COMMENTARY

Tracking Austronesian expansion into the Pacific via the paper mulberry plant

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One of the strategies the ancestors of Pacific peoples used for successful settlement of the islands of the Pacific Ocean was the concept of transported landscapes (1). Pacific peoples carried their culturally and economically important plants and animals in their colonizing canoes and introduced these species to the islands they settled, which were relatively impoverished in terms of terrestrial resources. It has been demonstrated that phylogeographic analyses of these plants and animals can serve as proxies for reconstructing the pathways of colonizing canoes, and thus trace the movement of Pacific peoples and identify their likely origins. This "commensal approach" to tracking the movement of prehistoric Pacific peoples has to date focused primarily on the animals transported by Pacific colonists, including the Pacific rat (2, 3), pigs (4), and chickens (5). In PNAS, Chang et al. (6) now present genetic analyses of one of the important plant species carried into and across the Pacific in colonizing canoes, with their study of the paper mulberry (*Broussonetia papyrifera*).

The settlement of the Remote Pacific has been associated and identified archaeologically with the Lapita Cultural Complex (1). The Lapita culture first appears in the Bismarck Archipelago some 3400 years before present (BP) and rapidly spreads into the previously uninhabited islands of Remote Oceania, reaching Tonga and Samoa, on the edge of the Polynesian Triangle by about 2900 BP (7). It is generally accepted that the Lapita culture is an extension of the Neolithic expansion of Austronesian-speaking peoples through Island Southeast Asia, from the Austronesian homeland in Taiwan (8–11). Migration to and settlement of the rest of the Polynesian Triangle did not begin until some 1,700 years after the colonization of Samoa and Tonga, with settlement of Aotearoa/New Zealand around 730 BP, marking the end of Austronesian expansion into the Pacific (Fig. 1). Although Taiwan has been identified as the homeland of the Austronesian languages, all previous commensal animal studies indicate origins and migration pathways that do not include Taiwan, suggesting a complex history for the various components of Austronesian and Lapita cultures. Most of the economically important plant species introduced to Remote Oceanic islands during prehistory, such as banana, taro, breadfruit, and sugarcane, have Near Oceanic origins, whereas the sweet potato and the bottle gourd are of South American origin. Thus, the results presented by Chang et al. (6), indicating that the most common variant of paper mulberry found in the Pacific, and the one most likely introduced by the early colonists, has a clear Taiwanese origin, are significant, providing (to my knowledge) the first direct genetic link between Taiwan and one of the Pacific commensal species.

Native to Asia, including Taiwan, paper mulberry is a dioecious plant (plants are either male or female) that gets its common name from the fact that it was used in China and Japan to make paper. In the Pacific, paper mulberry was an extremely important plant used for producing barkcloth or tapa, which was not only used for clothing, but for ceremonial artifacts and as an important indicator of wealth in gift exchange, still seen today in places like Tonga. Tapa production diminished in many Pacific cultures with the introduction of European woven cloth, and as a result, so did the cultivation of paper mulberry. Barkcloth is produced by beating the inner bark of various trees, but most commonly the paper mulberry, into a thin, pliable, felt-like fabric. Evidence of wooden tapa beaters have been found in an early, waterlogged site in East Polynesia, indicating it was clearly important for the first colonists (12). These artifacts link the tradition to early Austronesian cultures in Island Southeast Asia and on the mainland, where the earliest stone barkcloth beater has been found in Guangxi, Southern China, and dates to around 8000 BP (13).

To identify the geographic origins of paper mulberry and reconstruct its spread through Island Southeast Asia and into the Pacific, Chang et al. (6) studied genetic variation in a 1,233-bp region of the chloroplast DNA

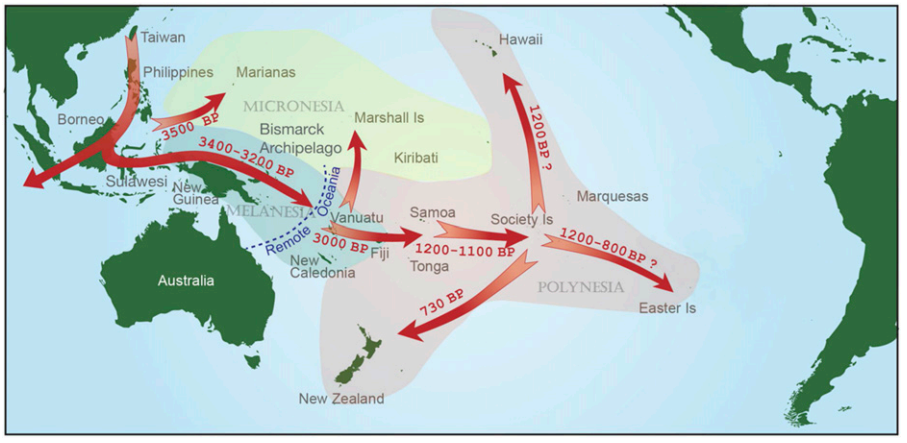

Fig. 1. Map showing the direction of Austronesian expansion from Taiwan and likely timing of expansion into the Pacific. Dates are expressed in years before present (BP) and are based on current archaeological evidence. The dotted line separates Near Oceania and Remote Oceania. Adapted from ref. 20, with permission from Elsevier.

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(cpDNA), which, like mtDNA in humans, is maternally inherited. A total of 604 samples of paper mulberry were collected from south China, Cambodia, Vietnam, Thailand, Japan, Taiwan, the Philippines, Sulawesi, the Solomon Islands, Fiji, and several islands in Polynesia. After sequencing, a total of 48 haplotypes, or distinct lineages, were identified, 31 of which were shared. One haplotype, designated cp-20, was found throughout the native range (southern China, Taiwan, Vietnam, Cambodia, and Thailand) and was identified as the likely ancestral type. As might be expected, samples collected in this native range also showed the greatest cpDNA variation, with 27 haplotypes identified from China, 20 of which were exclusively found there. Another five haplotypes were found in Indochina (Vietnam, Cambodia, and Thailand). Interestingly, the comparatively small island of Taiwan harbored 19 haplotypes, 16 of which were endemic.

The Taiwanese samples showed surprising geographic structuring, with different lineages found in the north, the east, and southern/central parts of the island. The haplotypes found in the north of the island, particularly cp-1, were shared with samples from the east coast region of the mainland of China, and were believed to have been introduced from there during the early phase of Austronesian expansions to the island dating between 8000 and 6000 BP (6). These northern varieties were not introduced further south, where the endemic Taiwanese lineages are found.

The most common variant found in the Pacific, cp-17, has a clear south/central Taiwanese origin. Haplotype cp-17 is the only lineage found in Sulawesi, Fiji, and in all of the Polynesian Islands sampled (Samoa, Tonga, Niue, the Austral Islands, the Marquesas, Pitcairn, and Rapa Nui/Easter Island) except for Hawaii, which also has plants with cpDNA assigned to haplotypes cp-41, likely introduced from Japan, and the ancestral type, cp-20. It is suggested (6) and highly likely that these varieties were introduced historically by the Japanese and Chinese workers brought in to Hawaii to work in the sugarcane fields during the colonial period. Haplotype cp-17 was also identified in one sample from New Guinea, as was haplotype cp-34, which is a common Indochinese lineage, indicating multiple introductions to the island. In total, five different lineages were identified in Near Oceanic paper mulberry. Interestingly, cp-17 was not found in the Philippines or the Solomon Islands; otherwise the distribution of this haplotype would be totally consistent with the expansion of Austronesian languages.

The fact that a single haplotype, cp-17, is dominant across the vast region of Polynesia is consistent with suggestions that Polynesian varieties consist of only male plants that are clonally propagated (14, 15) and strongly supports that they did not disperse naturally but were transported intentionally by humans. This form of propagation may also explain the possible loss of the species in particular locations when barkcloth manufacture is abandoned.

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Chang et al. (6) have contributed significantly to our understanding of Neolithic expansions from the mainland of China to Taiwan and the subsequent Austronesian migrations through Island Southeast Asia and into the Pacific. The clear Taiwanese origins of cp-17, the likely lineage introduced to Polynesia by early Polynesian colonists, is most exciting. A much more complex introduction history is indicated for Near Oceania, and further sampling in both Near Oceania, particularly locations in the Bismarck Archipelago (locations with evidence of Lapita settlement) and investigations into the distribution and genetic origins of paper mulberry plants in Vanuatu and New Caledonia will be most interesting. Such information would help to determine whether paper mulberry was likely introduced by Lapita colonists or if the introduction of cp-17 to Polynesia may have been the result of a post-Lapita introduction possibly directly from cp-17 harboring locations in Island Southeast Asia (either Taiwan or Sulawesi) or via Micronesia (16). Previous studies of commensal species such as the Pacific rat (17) and Pacific dogs (18) have demonstrated the need for specific, targeted sampling and full analysis of archaeological dates and distributions of commensal species that can reveal erroneous assumptions and errors in our interpretations of phylogeographic patterns and reconstructions of prehistoric human dispersals in the Pacific made based on limited sampling. The application of ancient DNA methods to identify the haplotypes in pre-European samples and artifacts made of tapa (19) will also assist in clarifying or confirming these interpretations from modern and historic samples and present exciting opportunities.

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