JOURNAL OF
Pacific
Archaeology

– ARTICLE –

Microfossil starch provides the first evidence for introduced taro (*Colocasia esculenta*) on the Marshall Islands, Micronesia, commencing c. 1800 cal. BP

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Abstract

Introduced taro (*Colocasia esculenta*) is assumed to have been ubiquitous in pre-contact societies across Oceania. However, there are few reports of direct, botanical evidence for its presence in Micronesia during this time. Here we report starch analysis of soil/sediment samples from Ebon Atoll in the Marshall Islands, eastern Micronesia. Starch grains, xylem cells, and calcium oxalate crystals of cf. taro were found at three sites, in habitation layers encompassing the period 1875-1715 cal. BP to 1060-920 cal. BP (95% CI). This study represents the first direct, botanical evidence for pre-European taro in the Marshall Islands, adding another archipelago to the scant list of such Micronesian sites, thus highlighting the importance of palaeoethnobotany in Micronesia.

***Keywords*:** domesticated plants; cultivars; Araceae; taro; *Colocasia esculenta*; atolls

To cite this article:
Horrocks, M., Weisler, M.I., & Hua, Q. 2025. Microfossil starch provides the first evidence for introduced taro (Colocasia esculenta) on the Marshall Islands, Micronesia, commencing c. 1800 cal. BP. Journal of Pacific Archaeology, 15(1): Article 2:1-22. DOI: https://doi.org/10.70460/jpa.v15i1.362

Submitted: 29/09/2024, Accepted 10/12/2024, First online 09/04/2025

The Journal of Pacific Archaeology is a peer-reviewed open access journal published by the New Zealand Archaeological Association

1. Introduction

Remote Oceania, comprising all Pacific Islands in Micronesia, Polynesia, and Melanesia east of the main Solomon Islands, was the last habitable area of the planet colonised by humans. Settlement commenced c. 3000 cal. BP with Lapita people arriving from the northwest, first appearing in the Reef and Santa Cruz Islands, and followed by rapid colonisation as far east as Tonga and Samoa by 2800 cal. BP (Bedford 2023; Burley et al. 2012; Summerhayes 2010). A lengthy pause was followed by a final eastward expansion commencing around 1000 cal. BP and finishing in New Zealand around 700 cal. BP (Barber and Benham 2024; Bunbury et al. 2022; Walter et al. 2010).

As people colonised these eastern islands, they carried a few domesticated and commensal animal species (dogs, pigs, chickens, and rats) (Collins et al. 2024) and a great diversity (70+) of domesticated plant species (Whistler 2009). Plant numbers reduced, mostly with island remoteness, and in the case of New Zealand, also a cooler, temperate climate. For example, at the time of European contact in the late 1700s, Fijians were cultivating at least 35 introduced species, Hawaiians 22-26, Easter Island Rapa Nui 10, and New Zealand Māori only six (Horrocks et al. 2017; Whistler 2009).

Of these introduced plants, taro (*Colocasia esculenta*), is one of the few ubiquitous species (Whistler 2009). This stemless perennial herb grows to 1 m or more in height and arises from a large, starch-rich corm. It continues to be cultivated throughout the Pacific Island region mostly vegetatively as a starch crop, with the leaves also eaten. All parts require cooking to destroy the noxious calcium oxalate crystals (needle-like raphides and composite druses) commonly highly concentrated in tissues of the Araceae (aroids) (Sunell and Healey 1979).

Based on this ubiquity, plus the large number of cultivars and its place in island mythologies, taro was probably one of the earliest introductions (Whistler 2009). It is cultivated from sea-level to 800+ m, in either wetland or dryland contexts, although the latter ideally requires sufficient rainfall or irrigation. Its natural habitat, or where it grows best, is shallow running water, but it is grown successfully on many atolls in excavated humus-filled pits (Burley et al. 2020; Chazine 2008; Weisler 1999) (Figure 1).

Despite this ubiquity of cultivation, direct, botanical evidence of pre-contact taro in Remote Oceania has, until relatively recently, relied on pollen studies. Yet, despite such studies on numerous archipelagos, few have identified taro pollen. These latter include the Society Islands (Parkes 1997), Hawaiian Islands (Athens and Ward 1997), Austral Islands (Prebble et al. 2019), and New Zealand (Handley et al. 2020; Horrocks, Brown, et al. 2022; Prebble et al. 2019). To our knowledge, only one Micronesian pollen study, centred on the high volcanic island of Kosrae, have reported taro pollen (*Colocasia esculenta* and *Cyrtosperma* sp.; Athens 1996: 843). This paucity is not surprising as taro is entomophilous and therefore produces little pollen, has particularly poor pollen preservation, and the pollen is prone to damage during the acetolysis process, therefore is rarely recovered (Nusaifa Beevi 2009).

In the last couple of decades, analysis of starch grains and associated material such as calcium oxalate crystals and xylem cells (tracheary tissue) from archaeological soils/sediments have provided another line

Figure 1: Taro (Colocasia esculenta) in centre foreground in a cultivation pit containing mostly the much taller giant swamp taro (Cyrtosperma merkusii) at archaeological site MLEb-1, Ebon Atoll, Marshall Islands (Photo, M. Weisler, 2012.)

of botanical evidence for taro (and several other starch rich crops) in Remote Oceania. Species' starch material can differ in morphology, with identification more secure in regions such as remote Oceania which are without close native relatives of many of the introduced species, including taro, for almost all the archipelagos. Pre-contact starch evidence for taro has been identified at numerous archipelagos in Remote Melanesia and Polynesia, namely Vanuatu, New Caledonia, Fiji, Tonga, the Society Islands, the Marquesas Islands, the Pitcairn Group, Easter Island, and New Zealand (e.g., Barber and Benham 2024; Burley et al. 2020; Flexner et al. 2024; Horrocks, Dodd et al. 2024; Horrocks et al. 2008, 2012, 2023; Horrocks and Nunn 2007; Kahn et al. 2014; Horrocks and Weisler 2006). It's worth noting that another recent, commonly investigated type of plant microfossil, phytoliths, is not relevant in this case because members of the Araceae, to which taro belongs, do not deposit it in their tissues (Piperno 2006). More recently, palmitone, an organic compound found in leaf waxes, has been identified as potentially indicating pre-contact *Colocasia esculenta* cultivation in Remote Oceania (Camperio et al. 2024).

Regarding the remaining Pacific Island culture area, Micronesia, comprising almost 2000 islands spread across 4000 km of the Northwest Pacific, at the time of writing taro findings appear limited to starch remains on Tarawa, Republic of Kiribati (Horrocks and Thomas 2022) and Guam, Mariana Islands (Dixon et al. 2020; Horrocks et al. 2015). Micronesia is relatively under-researched ethnobotanically (Arthur Whistler, pers. comm.), in part a result of fewer archaeological excavations. Here we address this research gap in the study of early Micronesian taro cultivation by the addition of another archipelago, with analysis of starch and associated material of excavated habitation layers on Ebon Atoll in the Marshall Islands, eastern Micronesia (Figure 2) (Weisler 1999; 2001a, b; 2002; in press).

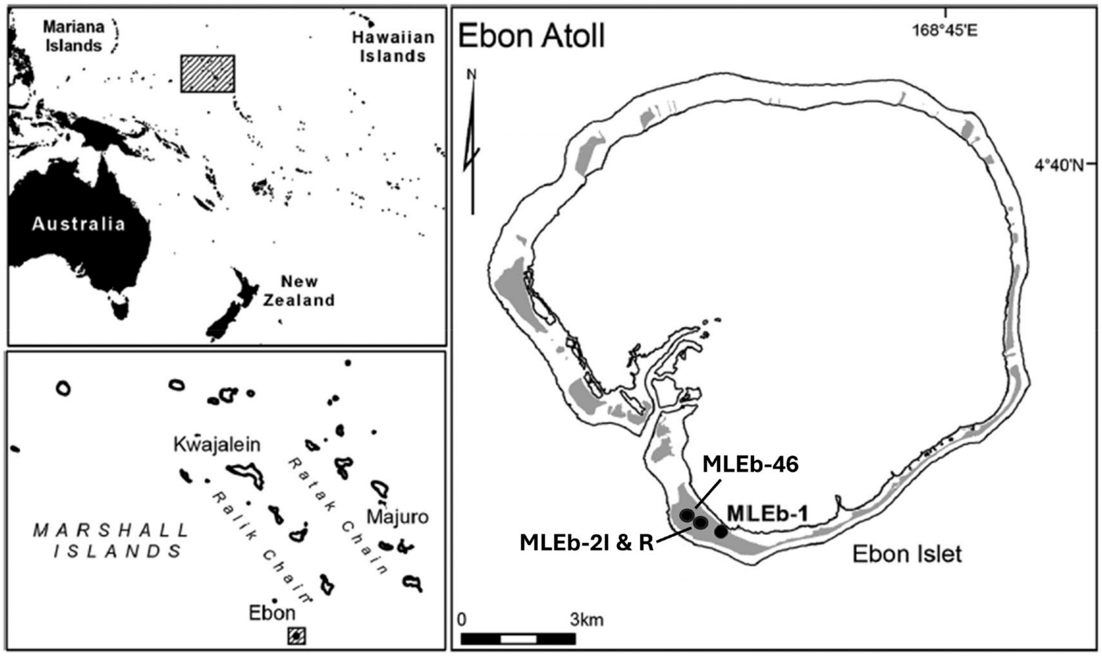

Figure 2: Map of the Republic of the Marshall Islands, showing Ebon Atoll and site locations

2. Study Area and Sites

Scattered across 2 million km^2 of ocean at the eastern limits of Micronesia, the Marshall Islands consist of 29 atolls, and five coral islands without lagoons (Figure 2). The islands are grouped in two roughly parallel alignments trending northwest-southeast over 1200 km between 4° and 12° latitude. Ebon Atoll is the southernmost, with a land area of 5.75 km^2 and comprising 16 islets surrounding a 12 km wide lagoon. Archaeological deposits at Ebon Atoll villages generally consist of gravelly sand layers, the result of reworked coral gravel pavements, deposited on top of sterile sands representing the original ground surface prior to human habitation (Weisler 2001b, in press).

Around four decades of archaeological research in the Marshall Islands, recently summarised by Weisler (in press), have revealed a sequence of occupation commencing soon after atoll emergence, just before 2000 cal. BP (Kayanne et al. 2011; Weisler in press; Weisler et al. 2012). Previous Ebon Atoll archaeological studies have included analysis of plant microfossils (Horrocks and Weisler 2006), land snails (Christensen and Weisler 2013), lizard bones (Pregill and Weisler 2007), fish bones (Lambrides and Weisler 2017), other vertebrates (Weisler 2001), and marine molluscs (Harris and Weisler 2018). The most recent study analysed a dog helminth parasite (Horrocks, Weisler et al. 2024). The plant microfossil study, of samples from Ebon Atoll, identified non-*Colocasia* starch and associated material which could be from *Cyrtosperma merkusii*, *Alocasia macrorrhiza*, or *Amorphophallus paeoniifolius* (Horrocks and Weisler 2006). A small number of fragments of possible taro starch amyloplasts (sub-cellular units specializing in starch grain synthesis and storage) were observed during that analysis but not reported because the specimens were too degraded and identification uncertain. In light of greater experience and using improved and new starch extraction and identification techniques (e.g., Horrocks et al. 2023), in the present study further starch analysis was carried out, using different samples from the Ebon sites.

Our study sites are situated along a 1 km stretch of Ebon islet, the largest landmass on Ebon Atoll, where a large village midden parallels the lagoon shore and is associated with cultivation pits just inland. Five habitation sites were originally recorded by Rosendahl (1987) based primarily on surface midden and artefacts. From a complete archaeological survey of all islets, and transection excavations on Ebon islet in 1995-96 and 2011-12 (Weisler 2002, unpublished), Weisler defined the subsurface boundaries of these sites and added additional sites to the inventory.

For the present study, five soil/sediment samples were analysed for starch from the following sites: two from MLEb-1, one from MLEb-2I, one from MLEb-2R, and one from MLEb-46 (Figure 2, Table 1). The samples were also checked for pollen.

Table 1: Provenance and age of analysed samples (from Horrocks, Weisler et al. 2024). Calibration performed using the IntCal20 calibration curve (Reimer et al. 2020) and the OxCal program v.4.4 (Bronk Ramsey 2009). *Starch identified; ** rounded to nearest multiple of five; "c." for entries in the Depth column designates dating samples collected from the screen during controlled stratigraphic excavations.

Site	Unit	Layer	Depth (cm)	Layer description	Lab no.	Material	δ^{13}C (‰)	Conventional ^{14}C age (BP)**	Calibrated age (cal. BP)**		
									68% CI	95% CI	Median
MLEb-1*	6	IIIA*	107	base of cultural	OZP925	*Cocos* endocarp	-23.3	1890 ± 30	1830-1745	1875-1715	1790
MLEb-1	18	IIA	c. 80	base of cultural	OZP928	*Cocos* endocarp	-24.9	920 ± 25	905-785	915-740	845
MLEb-2I	21	IIB	c. 80	cultural layer	OZP313	*Pandanus* drupe	-23.6	430 ± 30	515-475	530-335	495
MLEb-2I	14	IB	c. 40	cultural layer	Beta-92125	*Cocos endocarp*	-26.1	750 ± 40	725-660	735-570	685
MLEb-2R*	7	III*	c. 50	grey layer	OZP929	*Cocos* endocarp	-24.3	1060 ± 30	1050-925	1060-920	955
MLEb-46*	7	III*	c. 50	A horizon	OZP319	*Cocos* endocarp	-24.3	1840 ± 35	1820-1705	1830-1625	1745

3. Materials and methods

Controlled stratigraphic excavations were conducted at several habitation sites on Ebon islet, but it was not possible to correlate the cultural stratigraphy across the discontinuous 1+ km length of the cultural deposits; hence, several site numbers were assigned. All cultural sediments were dry- or wet-sieved with 6.4 mm screens and selected subsamples were also processed using 3.2 mm sieves. Sediment was collected from cultural and non-cultural layers by excavating bulk ~1 litre samples and bagging in either resealable plastic or cloth bags.

Starch and associated material were separated from the sediment samples by density separation (1.8 specific gravity) with sodium polytungstate (Horrocks 2020; Pearsall 2015) and presence/absence noted. Photomicrographs were taken with a Canon EOS 600D camera mounted on a Nikon 400E microscope. Starch and xylem are shown in greyscale, which is the usual natural colour of this material, to give better contrast and remove distracting background colours. Calcium oxalate crystals are shown in colour to display pleochroism (an optical phenomenon in which a substance has different colours when observed at different angles, especially with polarised light). Measurements were made using a calibration slide.

Pollen analysis was also commissioned and carried out for this study. The samples were prepared for this by the standard acetolysis method (Moore et al. 1991; Horrocks 2020).

Samples were collected for dating either in situ or during field screening. Short-lived, charred, and well-preserved terrestrial materials in the samples were selected for AMS ^{14}C age determinations from four habitation sites (Table 1). Short-lived materials were identified by Weisler using reference materials at the University of Queensland and identifications confirmed by archaeo-botanist Andy Fairbairn. The samples were pre-treated using the standard acid-alkali-acid method to remove all possible carbon contamination. The pre-treated samples were then combusted and graphitised using the H_2/Fe sealed-tube technique (Hua et al. 2001). AMS radiocarbon measurements were performed using the STAR 2MV accelerator at the Australian Nuclear Science and Technology Organisation (Fink et al. 2004).

4. Results

One type of starch was identified in this study, comprising amyloplasts or fragments thereof of the corms of cf. taro (*Colocasia esculenta*), found in three of the five samples (Fig. 3; 4A, B). Nine specimens were found in Sample MLEb-2R, five in Sample MLEb-46 and three in Sample MLEb-1 (22 x 40 mm coverslips) (Table 1). In addition, abundant raphides and druses (scores-100s), and one type of xylem cell (six specimens), mostly fragmented, were found in the same samples (Fig. 4C, D; 5). The material ranged from well preserved, to very degraded. This starch-associated material is very similar to that of aroids, the family to which taro belongs. Apart from abundant charcoal particles and the cf. aroid microfossils, the samples contained very little of any other material.

Pollen was extremely sparse in the samples, with none in Sample MLEb-1. All five had small amounts of fern spores, and Samples MLEb-2I and MLEb-2R also had small amounts of grass pollen. Sample MLEb-

2R had a single pollen grain of *Morinda citrifolia*, *Pandanus tectorius*, and *Cocos nucifera*. The former species is introduced; the latter two are present as wild varieties likely indigenous, with introduced varieties also present (Vander Velde 2003).

^{14}C results are also shown in Table 1. The age determinations for the three samples that had starch encompass 1875-1715 cal. BP to 1060-920 cal. BP (95% CI).

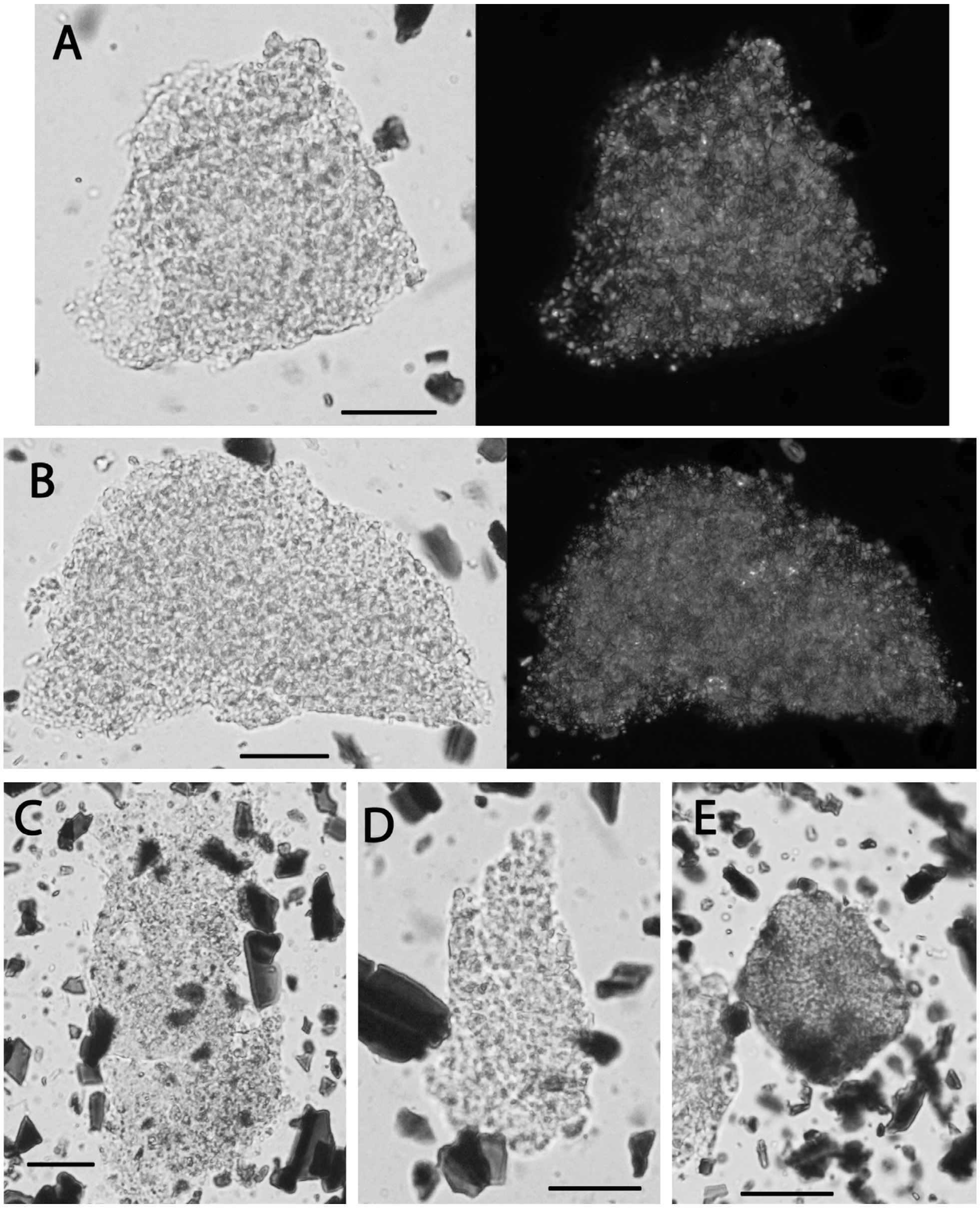

Figure 3: Fossil starch from Ebon Atoll. Sample labels in brackets; 600x; black background: cross-polarised light (CPL); scale bars: 20 µm. (A, B, D, E: MLEb-2R; C: MLEb-1.) A-E cf. Colocasia esculenta corm amyloplast remains, showing characteristic densely packed, sharply angular, tiny (mostly ≤ 4 µm) starch grains (hundreds-thousands), and the central vacuole seen as a dark gray/black dot giving a grainy appearance (cf. Fig. 6; 7); A and B show high visibility in CPL.

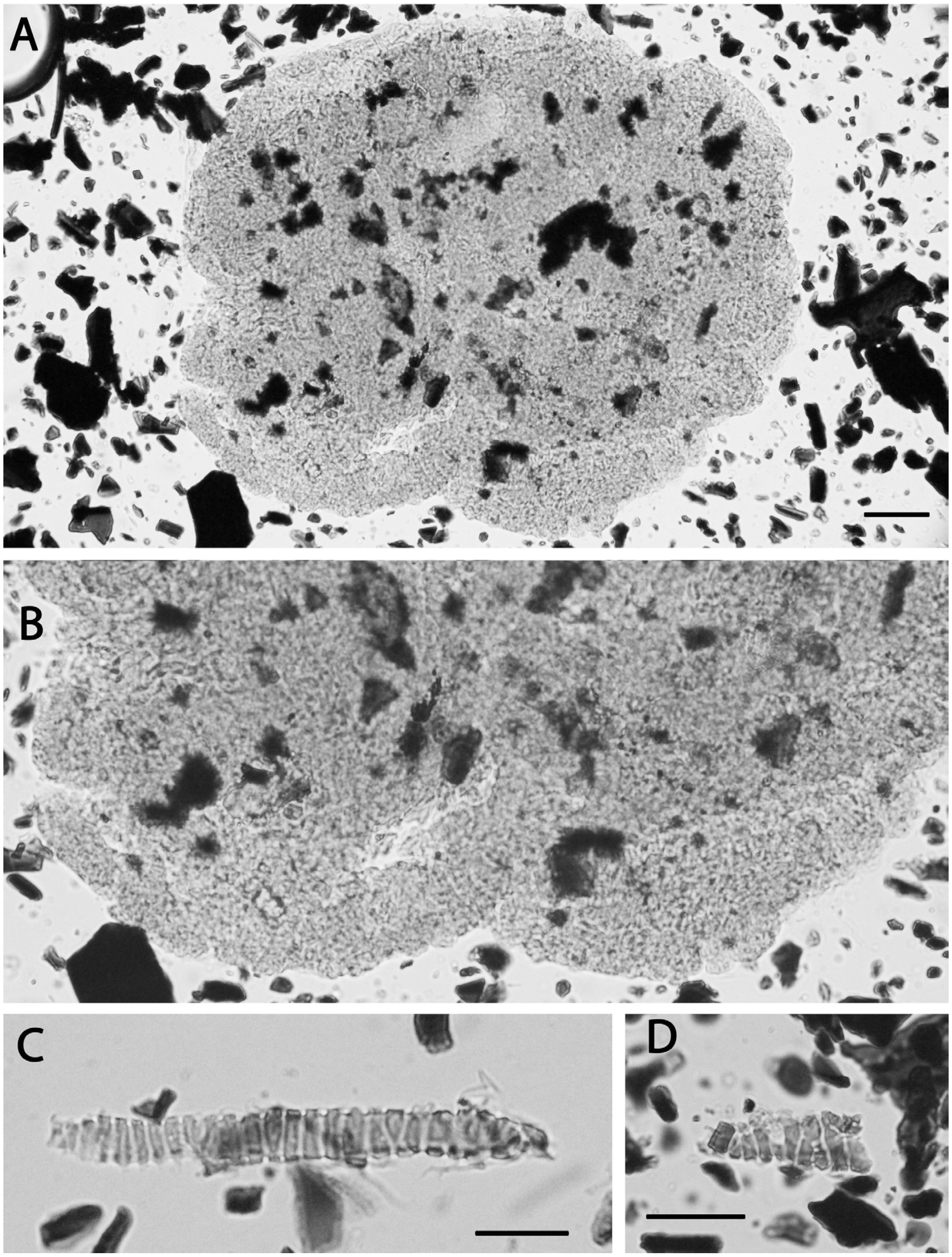

Figure 4: Fossil starch and xylem from Ebon Atoll. Sample labels in brackets; A 400x, remainder 600x; scale bars: 20 µm. (A, B: MLEb-46; C, D: MLEb-2R.) A a large mass of cf. Colocasia esculenta corm amyloplast remains, showing characteristic densely packed, sharply angular, tiny (mostly ≤ 4 µm) starch grains (hundreds-thousands), and the central vacuole seen as a dark gray/blasck dot giving a grainy appearance (cf. Fig. 6; 7). Typically curved amyloplast shapes (membranes not preserved/visible) can be seen as bulges. B lower portion of A shown at higher magnification (cf. Fig. 6B). C, D cf. Araceae xylem fragments, showing characteristic helical wall thickening (cf. Fig. 7E).

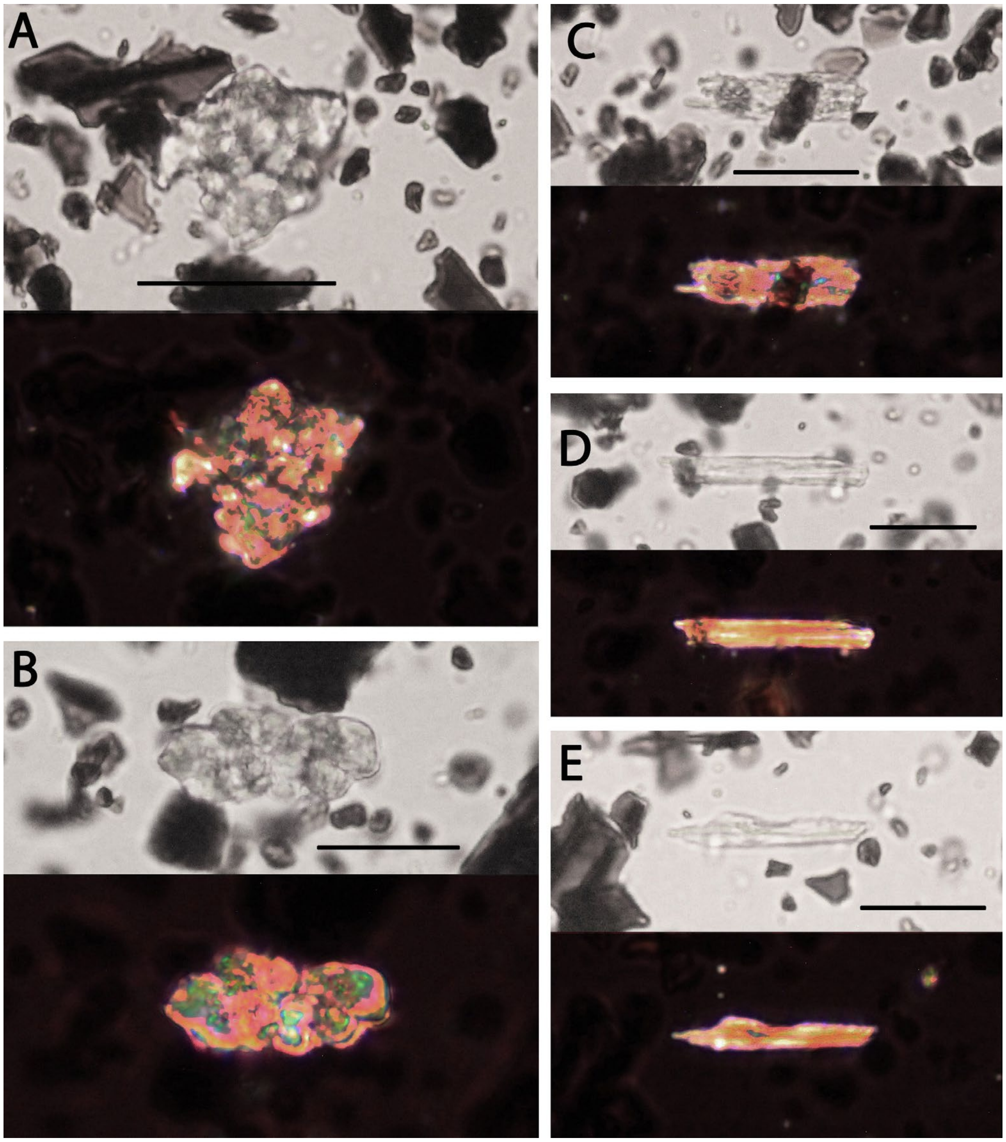

Figure 5: Fossil calcium oxalate crystals from Ebon Atoll. Sample labels in brackets; 600x; black background: cross-polarised light (CPL); scale bars: 20 µm. (A, C, E: MLEb-46; B, D: MLEb-2R; A, B degraded cf. Araceae druses with angular crystal projections mostly abraded, with characteristic pleochroism in CPL (cf. Fig 8A, B). C-E near complete (C) or partial (D, E) cf. Araceae raphide bundles, and showing characteristic pleochroism in CPL (cf. 8C-E).

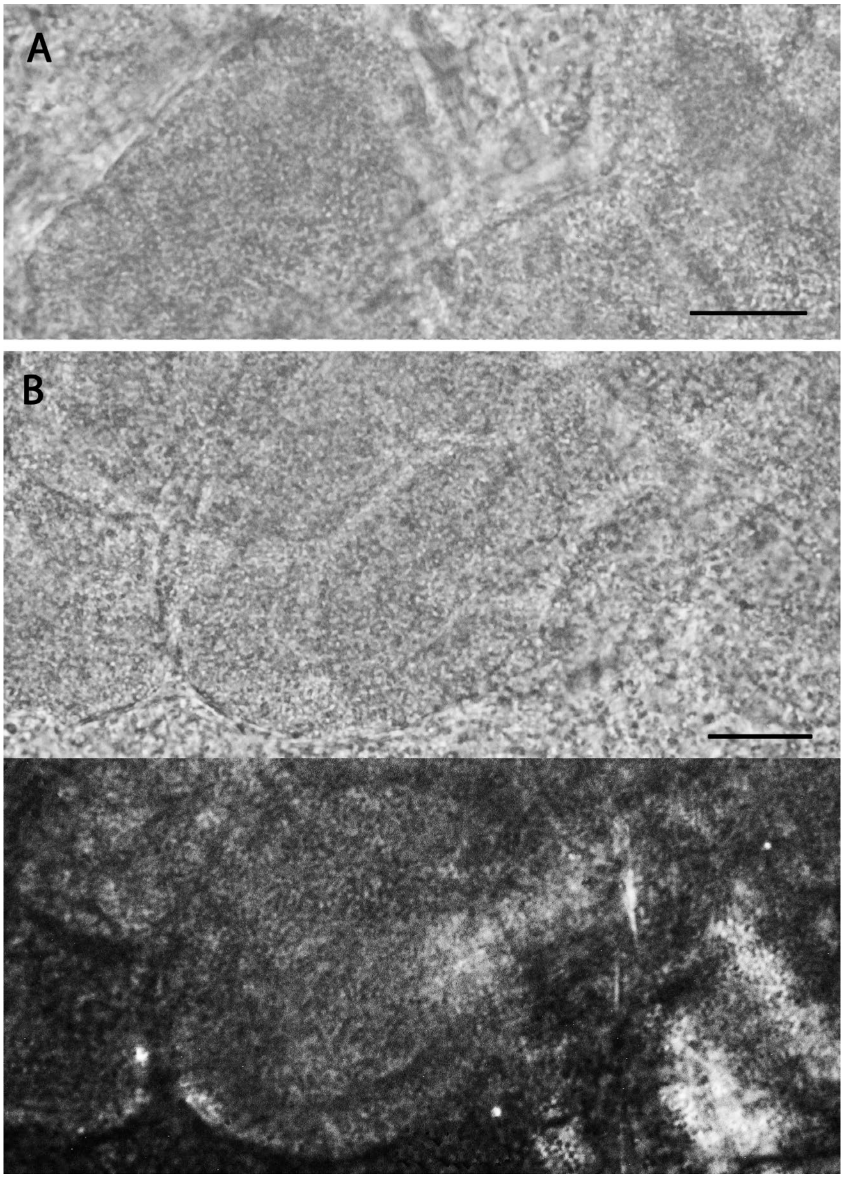

Figure 6: Modern reference material of Colocasia esculenta corm starch. 600x; black background: cross-polarised light (CPL); scale bars: 20 µm. A, B masses of corm amyloplasts, showing characteristic densely packed, sharply angular, tiny (mostly ≤ 4 µm) starch grains (hundreds-thousands), and the central vacuole seen as a dark gray/black dot giving a grainy appearance. B shows typical amyloplast curved shapes, and high visibility in CPL.

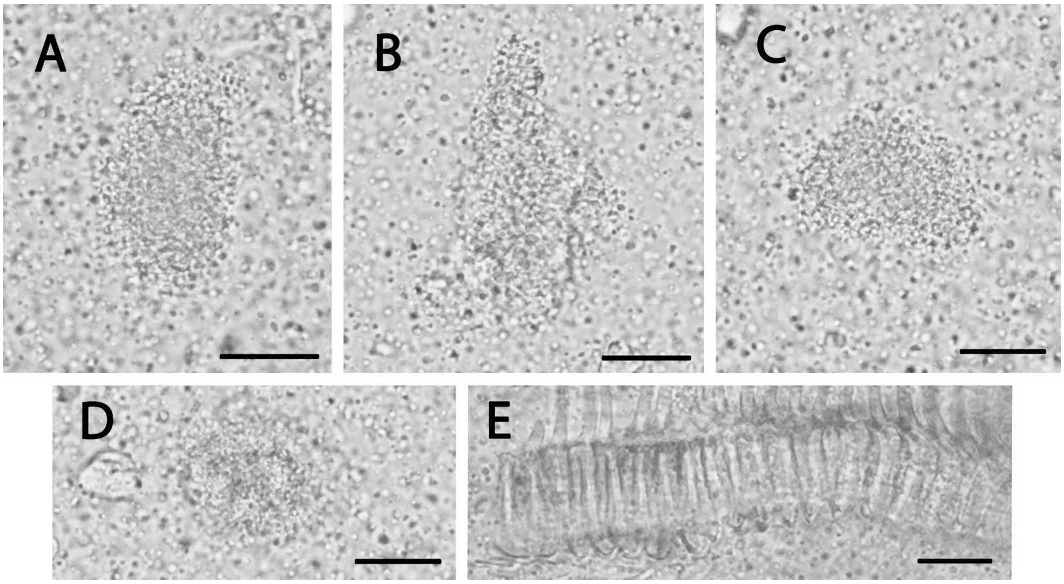

Figure 7: Modern reference material of starch and xylem of Colocasia esculenta corm. 600x; scale bars: 20 µm. A-D fragments of corm amyloplasts, showing characteristic densely packed, sharply angular, tiny (mostly ≤ 4 µm) starch grains (hundreds-thousands), and the central vacuole seen as a dark gray/black dot giving a grainy appearance. The clumps are surrounded by individual starch grains. E portion of a xylem cell, showing characteristic helical wall thickening.

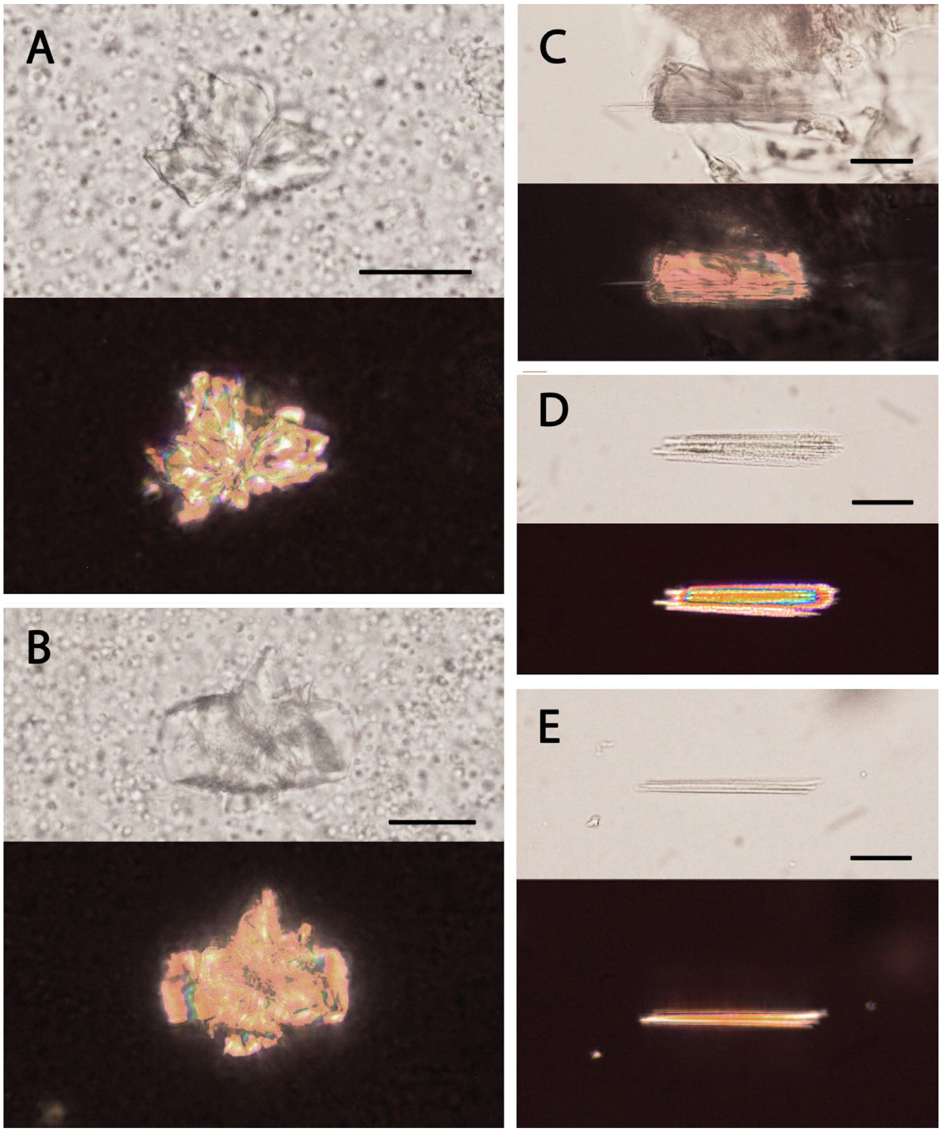

Figure 8: Modern reference material of calcium oxalate crystals of Colocasia esculenta corm (A, B, D, E) and leaf (C). 600x; black background: cross-polarised light (CPL); scale bars: 20 µm. A, B druses, showing angular crystal projections, and characteristic pleochroism in CPL (cf. Fig. 5A, B). C-E near complete (C) or partial (D, E) raphide bundles, with characteristic pleochroism in CPL (cf. 5C-E).

5. Discussion and conclusions

Detailed descriptions of *Colocasia esculenta* starch grains, calcium oxalate crystals, and xylem cells are given in the works of Fullagar et al. (2006), Horrocks, Bickler et al. (2024), and Horrocks, Dodd et al. (2024), Loy et al. (1992), Horrocks and Weisler (2006), and Seidemann (1966). *Leucocasia gigantea* (syn. *Colocasia gigantea*) has similar starch grains (Loy et al., 1992) but its natural range does not include Australia, Melanesia, or Remote Oceania (Matthews, 2004). The other three aroids introduced to the Marshall Islands - *Alocasia macrorrhiza*, *Amorphophallus paeoniifolius*, and *Cyrtosperma merkusii* - have starch grains similar to one another and many times larger than those of *C. esculenta*, hence can be definitively differentiated from the latter (Loy et al. 1992). These other three are known as "non-*Colocasia* aroids" (Loy et al. 1992).

Of relevance, Horrocks et al. (2023:6-9) note the following regarding degraded *Colocasia esculenta* fossil starch grains from archaeological sites on the Marquesas Islands:

> *Colocasia esculenta* starch has several distinctive features but can be challenging to identify. The corm amyloplasts contain hundreds of densely packed starch grains, are ovate, up to approximately 185 µm in diameter, and have very thin enclosing double membranes. The individual starch grains are mostly ≤4 µm in diameter, and appear sharply angular, while the central vacuole often appears as a dark gray/black dot. Starch grains of this species are much smaller than almost all other ancient subsistence starch taxa that have been described, allowing reasonably confident identification. However, the <4 µm grain size is near the limits of light microscopy, so grains are often best looked for in archaeological samples as groups, that is, amyloplasts or fragments thereof. In archaeological soils and sediments, *C. esculenta* amyloplasts are commonly fragmented and without visible membrane tissue.

Despite their tiny size, reasonably clear photomicrographic images of *Colocasia esculenta* starch grains can be obtained when working with stone tools or other types of archaeological samples preserved in permanently dry environments such as caves (Loy et al., 1992). When working with soils or sediments, however, the limitation of light microscopy in relation to this tiny size, and of depth of focus can present problems for photomicrography. It can be a major challenge to obtain clear focus on, and high magnification of, a large mass of these densely packed grains extracted from soils/sediments, especially if the grains are degraded. The effects are amplified when the mass is more three-dimensional, and decreased when it is flatter, i.e., more two-dimensional.

In addition, previously identified abraded and partially degraded masses of cf. *Colocasia esculenta* starch separated from soils/sediments appear very similar to those in Figures 3, 4A, and 4B when viewed in light microscopy (e.g., Barber and Benham 2024; Burley et al. 2020; Flexner et al. 2024; Horrocks, Dodd et al. 2024; Horrocks et al. 2008, 2012, 2023; Horrocks and Nunn 2007; Kahn et al. 2014; Horrocks and Weisler 2006). The photomicrographic appearance of this material can differ based on light-field/phase contrast microscope settings, camera settings (e.g., colour vs greyscale), digital photograph enhancements (e.g., brightness and contrast), and refractive index of the mounting media.

Along with other aroids, taro produces abundant calcium oxalate crystals in its corms and leaves (Sunell and Healey 1979). In this study, the crystals could therefore originate from the three other introduced aroids, although unlike in the previous microfossil study (Horrocks and Weisler 2006), we did not identify any starch grains that could be from those. Although having a higher specific gravity (2.2) than the starch density separation solution (1.8) used in lab processing, crystals can be caught up with other material in the separation. In Horrocks's experience, calcium oxalate crystals are generally poorly preserved (absent or very sparse) in most sediments and soils, unless the substrates are alkaline, where the crystals can often be observed in great abundance scattered on slide preparations. The Marshall Islands have sandy carbonate soils with pH ranging from 6.6 to 8.4, with subsoils up to 9.0 (Deenik and Yost 2006). We assume that the high crystal abundance in our case reflects high alkalinity of the sampled deposits. We note, however, that sediments from cultural layers in Marshall Islands archaeological sites generally have more organic matter that culturally sterile soils/subsurface sediments so pH can be somewhat lower (Weisler 1999: Table 1). Regarding the xylem cells, we also cannot rule out the other aroids as a source.

At nearly 2 km long, Ebon Atoll has perhaps the most extensive, near-continuous pit cultivation zone found on any atoll in Oceania yet documenting at least one of the aroids grown in the humus-rich sediments, and the antiquity of use, has not been realised until now. While identifying *Colocasia esculenta* mirrors a species of minor significance considering what is grown today (Fig. 1), was this the main aroid grown throughout the two millennia of human occupation? Possibly not, since giant swamp taro (*Cyrtosperma merkusii*) is the most common aroid grown today throughout the Marshall Islands, and has been cultivated since about 1800 cal. BP, with *Colocasia* on Tarawa, Kiribati (Horrocks and Thomas 2022). In contrast, *C. esculenta* is the dominant aroid grown in the Polynesian archipelago of the Tuamotus, French Polynesia (Chazine 1990; Emory 1975:36-38; Weisler 1999:626). These facts, then, beg the questions: did certain aroid species wax and wane in favourability over the centuries? If so, could this be linked to changing climates as giant swamp taro is more salt-tolerate (Lambert 1982; Thompson 1982) and could possibly withstand stormier conditions with increased salt-spray and perhaps tidal flooded cultivation pits? Since the southern Marshall Islands are situated in an area of high sensitivity to drought conditions (de Freitas et al. 2014) which are influenced during the cyclic periods of El Niño and La Niña that affect the thickness and extent of groundwater, the expanse of aroid cultivation, and the aroid species cultivated, may have mirrored long-term changes in precipitation. Or could one aroid species have been preferred due to taste, cultural preference or by supporting a larger corm; or had a shorter growing season, or could remain longer in the ground before harvest? While some of these questions may not be possible to conclusively address, identifying ancient aroid plant remains in dated archaeological contents can provide the necessary and sufficient information for at least investigating what we believe are important questions for future research.

This study represents the first direct, palaeo-botanical evidence for pre-European taro in the Marshall Islands, adding another archipelago to the currently scant list of such Micronesian sites, and addressing the relative under-researched topic of ethnobotany in Micronesia and throughout Oceania.

Funding

Radiocarbon dating was funded by grant number 12/004 to Weisler and Hua from the Australian Institute of Nuclear Science and Engineering. Analysis of Marshall Islands sediment samples was funded by the University of Queensland.

Data Availability Statement.

Data available on request from the authors.

Partnerships

This research did not use any primary data from Indigenous contexts.

Conflicts of Interest

The authors declare no conflicts of interest.

Author Contributions

Conceptualisation, M.I.W., M.H.; investigation, M.H., M.I.W., Q.H.; resources, M.H., M.I.W., Q.H.; writing—original draft preparation, M.H., M.I.W.; writing—review and editing, M.H., M.I.W., Q.H.; visualization, M.H.; funding acquisition, M.H., M.I.W., Q.H.

Acknowledgements

Permission to conduct the field work in 1995-96 and 2011-12 was granted to Weisler by the Historic Preservation Office, Republic of the Marshall Islands, and then Mayor Lajan Kabua.

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