Systematics and Species Limits of Breadfruit (Artocarpus, Moraceae)

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Communicating Editor: Wendy B. Zomlefer

ABSTRACT. Breadfruit (Artocarpus, Moraceae) is an important staple in Oceania and throughout much of the tropics. Interpretations of species delimitations among breadfruit and its closest relatives have varied from recognition of one to several species. To better understand the systematics and ultimately the origins of breadfruit, we considered evidence from molecular data. Amplified fragment length polymorphism data for 261 individuals of breadfruit, its closest relatives, putative hybrids, and nine outgroup taxa were analyzed using neighbor joining and parsimony analyses. Three species, A. altilis (domesticated breadfruit), A. camansi, and A. mariannensis, are recognized and the existence of hybrids (A. altilis × A. mariannensis) verified. A revised treatment based on the molecular results, as well as morphological and geographical considerations, is presented.

Artocarpus J. R. & G. Forster (Moraceae) comprises nearly 60 species (Jarrett 1959a, b, 1960; Kochummen 2000), including two widely cultivated throughout the tropics, breadfruit (A. altillis Parkinson) Fosberg and jackfruit (A. heterophyllus Lamark). The remaining species are primarily restricted to Malesia and Southeast Asia and include several utilized on a regional scale for food or timber. Breadfruit was domesticated in Oceania where it has been a traditional source of carbohydrates for millennia, and hundreds of cultivars have been selected for and named (Wilder 1928; Ragone 1997). Some cultivars are fertile diploids (2n = 2x = 56), but many are sterile hybrids or triploids (2n = 3x = ~84) and must be vegetatively propagated (Ragone 2001; Zerega et al. 2004). Within the last two centuries, a small percentage of Pacific breadfruit cultivar diversity has been introduced to other parts of the tropics including the Caribbean, Central and South America, Africa, and India, making breadfruit pantropically important (Ragone 1997). The great morphological diversity, particularly among Pacific cultivars and their closest relatives, has resulted in the publication of numerous binomials and various interpretations of species limits. While gross morphological leaf and syncarp characters have been useful for defining and selecting cultivars, the overlapping nature of some of these characters as well as the presence of hybrids has confounded taxonomists (Jarrett 1959b; Fosberg 1960).

Two fundamental issues remain unresolved regarding breadfruit systematics. The first, treated briefly here, is the correct binomial for domesticated breadfruit. Although this has been discussed by Merrill (1954), Jarrett (1959a), and Fosberg (1941, 1960), much inconsistency remains in the literature regarding the correct name. The generic name Artocarpus (from the Greek artos = bread and karpos = fruit) has been conserved (Fosberg 1939; Rousseau 1955), but there has been much confusion about the correct specific epithet. The earliest post-Linnaean binomial applied to breadfruit, Sitodium altile Parkinson, comes from the notes of Sydney Parkinson, one of the artists who accompanied Joseph Banks on the voyage of the Endeavour (Parkinson 1773). Sydney Parkinson died during the voyage, and his brother Stanfield Parkinson posthumously published his work. Merrill (1954) has argued that, in general, the names in this work were not validly published, because he maintained that a) Sydney Parkinson did not intend to publish them, b) the original author was probably Daniel Solander, and c) the descriptions lack botanical data. However, he also indicated that “in a very few cases, there may be reasons for accepting selected Parkinson entries as more or less validly published”—including Sitodium altile with a lengthy description adequate for proper identification of the plant (height, abundance of latex, leaf shape, the presence of separate male and female [flowers] inflorescences, gross morphological characters of the syncarp, and methods for food preparation).

 Nonetheless, Merrill (1954) and subsequent authors (Jarrett 1959a) still rejected Sitodium altile as validly published. Consequently, they referred to two other names, Artocarpus communis Forster (1776) and Radermachia incisa Thunberg (1776). Both names were published three years after Sitodium altile, but priority cannot be established between them (Merrill 1954; Jarrett 1959a). Jarrett (1959a, b) therefore adopted A. communis as the correct name on the grounds that it was more
widely used. However, since *Sitodium altile* was validly published with an adequate description accompanying the binomial, and the name has undisputed priority over all other published names, the correct name for breadfruit is *Artocarpus altillis* (Parkinson) Fosberg (Fosberg 1941, 1960).

The second issue regards species delimitations within the breadfruit complex that includes up to three species, *A. altilis* (domesticated breadfruit), *A. mariannensis* Trécult, and *A. camansi* Blanco (Fig. 1). Morphological diversity is partitioned differently among these species according to various authors. Jarrett (1959b) published the most recent treatment for the breadfruit complex and took a conservative approach, recognizing one highly variable species, *A. commnis*, that encompasses the diversity represented by both domesticated breadfruit and its closest relatives. However, she acknowledged that the material she examined was inadequate and mostly sterile, and suggested that further detailed studies were necessary. Trécult (1847) recognized two species, *A. incisa* L. f. (= *A. altilis*, domesticated sterile breadfruit) and a wild species endemic to the Mariana Islands and Palau, *A. mariannensis* (Figs. 1, 2). Fosberg (1960) also recognized two species, *A. mariannensis* and *A. altilis* that, in his assessment, encompassed seedless domesticated and “wild” seeded breadfruit (the “seeds” are technically thin walled achenes). Based on leaf indumentum and shape, as well as syncarp characters, he also suggested that hybridization between sterile *A. altilis* and fertile diploid *A. mariannensis* was occurring in Micronesia (Fosberg 1960). Blanco (1837) and Quisumbing (1940) both recognized two species, the seedless domesticated breadfruit (*A. rima* Blanco = *A. altilis*) and a wild relative, *A. camansi*, native to New Guinea, and possibly the Moluccas and the Philippines (Figs. 1, 2; Jarrett 1959b).

The problem of species limits within the breadfruit complex has not been examined in a phylogenetic framework or with molecular tools. The objective of our study was to reconstruct a phylogeny for *A. altilis*, *A. camansi*, and *A. mariannensis* with AFLP (amplified fragment length polymorphisms) data to test monophyly of putative species and to correlate the results with morphological and geographical characters for a revised treatment. The AFLP technique (Vos et al. 1995) has been shown to be a useful tool for studying relationships among closely related species, at the population level, or at the interface of the two (Yamamoto et al. 1998; Loh et al. 1999; Parsons and Shaw 2001; Buntjer et al. 2002; Beardsley et al. 2003; Dragoo et al. 2003). Additionally, AFLP data have proven to be highly reproducible (Jones et al. 1997). We collected AFLP data for 261 individuals representing the broad morphological diversity encompassed in all three putative species and hybrids, as well as data for nine outgroup taxa.

**Materials and Methods**

**Taxon Sampling.** The ingroup includes 24 putative *A. mariannensis* individuals, 29 putative *A. camansi* individuals, and 208 domesticated breadfruit individuals from throughout Oceania. Of the domesticated breadfruit, 74 have been classified as having arisen from *A. altilis × A. mariannensis* hybrids, and 134 as putative *A. altilis* individuals (Appendix 1). Ingroup samples were assigned to a species based on morphological characters discussed in the taxonomic treatment below. These characters come from the literature (Blanco 1837; Trécult 1847; Quisumbing 1940; Fosberg 1960; Ragone 1997) and personal observation of living trees and herbarium specimens (Appendix 1). Outgroup selection was based on previous molecular and morphological phylogenetic studies (Zerega 2003) and comprised the sister clade (*A. elasticus* Reinw. ex Blume, *A. kemandu* Miq., *A. janth King*, *A. maingay King*, *A. sictochen King*, and *A. tamara Becc.*) to the ingroup as well as members of the other clades (*A. trecolius* Elmer, *A. herophythus* Lamarc, and *A. lanceolatus Roxb.) in the same subgenus as the ingroup (*Artocarpus* subg. *Artocarpus*). Plants were collected in Papua New Guinea, Pohnpei Federated States of Micronesia, the Northern Mariana Islands, Singapore, Malaysia, and from the Breadfruit Institute, the most comprehensive breadfruit germplasm collection in the world, located at the National Tropical Botanical Garden (NTBG) in Hana, Maui, Hawaii.

**DNA Extraction and Amplified Fragment Length Polymorphisms.** A CTAB method (Zerega et al. 2002) was used to extract genomic DNA from approximately 1 cm² of leaf tissue dried in silica gel. DNA concentrations were estimated by comparing genomic DNA to known quantities on an agarose gel.

AFLP reactions were run using the AFLP Plant Mapping kit (Applied Biosystems, Foster City, California, USA) with a modified protocol (Zerega et al. 2002). Briefly, genomic DNA (0.2–0.3 μg) was digested with EcoRl and Msel enzymes, known flanking sequences which could be used as priming sites were ligated onto the restriction fragments, pre-selective PCR reactions with a single selective nucleotide on the 3' end of the primers were run, and this was followed by selective PCR with three selective nucleotides on the 3' end of the primers. Sixty-four selective primer combinations were screened on six samples (two each of *A. altilis*, *A. camansi*, and *A. mariannensis*), and three primer combinations were chosen based on having the highest number of bands and the highest percentage of polymorphic bands (*EcoRlCA/ Msel-CTC, EcoRF-CA/ Msel-CAT, EcoRl-AG/Msel-CTG*). The selective amplification products were separated and visualized on a 5% Long Ranger (Cambrex, Rockland, Maine, USA) gel on an ABI 377 sequencer using Genescan 3.1 and a Genescan Rox standard for each lane (Applied Biosystems). The standard contained 16 fluorescent-labeled fragments ranging in size from 35 to 500 base pairs so that the size of the AFLP fragments could be determined. The dataset and trees have been deposited in TreeBASE (study accession number S1261, matrix accession number M2203).

Genotyper 2.1 (Applied Biosystems) was used to visualize AFLP electropherograms and the data were scored manually for the presence and absence of different size fragments. Ambiguous size categories (those in which the intensity of the fragment varied so widely among samples that it was difficult to ascertain its presence or absence in some samples) were excluded. Fragments of the same size were considered homologous and were scored as either present or absent in each individual to create a binary data matrix. Homology of co-migrating bands among congenic species and within species has been previously addressed (Parsons and Shaw 2001; Rouppe van der Voort et al. 1997; Waugh et al. 1997). The studies found that same-sized fragments had very high sequence identity. As genetic distances decrease, the probability of correctly equating fragment size with homology increases (van de Zande and Bijlsma 1995). In addition, the use of polyacrylamide gels to separate AFLP bands rather than agarose gels and the presence
of a standard in every lane provide very accurate resolution of fragment size.

**Analyses.** Interspecific and intraspecific relationships within the breadfruit complex were explored using both neighbor joining (NJ) and maximum parsimony (MP) analyses. Although use of parsimony analysis for dominant marker data such as AFLP has been criticized (Baldeljui 1999), several studies have demonstrated that parsimony-based phylogenies based on sequence data yield the same robust topologies as those based on AFLP data, and that distance and parsimony analysis of the same AFLP dataset yield similar results (Zerega et al. 2002; Beardsley et al. 2003; Dragoo et al. 2003).

The AFLP data were treated as nonadditive, equally weighted characters and analyzed in PAUP* (Swofford 2002). The data were analyzed both with and without the hybrid accessions. Distance estimates for the NJ analyses were calculated using the index of Nei and Li (1979) and support was measured using one thousand bootstrap replicates. Maximum parsimony analyses used heuristic searches with 1000 random sequence addition replicates, holding no more than 100 trees per replicate, and TBR (tree-bisection-reconnection) branch swapping. Resulting trees were then used as starting trees in another round of TBR branch swapping holding up to 20,000 most parsimonious trees (MPT). To ascertain the relative degree of support for MP trees, bootstrap values were estimated using 100 replicates with 10 random addition sequence replicates each. To investigate the collapse of the monophyly of *A. altilis* in the parsimony analysis, the monophyly of *A. altilis* was enforced and used as a constraint in heuristic searches of the data. The topologies of randomly chosen most parsimonious trees (MPTs) from the constrained and unconstrained searches were compared statistically (Shimodaira and Hasegawa 1999).

**RESULTS**

**Hybrids Excluded.** Data from three AFLP primer pair combinations for *A. altilis*, *A. camansi*, *A. mariannensis*, and outgroup taxa were combined and yielded 171 polymorphic bands, 146 of which were parsimony informative. In the NJ analysis all three species form a monophyletic group with 98% bootstrap support (Fig. 3). *Artocarpus mariannensis* is monophyletic (87% support) and sister to a cluster containing *A. altilis* and *A. camansi*. Within this cluster, *A. camansi* is monophyletic and sister to a monophyletic group comprising 132 of the 134 *A. altilis* individuals. Thus, with the exception of two accessions (Zerega 194 and Ragone 326), *A. altilis* forms a monophyletic group. Although cultivars from the same region tend to cluster more closely together, there is no consistent geographic pattern. Additionally, cultivars with the same name do not necessarily group together.

Results of the first round of MP analysis yielded 13 MPTs with 890 steps, which were then swapped to completion and yielded 8664 MPTs with 889 steps, consistency index (CI) = 0.16, and retention index (RI) = 0.72. The topology of the strict consensus shares important features with the NJ tree (Fig. 4). The monophyly of the ingroup has 80% bootstrap support. *Artocarpus mariannensis* is monophyletic, but with very low support (52%), and nested within a clade of *A. altilis* from throughout Oceania, and the monophyly of *A. camansi* has no bootstrap support. *Artocarpus altilis* is nonmonophyletic, and most of the samples form a polytomy at the base of the ingroup. A statistical comparison of tree topologies from unconstrained and constrained searches enforcing the monophyly of *A. altilis* revealed that a topology with a constrained, monophyletic *A. altilis* is not significantly different than an unconstrained MPT (*p* = 0.7656) (Shimodaira and Hasegawa 1999).

**Hybrids Included.** With 74 *A. altilis* × *A. mariannensis* hybrids also included in the analyses, there were 174 polymorphic bands, 152 of which were parsimony informative. In NJ analyses the ingroup is monophyletic with 92% bootstrap support, *A. camansi* is resolved as a monophyletic lineage with no support, but both *A. mariannensis* and *A. altilis* are polyphyletic (Fig. 5). The hybrids are scattered throughout the tree with most of them in a cluster with *A. mariannensis* and a few clustered with *A. altilis*. Maximum parsimony analysis of the same data set reveals the same interspecific topology (tree not shown).

**DISCUSSION**

*Artocarpus camansi* and *Artocarpus mariannensis*. *Artocarpus camansi* is indigenous to New Guinea where it is common in the lowlands and grows in flooded riverbanks, secondary and primary growth forest, freshwater swamps, and in cultivation (Jarrett 1959b). It may also be indigenous to the Moluccas (Rumphius 1741) and possibly the Philippines (Quismumbing 1940). However, it may have been introduced and naturalized in the Philippines during the 1600s (Jarrett 1959b; Zerega et al. 2004). The introduction of *A. camansi* into cultivation for its edible seeds in other tropical regions outside of Oceania over the last few hundred years is well documented (Leakey 1977; Ragone 1997).

The range of *Artocarpus mariannensis* is not sympatric with *A. camansi* (Fig. 2). The former grows naturally in the uplifted limestone islands and coastal areas of Palau and in limestone and ravine forests in the Northern Mariana Islands where its fruits and seeds are harvested. It has been introduced to other islands in Micronesia including Chuuk, Yap, Pohnpei, Kosrae, and various atolls, and recently into the Polynesian islands of Tokelau, Tuvalu, and Hawaii (Ragone 2001). In addition to their distinct geographic ranges, *A. camansi* and *A. mariannensis* each have a suite of unique diagnostic leaf and infructescence characters, elaborated upon in the taxonomic treatment below (Fig. 1; Blanco 1837; Trécul 1847; Quismumbing 1940).

Molecular data further support the monophyly of *A. camansi* and *A. mariannensis*, as well as their close relationship with domesticated breadfruit (Fig. 3). As would be expected, the inclusion of cultivars, which are considered to be hybrids (*A. altilis* × *A. mariannensis*) based on morphological characters, had no effect on the monophyly of *A. camansi* but caused the collapse of monophyly in the putative parents. The distribution of the hybrids among both *A. altilis* and *A.
**Artocarpus camansi** may also be native to the Philippines and Moluccas.

**Artocarpus mariannensis** clusters is consistent with a hybrid nature of the accessions (Fig. 5). The presence of uniquely derived molecular and morphological characters and the non-overlapping geographical distributions of **Artocarpus camansi** and **Artocarpus mariannensis** indicate that they represent distinct monophyletic evolutionary lineages. There is no bootstrap support for the monophyly of **Artocarpus camansi**, but this may be due to selection of **Artocarpus altilis** from **Artocarpus camansi** being a relatively recent event (within the last 5,000 years, Zerega et al. 2004). Following the phylogenetic species concept, **Artocarpus camansi** and **Artocarpus mariannensis** are here recognized as two closely related, but separate, apospecies (Olmstead 1995).

**Domesticated Breadfruit.** The Pacific basin is breadfruit’s area of greatest morphological and genetic diversity (Ragone 1991; Zerega et al. in press), and the area where breadfruit was originally domesticated (Ragone 1997). In the eighteenth century, Europeans began distributing a few chosen cultivars beyond the Pacific Islands into tropical Madagascar, Africa, Central and South America, and the Caribbean (Powell 1973; Leakey 1977; Ragone 1997). Today it is grown throughout the tropics. Cladistic analysis excluding hybrids did not resolve a monophyletic **Artocarpus altilis** (Fig. 4), but a statistical comparison of trees from an unconstrained search and a search with **Artocarpus altilis** constrained as monophyletic indicated that the two topologies are not significantly different. In the distance analysis **Artocarpus altilis** is monophyletic, with the exception of two Micronesian cultivars (discussed further below) and sister to **Artocarpus camansi** (Fig. 3). These results support **Artocarpus altilis** as derived from **Artocarpus camansi**, a hypothesis originally suggested by Blanco (1940) and corroborated by historical human migration routes (Zerega et al. 2004). In addition to the sister relationship between **Artocarpus altilis** and **Artocarpus camansi** based on molecular evidence, the two species share morphological synapomorphies such as leaves that are typically pinnately lobed for most of the length of the leaf blade, yellowish green syncarp and infructescence surfaces, white to pale yellow perianth flesh, and oblong or reniform seeds.

Several Micronesian cultivars growing in the breadfruit germplasm collection at NTBG are recognized as hybrids because they exhibit morphological characters...
FIG. 3. Neighbor joining tree based on data from three AFLP primer pair combinations for *A. camansi*, *A. mariannensis*, and *A. altillis*, and outgroup taxa. Hybrids were excluded. For breadfruit cultivars (*A. altillis*) all of the following relevant information is indicated: grid number from the NTBG germplasm collection, collection numbers (DR = D. Ragone, NZ = N. Zerega), cultivar name, and the island of origin. Bootstrap values above 50% are indicated for interspecific relationships within the ingroup.
from both *A. altillis* and *A. mariannensis*. Hybrid combinations of characters are discussed in the taxonomic treatment below. Fosberg (1960) first recognized the morphological diversity of Micronesian breadfruit compared to other parts of Oceania and noted that many cultivars there had a random recombination of characters from both *A. altillis* and *A. mariannensis*. He suggested that introgressive hybridization involving sterile breadfruit and *A. mariannensis* was occurring in Micronesia. However, sterile *A. altillis* cultivars in Mi-
Cronesia are triploid (Ragone 2001), and triploids very rarely make it through meiosis I to successfully produce viable gametes. An alternative hypothesis proposes that diploid *A. altillis* cultivars, derived from selection from *A. camansi*, were introduced into Micronesia from Melanesia thousands of years ago by Lapita voyagers (Zerega et al. 2004). This was followed by hybridization and subsequent introgression with either *A. mariannensis* or *A. altillis*, as well as human selection and vegetative propagation, resulting in the great diversification of breadfruit cultivars in Micronesia (Zerega et al., in press). The presence of hybrid cultivars of recent origin from the Polynesian island group of Tokelau (Appendix 1) indicates that hybridization between the two species can produce fertile offspring. After most of the breadfruit trees on the island of Fakaofo in Tokelau were destroyed during a storm in 1914, diploid *A. altillis* cultivars and *A. mariannensis* were introduced. New cultivars with characteristics of both species have since arisen and are referred to as ulu afo (half-cast breadfruit) (Ragone 1988). Most of the hybrids appear to be genetically more similar to *A. mariannensis* than *A. altillis* (Fig. 5), suggesting they have introgressed more readily with the former. This may be the result of two circumstances. First, since *A. mariannensis* is native to Micronesia, it may have been more prevalent than introduced diploid *A. altillis*. Second, *A. mariannensis* is better adapted than *A. altillis* to atoll conditions common in Micronesian islands, making hybrids introgressing with *A. mariannensis* more likely to survive.

The Micronesian cultivars identified as hybrids in this study have recognizable morphological hybrid characters, especially when fertile (Ragone, unpubl. data), and differing degrees of introgression with either parent species may account in part for the morphological diversity among cultivars. However, cultivars of hybrid origin that have introgressed significantly more with one of the parent species may not exhibit morphological hybrid characters. The two accesses (Zerega 194 and Ragone 326), identified as *A. altillis* based on morphology but not part of a monophyletic *A. altillis* lineage, may be of hybrid origin but have introgressed significantly more with *A. altillis* (Fig. 3).

**Breadfruit Taxonomy.** *Artocarpus altillis*, *A. camansi*, and *A. mariannensis* comprise a well-supported monophyletic lineage (Figs. 3–5) that has been treated as one species (sensu Jarrett 1959), an approach that obscures the evolutionary history of the group and the origins of breadfruit. Jarrett (1959) acknowledged that her decision was based on limited, often sterile herbarium material, and suggested that further studies may show that two or more taxonomic entities and complex hybridization may have been involved in the ancestry of breadfruit. Live, fertile material from a broad geographic range and molecular evidence have allowed for more heuristic study and indicate that *Artocarpus camansi* and *A. mariannensis* represent two morphologically and geographically distinct monophyletic lineages, which both contributed to the evolution of domesticated breadfruit. *Artocarpus camansi*-derived breadfruit (*A. altillis*) appears to represent a monophyletic lineage (Fig. 3), and thousands of years of vegetative propagation and human selection have led to a unique combination of characters, making *A. altillis* morphologically distinct from its progenitor species (Fig. 1). Hybrids between *A. altillis* and *A. mariannensis* also occur. Therefore, the treatment below recognizes three monophyletic apecies, *A. camansi*, *A. mariannensis*, and *A. altillis* as well as natural *A. altillis × A. mariannensis* hybrids.

**Taxonomic Treatment**

Major distinguishing characters of the species come from leaf and syncarp morphology. The unique syncarp structure of *Artocarpus* is derived from a pistillate compound inflorescence condensed into a capitately structure made up of numerous fleshy tubular perianths containing a single ovary. The perianths are tightly packed together on a fleshy receptacle. The proximal portions of adjacent perianths are distinct, but the distal portions are completely or partially fused. When partially fused, the distinct distal portion provides taxonomic characters and is referred to as the anthocarp apex. (See Jarrett 1976 for additional detail). Measurements listed for each species are based on the specimens indicated in Appendix 1 and on Quisumbing (1940) and Fosberg (1960).

**Key to Breadfruit and Its Closest Relatives (Artocarpus)**

1. Leaf margin entire or with three to seven lobes in the distal third of leaf; leaf blade with abundant appressed reddish-brown hairs on midrib and abaxial veins; infructescence with dark green surface, oblong or irregularly shaped ... *A. mariannensis*

1. Leaf margin typically pinnately lobed, rarely entire with a praemorse apex; leaf blade glabrous to pubescent with colorless to pale white spreading and erect hairs on veins and blade; infructescence with yellowish green or rarely pink surface, globose to oblong.

2. Leaves densely pubescent with spreading or erect rough-walled straight white hairs, and smooth-walled uncinate white hairs; numerous achenes (commonly referred to as seeds) with dull, light brown, thin, flexible walls; infructescence surface echinate, with anthocarp apices narrowly conical and 5–12 mm long ... *A. camansi*

2. Leaves glabrous to moderately pubescent with spreading or erect rough-walled straight pale hairs, juvenile leaves may be densely pubescent; achen (commonly referred to as seeds) development often aborted but when present with dull light brown or shiny dark brown hard walls; infructescence surface flat to bumpy, with anthocarp apices rounded and barely protruding, or echinate with anthocarp apices conical and up to 5 mm long ... *A. altillis*


*Artocarpus rima* Blanco, Fl. Filip. 671. 1837. (spelled *Arctocarpus*)

*Artocarpus laevis* Hassk. Flora 25 (2), Beibl. 18. 1842.—HOLOTYPE: Java, *Batavia (cult.), Hasskarl s. n.* (L).

Domesticated breadfruit. Evergreen tree to 30 m tall. Leaves: 12–59 cm long × 10–47 cm wide, but juvenile leaves often larger, usually deeply pinnately lobed with up to 13 lobes cut from 1/3 to 4/5 of the way to midrib, rarely nearly entire with a praemorse apex, varying in size and shape on the same tree; glabrous to moderately pubescent, juvenile leaves may be densely pubescent, with pale or colorless, rough-walled hairs on midrib, adaxial and abaxial blade, and/or petiole; young leaves sometimes densely pubescent. Infructescence: interfloral bracts lacking, globose to cylindrical, 9–29 cm long × 6–20 cm wide; surface color typically yellowish-green, rarely pinkish; surface typically flat, especially in seedless cultivars with anthocarp apices rounded and barely protruding, but sometimes echinate, especially in fertile cultivars with conical, flexuous anthocarp apices up to 5 mm at the base and 3–5 mm long; flesh creamy white to pale yellow, dense due to fusion between medial portions of adjacent perianths; frequently seedless with tiny aborted ovules but some cultivars with few to several developed, typically ellipsoid, oblong, or reniform achenes with a hard, dull light brown or shiny dark brown wall. Stamine inflorescence: cylindrical to club-shaped, 10–29 (45) cm long × 1.8–4.4 cm in diameter.

**Distribution.** Pantropical, with greatest morphological diversity in Oceania.

**Vernacular Names.**


**Hybrids.** Natural *A. altilis × A. mariannensis* hybrids are also considered to be domesticated breadfruit. These hybrids are found primarily in Micronesia but also in the Polynesian island group of Tokelau, and exhibit characteristics of both parent species. Common characters contributed by *A. altilis* include deeply dissected leaves with more than seven lobes, white hairs, dense infructescences, decreased fertility, and flattened infructescence surface. *Artocarpus mariannensis* characters include entire to shallowly lobed leaves with seven or fewer lobes, reddish-brown hairs on leaf veins, spongy infructescences due to minimal fusion of adjacent perianths, bumpy infructescence surface, and dark yellow flesh. Various combinations of characters may occur including deeply dissected leaves of *A. altilis* with sparse reddish-brown hairs of *A. mariannensis* on the midrib and abaxial veins, or entire to shallowly lobed leaves of *A. mariannensis* with a yellowish, flat infructescence surface.


Evergreen tree to 35 m tall. Leaves: 40–60 cm long × 25–45 cm wide but juvenile leaves may be larger, typically pinnately lobed with fewer than 7–11 lobes cut from 1/3 to 1/2 way to midrib; sparsely to densely pubescent with white, uncinate, smooth-walled, and straight rough-walled hairs on midrib, adaxial and abaxial blade, and petiole. Infructescence: interfloral bracts lacking, globose to subglobose, 16–20 cm long × 8–15 cm wide; surface color yellowish-green; surface echinate with narrowly conical, flexuous anthocarp apices up to 5 mm at the base and 5–15 mm long; flesh white, spongy due to limited fusion between medial portions of adjacent flowers; numerous, developed typically oblong or reniform achenes with thin, flexible, dull light brown wall. Stamine inflorescence: cylindrical, 15–25 cm long × 1–4 cm in diameter.

**Distribution.** Native to New Guinea and Moluccas, probably naturalized in the Philippines. Cultivated in Indonesia, Malaysia, the Caribbean Islands, tropical Central and South America, and coastal West Africa.


Evergreen tree to 25 m tall. Leaves: 10–31 cm long × 5–21 cm wide, entire or with three to seven lobes cut less than 1/2 way to midrib in the distal third or half
of the leaf, varying in lobe number on the same tree; densely pubescent with reddish-brown, smooth-walled hairs on midrib and abaxial veins and petiole. 

Infructescence: interfloral bracts lacking, cylindrical to irregularly-shaped, 7–11 (18) cm long × 5–8.5 (12) cm wide; surface color dark green; surface bumpy with rounded or raised flattened anthocarp apices up to 5 mm at the base and 1 mm long; flesh dark yellow, spongy due to limited fusion between medial portions of adjacent flowers; several developed spherdoid achenes with hard, shiny dark brown wall. 

Staminate inflorescence: cylindrical, 6–10 cm long × 2–3.5 cm in diameter. 

**Distribution.** Native to the uplifted limestone islands and coastal areas of Palau and in limestone and ravine forests in the Northern Mariana Islands. Introduced and cultivated in other Micronesian islands including Chuuk, Yap, Pohnpei, Kosrae, and numerous atolls, and in the Polynesian islands of Tokelau, Tuvalu, and Hawaii.

**Vernacular Names.** Northern Mariana Islands: dugdug, Palau: chebei.

**Acknowledgements.** For field assistance and advice, the authors thank Laura Arriola, Abu Hussein, Robert Kiparanis, Ruth Kiew, John Kostka, Mark Kostka, Sean Lum, Supardi Noor, Vojtech Novotny, Lynn Raulerson, William Raynor, Agnes Rinherht, George Weiblen, Chan Yee Chong, and Lee Ying Fang. We also acknowledge the Nature Conservancy in Pohnpei, Federated States of Micronesia; University of Guam; National Research Institute of Papua New Guinea; Forest Research Institute of Papua New Guinea; Parataxonomist Training Center of Papua New Guinea; Singapore Botanic Garden; Forest Research Institute of Malaysia; The Breadfruit Institute, National Tropical Botanical Garden; and the Division of Fish and Wildlife and Department of Land and Natural Resources in the Northern Mariana Islands. This research was funded by the Lewis B. and Dorothy Cullman Foundation, National Science Foundation Dissertation Improvement Grant (DEB-0073161), Garden Club of America, the Explorers Club, and the Margaret and Herman Sokol Travel and Research Award.

**Literature Cited.**


Roupp van der Voort, J. N. A. M., P. van Zandvoort, H. J. van Eck, R. T. Folkertsma, R. C. B. Hutten, J. Draaijstra,
List of accesses used in this study. For each collection, the collector and collection number, NTBG # (grid #), the region of Oceania, the specific locality, and the cultivar are given, in that order. Samples with an NTBG accession number and/or grid number are deposited at PTBG. Ragone collections above 500, Hiyane, Perlman, and Whitter collections, and collection numbers indicated by NA are represented by living trees at the Breadfruit Institute. Superscript letters indicate specimens that were used for measurements in the species descriptions; a = leaf measurements, b = infructescence measurements, and c = stamine inflorescence measurements.

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