

## Systematics and Species Limits of Breadfruit (*Artocarpus*, Moraceae)

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**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. altilis* (Parkinson) Fosberg) and jackfruit (*A. heterophyllus* Lamarck). 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 ( $2n = 3x = \sim 84$ ) 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 *Sitodidium 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 altilis* (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* Trécul, 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. communis*, 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. Trécul (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; Trécul 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. kemando* Miq., *A. lowii* King, *A. maingayi* King, *A. scortecheenii* King, and *A. tamaran* Becc.) to the ingroup as well as members of the three other clades (*A. treculianus* Elmer, *A. heterophyllus* Lamarck, and *A. lanceifolius* 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 cm<sup>2</sup> 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 *EcoRI* and *MseI* 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 (*EcoRI*-ACA/*MseI*-CTC, *EcoRI*-ACA/*MseI*-CAT, *EcoRI*-AAG/*MseI*-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 in each lane (Applied Biosystems). The standard contained 16 fluorescently 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 congeneric 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 (Backeljau 1995), 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 com-

parison 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 (Quisumbing 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; Quisumbing 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.*



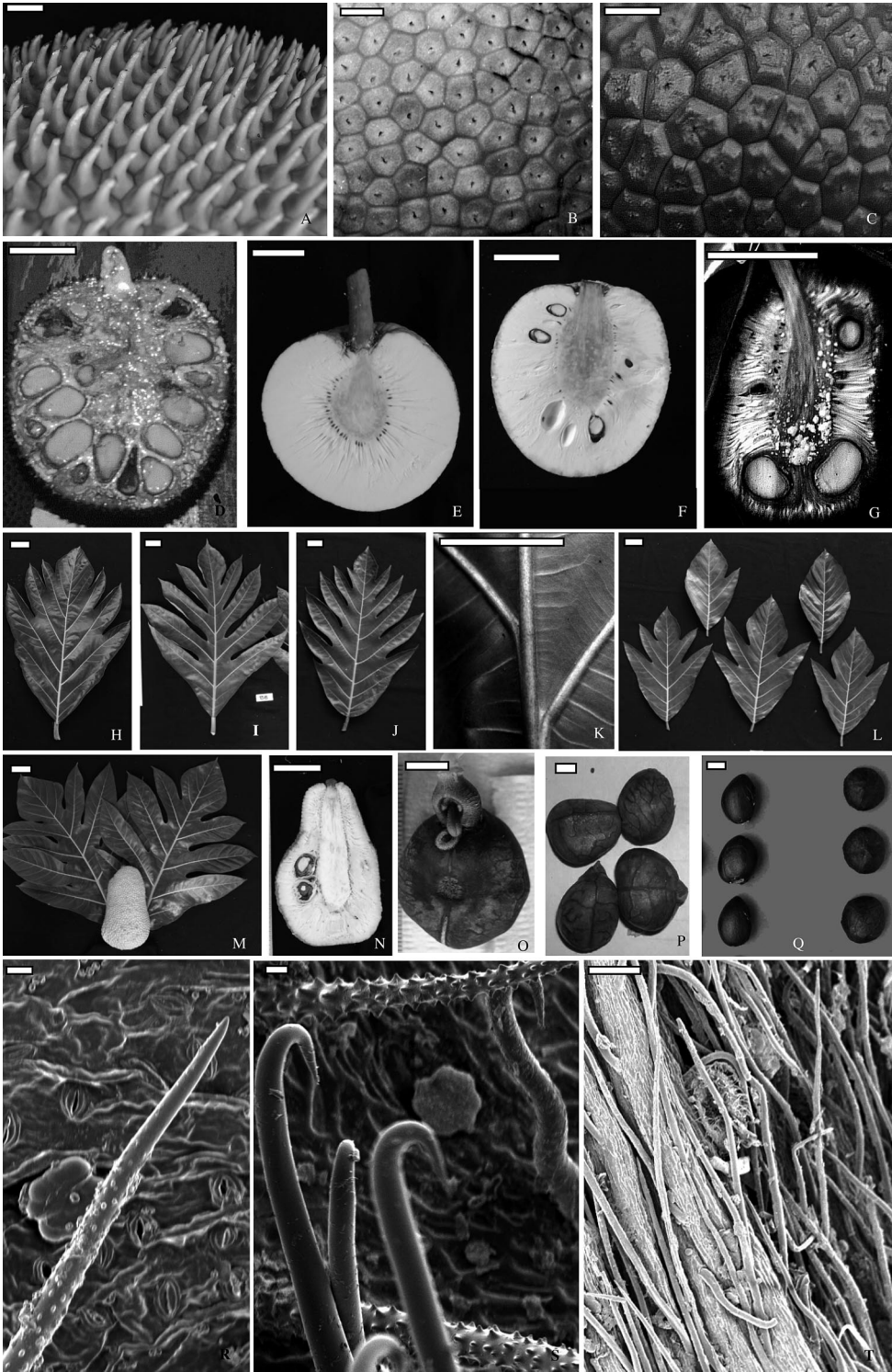


FIG. 1. Morphological characters of breadfruit and its closest relatives. A–C. Infructescence surfaces. A. *Artocarpus camansi*, Ragone 531. B. *A. altilis*, Zerega 102 (NY). C. *A. mariannensis*, Zerega 146 (NY). D–G. Sections of ripe infructescences. D. *A. camansi*, Zerega 88 (NY). E. *A. altilis*, Ragone 231 (PTBG). F. *A. altilis*, Ragone 528. G. *A. mariannensis*, Zerega 146 (NY). H–L. Leaves. H. *A. camansi*, NTBG grid # 50, I. *A. altilis*, Ragone 245 (PTBG). J. *A. altilis*, Ragone 231 (PTBG). K. *A. mariannensis*, Zerega 141. L. Variation in leaf morphology of *A. mariannensis*, Ragone 313 (PTBG). M. Leaf and infructescence of *A. altilis* × *A. mariannensis*, Ragone 53 (PTBG). N. Section of ripe infructescence, *A. altilis* × *A. mariannensis*, Ragone 53 (PTBG). O–Q. Seeds. O. *A. mariannensis*,

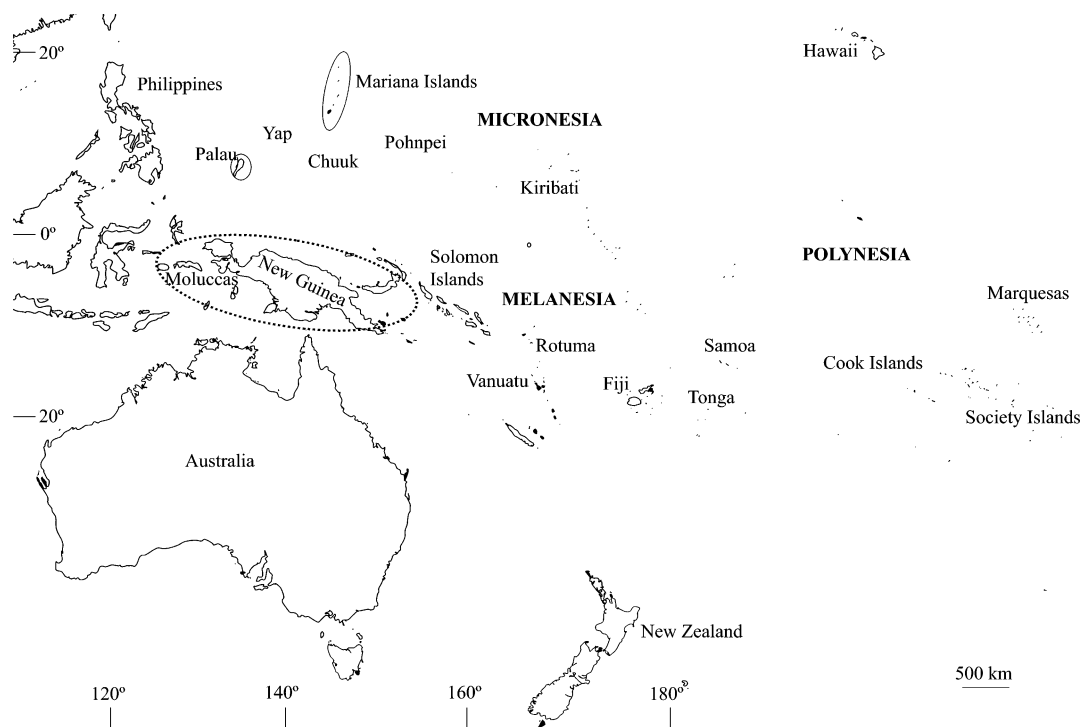


FIG. 2. Map showing natural ranges of *A. camansi* and *A. mariannensis*, indicated by dashed and solid lines, respectively. *Artocarpus camansi* may also be native to the Philippines and Moluccas.

*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 *A. camansi* and *A. mariannensis* indicate that they represent distinct monophyletic evolutionary lineages. There is no bootstrap support for the monophyly of *A. camansi*, but this may be due to selection of *A. altilis* from *A. camansi* being a relatively recent event (within the last 5,000 years, Zerega et al. 2004). Following the phylogenetic species concept, *A. camansi* and *A. mariannensis* are here recognized as two closely related, but separate, apecies (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 *A. altilis* (Fig. 4), but a statistical comparison of trees from an unconstrained search and a search with *A. altilis* constrained as monophyletic indicated that the two topologies are not significantly different. In the distance analysis *A. altilis* is monophyletic, with the exception of two Micronesian cultivars (discussed further below) and sister to *A. camansi* (Fig. 3). These results support *A. altilis* as derived from *A. 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 *A. altilis* and *A. 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

←

Ragone 313 (PTBG). P. *A. camansi*, Ragone 531. Q. Left, *A. altilis*, Ragone 426 (PTBG), right *A. altilis* × *A. mariannensis*, Ragone 363 (PTBG). R–T. Scanning electron micrographs of leaf trichomes. R. *A. altilis*, Ragone 123 (PTBG). S. *A. camansi*, Zerega 69 (NY). T. *A. mariannensis*, Zerega 160 (NY). Scale bars: A–C = 5 mm, D–M = 5 cm, O–Q = 1 cm, R–S = 10 μm, T = 100 μm.

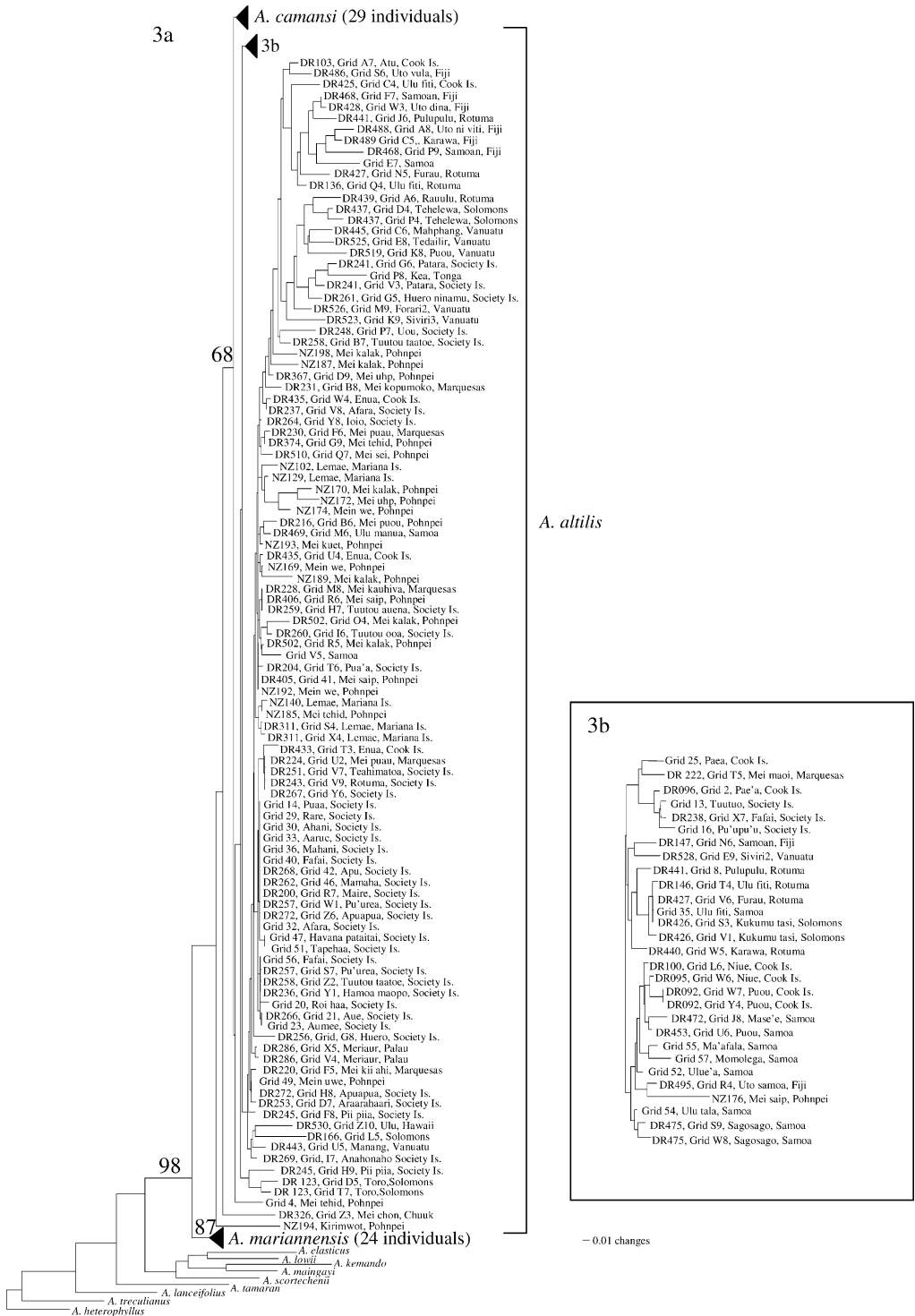


FIG. 3. Neighbor joining tree based on data from three AFLP primer pair combinations for *A. camansi*, *A. mariannensis*, *A. altilis*, and outgroup taxa. Hybrids were excluded. For breadfruit cultivars (*A. altilis*) all of the following relevant information is indicated: grid number from the NTBG germplasm 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.

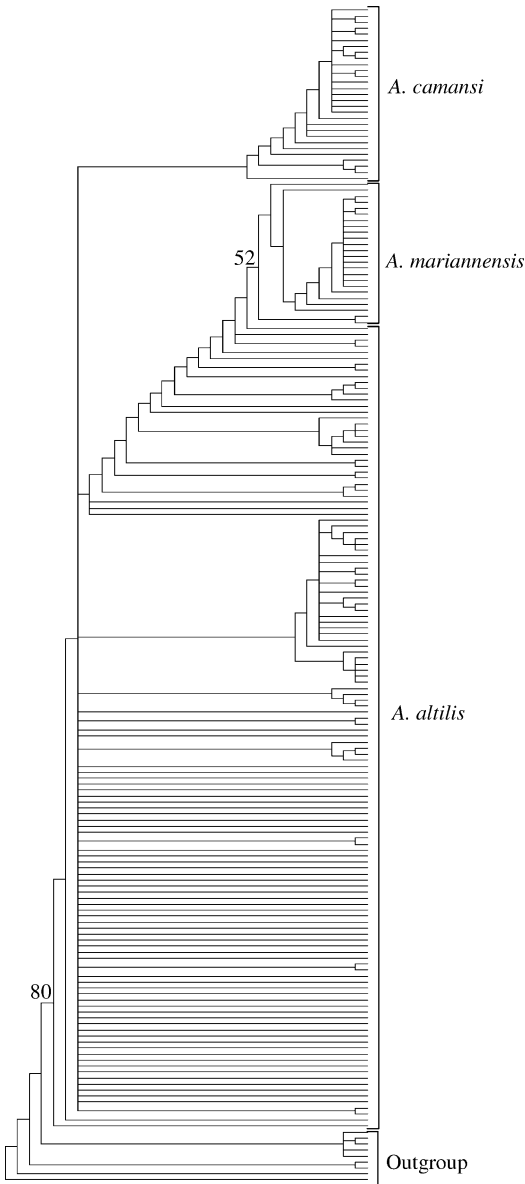


FIG. 4. Strict consensus tree of 8664 MPTs based on data from three AFLP primer combinations. Taxa groups are indicated to the right of the brackets. Bootstrap support values above 50% are indicated for interspecific relationships within the ingroup.

from both *A. altilis* 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. altilis* and *A. mariannensis*. He suggested that introgressive hybridization involving sterile breadfruit and *A. mariannensis* was occurring in Micronesia. However, sterile *A. altilis* cultivars in Mi-

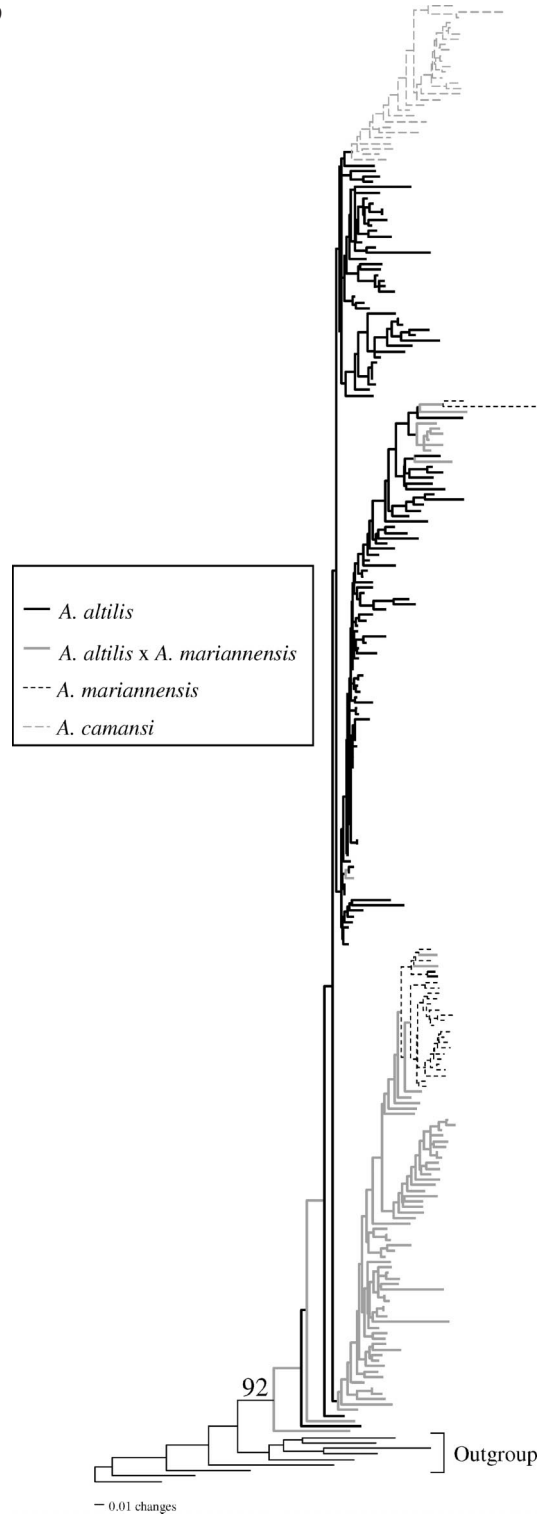


FIG. 5. Neighbor joining tree based on data from three AFLP primer pair combinations for *A. camansi*, *A. mariannensis*, *A. altilis*, *A. altilis* × *A. mariannensis*, and outgroup taxa. Thick black lines indicate *A. altilis*, solid gray lines indicate *A. altilis* × *A. mariannensis*, dashed black lines indicate *A. mariannensis*, and dashed gray lines indicate *A. camansi*. Bootstrap support values above 50% are indicated for interspecific relationships within the ingroup.



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. altilis* 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. altilis*, 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. altilis* cultivars and *A. mariannensis* were introduced. New cultivars with characteristics of both species have since arisen and are referred to as ulu afa (half-cast breadfruit) (Ragone 1988). Most of the hybrids appear to be genetically more similar to *A. mariannensis* than *A. altilis* (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. altilis*. Second, *A. mariannensis* is better adapted than *A. altilis* 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 accessions (Zerega 194 and Ragone 326), identified as *A. altilis* based on morphology but not part of a monophyletic *A. altilis* lineage, may be of hybrid origin but have introgressed significantly more with *A. altilis* (Fig. 3).

**Breadfruit Taxonomy.** *Artocarpus altilis*, *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 extensive 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. altilis*) 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. altilis* morphologically distinct from its progenitor species (Fig. 1). Hybrids between *A. altilis* and *A. mariannensis* also occur. Therefore, the treatment below recognizes three monophyletic aposespecies, *A. camansi*, *A. mariannensis*, and *A. altilis* as well as natural *A. altilis* × *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 capitate 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 or 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 uncinata 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; achene (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 5mm long. . . . . *A. altilis*



ARTOCARPUS ALTILIS (Parkinson) Fosberg, Jour. Wash. Acad. 31: 95. 1941. *Sitodium altile* Parkinson Jour. Voy. Endeavour. 45. 1773. *Artocarpus communis* J.R. & G. Forst. Char. Gen. 101. 1776.—LECTOTYPE: without provenance, *Forster s. n.* (BM).

*Radermachia incisa* Thunb. Handl. Vet-Akad. Stockh. 37: 253. 1776. *Artocarpus incisus* (Thunb.) L. f. Suppl. 411. 1781.—HOLOTYPE: Java, *Thunberg s. n.* (UPS) (isotype: L).

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

*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. *Staminate 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*. English: breadfruit, French: *arbre à pain*, Spanish: *árbol de pan*, German: *Brotfruchtbaum*, Philippines: *rima*, Indonesia: *sukun*, *timbul*, Malaysia: *kulur*, *kuror*, Papua New Guinea: *kapiak*, Fiji: *uto*, *kulu*, Solomon Islands: *bia*, *nimbalu*, Vanuatu: *beta*, Hawaii and Samoa: *ulu*, Society Islands: *uru*, Cook Islands: *kuru*, Micronesia, Tonga, and the Marquesas: *mei*, *mai*, Northern Mariana Islands: *lemae*, Kosrae: *mos*. Numerous cultivar names also exist throughout the islands of Oceania (see Ragone 1997 for a list of publications).

*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.

2. ARTOCARPUS CAMANSI Blanco Fl. Filip. 670. 1837 (*Arthocarpus*).—NEOTYPE: Manila, Luzon, Philippines, *Merrill Species Blancoanae* 830, designated by Merrill in Sp. Blanco. 124. 1918 (US!, No. 00904515).

*Artocarpus incisa* L. f. var. *muricata* Becc. For. Borneo. 628.—HOLOTYPE: New Guinea, *Beccari PP25* (FI).

*Artocarpus leeuwenii* Diels, Bot. Jahrb. 67: 175. 1935.—HOLOTYPE: New Guinea, *Docters van Leeuwen 11163* (B) (isotypes: BO, L, U).

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, uncinat, 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. *Staminate 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.

*Vernacular Names*. English: breadnut, Papua New Guinea: *kapiak*, Phillipines: *camangsi*, *pakok*.

3. ARTOCARPUS MARIANNENSIS Trécul Ann. Sci. Nat. Bot. III. 8: 114. 1847.—HOLOTYPE: Marianas Islands, *Gaudichaud s.n.* (P).

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  $\times$  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 spheroid achenes with hard, shiny dark brown wall. *Staminate inflorescence*: cylindrical, 6–10 cm long  $\times$  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: *dug-dug*, Palau: *chebiei*.

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- Measurements in the species descriptions; a = leaf measurements, b = infructescence measurements, and c = staminate inflorescence measurements.
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NA, 880690001 (P8) <sup>a, b</sup>, W Poly, Tonga, Kea. *Perlman s.n.*, 780332001 (33) <sup>a, b</sup>, E Poly, Society Is., Aarue. *Perlman s.n.*, 780325001 (32) <sup>a, b, c</sup>, E Poly, Society Is., Afara. *Perlman s.n.*, 780333001 (30) <sup>a, b</sup>, E Poly, Society Is., Ahani. *Perlman s.n.*, 780335001 (23) <sup>a, b</sup>, E Poly, Society Is., Aumea. *Perlman s.n.*, 780330002 (40) <sup>a, b</sup>, E Poly, Society Is., Fafai. *Perlman s.n.*, 780291001 (47) <sup>a, b</sup>, E Poly, Society Is., Havana pataitai. *Perlman s.n.*, 800269001 (36) <sup>a, b</sup>, E Poly, Society Is., Mahani. *Perlman s.n.*, 780328001 (14) <sup>a, b, c</sup>, E Poly, Society Is., Pua'a. *Perlman s.n.*, 790492001 (16) <sup>a, b</sup>, E Poly, Society Is., Pu'upu'u. *Perlman s.n.*, 780329001 (29) <sup>a, b</sup>, E Poly, Society Is., Rare. *Perlman s.n.*, 790486001 (20) <sup>a, b</sup>, E Poly, Society Is., Roi haa. *Perlman s.n.*, 780338001 (51) <sup>a, b</sup>, E Poly, Society Is., Tapehaa. *Perlman s.n.*, 790491001 (13) <sup>a, b</sup>, E Poly, Society Is., Tuutou. *Perlman s.n.*, 780330001 (56), W Poly, Society Is., Fafai. *Ragone 092*, 890156002 (W7) <sup>b, c</sup>, E Poly, Cook Is., Tahitian (Puou). *Ragone 092*, 890156001 (Y4) <sup>a, b, c</sup>, E Poly, Cook Is., Tahitian (Puou). *Ragone 095*, 890454001 (W6) <sup>b</sup>, E Poly, Cook Is., Niue. *Ragone 096*, 890153002 (2) <sup>b</sup>, E Poly, Cook Is., Paea. *Ragone 096*, 890153001 (25), E Poly, Cook Is., Paea. *Ragone 100*, 900231001 (L6) <sup>a, b</sup>, E Poly, Cook Is., Niue. *Ragone 103*, 900232001 (A7) <sup>a, b</sup>, E Poly, Cook Is., Atu. *Ragone 123*, 890456002 (D5) <sup>a, b</sup>, Mela, Solomon Is., Toro. *Ragone 123*, 890456001 (T7) <sup>b</sup>, Mela, Solomon Is., Toro. *Ragone 136*, 890458002 (Q4), Mela, Rotuma, Ulu fiti. *Ragone 136*, 890458001 (T4) <sup>b, c</sup>, Mela, Rotuma, Ulu fiti. *Ragone 136*, 890258001 (35) <sup>a, b, c</sup>, W Poly, Samoa, Ulu fiti. *Ragone 147*, 900234001 (N6), Mela, Fiji, Samoa. *Ragone 166*, 900235001 (L5) <sup>b</sup>, Mela, Solomon Is., unnamed. *Ragone 200*, 890459001 (R7) <sup>b</sup>, E Poly, Society Is., Maire. *Ragone 204*, 890460001 (T6) <sup>a</sup>, E Poly, Society Is., Puaa. *Ragone 216*, 900237001 (B6) <sup>a, b</sup>, E Poly, Marquesas, Mei puou. *Ragone 220*, 900238001 (F5) <sup>a</sup>, E Poly, Marquesas, Mei kii ahi. *Ragone 222*, 900239001 (T5) <sup>a, b</sup>, E Poly, Marquesas, Mei maoi. *Ragone 223*, 900240001 (M8), E Poly, Marquesas, Mei kauhiva. *Ragone 224*, 890462001 (U2) <sup>b</sup>, E Poly, Marquesas, Mei puau. *Ragone 230*, 900241001 (F6) <sup>a</sup>, E Poly, Marquesas, Mei aueka. *Ragone 231*, 900242001 (B8) <sup>b</sup>, E Poly, Marquesas, Mei kopumoko. *Ragone 236*, 890154001 (Y1) <sup>a, b, c</sup>, E Poly, Society Is., Hamoa (Maopo). *Ragone 237*, 910267001 (V8) <sup>a, b</sup>, E Poly, Society Is., Afara. *Ragone 238*, 890151001 (X7), E Poly, Society Is., Fafai. *Ragone 241*, 890463002 (G6) <sup>a</sup>, E Poly, Society Is., Patarā. *Ragone 241*, 890463001 (V3) <sup>b</sup>, E Poly, Society Is., Patarā. *Ragone 243*, 910265001 (V9) <sup>b, c</sup>, E Poly, Society Is., Rotuma. *Ragone 245*, 910266002 (F8) <sup>a</sup>, E Poly, Society Is., Pii-piia. *Ragone 245*, 910266001 (H9) <sup>a</sup>, E Poly, Society Is., Pii-piia. *Ragone 248*, 890464001 (P7) <sup>b</sup>, E Poly, Society Is., Ouo. *Ragone 251*, 890465001 (V7) <sup>a, b</sup>, E Poly, Society Is., Teahimatoa. *Ragone 253*, 900243001 (D7) <sup>b</sup>, E Poly, Society Is., Araaraahaari. *Ragone 256*, 900245001 (G8) <sup>a</sup>, E Poly, Society Is., Huero. *Ragone 257*, 890152002 (S7) <sup>a, b</sup>, E Poly, Society Is., Puurea. *Ragone 257*, 890152001 (W1) <sup>b</sup>, E Poly, Society Is., Puurea. *Ragone 258*, 890186002 (B7), E Poly, Society Is., Tuutou taatōe. *Ragone 258*, 890186001 (Z2) <sup>b</sup>, E Poly, Society Is., Tuutou taatōe. *Ragone 259*, 900246001 (H7) <sup>a, b</sup>, E Poly, Society Is., Tuutou auena. *Ragone 260*, 900247001 (I6) <sup>b</sup>, E Poly, Society Is., Tuutou ooa. *Ragone 261*, 900248001 (G5), E Poly, Society Is., Huero ninamu. *Ragone 262*, 890149001 (46) <sup>a, b</sup>, E Poly, Society Is., Mamaha. *Ragone 264*, 890150001 (Y8) <sup>a, b</sup>, E Poly, Society Is., Ioio. *Ragone 266*, 890147001 (21) <sup>a, b</sup>, E Poly, Society Is., Aue. *Ragone 267*, 890148001 (Y6) <sup>a, b</sup>, E Poly, Society Is., Unknown. *Ragone 268*, 890157001 (42) <sup>a, b</sup>, E Poly, Society Is., Apu. *Ragone 269*, 900249001 (I7) <sup>b</sup>, E Poly, Society Is., Anahonaho. *Ragone 272*, 890158002 (H8) <sup>a</sup>, E Poly, Society Is., Apuapua. *Ragone 272*, 890158001 (Z6), E Poly, Society Is., Apuapua. *Ragone 286*, 890159002 (V4) <sup>a, b</sup>, Micro,

## APPENDIX 1

List of accessions 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 located at the NTBG living breadfruit germplasm collection. Separate accessions with the same collection number indicate trees grown from either seeds or root cuttings of the same parent tree. SBG = from living collections of the Singapore Botanic Garden, E Poly = Eastern Polynesia, W Poly = Western Polynesia, Micro = Micronesia, Mela = Melanesia. Zerega voucher collections are deposited at NY, and Ragone collections through 499 are deposited at PTBG. Ragone collections above 500, Hiyane, Perlman, and Whistler collections, and collection numbers indicated by NA are represented by living trees at the Breadfruit Institute. Superscript letters indicate specimens that were used for mea-



Palau, Meriaur. *Ragone* 286, 890159001 (X5), Micro, Palau, Meriaur. *Ragone* 311, 890162002 (S4) <sup>a, b, c</sup>, Micro, Mariana Is., Lemae. *Ragone* 311, 890162001 (X4) <sup>a, b</sup>, Micro, Mariana Is., Lemae. *Ragone* 326, 890165001 (Z3), Micro, Chuuk, Mei chon. *Ragone* 367, 910271001 (D9) <sup>a, b</sup>, Micro, Pohnpei, Mei uhpw. *Ragone* 374, 910273002 (G9) <sup>a</sup>, Micro, Pohnpei, Mei tehid. *Ragone* 405, 890167001 (41) <sup>a, b</sup>, Micro, Pohnpei, Mei saip. *Ragone* 405, 890167002 (R6), Micro, Pohnpei, Mei saip. *Ragone* 425, 900368001 (C4) <sup>a, b, c</sup>, E Poly, Cook Is., Ulu fiti. *Ragone* 426, 890469002 (S3) <sup>a, b</sup>, Mela, Solomon Is., Kukumu tasi. *Ragone* 426, 890469001 (V1), Mela, Solomon Is., Kukumu tasi. *Ragone* 427, 890470001 (V6) <sup>b</sup>, Mela, Rotuma, Furau. *Ragone* 427, 890470002 (N5) <sup>a, b</sup>, Mela, Rotuma, Furau. *Ragone* 428, 890471001 (W3) <sup>a, b</sup>, Mela, Fiji, Uto dina. *Ragone* 433, 900256001 (T3) <sup>a, b</sup>, E Poly, Cook Is., Enua. *Ragone* 435, 890472002 (U4), E Poly, Cook Is., Enua. *Ragone* 435, 890472001 (W4) <sup>b</sup>, E Poly, Cook Is., Enua. *Ragone* 437, 900281002 (D4) <sup>a</sup>, Mela, Solomon Is., Tehelewa. *Ragone* 437, 900281001 (P4), Mela, Solomon Is., Tehelewa. *Ragone* 439, 900257001 (A6) <sup>a, b, c</sup>, Mela, Rotuma, Raulu. *Ragone* 440, 890457001 (W5) <sup>b</sup>, Mela, Rotuma, Karawa. *Ragone* 441, 900233002 (8) <sup>a, b</sup>, Mela, Rotuma, Pulpulu. *Ragone* 441, 900233001 (J6), Mela, Rotuma, Pulpulu. *Ragone* 443, 890473001 (U5) <sup>a</sup>, Mela, Vanuatu, Manang. *Ragone* 445, 900259001 (C6) <sup>a</sup>, Mela, Vanuatu, Malphang. *Ragone* 453, 890474001 (U6) <sup>b, c</sup>, W Poly, Samoa, Puou. *Ragone* 468, 900261001 (F7) <sup>a</sup>, Mela, Fiji, Samoan. *Ragone* 468, 900261002 (P9), Mela, Fiji, Samoan. *Ragone* 469, 900262001 (M6) <sup>b</sup>, W Poly, Samoa, Ulu manua. *Ragone* 472, 900263001 (J8) <sup>b</sup>, W Poly, Samoa, Mase'e. *Ragone* 475, 890475001 (W8), W Poly, Samoa, Sagosago. *Ragone* 475, 890475002 (S9) <sup>a</sup>, W Poly, Samoa, Sagosago. *Ragone* 486, 890476002 (S6) <sup>a, b</sup>, Mela, Fiji, Uto vula. *Ragone* 488, 900264001 (A8) <sup>a</sup>, Mela, Fiji, Uto ni viti. *Ragone* 489, 900265001 (C5) <sup>a</sup>, Mela, Fiji, Karawa. *Ragone* 495, 890477001 (R4) <sup>a, b, c</sup>, Mela, Fiji, Uto samoa. *Ragone* 502, 890478002 (O4) <sup>a, b</sup>, Micro, Pohnpei, Mei kalak. *Ragone* 502, 890478001 (R5), Micro, Pohnpei, Mei kalak. *Ragone* 510, 890479001 (Q7), Micro, Pohnpei, Mei sei. *Ragone* 519, 910275001 (K8) <sup>a, b, c</sup>, Mela, Vanuatu, Puou. *Ragone* 523, 910276001 (K9), Mela, Vanuatu, Siviri3. *Ragone* 525, 910277001 (E8) <sup>a</sup>, Mela, Vanuatu, Tedailir. *Ragone* 526, 910278001 (M9), Mela, Vanuatu, Forari2. *Ragone* 528, 910279001 (E9) <sup>b</sup>, Mela, Vanuatu, Siviri. *Ragone* 530, NA (Z10) <sup>a, b, c</sup>, E Poly, Hawaii, Ulu. *Whistler s.n.*, 770519001 (57) <sup>a</sup>, W Poly, Samoa, Momolega. *Zerega* 102 b, NA, Micro, Mariana Is., Lemae. *Zerega* 129, NA, Micro, Mariana Is., Lemae. *Zerega* 140, NA, Micro, Mariana Is., Lemae. *Zerega* 169 b, NA, Micro, Pohnpei, Mein we. *Zerega* 170, NA, Micro, Pohnpei, Mei kalak. *Zerega* 172 b, NA, Micro, Pohnpei, Mei uhp. *Zerega* 174, NA, Micro, Pohnpei, Mein we. *Zerega* 176, NA, Micro, Pohnpei, Mei saip. *Zerega* 185, NA, Micro, Pohnpei, Mei tehid. *Zerega* 187, NA, Micro, Pohnpei, Mei kalak. *Zerega* 189, NA, Micro, Pohnpei, Mei kalak. *Zerega* 192, NA, Micro, Pohnpei, Mein we. *Zerega* 193 b, NA, Micro, Pohnpei, Mei kuet. *Zerega* 194, NA, Micro, Pohnpei, Kirimwot. *Zerega* 198, NA, Micro, Pohnpei, Mei kalak.

*A. altilis* × *A. mariannensis*—*Hiyane s.n.*, 790494001 (Z9), Micro, Pohnpei, Mein padahk. *Perlman s.n.*, 790487001 (Z7), E Poly, Society Is., Huehue. *Perlman s.n.*, 790490001 (15), E Poly, Society Is., Rotuma. *Perlman s.n.*, 790488001 (12), E Poly, Society Is., Toneno. *Ragone* 041, 890169001 (Y2), W Poly, Tokelau, Ulu afa. *Ragone* 043, 89017002 (Z33), W Poly, Tokelau, Ulu hamoa. *Ragone* 043, 890170001 (X1), W Poly, Tokelau, Ulu hamoa. *Ragone* 044, 890171002 (7), W Poly, Tokelau, Ulu afa. *Ragone* 044, 890171001 (X6), W Poly, Tokelau, Ulu afa. *Ragone* 045, 890172002 (ZZ5), W Poly, Tokelau, Ulu afa. *Ragone* 045, 890172001 (37), W Poly, Tokelau, Ulu afa. *Ragone* 046, 890173002 (ZZ7), W Poly, Tokelau, Ulu afa. *Ragone* 046, 890173001 (11), W Poly, Tokelau, Ulu afa elise. *Ragone* 048, 890174001 (18), W Poly, Tokelau, Ulu afa. *Ragone* 049, 890175001 (34), W Poly, Tokelau, Ulu afa hamoa. *Ragone* 051, 890176002 (Z38), W Poly, Tokelau, Ulu afa. *Ragone* 051, 890176001 (Z8), W Poly, Tokelau, Ulu afa. *Ragone* 052, 890257001 (X3), W Poly, Tokelau, Ulu afa. *Ragone* 053, 890177001 (31), W Poly, Tokelau, Ulu afa. *Ragone* 053, 890177002 (5), W Poly, Tokelau, Ulu afa. *Ragone*

053, 890177003 (3), W Poly, Tokelau, Ulu afa. *Ragone* 054, 900230001 (6), W Poly, Tokelau, Ulu afa. *Ragone* 056, 890178001 (26), W Poly, Tokelau, Ulu afa. *Ragone* 057, 890453001 (O5), W Poly, Tokelau, Ulu afa. *Ragone* 058, 890179001 (44), W Poly, Tokelau, Ulu afa. *Ragone* 059, 890180001 (24), W Poly, Tokelau, Ulu hamoa. *Ragone* 063, 890185001 (28), W Poly, Tokelau, Ulu elise. *Ragone* 065, 890182001 (X9), W Poly, Tokelau, Ulu elise. *Ragone* 065, 890182002 (ZZ6), W Poly, Tokelau, Ulu elise. *Ragone* 287, 900250001 (A5), Micro, Palau, Yap variety. *Ragone* 288, 890160001 (X8), Micro, Palau, Ebechad. *Ragone* 290, 890183001 (Y3), Micro, Palau, Midolab. *Ragone* 291, 910652001 (U8), Micro, Palau, Errud. *Ragone* 301, 890184001 (10), Micro, Yap, Luthar. *Ragone* 303, 890161001 (19), Micro, Yap, Yuley. *Ragone* 314, 890163002 (U9), Micro, Mariana Is., Lemae. *Ragone* 314, 890163001 (X2), Micro, Mariana Is., Lemae. *Ragone* 320, 890164002 (T9), Micro, Chuuk, Sewan. *Ragone* 320, 890164001 (22), Micro, Chuuk, Sewan. *Ragone* 322, 910268001 (J9), Micro, Chuuk, Meion. *Ragone* 331, 910269001 (A9), Micro, Chuuk, Faine. *Ragone* 351, 890466002 (Q9), Micro, Chuuk, Mei koeng. *Ragone* 354, 890166001 (Y7), Micro, Chuuk, Mei chocho. *Ragone* 363, 900253002 (J5), Micro, Chuuk, Mei chocho. *Ragone* 363, 900253001 (Q6), Micro, Chuuk, Mei chocho. *Ragone* 365, 910270001 (D8), Micro, Pohnpei, Lipet. *Ragone* 373, 910272002 (E6), Micro, Pohnpei, Mein pohnsakar. *Ragone* 373, 910272001 (F9), Micro, Pohnpei, Mein pohnsakar. *Ragone* 385, 900254001 (H6), Micro, Pohnpei, Mei kole. *Ragone* 386, 900255001 (B5), Micro, Pohnpei, Mein pwahr. *Ragone* 387, 910274001 (Q10), Micro, Pohnpei, Nahnmal. *Ragone* 388, 890467001 (W9), Micro, Pohnpei, Mein pwuht. *Ragone* 421, 890468002 (L9), Micro, Kiribati, Te bukiraro. *Ragone* 421, 890468001 (V2), Micro, Kiribati, Te bukiraro. *Ragone* 511, 890480003 (R8), Micro, Pohnpei, Lipet. *Zerega* 143, NA, Micro, Marianas, Lemae. *Zerega* 152, NA, Micro, Marianas, Lemae. *Zerega* 157, NA, Micro, Marianas, Lemae. *Zerega* 158, NA, Micro, Marianas, Lemae. *Zerega* 159, NA, Micro, Marianas, Lemae. *Zerega* 168, NA, Micro, Pohnpei, Mein padahk. *Zerega* 178, NA, Micro, Pohnpei, Mein padahk. *Zerega* 180, NA, Micro, Pohnpei, Mei tek. *Zerega* 181, NA, Micro, Pohnpei, Lukual. *Zerega* 183, NA, Micro, Pohnpei, Mein padahk. *Zerega* 184, NA, Micro, Pohnpei, Mei oang. *Zerega* 186, NA, Micro, Pohnpei, Luhkual-lukiamas. *Zerega* 188, NA, Micro, Pohnpei, Mei pwet. *Zerega* 190, NA, Micro, Pohnpei, Mei serih seng. *Zerega* 195, NA, Micro, Pohnpei, Luhki. *Zerega* 196, NA, Micro, Pohnpei, Mein pwahr. *Zerega* 199, NA, Micro, Pohnpei, Mei arepe. *Zerega* 200, NA, Micro, Pohnpei, Mei ti. *Zerega* 201, NA, Micro, Pohnpei, Mei aoup.

*A. camansi*—NA, 770444001 (50) <sup>a, b</sup>, E Poly, Society Is., Camansi. *Ragone* 529, 910280001 (B9) <sup>a, b</sup>, Micro, Pohnpei, Mei kole. *Ragone* 531, 910281001 (M10) <sup>b</sup>, Philippines, Luzon, Camansi. *Ragone* 540, 910283001 (R10), Indonesia, Bogor, Timbul. *Ragone* 018, NA, Mela, Papua New Guinea, Kapiak. *Zerega* 019 a, b, NA, Mela, Papua New Guinea, Kapiak. *Zerega* 027, NA, Mela, Papua New Guinea, Kapiak. *Zerega* 030, NA, Mela, Papua New Guinea, Kapiak. *Zerega* 032, NA, Mela, Papua New Guinea, Kapiak. *Zerega* 035, NA, Mela, Papua New Guinea, Kapiak. *Zerega* 044, NA, Mela, Papua New Guinea, Kapiak. *Zerega* 046, NA, Mela, Papua New Guinea, Kapiak. *Zerega* 047, NA, Mela, Papua New Guinea, Kapiak. *Zerega* 052, NA, Mela, Papua New Guinea, Kapiak. *Zerega* 055, NA, Mela, Papua New Guinea, Kapiak. *Zerega* 057, NA, Mela, Papua New Guinea, Kapiak. *Zerega* 059, NA, Mela, Papua New Guinea, Kapiak. *Zerega* 069, NA, Mela, Papua New Guinea, Kapiak. *Zerega* 070, NA, Mela, Papua New Guinea, Kapiak. *Zerega* 083, NA, Mela, Papua New Guinea, Kapiak. *Zerega* 085, NA, Mela, Papua New Guinea, Kapiak. *Zerega* 087 b, NA, Mela, Papua New Guinea, Kapiak. *Zerega* 088, NA, Mela, Papua New Guinea, Kapiak. *Zerega* 091, NA, Mela, Papua New Guinea, Kapiak. *Zerega* 093, NA, Mela, Papua New Guinea, Kapiak. *Zerega* 094, NA, Mela, Papua New Guinea, Kapiak. *Zerega* 095, NA, Mela, Papua New Guinea, Kapiak. *Zerega* 100, NA, Mela, Papua New Guinea, Kapiak. *Zerega* 101 b, NA, Mela, Papua New Guinea, Kapiak.

*A. mariannensis*—*Ragone* 036, 890452001 (U3) <sup>a</sup>, Micro, Kiribati,



- Te mai. *Ragone* 313, 900252002 (A4)<sup>a, b</sup>, Micro, Mariana Is., Dugdug. *Ragone* 313, 900252001 (H5), Micro, Mariana Is., Dugdug. *Ragone* 313, 900252003 (N9), Micro, Mariana Is., Dugdug. *Zerega* 125, NA, Micro, Mariana Is., Dugdug. *Zerega* 126, NA, Micro, Mariana Is., Dugdug. *Zerega* 127, NA, Micro, Mariana Is., Dugdug. *Zerega* 131, NA, Micro, Mariana Is., Dugdug. *Zerega* 135 b, NA, Micro, Mariana Is., Dugdug. *Zerega* 136, NA, Micro, Mariana Is., Dugdug. *Zerega* 137, NA, Micro, Mariana Is., Dugdug. *Zerega* 138, NA, Micro, Mariana Is., Dugdug. *Zerega* 146, NA, Micro, Mariana Is., Dugdug. *Zerega* 148, NA, Micro, Mariana Is., Dugdug. *Zerega* 150, NA, Micro, Mariana Is., Dugdug. *Zerega* 153, NA, Micro, Mariana Is., Dugdug. *Zerega* 154, NA, Micro, Mariana Is., Dugdug. *Zerega* 155, NA, Micro, Mariana Is., Dugdug. *Zerega* 160, NA, Micro, Mariana Is., Dugdug. *Zerega* 161, NA, Micro, Mariana Is., Dugdug. *Zerega* 162, NA, Micro, Mariana Is., Dugdug. *Zerega* 163, NA, Micro, Mariana Is., Dugdug. *Zerega* 164, NA, Micro, Mariana Is., Dugdug. *Zerega* 167 b, NA, Micro, Mariana Is., Mei kole.
- A. elasticus*—*Zerega* 243, NA, Malaysia, Negeri Sembilan, NA. *A. heterophyllus*—*Zerega* 13, NA, Hawaii, Maui (cultivated), Jackfruit. *A. kemando*—*Zerega* 257, NA, Malaysia, Negeri Sembilan, NA. *A. lanceifolius*—*Zerega* 256, NA, Malaysia, Negeri Sembilan, NA. *A. lowii*—*Zerega* 246, NA, Malaysia, Negeri Sembilan, NA. *A. main-gayi*—*Zerega* 233, NA, Malaysia, Negeri Sembilan, NA. *A. scortechenii*—*Zerega* 218, NA, NA, Singapore, NA. *A. tamaran*—SBG, NA, NA, Singapore, NA. *A. treculianus*—*Zerega* 203, NA, Hawaii, Oahu (cultivated), NA