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Amis Pacilo and *Yami Cipoho* are not the same as the Pacific breadfruit starch crop—Target enrichment phylogenomics of a long-misidentified *Artocarpus* species sheds light on the northward Austronesian migration from the Philippines to Taiwan

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Abstract

‘Breadfruit’ is a common tree species in Taiwan. In the indigenous Austronesian Amis culture of eastern Taiwan, ‘breadfruit’ is known as *Pacilo*, and its fruits are consumed as food. On Lanyu (Botel Tobago) where the indigenous Yami people live, ‘breadfruit’ is called *Cipoho* and used for constructing houses and plank-boats. Elsewhere in Taiwan, ‘breadfruit’ is also a common ornamental tree. As an essential component of traditional Yami culture, *Cipoho* has long been assumed to have been transported from the Batanes Island of the Philippines to Lanyu. As such, it represents a commensal species that potentially can be used to test the hypothesis of the northward Austronesian migration ‘into’ Taiwan. However, recent phylogenomic studies using target enrichment show that Taiwanese ‘breadfruit’ might not be the same as the Pacific breadfruit (*Artocarpus altilis*) that was domesticated in Oceania and widely cultivated throughout the tropics. To resolve persistent misidentification of this culturally and economically important tree species of Taiwan, we sampled 36 trees of Taiwanese *Artocarpus* and used the Moraceae probe set to enrich 529 nuclear genes. Along with 28 archived *Artocarpus* sequence datasets (representing a dozen taxa from all subgenera), phylogenomic analyses showed that all Taiwanese ‘breadfruit’ samples, together with a cultivated ornamental tree from Hawaii, form a fully supported clade within the *A. treculianus* complex, which is composed only of endemic Philippine species. Morphologically, the Taiwanese ‘breadfruit’ matches the characters of *A. treculianus*. Within the Taiwanese samples of *A. treculianus*, Amis samples form a fully supported clade derived from within the paraphyletic grade composed of Yami samples, suggesting a Lanyu origin. Results of our target enrichment phylogenomics are consistent with the scenario that *Cipoho* was transported northward from the Philippines to Lanyu by Yami ancestors, though the possibility that *A. treculianus* is native to Lanyu cannot be ruled out completely.

Introduction

Prior to western colonial expansion, Austronesian languages were the most widely spoken language family, covering 206° of longitude from Madagascar in the west to Rapa Nui (Easter Island) in the east and 72° of longitude from Taiwan in the north to Aotearoa (New Zealand) in the south [1]. Given the extraordinarily wide distribution, the quest into the ancestral homeland of Austronesian-speaking peoples (hereafter Austronesians) has been central in Pacific anthropology [1]. Recent studies in historical linguistics [1, 2], archaeology [3, 4], human genomics [5], and phylogeography of Pacific paper mulberry [6, 7] overwhelmingly support the Bellwood-Blust Model, positing that the epic Austronesian diaspora that eventually colonized almost all habitable Remote Oceanic islands by ca. 1,300 A.D. started from the “Out of Taiwan” southward migration to the Philippines ca. 4,200–4,000 B.P. [3, 4, 8, 9]. However, Austronesian expansion and migration is by no mean unidirectional [10]. While all indigenous tribes of Taiwan’s main island speak Formosan languages that constitute nine of the 10 subgroups of the Austronesian languages, the language of the Yami (also known as Tao) people of Lanyu (Botel Tobago; Fig 1) belongs to the Batanic languages, which are part of the Malayo-Polynesian languages (the 10th subgroup of the Austronesian language family) [1, 11]. As Yami are also culturally different from other Formosan indigenous peoples, it is

generally assumed that the Yami are closely related to (and even descendants from) the Ivatan people of the Itbayat Island of the Batanes archipelago [12, 13], the northernmost Philippine islands ca. 100 km south of Taiwan and Lanyu [11, 14] across the Bashi Channel (Fig 1). The conjecture that Yami represents a northward Austronesian migration from the Philippines to Taiwan is also consistent with the idea that Neolithic Taiwan was part of the integral maritime trade networks around the South China Sea [15-17]. Surprisingly, however, archaeological and genetic studies both suggest that Yami are closer to Formosan indigenous peoples than the Ivatan [18, 19]. Bellwood and Dizon [20] surmised that the conflict among linguistic, archaeological, and human genetic evidence could have resulted from the replacement of earlier Formosan and non-Malayo-Polynesian by the Batanic speakers, suggesting a much more complicated origin of Yami people.

Fig. 1. Maps of Taiwan and the Philippines and sampling localities of Taiwanese *Artocarpus*. In the sampling map, the traditional distribution range of Amis people [21] is highlighted in light blue. See Table 1 for sample code abbreviation and detailed collection information.

According to the “Farming-Language Dispersal Hypothesis”, the key to Austronesians’ rapid and successful expansion and migration was their early adoption of the farming and sedentary lifestyle that had enabled the increase and spread of Austronesian ancestral populations as well as the languages they spoke [4, 9, 22, 23]. Accompanying their migration, Austronesian ancestors also carried a suite of domesticated animals and crop species to increase the likelihood of surviving in remote and resource-poor islands [24]. Phylogeographic studies of these commensal organisms thus can serve as proxies for tracking Austronesian migration [25, 26], providing additional insights into the complexity of Polynesian seafaring [6, 27, 28]. Amongst the ca. 200 plant species used by Yami people [29], ‘breadfruit’ has long been regarded as one of the possible plant species transported from the Philippines to Lanyu [14, 30].

Breadfruit [*Artocarpus altilis* (Parkinson) Fosberg] (Fig 2) is a fast-growing, low-maintenance, and high-yield traditional staple crop in Oceania [31, 32]. Though in the western world it is known primarily for its large, starchy, seedless fruits that were part of the infamous “Mutiny on the Bounty,” in the Pacific, breadfruit comprises hundreds of cultivars (seeded and seedless), and it is a multipurpose tree species whose seeds, latex, inner bark, wood, leaves, and male inflorescences are traditionally used for food, medicines, house construction, boat making, carving, clothing, cordage, animal feed, wrapping, bird trapping, insect repellent, and fish poison [32, 33]. What we refer to as the ‘fruit’ of breadfruit throughout this manuscript is actually botanically a syncarp and is made up of tightly packed accessory fruits composed mainly of fleshy floral tissues. Breadfruit was domesticated in Near Oceania over 3,000 years ago and transported by Austronesian ancestors across Oceanic islands during their epic migration [24, 27]. Over millennia, hundreds of breadfruit cultivars (varying in fruiting season, fruit shape, color and texture of the flesh and skin, presence or absence of seeds, flavor, cooking and storage qualities, leaf shape, and horticultural needs) were selected by humans, and a small portion of that diversity was introduced to the Caribbean, Central and South America, Africa, India, Southeast Asia, and islands of the Indian Ocean [34]. Because of its high nutritional and medicinal values [35], breadfruit has been exalted as a sustainable crop for alleviating hunger and treating diabetes in Oceania and around the world [36, 37].

Fig. 2. *Artocarpus altilis* (Parkinson) Fosberg. (A) Pistillate and staminate inflorescences. (B) Staminate inflorescence. (C) Fallen staminate inflorescences. (D) Syncarp surface. (E) Leaf. (F) Cross-section of syncarp. (G) Syncarp. (H) Tree (AaCCR200) planted on the campus of National Pingtung University (NPTU). (I) *Uru* planted on the campus of the University of Hawai'i at Mānoa. All photographs except for (I) was taken from tree planted in NPTU. A–C & H taken by C.-M. Wang, D–G by C.-L. Hsieh, and I by K.-F. Chung.

Despite its cultural and economic importance, species delimitation of breadfruit and its closest wild relatives has been difficult. This is in part due to its long taxonomic history and its complex domestication [38–41]. Numerous synonyms exist for the cultivated breadfruit. While the valid name is *Artocarpus altilis* (Parkinson) Fosberg [42], two synonyms are especially prevalent due to long history of use and taxonomic confusion: *A. communis* J.R.Forst. & G.Forst. [43] and *A. incisus* (Thunb.) L.f. [44]. Additionally, the circumscription of breadfruit has also varied. Jarrett [43] and Berg et al. [45], who mainly examined herbarium specimens, favored a broad approach that encompasses breadfruit's wild relatives. However, Zerega et al. [38], who worked with fresh specimens, molecular data, as well as herbarium specimens, took a narrower approach, recognizing *A. camansi* Blanco (breadnut) and *A. mariannensis* Trécul (*dugdug*) as distinct, closely related species of the cultivated breadfruit *A. altilis*. This latter approach has been widely adopted [32, 34, 45], including in the current study.

In Taiwan, the local name for 'breadfruit' is “麵包樹 *miao-bao-shu*” (where “*mian-bao*” means bread and “*shu*” means tree in Mandarin Chinese), which is a common tree species occurring both in cultivation throughout much of the island and in forests of Lanyu [46]. The earliest traceable record of 'breadfruit' of Taiwan appeared in the diary (6th September 1890) of Rev. George Leslie Mackay (1844–1901) [47], a Canadian Presbyterian missionary who had profound influence on Taiwan's Christianity and medical education [48]. Mackay recorded “*Pat-chi-lút* Bread fruit tree” from *Chhit-kha-chhoan* [47], a *Lam-si-hoan* (Amis) village in eastern Taiwan [49] (Fig 1). In his memoir “From Far Formosa”, Mackay wrote that “Breadfruit (*Artocarpus incisa*)” was “used by the aborigines exclusively” [50]. In Amis' oral history, *Pacilo* (≡*Pat-chi-lút*) [51] (also known as 'Apalo [51] / Qapalo [14], or *Facidol* called by central and southern Amis [14, 30]) was said to be introduced by Amis ancestors from overseas [52]. Nowadays, *Pacilo* is still commonly planted in eastern Taiwan especially around Amis households as food [51] and has become a popular ethnic cuisine of eastern Taiwan.

In Yami language, 'breadfruit' is called *Cipoho* or *Ciporo*, almost identical to *Cipoho* or *Tipoho* of the other Batanic languages [14]. In forests managed by Yami people, *Cipoho* is the third most dominant tree species [53]; traditionally, however, fruits of *Cipoho* are rarely consumed as food on Lanyu [54, 55]. Instead, Yami people use the light red wood of *Cipoho* for making houses, hats, plates, mortars (for crushing millet seeds), and the plank-boats *Tatala* and *Cinedkeran* that are central to the Yami culture [55–59]. Given the phonetic similarity of the names for 'breadfruit' in Batanic languages [14] and its appearance as a timber tree in managed and semi-naturalized forests of Lanyu [53, 60, 61], *Cipoho* has long been regarded as non-native [30, 61], possibly introduced by Yami ancestors along with their northward migration from Batanes Island [30].

However, in the earliest record of Lanyu's 'breadfruit', which was documented by Yasusada Tashiro [60] during the early period of the Japanese occupation, the species appeared to have been confused with the jackfruit "*Artocarpus integrifolia* L." (= *A. heterophyllus* Lam.), which was introduced during the Dutch colonization (1624–1662 A.D.) and has been widely grown in Taiwan since [52, 62]. In 1900 A.D., Tashiro was amongst the earliest botanists who ever visited Botel Tobago, and in "A guide to planting trees in urban Taiwan," he recorded 'breadfruit' as growing naturally and abundantly on Botel Tobago and commonly planted around indigenous villages of eastern Taiwan [60]. To promote 'breadfruit' as an urban tree species suitable even in northern Taiwan, Tashiro also referred to a 'breadfruit' tree grown in Mackay's residence in Tamsui (Fig 1) where he lived during his mission. Based on a widely circulated anecdote, that vibrant tree was grown from a *Pat-chi-lút* seedling given to Mackay by the *Nan-shih* Amis [63]. Likely due to Tashiro's promotion [60, 64], 'breadfruit' is now widely cultivated throughout Taiwan and is amongst the most common tree species planted on school campuses [65-67]. Because 'breadfruit' trees are easily accessible, its natural compounds and pharmaceutical properties have been extensively studied in Taiwan [68-70].

Although 'breadfruit' is fairly common in Taiwan, its taxonomy has been confusing. In addition to early confusion with the jackfruit [60, 71], Li [72] also confused the species with *A. lanceolatus* Trécul (= *A. lamellosus* Blanco) in the "Woody Flora of Taiwan," an important post World War II floristic work. Moreover, the above mentioned three common binomials used for the true Pacific breadfruit, (i.e., *Artocarpus altilis* [53, 69, 73, 74], *A. communis* [52, 53, 75-80], and *A. incisus* [29, 46, 61, 64, 81-84]) have been variously adopted even within a single publication [53], resulting in much confusion (S1 Appendix). And yet, the taxonomy of Taiwanese 'breadfruit' has never been rigorously studied. In recent phylogenomic studies of *Artocarpus* using target enrichment (Hyb-Seq), an herbarium sample collected from Lanyu (Yang13056), initially identified as '*Artocarpus incisus*' (= *A. altilis*), was determined to be *Artocarpus treculianus* Elmer based on morphology and grouped with NZ203 (a specimen of *A. treculianus* collected from cultivation in Hawaii). Both of these specimens were referred to as "*A. treculianus* 'ovatifolius'" for their morphological similarities with the type specimen of *A. ovatifolius* Merr. [85]. These samples were within the 'Philippinensi' clade of Sect. *Artocarpus*, Subgenus *Artocarpus*, a clade comprised of species thought to be endemic to the Philippines [86]. Since *A. treculianus* (including *A. ovatifolius* Merr.) has long been considered endemic to the Philippines [43, 45, 86], the likely persistent misidentification of the Taiwanese 'breadfruit' prompted us to conduct the present study. Additionally, considering the close geographic proximity and phytogeographic similarity between Lanyu and the Philippines [87] (Fig 1), the native status of *A. treculianus* has to be reconsidered. Indeed, in the earliest record by Tashiro [60], *Cipoho* was regarded as a native species on Lanyu, though latter scholars assumed that the species was not native since it was "breadfruit" [30, 61]. By taking advantage of recent phylogenomic studies in *Artocarpus* [88] using Hyb-Seq [85, 86, 89], we asked the following questions: (1) How many species of *Artocarpus* constitute the 'breadfruit' species of Taiwan and what is the correct name of the most common 'breadfruit' of Taiwan? (2) Is *Cipoho* native to Lanyu? and (3) What are the likely geographic origins of these 'breadfruit' species? By answering these questions, we also hope to contribute to our understanding of Yami's ancestry.

Materials and methods

Sampling

In Taiwan, the “breadfruit” is considered to be *Artocarpus incisus* (Thunb.) L.f. (= *A. altilis*), which in “The Red List of Vascular Plants of Taiwan 2017” is listed as “Least Concern” [84]. So only oral permissions from local land owners were needed to sample the species. Since there is a strong indigenous consciousness on Lanyu, we also obtained a collecting permit from the Lanyu Township Office. Prior to sampling, we thoroughly examined specimens in major herbaria (TAI, TAIF, TNM, and HAST [90]), literature [46, 72, 74, 76, 79, 81], and online information pertaining to the ‘breadfruit’ of Taiwan. Our preliminary investigation concluded that the morphology of almost all Taiwanese ‘breadfruit’ trees matched *A. treculianus* as recently circumscribed by Gardner and Zerega [86], rather than the true Pacific breadfruit, *A. altilis*. Because *A. treculianus* is considered a species complex and its taxonomy remains unsettled [86], we proceeded to sample ‘breadfruit’ from multiple localities of Taiwan, with a special focus on the traditional territory of the Amis of eastern Taiwan and Lanyu (Fig 1). In addition to the Taiwanese ‘breadfruit’, a genuine *A. altilis*, which is extremely rare in Taiwan, was located in National Pingtung University (NPTU) and sampled (Fig 2). We also sampled one jackfruit (*A. heterophyllus*), one *A. odoratissimus* Blanco [91], and one *A. xanthocarpus* from National Chiayi University (NCYU), National Pingtung University of Science and Technology (NPUST), and National Museum of Natural Science (NMNS), respectively, to improve *Artocarpus* sampling within Taiwan. Voucher information of the 36 samples collected in current study is detailed in Table 1. Voucher specimens were deposited in the Herbarium of Academia Sinica, Taiwan (HAST). To assure species identification of our samples, 28 already-sequenced accessions (S1 Table), including 10 accessions of the ‘Philippinensi’ clade *sensu* Gardner and Zerega [86], two accessions of *A. xanthocarpus*, one accession of *A. heterophyllus*, two accessions of *A. mutabilis* Becc. (*Pingan*), one accession of *A. odoratissimus* (*Lumok*) [91], two accessions of *A. altilis*, and five accessions of *A. camansi*, were also included, with *A. frutescens* Renner, *A. limpatu* Miq., and *A. papuanus* Renner selected as outgroups according to Gardner et al. [85].

Table 1. Sampling information of *Artocarpus* species of Taiwan.

Code	Species	Voucher	HAST specimen ID	Locality	Coordinate
AaCCR200	<i>A. altilis</i>	C.-R. Chuang 200	145709	Pingtung, NPTU ^a	22.6650, 120.5043
AhCCR207	<i>A. heterophyllus</i>	C.-R. Chuang 207	145712	Chiayi, NCYU ^b	23.4688, 120.4859
AoMYT20	<i>A. odoratissimus</i>	M.-Y. Tsai 20	145690	Pingtung, NPUST ^c	22.6454, 120.6057
CHW72	<i>A. treculianus</i>	H.-W. Chen 72	145811	Yilan, Jiaoxi	24.8236, 121.7707
CHW75	<i>A. treculianus</i>	H.-W. Chen 75	145812	Yilan, Jiaoxi	24.8164, 121.7458
CCR089	<i>A. treculianus</i>	C.-R. Chuang 089	145784	Taipei, AS ^d	25.0399, 121.6154
CCR114	<i>A. treculianus</i>	C.-R. Chuang 114	145644	Hualien, Sioulin	24.3166, 121.7442
CCR120	<i>A. treculianus</i>	C.-R. Chuang 120	145653	Hualien, Shoufeng	23.9196, 121.5335
CCR123	<i>A. treculianus</i>	C.-R. Chuang 123	145658	Hualien, Guangfu	23.6812, 121.4166
CCR127	<i>A. treculianus</i>	C.-R. Chuang 127	145785	Hualien, Guangfu	23.6638, 121.4208
CCR129	<i>A. treculianus</i>	C.-R. Chuang 129	145786	Hualien, Rueisuei	23.4951, 121.3633
CCR131	<i>A. treculianus</i>	C.-R. Chuang 131	145787	Hualien, Yuli	23.4281, 121.3477

CCR134	<i>A. treculianus</i>	<i>C.-R. Chuang 134</i>	145788	Hualien, Fuli	23.2600, 121.2989
CCR146	<i>A. treculianus</i>	<i>C.-R. Chuang 146</i>	145789	Taitung, Taitung	22.7469, 121.0569
CCR155	<i>A. treculianus</i>	<i>C.-R. Chuang 155</i>	145790	Taitung, Beinan	22.8212, 121.1890
CCR161	<i>A. treculianus</i>	<i>C.-R. Chuang 161</i>	145791	Taitung, Chenggong	23.0014, 121.3194
CCR168	<i>A. treculianus</i>	<i>C.-R. Chuang 168</i>	145792	Taitung, Changbin	23.3541, 121.4692
CCR172	<i>A. treculianus</i>	<i>C.-R. Chuang 172</i>	145793	Taitung, Guanshan	23.0143, 121.1517
CCR174	<i>A. treculianus</i>	<i>C.-R. Chuang 174</i>	145794	Taitung, Luyeh	22.9313, 121.1455
CCR176	<i>A. treculianus</i>	<i>C.-R. Chuang 176</i>	145795	Hualien, Fengbin	23.5147, 121.5024
CCR178	<i>A. treculianus</i>	<i>C.-R. Chuang 178</i>	145796	Hualien, Shoufeng	23.7685, 121.5611
CCR179	<i>A. treculianus</i>	<i>C.-R. Chuang 179</i>	145797	Taipei, NTU ^e	25.0186, 121.5407
CCR182	<i>A. treculianus</i>	<i>C.-R. Chuang 182</i>	145798	Taipei, TPBG ^f	25.0317, 121.5091
CCR184	<i>A. treculianus</i>	<i>C.-R. Chuang 184</i>	145799	Taipei, TPBG ^f	25.0318, 121.5079
CCR195	<i>A. treculianus</i>	<i>C.-R. Chuang 195</i>	145800	Pingtung, Pingtung	22.6726, 120.5088
CCR198	<i>A. treculianus</i>	<i>C.-R. Chuang 198</i>	145801	Pingtung, Pingtung	22.6588, 120.5088
CCR202	<i>A. treculianus</i>	<i>C.-R. Chuang 202</i>	145802	Pingtung, NPTU ^a	22.6666, 120.5048
CCR203	<i>A. treculianus</i>	<i>C.-R. Chuang 203</i>	145803	Taichung, Shigang	24.2652, 120.8093
CCR205	<i>A. treculianus</i>	<i>C.-R. Chuang 205</i>	145804	Taichung, NMNS ^g	24.1586, 120.6685
CCR208	<i>A. treculianus</i>	<i>C.-R. Chuang 208</i>	145805	Chiayi, CYBG ^h	23.4833, 120.4687
CCR209	<i>A. treculianus</i>	<i>C.-R. Chuang 209</i>	145806	Chiayi, CYBG ^h	23.4833, 120.4672
CCR217	<i>A. treculianus</i>	<i>C.-R. Chuang 217</i>	145807	Taitung, Lanyu	22.0281, 121.5780
CCR218	<i>A. treculianus</i>	<i>C.-R. Chuang 218</i>	145808	Taitung, Lanyu	22.0291, 121.5767
CCR219	<i>A. treculianus</i>	<i>C.-R. Chuang 219</i>	145809	Taitung, Lanyu	22.0291, 121.5767
CCR220	<i>A. treculianus</i>	<i>C.-R. Chuang 220</i>	145810	Taitung, Lanyu	22.0061, 121.5745
AxCCR204	<i>A. xanthocarpus</i>	<i>C.-R. Chuang 204</i>	145711	Taichung, NMNS ^g	24.1590, 120.6676

^aNPTU: National Pingtung University. ^bNCYU: National Chiayi University. ^cNPUST: National Pingtung University of Science and Technology. ^dAS: Academia Sinica. ^eNTU: National Taiwan University. ^fTPBG: Taipei Botanical Garden. ^gNMNS: National Museum of Natural Science. ^hCYBG: Chiayi Botanical Garden.

DNA extraction, library preparation, and sequencing

Genomic DNA was extracted from 0.01 g silica-dried young leaves using the modified CTAB method [92], purified using NEB (Ipswich MA, USA) Monarch® PCR & DNA Cleanup Kit (5 µg), and qualified and quantified using 1% agarose gel and a Qubit™ Fluorometer 4 (Invitrogen, Life Technology, CA, USA). DNA was randomly fragmented using Bioruptor® Pico B01060010 (Diagenode, Liège, Belgium) into 300–400 bp fragments, and libraries were prepared using NEBNext® Ultra™ II DNA Library Prep Kit for Illumina® (NEB, Ipswich MA, USA). Libraries were then quantified using Qubit™ Fluorometer 4 and Fragment analyzer 5200 (Agilent, CA, USA) to ensure the average final insert sizes of 450–550 bp. Three pools of 12 libraries were enriched for 529 targeted phylogenetic markers designed for *Artocarpus*-Moraceae [89] using MYbaits v5.01 custom probes (MYcroarray, Ann Arbor, MI, USA) following manufacturer's protocol, and subsequently reamplified with 14 PCR cycles based on parameters detailed in Gardner et al. [89]. A total of 36 enriched samples of *Artocarpus* were pooled with 22 samples of

other projects into a lane and sequenced by NGS High Throughput Genomics Core at Biodiversity Research Center, Academia Sinica (BRCS) using an Illumina HiSeq 2,500 (Illumina, San Diego, CA, USA) with paired end 150 bp HiSeq Rapid mode. Raw reads for all newly sequenced samples have been deposited in GenBank (Bioproject no. PRJNA855987).

Sequence assembly and phylogenetic analysis

The sequencing quality of raw reads of 36 newly sequenced and 28 archived samples were evaluated using FastQC v0.11.5 [93] and trimmed using Trimmomatic v0.39 [94] to filter out low-quality reads under quality score 20 with 4-bp window size, discarding any reads under 50 bp. Following the procedures detailed in Gardner et al. [85], the trimmed paired-reads were assembled using HybPiper 1.3.1 [95], a pipeline that produces gene-by-gene, reference-guided assemblies for phylogenomic analyses. In brief, trimmed paired-reads were first mapped to reference genes [85] using BWA v0.7.17 [96] and those successfully mapped were assembled into contigs using SPAdes v3.13.0 [97]. Exonerate [98] was then used to align the assembled contigs to their associated target sequences that contains exons and introns. To evaluate impact of noncoding sequences on our analyses, we used HybPiper to generate both the default ‘exon’ output as well as ‘supercontig’ sequences (consisting of exons plus flanking noncoding sequences). In the ‘exon’ dataset, genes that received a ‘paralogs warning’ from HybPiper were all removed. Assembled sequences that were shorter than 100 bp or 20% of average length as well as genes possessed by less 30 samples were removed, subsequently aligned with MAFFT v7.310 [99], and then trimmed by trimAl 1.2 rev59 [100] to filter out columns containing over 75% gaps. For the ‘supercontig’ alignment, an additional pipeline Putative Paralogs Detection (PPD) was used for potential paralogs detection and removal using a default setting [101], subsequently aligned by MAFFT v7.310 [99], and then trimmed by trimAl 1.2 rev59 [100] to filtered out the column containing over 49% gaps. Gene trees were reconstructed by IQ-TREE 2.0 [102] using the parameter `-m MFP -B 1000`. The coalescent based species trees were then calculated by ASTRAL v5.7.8 using default settings [103].

Results and discussion

A total of 30,843 Mb of raw reads were acquired for the 36 newly sequenced samples, with an average of 857 Mb per sample. For the 28 archived samples, a total of ca. 6,804 Mb of raw reads were downloaded, with an average of ca. 243 Mb per sample. Statistics of the assembled quality and summaries of the exon and supercontig alignments are detailed in S1 Table. On average, 524 loci were assembled for each sample, with the final species trees including 296 loci and 524 loci in the ‘exon’ and ‘supercontig’ datasets, respectively. The exon alignment included 64 accessions and contained 357,666 characters, while the supercontig alignment included 64 accessions and contained 890,946 bp.

Artocarpus is a taxonomically challenging genus [38, 86, 88, 104]. Recent studies using target enrichment phylogenomics suggest that the morphology-based taxonomy has both under- and overestimated species diversity in *Artocarpus*. For instance, Gardner et al. [91] demonstrated that *A. odoratissimus* s.l. circumscribed in the Linnaean taxonomy for two centuries [45] actually comprises two distinct species: *Lumok* (= *A. odoratissimus* s.s.) and *Pingan* (= *A. mutabilis* Becc.) long recognized by indigenous populations

in Borneo [91]. Meanwhile, *A. multifidus* F.M.Jarrett, a species recognized by its number of leaf lobes, is genetically indistinguishable from *A. pinnatisectus* Merr. [86].

In ASTRAL trees reconstructed based on both exons and the supercontigs (Fig 3), phylogenetic relationships of all major clades are fully supported and identical to those proposed in Gardner and Zerega [86] and Gardner et al. [85]. Specifically, *Artocarpus* subg. *Prainea* is sister to the clade of Subg. *Pseudojaca* + Subg. *Artocarpus*. Within Subg. *Artocarpus*, Sect. *Cauliflori* (*sensu* Gardner and Zerega [86]) is sister to the clade of Sect. *Duricarpus* + Sect. *Artocarpus*. Within Sect. *Artocarpus*, Clade ‘*Incisifolii*’ is sister to Clade ‘*Philippinensi*’ (the ‘*Rugosi*’ clade not having been sampled for this study). Within the Clade ‘*Incisifolii*’, our sampled *A. altilis* (AaCCR200) cultivated in Taiwan is placed sister to a clade composed of two Pacific *A. altilis* samples (K7 from Somoa and V8 from French Polynesia), confirming our species identification. Together with two *A. treculianus* (NZ203 and Yang13056) sequenced by Gardner et al. [85], all of our 32 samples of the Taiwanese ‘breadfruit’ form a fully supported clade within the *A. treculianus* complex clade, which is sister to the clade containing *A. nigrescens* and *A. pinnatisectus* that are both endemic to the Philippines.

Fig. 3. Comparison between ASTRAL trees based on exon and supercontig. Taiwanese samples of *Artocarpus* are shown in colors, with samples of ‘breadfruit’ colored in blues. Node labels denote posterior probabilities that are not 1.00. CY: Chiayi; HL: Hualien; PT: Pingtung; TC: Taichung; TP: Taipei; TT: Taitung. See Table 1 for other abbreviations.

The placement of the 32 samples of the Taiwanese ‘breadfruit’ within the *Artocarpus treculianus* complex confirms our conjecture that this common plant has been misidentified since Rev. Mackay’s earliest documentation [50]. Our ASTRAL trees also confirms the identification of *A. altilis*, *A. heterophyllus*, *A. odoratissimus*, and *A. xanthocarpus* (Fig 3) in Taiwan. Specifically, within Sect. *Duricarpus*/Clade ‘*Asperifolii*’, AoMYT20 and NZ618 (*A. odoratissimus* s.s. “*Lumok*”) form a clade sister to the clade of *A. mutabilis* “*Pingan*”, indicating that the Taiwanese *A. odoratissimus* s.l. is the *Lumok* [91].

Taxonomy of the *A. treculianus* complex remains unsettled [86], as there is considerable variation in leaf shape and pubescence, as well as the length of staminate inflorescence (ranging from 1–21 cm), and in the shape of the syncarp. Nevertheless, morphology of the Taiwanese ‘breadfruit’ sampled in the current study (Fig 4) differs from the closely allied *A. blancoi* and matches *A. treculianus* as circumscribed by Gardner and Zerega [86], confirming our preliminary identification. It is important to note that our current understanding of *A. treculianus* has been based on limited herbarium collections, which often do not well represent the morphological variation, even within an individual tree. For instance, leaves of *A. treculianus* observed in Taiwan often show considerable variation during different developmental stages (Fig 4L) as well as within a single tree (Fig 4M). An even greater variation is observed in staminate inflorescences (Fig 5), which can be important in the classification of *Artocarpus* species [86].

Fig. 4. *Artocarpus treculianus* Elmer. (A) Tree. (B) Staminate inflorescences. (C) Staminate flowers, top view. (D) Staminate flowers, side view. (E). Pistillate inflorescences and stipules. (E) Pistillate flowers, top view. (G) Pistillate flowers, side view. (H) Syncarps and leaves. (I) Syncarp surface. (J) Cross-section of

syncarp. (K) Syncarps and leaves of a tree from Batan Island. (L). A branch from a mature tree (left) and a seedling (right). (M) Variation of leaf shapes. Except for (K), all other photographs were taken in Taiwan. A, B, E, H, & L taken by K.-F. Chung, C, D, F, G, I, J, & M by C.-L. Hsieh, and K by D. N. Tandang.

Fig. 5. Variation in staminate inflorescences in *Artocarpus treculianus*. These staminate inflorescences all fell from a single tree planted on the campus of Academia Sinica, Taipei (CCR089) and gathered in June 1, 2022. Taken by K.-F. Chung.

Since Jarrett’s [43] seminal taxonomic work, *Artocarpus treculianus* has been regarded as an endemic taxon of the Philippines, with its northern distributional limit in the Batanes Islands [45, 86], where this “vulnerable” species grows both around human habitations as well as “in secondary forests and edges of forests” [105]. As a popular shade tree, its fruits are also eaten and leaves of this tree (Fig 4K) are also eaten and used as plates and to wrap food during festivities [105]. Additionally, its wood is used for making *Bangka* (a type of fishing boat common in the Philippine coastal villages), *Bangka* trusses, and doors and windows of traditional houses. Moreover, its white latex is cooked and used as bird-trap [105]. All these traditional utilities are highly similar to the traditional Yami culture [29, 55, 59, 75]. The presence of *A. treculianus* in Lanyu thus is consistent with a northward transport by ancestors of speakers of the Batanic languages, providing a commensal species likely brought by the ‘into Taiwan’ Austronesian migration [14, 30]. On the other hand, the possibility that *A. treculianus* is a native species of Lanyu cannot be ruled out, given the close geographical proximity and phytogeographic similarity between Lanyu and the Philippines [87]. Indeed, Tashiro recorded the tree was native and abundant in the forests of Lanyu after his first visit to the island in 1900 A.D. [60]. Though seeds and large syncarps of *Artocarpus* (Figs. 2 and 5) are generally assumed to be dispersed by forest ungulates [45], Gardner et al. [106] proposed a 1,600 km bird-mediated dispersal across Wallacea for the origin of *A. buyangensis* E.M.Gardner, Jimbo & Zerega, a recently described species endemic to Manus Island, Papua New Guinea. Given this, a seed of *A. treculianus* carried by a bird or possibly a flying fox (*Pteropus* sp.) flying across the 185 km-wide Bashi Channel (Fig 1) separating Lanyu and the Batanes Island is highly plausible. To test these alternative scenarios, further sampling in the Batanes Islands and from throughout the Philippines is essential.

Despite limited sampling, our ASTRAL trees reveal a marked geographic structure. Considering just the samples collected from traditional territories of Amis and Yami (bold-faced in Fig 3), the Amis samples form a fully supported clade (i.e., *Pacilo* clade) deriving from a paraphyletic grade consisting of the Lanyu samples (i.e., *Cipoho* grade), suggesting that the Amis samples originated from Lanyu. This inference is consistent with the Amis tale that their ancestors came from the overseas island Vutul (i.e., Botel Tobago) or Sanasai (i.e., Lyudao, an island. 73 km north of Lanyu; Fig 1) [107]. On the contrary, the lack of structure within the *Pacilo* clade suggests that this popular fruit crop of the Amis people may have been extensively translocated across eastern Taiwan. Additionally, within the *Pacilo* clade, the generally poor support values and highly discordant and entangled relationships between the exon and supercontig trees indicate the reticulated nature of tokogenetic relationships. Nevertheless, based on the ASTRAL trees (Fig 3), it is evident that *A. treculianus* cultivated in CYBG (CCR208 and 209), NMNS (CCR205), and NTU (CCR179) originated from Lanyu, while trees planted in AS (CCR089), TPBG (CCR182 and 184), NPTU (CCR202),

and other localities (CCR195, 198, and 203, and CHW72 and 75) were derived from eastern Taiwan (Fig 1), indicating multiple introductions of the ‘breadfruit’ to various parts of the island. Additionally, the placement of NZ203, a sample cultivated at the Fort de Russey Park in Honolulu, suggest a possible Lanyu origin. Our data thus demonstrate that the *Artocarpus*-Moraceae probe set [89] is efficient in detecting phylogeographic structure even on a small geographic scale, providing a genomic tool for unraveling the origin of *A. treculianus* with a more comprehensive sampling.

The correction of a persistent misidentification of the Taiwanese ‘breadfruit’ also underscores the possibility that the taxonomy of many common species might still be problematic. Unlike rare species, common plants may be less attractive for taxonomic research because their taxonomy is usually just assumed to be well-studied. On the other hand, because common species are often easily accessible, they are often used for applied research. For instance, a quick ‘Google Scholar’ search with the key words ‘breadfruit’ and ‘Taiwan’ resulted in more than 30 research articles of natural compound and pharmaceutical studies of either ‘*Artocarpus altilis*’ or ‘*A. communis*’, which were all mis-identifications of *A. treculianus* (S1 Appendix). This has major impacts on downstream use of such data! Although *A. treculianus* and *A. altilis* are both members of Sect. *Artocarpus*, the crown age of the diversification of the two species was estimated at ca. 25 million years ago in the Oligocene [108]. The long time elapsed since the split of their most recent common ancestor surely would have resulted in numerous evolutionary changes including the properties of chemical compounds. If readers of those research articles are not aware of this species mis-identification, the scientific values of these studies would be greatly undermined [109].

Conclusions

Our phylogenomic analysis (Fig 3) based on 529 nuclear genes enriched using the *Artocarpus*-Moraceae probes [89] confirms that the correct name for the Taiwanese ‘breadfruit’ is *Artocarpus treculianus* Elmer (Fig 3) according to the most updated taxonomic revision [86], while the true breadfruit, *A. altilis*, is extremely rare in Taiwan (Fig 2). Since *A. treculianus* is thought to be endemic to the Philippines, our study suggests that the species was likely transported from the Philippines to Lanyu in prehistorical time, providing a candidate study system to test the northward Austronesian migration into Taiwan using a commensal approach. Our study also indicates that *Pacilo* of eastern Taiwan originated from Lanyu, while both *Pacilo* and *Cipoho* were sources of modern introductions of *A. treculianus* to other parts of Taiwan.

Taxonomic treatment

Artocarpus treculianus Elmer, Leaf. Philipp. Bot. 2: 617 (1909); Merrill, Enum. Philipp. Fl. Pl. 2: 43 (1923); Jarrett, J. Arnold Arbor. 40(3): 302 (1959), *pro parte*, excl. *syn. Artocarpus nigrescens* Elmer; Gardner & Zerega, Gard. Bull. Singapore 73(2): 348 (2021). Type:—Philippine, Negros Oriental, Dumagueta, Cuenos Mountains, June 1908, *Elmer 10406* (lectotype BM, designated by Jarrett [43]; isotypes A, BO, L). Figs 5 & 6

Artocarpus ovatifolius Merr., Philipp. J. Sci. C 9: 268 (1914). Type:—Philippines, Luzon, San Antonio, June

- 34 1912, *Ramos BS 15040* (lectotype BM, designated by Jarrett [43]; isolectotypes B, US).
- 35 *Artocarpus ovatifolius* var. *dolichostachys* Merr., Enum. Philip. Pl. 2: 43 (1923). Type:—Philippines, Samar,
- 36 Apri 1914, *Ramos 1603* (lectotype BM, designated by Jarrett [43]; isolectotypes BO, GH, L, NY, P, SING).
- 37 *Artocarpus altilis* auct. non (Parkinson) Fosberg; Liu, Ill. Nat. Intr. Lign. Pl. Taiwan 2: 704 (1962);
- 38 Hatusima, Mem Fac. Agric. Kagoshima Univ. 5(3): 24 (1966); Liu & Liao, Fl. Taiwan 2: 118, *pl.* 233
- 39 (1976).
- 40 *Artocarpus communis* auct. non J.R.Forst. & G.Forst.: Merrill, Philipp. J. Sci., Bot. 3 (1908) 401; Sasaki,
- 41 List. Pl. Formosa 151 (1928); Kudo, Iconography of Tropical Plants in Formosa 1: 6, *pl.* 6 (1934); Yang,
- 42 Manual of Fruit Trees in Taiwan 101, *fig.* 63 (1951); Lin, Manual of Taiwan Vascular Plants 2: 46 (1999);
- 43 Cheng & Lu, Botel Tabaco, Yami & Plants 48 (2000); Chung, Illustrated Flora of Taiwan 4: 298 (2017).
- 44 *Artocarpus incisus* auct. non (Thunb.) L.f.: Mackay, From Far Formosa 63 (1896); Kawakami, List Pl.
- 45 Formosa. 103 (1910); Hayata, J. Coll. Sci. Imp. Univ. Tokyo 30: 278 (1911); Sasaki, J. Nat. Hist. Soc.
- 46 Taiwan 3(9): 35 (1913); Chang, J. Phytogeogr. Taxon. 29(1): 2 (1981); Yamazaki, J. Phytogeogr. Taxon.
- 47 30(2): 72 (1982); Liao, Quart. J. Exp. For. Natl. Taiwan Univ. 3(1): 146 (1989); Liao, Fl. Taiwan 2nd 2: 137,
- 48 *pl.* 66 (1996).
- 49 *Artocarpus integrifolia* auct. non L.f.: Tashiro, A guide to planting trees in urban Taiwan 238 (1900);
- 50 Matsumura & Hayata, J. Coll. Sci. Imp. Univ. Tokyo 22: 381 (1906).
- 51 *Artocarpus lanceolata* auct. non Trécul; Li, Woody Flora of Taiwan 115, *fig.* 40 (1963).

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- 64 **Funding Acquisition:** K-FC
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- 67 **Visualization:** C-RC, C-LH, DNT, K-FC
- 68 **Writing – Original Draft Preparation:** K-FC

Writing – Review & Editing: C-RC, C-LH, C-SC, C-MW, DNT, EMG, LA, NJCZ, K-FC

References

1. Blust R. The Austronesian homeland and dispersal. *Annu Rev Linguist.* 2019; 5:417–34. doi: 10.1146/annurev-linguistics-011718-012440.
2. Gray RD, Drummond AJ, Greenhill SJ. Language phylogenies reveal expansion pulses and pauses in Pacific settlement. *Science.* 2009; 323(5913):479–83. doi: 10.1126/science.1166858.
3. Bellwood P. *First islanders: Prehistory and human migration in Island Southeast Asia.* Oxford: John Wiley & Sons, Inc.; 2017.
4. Hung H-C. History and current debates of archaeology in Island Southeast Asia. In: Smith C, editor. *Encyclopedia of Global Archaeology.* Cham: Springer; 2019. p. 1–22.
5. McColl H, Racimo F, Vinner L, Demeter F, Gakuhari T, Moreno-Mayar JV, et al. The prehistoric peopling of Southeast Asia. *Science.* 2018; 361(6397):88–91. doi: 10.1126/science.aat3628.
6. Chang C-S, Liu H-L, Moncada X, Seelenfreund A, Seelenfreund D, Chung K-F. A holistic picture of Austronesian migrations revealed by phylogeography of Pacific paper mulberry. *Proc Natl Acad Sci USA.* 2015; 112(44):13537–42. doi: 10.1073/pnas.1503205112.
7. Peñailillo J, Olivares G, Moncada X, Payacán C, Chang C-S, Chung K-F, et al. Sex distribution of paper mulberry (*Broussonetia papyrifera*) in the Pacific. *PLoS ONE.* 2016; 11(8):e0161148. doi: 10.1371/journal.pone.0161148.
8. Carson MT, Hung H-C. Learning from Paleo-Landscapes: Defining the land-use systems of the ancient Malayo-Polynesian homeland. *Curr Anthropol.* 2018; 59(6):790–813. doi: 10.1086/700757.
9. Deng Z, Kuo S-C, Carson MT, Hung H-c. Early Austronesians cultivated rice and millet together: Tracing Taiwan’s first Neolithic crops. *Front Plant Sci.* 2022; 13:e962073. doi: 10.3389/fpls.2022.962073.
10. Bellwood P. The expansion of farmers into Island Southeast Asia. In: Higham CFW, Kim NC, editors. *The Oxford Handbook of Early Southeast Asia.* Oxford: Oxford University Press; 2022. p. 376–82.
11. Ross M. The Batanic languages in relation to the early history of the Malayo-Polynesian subgroup of Austronesian. *J Austron Stud.* 2005; 1(2):1–23.
12. Yu G-H. Ancient Batanese culture and Yami culture. *J East Taiwan Stud.* 2001; 5:15–45. doi: 10.6275/JETS.6.15-45.2001.
13. Chen Y-M. Cultural contact and material culture change: an ethnoarchaeological example from the Yami, Orchid Island, Taiwan. *Bull Inst Hist Philol Acad Sinica.* 1996; 67(2):415–44.
14. Li PJ-K. Some plant names in Formosan Languages. In: Pawley AK, Ross MD, editors. *Austronesian Terminologies: Continuity and Change.* Pacific Linguistics, C-127. Canberra: The Australia National University; 1994. p. 241–66.
15. Hung H-C, Iizuka Y, Bellwood P, Nguyen KD, Bellina B, Silapanth P, et al. Ancient jades map 3,000 years of prehistoric exchange in Southeast Asia. *Proc Natl Acad Sci USA.* 2007; 104(50):19745–50. doi: 10.1073/pnas.0707304104.
16. Alam O, Gutaker RM, Wu C-C, Hicks KA, Bocinsky K, Castillo CC, et al. Genome analysis traces regional dispersal of rice in Taiwan and Southeast Asia. *Mol Biol Evol.* 2021; 38(11):4832–46. doi:

10.1093/molbev/msab209.

17. Hung H-c, Nguyen KD, Bellwood P, Carson MT. Coastal connectivity: long-term trading networks across the South China Sea. *J Isl Coast Archaeol.* 2013; 8(3):384–404. doi: 10.1080/15564894.2013.781085.
18. Tsang C-H. On the origin of the Yami people of Lanyu as viewed from archaeological data. *J Austron Stud.* 2005; 1(1):135–51.
19. Loo J-H, Trejaut JA, Yen J-C, Chen Z-S, Lee C-L, Lin M. Genetic affinities between the Yami tribe people of Orchid Island and the Philippine Islanders of the Batanes archipelago. *BMC Genet.* 2011; 12:e21. doi: 10.1186/1471-2156-12-21.
20. Bellwood P, Dizon E. The Batanes Islands, their first observers, and previous archaeology. In: Bellwood P, Dizon E, editors. 4000 years of migration and cultural exchange: the archaeology of the Batanes Islands, Northern Philippines. Canberra: ANU E Press; 2013. p. 1–8.
21. Sanchez-Mazas A, Blench R, Ross M, Peiros I, Lin M, editors. *Past Human Migrations in East Asia.* London & New York: Routledge; 2007.
22. Bellwood P. Asian farming diasporas? Agriculture, languages, and genes in China and Southeast Asia. In: Stark MT, editor. *Archaeology of Asia.* Malden: Blackwell Publishing Ltd; 2006. p. 96–118.
23. Diamond JM, Bellwood PS. Farmers and their languages: The first expansions. *Science.* 2003; 300(5619):597–603. doi: 10.1126/science.1078208.
24. Kirch PV. Peopling of the Pacific: a holistic anthropological perspective. *Annu Rev Anthropol.* 2010; 39(1):131–48. doi: 10.1146/annurev.anthro.012809.104936.
25. Matisoo-Smith E. The commensal model for human settlement of the Pacific 10 years on—What can we say and where to now? *J Isl Coast Archaeol.* 2009; 4:151–63. doi: 10.1080/15564890903155273.
26. Storey AA, Clarke AC, Ladefoged T, Robins J, Matisoo-Smith E. DNA and Pacific commensal models: applications, construction, limitations, and future prospects. *J Isl Coast Archaeol.* 2013; 8(1):37–65. doi: 10.1080/15564894.2012.761299.
27. Zerega NJC, Ragone D, Motley TJ. Complex origins of breadfruit (*Artocarpus altilis*, Moraceae): implications for human migrations in Oceania. *Am J Bot.* 2004; 91(5):760–6. doi: 10.3732/ajb.91.5.760.
28. Matisoo-Smith E, Robins JH. Origins and dispersals of Pacific peoples: Evidence from mtDNA phylogenies of the Pacific rat. *Proc Natl Acad Sci USA.* 2004; 101(24):9167–72. doi: 10.1073/pnas.0403120101.
29. Wang H-H, Cheng H-W, Pan F-J. Plants utilization of Yami in Orchid Island. *J Natl Park.* 2000; 10(2):228–48.
30. Kano T. Some cultivated plants of the Formosan aborigines, and their relation of the ethnic history of Formosa. *J Anthropol Soc Nippon.* 1941; 56(10):522–8. doi: 10.1537/ase1911.56.522.
31. Ragone D. Breadfruit, *Artocarpus altilis* (Parkinson) Fosberg. Rome, Italy: IPGRI; 1997.
32. Ragone D. *Artocarpus altilis* (breadfruit). In: Elevitch CR, editor. *Traditional Trees of Pacific Islands: Their Culture, Environment, and Use.* Holualoa, Hawai'i: Permanent Agriculture Resources (PAR); 2006. p. 85–100.

33. McCoy MD, Graves MW, Murakami G. Introduction of Breadfruit (*Artocarpus altilis*) to the Hawaiian Islands. *Econ Bot.* 2010; 64(4):374–81. doi: 10.1007/s12231-010-9140-1.
34. Zerega N, Wiesner-Hanks T, Ragone D, Irish B, Scheffler B, Simpson S, et al. Diversity in the breadfruit complex (*Artocarpus*, Moraceae): genetic characterization of critical germplasm. *Tree Genet Genomes.* 2015; 11(1):e4. doi: 10.1007/s11295-014-0824-z.
35. Jones AMP, Murch SJ, Ragone D. Diversity of breadfruit (*Artocarpus altilis*, Moraceae) seasonality: A resource for year-round nutrition. *Econ Bot.* 2010; 64(4):340–51. doi: 10.1007/s12231-010-9134-z.
36. Turi CE, Liu Y, Ragone D, Murch SJ. Breadfruit (*Artocarpus altilis* and hybrids): A traditional crop with the potential to prevent hunger and mitigate diabetes in Oceania. *Trends Food Sci Tech.* 2015; 45(2):264–72. doi: 10.1016/j.tifs.2015.07.014.
37. Jones AMP, Ragone D, Tavana NuG, Bernotas DW, Murch SJ. Beyond the Bounty: Breadfruit (*Artocarpus altilis*) for food security and novel foods in the 21st Century. *Ethnobot Res Appl.* 2011; 9:129–49.
38. Zerega NJC, Ragone D, Motley TJ. Systematics and species limits of breadfruit (*Artocarpus*, Moraceae). *Syst Bot.* 2005; 30(3):603–15. doi: 10.1600/0363644054782134.
39. Ferrer-Gallego PP, Boisset F. The naming and typification of the breadfruit, *Artocarpus altilis*, and breadnut, *A. camansi* (Moraceae). *Willdenowia.* 2018; 48(1):125–35. doi: 10.3372/wi.48.48109.
40. St. John H. Report on the flora of Pingelap Atoll, Caroline Islands, Micronesia, and observations on the vocabulary of the native inhabitants: Pacific plant studies. *Pacific Sci.* 1948; 2(2):97–113.
41. Merrill ED. The botany of Cook's voyages and its unexpected significance in relation to anthropology, biogeography and history. *Chron Bot.* 1954; 14(5/6):161–384.
42. Fosberg FR. Names in *Amaranthus*, *Artocarpus*, and *Inocarpus*. *J Wash Acad Sci.* 1941; 31(3):93–6.
43. Jarrett FM. Studies in *Artocarpus* and allied genera, III. A revision of *Artocarpus* subgenus *Artocarpus*. *J Arnold Arbor.* 1959; 40(3):113–55, 298–326.
44. Corner EJH. Notes on the systematy and distribution of Malayan phanerogams III. *Gard Bull Singap.* 1939; 10:239–329.
45. Berg CC, Corner EJH, Jarrett FM. Moraceae, genera other than *Ficus*. In: Nooteboom HP, editor. *Flora Malesiana, Series I Vol 17 / Part 1*. Leiden: National Herbarium Nederland; 2006. p. 1–152.
46. Liao J-C. Moraceae. In: Editorial Committee of the Flora of Taiwan, editor. *Flora of Taiwan*, vol 2, 2nd edn. Taipei, Taiwan: Department of Botany, National Taiwan University; 1996. p. 136–95.
47. Mackay GL. The Diary of George Leslie Mackay, 1871–1901. Taipei: Institute of Taiwan History, Academia Sinica; 2015.
48. Rychetská M. Thirty years of mission in Taiwan: The case of Presbyterian missionary George Leslie Mackay. *Religions.* 2021; 12(3):e190. doi: 10.3390/rel12030190.
49. Kang P. A preliminary inquiry on the settlement and population of the Nan-shih Amis: from the seventeenth century to the nineteenth century. *Taiwan Historical Research.* 1999; 4(1):5–48.
50. Mackay GL. From Far Formosa: The Islands, its People and Mission. MacDonald JA, editor. New York, Chicago and Toronto: Fleming H. Revell Company; 1896.
51. Aits Butal, Tung G-S. Pangcah Miaraw—The Ethnobotany of Amis in Eastern Formosa. Taipei:

- Forestry Bureau, Council of Agriculture, Executive Yuan & Taiwan Environmental Information Association; 2009.
52. Yang C-F. Manual of Fruit Trees in Taiwan. Chiayi: Chiayi Experiment Station, Taiwan Agricultural Research Institute; 1951.
53. Wang H-H, Chang L-W, Kao R-C. Forest management of aborigines Tao in Lanyu (Botel Tabaco) and its effects to forest structure and species composition. J Natl Park. 2003; 13(1):75–94.
54. Yu G-H. The socio-cultural significance of Yami food classification. Bull Inst Ethnol Acad Sinica. 1993; 76:21–42.
55. Cheng H-W. The ethnic plant of Yami. J East Taiwan Stud. 1996; 1:67–104. doi: 10.6275/JETS.1.67-104.1996.
56. Cheng H-W, Wang K-C, Liao S-H, Sh N-P. The structure and woody material of the Yam's planked boats on Botel Tobago. J East Taiwan Stud. 2002; 7:3–44. doi: 10.6275/JETS.7.3-44.2002.
57. Jeng H-I. The Yami boat culture. Bull Inst Ethnol Acad Sinica. 1984; 57:95–155.
58. Kano T. The building of plank-boat and the festival thereof among the Yami People of Botel Tobago. J Anthropol Soc Nippon. 1938; 53(4):1–22. doi: 10.1537/ase1911.53.125.
59. Tung G-S, Aits Butal, Chang T-P. Pongso Inawan—The Ethnobotany of Tao on Orchid Island. Taipei: Forestry Bureau, Council of Agriculture, Executive Yuan & Taiwan Environmental Information Association; 2013.
60. Tashiro Y. A guide to planting trees in urban Taiwan. Taihoku: Bureau of Productive Industry, Government of Formosa; 1900. (In Japanese, title translated by K-FC)
61. Sasaki S. Important plants of Botel Tobago. J Nat Hist Soc Taiwan. 1913; 3(9):35–43. (In Japanese, title translated by K-FC)
62. Henry A. A list of plants from Formosa. Trans Asiat Soc Japan. 1896; 24 Supplement:1–118.
63. Open Museum.
https://openmuseum.tw/muse/digi_object/d2006042b74a1411ae4a536e508883f2#104311 2022.
64. Tashiro Y. A guide to street trees and planting trees in urban Taiwan. Taihoku: Bureau of Forest Management, Government of Formosa; 1920. (In Japanese, title translated by K-FC)
65. Su M-C. Diversity investigation and analysis of woody plants in junior high school campus of Pingtung City. Quart J For Res Taiwan. 2001; 23(2):47–62.
66. Liu S-F, Yang C-K. Investigation and analysis of woody plants in Tai-Ping City School campus of Taichung County. J Exp For Nat Taiwan Univ. 2007; 21(3):259–74.
67. Yang C-K, Wang Y-N, Huang Y-R, Chen Y-F. Diversity investigation and analysis of woody plants in elementary school campus of Chu-Shan Township, Nantou County. J Exp For Nat Taiwan Univ. 2008; 22(4):241–60.
68. Chen C-C, Huang Y-L, Ou J-C, Lin C-F, Pan T-M. Thre new prenylflavones from *Artocarpus altilis*. J Nat Prod. 1993; 56(9):1594–7. doi: 10.1021/np50099a021.
69. Lan W-C, Tzeng C-W, Lin C-C, Yen F-L, Ko H-H. Prenylated flavonoids from *Artocarpus altilis*: Antioxidant activities and inhibitory effects on melanin production. Phytochemistry. 2013; 89:78–88. doi: 10.1016/j.phytochem.2013.01.011.
70. Lee CW, Hsu LF, Lee MH, Lee IT, Liu JF, Chiang YC, et al. Extracts of *Artocarpus communis*

- induce mitochondria-associated apoptosis via pro-oxidative activity in human glioblastoma cells. Front Pharmacol. 2018; 9:e411. doi: 10.3389/fphar.2018.00411.
71. Matsumura J, Hayata B. Enumeratio plantarum in insula Formosa sponte crescentium hucusque rite cognitarum adjectis descriptionibus et figuris specierum pro regione novarum. J Coll Sci Imp Univ Tokyo. 1906; 22:1–702.
72. Li H-L. Woody Flora of Taiwan. Narberth, Pennsylvania: Livingston Publishing Company; 1963.
73. Liu T-S. Illustrations of Native and Introduced Ligneous Plants of Taiwan, Vol. 2. Taipei: College of Agriculture, National Taiwan University; 1962.
74. Liu T-S, Liao J-C. Moraceae. In: Li H-L, Liu T-S, Huang T-C, Koyama T, DeVol CE, editors. Flora of Taiwan, Vol 2. Taipei, Taiwan: Epoch Publishing Co.; 1976. p. 117–61.
75. Cheng H-W, Lu S-Y. Botel Tabaco, Yami & Plants. Taipei: Lamper Enterprises Co., Ltd.; 2000.
76. Chung S-W. Illustrated Flora of Taiwan, Vol. 4. Taipei: Owl Publishing House Co., Ltd.; 2017.
77. Sasaki S. List of Plants of Formosa. Taihoku: Natural History Society of Formosa; 1928.
78. Yang Y-P, Liu H-Y, Lu S-Y, editors. Manual of Taiwan Vascular Plants, vol. 2. II. Spermatophyta. Taipei: The Council of Agriculture, The Executive Yuan; 1997.
79. Lin C-C. Moraceae. In: Yang Y-P, Liu H-Y, Lu S-Y, editors. Manual of Taiwan Vascular Plants, Vol 2. Taipei: The Council of Agriculture, The Executive Yuan; 1999. p. 46–57.
80. Kudô Y. Iconography of Tropical Plants in Taiwan, Vol. 1. Tokyo: Meibundo & Co.; 1934.
81. Liao J-C. A taxonomic revision of the family Moraceae in Taiwan (1) Genera *Artocarpus*, *Broussonetia* and *Fatoua*. Quart J Exp For Natl Taiwan Univ. 1989; 3(1):145–51.
82. Yang C-K, Jung M-C. An ethnobotanical Memory of Taiwan. Taichung: Morning Star Publishing Inc.; 2012.
83. Kawakami T. A List of Plants of Formosa. Taihoku: Bureau of Productive Industry, Government of Formosa; 1910.
84. Editorial Committee of the Red List of Taiwan Plants. The Red List of Vascular Plants of Taiwan, 2017: Endemic Species Research Institute, Forestry Bureau, Council of Agriculture, Executive Yuan and Taiwan Society of Plant Systematics; 2017.
85. Gardner EM, Johnson MG, Pereira JT, Puad ASA, Arifiani D, Sahrmi, et al. Paralogs and off-target sequences improve phylogenetic resolution in a densely sampled study of the breadfruit genus (*Artocarpus*, Moraceae). Syst Biol. 2021; 70(3):558–75. doi: 10.1093/sysbio/syaa073.
86. Gardner EM, Zerega NJC. Taxonomic updates to *Artocarpus* subgenus *Artocarpus* (Moraceae) and allied taxa with a particular focus on the species native to Singapore. Gard Bull Singap. 2021; 73(2):309–74. doi: 10.26492/gbs73(2).2021-08.
87. Chang C-E. The phytogeographic position of Botel Tobago based on the woody plants. J Phytogeogr Taxon. 1986; 34(1):1–8. doi: 10.24517/00056105.
88. Zerega NJC, Supardi MNN, Motley TJ. Phylogeny and recircumscription of Artocarpeae (Moraceae) with a focus on *Artocarpus*. Syst Bot. 2010; 35(4):766–82. doi: 10.1600/036364410x539853.
89. Gardner EM, Johnson MG, Ragone D, Wickett NJ, Zerega NJC. Low-Coverage, whole-genome sequencing of *Artocarpus camansi* (Moraceae) for phylogenetic marker development and gene discovery. Appl Plant Sci. 2016; 4(7):e1600017. doi: 10.3732/apps.1600017.

90. Thiers BM. Index Herbariorum: New York Botanical Garden's Virtual Herbarium; Updated continuously. Available from: <http://sweetgum.nybg.org/science/ih/> (accessed 02.05.2022).
91. Gardner EM, Ahmad Puad AS, Pereira JT, Tagi Ja, Nyegang Sa, Miun P, et al. Engagement with indigenous people preserves local knowledge and biodiversity alike. *Curr Biol*. 2022; 32(11):R511–2. doi: 10.1016/j.cub.2022.04.062.
92. Doyle JJ, Doyle JL. A rapid DNA isolation procedure for small quantities of fresh leaf tissue. *Phytochem Bull*. 1987; 19(1):11–5.
93. de Sena Brandine G, Smith AD. Falco: high-speed FastQC emulation for quality control of sequencing data. *F1000Res*. 2019; 8:e1874. doi: 10.12688/f1000research.21142.2.
94. Bolger AM, Lohse M, Usadel B. Trimmomatic: a flexible trimmer for Illumina sequence data. *Bioinformatics*. 2014; 30(15):2114–20. doi: 10.1093/bioinformatics/btu170.
95. Johnson MG, Gardner EM, Liu Y, Medina R, Goffinet B, Shaw AJ, et al. HybPiper: Extracting coding sequence and introns for phylogenetics from high-throughput sequencing reads using target enrichment. *Appl Plant Sci*. 2016; 4(7):e1600016. doi: 10.3732/apps.1600016.
96. Li H, Durbin R. Fast and accurate short read alignment with Burrows-Wheeler transform. *Bioinformatics*. 2009; 25(14):1754–60. doi: 10.1093/bioinformatics/btp324.
97. Bankevich A, Nurk S, Antipov D, Gurevich AA, Dvorkin M, Kulikov AS, et al. SPAdes: a new genome assembly algorithm and its applications to single-cell sequencing. *J Comput Biol*. 2012; 19(5):455–77. doi: 10.1089/cmb.2012.0021.
98. Slater GS, Birney E. Automated generation of heuristics for biological sequence comparison. *BMC Bioinformatics*. 2005; 6:e31. doi: 10.1186/1471-2105-6-31.
99. Katoh K, Standley DM. MAFFT Multiple Sequence Alignment Software Version 7: Improvements in performance and usability. *Mol Biol Evol*. 2013; 30(4):772–80. doi: 10.1093/molbev/mst010.
100. Capella-Gutiérrez S, Silla-Martínez JM, Gabaldón T. trimAl: a tool for automated alignment trimming in large-scale phylogenetic analyses. *Bioinformatics*. 2009; 25(15):1972–3. doi: 10.1093/bioinformatics/btp348.
101. Zhou W-B, Soghigian J, Xiang Q-YJ. A new pipeline for removing paralogs in target enrichment data. *Syst Biol*. 2022; 71(2):410–25. doi: 10.1093/sysbio/syab044.
102. Nguyen LT, Schmidt HA, von Haeseler A, Minh BQ. IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Mol Biol Evol*. 2015; 32(1):268–74. doi: 10.1093/molbev/msu300.
103. Zhang C, Rabiee M, Sayyari E, Mirarab S. ASTRAL-III: polynomial time species tree reconstruction from partially resolved gene trees. *BMC Bioinformatics*. 2018; 19:e153. doi: 10.1186/s12859-018-2129-y.
104. Aneklaphakij C, Bunsupa S, Sirichamorn Y, Bongcheewin B, Satitpatipan V. Taxonomic notes on the 'Mahat' (*Artocarpus lacucha* and *A. thailandicus*, Moraceae) species complex in Thailand. *Plants*. 2020; 9(3):e391. doi: 10.3390/plants9030391.
105. Madulid DA, Agoo EMG. A pictorial guide to the noteworthy plants of Batanes Isladns. Manila: UNESCO National Commission of the Philippines, Science and Technology and National Museum of the Philippines; 2006.

106. Gardner EM, Jimbo T, Zerega NJC. *Artocarpus buyangensis* (Moraceae), a new species from Papua New Guinea. Syst Bot. 2022; 47(2):452–6. doi: 10.1600/036364422X16512564801542.
107. Mabuchi T. Tales concerning the origin of grains in the insular areas of Eastern and Southeastern Asia. Asian Folklore Studies. 1964; 23(1):1–92.
108. Williams EW, Gardner EM, Harris R, Chaveerach A, Pereira JT, Zerega NJC. Out of Borneo: biogeography, phylogeny and divergence date estimates of *Artocarpus* (Moraceae). Ann Bot-London. 2017; 119(4):611–27. doi: 10.1093/aob/mcw249.
109. Kholia BS, Fraser-Jenkins CR. Misidentification makes scientific publications worthless—save our taxonomy and taxonomists. Curr Sci. 2011; 100(4):458–61.

58 **Supporting information**

59 **S1 Table. Summary statistics of assembly quality of the 64 samples used in this study.**

70 **S1 Appendix. List of literature of the Taiwanese ‘breadfruit’ and the misused scientific names.**

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