

Archaeological identification of fragmented nuts and fruits from key Asia-Pacific economic tree species using anatomical criteria: Comparative analysis of *Canarium*, *Pandanus* and *Terminalia*

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ABSTRACT

The fats, protein and carbohydrates afforded by tree nuts and fruits are key resources for communities from Southeast Asia, through Melanesia, Australia and across Oceania. They are important in long-distance marine trade networks, large-scale ceremonial gatherings, and are core resources in a wide range of subsistence economies, including foraging systems, horticulture and swidden agriculture. Recent archaeobotanical evidence has also shown their deep-time importance, being amongst the earliest foods used in the colonisation of novel environments in Australia and New Guinea, as well as the later colonisation of Near and Remote Oceania. The archaeobotanical methods used to identify fruit and nut-derived plant macrofossils have been largely limited to use of morphological characters of near whole or exceptionally preserved remains, most commonly endocarps, the hard, nutshell-like interior layer of the fruit protecting the seed. Here we detail how anatomical characteristics of endocarps, visible in light and scanning electron microscopy (SEM), can be used with surviving morphological features to identify confidently the use of key Asia-Pacific economic trees, in this case, *Canarium*, *Pandanus* and *Terminalia*. Systematic anatomical description allows the identification of these important economic taxa, and separation from the remains of others such as *Aleurites* and *Cocos*, when found in a range of archaeological assemblages. This includes the often highly fragmented charred assemblages that can be recovered routinely from most sites with appropriate fine-sieving and flotation methods. These methods provide the basis for a more representative and nuanced understanding of ancient plant use, economy and social systems operating in the region and, being particularly useful in tropical regions, will broaden the archaeobotanical database on ancient foods globally.

Keywords: archaeobotany, macrofossils, endocarps, Sahul, scanning electron microscope (SEM)

RÉSUMÉ

Les graisses, les protéines et les glucides fournis par les noix et les fruits sont des ressources essentielles pour les communautés d'Asie du Sud-Est, de Mélanésie, d'Australie et d'Océanie. Ils sont importants dans les réseaux commerciaux maritimes à longue distance, les rassemblements cérémoniels à grande échelle et sont des ressources essentielles dans un large éventail d'économies de subsistance, y compris les systèmes de recherche de nourriture, l'horticulture et l'agriculture itinérante. Des preuves archéobotaniques récentes ont également montré leur importance dans le temps, étant parmi les premiers aliments utilisés dans la colonisation de nouveaux environnements en Australie et en Nouvelle-Guinée, ainsi que dans la colonisation ultérieure de l'Océanie proche et lointaine. Les méthodes archéobotaniques utilisées pour identifier les macrofossiles de plantes dérivées de fruits et de noix ont été largement limitées à l'utilisation de caractères morphologiques de restes presque entiers ou exceptionnellement préservés, le plus souvent des endocarpes, la couche intérieure dure en forme de coquille de noix du fruit protégeant la graine. Nous détaillons ici comment les caractéristiques anatomiques des endocarpes, visibles en microscopie optique et électronique à balayage, peuvent être utilisées avec les caractéristiques morphologiques survivantes pour identifier en toute confiance l'utilisation des principaux arbres économiques de l'Asie-Pacifique, dans ce cas *Canarium*, *Pandanus* et *Terminalia*. La description anatomique systématique permet l'identification de ces taxons économiques importants et la séparation des restes d'autres tels que les *Aleurites* et les *Cocos*, lorsqu'ils se trouvent dans une gamme d'assemblages archéologiques. Cela comprend les assemblages calcinés souvent très fragmentés qui peuvent être récupérés de façon routinière sur la plupart des sites avec des méthodes appropriées de tamisage fin et de flottation. Ces méthodes fournissent la base d'une compréhension plus représentative et nuancée de l'utilisation des plantes anciennes, de l'économie et des systèmes sociaux opérant dans la région et, étant particulièrement utiles dans les régions tropicales, élargiront la base de données archéobotanique sur les aliments anciens à l'échelle mondiale.

Mots-clés archéobotanique, macrofossiles, endocarpes, Sahul, microscope électronique à balayage (MEB)

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INTRODUCTION

Recent archaeobotanical research has transformed our understandings of ancient tropical subsistence systems and the varied global trajectories towards agriculture in tropical environments (Castillo et al., 2018; Crowther et al., 2016; Levis et al., 2018; Shaw et al., 2020). Suggestions that tropical rainforest provided an unviable long-term subsistence base for foragers have been proved incorrect on several continents (Roberts et al., 2017), with research in Southeast Asia and Sahul demonstrating unequivocally that early humans adopted complex plant and animal-based subsistence strategies in lowland and upland tropical environments before 40,000 years ago (e.g., Barker et al., 2007; Florin et al., 2020; Summerhayes et al., 2010; Veth et al., 2017). A key component of these early, and indeed later, economies across the Asia-Pacific region appears to be tree nuts and fruits, and a reliance on the fats, proteins and carbohydrates they provide. This includes during early and later human expansions (Latinis, 2000; Florin, 2021b; Kirch et al., 1995); and within a range of complex food production systems, such as the early agricultural systems of the New Guinea highlands (Denham et al., 2003, 2004), the managed rainforest landscape of the Wet Tropics of northeastern Queensland (Ferrier & Cosgrove, 2012; Roberts et al., 2021), and horticultural systems developed across lowland New Guinea, Oceania and the Pacific (Fairbairn, 2005; Kirch, 1989; Lentfer & Torrence, 2007).

Whilst the historical trajectories of some of these practices are well understood, more detailed archaeological investigation of arboricultural practices across this region have been hindered by a lack of systematic methodological research into identifying plant macrofossils, including the fragmented remains of economically exploited nuts and fruits (Denham et al., 2009; Fairbairn, 2005; Florin & Carah, 2018). In the majority of cases, identification of such remains in archaeological assemblages is heavily dependent on the morphological characteristics, that is the shape, size and physical form, of near whole and exceptionally well-preserved remains. An alternative approach that maximises the chances of identifying fragmented endocarp remains is that of using the anatomical characteristics preserved in fragmented endocarp tissue. Used successfully to identify the parenchymatous tissue of underground storage organs (USOs; see Florin et al., 2020, 2022; Hather, 1994, 2000a) and wood charcoals (Dotte-Sarout et al., 2015), anatomical features include the type and arrangement of the ground cells and vascular tissues, and the cell contents present in archaeological fragmented remains. In this paper, we explore the potential for anatomical identification of fragmented endocarp remains of three key genera of Asia-Pacific tree nuts and fruits, *Canarium*, *Pandanus* and *Terminalia*, an approach that has shown increasing promise over recent decades (Fairbairn in Summerhayes et al., 2010; Fairbairn et al., 2014; Florin et al., 2020, 2022; Oliveira, 2008). We test this approach on archaeological finds from New Guinea and Australia, demonstrating its potential to more effectively identify the

use of these key genera in the past, not only in archaeological sites from Southeast Asia to the Pacific, but also in the Old World tropics of Africa and South Asia.

BACKGROUND

Definition of tree fruits and nuts

Trees are economically important across Southeast Asia, Sahul and Oceania, their seeds and fruits providing key sources of fats, protein and carbohydrates in a range of economies, including those that are predominately forager, monocultural or polycultural food systems (see Figure 1). Trees are large, plants with persistent, woody stems. They are typically long-lived, commonly extending through several human generations (Kennedy, 2012, p. 6), and provide spatially fixed sources of food that often have inter-annual variations in abundance (mast cycles). The seeds, fruits and nuts exploited by humans are all derived from the reproductive parts of the plant used in sexual reproduction, namely the fertilised ovules, which become seeds – a new generation of plants awaiting growth – held within the pericarp, the tissues derived from the ovary (in which the ovules develop). The seeds and pericarp vary widely in size, structure, combination and shape, depending on the plant family (Figure 2; see Simpson, 2019). Pericarp structure varies from true nuts, in which the whole pericarp is toughened and forms a persistent shell, to drupes, in which a single seed is surrounded by a toughened inner pericarp layer (endocarp) within a fleshy outer layer (mesocarp and exocarp), to berry fruits in which multiple seeds are embedded in a soft, pulpy edible pericarp. These fruiting structures vary in the extent to which the fruits and seeds are likely to be preserved archaeologically, especially when charred by exposure to fire, and produce structurally varied plant remains (Figure 2, likely archaeological remains are coloured black). While commonly referred to as nuts, the three target genera for this paper do not produce true nuts in the botanical sense, but endocarps derived from the tough inner pericarp layer, which have been called elsewhere "nut-a-likes" (Fuller 2022, Chapter 18).

Structure and use of Canarium

Canarium is a widespread genus of about 100 tropical and sub-tropical trees in the family Burseraceae, growing in low to middle elevation primary and secondary forest in Africa, Asia, Island Southeast Asia, Australia, Melanesia and Oceania (see Figure 3a for historical distribution maps of key Asia-Pacific species; Leenhouts, 1956; Walter & Sam, 2002; Weeks, 2008). *Canarium* species are long-lived, medium to large-sized trees, standing between ~15 m and 50 m in height. Their trunks are used in construction, canoe building and manufacture of wooden artefacts, and the resinous extract of some species is used in the caulking of canoes (Kennedy & Clarke, 2004; Yen, 1996). *Canarium* species produce drupaceous fruits, their endocarp typically surrounding three seed cavities/locules (Figures 1 and 4). In most, but not all, varieties, only one seed locule is fertile

Figure 1. Economic tree species considered in this paper. (a) Fruits of *Terminalia ferdinandiana* in Jabiru, Mirarr Country, Northern Territory, Australia; (b) fallen *Terminalia grandiflora* fruits growing near Madjedbebe, Mirarr Country, Northern Territory, Australia; (c) immature fruits of *Canarium indicum* on Koil Island, Papua New Guinea (PNG); (d) polycultural garden on Koil Island, PNG with tree crops in background; (e) cephalium of polydrupe *Pandanus* from Koil Island, PNG; (f) cephalium of monodrupe *Pandanus julianettii* from Kosipe, PNG; (g) *Pandanus* agroforest in the Ivane Valley, PNG.

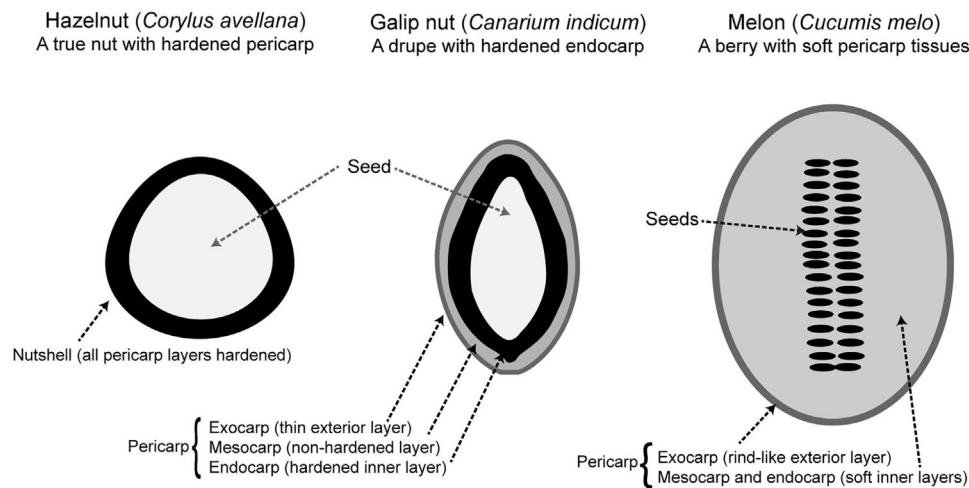


(i.e., seed-producing), while the other two remain immature and sterile (Evans, 1999). Several species are considered domestic, being cultivated for their large edible nuts in lowland tropical polyculture farming systems (see Lebot et al., 2008; Yen, 1991, 1995, 1996), including *Canarium indicum*, a crop that is showing promise

as a commercial plantation species (Carter & Smith, 2017).

The main edible portion of Asia-Pacific *Canarium* species are their seeds or "nuts", which are high in fat, ~70% in some species (Pham, 2016, p. 334). They are important seasonal resources across Island Southeast Asia,

Figure 2. Schematic showing radial longitudinal sections of different fruit types (not to scale), detailing the arrangement and structure of seed and fruit tissues, with those coloured black most likely to be preserved as charred archaeological plant macrofossils.



New Guinea and the Pacific (Walter & Sam, 1999, pp. 125–130; Yen, 1996). In the northern Solomon Islands, communities seasonally leave their hamlets to live close to and harvest stands of galip nuts (*C. indicum*) in the forest (Kimmerley 1995 in Spriggs, 1997, p. 56). These nuts are smoked and sealed in bamboo tubes, in which they can be kept for three to four years, either to be sold for cash or to support large community feasts. *Canarium* nuts were also traded in traditional exchange systems from the inshore islands of the north coast to the New Guinea highlands (Hogbin, 1970), a process that continues today. Some Melanesian species, including *Canarium decumanum* and *Canarium salmonense*, also have edible fruit pulp. In northern Australia, the smaller nuts of *Canarium australianum* are eaten but are considered as snack foods, rather than important resources by local Aboriginal communities (Jones & Meehan, 1989, p. 122). In the Philippines, pili nut (*Canarium ovatum*) is commercially harvested from cultivated forest stands primarily for its edible nuts (Pham, 2016). However, the young shoots and fruit pulp of this species are also edible – the latter after boiling – and oil is extracted from its nuts for use in cooking and soap manufacture. Further, its endocarps are used for fuel and in gardening mulches, and its resin as a fire-starter.

Structure and use of *Pandanus*

Pandanus is a diverse genus of palm-like plants in the family Pandanaceae with a thickened wood-like stem, thick aerial roots and a crown of strap-shaped leaves (Figure 1g), the latter commonly used in mat and basket production (see Figure 3b for historical distribution maps of key Asia-Pacific species; Stone, 1983). *Pandanus* species are variable in form and habitat, with lowland species up to 5 m in height and the endemic highland species in New Guinea reaching heights well in excess of 15 m, with a single thick stem that may be used in building construction. *Pandanus* species produce large compound fruits known as cephalia

(singular cephalium – Figure 1e, 1f) comprised of numerous keys or phalanges. Depending on the species, the keys consist of a single carpel (plant ovary) and surrounding tissue, or several fused into one structure. The basic fruiting unit in *Pandanus* is a drupe, with an endocarp surrounding a seed or kernel (Figure 4). Fruits from species in which the keys are predominantly single-seeded are thus known as monodrupes (Figure 4c), and species with keys consisting of several fused fruits are called polydrupes (Figure 4d).

Pandanus species produce a range of edible parts, with the kernels of large-seeded species high in fat and protein (Low, 1991, p. 42; Powell, 1976, p. 116) and superior in food value to the coconut (Kennedy & Clarke, 2004). Exploitation of *Pandanus* kernels is most developed in the highlands of New Guinea where the domestic crop karuka (*Pandanus julianetii*; Figure 1f, 1g) and its relatives are major components of the subsistence system, especially in resource-poor higher altitudes, at and above 2000 m (Bourke, 1996, 2017). This is towards the upper limit of tropical tuber-based cropping and the kernels provide an important dietary source in an otherwise fat-poor environment.

Pandanus tectorius and other polydrupe species are commonly found in lowland coastal settings around the Pacific, being commonly planted amenity trees in parks and leisure areas. On the driest Pacific atolls, with less than 900 mm annual rainfall, *Pandanus* is one of only 20–30 floristic taxa, and alongside coconut, the only one of importance for subsistence (Bayliss-Smith, 1990, p. 59). In northern Australia, New Guinea and the Melanesian islands use of these varieties is quite variable, with the species viewed as anything from a staple seasonal resource to a famine food. As well as the kernels, the soft base of the keys is eaten in many areas, sometimes after additional processing (e.g., roasting of *Pandanus spiralis*; Meehan et al., 1978). The soft, oily fruit of the monodrupe variety marita (*Pandanus conoideus*) and other related species are

Figure 3. Historical distribution maps of key taxa mentioned in-text; polymorphs refer to species distribution pre-European colonisation, and arrows refer to post-colonial introductions. (a) Historical distribution maps of *Canarium* species, *C. australianum*, *C. harveyi* and *C. indicum*, developed from Atlas of Living Australia (2022a) and Walter and Sam (2002); (b) Historical distribution maps of *Pandanus* species, *P. julianettii*, *P. spiralis* and *P. tectorius*, developed from (Atlas of Living Australia, 2022b) and Walter and Sam (2002); (c) Historical distribution maps of *Terminalia* species, *T. catappa*, *T. ferdinandiana* and *T. kaernbachii*, developed from Atlas of Living Australia (2022c), Bourke (1996) and Walter and Sam (2002).

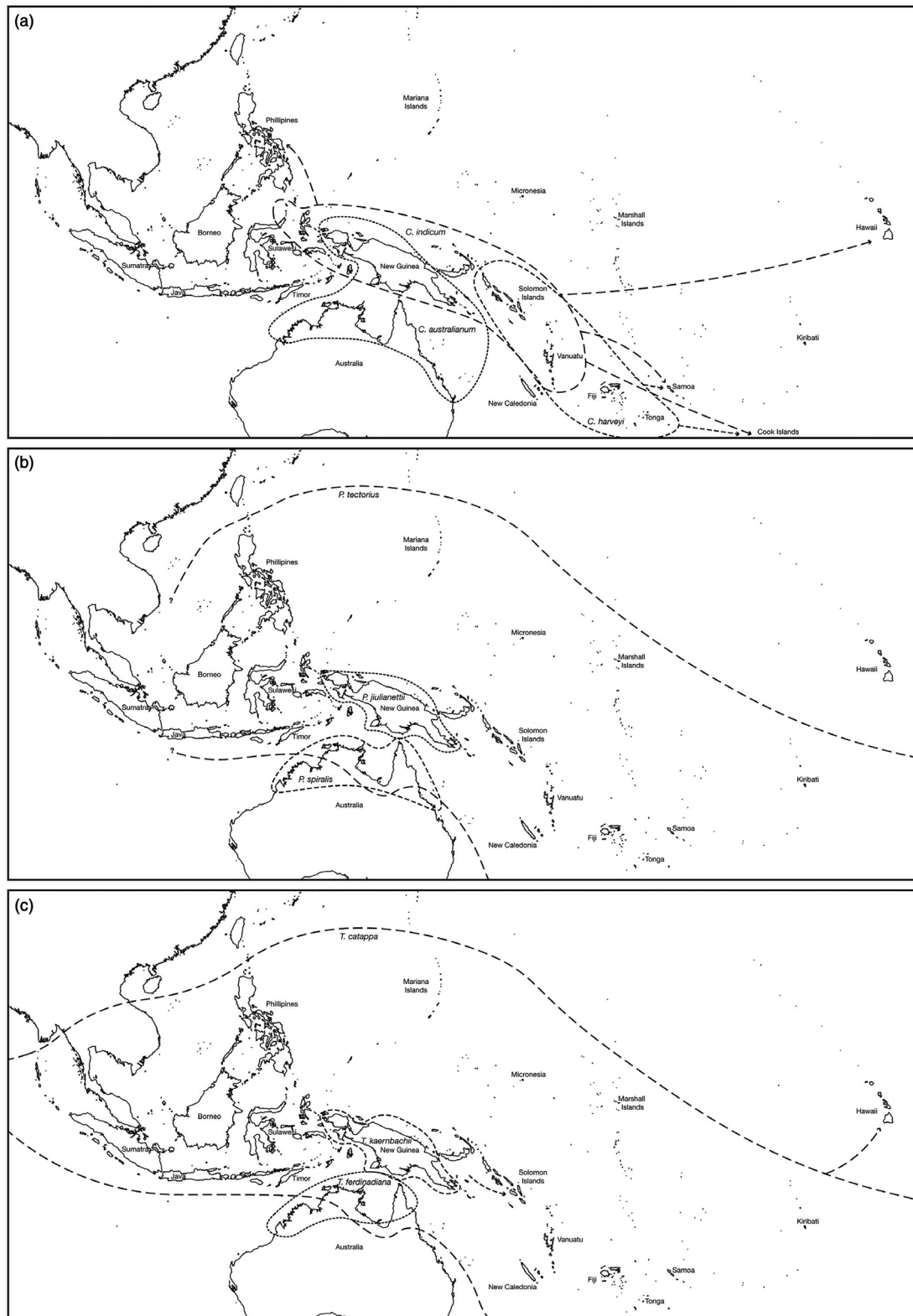
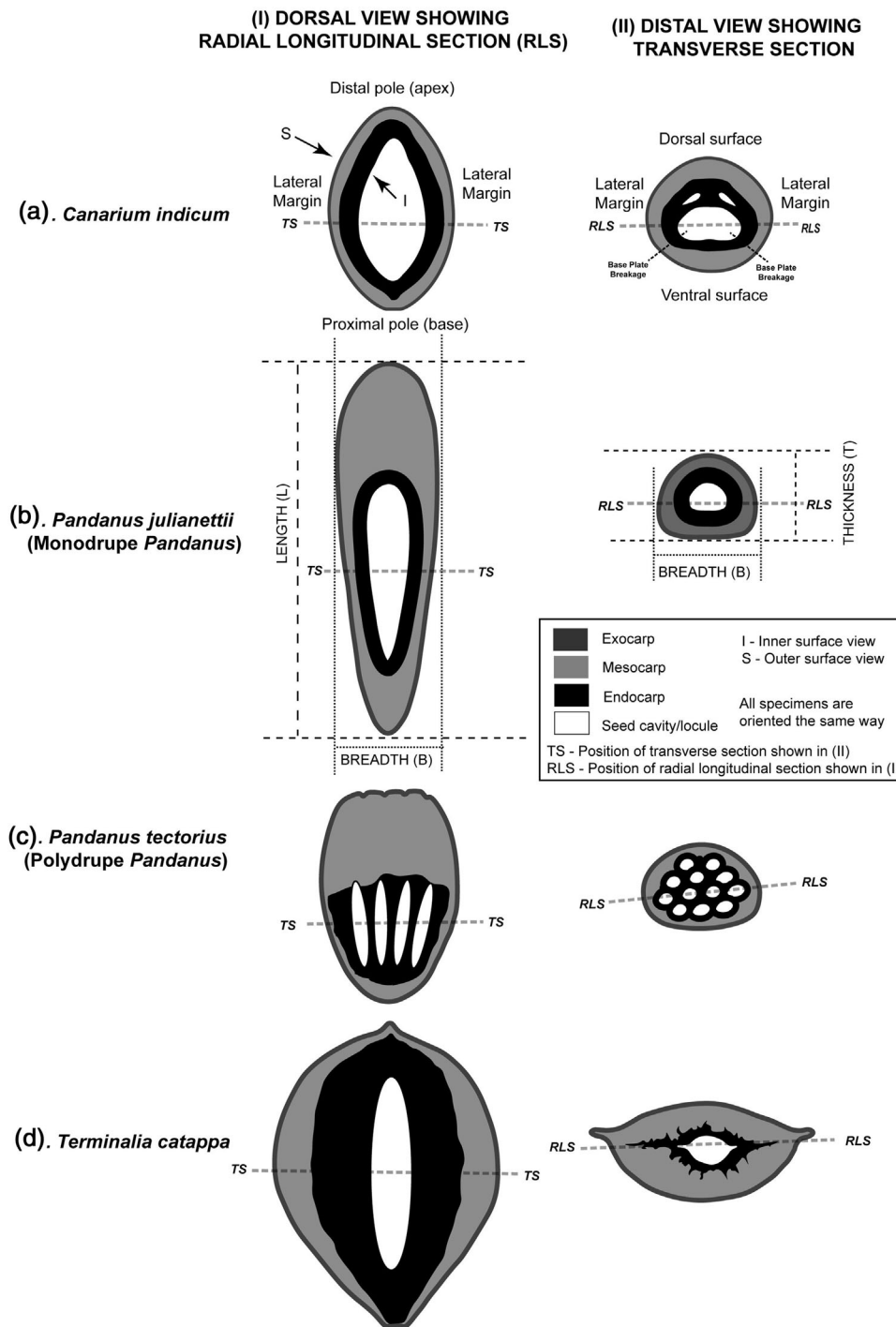


Figure 4. Schematic representation of orientation, structure, landmarks, measurements and sections for whole *Canarium*, *Pandanus* and *Terminalia* fruits.



cooked and eaten in the highlands of New Guinea, as well as being used to make a syrup-like food (Bourke, 2017).

Structure and use of *Terminalia*

Terminalia is a widespread genus, composed of nearly 300 species and distributed across the tropics and subtropics (see Figure 3c for historical distribution maps of key Asia-Pacific species; Exell, 1954; Walter & Sam, 2002).

Terminalia species range from small to large trees and have a unique arrangement of leaves: grouped at the terminus, or tips, of their branches. Hence their genus name. The fruit of *Terminalia* are single locule drupes, which range in length from ~1.5 cm to 11 cm, the largest of which is the New Guinea species, okari (*Terminalia kaernbachii*) (Walter & Sam, 2002). Two species, *Terminalia catappa* and *T. kaernbachii*, cultivated by communities in New Guinea and

in the former case, also in the Pacific, are considered domestic (see Lebot et al., 2008; Yen, 1991, 1995, 1996).

Terminalia species are both used for their edible seeds or "nuts", and fruit (Figure 1a, 1b). The large-fruited okari is cultivated in the inland lowland forests of New Guinea, through tending of wild stands and planting in villages (Walter & Sam, 2002). Its nuts are eaten raw or cooked and commonly sold in Port Moresby and other regional markets (Bourke, 1996). The raw or dried nuts of the sea almond (*T. catappa*), which has a widespread coastal distribution from Sri Lanka to the Pacific (see Figure 3c), range from being an occasionally eaten food to an important commercial product. In Vanuatu, nuts are dried and sold commercially in groceries (Walter & Sam, 2002), and on Iwa island in the Marshall Bennett Group in the Bismarck Archipelago, a particularly prized variety, renowned for its soft-shelled nuts, is preserved via smoking and exported to nearby islands (Bourke, 1996). In northern Australia, several species are exploited for both their fruit and nuts. The most famous of these is the Kakadu plum (*T. ferdinandiana*; see Figure 1a), the flesh of which is renowned for its extremely high levels of ascorbic acid (Gorman et al., 2019). This fruit is in demand in the Australian and international markets for its nutritional and antimicrobial properties, and it has both been grown in plantations and commercially wild-harvested as part of Indigenous-owned agribusinesses.

Archaeological visibility

Endocarps are highly visible in the archaeological record, and archaeological finds of *Canarium*, *Pandanus* and *Terminalia* endocarp demonstrate these genera have been exploited in Australia and New Guinea from the Pleistocene (Australia: Dilkes-Hall et al., 2019; Florin et al., 2020; New Guinea: Fairbairn et al., 2006; Summerhayes et al., 2010; Yen, 1990). At Madjedbebe, a rockshelter on Mirarr Country in the Alligator Rivers region of northern Australia, the exploitation of all three of these genera are associated with earliest occupation, 65–53,000 years ago (Florin et al., 2020). In particular, the considerable labour expended on the extraction of the nuts of *P. spiralis* (a polydrupe species endemic to northern Australia; see Figure 1b) evidenced at Madjedbebe, has been argued to demonstrate the importance of the fat-content of tree nuts to early human populations in this region (Florin, 2021b; Florin et al., 2020).

In Sahul's north, there has been more consideration of the topic of management, translocation and exchange of fruit trees, including the earliest evidence from Papua New Guinea for plant use with the exploitation of the monodrupe species *P. iwen* (previously referred to as "Taip") in the Ivane Valley, New Guinea highlands, 49–43–30–26,000 BP. Those finds do not imply the same labour-intensive nut extraction as seen in Madjedbebe, however, its use contemporary with anthropogenic vegetation burning and the presence of waisted axes has been suggested as indicative of landscape modification and management of resources (Fairbairn et al., 2006; Summerhayes et al., 2010). Early reports from excavations in Manim valley in

the New Guinea highlands, suggested a notable decrease in endocarp thickness over time, which was suggested to indicate a *Pandanus* domestication process in this region, about 6000 years ago (Golsen in Christensen, 1975, p. 24). However, more extensive archaeobotanical research by Donoghue (1988, p. 94) found that "visible morphological change" in *Pandanus* drupes between sites in the Manim Valley, was an indicator of the use of several wild species of *Pandanus* (*P. antarensis*, *P. brosimus* and *P. iwen*) and, therefore, evidence of different foraging environments, rather than domestication.

Use of *Canarium* is evidenced by c. 14,000 BP in the Sepik Valley of northern New Guinea (Yen, 1990, p. 262), and soon after at Pamwak rockshelter on Manus Island (Fredricksen et al., 1993). Alongside phytogeographical data, this has been used to support claims for early domestication of *C. indicum* and its Pleistocene translocation from northern New Guinea to Manus and the Bismarck Archipelago (Swadling & Hide, 2005). This translocation event, and evidence for the use and possible cultivation of *Pandanus* in the highlands, easily predates the appearance of Lapita pottery, and suggests the presence of cultivation-based subsistence systems in this region prior to the expansion of Austronesian speakers into Melanesia. Matthews and Gosden (1997), and Kirch (1988) have further argued similarities between this and later evidence for Lapita plant use in near Oceania demonstrates a system of Indigenous arboriculture, that both predated and influenced the later Lapita expansion.

Much of the interest in these Asia-Pacific genera of tree nuts and fruits has been part of a re-consideration of tropical subsistence practices in light of claims and counterclaims concerning the suitability of tropical ecosystems for gathering, and the emerging evidence for prehistoric complexity in pathways to tropical agriculture. In Highland New Guinea, microfossil evidence (starches, phytoliths and pollen) has been deployed to understand early plant exploitation practices and was the main source of plant data to confirm an independent centre of origin for agriculture at Kuk at 8–4000 BP (Denham et al., 2003, 2004). A similar methodological approach has argued for the presence of garden and tree-based food production at Waim (Shaw et al., 2020) around 4–5000 BP, developing from an earlier system of plant collection.

Although relatively well-represented in the archaeological literature, the prehistory of these genera in the Asia-Pacific is based on a small number of endocarp finds. With the exception of recent research by the authors (Fairbairn in Summerhayes et al., 2010; Florin et al., 2020, 2022), all published identifications of endocarp macrofossils, including the few reports which have recorded identification criteria (e.g., Donoghue, 1988; Hayes, 1992; Kirch, 1988; Matthews & Gosden, 1997; Yen & McEldowney in Swadling et al., 1991), have relied on the morphological features (i.e., overall nut shape and size) visible in complete preserved specimens or large fragments. Several of the key assemblages in New Guinea and near Oceania have been preserved in anaerobic, water-logged

conditions, which allow large uncharred – that is unburnt – macrobotanical remains to persist in the archaeological record (see Table 1). More commonly excavated are archaeological sites with aerobic strata in which only charred (partially burnt) plant remains are preserved (Fairbairn, 2005). In most cases charring only preserves a small portion of the original plant material exposed to burning and produces brittle plant remains prone to fragmentation during deposition and subsequent archaeological recovery. Fragmentation, combined with low preservation rates, reduces the potential for identification of charred macrofossil remains using morphological identification criteria and has imposed a methodological upper limit on the archaeobotanical investigation of these genera and their use in the Asia-Pacific.

METHODS

Archaeobotanical analysis of modern comparative material

Modern comparative specimens of *Canarium*, *Pandanus* and *Terminalia* species were used to develop reference criteria for identification of archaeological specimens, including a combination of specimen morphology (shape/size) and anatomy (presence and organisation of tissues). Modern reference specimens of individual endocarps and, in the case of polydrupe *Pandanus*, drupes were dissected and analysed in both fresh and charred states, the latter burnt at 400–500°C in a muffle furnace in reducing conditions.

Canarium, *Pandanus* and *Terminalia* are large and complex genera, with many species and sub-species. Reference specimens were investigated from a narrow range of the more common taxa encountered in the Asia-Pacific. All specimens were derived from the archaeobotany reference collection of The University of Queensland in Brisbane. For *Canarium*, this included *C. australianum*, *C. harveyi* and *C. indicum*. For *Pandanus*, this included both polydrupe species, *P. spiralis*, *P. basedowii* and *P. tectorius*, and monodrupe species, *P. brosimus*, *P. iwen* and *P. julianetti*. For *Terminalia*, this included *T. catappa*, *T. carpentariae*, *T. ferdinandiana*, *T. grandiflora* and *T. kaernbachii*.

Identification criteria were recorded using standard views and sections produced by fracturing the charred comparative reference specimens. The system developed here is based on standard procedures for orienting and describing whole seeds and fruits, combined with approaches adapted from the anatomical identification of wood (Hather, 2000b; Hillman et al., 1996; Simpson, 2019).

Correct orientation of the endocarps is essential for correct description and sectioning and is done using landmarks, assigned with reference to the proximal pole of the nut, that is the end attached to the parent plant, usually marked by a clear circular abscission scar (Figure 4). This is opposed by the distal pole, which has a variety of forms

depending on species, varying from a simple point to, in the case of *C. indicum*, three shallow flanges. The line between proximal and distal poles is the longitudinal axis of the nut. Transverse section (TS, Figure 4) is a fracture plane perpendicular to the longitudinal axis (i.e., axis running between proximal and distal poles of the fruit) in a line running between the lateral margins. The radial longitudinal section (RLS, Figure 4) is a fracture plane perpendicular to the endocarp surface and running to its longitudinal axis. Use of these two sections allows for an understanding of the shape and arrangement of cells in the endocarp in three dimensions. In addition, surface views of the endocarp specimens were recorded from both the outer surface (S, Figure 4) and inner surface (i.e., the view of the locule surface; I, Figure 4). In wood anatomical studies the RLS is accompanied by the tangential longitudinal section (TLS), that is a section running perpendicular to the RLS which allows the radial arrangement of tissues to be understood. This was found to have less utility in endocarp studies.

Specimens from all plant genera were described using the same sections and surface views, taking into account the peculiarities of species morphology. Morphological identification criteria were recorded using light microscopy and anatomical identification criteria using high-powered light microscopy and scanning electron microscopy (SEM). The following features were recorded where visible in transverse and RLS, and outer surface and inner surface views: cell size, shape and orientation; cell wall thickness; surface texture; inner surface cell pattern; presence of cell inclusions; and endocarp thickness (see Table 2).

Archaeobotanical analysis of archaeological material

Plant macrofossil assemblages from several sites within the Asia-Pacific region were used to develop and explore the efficacy of these methods. Charred probable endocarp remains were recovered from legacy archaeological assemblages, and new assemblages, collected during fieldwork by flotation or wet-sieving from 2004 onwards by the authors. Some of the legacy assemblages were worked on by Doug Yen (see references below). His identifications, which were made largely on the basis of morphology, provided already identified specimens with which we could evaluate the anatomical approach. The new assemblages were analysed and worked on with reference to these finds and the modern reference specimens, which underpinned all identification efforts. The legacy assemblages came from Papua New Guinea, namely the Yomining Complex (DGD) and Lebang Tatale (DGW) sites in Nissan (Spriggs, 1991), and Dongan (Swadling et al., 1991) and Seraba in the Sepik Ramu region (Swadling & Hide, 2005). Recently collected floated or wet-sieved assemblages came from Taora, Lachitu and Watinglo (Sandaun Province, PNG; O'Connor et al., 2011), Madjedbebe (Mirarr Country, Northern Territory, Australia; Clarkson et al., 2017), Kosipe Mission (Ivane Valley, Central Province, PNG; Summerhayes et al., 2010) and Mamatu in the same region. The examples included in this paper have been selected to demonstrate

Table 1. Archaeological finds of *Canarium*, *Pandanus* and *Terminalia* endocarp in the Asia-Pacific region.

Site	Location	Age	Taxa	Preservation	Recovery method	References
Island Southeast Asia						
Matja Kuru 1	Lake Ira Laloro, East Timor	11,100–4,400 BP	<i>P. cf. tectorius</i>	Charred	Wet-sieving (2 mm mesh)	(Oliveira, 2008)
Ulu Leang Cave	Sulawesi, Indonesia	11,000–3,500 BP	<i>Canarium</i> sp.	Charred	Wet-sieving	(Glover, 1979)
Niah Cave	Sarawak, Borneo	10,000 BP	<i>Canarium</i> spp.	Charred	Flotation	(Paz, 2005)
Buri Ceri Uato Mane	Baucau, East Timor	8600 BP to present	<i>P. cf. tectorius</i> , cf. <i>T. catappa</i>	Charred	Flotation	(Oliveira, 2008)
Leang Burung 1	Sulawesi, Indonesia	5500 BP	cf. <i>Canarium</i> sp., cf. <i>Pandanus</i> sp.	Charred	Flotation	(Paz, 2001, 2005)
Jerimalai	Tutuala, East Timor	5453–5168 BP	cf. <i>T. catappa</i>	Charred	Flotation	(Oliveira, 2008)
Bekes	Bontoc province, Philippines	1380–1270 BP	cf. <i>Pandanus</i> sp.	-	Flotation	(Paz, 2001)
Batususu	Ambon Island, Indonesia	850–300 BP	<i>C. indicum</i> , <i>C. lamii</i> endocarp	-	-	(Latinis & Stark, 1996)
Australia						
Madjedbebe	Alligator Rivers region, Australia	65,000 BP to present	<i>C. australianum</i> , <i>P. spiralis</i> , <i>T. grandiflora</i> , <i>Terminalia</i> spp. endocarp	Charred	Flotation	(Florin et al., 2022; Florin et al., 2020)
Carpenter's Gap 1	Kimberley, Australia	47,000 BP to present	<i>Terminalia</i> spp.	Desiccated, charred	Flotation	(Dilkes-Hall et al., 2019; McConnell & O'Connor, 1997)
Riwi	Kimberley, Australia	7000 BP to present	<i>Terminalia</i> spp.	Desiccated, charred	Sieving (1.5 mm mesh)	(Dilkes-Hall et al., 2020a)
Brooking Gorge 1	Kimberley, Australia	> 1554–1270 BP to present	<i>Terminalia</i> cf. <i>ferdinandiana</i>	Desiccated, charred	Sieving (3 mm mesh)	(Dilkes-Hall et al., 2020b)
Widingarri Shelter 1	Kimberley, Australia	1435–905 BP to present	<i>Canarium australianum</i> , <i>Pandanus</i> sp., <i>Terminalia</i> cf. <i>ferdinandiana</i>	Desiccated, charred	Sieving (3 mm mesh)	(Dilkes-Hall et al., 2020b)
Widingarri Shelter 2	Kimberley, Australia	1218–761 BP to present	<i>Canarium australianum</i> , <i>Terminalia</i> cf. <i>ferdinandiana</i>	Desiccated, charred	Sieving (3 mm mesh)	(Dilkes-Hall et al., 2020b)

(Continued)

Table 1. (Continued).

Site	Location	Age	Taxa	Preservation	Recovery method	References
Wandjina	Kimberley, Australia	1181–956 BP to present	<i>Canarium australianum</i> , <i>Terminalia</i> cf. <i>ferdinandiana</i>	Dessicated, charred	Sieving (3 mm mesh)	(Dilkes-Hall et al., 2020b)
Shelter 2, Moonggaroonggoo	Kimberley, Australia	<464–313 BP to present	<i>Terminalia</i> sp.	Desiccated, charred	Sieving (1.5 mm mesh)	(Dilkes-Hall, 2019; Maloney, Dilkes-Hall, & Davis, 2017)
Mainland New Guinea Ivane Valley sites	Owen Stanley Range, PNG	49–43,000–30–26,000 BP	<i>P. iwen</i> (formerly described as cf. Taip)	Charred	Dry- and wet-sieving (2 mm mesh)	(Fairbairn et al., 2006; Summerhayes et al., 2010)
Seraba Manim	Sepik-Ramu, PNG Western Highlands, PNG	14,000 BP 10,900 to present	<i>C. indicum</i> endocarp <i>P. antaresensis</i> , <i>P. brosimus</i> and <i>P. iwen</i> endocarp	- Charred	- Flotation; wet-sieving (2 mm mesh)	(Yen, 1990) (Christensen, 1975; Donoghue, 1988)
Taora	West Sepik, PNG	7421–6599–6375–5965 BP	<i>Pandanus</i> sp., <i>Terminalia</i> cf. <i>catappa</i> endocarp	Charred	Flotation	(Fairbairn, 2005)
Dongan	Sepik-Ramu, PNG	7–6000 BP	<i>Canarium</i> cf. <i>indicum</i> , <i>Pandanus</i> sp.	Waterlogged	-	(Fairbairn & Swadling, 2005; Yen & McEldowney in Swadling et al., 1991)
Yuku	Western Highlands, PNG	<300 BP to present	<i>P. conoideus</i> endocarp	-	-	(Bulmer, 1975, 2005; Denham, 2016)
Near Oceania Pamwak Rockshelter	Manus Island, PNG	12,400±80 BP to present	<i>Canarium</i> sp. endocarp	Charred	Wet-sieving (1.4 mm mesh)	(Fredricksen et al., 1993)
Kilu Cave	Buka Island, Solomon Islands	9400–6600 BP	<i>C. indicum</i> and <i>C. salomonense</i> endocarp	Charred	Wet-sieving	(Wickler & Spriggs, 1988)
Panakiwuk	New Ireland, PNG	8000 BP; 1550BP	<i>Canarium</i> sp. endocarp (possibly wild); <i>Canarium</i> cf. <i>indicum</i> , <i>Canarium</i> sp. endocarp	-	Sieved (3 mm mesh)	

(Continued)

Table 1. (Continued).

Site	Location	Age	Taxa	Preservation	Recovery method	References
Vatulum Posovi	Guadalcanal, Solomon Islands	6285–2600 BP	<i>Canarium</i> sp. endocarp	Charred	-	(Roe, 1992; Spriggs, 1997, pp. 81–82)
Tatale	Nissan Island, PNG	4600–3400 BP	<i>C. indicum</i> , <i>Canarium</i> spp., cf. <i>Terminalia</i> sp. endocarp	Charred	-	(Spriggs, 1997, p. 80)
Vatulum Tavuro	Guadalcanal, Solomon Islands	4230–3680–3650 BP	<i>C. indicum</i> , <i>Canarium</i> sp. endocarp	-	-	(Roe, 1992; Spriggs, 1997, pp. 81–82)
Maklo	Maklo Island, PNG	3840±60 BP	<i>C. indicum</i> , polydrupe <i>Pandanus</i> sp., <i>Terminalia</i> sp. endocarp	Waterlogged	Wet-sieving	(Matthews & Gosden, 1997)
Lebang Hatika (DFF)	Nissan Island, PNG	3650–2900 BP	<i>C. indicum</i> , <i>Canarium</i> cf. <i>harveyii</i> , <i>Canarium</i> cf. <i>decumanum</i> , <i>Pandanus</i> sp., <i>T. cf. catappa</i>	-	Sieving (5 mm mesh)	(Spriggs, 1991, pp. 233–235; 1997, p. 81)
Kamgot	Anir Islands, PNG	3300–3000 BP	<i>Canarium</i> sp., polydrupe <i>Pandanus</i> spp., <i>T. catappa</i>	Charred	Flotation; wet-sieving (2 mm mesh)	(Summerhayes et al., 2019, pp. 396–397)
Yominig Complex sites (DGD/1-3)	Nissan Island, PNG	3200–850 BP	<i>C. cf. harveyii</i> , <i>C. indicum</i> , cf. <i>C. salomonense</i> , <i>Pandanus</i> sp.	-	Sieving	(Spriggs, 1991, pp. 230–232)
Lebang Tatale (DGW)	Nissan Island, PNG	3500–860 BP	<i>C. cf. indicum</i> , <i>C. cf. harveyii</i> , <i>C. cf. salomonense</i> and cf. <i>Terminalia</i> spp.	-	Sieving (5 mm mesh)	(Spriggs, 1991, pp. 227–232)
Talepakemalai	Eloaia Island, Mussau Islands	3150–2750 BP	<i>C. indicum</i> (showing evidence of nut-cracking), polydrupe <i>Pandanus</i> spp., <i>T. catappa</i>	Waterlogged	Wet-sieving (5 mm and 3 mm mesh)	(Kirch, 1989)
Apalo	Kumbun Island, PNG	2900±80 BP	<i>C. indicum</i> , <i>Canarium</i> sp., polydrupe <i>Pandanus</i> sp., <i>Terminalia</i> sp.	Waterlogged	Wet-sieving	(Hayes, 1992; Matthews & Gosden, 1997)

(Continued)

Table 1. (Continued).

Site	Location	Age	Taxa	Preservation	Recovery method	References
Makekur	Adwe Island, PNG	1580±60 BP	<i>C. indicum</i> , polydrupe <i>Pandanus</i> sp., <i>Terminalia</i> sp.	Waterlogged	Wet-sieving	(Matthews & Gosden, 1997)
Site 6, Rakival Village	Watom Island, PNG	315±53 BP	<i>Canarium</i> sp., <i>Terminalia</i> sp.	Waterlogged	-	(Specht, 1968)
Remote Oceania						
ScMo-341	Mo'orea, Society Islands	4650±50–2430±30 BP	<i>Pandanus</i> sp.	Waterlogged	Sieving (1/16in or 1.6 mm mesh)	(Kahn et al., 2014)
ScMo-343	Mo'orea, Society Islands	4610±30 BP	<i>Canarium</i> sp., <i>Pandanus</i> sp.	Waterlogged	Sieving (1/16in or 1.6 mm mesh)	(Kahn et al., 2014)
ScMo-342	Mo'orea, Society Islands	3740±30 BP–3,030±30 BP	<i>Pandanus tectorius</i> , <i>Terminalia</i> sp.	Waterlogged	Sieving (1/16in or 1.6 mm mesh)	(Kahn et al., 2014)
Te Bakoa	Nikunau Island, Republic of Kiribati	2000 BP	<i>Pandanus</i> sp.	Charred	Sieving (4 mm mesh)	(di Piazza, 1999)
Site 1, Utrök Islet	Utrök Atoll, Marshall Islands	1930–1630 BP to present	<i>Pandanus</i> sp.	Charred	Sieving (6.4 mm mesh)	(M. Weisler, 2001)
Tangata	Mangaia Island, Cook Islands	950–250 BP	<i>P. tectorius</i>	Charred	Sieving (“fine” mesh)	(Kirch et al., 1995)
Henderson sites	Henderson Island, Pitcairn Islands	900–300 BP	<i>Pandanus</i> sp.	Charred	-	(M. I. Weisler, 1995)
Moturakau rockshelter	Moturakau Islet, Cook Islands	750–150 BP	<i>Pandanus</i> sp.	Charred	-	(Allen & Huebert, 2016)

Table 2. Morphological and anatomical characteristics considered in the endocarp identification process (following Fairbairn in Summerhayes et al., 2010; Florin, 2021; University of Queensland, 2014).

Morphological criteria	Anatomical criteria
<ul style="list-style-type: none"> • Shape (2D, 3D, basal form, apical form) • Size (length, breadth, thickness; endocarp thickness) • Surface features (attachment scars, floral insertions etc.) • Surface texture/patterning • Internal texture/patterning 	<ul style="list-style-type: none"> • Patterning of endocarp ground tissue (sclerenchyma) • Patterning of vasculature (Monocotyledons only) • Presence and form of parenchymatous tissue • Cell inclusions (e.g., phytoliths) • Exocarp structure

and illustrate the method, and fuller treatment of the site datasets will be or has been published elsewhere.

For charred samples, fragments of endocarp were separated from the samples after assay using low-powered microscopy. The first task in this phase was to separate obvious wood charcoal specimens from the endocarp, identified on the basis of wood's distinctive and easily observable three-dimensional structure (Hather, 2000b). In most cases, endocarp fragments usually dominated the samples once wood charcoals were accounted for, and it was relatively easy to separate other charred matter, such as leaf remains, vegetative parenchyma, palm tissue and seeds.

Possible endocarp fragments could be recognised by their dense tissue, made up of thick-walled sclerenchyma, and remnant morphology such as curved walls, the presence of locules (seed cavities), attachment point to the parent plant, apex, the outer and inner surfaces (the endocarp outer wall and the seed locule surface) and, in the case of monocotyledons, such as *Pandanus* species, the longitudinally arranged vascular bundles. Many of these features survived even in highly fragmented specimens and were important for verifying that the specimen was a possible endocarp fragment. Furthermore, these features also allowed orientation of the specimen so the visible anatomy could be understood in relation to the reference collection. In complex three-dimensional anatomical specimens this is important and could not always be determined from fragments of tissue without clear morphological features, unlike wood charcoals.

Once recovered and oriented, specimens were subject to investigation using reflected/incident light microscopes, including standard ~4-50× magnification dissecting microscopes and high-powered models (~50-400× magnification) with Z-Stack and other image merging technologies. SEM was also used to investigate tissues at a higher magnifications (>1000× magnification) and levels of visual resolution. Samples for SEM analysis were mounted on standard stubs using carbon tape and, where necessary, carbon cement, with the surface or section to be viewed uppermost. Gold coating of specimens was in some cases necessary to help conductivity with the SEM, though the necessity of coating varied with machine and uniqueness of the specimen. As coating renders specimens unrecoverable, newer low-vacuum instruments, less likely

to require coating are often preferable. All specimens were subject to drying in an incubator before entering the SEM chamber.

Morphological features and then anatomical features visible in section were recorded. Almost inevitably, new sections had to be cut to allow clear view of the anatomical features. Those exposed during burial were often heavily eroded and cell lumen filled with sediment. Sectioning was undertaken with a scalpel or backed razor blade. As with all archaeological charred specimens, sectioning of this type is unpredictable due to the presence of unseen cracks and cavities in the tissue and it was not always possible to provide optimal sections to work with. Furthermore, some specimens collapsed, cracked or accumulated charge when in the SEM in an unpredictable manner. SEM work required rapid sample handling and imaging to minimise charging. In some cases, useful images could simply not be recovered or required significant modification in image processing software to render details clearly.

RESULTS

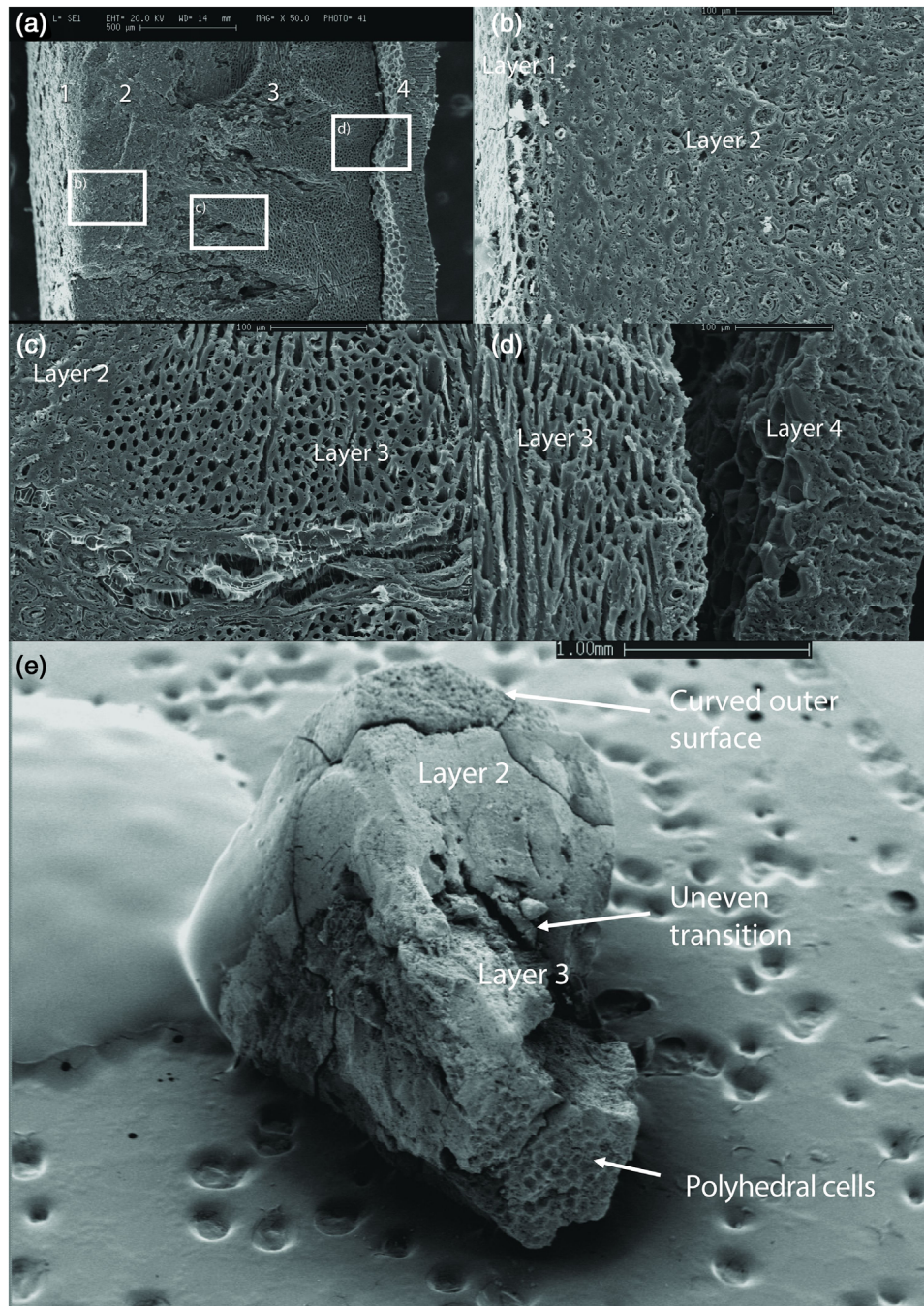
Canarium

Canarium endocarp has distinctive dense tissue that can be confidently assigned to genus even when fragmented.

Surface morphology: The surface of *Canarium* endocarp is smooth, lacks pores and consists of small, thick-walled isodiametric (spherical to elliptical) cells. The attachment point of the endocarp to the parent plant is often preserved at the proximal pole as an irregular aperture, and flanges can be preserved at the distal pole, often marked by a point. Longitudinal ridges extend the length of the endocarp in many species, varying from rounded cross-section to more angled or flanged forms, depending on the species and number of fertile locules.

Fragment morphology: Fragmentation in charred *Canarium* endocarps is varied in form and extent, with endocarps often fracturing longitudinally along their ridges and also following locule margins. This leads to fragments commonly preserving only a single curved (above the infertile locules) or flattened (above the fertile locule) endocarp wall. Fragmentation, especially close to the proximal or distal pole, does also, at times, cross the TS,

Figure 5. Anatomical features of *Canarium*. (a-d) SEM images of charred *C. indicum* endocarp, showing Layers 1-4 as described in the text; (a) TS with inner locule surface to left (boxes inset show position of (b-d)); (b) close up of Layers 1 and 2; (c) close-up of Layers 2 and 3; (d) close up of Layers 3 and 4; and (e) Small fragment of *Canarium* sp. endocarp from Taora, PNG, showing the tripartite structure typical of the genus and some key diagnostic features.



which allows all three seed locules and/or conjoins to be viewed.

Anatomy of endocarp ground tissue: In section, *Canarium* endocarp is comprised of at least four distinctive layers (Figure 5). An outer layer (Layer 1) is formed from tangentially flattened cells, generally smaller and with thinner walls than adjacent cells in Layer 2 and clearly identifiable lumen (cell cavities). In surface view (S on

Figure 4) cell margins were varied in their definition and shape, some being rectangular and others circular to elliptical. In some areas, distinct cells could not be identified at all. Layer 1 was generally thin, perhaps 5–10 cells thick at most, and had an indistinct transition into Layer 2 comprised of a mass of thick-walled isodiametric cells with clearly visible pores in the cell walls – this is a characteristic of all cells in *Canarium* endocarps. In Layer 2 these

generally decrease in size towards the indistinct boundary with Layer 1. The cells in Layer 1 had small to non-existent lumen (cavities) and the cell walls often fused into an indistinct mass, with cells only identifiable on the basis of the preserved cell lumen and small intercellular spaces.

Layer 2 had a variable transition to an inner layer (Layer 3) comprising of an interwoven mass of elongated, tangentially to radially arranged, porous cells with undulating margins. Layer 3 could be narrow, comprising 20% or less of the endocarp diameter or be much wider and extend into Layer 2 in a flaming pattern. Fragments of *Canarium* endocarp commonly broke in a stepwise pattern at the transition between Layers 2 and 3, following the contours of the transitional zone. Layers 2 and 3 often have different reflective properties under light microscopy.

The inner surface of *Canarium* endocarps, that is the seed locule, is highly distinctive and consists of a layer of irregular, radially aligned cells with a smooth inner surface that often fused into an indistinct mass during charring (Layer 4). This is attached to the rest of the endocarp by a layer of thin-walled polyhedral cells that commonly ruptured in broken specimens, causing the inner layer to separate and expose a highly distinctive layer of polyhedral cells on the locule surface. These cells typically measuring 50 μm in diameter and have raised cell margins and visible pores. This feature is found in all *Canarium* species, though in some specimens the inner layer remained attached to the endocarp and appeared as a smooth surface, where in others the layer was partially or totally detached.

Distinction between *C. indicum* (Figure 5), *C. harveyii* (Figure 6a, 6c, 6e, 6g) and *C. salomonense* (Figure 6b, 6d, 6f, 6h) was not possible at this time using anatomical criteria alone. Further work is required to determine whether it is possible at all. Size, shape and species distribution were the main methods of identifying species, such as *C. australium* at Madjedbebe (Florin et al., 2020, p. S1), and further work is required to evaluate the extent to which larger fruited species can be distinguished on the basis of morphology and also which morphological traits allow species identification in fragmented remains.

Archaeological specimens: Hundreds of archaeological specimens of *Canarium* were identified in the assemblages surveyed for this study and it was the most common of the species preserved. Anatomical features were preserved well, even in specimens where cells had become glassy due to high heat exposure, such as those from Pamwak (Figure 7a), and could be identified in relatively small fragments, such as those from Madjedbebe and Taora. A combination of anatomical features seen in Layers 1-4 is required to confirm identification of *Canarium* specimens in the target species group to genus level, including the outer smooth surface, isodiametric cells of Layer 2, tangential/radial cells of Layer 3 and polyhedral cell pattern on the locule inner surface following the detachment of Layer 4. Figure 5e shows a specimen from Taora in PNG of less than 2 mm in diameter, initially distinguished because of the preservation of the polyhedral pattern of cells on the locule inner surface. Close inspection showed the curved,

smooth outer surface of the endocarp and a clear distinction between outer (Layers 1 and 2) and inner cell layers (Layer 3) could be seen in the section. The polyhedral pattern of broken cells on the inner surface of Layer 3 in *Canarium* endocarps preserves well even in heavily eroded charred archaeological specimens, as shown in the case of two specimens from Pamwak, which also preserved the Layer 3 cell pattern in partially vitrified/glassy cells (Figure 7a-d). This pattern was also preserved in waterlogged specimens from Dongan (Figure 7g, 7h) when cells in the endocarp visible in section had clearly collapsed (Figure 7e, 7f).

Pandanus

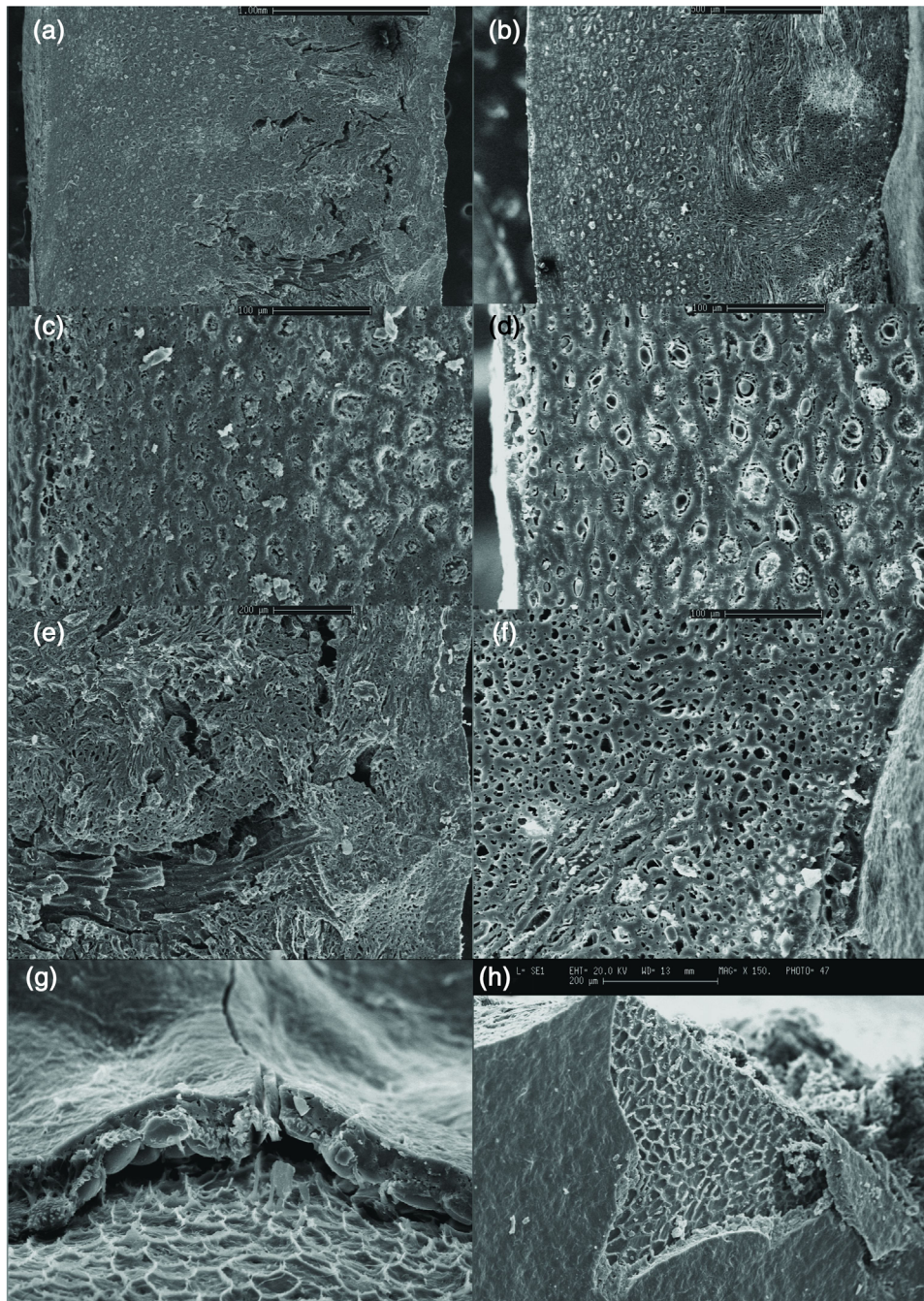
Using both morphological and anatomical criteria, *Pandanus* can be identified even following high levels of fragmentation. Further, even at high fragmentation, monodrupe and polydrupe species of *Pandanus* can be distinguished based on anatomical criteria. Further speciation is possible in some cases, either via cell wall thickness of monodrupe varieties (Donoghue, 1988; Fairbairn in Summerhayes et al., 2010) or through the identification of further anatomical criteria (e.g., the presence of distinctive mesocarp anatomy; Florin et al., 2020, 2021).

Surface morphology: In monodrupe species, the *Pandanus* endocarp breaks cleanly from the fibrous mesocarp and exocarp when dry or charred leaving a smooth surface with longitudinal ridges, and a rounded proximal pole and, depending on species, a slightly pointed distal pole (see Figure 8g, 8h). The proximal pole often has an irregular opening to the seed cavity. The ridges are formed by the cylindrical vascular bundles that ramify longitudinally, in parallel through the tissue, and that also project from the poles of the endocarp, looking like thick hairs (Figure 8g). In cross-section these are formed by a mass of circular to elliptical thick-walled cells that are very dense in low magnification – known as bundle sheath cells – surrounding the vascular tissues that in charred specimens often collapse leaving a series of circular voids. These are not always clearly visible in the bundles. The exocarp and mesocarp of polydrupe species usually collapses and falls away when charred, leaving an irregular surface to the endocarp (e.g., Figure 9f). In dried specimens the tissue of the mesocarp often remains, but may slightly collapse leaving longitudinal ridges from the vascular bundles within.

Fragment morphology: Fragments of monodrupe species usually retain some element of the external endocarp shape – the smooth external wall or the proximal/distal surfaces with projecting vascular bundles – and/or the smooth seed locule inner surface (see below; Figure 8d, 8f). Wall fragments usually preserve both inner and outer surfaces. Fragments of polydrupe species are much less regular in form (e.g., Figure 9h) and can be difficult to orientate unless sections of the seed locules are preserved (e.g., Figure 9d).

Locule surface: The seed locules are roughly cylindrical cavities within the endocarp, forming much of the volume of the drupe in monodrupe species and a series of smaller

Figure 6. SEM images of charred endocarps of *Canarium harveyii* (left column) and *C. salomonense* (right column). (a, b) complete TS with locule inner surface (I in Figure 4) to right and outer endocarp surface (S) to left; (c, d) close up of Layers 1 and 2; (e, f) close-up of Layers 3 and 4; (g, h) close-up of polyhedral cells on the locule surface.



voids in polydrupe species. They often include a single jutting-out ridge, or kernel attachment scar, which runs in parallel to the cavity (see Figure 8e). The locule surface is smooth but may preserve a series of very fine tangentially aligned striations.

Anatomy of endocarp ground tissue: In both monodrupe and polydrupe species of *Pandanus* the ground tissue consists of irregularly shaped cells which can appear to make flame-like patterns within the tissue in both TS and

LS. The closed collateral vascular bundles are circular to oval in shape. The xylem and phloem are present at one end of the bundle, the phloem often having collapsed, with sclerenchymatous cells or bundle sheath surrounding this vascular tissue in a non-symmetrical manner (see Figures 8a, 8b, and 9a, 8b). In monodrupes, the vascular bundles are uniformly arranged; the vascular tissue is positioned towards the inner surface of the endocarp, and the vascular bundles form evenly spaced concentric rings

Figure 7. SEM images of variable preservation of *Canarium* endocarp features in archaeological specimens. (a) cell fusion and glassiness in TS of specimen from Pamwak, PNG; (b) polyhedral cell impressions in same Pamwak specimen; (c) Survival of polyhedral cells and Layer 3 in small fragment of *Canarium* endocarp from Pamwak, PNG; (d) close-up of same specimen; (e) TS of waterlogged *Canarium* endocarp from Dongan section showing collapse of cells; (f) close up of collapsed cells in same specimen; (g, h) I in same specimen showing preservation of cell pattern.

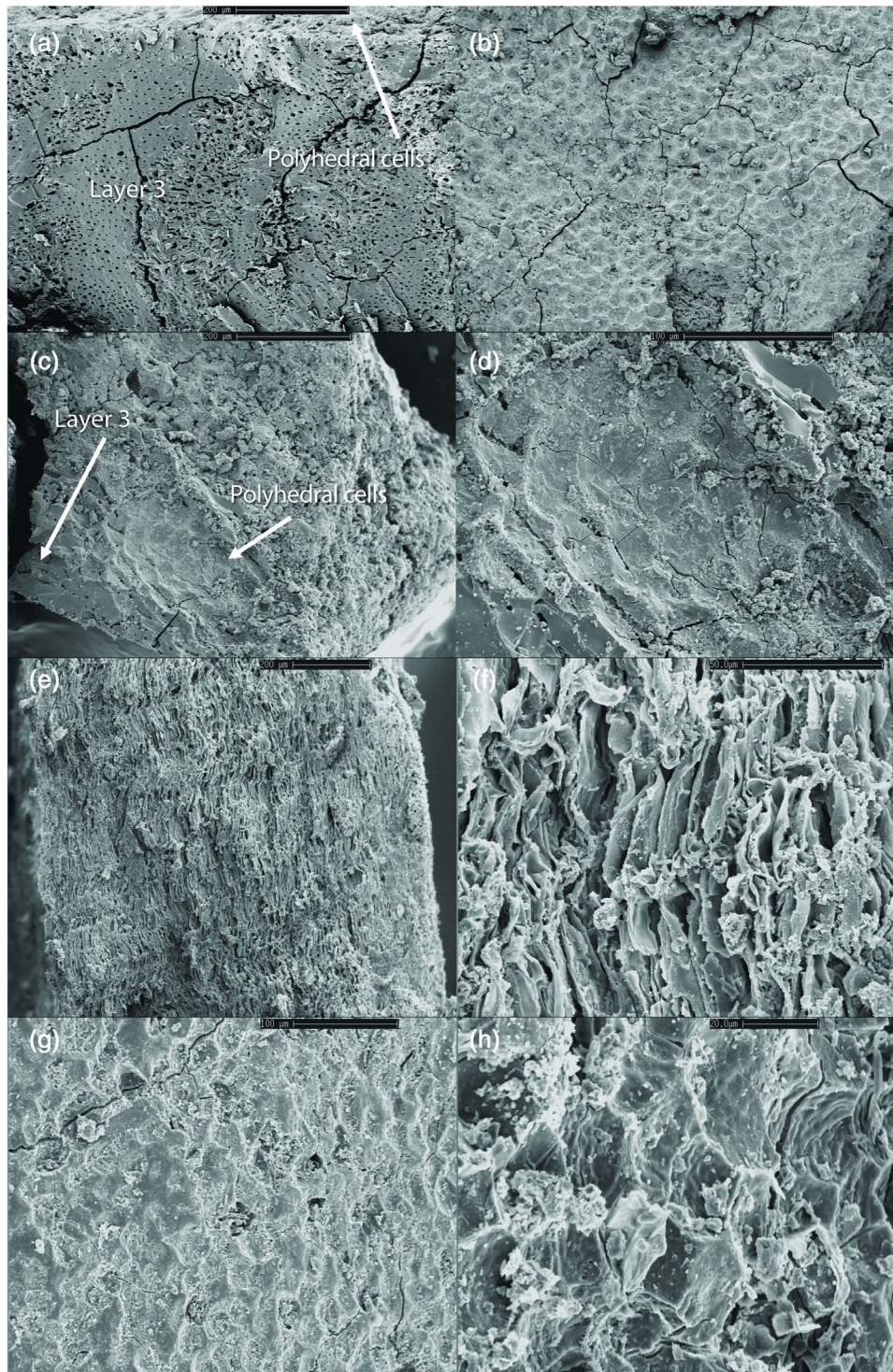


Figure 8. SEM images of charred reference (left) and archaeological (right) monodrupe *Pandanus*. (a) TS of *P. iwen* endocarp, displaying a close-up of a vascular bundle; (b, d) TS of *P. iwen* from Kosipe Mission (AER), Ivane Valley, PNG, (b) displays a close-up of a vascular bundle; (c) TS of *P. julianettii* endocarp, note the relatively thin-walled endocarp; (e) TS of *P. brosimus* endocarp, note the relatively thick-walled endocarp and the visible primary ring of larger vascular bundles and the outer ring of smaller vascular bundles; (f) TS of monodrupe *Pandanus* from Mamatu, PNG, note the visible primary ring of larger vascular bundles and the outer ring of smaller vascular bundles; (g) distal S of *P. Iwen*, displaying the vascular bundles, which form longitudinal ridges on the outer surface; (h) S of *P. iwen* from Kosipe Mission (AER), Ivane Valley, PNG, note the longitudinal ridges.

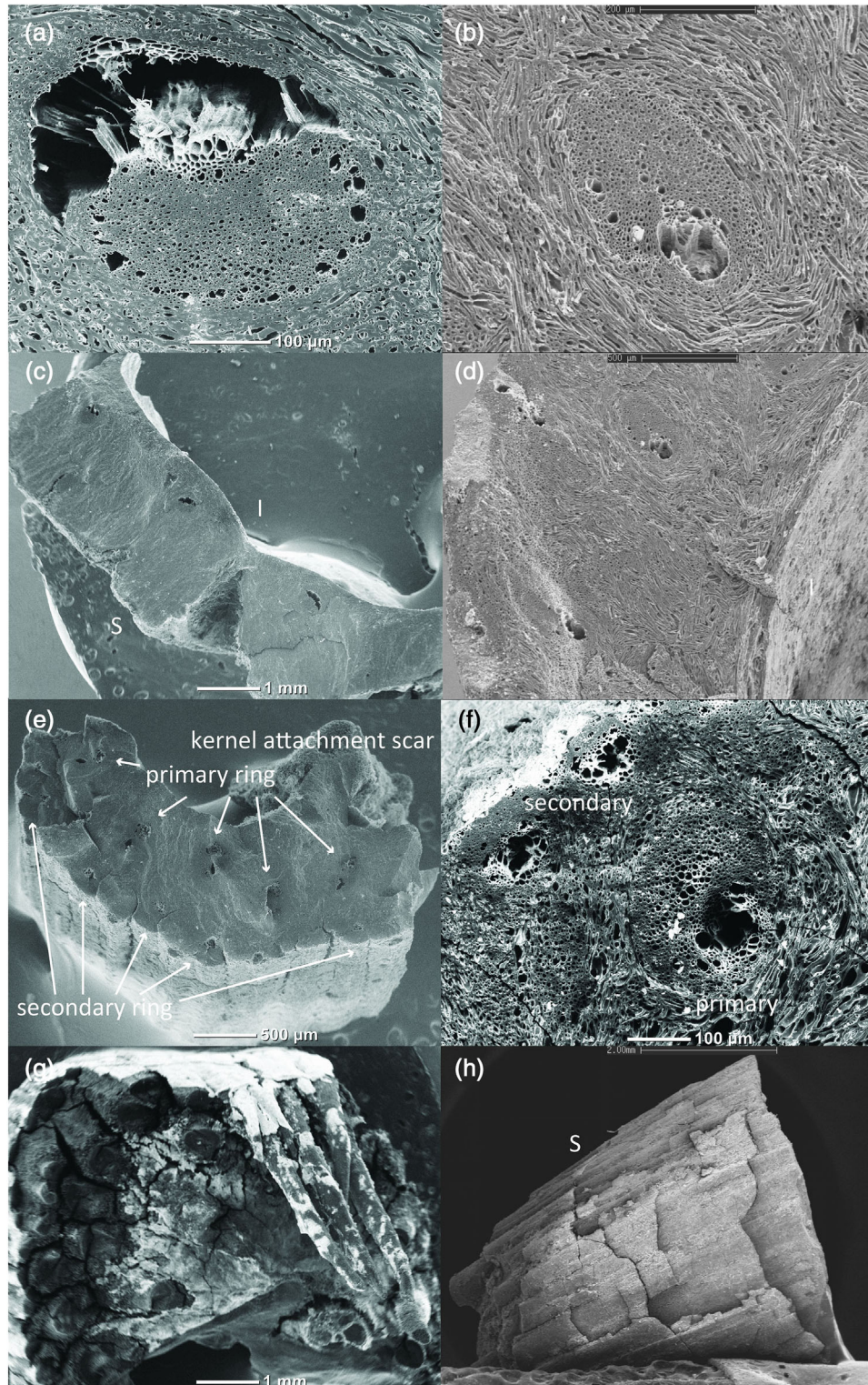
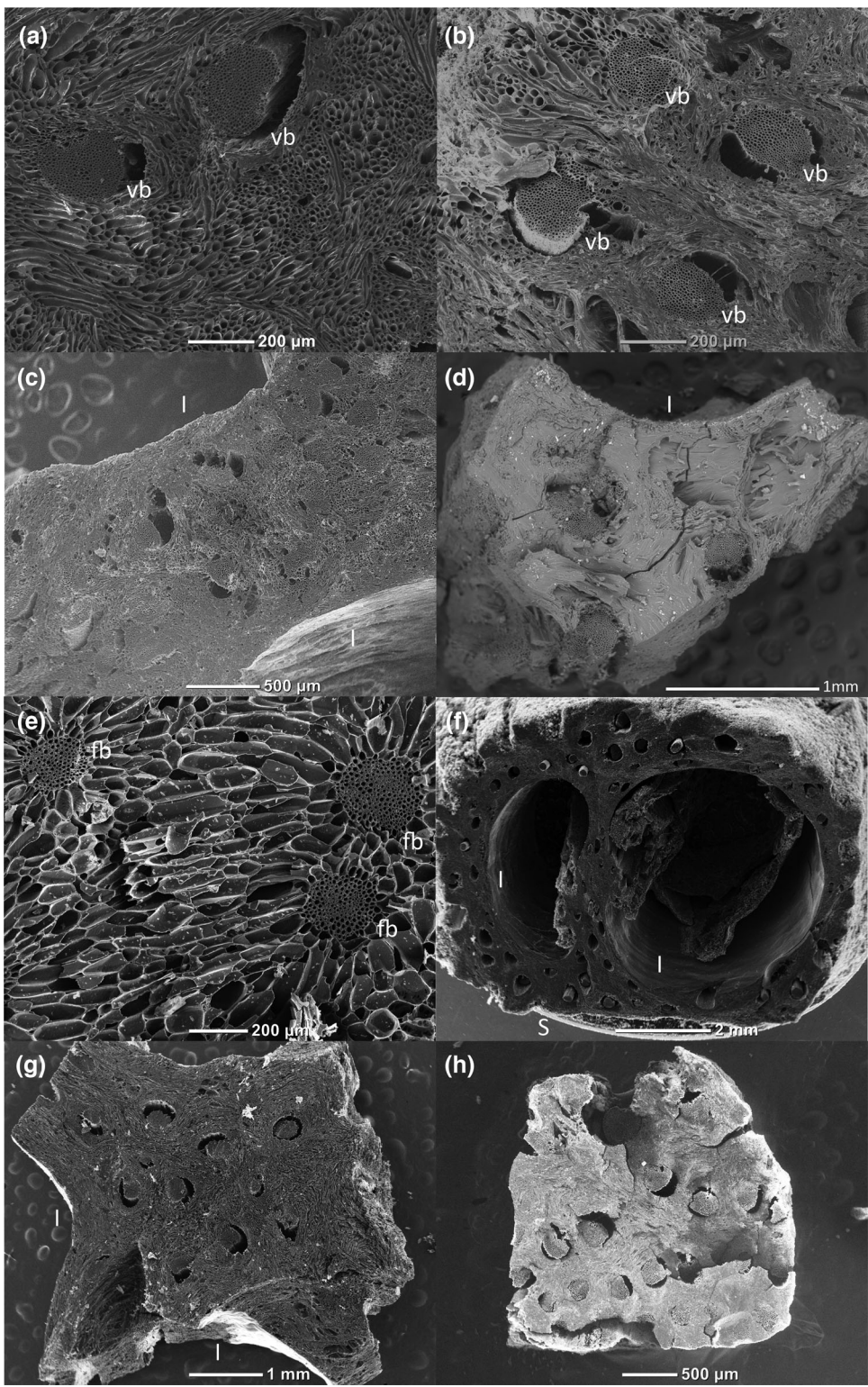


Figure 9. SEM images of charred reference (left) and archaeological (right) polydrupe *Pandanus*; vb: vascular bundles, fb: fibre bundle, I: inner surface, S: outer surface. (a, c) TS of *P. spiralis* endocarp; (b, d) TS of *P. spiralis* from Madjedbebe, Mirarr Country, northern Australia; (e) TS of *P. spiralis* mesocarp; (f) TS of *P. basedowii* "duo-drupe" endocarp; (g) TS of *P. tectorius*; (h) TS of polydrupe *Pandanus* sp. from Dongan, Sepik-Ramu, PNG.



around the seed locule. In many species, a primary, inner ring consists of larger vascular bundles than the secondary, outer ring or rings (Figure 8c-f). In comparison, polydrupe species are less uniform and, like in most monocotyledonous tissue, their vascular bundles are arranged randomly through the ground tissue often at a range of angles (Figure 9a-d, 9f). Large vessels, possible xylem elements, are found in the sclerenchyma in monodrupes and in those taxa phloem appears to be present on both sides of the xylem, though it is difficult to tell in charred specimens.

Archaeological specimens. Monodrupe *Pandanus* remains were widely found in sites from the Ivane Valley (Summerhayes et al., 2010), and preserved the distinctive anatomical features of the genus, including flaming cell pattern in TS and regularly distributed large vascular bundles with well-developed bundle sheaths (see Figure 8b, 8d). Also well preserved were the longitudinal ridges on the outside of the endocarp (Figure 8h). The anatomy of monodrupe *Pandanus* species was very similar and at this time species could not be distinguished on the basis of anatomy alone. Monodrupe *Pandanus* was also found at Mamatu, PNG (Figure 8f).

The assemblage at Madjedbebe was dominated by fragments of polydrupe *Pandanus* endocarp, identified as *P. spiralis* (Florin et al., 2020, 2021). Even though most fragments were small and did not permit for identification on morphological grounds (i.e., through the presence of multiple seed locule walls), the non-uniform nature of the vasculature patterning allowed for their identification as polydrupe *Pandanus* (see Figure 9b, 9d). Two species of polydrupe *Pandanus* grow in western Arnhem Land, *P. basedowii* and *P. spiralis*. A number of lines of evidence were used for further species identification: the presence of *P. spiralis* mesocarp (Figure 9e), which is more robust than that of *P. basedowii* and is composed of parenchyma oriented around small fibre bundles; the absence of "duo-drupe" endocarp, indicative of *P. basedowii* (Figure 9f); and the growth habitat of *P. basedowii*, which is today found on the elevated Arnhem Land Escarpment proper, approximately 10km away from the rockshelter, compared to the locally growing *P. spiralis*. Fragmented and waterlogged polydrupe *Pandanus* were found in the Dongan assemblage. These were identified by both morphological and anatomical criteria (Figure 9h).

Terminalia

Highly-fragmented *Terminalia* endocarp can be identified to genus, and in some cases even species, on the basis of its morphological and anatomical criteria (e.g., *T. grandiflora*; Florin et al., 2022).

Surface morphology: *Terminalia* fruits vary in the proportion and durability of the mesocarp tissue, with some persistent, such as *T. grandiflora* (Figure 10e) and *T. kaernbachii*, and others prone to full or partial collapse on charring, such as *T. catappa*, *T. carpentariae* and *T. ferdinandiana* (Figures 10a, and 11a, 11b). The surface of

the surviving structures in charred fruit assemblages is thus varied: that of *T. catappa* preserves the irregular edge of the endocarp; that of *T. carpentariae* and *T. ferdinandiana* preserves the exocarp surface, with the mesocarp partially collapsed beneath, creating a rough surface, with a longitudinally aligned reticulum (net-like pattern) running across it (much like an olive; Figure 10a); and that of *T. grandiflora* preserves the robust mesocarp tissue (see below) with the exocarp usually worn away (Figure 10e). Small evenly-spaced pores are found at the conjoins of the channels making up the reticulum in *T. carpentariae* and *T. ferdinandiana*, with only the pores and not the reticulum being usually preserved in archaeological samples (Figure 10g).

Fragment morphology: Composed of two convex sections fused together (Figures 4 and 10b), *Terminalia* endocarp usually fractures longitudinally following the locule margin, leaving a single curved inner endocarp wall. Further, transverse fractures are also common in charred specimens.

Anatomy of endocarp ground tissue: *Terminalia* ground tissue is composed of three layers (labelled in Figure 10d). In some species (e.g., *T. grandiflora*), the mesocarp tissue is more robust and acts as a further outer layer, composed of thin-walled isodiametric cells, which are located in corrugated furrows, intersecting with Layer 1 (Figure 10e). Layer 1 is an interwoven mass of transversely arranged porous, elongated cells with undulating cell walls. This layer is similar to the ground tissue in *Pandanus* and in some species forms small voids (e.g., *T. grandiflora*), which can be confused for the empty spaces left by vascular bundles in fragmented and disintegrated archaeological *Pandanus* specimens (see Figure 10e). Layer 1 fuses to a narrow band of a homogeneous mass of thick-walled isodiametric cells (Layer 2). These cells can fuse together in the charring process to create an indistinct mass, with only cell lumens visible. Layer 3 is a thin inner layer, which, along with parts of Layer 2, is often worn away. This results in the appearance of fine tangentially aligned striations on the locule surface.

While being consistent with the same layered structure, *T. catappa* and *T. kaernbachii* contain groups of large spherical voids throughout the endocarp and mesocarp tissue. These large voids (see Figure 11), presumably buoyancy aids for seeds that are easily distributed in water, are visible under low-powered microscopy and their inner surfaces retain the impression of the surrounding cell margins. While these species are very similar anatomically, there were differences that have the potential to be diagnostic. The mesocarp cells in both species were noticeably thinner-walled and less robust than the endocarp cells (Layer 1), but in *T. kaernbachii* they are thicker than corresponding tissue in *T. catappa*, which fragmented easily on charring and break away from the tougher endocarp. In the case of *T. kaernbachii*, like *T. grandiflora*, the mesocarp tissue was robust and appeared to survive charring well, holding together on the endocarp. The large voids seen in *T.*

Figure 10. Light-microscopy and SEM images of charred *Terminalia* fruits. (a) S and (b) TS of *T. fernandiana*; (c, d) SEM detail of *T. fernandiana* TS; (e, f) TS of *T. grandiflora*; (g, h) *T. ferdinandiana/carpentariae* from Madjedbebe, Mirarr Country, northern Australia, displaying S (g) and TS (h).

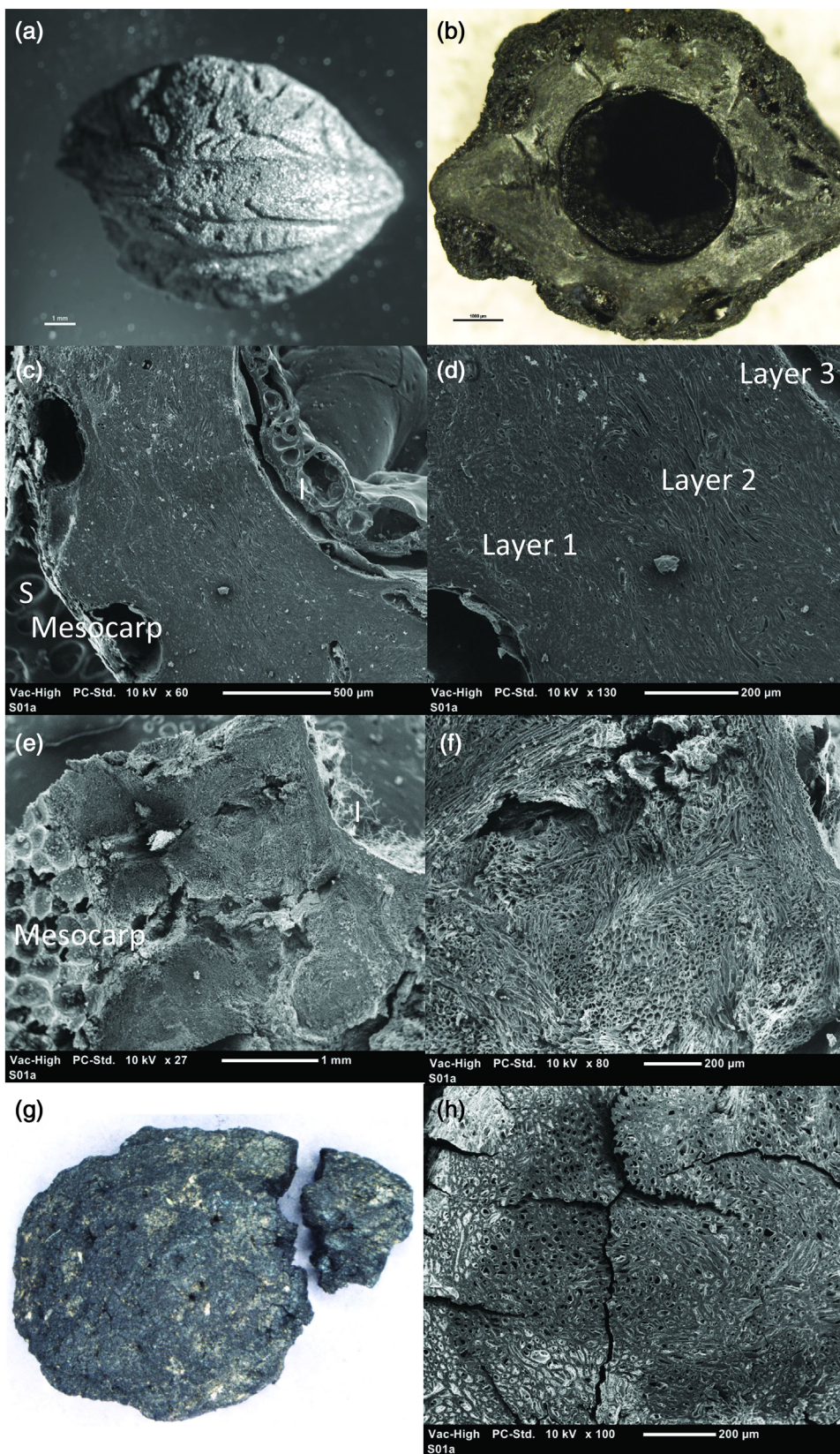
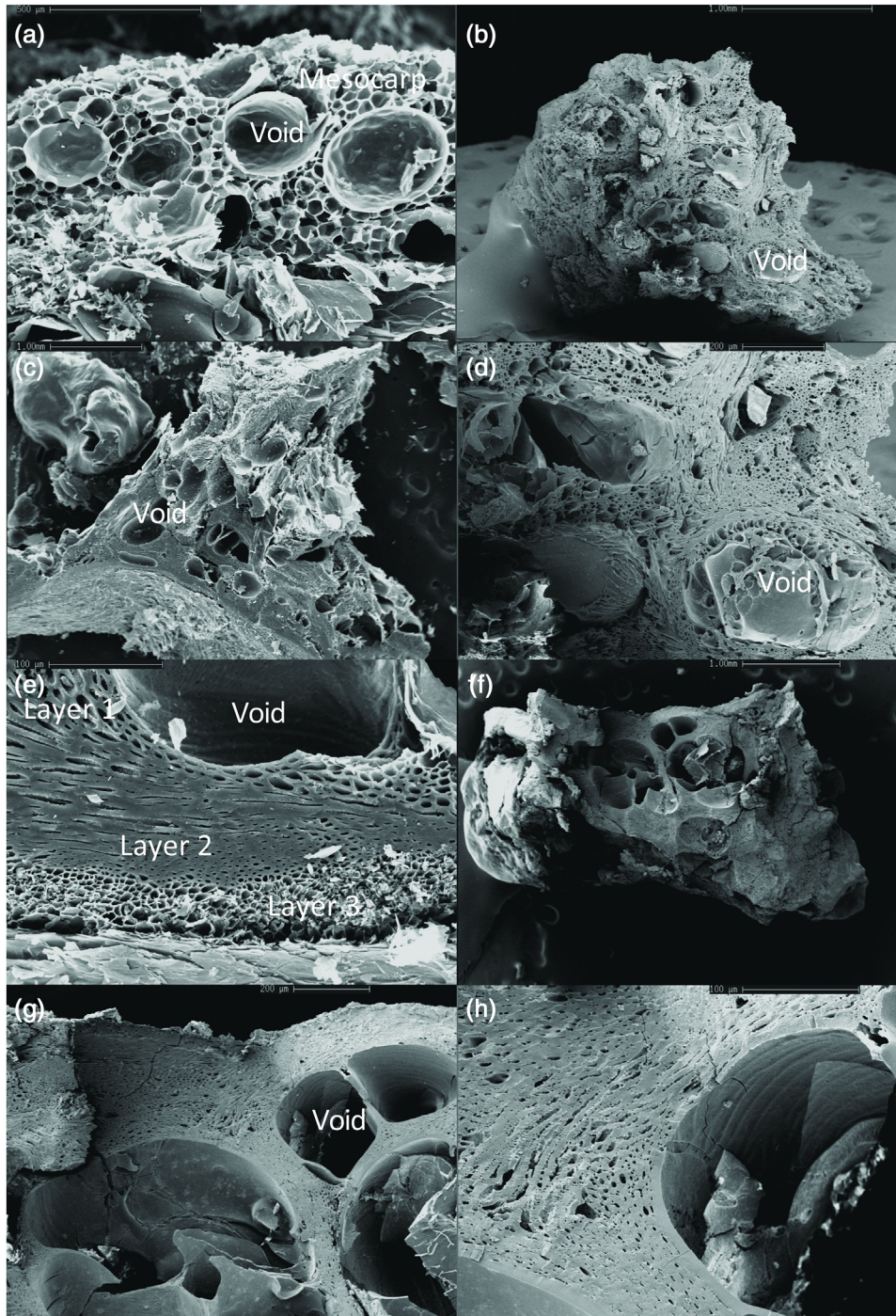


Figure 11. SEM images of charred *Terminalia* specimens. (a) TS of *T. catappa*; (b) *T. catappa* endocarp fragment; (c) *T. catappa* endocarp close-up; (d, e) *T. catappa/kaernbachii* from Yomining Site 3 (DGD/30) 130 cm–140 cm (D = fragment view; E = section view); (f–h) *T. catappa/kaernbachii* archaeological endocarp from Labang Tatale 140 cm–150 cm; (f) fragment view; (g, h) TS.

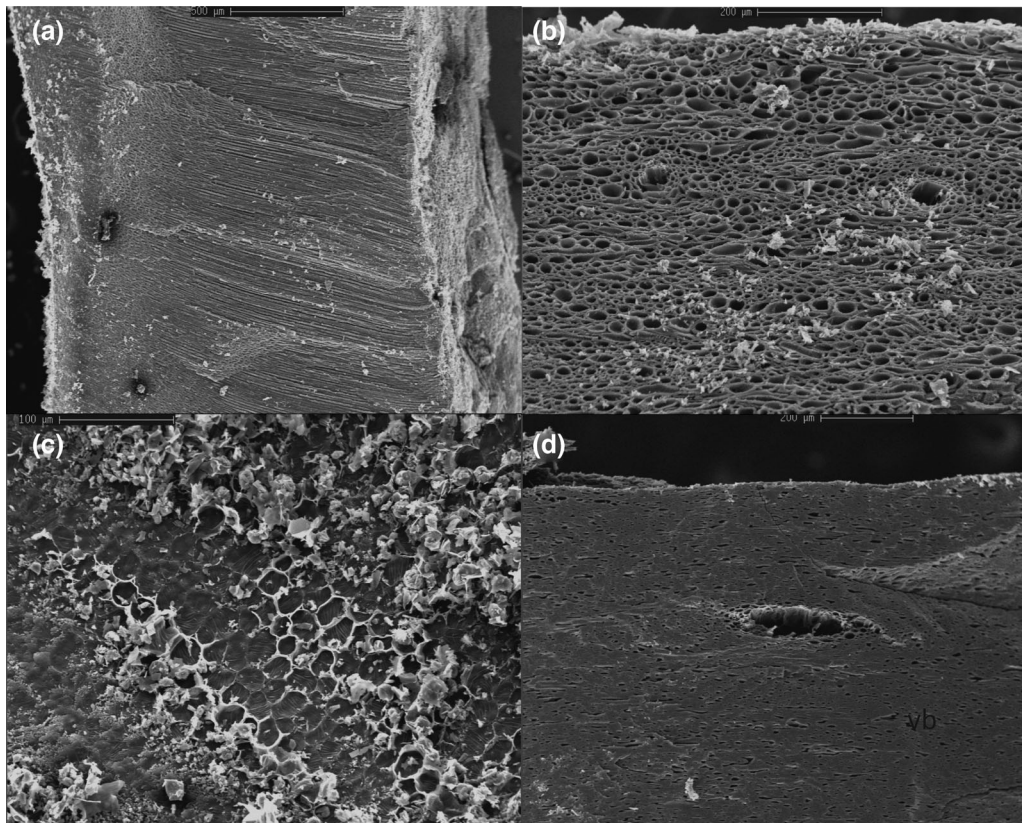


kaernbachii also formed distinctive clusters, separated by patches of smaller-celled ground tissue. Further work is required to determine if such characteristics are diagnostic and useful in determining species in charred remains.

Archaeological specimens: At Madjedbebe, archaeological specimens of *T. grandiflora* and *Terminalia*

spp. have been identified (Florin et al., 2020, 2022). The former is distinguished by its size (2 cm–4 cm, which is larger than *T. ferdinandiana* and *T. carpentariae*) and its outer mesocarp tissue, consisting of robust and large isodiametric cells (Figure 10e). Fragmentary specimens of *Terminalia* spp., based on size (1 cm–2 cm long), either

Figure 12. SEM images of *Aleurites molucanna* (a,b) and *Cocos nucifera* (c,d). (a) TS of *A. molucanna* endocarp reference specimen; (b) *A. molucanna* endocarp inner surface on reference specimen; (c) *Cocos nucifera* TS of immature endocarp reference specimen; (d) archaeological *Cocos nucifera* from Taora, PNG.



belong to *T. carpentariae* or *T. ferdinandiana* endocarp (Figure 10g, 10h). However, these drupes cannot be distinguished from each other using anatomical or morphological criteria. Their distinct characteristics, instead, relate to their exocarp colour and texture (*T. carpentariae* drupes are hairy or glabrous); criteria which are not archaeologically visible.

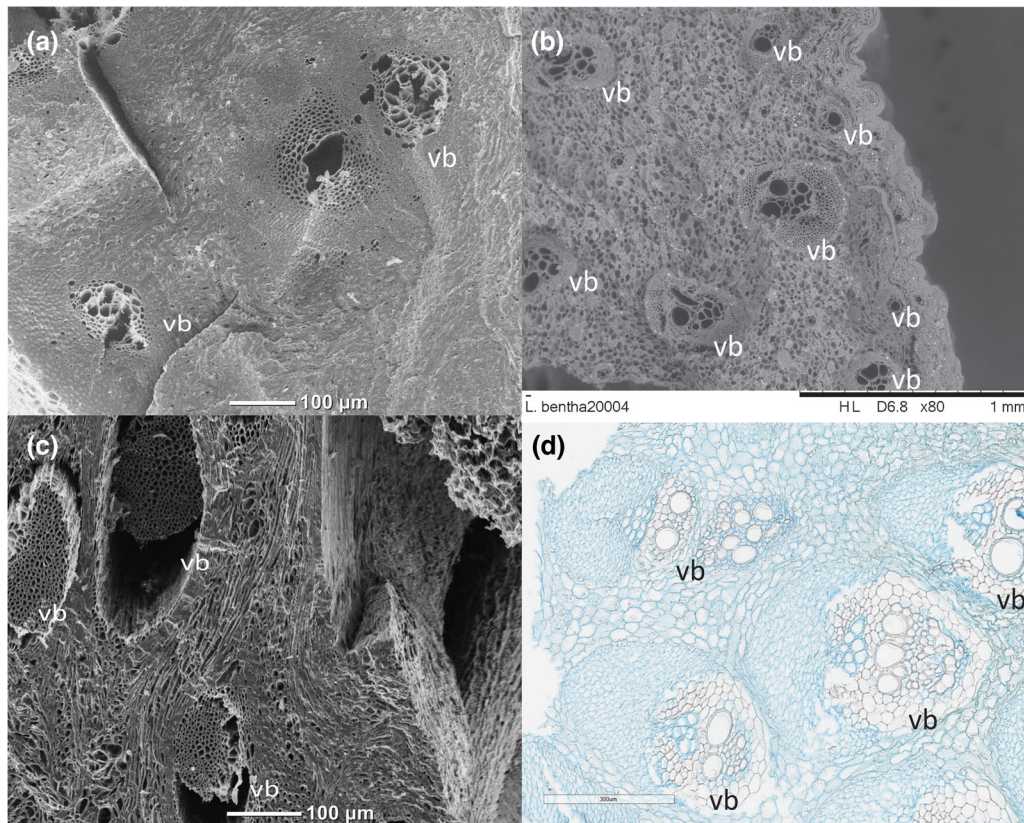
Archaeological fragments of charred archaeological endocarp from Yomining Complex site 3 (130 cm–140 cm, <900 BP; Figure 11d, 11e) and Lebang Tatale (140 cm–150 cm, 1310 BP; Figure 11f–h) were confidently identified as *T. catappa* or *T. kaernbachii* on the basis of their preserved anatomy. Given the distribution of both species, with *T. kaernbachii* only found on mainland New Guinea (Bourke, 1996; with a few potential outliers suggested beyond, Walter & Lebot, 2003, p. 241), it seems highly probable that the specimens come from *T. catappa*, which is very widespread in coastal regions. Further work is required to establish whether the two species can be adequately distinguished on the basis of their fruit anatomy. Only an uncertain identification of *Terminalia* was otherwise offered in foundation work by Doug Yen for specimens from other layers in the Nissan sites (Spriggs, 1991, p. 230, Table 6), and this exploratory work has thus expanded the data for plant exploitation on Nissan.

DISCUSSION

Our research demonstrates that by using anatomical criteria developed from modern reference specimens, charred and heavily fragmented archaeological specimens of *Canarium*, *Pandanus* and *Terminalia* endocarp can be separated from each other and identified confidently to genus level. The methods we have developed and described here, which are based on standard procedures for orienting and describing whole seeds and fruits combined with approaches adapted from the anatomical identification of wood charcoals, allow not only for the identification of these genera but for standardised comparison of modern reference material and archaeological endocarp specimens more widely. Furthermore, they allow for the systematic comparison of other seed and fruit remains, especially larger forms that are typically fragmented in archaeological sites.

While we have focused on *Canarium*, *Terminalia* and *Pandanus*, we have also reviewed endocarps from a wider range of economic taxa from the Asia-Pacific region. Candlenut (*Aleurites molucanna*; Figure 12a, 12b) and coconut (*Cocos nucifera*; Figure 12c, 12d) are two of the most commonly reported taxa in the Asia-Pacific and their endocarps are easily differentiated from those described here using our approach. *Aleurites* has a highly distinctive cell arrangement in TS, with long cells radially arranged

Figure 13. SEM images of *Pandanus* (a, c) and *Livistona* (b, d) endocarp and palm stem reference specimens. (a) TS of *P. brosimus*, displaying vascular bundles surrounded by thick-walled sclerenchyma. The sclerenchyma is partially vitrified. (b) TS of *L. benthamii*, displaying vascular bundles surrounded by thin-walled parenchyma. At the outer edge of the stem the ground tissue have collapsed due to the specimens drying prior to charring. (c) TS of *P. basedowii*, displaying vascular bundles surrounded by thick-walled sclerenchyma patterned in a flame-like manner. (d) Thin-section of *L. humilis*, displaying vascular bundles surrounded by thin-walled and delicate parenchyma.



across the whole endocarp thickness (Figure 12a). While the inner surface superficially resembles *Canarium*, the polyhedral cells are larger (Figure 12b) and in combination with the anatomical features in TS mean confusion of the two should not be possible. *Cocos* has a distinctive anatomy in TS with layers of elongated cells running perpendicular to each other, interrupted by secretory cavities (Figure 12c, 12d). Its fragments also have a shallow arc, indicative of the large size of the fruit and surface ridges. Again, the features are distinctive from the *Canarium*, *Terminalia* and *Pandanus*, as were the endocarps of *Barringtonia*, *Pometia*, *Elaeocarpus*, *Dracontomelon* and others.

Similarly, whilst *Pandanus* endocarp is superficially similar to monocotyledonous stem tissue, such as that from palm stem or USOs, it can easily be distinguished from these. Figure 13 compares the anatomical structure of *Pandanus* to *Livistona* spp. palm. Both have vascular bundles arranged randomly through ground tissue. However, their ground tissue is markedly different. Whilst that of *Pandanus* is made up of thick-walled and elongated cells (sclerenchyma), that of *Livistona* is made up of thin-walled and delicate, isodiametric cells (parenchyma). The latter can be easily transformed in shape with drying

and charring (see Figure 13b) and is much less dense than endocarp – a feature that can be felt when sectioning, and heard when dropping a specimen from height into a glass petri dish. The charred tissues of monocotyledonous stem-based USOs are also made up of parenchyma and are often even less dense again.

Anatomical features were surprisingly well preserved in the archaeological specimens, but there was considerable variation between specimens in clarity of resolution. Specimens varied in the degree of cell fusion and differentiation, probably reflecting the charring environment, as well as the age and development of the endocarp when charred. Furthermore, erosion of the specimen surfaces was often seen, leading to obliteration of the visible features, though fresh sectioning could revive the sample when it was large enough to split. When cell structure was visible, it was sometimes difficult to assign a fractured section to TS or RLS in fragmented archaeological specimens as fragment orientation was difficult due to the lack of preserved landmarks. A key requirement for success in this method was familiarity with complete and dissected reference specimens from the target genera. This allowed informed assessment of the probable

orientation of the specimen, using for example surviving macroscopic features. Where such assessment was fruitless, fragments were fractured perpendicular to the endocarp surface (S), which in most cases yielded satisfactory results.

A technical limit was imposed on identification by the size of fragments required to preserve intact specimens of the key anatomical features. The smallest identified fragments were 1 mm–2 mm in maximum dimension (e.g., Figure 5e). It is doubtful that smaller fragments could be identified as secure identification required the observation of sets of features, which are not preserved together in heavily fragmented specimens (<1 mm in size).

Some archaeological specimens were also extremely fragile and fragmented due to handling and pressure changes during SEM work, in some cases leading to charring and poor image retrieval, and in others the loss of the specimen. Fragility increased with sample age, with early specimens from Pamwak failing in several cases. Sample preparation (coating, drying, gradual introduction to low-pressure environments) reduced these problems, as did the use of low vacuum SEM, which is recommended in all cases. In some cases, the deterioration of tissue was such that identification was simply not possible.

While many anatomical criteria were best visualised using SEM and high-powered light microscopy, the authors found that initial sorting of specimens under low-powered light microscopy was sufficient for identification of key features in archaeological specimens once reference specimens had been extensively observed. This greatly sped up analysis and reduced the exposure of rare specimens to damaging instrumental conditions. However, use of SEM and/or high-powered incident light microscopy was required for some difficult specimens and when encountering unfamiliar taxa.

While work has demonstrated that *Canarium*, *Terminalia* and *Pandanus* specimens can be identified at a genus level using anatomical criteria alone, higher level identification using only anatomical criteria is limited in potential. For example, *C. indicum*, *harveyii*, *salomonense* and *australianum* endocarp have very similar anatomical structure, as did those of *T. catappa* and *T. kaernbachii*. The anatomical criteria in *Pandanus* could be used to distinguish between fragmented monodrupe and polydrupe endocarps and some species could be identified using a mixture of anatomical and morphological characteristics (e.g., *T. grandiflora*; Florin et al., 2022). However, in many cases species level identification requires morphometric analysis. Morphometric studies have been shown to be efficacious for identifying monodrupe *Pandanus* species (Donoghue, 1988; Summerhayes et al., 2010) and in analysing possible domestication in *Canarium* (Lepofsky et al., 1998).

Whilst morphological analysis has allowed for the identification of tree crop remains in many places across the Asia-Pacific and is important for identification at the species level, in archaeological sites with less than the ideal preservation environment specimens preserving these characteristics are often limited in number. This is

especially true with increasing antiquity. At Madjedbebe, whilst it was not abnormal for late Holocene specimens to be preserved as larger fragments (i.e., >4 mm in size), the majority of identified endocarp specimens in the earliest phase of occupation (Phase 2) were between 1 mm and 2 mm in size. These specimens would not have been identifiable without the use of anatomical criteria, and importantly, would not have been recovered without flotation or by using an appropriate sieve size. This observation emphasises the importance of using fine-meshed sieves to recover the least biased assemblages and widest range of plant macrofossils from excavated archaeological sediments. In the legacy sample set, *Terminalia* remains, probably from *T. catappa*, were identified for the first time with a high level of confidence in two sites from Nissan. Both fragments lacked coherent morphological indicators of their identity and had not been identified in earlier work. The method described here empowers archaeobotanists to produce better justified and systematic identifications for a wider range of preserved specimens. As shown by the analyses discussed here, it has shown the potential to greatly expand the database available for understanding ancient plant use in the tropics of Australia and Oceania, but as tree fruits and nuts are found widely around the world, the method also has much wider geographical potential.

CONCLUSION

Endocarp is durable and widely preserved in a range of archaeological contexts. Its recovery and identification also has a lot to offer to studies of past human movements, economies, culinary traditions, and cultural contact and exchange. Our research demonstrates that anatomical criteria can be used, alongside available morphological criteria to identify charred and heavily fragmented archaeological specimens of *Canarium*, *Pandanus* and *Terminalia* endocarp. Initial comparative research suggests that the method is a powerful means of identifying a broad range of economic taxa, including the most commonly exploited fruits of the Asia-Pacific, and further analysis on reference specimens will test and extend the observations made here. Many other genera are economically valuable across the Asia-Pacific region. Most are large and have little chance of routinely surviving in morphologically identifiable form in charred plant remain assemblages. The method outlined here has the potential to greatly increase the range and number of plant species represented in Asian-Pacific and, indeed, global archaeobotany from a greater number of sites, including dryland sites in which charring is the only preservation medium. Alongside, the use of systematic archaeobotanical recovery, including flotation, fine dry- and wet-sieving (i.e., using 0.5mm and 1mm meshes), it clearly has the potential to improve archaeological data for plant-based subsistence.

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