

The Role of Plant Foods in the Evolution and Dispersal of Early Humans: A Perspective from Across the Wallace Line

Die Rolle pflanzlicher Nahrung bei der Evolution und Verbreitung früher Menschen: Ein Blick von jenseits der Wallace-Linie

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ABSTRACT

In recent years, new evidence for the early use of plant foods has challenged the stereotype of the meat-eating Paleolithic. Whilst often making up the smaller component of the diet, plant foods are key to hominin diets, carbohydrates especially providing an efficient energy resource. This paper reviews the current evidence for the role of plant foods in the evolution and dispersal of early modern humans and our closest ancestors, with a focus on new evidence for early diet from Island Southeast Asia, Australia and New Guinea. It demonstrates the importance of plant foods and their processing, to the dietary flexibility and adaptive capacity of our species.

Keywords: Wallacean Archipelago, Sahul, Madjedbebe, plant food, human evolution, dietary flexibility

ZUSAMMENFASSUNG

In den letzten Jahren haben neue Belege für die frühe Verwendung pflanzlicher Nahrungsmittel das Stereotyp des fleischiessenden Paläolithikums in Frage gestellt. Obwohl sie oft den kleineren Teil der Ernährung ausmachen, sind pflanzliche Nahrungsmittel der Schlüssel zur Ernährung der Homininen, wobei insbesondere Kohlenhydrate eine effiziente Energiequelle darstellen. Dieser Beitrag gibt einen Überblick über die aktuellen Belege für die Rolle pflanzlicher Nahrungsmittel bei der Evolution und Verbreitung des frühen modernen Menschen und unserer nächsten Vorfahren. Der Fokus liegt dabei auf neuen Belegen von den Inseln Südostasiens,

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Australien und Neuguinea. Deutlich wird die Bedeutung pflanzlicher Nahrungsmittel und ihrer Verarbeitung für die ernährungsmäßige Flexibilität und Anpassungsfähigkeit unserer Spezies.

Schlagwörter: Wallacea, Sahul, Madjedbebe, Pflanzennahrung, menschliche Evolution, ernährungsmäßige Flexibilität

Introduction

As a species, *Homo sapiens* have thrived beyond the extinction of our closest hominin ancestors and have adapted to many and diverse environments, using cultural innovations to not only survive within but to shape the world around us. Diet, and the ability to extract energy and nutrition from diverse resources and ecological niches, has long been seen as key to this process of evolution and dispersal. However, research into Paleolithic diets has historically focused on the animal component: meat and its associated hunting behaviors and technologies. Whilst this focus reflects the biases of the archaeological record, it has also been broadly supported by an assertion that most calories in modern hunter-gatherer (Cordain et al. 2000; cf. Milton 2000) and—where isotopic analysis has offered an insight—Paleolithic diets are derived from animal sources (Richards et al. 2000; Bocherens et al. 2005; Bocherens 2009; Richards and Trinkaus 2009; Wißing et al. 2016; Jaouen et al. 2019; cf. Naito et al. 2016; Drucker et al. 2017). However, more recent research has revisited the importance of plant foods to Paleolithic diets. This has been a result of new evidence and, in many cases, novel methods (e.g., analysis of plant microfossils in dental calculus). It has also been a result of a shift in focus to understand the macro-nutrient requirements of hominin populations, and the role of hard-to-process and non-preferred or ‘fallback’ foods, including many plant foods (Robinson and Wilson 1998; Laden and Wrangham 2005), in their evolution and dispersal. This has led to new considerations of the importance of plant foods in the movement of archaic and modern humans into more marginal environments (Jones 2009; Hardy 2010), and of the ultimate success of modern human populations (Stiner and Kuhn 2009; Power and L'Engle Williams 2018).

Whilst much of this debate has been centered on Africa and Eurasia, the archaeology of Island Southeast Asia, Australia and New Guinea has in recent years provided new evidence for the role of plant foods in early adaptations to novel environments (see Fig. 1; Barton 2005; Barker et al. 2007; Summerhayes et al. 2010; Dilkes-Hall et al. 2019; Florin et al. 2020). The movement of humans across the Wallacean Archipelago and the peopling of Sahul (the Pleistocene continent encompassing Australia, New Guinea and the Aru Islands) represents a critical threshold in human history, human populations crossing a series of biogeographic boundaries impassable for all kinds of animals, including several of our hominin ancestors (*H. floresiensis*; Brown et al. 2004; Sutikna et al. 2016; *H. luzonensis*; Détroit et al. 2019; and, possibly, Denisovans; Carlhoff et al. 2021; Teixeira et al. 2021). This paper reviews the current evidence for the role of plant foods in the evolution and dispersal of modern humans and our closest ancestors, and uses evidence from the southern dispersal arc to provide new perspectives on the importance of plant gathering, cooking and processing to the adaptive capacity of humans across a range of environments.

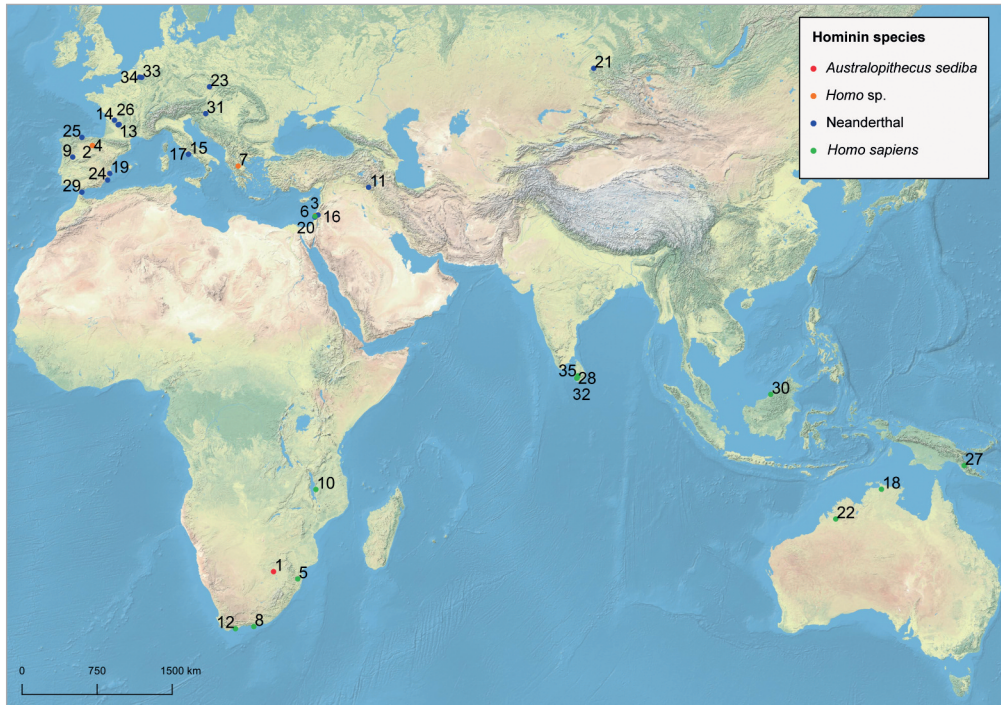


Fig. 1: Map of archaeological sites with direct evidence for early plant food use, dating from >35 kya, in chronological order.

Abb. 1: Karte archäologischer Stätten mit direkten Hinweisen auf eine frühe pflanzliche Nahrungsnutzung älter als 35.000 Jahre vor heute in chronologischer Reihenfolge.

1: Malapa, South Africa; 2: Sima del Elefante, Spain; 3: Gesher Benot Ya'aqov, Israel; 4: Gran Dolina, Spain; 5: Border Cave, South Africa; 6: Skhul Cave, Israel; 7: Theopetra Cave, Greece; 8: Klasies River Caves, South Africa; 9: Figueira Brava Cave, Portugal; 10: Ngalue Cave, Mozambique; 11: Shanidar Cave, Iran; 12: Blombos Cave, South Africa; 13: La Ferrassie I and II, France; 14: La Quina, France; 15: Grotta del Fossellone, Italy; 16: Amud Cave, Israel; 17: Grotta Guattari, Italy; 18: Madjedbebe, Australia; 19: El Salt, Spain; 20: Kebara Cave, Israel; 21: Chagyrskaya Cave, Siberia; 22: Carpenter's Gap 1, Australia; 23: Kůlna Cave, Czech Republic; 24: Sima de las Palomas del Cabezo Gordo, Spain; 25: El Sidrón, Spain; 26: Abris des Merveilles, France; 27: Ivane Valley, New Guinea; 28: Fa-hien Lena, Sri Lanka; 29: Gorham's Cave, Gibraltar; 30: Niah Cave, Borneo; 31: Vindija Cave, Croatia; 32: Kitulgala Beli-lena, Sri Lanka; 33: Goyet Caves, Belgium; 34: Spy Cave, Belgium; 35: Batadomba-lena, Sri Lanka; ESRI base map.

Diet, and hominin evolution and dispersal in Africa and Eurasia

Diet has long been considered important to hominin evolution. Many of the physiological traits unique to the *Homo* genus, including our relatively large brain size, decreased gut size, and changes in dental morphology and locomotive adaptations suggest innovative dietary choices comparative to other primates. However, the evidence available to directly consider the diet of different hominin species is scarce, especially in earlier time periods, and tends to favor evidence for the more robust, animal component of diet. Where the remains of plant foods do preserve,

it is often as charred macrofossils—the processes of cooking, burning fuel or disposing of rubbish in hearths allowing for continued preservation of these materials through carbonization; as more robust fossil remains (e.g., phytoliths, mineralized seeds); or in special preservational environments (e.g., water-logged sites, within dental calculus). However, with increased antiquity, the recovery of plant food remains requires both exceptional preservational environments and the implementation of systematic archaeobotanical recovery techniques. Therefore, a range of indirect evidence, including changes in phenotypic traits and genetics, and comparisons to contemporary human and nonhuman primate populations are often required, alongside archaeological evidence, to build a picture of evolving hominin diet.

For the majority of hominin evolution diet has been heavily plant-based, and early australopiths likely ate a diet similar to that of their closest ancestors, great apes. This meant a diet heavily focused on fruits, with leaves, flowers and stem consumed as secondary or fallback foods (Doran et al. 2002; Rothman et al. 2008; Hohmann et al. 2010; Watts et al. 2012; Vogel et al. 2017). All great apes also consume some insect matter, which provide trace nutrients. Chimpanzees and bonobos, especially dominant males, hunt and kill small vertebrates and monkeys, which can make up to 10-20% of their diet (Milton 1987; Watts 2020). However, the majority of chimpanzees and bonobos, and likely early hominins, acquire the substantive proportion of their calories from fruit (~60-70%) and leaves (20%; Pontzer and Wood 2021). Changes in the microwear and dental morphology of *Australopithecus*, and to a greater degree *Paranthropus*, including increases in molar size, enamel thickness and decreases in shearing quotients, has been suggested to indicate a shift to a broader plant-based diet, with focus potentially shifting from leaves to underground storage organs (USOs) as a fallback food 4-2 million years ago (mya; Ungar 2004; Laden and Wrangham 2005). This is supported by isotopic evidence for C4 resource consumption by *A. bahrelghazali* individuals from Koro Toro in Chad, which is argued to demonstrate the exploitation of the above- and below-ground parts of grasses (*Poaceae*) and sedges (*Cyperaceae*), especially sedge tubers and corms (Lee-Thorp et al. 2012).

Meat-eating

More than 2.5 mya (Bunn 1981; Potts and Shipman 1981; Domínguez-Rodrigo et al. 2005), and possibly as early as 3.3 mya (McPherron et al. 2010), cut marks found on fossil faunal assemblages attest to the hunting and confrontational scavenging of large herbivores by African hominids (Domínguez-Rodrigo and Pickering 2003; cf. O'Connell et al. 2002). This increase in meat-eating associated with late *Australopithecus* and early *Homo*, broadly corresponds to the evolution of a significantly larger relative brain size, increased body size, simplified digestive anatomy, and greatly expanded geographical range occurring with *H. erectus* by 1.8 mya (Wood and Collard 1999a, b). As such, increased carnivory has been argued to be a central mechanism in the evolutionary development of *Homo* (Aiello and Wheeler 1995; Milton 1999; Bunn 2007; Zink and Lieberman 2016).

Aiello and Wheeler's (1995) 'expensive-tissue hypothesis' argues that the energy expenses of relative increases in brain size in *Homo* were offset by decreasing gut size and, therefore, required

a high-quality, easy-to-digest diet. The addition of hunting into the Hominin behavioral repertoire is argued to have provided such a high-calorie, low-fiber resource (Bunn 2007), and evidence of changing masticatory capacity in *Homo*, including decreased enamel thickness and increases in the shearing quotients compared to *Australopithecus*, supports the inclusion of more, tough and elastic resources, such as meat, into early Pleistocene diets (Ungar 2004). However, whilst meat is high-calorie and provides easily digestible essential amino acids, minerals and vitamins, the metabolic cost of converting protein into energy, required for brain function and the physical demands of hunting (e.g., endurance running; Bramble and Lieberman 2004), greatly exceeds that of carbohydrates (Milton 1999). Meat-eating has usually been argued, therefore, to have been incorporated into a mixed diet, potentially also allowing for a shift towards the consumption of a higher-proportion of energy-rich, rather than nutrient-rich, plant resources, such as seeds, nuts and USOs (Milton 1999, 2003). Early direct evidence for plant food use is sparse. However, there is evidence for the use of uncooked starchy plant foods and nut-cracking, dating to ~1.2 mya and 790 kya, respectively (see Table 1; Goren-Inbar et al. 2002; Hardy et al. 2017).

Cooking and starchy plant foods

Changes in dietary composition are not the only way to improve dietary quality. The processing of foods, especially cooking, has also been implicated in the evolution of increased hominin brain size (Wrangham et al. 1999; Wrangham 2007; 2017; Wrangham and Carmody 2010). Wrangham et al.'s 'cooking hypothesis' argues that the ability to cook food, rather than meat-eating, was the likely driver for the encephalization of our species ~2 mya. This is because cooking makes many foods easier to digest, especially starchy plant foods (e.g., USOs, grass seeds) through the conversion of resistant starches to soluble forms; kills foodborne pathogens; and necessitates the assembly of foods into a shared location, heightening competition and facilitating new social relationships (Wrangham et al. 1999; Carmody and Wrangham 2009; see also O'Connell et al. 1999). There is, however, no archaeological evidence for the use of fire by hominins prior to ~1.5–1 mya (Brain and Sillen 1988; Bellomo 1994; Berna et al. 2012), and repeated and consistent fire use is not apparent until 400–200 thousand years ago (kya; Roebroeks and

Table 1 (pages 18–21): Direct evidence for the use of plant foods, dating to >35 kya; †*Homo sapiens* also occupied the site, but not during this time period; **Celtis* spp. endocarp have also been found at several other Early and Middle Pleistocene archaeological sites (Chaney 1935; Aigner 1969; de Lumley et al. 1976; Laville and Renault-Miskovsky 1977; Binford and Ho 1985; Matsutani 1987; Bittman 1992; Gabunia et al. 2000; Messenger et al. 2008). However, these assemblages have been largely interpreted as environmental in origin.

Tabelle 1 (Seiten 18–21): Direkte Belege für die Verwendung pflanzlicher Lebensmittel, datiert auf älter als 35.000 Jahre vor heute; †*Homo sapiens* bewohnte die Stätte ebenfalls, jedoch nicht während dieser Zeit; **Celtis* spp. Endocarpe wurden auch an mehreren anderen archäologischen Stätten des Alt- und Mittelpleistozäns gefunden (Chaney 1935; Aigner 1969; de Lumley et al. 1976; Laville und Renault-Miskovsky 1977; Binford und Ho 1985; Matsutani 1987; Bittman 1992; Gabunia et al. 2000; Messenger et al. 2008). Diese Fundanhäufungen wurden jedoch weitgehend als umweltbedingten Ursprungs interpretiert.

#	Site	Age	Associated hominin	Type of evidence
1	Malapa, South Africa	2 mya	<i>Australopithecus sediba</i>	Plant microfossils recovered from dental calculus
2	Sima del Elefante, Spain	1.2 mya	<i>Homo</i> sp.	Plant microfossils recovered from dental calculus
3	Gesher Benot Ya'aqov, Israel	790 kya	<i>Homo</i> sp.	Usewear analysis of pitted stone artifacts; Waterlogged macrofossils (preserved in a lake margin environment)
4	Gran Dolina, Spain	780 kya	<i>Homo</i> sp.	Mineralized plant macrofossils
5	Border Cave, South Africa	170 kya	<i>Homo sapiens</i>	Charred plant macrofossils
6	Skhul Cave, Israel	130-100 kya	<i>Homo sapiens</i>	Plant microfossils recovered from dental calculus; Plant microfossils recovered from stone tool surfaces
7	Theopetra Cave, Greece	129 kya, 124 kya, 57 kya	<i>Homo</i> sp.	Charred and mineralized plant macrofossils; Phytoliths recovered from anthropogenic sediment samples, including hearths
8	Klasies River Caves, South Africa	120 kya, 65 kya; 102-98 kya; 102-98 kya	<i>Homo sapiens</i>	Charred plant macrofossils; Plant microfossils recovered from dental calculus; Plant microfossils recovered from stone tool surfaces
9	Figueira Brava Cave, Portugal	106-86 kya	Neanderthal	Charred plant macrofossils
10	Ngalue Cave, Mozambique	105 kya	<i>Homo sapiens</i>	Plant microfossils recovered from stone tool surfaces
11	Shanidar Cave, Iran	100-44 kya; 50-46 kya	Neanderthal ¹	Plant microfossils recovered from Mousterian stone tool surfaces; Plant microfossils recovered from dental calculus
12	Blombos Cave, South Africa	99-70 kya	<i>Homo sapiens</i>	Plant microfossils recovered from dental calculus
13	La Ferrassie I and II, France	74-68 kya	Neanderthal	Plant microfossils recovered from dental calculus
14	La Quina, France	71-48 kya	Neanderthal	Plant microfossils recovered from dental calculus; Plant microfossils recovered from stone tool surfaces
15	Grotta Fossellone, Italy	70 kya	Neanderthal	Plant microfossils recovered from dental calculus
16	Amud Cave, Israel	70-55 kya	Neanderthal	Phytoliths recovered from anthropogenic sediment samples, including hearths
17	Grotta Guattari, Italy	67 kya, 55 kya	Neanderthal	Plant microfossils recovered from dental calculus

#	Evidence	Reference
1	Phytoliths from dicotyledonous plants, including from leaves, fruit and wood or bark, and from monocotyledonous plants, including from sedges, palm and possible grasses	Henry et al. 2012
2	Starch grains, including from a Poaceae seed (Triticeae or Bromideae tribe), no signs of cooking or processing	Hardy et al. 2017
3	Usewear evidence for nut-cracking, likely including the extraction of acorns (<i>Quercus</i> spp.); Waterlogged remains of 55 taxa of plants known to be eaten ethnographically, although many are found naturally within the lake margin and may have been deposited via natural or hominin agents	Goren-Inbar et al. 2002; Melamed et al. 2016
4	Mineralized hackberry (<i>Celtis</i> sp.) endocarps, associated with human occupation of the site*	Allué et al. 2015
5	Charred star-lily (<i>Hypoxis</i> sp.) rhizomes recovered from hearth features	Wadley et al. 2020
6	Starch grains, including from Triticeae tribe grass seeds, and phytoliths from date palm (<i>Phoenix</i> spp.) fruits, some starch show signs of cooking and processing; 100 starch grains on 26 tools, including from Triticeae and Adropogoneae or Paniceae tribe grass seeds, and probable USOs, and phytoliths from date palm (<i>Phoenix</i> spp.) fruits	Henry et al. 2014
7	Charred and mineralized remains of 14 taxa of wild legumes, and fruits; Phytoliths, including dendritic grass phytoliths from mature grass spikelets, sedges (Cyperaceae family), and celtis (<i>Celtis</i> sp.) fruits	Tsartsidou et al. 2014; Kotzamani 2009
8	Charred parenchyma fragments from underground storage organs recovered from hearth features; Starch grains, including from Triticeae and Adropogoneae or Paniceae tribe grass seeds, and probable USOs; 48 starch grains on 23 tools, including from Triticeae and Adropogoneae or Paniceae tribe grass seeds, and probable USOs	Henry et al. 2014; Larbey et al. 2019
9	Large quantities of charred stone pine (<i>Pinus pinea</i>) bracts and nutshell	Zilhão et al. 2020
10	Starch grains, mostly from wild <i>Sorghum</i> spp., especially prevalent on scrapers and core/grinding tools, some show evidence of damage, potentially from processing such as grinding	Mercader 2009
11	35 starch grains on 32 tools, including from Triticeae and Adropogoneae or Paniceae tribe grass seeds, probable legumes and probable USOs; Starch grains, including from Triticeae tribe grass seeds, some of which show signs of cooking, probable legumes and probable USOs, and phytoliths from date palm (<i>Phoenix</i> spp.) fruits	Henry et al. 2011
12	Starch grains, including from Adropogoneae or Paniceae tribe grass seeds	Henry et al. 2014
13	2 starch grains	Henry et al. 2014
14	3 starch grains; Starch grains, including from Triticeae and Adropogoneae or Paniceae tribe grass seeds	Henry et al. 2014
15	Some starch grains, a phytolith from a grass, and other plant tissue	Power et al. 2018
16	Phytoliths, including high proportions of dendritic grass phytoliths from mature grass spikelets	Madella et al. 2002
17	Starch grains, including from probable Lily (<i>Lilium</i> sp.) and Triticeae grass seeds, and phytoliths from monocotyledonous and dicotyledonous plants	Power et al. 2018

#	Site	Age	Associated hominin	Type of evidence
18	Madjedbebe, Australia	65-53 kya	<i>Homo sapiens</i>	Charred plant macrofossils; Residue and use-wear analysis of grinding stones
19	El Salt, Spain	60.7-45.2 kya	Neanderthal	Gas chromatography of coprolite samples
20	Kebara Cave, Israel	60-48 kya	Neanderthal	Charred plant macrofossils
21	Chagyrskaya Cave, Siberia	51-45 kya	Neanderthal	Plant microfossils recovered from dental calculus
22	Carpenter's Gap 1, Australia	51-38.8 kya	<i>Homo sapiens</i>	Charred and dried plant macrofossils
23	Kůlna Cave, Czech Republic	50-40 kya	Neanderthal	Plant microfossils recovered from dental calculus
24	Sima de las Palomas del Cabezo Gordo, Spain	50 kya	Neanderthal	Plant microfossils recovered from dental calculus
25	El Sidrón, Spain	49 kya	Neanderthal	aDNA analysis of eukaryotic diversity recovered from dental calculus
26	Abris des Merveilles, France	49-39 kya	Neanderthal'	Plant microfossils recovered from Mousterian stone tool surfaces
27	Ivane Valley, New Guinea	49-36 kya	<i>Homo sapiens</i>	Charred plant macrofossils; Plant microfossils recovered from stone tool surfaces
28	Fa-hien Lena, Sri Lanka	48-34 kya	<i>Homo sapiens</i>	Charred plant macrofossils; Plant microfossils recovered from sediment samples
29	Gorham's Cave, Gibraltar	47-33 kya	Neanderthal'	Charred plant macrofossils; Plant microfossils recovered from Mousterian stone tool surfaces
30	Niah Cave, Borneo	46-34 kya	<i>Homo sapiens</i>	Charred and dried plant macrofossils; Plant microfossils recovered from stone tool surfaces and sediment samples
31	Vindija Cave, Croatia	45.5 kya, 34.3 kya	Neanderthal	Plant microfossils recovered from dental calculus
32	Kitulgala Beli-lena, Sri Lanka	44.9-31.6 kya	<i>Homo sapiens</i>	Charred plant macrofossils
33	Goyet Caves, Belgium	41-40 kya	Neanderthal	Plant microfossils recovered from dental calculus
34	Spy Cave, Belgium	37-36 kya	Neanderthal	Plant microfossils recovered from dental calculus; aDNA analysis of eukaryotic diversity recovered from dental calculus
35	Batadomba-lena, Sri Lanka	36.3-31.5 kya	<i>Homo sapiens</i>	Plant microfossils recovered from sediment

#	Evidence	Reference
18	Charred remains of 5 fruit and nut taxa, including pandanus (<i>Pandanus spiralis</i>) endocarp, a hard-to-extract tree nut; 3 underground storage organs and 2 types of palm pith; Residue and usewear consistent with grinding of small siliceous seeds on a grinding stone fragment	Clarkson et al. 2017; Florin et al. 2020
19	Phytosterol metabolites, including 5 β -stigmastanol and 5 β -epistigmastanol, were present, showing the direct dietary input of plant sterols	Sistiaga et al. 2014
20	Charred remains of 45 taxa of plants known to be eaten ethnographically, dominated by legumes and, to a lesser degree, pistachio (<i>Pistachia atlantica</i>)	Lev et al. 2005
21	Starch grains, phytoliths, including from grass, and other plant tissues	Salazar-García et al. 2021
22	Charred and dried endocarp of <i>Terminalia</i> sp. fruits/nuts and black plum (<i>Vitex cf. glabrata</i>) fruits	McConnell and O'Connor 1997; Dilkes-Hall et al. 2019
23	Starch grains, including from Triticeae tribe grass seeds	Henry et al. 2014
24	Small number of starch grains and phytoliths	Power et al. 2018; Salazar-García et al. 2021
25	aDNA from split gill mushrooms (<i>Schizophyllum commune</i>), pine nuts (<i>Pinus koraiensis</i>) and forest moss (<i>Physcomitrella patens</i>)	Hardy et al. 2012; Weyrich et al. 2017
26	15 starch grains on 7 tools, including from Triticeae and Adropogoneae or Paniceae tribe grass seeds	Henry et al. 2014
27	Charred monodrupe pandanus (<i>Pandanus</i> cf. <i>taip</i>) endocarps; 753 starch grains on 3 stone artifacts, including from probable yam (cf. <i>Dioscorea</i> sp.) tubers	Fairbairn et al. 2006; Summerhayes et al. 2010
28	Charred canarium (<i>Canarium</i> sp.) endocarps; Phytoliths from grasses, shrubs and trees, including bananas (<i>Musa accuminata</i> , <i>Musa balbisinia</i>), wild rice (<i>Oryza</i> spp.), palm (Arecaceae), breadfruit (<i>Artocarpus</i> sp.), canarium (<i>Canarium</i> sp.) and durians (<i>Durio</i> sp.)	Premathilake and Hunt 2018a, b; Wedage et al. 2019b
29	Charred wild olive (<i>Olea</i> sp.) and stone pinenut (<i>Pinus pinea</i>) endocarps; 17 starch grains on 16 tools, including from Triticeae and Adropogoneae or Paniceae tribe grass seeds	Barton et al. 1999; Henry et al. 2014
30	Charred and dried remains of 13 plant taxa, including two likely toxic species, wild yam (cf. <i>Dioscorea hispida</i>) and kepayang (<i>Pangium edule</i>) nuts; Starch grains from birah (<i>Alocasia longifolia</i>), yam (<i>Dioscorea</i> sp.) and palm pith, the latter of which was recovered from a stone tool as well as sediment samples	Barton 2005; Barker et al. 2007; Barton and Paz 2007
31	Starch grains, including from Triticeae and tribe grass seeds, probable legumes and probable USOs; phytoliths from monocotyledonous and dicotyledonous plants, fungal spores and other plant tissue	Power et al. 2018
32	Probable charred breadfruit (cf. <i>Artocarpus</i> sp.) and canarium (cf. <i>Canarium</i> sp.) endocarp	Wedage et al. 2020
33	A starch grain	Henry et al. 2014
34	Starch grains, including from a probable waterlily (Nymphaeaceae family) USO, and Adropogoneae or Paniceae tribe grass seeds; aDNA from grey shag mushroom (<i>Coprinopsis cinerea</i>)	Henry et al. 2011, 2014; Weyrich et al. 2017
35	Phytoliths from grasses, shrubs and trees, including palm (Arecaceae), banana (<i>Musa</i> sp.) and breadfruit (<i>Artocarpus</i> sp.), likely deposited by natural and human agents	Perera et al. 2011

Villa 2011; Shahack-Gross et al. 2014; Sandgathe 2017; Sorensen 2019). It is, therefore, possible that cooking was not a key driver of earlier hominin evolution, including physiological and behavioral changes evident in early *H. erectus*. However, its effect on modern human physiology is readily apparent, as, even with access to domesticates and electric blenders, the contemporary choice to subsist on uncooked plant foods has been shown to cause undernutrition, reduced libido, amenorrhea and fatigue (Koebnick et al. 1999).

One hypothesized effect of cooking and other plant-processing practices on human physiology is copy number expansion (increased repetition of the relevant section of the genome) in the α -amylase gene responsible for the production of salivary amylase, *AMY1* (Hardy et al. 2015; Inchley et al. 2016). α -amylase is an enzyme responsible for catalyzing the hydrolysis of starch into sugars, and is produced in the pancreas and salivary glands of humans. Whilst the role of salivary, as opposed to pancreatic, amylase in starch breakdown is still somewhat unclear (Sonestedt 2018), increased salivary amylase has been associated with changes in the oral perception of starches, leading to increased palatability, and the body's pre-absorptive metabolic signalling, allowing for more effective digestion (Hoebler et al. 1998; Mandel et al. 2010; Mandel and Breslin 2012; Peyrot des Gachons and Breslin 2016; Atkinson et al. 2018). Further, high copy numbers of *AMY1* (up to 30) and associated increased salivary amylase production, correlate with the consumption of high-starch diets both within contemporary human populations, and between humans and non-human primates, the latter only possessing two copy numbers (Samuelson et al. 1996; Perry et al. 2007). A recent study investigating the *AMY* gene locus in ancient and modern DNA found that a copy number expansion occurred in *AMY1* following the split between Neanderthals and modern humans ~650 kya and prior to the movement of humans outside Africa (Inchley et al. 2016). Inchley et al. (2016) argue this copy number expansion occurred in a selective environment in which increased starch consumption favored changes in starch-digestion efficiency. This increased starch consumption was, they argue, facilitated by the development of plant processing practices in the Middle Pleistocene, such as cooking, grinding, and leaching.

Whilst Neanderthals only possess two *AMY1* copy numbers (Prüfer et al. 2014), a recent genomic analysis of ancient and modern oral microbiomes of *Homo* and nonhuman primates, provided evidence for abundant oral *Streptococci* bacteria in both modern humans and Neanderthals, but not in nonhuman primates (Fellows Yates et al. 2021). These bacteria possess amylase-binding protein genes, which when expressed capture salivary amylase, for their nutrition and dental adhesion. This suggests starch consumption had begun to increase prior to the split between Neanderthals and modern humans. Later copy number variations in *AMY1* likely reflected a growing trend in the increasing use and processing of starchy plant foods, potentially with roots in the pre-*Homo* dietary incorporation of USOs 2-4 mya.

This is supported by a sparse, but growing body of direct evidence for the use, cooking and processing of starchy plant foods by both modern humans and Neanderthals in Africa and Eurasia (see Table 1). This includes macrobotanical evidence for the cooking of USOs by modern humans by 170 kya in South Africa (Larbey et al. 2019; Wadley et al. 2020); and diagnostic pro-

cessing damage on starch grains recovered from both modern human and Neanderthal dental calculus, 130-100 kya and 50-46 kya, respectively, in Israel, suggesting the cooking and eating of starchy plant foods (Henry et al. 2011, 2014). Wild grass starch grains with processing damage consistent with grinding, recovered from the surfaces of stone tools, such as scrapers and core/grinding tools, at Ngalue Cave in Mozambique also attest to seed-grinding by modern humans by 105 kya (Mercader 2009).

Hyper-carnivorism and animal fat

However, this evidence does not allow for easy interpretations of the proportional contributions of plant and animal foods to diet, and some researchers still argue for a heavy reliance on large animal foods by Middle Pleistocene *Homo* in Africa and Eurasia (Ben-Dor et al. 2011, 2021; Ben-Dor and Barkai 2021). The ‘hyper-carnivore hypothesis’ argues *H. erectus* and later Middle Paleolithic hominins (including Neanderthals and early modern humans) relied on animal foods for over 70% of their caloric intake. To achieve this, they required high animal fat contributions to their diet, to offset protein consumption. This is because protein consumption has a physiological limit in humans, placed at ~20-50% of daily calorie intake (Billsborough and Mann 2006; Speth and Spielmann 1983; Noli and Avery 1988). This limit is due both to the high metabolic cost of processing protein for energy, which raises daily caloric requirements, and the limited ability of the liver and kidneys to remove the by-products of protein metabolism, especially nitrogen-containing urea (Billsborough and Mann 2006; Rudman et al. 1973). The documented effects of eating a diet based primarily in lean protein, known as ‘rabbit starvation’, are starvation despite high-calorie consumption, loss of body protein, protein toxicity and, after several weeks, death (Stefansson 1944; Speth and Spielmann 1983). Both fats and carbohydrates spare the metabolism of protein for energy and their consumption is required to maintain a high-protein intake. Ben-Dor and colleagues (Ben-Dor et al. 2011, 2021; Ben-Dor and Barkai 2021) hypothesize that a specialization in large prey, epitomized by the hunting of elephants, by Middle Pleistocene *Homo* allowed them to consume the high-fat diet required to live as hyper-carnivores. Decreases in prey-size, due to a mixture of over-exploitation and changing environments, they argue, led to decreased fat-intake, a subsequent broadening of diet to offset this, and increasingly complex behavioral and cultural adaptations (Ben-Dor and Barkai 2021).

However, numerous studies have shown that under conditions of marginal calorie, protein or glucose intake, carbohydrates spare protein more efficiently than fat, making plant foods an often more efficient substitute to fatty animals despite their higher processing requirements (Speth and Spielmann 1983). Further, modern examples of hyper-carnivorism—such as arctic-living, where a high-fat intake is met by blubber-rich marine mammals, or pastoralism, which relies on domestication and secondary products for fat and protein consumption—are recent adaptations to marginal environments (Vasil’ev et al. 2016; Arbuckle and Hammer 2018; Flegontov et al. 2019; Pontzer and Wood 2021). Wild animals from sub-arctic environments typically have much lower levels of body fats than those involved in these examples (<5%; Cordain et al. 2000; Hardy 2010). Hyper-carnivorism, therefore, demonstrates the extreme flexibility of the human

dietary niche. However, it is very unlikely, even given the higher fat content of larger extinct Pleistocene mammals (Ben-Dor and Barkai 2021), that it was a preferred diet across Middle Pleistocene Africa and Eurasia, especially in warmer tropical and temperate regions. Indeed, contemporary hunter-gatherer groups from temperate and tropical regions depend on gathered plant foods for at least ~26-55% of their calories (Cordain et al. 2000), and it is argued that the risk involved in large game hunting in many of these societies means it is practiced as much for its benefits as a competitive male display and its role in the production of reciprocal relationships through meat-sharing, as it is for its nutritional advantages (Hawkes et al. 1991; O'Connell et al. 2002). It is only in the northern coniferous forest and tundra that plant foods make up less than 25% of hunter-gatherer calories (Cordain et al. 2000; cf. Milton 2000).

The dietary breadth of Neanderthals and modern humans in Europe

In the glacial, high-altitude environments of Middle Paleolithic Europe, it is, therefore, not surprising that there is both zooarchaeological and isotopic evidence to suggest that Neanderthal populations may have relied heavily on the hunting of woolly mammoths and large ungulates, such as gazelle, deer, wild horses, boar, bison, and wild cattle (Hoffecker 1991; Stiner 1994; Gaudzinski 1995; Thieme 1997; Marean and Assefa 1999; Burke 2000; Richards et al. 2000; Griggo 2004; Bocherens et al. 2005; Kuhn and Stiner 2006; Bocherens 2009; Richards and Trinkaus 2009; Stiner and Kuhn 2009; Wißing et al. 2016; Jaouen et al. 2019). Kuhn and Stiner (Kuhn and Stiner 2006; Stiner and Kuhn 2009) have argued the archaeological signature of this dietary pattern is markedly different to that of Upper Paleolithic modern human populations in Europe, who were increasingly more reliant on small hard-to-capture prey, aquatic resources and plant carbohydrates evidenced by the increased frequency of grinding stone technologies in archaeological sites. They link this dietary shift, to other technological changes in the Upper Paleolithic, including the development of bone needles and awls required for the production of clothing and shelter, which are associated with gendered division of labor ethnographically. As such, they argue, Upper Paleolithic populations broadened their dietary breadth through the development of complimentary, gendered economic roles, comparable to those of most modern hunter-gatherer economies. The adaptive advantages of specialized division of labor, namely increased dietary breadth, rather than a specific difference in cognitive or physiological capabilities, is argued to have allowed the demographic expansion of modern human populations and, eventual, out-competition of contemporary Neanderthal populations in Europe.

However, whilst there is compelling evidence for the hunting of woolly mammoths and large ungulates by Middle Paleolithic populations, there is also a growing body of evidence to suggest Neanderthal diet may have been broader than previously argued. First, the isotopic evidence used to construct the trophic position of Neanderthal populations has been questioned. This is because nitrogen isotope data only provides evidence for protein consumption. This leads to a significant undercalculation of plant food use in diets, because such resources usually contribute to carbohydrate and fat, rather than protein, intake. Even when specifically investigating the percentage contribution of animal and plant foods to protein intake, the analysis of nitrogen

isotopes from bulk collagen samples has been shown to underestimate the significance of plant foods (Wißing et al. 2016). Where analysis has instead been completed on individual amino acids, estimations of plant food contributions to protein intake have been significant even in cold environments (e.g., >20% at Buran Kaya III, south Crimea: Drucker et al. 2017; up to 20%, at Spy Cave, Belgium: Naito et al. 2016). Further, this isotopic data is preferentially available at archaeological sites from colder climates, where plants likely played a smaller role in Neanderthal diets, as warmer climates are less conducive to the survival of ancient collagen in human bones (Power and L'Engle Williams 2018).

Second, there is a growing body of direct evidence for a significant contribution of plant foods and fungi to Neanderthal diets (see Table 1). Across Eurasia, microfossils and eukaryotic aDNA preserved in dental calculus have attested to the likely consumption of a range of plant foods and fungi by Neanderthals, including fruits, nuts, wild grass seeds, legumes, USOs, and mushrooms (Henry et al. 2011, 2014; Weyrich et al. 2017; Power et al. 2018; Salazar-García et al. 2021). Whilst this data does not attest to the proportion of plant foods eaten by Neanderthal populations, direct comparison to modern human dental calculus from Middle and Upper Paleolithic Europe has shown no obvious difference either in the range of plant taxa consumed or the evidence for cooking practices (Henry et al. 2014). Further to this, phytolith analysis of sediment samples at Amud Cave, Israel, provides clear and repetitive evidence for the collection and likely consumption of grass seeds by its Neanderthal population, 70-55 kya (Madella et al. 2002), and recent macrobotanical evidence from Figueira Brava Cave, Portugal, provides evidence for continued harvesting of pine nuts, requiring the climbing of mature pine trees, 106-86 kya (Zilhão et al. 2020). The latter is one of several Neanderthal sites to provide macrobotanical evidence for the exploitation of fatty tree nuts and fruits (see Table 1; Barton et al. 1999; Lev et al. 2005). It is, therefore, likely that plant foods made a more significant contribution to Neanderthal diets than previously thought, especially in the more southern range of their distribution. Third, there is also evidence for the exploitation of significant quantities of small vertebrates, avifauna, fish, and marine mammals and shellfish by some Neanderthal populations in the southerly latitudes of Europe (Stringer et al. 2008; Blasco and Fernández Peris 2012; Will et al. 2019; Zilhão et al. 2020).

This evidence suggests that the large-game hunting focus of Neanderthals in high-latitude Europe was likely supported by the consumption of carbohydrates and fats from plant foods, especially in late winter when animal prey had lower body fats (Jones 2009; Hardy 2010). Further, much like early modern human populations, Neanderthals likely exploited a range of resources dependent on their local environment, including hard-to-process plant foods, such as grass seeds, fish and animal prey requiring a range of capture technologies. This does not, however, negate a general trend visible in the Upper Paleolithic, which saw continued increases in the contribution of small game to modern human diets (Stiner 2001), and a range of technological changes, including the increased use of grinding technologies. Power and L'Engle Williams (2018) reviewed the archaeological evidence for increases in grinding stones in the Upper Paleolithic, and found an increase in this technology beyond that hypothesized for increasing

population size in this period. They argued this archaeologically-more-robust evidence for plant-processing indicated increasing processing practices in the Upper Paleolithic, and especially following the Last Glacial Maximum. This may be linked to an increased gendered division of labor in early modern human populations. Alongside other factors, such as the local availability of plant foods with changing climate, increasingly distinct economic roles may have allowed for the individual technological specialization required to produce a broader group diet. However, this appears to be a more gradual and spatially diverse pattern than originally proposed by Kuhn and Stiner (Kuhn and Stiner 2006; Stiner and Kuhn 2009), and a continuation of foraging practices already displayed by Neanderthals. It is, therefore, hard on present evidence to conclude as to whether an increased gendered division of labor and specialization in plants and other foods was responsible for the out-competition of Neanderthals in Eurasia, or if its increased archaeological visibility was an effect of increasing modern human population size following Neanderthal extinction (Martínez 2006).

Diet and peopling of the Wallacean Archipelago and Sahul

The Wallacean archipelago and Sahul provide a valuable case study for further disentangling the early diets, plant food use and adaptive capacities of modern humans and other hominin species. The earliest evidence for hominin dispersal into this region comes from stone tools on the island of Flores 1 mya (Brumm et al. 2010; see also van den Bergh et al. 2016a), the Philippines 709 kya (Ingicco et al. 2018) and Sulawesi 200 kya (van den Bergh et al. 2016b). These artifacts are likely the result of *H. erectus* making limited water-crossings onto these island environments, alongside several proboscoid and rodent species (Dennell et al. 2014; Gaffney 2020). These appear to be outlier events, genetic restrictions from Asian mainland populations eventuating in the allopatric speciation of dwarfed hominins, including *H. floresiensis* and *H. luzonensis*, and there is no evidence for successful water-crossings into the smaller and more faunally depauperate islands of the Wallacean Archipelago. Recent genetic evidence for admixture with early Australian and New Guinean populations, also suggests Denisovans may have been present in the Wallacean Archipelago (Carlhoff et al. 2021; Teixeira et al. 2021). However, there is no definitive fossil evidence for this species outside the Altai Mountains. Where evidence for diet is available for *H. floresiensis*, they appear to have been restricted to terrestrial resources, likely including stegodons and rats (van den Bergh et al. 2009; Brumm et al. 2016; Sutikna et al. 2016; O'Connor et al. 2017). This is despite some evidence from Java for the exploitation of shellfish by *H. erectus* (Choi and Driwantoro 2007; Joordens et al. 2009). Interestingly, at Liang Bua, Flores, there is no micromorphological evidence for the presence of hearths within the archaeological layers associated with *H. floresiensis*, suggesting cooking may not have been a part of their behavioral toolkit (Morley et al. 2017).

Early evidence for modern humans in this region has been argued to be markedly different, with early populations relying on marine resources to people smaller Wallacean islands, and mainland Sahul (O'Connor et al. 2017; Allen and O'Connell 2020; Shipton et al. 2021). Early evidence for *H. sapiens* diet at Laili Cave, 44.6 kya, Asitau Kuru, 44 kya and Lene Hara Cave,

42 kya, on Timor, and Makpan, 40 kya, on Alor Island attests to the exploitation of marine shellfish, fish, including fast-moving pelagic species (O'Connor et al. 2011; cf. Anderson 2013), sea turtle, crab and urchin (Hawkins et al. 2017; O'Connor et al. 2017; Shipton et al. 2019; Kealy et al. 2020). This is supported by isotopic evidence from a *H. sapiens* tooth recovered from earliest occupation at Asitau Kuru, which indicates a reliance on marine resources (Roberts et al. 2020). This evidence has been used to characterize early modern human movement through Wallacea as rapid and underpinned by the pull of high-ranked, yet easily over-predated, coastal resources (O'Connell and Allen 2012). Populations with narrow diets in the early stages of expansion, chose to relocate to new coastal habitats rather than invest in more labor-intensive resource acquisition.

However, evidence from other early sites in Wallacea suggest early modern humans exploited inland environments at similar or, even, earlier time depths. The earliest figurative art in this region, dating to 45.5 kya at Leang Tedongnge and 43.9 kya at Leang Bulu' Sipong 4, Sulawesi, depicts wild pigs and dwarf bovids hunted by therianthropes (Aubert et al. 2019; Brumm et al. 2021). Zooarchaeological evidence from inland archaeological sites in Flores (Liang Bua, 47-46 kya), Sulawesi (Leang Sakapao 1 and Leang Burung 2, ~36 kya), and Timor (Matja Kuru 2, 36.3-35 kya) attributed to *H. sapiens* suggest a reliance on terrestrial resources (Bulbeck et al. 2004; O'Connor et al. Aplin 2014; Sutikna et al. 2016; Brumm et al. 2018). Further, early occupation at Niah Cave, Borneo, 46-34 kya, then part of mainland Asia, demonstrates adaptation to tropical forest, predicated on the exploitation of a wide range of resources, including pigs, small primates, and plant resources (Barton 2005; Barker et al. 2007; Barton and Paz 2007). This included plant foods that required processing, including leaching for toxicity, such as wild yam (cf. *Dioscorea hispida*) and kepayang (*Pangium edule*) nuts. This is in keeping with other archaeological evidence from across the southern dispersal arc, which demonstrates early adaptations to a range of non-coastal environments, including rainforest (Roberts et al. 2017; Wedage et al. 2019a), high-altitude (Fairbairn et al. 2006; Summerhayes et al. 2010) and arid environments (Blinkhorn et al. 2017; Groucutt et al. 2018, 2021).

Rather than providing evidence for the pull factors of high-calorie, easy-to-capture resources available to foragers in Wallacea, O'Connor et al. (2017) argue that evidence for the use of a range of shellfish, fish and other marine resources by early modern humans in the Wallacean Archipelago demonstrates their adaptive capacity and dietary flexibility. In comparison to Sulawesi, Luzon and Flores, the smaller islands of Wallacea have few large- and medium-bodied terrestrial fauna, and their settlement in the Pleistocene and Holocene was almost entirely reliant on marine fauna until the introduction of domesticated plants and animals (Samper Carro et al. 2016; Hawkins et al. 2017). Whilst some of these resources are easily harvested (e.g., tridacnids; O'Connell and Allen 2012), many also require specialized technologies, such as line-fishing (evidenced by 23-16 kya; O'Connor et al. 2011). Alongside the technological requirements of watercraft, and the cognitive capacities for planning and forethought requisite for longer sea-voyages made by early modern humans (Leppard 2015; Shipton et al. 2021), the ability to exploit a broad range of marine resources is argued to have both underpinned successful

Homo sapiens dispersal and limited earlier hominin movements through Wallacea (O'Connor et al. 2017; Gaffney 2020).

The importance of plant foods for early movement in Wallacea and Sahul

Whether a pull factor or a demonstration of adaptive flexibility, a heavy reliance on lean, marine proteins, such as shellfish and fish, to people the Wallacean Archipelago must necessarily have been supported by access to fats and carbohydrates from other sources (Noli and Avery 1988). With a lack of large- and medium-bodied fauna on smaller islands, this means early modern humans would have had to, at least in part, rely on plant resources for these nutrients. Due to poor preservation and a lack of systematic archaeobotanical recovery, there is, however, no direct evidence for Pleistocene plant food use in the Wallacean Archipelago by *H. sapiens* or earlier hominin populations. However, early archaeobotanical evidence from northern Sahul indicates that early human populations used and processed a wide range of plant foods shared across the Wallacean Archipelago.

The earliest archaeobotanical evidence from Sahul is recovered from Phase 2 at Madjedbebe, northern Australia, dating from 65-52.7 kya (Clarkson et al. 2017; Florin et al. 2020). This phase, representing the earliest known archaeological evidence for humans in Sahul, includes evidence for complex technologies, such as grinding stones and ground-edge axes, the material evidence of symbolic behavior, including the production of a compound, reflective (micaceous) pigment, and evidence for a broad plant diet. The latter includes macrobotanical, and residue and usewear evidence for the use of a range of plant foods and processing techniques, including cooking, pounding and grinding (Florin et al. 2020). There is no evidence for the animal component of the diet in this phase. However, as most Australian fauna, and wild animals globally, are low in fat (Naughton et al. 1986), it can be inferred that it consisted of mostly lean proteins. It is, therefore, unsurprising that considerable labor was expended on the extraction of polydrupe pandanus (*Pandanus spiralis*) kernels, which are rich in fat (44-50%; Low 1991), and that a range of plant carbohydrates, including USOs and palm pith, requiring roasting and pounding (Russell-Smith et al. 1997), and, likely, seeds were exploited.

Many of the genera known to be exploited at Madjedbebe (*Buchanania*, *Canarium*, *Livistona*, *Pandanus* and *Terminalia*) are shared across the Wallacean Archipelago and, in many cases, are also found in tropical and sub-tropical vegetation across the southern dispersal arc (Golson 1971; Crisp et al. 2010; van Welzen et al. 2011). The same is true of plant foods used at other early archaeological sites in northern Sahul, including *Terminalia* sp. and black plum (*Vitex* cf. *glabrata*) fruits and nuts, from Carpenter's Gap 1, northern Australia, 51-38.8 kya (McConnell and O'Connor 1997; Dilkes-Hall et al. 2019), and monodrupe pandanus (*Pandanus* cf. *taip*) and yam (cf. *Dioscorea* sp.) tubers from the Ivane Valley, highland New Guinea, 49-36 kya (Fairbairn et al. 2006; Summerhayes et al. 2010). The latter evidence even suggests the transportation of low-altitude yams into the New Guinea highlands to support the early use of this region. It is, therefore, likely that early human populations drew upon their culturally transmitted knowledge of the ecology and processing requirements of tropical plant foods, as well as cognitive capacity

to apply this knowledge flexibly to novel species and environments, to move across the Wallacean Archipelago and into Sahul. Alongside dietary flexibility and marine-specialized technologies, the ability to extract nutrients from a broad range of plant foods, would have allowed early humans to adapt to a range of environments, including marginal zones, such as faunally depauperate islands and high-latitudes.

H. floresiensis and *H. luzonensis* species likely also used a range of plant foods. However, there is little evidence in Wallacea to suggest they routinely cooked, or otherwise used complex technologies to process plant foods, and some evidence to suggest they did not (Morley et al. 2017). This may be an artifact of preservation as direct evidence for plant food use is sparse. However, it may also be that these activities are part of a gradual development of dietary specialization and flexibility epitomized by *H. sapiens*, but also evidenced in Neanderthals (and likely Denisovans), that allowed for adaptations to a range of environments globally.

Labor specialization in Sahul

Alongside evidence for a broad plant diet at Madjedbebe, there is also evidence for specialized technology, including grinding stones and ground-edge axes, from the earliest phase of occupation (Clarkson et al. 2017). The latter of these technologies, ground-edge axes, is a multi-purpose tool requiring both a high-level of knapping skill, and a large investment of labor to produce and grind (Hiscock et al. 2016; Shipton et al. 2020; Ford and Hiscock 2021). As such, this technology suggests a specialized division of labor for its production. The presence of these technologies and a broad plant diet may, therefore, point to a specialized and gendered division of labor like that argued for the Upper Paleolithic in Eurasia (Kuhn and Stiner 2006; Stiner and Kuhn 2009), albeit without its extensive osseous record. This would suggest early modern humans peopling Australia by 65 kya had specialized economic roles, allowing them to adeptly exploit a range of resources, including hard-to-process plant foods. Neither grinding stones nor ground-edge axes are, however, part of the archaeological record in Pleistocene Wallacea (Shipton et al. 2020) and, in the case of ground-edge axes, they are also limited to northern Sahul in the Pleistocene (Ford and Hiscock 2021). As such, these technologies are at present understood regionally to be innovations occurring with the peopling of northern Australia. Whilst this may suggest that intensive plant processing and specialized division of labour also only occurred with the peopling of Sahul, given the extent of plant-processing evidenced at Niah Cave without grinding stone technology, it is more likely that these more archaeologically visible technologies cannot be relied upon to denote such behavior. Many technologies associated with plant processing and other specialized labor are ethnographically known to have been made with less durable materials, and even the grinding of grass seeds need not have always required specialized stone technologies (e.g., Mercader 2009). Absence of evidence for specialized labor roles and dietary breadth cannot be equated with evidence for absence, and the role of specialized archaeobotanical recovery methods and analysis must not be underestimated if we are to better understand such practices in Wallacea and Sahul, and indeed, globally.

Conclusion

Evidence for the use of plant foods by early modern humans and our closest ancestors from Africa, Eurasia, Wallacea and Sahul, suggests plant foods and processing technologies, such as cooking, grinding and leaching, were important to people's dietary flexibility and adaptive capacity. The necessity for fats and carbohydrates in the diets of hominins means that, except in extreme and mostly recent circumstances (e.g., arctic living and pastoralism), plant foods would have been required in considerable amounts. The ability to process nutrients available within plants effectively allowed for increased dietary breadth, and likely, alongside the ability to better exploit a large range of animal foods, underpinned the ability of our species to move into new and marginal environments globally. This appears especially true of the early movement into Sahul, where a broad plant diet and associated processing technology is evidenced with first peopling. However, like many traits considered to be behaviorally modern it is increasingly apparent that plant processing was not unique to our species. Indeed, with increased direct evidence for Neanderthal plant food use, there is a growing awareness of similarities in the dietary niche of modern and archaic humans in Eurasia. Importantly, if we are to further elucidate the role of plant foods in hominin evolution and dispersals, it is critical that systematic archaeological recovery and analysis of macro- and micro-fossils becomes a universal practice in Palaeolithic archaeology globally.

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