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# Breadfruit in the Pacific Islands, its domestication and origins of cultivars grown in East Polynesia and Micronesia

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## ABSTRACT

Cultivated breadfruit comprises domesticated cultivars of *Artocarpus altilis* (breadfruit), a species native to Remote Oceania, with hybrid cultivars with *A. mariannensis* (*dugdug*), a species from Palau and Mariannas Islands. *Artocarpus altilis* is not a domesticated cultivar group of *A. camansi* (breadnut), as currently understood, but rather a genetically and morphologically distinctive sister taxon, that has been reproductively long isolated from *A. camansi. Artocarpus altilis* regenerates rapidly from root suckering following canopy and root damage: this is an important trait both for adaptation to the South Pacific Tropical Cyclone zone and for its domestication. This trait is not known in *A. camansi* which can be propagated only by seeds. The pre-historic domestication of *A. altilis* and selection of breadfruit cultivars was initiated by Austronesian peoples in Remote Oceania—in its putative natural range in the south-eastern Solomon Islands and/or northern Vanuatu. Major secondary centres of breadfruit selection and cultivar diversity are in the south-west Pacific (Fiji and adjacent central-western Polynesia viz. Sāmoa and Tonga), the eastern Caroline Islands (Pohnpei) and eastern Polynesia (Marquesas and Tahiti). Generic terms for breadfruit in Polynesian languages derive mainly from proto-Oceanic **kulu* (*A. camansi* and *A. altilis*), and proto-Micronesian **mai* (*A. mariannensis* × *A. altilis* hybrids in Micronesia). Morphological and genetic studies of *A. altilis* show eastern Polynesian breadfruit cultivars to be closely related to Micronesian cultivars, while central-western Polynesian cultivars are related to those from eastern Melanesia (Solomon Islands, Vanuatu, and Fiji). The most widely grown seedless and few-seeded diploid cultivars in Fiji and adjacent central-western Polynesia (Sāmoa and Tonga) are genetically very different from the seedless triploid cultivars in eastern Polynesia. A striking finding of breadfruit genetic studies is that a single 'genotype' (*mä'ohi*) accounts for half of the prolific assortment of morphologically diverse, triploid breadfruit cultivars in eastern Polynesia and Micronesia. Given that there is no compelling documented historical, archaeological, linguistic, or genetic support for direct human contact and ancient exchanges between Micronesia (Caroline Islands) and eastern Polynesia, it is postulated that selected breadfruit cultivars, including triploid or polyploid cultivars of *A. altilis*, were introduced into eastern Polynesia (Marquesas) and the Caroline Islands (Pohnpei) from Polynesian Outlier Islands.

**Key words:** *Artocarpus altilis*, *A. mariannensis*, *A. camansi*, breadfruit, tree domestication, Near Oceania, Remote Oceania, Green's line, Micronesia, Polynesia, Solomon Islands, Vanuatu

### *Breadfruit – an untapped potential for addressing food security and climate change in Polynesia, the Pacific Islands, and the humid tropics*

Breadfruit has traditionally acted as both a staple and famine food throughout Polynesia. It is a vital element in Polynesian mythology—including in Hawaii (Mabberley 1989), Tahiti and Kapingamarangi—and connected with sacrifice of one's self for family, and staving off famine (Roosman 1970). When there are famines in Hawai ʻi, the god Ku saves the life of his earthly wife by standing on his head and becoming a breadfruit tree (Pukui 2003: 8). On Rai ʻatea, near Tahiti, a father bids farewell to his starving family, but then becomes a breadfruit tree which saves them from famine (Beckwith 1940: 100–101). The poignant focus of breadfruit in Polynesian mythology can be developed beyond a metaphor for global food security in these challenging times.

The modern spread of breadfruit was largely fuelled by the Englishman, Sir Joseph Banks (1743-1820). After seeing it on the 1768-1771 voyage on HMS *Endeavour* Banks recommended the introduction of breadfruit to the Caribbean as a source of food for plantation slave workers. In 1787 Captain William Bligh led a failed attempt to introduce Tahitian breadfruit into the Caribbean because of the famed mutiny on the HMS *Bounty* (Bligh 1792, Mabberley 1989). Bligh subsequently led a successful expedition transporting more than 600 breadfruit plants to Jamaica and St. Vincent in 1772 (Powell, 1977), and breadfruit remains an important food-tree crop in the Caribbean, and is increasingly being exported to the United States.

Breadfruit timber and latex have many local uses (Mabberley 1989) but more importantly the species is an Annex 1 crop in the International Treaty on Plant Genetic Resources for Food and Agriculture. However, there is an urgent need to revitalise breadfruit agroforestry systems—as traditional knowledge and farming systems is being lost in an era of imported processed food and with a breakdown in intergenerational sharing of traditional knowledge—throughout the Pacific Islands. This will require relevant Government Departments, Pacific Community (SPC), Breadfruit People online community, farmer organisations, NGOs, and the private sector to

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assist current and prospective growers of breadfruit to make better and more informed choices with respect to the most suitable cultivars for particular habitats and end uses. Fortunately, essential and well-compiled information on breadfruit cultivation is becoming more widely available, e.g. https://www.pardi.pacificfarmers.com/breadfruit-compendium / Taylor 2021, https://www.breadfruitpeople.com/ and https://ntbg.org/breadfruit/.

Maintaining cultivar diversity in breadfruit will be vital to produce a range of end products (human food, animal feed, fibre, wood, medicine) and year-round fruit production. Certain breadfruit cultivars will be better adapted to the predicted new climates, including a more variable climate with greater extremes, rising sea-levels and more severe king tide events[6]. It is noted that breadfruit can assist with both climate change mitigation—through carbon sequestration in its wood and low-fossil fuel input systems for carbohydrate/food production—and climate change adaptation, given the tree's resilience to tropical cyclones and protection of soils, especially near-coastal and sloping lands prone to soil erosion. Furthermore, breadfruit is an exceptionally healthy source of carbohydrates, being high in fibre, the essential amino acid lysine, and antioxidants, as well as being gluten-free.

An improved understanding of the nature and origins of breadfruit diversity, as elaborated in this paper, will assist in both the enhanced use of breadfruit cultivars in tropical agroforestry food production systems and their future conservation.

### *Breadfruit in Eastern Polynesia*

The importance of the breadfruit as a food staple in the Pacific Islands, and the circumstances of its introduction to Polynesia (e.g., Ishikawa 1987, Langdon 1989, Ragone 1991, 1991a) and Micronesia (Petersen 2006; Ragone and Raynor 2009) have been well-documented. Marquesan agriculture was dominated by breadfruit with orchard gardens of breadfruit occupying most of the lower parts of the landscape (Handy 1923: 181–202). Preserved breadfruit or *mā*, fermented semi-anaerobically in pits, was the mainstay of the Marquesan diet and vital for optimal utilisation of the seasonal breadfruit crop (Handy 1923: 189–195). Similarly in Tahiti and the Society Islands, breadfruit was traditionally widely cultivated, occupying extensive portions of the coastal plains and adjacent lower hill slopes (Oliver 1975: 234). It was a major food source with every family owning or sharing ownership of trees. Wilder (1928: 15) noted that Tahitians were discriminating judges of breadfruit, thoroughly enjoying the finer cultivars, and eating inferior 'fruits' (compacted infructescences) only in times of scarcity. In selecting cultivars, the most important qualities were flavour and length of cooking time (Wilder 1928: 20). Food preparation included roasting over an open fire, baking for incorporation into the starchy staple *pöpoi*, and fermenting and beating into the sour paste *mahi* (Wilder 1928: 15 & 18).

### *Breadfruit taxonomic complex*

The breadfruit taxonomic complex in the Pacific Islands comprises six entities, viz. *Artocarpus altilis* (Parkinson) Fosberg –diploid and triploid, *A. mariannensis* Trécul –diploid, *A. altilis* × *A. mariannensis* hybrid –diploid and triploid, with the latter including two entities with different genomic contributions from the parental species (Ragone 1997, Ragone 2006, Ragone and Manner 2006, Zerega *et al.* 2015, Ragone 2018, Lincoln et al. 2019). *Artocarpus camansi* or breadnut—characterised by its soft spine-covered, seed-filled fruits—is closely related to both *A. altilis* and *A. mariannensis*, and has been posited as the wild ancestor of *A. altilis* (e.g., Quisumbing 1940: 334, Zerega et al. 2004: 763–764). *Artocarpus bergii* E.M. Gardner et al., with smaller infructescences, is a recently described species related to breadfruit, and known only from the Maluku Islands in eastern Indonesia (Gardner *et al.* 2021).

### *Artocarpus altilis*

*Artocarpus altilis* represents a monophyletic lineage (e.g., Zerega *et al.* 2005, 2015). It has been recorded as a naturalised, possibly natural, species throughout the south-western Pacific Islands, including Nendö, south-eastern Solomon Islands (Yen 1974: 260); Pentecost, Vanuatu where the cultivars *betawotan* and *wo* reproduce without human intervention (Walter 1989: 8); and Fiji (Seemann 1868:255), as well as being widely cultivated in the south-eastern Solomon Islands, Vanuatu, Fiji, Rotuma, and throughout Polynesia (except New Zealand and Easter Island), and Micronesia (Ragone 1991).

Further east in the south-west Pacific, seedless breadfruit (*A. altilis*) cultivars begin to predominate in Fiji which is geographically, culturally and linguistically closely related to Polynesia. Most cultivated breadfruit trees in Fiji, including the widely grown traditional cultivars or cultivar groups *uto dina* (comprising several cultivars), *balekana* and *buco*, as well as *bokasi*, *lolō*, *varaqā, votovoto* and *utovula*[7], are seedless, or nearly so (Seemann 1868, Koroveibau 1967, Ragone 1991, MacGregor et al. 2021). On the other hand, there are still many few-seeded forms of breadfruit in Fiji—sometimes deliberately cultivated using vegetative propagation and/or protected when naturally regenerating; these include *utoniviti*, *karawa*, *maliva*, *matavude*, and *utosore*/*utovakasorena*. There has been a considerable introduction of breadfruit cultivars into Fiji, including *balekana ni Sāmoa*, *buco ni Sāmoa*, *uto ni Sāmoa*, which, from their cultivar names indicate they have a Sāmoan origin, and also introduced by resettled islanders from Ocean Island (Kiribati) to Rabi Island who bought with them in the 1940s *mai keang*, *mai koro*, *mai wea*, and *bukiraro*, and from Vaitupu (Tuvalu) who brought *uto Elise* to Kioa Island, with this cultivar now also grown on nearby Vanualevu.

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[6] For example, in South Tarawa the variety *mai bokēkē* appears to be more tolerant of new stresses connected with climate change (L. Thomson observations in January 2023).

[7] *Uto vula* was the only Fijian cultivar assessed as triploid *A. altilis* in the Zerega et al. (2015) study, but this accession was recorded as seeded (Ragone 1991) and its ploidy level needs checking

Further east in central-west Polynesia (including Sāmoa, Tonga and Niue) seedless/near seedless diploid breadfruit (*A. altilis*) cultivars predominate (Fig. 1), although the presence of occasional triploid cultivars cannot be excluded. The Sāmoan cultivar *ʻulu eʻa* (Fig. 1A) was assessed as triploid by Ragone (1991), but then a Tokelau cultivar of the similar name *ulu ea* (and likely a recent import from Sāmoa) was assessed as diploid (Zerega et al. 2015). The Sāmoan cultivar ʻ*ulu tala* had one triploid locus (Zerega et al. 2015) but sometimes produces seeds (Ragone 1991), and, accordingly, its bizarre genome may be a mixture of diploid and triploid. The Fijian cultivar *uto vula* had a single triploid locus (Zerega et al. 2015). There is another Fijian cultivar *uto savisavi* (MacGregor et al. 2021) that is morphologically like ʻ*ulu eʻa* and so the ploidy status of these two Fijian cultivars warrants further investigation.

**Figure 1** Well-known Sāmoan breadfruit cultivars (*A. altilis*, Upolu, Sāmoa) 1A. *ʻUlu eʻa triploid* (top left). 1B. *Māʻopo diploid* (top right). 1C. *Maʻafala diploid* (bottom left). 1D. *Puʻou diploid* (bottom right); Images: Lex Thomson

### *Artocarpus camansi*

*Artocarpus camansi*, with its distinctive spine-covered and seed-filled infructescences (Fig. 2), is considered a close relative or sister species of *A. altilis*. It occurs widely in lowland New Guinea (e.g., Barrau, 1957, Jarrett 1959, Croft 1987, Ragone 1991:114); and in the Solomon Islands (e.g., Yen, 1974: 260), readily colonising disturbed sites such as alluvial sediments (e.g., Paijmans 1976). Yen (1974: 260) observed that breadfruit *sensu lato* was relatively unimportant in the subsistence systems of the main Solomon Islands with seeded cultivars predominating, these including some very seedy forms (i.e., *A. camansi*). The native range of *Artocarpus camansi* almost certainly extends beyond New Guinea. For introduced into Kiribati and Tuvalu, and more recently into Tokelau from Tuvalu (Ragone 1991: 17, 77).

Morphologically diverse *A. altilis* × *A. mariannensis* hybrids—including both few-seeded diploid and sterile triploid cultivars—have been selected and dispersed throughout Micronesia (Fig. 3B,C,D). These hybrids have proved to be better adapted to atoll island environments than is *A. altilis*—including more saline and periodically dry sites—and with higher yields of fleshy infructescences than *A. mariannensis*. Petersen (2006) has argued that the sociocultural transformations within Micronesia between 1000–1500 AD are attributable to a ‘breadfruit revolution’, with hybrid breadfruit transforming agricultural and food production firstly in eastern Caroline Islands (notably Pohnpei) and then more widely in Micronesia. It is also possible that the introduction or development of seedless triploid *A. altilis* (*mao'i* genotype; see below), around the same period, also contributed to the Micronesian ‘breadfruit revolution’, at least in the volcanic islands, such as Pohnpei, where salt and drought tolerance are far less important than on the low-lying atolls.

**Figure 3** Micronesian breadfruit species and cultivars. 3A. *Artocarpus mariannensis* (top left); 3B. *Yuley;* triploid *A. altilis* × *A. mariannensis* (Butaritari, Kiribati; recent introduction from Yap) (top right); 3C. *Meinpadahk*, triploid *A. altilis* × *A. mariannensis* Pohnpei, FSM (bottom left). 3D. *Mei tehid*; triploid *A. altilis* (bottom right). Images: JB Friday (3A,C,D), Lex Thomson (3B).

### *Is Artocarpus altilis a domesticated cultivar group of A. camansi?*

*Artocarpus camansi* (breadnut) is distinguished from *A. altilis* by both its infructescences, covered in ±long flexible spines, and comprised mostly of seeds and a large pithy core; and its leaves which are more densely pubescent (Jarrett 1959, Zerega *et al.* 2005, Ragone 2006a, Jones 2010; Fig.1). *Artocarpus camansi* is considered native in New Guinea and the Maluku Islands (eastern Indonesia) and possibly also Philippines; however, the area of its original natural distribution is difficult to establish due to its likely, but undocumented, prehistoric movement by humans. In the Pacific Islands, *A. camansi* has been rarely cultivated (Ragone 1997: 7) with records from the island of Epi, Vanuatu[8], and as far east as Sāmoa and the Society Islands, and north to Pohnpei in Micronesia (Zerega *et al.* 2015). It also occurs in the hinterland at Mamfiri, Rotuma where it was grown in ancient times for its inner fibre and production of canoe hulls (John Bennett, pers. comm.). In Fiji there is an uncommon cultivar known as '*Votovoto*' (meaning thorny or prickly) with infructescences covered in long spines but with either no seeds (Seemann 1868: 256) or few as observed in Manukasi village, Natewa peninsula, Vanualevu (Kaitu Erasito, pers. comm.). In Vanuatu there are also several cultivars that have either numerous large seeds, i.e., *bi* and *wabi* on Pentecost (Walter 1989: 6), or very prickly skin, i.e., *puka* on Vate (Walter 1989: 17). It is possible that such cultivars (i.e., *votovoto*, *bi*, *wabi* and *puka*) are hybrids between *A. camansi* and *A. altilis*, but such hybrids are yet to be detected in any of the comprehensive DNA studies undertaken on breadfruit and breadnut.

Zerega and Ragone (2005: 607) reported that their Amplified Fragment Length Polymorphism (AFLP) studies supported a theory that *A. altilis* was derived from *A. camansi*: if so, this species complex with its cultivars would have to be known as *A. altilis* (syn. *A. camansi* – cf. Mabberley 2017: 76). However, AFLP studies are now considered to be of limited use in reconstructing the evolutionary history of any particular group of organisms (Allan and Max 2010).

Given the likely natural, certainly naturalised, occurrences of seeded and genetically diverse *Artocarpus altilis* in Remote Oceania/south-western Pacific we believe that the species is not an ancient cultigen of *A. camansi*. It is noted that:

1. The first settlers bearing the Lapita Cultural Complex arrived and settled in the Bismarck Archipelago around 3,600 years CE (Kirch 1988). Whilst these immigrants were based in coastal settlements, quite likely they observed Papuans utilising *A. camansi* as a food source for its edible seeds. The Lapita settlers had major carbohydrate sources from their gardens, including taro [*Colocasia esculenta* (L.) Schott], swamp taro [*Cyrtosperma merkusii* (Hassk.) Schott], various yams, notably *Dioscorea alata* L., and bananas (*Musa* spp. and hybrids), so there was no driving imperative to attempt domestication of an edible seed-producing tree into one providing carbohydrate. Over several hundred years, the Lapita peoples crossed into Remote Oceania, perhaps leap-frogging the main Solomon Islands, before reaching Nendö (Sheppard 2019), the main island of the Santa Cruz Group, and then rapidly—within one or two centuries—colonising islands throughout the Pacific (Pawley 2006: 247) including eastwards to Sāmoa and south to New Caledonia where only *A. altilis* is found. It seems improbable that in such a short space of time, i.e., <300 years, the Lapita settlers could have drastically modified a nut tree *A. camansi* into a genetically and morphologically much more diverse, food carbohydrate staple tree species, *A. altilis*.

2. The spine-covered, typically seed-filled *Artocarpus camansi* occurs in eastern Indonesia (Maluku Islands) and is the predominate *Artocarpus* species throughout New Guinea (Jarrett 1959), as well much of the Solomon Islands, viz. Western Province, including New Georgia; Choiseul, Santa Isabel, Guadalcanal, Malaita, and San Cristobal/Makira (Yen 1974: 260; Basil Gua & Gideon Bouru, pers. comms.); whereas *A. altilis* predominates in Remote Oceania, i.e. Temotu Province in the SE Solomon Islands, northern Vanuatu and then in all directions throughout the Pacific Islands. *Artocarpus altilis* is uncommon in Near Oceania and adjacent south-east Asia, and invariably associated with cultivation. It is infrequently cultivated in the Solomon Islands (e.g., Ranogga Island in Western Province, Dr Richard Pauku pers. comm.) and Papua New Guinea including from the Manus Islands, where seedless forms of breadfruit (with aborted embryos) have been observed (Yen 1991: 87). It is also cultivated in eastern Indonesia, including on Biak in West Papua (Beccari, 1902: 628–629), where it was described as *Artocarpus incisus* (Thunb.) L. f. var. *muricatus* Becc., and in the Maluku Islands, e.g., Rumphius (1741) where it is described as *Soccus lanosus*, a breadfruit which had low facets on the syncarp and glabrous leaves, and morphologically corresponding to *A. altilis*. Its early cultivation extended as far west as Java, under the names *Radermachia incisa* Thunb. and *Artocarpus laevis* Hassk. (Zerega et al. 2005: 611).

3. While sharing a few morphological synapomorphies, the species have several different morphological characters (Zerega and Ragone 2005) that would not be expected to have arisen due to mild human selective pressure. Firstly, they have different leaf pubescence, with the mature leaves of *A. camansi* being densely pubescent, while those of *A. altilis* are glabrous to moderately

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[8] The *sur* has prickly-skinned. rounded infructescences full of seeds (Walter 1989: 10) and presumably is *A. camansi*. Walter records three other prickly-skinned cultivars on Epi, viz. *bombouro, bresa* and *surnamarbumba.*

pubescent. Secondly, the skin texture of *A. camansi* infructescences is invariably echinate or with long (5-12 mm) flexible, narrowly conical spines, while that of *A. altilis* consists of short spikes, pebbly ±flat or rounded, sandpaper-like with persistent stigma dots, smooth± irregularly raised sections (and only extremely infrequently with longer spines) (Jones, 2010). Thirdly, the seeds of *A. camansi* have a thin, light-brown outer coat, patterned with darker veins, whereas *A. altilis* seeds typically have a dark brown shiny coat (Ragone 2006a).

4. The two species have different propagation strategies. Both *A. camansi* and seeded types of *A. altilis* may be readily propagated from their large, recalcitrant seeds. However, according to Ragone (2006a), *A. camansi* trees do not produce root shoots and cannot be grown from root cuttings, whereas *A. altilis* is readily propagated vegetatively from both root suckers and root cuttings. Furthermore, *Artocarpus altilis* regenerates and freely spreads in both natural and cultivated settings, especially following root disturbance and damage. The latter regeneration method is well suited to environments which are subject to frequent disturbance such as from tropical cyclones.

5. DNA studies, using AFLP, microsatellite and SNP markers, have shown *A. altilis* to be genetically distinct from *A. camansi* (Zerega et al. 2005; Zerega et al. 2015, Diczbalis et al. 2019), with intermediate genotypes absent and little or no evidence of introgression in these studies. Indeed Zerega et al. (2015) noted this anomaly "*there is little overlap of the A. camansi group in any of the breadfruit or hybrids (Fig. 6), although it is thought to be the wild progenitor of non-hybrid breadfruit (Zerega et al. 2004, 2005)*". This contrasts with the situation with the other close wild relative of *A. altilis*, viz. *A. mariannensis*, with spontaneous hybridisation seemingly frequent in their shared cultivated range (e.g., Tokelau, Ragone 1971:77). Furthermore, *A. camansi* displays lower levels of genetic diversity than cultivated breadfruit (Zerega et al. 2015:22), whereas the opposite would be expected if *A. altilis* had been domesticated from *A. camansi* by Lapita and/or Melanesian peoples, given genetic bottlenecks sometimes associated with human selection in tree crops.

6. Gardner and Zerega (2021: 322) note that *A. altilis* and *A. camansi* "*form reciprocally monophyletic clades (Audi, 2018; Gardner et al., 2021a) in contrast to domesticated systems such as Zea mays L., in which the wild members of the species form a paraphyletic clade (Matsuoka et al., 2002)*". The finding that *A. altilis* and *A. camansi* are reciprocally monophyletic suggests that they have been isolated for a very long time.

Traditional tree domestication is most often a long, quasi-directional process involving modest selective pressure over many generations, such as for *Canarium* spp. in Melanesia: in the Pacific it is believed to have been devoid of active and highly directed breeding activities. However, the appearance, identification, and propagation of selected seedless triploids (and their sports), as has been the case with seedless triploid breadfruit in Micronesia and eastern Polynesia, is akin to domestication in the fast lane, when a key objective is selection of starchy fruits devoid of seeds.

The earlier postulated domestication of *A. altilis* in New Guinea from *A. camansi* requires further investigation to be proven. If true, it would indeed be a remarkable achievement as it would have required ±concurrent selection for multiple, likely-independent traits including fewer seeds, smaller seeds, reduction in the length and width of the core of infructescence, ability to be propagated from root cuttings-vegetative propagation, and a thinner/flatter skin surface (suggested to be suited to easy peeling) over just some hundreds of years. Selection and simultaneous improvement of multiple independent traits is a long process even for annual crops subjected to active breeding and selection, let alone for tree crops with longer generation intervals and not subjected to active breeding such as most tropical fruit and nut tree species.

It is also noted that several morphological traits that would not have been expected to be under human selective pressure differ between *A. camansi* and *A. altilis*: these include leaf size, leaf indumentum density, length, and appearance of leaf trichomes, peduncle collar and insertion (Zerega et al. 2005, Jones 2010). It is possible that some differences in infructescence characteristics between *A. altilis* and *A. camansi* are related to favouring seed dispersal by fruit bats (*Pteropus* spp.), with smaller infructescences containing smaller seeds providing a greater reward in terms of more starchy flesh and more easily carried longer distances by them.

### *Postulated wild origin for breadfruit in SE Solomon Islands and northern Vanuatu*

It is postulated here that breadfruit (*Artocarpus altilis*) is a wild species from Remote Oceania, most likely south-east Solomon Islands and/or northern Vanuatu. The biogeographic delineation between Near and Remote Oceania (Pawley and Green1973; Green 1991), here termed the Green's line, is significant for understanding the origins of *Artocarpus altilis*. Between the most easterly of the Solomon Islands chain (eastern tip of Makira/San Cristobal) and the Santa Cruz group there is 352 km stretch of sea, across which people could not see new land, and which, pre-Lapita or up to c. 1,500 BCE, acted as a barrier to further ocean voyaging and exploration. It also acted as a major biogeographic boundary. Distances between islands increase markedly beyond the Solomon Islands chain proper and this has significantly affected the distribution of plants and animals, with 162 genera of seed-plants, about 24% of the total, having their eastern limit in the main Solomon Islands (Green, 1991).

As noted by Jarrett (1976: 38) the distribution of *Artocarpus* species '*suggest[s] that water is a strong* *barrier to dispersal, as might be expected with such large seeds lacking dormancy*'. It is here argued that the Green's line acted as a reproductive and dispersal barrier to the recalcitrant, large-seeded *A. camansi* and *A. altilis* that enabled them to evolve in near-complete isolation, well before the arrival of humans in Remote Oceania, and helps to explain the considerable morphological (see Table 1) and genetic differences (Zerega and Ragone 2015) between the two species. However, it should be noted that large recalcitrant seeds can spread infrequently across substantial ocean barriers, as evidenced, for example, by the presence of the largely Australian black bean (*Castanospermum australe* A.Cunn. ex Mudie) in Vanuatu, and here also posited for the immediate ancestor of *A. altilis* across the oceanic barrier of the Green's line.

The evolution of a root suckering habit in *A. altilis* is considered especially significant, not due to human selection, but rather likely related to the differences in tropical cyclone frequency and intensity between Near and Remote Oceania, with cyclones being absent in New Guinea and the main Solomon Islands[9] experiencing an average of 1.5 cyclones per year mostly in low intensity categories. By contrast, in the adjacent south-western edge of Remote Oceania (Temotu Province, Solomons Islands [cf. Whitmore, 1974] and Torba Province, Vanuatu), tropical cyclones are more frequent and intense including some in Category 5, e.g., Cyclone Zoe in 2002 which devastated Tikopia (Temotu), with 2-3 cyclones passing over the Vanuatu archipelago each year, and with around 3–5 per decade of sufficiently high intensity to cause severe damage (Anon. 2014: 25). The ability to regenerate rapidly from root suckers, often pre-formed, following major cyclone canopy damage and root damage to *A. altilis*, and other tree species such as *Santalum austrocaledonicum* and an undescribed riparian *Casuarina* species (Santo, Vanuatu), is of tremendous adaptive advantage in the cyclone-prone environments to the east of Green's line.

The Santa Cruz group, Temotu Province of Solomon Islands is a centre of breadfruit diversity with 39 named breadfruit cultivars, including 19 from Neboi Village, Nendö and 20 names in *Äiwoo* language, Otelo Village, Lomlom, Reef Islands, with the latter cultivars being distinguished on yield and maturation time; fruit size, shape, flesh colour, cooking time, taste and smell; and leaf shape (Jackson, 1982). Major cultivation and intensive domestication of breadfruit is here posited to have taken place in the Santa Cruz Islands (south-east Solomon Islands) and the adjacent Torres and Banks Islands, as well as Santo, Malo, and Pentecost (northern Vanuatu). As observed by Ragone (1997: 19) "*the greatest diversity of seeded and few-seeded cultivars is found in the eastern Solomon Islands and Vanuatu, and it was probably in the Santa Cruz and possibly the Banks Islands that breadfruit was first extensively cultivated and selected*". This involved the selection of few-seeded or seedless diploids (2n = 56) and likely also seedless triploids (3n = 84), vegetatively- propagated cultivars with more starchy and less seedy infructescences, as well other unique cultivars such as the purple-fleshed cultivar *bia ningabo* (Malo language; Neo Island on the western end of Santa Cruz, Rev. Jasper Bonnie pers. comm.). The human selective pressure for seedless breadfruit is attributed to greater suitability in the preparation of pit-fermented breadfruit—traditionally a very important food throughout Polynesia (Ragone 1991a, 2002), including Polynesian Outliers (Kapingamarangi, Nukuoro, Tikopia), as well as in Micronesia (Yen 1991: 87) and Vanuatu, Melanesia (Walter 1989: 9–10).

One putative location for wild *A. altilis* is Nendö where Yen (1974: 260) has recorded that the species grows in valleys in the interior of the island. However, in this case and most others, the local observers consider the species was likely introduced. However, within 5 to 10 years breadfruit can naturalise and appear to be wild or semi-wild, such as in many parts of Fiji (Kaitu Erasito, pers. comm.). Over three thousand years (i.e., since initial Lapita colonisation of Remote Oceania), it is quite possible that the origins of breadfruit in any part of its natural range may have been lost. Furthermore, assuming *A. altilis* had similar ecological requirements to its sister species *A. camansi*, and favoured fertile, alluvial soils, then such zones are likely among the first to be utilised for gardens, and might help explain the absence of undisturbed forest sites with *A. altilis* being present as a constituent species.

In Vanuatu, breadfruit is naturalised, possibly wild, in the northern islands, i.e., north of Efate (Presley Dovo, Jon Naupa, pers. comms 10/2023), although there is also one field note made by S. Frank Kajewski of its appearing to be wild in the forests of Erromango (Guillaumin 1932: 106). Northern and central Vanuatu is a breadfruit domestication hotspot: in ten local languages from this region there are at several hundred named breadfruit cultivars, exhibiting extreme variation in infructescence characteristics (size, shape, skin, pulp texture and colour, seediness), as well as variation in leaf form, tree habit, culinary and gustatory properties: there are also local myths related to breadfruit domestication (Walter 1989: 7–9).

The greatest cultivar diversity has been recorded from the northern islands. In the Torres and Banks Group, Codrington (1891: 304) noted 60 cultivars of breadfruit on Mota, and Walter (1989: 6) recorded 17 cultivars on Vanua Lava in the Banks Islands, while Walter and Sam (1991) recorded 31 in the Torres Islands. In her surveys from 1982 to 1986 Annie Walter recorded 78 morphotypes on Santo and 137 morphotypes on adjacent Malo (Mies 2009: 20), including 108 locally-named and recognised morphotypes around Avunatari (Walter, n.d.). On Pentecost, 44 morphotypes have been recorded (Walter, 1989: 6); and on Ambrym 65 cultivars were recorded in the village of Ranon by Murray (1894: 36).

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[9] The Solomon Islands are located south of the equator, just north of an area known for the frequent occurrence of tropical cyclones https://pcric.org/wp-content/uploads/2022/03/Solomon-Islands-2.pdf

**Table 1**. Morphological differences between *Artocarpus camansi* and *A. altilis*

| Character | *A. camansi* | *A. altilis* | Notes |
|---|---|---|---|
| Propagation method and root suckering habit | Always propagated from seed and does not produce root suckers (Morton 1987, Ragone 2006a, Kaitu Erasito and Quito Braun-Ortega pers. comms.). Adventitious shoot growth from the base of breadfruit trees in New Guinea is rare (Yen 1991a: 565). | All cultivars are recorded as developing shoots from their roots which can be used for propagation or develop into a clonal thicket | Character likely under genetic control as observations made of trees of both species growing in the same environment at the NTBG Kahanu Garden on Maui, Hawai‘i. |
| Leaf size (Jones, 2010) | Av. 57 cm x 41 cm, 8 lobes per leaf | Av. 41 x 34 cm, 7 lobes per leaf | There is a major difference in average leaf size on trees grown in the NTBG Kahanu Garden with *A. camansi* leaves (2920 cm$^2$) being twice the size of those of *A. altilis* (1400 cm$^2$) |
| Leaf indumentum density | Moderately to densely pubescent | Near-glabrous to moderately pubescent | |
| Length and appearance of leaf trichomes | Straight, pale trichomes | White or reddish-white trichomes found primarily along the veins. Trichomes longer on Melanesian cultivars (Jones 2010) | |
| Infructescence shape | Ellipsoid | Round, oval, oblong, ellipsoid, heart-shaped, and irregular-shaped | Character may be affected by human selection |
| Infructescence peduncle collar and insertion (Jones 2010) | Peduncle collar generally absent | Raised or flattened, elongated collar | Character unlikely to be affected from human selection |
| Infructescence core (Jones, 2010) | Av. 13.5 cm x 5.3 cm | Av. 10.4 x 4.2 cm | The average sectioned core dimension is much greater for *A. calamansi* cf. *A. altilis*, viz. 72 cm$^2$ vs. 44 cm$^2$. |
| Infructescence surface (Jones, 2010) | Covered by long (5 -15 mm) flexible, narrowly conical spines | Surface texture is variable, but mostly smooth ± irregularly raised sections. The surface is covered with small sharp spikes, pebbly ±flat or rounded or sandpaper-like with persistent stigma dots (infrequently covered with longer spines perhaps due to hybridisation). | Infructescence surface suggested to have been transitioned during domestication from being covered by long flexible spines towards a smoother texture (Jones, 2010) |
| Colour of infructescence skin (Ragone 1997) | Light green | Light green, yellowish-green or yellow | New colours of infructescence skin would not have been expected from human selective pressure |
| Colour of infructescence flesh | White | Creamy white or pale yellow (or yellow when overmature) | Change in flesh colour not expected from human selective pressure, but could be associated with change in ratio of seed:flesh. |
| Number and type of seeds per infructescence (from Jones 2010) | Many large, hard-coated seeds. Average of c. 35 seeds per infructescence | Average number of c. 2 seeds per infructescence. | Very low number of seeds for *A. altilis* infructescences is due to the inclusion of seedless triploids in these samples. |
| Seed coat surface (from Ragone 2006a) | Thin, light-brown outer seed coat, patterned with darker veins | Dark brown shiny seed coat | Difference in seed coat colour not expected to be under human selective pressure |

### *Linguistic origins of generic terms for breadnut (Artocarpus camansi) and breadfruit (A. altilis)*

In the Philippines, the seeded breadfruit or breadnut (*Artocarpus camansi*) is known in local Western Malayo-Polynesian languages as *kamánsi* (Casiguran Dumagat spoken in NE Luzon, Hanunóo spoken in Mindoro), *kamansi* (Cebuano spoken in Cebu; Mansaka spoken in Mindanao), *kamansí?* (Tagalog; Maranao in Mindanao), *kemasi* (Manobo spoken in Mindanao), *kemasey* (Tiruray spoken in Mindanao) (Blust and Trussel 2016). These terms have sometimes been considered to have been derived from **kamansi* and/or **kamansiq*, in reconstructed/hypothetical Proto-Philippines (PPh) or Greater Central Philippines (GCP) languages (Blust 1991), and possibly attest to the antiquity or indigenous nature of *A. camansi* in the Philippines. However, there is scant evidence that Austronesian peoples moving through the Philippines to New Guinea adopted any of these names for *A. camansi.* One of the West Papuan language names for breadfruit *sensu lato* is *kamandi* (Barrau 1957: 119), and requires further investigation. An alternative interpretation for PPh **kamansi* would be that it is an innovation replacing PMP **kulu*. Indeed, *kolō* is used for seedless breadfruit in the Visayan language of the southern Philippines (Yap 1971), but here this name is considered a relatively recent term, implying that seedless breadfruit arrived in the southern Philippines from the South Pacific, rather than Micronesia.

Wolff (1994) regarded the term ***kuluɣ* for breadfruit *sensu lato* to have a 'Pacific' origin, while Dempwolff (1934–37; Vol 3:83) considered that **kulu(l),* derives from Proto Malayo-Polynesian for breadfruit (German: Brotfruchtbaum). Wolff (1994: 522–523) noted the spread from east to west of the name *sukun*[10] for the seedless breadfruit, as in languages of the Moluccan Islands as well as in Javanese and Malay, while names connected with ***kuluɣ* refer to the seeded breadfruit in these languages. There are numerous names for the seeded breadfruit (*A. camansi*) in traditional Indonesian languages, attesting to its ancient presence in that extensive archipelago: these include *sukun biaji*[11] and *kullur* (for Malay and Javanese), *timbul* (Balinese), *goma* (Ternate – a north Halmahera/Papuan language) and *gomassi* (Maluku Islands), *amakir* & *umare* (Ambon), and *sukun utan* (or forest *sukun*) (Note: some of these names have been modernised from Rumphius 1741a with a current spelling), as well as *suune* (Ambon), *amo* (North Maluku), *kamandi, urknem* and *beitu* (West Papua), *karara* (Bima, Sumba, Flores), *susuaek* (Rote), *hotopul* (Batak), *arise, kulur* (Sundanese), *kluwih* (Javanese), *kulu* (Aceh), *kalawi* (Minang), and in Sulawesi there is *bakara* (Makassan) and *baka* (Bugis).

We consider it likely that the term **kuluR* entered Malayo-Polynesian languages not long before languages ancestral to those of eastern Indonesia and Oceania separated from their more westerly relatives. Names such as *sukun* in Indonesia, and *kolō* in Cebuan (which likely reflects **kuluR*) needed to be developed with the arrival of seedless/ few-seeded breadfruit—subsequent to its discovery in Remote Oceania—to differentiate them from seeded breadfruit (*A. camansi*). In Papua New Guinea, there is a striking link between the language family that people speak and which type of *Artocarpus* that they eat: most people who consume breadfruit speak an Austronesian language while most people who consume breadnut speak a Papuan language (Michael Bourke, pers. comm.).

The two generic terms for breadfruit in Polynesian languages likely have their origin in morphologically distinctive taxonomic entities, viz. **kulu* for both *A. camansi* in New Guinea & Solomon Islands and *A. altilis* in SE Solomons & Vanuatu, and **mai* for *A. altilis* × *A. mariannensis* hybrids in Federated States of Micronesia (FSM); the natural distributions of *A. altilis* & *A. camansi* and *A. mariannensis* being separated by more than 1000 km of mainly ocean. **baReko* is another POc reconstruction for breadfruit (or breadnut) reflected in Western Oceanic, SE Solomonic, Temotu, North-Central and Southern Vanuatu languages (Ross 2008: 282) but this term and cognates do not extend to any Polynesian languages. Ross (2008: 283) speculated that **baReko* (or **beta*) may have denoted *A. camansi* or a particular cultivar or breadfruit cooking preparation. He also noted that the reflexes of **baReko* are generally regular, suggesting that replacement took place very early in the history of Oceania languages. Given the distribution of the term **baReko*—in our putative origin of *A. altilis*—it may refer to seedless/near seedless breadfruit and/or an associated preparation of a preserved starchy food, that was made shortly after the discovery *A. altilis* by the early Lapita settlers.

Proto-Polynesian **kulu* and its reflexes are widely distributed in Polynesia as a primary name for the breadfruit tree and its 'fruit', including Sāmoa (*'ulu*) and nearby atolls of Tokelau (*ulu* – borrowing from Sāmoan); Cook Islands (*kulu* in Pukapuka and *kuru* elsewhere); Hawaiʻi (*'ulu*); French Polynesia: Raʻivavae, Austral Islands (*'ugu*); Society Islands (*'uru*); Tuamotu Islands (*kuru*, *'uru*); Vaeakau-Taumako of the southeast Solomons Outliers (*kulu*), and north from there in Northern Outliers, viz. Luangiua, (*ulu*) and Sikaiana (*kulu*) in Solomon Islands; Nuguria (*ulu, kuru*), Nukumanu and Takuu (*kuru*) in PNG; Nukuoro (*guru*) and Kapingamarangi (*kuru*) in FSM, and sporadically in the southern Polynesian Outliers including Ifira-Mele and West Futuna (*kuru*). Outside Polynesian languages, cognates of POc **kuluR* 'breadfruit' may be found in Papua New Guinea languages, e.g. Gedaged, Takia (*ul*); Bola, Mussau, Nakanai (*ulu*); Ali, Titan, Wogeo (*kul*); Manam, Vitu, Wayan (*kulu*); Western Fiji (*kulu*), New Caledonia (*cin*, *i-oun*) (Ross *et al.* 2008) and Rotuma (*'ulu*) (Churchward 1940).

The Proto Micronesian term for breadfruit is **mai*, and it is probable that reflexes such as Kiribati *mai* and Pingelap *mey* are the sources of the Polynesian name *mei*/*mai* for breadfruit. The term**mei*/**mai* has a wide and unusual distribution in Polynesia, extending over 6,500 km of ocean, with external cognates in Micronesia and southern Vanuatu (Geraghty 1990). *Mei* is widely used for breadfruit in central-western Polynesia (Niue, Tonga including Niuafoʻou, East Futuna, East ʻUvea and Tuvalu, but not in Sāmoa). *Mei* is used in the Southeast Solomons Outliers (Anuta, Tikopia and Rennell) with the exception of Vaeakau-Taumako which has *kulu*; in scattered locations in the Southern Outliers (Emae, Ouvéa), while Mele-Fila and West Futuna have *kuru* and Emae has a variety named *kuro*. *Mei* is used in two island archipelagos of East Polynesia, the Marquesas and Mangareva/Gambier Islands, the latter having a history of late influence from Marquesan (Wilson 2022). *Mai*, rather than *mei*, is found only in parts of northern Tuvalu, and may be the base of Tahitian *maiore*, an older name for breadfruit (but see alternative etymology below).

Marquesan and Mangarevan *mei* is part of a group of late borrowings into Marquesan proposed by Wilson (n.d.) as being from the Tikopia area and that had earlier spread to the area around Tikopia as part of the Tongan expansion. Wilson relates it to what he sees as other borrowings that postdate the formation of PEPn, which he derives from Tongan- and Nuclear Polynesian-derived terms from the Tikopia-area found in other EPn languages. Such borrowings are consistent with historical voyages from the Northern Outliers to Tikopia as well as the evidence collected by Wilson that the initial settlement of East Polynesia was from the Northern Outliers along a corridor running east of the Northern Outliers through the Phoenix and Line Islands to the Marquesas (Wilson 2014: 344,

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[10] *Sukun* means seedless in Javanese

[11] *Biaji/biji* means seeded in Bahasa Indonesia

Wilson 2021). He has provided evidence that the Northern Outliers subgroup with the Southeast Solomons Polynesian Outliers and that traditional Northern Outlier voyages to that area provided a means to maintain knowledge of high island flora and fauna and spread such knowledge into Proto East Polynesian and early descendants of Proto East Polynesian (Wilson 2012: 335-337; 2018: 405-407; 2021) https://pollex.eva.mpg.de/entry/mei2

**Figure 4** *Pokēkē* cultivar (*Artocarpus altilis* × *A. mariannensis* hybrid) in southern Tuvalu (Image: Mr Uatea Vave)

Marquesan and Mangarevan also have names for cultivars of breadfruit that incorporate regular cognates of PPn **kulu,* as does Emae in the Southern Outliers. Tahitian *maiore,* a doublet of *ʻuru,* has been seen by some as related to Marquesan *mei*, but another possible source is PEPn **kai/uore* ʻwizened fruit that falls before ripe, especially of breadfruitʼ, Hawaiian ʻ*aʻaiole*; Tahitian *ʻaiore*, Marquesan *kauoʻe*, and Rarotonga *mākaiore* (Wilson n.d.)

Distribution of the term *mei* within Polynesia as a whole is likely indicative of borrowing from Tuvalu, Tonga and/or Tikopia. Hybrid breadfruit cultivars under the name *mei* may have been introduced into Polynesia from Pohnpei (FSM) by Tongans (c. 1000–500 BP) who then took the name ±the plant to the Southeast Solomons Outliers, some of the Southern Outliers and back to heavily Tongan-influenced East ʻUvea, Niuafoʻou, and East Futuna. Another possible route for introduction of hybrid breadfruit to Polynesia is via Kiribati (*mai*) into northern Tuvalu (*mai*) and southern Tuvalu (*mei*). Some breadfruit hybrids survive in Polynesian atolls, such as the cultivar *pokēkē* in southern Tuvalu (Fig. 4), and also in the Carolinean/Northern Polynesian Outliers of Kapingamarangi (Fig. 5), and Nukuoro, which has breadfruit cultivars with both rough skin (*gulu daladala*)[12] and smooth skin (*gulu maimai* and *gulu malali*) (Carroll and Soulik, 1973: 95). The Carolinean Polynesian Outliers have clearly had considerable contact with Micronesia and may have received their hybrid breadfruit directly from there. In summary, the term *mei* appears to be a late borrowing into Polynesian languages resulting in a geographically patchy overlay of *mei* over *kulu*.

**Figure 5** Kapingamarangi villagers provide hybrid breadfruit (*A. altilis* × *A. mariannensis*) to visiting sailors from SV Manjana (Image: Mr Are Christian Sveen; 15/4/2019)

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[12] The roughened texture is likely due to *A. mariannensis* which often contributes conical, flattened perianth disks to the fruit of hybrids (Ragone 1991: 17)

### *Proliferation and distribution of breadfruit cultivar names*

There are more than 2000 cultivar names for breadfruit in the Pacific Islands (Ragone 1991, Jardin 1974), including in:

*Melanesia:*

- 20–147 cultivars in Solomon Islands (Ragone 1991); 18-39 cultivars in the Santa Cruz Islands (Yen 1974; Jackson 1982),
- More than 500 cultivars in Vanuatu, mostly in the northern islands (e.g., Murray 1894, Walter 1989, Navarro et. al. 2007, Mies 2009, Labouisse 2016); 76 cultivars in the Vanuatu Southern Polynesian Outliers of Aniwa and Futuna (Dougherty 1983),
- 13–55 cultivars in Fiji (Seemann 1868, Koroveibau 1967, Ragone 1991, MacGregor et al. 2021), nine in Rotuma, Fiji (Churchward 1940) and five in Lau, Fiji (Thompson 1940).

*Micronesia:*

- 45–131 cultivars in Pohnpei, Federated States of Micronesia (FSM), (Christian 1897, Soucie 1978, Raynor 1989),
- 31–56 cultivars in Chuuk, FSM (Bascom 1946, Elbert 1947),
- 23 cultivars in Marshall Islands (Mackenzie 1964),
- 18–21 cultivars in Kosrae, FSM (Sarfert 1919, Lee 1976, Merlin et al. 1993),
- 5 cultivars in Kiribati (Catala 1957).

*Polynesia:*

- Outliers: 13 cultivars on Anuta, Solomon Islands (Yen 1973), nine on Tikopia, Solomon Islands (Ms Gabrietta Tofisoaki, pers. comm.), and three on Kapingamarangi, Carolinean Polynesian Outlier, FSM (Coenan and Barrau 1961),
- 24–66 cultivars in Society Islands, French Polynesia (FP) (Ellis 1829, Bennett 1860: 396, Wester 1924, Henry 1928, Wilder 1928, Petard 1986, Ragone 1991),
- 25–34 cultivars in Marquesas, FP (Jardin 1862, Guillaume Lebronnec from informant Stanislas Taupotini on Nuku Hiva c. 1948, Christian 1910, Wester 1924, Ragone 1991),
- 13 cultivars in Mangareva, FP (Buck 1938),
- 20–46 cultivars in Sāmoa (Christophersen 1935, Parham 1966, Ragone 1991, Ragone et al. 2004),
- 5–11 cultivars in Tonga (Yuncker 1959, Tupoulahi-Fusimalohi 1999),
- 8 cultivars in East Futuna/Wallis and Futuna (Burrows, 1936),
- 6–10 cultivars in Tuvalu (Ragone 1991, Thaman et al. 2017),
- 4–5 cultivars in Cook Islands (Cheeseman 1903, Wilder 1931),
- 5 cultivars in Niue (Yuncker 1943).
- 1 cultivar in Hawaiʻi

In some cases, cultivar names are synonyms, i.e., the same cultivar being grown under a different name in a different place. For example, the distinctive Sāmoan and Tongan cultivar māʻopo—with near entire leaves and ellipsoid infructescences (Fig. 1B)—is known as uto lolō/uto cokocoko in Fiji and ʻulu pulpul/pulupulu in Rotuma (Seemann 1868: 256, Erasito 2019, Ragone et al. 2004, Elevitch and Ragone 2018).

### Development of seedless breadfruit

While completely seedless breadfruit is almost unknown in PNG, Bougainville and Solomon Islands, such cultivars occur on nearby Northern Polynesian Outlier Islands such as Takuu (politically part of PNG) as well as Polynesian Outliers in the Santa Cruz Islands (SE Solomon Islands) (Yen 1974: 258 and 1991: 87, including references and pers. comms.). Two seedless breadfruit cultivars have been reported from Nendö, Temotu Province SE Solomon Islands (Yen 1974: 258). A seedless cultivar with large infructescences is also grown in the Reef Islands (Temotu Province) where it is known as *blosi miboa nadola* (Äiwoo language name meaning '*blosi* variety without seed') and near identical with the seedless cultivar *metu nonabe* on Nendö Island, with its name meaning 'similar smell to *Terminalia catappa*' in Graciosa Bay language (Rev. Jasper Bonnie, pers. comm.). A seedless breadfruit cultivar is reportedly grown on Tikopia (Ms Gabrietta Tofisoaki, pers. comm.).

Seedless breadfruit cultivars, including some morphologically resembling those in eastern Polynesia, are also found throughout the northern Pacific Islands from Palau, through Marianas and FSM to Marshall Islands in the east (Ragone 1991: 15), and have long been documented in Micronesia. The Spanish introduced seedless breadfruit from Guam to the Philippines in the 17th century (Wester 1924), while Dampier (1729), who coined the name breadfruit (Mabberley 1989), documented the use of seedless breadfruit in the Mariana Islands. Furthermore, recent genetic studies indicate that these sterile triploids in Micronesia include numerous named cultivars/unique genotypes of both *A. altilis* (c. 14 cultivars) and *A. altilis* × *A. mariannensis* (c. 25 cultivars) (Zerega et al. 2015), suggestive of a considerable period of domestication and cultivar selection. An archaeological record of breadfruit charcoal and pollen from Kosrae has been interpreted as the introduction of a set of food plants with a strong arboricultural component at first settlement, i.e., about 2000 years ago (Athens et al. 1996). This conclusion implies the existence by this date of breadfruit of Polynesian type, seedless and propagated by suckers like that of Kosrae today (Kennedy and Clarke 2004: 28).

As discussed above, the seedless trait in breadfruit becomes more prevalent further east in the South Pacific Islands. It is here considered likely that seedless triploid breadfruit was first selected in the south-east Solomon Islands (Santa Cruz Islands) or adjacent northern Vanuatu, given that these are known hotspots for early species domestication of food trees such as *Canarium indicum* L., *C. harveyi* Seem. var. *nova-hebridiense* Leenh., *Terminalia catappa* L. and *Barringtonia* spp. (Evans 1999), including breadfruit (Yen 1974; Ragone 1991), and with Mies (2009) recording 14 seedless (±aborted seeds) breadfruit cultivars/ morphotypes from seven islands on Vanuatu. It is further posited here that selected breadfruit cultivars, including few-seeded cultivar(s) of diploid *A. altilis* and seedless triploid cultivar(s) of *A. altilis*, were first introduced into eastern Polynesia from the south-western Pacific, perhaps South-east Solomons Polynesian Outliers such as Tikopia.

### *Proliferation of one seedless triploid Artocarpus altilis lineage into different cultivars in eastern Polynesia and Micronesia (Pohnpei)*

A striking finding of the breadfruit isozyme studies of Ragone (1991) was that more than 30% of breadfruit accessions (74 out of 204) had the same profile (zymotype) for the six enzyme systems studied. This frequent zymotype was unique to the typically seedless *A. altilis* cultivars characteristic of eastern Polynesia (Marquesas, Society Islands, Cook Islands, Hawai‘i) and Micronesia (Palau, Marianas, Kosrae, Chuuk, and Pohnpei), but with one representative from each of Fiji (*uto lolō*) and Sāmoa (*‘ulu e‘a*). These findings were mirrored in the microsatellite marker studies of Zerega *et al.* (2015) where a single genotype[13], here referred to as the *mä'ohi* genotype, accounted for 49% of triploid *A. altilis* cultivars examined. These included 43 different cultivar names from Cook Islands (*enua*), Federated States of Micronesia (Chuuk *mei chon* and Pohnpei seven cultivars), French Polynesia (Society Islands 26 cultivars; and Marquesas four), Hawai‘i (*‘ulu*), Marianas Islands (*lemae)* and Palau (*meriaur*). In the same lineage[14] as this predominate genotype, there were a further 25 closely related genotypes of 24 named cultivars, mainly from French Polynesia (Society Islands and Marquesas), Hawai‘i and Micronesia.

This triploid cultivar group (viz. *mä'ohi* genotype), including very closely related cultivars, is considered ancient in the Marquesas (*mei mä'ohi*), Society Islands (*‘uru ma‘ohi*), and Cook Islands (*kuru maori*) (Christian 1910; Hugenin 1902; Henry 1928; Ragone 1987 and 1991; Wilder 1928). These cultivar names viz. Marquesan *mä'ohi*, Tahitian *ma‘ohi*, and Rarotongan *maori,* are all derived from *maori (*maqoli*) which translates as “the regular type that everybody knows”. It is also the only breadfruit, under the name *‘ulu,* to have reached Hawai‘i in prehistoric times (Ragone 1991, Mabberley 1998: 48), likely around 1300 CE (McCoy et al. 2010). Four related breadfruit genotypes—here presumed to be sports of the original introduction—have been identified in Hawai‘i (Zerega *et al.* 2015). The widespread distribution and antiquity of the *mä'ohi* genotype including sports, likely make it one of the earliest seedless triploid cultivars, if not the original one (Ragone 1991).

As described by Ragone (1991) the *mä'ohi* genotype/ lineage is ancient and highly valued due to its seedless character. It is here posited that *mä'ohi* was discovered and selected in south-eastern Solomon Islands/northern Vanuatu (Remote Oceania) sometime after the Lapita people had first voyaged to and settled Western Polynesia, i.e., after 2800 BP. Subsequently it was moved both north to Micronesia and east to Marquesas[15], and then from Marquesas to the Society Islands and Cook Islands. In each of these islands the highly desirable *mä'ohi* lineage cultivar(s) appears to have been widely cultivated providing opportunities for vegetative mutations or sports, either canopy or root sucker sports—and followed by discovery, selection, and propagation by observant and skilled local horticulturists. The more promising of these sports or mutants were then named, propagated, shared, and dispersed. While triploid *A. altilis* cultivars are genetically closely inter-related they exhibit major variation in morphological (see Fig. 6) and economically important traits. It is postulated that meristematic tissues in breadfruit triploids are less stable at mitosis and have higher rates of mutation than diploids, making them ideal candidates for rapid development of cultivar diversity. This is illustrated in another remarkable finding that a single accession (NTBG 900245.001), *huero* (Fig. 6D), in the Zerega et al. (2015) study was found to comprise two lineages and genotypes: viz. a triploid with the *mä'ohi* lineage/genotype which occasionally produces seeds (Kahanu, Maui, Hawai‘i) and a putative more seedy diploid (i.e. only diploid loci observed) with a different lineage/genotype at Hilo, Hawai‘i: the implication is that the meristematic tissues of this cultivar are unstable and may partly explain variation in seediness in *huero* and *kakano*[16] grown in Society Islands and Marquesas, respectively, and also the rapid evolution of different infructescence and leaf forms found in cultivars in the *mä'ohi* lineage/genotype group (Zerega et al. 2015: 22–23).

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[13] Whilst assessed as having the same ‘genotype’ (identical at all assessed microsatellite loci) these cultivars are unlikely to be genetically identical (clones) as they may differ from one another at non-assessed loci and/or have a different parental allele dosage in the case of triploids. Critically, they display variation in traits that are locally valued and maintained, under a different cultivar name.

[14] Samples in the same lineage group, i.e. derived from a close common ancestor, were assigned based on a threshold number of mutation steps, adjusted for ploidy level.

[15] Seedless breadfruit in Marquesas were described more than 400 years ago (Queirós, 1615)

[16] *Huero* means seed in Tahitian; *kakano* means seed in Marquesan

**Figure 6** Morphological diversity in east Polynesian breadfruit (triploid *A. altilis* cultivars of same genotype and lineage). 6A. *Rare ʻautiʻa*, Pāʻea, Tahiti (top left). 6B. *'äfara,* Ua Huka, Tahiti (top right); 6C. *Mei puʻou,* Hakaui, Marquesas (bottom left). 6D. *Huero*, Anaa, Tuamotus (bottom right). Images: Jean-François Butaud (6A, 6B, 6D), Walter Teamotuaitau (6C).

### *Other breadfruit lineages in Eastern Polynesia*

Another astonishing finding in the Zerega et al. (2015) study was the composition of their lineage 4 which comprised one triploid *A. altilis* cultivar *tuʻutou* from the Society Islands (note: one of several different lineages/genotypes known by the same cultivar name) and three genotypes of *A. altilis* × *A. mariannensis* hybrids from Palau, under the cultivar names *ebechab* and *midolab*. There is a greater genetic contribution from the *A. altilis* parent in the latter hybrids, suggesting that these triploids arose through a spontaneous hybridisation of an autotetraploid *A. altilis* (an infrequent or rare individual)

× diploid *A. mariannensis*[17]. This remarkable lineage 4 comprises breadfruit cultivars with a shared ancestry on small islands on opposite sides of the Pacific Ocean, separated by 9,745 km of ocean. Given that these cultivars almost certainly reflect ancient dispersal[18], it is posited here that a common tetraploid *A. altilis* ancestor was moved in different directions from the zone of intensive breadfruit domestication (Temotu Province, south-eastern Solomon Islands and northern Vanuatu):

1. North-north west to eastern Caroline Islands (Pohnpei) or Palau, where it spontaneously hybridised with diploid *A. mariannensis*, sometime after 2000 BP[19] and

2. East from the Central Northern Polynesian Outliers to Marquesas/Society Islands, perhaps already incorporated into the triploid *A. altilis* cultivar *tu'utou* or as the original tetraploid which then spontaneously hybridised with another diploid *A. altilis* cultivar, such as *huero* (in a related lineage 6 from Society Islands).

There are at least three other breadfruit lineages identified in the Zerega et al. (2015) study which may also have been early introductions into eastern Polynesia, but likely introduced sometime after the prolific *mä'ohi* and *tu'utou* lineages, viz. lineage 2 (five *A. altilis* triploid genotypes including cultivars *fafai*, *pätara*, *pu'upu'u* and *tu'utou* from Society Islands), lineages 29 & 30 (three *A. altilis* diploid genotypes including cultivars *mei kakano* and *huero nïnamu*, from Marquesas and Society Islands, respectively) and lineages 40 and 41 (two *A. altilis* diploid genotypes, comprising cultivars *pi'ipi'ia* and *porohiti* from Society Islands).

Whilst there is a shared generic term *mei* for breadfruit in Micronesia and in Marquesas & Mangareva, there is no evidence for Micronesian hybrids of *A. altilis* × *A. mariannensis* having been introduced into eastern Polynesia in prehistoric times. This is somewhat surprising given their likely better adaptation and superior performance compared with pure *A. altilis* cultivars in atoll archipelago environments in eastern Polynesia such as Mangareva/Gambier Islands and the Tuamotu Islands. However, the possibility that the *A. altilis* × *A. mariannensis* hybrid was introduced to Marquesas—but then either died out or else survives as infrequent or rare specimens, possibly in remote locations—cannot be discounted.

The evidence from breadfruit genetic and morphological studies is that eastern Polynesian cultivars of *Artocarpus altilis* are more closely related to the Micronesian cultivars, while the western Polynesian cultivars of *A. altilis* (Sāmoa/Tonga/Rotuma) are more closely related to those from Melanesia (Ragone 1991, Jones 2010, Zerega *et al.* 2015). The most highly valued and widely grown breadfruit cultivars in central-western Polynesian are unknown in eastern Polynesia, notwithstanding possible recent post-European introductions. *Ma'afala* (Fig. 1C) produces a highly regarded 'fruit' and is a widely cultivated breadfruit cultivar in central-western Polynesia, including in Tuvalu (*mei maafala*) and Niue (*mei mafala*) and was the most frequently recorded breadfruit cultivar in Sāmoa (Ragone *et al.* 2004), with this cultivar name identified by 90% of respondents, as well as being a well-recognised cultivar in Tonga (Tupoulahi-Fusimalohi 1999). However, *ma'afala* is not recorded in eastern Polynesia except for Cook Islands where it is known as 'Niue'; the later name suggesting it to be a recent introduction from Niue.

In Sāmoa, *pu'ou*—a diploid cultivar of *A. altilis*—was the second-most frequently recorded breadfruit cultivar name in the Ragone *et al.* (2004) study, and recognised by 81% of Sāmoan respondents, but *pu'ou* has never been recorded from French Polynesia. *Pu'ou* is a recent introduction from central-western Polynesia (Sāmoa/ Tonga/ Futuna) to several other Pacific Islands including Fiji (*uto ni Sāmoa*), Rotuma (*'ulu Sāmoa*), Kosrae (*mos en Sāmoa*), Pohnpei (*meiuhpw en Sāmoa*) and Vanuatu ('*puou*' introduced from Wallis & Futuna; Ragone 1991: 90). The Marquesan cultivar *mei pu'ou* is recorded as a triploid *A. altilis* (Zerega et al. 2015) and is morphologically quite different from Sāmoan *pu'ou* (Fig. 6C cf. Fig. 1D). However, *mei pu'ou* is morphologically near-identical to *'uru tu'utou* from Tahiti sharing the traits of twisted leaves, short fruit peduncles and a large ovoid infructescences (Walter Teamotuaitau pers. comm.). A seeded diploid cultivar, known locally as '*Tahitian*' in Cook Islands shares the same lineage/genotype as Sāmoan *pu'ou* (Ragone 1991, Zerega et al. 1995) but this cultivar appears to be of recent origin as suggested by its name, that was not recorded by Cheeseman (1903) or Wilder (1931).

The third-most frequently recorded cultivar name in Sāmoa was *'aveloloa*: it was recorded by 68% of respondents (Ragone *et al.* 2004). *'Aveloloa* provides a timber valued for house building in Sāmoa (Christophersen 1935) and is also widely grown in Tonga (Tupoulahi-Fusimalohi 1999). It is recorded in Tuvalu under the name *mei aveloa*, but is absent from eastern Polynesia.

The fourth-most recorded cultivar name in Sāmoa, recognised by 62% of Sāmoan respondents, was *mā'opo* (Fig. 1B). This seedless diploid/possibly triploid[20] cultivar and/or morphologically similar sports are widely cultivated, sometimes under similar names, in central-western Polynesia including Tonga (*mā'opo*), Futuna (*lautoko mā'opo*) and Niue (*mei mā'opo*) as well as Fiji

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[17] Autotetraploids are more common in plants than previously thought (Tate et al. 2005) and in nature, triploids typically arise spontaneously through crosses between diploid and tetraploid plants in the same population (e.g. Pearson 2001). Alternatively, Ragone (1991) has postulated that triploids in breadfruit may arise from unreduced gametes in one parental entity (especially an unstable hybrid), which on fusion with a reduced gamete results in a triploid.

[18] There is a possibility, elaborated by Ragone (1991: 127), that the Spanish were responsible for introducing Polynesian breadfruit (presumably from Marquesas) to Guam (Micronesia), but Lineage 4 was not detected in Society Islands or in Palau (approx. 1200 km SW of Guam) and Marianas.

[19] This breadfruit translocation would likely correspond with a migration from the south-west Pacific (before 2100 BP) or northern New Guinea (before 1800 BP), viz. human migration streams identified by the DNA studies of Liu *et al.* 2022.

[20] *Pulupulu* from Rotuma was determined as diploid (Zerega *et al.* 2015), while Ragone (1991: 118) reported that *mā'opo* was triploid.

(*uto lolo*, *uto cokocoko*, *uto dogodogo* and *uto draucoko*) and Rotuma (*pulupulu*) (Seemann 1868, Ragone 1991, MacGregor et al. 2021). *Mā'opo* is not recorded in eastern Polynesia although it has been suggested as the same as the morphologically similar *rare 'auti'a* from Society Islands (Ragone 2006): *rare 'auti'a* is a triploid (Zerega *et al.* 2015: 4) and distinguishable from *mā'opo* in its variably shaped, frequently rounded-spherical infructescences (Wilder 1931: 74–75) and yellow-greenish midrib and costae on the adaxial leaf surface cf. whitish midrib ones.

### *Conclusions*

Taken together our analyses challenge at least two accepted beliefs: (1) that *Artocarpus altilis* is a domesticated cultivar species of *A. camansi*, and (2) that the original and other early introductions of breadfruit into eastern Polynesia came from central-western Polynesia. Our proposal with regards to (1) is that *Artocarpus altilis* is a native species from remote Oceania (most likely south-eastern Solomon Islands and/or northern Vanuatu), and with regards to (2) that breadfruit was introduced into Eastern Polynesia from the eastern Solomon Islands or northern Vanuatu. Our analysis also challenges the definition of Proto Malayo-Polynesian **kulu* as 'breadfruit' whereas if it was indeed a PMP word it would have meant 'breadnut'.

Accordingly, the pre-historic domestication of *A. altilis* and selection of breadfruit cultivars was initiated by Austronesian peoples in Remote Oceania—in its putative natural range in the south-eastern Solomon Islands and/or northern Vanuatu. Major secondary centres of breadfruit selection and cultivar diversity are in the south-west Pacific (Fiji and adjacent central-western Polynesia viz. Sāmoa and Tonga), the eastern Caroline Islands (Pohnpei) and eastern Polynesia (Marquesas and Tahiti). Morphological and genetic studies of *A. altilis* show eastern Polynesian breadfruit cultivars to be closely related to Micronesian cultivars, while central-western Polynesian cultivars are related to those from eastern Melanesia (Solomon Islands, Vanuatu, and Fiji). The most widely grown seedless and few-seeded diploid cultivars in Fiji and adjacent central-western Polynesia (Sāmoa and Tonga) are genetically very different from the seedless triploid cultivars in eastern Polynesia.

The patterns of breadfruit cultivar diversity and distribution provide further support for Wilson's hypothesis (2012, 2018) that eastern Polynesia was settled from Polynesian Outliers in the south-western Pacific (near to Solomon Islands and northern Vanuatu) rather than directly from Sāmoa as earlier assumed (Hale 1846: 119–25, 148; Kirch 2000, Kirch and Green 1987, 2001; Bellwood 2011). The breadfruit genetic lineages shared between Micronesia and eastern Polynesia (Zerega et al. 2015) indicate that these widely separated regions have the same or closely related and overlapping introductions of *A. altilis* cultivars. Our findings for breadfruit dispersal to eastern Polynesia are in concert with those for fehi bananas (*Musa* series *Australimusa*) for which it is postulated that fehi founder clones were dispersed from around the Solomon Islands (possibly Makira), first reaching eastern Polynesia (Marquesas and Tahiti) and, later, Cook Islands, and Hawai'i (Thomson *et al.* 2022). Pacific breadfruit cultivar diversity, much of it developed over millennia by Austronesians (Lapita peoples), Polynesians, and Micronesians, is a vital global public good and genetic resource which needs to be made more widely available—using well-established international protocols—throughout the humid tropics for food security, soil protection and improvement, climate change adaptation and mitigation.

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