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parallel text in Chinese and English

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構樹 DNA 佐證臺灣為南島語族原鄉

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關鍵詞：
葉綠體 DNA、共生物種研究、民族植物學、出臺灣說、性別鑑定分子標記、樹皮布

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1. 引言

「南島語族的起源與擴張」與「史前島嶼東南亞及大洋洲族群形成」是兩個與臺灣及太平洋史前史密切相關的學術議題，也是推展南島語言復振的理論基礎。在本論文集中，Peter Bellwood (2021) 及 Matthew Spriggs (2021) 根據近年來語言學、考古學及古 DNA 基因體學的進展分別就此兩個議題做了前瞻及精要的回顧，其相關證據均支持以「農業／語言擴張假說」為基礎的「出臺灣說」，佐證臺灣為南島語族原鄉。兩位學者同時也一再強調新石器時代人類拓殖太平洋歷史的複雜性，並指出跨領域研究整合的重要性。本文進一步以近年來太平洋構樹的親緣地理研究，為「出臺灣說」提出民族植物學的證據。

2. 南島語族與「共生物種」的遷徙

人類因為食、衣、住、行等需求，以及文明、文化的發展，與他們所利用的「動、植物」間產生緊密的「共生」關係，當人群移動與遷徙時，有意無意間也改變了這些「共生物種（commensal species）」自然的地理分布。南島語族為農業民族（圖 1A），根據「農業／語言擴張假說」，新石器時代人類由採集狩獵轉為定居的

農業族群時，因為糧食生產促成的人口增長激化了土地競爭，在此雙重壓力下，南島語族不可避免地向外遷徙與擴張，南島語亦隨之擴散。同時，豬、雞、狗、太平洋鼠等動物，以及麵包樹、芋頭、山藥、構樹等大約 70 種植物所構成的南島「農業包裹（agriculture package）」也隨之被攜帶至大洋洲各島嶼，考古人類學者以南島農業包裹的「轉移地景（transported landscape）」來形容南島農業的擴散（圖 1A），而地景轉移也被認為是南島語族能成功拓殖遠大洋洲資源匱乏小島的關鍵策略（Matisoo-Smith 2009, Kirch 2010）。

由於組成南島農業包裹的共生物種全賴南島語族才得以跨越大洋傳播，這些共生物種的 DNA 也記載了南島遷徙的歷史足跡，提供了歷史語言學、考古學與人類遺傳學之外的第四類證據。1994 年，目前任教紐西蘭奧塔哥大學（University of Otago）的生物人類學家馬諦索 - 史密斯（Lisa Matisoo-Smith）首開太平洋「共生物種」的親緣地理研究，以太平洋島嶼常見的波里尼西亞鼠（*Rattus exulans*）的 DNA 見證了南島祖先卓越的航海能力。之後，學者接著以豬、雞、狗等動物，以及麵包樹、香蕉、芋頭、椰子、番薯等的親緣地理研究，揭開了南島語族拓殖與往返島嶼間的複雜歷史（Matisoo-Smith 2009, Storey et al. 2013）。然而，由於多數傳入太平洋的共生物種是起源於東南亞及近大洋洲（例如：新幾內亞）

的作物或豢養動物，因此，前述研究都無法測試南島語族出臺灣說這個最重要的議題。

3. 打樹成衣

十八世紀英國庫克船長（Captain James Cook）奉命執行了三次橫渡太平洋的遠征，在航海日誌中，庫克詳細的記錄了航程的所見所聞，包括他對於大溪地人「布」的觀察。庫克提到，大溪地人的布是由樹皮製成的，當地人稱之為 *tapa*，*tapa* 主要製作原料來自一種他們細心種植照料樹木的樹皮，當地人採收其樹皮並將之浸水，再用由硬木製成的「打棒」（beater）把樹皮拍打製成非常細緻的布（圖 1B），提供大溪地人在日常生活、儀式、慶典之所需。庫克船隊中隨行的植物學家索蘭德（Solander）指出當地種來製作 *tapa* 的植物即是中國人用於造紙的「構樹」。庫克在航海日誌中除了詳細描述 *tapa* 的製作過程，也提及波里尼西亞各島嶼都種有原住民以根部萌檗（root suckers）繁殖的構樹（圖 1D）。

將植物樹皮經槌氈拍打所製成的「樹皮布」文化，在西非、東南亞、太平洋、中南美洲等地都可發現，但以太平洋島嶼的 *tapa* 最廣為人知（張至善 2011）。在西方紡織品傳入前，*tapa* 是太平洋島民日常生活的基本所需，可用於衣著、家居布置、打扮裝飾及藝術創作

（圖 1C）。雖然可用於製作樹皮布的植物種類繁多，包括桑科的麵包樹屬（*Artocarpus*）、榕屬（*Ficus*）及構樹、以及錦葵科的黃槿等，但構樹為太平洋南島語族製作 *tapa* 最常用的樹種，由構樹製成的 *tapa* 質地也最為細緻（張至善 2011）。

圖 1 A. 夏威夷大學民族植物園內重建的傳統波里尼西亞村落；B. 巴布亞新幾內亞 Oro 省 Tufi 原住民身著傳統服飾製作「樹皮布」；C. 巴布亞新幾內亞 Oro 省 2018 Tufi Tapa and Tattoo 慶典；D. 智利復活節島（Rapa Nui）構樹植栽，Rapa Nui 稱構樹為 *Mahute*。

4. 臺灣最常見卻最視而不見的樹種

構樹（*Broussonetia papyrifera* (L.) L'Hér. ex Vent.）是雌雄異株（圖 2）的桑科植物，廣泛分布在中國黃河流域以南到中南半島、臺灣及韓國，同時，因為其快速生長的特性與其樹皮纖維的價值，構樹在很早就被引入日本、歐洲、美國、太平洋島嶼等地，甚至在巴基斯坦、菲律賓等地已歸化成為入侵植物（Chung et al. 2017）。在臺灣，構樹在都市鄉村無所不在、隨處可見，路旁、牆角、人行道，或偶而路過的荒地、河岸、山徑旁，可說是臺灣最常見，但人們最視而不見的樹種。構樹葉面、葉柄與幼莖上均被毛，質感粗糙，富含纖維，為梅花鹿、山羊喜歡的食物，因此臺灣民間慣以鹿仔樹稱之。初夏時，構樹聚合果成熟，橘紅色鮮豔的果肉柔軟多汁，吸引大群的各式鳥類及小型哺乳動物前來覓食（圖 2C），為低海拔各種動物的夏日饗宴。

人類利用構樹的歷史十分悠久，《詩經．小雅．鶴鳴》中傳世的「樂彼之園，爰有樹檀，其下維穀」，其中的「穀」字指的便是構樹，此詩句述說「濃密的檀樹林下長了低矮的構樹」，以兩種多用途的植物來比喻人才，有招才納賢之意。而構樹確實全身是寶，在臺灣，構樹除了是養鹿人家的最愛，亦可用於餵豬；構樹種子、葉、乳汁、甚至樹皮都可入藥。由於生長快速，構樹也廣為世界各國引入做為綠化

樹種，也在許多地區變成入侵植物。不過構樹對人類最重要的用途，在於它樹皮內層中極長的韌皮纖維，為極佳的纖維作物。

三國時代吳國人陸璣在《詩疏》中，以「今江南人績其皮以為布，又擣以為紙」註釋《詩經．小雅．鶴鳴》文句中的「穀」字，其中「擣

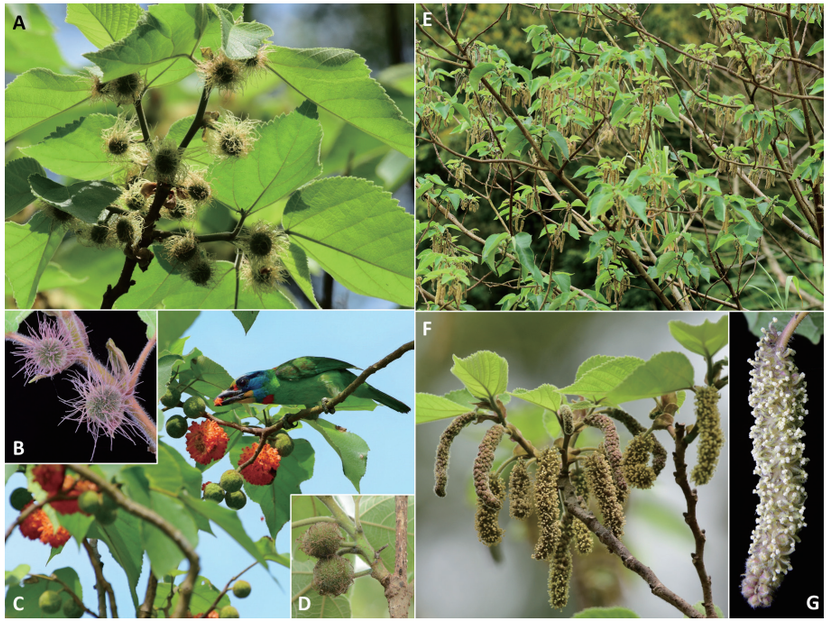

圖 2　構樹是雌雄異株的植物。A. 雌構樹開花的枝條；B. 構樹的雌花序近照；C. 五色鳥取食構樹果實；D. 新幾內亞東高地省（Eastern Highlands Province）的構樹為雌性，此為開花後無法受粉的柱頭凋萎的雌花序；E. 雄構樹開滿花的枝條；F. 雄構樹開花的枝條；G. 構樹雄花序近照。除 D 外，其餘照片均在臺灣拍攝。

以為紙」記載了三國時代江南人用構樹造紙的過程，此技術傳承千百年至今，當代書法用紙「棉紙」仍以構樹為主要原料。那「績其皮以為布」中的「布」所指為何呢？在考據古文獻與民族誌後，民族學者凌純聲認為「績其皮以為布」中的「布」字，與《史記．貨殖列傳》中的「榖布」同義，也就是太平洋原住民所稱的 *tapa*，都是指以構樹製作的樹皮布。凌純聲進一步推論，史載東漢宦官蔡倫以破布魚網等材料發明造紙術，這些破「布」魚網事實上都是構樹纖維的利用，而出生江南地區的蔡倫，極有可能受到東漢江南地區仍存在的樹皮布製作程序啟發，而「發明」了造紙術製作出蔡侯紙（凌純聲 1961）。

儘管古籍中記載以槌氈拍打製成的「榖布」對我們來說已是無從想像的遙遠，然而 *tapa* 對於太平洋地區的南島語族而言，卻曾是日常生活的必需及文化上無可取代的象徵（圖 1C）。十八世紀庫克船長記載波里尼西亞各島嶼均遍植構樹用以製作 *tapa*，而在所有遠大洋洲南島語族栽種或豢養的共生物種中，構樹是唯一原生地在中國、臺灣、中南半島的共生物種，具備檢測南島語族出臺灣說的條件。雖然隨著紡織衣物的引入，*tapa* 已不再是現代太平洋島民生活中必要的元素，樹皮布文化也由許多地區消失，卻也正因如此，構樹更有可能保持古老的遷徙印記，加上太平洋地區並沒有構樹的近緣植物，排除了物種之間雜交的可能。

5. 構樹 DNA 記述的南島語族遷徙路

2008 年春天，時任教於臺灣大學森林環境暨資源學系的筆者，接到國立臺灣史前文化博物館張至善博士的邀約，嘗試從「衣」出發，以構樹的親緣地理（phylogeography）測試南島語族遷徙的假說，同時，太平洋彼端的智利考古學者 Andrea Seelenfreund 與生化學者 Daniela Seelenfreund 也正埋首鑽研相同議題。我們這支跨領域的跨國團隊，於是展開橫跨太平洋的遠征，足跡遍布臺灣、中國、越南、日本、菲律賓、新幾內亞、斐濟、東加、薩摩亞、夏威夷、大溪地、復活節島等遠、近大洋洲各島嶼，採集了超過 600 個構樹樣本（Chang et al. 2015）。

DNA 序列在複製的過程中偶爾會發生突變，產生了遺傳變異，這些等位但序列不盡相同的 DNA 稱為「單倍體基因型（haplotypes）」，簡稱單倍型；而親緣地理學則是藉由分析種內、近緣種間單倍型的地理分布以研究族群（demographic）及歷史因素（如第四紀冰河期）對物種分布的影響。構樹研究團隊在母系遺傳的葉綠體基因組中 *ndhF* 至 *rpl32* 兩基因間隔區（intergenic spacer）的 DNA 序列中偵測到 48 個單倍型，在描述這 48 個基因單倍型演化關係的網狀圖中（圖 3），可以看出臺灣、中國與中南半島擁有最高的單倍型多樣性，根據分子演化學的理論，這些地區為構樹

可能的「原生地」。而與原生地相比，太平洋上的單倍型多樣性則明顯較低，且絕大多數的構樹均攜帶紅色、編號 17 的單倍型（cp-17），而除了大洋洲外，cp-17 僅分布在臺灣南部。在演化上，cp-17 位在由 cp-9 至 cp-19 等僅分布在臺灣的特有單倍型支序的最末端 （圖 3），顯示 cp-17 源自臺灣，因此遠大洋洲帶有 cp-17 的構樹無疑源自於臺灣，證明了臺灣是太平洋攜帶 cp-17 構樹的原鄉，Chang et al. (2015) 因此提供了第一個以共生物種、民族植物學支持臺灣為南島原鄉出臺灣說的研究。

接著，研究團隊開發出可鑑定構樹性別的分子標記，並分析了太平洋地區由蘇拉威西至大洋洲超過 300 株構樹的性別（Penailillo et al. 2016），結果發現太平洋地區攜帶 cp-17 的構樹皆為雌性（圖 4），顯示太平洋地區的構樹絕非藉由有性生殖種子繁衍，與文獻記載南島語族藉由根部萌糵扦插無性繁殖的記載與觀察一致，輔以 Chang et al. (2015) 的發現，更加證明了太平洋的構樹係人類由臺灣傳入，與南島農民出臺灣說的立論不謀而合。

然而，由於 Chang et al. (2015) 的研究所使用的 DNA 分子序列缺乏足夠的變異用以檢測太平洋構樹傳播的歷史年代與路徑是否與「出臺灣說」一致，同時，我們也無法排除太平洋構樹源自近代太平洋海上貿易。Seelenfreund et al. (2016) 分析了在法屬波里尼西亞 Gambier 群島 Agakauitai 島上一洞穴中發現的一捆古老的 *tapa*，

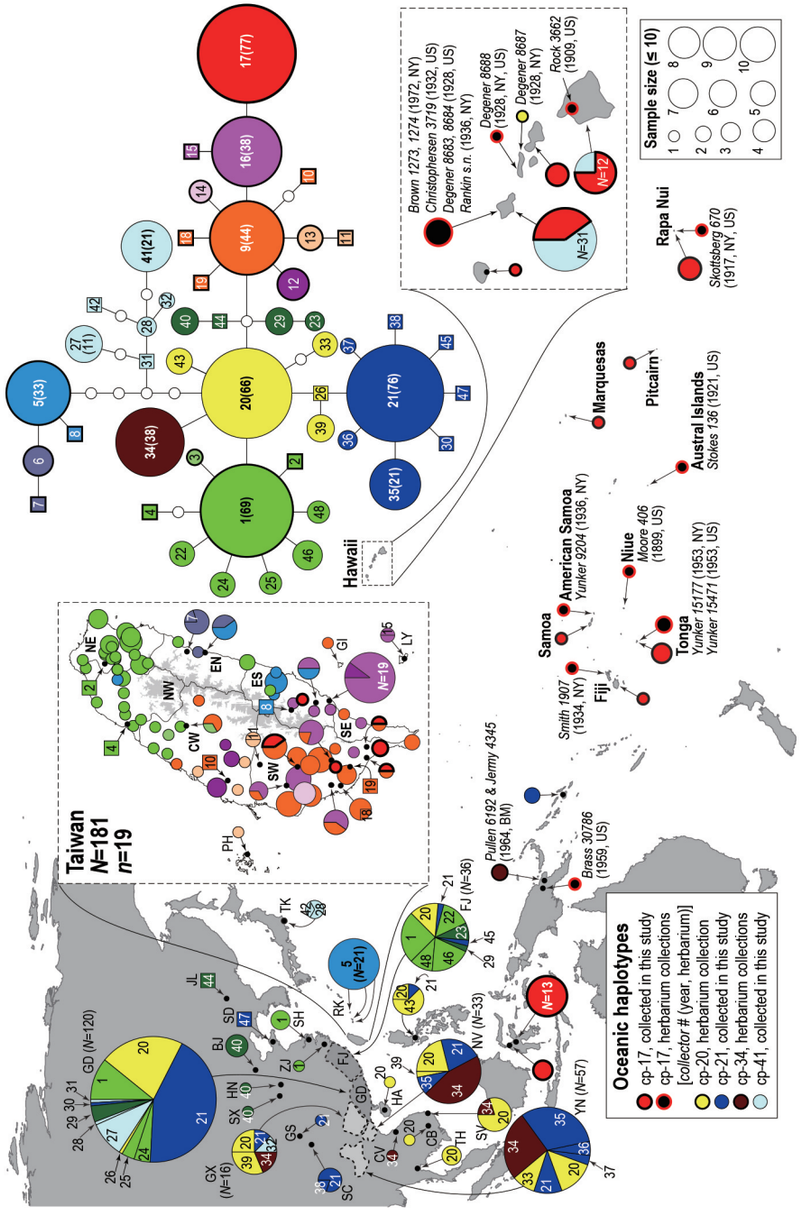

圖 3 構樹葉綠體 *ndhF-rpl32* 單倍體基因型之地理分布與單倍體網狀圖。構樹在原生地（中國、臺灣、中南半島）有非常高的單倍型多樣性，相較之下，絕大多數在蘇拉威西、新幾內亞、大洋洲島嶼的構樹都攜帶 cp-17（紅色）的單倍型，該單倍型除了太平洋島嶼外，僅分布在臺灣南部，證明太平洋構樹源自臺灣，佐證了「南島語族出臺灣說」。原文刊載於 Chang et al. (2015) (doi:10.1073/pnas.1503205112)。

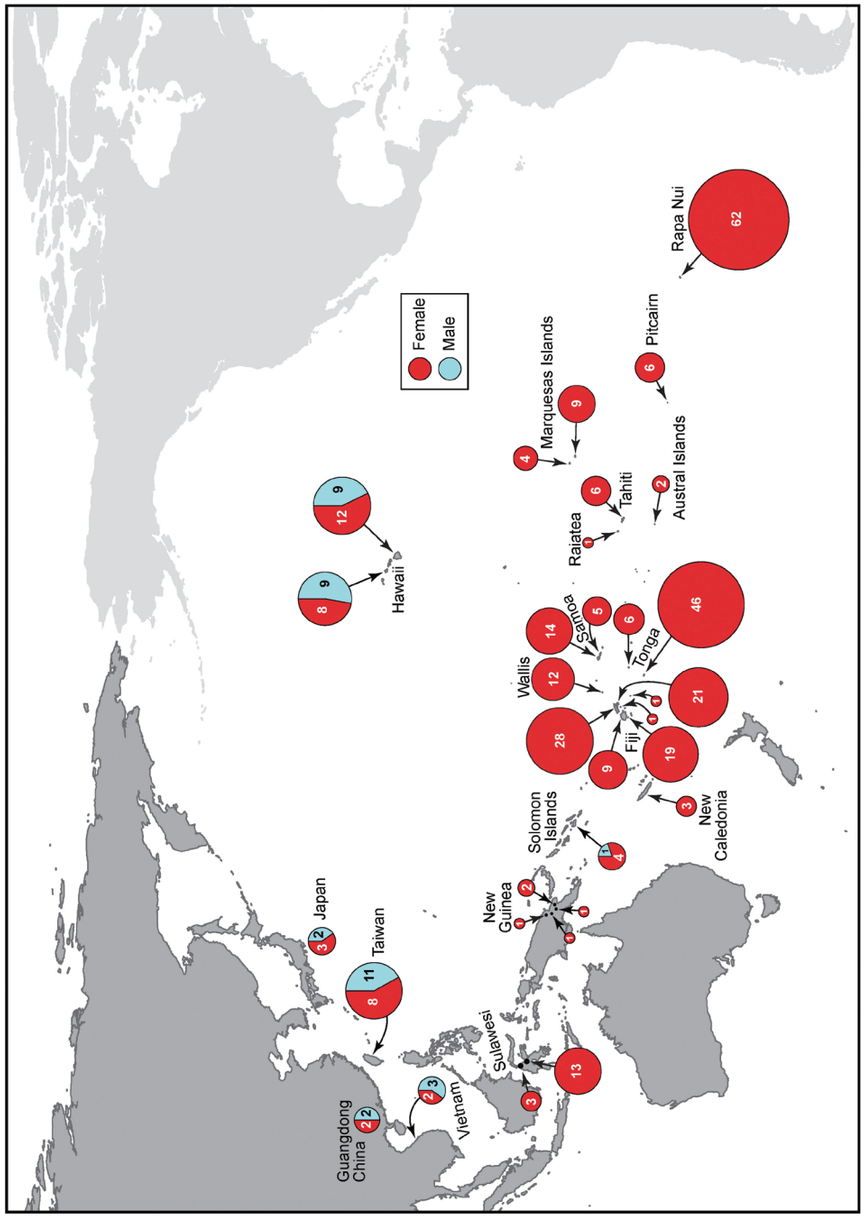

圖 4 太平洋構樹的性別。紅色為雌株構樹，淺藍色為雄株構樹，圓形的大小與樣本數成比例。原文刊載於 Penaliillo et al. (2016) (doi:10.1371/journal.pone.0161148.g005)。

經由加速器質譜法定年，顯示這些 *tapa* 製作的年代可追溯自 17 世紀該島島民與歐洲人接觸前，同時以具物種鑑定力的分子標記定序證實該 *tapa* 係以構樹為原料製作，顯示遠大洋洲構樹的傳入與大航海時代西方人的活動無關。

為了能進一步分析構樹傳入大洋洲的歷史，本研究團隊利用次世代定序技術組裝構樹的全葉綠體基因組，用於解析太平洋構樹的傳播史。圖 5 為筆者在 2019 南島語言復振國際論壇中發表的初步分析結果。我們取樣了太平洋地區 13 個構樹樣本，並以分子標記確認這些樣本均為雌株、並攜帶 cp-17 及其衍生的 cp-49 和 cp-51 單倍型（圖 5 中的紅色樣本），並以人類最早拓殖復活節島的可能年代 1300±200 年作為校正點定年。如圖 5 中所示，本分析中 13 個太平洋構樹的樣本都被歸為一群，而臺灣的樣本則為太平洋群的「姊妹群」，兩群約在 5,400 年前分離。而在太平洋群中，蘇拉威西被置於遠大洋洲的姊妹群，兩群在 5,080 年前分離。在遠大洋洲群的構樹樣本可再分為 A、B 兩群，兩群在距今 3,834 年前分隔，在 A 群中，斐濟樣本與東加樣本關係密切，夏威夷與瓦利斯島互為姊妹群，而在 B 群中，斐濟樣本與兩個大溪地樣本則漸次為復活節島的姊妹群。我們的分析顯示構樹在 5,400 年前被帶離臺灣，在 5,080 年前抵達蘇拉威西，並在 3,834 年前進入遠大洋洲。由於我們使用的校正點年代較為久遠，因此計算出來太平洋構樹傳入的年代（圖 5）較 Peter

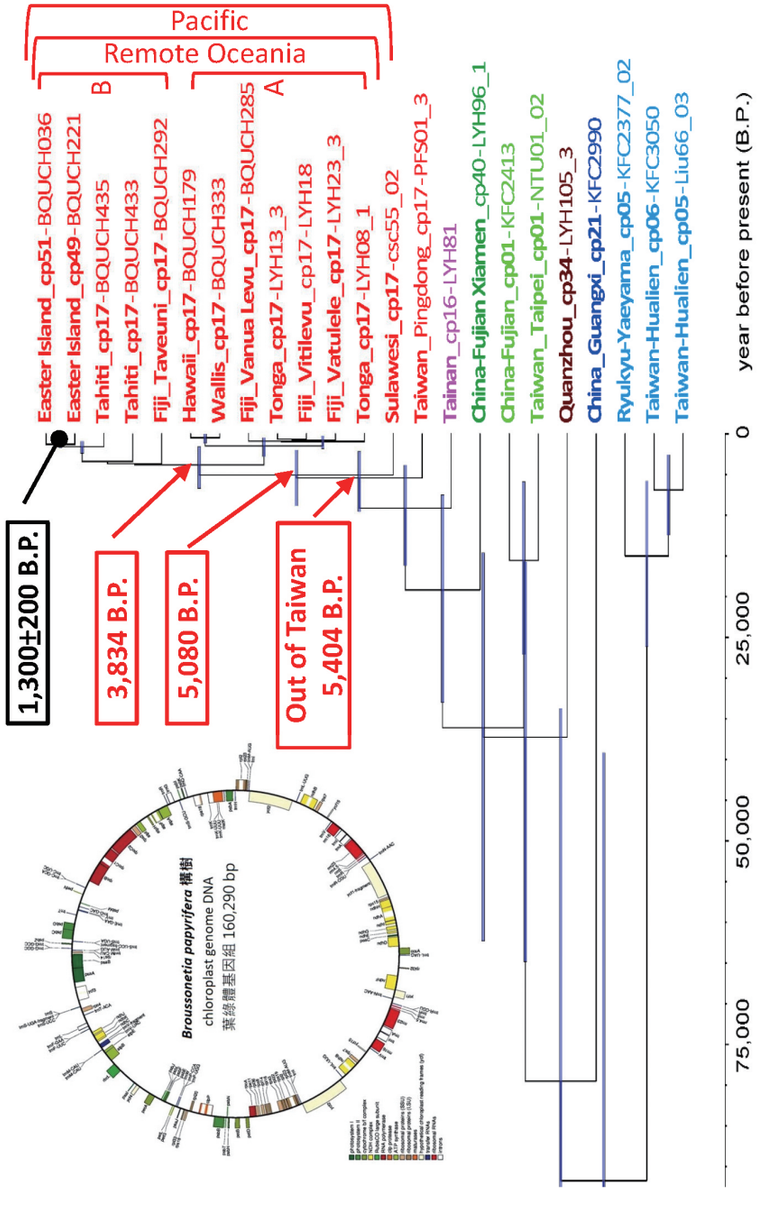

圖 5　以全葉綠體基因組序列分析太平洋構樹的傳播歷史。

Bellwood 在本論文集中（Bellwood 2021：圖 2）提出的模型古老了許多。但該分析顯示，構樹被帶離臺灣至東南亞、最終抵達遠大洋洲的年代，還是遠比歐洲殖民前早了許多，同時太平洋構樹由北而南，再由西往東的傳播方向，也與 Peter Bellwood 的模型高度符合。近來我們根據更多太平洋構樹的葉綠體基因組序列與更合理的校正年代，發現構樹在太平洋的傳播年代與路徑，與 Peter Bellwood 出臺灣說的模型高度契合，此研究成果目前已完成分析，將在近期內投稿。

根據植物親緣地理分析，我們首先證明臺灣是太平洋構樹的原鄉，而進行中的族群基因體研究，顯示構樹 DNA 記載了南島語族航海家乘風破浪的遷徙路徑與年代等航海史。此外，具性別辨識能力的分子標記顯示，太平洋用於製作樹皮布的構樹全為雌株，顯示出臺灣的構樹係由南島語族藉由阡插萌檗傳遍遠大洋洲島嶼，也證實了出臺灣的南島語族先祖是具備農耕技術的「農民」，支持了以「農業／語言擴張假說」為基礎的「出臺灣說」，再次見證了臺灣在南島研究上的重要性。

6. 有「構」厲害

構樹，串聯起生物親緣地理學、考古人類學、歷史語言學與

人類遺傳學等學門知識，由研究臺灣最常見的本土樹種，提供了臺灣為南島原鄉出臺灣說的堅實佐證。2018 年，筆者與中央研究院數位文化中心合作，建立「生物多樣性數位博物館 http://brmas.openmuseum.tw/」，嘗試將科學研究以另一種方式呈現，藉由創新的媒介與多元內容，讓民眾得以從不同角度接觸艱深的研究主題，在專業中尋得與生活、文化與歷史的連接，了解研究之於學術之外的價值，希望能將生物多樣性研究的成果及意義落實於社會中（章璿 & 鍾國芳 2019）。生物多樣性數位博物館以「有『構』厲害」為題，透過「子曰：必也正名乎」、「打樹成衣」及「植物學家的人類學之旅」三個主題，從臺灣最常見的植物「構樹」連結至南島文化這份臺灣給世界的禮物（Diamond 2000），在科普知識的傳遞之餘，讓深受漢文化影響的我們從而思考與探索臺灣為南島原鄉的深層意義。

謝辭

作者感謝中華民國原住民族委員會邀請至帛琉共和國參加 2019 南島語言復振國際論壇。本文撰寫期間承李壬癸院士給予諸多建議，特此致謝。本研究於 2008 年由張至善博士發想而展開，劉筱蕾博士於碩士研究期間收集葉綠體 DNA 序列，並與智利研究團隊 Andrea Seelenfreund 與 Daniela Seelenfreund 密切合作。本研究承中央研究院主題研究計畫（AS-107-TP-B18）、中央研究院數位文化中心計畫（ASCDC-107-11）、科技部南島文化跨領域研究：從南島語族到原住民族（107-2420-H-002-034）經費支持。

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Paper mulberry DNA attests Taiwan as Austronesian ancestral homeland

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Keywords:
chloroplast DNA, commensal approach, ethnobotany, out of Taiwan hypothesis, sex marker, *tapa* cloth

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1. Introduction

"The Origin and Spread of Austronesian-Speaking Peoples" by Peter Bellwood (2021) and "The Genetic History of Pacific Islanders" by Matthews Spriggs (2021) in this volume are two topics closely related to the prehistories of Taiwan and the Pacific as well as the theoretical justification for the revitalization of Austronesian languages. These two insightful and succinct reviews summarize recent advances in historical linguistics, archaeology, and paleogenomics underscoring the "Farming/Language Dispersal Hypothesis", supporting the "Out of Taiwan" hypothesis positing Taiwan as the Austronesian homeland. Both scholars also emphasize the complexity of the prehistory of the Neolithic colonization into the Pacific, and the importance of integrating interdisciplinary research. In this contribution, I present how studies of Pacific paper mulberry provide further evidence from an ethnobotanical perspective for the Out of Taiwan hypothesis.

2. Commensal approach to the study of Austronesian expansion and migration

When Neolithic humans shifted from hunter-gatherer to sedentary farming communities, population growth as the result of food production would intensify competition for land. Under these dual pressures, farming communities would inevitably migrate and expand, resulting in the spread of languages as expounded by the Farming/Language Dispersal Hypothesis. Ancestors of Austronesian-speaking peoples (thereafter Austronesians) were farmers (Fig. 1A) and their transition from hunter-gathering into an agricultural economy also entailed a close and symbiotic relationship with plants and animals utilized. Consequently, domesticated animals such as pigs, chickens, and dogs as well as Pacific rats, and a suite of ca. 70 plant species, such as breadfruits, taros, yams, and paper mulberry, that constituted the Austronesian "agricultural package" were also transported across Oceanic islands. Archaeologists and anthropologists describe the spread of Austronesian agriculture as "transported landscapes", a strategy that had maximized their chances of surviving in the increasingly

resource depauperate island environments, facilitating their successful colonization of Remote Oceanic islands (Matisoo-Smith 2009, Kirch 2010).

Because those "commensal species" constituting the agricultural package depended fully on Austronesian ancestors to overcome the large expanses of water, their DNA likely recorded traces of Austronesian migration, providing the fourth category of evidence in addition to historical linguistics, archaeology, and human genetics that can test theories of Austronesian expansion and migration. In 1994, Lisa Matisoo-Smith, currently a professor of the University of Otago, New Zealand, pioneered the phylogeographic studies of the Austronesian commensal species, analyzing DNA variation of the Pacific rats (*Rattus exulans*) to demonstrate the extraordinary navigation ability of Polynesian seafarers. Subsequent studies of domestic animals, including pigs and chickens, and crop species, such as breadfruits, bananas, taros, coconuts, and sweet potatoes, revealed complicated histories of colonization and inter-island transportation (Matisoo-Smith 2009, Storey et al. 2013). However, as a majority of Austronesian commensal species introduced into the Pacific have their geographic

origins in SE Asia and/or Near Oceania (e.g., New Guinea), none of the aforementioned studies were able to test the "Out of Taiwan" hypothesis.

Figure 1 A: A Polynesian village reconstructed in Kamakakuokalani Center for Hawaiian Studies, University of Hawai'i at Mānoa; B: A Korafe (Tufi, Oro Province, Papua New Guinea) lady dressing traditional cloth making *tapa*; C: 2018 Tufi Tapa and Tattoo Festival; D: Paper mulberry plantation in Easter Island (Rapa Nui), Chile. In Rapa Nui, paper mulberry is called *Mahute*.

3. Felting Bark to Make Cloth

In the 18th Century, British Royal Navy Captain James Cook was commissioned to make three voyages to the Pacific Ocean. In his travel log, Cook carefully recorded all details observed during the journeys, including an observation of the Tahitian Cloth, which he wrote (Cook 1893:99–100):

> I shall now describe their way of making Cloth, which, in my opinion, is the only Curious manufacture they have. All their Cloth is, I believe, made from the Bark of Trees; the finest is made from a plant which they Cultivate for no other purpose. Dr. Solander think it is the same plant the bark of which the Chinese make paper of. They let this plant grow till it is about 6 or 8 feet high, the Stem is then about as thick as one's Thunb or thicker; after this they cut it down and lay it a Certain time in water. This makes the Bark strip off easy, the outside of which is scraped off with a rough Shell. After this is done it looks like long strips of ragged linen; these they lay together, by means of a fine paste made of some sort of a root, to the Breadth of a yard more or less, and in length 6, 8 or 10 Yards or more according to the use it is for. After it is thus put together it is beat out to its proper breadth and fineness, upon a long square piece of wood, with wooden beaters, the Cloth being kept wet all the time. The beaters are made of hardwood with four square sides, are about 3 or 4 inches broad and cut into grooves of different fineness; this makes the Cloth

look at first sight as if it was wove with thread, but I believe the principal use of the Grooves is to facilitate the beating it out, in the doing of which they often beat holes in it, or one place thinner than another; but this is easily repaired by pasting on small bits, and this they do in such a manner that the Cloth is not the least injured. The finest sort when bleached is very white and comes nearest to fine Cotton.

Tapa, or bark cloth, is a non-woven textile made of tree bark via beating (Fig. 1B). Bark cloth is found in West Africa, Southeast Asia, Oceania, and Latin America; however, it is the *tapa* of the Pacific that is most widely known (Chang 2011). Prior to the introduction of western weaving textiles, *tapa* was essential to Pacific daily life, having been used for clothing, decoration, room partitioning, and arts and crafts (Fig. 1C). In the Pacific, although many species of the Mulberry Family (Moraceae), such as breadfruits (*Artocarpus* spp.), fig trees (*Ficus* spp.), paper mulberry as well as *Hibiscus tiliaceus* of the Mallow Family (Malvaceae) can be used to make bark cloth, paper mulberry (*Broussonetia papyrifera*) has been the most widely and commonly used tree, producing the finest tapa cloth (Chang 2011).

4. Most common and yet neglected plant species in Taiwan

Paper mulberry [*Broussonetia papyrifera* (L.) L'Hér. ex Vent.] is a dioecious (Fig. 2) tree species of the Mulberry Family widely distributed in China, Indochina, Taiwan, and Korea. Because of its fast growing and extremely long fiber in the inner bark, paper mulberry has long been introduced to Japan, Europe, United States, and the Pacific islands, becoming invasive plants in countries such as Pakistan and the Philippines (Chung et al. 2017). In Taiwan, paper mulberry can be found almost everywhere in both urban and rural areas: on roadsides, wall corners, sidewalks, wasteland, riverbanks, and mountain paths. Arguably, paper mulberry is the most common and yet neglected plant species in Taiwan. Paper mulberry leaves, as well as petioles and young branches, are hairy, coarse, and fibrous, and they are favorable food for deer and goats. Consequently, paper mulberry is often called "*Luzishu* 鹿仔樹 [deer tree]" by Taiwanese locals. In June and July, the soft and juicy tissues of mature fruits of paper mulberry are abundantly available, providing a summer feast for birds and small mammals (Fig. 2C).

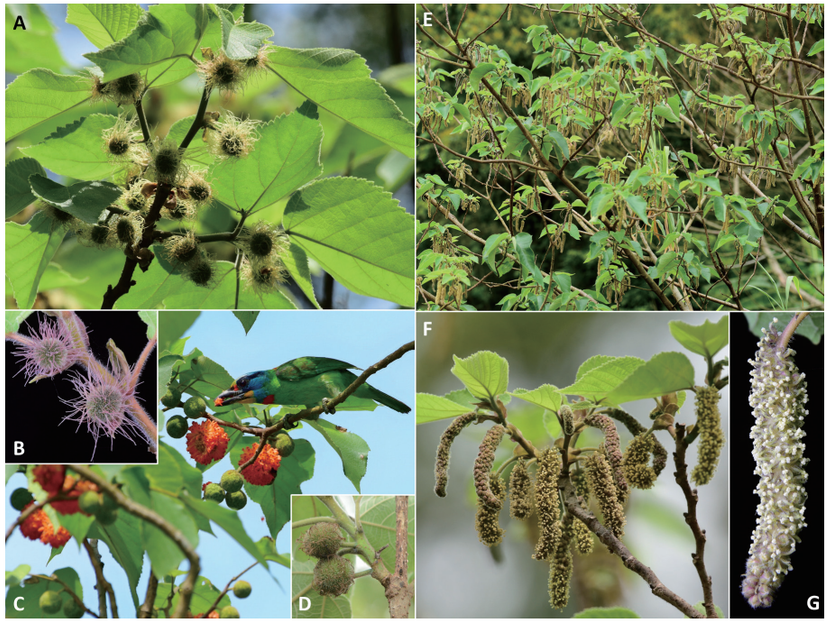

Figure 2 Paper mulberry is a dioecious tree species. A: Female paper mulberry tree in full blossom; B: A close-up of female inflorescences; C: A Taiwan Barbet feeding on fruits of paper mulberry; D: Wilted female inflorescences of a paper mulberry tree in Eastern Highlands Province, Papua New Guinea; E: Male paper mulberry tree in full blossom; F: Male inflorescences; G: A close-up of a male inflorescence.

Paper mulberry has been utilized for millenia. In the existing oldest collection of Chinese poetry *Shijing* 詩經 [Book of Poetry] (1046–771 BC), paper mulberry was recorded in a verse of *He-Ming* 鶴鳴 [Crane cries], *Xiao-ya* 小雅 [Minor odes of the kingdom] as "*Le Bi Zhi Yuan, Yu You Shu Tan, Qi Xia Wei Gu* 樂彼之園、爰有樹檀、其下維穀 [Pleasant is that garden, In which are the sandal trees; But beneath them is the paper mulberry (https://ctext.org/book-of-poetry/he-ming)]". The verse uses two multi-purpose tree species "sandalwood" and "paper mulberry" as metaphors for gifted persons, implying a desire to recruit talents. Indeed, paper mulberry leaves are not only highly praised as deer and pig fodder, its leaves, seeds, latex, and even bark are valuable traditional medicine. Because it is fast growing, paper mulberry has also been widely introduced for quick afforestation and erosion control. Consequently, it has become an invasive species in many parts of the world (Chung et al. 2017). However, paper mulberry's most important property is its extremely long fiber in the inner bark, making it an exceptional fiber crop.

Lu Chi 陸　璣 (261–303 AD), a scholar born in Wu of the Three Kingdoms Period (220–280 AD), explained the word *Gu* 穀 in his *Shih Shu* 詩疏 [Annotation of the Book of Poetry]. *Lu* annotated that *Gu*　穀 is synonymous with paper mulberry, which was still used by *Jiangnan*　江　南 peoples during the Three Kingdoms Period for felting into cloth and beating into

paper. While it has been long known that paper mulberry was used to make paper during the period and the tree remains the most important resource for making *Mianzhi* 棉紙 [cotton paper] and for calligraphy up to now, exactly what "felting into cloth" means remains controversial. Ethnologist Ling Shun-Sheng 凌純聲 surmised that the "cloth" is what was recorded in Vol. 129 of *Shih chi* 史記 [The Historical Memoirs] (90 BC) as *tapu* 榻布, identical as the cloth made of paper mulberry tree bark known as *tapa* in the Pacific. Although *Tsai Lun* 蔡倫 (63–121 AD), a eunuch in the Eastern Han Dynasty (25–220 AD), has long been accredited for inventing the paper-making technique using rags, fishing nets and other materials, Ling (1961) argued that those materials were actually made of the bark fiber of paper mulberry trees. Given that the making of bark cloth still existed in the *Jiangnan* area where *Tsai Lun* was born, he might have been inspired by the process of bark cloth-making and eventually "invented" the technique that produced the *Tsaihou Chih* 蔡侯紙 [paper of Marquis Tsai].

Though *tapu* recorded in ancient Chinese literature has long gone, *tapa* was once essential for Austronesians' daily lives and still remains culturally irreplaceable in

the Pacific up to now (Fig. 1C). As documented in Captain Cook's travel log, paper mulberry was widely planted across the Pacific in the 18th Century as prime material for making *tapa*, presenting the only commensal species that is native to East Asia, and which is suitable for testing the "Out of Taiwan" hypothesis of Austronesian expansion and migration. With the introduction of western weaving textiles, *tapa* is no longer used for day-to-day life in the Pacific and tapa culture has disappeared from many Pacific Islands. However, because of its rarity, paper mulberry is more likely to preserve the genetic legacy of the ancient migration. Moreover, because there is no close relative of paper mulberry in the Pacific, the possibility of interspecific hybridization can be precluded.

5. Austronesian migration recorded in paper mulberry DNA

In spring 2008, the author received an invitation from Chi-Shan Chang 張至善 of the National Prehistory Museum 國立臺灣史前博物館 to test hypotheses of Austronesian expansion and migration from the "clothing" perspective using

phylogeography of paper mulberry. Concurrently, Chilean archaeologist Andrea Seelenfreund and biochemist Daniela Seelenfreund independently conceived a similar idea. Together, our international interdisciplinary collaboration embarked on fieldwork across the Pacific, collecting more than 600 paper mulberry trees from Taiwan, China, Vietnam, Japan, the Philippines, New Guinea, Fiji, Tonga, Samoa, Hawaii, Tahiti, Rapa Nui, etc. (Chang et al. 2015).

DNA sequences mutate occasionally during the process of replication, resulting in different "haplotypes" that are a group of DNA sequences inherited from a common ancestor and yet differing slightly in their sequences. Phylogeography aims to research what demographic and/or historical events have generated the observed geographic distribution of haplotypes within and among closely related species. By sequencing the intergenic spacer between the genes *ndhF* and *rpl32* of the maternally inherited chloroplast genome, 48 haplotypes were detected in the 604 sampled paper mulberry trees (Chang et al. 2015). Figure 3 shows the sampling localities and the evolutionary relationship of the 48 haplotypes. As shown in Fig. 3, China, Taiwan, and Indochina have the highest number of haplotypes, indicating that these areas are indeed the native distribution range of paper mulberry as predicted by evolutionary theories. Compared to the native range, Pacific paper mulberry trees are genetically homogeneous and predominately carry haplotype cp-17 (red haplotype). Except for the Pacific, cp-17 is found only in southern Taiwan. Because cp-17 is a tip haplotype of the clade composed of cp-9 to cp-19 that are exclusively distributed in Taiwan, the Pacific cp-17 has an unambiguous geographic origin from Taiwan, indicating that Taiwan is the homeland of the Pacific paper mulberry trees and providing the first ethnobotanical support of a commensal species concurring with the prediction of the out of Taiwan hypothesis of Austronesian expansion and migration (Chang et al. 2015).

Subsequently, a molecular marker that can identify paper mulberry sex was developed using a duplex PCR protocol based on the male-specific sequence (Penailillo et al. 2016). After analyzing more than 300 samples collected from Sulawesi to all across Oceania, Penailillo et al. (2016) showed that all Pacific paper mulberry trees carrying haplotype cp-17 are female (Fig. 4), indicating the absence of sexual reproduction, congruent with the historical

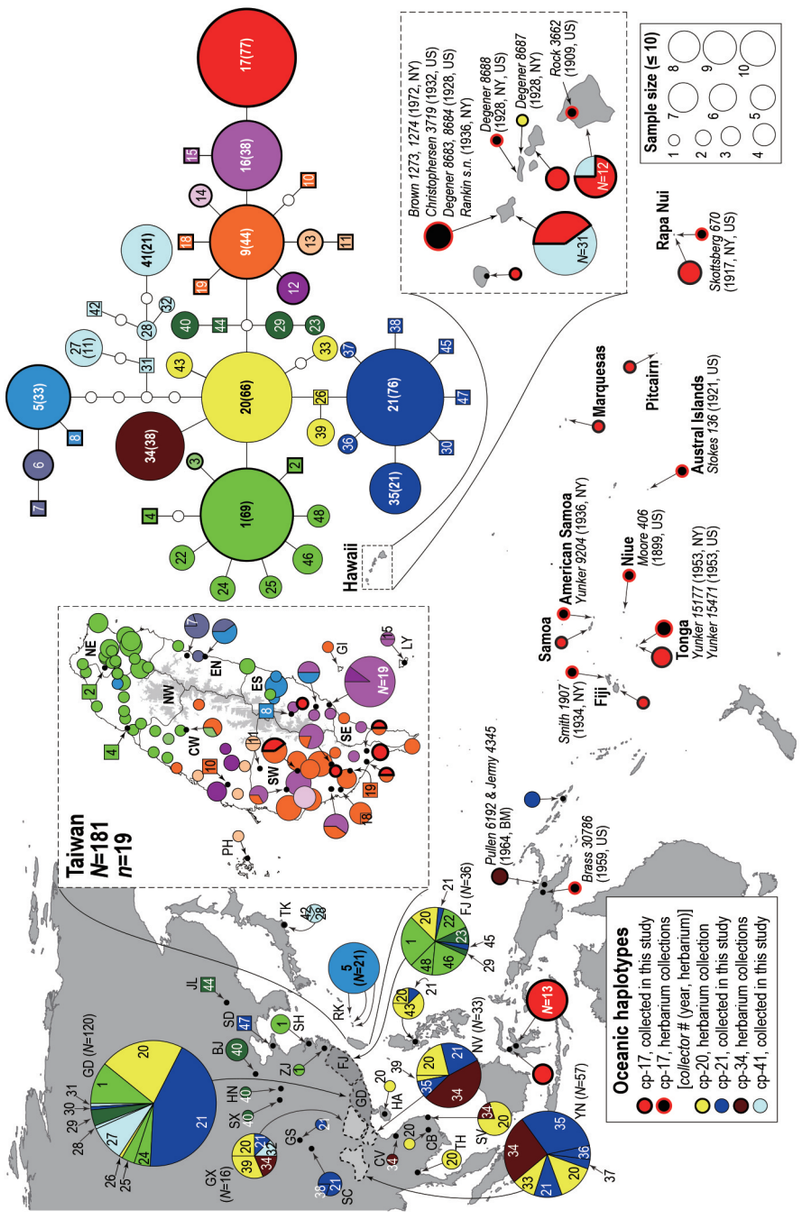

Figure 3 Distribution of *ndhF-rpl32* haplotypes and haplotype network. Published in Chang et al. (2015) (https://doi.org/10.1073/pnas.1503205112).

account on the clonal propagation and anthropogenic introduction of the Pacific paper mulberry, corroborating Chang et al. (2015) in supporting Taiwan as the ancestral homeland for both Austronesians and the Pacific paper mulberry.

However, because the chloroplast *ndhF-rpl32* intergenic spacer lacks genetic variation needed to reconstruct the detailed route and chronology of the transportation of Pacific paper mulberry, results inferred from Chang et al. (2015) cannot rule out the possibility of recent introduction via modern international trades. This concern was first addressed by analyses of a bundle of ancient *tapa* discovered at a cave on the Agakauitai Island of the Gambier Archipelago, French Polynesia (Seelenfreund et al. 2016). Using a species-specific molecular marker, the *tapa* was shown to be made of paper mulberry. Based on an Accelerator Mass Spectrometry (AMS), the dating suggests that the *tapa* was made in the 17th Century before islanders' first contact with Europeans (Seelenfreund et al. 2016).

To further elucidate the history of paper mulberry's introduction into the Pacific, we reconstructed a dated

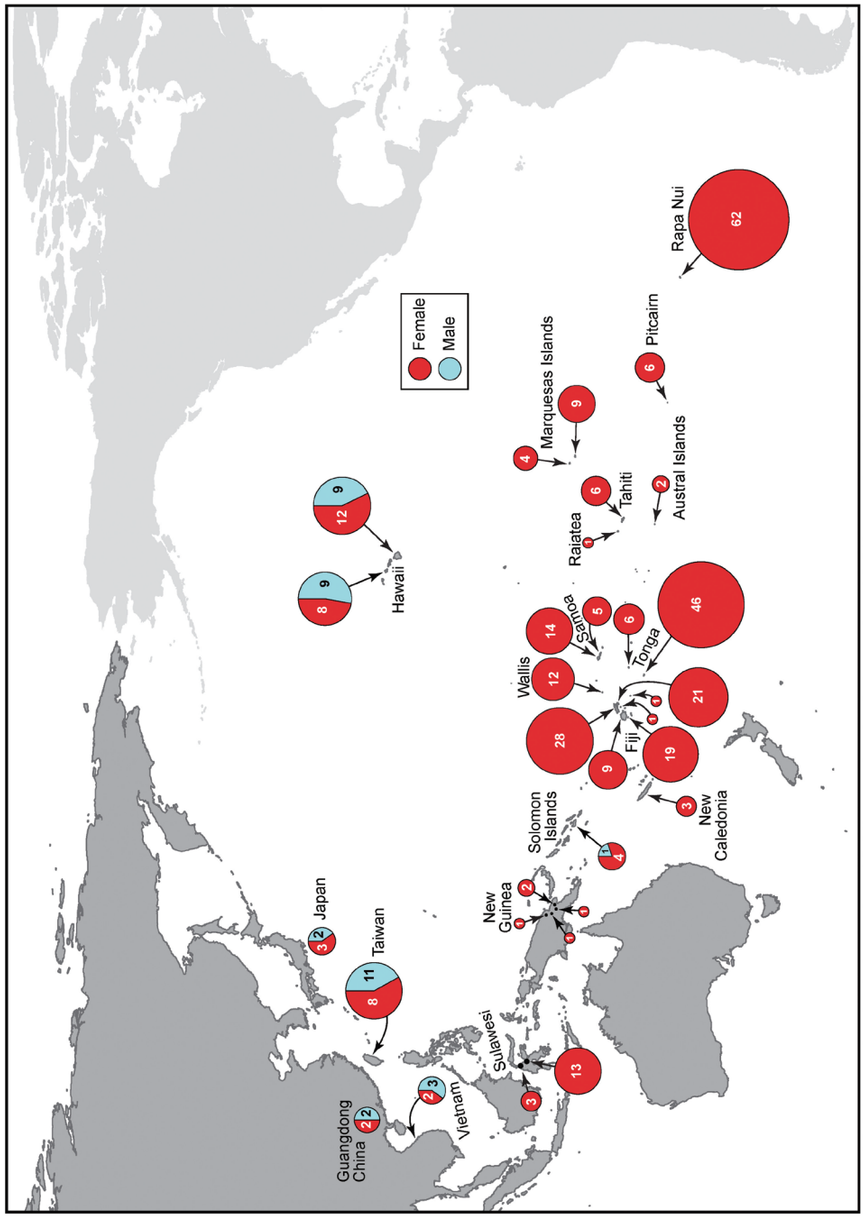

Figure 4 Sex distribution of Pacific paper mulberry. Size of the circles is proportional to the number of samples. Published in Penaililllo et al. (2016) (doi:10.1371/journal.pone.0161148.g005).

phylogeny (i.e., chronogram) based on whole chloroplast genome sequences assembled using the next-generation sequencing (NGS) technology. Figure 5 shows a preliminary result presented in the 2019 International Austronesian Language Revitalization Forum. In this analysis, we sampled 13 Pacific paper mulberry trees that are all female and carry cp-17 haplotype or its derived haplotypes cp-49 and cp-51 (red samples in Fig. 5), calibrated with the proposed date of first settlement to Rapa Nui 1300±200 years before present (BP). As shown in Figure 5, all 13 Pacific samples are grouped together with cp-17 of Taiwan placed as the basal "sister group" separating from the Pacific Group ca. 5,400 BP. Within the Pacific Group, Sulawesi in turn is placed as a basal sister group to the Remote Oceanic Group separating from the former 5,080 BP. The Remote Oceanic Group is placed in two groups A and B, separating at 3,834 BP. In Group A, Fijian samples are closely related to Tongan samples and the Hawaiian sample is placed as sister to the Wallis sample. In Group B, the Fijian sample and two Tahitian samples are placed as successive basal sister groups to Easter Island samples. Our analysis suggests that paper mulberry was brought out of Taiwan 5,400 BP, arriving in Sulawesi 5,080

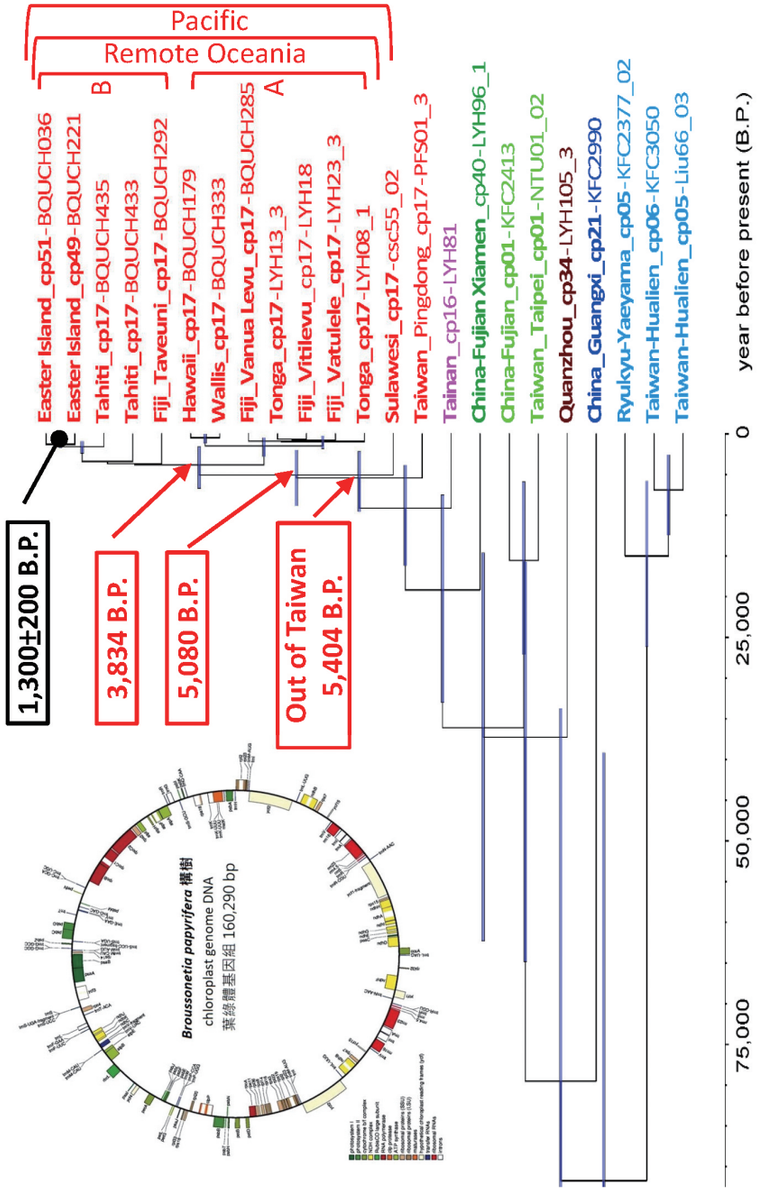

Figure 5 Chronogram of the Pacific paper mulberry based on whole chloroplast genome sequences.

BP, and transported into Remote Oceania 3,834 BP (Fig. 5). Since the calibration point used in this analysis is relatively old, the resulting dates are much earlier than the model proposed by Peter Bellwood (2021: Fig. 2). However, it is clear from our preliminary analysis that the tree was brought out of Taiwan into Island Southeast Asia and Remote Oceania prior to the European colonial period, and its direction of transportation was from north to south and west to east, highly congruent with Peter Bellwood's model. Recently, we have completed a study based on chloroplast genome sequences of additional Pacific paper mulberry trees using more plausible calibrations. Our analyses reveal phylogenetic relationships and chronology of the dispersal of Pacific paper mulberry that are highly consistent with Peter Bellwood's model of the "Out of Taiwan" hypothesis. This manuscript is currently under preparation and will be submitted for publication soon.

Based on phylogeographic analysis (Chang et al. 2015), we first demonstrated that Taiwan is the homeland of Pacific paper mulberry. Our ongoing population genomic analyses further show that the genome of paper mulberry preserves the history of the epic journey of Austronesian

seafaring, recording paths and chronology accompanying Austronesian expansion and migration from Taiwan to Remote Oceania (Fig. 5). Additionally, a sex marker showed that all Pacific paper mulberry carrying cp-17 used for making *tapa* are female (Penailillo et al. 2016), indicating the clonal nature of the Pacific paper mulberry progagated via root suckers by Austronesian ancestor across Remote Oceanic islands. Our studies of the Pacific paper mulberry thus not only support the "out of Taiwan" hypothesis but also confirm that the Austronesian ancestors were farmers, corroborating the "Farming/Language Dispersal Hypothesis."

6. The Great Paper Mulberry—an Open Museum Exhibition

Our studies of paper mulberry, one of the most common and yet most neglected plant species of Taiwan, connect biogeographical, archaeological, anthropological, historical linguistic, and human genetic studies, demonstrating the species as an Austronesian commensal species whose DNA provides an unexpected and yet unambiguous

support for the "out of Taiwan" hypothesis of Austronesian expansion and migration. To make our series of studies more accessible to the general public, an online exhibition "The Great Paper Mulberry" was designed in the OPEN MUSEUM website (http://openmuseum.tw/muse/exhibition/9c9c5736e4d5d727e393b1f710c49bba) of Academia Sinica Center for Digital Cultures (Chang & Chung 2019). Through the three exhibitions titled "Rectification of Names", "Anthropological Journey of a Botanist", and "Felting Bark to Make Cloth", we demonstrate how paper mulberry DNA tells a story of Austronesian expansion and migration, affirming paper mulberry as a genuine "Taiwan's Gift to the World" (Diamond 2000). In addition to conveying scientific knowledge, the exhibition also allows us, who are deeply influenced by the Han Chinese culture, to think about and explore the deeper meaning of Taiwan as an Austronesian homeland.

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