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Palaeoecological studies at four archaeological sites in the New Guinea Highlands document local vegetation histories and plant use from c. 18,000 cal BP to the recent past

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Abstract

Plant microfossils at archaeological sites in the New Guinea Highlands have received little attention compared to lithic and faunal analyses. Here we analyse plant microfossils (pollen, charcoal particles, phytoliths, and starch) from three rockshelters (Yuku, Kiowa, and Manim) and one open site (Wañelek), dating from c. 18,000 cal BP. Pollen results show a diverse range of taxa, and record major as well as subtle changes in vegetation history, with complimentary phytolith results. Vegetation changes, especially *Nothofagus* spp. decline, were driven by post-LGM climatic warming and anthropogenic deforestation, respectively, yielding mixed *Castanopsis-Lithocarpus* lower montane forest, and secondary forest, disturbance taxa, and grasslands. Low charcoal counts and ground fern establishment suggest periods of limited use within some rockshelters. Subsistence plant remains include starch of cf. *Castanopsis acuminatissima* nuts and cf. *Colocasia esculenta* corms, and a leaf phytolith of *Musa* sp. A new type of aquatic archaeological marker, cf. euglenoid cysts, was also identified.

Keywords: Plant microfossils; pollen; phytoliths; starch grains; archaeobotany; *Castanopsis*; *Colocasia esculenta*

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1. Introduction

The Sahul landmass, comprising New Guinea and Australia during times of lower sea level, was settled by people at least 55,000 years ago (Clarkson *et al.* 2015). The dispersal of people into an area of high biodiversity and endemism resulted in extensive ecological transformations, including deforestation and faunal extinctions, which became more marked following the emergence of agriculture (Denham 2024). Agriculture is thought to have developed independently on the island of New Guinea (Denham *et al.* 2003; Golson *et al.* 2017) and been based primarily on vegetatively propagated crops (Denham 2011, 2018).

Archaeological research in the New Guinea Highlands, commencing in the late 1950s, initially focused on faunal and stone tool analyses, enabling long-term historical framing of the nature and timing of cultural activity and transformation (Bulmer and Bulmer 1966; Christensen 1975; Denham and Muke 2024; Mountain 1991; Sutton *et al.* 2009). Subsequently, archaeobotanical research identified macrobotanical and microbotanical remains of the plants gathered and cultivated (Denham *et al.* 2003; Donoghue 1989; Field *et al.* 2020; Fullagar *et al.* 2006; Horrocks *et al.* 2008).

We aim to build on previous Highlands research by analysing plant microfossils - pollen, charcoal particles, phytoliths, and starch - in archaeological deposits at four occupation sites (Yuku, Kiowa, Wañelek, and Manim) in the Highlands (Fig. 1). The analyses are designed to provide local vegetation histories that accompany the material cultural record and to thereby shed light on plant subsistence activities in the region.

Figure 1: Map of Papua New Guinea showing site locations

2. The study area and sites

The Highlands comprise a long chain of mountain ranges on the island of New Guinea, including Puncak Jaya, Indonesia, at 4,884 m above sea level, the highest mountain in Oceania. The ranges run generally east-west along the length of the island and have numerous intermontane river valleys. The study sites (Yuku, Kiowa, Wañelek, and Manim) are in the eastern Central Range (or Cordillera) montane rainforests, a tropical moist forest ecoregion at 1000-3000 m elevation (Fig. 1).

There are three broad vegetation zones in the Central Range (Paijmans 1976): lower montane forest, upper montane forest, and high mountain forest. The sites are within the first two zones. Lower montane forest extends from the lowland forest transition at c. 1000 m up to 2500 m, depending on the region. The canopy of this zone is characterized by Fagaceae, including *Castanopsis acuminatissima* and species of Elaeocarpaceae and Lauraceae. The conifers *Araucaria cunninghamii* var. *papuana* and *Araucaria hunsteinii* can form thick stands (Wikramanayake *et al.* 2000). People have intensified various tree species within the forest for subsistence and ritual purposes (Ash *et al.* 2023; Stone 1982). Upper montane forest occurs above c. 1500 m, with the canopy characterized by various *Nothofagus* spp., either in mixed stands with other species or in monostands, especially on ridge crests and upper slopes. Mosses and other epiphytes cover the trees (Wikramanayake *et al.* 2000).

The Central Range has the greatest diversity of species from *Nothofagus* subgenus *Brassospora* (Read *et al.* 1990; Read and Hope 1996). As well as considerable canopy diversity, these two montane forest zones (lower and upper) have a large diversity of genera and species in their mixed under-layers, including palms (Arecaceae), *Pandanus*, tree ferns such as *Cyathea* and *Dicksonia*, and climbing forest bamboo (Bambusoideae, a Poaceae subfamily) in the understory, as well as ferns, herbaceous plants, and bryophytes in the ground cover. The diversity of edible understory and ground cover species generally decreases with increasing altitude in these montane forests, especially within *Nothofagus* dominated tracts (Denham 2007; Golson 1991; Mountain 1991).

High mountain forest commences above c. 2400 m, and extends to the tree line, in places extending to 3900 m in the higher-elevation subalpine grasslands ecoregion. High altitude trees are conifers - *Podocarpus, Dacrycarpus, Dacridium, Papuacedrus, Araucaria*, and *Libocedrus* - along with broadleaf trees in the Myrtaceae family. This forest generally has a thin canopy, shorter than the upper montane forests, with a thick understory (Wikramanayake *et al.*, 2000), and lacking *Pandanus* and bamboo (Robbins 1961).

Pollen core records from wetlands across the Highlands have reconstructed the vegetation history since the Terminal Pleistocene (Haberle 2007; Hope and Golson 1995; Powell 1982). These records show a general decline in *Nothofagus* (a cool climate indicator) forest and its retreat to higher elevations following climatic warming leading into the Holocene, and further declines with forest clearance by people during the early, mid- or late Holocene depending on location within the Highlands (Powell, 1982; Hope and Haberle, 2005). For example, various pollen records in the Wahgi Valley (Haberle *et al.* 2012; Powell 1982; Robbins 1961) show long periods of disturbance and periodic burning during the Pleistocene, followed by extensive forest clearance during the early-to-mid Holocene at several places on the valley floor (Denham and Haberle 2008). Until recently, clearance had mainly occurred on the floors and lower slopes of the larger intermontane valleys, denuding the landscape to open grassland (Poaceae) with groves of *Casuarina* and *Pandanus*, clumps of bamboo, tall grasses, remnant forest outliers, abandoned gardens, and various herb species, which are mostly tropical weeds. These entrenched disclimax grasslands are perpetuated and extended by periodic burning (Robbins 1961).

Previous plant microfossil studies at several archaeological sites in the New Guinea Highlands, namely Kuk Swamp (Denham *et al.* 2003; Fullagar *et al.* 2006), Yuku rockshelter (Horrocks *et al.* 2008), and the open sites of Waim, Bismarck Mountain Range (Shaw *et al.* 2020), and Joe's Garden in the Ivane Valley (Field *et al.* 2020), have provided information regarding plant utilisation. At Kuk, pollen, phytolith, and microcharcoal analyses of archaeological stratigraphy and feature fills thought to be associated with early agricultural activities provide evidence for increasing forest disturbance, leading to eventual replacement with grassland by c. 7000 cal BP. *Musa* (banana) spp. leaf phytoliths increased in association with a mounded palaeosurface dated to 7000-6400 cal BP and a drainage feature dated to 4800-4400 cal BP (Denham *et al.* 2003; Haberle *et al.* 2012; Lentfer and Denham 2017). Use wear and residue analyses of stone tools associated with plant exploitation and early agricultural activities during the early and mid-Holocene identified the processing of *Colocasia esculenta* (taro) and a *Dioscorea* (yam) species (Fullagar *et al.* 2006). At Yuku, putative starch and calcium oxalate crystals of *Dioscorea* spp. were reported at points throughout the sequence (Horrocks *et al.* 2008). At Waim, excavations revealed structural remains and stone tools, including broken pestle bases, dating to 5050-4200 cal BP (Shaw *et al.* 2020). Use wear and residue analyses of the pestles identified plant tissue fragments, phytoliths, and starch grains interpreted to derive from a range of edible plants, including *Castanopsis acuminatissima* (nuts), *Dioscorea* spp., *Pueraria lobata* (tubers), and a *Musa* species (fruits). At Joe's Garden, Field *et al.* (2020) identified *C. acuminatissima* and *P. lobata* starch grains on a stone mortar from a c. 4400 cal BP context.

Summaries of the archaeological research conducted at each site are provided below. The term "occupation" does not imply prolonged or permanent residency by people in the past. Rather, the "main period of occupation" refers to the time when people visited and used the site more intensively; individual visits could have been periodic, seasonal, or for extended periods, yet these stays were likely recurrent.

2.1. Yuku

Yuku rockshelter (1280 m) is situated in the valley of the Yuem River, a tributary of the Lai River, and west of the Baiyer Valley, Western Highlands Province (Fig. 1). The shelter, with c. 21 m2 of ground protected by the overhang, was excavated in 1959-1960 by Sue Bulmer (1966, 2005). It contained up to 3.6 m depth of stratified deposits, which were excavated in seven main layers defined by changes in components such as colour, texture, and density of cultural materials. The more complex, thicker layers were subdivided (e.g., Layer 3A-C).

All layers contained artefactual material and radiocarbon dates suggested occupation by at least 17,500 cal BP (Table S1; Gaffney *et al.* 2021). The stone tool assemblage was reviewed by Bulmer (e.g., Bulmer 2005; Bulmer and Bulmer 1966), with multiple analyses undertaken on Bulmer's excavated materials. The latter included plant microfossil analysis of sediments (Horrocks *et al.* 2008), review of faunal distributions (Sutton *et al.* 2009), reanalysis of faunal material (Gaffney *et al.* 2021), and ^{14}C dating of charcoal, macrobotanical remains (Denham 2016), and bird eggshell (Gaffney *et al.* 2021).

Previous dating estimates at Yuku for *Saccharum officinarum* (sugarcane) of c. 5650-4550 cal BP and *Pandanus conoideus* (marita) of c.14,000 BP (Bulmer 1975, 2005) have been ruled out by direct AMS dating, which provided dates <300 years old (Denham 2016). The chronostratigraphic integrity of the site is currently uncertain (see Denham 2016 and Gaffney *et al.* 2021) and is discussed further below.

Table 1: Sediment samples used for microfossil analysis and radiocarbon dating. Provenance and descriptive information for Yuku, Kiowa and Wañelek derive from Bulmer's bag labels and fieldnotes, as well as reclassifications undertaken by Bulmer at Yuku (see Denham 2016: Table S2), while those for Manim derive from Christensen's bag labels (see Christensen 1975; Denham 2019). The dates have all been previously published, although some have been recalibrated (Bulmer 1964, 1966, 1991; Gaffney *et al.* 2015b, 2021; Denham 2016, 2019). Where there are multiple dates for a single layer or context derived from recent dating (reported in Denham 2016, 2019) on charcoal from the same bag samples used for microfossil analysis, the widest combined range of the calibrated date ranges (excluding date range with less than c.1.0% probability) is given. Dates derived from earlier research or derived from other bag samples within the same context are given in italicised date ranges.

Sample Code	Unit	Layer	Description	Radiocarbon Date Ranges (Cal BP)
Yuku				
Y2	1A	2	Layer 2	313-modern
Y3A	1A	3A	Layer 3A	*5841-4626*
Y3B	1-2	3B	Layer 3B	
Y4A	1A	4A	Layer 4A	
Y4C	1-2	4C	Layer 4C	*11,748-10,710*
Y4f	1	4	Fill of fireplace in top of Layer 4	
Y5A	unknown	5A	Top of Layer 5A	
Y5C	2	5C	Layer 5C (formerly 5E)	
Y6	1A	6	Layer 6 (formerly 5D)	*17,819-16,601*
Y7B	1A	7B	Layer 7B	
Kiowa				
K3		3	Main layer	*5916-5294*
K7		7	Main layer	10,168-9532
K8		8	Main layer	
K8f		8	Fill of 'fireplace' mixed with sediment	
K10		10	Upper part of main layer	*12,126-10,146*
K11		11	Upper part of main layer	11,237-10,661
K11f		11	Fill of 'fireplace' mixed with sediment	
K12		12	Upper part of main layer	12,173-11,706
Wañelek				
W1	105Z	I	Topsoil (Layer A)	270-17
W2	105Z	II	Garden soil (Layer B)	
W3	105Z	III	Orange Subsoil (Layer C)	

W4	105Z	IV	Upper grey-black soil (upper Layer D)	5296-5045
W5	105Z	V	Lower grey-black soil (lower Layer D)	4146-3929
W6	105Z	VI	Transition to natural (upper Layer E)	
W7	105Z	VII	Reddish transition to natural (lower Layer E)	
W8	105Z	VIII	Natural (Layer F)	
W101Y6	W101	6	Charcoal rich deposit in top of Layer 6	17,495–16,991
W101Y7	W101	7	Charcoal rich deposit in Layer 7	15,825–15,281
W101Y8	W101	8	Charcoal rich deposit in Layer 8	17,549–17,009
W101Y9	W101	9	Charcoal rich deposit in Layer 9	17,590–17,051
W101Y9sur	W101	9	Charcoal rich deposit at the top of Layer 9	
W101Y9ph	W101	9	Charcoal from fill of 'posthole' in Layer 9	17,708–17,145
WB(II)4	17-18/B(I+II)	4	Black soil lens at top of Layer 4	
WB(II)5lith	17-18/B(I+II)	5	Layer 5 around 'western' group of flakes	3357–3172
WB(II)6f	17-18/B(I+II)	6	Fill of fireplace at the top of Layer 6	
WB(I)7f	17-18/B(I+II)	7	Fill of fireplace at the top of Layer 7	*4154-3326*
WB(II)8f	17-18/B(I+II)	8	Fill of fireplace/oven pit at the top of Layer 8	*3847-2852*
WB(I)11ph	17-18/B(I+II)	11	Fill of posthole at the top of Layer 11	4868-4643
Manim				
M1	I	I	Level 1, Clay-rich topsoil (Layer I)	
M2	I	I	Level 2, Clay-rich topsoil (Layer I)	270-12
M3	I	I	Level 3, Clay-rich topsoil (Layer I)	
M4	I	II	Level 4, Dark organic-rich sand (Layer II)	437-155
M5	I	II	Level 5, Dark organic rich sand (Layer II)	900-693
M6	I	II	Level 6, Dark organic rich sand (Layer II)	673-556
M7	I	II	Level 7, Dark organic rich sand (Layer II)	
M8	I	III	Level 8, Banded sands (Layer III)	
M9	I	III	Level 9, Banded sands (Layer III)	
M10	I	III	Level 10, Banded sands (Layer III)	2340-2155
M11	I	III	Level 11, Banded sands (Layer III)	
M12	I	III	Level 12, Banded sands (Layer III)	2791-2727

2.2. Kiowa

Kiowa rockshelter (1500 m) is situated approximately 2 km southeast of Chuave Station, Chimbu Province (Fig. 1). It was excavated in 1960 by Bulmer (1966) and dates from the Terminal Pleistocene, c. 12,500 years ago (Table S2; Denham 2016; Gaffney *et al.* 2021), with continued and perhaps seasonal occupation through to the Late Holocene (Bulmer 1964, 1966). Deposits containing multiple fire ash lenses interbedded with adjacent soils at the edges of the rockshelter were excavated to a maximum depth of 3.65 m. Twelve stratigraphic layers were identified.

All layers contained some artefactual material. The stone tool assemblage was reviewed by Bulmer (e.g., Bulmer 2005; Bulmer and Bulmer 1966), with a range of subsequent analyses undertaken on Bulmer's excavated materials. The latter include reassessment of the lithic assemblage (Gaffney *et al.* 2015a), review of faunal identifications (Sutton *et al.* 2009) and reanalysis of faunal material (Gaffney *et al.* 2021), examination of shell artefacts as trade items (Gaffney *et al.* 2018), and radiocarbon dating of charcoal (Denham 2016) and bird eggshell (Gaffney *et al.* 2021).

2.3. Wañelek

Wañelek (1710 m) is an open site located on a ridge in the Kaironk Valley of the Bismarck Schrader Ranges (Fig. 1). In 1972 and 1973, Bulmer excavated four areas, with radiocarbon dating suggesting occupation by people at four different times from the Last Glacial Maximum (LGM) to the late Holocene (Table 3). In contrast to Kiowa and Yuku, the archaeological investigations at Wañelek have not been written up except in preliminary form (Bulmer 1977, 1991; Gaffney *et al.* 2015b).

Only limited re-examination of materials collected from the site has occurred. Gaffney *et al.* (2015b) used petrographic and geochemical data from pottery, together with new ^{14}C dates, to show that pottery was found in secure archaeological contexts associated with an occupation around 3000 cal BP. Sherds included one likely made on the north coast, whereas others were possibly locally made. Denham (2016) redated the site to investigate the c. 4000-3000 cal BP occupation as well as a previously claimed Terminal Pleistocene house structure. He concluded that recurrent site occupation had occurred 4100-2800 cal BP, and possibly earlier, and that the putative Terminal Pleistocene house structure was most plausibly a major burning event of local forest, c. 17,700-17,000 cal BP.

2.4. Manim

Manim rockshelter (1770 m; also referred to as "Manim 2") is named after the adjacent Manim Creek and is situated in the Wurup Valley, a tributary to the Upper Wahgi Valley (Fig. 1). Today, the rock-shelter is relatively small, covering c. 4 m^2; however, its morphology suggests that it was more extensive in the past prior to partial infilling. Ole Christensen excavated the shelter in 1973 (Christensen 1975). A robust chronology has been established for Manim, extending to at least 10,200 cal BP (Table S4; Denham 2019) and possibly to c. 12,000 cal BP (Christensen 1975; Mangi 1984). Analyses of the abundant archaeobotanical (Donoghue, 1989) and dense lithic assemblages (Burton 1984; Mangi 1984) have been reported.

There were two main occupation periods at Manim, with the most intensive occurring from before 9000 cal BP to c. 6600-6400 cal BP and a later one at c. 3400-3200 cal BP (Denham 2019). Ground stone tool technology occurred from at least c. 9000 cal BP and was more widely adopted by c. 6600-6400 cal BP (Christensen 1975; Denham 2019; Mangi 1984). Ground stone axe-adzes may have facilitated the clearance of forest for cultivation, in which case the findings from Manim complement those for forest clearance and early mound cultivation at c. 7000-6400 cal BP at Kuk Swamp (Denham *et al.* 2003) only 17 km away (Denham and Haberle 2008).

3. Materials and methods

Pollen and microcharcoal analyses were carried out on 36 sediment samples (Table 1): nine from Yuku, eight from Kiowa, eight from Wañelek, and 11 from Manim. Analyses of phytoliths and starch grains were conducted mostly on paired samples to those used for pollen and microcharcoal analysis, as well as other samples of interest: 12 samples from Manim, which corresponded to 11 of those examined for pollen and microcharcoal; only four samples from Yuku (Layers 3A, 3B, 4f and 5C), to avoid replication of samples previously analysed by Horrocks *et al.* (2008); six samples from Kiowa; and 20 samples from Wañelek, including eight paired (W1-W8) through the stratigraphic sequence, as well as six samples from stratigraphic units and feature fills associated with the c. 4100-2800 cal BP multiperiod occupation and six samples associated with the Terminal Pleistocene burning event at 17,700-17,000 cal BP (W101).

Pollen samples were treated with 10% sodium pyrophosphate and sieved using 180 µm and 8 µm mesh. The fraction <180 µm and >8 µm was treated with 10% HCl, then acetolysis was undertaken, followed by heavy liquid separation using sodium polytungstate (s.w. 2.0, for 20 min at 2000 rpm). This last step was repeated twice; the floating residue was dehydrated with 96% ethanol. Slides were mounted with glycerol and sealed with paraffin wax. Pollen and spore preservation was highly variable within and between sites, with pollen sparse in many samples. Total pollen sum counts (dryland pollen sum) are shown on the pollen diagrams. For concentration calculations, one tablet, containing 18584 *Lycopodium* spores, was added to each sample prior to processing.

Samples were prepared for phytolith analysis with 0.1 molar sodium pyrophosphate and 10% KOH, followed by 10% HCl, then 500 °C for 4-5 hr. This was followed by heavy liquid separation using sodium polytungstate (s.w. 2.3, for 5 min. at 2000 rpm) (Horrocks 2020; Piperno 2006). Slides were mounted with Canada balsam. A sum of at least 200 phytoliths was counted for each sample and slides were scanned for types not found during the counts. Volumetric measurements were not carried out for phytoliths.

Samples were prepared for starch analysis with 5% Calgon followed by heavy liquid separation using sodium polytungstate (s.w. 1.7-1.8, for 3 min. at 1500 rpm) (Horrocks 2020; Piperno 2006). Starch was assessed qualitatively, simply as presence or absence. Measuring starch grains separated from soils and sediments quantitatively is difficult, and perhaps meaningless or misleading, because unlike pollen grains and to a large extent phytoliths, they are not part of a background "rain". Rather, they tend to be very much directly *in situ* deposited and can be present tightly packed in a single microscopic amyloplast material thereof in their scores, hundreds, or thousands. This effect is increased with a reduction in relative grain size. For example, a single *Colocasia esculenta* amyloplast or degraded mass of these amyloplasts where enclosing membranes are not preserved or visible may comprise up to many thousands of starch grains. Variation in the size of amyloplast fragments therefore also means potentially large differences in starch grain numbers. Thus, individual starch grain or amyloplast fragment numbers do not necessarily represent plant cultivation frequency or intensity. Slides were mounted with glycerol jelly. Other material of interest, in this case euglenoid cysts, can be separated along with starch in this preparation.

Identification of phytoliths and starch was aided using a modern reference collection of specimens of species cultivated by early Oceania peoples. The collection is housed at Microfossil Research Ltd., Auckland.

The software package Tilia 3.0.3 was used to construct the graphical diagrams. Photomicrographs of microfossils were taken with a Canon EOS 600D camera mounted on a Nikon 400E microscope. Measurements were made using a calibration slide.

The radiocarbon dates (all calibrated to two sigma) used for the sampled profiles in this study are shown next to the relevant samples on the graphical diagrams (taken from Table 1). The dates have all been previously published, although some have been recalibrated (Bulmer 1964, 1966, 1991; Denham 2016, 2019; Gaffney *et al.* 2015b, 2021). In several cases, dates on fragments of charcoal were obtained from the same sediment sample used for microfossil analysis; these are indicated by italics in the figures.

4. Results

4.1 Pollen and spores

Pollen concentration was highly variable, ranging from zero to several hundred pollen grains and spores per slide. This result is not uncommon in archaeological contexts where substrates are frequently disturbed by human activity. Caution is required in the interpretation of the microcharcoal record at occupation sites, as the particles could derive from on-site burning by people, such as in hearths and earth ovens, as much as from burning in the vicinity of the site.

4.1.1. Yuku (1280 m)

One (Layer 5C) of the nine samples from Yuku rockshelter, in the lower montane forest zone, had insufficient pollen and spores for analysis. The pollen record commenced c. 17,000 cal BP, around the end of the LGM, when ice cover remained near maximum levels in the region until after c. 15,400-15,000 BP, when it retreated rapidly over the next 4000 years approaching the Holocene (Barrows *et al.* 2011; Mills *et al.* 2016). Layer 6 showed a very high charcoal concentration, possibly reflecting an on- or off-site burning episode (Fig. 2). Except for the uppermost sample, the pollen assemblages were overwhelming dominated by Piper type pollen. Small shrubs or semi-climbers of this genera are part of the understory in the montane forests (Robbins 1961). This taxon has been used by people for a variety of functions, including food, medicines, rituals, rope, torches, tube snares, and every day and ceremonial dress (Powell 1976). Given that Piper is primarily insect-pollinated (Semple 1974), it does not have long distance pollen transport (LDT) on air currents; consequently, the high frequencies suggest either growing locally in the immediate vicinity of the rockshelter or use of Piper plants within the rockshelter. This pollen type was not included in the earlier Yuku study as pollen preservation was poor, with possible examples showing extreme ghosting (Moore *et al.* 1991) and decay, precluding definitive identification (Horrocks *et al.* 2008).

4.1.2. Kiowa (1500 m)

Four (K3, K8, K8f, and K11) of the eight samples from Kiowa rockshelter, which is situated at the transition of the lower and higher montane forest zones, had insufficient pollen and spores for analysis. The four remaining samples encompassed the Pleistocene-Holocene transition, from c. 12,000-10,000 cal BP. The pollen assemblages showed variably high *Nothofagus brassii* type pollen and fern (e.g., *Davallia* type) spore values (Fig. 3). The former has high pollen production and LDT (Macphail and McQueen 1983), so in this case perhaps reflects more the regional forest rather than vegetation in the immediate vicinity of the shelter. Alternatively, medium to large amounts of spherical verrucose phytoliths in these samples (see phytolith results below), possibly from the wood and leaves of *Nothofagus* (Kondo *et al.* 1994), could reflect use in the shelter. The wood of this taxon has been used by people for a variety of functions, including spears, digging sticks, spades, and house construction (Powell 1976).

The large numbers of fern spores in the lower samples could reflect variable rates of use of the shelter, allowing ground ferns to colonise damper parts between periods of more intensive human occupations (Fig. 3). Other fern spore types, namely Cyatheaceae and *Pteris* in the uppermost sample, have been used as a food source by people, notably *Cyathea* spp. and *Pteris moluccana* fronds (Croft 1982; Powell 1976). Charcoal concentrations were generally high, suggesting on-site activities within the shelter by people during the associated time periods.

4.1.3. Wañelek (1710 m)

We discuss the Wañelek results in three parts: general trends through the stratigraphy (Samples W1-W8), the multiphase occupation c. 4100-2800 cal BP, and the burning event at c. 17,700-17,000 cal BP. Samples W1-W8 were collected through the stratigraphy in Area D, excavation unit 105Z at the site (Table 1; see Gaffney *et al.* 2015b: Fig. 1) and likely extend from modern (W1) to potentially the Pleistocene (W8). The middle samples (W4-W5) are c. 5000-4000 cal BP in age. The inversion in the radiocarbon dates for charcoal from W4 and W5 is not unexpected in an open site location in a tropical environment, where pedogenesis could be expected to mix fine materials within active A and B horizons. This type of disturbance is reduced following burial of the palaeosol and thus removal from the zone of active pedogenesis. As a result of pedogenic admixture, plant microfossil assemblages within a soil unit likely include older materials, resulting in "smoothed" assemblages, with data points representing a "moving average" as the stratigraphy progressively builds up. Pedogenesis is less of a problem for preserved feature fills or discrete deposits, as they would not have been preserved if subjected to intensive pedoturbation.

The pollen assemblages from W8 to W1 show an initial, major decline of *Nothofagus* forest, replaced by lower montane, secondary forest and disturbance taxa from Samples W6 to W5 by c. 5000-4000 cal BP (Fig. 4). Coincident with the increased charcoal, this shift likely represents increased forest disturbance and clearance in the vicinity for settlement and agriculture. The high Poaceae and fern spore values in the uppermost sample (W1) reflect the open environment at Wañelek in the recent past.

The microfossil assemblages from Area B, excavation units 17/18B(I) and 17/18B(II), and from Area D, excavation unit 105Z, provide a window on environments and plant use during multiphase occupations c. 4100-2800 cal BP (following Bulmer 1977, 1991; Gaffney *et al.* 2015b) (Table 1). The several samples from feature fills, including of posthole and fireplaces/oven pits, are relatively undisturbed and directly associated with site use by people compared to the strata samples. Remains of the two starch-rich species identified at this site were found in multiple contexts: cf. *Colocasia esculenta* in B(I) posthole fill and Layers 4 and 5, and cf. *Castanopsis acuminatissima* in WB(I)11ph posthole fill and in all 105Z samples (Fig. 6). *Colocasia esculenta* is a major staple in the Indo-Pacific region and New Guinea (Li 1970; Yen 1973; Denham 2011) and its microfossil presence suggests cultivation in the vicinity, while *C. acuminatissima* is a major Highlands staple. *Castanopsis acuminatissima* nuts are thought to have been widely exploited in the Highlands for millennia, with the trees almost certainly managed by people, resulting in increased density. A later phase (c. 3000 cal BP) during this occupation period is associated with pottery, including a sherd likely from the north coast (Gaffney *et al.* 2015b).

Multiple samples associated with a major burning event c. 17,700-17,000 cal BP were collected in Area D, excavation unit 101Y, Layers 6-9 (including multiple samples from the Layer 9 contexts). These samples all show broadly comparable phytolith frequencies (Fig. 6) and apparently no economic species. The event deposited large amounts of wood charcoal that are well-preserved in this portion of the site.

4.1.4. Manim (1770 m)

All 11 samples from Manim rockshelter, a little more elevated than the open site of Wañelek in the montane forest zone, had sufficient pollen and spores for analysis. The profile encompasses the late Holocene, from c. 2750 cal BP. The samples showed initially high pollen values of *Nothofagus brassii* type, followed by increasing values of a diverse range of tree, shrub, herbaceous, and fern pollen and spore types at the expense of *Nothofagus* (Fig. 5). The more dominant types are Casuarinaceae, *Lithocarpus* type, *Macaranga*, *Nauclea* type, *Piper* type, Proteaceae, *Trema*, and Poaceae. The less abundant types are *Dodonaea* type, *Engelhardia*, Moraceae/Urticaceae, Proteaceae, Rutaceae, Sapotaceae, Amaranthaceae/Chenopodiacerae, Asteraceae, Labiatae, and *Aspidium* type. As with Wañelek (Fig. 4), higher charcoal concentrations appear linked to this change, most likely a result of increased vegetation disturbance and eventual clearance by people.

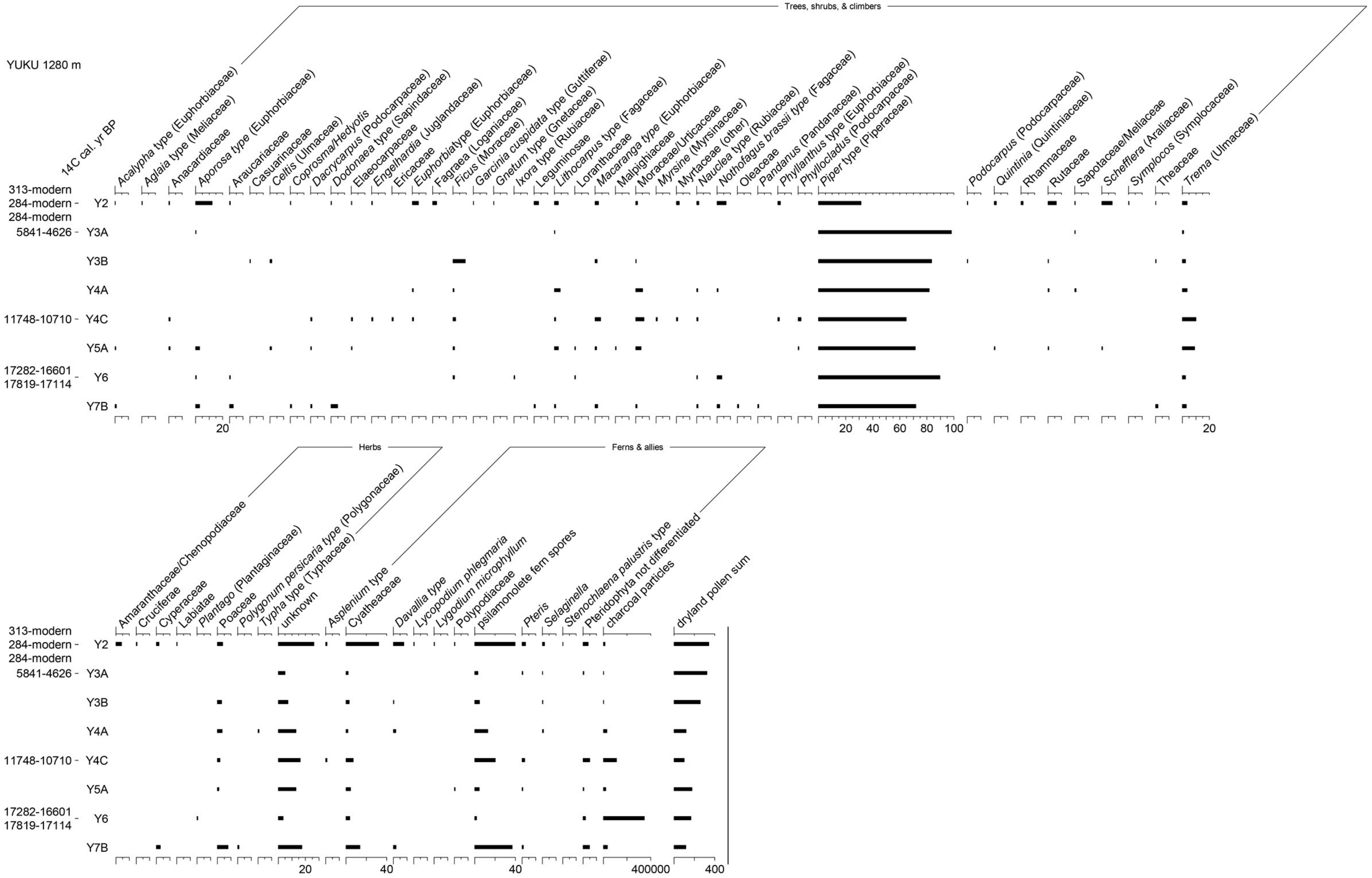

Figure 2: Pollen percentage diagram of samples from Yuku (ferns, fern allies, and *Anthoceros* type not included in sum)

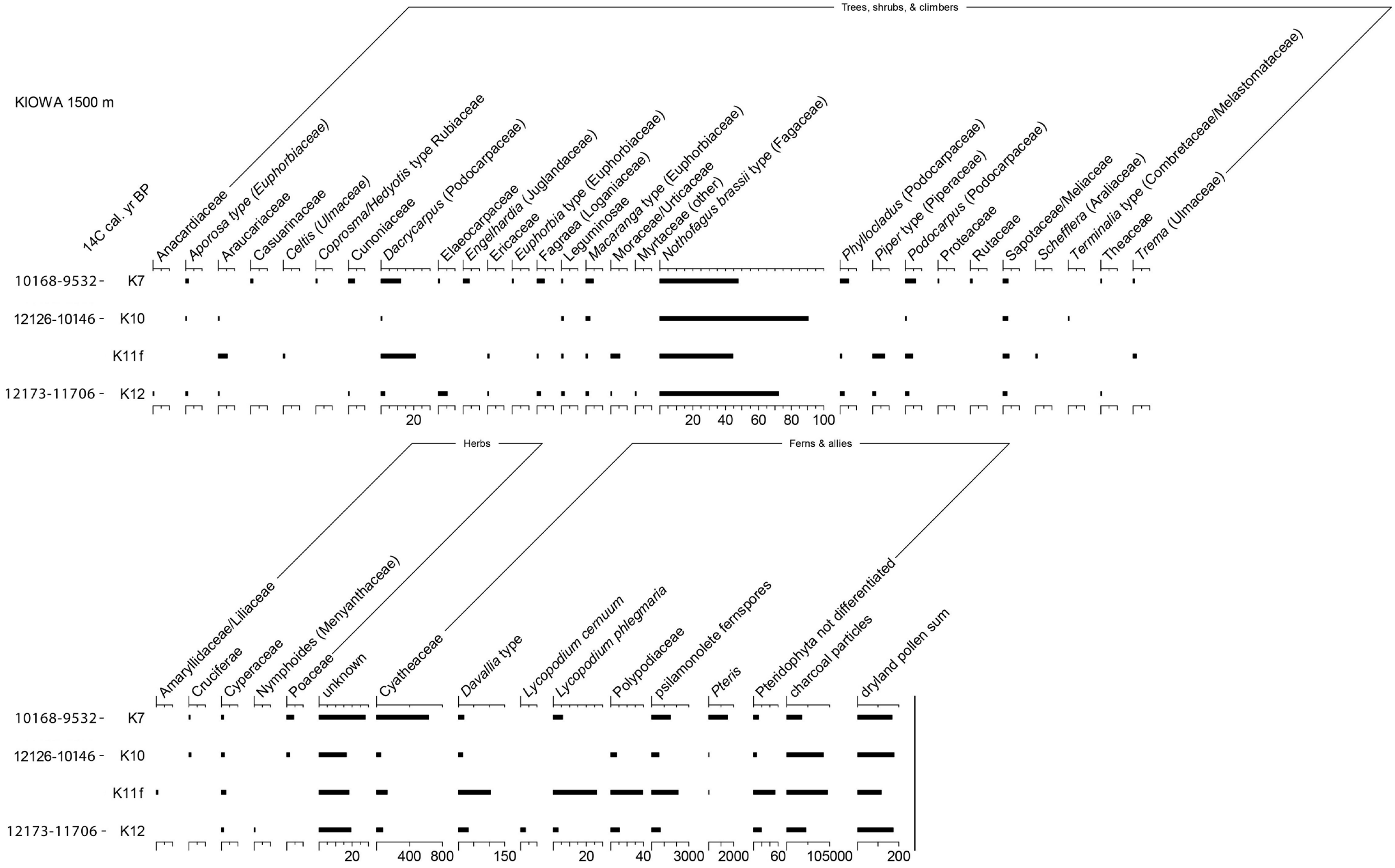

Figure 3: Pollen percentage diagram of samples from Kiowa (ferns and fern allies not included in sum)

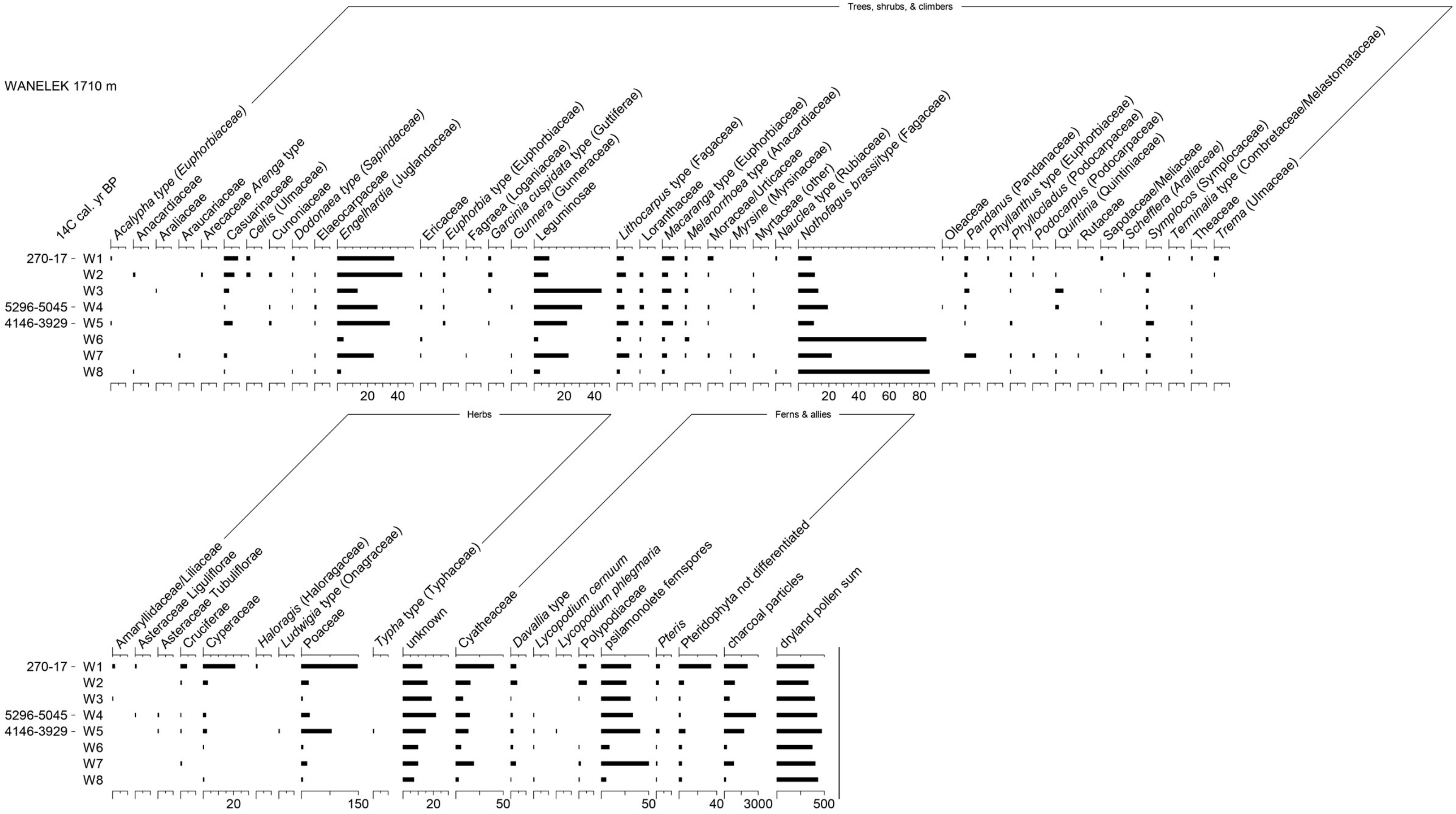

Figure 4: Pollen percentage diagram of samples from Wañelek (Poaceae, ferns, and fern allies not included in sum)

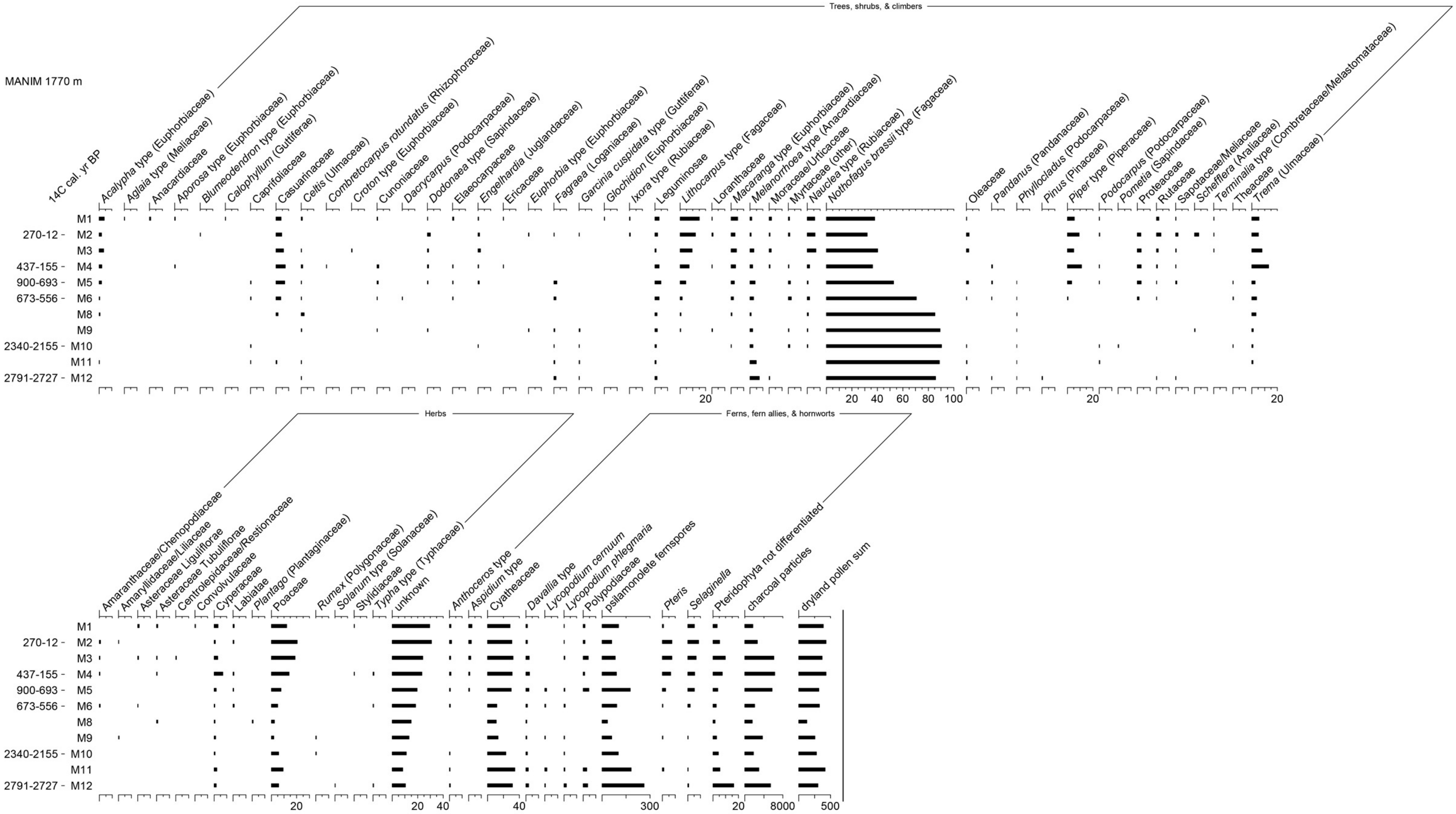

Figure 5: Pollen percentage diagram of samples from Manim (ferns and fern allies not included in sum)

4.2. Phytoliths

All samples except Layer 5C at Yuku had sufficient phytoliths for analysis. The phytolith assemblages of all except the Kiowa samples were dominated by Poaceae leaf phytoliths, notably bulliform type (Fig. 6). Although the coincident pollen assemblages show variable frequencies of Poaceae pollen (Fig. 2), the high Poaceae phytolith frequencies likely reflect the relatively very high production rate of phytoliths within this family relative to most other taxa (Piperno 2006). Various uses of grasses by people in rockshelters, especially for bedding, should also be considered.

The Kiowa samples had several high bulliform percentages and relatively high values of spherical verrucose phytoliths (Fig. 6). The lowermost sample at this site (Layer 12) had a high percentage of spherical nodular phytoliths. These non-Poaceae phytoliths, which at this stage of New Guinea Highlands phytolith research are deemed to be from unknown taxa, could be from woody tissue or leaves (Kondo *et al.* 1994).

Another major difference between the sample groups is that the Wañelek WB samples had higher values of another type of Poaceae leaf phytolith, namely rondel, potentially from several grass subfamilies (Fig. 6). These phytoliths could reflect the more open, ridge-top location of Wañelek compared to the other three, rockshelter sites.

Changes in up-profile phytolith frequencies in the Manim spectra were limited to small increases in rondel type Poaceae leaf phytoliths and subsequently in spherical verrucose type (Fig. 6). Although subtle, these changes could be environmental or reflect use by people of different plant taxa. Small amounts of Bambusoideae and saddle Poaceae leaf phytoliths were present in most of the Manim samples while notably lacking in samples from the other sites. Several bamboo (Bambusa) species have numerous uses by people, from construction materials and for cooking, to making musical instruments and for food (Powell 1976).

The intra- and inter-site variations in phytolith types probably reflect local environmental conditions and use of different plant taxa by people. Although the predominance of Poaceae phytoliths in this case could in some cases reflect open grassland environments, the aforementioned very high production of Poaceae phytoliths compared to most other taxa should be borne in mind.

A single *Musa* (banana) sp. leaf phytolith was found in Layer 3A from Yuku (Fig. 6; Fig. 7A). Detailed descriptions of *Musa* phytoliths are well documented (Horrocks *et al.* 2009; Lentfer 2009; Mindzie *et al.* 2001; Vrydaghs *et al.* 2009). *Musa* species were likely initially domesticated in the New Guinea region (Perrier et al. 2011). Although many *Musa* cultivar groups are eaten by people, some, including the endemic highland *Musa ingens*, are not usually, yet they can be used for many other purposes (Kennedy 2009).

Other biosilicates, namely fragments of diatoms and sponge spicules, were found in some samples from Wañelek and Kiowa (Figure 6). These fragments are from aquatic sources.

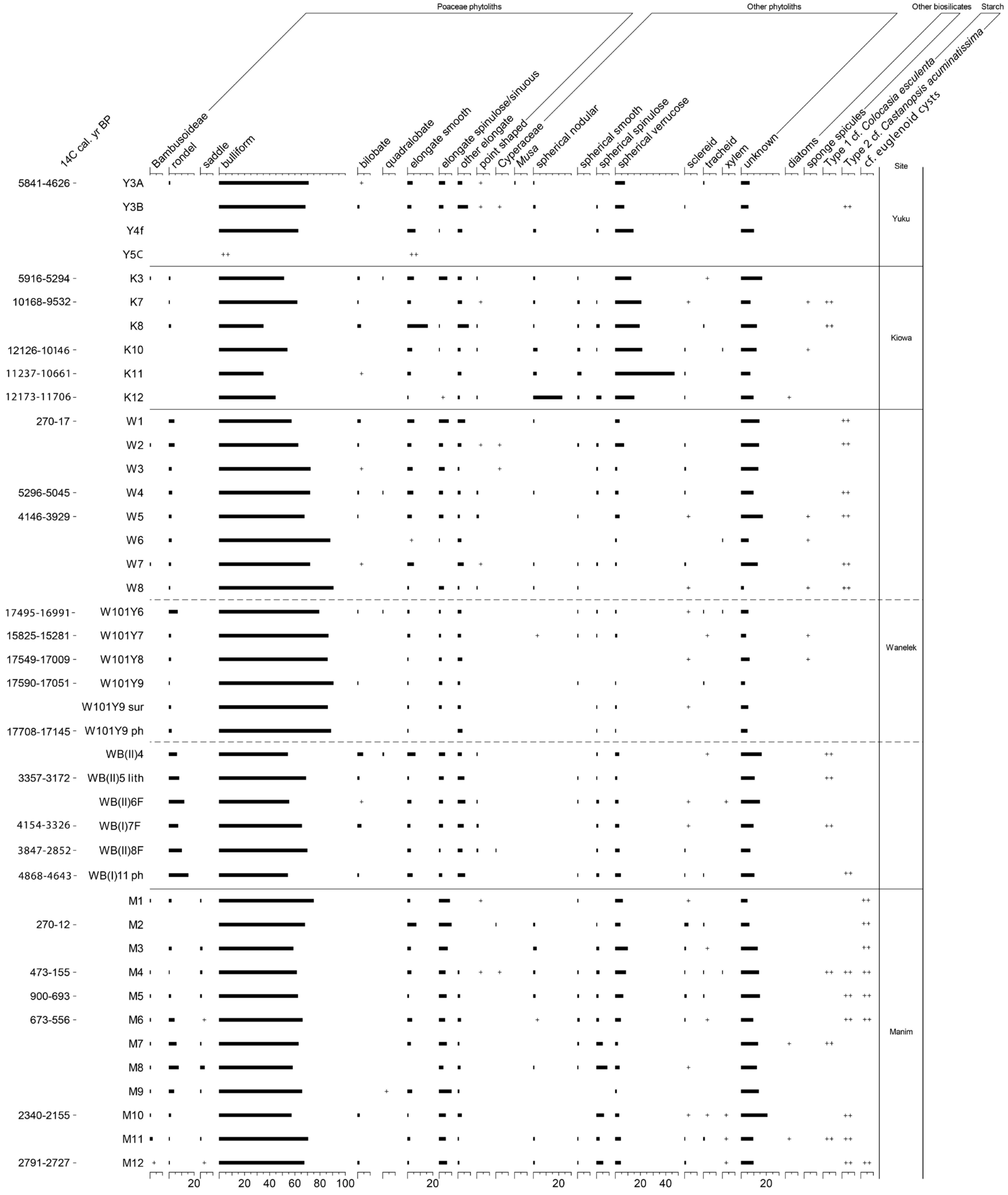

Figure 6: Phytolith percentage, starch, and euglenoid cyst diagram of samples from Yuku, Kiowa, Wañelek, and Manim (diatoms and sponge spicules not included in sum, + = found after count, ++ = present).

4.3. Starch

Given the great diversity of the New Guinea native flora (and potentially its starch) and that ancient starch is under-researched compared to phytoliths and especially pollen, the starch results should be treated cautiously. Two types of starch were identified in this study. Type 1, found in samples from Kiowa, Wañelek, and Manim, comprised abraded amyloplast (organelles specialised for starch grain synthesis and storage) clumps and fragments thereof, most probably derived from the corms of cf. *Colocasia esculenta* (taro) (Fig. 6, Fig. 7B-E; Fig. 8-11). The archaeological microfossils are consistent with detailed descriptions of *C. esculenta* starch grains (Fullagar *et al.* 2006; Horrocks *et al.* 2023, 2024a; Horrocks and Weisler 2006; Loy *et al.* 1992; Seidemann 1966). *Leucocasia gigantea* (syn. *Colocasia gigantea*) has similar starch grains (Loy *et al.* 1992) but is ruled out because its natural range does not include Melanesia or Australia (Matthews 2004).

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 7B-E, 8, and 9 when viewed in light microscopy (e.g., Burley *et al.* 2018; Flexner *et al.* 2024; Horrocks *et al.* 2007, 2008a, 2008b, 2011, 2012a, 2012b, 2015, 2020, 2022, 2023a, 2023b, 2024a, 2024b; Horrocks *et al.* 2025, in press; Horrocks and

Nunn 2007, Horrocks and Thomas 2022; Horrocks and Weisler 2006; Kirch *et al.* 2024, Peterson *et al.* 2020). 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.

The antecedent of *Colocasia esculenta* evolved in Southeast Asia (Matthews 1991, 2014) and is thought to have expanded to Sahul during the late Miocene to late Pliocene (Matthews 1991; Ahmed *et al.* 2020). There are several lines of archaeological evidence for exploitation and possible cultivation of *C. esculenta* in New Guinea from c. 10,000 yr BP (Fullagar *et al.* 2006). A recent study of DNA diversity in cultivated and wild *C. esculenta* specimens did not support the hypothesis of domestication in New Guinea (Ahmed *et al.* 2020). However, it is possible that this species underwent recurrent localised domestications across the Indo-Pacific in the past, with recurrent subsequent marginalisation and loss of many local varieties following sequential introductions of cultivars, initially diploids and then triploids, from a few source regions on mainland and island Southeast Asia (Denham 2018). The cf. *C. esculenta* findings were all in substrates dated <c. 4700 cal BP and are associated with multiple occupations at Wañelek from 4700-2800 cal BP and agricultural development in the Upper Wahgi Valley at Manim (see Bayliss-Smith *et al.* 2017) (Fig. 6).

Type 2 starch found scattered on slides of the lowermost samples at Wañelek and Manim, and in Sample Y3B at Yuku, comprised large individual grains, up to c. 40 µm (occasionally more) along their longest axis. The grains are irregular polyhedral with a centric hilum (the point around which starch layers are deposited) (Fig. 6; Fig. 12-14). These features are consistent with starch grains from the nuts of the common native tree *Castanopsis acuminatissima*. All the grains showed some degree of decay, with only faint visibility in cross-polarised light. Using quadratic discriminant analysis of a variety of subsistence species' starch grains of the New Guinea Highlands, Field *et al.* (2020) showed that *C. acuminatissima* grains were relatively easy to separate from other species in their reference collection (see also Li *et al.* 2022 for starch descriptions of several Southeast Asian *Castanopsis* spp.). The nuts of this species have been used as a food source and the wood used for shields and house construction (Powell 1976).

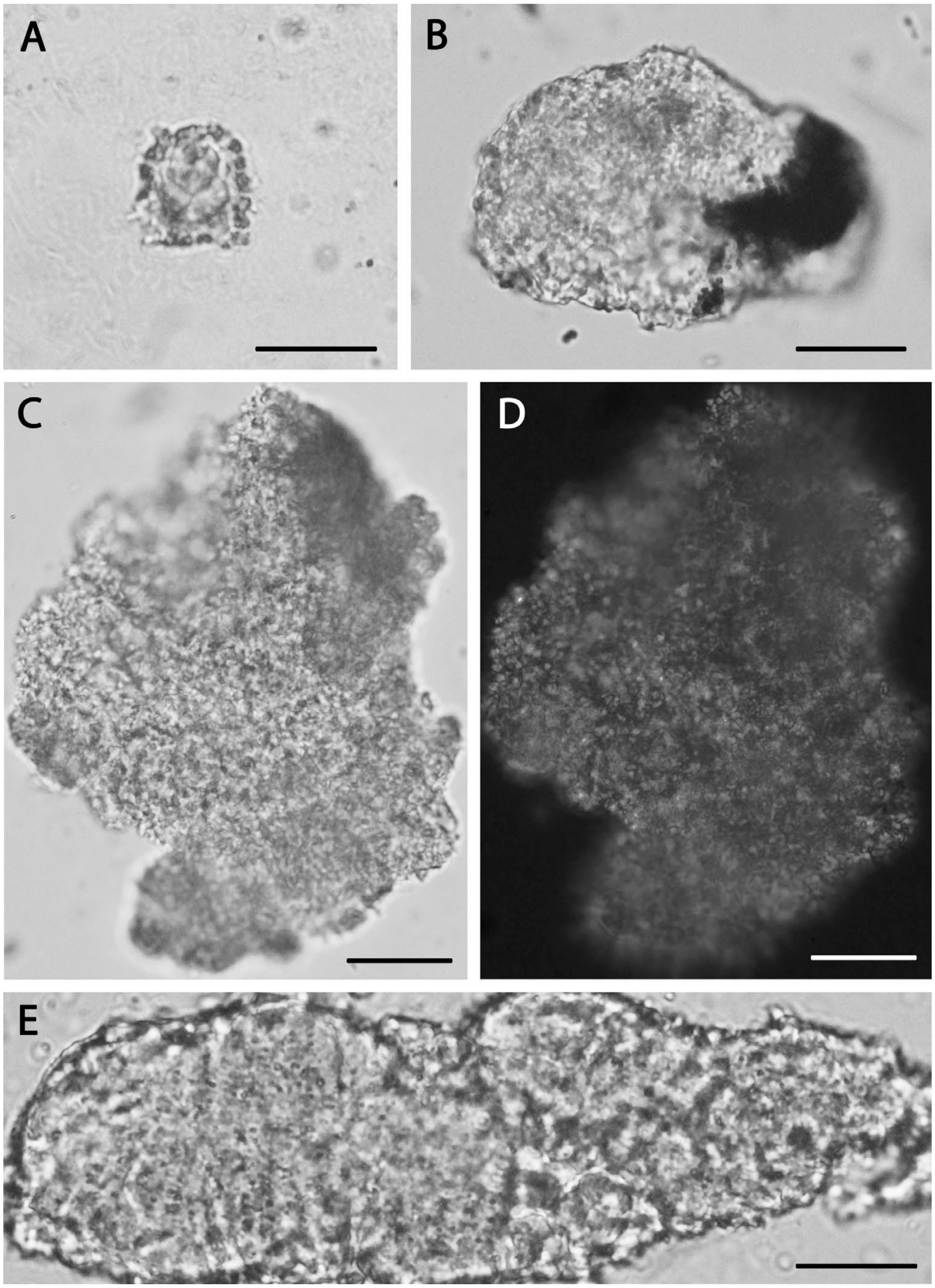

Figure: 7. Fossil *Musa* sp. phytolith and cf. *Colocasia esculenta* (Type 1) starch. 600x; black background = cross-polarised light (CPL); scale bars = 20 µm. The sample labels (in brackets) refer to the Yuku, Kiowa, and Manim sites, and are explained in Table 1. A (Y3A) *Musa* sp. phytolith, showing characteristic rectangular/squarish shape, basal protuberances, and raised crater. B (K8), C, D (M7), E (M11) amyloplast material containing high concentration (up to 1000s) of densely packed, tiny angular starch grains (cf. *C. esculenta* starch, Fig. 10; Fig. 11). Hila appear mostly as dark grey/black dots, imparting a grainy appearance to the mass. D is the material in C, showing high visibility in CPL (cf. *C. esculenta* starch, Fig. 10C).

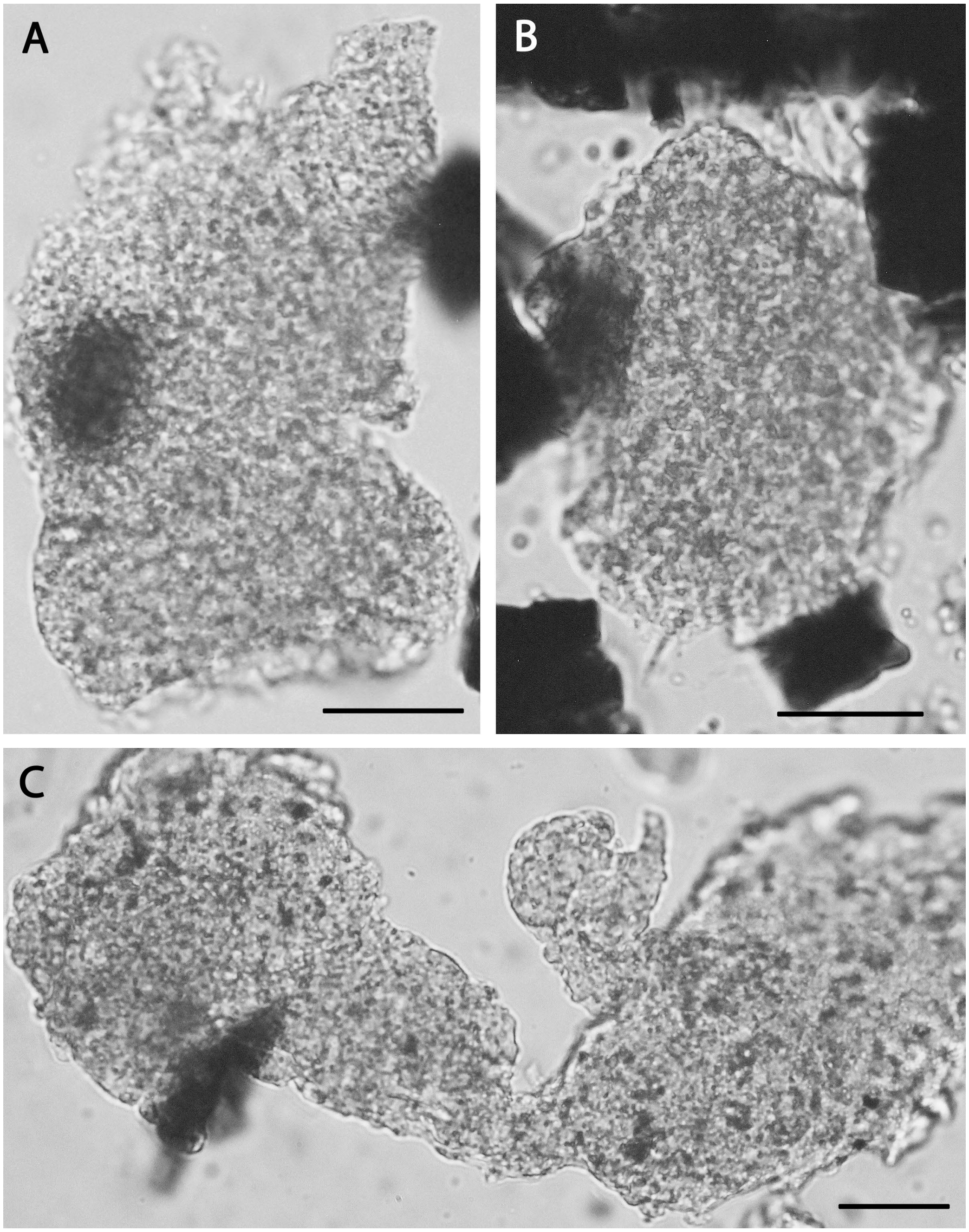

Figure 8: Fossil cf. Colocasia esculenta (Type 1) starch, continued. 600x; scale bars = 20 µm. The sample labels (in brackets) refer to the Wañelek and Manim sites and are explained in Table 1. A, B (WB7), C (M4) amyloplast material containing high concentration (up to 1000s) of densely packed, tiny angular starch grains (cf. C. esculenta starch, Fig. 10; Fig. 11). Hila appear as dark grey/black dots, imparting a grainy appearance to the mass.

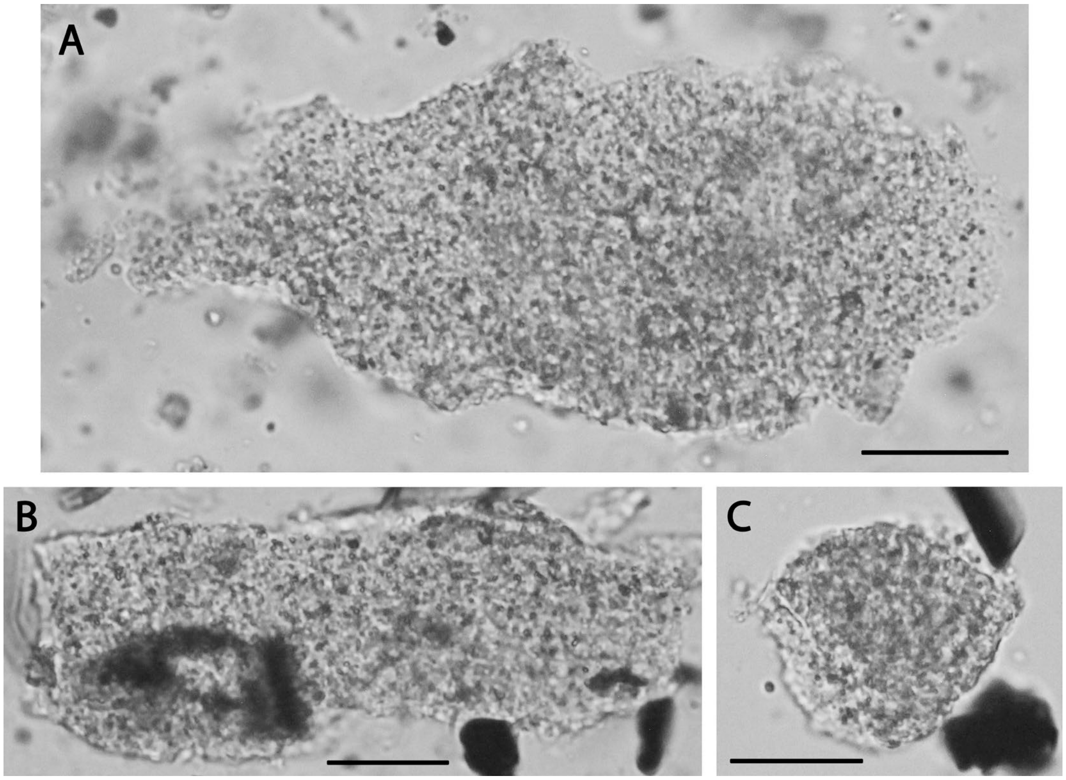

Figure 9: Fossil cf. *Colocasia esculenta* (Type 1) starch, continued. The sample labels (in brackets) refer to the Wañelek and Kiowa sites and are explained in Table 1. A (WB5), B (K7), C (WB7) amyloplast material containing high concentration (up to 1000s) of densely packed, tiny angular starch grains (cf. *C. esculenta* starch, Fig. 10; Fig. 11). Hila appear as dark grey/black dots, imparting a grainy appearance to the mass.

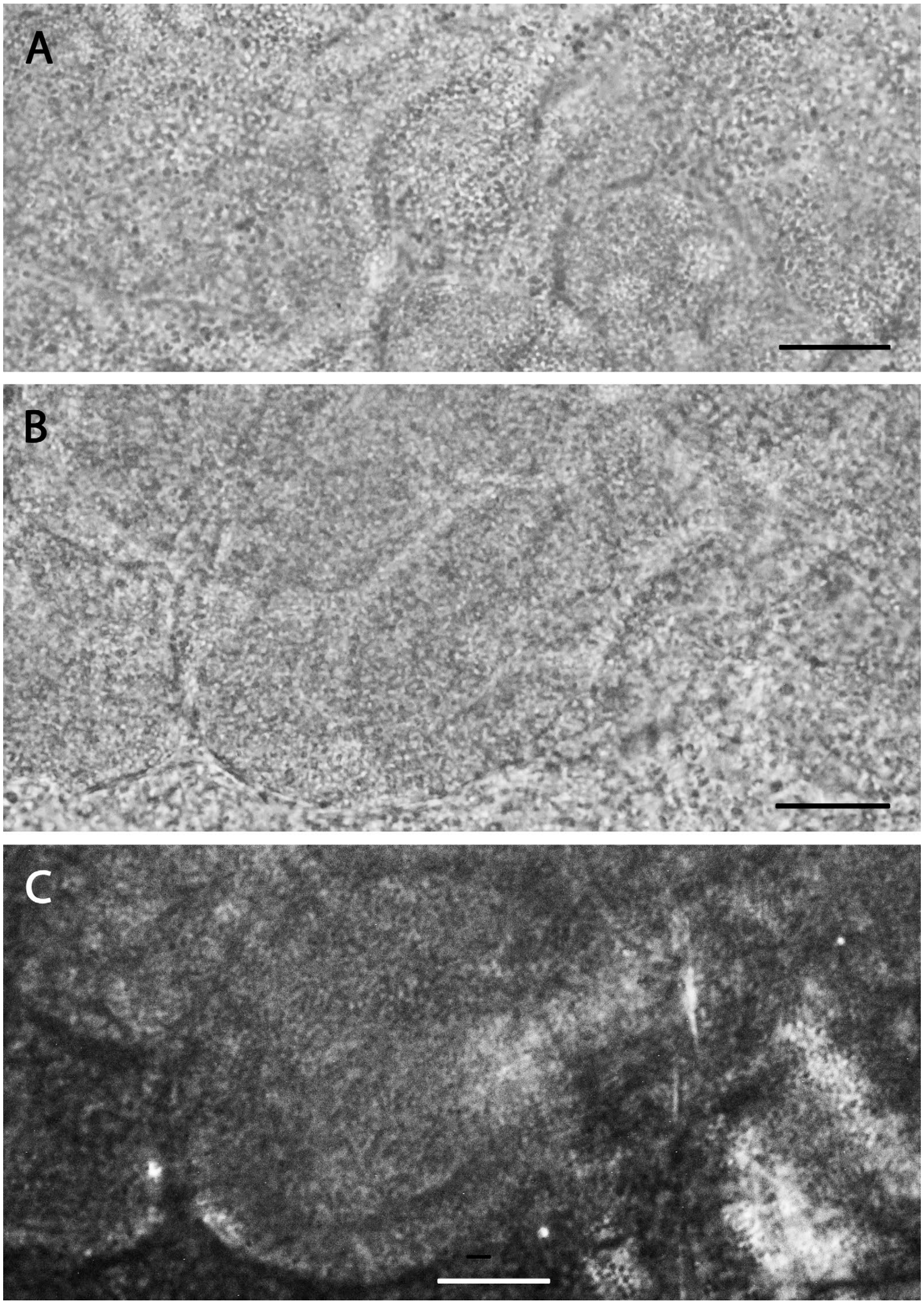

Figure 10: Modern reference *Colocasia esculenta* starch. 600x; black background = cross-polarised light (CPL); scale bars = 20 µm. A-C amyloplast material containing high concentration (up to 1000s) of densely packed, tiny angular starch grains. Hila appear as dark grey/black dots, imparting a grainy appearance to the mass. C is the material in B, showing high visibility in CPL.

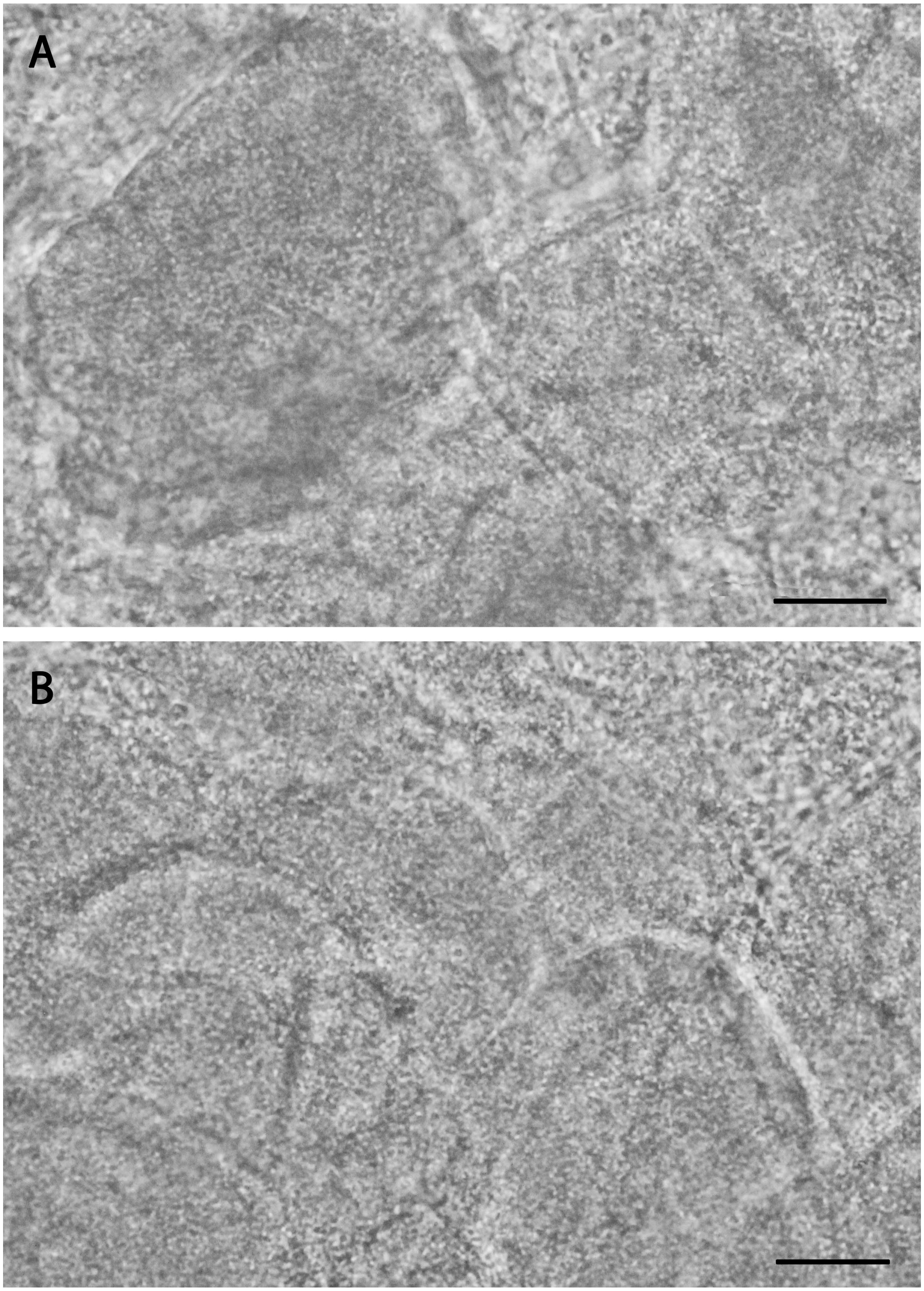

Figure 11: Modern reference *Colocasia esculenta* starch. 600x; scale bars = 20 µm. A, B amyloplast material containing high concentration (up to 1000s) of densely packed, tiny angular starch grains. Hila appear as dark grey/black dots, imparting a grainy appearance to the mass.

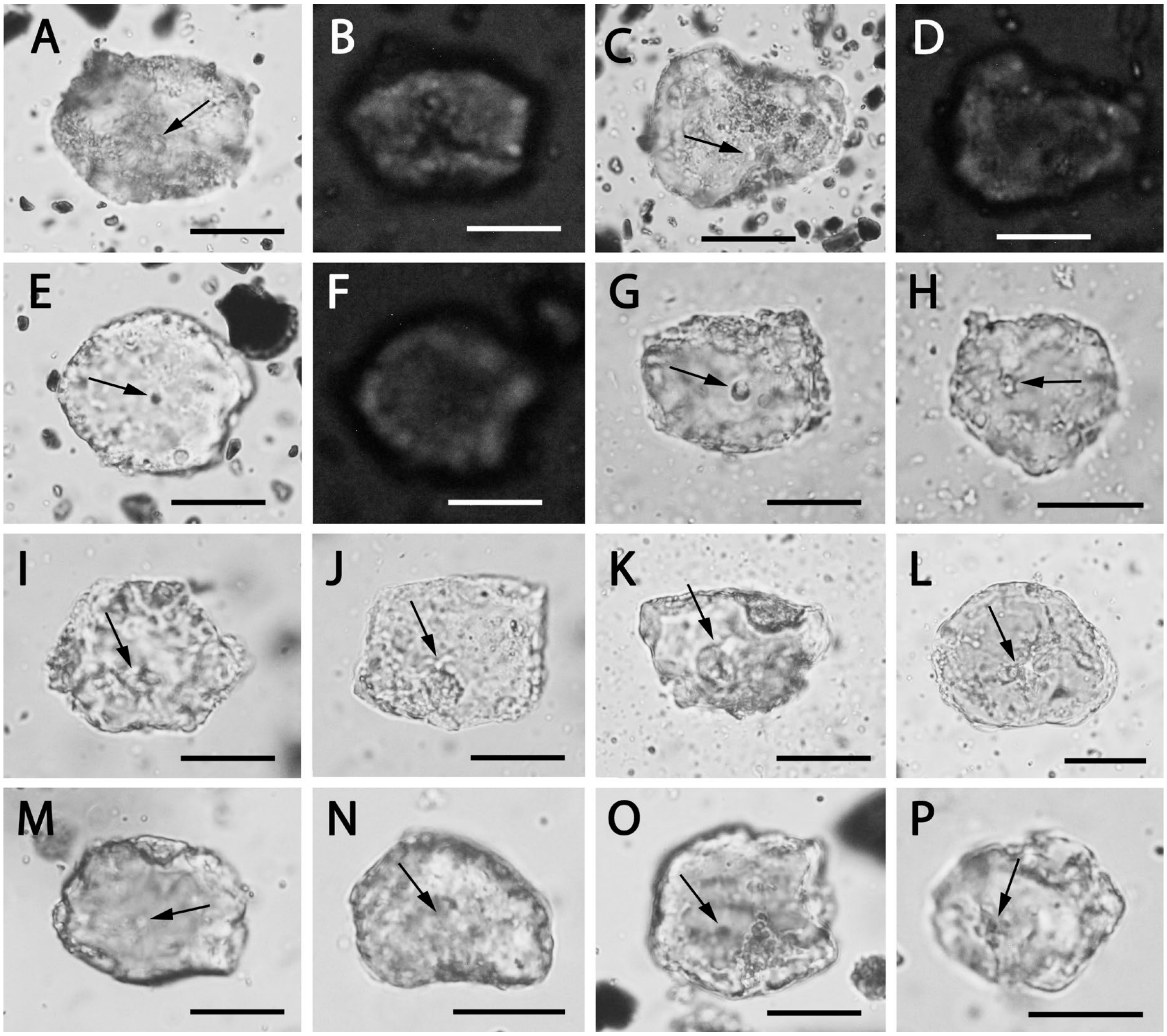

Figure 12: Fossil cf. *Castanopsis acuminatissima* (Type 2) starch. 600x; black background = cross-polarised light (CPL); scale bars = 20 µm. The sample labels (in brackets) refer to the Yuku, Manim, and Wañelek sites, and are explained in Table 1. A-F (Y3B), G, H (M12), I (M10), J (M6), K (M5), L (WB 11 ph), M (W8), N, O (W5), P (W4). A-P individual, degraded, irregular polyhedral grains (cf. *C. acuminatissima* starch, Fig. 13; Fig. 14). Centric hila appear as dots or circles (arrows), often fissured (I, J, L, P) and occasionally expanded (J, K). B, D, and F are the grains shown in A, C, and E, respectively, showing some visibility in CPL, with clear extinction cross not preserved (cf. *C. acuminatissima* starch, Fig.13B; Fig. 14B).

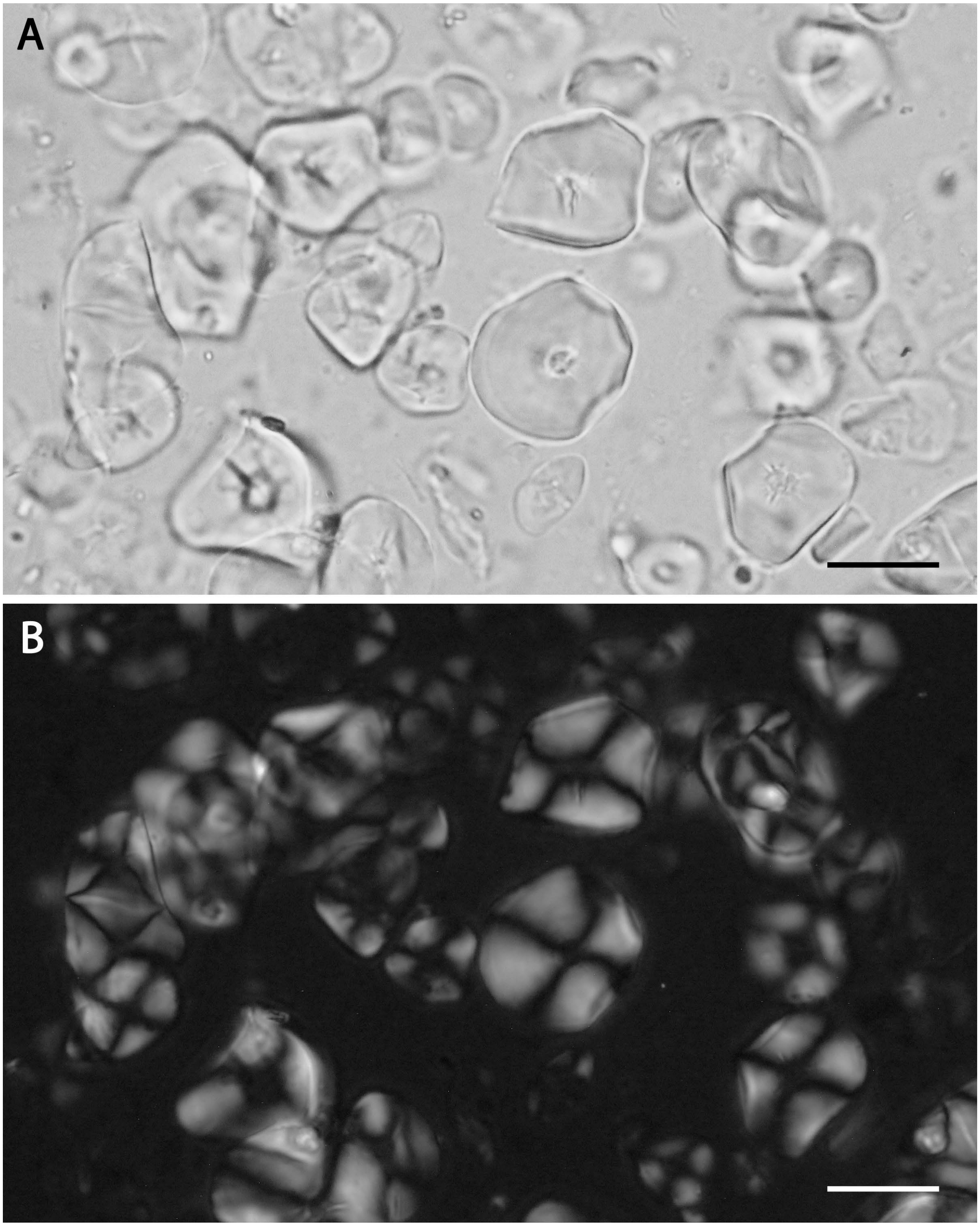

Figure 13: Modern reference *Castanopsis acuminatissima* starch. 600x; black background = cross-polarised light (CPL); scale bars = 20 µm. A scattered individual grains, characteristically irregular polyhedral in shape, with centric hila. B shows A in CPL, with distinct centric extinction crosses.

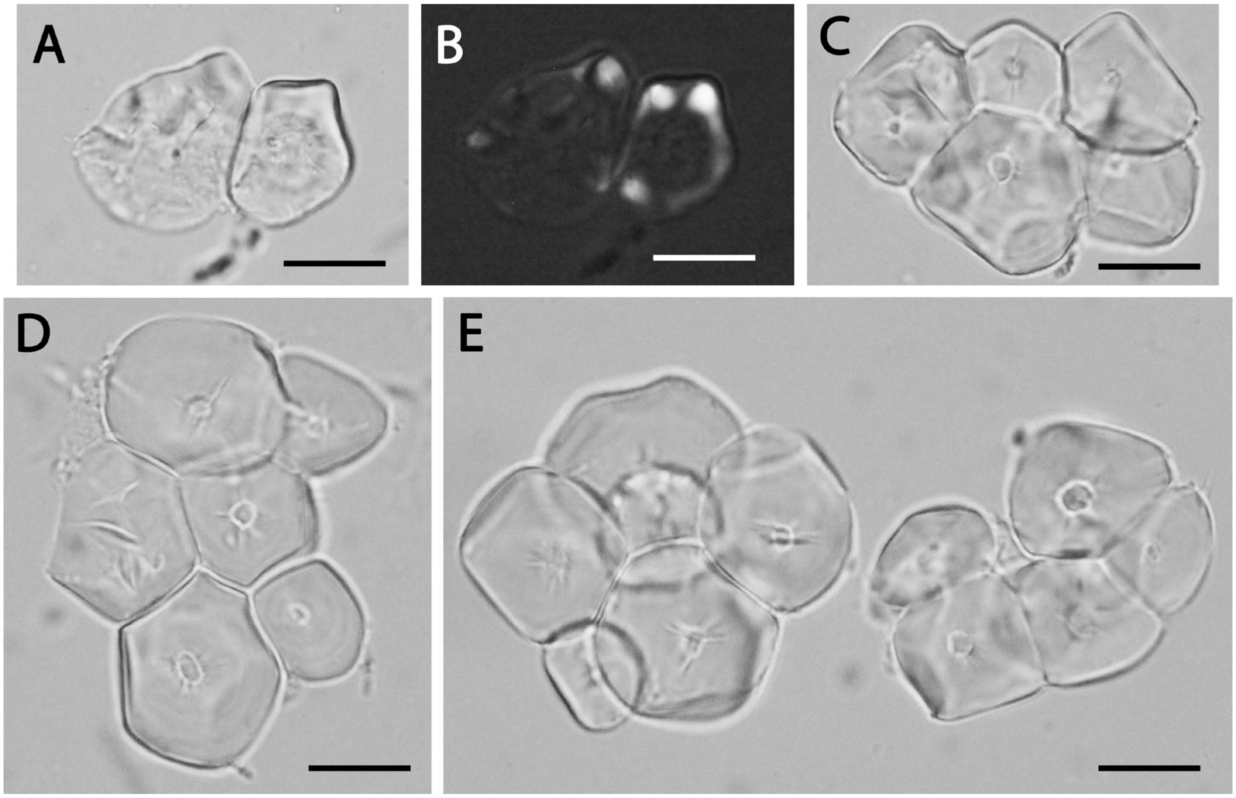

Figure 14: Modern reference *Castanopsis acuminatissima* starch. 600x; black background = cross-polarised light (CPL); scale bars = 20 µm. A-E clumps of grains, characteristically irregular polyhedral in shape, with centric hila. B shows A in CPL, with indistinct centric extinction crosses, occasionally found in this taxon.

4.4. Euglenoid cysts

Another type of microfossil, namely euglenoid cysts, was found in the starch extractions. These microfossils were observed in Samples M1-6 and M12 from Manim Rockshelter (Fig. 6; Fig. 15). Only one specimen was found in Sample 12, while the other samples had 10-20+ specimens per slide. The cysts are discoidal, circular, 46-49 x 23-26 µm in diameter, with concentric, fingerprint-like surface ornamentation. These features are consistent with those of a species of *Chromotriletes* s.l. (van de Schootbrugge *et al.* 2024). The cysts appear to be from euglenoids, single celled protists that inhabit shallow freshwater ponds and freshwater environments with abundant organic matter (Gojdics 1953; Hindák *et al.* 2000; Leander *et al.* 2017).

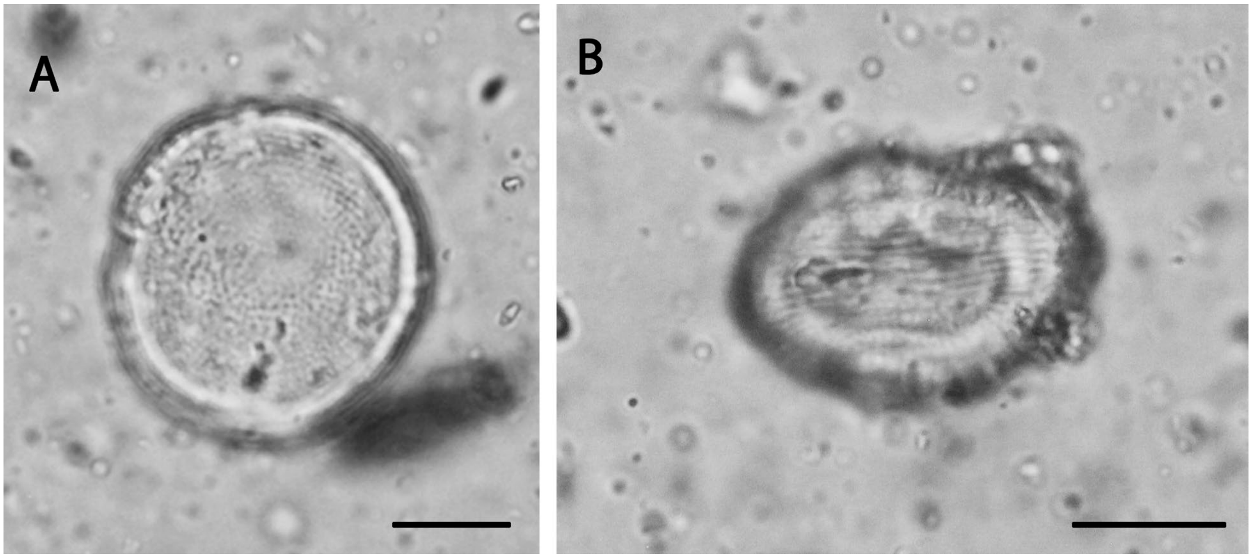

Figure 15: Fossil cf. euglenoid cysts. 600x; scale bars = 20 µm; from Manim Sample M5. A, B show characteristic discoidal, circular shape, with concentric, fingerprint-like surface ornamentation. B is a side view.

5. Discussion

The combined microfossil analyses at four archaeological sites in the Highlands of Papua New Guinea show changes in vegetation history in the vicinity of each site, and information on plant use within domestic contexts. The interpretative value of the results varies between sites.

5.1. Yuku (1280 m)

The reliability of the Yuku chronology is currently uncertain. Gaffney *et al.* (2021) derived a chronology from the available radiocarbon evidence, interpreting dates for multiple layers. Based on previous radiocarbon determinations, Denham (2016) suggested that disturbance or contamination of organic materials had occurred. In contrast to those of Wañelek and Manim, the Yuku pollen data do not show clear temporal trends; clear trends could be expected if the strata represent climatic warming from the end of the LGM to the present (Fig. 2; Fig. 4; Fig. 5). This potential anomaly could reflect stratigraphic disturbance or contamination and is perhaps supported by the high *Piper* pollen frequencies throughout the stratigraphy. It is possible that the coarse matrix, including lithics and faunal material, is less disturbed (following Gaffney *et al.* 2021), but that there has been displacement of fine materials (<2 mm) post-depositionally or during excavation. If this is the case, the Yuku microfossil data generally, including the *Musa* phytolith in Layer 3A, are chronologically unreliable.

5.2. Kiowa (1500 m)

Kiowa has a generally accepted reliable chronology, with chronostratigraphic agreement replicated in multiple dating exercises on different material types (Bulmer 1966; Denham 2016; Gaffney *et al.* 2021). The four samples with sufficient pollen for analysis date to the beginning of the Holocene or the Holocene-

Pleistocene transition. The high *Nothofagus* values represent upper montane forest in the vicinity, which was presumably replaced by lower montane forest during the warmer, stable early Holocene (Fig. 3). Fluctuating and lower frequencies of bulliform Poaceae phytoliths compared to some of the other sites examined here, could reflect the persistence of local forest to the mid Holocene (Layer 3) (Fig. 6). The occurrence of cf. *Colocasia esculenta* starch in Layers 7 and 8, dating to c. 10,170-9530 cal BP, likely represents gathering and processing of the wild form, although the possibility of very early cultivation cannot be ruled out.

5.3. Wañelek (1710 m)

We discuss the Wañelek results in three parts: general trends through the stratigraphy (Samples W1-W8), the multiphase occupation c. 4100-2800 cal BP, and the burning event at c. 17,700-17,000 cal BP.

Samples W1-W8 were collected through the stratigraphy in Area D, excavation unit 105Z at the site (Table 1; see Gaffney *et al.* 2015b: Fig. 1) and likely extend from modern (W1) to potentially the Pleistocene (W8). The middle samples (W4-W5) are c. 5000-4000 cal BP in age. As discussed previously, the inversion in the radiocarbon dates for charcoal from W4 and W5 represents pedogenesis, which would admix fine materials within active A and B horizons. As a result of pedogenic admixture, plant microfossil assemblages within a soil unit likely represent a "moving average" as the stratigraphy progressively builds up. As noted, pedogenesis is less of a problem for preserved feature fills or discrete deposits, because they would not have been preserved if subjected to intensive pedoturbation. The pollen assemblages from W8 to W1 show an initial, major decline of *Nothofagus* forest, replaced by lower montane, secondary forest and disturbance taxa from Samples W6 to W5 by c. 5000-4000 cal BP (Fig. 4). Coincident with the increased charcoal, this shift likely represents increased forest disturbance and clearance in the vicinity for settlement and agriculture. The high Poaceae and fern spore values in the uppermost sample (W1) reflect the open environment at Wañelek in the recent past.

The microfossil assemblages from Area B, excavation units 17/18B(I) and 17/18B(II), and from Area D, excavation unit 105Z, provide a window on environments and plant use during multiphase occupations c. 4100-2800 cal BP (following Bulmer 1977, 1991; Gaffney *et al.* 2015b) (Table 1). The several samples from features fills, including of posthole and fireplaces/oven pits, are relatively undisturbed and directly associated with site use by people compared to the strata samples. Remains of the two starch-rich species identified at this site were found in multiple contexts: cf. *Colocasia esculenta* in B(I) posthole fill and Layers 4 and 5, and cf. *Castanopsis acuminatissima* in WB(I)11ph posthole fill and in all 105Z samples (Fig. 6). *Colocasia esculenta* is a major staple in the Indo-Pacific region and New Guinea (Li 1970; Yen 1973; Denham 2011) and its microfossil presence suggests cultivation in the vicinity, while *C. acuminatissima* is a major Highlands staple. *Castanopsis acuminatissima* nuts are thought to have been widely exploited in the Highlands for millennia, with the trees almost certainly managed by people, resulting in increased density. A later phase (c. 3000 cal BP) during this occupation period is associated with pottery, including a sherd likely from the north coast (Gaffney *et al.* 2015b).

Multiple samples associated with a major burning event c. 17,700-17,000 cal BP in Layers 6-9, Area D, excavation unit 101Y contained similar phytolith frequencies (Fig. 6), with no economic species.

5.4. Manim (1770 m)

The late Holocene stratigraphy at Manim post-dates the main periods of site occupation. Within the last 3000 years, the rockshelter was probably used as a temporary shelter or camp by people hunting, gathering, and gardening in the vicinity (Christensen 1975). Despite spanning only the last c. 3000 years, there are clear trends within the pollen record. *Nothofagus* forest predominated locally from c. 2800-2700 cal BP to c. 1000 cal BP (Fig. 5). The reduced but continuing *Nothofagus* presence after c. 1000 cal BP reflects the site's higher altitude; this forest type characterises Pleistocene and early Holocene periods at lower elevation sites in the Highlands (Denham 2007) (Fig. 5). Several plant taxa increased following the *Nothofagus* decline: some lower montane forest species, e.g., *Lithocarpus*; secondary forest, e.g., *Macaranga*; disturbance taxa, e.g., Poaceae; and species planted by people, such as *Casuarina*. The latter is planted in the Highlands around settlements and as a form of tree-fallowing in abandoned garden plots (Powell *et al.* 1975). The practice is thought to have originated c. 1200 cal BP in the Highlands (Haberle 2007), although potentially slightly earlier in the Upper Wahgi Valley (Sniderman *et al.* 2009). These transitions suggest the expansion of settlement and gardening up the Wurup Valley walls to the vicinity of Manim from c. 1000 cal BP, with concomitant reduction in forest cover.

The single apparent change in the phytolith record at Manim is the subtle, mid-profile peak in Poaceae rondel phytoliths (Fig. 6). This change is likely related to the forest clearance. Apart from this one effect, the changes in the large number of pollen taxa frequencies at Manim (Fig. 5) are not reflected in the phytolith record, illustrating the general limitations of phytolith analysis compared to pollen analysis in showing vegetation history. There are exceptions to this, e.g., in substrate types where pollen is not preserved and phytoliths are (Piperno 2006). Of similar microscopic size to pollen grains and spores, phytoliths are not adapted for dispersal, but will be carried as dust on wind, along waterways, and in fires, among other pathways. Methodological limitations are due to high overlap of many phytolith types between taxa and often high over-representation of a small number of taxa, notably Poaceae and Arecaceae (palms) (Piperno 2006). Regarding the latter, mostly very small amounts of Arecaceae phytoliths (spherical spinulose, from the fronds) in this study of four separate locations suggests that fronds were little utilised at the sites, if at all. (Arecaceae pollen is recorded only at Wañelek, in a small amount.) Similarly, although *Musa* leaf phytoliths are not over-represented in phytolith spectra, they are distinctive (Mindzie *et al.* 2001) and commonly found in Oceania (Horrocks 2020), so the finding of only a single *Musa* phytolith in this study (at Yuku) is perhaps surprising given the importance of this staple genus in the Highlands, and the known common use of leaves in food preparation.

The starch analysis at Manim identifies the two economic species: the widely utilised nut of cf. *Castanopsis acuminatissima* (Layers 4-7 and 10-12) and corms of cf. *Colocasia esculenta* (Layers 4, 7, and 11) (Fig. 6). The latter in late Holocene contexts at Manim was probably cultivated in adjacent gardens rather than collected from the wild.

The cf. euglenoid cysts (an aquatic marker) found in Manim rockshelter could reflect processing of wetland resources by people, such as Osteichthyes (boney fish) (Sutton *et al.* 2009).

6. Conclusion

The combined charcoal particle, phytolith, and starch grain analyses at four archaeological sites in the New Guinea Highlands have yielded new information on vegetation history and plant exploitation. Although the analyses have been constrained by the sampling and record keeping of the original excavators, the pairing of pollen/charcoal particle and phytolith/starch analyses, as well as many radiocarbon dates for the same contexts, has increased the potential rigour of interpretation.

The pollen records show different histories of palaeoecological change for sites at different elevations, with the reduction in *Nothofagus* forests muted and later at higher elevations. The transitions to other vegetation communities during the Terminal Pleistocene and early Holocene at lower elevations (e.g., Kiowa) were primarily climatically driven, namely, the establishment of mixed lower montane forests following climatic warming after the LGM, whereas the transitions at higher elevation were primarily anthropic, namely, disturbance and clearance for settlement and agriculture (e.g., Wañelek and Manim). Frequency distributions of major phytolith types do not readily compare to the pollen records, which could reflect differences between on-site and off-site microfossil taphonomy, selective use of some species on site (e.g., Poaceae for bedding in rockshelters and for construction materials in buildings), and relatively very high production of Poaceae phytoliths diluting other taxa in the counts.

The starch analysis has yielded tentative results of interest, in particular the use of *Colocasia esculenta* during a multiphase occupation c. 4700-2800 cal BP at Wañelek, and the persistent use from c. 2800-2700 cal BP to the recent past at Manim. People using these sites were likely growing this crop in the adjacent landscape, and thus, were associated with agricultural communities. Present day cultivation in the New Guinea Highlands has a mean usual altitudinal range up to 1400 m and an extreme altitudinal range up to 2760 m (Bourke 2010). Expanded reference collections and technical refinement should advance the taxonomic specificity and accuracy of phytolith and starch analyses in the Highlands, and adjacent regions, as they become more routinely included in archaeological investigations.

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Data Availability Statement.

Data is 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, T.P.D., M.H.; investigation, M.H., S.v.d.K.; resources, M.H., S.v.d.K., T.P.D., S.B.; writing—original draft preparation, M.H., T.P.D., S.v.d.K.; writing—review and editing, M.H., T.P.D., S.v.d.K.; visualization, M.H., T.P.D.; funding acquisition, M.H., T.P.D., S.v.d.K., S.B.

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