *Artocarpus vrieseanus* + *A. xanthocarpus* clade, the complete fusion of adjacent pistillate perianths, is incompatible with the broad view of *A. nitidus* sensu Berg et al. We have also observed specimens intermediate between *Artocarpus nitidus* subsp. *borneensis* and *A. longifolius* Becc. subsp. *adpressus* C.C.Berg as well as between *A. lamellosus* (previously *A. nitidus*

subsp. *nitidus*) and *A. rubrovenius*, which is not surprising given their phylogenetic affinity.

Based on the morphological and molecular evidence, it therefore seems best to recognise these taxa as distinct following Jarrett, but all at the species level with the exception of *Artocarpus vrieseanus* var. *subsessilis* (the *A. vrieseanus* complex awaits further scrutiny). A case might be made for subsuming *Artocarpus humilis* within *A. griffithii*. The latter was already broadly circumscribed in Jarrett's system, encompassing material from Thailand and Vietnam with syncarps that ripen yellow rather than pink (likely corresponding to *Artocarpus eberhardtii* Gagnep.) and material from Borneo with leaves similar to those of *A. humilis*. In addition, *Artocarpus humilis* and *A. griffithii* form sister clades in at least some analyses (Fig. 1A). However, *Artocarpus griffithii* is consistently diagnosable throughout its range on the basis of its shiny subglabrous syncarps that are nigrescent upon drying, so subsuming *A. humilis* seems unwarranted at this time. Likewise, the close affinity of *Artocarpus xanthocarpus* and *A. vrieseanus*, as well as the morphological heterogeneity of the latter, might support combining those taxa into a broadened *A. vrieseanus*. Well-sampled population genetic studies would do much to clarify the proper limits of both *Artocarpus griffithii* and *A. vrieseanus*.

2. *Artocarpus lacucha* s.l.

Berg et al. (2006) united four species and two varieties of a fifth, long recognised as distinct, into a broadly circumscribed *Artocarpus lacucha*. As with *Artocarpus nitidus* s.l., they recognised informal forms corresponding roughly to the subsumed taxa: *A. dadah* Miq., *A. ovatus* Blanco, *A. fretessii* Teijsm. & Binn. ex Hassk., *A. vrieseanus* Miq. var. *refractus* (Becc.) F.M.Jarrett and *A. vrieseanus* Miq. var. *papillosus* F.M.Jarrett (the latter two treated as the same form).

As described above, the varieties of *Artocarpus vrieseanus* are distinct in the complete fusion of adjacent pistillate perianths, a character not shared with any other taxa treated here. *Artocarpus fretessii* is distinct in its deeply-lobed syncarps with one seed per lobe and its tiny globose staminate inflorescences, usually clustered together on short shoots. *Artocarpus ovatus* can be distinguished by its long peduncles and clavate staminate inflorescences as well as by the distinctive deflexed position of its inflorescences (Fig. 12). *Artocarpus dadah* can be distinguished from *A. lacucha* by the entire margins on mature leaves (often denticulate in *A. lacucha*), more shallowly lobed syncarps, longer peduncles, and smaller staminate inflorescences. These taxa can be distinguished even when sterile by recourse to leaf morphology and geography (detailed below).

On the other hand, the Borneo endemic *Artocarpus albobrunneus* is not readily distinguishable from *A. fretessii*. The type has dry syncarps with contrasting pale centres and darker lobes, but the label indicates that the syncarps were yellow when fresh, a character consistent with Bornean *Artocarpus fretessii*.

Maintaining *Artocarpus lacucha* sensu Berg et al. might be justified despite its morphological and geographic heterogeneity if the components formed a monophyletic clade, but phylogenetic analyses over the past decade have consistently demonstrated its non-monophyly (Zerega et al., 2010; Williams et al., 2017; Gardner, 2017) (Fig. 1). We therefore adopt the species concepts of Jarrett (1960), which are consistent with both morphological and phylogenetic evidence.

3. *Artocarpus gomezianus*

The type subspecies of *Artocarpus gomezianus* Wall. ex Trécul is found in mainland Southeast Asia, Singapore, Sumatra and Java. It can be recognised by the reddish abaxial venation on its leaves (Fig. 14). *Artocarpus gomezianus* subsp. *zeylanicus* F.M.Jarrett is found only in India and Sri Lanka, and within it two distinct forms are discernable: the first with soft whitish pubescence on its leaves, found in India and Sri Lanka, and the second with subglabrous vegetative parts, found only in Sri Lanka. Both have small (c. 3 cm), velutinous syncarps that might be considered unremarkable within *Artocarpus* subgen. *Pseudojaca*. The difficulty in distinguishing dry specimens of the subglabrous form from *Artocarpus gomezianus* led Jarrett (1960) to treat all of these specimens as *A. gomezianus* subsp. *zeylanicus,* but she questioned whether the two forms should be treated as two taxa or whether they might simply represent different developmental stages. The absence of the subglabrous form from India as well as the apparent absence of intermediate specimens counsel in favour of treating these two entities separately. The type is from India and belongs to the first (pubescent) form, whose vegetative characters are clearly closer to *Artocarpus lacucha* than to *A. gomezianus*, although the syncarp may be considered in some ways intermediate between those two species, with a pale velutinous indumentum as in *A. gomezianus* but deep lobes as in *A. lacucha* (Fig. 15). The subglabrous form was previously treated as *Artocarpus lacucha* var. β *gomezianus* (Wall. ex Trécul) Trimen.

The single sample of *Artocarpus gomezianus* subsp. *zeylanicus* in our phylogenetic analyses is from India and represents the pubescent form; as was expected based on morphology, it was sister to *A. lacucha* s.s. in all analyses. No phylogenetic information is available for the subglabrous form.

The distinctiveness of the type (pubescent) form of *Artocarpus gomezianus* subsp. *zeylanicus* counsels strongly in favour of recognising it at the species level. Sterile specimens of the subglabrous form are distinguishable from *Artocarpus gomezianus* subsp. *gomezianus* primarily based on geography, and usually the somewhat narrower aspect of the leaf, but the reproductive parts match the type of *A. gomezianus* subsp. *zeylanicus*. Until further evidence such as a population genetic study supports a different course of action, it seems best for now to maintain Jarrett's geographically coherent delimitation of the taxon, recognising the possibility that the subglabrous form may simply be a regional variant of *Artocarpus gomezianus* subsp. *gomezianus*.

A phylogenetic or population genetic study of examples from throughout the range of *Artocarpus gomezianus*, including Sri Lanka, may highlight any distinctions.

Summary of taxonomic changes

As a precursor to the forthcoming treatment of *Artocarpus* for *Flora of Singapore*, we revise the taxa recently included by Berg et al. (2006) in *A. nitidus* s.l. as follows. We reinstate the Philippine endemic *Artocarpus lamellosus*, consisting only of the material comprising Jarrett's *A. nitidus* subsp. *nitidus* but under an earlier name that must supersede Trécul's (discussed below). We reinstate *Artocarpus parvus* Gagnep. (corresponding to *A. nitidus* subsp. *lingnanensis* (Merr.) F.M.Jarrett), *A. humilis* Becc. (= *A. nitidus* subsp. *humilis* (Becc.) F.M.Jarrett), *A. borneensis* Merr. (= *A. nitidus* subsp. *borneensis* (Merr.) F.M.Jarrett), and *A. griffithii* (King) Merr. (= *A. nitidus* subsp. *griffithii* (King) F.M.Jarrett) as species-level taxa, corresponding to Jarrett's subspecies, and we reinstate *A. vrieseanus* var. *subsessilis*, noting that the *A. vrieseanus* complex requires additional work. *Artocarpus griffithii*, the only one of these taxa found in Singapore is easily distinguished from the others by its nearly glabrous syncarps, with a pink exterior and a dark red juicy interior when ripe. Whether a form of *Artocarpus griffithii* with externally yellow (but apparently still internally pink to red) syncarps, found in the northern part of its distribution including Thailand, should be recognised as a distinct entity, perhaps corresponding to *A. eberhardtii* Gagnep., awaits further study.

We reinstate *Artocarpus dadah* Miq. as a species distinct from *A. lacucha*, recognising the latter only in the strict sense (Jarrett, 1960). *Artocarpus dadah* occurs in Borneo, Sumatra and from the Malay Peninsula (including Singapore) through Thailand, overlapping with *A. lacucha* only in the latter. In contrast to *Artocarpus lacucha,* mature trees of *A. dadah* never have dentate leaf margins and the syncarps never have raised perianth apices. In *Artocarpus dadah*, the peduncles are usually longer (staminate to c. 1.5 cm and pistillate to c. 2.5(–10 in Borneo) cm) than in *A. lacucha* (staminate to c. 0.5 cm and pistillate to c. 1.5(–2.5) cm), the leaves of *A. dadah* are usually proportionally more elongate with more lateral veins (10–20 in *A. dadah* as opposed to 9–18 in *A. lacucha*), and the lamina often dries reddish brown in *A. dadah* (rather than pale brown in *A. lacucha*). We maintain *Artocarpus peltatus* Merr. in the synonymy of *A. dadah*; although some Bornean material appears distinct in its long peduncles and auriculate to peltate leaf attachments, phylogenetic evidence so far has not supported the distinction (Williams et al., 2017). The remaining entities included in *Artocarpus lacucha* s.l. by Berg et al. (2006), *Artocarpus ovatus* Blanco (Philippines), *Artocarpus fretessii* Teijsm. & Binn. ex Hassk. (Borneo to the Moluccas) and *Artocarpus vrieseanus* var. *refractus* (Moluccas through the Solomon Islands), are also reinstated. We include *Artocarpus albobrunneus* in the synonomy of *A. fretessii* due to the lack of distinguishing characters.

Finally, we restrict *Artocarpus gomezianus* to the type subspecies, elevating *Artocarpus gomezianus* subsp. *zeylanicus* to species level.

Below we provide synonomies and diagnostic characters for the reinstated and recircumscribed taxa. Complete citation histories may be found in Jarrett (1960), Kochummen (2000) and Berg et al. (2006, 2011). Neotypes are designated for *Artocarpus lamellosus* Blanco and *A. pomiformis* Teijsm. & Binn., and lectotypes are designated for the following: *A. dasyphyllus* var. *flavus* J.J.Sm., *A. eberhardtii* Gagnep., *A. eberhardtii* var. *poilanei* Gagnep., *A. fretessii* Teijsm. & Binn. ex Hassk., *A. gomezianus* var. *griffithii* King, *A. lacucha* Roxb. ex Buch.-Ham., *A. lakoocha* Roxb., *A. lakoocha* var. *malayana* King, *A. lanceolatus* Trécul, *A. lingnanensis* Merr., *A. masticata* Gagnep., *A. nitidus* Trécul, and *Ficus tampang* Miq.

Unless otherwise stated, all types were examined either in person or via photographs, the latter sometimes via JSTOR Global Plants (plants.jstor.org).

Taxonomic revisions

Artocarpus J.R.Forst. & G.Forst. subgen. ***Pseudojaca*** Trécul, Ann. Sci. Nat., Bot., sér. 3, 8: 117 (1847). – *Artocarpus* sect. *Pseudojaca* (Trécul) Renner, Bot. Jahrb. Syst. 39: 368 (1907). – TYPE: *Artocarpus lakoocha* Roxb., designated by Jarrett (1960) (= *Artocarpus lacucha* Roxb. ex Buch.-Ham.).

Species and distribution. Approximately 29 species distributed from India to the Solomon Islands, comprising two clades: one with peltate interfloral bracts corresponding to *Artocarpus* ser. *Peltati* F.M.Jarrett (*A. borneensis* Merr., *A. dadah* Miq., *A. fretessii* Teijsm. & Binn. ex Hassk., *A. fulvicortex* F.M.Jarrett, *A. gomezianus* Wall. ex Trécul, *A. humilis* Becc., *A. glaucus* Blume, *A. griffithii* (King) Merr., *A. lacucha* Roxb. ex Buch.-Ham., *A. lamellosus* Blanco, *A. longifolius* Becc. (subsp. *longifolius* and subsp. *adpressus* C.C. Berg), *A. ovatus* Blanco, *A. parvus* Gagnep., *A. primackii* Kochummen, *A. reticulatus* Miq., *A. rubrosoccatus* E.M.Gardner, Chaveer. & Zerega, *A. rubrovenius* Warb., *A. subrotundifolius* Elmer, *A. thailandicus* C.C.Berg, *A. tomentosulus* F.M.Jarrett, *A. vrieseanus* Miq. (var. *vrieseanus*, var. *refractus* (Becc.) F.M.Jarrett, var. *subsessilis* F.M.Jarrett and var. *papillosus* F.M.Jarrett), *A. xanthocarpus* Merr., *A. zeylanicus* (F.M.Jarrett) E.M.Gardner & Zerega) and one with mostly clavate interfloral bracts corresponding for the most part to *Artocarpus* ser. *Clavati* F.M.Jarrett (*A. hypargyraeus* Hance ex Benth., *A. gongshanensis* S.K.Wu ex C.Y.Wu & S.S.Chang, *A. nanchuanensis* S.S.Chang, S.C.Tan & Z.Y.Liu, *A. nigrifolius* C.Y.Wu, *A. petelotii* Gagnep., *A. pithecogallus* C.Y.Wu, *A. styracifolius* Pierre, *A. tonkinensis* A.Chev.), the only difference being the position of *A. tonkinensis* in the clavate clade (Fig. 1).

1. Key to taxa formerly comprising *Artocarpus nitidus* s.l. (Berg et al., 2006)

1a. Adjacent pistillate flowers proximally free 2
1b. Adjacent pistillate flowers completely fused 6

2a. Syncarp subglabrous; nigrescent when dry ..... *A. griffithii*
2b. Syncarp pubescent; not nigrescent when dry 3

3a. Syncarp pubescence dark red-brown ..... *A. borneensis*
3b. Syncarp pubescence otherwise 4

4a. Syncarps up to 5 cm across, velutinous, flesh bright pink ripening orange-pink; leaf apices rather blunt (China to Thailand and Vietnam, sometimes cultivated) .. .. *A. parvus*
4b. Syncarps seldom exceeding 3 cm, short-pubescent, flesh otherwise; leaves acuminate (Borneo and Philippines, not usually cultivated) 5

5a. Syncarps seldom deeply lobed; leaf acumen up to 3 cm, lateral veins markedly ascending, usually drying brown, attachment cuneate (Borneo) ..... *A. humilis*
5b. Syncarps usually deeply lobed; leaves shortly acuminate, without markedly ascending lateral veins, often drying blue-grey above, attachment often rounded to subcordate (Philippines) ..... *A. lamellosus*

6a. Syncarps with a few persistent interfloral bracts, the surface not visibly areolate; leaf base cuneate to decurrent (Philippines)..... *A. xanthocarpus*
6b. Syncarps without persistent interfloral bracts, the surface often visibly areolate; leaf base rounded to subcordate (New Guinea, Solomon Islands) .... *A. vrieseanus* var. *subsessilis*

1.1 *Artocarpus borneensis* Merr., J. Straits Branch Roy. Asiat. Soc. 85: 165 (1922). – *Artocarpus nitidus* Trécul subsp. *borneensis* F.M.Jarrett, J. Arnold. Arbor. 41: 127 (1960). – *Artocarpus nitidus* auct. non Trécul: Berg, Fl. Males., Ser. 1, Spermat. 17(1): 121 (2006), as "borneensis" form. – TYPE: [Malaysia], British North Borneo [Sabah], Sandakan and vicinity, September–December 1920, *M. Ramos 1592* (lectotype PNH n.v., designated by Jarrett (1960); isotypes A [A0046792, A0046793], B [B 10 0294378], BM [BM000951876], BO, GH [GH00034348] K [K001051140], L [L0039898], OSC [OSC0000745], P [P06777462], SING [SING0052138], US [US00089831]). (Fig. 2).

Artocarpus nitidus auct. non Trécul: Kochummen, Tree Fl. Sabah & Sarawak 3: 201 (2000); Berg, Fl. Thailand 10(4): 17 (2011).

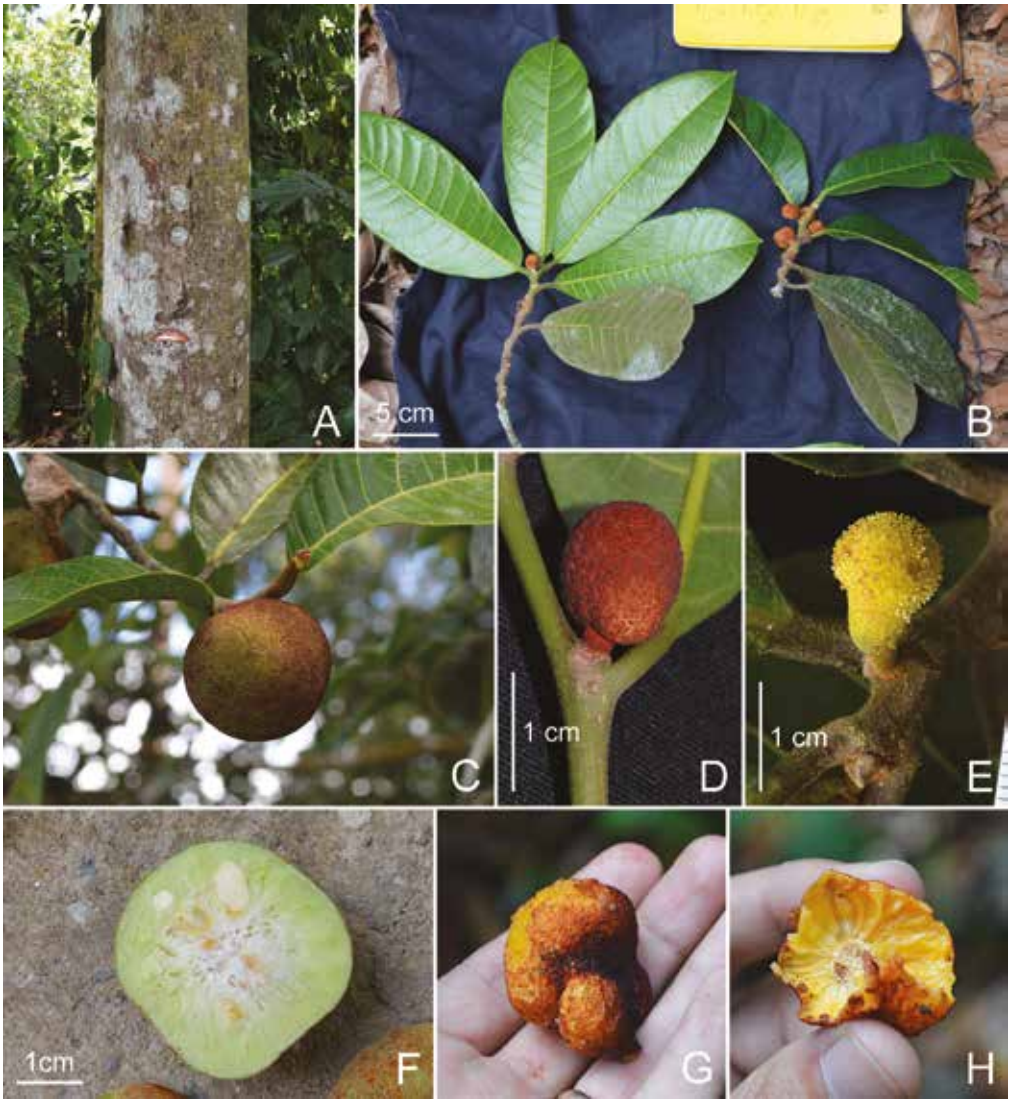

Fig. 2. *Artocarpus borneensis* Merr. **A.** Bole. **B.** Shoot with pistillate infloresences. **C.** Shoot with immature syncarp. **D.** Pistillate inflorescence. **E.** Staminate inflorescences. **F.** Unripe syncarp in section. **G & H.** Ripe syncarps. All from Sabah. (Photos: A–E, G & H, E.M. Gardner; F, N.J.C. Zerega).

Diagnostic characters. Leaves often rather thickly coriaceous with (8–)10–15 lateral veins, the lamina often grey-brown and very shiny *in sicco*, sometimes noticeably pubescent. Ripe syncarp to c. 6 cm across, surface yellow, drying brown, with a dense covering of fine red-brown hairs (present also on pistillate inflorescences), flesh yellow-orange.

Distribution. Endemic to Borneo.

Notes. Merrill did not specify the location of his type material, so the duplicates must all be considered syntypes, and Jarrett's (1960) "holotype citation" was therefore an effective lectotypification. We have not yet been able to confirm the status of the lectotype at PNH, which Jarrett apparently did not see. If it was destroyed, a new lectotype will need to be designated.

1.2 ***Artocarpus griffithii*** (King) Merr., Pap. Michigan Acad. Sci., Part 1, 24: 64 (1939). – *Artocarpus gomezianus* Wall. ex Trécul var. *griffithii* King in Hook.f., Fl. Brit. India 5: 544 (1888), as '*gomeziana* var. *griffithii*'; King, Ann. Bot. Gard. (Calcutta) 2: 16, t. 14B (1889). – *Artocarpus nitidus* Trécul subsp . *griffithii* (King) F.M.Jarrett, J. Arnold Arbor. 41: 128 (1960). – *Artocarpus nitidus* auct. non Trécul: Berg, Fl. Males., Ser. 1, Spermat. 17(1): 121 (2006), as "griffithii" form. – TYPE: [Malaysia], Malacca [Melaka], 1863, *W. Griffith 4665* (lectotype K [K000357626], designated here; isolectotypes CAL, GH [GH00046795], P [P00756673]). (Fig. 3).

Artocarpus eberhardtii Gagnep., Bull. Soc. Bot. France 73: 87 (1926). – TYPE: [Vietnam], Annam, environ de Hué, s.d., *P.A. Eberhardt 3288* (lectotype P [P00756676], designated here; isolectotype P [P00756677]).

Artocarpus eberhardtii Gagnep. var. *poilanei* Gagnep., Bull. Soc. Bot. France 73: 87 (1926). – TYPE: [Laos], près de Savannaket, 12 February 1925, *E. Poilane 11955* (lectotype P [P00756674], first step designated by Jarrett (1960), second step designated here; isolectotype P [P00756675]).

Artocarpus gomezianus auct. non Trécul: Ridley, J. Straits Branch Roy. Asiat. Soc. 33: 147 (1900); Ridley, Fl. Malay Penins. 3: 355 (1924); Corner, Wayside Trees Mal. 654, t. 195 (1940).

Artocarpus lanceolatus auct. non Trécul: Gagnepain in Lecomte, Fl. Indo-Chine 5: 738 (1928).

Artocarpus nitidus auct. non Trécul: Kochummen, Tree Fl. Sabah & Sarawak 3: 201 (2000); Berg, Fl. Thailand 10(4): 17 (2011).

Diagnostic characters. Leaves with (7–)9–15 lateral veins, the midrib often reddish or nigrescent *in sicco*. Ripe syncarp to c. 4.5 cm across, surface orange-pink or red (to yellow in Kelantan and further north), nigrescent *in sicco*, nearly glabrous, flesh deep red to bright pink.

Distribution. Southern China to Sumatra (including Singapore) and Borneo.

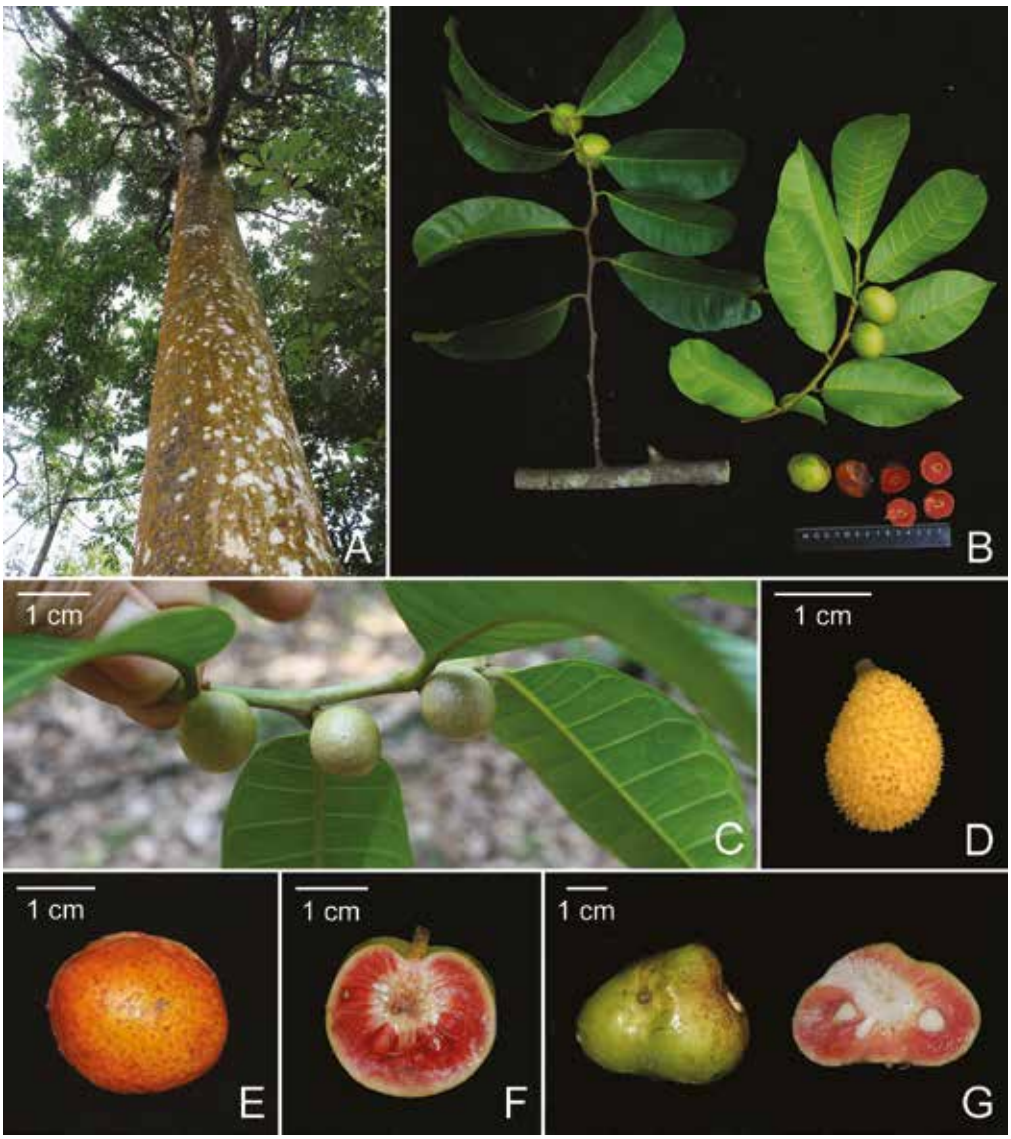

Fig. 3. *Artocarpus griffithii* (King) Merr. **A.** Bole. **B.** Leafy shoot. **C.** Pistillate inflorescences. **D.** Staminate inflorescence. **E.** Ripe syncarp. **F.** Section of mature but unripe syncarp. **G.** Syncarps. A & C from Peninsular Malaysia, B & D from Singapore, H from Borneo. (Photos: A & C, A.F. Morad; B, P.K.F. Leong; D, E.M. Gardner; E & F, R. Lim; G, A. Ronaldo).

Notes. King's *Artocarpus gomezianus* var. *griffithii* first appeared in the *Flora of British India* in December 1888 (Stafleu & Cowan, 2011), with a note, "King mss.," no doubt referring to King's *The Species of Artocarpus Indigenous to British India*, which appeared the next year. These two publications have slightly different lists of type material, with *Curtis s.n.* appearing only in the former and *King 6551* and *7533*

appearing only in the latter. Although we consider them all original material, we have chosen a lectotype that was cited in both publications (*Griffith 4665*).

1.3 ***Artocarpus humilis*** Becc., Nelle Foreste di Borneo 629 (1902). – *Artocarpus nitidus* Trécul subsp. *humilis* (Becc.) F.M.Jarrett, J. Arnold Arbor. 41: 126 (1960). – TYPE: [Malaysia], Sarawak, a Marop prov. del Batàn-Lupàr [Batang Lupar], March 1866, *O. Beccari PB 3128* (lectotype FI [FI013392, herb no. 9410, a single specimen over 2 sheets], designated by Jarrett (1960); isolectotypes K [K001051139], P [P06777581], S [S07-8177]). (Fig. 4).

Artocarpus nitidus auct. non Trécul: Kochummen, Tree Fl. Sabah & Sarawak 3: 201 (2000); Berg, Fl. Males., Ser. 1, Spermat. 17(1): 121 (2006); Fl. Thailand 10(4): 17 (2011).

Diagnostic characters. Lateral leaf veins 5–9, often markedly ascending, the midrib often prominently raised; ripe syncarp to c. 4 cm across, surface yellow, pale brownish pubescent, flesh yellow(?).

Distribution. Endemic to Borneo.

Notes. Because Beccari's protologue did not specify the location of his type material, Jarrett's "holotype" citation was instead an effective lectotypification.

1.4 ***Artocarpus lamellosus*** Blanco, Fl. Filip. 667 (1837), as '*lamellosa*'. – TYPE: Philippines, Luzon, Batangas Prov., August 1914, *E.D. Merrill Species Blancoanae 100* (neotype P [P06777305], designated here; isoneotypes A n.v., BM, BO, F, GH n.v., K, L [L.1591655], MO). (Fig. 5).

Artocarpus nitidus Trécul, Ann. Sci. Nat., Bot., sér. 3, 8: 119 (1847), as '*nitida*'. – *Artocarpus nitidus* Trécul subsp. *nitidus*: Jarrett, J. Arnold Arbor. 41: 123 (1960). – TYPE: Philippines, Luzon, Albay Prov., 1841, *H. Cuming 1078* (lectotype P [P00507965], first step designated by Jarrett (1960), second step designated here; isolectotypes BM [BM000951874], E [E00504533], K [K001051598], MO, NY [NY00025196], P [P00507964] , SING [SING0052139]).

Artocarpus lanceolatus Trécul, Ann. Sci. Nat., Bot., sér. 3, 8: 121 (1847), as '*lanceolata*'. – TYPE: Philippines, [Luzon], Manille-Calawan [Manila-Calauan], 1840, *J.M.M. Callery 60* (lectotype P [P00507966], first step designated by Jarrett (1960), second step designated here; isolectotype P [P06777205]).

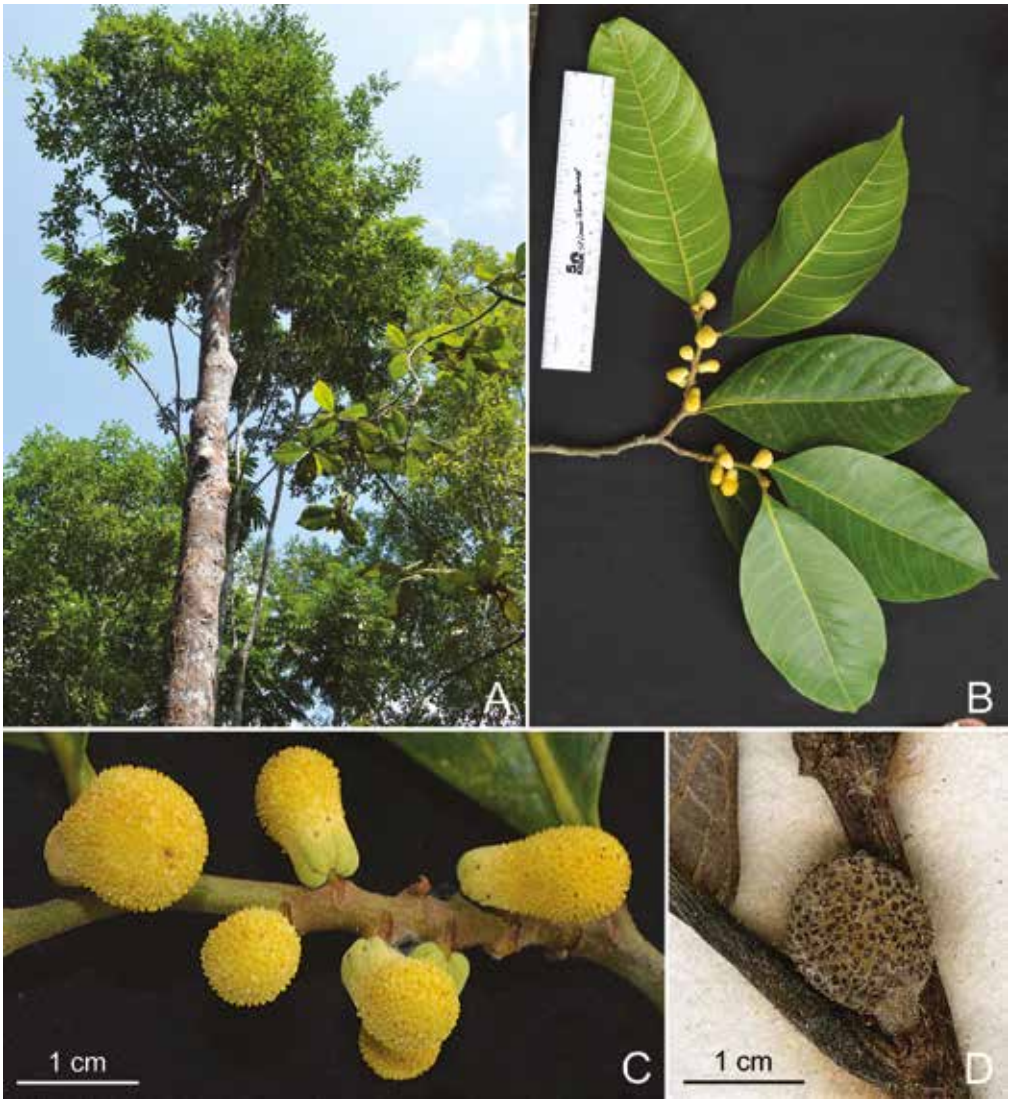

Fig. 4. *Artocarpus humilis* Becc. **A.** Bole. **B.** Leafy shoot with staminate inflorescences. **C.** Detail of staminate inflorescences. **D.** Pistillate inflorescence on the holotype, *Beccari PB3128*. A from Sarawak, B from Sabah. (Photos: A, E.M. Gardner; B, & C, N.J.C. Zerega; D, reproduced by permission from the Director of FI herbarium).

Diagnostic characters. Lateral leaf veins c. 5–6, ripe syncarp to c. 3 cm across, surface yellow, velutinous; flesh yellow. Differs from *Artocarpus xanthocarpus* (the only species in its range with which it might be mistaken) in the smaller, deeply lobed, syncarps (up to 3 cm across, with c. 3 seeds), and the clavate staminate inflorescences.

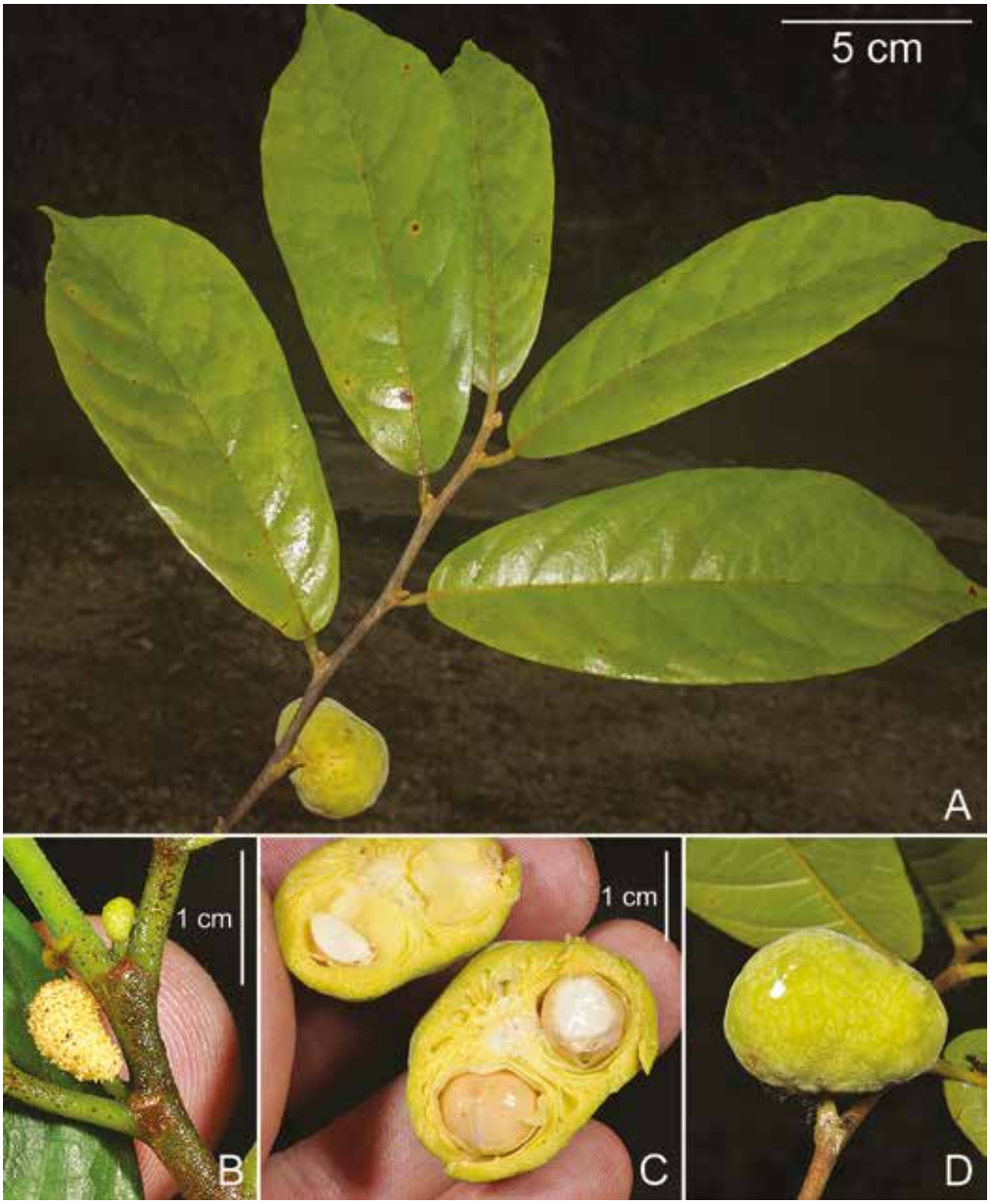

Fig. 5. *Artocarpus lamellosus* Blanco. **A.** Leafy shoot; **B.** Staminate inflorescence; **C & D.** Syncarp. All from Cebu. (Photos: P. Pelser & J. Barcelona, reproduced from Pelser et al. (2011 onwards) with permission).

Distribution. Endemic to the Philippines.

Notes. No original material for *Artocarpus lamellosus* could be traced. Merrill (1922) considered it equivalent to *Artocarpus nitidus*, but Jarrett (1960) disagreed,

considering *A. lamellosus* a *nomen dubium* that could apply to *A. xanthocarpus* or *A. rubrovenius* Warb. but not to *A. nitidus*. A reconsideration of the protologue (Blanco, 1837) leads us to agree with Merrill. Blanco described the syncarp as full of seeds ("lleno de semillas") and like a hen's egg ("como un hueve de gallina"), and it was on this basis that Jarrett discounted the association with *Artocarpus nitidus*, the latter typically having few seeds in a syncarp smaller than a hen's egg. We consider the syncarp description too vague to rule out the association, however, as the comparison to a hen's egg (which may be found in a variety of sizes) may refer to shape rather than size, and a small fruit might be considered full with few seeds. Consideration of the other characters also points to *Artocarpus nitidus*. Blanco described the leaves as 5 × 2+ inches (roughly 12 × 5.5 cm) and glabrous, with revolute margins, which could fit well with *A. xanthocarpus* or *A. nitidus* but is so small as to be nearly out of range for *A. rubrovenius*, which in any event generally does not have revolute margins (Berg et al., 2006). The pistillate inflorescences were described as very small, sessile and oval, which best describes *Artocaprus nitidus*. While the inflorescences of both *Artocarpus nitidus* and *A. rubrovenius* can be described as oval, those of *A. nitidus* are more nearly sessile and in any event have a better claim to being "very small." At the very least, *Artocarpus lamellosus* predates all three other taxa under discussion and must take priority over one of them, and we must acknowledge the possibility that Blanco may have considered all of them conspecific. For the reasons outlined above, we follow Merrill's approach and neotypify *Artocarpus lamellosus* with his *Species Blancoanae 100* (= *A. nitidus*).

1.5 ***Artocarpus parvus*** Gagnep., Bull. Soc. Bot. France 73: 89 (1926), as '*parva*'. – TYPE: [Vietnam], Tonkin, Haïphong, dans les jardins [cultivated], March 1889, *B. Balansa 4112* (lectotype P [P00756680], designated by Jarrett (1960)). (Fig. 6).

Artocarpus sampor Gagnep., Bull. Soc. Bot. France 73: 90 (1926). – TYPE: [Vietnam] Annam, Presqu'île de Núi han heo, prov. de Nhatrang, 12 June 1923, *E. Poilane 6879* (lectotype P [P00756678], designated by Jarrett (1960); isolectotypes F, P [P00756679]).

Artocarpus lingnanensis Merr., Lingnan Sci. J. 7: 302 (1931); Merr., Lingnan Sci. J. 13: 56 (1934). – *Artocarpus nitidus* Trécul subsp. *lingnanensis* (Merr.) F.M.Jarrett, J. Arnold Arbor. 41: 124 (1960). – TYPE: China, Kwangtung [Guangdong] Prov., Canton Christian College Campus, 10 May 1925, *F.A. McClure 1647, herb. no. 13471* (lectotype UC [UC287882], designated here; isolectotypes K, P [P00756681], PE [PE00024102, PE00024103, PE00024104]).

Artocarpus nitidus auct. non Trécul: Kochummen, Tree Fl. Sabah & Sarawak 3: 201 (2000); Berg, Fl. Males., Ser. 1, Spermat., 17(1): 121 (2006); Berg, Fl. Thailand 10(4): 17 (2011).

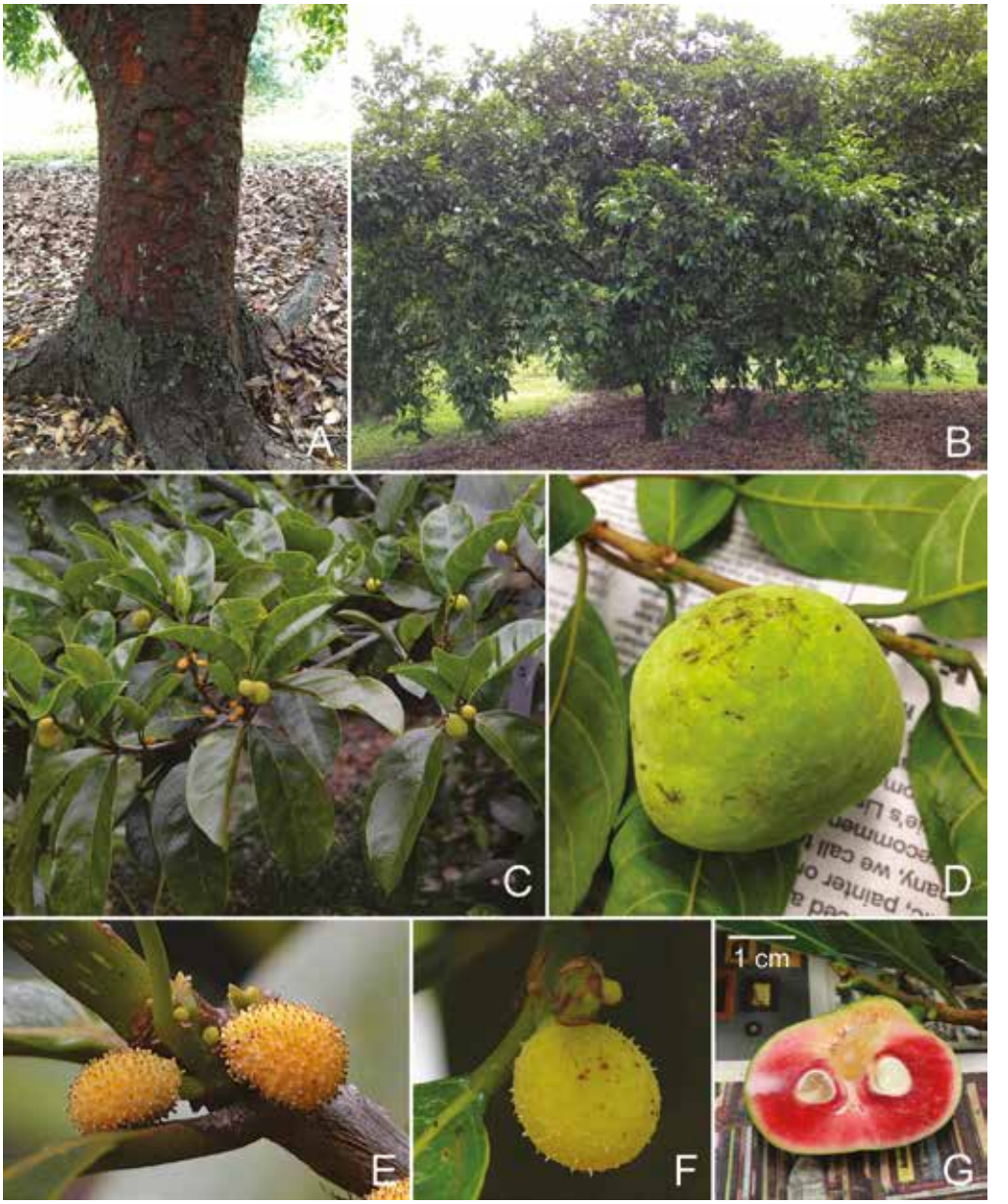

Fig. 6. *Artocarpus parvus* Gagnep. **A.** Bole. **B.** Habit. **C.** Leafy shoot with inflorescences. **D.** Syncarp. **E.** Staminate inflorescences. **F.** Pistillate inflorescence. **G.** Syncarp in section. All from Montgomery Botanical Center, Florida, USA. (Photos: E.M. Gardner).

Diagnostic characters. Lateral leaf veins usually 6–9(–14), acumen rather blunt; ripe syncarp to c. 5 cm across, surface yellow-orange and velutinous, flesh pink-orange. The dark rough bark is also distinctive.

Distribution. Southern China, Thailand and Vietnam, but cultivated worldwide in tropical and subtropical areas.

Notes. This is the *kwai muk* (Cantonese), often cultivated for its fruits. Two rather obscure names, published simultaneously by Gagnepain, unfortunately have priority over *Artocarpus lingnanensis*, the epithet under which this species has been widely known. Because the type material of *Artocarpus sampor* contains mixed material (a syncarp probably from *A. gomezianus* Miq.), it seems advisable to accept the name *A. parvus*.

For *Artocarpus lingnanensis*, Merrill designated both a male and female type. The latter is cited as *McClure s.n.*, September 1924, from Honam Island. Although no unnumbered *McClure* specimen bearing that date could be located, an annotation as the female type appears in Merrill's handwriting on *McClure 1*, Oct. 1, 1924 (UC), whose locality is given as a college campus in Canton (Guangdong), presumably Canton Christian College, located on Honam Island in Guangzhou. The vague citation to this syntype as well as the lack of duplicates counsel in favour of lectotypifying the male type.

1.6 ***Artocarpus vrieseanus*** Miq. var. ***subsessilis*** F.M.Jarrett, J. Arnold Arbor. 41: 101 (1960). – *Artocarpus nitidus* auct. non Trécul: Berg, Fl. Males., Ser. 1, Spermat., 17(1): 121 (2006), as "subsessilis" form. – TYPE: Territory of New Guinea [Papua New Guinea], Madang Distr., near Jal village, about halfway along road to Bamesos, Gogol River Valley, 14 July 1955, *R.D. Hoogland 4999* (holotype A [A00034354]; isotypes CANB [CANB68502, CANB68503], K [K001051125], L [L0039910], MEL [MEL2085484], US [US00089820]). (Fig. 7).

Diagnostic characters. Leaves rather thinly coriaceous and not shiny *in sicco*. Staminate inflorescences visibly pedunculate and subglobose to ellipsoid. Adjacent pistillate flowers completely fused without a proximal free portion. Ripe syncarp surface subglabrous, usually not lobed and often with an areolate pattern formed by the flat perianth apices; peduncles up to 7 mm long.

Distribution. New Guinea to the Solomon Islands.

Notes. Berg et al. (2006) provisionally considered *Artocarpus antiarifolia* Becc. to be synonymous with the "subsessilis" form; however, an examination of the type (FI) indicates that it matches *A. vrieseanus* Miq. var. *vrieseanus* (cf. Jarrett, 1960), particularly in the long slender peduncle and the lack of a reticulate surface on the syncarp.

Fig. 7. *Artocarpus vrieseanus* Miq. var. *subsessilis* F.M.Jarrett. **A.** Isotype (*Hoogland et al. 4999*, L). **B**. Staminate inflorescences (*Anon. AQ356914*, SING [SING0243385]). **C.** Syncarps (*E.E. Henty NGF10586*, SING [SING0276196]).

1.7 ***Artocarpus xanthocarpus*** Merr., Publ. Bur. Sci. Gov. Lab. 17: 10 (1904), as '*xanthocarpa*'. – TYPE: Philippines, Luzon, Bataan Prov., Lamao Riv., Mt. Mariveles, June 1904, *H.N. Whitford 367* (lectotype: P [P00756672], designated by Jarrett (1960); isolectotypes K [K001051129], NY [NY00025208], PNH (destroyed), US [US00089817]). (Fig. 8).

Artocarpus nitidus auct. non Trécul: Berg, Fl. Males., Ser. 1, Spermat., 17(1): 121 (2006); Berg, Fl. Thailand 10(4): 17 (2011).

Artocaprus lanceolatus auct. non Trécul: Merr., Enum. Philipp. Fl. Pl. 2: 42 (1923).

Artocarpus rubrovenius auct. non Warb.: Merr., Philipp. J. Sci., C: 401 (1908).

Diagnostic characters. Leaf acumens up to 3 cm long. Staminate inflorescences subglobose to obovoid. Adjacent pistillate flowers completely fused without a proximal free portion. Ripe syncarps shallowly lobed, up to 5 cm across with at least several seeds (in contrast to the few-seeded *Artocarpus lamellosus*, the only species

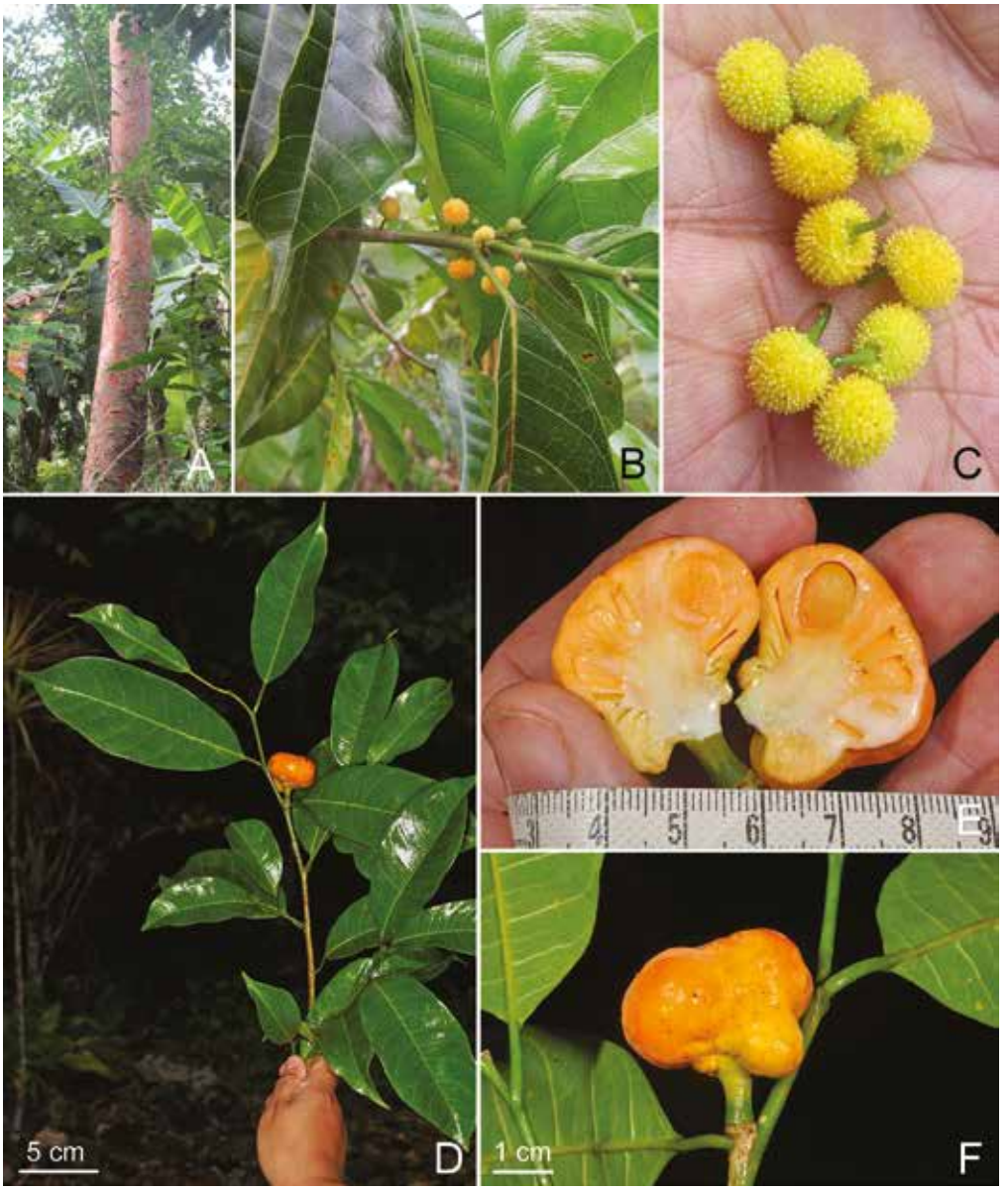

Fig. 8. *Artocarpus xanthocarpus* Merr. **A.** Bole. **B.** Leafy shoot with staminate inflorescences. **C.** Staminate inflorescences. **D.** Leafy shoot with syncarp. **E & F.** Syncarp. A–C from Panay; D–F from Cebu. (Photos: A–C, H. Cabria; D–F, P. Pelser & J. Barcelona reproduced from Pelser et al. (2011 onwards) with permission).

with which it might be confused). The leaf base is cuneate, whereas it is typically rounded to subcordate in *Artocarpus lamellosus*.

Distribution. Endemic to the Philippines.

2. Key to taxa formerly comprising *A. lacucha* s.l. (Berg et al. 2006)

1a. Adjacent pistillate flowers proximally free 2
1b. Adjacent pistillate flowers proximally fused 5

2a. Staminate inflorescences less than 1 cm in diameter, usually clustered on short shoots; pistillate inflorescences deeply lobed and papillate between the lobes .... *A. fretessii*
2b. Staminate inflorescences ≥1 cm in diameter, not usually clustered on short shoots; pistillate inflorescences lobed or not but not usually papillate between the lobes 3

3a. Inflorescences deflexed upwards away from twig; staminate peduncle up to 4.5 cm long; leaf base ±cordate (Philippines) ..... *A. ovatus*
3b. Inflorescences not deflexed upwards away from twig; staminate peduncle up to 1.5 cm long; leaf base usually not cordate but may be auriculate or peltate (not in the Philippines) 4

4a. Styles exserted to 1.5 mm or more; peduncles shorter than inflorescences; margin often denticulate even on mature leaves ..... *A. lacucha*
4b. Styles barely exserted to 0.5 mm; peduncles usually longer than inflorescences; margin entire on mature leaves ..... *A. dadah*

5a. Pistillate inflorescences smooth at anthesis (New Guinea) … *A. vrieseanus* var. *refractus*
5b. Pistillate inflorescences papillate at anthesis (Solomon Islands) … *A. vrieseanus* var. *papillosus*

2.1 ***Artocarpus dadah*** Miq., Fl. Ned. Ind., Eerste Bijv. 3: 420 (1861). – *Artocarpus lacucha* auct. non Roxb. ex Buch.-Ham.: Berg, Fl. Males., Ser. 1, Spermat., 17(1): 118 (2006), as "dadah" form. – TYPE: [Indonesia], Sumatra australis in prov. Lampong [Lampung Prov.], prope Mangala [Menggala], s.d., *J.E. Teijsmann H.B. 4391* (lectotype U [U0004426], designated by Jarrett (1960); isolectotypes BO, K [K000357623], L [L0039872]). (Fig. 9).

Artocarpus mollis Miq., Fl. Ned. Ind., Eerste Bijv. 3: 420 (1861). – TYPE: [Indonesia], Sumatra australis in prov. Lampong [Lampung Prov.], prope Kebang, s.d., *J.E. Teijsmann H.B. 4211* (lectotype L [L0039876], designated by Jarrett (1960); isolectotypes BO, U [U0004425]).

Artocarpus rufescens Miq., Fl. Ned. Ind., Eerste Bijv. 3: 420 (1861). – TYPE: [Indonesia], Sumatra orientalis in regione Palembanica [South Sumatra Prov.], prope Dermo-enim, s.d., [*J.E. Teijsmann*] *H.B. 3793* (lectotype U [U0004425], designated by Jarrett (1960); isolectotypes BO, K [K001051086], L [L0039877]).

Artocarpus tampang Miq., Fl. Ned. Ind., Eerste Bijv. 3: 421 (1861). – TYPE: [Indonesia], Sumatra orientalis in regione Palembanica [South Sumatra Prov.], prope Panan-donan [Pengandonan], in Ogan-ulu [Ogan Komering Ulu], s.d., *J.E. Teijsmann H.B. 3997* (lectotype U [U0004427], designated by Jarrett (1960); isolectotypes BO, K [K001051085], L [L0039875]).

Ficus tampang Miq., Fl. Ned. Ind., Eerste Bijv. 3: 425 (1861). – TYPE: [Indonesia], Sumatra occidentalis [West Sumatra Prov.] prope castellum de Kock [Bukittingi], in Kota-nopan, s.d., *J.E. Teijsmann H.B. 710* (lectotype U, designated by Jarrett (1960), apparently lost; new lectotype BO, designated here).

Ficus inconstantissima Miq., Fl. Ned. Ind., Eerste Bijv. 3: 431 (1861). – *Artocarpus inconstantissimus* (Miq.) Miq., Ann. Mus. Bot. Lugduno-Batavi 3: 211 (1867), as '*inconstantissima*'. – TYPE: [Indonesia], Sumatra orientale in regione Palembang [South Sumatra Prov.], prope Batu-radja, s.d., *J.E. Teijsmann H.B. 3529* (lectotype U [U0004423], designated by Jarrett (1960); isolectotypes BO, CAL, K [K001051084], L [L0039874], MEL [MEL2414813]).

Artocarpus dadah Miq. var. *pubescens* Miq., Ann. Mus. Bot. Lugduno-Batavi 3: 213 (1867), as 'var. γ *pubescens*'. – *Artocarpus erythrocarpus* Korth. in Miquel, Ann. Mus. Bot. Lugduno-Batavi 3: 213 (1867), non Teijsm., pro syn., nom. inval., as '*erythrocarpa*' – TYPE: [Indonesia], Sumatra occidentalis, s.d., *P.W. Korthals s.n.* (lecotype L [L0816778], designated by Jarrett (1960); possible isolectotypes (or syntypes) L [L0816775, L0816776, L0039878], U [U0004424, U.1423884]).

Artocarpus lakoocha Roxb. var. *malayanus* King in Hook.f., Fl. Brit. India 5: 544 (1888); King, Ann. Roy. Bot. Gard. (Calcutta) 2: 15 (1889), p. p. m., as '*malayana*'. – TYPE: Malaya [Peninsular Malaysia], Perak, Larut, Chanderiang [Chenderiang], March 1884, *G. King 5653* (lectotype K [K001328358], designated here; isolectotypes BM [BM000951753], CAL n.v., K [K001051067], L [L.1582775], P [P06777568]).

Artocarpus reniformis Becc., Nelle Foreste di Borneo 631 (1902). – TYPE: [Malaysia], Sarawak, Kutcin [Kuching], February 1867, *O. Beccari PB 3107* (lectotype FI [herb. no. 9412, a single specimen over 3 sheets], designated by Jarrett (1960); isolectotype K [K001051083]).

Artocarpus peltatus Merr., J. Straits Branch Roy. Asiat. Soc. 85: 166 (1922), as '*peltata'*. – *Artocarpus lacucha* auct. non Roxb. ex Buch.-Ham.: Berg, Fl. Males., Ser. 1, Spermat., 17(1): 118 (2006), as "peltatus" form. – TYPE: [Malaysia], British North Borneo [Sabah], January–March 1916, *A. Villamil 168* (lectotype PNH, designated by Jarrett (1960); isolectotypes BO, US [US00089825]).

Artocarpus lakoocha auct. non Roxb., Ridley, J. Straits. Branch Roy. Asiat. Soc. 33: 147 (1900); Ridley, Fl. Malay Penins. 3: 355 (1924); Berg, Fl. Thailand 10(4): 15 (2011).

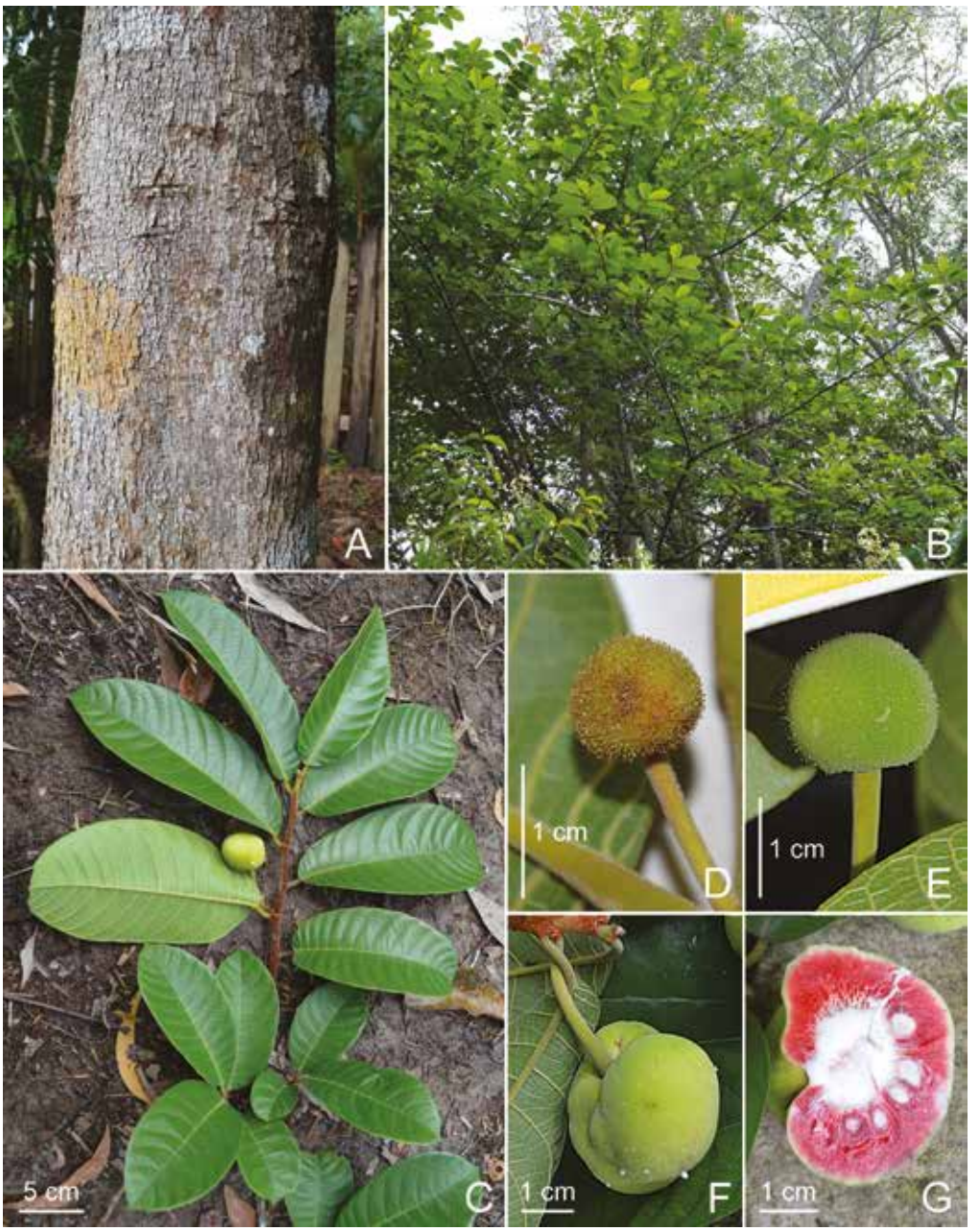

Fig. 9. *Artocarpus dadah* Miq. **A.** Bole. **B.** Habit. **C.** Leafy shoot with syncarp. **D.** Staminate inflorescence. **E.** Pistillate inflorescence. **F & G.** Syncarps. A from Sarawak, B– G from Sabah. (Photos: A, B, D & E, E.M. Gardner; C, F & G, N.J.C. Zerega).

Diagnostic characters. Mature leaves with entire margins, attachment sometimes auriculate to peltate; syncarp surface smooth, without persistent interfloral bracts,

peduncle up to 4(–8) cm long; staminate inflorescences globose with peduncles up to 1.5 cm long.

Distribution. Thailand, Malay Peninsula (including Singapore), Sumatra and Borneo.

Notes. Miquel did not specify the location for his type material, specifying only a locality and a collector, for example, "Sumatra austr. in prov. Lampong, propre Mangala (T.)" [Teijsmann] for *Artocarpus dadah*. In most cases here, Teijsmann collections from the H.B. series exist at L and U precisely matching Miquel's localities. The L labels state "Ex Herb Univ Ultraj.[,]" indicating that the L and U material were once together at Utrecht but that part of the gathering was sent to L, undoubtedly as part of the two-way exchange of specimens that Miquel oversaw in the period after he was appointed director of the Rijksherbarium but retained his position in Utrecht (Stafleu, 1966). In one case (*Artocarpus mollis*, *H.B. 4211*) the L specimen seems to have been cut off the top of the U specimen. Thus, although Jarrett typically cites the U sheet as a holotype, Miquel's citation might apply equally to the material now at L. We therefore treat Jarrett's "holotype" citations as effective designations of lectotypes. In the case of *Ficus tampang* Miq., the "holotype" cited by Jarrett, *H.B. 710*, could not be located at U; however, a duplicate exists at BO, and we therefore designate that collection as a new lectotype. We note that in most of these cases, the L and U sheets list no collector; however, the BO duplicates invariably identify Teijsmann.

In her revision, Jarrett (1960) indicated a holotype at Leiden for *Artocarpus dadah* var. *pubescens* Miq. Miquel's protologue introduces the new name as "*var.* γ *pubescens (A. erythrocarpa* KORTH. *herb.*)", citing an unpublished name attributed to Korthals, and indeed, there exists a single Korthals sheet in Leiden that is annotated "*Artocarpus erythrocarpa*." Following his description, though, Miquel states simply, "*Sumatra occidentalis:* KORTHALS." There are five additional Korthals sheets in L and U annotated as "*pubescens dadah* var. *pubescens*"; five years before her monograph was published, Jarrett annotated three of them as syntypes and one as a lectotype. These specimens would have all come from Korthals' single expedition to Sumatra in 1836 (Van Steenis-Kruseman, 1950), so all of them should have been available to Miquel. We therefore tend to agree with Jarrett's first impulse and therefore treat her "holotype" citation of the "*erythrocarpa*" sheet as an effective lectotypification.

A short description of *Artocarpus lakoocha* var. *malayana* appeared in the *Flora of British India* (King, 1888), which slightly predated and was likely a summary of King's more complete description in his account of *Artocarpus* (King, 1889). We therefore treat the specimens cited in both treatments as original material but designate a lectotype cited in both.

Because Merrill did not specify the location of his type for *Artocarpus peltatus*, Jarrett's "holotype" citation must be interpreted as an effective lectotypification.

2.2 *Artocarpus fretessii* Teijsm. & Binn. in Hasskarl, Abh. Naturf. Ges. Halle 9: 189 (1866), as '*fretissi*', based on *Metrosideros spuria* Rumph., Herb. Amb. 3: 26, t. 13 (1743). – *Antiaris fretessii* Teijsm. & Binn., Cat. Hort. Bog. 84 (1866), nom. nud. – *Prainea rumphiana* Becc., Nelle Foreste di Borneo 636 (1902), nom. illeg. superfl. – *Artocarpus lacucha* auct. non Roxb. ex Buch.-Ham.: Berg, Fl. Males., Ser. 1, Spermat., 17(1): 118 (2006), as "fretessii" form. – TYPE: [Published illustration] Rumphius, Herb. Amb. 3: t. 13 (1743), lectotype designated here. (Fig. 10).

Artocarpus dasyphyllus Miq., Ann. Mus. Bot. Lugduno-Batavi 3: 212 (1867), as '*dasyphylla*'. – *Artocarpus erythrocarpus* Teijsm. in Miquel, Ann. Mus. Bot. Lugdundo-Batavi 3: 212 (1867), non Korth. pro. syn., nom. inval., as '*erythrocarpa*'. – TYPE: [Indonesia], Celebes borealis [North Sulawesi Prov.], Menado [Manado], s.d., *J.E. Teijsmann H.B. 5789* (lectotype U [U0004428], designated by Jarrett (1960); isolectotype BO n.v.).

Artocarpus dasyphyllus var. *flavus* J.J.Sm. in Boerlage, Icon. Bogor. 3: 85, t. 234 (1907), as '*dasyphylla* var. *flava*'. – TYPE: [Published illustration] Smith in Boerlage, Icon. Bogor. 3: t. 234 (1907), lectotype designated here.

Artocarpus leytensis Elmer, Leafl. Philipp. Bot. 1: 279 (1908). – *Artocarpus rotundifolius* Elmer ex Merr., Enum. Philipp. Fl. Pl. 2: 42 (1923), pro syn., nom. inval., as '*rotundifolia*'. – TYPE: Philippines, Leyte Prov., Palo, January 1906, *A.D.E. Elmer 7243* (lectotype K [K001051127], designated by Jarrett (1960); isolectotypes A [A00034355], BO, E [E00504528], NY [NY00025194], PNH (destroyed)).

Artocarpus paloensis Elmer, Leafl. Philipp. Bot. 1: 280 (1908). – TYPE: Philippines, Leyte Prov., Palo, January 1906, *A.D.E. Elmer 7244* (lectotype K [K001051128], designated by Jarrett (1960); isolectotypes A [A00034359], BO n.v., E [E00504530], NY [NY00025200], PNH(destroyed)).

Artocarpus albobrunneus C.C.Berg, Blumea 50(3): 541, fig. 2 (2005). – TYPE: Indonesia, East Kalimantan, Jl. Akbar, Km 39, along Sakakanan river, 13 March 2000, *Adriansyah AA 2243* (holotype L [L0370847]; isotypes A [A00993767], K [K000442528], SAN, WAN n.v.).

Artocarpus lacucha auct. non Roxb. ex Buch.-Ham.: Berg, Fl. Thailand 10(4): 15 (2011).

Diagnostic characters. Mature leaves usually with entire margins; syncarps deeply lobed, with one seed per lobe and the unexpanded papillate surface of the inflorescence visible between the lobes, with numerous persistent bracts, peduncle c. 2–3 cm long; staminate inflorescences globose and often clustered on short shoots on older wood, peduncles c. 3–7 mm long.

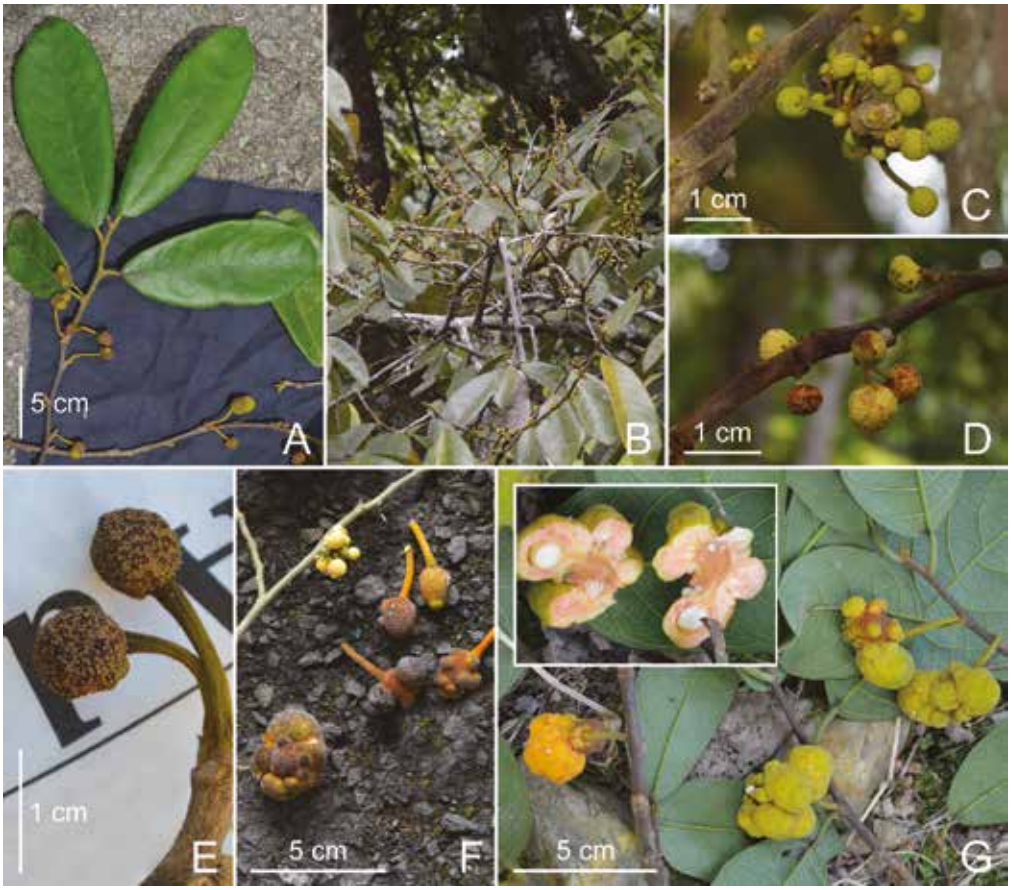

Fig. 10. *A. fretessii* Teijsm. & Binn. ex Hassk. **A.** Leafy shoot with immature syncarps. **B.** Staminate inflorescences on deciduous shoots. **C.** Immature staminate inflorescences on short shoot. **D.** Staminate inflorescences on normal shoot. **E.** Pistillate inflorescences. **F.** Tree *VII G 105* in Kebun Raya Bogor with atypical syncarps and yellow flesh. **G.** Syncarps. A–E & G from Sabah; F from Bogor. (Photos: A–F, E.M. Gardner; G, N.J.C. Zerega).

Distribution. Philippines, Sulawesi and the Moluccas.

Notes. Although *Artocarpus fretessii* was published without a description or diagnosis, the name was validly published under Article 38.1 of the Shenzhen Code (notwithstanding recommendation 38A.1) because the protologue refers to Rumphius's *Metrosidero spuria*, described and illustrated in detail in the *Herbarium Amboinense*. For this reason, we lectotypify Rumphius's plate, noting that the involucre appearing on one of the syncarps is simply an embellishment added by the artist. The protologue gives the epithet "*fretissi*," apparently in honour of De Fretes, a resident of Ambon. The improperly declined ending must certainly be corrected under Article 60.8. Although the spelling should be corrected only with reserve (Art. 60.3), "fretissi" is an obvious orthographic error, highlighted by the appearance in the same year of

"*Antiaris fretessii*" in a catalogue of plants cultivated in the Bogor Botanical Garden. We therefore follow Jarrett (1960) in using the epithet *fretessii*.

Smith's protologue for *Artocarpus dasyphyllus* var. *flavus* does not cite unique type material connected to the yellow-fruited tree in Bogor but merely refers to the material cited by Miquel for the red-fruited type variety. Because Smith's variety has no ascertainable specimens constituting original material, we typify the detailed plate published along with the name. As discussed by Jarrett (1960), Rumphius's description said that the fruits were yellow, but the significance of the differences in fruit colour is unclear as they do not correlate with geography. We note that yellow fruits may also have red interiors (cf. the type of *Artocarpus albobrunneus* and Fig. 10-G), adding to the confusion. An extant tree from Sulawesi in the Bogor Botanical Garden, *VII G 105*, has fruits with yellow interiors and may be this variety. A specimen of that tree at L examined by Jarrett (1960) was annotated as "*Antiaris fretessii*," referring to the nomen nudum in Teijsmann's and Binnendjik's catalogue of the Garden. However, fruits collected from *VII G 105* are uncharacteristically large and do not especially resemble either Rumphius' or Smith's plates (Fig. 10F).

2.3 *Artocarpus lacucha* Roxb. [Hort. Beng. 66 (1814), nom. nud.] ex Buch.-Ham., Mem. Wern. Nat. Hist. Soc. 5: 333 (1826). – TYPE: [Myanmar], Rangoon [Yangon], s.d., *F. Buchanan-Hamilton s.n.* (lectotype BM [BM013717453], designated here) (Fig. 11).

Artocarpus lakoocha Roxb., Fl. Ind. 3: 24 (1832). – TYPE: India, Bengal, September 1812, *W. Roxburgh s.n.*(lectotype BM [BM000900563], designated by Jarrett (1960)).

Artocarpus benghalensis Roxb. ex Wall., Numer. List 4655C (1831), nom. nud.

Artocarpus reticulatus B.Heyne ex Wall., Numer. List 4655D (1831), nom nud., non Miq., as '*reticulata*'.

Artocarpus mollis Wall., Numer. List 4661 (1831), nom nud., non Miq.

Artocarpus yunnanensis Hu, Bull. Fan. Mem. Inst. Biol. Bot. 8: 32 (1937). – TYPE: China, Yunnan, Mon-hun, Fo-hai 1400 m, June 1936, *C.W. Wang 77078* (holotype PE [PE00024113]; isotypes A [A00034345], PE [PE00024111, PE00024112]).

Artocarpus ficifolius W.T.Wang, Acta Phytotax. Sin. 6: 274, t. 15, fig. 23 (1957), as '*ficifolia*'. – TYPE: China, Yunnan, Chin-ping, Meng-la, 350 m altitude, 16 April 1956, *Exped. Biol. Sino-ross. ad prov. Yunnan 676* (holotype PE [PE00024095]; isotype A [A00034343]).

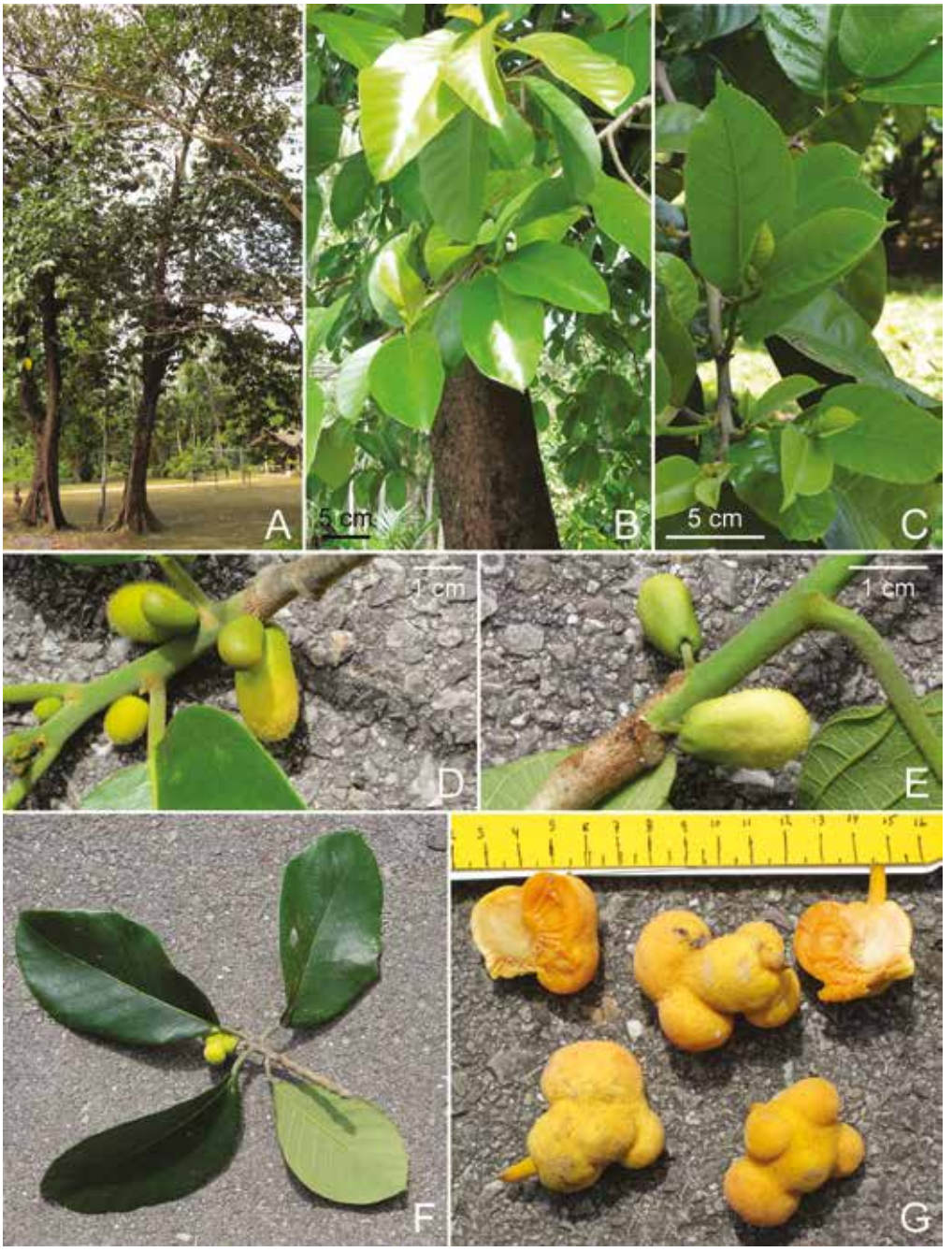

Fig. 11. *Artocarpus lacucha* Roxb. ex Buch.-Ham. **A.** Habit. **B.** Leafy shoot. **C.** Young leaves with denticulate margins. **D.** Shoot with inflorescences. **E.** Staminate inflorescence. **F.** Leafy shoot with immature syncarp. **G.** Syncarps. A, B, D–G from Thailand, C from Kebun Raya Bogor. (Photos: A, B, D–G, N.J.C. Zerega; C, E.M. Gardner).

Diagnostic characters. Mature leaves often with a denticulate margin; styles exserted to 1.5 mm or more, forming a visible halo around the inflorescence; syncarp surface deeply lobed and often bumpy, peduncle up to 2.5 cm long; staminate inflorescences usually ellipsoid to obovoid with a peduncle up to 0.5 cm long.

Distribution. India to Nepal, southern China, Thailand and Vietnam.

Notes. Jarrett (1960) cited *Roxburgh s.n.* (BM000900563) as the "holotype (?)" of *Artocarpus lakoocha* Roxb. We consider Jarrett's citation to have been an effective lectotypification. Another specimen possibly constituting original material exists, with a label in Roxburgh's hand but no date or locality other than "India" (BM000900562).

2.4 *Artocarpus ovatus* Blanco, Fl. Filip. 666 (1837), as '*ovata*'. – *Artocarpus lacucha* auct. non Roxb. ex Buch.-Ham.: Berg, Fl. Males., Ser. 1, Spermat., 17(1): 118 (2006), as "ovatus" form. – TYPE: Philippines, Luzon, Rizal Prov., Antipolo, January 1914, *E.D. Merrill SB 254* (neotype BM n.v., designated by Jarrett (1960); isoneotypes A n.v., BO n.v., GH n.v., K n.v., L [L.1582620], NY [NY00025199], P n.v., PNH, US [00688536]). (Fig. 12).

Artocarpus cumingianus Trécul, Ann. Sci. Nat., Bot., sér. 3, 8: 119, t. 4, fig. 117, 118 (1847), as '*Cummingiana*'. – TYPE: Philippines, Cebu, 1841, *H. Cuming 1784* (holotype P [P06777794]; isotypes B [B 10 0294377], BM [BM000951752], CGE n.v., K [K001051130, K001051131]).

Artocarpus acuminatissimus Merr., Philipp. J. Sci. 18: 49 (1921), as '*acuminatissima*'. – TYPE: Philippines, Luzon, Tayabas Prov., April 1914, *R. De Mesa & N. Rosario 22777* (lectotype K [K001051132], designated by Jarrett (1960); isolectotypes PNH (destroyed), US [US00089832])

Artocarpus lacucha auct. non Roxb. ex Buch.-Ham.: Berg, Fl. Thailand 10(4): 15 (2011).

Diagnostic characters. Mature leaves with entire margins, attachment usually subcordate; syncarp shallowly lobed, surface smooth, peduncle up to 8 cm long; inflorescences deflexed, pointing upwards away from stem; staminate inflorescences obovoid to clavate, peduncles up to 4.5 cm long.

Distribution. Philippines.

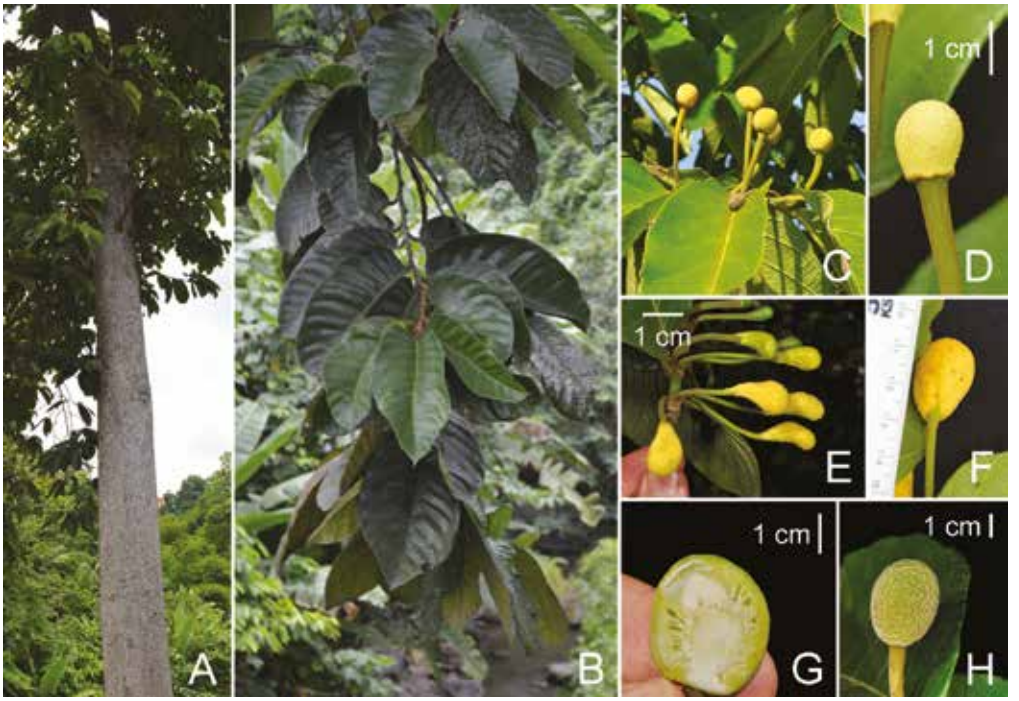

Fig. 12. *Artocarpus ovatus* Blanco. **A.** Bole. **B.** Leafy shoot. **C & D.** Pistillate inflorescences. **E & F**. Staminate inflorescences. **G & F.** Immature syncarps. A, B, D, E & F from Luzon, C, G & H from Panay. (Photos: A, B, D & F, E.M. Gardner; C, G & H, P. Pelser and J. Barcelona, reproduced with permission from Pelser et al. (2011 onwards)).

2.5 ***Artocarpus vrieseanus*** Miq. var. ***refractus*** (Becc.) F.M.Jarrett, J. Arnold Arbor. 41: 98 (1960). – *Artocarpus refractus* Becc., Nelle Foreste di Borneo 630 (1902), as '*refracta*'. – *Artocarpus lacucha* auct. non Roxb. ex Buch.-Ham.: Berg, Fl. Males., Ser. 1, Spermat., 17(1): 118 (2006), as "refractus" form. – TYPE: [Indonesia], Isole Aru [Maluku Prov., Aru Islands Regency], Giabu-lengan [Jabulenga], May 1873, *O. Beccari s.n.* (lectotype FI [FI008155], designated by Jarrett (1960); isolectotype FI [FI008156]). (Fig. 13A)

Artocarpus lacucha auct. non Roxb. ex Buch.-Ham.: Berg, Fl. Thailand 10(4): 15 (2011).

Diagnostic characters. Mature leaves with entire margins; syncarp surface smooth, peduncle up to 3 cm long; staminate inflorescences with peduncles 3–15 mm long.

Distribution. Philippines, Moluccas and New Guinea.

Fig. 13. *Artocarpus vrieseanus* Miq. **A.** Leafy shoot with staminate inflorescences of *Artocarpus vrieseanus* Miq. var. *refractus* (Becc.) F.M.Jarrett., with syncarps in the inset. **B.** Type specimen of *Artocarpus vrieseanus* var. papillosus from K. (Photos: A from Bell Museum, B, © copyright of the Board of Trustees of the Royal Botanic Gardens, Kew, reproduced with permission).

Notes. Because Beccari's protologue cited two collections, Jarrett's (1960) "holotype" citation of *Beccari s.n.* was an effective lectotypification.

2.6 *Artocarpus vrieseanus* Miq. var. ***papillosus*** F.M.Jarrett, J. Arnold Arbor. 41: 99 (1960). – TYPE: Solomon Islands, Malaita, Quoimonapu, 12 December 1930, *S.F. Kajewski 2360* (holotype A [A00034353]; isotypes BM [BM001014692], K, L [L.1583150], P n.v.). (Fig. 13B).

Artocarpus lacucha auct. non Roxb. ex Buch.-Ham.: Berg, Fl. Males., Ser. 1, Spermat., 17(1): 118 (2006), as "refractus" form; Berg, Fl. Thailand 10(4): 15 (2011).

Diagnostic characters. Mature leaves with entire margins; pistillate inflorescences distinctly papillate at anthesis; syncarp often shallowly lobed and papillate between the lobes but the lobes much shallower and less distinct than in *Artocarpus fretessii*, peduncle up to 3.5 cm long; staminate inflorescence with peduncles 3–5 mm long.

Distribution. Solomon Islands.

3. Taxa formerly comprising *A. gomezianus* s.l. (Berg et al. 2006)

3.1 ***Artocarpus gomezianus*** Wall. ex Trécul, Ann. Sci. Nat., Bot., sér. 3, 8: 118 (1847), as '*gomeziana*'. – *Artocarpus lakoocha* Roxb. var. β *gomezianus* (Wall ex Trécul) Trimen, Handb. Fl. Ceylon 4: 99 (1898), as '*gomeziana'*. – TYPE: [Myanmar], Tavoy, 1832, *N. Wallich [Gomez] s.n.* [EIC 4660] (holotype G [G00438018]; isotypes CAL, CGE, K-W [K001039620, K000357624]). (Fig. 14).

Artocarpus petiolaris Miq., Fl. Ned. Ind., Eerste Bijv. 3: 422 (1861). – TYPE: [Indonesia], Sumatra borealis [North Sumatra Prov.] in prov. Baros [Barus], s.d., *J.E. Teijsmann H.B. 752* (lectotype U [U0004432], designated by Jarrett (1960); isolectotype BO).

Artocarpus pomiformis Teijsm. & Binn., Natuurk. Tijdschr. Ned.-Indië. 25: 400 (1863). – TYPE: [Indonesia], West Java, cult. in Hort. Bot. Bog., s.d., [*Unknown*] *H.B. 7289* (neotype BO, designated here; isoneotype P [P06777334]).

Artocarpus masticatus Gagnep., Bull. Soc. Bot. France 73: 88 (1926), as '*masticata*'. – TYPE: [Vietnam], Annam, Phu hu, prov. Nhatrang [Khánh Hòa Prov., Nha Trang], entre Nhatrang [Nha Trang] et Niubhoa, 25 January 1923, *E. Poilane 5492* (lectotype P [P00756688], designated here; isolectotypes K [K001051105], P [P00756689, P00756690], US [US00089828]).

Diagnostic characters. Leaves subglabrous, main veins reddish below; syncarps smooth, velutinous, peduncles up to 4.5(–6 in Thailand) cm long.

Distribution. India (Andaman Islands), Myanmar to Vietnam, Malay Peninsula (including Singapore), Sumatra, Java and Philippines

Notes. Jarrett (1960) cited a "holotype" for *Artocarpus petiolaris*; however, Miquel's brief citation states simply "Sumatra bor. in prov. Baros (T.)." In addition to *H.B. 752* in Utrecht, there exists in Leiden *H.B. 721*, marked "Ex Herb Univ Ultraj." Because both specimens are syntypes, Jarrett's citation of *H.B. 752* was actually an effective lectotypification.

Teijsmann and Binnendijk described *Artocarpus pomiformis*, which is just *A. gomezianus* in Java, from the living collections of the Bogor Botanical Garden. The protologue gives no indication of a type, and it was not possible to identify original material with any certainty. We have therefore neotypified the name with *H.B. 7289*, a specimen collected from the Garden, perhaps under the auspices of Teijsmann, whose name appears on at least 18 nearby (72--) H.B. numbers in the Leiden herbarium.

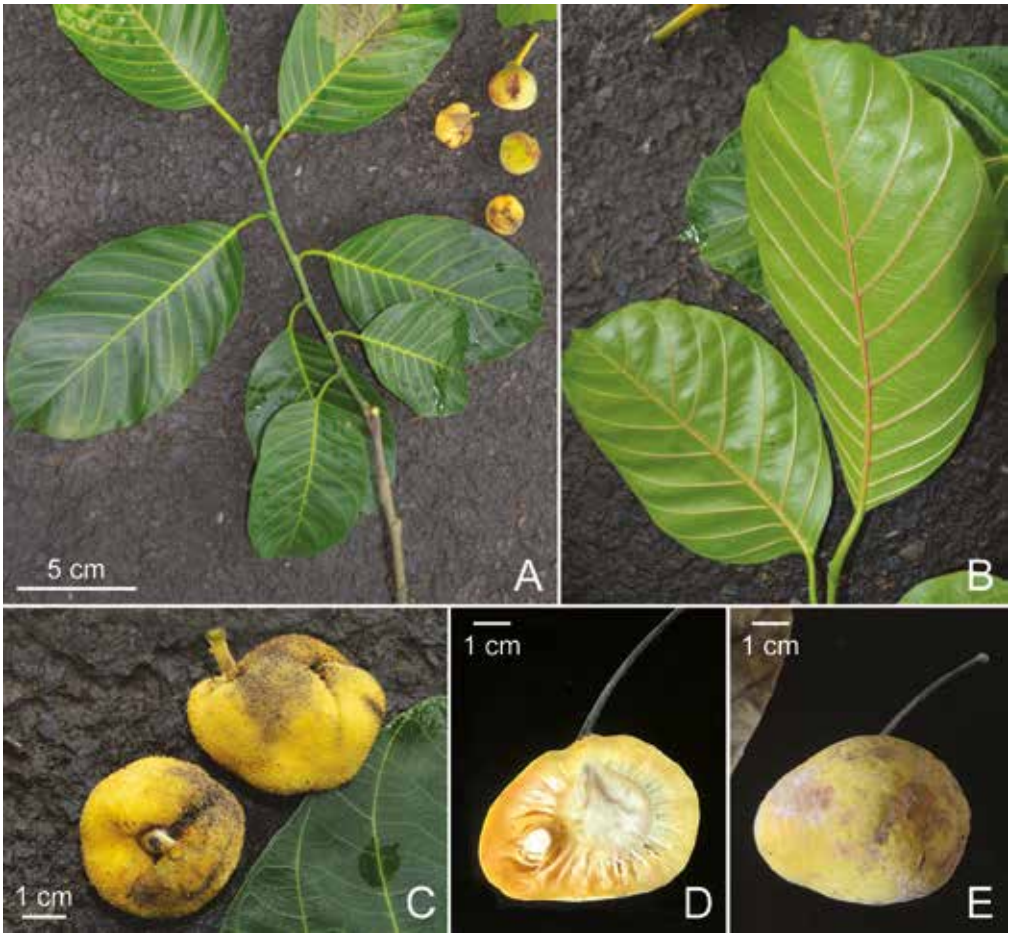

Fig. 14. *Artocarpus gomezianus* Wall. ex Trécul s.s. **A.** Leafy shoot. **B.** Abaxial leaf surface showing reddish venation. **C.** Staminate inflorescences. **D–E.** Syncarps. A–C from Kebun Raya Bogor & D–E from Peninsular Malaysia (Photos: A–C, E.M. Gardner; D–E, M.L. Chan).

3.2 *Artocarpus zeylanicus* (F.M.Jarrett) E.M.Gardner & Zerega, **stat. nov.** – *Artocarpus gomezianus* subsp. *zeylanicus* F.M.Jarrett, J. Arnold Arbor. 41: 90 (1960). – TYPE: India, [Karnataka], Madras [Presidency], Mangalore, March 1852, *R. Wight 2717* (holotype K [K000357625]; isotypes C n.v., GH [00035005], L [L0039889]). (Fig. 15)

Artocarpus bengalensis Roxb. ex Buch.-Ham., Journey Mysore 3: 205 (1807), nom. inval. Based on: India, Western Ghats, Cutaki, 9 March 1801, *F. Buchanan-Hamilton s.n.* (BM).

Artocarpus lakoocha auct. non Roxb.: Thwaites, Enum. Pl. Zeylan 262 (1861), as var. β. – *Artocarpus lakoocha* Roxb. var. β *gomezianus* auct. non (Wall ex Trécul) Trimen: Trimen, Handb. Fl. Ceylon 4: 99 (1898), as '*gomeziana*'. – Based on Sri Lanka, s.d., *G.H.K. Thwaites CP 2232* (BM, PDA [PDA00005813]) and *CP 2463* (K, PDA n.v.).

Fig. 15. *Artocarpus zeylanicus* (F.M.Jarrett) E.M.Gardner & Zerega. Pubescent form, matching the type. **A.** Bole; **B.** Leafy shoot with inset showing the staminate inflorescences; **C.** Syncarps. A–C from Sri Lanka, B from India. (Photos: A–C, Z. Jamil, B inset, S. Machado).

Diagnosis characters. Differs from *Artocarpus gomezianus* in the densely and softly whitish pubescent stipules, young twigs, and abaxial surface of the leaves, which are often ovate-attenuate. Differs from *Artocarpus lacucha* in the softer and whitish (rather than brown) pubescence, the entire margins of mature leaves, and smooth surface of the syncarps.

Distribution. Eastern India and Sri Lanka.

Notes. Much of the Sri Lankan material differs from the type in having subglabrous vegetative parts, making it difficult to distinguish from *Artocarpus gomezianus* and leading Jarrett (1960) to include *A. zeylanicus* in synonymy. The type, however, is clearly distinguishable and in many ways bears a stronger resemblance to *Artocarpus lacucha*. Determining the proper status of the subglabrous material requires further investigation, but for now it is maintained as part of *Artocarpus zeylanicus* following Jarrett's (1960) circumscription. The lack of reddish venation on the abaxial surface of the leaf, common in *Artocarpus gomezianus* but not mentioned on any specimen labels for subglabrous *A. zeylanicus*, may be a distinguishing character.

Had it been validly published, the legitimate name for *Artocarpus zeylanicus* would be *A. bengalensis* Roxb. ex Buch.-Ham.; however, the protologue is insufficient as it contains only the size and uses of the fruit, as well as a vernacular name (Mabberley, 1977). Some Hohenracker collections are labelled "*Artocarpus cuspidata* Miq. n. sp." This is not Griffith's *Artocarpus cuspidatus* (= *A. rigidus* Blume) but rather an apparently unpublished name that corresponds to *A. zeylanicus*.

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Appendix 1. Accessions used in this study, showing species (in bold), country, year collected, collector and collection number (in italics), standard acronym of the herbarium where the specimen is deposited and Genbank accession number. Asterisks placed after collection number denote samples newly prepared for this study. Reads for all samples have been deposited in GenBank under BioProject PRJNA322184.

***Artocarpus altissimus* (Miq.) J.J.Sm.,** Java (cult.), 2016, *Gardner et al. 441* (F), SRR12283100; Thailand, 2012, *Sinbu s.n.* (F), SRR12283081.

***Artocarpus borneensis* Merr.,** Borneo, 2013, *Zerega et al. 686* (F), SRR12283067; Borneo, 2005, *Yabainus SP 11399** (SNP), SRR12834862.

***Artocarpus dadah* Miq.,** Borneo, 1991, *Adriansyah AA W882* (L), SRR12283104; Borneo, 1991, *deWilde et al. 21278* (L), SRR12283013; Thailand, 1992, *Larsen et al. 42826** (MO), SRR12834861; Peninsular Malaysia, 2002, *Zerega et al. 245* (NY), SRR12283078; Borneo, 2013, *Zerega et al. 694* (F), SRR3907210; Borneo, 2013, *Zerega et al. 794* (F), SRR12283077; Borneo, 2013, *Zerega et al. 894* (F), SRR12283076; Borneo, 1990, *Sidiyasa 3465* (L), SRR12283011.

***Artocarpus elasticus* Reinw. ex. Blume,** Borneo, 2014, *Gardner et al. 87* (F), SRR3907457.

***Artocarpus fretessii* Teijsm. & Binn. ex Hassk. (*A. albobrunneus* C.C.Berg),** Borneo, 2000, *Adriansyah AA2243* (L), SRR12282906; Borneo, 2013, Zerega eta l. 929 (F), SRR3907410.

***Artocarpus fretessii* Teijsm. & Binn. ex Hassk.,** Sulawesi, 1990, *Burley et al. 4171* (L), SRR12283010; Philippines, 1992, *Barbon et al. PPI6044* (F), SRR12283009; Philippines, 1920, *Wenzel 811* (F), SRR12283008.

***Artocarpus fulvicortex* F.M.Jarrett,** Singapore, 2018, *Ibrahim et al. EG711** (SING), SRR12283090; Singapore, 2012, *Lee Y.Q. 35* (F), SRR12283075.

***Artocarpus glaucus* Blume**, Australia, 1979, *Dunlop 5189* (L), SRR12283007; Borneo, 2013, *Zerega et al. 852* (F), SRR12283074.

***Artocarpus gomezianus* Wall. ex Trécul,** Thailand, 2012, *Zerega et al. 533* (F), SRR12283072.

Artocarpus gongshanensis S.K.Wu ex. C.Y.Wu & S.S.Chang, China, 2005, *Gaoligong Shan Biodiversity Survey 24987* (HAST), SRR12283006.

***Artocarpus griffithii* (King) Merr.,** Sumatra, 2013, *Krukoff 4372* (US), SRR12282996; Peninsular Malaysia, 2002, *Zerega et al. 216* (F), SRR12283066.

***Artocarpus heterophyllus* Lam.,** Borneo (cult.), 2014, *Gardner et al. 98* (F), SRR3907497.

***Artocarpus humilis* Becc.,** Borneo, 2016, *Gardner et al. 258* (F), SRR12283050; Borneo, 2013, *Zerega et al. 834* (F), SRR12283065.

***Artocarpus hypargyreus* Hance ex. Benth.**, China, 2016, Gardner et al. 170 (F), SRR12283054; China, 1941, *Taam 2259* (US), SRR12282899.

***Artocarpus lacucha* Roxb. ex Buch.-Ham.**, China (cult.), 2012, *Hu J.-X. CAS7* (F), SRR12283070; Myanmar, 2006, *Fujikawa 35726* (MO), SRR12283002; Thailand, 2012, *Zerega et al. 420* (F), SRR3907082.

***Artocarpus lamellosus* Blanco,** Philippines, 1917, *Elmer 18279** (L), SRR12834860; Philippines, 1992, *Gaerlan et al. PPI10374* (F), SRR12282893.

***Artocarpus limpato* Miq.,** Borneo, 2013, *Zerega et al. 609* (F), SRR3907129.

Artocarpus longifolius Becc. subsp. **adpressus** C.C. Berg, Borneo, 2016, *Gardner & Zerega 412* (F), SRR12283094; Borneo, 1994, *Nangkat 15511* (L), SRR12282897.

***Artocarpus longifolius* Becc. subsp. *longifolius*,** Borneo, 1985, *Fidilis & Asik SAN110834* (L), SRR12282999.

Appendix 1. Continuation.

***Artocarpus nanchuanensis* S.S.Chang, S.C.Tan & Z.Y.Liu,** China, 2011, *Sirong Yi YISR20130717024** (KUN), SRR12283101.

***Artocarpus ovatus* Blanco**, Philippines, 1988, *Fernando* 786 (F), SRR12283045; USA (cult.), 2000, *Zerega 202* (F), SRR12283063.

***Artocarpus parvus* Gagnep.**, Borneo (cult.), 2013, *Zerega et al. 911* (F), SRR3907350; China, 1981, *Yip 283* (L), SRR12282994.

***Artocarpus petelotii* Gagnep.**, Vietnam, 2009, *Soejarto et al. DDS14435* (F), SRR12282891.

***Artocarpus pithecogallus* C.Y.Wu,** China, 2013, *Li Jianwu 3200* (KUN), SRR12282992.

***Artocarpus primackii* Kochummen,** Borneo, 2013, *Zerega et al. 687* (F), SRR3907189; Borneo, 2013, *Zerega et al. 924* (F), SRR12282991.

***Artocarpus rubrosoccatus* E.M.Gardner, Chaveer. & Zerega,** Thailand, 2012, *Zerega et al. 517* (F), SRR12283080.

***Artocarpus rubrovenius* Warb.,** Philippines, 1987, *Madulid et al. DAM6810* (F), SRR12283020; Philippines, 1987, *Burley 84* (F), SRR12282884.

***Artocarpus sepicanus* Diels,** Papua New Guinea, 2000, *Weiblen 1701* (MIN), SRR3907521.

***Artocarpus styracifolius* Pierre,** China, 2016, *Gardner et al. 176* (F), SRR12283038; Vietnam, 2006, *Loc NY-HN 611* (MO), SRR12282888.

***Artocarpus subrotundifolius* Elmer,** Philippines, 1915, *Wenzel 1576* (F), SRR12282887.

***Artocarpus thailandicus* C.C.Berg,** Thailand, 2012, *Zerega et al. 402* (F), SRR3907065.

***Artocarpus tomentosulus* F.M.Jarrett,** Borneo, 2013, *Zerega et al. 617* (F), SRR12283060.

***Artocarpus tonkinensis* A.Chev. ex. Gagnep.,** China (cult.), 2012, *Hu J.-X. CAS8* (F), SRR12283059; China, 2016, *Gardner et al. 174* (F), SRR12283037.

***Artocarpus vrieseanus* Miq. var. *papillosus* F.M.Jarrett,** Solomon Islands, 1930, *Kajewski 2360* (L), SRR12282983.

***Artocarpus vrieseanus* Miq. var. *refractus* (Becc.) F.M.Jarrett,** Papua New Guinea, 1940, *Clemens 11174** (US), SRR12834859; Papua New Guinea, 1954, *Hoogland 4822* (L), SRR12282981.

***Artocarpus vrieseanus* Miq. var. *subsessilis* F.M.Jarrett,** Papua New Guinea, 1953, *Brass 21660* (L), SRR12282982; Papua New Guinea, 1954, *Hoogland 4813* (L), SRR12282980.

***Artocarpus vriesianus* Miq. var. *vrieseanus*,** Moluccas, 2013, *Tjut Bangun et al. 684** (BO), SRR12834858; Papua New Guinea, 2000, *Weiblen 1229* (MIN), SRR12283057.

***Artocarpus xanthocarpus* Merr.,** Philippines, 1916, *Elmer 16247* (F), SRR12282885; Taiwan, 2003, *Yang 15648* (MO), SRR12283033.

***Artocarpus zeylanicus* (Jarrett) E.M.Gardner & Zerega,** India, 2013, *Zerega et al. 956* (CHIC, photo voucher), SRR12283117.

***Artocarpus sp.* aff. *borneensis*,** Borneo, 2016, *Gardner & Zerega 410* (F), SRR12283103.

***Artocarpus sp.* aff. *fretessii*,** Borneo, 1992, *Adriansyah AA440* (L), SRR12282988.

***Batocarpus costaricensis* Standl. & L.O.Williams,** Cost Rica, 2000, *Weiblen 1463* (MIN), SRR12283111.