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Taxonomic updates to *Artocarpus* subgenus *Artocarpus* (Moraceae) and allied taxa with a particular focus on the species native to Singapore

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ABSTRACT. The breadfruit genus *Artocarpus* J.R.Forst. & G.Forst. (Moraceae) has sixteen species in Singapore, fourteen of them native. In this precursory study to the treatment of *Artocarpus* for the *Flora of Singapore*, we present updated phylogenomic analyses of *Artocarpus* subgenus *Artocarpus* based on 517 nuclear genes. The following taxonomic changes based on recent phylogenetic analyses, review of herbarium specimens, and field observations, are proposed. *Artocarpus* subg. *Cauliflori* (F.M.Jarrett) Zerega is reduced to a section within *Artocarpus* subg. *Artocarpus*, and *Artocarpus* sect. *Glandulifolium* F.M.Jarrett is raised to subgenus status. The new monotypic subgenus *Artocarpus* subg. *Aenigma* E.M.Gardner & Zerega is proposed for *Artocarpus sepicanus* Diels, whose phylogenetic position remains uncertain and may be of ancient hybrid origin. *Artocarpus elasticus* Reinw. ex Blume, *A. scortechinii* King and *A. corneri* Kochummen are recognised as distinct species. *Artocarpus clementis* Merr. is reinstated as distinct from *A. lanceifolius* Roxb. *Artocarpus calophyllus* Kurz and *A. melinoxylus* Gagnep. are reinstated as distinct from both *A. chama* Buch.-Ham. and *A. rigidus* Blume. *Artocarpus nigrescens* Elmer is reinstated as distinct from *A. treculianus* Elmer. Keys to the subgenera, the sections of *Artocarpus* subg. *Artocarpus* and to the species found in Singapore are presented. A nomenclatural synopsis of subgenera *Artocarpus*, *Aenigma* and *Glandulifolium* is presented with taxonomic notes to aid in identification. Seventeen lectotypes, six of them in a second step, and two neotypes are designated.

Keywords. *Artocarpus clementis*, *Artocarpus corneri*, *Artocarpus elasticus*, *Artocarpus lanceifolius*, *Artocarpus scortechinii*, *Flora of Singapore*, typification

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). This is a precursory study for the *Artocarpus* treatment for the *Flora of Singapore* and a monograph of the genus.

Artocarpus was revised by Jarrett (1959a,b, 1960) with subsequent taxonomic work for the *Tree Flora of Malaya* and the *Tree Flora of Sabah and Sarawak* by Kochummen (1978, 2000) and for *Flora Malesiana and Flora of Thailand* by Berg et al. (2006, 2011). The subgenera were revised following a phylogenetic study by Zerega et al. (2010). Additional phylogenetic work has provided a molecular framework for taxonomic revisions (Williams et al., 2017; Gardner et al., 2021), several of which affect the Singapore species. Those pertaining to *Artocarpus* subg. *Pseudojaca* Trécul were proposed by Gardner & Zerega (2020a). This account focuses on the species of *Artocarpus* subg. *Artocarpus*, of which 12 species occur in Singapore.

Higher classification within *Artocarpus*

Under the most recent circumscription, *Artocarpus* contains four subgenera: *Artocarpus*, *Pseudojaca*, *Cauliflori* (F.M.Jarrett) Zerega and *Prainea* (King) Zerega, Supardi & T.J.Motley, distinguished on the basis of phyllotaxy and the degree of fusion between adjacent pistillate flowers (Zerega et al., 2010). Recent phylogenomic analyses based on 517 nuclear genes have provided strong support for backbone relationships within *Artocarpus* (Gardner et al., 2021). In most analyses, the subgenera were largely monophyletic, with two notable exceptions. *Artocarpus sepicanus* Diels (*Artocarpus* subg. *Artocarpus*) and *A. altissimus* (Miq.) J.J.Sm. (*Artocarpus* subg. *Pseudojaca*) usually formed a clade sister to subgenera *Artocarpus* + *Cauliflori*, although in some cases *A. sepicanus* has been sister to *Artocarpus* subg. *Pseudojaca*. Although *Artocarpus altissimus* shares distichous leaves and non-amplexicaul stipules with *Artocarpus* subg. *Pseudojaca*, it has bifid styles, a character not otherwise found in the subgenus but common in *Artocarpus* subg. *Artocarpus*. While *Artocarpus sepicanus* has amplexicaul stipules, resulting in its traditional placement in *Artocarpus* subg. *Artocarpus*, the exfoliating petiole epidermis is a character common in *Artocarpus* subg. *Pseudojaca* but nearly absent from *Artocarpus* subg. *Artocarpus* (but see *A. calophyllus* Kurz). *Artocarpus altissimus* was excluded from *Artocarpus* subg. *Pseudojaca* by Gardner & Zerega (2020a), but the appropriate positions of both species remain doubtful.

Artocarpus subg. *Artocarpus* as circumscribed by Jarrett (1959b, 1960) and as modified by Gardner et al. (2021) consists of two monophyletic sections: *Artocarpus* sect. *Duricarpus* F.M.Jarrett (with indurated perianth apices) and *Artocarpus* sect. *Artocarpus* (with non-indurated perianth apices). The series within these sections are not monophyletic but mostly correspond to clades that can be distinguished on the basis of morphology. Within *Artocarpus* sect. *Artocarpus*, the species of *Artocarpus* ser. *Rugosi* F.M.Jarrett mostly have pistillate flowers of dimorphic lengths and rugose to tuberculate staminate inflorescences. The species of *Artocarpus* ser. *Angusticarpus* F.M.Jarrett do not form a clade and reside within the *Rugosi* clade. *Artocarpus* ser. *Incisifolii* F.M.Jarrett consists of two clades, both mostly with pinnately-incised leaves

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* subg. *Artocarpus*.

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.	Made consistent with the other entries, in *A. lacucha* Roxb. ex Buch.-Ham.)
Artocarpus elasticus Reinw. ex Blume	In the strict sense, not including *A. corneri* Kochummen and *A. scortechinii* King
Artocarpus fulvicortex F.M.Jarrett	
Artocarpus gomezianus Wall. ex Trécul	
Artocarpus griffithii (King) Merr.	Included by Berg et al. (2006) in in *A. nitidus* Trécul
Artocarpus heterophyllus Lam.*	
Artocarpus hispidus F.M.Jarrett	
Artocarpus integer (Thunb.) Merr.	
Artocarpus kemando Miq.	In the strict sense, not including *A. maingayi* King
Artocarpus lanceifolius Roxb.	In the strict sense, not including *A. clementis* Merr.
Artocarpus lowii King	
Artocarpus rigidus Blume	
Artocarpus scortechinii King	Included by Berg et al. (2006) in *A. elasticus* Reinw. ex Blume

on mature trees; one clade is restricted to the Philippines, while the other extends from the Moluccas to the Pacific. A fourth clade consists solely of *Artocarpus montanus* E.M.Gardner & Zerega. Within *Artocarpus* sect. *Duricarpus*, *Artocarpus* ser. *Laevifolii* F.M.Jarrett and *Artocarpus* ser. *Asperifolii* F.M.Jarrett, with minor modifications as outlined in Gardner et al. (2021), correspond to clades distinguished by the strength of the leaf indumentum.

In this precursory study to the treatment of *Artocarpus* for the *Flora of Singapore*, we present updated phylogenomic analyses of *Artocarpus* subg. *Artocarpus* followed by taxonomic updates. We focus in particular on four taxa native to Singapore with problematic circumscriptions: *Artocarpus elasticus* Reinw. ex Blume (in the broad sense of Berg et al. (2006) including *A. corneri* Kochummen and *A. scortechinii* King),

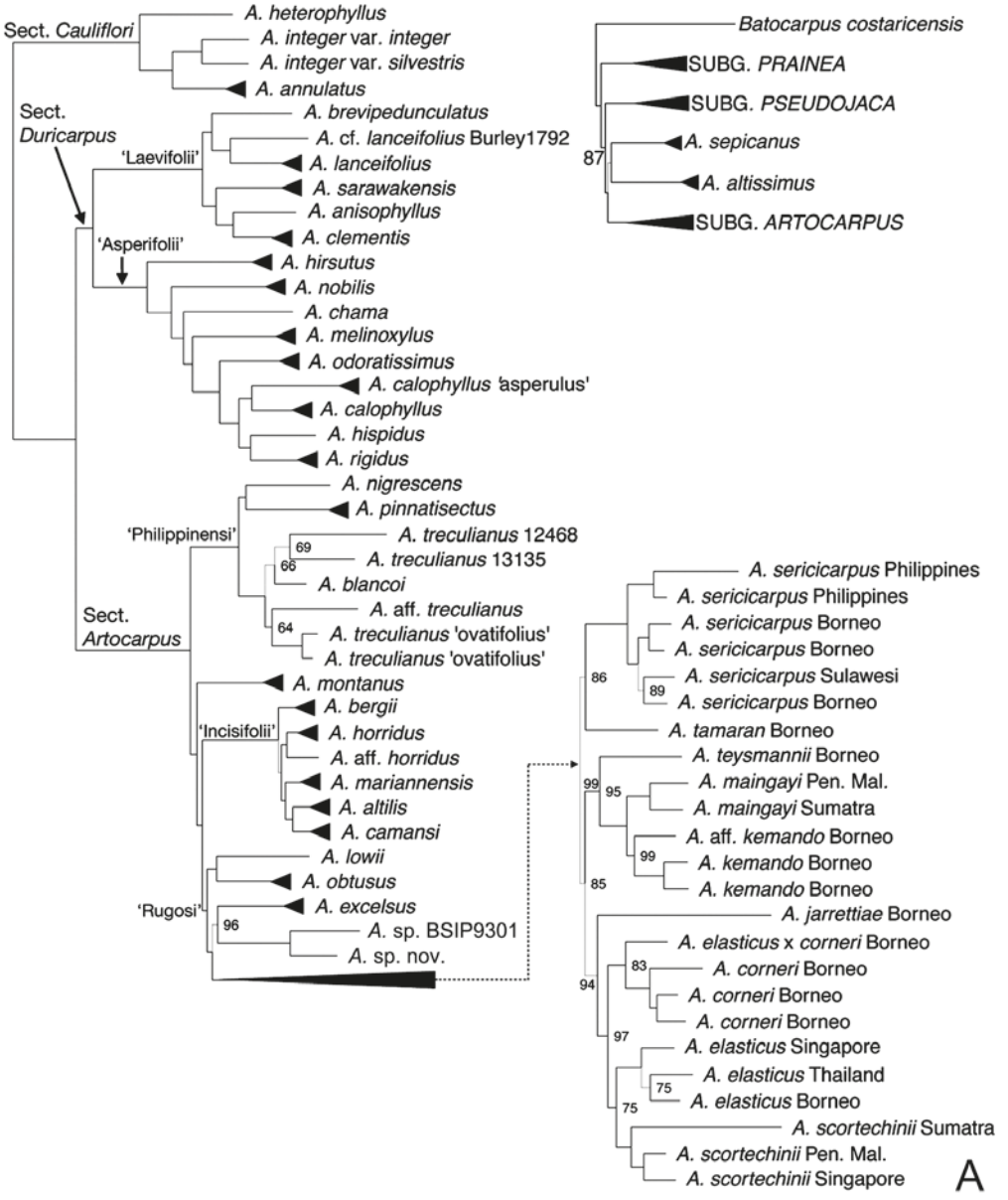

Fig. 1A. Phylogenetic tree based on a supermatrix of all exon sequences, with branch lengths proportional to substitutions. Nodes without labels have 100% bootstrap support. Monophyletic taxa have been collapsed for clarity, indicated by black triangles. Branches disagreeing with the ASTRAL species tree (Fig. 1B) appear in grey. Upper right inset shows the positions of the subgenera of *Artocarpus*, *A. sepicanus*, and *A. altissimus*.

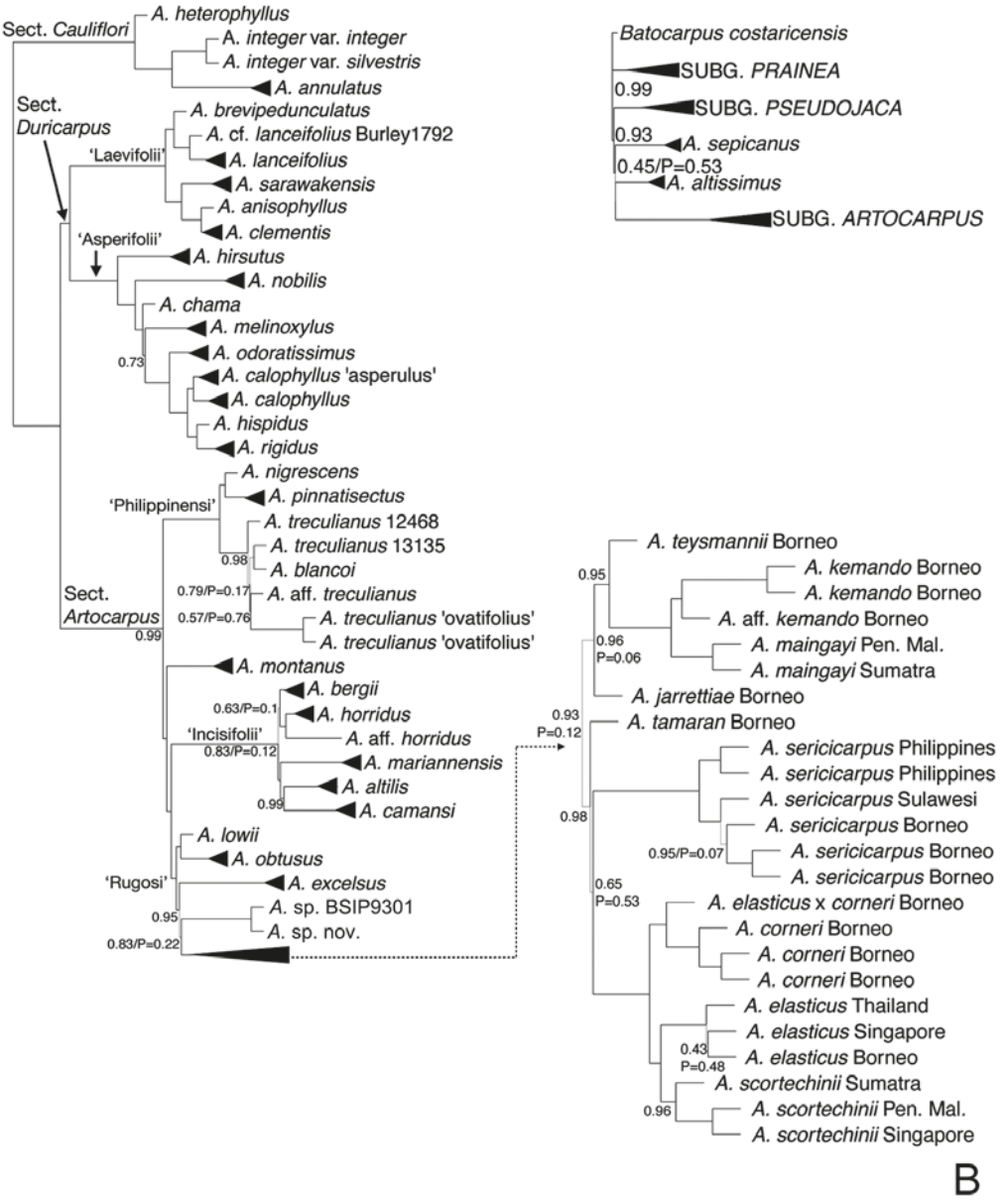

Fig. 1B. ASTRAL species tree based on gene trees for all exon sequences, with branch lengths proportional to coalescent units. Nodes without labels have local posterior probability of 1.0 and $P < 0.05$ (indicating rejection of the polytomy hypothesis). Monophyletic taxa have been collapsed for clarity, indicated by black triangles. Branches disagreeing with the supermatrix tree (Fig. 1A) appear in grey. Upper right inset shows the positions of the subgenera of *Artocarpus*, *A. sepicanus*, and *A. altissimus*.

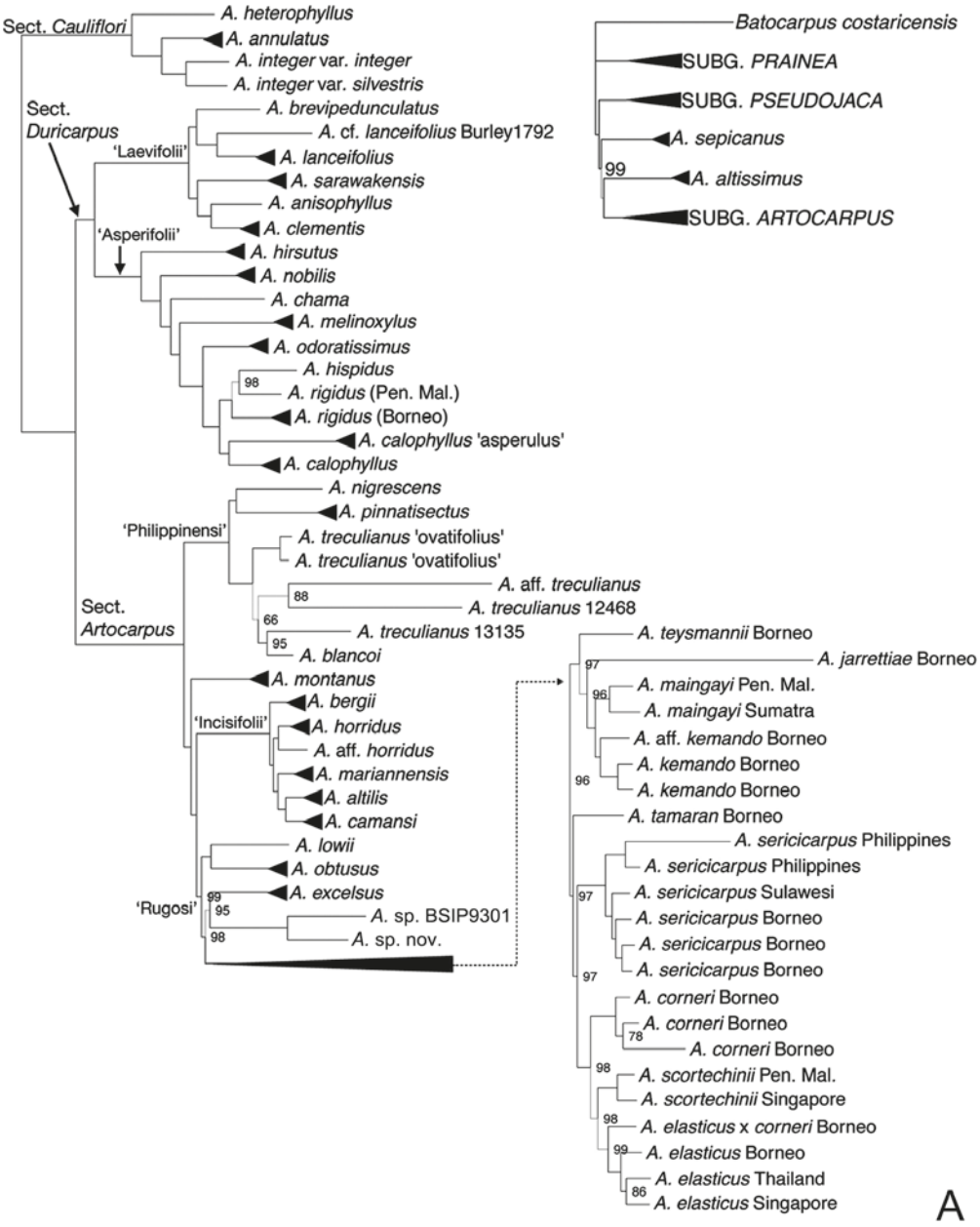

Fig. 2A. Phylogenetic tree based on a supermatrix of all "supercontig" sequences (exons and flanking noncoding sequences), with branch lengths proportional to substitutions. Nodes without labels have 100% bootstrap support. Monophyletic taxa have been collapsed for clarity, indicated by black triangles. Branches disagreeing with the ASTRAL species tree (Fig. 1B) appear in grey. Upper right inset shows the positions of the subgenera of *Artocarpus*, *A. sepicanus*, and *A. altissimus*.

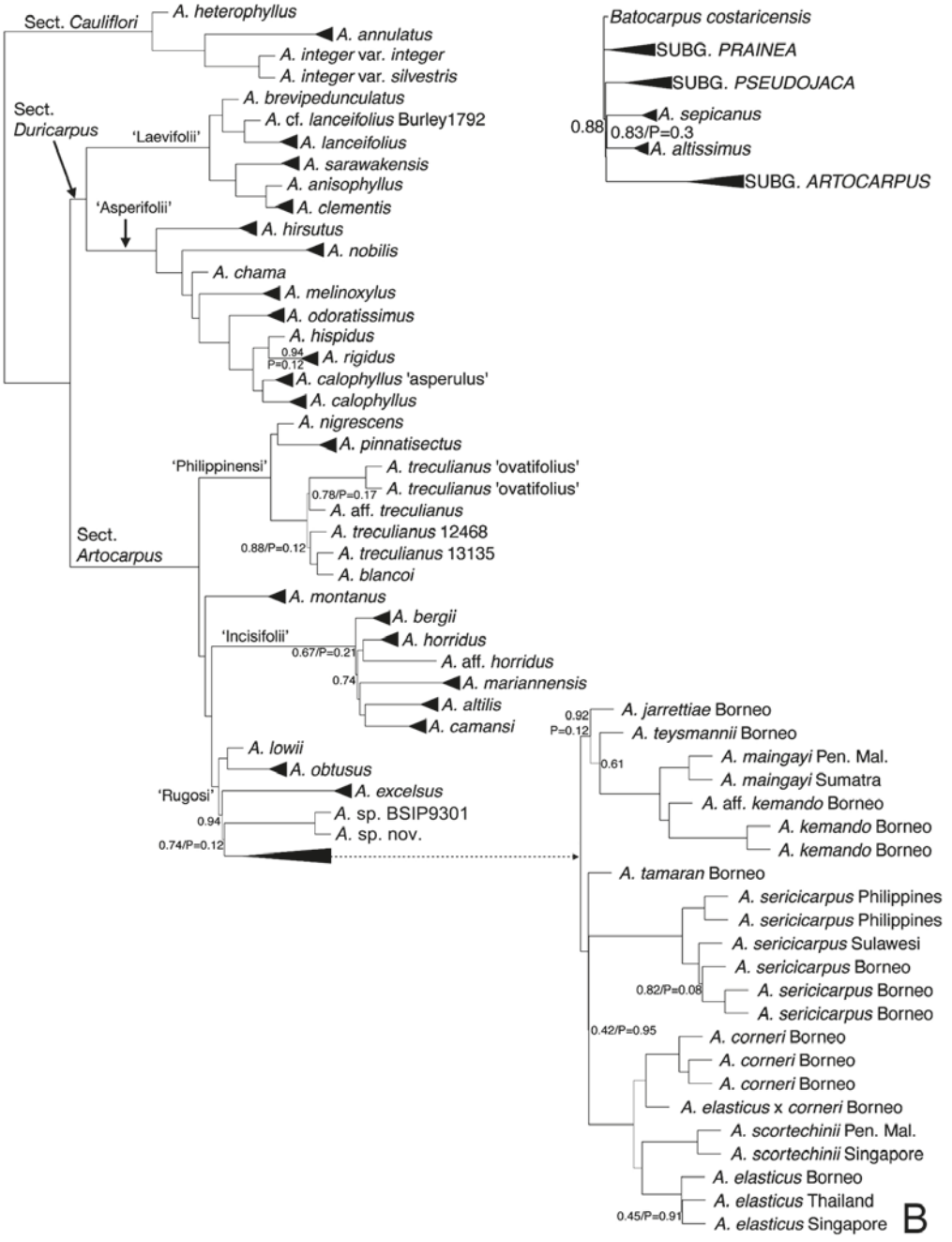

Fig. 2B. ASTRAL species tree based on gene trees for all "supercontig" sequences (exons and flanking noncoding sequences), with branch lengths proportional to coalescent units. Nodes without labels have local posterior probability of 1.0 and $P < 0.05$ (indicating rejection of the polytomy hypothesis). Monophyletic taxa have been collapsed for clarity, indicated by black triangles. Branches disagreeing with the supermatrix tree (Fig. 1A) appear in grey. Upper right inset shows the positions of the subgenera of *Artocarpus*, *A. sepicanus*, and *A. altissimus*.

A. kemando Miq. (including *A. maingayi* King and *A. sumatranus* F.M.Jarrett), *A. lanceifolius* Roxb. (including *A. clementis* Merr.) and *A. rigidus* Blume (including, in the broad sense of Jarrett (1959b), *A. asperulus* Gagnep. and *A. calophyllus* Kurz). We also clarify the circumscriptions of some Philippine-endemic taxa currently in the process of being assessed for the IUCN Red List of Threatened Species. Revisions presented here are based on phylogenetic results as well as a review of specimens at BKF, BM, F, IBSC, K, L, MO, SAN, SAR, SING, SNP and US, and images of specimens from CAL, FI, KUN, P and PE.

Phylogenetic methods and results

For phylogenomic reconstruction, we employed target enrichment (HybSeq) to capture 517 nuclear genes developed by Gardner et al. (2016). Due to the uncertainty in the positions of *Artocarpus jarrettiae* Kochummen and *A. sepicanus*, four phylogenomic analyses were performed using both coding and non-coding sequences and under two different analysis methods. The exon and 'supercontig' (exon + noncoding sequences) data sets described by Gardner et al. (2021) were augmented with 12 additional samples, including replication for select species and geographically expanded sampling for *Artocarpus elasticus* and *A. scortechinii.* The samples included one putative hybrid between *Artocarpus elasticus* and *A. corneri*, *E. Gardner et al. 336* (F, SAR). Library preparation, target enrichment, sequencing, and assembly with HybPiper (Johnson et al., 2016) followed the same methods used in that study, and the additional sequences were added to a subset of the sequences from the same study (Appendix 1). This data set contained all species in subgenera *Artocarpus* and *Cauliflori*, *Artocarpus altissimus* (with most species replicated), one sample per species from subgenera *Pseudojaca* and *Prainea*, and the outgroup *Batocarpus costaricensis* Standl. & L.O.Williams (Neotropical Artocarpeae).

For each gene in both the exon and 'supercontig' data sets, sequences were filtered to remove those whose length was less than 100 bp or 20% of the average length of that gene, and samples with less than 50 genes remaining after filtering were discarded. Filtered sequences were aligned with MAFFT 7.450 (Katoh & Standley, 2013), sites with over 75% gaps were removed using TrimAl (Capella-Gutiérrez et al., 2009), and for samples that were over 100 years old or had fewer than 300 assembled genes, poorly aligned termini were removed using HerbChomper 0.3 (Gardner, 2020). An initial set of gene trees was estimated using FastTree 2.1.10 (Price et al., 2009), and sequences corresponding to outlier branches were removed from the alignments using TreeShrink in 'all-genes' mode. Gene trees were generated using IQTree 2.0.3 (Nguyen et al., 2015) under the best-fit model for each gene as determined by Bayesian Information Criterion, and node support was calculated using 1000 ultrafast bootstrap replicates. After collapsing nodes with less than 30% support using TreeCollapseCL 3.0 (Hodcroft, 2013), the gene trees were used to estimate a species tree using ASTRAL-III 5.7.1 (Zhang et al., 2018) ('*exon-ASTRAL*' and '*supercontig-ASTRAL*'). Node support was estimated using local posterior probability (LPP), a metric based on quartet scores

that represents gene tree concordance. We also carried out a polytomy test in ASTRAL (-t 10) to investigate whether the polytomy hypothesis could be rejected for each node. Finally, a maximum-likelihood tree was inferred from a partitioned concatenated supermatrix of all loci using IQTree, under the best-fit model for each gene ('*exon-supermatrix*' and '*supercontig-supermatrix*').

The phylogenetic analyses (Fig. 1, 2) generally agreed with those of Gardner et al. (2021). *Artocarpus sepicanus* fell near *Artocarpus* subg. *Artocarpus* in all analyses. In two analyses (*exon-ASTRAL* and *supercontig-supermatrix*), *A. sepicanus* and *A. altissimus* formed a clade, which in turn was sister to *Artocarpus* subg. *Cauliflori* and the rest of *Artocarpus* subg. *Artocarpus*; however, the polytomy hypothesis for the sister relationship of *A. sepicanus* and *A. altissimus* could not be rejected (P = 0.2969). In the other two analyses (*exon-supermatrix* and *supercontig-ASTRAL*), it was sister to *A. altissimus* + *Artocarpus* subg. *Cauliflori* + the rest of *Artocarpus* subg. *Artocarpus*; however, the polytomy hypothesis for the position of *A. altissimus* as sister to *Artocarpus* subg. *Cauliflori* and *Artocarpus* not including *A. sepicanus* could not be rejected (P = 0.5318).

Augmented sampling revealed that although *Artocarpus elasticus* s.l. was monophyletic, relationships within that clade reflected the three-species concept rather than geography; for example, *A. elasticus* samples from Singapore, Borneo and Thailand formed a clade, as did *A. scortechinii* samples from Singapore, Sumatra and Peninsular Malaysia—even though the Singapore samples of *A. elasticus* and *A. scortechinii* were collected at the same locality. By contrast, the sister clade of *Artocarpus sericicarpus* F.M.Jarrett showed geographic structure. *Artocarpus kemando* s.l. was monophyletic; the two samples of *A. kemando* s.s. (both from Borneo) formed a clade sister to *Ambriansyah AA2766* (Borneo; identified by Gardner et al. (2021) as *A. sumatranus* but reconsidered below). The two samples of *Artocarpus maingayi* (Peninsular Malaysia and Sumatra) formed a clade sister to those three samples. The position of *Artocarpus jarrettiae* was unstable. In the *exon-supermatrix* analysis, it was sister to *Artocarpus elasticus* s.l. with high bootstrap support (94%), while in the *supercontig-supermatrix* analysis, it was sister to *A. kemando* s.l. with high bootstrap support (96%). In both ASTRAL analyses, *Artocarpus jarrettiae* was sister to *A. teysmannii* Miq. + *A. kemando* s.l.; however, the polytomy hypothesis could not be rejected in either analysis (*exon-ASTRAL*: P = 0.063; *supercontig-ASTRAL*: P = 0.1162).

Although the polytomy hypothesis was rejected for its placement, results were consistent with a hybrid origin for *E. Gardner et al. 336*, which was allied to *Artocarpus elasticus* s.s. and *A. corneri* with nearly equal frequency in the gene trees. It was closest to *Artocarpus elasticus* s.s. in 36.9% (*exon* data set) or 39.2% (*supercontig* data set) of gene trees and *A. corneri* in 37.5% (*exon*) or 38.6% (*supercontig*) of gene trees.

In all analyses, *Artocarpus rigidus* s.l. was paraphyletic, with *A. hispidus* F.M. Jarrett completing the clade. *Artocarpus lanceifolius* was also not monophyletic, with *A. lanceifolius* subsp. *clementis* (Merr.) F.M.Jarrett and *A. anisophyllus* Miq. forming a clade and *A. lanceifolius* subsp. *lanceifolius* forming a clade with *A. brevipedunculatus* (F.M.Jarrett) C.C.Berg. In one analysis (*supercontig-supermatrix*), *Artocarpus hispidus* was nested within *A. rigidus* s.s.

As in Gardner et al. (2021), *Artocarpus treculianus* Elmer was not monophyletic; *A. nigrescens* Elmer, included in *A. treculianus* in Berg et al. (2006), was sister to *A. multifidus* F.M.Jarrett and *A. pinnatisectus* Merr. in all analyses. While its exact position varied, the single sample of *Artocarpus blancoi* (Elmer) Merr. was nested within the *A. treculianus* clade in all analyses. *Artocarpus multifidus* was also not monophyletic, as the type of *A. pinnatisectus* was nested within it in all analyses.

Taxonomic discussion

Artocarpus sepicanus and *A. altissimus*

The position of *Artocarpus sepicanus* has varied in past analyses (Williams et al., 2017; Kates et al., 2018; Gardner et al., 2021). Here, the polytomy hypothesis could not be rejected for its exact placement despite the employment of 517 loci and triplicate sampling for that species as well as its sometimes-closest ally, *Artocarpus altissimus*. For now, this appears to be a 'hard' polytomy, perhaps reflecting reticulation in the lineage of *Artocarpus sepicanus*, although further investigation is certainly warranted. Despite its spiral leaf arrangement, which fits well within *Artocarpus* subg. *Artocarpus*, *A. sepicanus* also has some affinities with *Artocarpus* subg. *Pseudojaca*, to which it was sister in some analyses in Kates et al. (2018). *Artocarpus sepicanus* has exfoliating petiole epidermis, a character present in some species of *Artocarpus* subg. *Pseudojaca* but nearly absent from *Artocarpus* subg. *Artocarpus*. In addition, the perianth apices are barely free, and the seeds are unusually small (< 5 mm) for a member *Artocarpus* subg. *Artocarpus*. Maintaining the traditional placement of *Artocarpus sepicanus* within *Artocarpus* subg. *Artocarpus* would require the inclusion of *A. altissimus* in that subgenus, a problematic idea as *A. altissimus* lacks the two consistent synapomorphies of *Artocarpus* subg. *Artocarpus*: free perianth apices and spirally-arranged leaves with fully-amplexicaul stipules. Although some members of *Artocarpus* subg. *Artocarpus* have barely-free apices (e.g., *A. altilis*), the edges of the apices are never connate; likewise, within *Artocarpus* subg. *Pseudojaca*, even though some species may have protrusions from the centres of the perianth apices (e.g., *Artocarpus reticulatus* Miq. and *A. rubrosoccatus* E.M.Gardner et al.), the edges of the latter are always connate. By the same token, *Artocarpus altissimus* diverges from *Artocarpus* subg. *Pseudojaca* in its bifid styles, not present in any other species of *Artocarpus* subg. *Pseudojaca*, and its glandular-crenate leaf margins, unique within the genus. In light of the uncertain phylogenetic position, intermediate morphology, and possible hybrid origin of *Artocarpus sepicanus*, we therefore place it into a new monotypic subgenus, styled here *Artocarpus* subg. *Aenigma* E.M.Gardner & Zerega. We likewise raise the monotypic *Artocarpus* subg. *Pseudojaca* sect. *Glandulifolium* F.M.Jarrett (*A. altissimus*) to subgenus level.

In light of these changes, the primary feature distinguishing *Artocarpus* subg. *Cauliflori*, the cauliflorous or ramiflorous position of the inflorescence-bearing shoots, no longer warrants subgenus-level status, especially in light of its consistent position as sister to *Artocarpus* subg. *Artocarpus* in all phylogenomic analyses (Johnson et al.,

2016; Kates et al., 2018; Gardner et al., 2021). We further note that Jarrett (1959b) included the *Cauliflori* species as a series within *Artocarpus* sect. *Artocarpus* based on their spiral leaf arrangement (*Artocarpus* subg. *Artocarpus*) and flexuous (rather than indurated) apices of the pistillate flowers (*Artocarpus* sect. *Artocarpus*). This morphology and the position of *Artocarpus* subg. *Cauliflori* in our phylogenetic analyses are compatible with its reduction to a section within *Artocarpus* subg. *Artocarpus*.

***Artocarpus elasticus* s.l.**

Artocarpus elasticus (widespread from Thailand to Borneo and Java), *A. scortechinii* (Malay Peninsula and Sumatra) and *A. corneri* (Borneo) form a complex of species that were treated as informal forms under a broadly-circumscribed *A. elasticus* by Berg et al. (2006). *Artocarpus scortechinii* and *A. corneri*, while less widespread than *A. elasticus* s.s., appear to be more than mere geographic variants as they grow in sympatry with *A. elasticus* s.s., and phylogenetic results as well as morphology reflect the three-species concept rather than geography. *Artocarpus elasticus* s.s. has dimorphic pistillate flowers (long sterile ones and short fertile ones) and wavy leaves with a rough hispidulous upper surface. *Artocarpus scortechinii* (sympatric with *A. elasticus*) lacks dimorphic pistillate flowers and has flatter, narrower leaves with a smooth upper surface. *Artocarpus corneri* (sympatric with *A. elasticus* but not with *A. scortechinii*) lacks long sterile pistillate flowers (although in some cases a few are thickened rather than elongate) and has flatter leaves than *A. elasticus* with a much sparser indumentum, although the lower surface may be softly pubescent at lower elevations. These morphological differences are great enough that *Artocarpus elasticus* trees can be distinguished from their two sympatric close allies at a fair distance. In light of the phylogenetic and morphological distinctiveness of these three entities, we recognise them as distinct taxa following Kochummen (2000) rather than as informal entities following Berg et al. (2006). Because *Artocarpus elasticus* is consistently distinguishable from and grows in sympatry with *A. corneri* and *A. scortechinii*, we consider any rank below that of species unwarranted. The existence of an apparent natural hybrid (*E. Gardner et al. 336*) between *Artocarpus elasticus* and *A. corneri* is noteworthy and worthy of further investigation and complements Jarrett's (1959b) documentation of an apparent hybrid between *A. elasticus* and *A. scortechinii*. However, the possibility of hybridisation alone is not a reason to combine otherwise distinct taxa. Hybridisation is already well-known in the breadfruit clade between *Artocarpus altilis* and *A. mariannensis* Trécul. (Fosberg, 1960; Zerega et al., 2005), and investigation is currently underway into apparent hybridisation in other clades of *Artocarpus*.

***Artocarpus kemando* s.l.**

Berg et al. (2006) recognised a broad *Artocarpus kemando* and included *A. maingayi* King and *A. sumatranus* in synonomy. *Artocarpus kemando* (Borneo and southern/eastern Malay Peninsula and Sumatra) and *A. maingayi* (northern/western Malay Peninsula and Sumatra) are essentially geographic variants with little range overlap

(perhaps in Johor and Peninsular Thailand), the latter distinguished primarily by its much shorter peduncle (3–8 mm in *A. maingayi* vs. 15–40 mm long in *A. kemando*), the more flattened aspect of the pistillate perianth apices, and in much of its distribution, the rounded leaf apices. Their affinity has long been recognised; Beccari (1902) treated them as a single taxon, and Corner (1940) suggested that *Artocarpus maingayi* might be reduced to a variety. However, Berg et al. (2006), despite treating these names as synonymous, noted the near-absence of intermediate forms when considering the peduncle length. The rarely-collected *Artocarpus sumatranus* is distinguishable from *A. kemando* only by its generally larger parts and somewhat longer apices of the conical pistillate perianths. Phylogenomic analyses have supported the monophyly of a broad *Artocarpus kemando*, with sub-clades compatible with the three-species concept (Gardner et al., 2021). However, closer examination of the only specimen identified in these studies as *Artocarpus sumatranus*, *Ambriansyah AA2766* (Indonesia, Central Kalimantan, 30 March 2004, K, L [L.1583716]), has revealed that it does not match the type; indeed, it differs from all of the species included in *Artocarpus kemando* s.l. in its bifid styles, fluted pistillate perianths, and retuse leaf apices. Collected in a peat swamp forest, it matches other collections from peat swamp forests in Borneo (Agusti Randi, pers. comm.) and appears to be a distinct undescribed taxon. Because *Ambriansyah AA2766* was sister to *Artocarpus kemando* s.s. in our phylogenetic analyses as well as in Gardner et al. (2021), recognising it as a distinct entity would require doing the same for *A. maingayi*. Despite the closeness of *Artocarpus kemando* and *A. maingayi*, they are easily distinguishable when fertile, and we therefore maintain Jarrett's (1959b) treatment of them as separate species pending further study of *Ambriansyah AA2766* and the resolution of its status. However, we maintain *Artocarpus sumatranus* as a synonym of *A. kemando* in light of the minor characters distinguishing the type of that species and the absence of phylogenetic evidence requiring a different approach.

Artocarpus jarrettiae

Artocarpus jarrettiae is an enigmatic species collected perhaps only once and included in the synonymy of *A. elasticus* by Berg et al. (2006). Its vegetative and reproductive characters are intermediate between *Artocarpus elasticus* and *A. kemando*, and its placement in phylogenomic analyses (based on the type specimen) has been similarly equivocal (Gardner et al., 2021), raising the possibility that it is of hybrid origin. Here, its alliance (*Artocarpus kemando* s.l. or *A. elasticus* s.l.) shifted depending on the analysis employed, and the polytomy hypothesis could not be rejected. In light of this evidence, it cannot be maintained in the synonymy of *Artocarpus elasticus*.

***Artocarpus lanceifolius* s.l.**

Artocarpus lanceifolius in Roxburgh's original sense was described from Penang and can be found from Peninsular Thailand to Sumatra including Singapore, and perhaps in Batang Ai in Sarawak. Jarrett (1959b) reduced *Artocarpus clementis* to *A. lanceifolius* subsp. *clementis*. The latter differs primarily in having generally smaller parts, infructescences with persistent interfloral bracts, and leaves on juvenile trees that are dissected all the way to the midrib, appearing almost compound and somewhat

resembling the mature leaves of the allied *Artocarpus anisophyllus*. Phylogenetic analyses do not support the monophyly of a broadly circumscribed *Artocarpus lanceifolius* that would include *A. clementis,* the latter being more closely allied to *A. anisophyllus*. Restricted to Borneo, *Artocarpus clementis* has strongly-scented inflorescences with short stamens and deflexed simple styles, in marked contrast to *A. lanceifolius* (now corresponding only to Jarrett's subsp. *lanceifolius*), which has unscented inflorescences with larger stamens and long, bifid styles. Although further study is warranted, it therefore appears likely that *Artocarpus clementis* is insect pollinated while *A. lanceifolius* is wind pollinated. Sterile specimens can be usually distinguished from one another by the substantially smaller leaves of *Artocarpus clementis*. The affinity of *Artocarpus clementis* to *A. anisophyllus* is apparent in the striking resemblance of their juvenile leaves, which appear compound because the lamina is incised all the way to the midrib. Leaves on juvenile *Artocarpus lanceifolius* may be pinnately incised, but generally not all the way to the midrib. The similarity of the fruity inflorescence odours of *Artocarpus clementis* and *A. anisophyllus* is also noteworthy. The morphological and phylogenetic distinctiveness of *Artocarpus clementis* therefore counsels in favour of its recognition as a species. Moreover, making the broad *Artocarpus lanceifolius* monophyletic would require the absurdity of subsuming all members of this morphologically diverse clade, including the very distinctive *Artocarpus anisophyllus*, *A. brevipedunculatus* and *A. sarawakensis* F.M.Jarrett, into a single species.

***Artocarpus rigidus* s.l. and *A. chama* s.l.**

Authorities have likewise disagreed as to the proper circumscription of *Artocarpus rigidus*. Plants matching the type from Sumatra can be found from Peninsular Thailand to Java and Borneo, including Singapore. Jarrett (1959b) reduced two species from continental Southeast Asia, *Artocarpus asperulus* and *A. calophyllus* to *A. rigidus* subsp. *asperulus* (Gagnep.) F.M.Jarrett. This resembles *Artocarpus rigidus* s.s. but has a stronger indumentum than *A. rigidus.* Additionally, *Artocarpus calophyllus* s.s. typically has a longer peduncle (10–50 mm in *A. calophyllus* s.s. compared to 0.3–20 mm in *A. rigidus* s.s. and *A. asperulus* s.s.) and longer pistillate perianth apices (6–10 mm in *A. calophyllus* s.s. compared to 3–8 mm in *A. rigidus* s.s. and *A. asperulus* s.s.). Kochummen (1978) proposed also reducing *Artocarpus hispidus* to subordinate status under *A. rigidus,* reasoning that the differences between those two species (in indumentum, leaf shape and peduncle length) were not greater than those between *A. rigidus* and *A. asperulus*. Berg in the *Flora Malesiana* treatment restricted *Artocarpus rigidus* to its original circumscription and subsequently in the *Flora of Thailand* transferred *A. asperulus* and *A. calophyllus* to the synonomy of the Indian species *A. chama* Buch.-Ham., albeit with some hesitation, recognising four informal forms within the latter, including 'asperulus' and 'calophyllus' forms (Berg et al., 2006, 2011). Phylogenomic analyses here and in Gardner et al. (2021) support Kochummen's hypothesis that a broad *Artocarpus rigidus* that includes *A. asperulus* must also include *A. hispidus*; these analyses also supported the validity of *A. calophyllus* and *A. asperulus* as distinct entities, as proposed by Berg. Our

phylogenetic analyses do not support the broad and morphologically heterogeneous *Artocarpus chama* proposed by Berg, supporting instead Jarrett's (1959b) restriction of that species to the form found in India and Bangladesh with pubescent leaves and short, blunt pistillate perianth apices, and her corresponding recognition of the Vietnamese *A. melinoxylus* Gagnep., with its subglabrous upper leaf surface, at species level. The existence in sympatry of *Artocarpus rigidus* s.s. and *A. hispidus* in Singapore and Peninsular Malaysia also counsels against recognising a broadened *A. rigidus*, as does their phylogenetic distinctness in most analyses, and maintaining separate species is therefore the best course of action. Because the boundary between *Artocarpus calophyllus* and *A. asperulus* appears to be fluid based on our review of specimens, we prefer for now to keep them as a single entity, although it is likely that additional investigation may warrant the recognition of distinct taxa, if not at species level then perhaps as subspecies.

Artocarpus altilis and the Philippine-endemic species

Finally, disagreements over species limits have confused the circumscription of *Artocarpus altilis* (= *A. communis* J.R.Forst & G.Forst.). The narrowest circumscription recognises *Artocarpus altilis* as applying only to the few-seeded to seedless cultivated breadfruit; this approach has support from population-genetic analyses and has been favoured by breadfruit specialists and the horticultural community (Zerega et al., 2005, 2015). It also closely tracks the species recognised by Rumphius, who recognised 'Soccus lanosus' (= *Artocarpus altilis*), 'Soccus granosus' (= *A. camansi* Blanco), and two taxa within 'Soccus silvestris' corresponding to *A. horridus* F.M.Jarrett. An intermediate approach taken by Jarrett (1959b) includes the wild relatives *Artocarpus camansi* and *A. mariannensis* Trécul within *A. altilis* (as *A. communis*) but recognises *A. horridus* (including *A. bergii* E.M.Gardner et al.) as separate. Fosberg (1960) subsequently maintained *Artocarpus camansi* in the synonomy of *A. altilis* but recognised the Micronesian *A. mariannensis* as distinct. The broadest approach, proposed by Berg et al. (2006), has all of the above-mentioned taxa as well as nearly all of the Philippine-endemic members of *Artocarpus* subg. *Artocarpus* (*A. blancoi*, *A. multifidus*, *A. pinnatisectus*) subsumed under *A. altilis*. The broadest circumscription is not compatible with phylogenetic evidence, as the Philippine species form their own clade. Leaving aside the Philippine species and the paraphyly of Jarrett's circumscription of *Artocarpus horridus* in some analyses, phylogenetic evidence is compatible with all of these approaches. Reasonable arguments might be made for any of these circumscriptions or even for the recognition of subspecies. In particular, *Artocarpus altilis* and *A. camansi* might easily be combined as the former has been considered a domesticated version of the latter (Zerega et al., 2005). However, further investigation is required as phylogenomic analyses have thus far shown these taxa to form reciprocally monophyletic clades (Audi, 2018; Gardner et al., 2021) in contrast to domesticated systems such as *Zea mays* L., in which the wild members of the species form a paraphyletic grade (Matsuoka et al., 2002). Given the widespread use of the narrow approach in the breadfruit research and growing community, we choose to

maintain *Artocarpus altilis*, *A. camansi* and *A. mariannensis* as distinct species unless and until further evidence requires a different treatment.

Within the Philippine clade, *Artocarpus multifidus* and *A. pinnatisectus* do not appear to be distinct, either in a phylogenetic or morphological sense (discussed further under *A. pinnatisectus* below) and should be treated as a single entity. The *Artocarpus treculianus* complex also requires re-evaluation. While it is clear that *Artocarpus nigrescens* should be recognised as a distinct species, both on the basis of its phylogenetic position as well as its striking coal-black syncarps, the proper boundaries between *A. treculianus* s.s., *A. ovatifolius* Merr. (included in *A. treculianus*), *A. blancoi*, and a possible undescribed entity from the northern Philippines, require further study. While the types of *Artocarpus treculianus* and *A. ovatifolius* are distinct from one another, intermediate forms abound, and our present inability to draw a clear line between them counsels against premature splitting. Likewise, *Artocarpus blancoi* is so distinct from *A. treculianus* in both reproductive and vegetative characters that combining them on the basis of the sparse sampling employed here (two samples of *A. treculianus* s.s. and one of *A. blancoi*, all over 100 years old) would be too precipitous. We hope that further study will further clarify the species limits of the Philippine clade.

Taxonomic and nomenclatural synopsis

Below we present a key to the sections of *Artocarpus* subg. *Artocarpus*, and a set of informal clade names roughly corresponding to Jarrett's series, summarised in Table 2. Because the revisions proposed here affect so many taxa, below we provide a nomenclatural synopsis of all species in *Artocarpus* subg. *Artocarpus*, with taxonomic notes including key characters to aid in rapid identification of species. We also provide diagnostic spot characters that in combination with geography will aid in field identification. Complete citation histories may be found in Jarrett (1959b) and Berg et al. (2006, 2011). Jarrett took a broader view of holotypes than the present Code, we therefore interpret most of her 'holotype' citations as effective lectotypifications under Art. 9.10 of the Shenzhen Code (Turland et al., 2018). Lectotypes are designated for *Artocarpus brasiliensis* Gomes, *A. chama* Buch.-Ham., *A. hirsutus* Lam., *A. incisifolius* Stokes var. *seminiferus* Stokes, *A. incisus* L.f. var. *non-seminiferus* Duss, *A. klidang* Boerl., *A. kunstleri* King, *A. lanceifolius* Roxb., *A. maingayi* King, *A. scortechinii* King, and *A. champeden* Lour. Second-step lectotypes are designated for *Artocarpus blumei* Trécul, *A. chaplasha* Roxb., *A. heterophyllus* Lam., *A. lowii* King, *A. papuanus* Diels, and *A. philippensis* Lam. Neotypes are designated for *Artocarpus maximus* Blanco and *A. reticulatus* W.Hunter.

Table 2. Summary of the infrageneric taxa and informally-named clades treated here.

Taxonomic level	Key characters	Species	Geographic range
SUBGENUS *Artocarpus*	Leaves spirally arranged, stipule scars annulate, pistillate perianth apices free	39 species	From India to Oceania, with *A. altilis* (and to a lesser extent *A. camansi*) cultivated throughout the tropics
Section *Artocarpus*	Pistillate perianth apices not indurated and usually flexuous, staminate inflorescences usually spicate (elongate heads)	23 species	Singapore; Nicobar Islands east through Thailand, Indonesia, Papua New Guinea, Oceania, Philippines
'Philippinenses' clade	Leaves on mature trees usually incised, pistillate inflorescences with persistent interfloral bracts	4 species: *A. blancoi*, *A. nigrescens*, *A. pinnatisectus*, *A. treculianus*	Endemic to Philippines
'Incisifolii' clade	Leaves on mature trees usually incised, pistillate inflorescences lacking interfloral bracts	5 species: *A. altilis*, *A. bergii*, *A. camansi*, *A. horridus*, *A. mariannensis*	Singapore; Moluccas east through Oceania and Philippines (*A. altilis*, and to a lesser extent *A. camansi,* cultivated throughout the tropics)
'Rugosi' clade	Leaves on mature trees all or predominantly entire, pistillate inflorescences often with dimorphic processes and with or without interfloral bracts, surface of staminate inflorescences often rugose to tuberculate	13 species: *A.* sp. nov., *A. corneri*, *A. elasticus*, *A. excelsus*, *A. kemando*, *A. lowii*, *A. maingayi*, *A. obtusus*, *A. scortechinii*, *A. sericicarpus*, *A. tamaran*, *A. teysmannii*, and the probable interspecific hybrid *A. jarrettiae*	Singapore; Nicobar Islands, Thailand, peninsular Malaysia, Sumatra, Java, Borneo, Sulawesi, the Moluccas, New Guinea, Palawan
Artocarpus montanus clade	Leaves on mature trees entire, pistillate inflorescences with monomorphic filiform perianth apices and without interfloral bracts.	*A. montanus*	Southern Vietnam, eastern Thailand
Section *Duricarpus*	Pistillate perianth apices usually indurated and not flexuous; staminate inflorescences usually not spicate (subglobose to ovoid heads)	13 species	From India east through southeast Asia, Sumatra, Borneo, Java, Philippines
'Laevifolii' clade	Leaves mostly subglabrous and staminate inflorescences mostly ellipsoidal	5 species: *A. anisophyllus, A. brevipedunculatus*, *A. clementis*, *A. lanceifolius*, *A. sarawakensis*	Singapore, Borneo, Peninsular Malaysia, Thailand, Sumatra, Philippines

Table 2 (continued).

Taxonomic level	Key characters	Species	Geographic range
'Asperifolii' clade	Leaves mostly pubescent and staminate inflorescences varying from subglobose to spicate	8 species: *A. calophyllus*, *A. chama*, *A. hirsutus*, *A.hispidus*, *A. melinoxylus*, *A. nobilis*, *A. odoratissimus*, *A. rigidus*	Singapore, Borneo, Java, Lesser Sunda Islands, Myanmar, Peninsular Malaysia, Sumatra, Thailand, Philippines, Sri Lanka, Vietnam, India, Bangladesh, Cambodia
Section *Cauliflori*	Inflorescences on cauliflorous or ramiflorous short shoots	3 species: *A. annulatus*, *A. heterophyllus*, *A. integer*	Singapore, India, Thailand, Sumatra, peninsular Malaysia, Borneo, Java, Sulawesi, Moluccas (*A. heterophyllus,* and to a lesser extent *A. integer,* cultivated in many tropical areas)
SUBGENUS *Glandulifolium*	Leaves distichous, stipule scars not annulate, leaf margins glandular-crenate, pistillate perianth apices connate, styles bifid	*A. altissimus*	Borneo (West Kalimantan), Sumatra, Thailand
SUBGENUS *Aenigma*	Leaves spirally arranged, petioles with exfoliating epidermis, stipule scars annulate, pistillate perianth apices barely free, seeds < 5 mm long	*A. sepicanus*	New Guinea

Artocarpus J.R.Forst. & G.Forst., Char. Gen. Pl., ed. 2 (1776) 101, t. 51, 51a, nom. cons. – TYPE: *Artocarpus communis* J.R.Forst. & G.Forst. (= *A. altilis* (Parkinson) Fosberg).

Key to the subgenera of *Artocarpus*

1a. Leaves spirally arranged 2
1b. Leaves distichous 3

2a. Petiole epidermis usually persistent; seeds > 5 mm long ..... subg. *Artocarpus*
2b. Petiole epidermis exfoliating; seeds < 5 mm long ..... subg. *Aenigma*

3a. Pistillate perianths free ..... subg. *Prainea*
3b. Pistillate perianths connate 4

4a. Leaf margins not glandular-crenate; styles simple ..... subg. *Pseudojaca*
4b. Leaf margins glandular-crenate; styles bifid ..... subg. *Glandulifolium*

Artocarpus subg. ***Artocarpus*** – *Artocarpus* subg. *Jaca* Trécul, Ann. Sci. Nat. Bot. sér 3, 8: 110 (1847), nom. inval. – *Artocarpus* sect. *Jaca* (Trécul) Renner, Bot. Jahrb. Syst. 39: 363 (1907), nom. inval.

Pistillate perianth apices free; leaves spirally arranged with annulate stipule scars. A subgenus with 39 species, from India to Oceania.

Key to the sections of *Artocarpus* subg. *Artocarpus*

1a. Inflorescences on cauliflorous or ramiflorous short shoots ..... sect. *Cauliflori*
1b. Inflorescences axillary, never on cauliflorous or ramiflorous short shoots 2

2a. Pistillate perianth apices indurated and obviously free; staminate inflorescences seldom spicate ..... sect. *Duricarpus*
2b. Pistillate perianth apices not indurated, often flexuous, and sometimes not obviously free; staminate inflorescences almost always spicate ..... sect. *Artocarpus*

Key to the species of *Artocarpus* subg. *Artocarpus* found in Singapore

1a. Inflorescences usually on cauliflorous or ramiflorous short shoots 2
1b. Inflorescences never on cauliflorous or ramiflorous short shoots 3

2a. Leaves and petioles glabrous; female inflorescences with annulus surrounding peduncle attachment ..... *A. heterophyllus*
2b. Leaves (at least on the main veins) and petioles pubescent; female inflorescences without annulus surrounding peduncle attachment ..... *A. integer*

3a. Leaves always (sub)glabrous, petiole with prominent proximal pulvinus 4
3b. Leaves (sub)glabrous or pubescent, petiole without prominent proximal pulvinus 5

4a. Leaves on adult trees entire ..... *A. lanceifolius*
4b. Leaves on adult trees incised all the way to midrib, appearing compound, usually with alternating long and short ‘leaflets’ ..... *A. anisophyllus*

5a. Leaves on mature trees always lobed; staminate inflorescences spicate with smooth surface; pistillate inflorescences without interfloral bracts 6
5b. Leaves on mature trees usually entire; staminate inflorescences globose to spicate, surface smooth or sulcate; pistillate inflorescences mostly with interfloral bracts 7

6a. Syncarps with flattened processes ..... *A. altilis*
6b. Syncarps with pointed processes ..... *A. camansi*

7a. Staminate inflorescences subglobose, to 3 cm long, with a smooth surface; syncarp processes indurated and never dimorphic, with persistent interfloral bracts 8
7b. Staminate inflorescences cylindrical to spicate, at least 4 cm long, with a smooth or sulcate surface; syncarp processes dimorphic or not but never indurated, with or without persistent interfloral bracts 9

8a. Leaves hispid; peduncles at least 1 cm long ..... *A. hispidus*
8b. Leaves usually scabrid but never hispid; peduncles less than 1 cm long ..... *A. rigidus*

9a. Latex oily; leaves (sub)glabrous; staminate inflorescences with smooth surface ..... *A. lowii*
9b. Latex not oily; leaves pubescent at least on main veins; staminate inflorescences with sulcate surface 10

10a. Syncarps less than 5 cm long; leaves less than 18 cm long, shallowly once-pinnately lobed in juvenile trees and never lobed in mature trees; twigs c. 2–3 mm thick ..... *A. kemando*
10b. Syncarps more than 5 cm long; leaves more than 18 cm long, up to three times pinnately lobed in juvenile trees and sometimes lobed even in (sub-)mature trees; twigs at least 5 mm thick 11

11a. Leaves more or less flat, with plane margin; syncarp processes all the same length ..... *A. scortechinii*
11b. Leaves wavy, with repand margin; syncarp processes dimorphic ..... *A. elasticus*

1. *Artocarpus* J.R.Forst. & G.Forst. subg. ***Artocarpus*** sect. ***Artocarpus***

Diagnostic characters. Pistillate perianth apices not indurated and usually flexuous; staminate inflorescences usually spicate (elongate heads). A section with 23 species, from Nicobar Islands east through Thailand, Malaysia, Indonesia, Papua New Guinea, Philippines and Oceania. *Artocarpus altilis* (and to a lesser extent *A. camansi*) are cultivated throughout the tropics.

Four clades may be recognised:
1. **'Philippinenses'** (corresponding to *Artocarpus* ser. *Incisifolii* F.M.Jarrett, p.p.), sister to the rest of the subgenus: leaves on mature trees usually incised; pistillate inflorescences with persistent interfloral bracts. Four species, endemic to the Philippines: *Artocarpus blancoi* (Elmer) Merr., *A. nigrescens* Elmer, *A. pinnatisectus* Merr. and *A. treculianus* Elmer.

2. ***Artocarpus montanus*** E.M.Gardner & Zerega comprises its own clade, sister to Incisifolii + Rugosi.

3. **'Incisifolii'** (corresponding to *Artocarpus* ser. *Incisifolii* F.M.Jarrett, p.p.), sister to 'Rugosi': leaves on mature trees usually incised; pistillate inflorescences lacking interfloral bracts. Five species, from the Moluccas to Oceania: *Artocarpus altilis* (Parkinson) Fosberg, *A. bergii* E.M.Gardner et al., *A. camansi* Blanco, *A. horridus* F.M.Jarrett and *A. mariannensis* Trécul.

4. **'Rugosi'** (including *Artocarpus* ser. *Rugosi* F.M.Jarrett and *Artocarpus* ser. *Angusticarpi* F.M.Jarrett), sister to 'Incisifolii': surface of staminate inflorescences often rugose to tuberculate; pistillate inflorescences often with dimorphic processes. Approximately 13 species, from Thailand to Sumatra, Java, Borneo, Sulawesi, the Moluccas and New Guinea: *Artocarpus* sp. nov., *A. corneri* Kochummen, *A. elasticus* Reinw. ex Blume, *A. excelsus* F.M.Jarrett, *A. kemando* Miq., *A. lowii* King, *A. maingayi* King, *A. obtusus* F.M.Jarrett, *A. scortechinii* King, *A. sericicarpus* F.M.Jarrett, *A. tamaran* Becc., *A. teysmannii* Miq., and the probable interspecific hybrid *A. jarrettiae* Kochummen.

1.1 ***Artocarpus altilis*** (Parkinson) Fosberg, J. Wash. Acad. Sci. 31: 95 (1941). – *Sitodium altile* Parkinson, J. Voy. South Seas 45 (1773); Seemann, Fl. Vit. 255 (1868), as '*Sitodium utile*'. – TYPE: [Unpublished illustration] [Society Islands, Tahiti], 1769, watercolour by S. Parkinson (lectotype BM, designated by Ferrer-Gallego & Boisset (2018)). (Fig. 3)

Artocarpus communis J.R.Forst. & G.Forst., Char. Gen. Pl., ed. 2: 102, t. 51, 51a (1776). – *Artocarpus incisifolius* Stokes var. *apyrenus* Stokes, Bot. Mat. Med. iv. 331 (1812), as '*β apyrena*—(Variation)', nom. inval. – *Saccus communis* (J.R.Forst. & G.Forst.) Kuntze, Revis. Gen. Pl. 2: 633 (1891). – TYPE: [Society Islands, Tahiti, 1773], *J.R. Forster & G. Forster s.n.* (lectotype BM [BM000900567], designated by Jarrett (1959b); isolectotype? K [K000357659]).

Radermachia incisa Thunb. in Kongl. Vetensk. Acad. Handl. 37: 253 (1776). – *Artocarpus incisus* (Thunb.) L.f., Suppl. Pl. 411 (1782). – *Sitodium incisum* (Thunb.) Thunb. in Banks, Philos. Trans. Roy. Soc. London 69: 465 (1779). – *Artocarpus incisifolius* Stokes, Bot. Mat. Med. 4: 331 (1812), as '*incisifolia*', nom. illeg. superfl. – TYPE: [Indonesia], Java, *Thunberg s.n.* (lectotype UPS [V-135210], designated by Jarrett (1959b); isolectotype L [L0052850]).

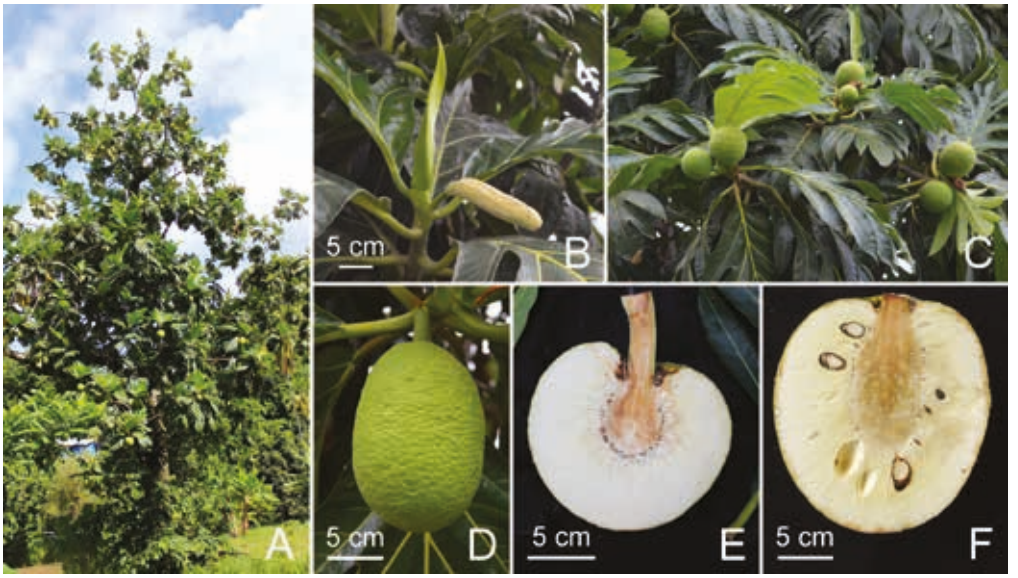

Fig. 3. *Artocarpus altilis* (Parkinson) Fosberg. **A.** Tree. **B.** Staminate inflorescence and stipule. **C.** Branch with syncarps. **D, E.** Seedless syncarps. **F.** Seeded syncarp. A–E from St. Vincent & Grenadines; F from Breadfruit Institute, Hawaii. (Photos: A–E, N.J.C. Zerega; F, J. Wiseman)

Artocarpus rima Blanco, Fl. Filip. 671 (1837). – TYPE: Philippines, Luzon, Manila, March 1914, *Merrill SB 603* (neotype US [US00688527], designated by Ferrer-Gallego & Boisset (2018); isolectotypes BO [2 sheets], PNH).

Artocarpus laevis Hassk., Flora 25(2): Beibl. 18 (1842). – *Artocarpus incisus* L.f. var. *laevis* (Hassk.) Miq., Fl. Ned. Ind. 1(2): 285 (1859), as '*incisa β laevis*'. – TYPE: [Indonesia], Java, Batavia [Jakarta], cult., *Hasskarl s.n.* (lectotype L n.v., designated by Jarrett (1959b)).

Artocarpus incisus L.f. var. *non-seminiferus* Duss, Fl. Phan. Antill. Franc. 3: 155 (1897), as 'α *non seminifera*'. – *Artocarpus altilis* (Parkinson) Fosberg. var. *non-seminiferus* (Duss) Fournet, Fl. Illustr. Phan. Guadeloupe & Martinique 1: 170 (2002). – TYPE: Martinique, 1 January–31 December 1882, *Duss 1402* (lectotype NY [NY01368002], designated here; isolectotypes US [US01068041, US01068049]).

Inocarpus edulis Vincendon-Dumoulin & Desgraz, Iles Marquises, ou Nouka-Hiva 206 (1843), nom. nud., non. J.R.Forst. & G.Forst. (1776). – *Artocarpus edulis* Eyries, Bull. Soc. Géogr. sér. 2, t. 19: 314 (1843), nom. nud.

Diagnostic characters. Leaves on mature trees incised, syncarps globose to ellipsoidal with barely-free perianth apices (sometimes with smooth syncarp surface) and few to no seeds.

Distribution. Cultivated throughout the tropics, but first domesticated in Oceania (Zerega et al., 2005).

Notes. This is the cultivated breadfruit, distinguishable from *Artocarpus camansi* by the paucity or absence (in triploid varieties) of seeds and the lack of long tapering perianth apices on the syncarps. Although it is likely that the basionym originated with Solander (although not certain, as we were unable to examine Solander's journals for this study), the protologue does not credit Solander, so 'Solander ex Parkinson' should not be used.

The protologue of Stokes's variety *apyrenus* cites in synonymy variety 'α' from Forster's *Plantae Esculentae* (Forster, 1786: 23) and the fourteenth edition of the *Systema Vegetabilium* (Von Linné et al., 1784), the latter of which refers to Forster's *Vom Brodbaum* (Forster, 1784: 33, t. 1, 2). It is clear from both sources that the variety is identical to Forster's original *Artocarpus communis*, and the two should therefore be considered homotypic. These sources did not cite but are synonymous with Thunberg's variety 'α' within *Radermachia incisa* (variety 'β' being referable to *Artocarpus camansi*).

The lectotype designated by Jarrett (1959b) for *Artocarpus laevis* Hassk. (as 'holotype') could not be located, but the identity of that species with *A. altilis* can be confirmed by the citation of Rumphius's 'Soccus lanosus' as the only synonym in the protologue.

The protologue of Duss's variety *non-seminiferus* cites two collections, *Duss 3771* and *Duss 1401*. The former could not be traced and was perhaps destroyed with the main set at B. The latter appears to be a typographical error for *1402*, which bears Duss's annotation; *1401* (MO) is *Celtis iguanaea* (Jacq.) Sarg. No material at P or B could be located, but the NY specimen [NY01368002], which is complete and whose image can be accessed online, can serve very well as the lectotype.

'*Artocarpus edulis*', a nomen nudum occasionally used for breadfruit, appears to have its origin in a partial correction (in a book review) of the mistaken application of '*Inocarpus edulis*' to breadfruit. *Inocarpus edulis* J.R.Forst. & G.Forst (Fabaceae) (= *Inocarpus fagifer* (Parkinson ex F.A.Zorn) Fosberg) was published in the same book as *A. communis*, likely explaining the original mistake.

1.2 *Artocarpus bergii* E.M.Gardner et al., Syst. Bot. 46(1): 91 (2021). – TYPE: Indonesia, N. Maluku Prov., Halmahera, Weda Bay, 24 December 2012, *Iska Gushilman et al. 285* (holotype BO; isotypes L [L.3969484], MO [MO-2702081]).

Diagnostic characters. Leaves entire and subglabrous on mature trees; staminate inflorescences slender (c. 1 cm wide); syncarps cylindrical, up to 7 cm long, with flattened processes.

Distribution. Moluccas.

Notes. Material assigned to this species was included in *Artocarpus horridus* by Jarrett (1959b), but it differs from the latter in having subglabrous, entire leaves on mature trees and more slender staminate inflorescences.

1.3 *Artocarpus blancoi* (Elmer) Merr., Enum. Philipp. Fl. Pl. 2: 40 (1923). – *Artocarpus communis* J.R.Forst. & G.Forst. var. *blancoi* Elmer, Leafl. Philipp. Bot. 2(32): 617 (1909), as '*Artocarpus communis blancoi* Elm. n. var.'. – *Artocarpus incisus* L.f. var. *blancoi* (Elmer) Merr., Enum. Philipp. Fl. Pl. 2: 40 (1923), pro syn., nom. inval. – TYPE: Philippines, Luzon, Bataan Prov., Mt Mariveles, Lamao River, August 1904, *Borden 488 (FB 1682)* (PNH untraced, presumed destroyed); Rizal Prov., February 1928, *Ramos BS 42018* (neotype K [K000798306], designated by Jarret (1959b); isoneotypes L [L.1591237], US [US01088811]). (Fig. 4)

Artocarpus communis auct. non J.R.Forst. & G.Forst.: Merrill, Sp. Blancoan. 124 (1918), as '*Artocarpus communis* Forst. var.'.

Artocarpus altilis auct. non Parkinson (Fosberg): Berg, Fl. Males., ser. 1, 17(1): 82 (2006), p.p.

Diagnostic characters. Leaves on mature trees shallowly to deeply incised; stipules with greyish hairs; syncarps with filiform perianth apices.

Distribution. Philippines.

Notes. Included in *Artocarpus altilis* by Berg et al. (2006) but distinguishable from that species by cylindrical syncarps with long, filiform perianth apices with inflated hairs, and persistent interfloral bracts.

1.4 *Artocarpus* sp. nov.

Diagnostic characters. Leaves on mature trees incised; syncarps with dimorphic perianth apices.

Distribution. Known only from Manus Province, Papua New Guinea.

Notes. This species, which will be published shortly, is the easternmost member of the 'Rugosi' clade and most closely resembles *Artocarpus elasticus*, differing primarily in its simple styles and minute indumentum.

1.5 *Artocarpus camansi* Blanco, Fl. Filip. 670 (1837). – TYPE: [Philippines], Luzon, Manila, February 1915, *Merrill SB 830* (neotype US [US00730771], designated by Ferrer-Gallego & Boisset (2018); isoneotype L [L0817646]). (Fig. 5)

Artocarpus incisus L.f. var. β Murray, Syst. Veg. (ed. 14) 838 (1784); Forster, Pl. Esc. 26 (1786). – *Artocarpus incisifolius* Stokes var. *seminiferus* Stokes, Bot. Mat. Med. iv. 331 (1812), as 'α *seminifera*—(Variation)'. – *Artocarpus incisus* L.f. var. *seminiferus*

(Stokes) Duss, Fl. Phan. Antill. Franc. 3: 156 (1897), as 'β *seminifera*'. – *Artocarpus altilis* (Parkinson) Fosberg var. *seminiferus* (Stokes) Fournet, Fl. Illustr. Phan. Guadeloupe & Martinique 1: 171 (2002), as '*seminifera* (Duss)'. – TYPE: [Published illustration] Sonnerat, Voy. Nouv. Guinée 99, t. 57 (1776), lectotype designated here.

Artocarpus incisus L.f. var. *muricatus* Becc., Nelle Foreste di Borneo 628 (1902). – TYPE: New Guinea [Papua New Guinea], Tandgiong Bair [Tangion Bair], 9 April 1872, *Beccari PP 25* (lectotype FI [FI008131], designated by Jarrett (1959b)).

Artocarpus leeuwenii Diels, Bot. Jahrb. Syst. 67: 175 (1935). – TYPE: New Guinea, [West Papua] Irian Jaya, Meervlakte, November 1926, *Docters van Leeuwen 11163* (lectotype B [B 10 0186974], designated by Jarrett (1959b); isolectotypes L [L0039871], U [U0124148]).

Artocarpus papuanus Diels, Bot. Jahrb. 67: 175 (1935), as '*papuana*', nom. illeg. non Renner (1909). – TYPE: [Papua New Guinea, E. Sepik Prov.] Northeast New Guinea, Lager 1, Aprilfluss, Mündung, 9 June 1912, *Ledermann 7513* (lectotype B [B 10 0294374], first step designated by Jarret (1959b), second step designated here; isolectotypes B [B 10 0294375], SING [SING0294208]).

Diagnostic characters. Leaves on mature trees incised; syncarps with tapering perianth apices and filled with seeds.

Distribution. Native to New Guinea, Moluccas, and possibly naturalised in the Philippines. Cultivated in several tropical regions, including Southeast Asia, the Caribbean Islands, Central and South America and coastal West Africa.

Notes. *Artocarpus camansi,* is commonly referred to as breadnut, the closest wild relative of cultivated breadfruit (Zerega et al., 2005). Unlike the cultivated *Artocarpus altilis*, the syncarps of *A. camansi* have long tapering perianth apices and are completely filled with seeds.

This species corresponds to variety 'β' of Thunberg's *Radermachia incisa*. *Artocarpus incisifolius* var. *seminiferus* was based on variety 'β' as described in the fourteenth edition of the *Systema Vegetabilium* (Von Linné et al., 1784: 838) and in Forster's *Plantae Esculentae* (Forster, 1786: 26), which was expressly based on the 'Rima' described by Sonnerat, whose illustrations unmistakably depict *Artocarpus camansi* (Sonnerat, 1776: 99). We therefore designate one of his illustrations as the lectotype of *Artocarpus incisifolius* var. *seminiferus*.

Jarrett (1959b) designated a lectotype for *Artocapus papuanus* by citing a 'holotype' in Berlin; two sheets exist there, a fertile one (B_10_0294374) bearing her annotation and a sterile one without her annotation. Although not explicitly stated in her published designation, clearly B_10_0294374 was intended; to avoid any doubt, the second step is designated here.

Fig. 4. *Artocarpus blancoi* (Elmer) Merr. **A.** Tree. **B.** Trunk. Inset: Bark slash. **C.** Sitpule. **D.** Branch with staminate inflorescences and syncarp. All from Luzon Philippines. Scale bars estimated. (Photos: A, B, E.M. Gardner; C, K. Hageman; D, L. Gocon; C, D reproduced from Pelser et al. (2011 onwards) with permission)

1.6 ***Artocarpus corneri*** Kochummen, Gard. Bull. Singapore 50: 197 (1998); Kochummen, Tree Fl. Sabah & Sarawak 3: 194, t. 3 (2000). – *Artocarpus elasticus* auct. non Reinw. ex Blume: Berg, Fl. Males., ser. 1, 17(1): 90 (2006), as 'corneriform'. – TYPE: [Malaysia], Borneo, Sarawak, Belaga, Dulit Range, Ulu Sg. Kayan, 20 October 1983, *Dayang Awa & P.C. Yii S 46878* (holotype KEP; isotypes CGE n.v., K [K001328347], L [L.1587733], SAN, SAR). (Fig. 6)

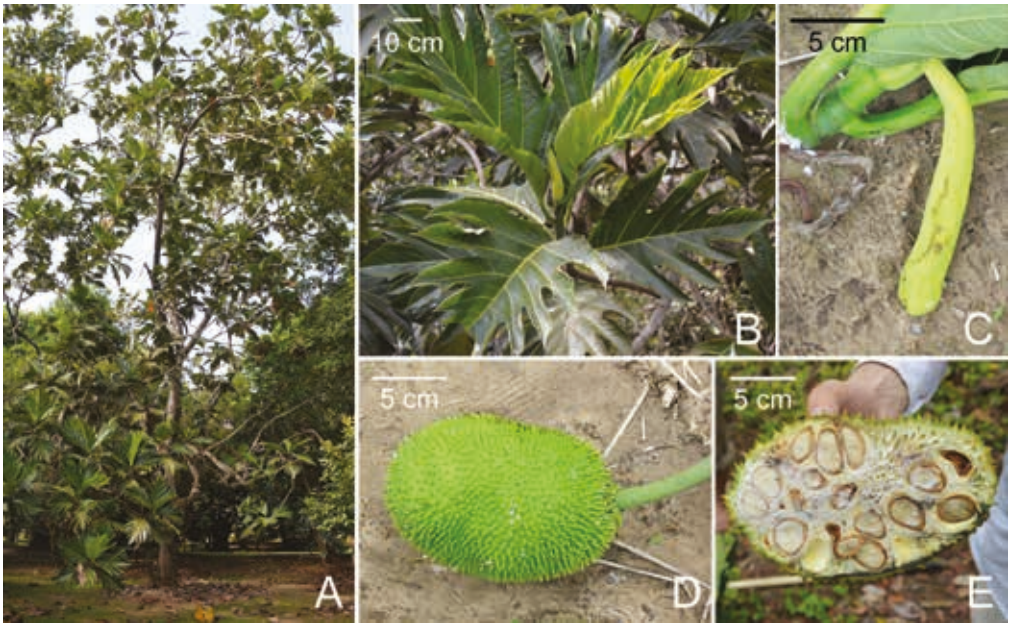

Fig. 5. *Artocarpus camansi* Blanco. **A.** Tree (*NZ916*). **B.** Leaves and stipule (*NZ916*). **C.** Staminate inflorescence (*NZ441*). **D.** Syncarp surface (*NZ441*). **E.** Open syncarp (*NZ718*). A, B, E from Malaysia; C, D from Thailand. (Photos: N.J.C. Zerega)

Diagnostic characters. Leaves on mature trees entire and not very wavy, with a smooth upper surface; syncarps without long curling sterile flowers but sometimes with sparse wide flowers.

Distribution. Borneo (Sarawak).

Notes. *Artocarpus corneri* differs from *A. elasticus* (Fig. 7) in the absence of elongate processes (sterile flowers) on the pistillate inflorescences and syncarps. The upper surface of the leaf may be smooth or (less often) scabridulous to the touch but is usually not short hispid as in *Artocarpus elasticus*. The leaves tend towards a more narrowly ovate shape than is typical for *Artocarpus elasticus*, and the stipules are covered in a soft brown pubescence as in *A. scortechinii*. While *Artocarpus corneri* syncarps lack the long processes typical of *A. elasticus*, some specimens (e.g., *Julaihi Jamree et al. S 79274*, SAR) have perianths that are dimorphic in width, with scattered wide flowers that may also protrude slightly. The two forms of *Artocarpus corneri* may correspond to two Iban names: *tekalong empurung*, matching the type, and *pedalai*, a name shared with *Artocarpus sericicarpus* F.M.Jarrett and *A. sarawakensis* F.M.Jarrett, matching the form with dimorphic flowers. Both forms are sweet and edible, but the *pedalai* form is apparently superior (Salang anak Nyegang, pers. comm.). Whether the two forms represent intraspecific variation or distinct entities requires further investigation.

The nomen nudum *Artocarpus blumei* Trécul var. *sarawakensis* Boerl. almost certainly refers to either *A. corneri* or *A. elasticus*.

Fig. 6. *Artocarpus corneri* Kochummen. **A.** Tree (*EG863*). Inset: Bark (*EG818*). **B.** Stipule (*EG818*). **C.** Syncarp and leaves on tree (*EG818*). **D.** Immature syncarp (*EG818*). **E.** Immature syncarp cut open (*EG818*). **F.** Staminate inflorescences (*EG818*). All photos from Sawarak, Malaysia. (Photos: E.M. Gardner)

1.7 ***Artocarpus elasticus*** Reinw. ex Blume [Cat. Gew. Buitenzorg 101 (1823), nom. nud.], Bijdr. Fl. Ned. Ind. 481 (1825). – TYPE: [Indonesia], Java, *Reinwardt(?) s.n.* (lectotype L [L0039879], designated by Jarrett (1959b)). (Fig. 7)

Artocarpus blumei Trécul, Ann. Sci. Nat. Bot. sér. 3, 8: 111, t. 4, fig. 116 (1847), as '*blumii*'. – TYPE: [Indonesia], [West] Java, near Tjicoja [Cikoja], 29 January 1843, *Zollinger 1058* (lectotype P [P00756663], first step designated by Jarrett (1959b), second step designated here; isolectotypes L [L.1587449], P [P00756664, P00756665], U [U.1423857]).

Artocarpus kunstleri King in Hooker, Fl. Brit. Ind. 5: 540 (1888); King, Ann. Roy. Bot. Gard. (Calcutta) 2: 9, t. 4 (1889). – TYPE: [Peninsular Malaysia] Malaya, 1871, *Maingay 1484* (lectotype K [K001051074], designated here; isolectotypes CAL [CAL0000014458], L [L0817365]).

Artocarpus pubescens auct. non. Willd.: Blume, Bijdr. Fl. Ned. Ind. 481 (1825).

Diagnostic characters. Leaves on mature trees wavy, with a scabrid upper surface; staminate inflorescences to 18 cm long, sulcate and often twisted; syncarps with dimorphic perianth apices, the sterile ones long and curling.

Distribution. Thailand, Peninsular Malaysia, Singapore, Sumatra, Java, Borneo and Palawan.

Notes. Artocarpus elasticus differs from *A. corneri* and *A. scortechinii* in the scabrid (short hispid) upper surface of the leaf and the consistent presence of elongate sterile processes on the pistillate inflorescences and syncarps.

The lectotype of *Artocarpus blumei* designated by Jarrett consists of multiple sheets, but only one of these, P00756663, contains both leaves and an inflorescence, and we therefore designate that sheet as the second-step lectotype.

King's condensed treatment of *Artocarpus* in the *Flora of British India* (King, 1888) appeared before his full account (King, 1889), which was cited as still in manuscript. As only *Maingay 1484* was cited in the first account for *Artocarpus kunstleri* King, we designate a duplicate in K as the lectotype.

1.8 *Artocarpus excelsus* F.M.Jarrett, Blumea 22(3): 409 (1975). – TYPE: [Malaysia], Borneo, Sabah, Mt Kinabalu, Mesilau River, 1 May 1964, *Chew & Corner RSNB 7046* (holotype K [K001051088, K001051089 – a single specimen over 2 sheets]; isotypes A [A00034350], CANB [CANB232762], L [L0039880], LE [LE00011403], SAN, SING [SING0052143], US [US00089829]).

Diagnostic characters. Vegetative parts subglabrous; leaves narrowly elliptic; staminate inflorescences finger-shaped, up to c. 3 cm long; syncarps small and cylindrical with a pebbly surface.

Distribution. Borneo (Sabah and Sarawak).

Notes. Artocarpus excelsus, restricted to lower montane forest in Borneo, resembles *A. lowii* in its (sub)glabrous parts and slender, finger-shaped staminate inflorescences; however, the leaves are narrower, and the perianth apices on the syncarps are more flattened.

The holotype is on two sheets, with the pistillate and staminate inflorescences mounted separately and marked 'sheet 1' and 'sheet 2' in Jarrett's hand.

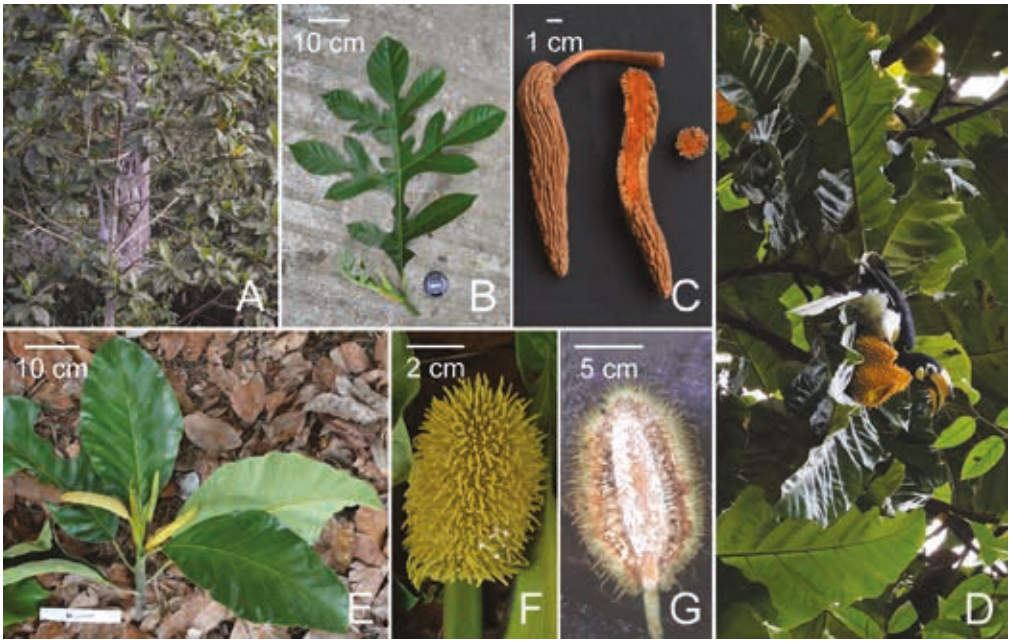

Fig. 7. *Artocarpus elasticus* Reinw. ex Blume. **A.** Tree. **B.** Juvenile leaf (*NZ605*). **C.** Staminate inflorescence in cross and longitudinal section. **D.** Branch with leaves, mature syncarp and a hornbill feeding on the fruit. **E.** Adult leaves with stipule and staminate inflorescence (*EG184*). **F.** Immature syncarp (*EG184*). **G.** Open immature syncarp. All photos from Sabah, Malaysia. (Photos: A–C, E, F, E.M. Gardner; D, P.K.F. Leong; G: N.J.C. Zerega)

1.9 *Artocarpus horridus* F.M.Jarrett, J. Arnold Arbor. 40: 306 (1959). – TYPE: [Indonesia, N. Maluku Prov.], Halmahera, Soa Tobaroe [Tobaru], 29 May 1922, *Béguin 1976* (holotype L [L0039890]; isotypes BO, L [L0039891]). (Fig. 8)

Artocarpus communis J.R.Forst. & G.Forst. var. *pungens* J.J.Sm. ex K.Heyne, Nutt. Pl. Ned.-Ind. ed. 2, 1: 557 (1927). – TYPE: [Published illustration] 'Soccus silvestris' in Rumphius, Herb. Amboin. 1: 114, t. 34 (1741), lectotype designated by Jarrett (1959b).

Artocarpus elasticus auct. non Reinw. ex Blume: Hassk., Abh. Naturf. Ges. Halle 9: 158 (1866); Merrill, Interp. Herb. Amboin. 191 (1917).

Diagnostic characters. Leaves on mature trees incised; leaves and stipules densely pubescent with sharp and unpleasant hairs.

Distribution. Moluccas.

Notes. *Artocarpus horridus* resembles *A. camansi*, but with generally smaller parts (e.g., syncarp up to 9 × 4.5 cm in *A. horridus* and up to 20 × 15 cm in *A. camansi*), and a shaggier and more ferocious indumentum, the latter making the specimens unpleasant to handle and giving rise to its specific epithet. The species corresponds to Rumphius's 'Soccus silvestris'. Within the latter, Rumphius recognised two entities: a pubescent form matching Jarrett's type of *Artocarpus horridus*, and a glabrous form matching collections from Buru (Rumphius, 1741: 114), which may warrant further attention.

1.10 ***Artocarpus jarrettiae*** Kochummen, Gard. Bull. Singapore 50: 198 (1998). – TYPE: [Malaysia], Borneo, Sabah, Langanan [Kinabalu NP], 14 August 1987, *Amin & Francis SAN 120933* (holotype SAN; isotypes K [K001051134], KEP, L [L.1587714]).

Diagnostic characters. Leaves like those of *Artocarpus elasticus* but much smaller (to 18 cm long); syncarps with long sterile flowers but otherwise similar to those of *A. kemando*, with short reddish hairs.

Distribution. Borneo (Sabah).

Notes. The type of *Artocarpus jarrettiae* displays leaf and syncarp characters intermediate between *A. elasticus* (Fig. 7) and *A. kemando* (Fig. 9) and may well represent a rare interspecific hybrid. No material known to us has been assigned to *Artocarpus jarrettiae* in the 22 years since it was described, despite the type locality being a well-collected protected area within Kinabalu National Park. The authors were unable to locate any plants matching *Artocarpus jarrettiae* during a 2013 trip to the type locality, made especially for that purpose, although we did collect *A. kemando*. The paratype appears to be simply a small-leaved specimen of *Artocarpus elasticus*.

1.11 ***Artocarpus kemando*** Miq., Fl. Ned. Ind., Eerste Bijv. 3: 418 (1861). – TYPE: [Indonesia], Sumatra, Lampong, near Kebang, *Teijsmann HB 4515* (lectotype L [L0039894], designated by Jarrett (1959b); isolectotypes BO, P [P06880102], U [U0004433]). (Fig. 9)

Artocarpus brunneifolius S.Moore, J. Bot. 63(Suppl.): 112 (1925), as '*brunneifolia*'. – TYPE: [Indonesia], Sumatra, Palembang, Hills above Moera Mengkoelem, R. Rawas, 1880, *Forbes 3046* (lectotype BM [BM000951750], designated by Jarrett (1959b); isolectotypes L [L0039895, L0039896], P [P06777257], SING [SING0052145]).

Artocarpus sumatranus F.M.Jarrett, J. Arnold Arbor. 40: 353 (1959). – TYPE: [Indonesia], Sumatra, East Coast, Selatpandjang, mouth of Kampar, 6 March 1937, *Sewandono bb 22055* (holotype BO [a single specimen over two sheets – BO-1297304, BO-1297305]; isotype L [L.1591802]).

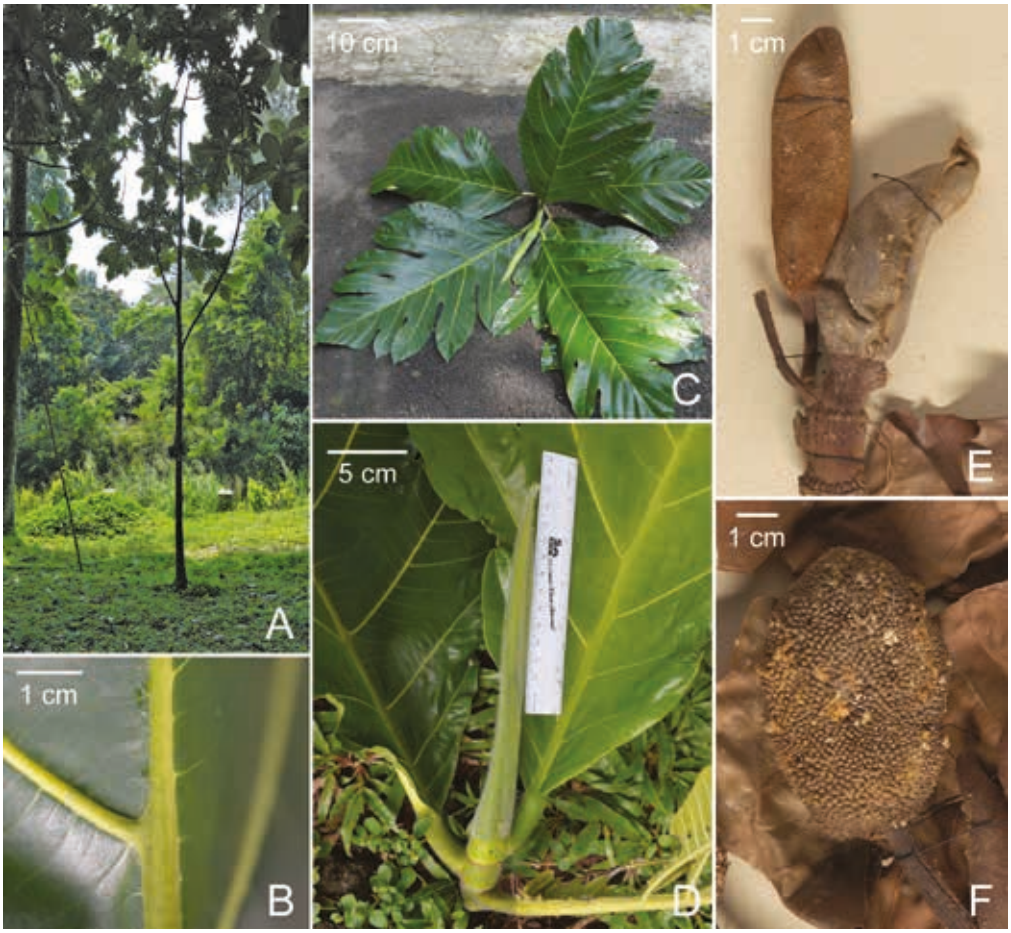

Fig. 8. *Artocarpus horridus* F.M.Jarrett. **A.** Tree (*EG437*). **B.** Leaf underside with hairs (*EG437*). **C.** Leaves and stipule (*EG437*). **D.** Stipule and stipule scars with hairs (*EG438*). **E, F.** *Béguin 1975* (L0817603), showing staminate inflorescence (E) and syncarp (F). All from Indonesia. (Photos A–D, E.M. Gardner; E, F, L herbarium)

Artocarpus maingayi auct. non. Miq.: Ridley, J. Straits Branch Roy. Asiat. Soc. 33: 147 (1900).

Diagnostic characters. Leaf apices acuminate; peduncle > 1.5 cm long; syncarps small (to c. 4 cm long), velutinous with raised apices.

Distribution. Southern and eastern Peninsular Malaysia, Singapore, southern Sumatra, and Peninsular Thailand.

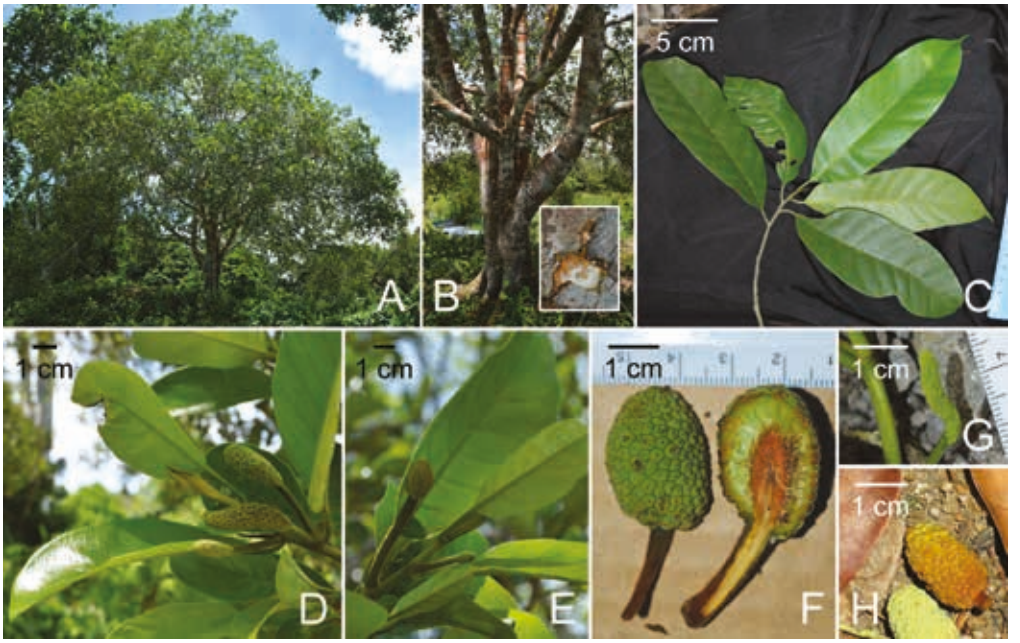

Fig. 9. A–G. *Artocarpus kemando* Miq. **A.** Tree (*EG196*). **B.** Trunk. Inset: Bark slash and exudate (*EG196*). **C.** Leaves (*NZ830*). **D.** Branch with leaves and staminate inflorescence (*EG196*). **E.** Branch with leaves and pistillate inflorescence (*EG196*). **F.** Open syncarp. **G.** Staminate inflorescence at pre-anthesis (*EG187*). **H.** Syncarp of the closely allied *A. maingayi* King. The flower apices are much more protruded than in *A. kemando*. All from Malaysia. (Photos: A–G: E.M. Gardner; H, Y.S. Yeoh)

Notes. *Artocarpus kemando* can be distinguished from *A. maingayi* as follows. The leaf apices are consistently acuminate (in *Artocarpus maingayi* they are rounded in Peninsular Malaysia to shortly acuminate in Sumatra), the peduncle is longer than 1.5 cm (shorter than 1 cm in *A. maingayi*), and the pistillate perianth apices are conical to umbonate (flattened in *A. maingayi*). The type of *Artocarpus brunneifolius* is subglabrous in nearly all its parts, and although it agrees better with *A. kemando*, the pistillate perianths appear somewhat intermediate between *A. kemando* and *A. maingayi*. The type of *Artocarpus sumatranus* also generally agrees with *A. kemando*; the broader leaves, somewhat thicker twigs, and slightly longer pistillate perianth apices (up to 3 mm long) do not at this time warrant recognition as a distinct species, although further study is needed. Some specimens from peat swamp forests in Borneo may, however, represent a distinct entity. These (*AA2766*, K, L, WAN; and *S 12902*, K, L, SAR) resemble the type of *Artocarpus sumatranus* in their broad leaves, but the leaf apices are rounded to emarginate, and the pistillate perianths have fluted apices with bifid styles (consistently simple in *A. kemando*).

1.12 ***Artocarpus lowii*** King in Hooker, Fl. Brit. India 5: 542 (1888); King, Ann. Roy. Bot. Gard. (Calcutta) 2: 10, t. 7A (1889), p.p. – TYPE: [Peninsular Malaysia], Perak, Larut, near Gunong Pando [Gunung Panti], June 1885, *King 7737* (lectotype CAL [CAL0000014464], first step designated by Jarrett (1960), second step designated here; isolectotypes BM [BM000951746], CAL [CAL0000014463], K [K001051077], SING [SING0052077]). (Fig. 10)

Diagnostic characters. Latex separating into a white sticky phase and a clear oily phase; vegetative parts subglabrous; leaves elliptic; syncarps to 6.5 cm long with a pebbly surface.

Distribution. Peninsular Malaysia, Singapore and Sumatra.

Notes. Artocarpus lowii is remarkable for its oily latex, which can be used as an ointment and even to fry fish (Corner, 1940). It resembles the montane species *Artocarpus excelsus* (Borneo) and *A. montanus* (Vietnam) but with somewhat larger leaves, and distinctive synarps whose pale apices appear outlined in dark green. As detailed by Jarrett (1959b), King's account containing the protologue transposed the descriptions and drawings of the staminate inflorescences for *Artocarpus lowii* and *A. peduncularis* Kurz (= *A. teysmannii*).

1.13 ***Artocarpus maingayi*** King in Hooker, Fl. Brit. India 5: 542 (1888); King, Ann. Roy. Bot. Gard. (Calcutta) 2: 11 (1889). – TYPE: [Peninsular Malaysia], Perak, Larut, November 1882, *King 3595* (lectotype K [K001051069], designated here; isolectotypes CAL [CAL0000014456, CAL0000014457]). (Fig. 9H)

Diagnostic characters. Leaf apices usually rounded; peduncles < 0.5 cm long; syncarps small (to c. 4 cm), with flattened, cushion-shaped perianth apices.

Distribution. Northern and western Peninsular Malaysia, northern Sumatra, and Peninsular Thailand.

Notes. Distinguishing characters are given above under *Artocarpus kemando*. We have designated *King 3595* as the lectotype of *Artocarpus maingayi* because although it was not widely distributed among herbaria, it is the only syntype we have seen containing both staminate and pistillate inflorescences.

1.14 ***Artocarpus mariannensis*** Trécul, Ann. Sci. Nat., Bot. sér. 3, 8: 114 (1847). – *Saccus mariannensis* (Trécul) Kuntze, Revis. Gen. Pl. 2: 633 (1891). – TYPE: Mariana Islands, Guam, *Gaudichaud s.n.* (holotype P [P00636904]). (Fig. 11)

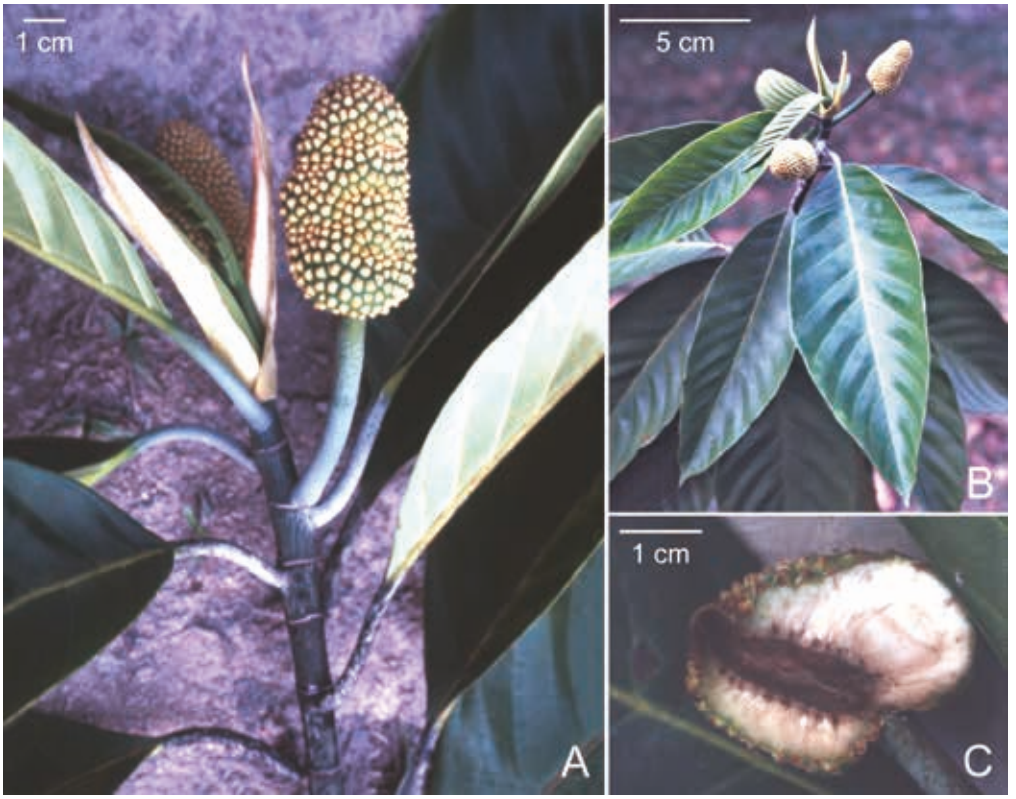

Fig. 10. *Artocarpus lowii* King. **A.** Branch with syncarp, stipule and stipule scars. **B.** Leaves and syncarps. **C.** Open syncarp. All from Malaysia, *NZ246*. (Photos: N.J.C. Zerega)

Diagnostic characters. Leaves on mature trees usually entire or shallowly trilobed, with rufous hairs on main veins on leaf underside; syncarps irregularly shaped with a dark green and pebbly surface when ripe.

Distribution. Micronesia.

Notes. *Artocarpus mariannensis* was included in *Artocarpus altilis* by Jarrett (1959b) and Berg et al. (2006) but it is readily distinguishable by its entire to shallowly lobed leaves with red-brownish hairs on the midrib of the leaf underside, smaller irregularly shaped syncarps with a knobbly dark green surface and yellow flesh, and smaller staminate inflorescences. This species is known to hybridise with *Artocarpus altilis* (Fosberg, 1960; Zerega et al., 2005, 2015).

1.15 ***Artocarpus montanus*** E.M.Gardner & Zerega, Phytotaxa 453(3): 270 (2020). – TYPE: Vietnam, Kon Tum Prov., Dak Gley Distr., about 10 km to N of Dak Gley town, between Dak Nen and Mang Khen (Dak Che) villages, 19 November 1996, *L.V. Averyanov et al. VH1819* (holotype P [P06777683]; isotypes HN n.v., LE, MO).

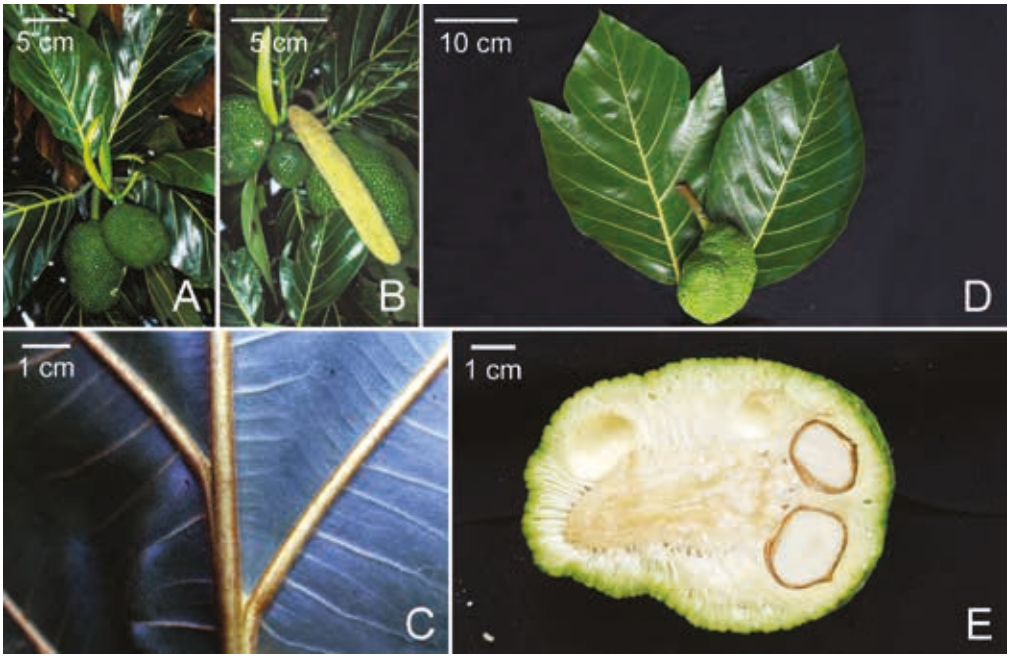

Fig. 11. *Artocarpus mariannensis* Trécul. **A.** Leaves, stipule, and syncarps. **B.** Staminate inflorescence and syncarps. **C.** Leaf underside with reddish hairs. **D.** Leaves and syncarp. **E.** Open syncarp. A–C from Rota, Northern Mariana Islands, D, E from Hawaii, Breadfruit Institute (NTBG acc. 900252.002, Provenance Mariana Islands). (Photos: A, B, T.J. Motley; C, N.J.C. Zerega; D, E, J. Wiseman)

Diagnostic characters. Vegetative parts subglabrous; leaves narrowly elliptic; syncarps subglobose with filiform perianth apices.

Distribution. Southern Vietnam and possibly eastern Thailand (Gardner et al., 2020).

Notes. Artocarpus montanus, restricted to montane areas, most resembles *A. excelsus* and *A. lowii* in its (sub)glabrous parts.

1.16 ***Artocarpus obtusus*** F.M.Jarrett, Blumea 22(3): 410 (1975). – TYPE: [Malaysia], Borneo, Sarawak, Kuching, Semenggoh FR, *Galau S 15740*, 29 November 1961 (holotype K [K000227611]; isotypes C, K [K000227610], L [L.4322786], SAR).

Diagnostic characters. Leaves on mature trees entire and thickly coriaceous with obtuse to retuse apices; syncarps with thick perianth apices that are dimorphic in length; staminate inflorescences shallowly sulcate with a smell rather like fermented green apples.

Distribution. Borneo.

Notes. Except for the leaves, which are unique, *Artocarpus obtusus* bears more resemblance to *A. elasticus* and allies than to its sister species *A. lowii*.

1.17 ***Artocarpus nigrescens*** Elmer, Leafl. Philipp. Bot. 2: 614 (1909). – TYPE: Philippines, Negros Oriental, Dumaguette (Cuernos Mts.), April 1908, *Elmer 9795* (lectotype BM, designated by Jarrett (1959b); isolectotypes A [A00034358], BM [BM000951744], BO, E [E00504531], L [L0039909], MO [MO-204395], NY [NY00025195], US [US00089827]). (Fig. 12)

Artocarpus treculianus auct. non Elmer: Jarrett, J. Arnold Arbor. 40: (1959); Berg, Fl. Males., ser. 1, 17(1): 106 (2006).

Diagnostic characters. Leaves on mature trees incised; syncarps coal black when mature on the tree.

Distribution. Philippines.

Notes. Fruiting *Artocarpus nigrescens* is unmistakable when on a live tree; the epithet refers to the syncarps that blacken on the tree. Jarrett (1959b) considered this an erroneous character likely associated with decaying fruits and reduced *Artocarpus nigrescens* to a synonym of *A. treculianus*. However, Elmer's detailed field notes on the type preserved in New York (apparently not seen by Jarrett) describes 'young fruit black …. nearly mature heads coal black.' His observations were corroborated by more recent ones in Cebu (D. Tandang, pers. comm., Fig. 12). Jarrett's hesitance to accept this character was understandable, as the black syncarps dry brown (Cebu, *D. Tandang et al. 65*, PNH).

1.18 ***Artocarpus pinnatisectus*** Merr., Philipp. J. Sci. 18: 50 (1921). – TYPE: Philippines, Luzon, Tayabas, Guinayangan, March 1913, *Escritor BS 20789* (lectotype US [US00089824], designated by Jarrett (1959b); isolectotype K [K001193747]). (Fig. 13)

Artocarpus multifidus F.M.Jarrett, J. Arnold Arbor. 40: 324 (1959) – TYPE: Philippines, Samar, Teft, Mt Calbiga, May 1948, *Sulit 6462* (holotype PNH n.v.; isotypes A [A00034356, A00034357]).

Artocarpus altilis auct. non Parkinson (Fosberg): Berg, Fl. Males., ser. 1, 17(1): 82 (2006).

Diagnostic characters. Leaves on mature trees pinnately incised with up to 20 lobes; trunks slender and pale with an almost palm-like habit.

Distribution. Philippines.

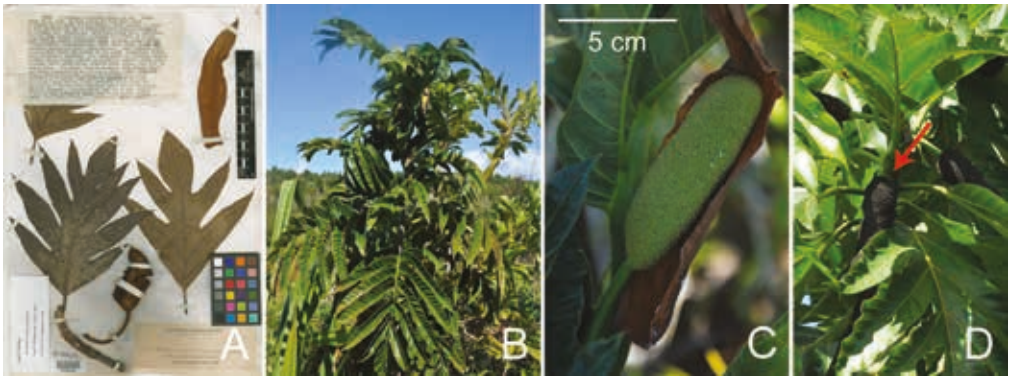

Fig. 12. *Artocarpus nigrescens* Elmer. **A.** Isotype (*Elmer 9795*, NY) with leaves, stipule and syncarp, which dries brown. **B.** Young tree. **C.** Pistillate inflorescence. **D.** Mature black syncarp (arrow). B–D from the Philippines. (Photos: A, NY herbarium; B–D, D. Tadang)

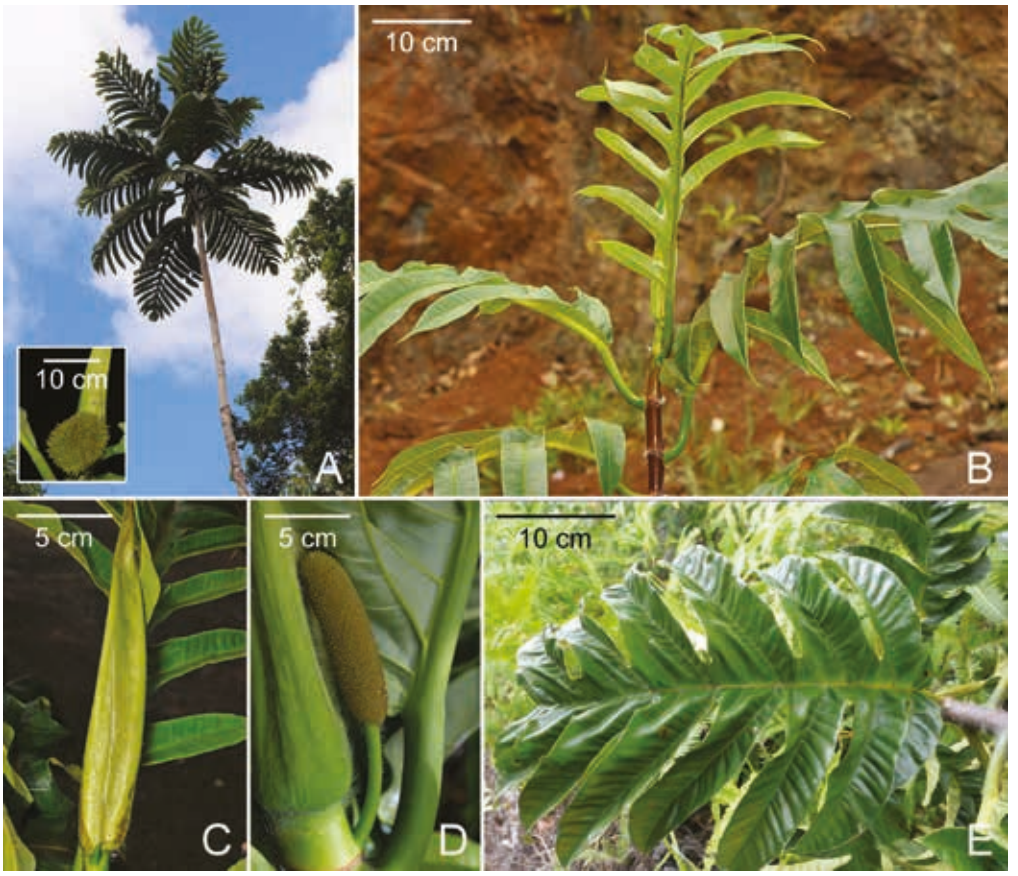

Fig. 13. *Artocarpus pinnatisectus* Merr. **A.** Tree. Inset: Syncarp. **B.** Sapling. **C.** Stipule. **D.** Staminate inflorescence. **E.** Leaf. All from Dinagat Islands, Philippines. Scale bars estimated. (Photos: A–C, P. Pelser & J. Barcelona; D, E, M. Manting; all reproduced from Pelser et al. (2011 onwards) with permission)

Notes. Jarrett distinguished *Artocarpus multifidus* from *A. pinnatisectus* based on the number of leaf lobes (7–10 in the former and 12–20 in the latter); however, additional collections made since 1959 have made it clear that this is a variable character that cannot be used to distinguish these taxa. This leaves the abnormal staminate inflorescences on the type of *Artocarpus pinnatisectus* as the only distinguishing character. The fusion of two inflorescences side-to-side is an abnormality found occasionally in other species such as *Artocarpus heterophyllus*. As noted by Jarrett, they were not mentioned by Merrill in the protologue. Moreover, in phylogenomic analyses, *Artocarpus pinnatisectus* is nested within the *A. multifidus* clade (Gardner et al., 2021). Maintenance of separate taxa therefore appears to be unjustified. Berg et al. (2006) included this species in *Artocarpus altilis*, a grouping inconsistent with phylogenetic evidence. Moreover, *Artocarpus pinnatisectus* can be distinguished from *A. altilis* by the longer leaves with more lobes, syncarps with longer perianth apices and persistent interfloral bracts, and stouter staminate inflorescences with scattered sterile processes and a banana-like scent (M. Manting, pers. comm.).

1.19 ***Artocarpus scortechinii*** King in Hooker, Fl. Brit. India 5: 542 (1888); King, Ann. Roy. Bot. Gard. (Calcutta) 2: 12, t. 9 (1889). – TYPE: [Peninsular Malaysia], Perak, July 1883, *King 7792* (lectotype SING [SING0052137], designated here; isolectotypes BM [BM000951747], CAL [CAL0000014536, CAL0000014538], K [K001051076]). (Fig. 14)

Diagnostic characters. Leaves on mature trees entire and not wavy, with a smooth upper surface and a soft velvety lower surface; staminate inflorescences smaller, more shallowly sulcate, and shorter than in *Artocarpus elasticus*; syncarps without dimorphic perianth apices.

Distribution. Peninsular Malaysia, Singapore and Sumatra.

Notes. *Artocarpus scortechinii* differs from the sympatric *A. elasticus* (Fig. 7) as described above. Because the leaves have a flatter and more narrowly ovate aspect than *Artocarpus elasticus*, the species can be distinguished with confidence at quite a distance.

1.20 ***Artocarpus sericicarpus*** F.M.Jarrett, J. Arnold Arbor. 40: 350 (1959). – TYPE: Philippines, Luzon, Quezon. Guinayangan, January–April 1903, *Merrill 2024* (holotype US [US00089823]; isotypes K, NY [NY00025202, NY00025203, NY00025204], US [US00089822, US01094841]).

Artocarpus elasticus auct. non Blume: Fern.-Vill., Nov. App. 202 (1880); Stapf, Kew Bull. 1894: 108 (1894); Wester, Philipp. Agric. Rev. 8: 109, t. 8a (1915); Merrill, Enum. Philipp. Fl. Pl. 2: 41 (1923); Wester, Bull. Bur. Agric. Philipp. 39: 78, t. 196, 32c (1924); Brown, Useful Pl. Philipp. 463, f. 188 (1941).

Artocarpus blumei auct. non Trécul: Vidal, Revis. Pl. Vasc. Filip. 254 (1886); Elmer, Leafl. Philipp. Bot. 2: 613 (1909).

Diagnostic characters. Leaves on mature trees very large, corrugated but not wavy, usually with a smooth upper surface; staminate inflorescences short, deeply sulcate, and not twisted; syncarps with dimorphic perianth apices, the sterile ones narrower, longer, and more pubescent than on *Artocarpus elasticus*.

Distribution. Borneo, Sulawesi, Moluccas and Philippines (Palawan).

Notes. Artocarpus sericicarpus differs from *A. elasticus* (Fig. 7) as described above, as well as in the reportedly much tastier fruit (A. Lamb, pers. comm.). References to *Artocarpus elasticus* in earlier literature pertaining to the Philippines are generally based on *A. sericicarpus*, as *A. elasticus* is restricted to Palawan in the Philippines.

1.21 ***Artocarpus tamaran*** Becc., Nelle Foreste di Borneo 626 (1902). – TYPE: [Malaysia], Borneo, Sarawak, Mte Mattang [Matang] a Vallombrosa, December 1866, *Beccari PB 2996* (lectotype FI [FI013394, herb. no. 9384 – a single specimen over 3 sheets], designated by Jarrett (1959b); isolectotype K [K001051087]).

Diagnostic characters. Leaves on juvenile trees pinnately incised and often > 1 m long, becoming entire and < 35 cm long on mature trees; inflorescences with a banana cream pie scent, the staminate ones tuberculate and hairy and the pistillate ones with dimorphic flowers; the sterile ones very narrow and wiry.

Distribution. Borneo.

Notes. Artocarpus tamaran displays the most striking dimorphism between juvenile and adult leaves in the genus. Leaves on juvenile trees are pinnately dissected all the way to the midrib, but the lanceolate lobes are connected by a narrow wing of lamina running along the midrib. The leaves can be over a metre long, and the overall impression is that of a palm leaf. The mature leaves are entire, do not exceed 35 cm in length, and have a corrugated appearance similar to those of its companion in the emergent layer of the forest, *Dipterocarpus applanatus* Slooten. The staminate inflorescences are tuberculate with brown hairs, and the pistillate inflorescences have dimorphic perianth apices, with the long flowers much narrower than those of *Artocarpus elasticus* (Fig. 7) or *A. sericicarpus*.

1.22 ***Artocarpus teysmannii*** Miq., Fl. Ned. Ind., Eerste Bijv. 418 (1861). – TYPE: [Indonesia], Sumatra, Lampung, near Kebang, *J.E. Teijsmann H.B. 4387* (lectotype U [U0004435], designated by Jarrett (1959b); isolectotypes BO, L [L0039906]).

Artocarpus peduncularis Kurz, J. Bot. 13: 331 (1875). – TYPE: India, Nicobar Islands, Kamorta, *Kurz s.n.* (lectotype CAL [CAL0000014467], designated by Jarrett (1959b); isolectotype? February 1875, *Kurz 26096*, K [K000357629]).

Diagnostic characters. Trunks pale, tall and smooth, often with buttresses; syncarps with abruptly tapering perianth apices that are dimorphic in length; spicate staminate inflorescences with brown subulate processes resembling fat long hairs.

Distribution. From Nicobar Islands eastward to Malay Peninsula and Indonesia (as far east as West Papua).

Notes. *Artocarpus teysmannii* is a distinctive species that can often be recognised from a distance. Miquel consistently used the spelling '*teysmannii*' for species named for Teijsmann, and we therefore decline to correct the epithet to '*teijsmannii*' (cf. Berg et al., 2006). Our concept of *Artocarpus teysmannii* corresponds only to *A. teysmannii* subsp. *teysmannii* sensu Berg et al. (2006); we consider *A. teysmannii* subsp. *subglabrus* C.C.Berg synonymous with *A. sepicanus*.

1.23 ***Artocarpus treculianus*** Elmer, Leafl. Philipp. Bot. 2: 617 (1909). – TYPE: Philippines, Negros Oriental, Dumaguete, Cuernos Mountains, June 1908, *Elmer 10406* (lectotype BM, designated by Jarrett (1959b); isolectotypes A, BO, L [L0039907]).

Artocarpus ovatifolius Merr., Philipp. J. Sci., C 9: 268 (1914). – *Artocarpus sorsogonensis* Elmer ex Merr., Enum. Philipp. Fl. Pl. 2: 42 (1923), pro syn., nom. inval. – TYPE: Philippines, Luzon, San Antonio, June 1912, *Ramos BS 15040* (lectotype BM, designated by Jarrett (1959b); isolectotypes B [B 10 0294373], US [US00089826]).

Artocarpus ovatifolius Merr. var. *dolichostachys* Merr., Enum. Philipp. Fl. Pl. 2: 43 (1923). – TYPE: Philippines, Samar, April 1914, *Ramos 1603* (lectotype BM, designated by Jarrett (1959b); isolectotypes BO, GH [GH00046636], L [L0039908], NY [NY00025198], P [P06777815], SING [SING0052136]).

Artocarpus communis auct. non J.R.Forst. & G.Forst.: Merrill, Philipp. J. Sci., C 3: 401 (1908) (based on Camiguin, *Fenix BS 4069* and Batan, Santo Domingo de Baseo, *Fenix 3613*).

Diagnostic characters. Leaves on mature trees entire or incised; staminate inflorescences narrow (< 1 cm) but varying widely in length; synarps with flattened processes.

Distribution. Philippines.

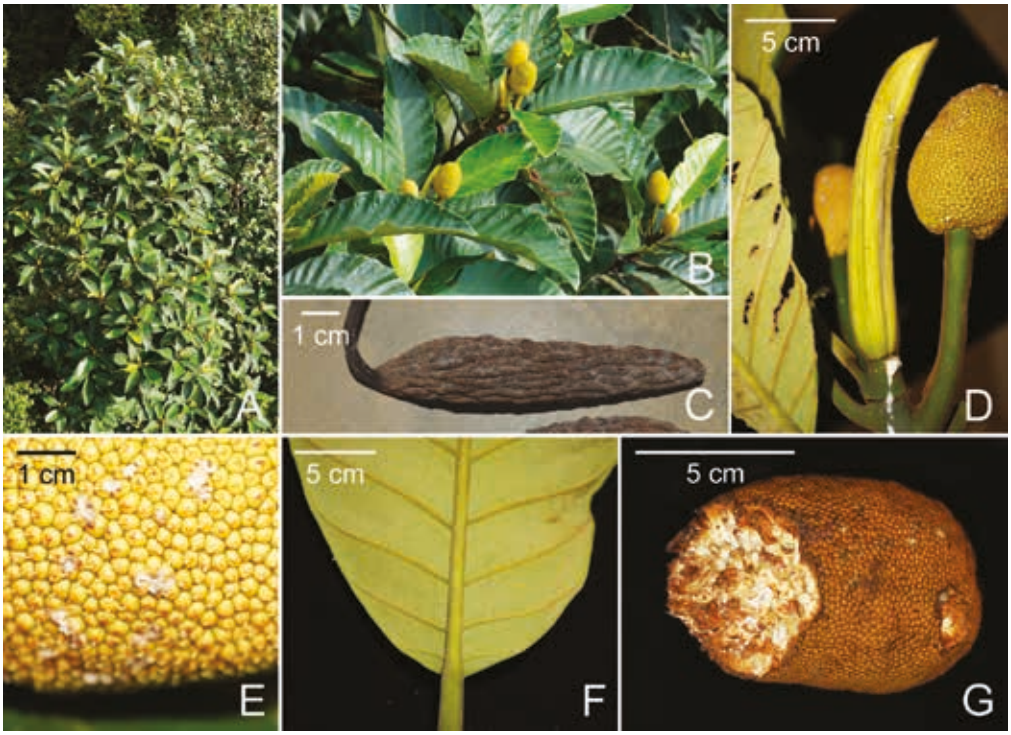

Fig. 14. *Artocarpus scortechinii* King. **A.** Tree. **B.** Leaves and pistillate inflorescences on tree. **C.** Dried staminate inflorescence. **D.** Stipule and immature syncarp. **E.** Pistillate inflorescence with stigmas. **F.** Leaf underside with pubescence. **G.** Open syncarp. All from Singapore. (Photos: A, B, D–G: R.C.J. Lim; C, E.M. Gardner)

Notes. Artocarpus treculianus can be distinguished from *Artocarpus blancoi* by the blunt rather than filiform perianth apices on the syncarps and the absence of grey villous pubescence on stipules. However, this heterogeneous complex requires more investigation; the mature leaves may be entire and nearly glabrous (cf. the type of *Artocarpus ovatifolius*) or pinnate and pubescent (cf. the type of *A. treculianus*), but intermediate forms abound as well. The length of the staminate inflorescences can vary by an order of magnitude (ranging from 1–21 cm), and syncarps range from irregularly ellipsoidal to almost perfectly globose.

2. *Artocarpus* subg. ***Artocarpus*** sect. ***Duricarpus*** F.M.Jarrett, J. Arnold Arbor. 40: 137 (1959). – TYPE: *Artocarpus rigidus* Blume.

Diagnostic characters. Pistillate perianth apices usually indurated and not flexuous; staminate inflorescences usually not spicate (subglobose to ovoid heads). A section of 14 species from India to Borneo and Java.

Two clades may be recognised:
1. **'Laevifolii'** (including *Artocarpus* ser. *Laevifolii* F.M.Jarrett): mostly (sub) glabrous leaves and mostly ellipsoidal staminate inflorescences (*Artocarpus brevipedunculatus* being the exception, with subglobose inflorescences). Five species: *Artocarpus anisophyllus* Miq., *A. brevipedunculatus* (F.M.Jarrett) C.C.Berg, *A. clementis* Merr., *A. lanceifolius* Roxb. and *A. sarawakensis* F.M.Jarrett.

2. **'Asperifolii'** (including most of *Artocarpus* ser. *Asperifolii* F.M.Jarrett): mostly pubescent leaves and subglobose to spicate staminate inflorescences. Eight species: *Artocarpus calophyllus* Kurz, *A. chama* Buch.-Ham., *A. hirsutus* Lam., *A. hispidus* F.M.Jarrett, *A. melinoxylus* Gagnep., *A. nobilis* Thwaites, *A. odoratissimus* Blanco and *A. rigidus* Blume.

2.1 ***Artocarpus anisophyllus*** Miq., Fl. Ned. Ind., Eerst Bijv. 422 (1861), as '*anisophylla*'. – TYPE: [Indonesia], [South] Sumatra, Palembang, Batoe Radja [Batu Raja], *Teijsmann HB 3698* (lectotype U [U0004422], designated by Jarrett (1959b); isolectotypes BO, K, L [L0039868, L0039869]). (Fig. 15)

Artocarpus klidang Boerl., Handl. Fl. Ned. Ind. 3: 333, 371 (1900), in clavi. – TYPE: [Indonesia], Bangka, *Teijsmann HB 7246* (lectotype L [L.1591494], designated here).

Artocarpus superbus Becc., Nelle Foreste di Borneo 625 (1902), as '*superba*'. – TYPE: [Malaysia], Borneo, Sarawak, Mte Mattang [Matang] a Valambrosa, December 1866, *Beccari PB 2997* (lectotype FI [FI013393, herb. no. 9399], designated by Jarrett (1959b); isolectotypes FI [FI013393, herb. no. 9399a], K [K001051100, K001051101]).

Artocarpus anisophyllus Miq. var. *sessilifolius* Kochummen, Gard. Bull. Singapore 50: 200 (1998). – TYPE: [Malaysia], Borneo, Sabah, Sandakan, Sepilok FR, 7 May 1955, *G.H.S. Wood s.n.* (holotype SAN; isotypes A [A01154841], SING [SING0046095]).

Diagnostic characters. Leaves on mature trees pinnately incised all the way to the midrib, with alternating long and short 'leaflets'.

Distribution. Thailand, Peninsular Malaysia, Singapore, Sumatra, Borneo and Philippines (Palawan).

Notes. This species is characterised by deeply dissected leaves that appear compound and anisophyllous, with alternating long and short 'leaflets' (lobes). Some plants in Borneo have somewhat smaller leaves, still appearing compound but often without marked anisophylly. Known as 'bensenge' in Central Kalimantan and 'karusung' in South Kalimantan, these plants have fruit characters intermediate between typical *Artocarpus anisophyllus* and *A. clementis* (Hanif Wicaksono, pers. comm.) and may correspond to the type of *A. anisophyllus* var. *sessilifolius* Kochummen. Further phylogenetic investigation of that complex of species, including the possibility

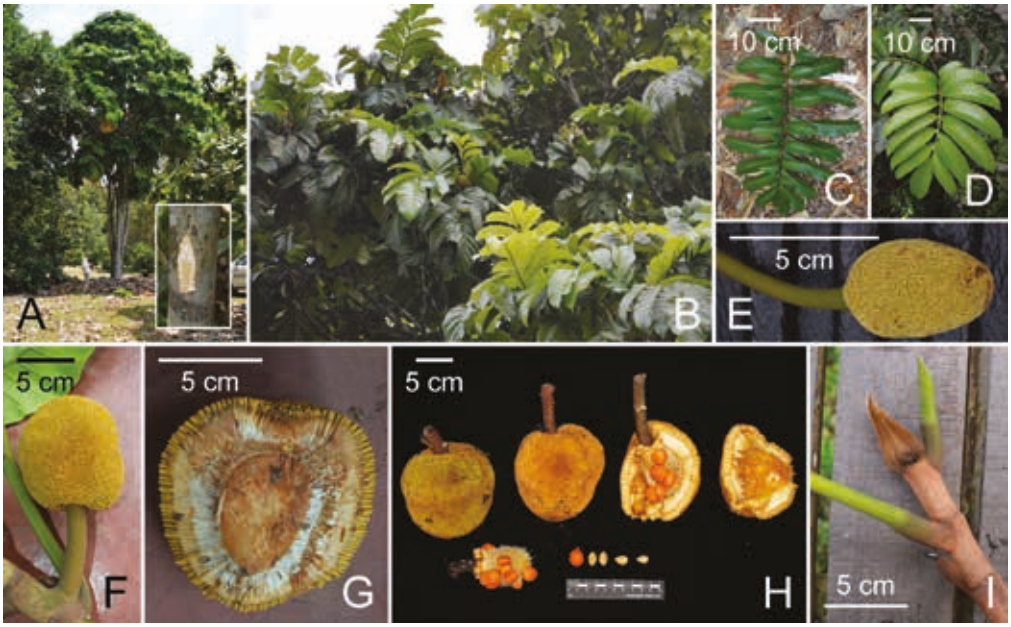

Fig. 15. *Artocarpus anisophyllus* Miq. **A.** Full tree (*EG229*). Inset: Bark (*NZ838*). **B.** Tree branches with syncarps. **C, D.** Variation in leaves from different trees (C, *EG251*). **E.** Staminate inflorescence. **F.** Branch with syncarp (*EG229*). **G.** Immature syncarp (*EG229*). **H.** Mature syncarp with orange perianth flesh surrounding achene fruits. **I.** Stipule and petiole (*NZ606*). A–G, I from Malaysia; H from Singapore. (Photos: A, B, I, N.J.C. Zerega; C, D–G, E.M. Gardner; H, R.C.J. Lim)

of hybridisation, may shed light on the issue. Boerlage's *Artocarpus klidang* was described only in his key to the species of *Artocarpus* found in the Dutch East Indies. The manuscript that was noted in an accompanying species list was presumably never published due to Boerlage's untimely death in Ternate. Although *klidang* (or *keledang*) is normally a vernacular name for *Artocarpus lanceifolius*, Boerlage associated it, albeit with some doubt, with *A. anisophyllus*, and indeed the original material from Bangka consists of juvenile specimens of the latter species.

2.2 *Artocarpus brevipedunculatus* (F.M.Jarrett) C.C.Berg, Blumea 50(3): 541 (2005). – *Artocarpus melinoxylus* Gagnep. subsp. *brevipedunculatus* F.M.Jarrett, J. Arnold Arbor. 40: 144 (1959). – TYPE: British North Borneo [Malaysia, Sabah], Beaufort, ½ mile N.E. from Beaufort Township, 6 May 1955, *Wood SAN A1733* (holotype A [A00034352]; isotypes BRI [BRI-AQ0064436], K not found, L [L0039897]).

Diagnostic characters. Twigs reddish pubescent; leaves thinly pubescent; staminate inflorescences subglobose without a strong scent; syncarps subglobose (up to 6 cm long) with orange flesh.

Distribution. Borneo.

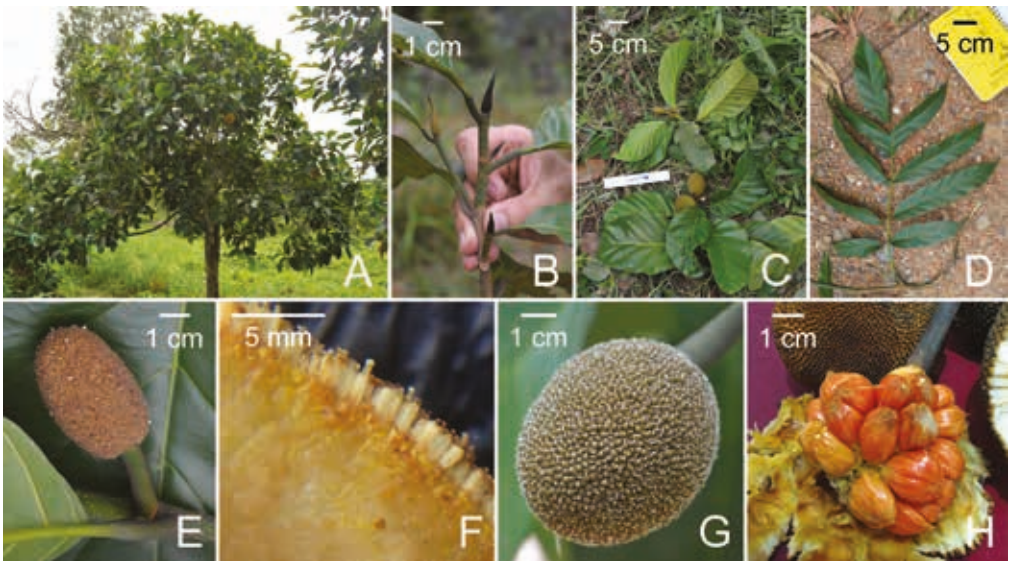

Fig. 16. *Artocarpus clementis* Merr. **A.** Tree (*EG183*). **B.** Branch with stipule (*NZ739*). **C.** Leaves and syncarps (*EG183*). **D.** Juvenile leaf (*NZ740*). **E.** Staminate inflorescence (*NZ739*). **F.** Close up of stamens (*EG183*). **G.** Pistillate inflorescence with simple stigmas. **H.** Ripe syncarp. A–G from Malaysian Borneo; H from Central Kalimantan. (Photos: A, C, F–G, E.M. Gardner; B, D, E, N.J.C. Zerega; H, E. Ednie)

Notes. The smaller syncarps of *Artocarpus brevipedunculatus* resemble those of its ally *A. clementis* (Fig. 16) in that they both have orange flesh.

2.3 *Artocarpus calophyllus* Kurz, Prelim. Rep. Forest Pegu App. A. p. cxxiv., App. B. 82, in clavi (1875), as '*calophylla*'; Kurz, Forest Fl. Burma 2: 431. (1877). – *Artocarpus chama* auct. non Buch.-Ham.: Berg, Fl. Thailand 10(4): 10, as 'calophyllus-form'. – TYPE: Burma [Myanmar], Tenasserim [Tanintharyi], *Kurz s.n.* (lectotype CAL [CAL0000014466], designated by Jarrett (1959b)). (Fig. 17)

Artocarpus asperulus Gagnep., Bull. Soc. Bot. France 73: 86 (1926), as '*asperula*'. – *Artocarpus rigidus* Blume subsp. *asperulus* (Gagnep.) F.M.Jarrett, J. Arnold Arbor. 40: 154 (1959). – *Artocarpus chama* auct. non Buch.-Ham.: Berg, Fl. Thailand 10(4): 10, as 'asperulus-form'. – TYPE: Annam [Vietnam], Nhatrang [Khanh Hoa] Prov., 24 May 1924, *Poilane 6644* (lectotype P [P00379050], designated by Jarrett (1959b); isolectotypes K [K001051063], P [P06777687]).

Artocarpus asperulus Gagnep. var. *hirtus* Bull. Soc. Bot. France 73: 87 (1926), as '*hirta*'. – TYPE: [Vietnam], Songlu, Bien Hoa Prov., August 1877, *Pierre 3777* (lectotype P [P06777709], designated by Jarrett (1959b); isolectotypes A [A00046768], F).

Fig. 17. *Artocarpus calophyllus* Kurz. **A.** Branches with leaves and pistillate inflorescences (*NZ507*). **B.** Juvenile leaf and stipule (*NZ512*). **C.** Syncarp and leaves (*NZ507*). All from Thailand. (Photos: N.J.C. Zerega)

Diagnostic characters. All parts pubescent, often yellowish; syncarps covered with straight tapering perianth apices.

Distribution. Myanmar, Thailand, Cambodia, Vietnam and northern Peninsular Malaysia.

Notes. This species as circumscribed here corresponds entirely to Jarrett's (1959) idea of *Artocarpus rigidus* subsp. *asperulus* and belongs to the clade (including *A. hispidus* (Fig. 18) and *A. rigidus* (Fig. 19)) with subglobose syncarps covered by straight, tapering perianth apices. *Artocarpus calophyllus* is consistently pubescent throughout, but not hispid as in *A. hispidus*. Two forms may be recognised as detailed by Berg et al. (2011). The 'asperulus' form has generally narrower leaves, usually subappressed, rough pubescence, persistent epidermis on the petioles, and pistillate inflorescences that are nearly sessile or at least on peduncles < 2 cm long with perianth apices 3–8 mm long. The 'calophyllus' form has proportionally broader leaves, more or less patent, denser, soft pubescence, exfoliating epidermis on the petioles, and pistillate inflorescences on peduncles up to 5 cm long, with somewhat longer perianth apices (6–10 mm). At least in Thailand, nearly all specimens can be sorted into one or the other of these forms, and further study may ultimately warrant the recognition of separate taxa.

2.4 ***Artocarpus chama*** Buch.-Ham., Mem. Wern. Nat. Hist. Soc. 5: 331 (1826). – TYPE: [Bangladesh], Rangamati, 17 April 1808, *Buchanan-Hamilton s.n.* [EIC 4657C] (lectotype K-W [K000357631], designated here).

Artocarpus chaplasha Roxb. [Hort. Beng. 66 (1814), nom. nud.], Fl. Ind. 3: 525 (1832). – TYPE: India, *Roxburgh s.n.* (lectotype K [K000357628], first step designated by Jarrett (1959b), second step designated here).

Urostigma chrysopthalmum Miq., London J. Bot. 6: 575 (1847). – *Ficus chrysophthalma* (Miq.) Miq., Ann. Mus. Bot. Lugduno-Batavi 3: 285 (1867). – TYPE: India, 1836, *Wight 949* (holotype E [E00288968]).

Diagnostic characters. Dense yellow pubescence throughout; peduncles up to 8 cm long; syncarps ellipsoidal to cylindrical with blunt perianth apices.

Distribution. India and Bangladesh.

Notes. The syncarps of *Artocarpus chama* have blunt perianth apices resembling those of *A. melinoxylus*, but the peduncles of *A. melinoxylus* are longer (7–13.5 cm), and the vegetative parts are not as pubescent.

Buchanan-Hamilton's protologue refers to specimens sent to Roxburgh from Chatigang [Chittagong] in 1798; as these could not be traced, another specimen at K-W with Buchanan-Hamilton's annotation must serve as the lectotype.

2.5 ***Artocarpus clementis*** Merr., J. Straits Branch Roy. Asiat. Soc. 85: 164 (1922). – *Artocarpus lanceifolius* Roxb. subsp. *clementis* (Merr.) F.M.Jarrett, J. Arnold Arbor. 40: 142 (1959). – TYPE: British North Borneo [Malaysia, Sabah], Mount Kinabalu, Gurulau Spur, November 1915, *Clemens 10770* (lectotype PNH n.v., designated by Jarrett (1959b); isolectotypes A [A00046794], BO, K [K001051099]). (Fig. 16)

Artocarpus lanceifolius auct. non Roxb.: Kochummen, Tree Fl. Sabah & Sarawak 3: 201 (2000); Berg, Fl. Males., ser. 1, 17(1): 97 (2006).

Diagnostic characters. Vegetative parts subglabrous; staminate inflorescences ellipsoidal with a strong fruity smell; syncarps subglobose, up to 8 cm long, with tapering, blunt perianth apices and orange flesh.

Distribution. Borneo.

Notes. Recognised by Jarrett (1959b) as a distinct subspecies but considered conspecific with *Artocarpus lanceifolius* (Fig. 20) by Berg et al. (2006), *A. clementis* differs from *A. lanceifolius* in having smaller staminate inflorescences (up to 6 cm long in *A. lanceifolius* but seldom exceeding 3 cm in *A. clementis*) with much shorter stamens (c. 3.5 mm long in *A. lanceifolius* but c. 1.5 mm in *A. clementis*), and a strong fruity odour (completely lacking in *A. lanceifolius* but similar to that of *A. anisophyllus*). The syncarps are smaller (to c. 8 cm long but up to 12 cm in *Artocarpus lanceifolius*) as are the peduncles (c. 4 cm long but 5–10 cm in *A. lanecifolius*) with vivid red-orange flesh and tapering, spreading perianth apices. The subglabrous leaves of *Artocarpus clementis* tend to be smaller than those of *A. lanceifolius*, rarely if ever attaining the upper range of the latter, which can reach 30 cm in length. Juvenile material can be easily distinguished by leaves that are dissected all the way to the midrib in *Artocarpus*

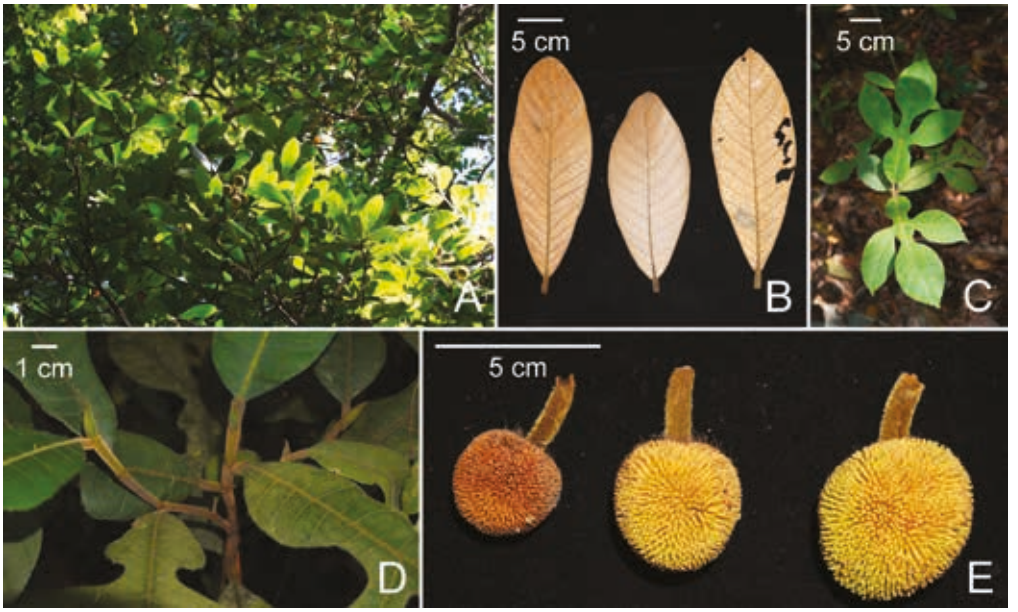

Fig. 18. *Artocarpus hispidus* F.M. Jarrett. **A.** Tree. **B.** Dried adult leaves. **C.** Juvenile leaves. **D.** Hispid twigs. **E.** Syncarps. All from Singapore. (Photos: R.C.J. Lim)

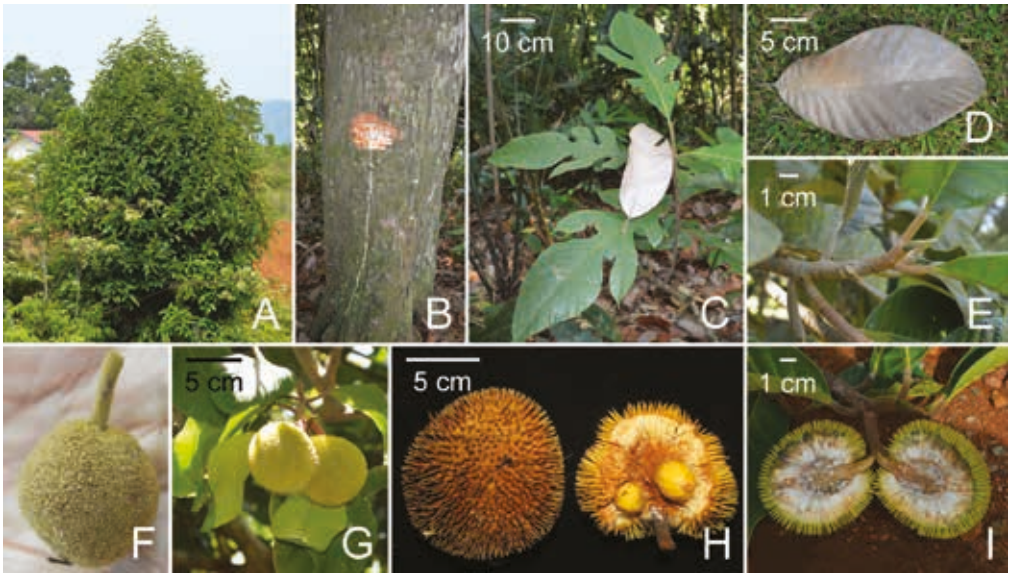

Fig. 19. *Artocarpus rigidus* Blume. **A.** Tree (*NZ728*). **B.** Bark with slash and exudate (*NZ831*). **C.** Juvenile leaves with dried mature leaf (*NZ832*). **D.** Mature dried leaf (*NZ920*). **E.** Stipule (*NZ831*). **F.** Staminate inflorescence at anthesis (*NZ920*). **G.** Pistillate inflorescences on branch with adult leaves. **H.** Mature syncarp. **I.** Open immature syncarp (*NZ728*). A–E, I from Malaysian Borneo; F, G from Philippines; H from Singapore. (Photos: A–E, I, N.J.C. Zerega; F, G, E.M. Gardner; H, R.C.J. Lim)

clementis, appearing compound and strongly resembling those of *A. anisophyllus*; in *A. lanceifolius* leaves on juvenile plants can be deeply pinnately lobed, but never all the way to the midrib and appearing compound.

2.6 ***Artocarpus hirsutus*** Lam., Encycl. 3(1): 211 (1789), as '*hirsuta*'. – *Artocarpus pubescens* Willd., Sp. Pl., ed. 4, 4(1): 189 (1805), nom. illeg. superfl. – *Saccus hirsutus* Kuntze, Revis. Gen. Pl. 2: 633 (1891), nom. illeg. superfl. – TYPE: [Published illustration] 'Ansjeli' in Rheede, Hort. Malab. 3, t. 32 (1682), lectotype designated here.

Ficus malabarica Miq., London J. Bot. 7: 457 (1848), p.p. – TYPE: India, Madras [Chennai], 1835, *Wight 873* (lectotype U [U.0245540], designated by Jarrett (1959b)).

Diagnostic characters. Staminate inflorescences spicate; syncarps yellow with abruptly tapering perianth apices and yellow-orange flesh.

Distribution. India.

Notes. The staminate inflorescences of *Artocarpus hirsutus* are spicate, which is unusual within *Artocarpus* sect. *Duricarpus*; the only other member of the section sharing this feature is *Artocarpus nobilis*.

Lamarck's protologue was based not on specimens but on Rheede's 'Ansjeli' in the *Hortus Indicus Malabaricus* (Van Rheede tot Draakestein, 1682). Rheede's plate leaves no doubt as to the identity of our species and we therefore designate it as the lectotype. The type of *Ficus malabarica* Miq. contains leaves of *Artocarpus hirsutus* and a fig of *Ficus palmata* Forssk.

2.7 ***Artocarpus hispidus*** F.M.Jarrett, J. Arnold Arbor. 40: 149 (1959). – TYPE: Singapore, Bukit Timah Nature Reserve, 2 June 1940, *Corner SFN 37035* (holotype SING [SING0051260]; isotype L [L0039892]). (Fig. 18)

Diagnostic characters. All parts dense yellowish pubescent; leaves obovate; peduncles 2.5–3.5 cm long; syncarps covered with straight tapering perianth apices.

Distribution. Peninsular Malaysia and Singapore.

Notes. This species is distinguishable from the sympatric *Artocarpus rigidus* (Fig. 19) by the stronger indumentum, longer peduncles (0.8–2.5 cm in *A. rigidus*) and obovate leaves.

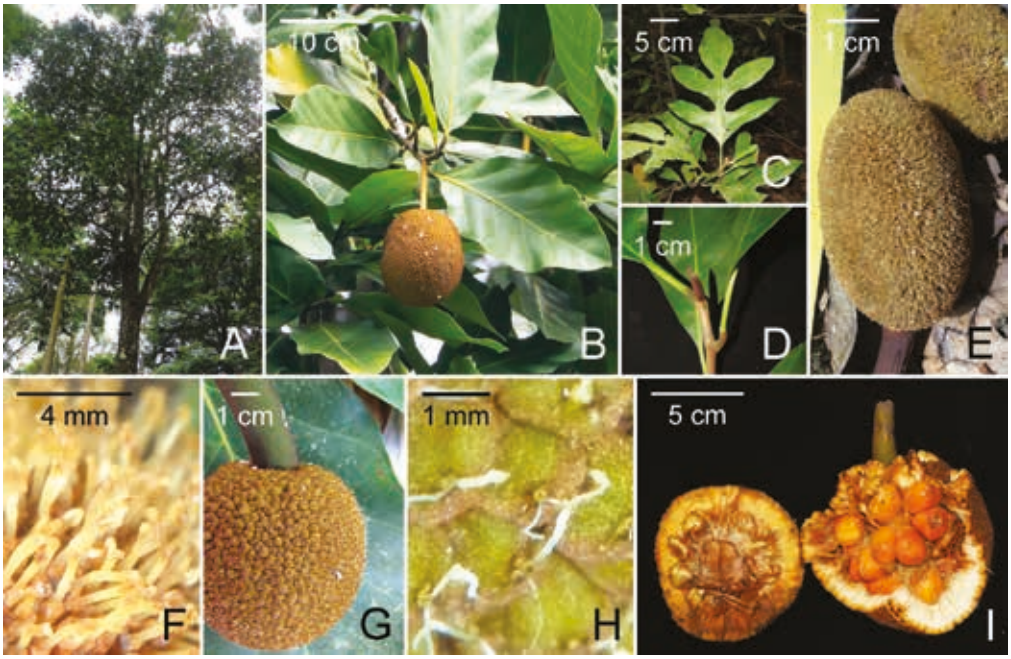

Fig. 20. *Artocarpus lanceifolius* Roxb. **A.** Tree. **B.** Syncarp on branch with leaves. **C.** Juvenile leaf. **D.** Stipule. **E.** Staminate inflorescence. **F.** Close up of stamens in staminate inflorescence at anthesis. **G.** Pistillate inflorescence with bifid receptive stigmas. **H.** Close up of pistillate inflorescence bifid stigmas. **I.** Open syncarp. A, E–H from Malaysian Borneo (*EG2*); B–D, I from Singapore. (Photos: A, E–H, E.M. Gardner; B, S.K. Ganesan; C, D, I, R.C.J. Lim)

2.8 ***Artocarpus lanceifolius*** Roxb. [Hort. Bengal. 103 (1814), nom. nud.], Fl. Ind. 3: 572 (1832), as '*lanceæfolia*'; Wight, Ic. Ind. Or. 2: 4, t. 679 (1843), as '*lanceæfolia*'. – TYPE: [Unpublished illustration] Drawing by Roxburgh, no. 1021, cat. no. 53-56-14 (lectotype CAL, designated here), cf. Wight, Icon. Pl. Ind. Orient. 2: t. 679 (1843). (Fig. 20)

Artocarpus reticulatus W.Hunter, J. Straits Branch Roy. Asiat. Soc. 53: 114 (1909), as '*reticulata*', nom. illeg. non Miq. (1867). – TYPE: [Unpublished illustration] Drawing by Roxburgh, no. 1021, cat. no. 53-56-14 (neotype CAL, designated here), cf. Wight, Ic. Ind. Or. 2: t. 679 (1843).

Diagnostic characters. Vegetative parts subglabrous; staminate inflorescences ellipsoidal, without a strong scent; syncarps subglobose, up to 12 cm long, with flattened processes.

Distribution. Thailand, Peninsular Malaysia, Singapore, Sumatra, and perhaps Borneo (Sarawak, Batang Ai).

Notes. Distinguishing characters are given above under *Artocarpus clementis* (Fig. 16). Roxburgh's 1832 description is frustratingly terse and contains no reference to a type: '*Leaves* broad-lanceolar, or oblong, acuminate, entire. *Fruit* terminal, spherical. A native of Prince of Wales' Island'. Nevertheless, the only species native to Penang Island matching this description is *Artocarpus lanceifolius*. While the leaf description might apply to *Artocarpus dadah* Miq. or *A. griffithii* (King) Merr., the inflorescences of the latter two arise serially from the leaf axils and would never be described as terminal. In our taxon, however, the inflorescences arise from the final leaf axil, appearing terminal. Any doubt is dispelled by Roxburgh's drawing (preserved at CAL), which formed the basis for the plate in Wight's *Icones* (1843). As the only original material that can be confidently associated with Roxburgh's name is the illustration, it must serve as the type. Roxburgh apparently originally thought to call the species '*Artocarpus elliptica*', which appears on the drawing, struck out, and replaced by '*Artocarpus lanceofolia*'. Kochummen (2000) cited the plate in Wight's *Icones* as the type; this would have been an effective designation of a neotype had the original drawing been lost.

Hunter's manuscript containing his *Artocarpus reticulatus* was published posthumously by Ridley, along with Ridley's annotations, the latter including a probable association with *A. lanceifolius*. Hunter's drawings were apparently already lost by the time Ridley published his manuscript, and no other original material is known; it therefore seems best to typify the name with the lectotype of *Artocarpus lanceifolius*.

Specimens from Batang Ai, Sri Aman, in Sarawak represent the only known Bornean material probably referable to *A. lanceifolius*.

2.9 *Artocarpus melinoxylus* Gagnep., Bull. Soc. Bot. France 73: 88 (1926). – TYPE: Annam [Vietnam], Ba na près de Tourane, 11 July 1923, *Poilane 7079* (lectotype P [P00756687], designated by Jarrett (1959b); isolectotype A [A00046635]). (Fig. 21)

Artocarpus chama auct. non Buch.-Ham.: Berg, Fl. Thailand 10(4): 10, as 'chama-form'.

Diagnostic characters. Leaves with a subglabrous upper surface, peduncle of the staminate inflorescence up to 5 cm long; syncarp subglobose with blunt perianth apices.

Distribution. Vietnam.

Notes. Artocarpus melinoxylus resembles *A. chama* with its blunt pistillate perianth apices, but it differs in the shorter and stouter peduncle of the staminate inflorescence (up to 50 × 3 mm in *A. melinoxylus*, compared to 60–75 × c. 1.5 mm in *A. chama*) and subglabrous upper surface of the leaf in *A. melinoxylus*, compared to dense indumentum in *A. chama*.

Fig. 21. *Artocarpus melinoxylus* Gagnep. **A.** Tree. **B.** Branch with leaves and syncarps. All from Vietnam. (Photos: J. Leong-Škorničková)

2.10 ***Artocarpus nobilis*** Thwaites, Enum. Pl. Zeyl. [Thwaites] 282 (1861). – TYPE: Ceylon [Sri Lanka], 1863, *Thwaites CP 2818* (lectotype PDA n.v., designated by Jarrett (1959b); possible isolectotypes BM [BM000951738, BM000951739], BR [BR0000005297108], C, FR [FR0031170], GH [GH00034346], K [K001051080, K001051081, K001051082], MEL [MEL2413290, MEL2413291], MPU [MPU017277], P [P06777225, P06777226, P06777227]).

Artocarpus pubescens auct. non Willd.: Moon, Cat. Pl. Ceylon 61 (1821).

Diagnostic characters. Leaf margins crenate, staminate inflorescences spicate, very long (over 7 cm) and narrow (c. 1.5 cm).

Distribution. Sri Lanka.

Notes. Within *Artocarpus* sect. *Duricarpus*, this distinctive species shares its spicate staminate inflorescences (70–130 × c. 15 mm) only with *A. hirsutus*.

2.11 ***Artocarpus odoratissimus*** Blanco, Fl. Filip. 671 (1837). – TYPE: Philippines, Mindoro, Calapan, May 1916, *Merrill SB 1019* (neotype BM, designated by Jarrett (1959b); isoneotypes F, L [L0039899, L0039900], NY [NY00025197], P [P06777811], US [US00688532, US00688533]).

Artocarpus mutabilis Becc., Nelle Foreste di Borneo 627 (1902). – TYPE: [Malaysia], Borneo, Sarawak, Kuching, Siul, October 1865, *Beccari PB 758* (lectotype FI [FI008133], designated by Jarrett (1960); isolectotypes FI [FI008139], K [K001051097, K001051098], P [P06777806, P06777807]).

Artocarpus tarap Becc., Nelle Foreste di Borneo 626 (1902). – TYPE: [Malaysia], Borneo, Sarawak, Kuching, November 1866, *Beccari PB 2697* (lectotype FI [FI008142], designated by Jarrett (1960); isolectotype K [K001051093]).

Artocarpus nuciferus J.V.Thomps., Cat. Exotic Pl. Mauritius 25 (1816), as '*nucifera*', nom. nud. (cf. P06827315); Thompson, Cat. Exotic Pl. Mauritius, ed. 2, 39 (1822).

Diagnostic characters. Leaves scabrid with yellow pubescence; syncarps ellipsoidal, up to 20 cm long, with straight, indurated perianth apices and sweet white flesh.

Distribution. Borneo (native), Philippines (probably introduced), and in cultivation.

Notes. Artocarpus odoratissimus can be recognised by its broad sandpapery leaves covered in yellowish hairs and its distinctive large syncarps. This species is widely cultivated in Borneo and Mindanao, where it is known as *tarap* and *marang*, respectively. Two taxa recognized by the Iban people in Sarawak correspond to this species: the cultivated *lumok*, and the wild *pingan*. The latter, characterized by smaller fruits often has long patent hairs on *stipules* and has sometimes been misidentified as *Artocarpus sarawakensis*; however it in fact belongs to *A. odoratissimus*. The Iban distinctions are supported by molecular evidence (Gardner, 2017).

2.12 ***Artocarpus rigidus*** Blume, Bijdr. Fl. Ned. Ind. 482 (1825), as '*rigida*'. – *Artocarpus cuspidatus* Griff., Not. Pl. Asiat. 4: 400 (1854), nom. illeg. superfl. – *Artocarpus muricatus* W.Hunter, J. Straits Branch Roy. Asiat. Soc. 53: 114 (1909), as '*muricata*', nom. illeg. superfl. – TYPE: [Indonesia], Java, *Blume 1364* (lectotype L [L0039903], designated by Jarrett (1959b); isolectotypes CAL [CAL0000033469], K [K001051092], P? [P06777771], S [S07-8181]). (Fig. 19)

Radermachia rotunda Houtt., Nat. Hist. II. 11: 455 (1779), nom. rejic. prop. – *Artocarpus rotundus* (Houtt.) Panzer, Pflanzensyst. 10: 380 (1783), as '*rotunda*'. – TYPE: not designated.

Artocarpus echinatus Roxb. [Hort. Bengal. 66 (1814), nom. nud.], Fl. Ind. 3: 527 (1832), as '*echinata*'. – TYPE: locality unknown, *Roxburgh s.n.* (lectotype BM [BM000900565], designated by Jarrett (1959b)).

Artocarpus runcinatus Reinw. ex Blume, Cat. Gew. Buitenzorg 101 (1823), as '*runcinata*', nom. nud.

Artocarpus kertau Zoll. ex Miq. in Zollinger, Syst. Verz. 2: 89, 95 (1854). – TYPE: [Indonesia], Java, Bantam [Banten], 15 March 1847, *Zollinger 1009* (lectotype P [P00507961], designated by Jarrett (1959b); isolectotypes A [A00034351], L [L0039904], U [U0245447]).

Artocarpus dimorphophyllus Miq., Fl. Ned. Ind., Eerste Bijv. 417 (1861), as '*dimorphophylla*'. – TYPE: [Indonesia], Sumatra, Jeboes Banka, *Teijsmann HB 3369* (lectotype U [U0004434], designated by Jarrett (1959b); isolectotype BO).

Artocarpus varians Miq., Fl. Ned. Ind., Eerste Bijv. 417 (1861). – TYPE: [Indonesia], Sumatra, Lampongs, *Teijsmann HB 4358* (lectotype U [U0124150], designated by Jarrett (1959b); isolectotypes BO, L [L0039902]).

Diagnostic characters. Pubescence usually sparse; leaves often with a smooth upper surface, drying grey; peduncles very short, the inflorescences appearing essentially sessile; subglobose syncarps covered in straight tapering processes.

Distribution. Myanmar, Peninsular Malaysia, Singapore, Sumatra, Borneo, Java, Lesser Sunda Islands, and perhaps Thailand.

Notes. The pubescence on *Artocarpus rigidus* is much sparser than that on *Artocarpus calophyllus* or *A. hispidus*, and the leaves are more classically elliptic.

The identity and status of *Artocarpus rotundus* (Houtt.) Panz. were reviewed by the authors in their proposal to reject that name (Gardner & Zerega, 2020b).

2.13 ***Artocarpus sarawakensis*** F.M.Jarrett, Blumea 22(3): 410 (1975). – TYPE: [Malaysia], Borneo, Sarawak, Bintulu, Segan FR, 23 November 1961, *Ilias S 15109* (holotype K [K000227612]; isotypes C, L [L0039905], SAN, SAR).

Diagnostic characters. Leaves very sparsely pubescent with a smooth upper surface; stipules densely covered with long yellow hairs; syncarps subglobose (up to 5 cm long), covered with closely-set obtuse perianth apices.

Distribution. Borneo (Sarawak).

Notes. Artocarpus sarawakensis is a distinctive and rare species often confused with *A. odoratissimus* but easily distinguishable from that species based on the characters given above. The Sumatran specimen (*Burley et al. 1792*, L0816142) assigned to this species by Berg et al. (2006) belongs instead to *Artocarpus lanceifolius*, although it differs from the usual form of that species in the pubescent stipules and abaxial surface of the leaves.

3. ***Artocarpus*** subg. ***Artocarpus*** sect. ***Cauliflori*** (F.M.Jarrett) Zerega & E.M.Gardner, **stat. nov.** – *Artocarpus* ser. *Cauliflori* F.M.Jarrett, J. Arnold Arbor. 40: 327 (1959). – *Artocarpus* subg. *Cauliflori* (F.M.Jarrett) Zerega, Syst. Bot. 35: 778 (2010). – TYPE: *Artocarpus integer* (Thunb.) Merr.

Diagnostic characters. Inflorescences on cauliflorous or ramiflorous short shoots.

3.1 ***Artocarpus annulatus*** F.M.Jarrett, Blumea 22: 409 (1975). – TYPE: [Malaysia], Borneo, Sarawak, Gn. Mentawa, Tiang Bekap [Teng Bukap], 25 July 1963, *W.L. Chew & J.R. Anderson CWL 665* (holotype K [K001051090, K001051091 – a single specimen over two sheets, plus carpological material]; isotypes A, K, KEP, L [L0039870], SAR, SING [SING0052146]).

Diagnostic characters. Bark fissured, showing red inner bark; leaves separating into layers when torn; staminate inflorescences with annulate constrictions; syncarps cauliflorous and cylindrical (to c. 10 cm long) with elongate perianth apices.

Distribution. Borneo (Sarawak).

Notes. This critically-endangered limestone-endemic species is easily distinguished from *Artocarpus heterophyllus* and *A. integer* based on the characters above, in particular the beehive-shaped staminate inflorescences.

3.2 ***Artocarpus heterophyllus*** Lam., Encycl. 3(1): 209 (1789), as '*heterophylla*' – *Artocarpus integrifolius* L.f. var. *heterophyllus* Pers., Syn. Pl. 2: 531 (1807), as 'ß *heterophylla*'. – TYPE: [Mauritius], *Commerson s.n.* (lectotype P-JU [P00307204], first step designated by Corner (1938), second step designated here; isolectotypes MPU [?MPU1281760, MPU1281761], P-JU [P00307420, P00307459]). (Fig. 22)

Artocarpus philippensis Lam., Encycl. 3(1): 210 (1789). – TYPE: [Philippines], *Sonnerat s.n.* (lectotype P-JU [P00382286] p.p., designated by Corner (1939), second step designated here, excluding the two inflorescences labelled 'fleurs femmelles du Rima').

Polyphema jaca Lour., Fl. Cochinch. 2: 546 (1790). – TYPE: Cochinchina [Vietnam], *Loureiro s.n.* (lectotype BM [BM000900564], designated by Corner (1938)).

Artocarpus nanca Noronha, Verh. Batavia. Genootsch. Kunst. 5(5): 7 (1790), nom. nud.

Artocarpus brasiliensis Gomes, Observ. Bot.-Med. Nonnullis Bras. Pl. 2: 34, t. 5 (1803). – TYPE: [Published illustration] Gomes, Observ. Bot.-Med. Nonnullis Bras. Pl. 2: t. 5 (1803), lectotype designated here.

Artocarpus maximus Blanco, Fl. Filip. 669 (1837), as '*maxima*'. – TYPE: Philippines, Luzon, Camarines, December 1913, *Merrill SB 415* (neotype PNH, designated here; isoneotypes F, L [L0817014], P [P06777323], US [US00688534]).

Artocarpus integrifolius auct. non L.f., mult. auct.

Fig. 22. *Artocarpus heterophyllus* Lam. **A.** Tree in cultivation (*NZ944*). **B.** Stipule (*N902*). **C.** Leaves (*NZ944*). **D.** Cauliflorous syncarps and staminate inflorescence. **E.** Open syncarps. **F.** Staminate inflorescence at anthesis. **G.** Staminate inflorescence with fungus and gall midges. **H.** Syncarp with annulus at base (*EG241*). **I.** Pistillate inflorescence with receptive stigmas. **J.** Mature syncarps. A–C, H from Malaysia; D, F from US (Florida); E from Indonesia; G, I from Thailand; J from Bangladesh. (Photos: N.J.C. Zerega)

Diagnostic characters. Leaves subglabrous; syncarps gigantic and cauliflorous, with an annular ring around the petiole attachment; perianth apices pyramidate.

Distribution. Probably native to India (Western Ghats) but cultivated throughout tropical and subtropical regions.

Notes. The cultivated jackfruit can be distinguished from the cempedak (*Artocarpus integer*) by the annular ring surrounding the peduncle where it attaches to the syncarp, as well as the more or less glabrous vegetative parts in *A. heterophyllus*.

The type material for *Artocarpus heterophyllus* consists of three sheets in Jussieu's herbarium. Corner's (1939) designation of the specimen with 'precocious male inflorescences and sapling leaves of a seedling' probably refers to P00307204; however, lest there be any doubt, we second-step designate that specimen as the lectotype.

The original material of *Artocarpus philippensis* in Lamarck's herbarium is mixed, containing material from both *Artocarpus heterophyllus* and (probably) *A. blancoi*. Corner, treating *Artocarpus philippensis* as a synonym of *A. heterophyllus*,

cited a Sonnerat collection as the type; this can only refer to P00382286 (excluding the inflorescences with long flowers, which probably belong to *A. blancoi* and are labelled separately as 'fleurs femmelles du Rima'), as the other sheet annotated as *A. philippensis* (P00382287) is only *A. blancoi*.

Many authors have misapplied the name *Artocarpus integrifolius* to *A. heterophyllus*, but as explained by Corner (1939) and Jarrett (1959b), the former is a superfluous name for *A. integer*. Merrill likewise intended his combination *Artocarpus integer* (the legitimate name for the cempedak, see 3.3 below) to apply to jackfruit (Corner, 1939).

A search of LISU herbarium turned up no *Artocarpus* specimens seen by Gomes; accordingly, we designate his illustration of *A. brasiliensis* Gomes as the lectotype.

3.3 ***Artocarpus integer*** (Thunb.) Merr., Interpr. Herb. Amboin. 190 (1917) – *Radermachia integra* Thunb., Kongl. Vetensk. Acad. Handl. 37: 254 (1776). – *Sitodium macrocarpon* Thunb., Philos. Trans. 69: 467 (1779), nom. illeg. superfl. – *Artocarpus integrifolius* L.f., Suppl. Pl. 412 (1781), as '*integrifolia*', nom. illeg. superfl. – *Sitodium cauliflorum* Gaertn. Fruct. Sem. Pl. 1: 345 (1788), nom. illeg. superfl. – [*Artocarpus jaca* Lam. var. *ß*, Encycl. 3: 209 (1789)]. – *Artocarpus macrocarpos* (Thunb.) Dancer, Cat. Bot. Gard. Jamaica I (1792), as '*macrocarpon*', nom. illeg. superfl. – *Artocarpus integrifolius* var. *hirsutus* Stokes, Bot. Mat. Med. 4: 330 (1812), as '*integrifolia* var. *hirsuta',* nom. illeg. superfl. – TYPE: [Indonesia], Java, *Thunberg s.n.* (lectotype UPS [UPS:BOT:V-135213], designated by Corner (1939); isolectotypes? L [L0052851, L0052852]). (Fig. 23)

Artocarpus hirsutissimus Kurz, Natuurk. Tijdschr. Ned.-Indië 27: 182 (1864), as '*hirsutissima*' – TYPE: [Indonesia], Bangka, *Kurz 1017* (lectotype CAL n.v., designated by Jarrett (1959b)).

Artocarpus pilosus Noronha, Verh. Batavia Genootsch. Kunst. 5(5): 7 (1790) nom. nud.

Polyphema champeden Lour., Fl. Cochinch. 547 (1790), p.p. – *Artocarpus polyphema* Pers., Syn. Pl. 2(2): 531 (1807), nom. illeg. superfl. – *Artocarpus champeden* (Lour.) Stokes, Bot. Mat. Med. 4: 330 (1812). – TYPE: [Published illustration] 'Soccus arboreus minor' in Rumphius, Herb. Amboin. 1: 107, t. 31 (1741), lectotype designated here.

Artocarpus pilosus Reinw. ex Blume, Cat. Gew. Buitenzorg 101 (1823), as '*pilosa*', nom. nud.

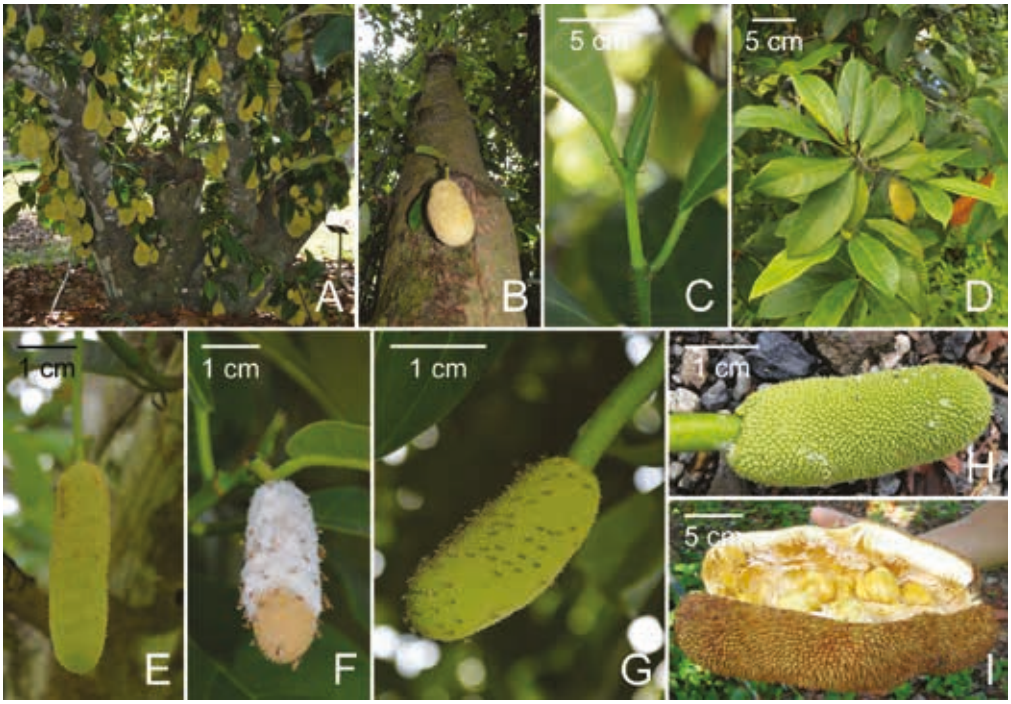

Fig. 23. *Artocarpus integer* (Thunb.) Merr. **A.** Tree in cultivation. **B.** Tree in forest (*EG402*). **C.** Stipule (*NZ710*). **D.** Branch with leaves (*NZ645*). **E.** Staminate inflorescence at anthesis. **F.** Staminate inflorescence with fungus and gall midges (*NZ725*). **G.** Pistillate inflorescence with gall midges. **H.** Pistillate inflorescence (*NZ616*). **I.** Mature syncarp. All from Malaysia. (Photos: A–H, N.J.C. Zerega; I, M. Wang)

3.3.1 *Artocarpus integer* (Thunb.) Merr. var. *integer*

Diagnostic characters. Leaves and twigs usually pubescent with wiry hairs; syncarps cauliflorous and smaller than in those of *Artocarpus heterophyllus* and without an annulus at the base of the peduncle; perianth apices usually with a pebbly look; mature fleshy perianth tissue surrounding the true fruit ('seed') separates readily from the syncarp rind, unlike in *A. heterophyllus*.

Distribution. Thailand, Peninsular Malaysia, Singapore, Sumatra, Borneo, Java, Sulawesi and Moluccas, but cultivated in many tropical areas.

Notes. This is the widely-cultivated *cemepedak*, distinguishable from *Artocarpus heterophyllus* by the lack of an annular ring where the peduncle attaches to the syncarp and the presence of wiry hairs at least on the stipule and at the nodes (but often throughout the vegetative parts).

Corner (1939) and Jarrett (1959b) extensively reviewed the taxonomic history of jackfruit and cempedak, but the status of *Polyphema champeden* Lour. remained

unsettled. In his commentary on Loureiro's *Flora Cochinchinensis*, Merrill (1935) stated that there was a type specimen for it at BM. However, Corner (1939) could find no evidence of such a specimen and viewed *Polyphema champeden* as a '*mixtum compositum*', because it was based on Rumphius's 'Soccus aboreus minor' (= *Artocarpus integer*) along with plants Loureiro had ostensibly seen in Malacca and Cochinchina (Vietnam), for which he used the vernacular 'cậy mit nai' (probably *Artocarpus calophyllus*). Jarrett (1959b) further noted that much of Loureiro's *Polyphema champeden* description was derived from the description and illustration of 'Soccus arboreus minor' of Rumphius (1741: 107, t. 31), with the exception of one statement ('spathae saepe repando-incisae') being derived from an illustration in Bontius' *Historiae Naturalis and Medicae Indiae Orientalis*, with the erroneous name 'champidaca' written above a drawing combining the incised leaves of breadfruit with a durian fruit (Bontius, 1658: 119). Because the majority of the description was based on Rumphius, his illustration is designated here as the lectotype in the absence of original specimen material.

3.3.2 ***Artocarpus integer*** var. ***silvestris*** Corner, Gard. Bull. Singapore, 10: 76 (1939). – TYPE: [Peninsular] Malaysia, Johore, *Corner 32988* (holotype SING [SING0069581, SING0069582, SING0069583 – a single specimen over three sheets]).

Distribution. Peninsular Malaysia.

Notes. This is thought to be the wild relative of cempedak known as *bangkong* in Peninsular Malaysia, with often glabrous leaves and smaller fruits without a strong taste or smell. Distinguishing characters were reviewed at length by Corner (1939), and a molecular study by Wang et al. (2018) supported Corner's taxonomy.

4. ***Artocarpus*** subg. ***Glandulifolium*** **(**F.M.Jarrett) E.M.Gardner & Zerega, **stat. nov.** – *Artocarpus* subg. *Pseudojaca* sect. *Glandulifolium* F.M.Jarrett, J. Arnold Arbor. 41: 134 (1960). – TYPE: *Artocarpus altissimus* (Miq.) J.J.Sm.

Diagnostic characters. Leaves distichous, leaf margins glandular-crenate.

4.1 ***Artocarpus altissimus*** (Miq.) J.J.Sm. in Boerlage, Icon. Bogor. 3: t. 233 (1907). – *Morus altissima* Miq., Fl. Ned. Ind., Eerste Bijv. 3: 415 (1861), as '*Morus? altissima*'. – TYPE: [Indonesia], Sumatra, Sekajoe, Moenie, *Teijsmann HB 3972* (lectotype L [L0039867], designated by Jarrett (1960); isolectotype BO n.v.).

Grewia subcordata Miq., Fl. Ned. Ind., Eerste Bijv. 3: 404 (1861), as '*Grewia? subcordata*'. – TYPE: [Indonesia], Sumatra, Palembang, Moeara Enim, *Teijsmann HB 4024* (lectotype L [L.1591513], designated by Jarrett (1960)).

Diagnostic characters. Leaves distichous with glandular-crenate margins.

Distribution. Thailand, Sumatra and Borneo (West Kalimantan).

Notes. With its glandular-crenate leaf margins, *Artocarpus altissimus* cannot be mistaken for any other member of its genus.

Jarrett's (1960) citation of *HB 4042* as the 'holotype' of *Grewia subcordata* Miq. appears to be a typographical error for *HB 4024*, corrected here.

5. ***Artocarpus*** subg. ***Aenigma*** E.M.Gardner & Zerega, **subg. nov.** – TYPE: *Artocarpus sepicanus* Diels.

Diagnostic characters. Leaves spirally arranged, petiole epidermis exfoliating, perianth apices barely free, endocarps small, up to c. 5 mm long.

Distribution. New Guinea.

Notes. The name of this subgenus refers to the enigmatic taxonomic position of its only member, *Artocarpus sepicanus*, which, as discussed above, displays characters intermediate between subgenera *Artocarpus* and *Pseudojaca* and may have originated from an ancient hybridisation between members of those two subgenera.

5.1 ***Artocarpus sepicanus*** Diels., Bot. Jahrb. Syst. 67: 176 (1935), as '*sepicana*'. – TYPE: [Papua New Guinea], Northeast New Guinea, Sepik, Malu, 17 January 1913, *Ledermann 10628* (lectotype B [B 10 0294371], designated by Jarrett (1959b)).

Artocarpus teysmannii subsp. *subglabrus* C.C.Berg, Blumea 50(3): 543 (2005), as '*teijsmannii* subsp. *subglabrus*'. – TYPE: Papua New Guinea, Morobe Prov., December 1944, *L.S. Smith NGF 1176* (holotype LAE; isotypes A [A00993769], BRI [BRI-AQ0064501], CANB [CANB213527.1], K [K000577448]).

Diagnostic characters. Leaves spirally arranged and subglabrous; petiole epidermis exfoliating; perianth apices barely free, seeds < 5 mm long.

Distribution. New Guinea.

Notes. Artocarpus sepicanus is notable for its unusually small seeds (c. 5 mm long) and for its petioles with exfoliating epidermis (common in *Artocarpus* subg. *Pseudojaca* but rare in *A.* subg. *Artocarpus*, where it was previously placed). The exfoliating epidermis character is, however, uncharacteristically lacking in the type of *Artocarpus teysmannii* subsp. *subglabrus*, which is nevertheless considered synonymous with *A. sepicanus* due to other morphological characters and its consistent placement with

A. sepicanus in phylogenetic analyses. Another specimen of interest here is *Ficus ralumensis* K.Schum., which is a *mixtum compositum* containing a fig of *Ficus calopilina* Diels (fide Berg & Corner (2005)) and leaves of an *Artocarpus* species of uncertain identity. Berg et al. (2006) included these under *Artocarpus teysmannii* subsp. *subglabrus*. However, the leaves of the *Ficus ralumensis* type specimen do not match those of *Artocarpus teysmannii* or *A. sepicanus*, and the *F. ralumensis* type was collected in New Britain, well outside the range of *A. teysmannii* s.s., which has so far not been recorded further east than West Papua, Indonesia. The leaf material may relate instead to an entity known from a single collection in Solomon Islands, *Bourale BSIP 9301* (L, SING), which is part of the 'Rugosi' clade and allied to a new species of *Artocarpus* to be described from Manus Island, Papua New Guinea.

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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 denote samples newly prepared for this study. Reads for all samples have been deposited in GenBank under BioProject PRJNA322184.

Artocarpus altilis (Parkinson) Fosberg, French Polynesia (cult. in USA), 2000, *Breadfruit Institute Grid no. V8* (National Tropical Botanical Garden, living accession), SRR12283102; Samoa (cult. in USA), 2000, *Breadfruit Institute Grid no. K7* (National Tropical Botanical Garden, living accession), SRR12282879.

Artocarpus altissimus (Miq.) J.J.Sm., Java (cult.), 2016, *Gardner et al. 441* (F), SRR12283100; Thailand, 2012, *Sinbu s.n.* (F), SRR12283081; Sumatra, 1934, *bb. 18789* (L), SRR12282904.

Artocarpus anisophyllus Miq., Borneo, 2013, *N. Zerega et al. NZ606* (F), SRR3907106.

Artocarpus annulatus F.M.Jarrett, Borneo, 2016, *N. Zerega et al. NZ985* (F), SRR12283099; Borneo, 1980, *S38722* (L), SRR12282903.

Artocarpus bergii E.M.Gardner et al., Moluccas, 2013, *R. Mahroji 160* (MO), SRR12283031; ibidem, 2013, *I. Haris 26* (MO), SRR12283019.

Artocarpus blancoi (Elmer) Merr., Philippines, 1920, *Ramos 42018* (L) (isoneotype), SRR12282902.

Artocarpus brevipedunculatus (F.M.Jarrett) C.C.Berg, Borneo, 2013, *N. Zerega et al. NZ814* (F), SRR3907332.

Artocarpus borneensis Merr., Borneo, 2013, *Zerega et al. 686* (F), SRR12283067.

Artocarpus calophyllus Kurz, Thailand, 2012, *N. Zerega et al. NZ512* (CHIC), SRR12283096; ibidem, 2012, *NZ507* (CHIC), SRR12283043.

Artocarpus calophyllus Kurz ('asperulus' form), Thailand, 1995, *WT52* (FTBG), SRR12283004; Vietnam, 2006, *NYHN 675* (MO), SRR12283041.

Artocarpus camansi Blanco, Honduras (cult. in USA), 2000, *Breadfruit Institute Grid no. MV2* (National Tropical Botanical Garden, living accession), SRR12283098; Papua New Guinea, 2000, *Breadfruit Institute Grid no. McB1* (National Tropical Botanical Garden, living accession), SRR12283119; Papua New Guinea, 1960, *Hoogland 10612* (BO), SRR12283003; Philippines, 2000, *Breadfruit Institute Grid no. M10* (National Tropical Botanical Garden, living accession), SRR12283118; Philippines, 1991, *Barbon et al. PPI1915* (L), SRR15903816*.

Artocarpus chama Buch.-Ham., Bangladesh, 2011, *N. Zerega et al. NZ354* (F), SRR12283079.

Artocarpus clementis Merr., Borneo, 2012, *N. Zerega et al. NZ739* (F), SRR3907263; Borneo, 2016, *E. Gardner et al. EG183* (F), SRR15903815*.

Artocarpus corneri Kochummen, Borneo, 1963, *Fuchs 21347* (K), SRR12283015; Borneo, 2016, *E. Gardner & N. Zerega EG333* (F), SRR12283093; Borneo, 2017, *E. Gardner et al. EG519* (F), SRR15903814*.

Artocarpus dadah Miq., Borneo, 2013, *Zerega et al. 694* (F), SRR3907210.

Artocarpus elasticus Reinw. ex. Blume, Borneo, 2014, *E. Gardner et al. EG87* (F), SRR3907457; Thailand, 2012, *N. Zerega et al. NZ458* (CHIC), SRR12283040; Singapore, 2018, *E. Gardner et al. EG722* (F), SRR15903813*.

Artocarpus elasticus* × *A. corneri, Borneo, 2016, *E. Gardner & N. Zerega EG336* (F), SRR12283092.

Artocarpus excelsus F.M.Jarrett, Borneo, 2016, *E. Gardner et al. EG222* (F), SRR12283091; Borneo, 2013, *N. Zerega et al. NZ780* (F), SRR3907331.

Artocarpus fretessii Teijsm. & Binn. ex Hassk., Borneo, 2013, *Zerega et al. 929* (F), SRR3907410.

Artocarpus fulvicortex F.M.Jarrett, Singapore, 2012, *Lee Y.Q. 35* (F), SRR12283075.

Artocarpus frutescens (Becc.) Renner, Borneo, 2016, *E. Gardner & N. Zerega EG411* (F, SAR), SRR12283088.

Artocarpus glaucus Blume, 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., Peninsular Malaysia, 2002, *Zerega et al. 216* (F), SRR12283066.

Artocarpus heterophyllus Lam., Borneo (cult.), 2014, *E. Gardner et al. EG98* (F), SRR3907497.

Artocarpus hirsutus Lam., India, 2013, *N. Zerega et al. NZ953* (CHIC, photo voucher), SRR12283116; India, 1969, *C.J. Saldanha 12423* (US), SRR12283005.

Artocarpus hispidus F.M.Jarrett, Peninsular Malaysia, 2002, *N. Zerega et al. NZ258* (F), SRR12283071.

Artocarpus horridus F.M.Jarrett, Moluccas (cult. in Java), 2016, *E. Gardner et al. EG437* (F), SRR12283095; *E. Gardner et al. EG438* (F), SRR15903822*.

Artocarpus cf. ***horridus*** F.M.Jarrett, Moluccas (cult. in Java), 2016, *E. Gardner et al. EG429* (F), SRR12283097.

Artocarpus humilis Becc., Borneo, 2016, *Gardner et al. 258* (F), SRR12283050.

Artocarpus hypargyreus Hance ex. Benth., China, 2016, *Gardner et al. 170* (F), SRR12283054.

Artocarpus integer (Thunb.) Merr. var. ***integer,*** Borneo, 2013, *N. Zerega et al. NZ918* (F), SRR3907371.

Artocarpus integer (Thunb.) Merr. var. ***silvestris*** Corner, Peninsular Malaysia, 2013, *M. Wang et al. MW201* (CHIC), SRR12282898.

Artocarpus jarrettiae Kochummen, Borneo, 1987, *SAN120933* (K), SRR12282898.

Artocarpus kemando Miq., Borneo, 2014, *E. Gardner et al. EG261* (F), SRR12283052; Borneo, 2013, *N. Zerega et al. NZ612* (F), SRR3907163.

Artocarpus aff. ***kemando*** Miq., Borneo, 2004, *AA2766* (L), SRR12282886.

Artocarpus lacucha Roxb. ex Buch.-Ham., Thailand, 2012, *Zerega et al. 420* (F), SRR3907082.

Artocarpus lamellosus Blanco, Philippines, 1992, *Gaerlan et al. PPI10374* (F), SRR12282893.

Artocarpus lanceifolius Roxb., Peninsular Malaysia, 2002, *N. Zerega et. al. NZ241* (F), SRR15903821*; Peninsular Malaysia, 2013, *E. Gardner et al. EG2* (KEP), SRR12283000.

Artocarpus cf. ***lanceifolius*** Roxb., Sumatra, 1988, *Burley 1792* (L), SRR12283021.

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

Artocarpus lowii King, Peninsular Malaysia, 2013, *M. Wang et al. MWL2* (CHIC), SRR3907544.

Artocarpus longifolius Becc. subsp. ***adpressus*** C.C.Berg, Borneo, 2016, *Gardner & Zerega 412* (F), SRR12283094.

Artocarpus maingayi King, Sumatra, 1972, *De Wilde 13584* (L), SRR12282998; Peninsular Malaysia, 2002, *N. Zerega et al. NZ257* (F), SRR12283069.

Artocarpus mariannensis Trécul, Cult. in USA from Micronesia, 2000, *Breadfruit Institute Grid no. DD4* (National Tropical Botanical Garden, living accession), SRR12283068; Cult. in USA from Micronesia, 2000, *Breadfruit Institute Grid no. CC5* (National Tropical Botanical Garden, living accession), SRR12283051.

Artocarpus melinoxylus Gagnep., Vietnam, 2008, *DDS14222* (F), SRR12282896; Vietnam, 2016, *J. Leong*-Škorničková *et al. 2924* (SING), SRR12283046*.

Artocarpus montanus E.M.Gardner & Zerega, Vietnam, 1995, *Averyanov et al. VH1819* (MO) (isotype), SRR12283017; *VH445* (MO), SRR12282907.

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

Artocarpus nigrescens Elmer, Philippines, 1919, *Ramos BS 34736* (US), SRR12282995.

Artocarpus nobilis Thwaites, Sri Lanka, 1985, *A.H.M. Jayasuriya 3283* (US), SRR12282892; Sri Lanka, 1973, *Kostermans 24593* (L), SRR12282993.

Artocarpus obtusus F.M.Jarrett, Borneo, 2016, *E. Gardner et al. EG248* (F), SRR12283049; Borneo, 2013, *N. Zerega NZ729* (F), SRR12283064; Borneo, 1972, *S31741* (L), SRR12283048.

Artocarpus odoratissimus Blanco, Borneo, 2016, *E. Gardner et al. EG294* (F), SRR12283047; Borneo, 2013, *N. Zerega et al. NZ618* (F), SRR12283115.

Artocarpus ovatus Blanco, USA (cult.), 2000, *Zerega 202* (F), SRR12283063.

Artocarpus parvus Gagnep., Borneo (cult.), 2013, *Zerega et al. 911* (F), SRR3907350.

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

Artocarpus pinnatisectus Merr., Philippines, 1992, *PPI3911* (K), SRR12282895; Philippines, 1913, *Escritor BS 20789* (US) (lectotype), SRR12282890; Philippines, 1991, *PPI2376* (L), SRR12282901.

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

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

Artocarpus rigidus Blume, Borneo, 2013, *N. Zerega et al. NZ728* (F), SRR3907233; Borneo, 2016, *E. Gardner et al. EG263* (F), SRR12549298; Peninsular Malaysia, 2002, *N. Zerega et al. 230* (F), SRR12283042.

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

Artocarpus rubrovenius Warb., Philippines, 1987, *Burley 84* (F), SRR12282884.

Artocarpus sarawakensis F.M.Jarrett, Sarawak, 1965, *S23876* (L), SRR12282881; Borneo, 2017, *E. Gardner et al. EG527* (F), SRR12282962*.

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Artocarpus styracifolius Pierre, China, 2016, *Gardner et al. 176* (F), SRR12283038.

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

Artocarpus tamaran Becc., Borneo, 2014, *E. Gardner et al. EG92* (F), SRR3907480.

Artocarpus teysmannii Miq., Borneo, 2013, *N. Zerega et al. NZ946* (F), SRR3907434.

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

Artocarpus tonkinensis A.Chev. ex. Gagnep., China, 2016, *Gardner et al. 174* (F), SRR12283037.

Artocarpus treculianus Elmer, Philippines, 1910, *Elmer 12468* (US), SRR12282985; Philippines, 1911, *Elmer 13135* (US), SRR12282984; Philippines, 2000, *N. Zerega et al. NZ203* (F), SRR12283058; Taiwan, 2000, *Yang 13056* (MO), SRR12283036.

Artocarpus aff. ***treculianus*** Elmer, Philippines, 1991, *PPI2741* (L), SRR12282882.

Artocarpus vriesianus Miq. var. ***vrieseanus***, Moluccas, 2013, *Tjut Bangun et al. 684* (BO), SRR12834858.

Artocarpus xanthocarpus Merr., Taiwan, 2003, *Yang 15648* (MO), SRR12283033.

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