The Breadfruit Trail

The wild ancestors of a staple food illuminate human migrations in the Pacific islands.

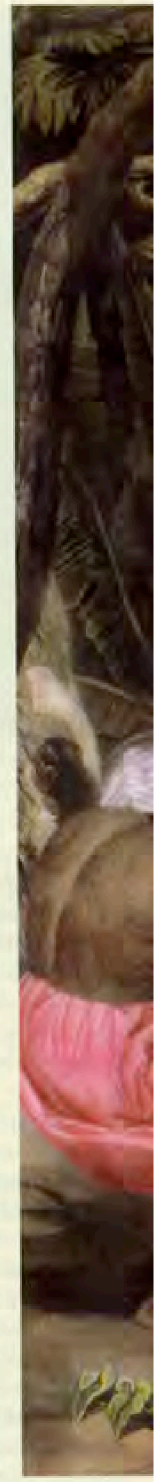
By Nyree J.C. Zerega

Many years ago a god named Ku came to Hawai'i and married a mortal woman. Together they had a large family, but Ku never told her he was a god. One year, a terrible famine came to the islands, and Ku's family became weak with hunger. When Ku could no longer bear his family's suffering, he confided to his wife: "If I go on a long journey, I can get food for our children and everyone on the island, but I will never be able to return." At first his wife would not hear of such a thing, but after watching her children slowly starve, she finally relented. The couple walked together into their garden, where Ku kissed his wife good-bye and disappeared into the earth. In her grief Ku's wife waited at the spot where he had disappeared, watering it for several days with her tears. Soon a sprout pushed up from the spot and rapidly grew into a tree. Within just a few days Ku's body had transformed into a large tree trunk, his arms into branches, his blood into a white latex flowing through the tree, and his head into a fruit that provided Ku's family with the food he had promised. The tree, and the food, was the breadfruit.

This legend is just one of many that are told to account for the origins of breadfruit *(Artocarpus altilis)*. It is little wonder that the plant is the stuff of legend, for it has been cultivated as a staple starch crop in the Pacific islands for thousands of years. Biologists, however, are still looking for a more down-to-earth explanation of the plant's origins. The puzzle begins with the fact that many breadfruit trees are seedless and sterile. Sometime in the past, cultivators must have transformed a fertile plant into one that needs human intervention to reproduce itself. But what was the ancestral tree? Breadfruit is scattered across thousands of islands in the Pacific, but no close wild relatives grow throughout much of this range. Thus there is no prime local candidate for botanists to name as breadfruit's ancestor. And if the transformation did not occur throughout the Pacific, it probably occurred in just one place, and the sterile trees must have been spread by human means. But where did these people come from?

Seafaring people reached Australia and New Guinea at least 40,000 years ago and, relaunching from those lands, settled the Solomon Islands by 30,000 years ago. But the broader peopling of Oceania—the middle and southern Pacific islands—did not get underway until about 4,000 years ago. Most scholars attribute the resurgence in settlement to a people they call the Lapita, after an archaeological site in New Caledonia. The main evidence for the patterns of their migrations comes from tracing a characteristic style of pottery, in which geometric and, occasionally, representational designs were stamped into the clay. Linguistic and genetic data generally support the archaeological conclusions.

The Lapita, thought to have come from somewhere in island Southeast Asia, first traveled to the northern coast of New Guinea. They continued their migrations eastward through Melanesia and into the far reaches of eastern Polynesia, making their way to Easter Island by about 1,700 years ago [*see map on pages 48 and 49*]. Micronesia is much more culturally and linguistically heterogeneous than Polynesia, and its island



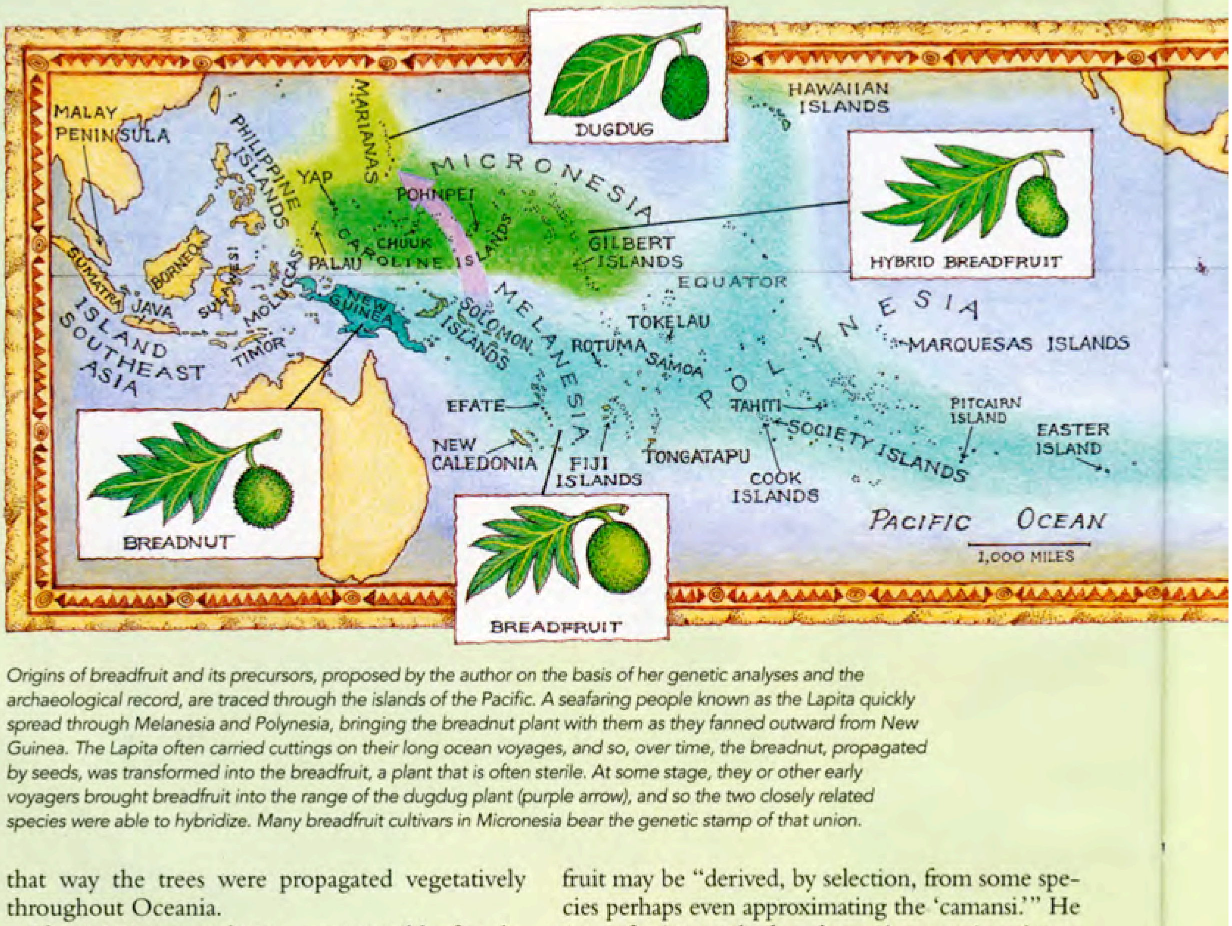
ist-
by
9].
sti-
ind

Thomas Gosse, Transplanting of the Bread-Fruit-Trees from Otaheite [Tahiti], *1796. Gosse's hand-colored mezzotint depicts Lieutenant William Bligh, standing at right in uniform, overseeing the collection of young breadfruit trees for transport to the Caribbean. Although the voyage, on* HMS Bounty, *ended in the famed mutiny in 1789, Bligh carried out his mission on a later voyage. Analysis of breadfruit DNA is enabling biologists to trace its wild origins, and the spread of related cultivars by Pacific islanders.*

groups were probably settled by migrants who came at various times from island Southeast Asia, Melanesia, New Guinea, and elsewhere. The last of the principal Oceanic islands to be settled were the Hawaiian Islands, about 1,700 years ago, and New Zealand, about 1,200 years ago—in both cases by Polynesians.

Prehistoric seafarers casting off from their home islands to settle elsewhere would have been sure to take along breadfruit trees, which provide an abundance of fruit. The first breadfruit trees, like their unknown progenitor, may have been capable of reproducing by means of seeds. At some point, however, the voyagers must have begun to transport and transplant root cuttings, which can be nicked with a sharp blade to produce shoots. In that way the trees were propagated vegetatively throughout Oceania.

If migrating people were responsible for the propagation of breadfruit, finding its wild progenitor might contribute to far more than the botanical problem of finding the origins of the plant. By tracing the paths of ancient breadfruit, light might be shed on the routes taken by the ancient mariners who transported it. Unfortunately, reconstructing the plant's botanical history has long proved difficult. During the millennia breadfruit has been cultivated, the trees changed with time and place. Mutations occurred, and cultivators on various islands selected for trees that grew best under local particularly conditions or whose fruits were particularly appealing in size, taste, and texture. My hope was that DNA evidence obtained through the new tools of molecular biology would finally resolve the puzzle of the species' origins.

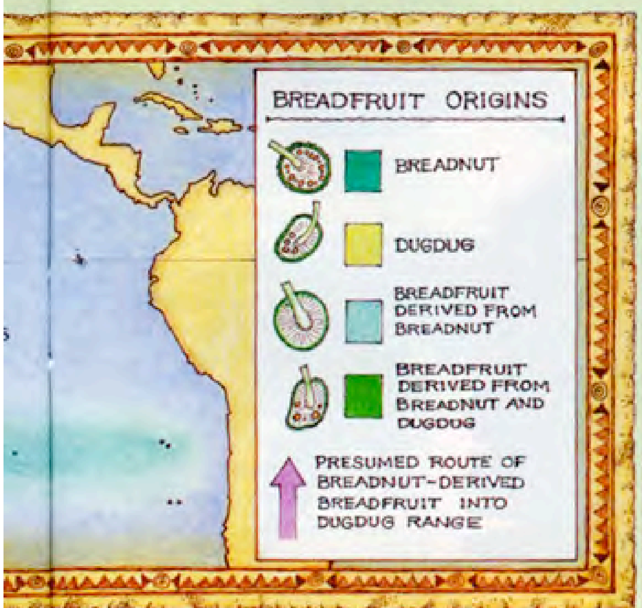


Origins of breadfruit and its precursors, proposed by the author on the basis of her genetic analyses and the archaeological record, are traced through the islands of the Pacific. A seafaring people known as the Lapita quickly spread through Melanesia and Polynesia, bringing the breadnut plant with them as they fanned outward from New Guinea. The Lapita often carried cuttings on their long ocean voyages, and so, over time, the breadnut, propagated by seeds, was transformed into the breadfruit, a plant that is often sterile. At some stage, they or other early voyagers brought breadfruit into the range of the dugdug plant (purple arrow), and so the two closely related species were able to hybridize. Many breadfruit cultivars in Micronesia bear the genetic stamp of that union.

Scholars have put forward at least two testable hypotheses about the origins of breadfruit. The first was advanced in 1940, when Eduardo Quisumbing, a Filipino botanist, suggested breadfruit may be "derived, by selection, from some species perhaps even approximating the 'camansi.'" He was referring to the breadnut, *A. camansi,* native to New Guinea and possibly the Philippines and the Moluccas. It produces edible, chestnutlike seeds. A second, much more complex hypothesis was proposed in 1960 by Francis Raymond Fosberg, an accomplished American botanist of the Pacific flora.

Fosberg implicated two other species in addition to the breadnut. One is the Philippine endemic commonly known as antipolo *(A. blancoi)*, which is used primarily for lumber. The other, often called dugdug *(A. mariannensis)*, is endemic to certain uplifted limestone islands in Micronesia, namely Palau and the Marianas. The islanders consume both its seeds and the surrounding flesh.

Fosberg suggested that antipolo first hybridized with breadnut, giving rise to sterile breadfruit. But he also noted that Micronesian breadfruit has its own unique characteristics. For example, some specimens have leaves like those of the dugdug but seedless fruit like that of breadfruit; others have deeply cut leaves like the breadfruit's, but those leaves have brownish and reddish hairs on the leaf veins, like the dugdug's. To account for those features, Fosberg suggested that in Micronesia the sterile breadfruit trees had somehow hybridized with dugdug.



To begin my own study into the origins of breadfruit, I wanted to test both these hypotheses about its wild progenitors. That led immediately to my first question: Are breadnut, dugdug, and antipolo the species most closely related to breadfruit, and if not, what is? Second, is there evidence that any of those species contributed to breadfruit's gene pool?

I determined the DNA sequences for two regions of the genome in nearly forty species in the breadfruit genus, *Artocarpus*. The genus belongs to the mulberry family (Moraceae) and encompasses many useful and curious species. On the basis of the DNA sequences, I constructed a family tree for *Artocarpus*, which showed that breadfruit is closely related to breadnut and dugdug but not to antipolo.

In DNA sequencing, the base pairs, or molecular building blocks, in a species' chromosomes are identified one by one. But a single genome can include billions of base pairs. Although the speed at which this kind of data can be generated is rapidly increasing, many biologists must content themselves with sequencing only small regions of an organism's genome. Unless those regions happen to be highly variable, they may not shed much light on the genetic relatedness among closely related species. The regions I had sequenced were just too similar to reveal how breadfruit, breadnut, and dugdug fit together on the tree of life. I needed more data.

I turned to a method of DNA fingerprinting called amplified fragment length polymorphisms (AFLP). In effect, the technique takes many snapshots of an organism's entire genome, increasing the chances that informative regions will be found. The first step in the process is to extract DNA and treat it with enzymes that slice it into many small fragments. Examining all of these fragments is not feasible, so the next step is to "amplify" (make many copies of) only a subset of the fragments. Among the amplified fragments, some will be unique to the single individual source of the DNA, whereas others will be shared with other members of the same species. Of the latter, some will prove to be unique to the species as a whole, and others will be shared with members of various other species. By sorting through the amplified fragments, the investigator can determined which of them are "fingerprints" of particular individuals, species, or even more distant genetic relations.

I realized I would have to analyze tissue from several individual specimens of breadfruit, dugdug, and breadnut. Would that force me to island-hop around the Pacific, collecting samples of trees from tropical forests and white-sand beaches? As arduous (and appealing) as that might be, there was a quicker (and cheaper) way.

Kahanu Garden, part of the National Tropical Botanical Garden, is situated on the Hawaiian island of Maui, near the Pi'ilanihale Heiau, a structure of lava rock thought to be the largest ancient Polynesian place of worship. Approximately ten acres of the garden is devoted to the largest known collection of breadfruit cultivars in the world: more than 200 trees have been collected from seventeen Pacific island groups and beyond. Although the collection was originally established in the 1970s, the bulk of it was assembled in the 1980s by Diane Ragone, the director of the National Tropical Garden's Breadfruit Institute. At this one location I obtained samples of breadfruit from Java and the Philippine Islands, in island Southeast Asia, and from various islands in Melanesia, Micronesia, and Polynesia. Only a handful of dugdug and breadnut trees grow at Kahanu, however, so I traveled, along with Timothy J. Motley of the New York Botanical Garden, to New Guinea and the Marianas. In both places knowledgeable local botanists helped me collect more samples.

When I examined the DNA from all the trees, I found many genetic fingerprints that were common to breadfruit, breadnut, and dugdug. That confirmed just how closely related the three species are. But I was also able to identify some dugdug fingerprints absent in all breadnut trees, and some breadnut fingerprints absent in all dugdug trees. Looking at the distribution revealed an intriguing pattern. Both breadnut and dugdug fingerprints were present in virtually all Micronesian breadfruit cultivars. But most of the breadfruit cultivars in Melanesia and Polynesia included only the fingerprints of breadnut, not of dugdug.

To some extent, then, both Quisumbing and Fosberg were correct. Overwhelmingly, in Melanesia and Polynesia, breadfruit cultivars were derived through selection from breadnut, just as Quisumbing surmised. But Fosberg was right to think there was something different about the Micronesian breadfruit trees. In Micronesia, breadnut or breadnut-derived breadfruit appears to have hybridized with dugdug, probably not in a single event but in a process known as introgression, in which a series of interspecies crosses are followed by repeated backcrosses. The result was a unique diversity of cultivars.

How do these findings tie in with the migrations of people across the Pacific? Here's a possible explanation. As the Lapita people voyaged eastward from New Guinea, they likely carried along whatever they needed of the wild breadnut, so that they could establish breadnut as a crop. But breadnut seeds remain viable for just a few weeks; seafarers who anticipated a long ocean voyage, such as the ones that led colonizers to regions east of the Solomon Islands, would have known to bring along root cuttings. (In fact, the Lapita vegetatively propagated several of their important crops, including yams and taro.) By propagating and spreading their breadnut trees via cuttings, generation upon generation of islanders transformed it into the breadfruit, a species that did not reliably produce viable or edible seeds but that could be consumed as a starch crop.

Human settlement of Micronesia was not so straightforward as it was in Melanesia and Polynesia, and several migration routes may have been established. One route scholars have suggested began in the eastern Solomon Islands or in the islands to their southeast, and followed a northward course to the Caroline Islands. Lapita or other people taking that route could have introduced the breadnut-derived breadfruit into Micronesia. Migrations and trade routes within Micronesia could then have brought the introduced breadfruit into the range of the native dugdug, where the two species could have cross-pollinated.

Breadfruit tree, shown here in an engraving made about 1800, grows to a height of sixty-five feet.

The earliest breadnut-derived breadfruit occurs in Melanesia, where breadfruit cultivars that produce seeds are still commonly found. I speculate that such fertile plants may be what hybridized with dugdug. Nothing like them persists in Micronesia, however, though the hybrid breadfruit trees themselves sometimes do produce seeds. The ancestral cultivars may have disappeared from the region because of a difference in environmental conditions or because people who lived there—perhaps owing to the availability of the edible dugdug seeds—preferentially selected seedless cultivars.

Finally, the route from Melanesia into Micronesia might well have been a two-way street. I discovered dugdug fingerprints in a small number of

Tahitian breadfruit is shown here as it was published in the journals of Captain James Cook, during Cook's first Pacific voyage, 1768–1771.

cultivars I sampled from the Solomon Islands and farther east, in Efate, the Fiji Islands, Samoa, and the Society Islands. The evidence suggests that hybrid breadfruit cultivars, developed in Micronesia, could later have joined the breadnut-derived breadfruit in Melanesia and Polynesia.

Much more remains to be learned about the finer details of how people selected and spread breadfruit trees. Because of the genetic scrambling that has taken place, and can still occur, between fertile plants, and because of the continual movement of humans, the picture is complex. Bringing it into sharper focus will keep us breadfruit botanists plying the Pacific for years to come. □