Evaluating the dietary micro-remain record in dental calculus and its application in deciphering hominin diets in Palaeolithic Eurasia

Power, R.C.F.

Evaluating the dietary microremain record in dental calculus and its application in deciphering hominin diets in Palaeolithic Eurasia

Proefschrift

ter verkrijging van

de graad van Doctor aan de Universiteit Leiden,

op gezag van Rector Magnificus prof. mr. C.J. J. M. Stolker,

volgens besluit van het College voor Promoties

te verdedigen op dinsdag 1 november 2016

klokke 16.15 uur

door

Robert Charles Fergal Power

Geboren te Waterford, Ierland

in 1989

Promotor: Prof. dr. Jean-Jacques Hublin (Universiteit Leiden and the Max-Planck-Gesellschaft)

Co-Promotor: Dr. Amanda G. Henry (Max-Planck-Gesellschaft)
Co-Promotor: Dr. Domingo C. Salazar-García (University of Cape Town, and the Max-Planck-Gesellschaft)

Promotie commissie:

Prof. dr. Wil Roebroeks (Universiteit Leiden)
Dr. Alexander Verpoorte (Universiteit Leiden)
Prof. dr. Annelou van Gijn (Universiteit Leiden)
Dr. Geeske Langejans (Universiteit Leiden and the University of Johannesberg)
Prof. dr. Marco Madella (Universitat Pompeu Fabra)

Cover design by Mariska Carvalho

This research has been made possible through a Max Planck Independent Research Group grant of the Max Planck Society, obtained by Dr. Amanda G. Henry. The research was supervised by Dr. Amanda G. Henry and Dr. Domingo C. Salazar-García.

Contents

List of Figures

List of Tables

1

Preface

Since William King first described Neanderthals as a distinct species in 1864, this hominin has provoked discussion, insight, and debate. This event in taxonomic history was a breakthrough in understanding human origins. Since this milestone, we have learned much more about Neanderthals and their relationship to ourselves. The application of ecological perspectives to this topic has addressed more comprehensively than ever before the subsistence, behavioural ability, and the ultimate fate of this extinct hominin. This doctoral thesis aims to continue the spirit of these advances by examining how frequently plants featured in Neanderthal dietary regimes and assessing what this means for the apparent distinctiveness of Neanderthal diets. It does this by developing dental calculus analysis as an archaeobotanical technique and exploring how it can reveal Neanderthal plant use. The scope of this thesis encompasses the development of high-resolution approaches for reconstructing food choice using dental calculus, and the use of these advances to revaluate Neanderthal diets in the context of Pleistocene ecological conditions. This thesis is comprised of six chapters, of which the middle three are stand-alone papers, two of which are published and one submitted for publication:

a) Introduction: The evolutionary context of Neanderthal dietary ecology (Chapter 2).

b) Assessing use and suitability of scanning electron microscopy in the analysis of microremains in dental calculus (Chapter 3). Published as Power RC et al., J Archaeol Sci 49:160–169. 2014.

c) Dental calculus evidence of Taï Forest Chimpanzee plant consumption and life history transitions (Chapter 4). Published as Power RC et al., Sci. Rep 5. 2015.

d) Dental calculus indicates widespread plant use within the Neanderthal dietary niche (Chapter 5). Submitted as Power RC et al. to the J Hum Evol.

e) Discussion: a pathway for reconstructing Neanderthal dietary ecology (Chapter 6).

My thesis initially contextualises the significance of the Neanderthal diet within the broader evolution of hominin diets. The importance of Neanderthal diets for understanding this Pleistocene hominin and explaining its fate are examined. It also discusses how dental calculus can assist dietary studies of this hominin. The first paper examines the shortfalls of conventional analytical dental calculus approaches, and develops a high–resolution workflow for optimising extractable dietary data from dental calculus. The second paper explores the representativeness of the dental calculus dietary record. It quantifies its resolution with dental calculus samples from chimpanzees with a documented dietary history. The third and last paper examines if the Neanderthal dental calculus dietary record from a variety of sites situated across their range in time and space suggest flexible or rigid diets. I use these results to place their diet within the current knowledge of hominin plant use, hominin dietary breadth, and the evolution of hominin diets.

2

Introduction: the evolutionary context of Neanderthal dietary ecology

2.1 The importance of understanding Palaeolithic diets

Energy provisioning is central to mammalian ecology. Understanding mammalian life requires examining its acquisition of energy. Dietary details, such as nutritional requirements, use of different environments, and trophic level may define a taxon (Hutchinson, 1959; Armstrong and McGehee, 1980). The importance of diet is no less true for our own lineage (Winterhalder and Smith, 2000). Dietary strategies are relevant for understanding the most basic and the most specialised level of organisation of human societies. Exposure to new environments and climatic cycles forced major subsistence changes because these presented energetic challenges that restricted, expanded, or otherwise shaped past populations. Scholars recognise that reconstructing ancient dietary niches is of central importance to early hominin palaeobiology. Many authors have suggested that niche switching is linked to landmark changes in hominin evolutionary history (O'Connell et al., 1999; Wrangham, 2000). This is evident from the emergence of distinct morphological and behavioural changes.

Among early Pleistocene hominins, for example, differences in the apparatus of mastication distinguish robust and gracile forms. Enormous, thickly enamelled teeth and robust mandibles that supported powerful mastication ability separate robust *Paranthropus boisei* and *Paranthropus robustus* from the less-developed forms including *Australopithecus afarensis* and *Australopithecus africanus*. Chipping of the enamel from the robust species is suggestive of the consumption of hard foods (Constantino et al., 2010), although microwear fails to support this view (Ungar et al., 2008). The ability to consume extremely hard and tough foods may have been an adaptation for processing fallback foods during seasonal bouts of food scarcity (Lee-Thorp et al., 1994; Ungar et al., 2008; Constantino et al., 2010). Stable isotopic evidence has told a different story on why this specialised robust anatomy evolved. *Paranthropus robustus* isotopic values suggest this hominin was reliant on C_4 grasses and sedges, in contrast to those of nearly all other hominins, which show more reliance on C_3 resources. This implies that the robust craniodental features are an

adaption to "repetitive loading" from consuming large quantities of low-quality vegetation rather than hard objects (Cerling et al., 2011). These craniodental traits represent differences in adaptive capabilities from more gracile forms even if their dietary niches were composed of similarly tough foods (Laden and Wrangham, 2005; Ungar et al., 2008).

Just as early Pleistocene robust hominins morphologically adapted to a dietary niche, other hominins have evolved morphologically in many other ways because of exploiting new dietary regimes. A dietary change is intertwined with the most dramatic externalisation of hominin evolution, the dramatic increased size of the hominin brain. According to the "expensive tissue hypothesis," the emergence of a large and energetically costly large brain and small gut in the *Homo* genus arose concomitant to an increasingly energy-dense diet (Aiello and Wheeler, 1995) . The trade-off between a larger brain size and a smaller digestive tract demanded a higher quality diet, which was possible through either consuming more high-energy classes of food or through external digestion (i.e. food processing or cooking). Some of the most recent anatomical changes in hominin history relate to diet. Present day human dentition is the outcome of a progressive reduction in the size and number of teeth since the first emergence of *Homo*. The process of diminishing tooth size accelerated in periods of dietary change such as the transition to agriculture (Loring Brace et al., 1987). A decrease in the loads exerted on teeth due to changing properties of diet explains this process, whether it is a phenotype relaxation, or selection for a reduction in size and number of teeth.

Other subsistence patterns that have developed recently in hominin history have also left their mark on parts of our biology. For example, the emergence of agriculture has instigated several distinctive changes that remain with us. The *AMY1* gene, which is responsible for producing salivary amylase, the enzyme that breaks down starch in the mouth by hydrolysing it into more useable sugars, is one such example. Present day humans have several copies of this gene (six is the average), and the more copies an individual has, the more amylase is expressed in their saliva (Bank et al., 1992). *AMY1* copy number variation follows a gradient, such that more copies are present in populations with historically heavy intake of starch, and few copies occur in populations with a low intake of starch (Squires, 1953; Perry et al., 2007; Carpenter et al., 2015; Hardy et al., 2015a). This indicates that some copy number variation evolved recently (during the last 10,000 years) in response to the proliferation of starch in diets from agriculture (Perry et al., 2007). The impact of the lower copy phenotype, a reminder of our hunter-gatherer past, reverberates today as

a lower estimated *AMY1* copy-number is linked to obesity and morbidity (Falchi et al., 2014).

As we have seen, our morphology and genome testify to millions of years of changing diets. Dietary adaptations are present from the earliest hominins in early Pleistocene Africa to recent populations in the last 10,000 years. Unsurprisingly, in the case of Neanderthals, subsistence strategies have been a preeminent focus of research. Just as diet was likely the main trait that differentiated early robust and gracile hominins, dietary behaviours are thought to have set Neanderthals apart from other hominins. Neanderthal diet has been suggested as narrow, specialised and profoundly conservative, unlike that of early modern humans, and this dietary niche influenced their range, population history and disappearance.

Neanderthals were closely related to early modern humans, and are even known to have interbred with them, but were distinct in anatomy, ontogeny and techno-cultural expression (Spoor et al., 2003; Smith et al., 2007; Klein, 2009; Gunz et al., 2010; Murray et al., 2015). It is less clear if their diet differed from that of early modern humans. The apparent distinctiveness of Neanderthal resource use has led researchers to link it to their displacement at the end of Middle Palaeolithic. Some consider that Neanderthal diet was reliant on a more restricted range of animal food staples than that of early modern humans (O'Connell, 2006; Stiner, 2013). An inflexible subsistence pattern, due perhaps to cultural or biological factors, may also have burdened Neanderthals with a competitive disadvantage when Upper Palaeolithic modern peoples began to enter Eurasia. Certainly, the more Neanderthals ascended the food chain the more prone they were to experiencing episodes of insufficient food supply. Potentially, this might explain their small isolated populations, their history of regional extinction events and displacement. Unfortunately, it is unclear if their foraging strategies were as inflexible as imagined in this scenario. Furthermore, it is unknown if their economy responded to different ecologies or was static across their range. Understanding their plant use in particular is fundamental because plant use has major implications for their trophic position and the adaptability of their diets. However, because we have limited knowledge on Neanderthal plant use we thus cannot answer these questions. To assess what diet may reveal about this hominin we must first consider Neanderthal origins and history.

2.2 Neanderthals: phylogeography and chronology

2.2.1 Neanderthal origins

Neanderthals evolved from hominins of African origin that entered western Eurasia at some point in the Pleistocene (Hublin, 2009). Revised genetic evidence indicates that the lineage that gave rise to Neanderthals split from the ancestors of early modern humans 550 to 765 ka depending on the pace of the mutation rates (Meyer et al., 2014; Prüfer et al., 2014). A date of about 500 ka would agree with hominin remains found in Europe at this time. Dental morphological evidence poorly converges and it may suggest a split as early as one million years ago (Gomez-Robles et al., 2013). Due to the breadth of these estimated time ranges, and discrepancies between the different lines of evidence, the last common ancestor species is contentious and the geographic setting where it evolved is unclear. Leaving this aside, there appears to be evolutionary continuity in morphology from the hominins found in Europe dated to 500-300 ka (Arago in France, Sima de los Huesos in Iberia, Petralona in Greece and Mauer in Germany) to Neanderthals. Arguably early African fossils have no such continuity to Neanderthals (Bermúdez de Castro, 1997). Palaeoanthropologists can only reliably assign skeletal remains to Neanderthals in the late Middle Pleistocene (230-180 ka) at European sites such as Biache-Saint-Vaast, Fontéchevade, La Chaise Suard, and La Lazaret in France (Churchill, 2014). Most of our knowledge about Neanderthals stems from their later chronological range from 130-30 ka.

2.2.2 Neanderthal range

Neanderthals are known from sites throughout Eurasia, such as Forbes' Quarry, Devil's Tower, Zafarraya, El Sidrón in Iberia; Le Moustier, La Ferrassie, Regourdou, Pech-de-l'Aze, Roc de Marsal and La Chapelle-aux-Saints in France; Neanderthal in Germany; Grotta Guattari in Italy; Krapina and Vindija in Croatia and Kůlna in the Czech Republic; Teshik-Tash in Uzbekistan; Shanidar in Iraq; Amud, Tabun and Kebara in Israel. Although applying a species concept to Neanderthals or any extinct hominin can be difficult and inevitably controversial, the skeletal remains from many of these sites exhibit morphological traits that typify Neanderthals. These sites suggest Neanderthals lived in much of western and central Eurasia. They occupied as far north as the German Coast while in the south their ranged stretched to the Mediterranean rim, the Levant and parts of Iraq (Fig. 1).

Their east to west range stretched from Atlantic Iberia in the west and central Siberia in the east. Skeletal remains show conclusively that they lived as far east as the Altai Mountains in central Asia (Krause et al., 2007). In this span of western Eurasia, there is variation and discontinuity. Occupation of northern areas varied according to glacial cycles (Van Andel et al., 2004). This is evident in the depopulation of northern areas in cold periods of MIS 6 and MIS 4, due to either the volatility of climate or the harshness of the climatic conditions themselves. These regions were subsequently recolonised in warmer phases. Archaeological and mitochondrial DNA evidence shows that this process occurred through a process of incremental local extinctions in northern zones on the onset of cold phases rather than Neanderthals tracking the movement of milder climates south (Hublin, 1998; Roebroeks et al., 2011).

Fig. 1: The area shaded in blue represents the largest known range of Neanderthals based on lithic and skeletal evidence. Krause et al., 2007 modified by Ryulong licenced under CC-BY-SA-3.0 and by author.

2.2.3 Neanderthal disappearance and its implications for dietary ecology

Although Neanderthals survive in part to this day as archaic DNA in the contemporary human genome, Neanderthals are an extinct branch of humanity. The manner of their disappearance has proven to be difficult to resolve. They roamed Eurasia well into the warm MIS 3 Phase (the interplenniglacial), but how late they survived and if their disappearance is a result of the spread of Upper Palaeolithic early modern people is hotly debated (Finlayson, 2008; Pinhasi et al., 2011; Higham et al., 2014). Late Neanderthals may have survived in far-flung pockets of their range, including in Southern Iberia where there are few Aurignacian remains

(Finlayson et al., 2006), and in the Caucasus Mountains (Ovchinnikov et al., 2000). In addition to these postulated refugia, a northern refuge near the Arctic Circle at Byzovaya has been suggested based on Mousterian tools dating to 34-31 ka cal BP (Slimak et al., 2011). This is an exceptionally northern site, outside of the conventional views of their range and it fits poorly with available data (Zwyns et al., 2012). Excavators found no hominin remains, meaning they were unable to clarify if this is a Late Neanderthal occupation. The evidence verifies that Neanderthals were gone across their range by 33 ka cal BP, but they could well have disappeared considerably earlier as dates this late are rare (Galván Santos et al., 2006; Wood et al., 2013a). Many argue that they survived no later than 40 ka cal BP (Pinhasi et al., 2011; Wood et al., 2013b; Higham et al., 2014; Hublin, 2015). One reason why this problem is difficult to resolve is that the period is at the temporal limit of the applicability of radiocarbon dating (Higham, 2011).

Both changes in stone tool technologies and variation within technocomplexes have influenced our interpretation of the disappearance of Neanderthals. Neanderthals developed a stone tool industry called the Mousterian Industrial Complex, characterised by the presence of large, specially prepared cores and specialised flakes often made using the Levallois technique (Klein, 2009). This is the dominant technology in western Eurasia until the arrival of early modern Upper Palaeolithic technocomplexes such as the Aurignacian. In some regions, the archaeological layers containing Neanderthal-associated Mousterian tools are separated from those containing Aurignacian tools by layers containing artefacts from so-called transitional industries. One of the best-studied examples is the Châtelperronian of central France and northern Iberia. Many aspects of the Châtelperronian are characteristically Upper Palaeolithic, leaving some to wonder if it was manufactured by Neanderthals (Ruebens et al., 2015). The Châtelperronian is the only transitional industry with directly associated Neanderthal remains (Hublin et al., 1996), strongly indicating that it was, in fact, created by Neanderthals. Reassessment of Châtelperronian tools appears to suggest that this complex emerged from the local Mousterian (Granger and Lévêque, 1997; Ruebens et al., 2015). This raises the question of Neanderthals groups interacted and exchanged culture with Upper Palaeolithic early modern humans. Resolving this issue is central to understanding the potential intensification of plant use suggested by Châtelperronian grindstones (See 2.5.1). If a process of acculturation occurred, it could have influenced multiple levels of Neanderthal culture including their diets. Debate has centred on whether the Châtelperronian appeared following contact with early moderns. Some have argued that the Châtelperronian was manufactured by

Neanderthals before Upper Palaeolithic modern humans arrived in Europe and that its stratigraphic overlap with moderns at the key Châtelperronian site of Grotte du Renne is a product of sediment disturbances and layer remixing and cannot be reliably interpreted (Zilhão et al., 2006). Indeed, at Grotte du Renne (Arcy-sur-Cure, France), there is evidence of remixing in the sequence (Higham et al., 2010). Reattempts at dating imply that Neanderthals were the makers of the Châtelperronian industry, and the Châtelperronian Neanderthal (Saint-Césaire) post-dated the arrival of early modern humans in western Europe (Hublin et al., 2012). This timing suggests a cultural diffusion from modern to Neanderthal groups.

We can also discern interaction by identifying gene flow between these hominins. Geneticists have pinpointed multiple events of introgression between Neanderthals and early modern humans. This introgression likely occurred in the Near East prior to the split of the ancestors of present day Europeans and Asians (86-37 ka) (Sankararaman et al., 2012). A second event may have occurred, presumably further east concerning the ancestors of present day Asians only (Vernot and Akey, 2015). An early modern human dated to 42-37 ka from Peştera cu Oase, Romania, one of the oldest modern humans found in Europe, showed recent admixture with Neanderthals, with 6–9 % of its genome from a Neanderthal ancestor. The completeness of the archaic DNA in the Oase individual indicates that this cross occurred four to six generations prior. The recent suggested date of this admixture indicates that admixture probably occurred in Europe (Fu et al., 2015).

What this cultural diffusion and population admixture tells us about the Neanderthal subsistence and its ability to adjust to new circumstances is unclear. The presence of two or more types of hominins in Eurasia inevitably led to overlapping territories. Both hominin groups would have sought the same high quality resources, leading to direct competition for the optimal foods. The impact of new hominins on Neanderthals would vary according to how numerous Neanderthals were; a large population could buffer against a large influx of competing hominins. Yet high-quality ancient genomes have revealed that Neanderthal demographic history differs from that of early moderns. Neanderthal genetic history displays a protracted history of small isolated populations and low genetic diversity (Castellano et al., 2014; Prüfer et al., 2014). Small populations could have left them highly vulnerable to even minor competition from early moderns. The inevitable increase in isolation may have reduced their ability to develop resilient subsistence patterns to cope with the arrival of early moderns.

Neanderthal admixture, decline and extinction may imply that their niche was susceptible to competition. It is easy to envisage early moderns who arrived in Europe creating ecological imbalances that disrupted Neanderthal foraging. Given chronological ambiguity, this is not currently detectable. On the other hand, competition may have led to an intensification of Neanderthal subsistence. The cultural diffusion may have led to Neanderthals adopting modern subsistence strategies, but this elucidates little about the dietary niche Neanderthals used for 200,000 years previously. To interpret their long-lived subsistence and dietary regime we must examine their diets using an interpretive framework loaned from ecological theory that allows us to make predictions about their foraging behaviour.

2.3 Applying a framework for studying ancient diets

2.3.1 Human Behavioural Ecology

Knowledge of Palaeolithic human diets is not useful if we have no means of interpreting this information. A theoretical framework that allows us to place dietary choices in a cultural and biological context is needed. Human Behavioural Ecology (HBE) is a useful framework for studying dietary choices and the environmental, biological, and cultural limitations that frame those choices. Behavioural ecology emerged in the 1960s and the 1970s amongst circles of ecological theorists seeking a basis for studying feeding, social, and reproductive behaviours (Bird and O'Connell, 2006). Behavioural ecology spread to researchers interested in human societies, as it allows human behaviour to be interpreted in the rubric of evolutionary ecology theory. Human behavioural ecology posits that individuals tend to adapt to their environment as necessary to maximise their fitness (Mulder and Schacht, 2012). On a daily basis, foragers will consider and weigh decisions on their costs and benefits. If behaviours diverge from this pattern, the possibility of social and cultural factors can be investigated. Behavioural ecologists attribute behavioural diversity to the cumulative impact of the strategies of individuals, the local ecological niches, and the cultural transmissions of information (Smith, 2011; Mulder and Schacht, 2012).

Human behavioural ecology has been widely adopted in anthropology as it offers a framework to generate testable hypotheses about behavioural variation. One group of HBE theories that are popular in studies of human origins are optimal foraging theory and diet breadth models. These models provide a powerful way to assess forager feeding strategies. In a diet breadth framework, researchers predict

whether a forager will collect a potential food item that it encounters while foraging (MacArthur and Pianka, 1966). To acquire a resource, the forager must bear both the search costs (e.g. location, hunting and digging) and the handling costs (e.g. preparing and processing), and will minimise these as far as possible although this does not influence a resource's ranking in the diet breadth model. A forager can seek to maximise their efficiency by incorporating the most profitable food items (plant or animal) available and ignoring lower ranked prey (Fig. 2). The inclusion of any given item relies on its ultimate profitability to the forager rather than its abundance (Bird and O'Connell, 2006). Researchers usually assume that foragers assign a rank to a potential food depending on its energy yield minus the cost of food preparation, but foods may also be ranked on other currencies, such as specific macro or micronutrients that are more physiologically important to the individual than total energy (Hockett and Haws, 2005). Food may even be ranked according to individual subjective preferences. The foraging cultures of Alaskan peoples give potential real world examples of non-energetic currencies. Alaskan foragers commonly rob nutritious foods such as sedge corms (Cyperaceae spp.) from rodent caches and nests, which rodents collect for winter food. They compensate the loss of their plunder with fish to sustain the rodent over the winter (Anderson, 1939). A desire to procure vegetable nutrients, rather than energy alone probably explains this behaviour. A low-ranked food item may also be a prey individual that is younger and smaller than normal for the taxon. A food type may be highly ranked, energy-rich and abundant but fast moving, and hard to catch and hence rarely entering diets. Improved technologies can dramatically lower handling costs (Kelly, 1995). For example, nets and weirs majorly abate the search costs for catching river fish, although maintaining nets and weirs is a substantial long-term cost and a constraint on mobility. For this reason, recognising technological change is important for deciphering foraging choices.

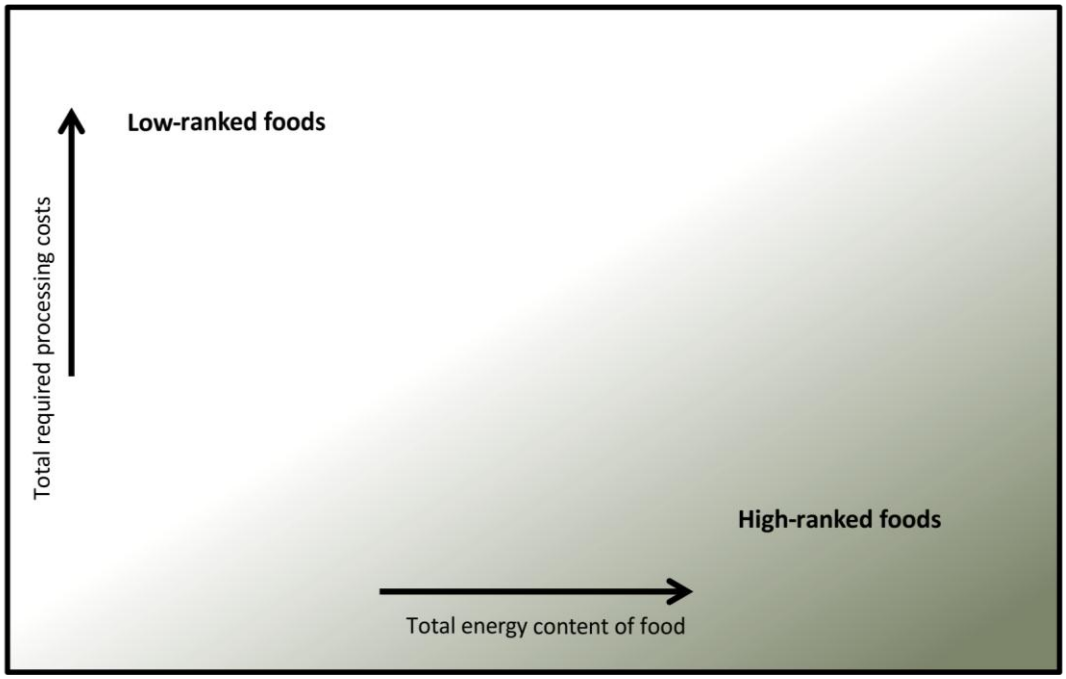


Fig. 2: Conceptional illustration of a diet breadth model that uses energy. Behavioural ecologists rank foods on their energy (or other nutritional metric) return net of the processing costs expended to obtain energy. Ranking in diet breadth models ignores prey abundance and prey search costs.

Given current data on handling costs, diet breadth models predict that due to the differences in energy yield, animal foods (especially meat and fat from medium and large ungulates) and honey are high-ranked, in contrast to the majority of plant foods (Table 1). However, plant foods are usually a more abundant staple and their collection is far more reliable than most types of hunting. Nevertheless, because of their laborious collection and handling most plants provide fewer calories (Kelly, 1995; Kuhn and Stiner, 2006), and are less preferred. Ethnographic studies of food preferences confirm this trend (Berbesque and Marlowe, 2009). Although recent foragers prefer animal foods, plant foods are still a ubiquitous feature of their diets. This is readily explained by the fact that the quest for food relies on reducing food supply volatility, rather than always attempting to maximise the amount of food one takes in (Winterhalder, 1986). Plants are usually more abundant and occur in large patches, they are more easily and reliably located than game. This is important because forager mobility is limited.

A lesson in the value of these diet breadth models in interpreting food choice may be found in the classic ethnography of the Aché of eastern Paraguay (Hawkes et al., 1982). The Aché hunt peccary, deer, and monkey, and they gather oranges, palm hearts, palm fibre and larvae in palms as well as honey. Hunting offers unreliable

returns yet the Aché are predominantly hunters. Game provide about ~78 % of dietary energy while plants provide only ~12 % (Gurven et al., 2001). Plants and fish available to the Aché offer more abundant, more reliable, and far more readily located foods. Aché hunting game will stop and collect honey, grubs, and the most highly ranked plants they pass such as oranges. Yet they often ignore other plant foods like palm fibre even though these are regularly consumed when little else is available. The Aché provide several lessons for studying ancient hominin food provision. Examination of energy returns reveals that hunting is typically the optimal strategy, although unreliable, hunting offers the highest overall returns. Although plants provide less energy (Kelly, 1995), they are crucial and ensure survival in periods of shortage. It also is a reminder of the uneven distribution of resources in the landscape (Hawkes et al., 1982). While this patchiness is unaccounted for in diet breadth models it is incorporated into other theories such as the patch choice model and the marginal value theorem. Although these theories are difficult to apply to Palaeolithic societies, they further illustrate why plants are collected for subsistence. The patchy nature of food distribution combined with labour specialisation favours the common use of both high- and low-ranked foods. This strategy is true in most societies worldwide.

Recent foragers exploit variations in the reliability and abundance of plant and animal foods with highly efficient systems of labour specialisation, usually according to sex. Generally, in recent forager societies females collect most plant foods while males tend to hunt, especially when the quarry is large and dangerous (Kelly, 1995).

This sex specialization pattern is true in almost all reported recent forager societies, except the Agta of the Philippines (Goodman et al., 1985). One advantage of this system is that it accommodates the difficulties that a highly mobile hunting lifestyle brings to aspects of reproduction such as breast-feeding. The gathering of plants and immobile animal foods like shellfish is more conductive than hunting to the feeding demands of infants, and reduces the risk starvation because gathering yields nutrients even when hunting fails (Brown, 1970). Moreover, hunting large game may have been useful to males as a method of building social status by signalling fitness to the group, this is known as “costly signalling” (Hawkes and Bird, 2002). A division of labour between hunting and foraging thus optimises the high-energy returns of meat and the reliability of plant collection. The risk of a diet that eschews plant food and depends on animal food is observed in the early records of arctic foraging peoples. Little plant nutrition was available to arctic foragers and

this coupled with extreme seasonality meant that stretches of hunger and even devastating starvation were a regular feature of life (Ackerknecht, 1948; Young, 1996). Records from isolated communities in eastern Greenland show that as many as 15 % of the population died of starvation between 1881 and 1883 (Holm, 1911).

2.3.2 The subsistence trajectory of Palaeolithic societies

Diet breadth models provide a starting point for exploring subsistence choices of past groups. They have formed the dominant paradigm to explain Palaeolithic subsistence. Prehistorians have invoked behavioural ecology to argue that there is a landmark point in hominin dietary history at which foragers switched prey in a transition termed the "Broad Spectrum Revolution" in the terminal Pleistocene (Binford, 1968; Flannery, 1969; Zeder, 2012). Hunters of medium and large game began to heavily rely on plants, fish, and fowl due to climatic and demographic pressures. In addition, broad spectrum foragers existed in higher densities and typically spent a high proportion of time processing food. An increasing use of plants was believed to induce a local lowering of the overall human trophic level. This changing strategy led to an increase in dietary breadth, and ushered in the first experiments in providing food through agriculture and pastoralism.

Zooarchaeologists have since argued that the process of prey switching and diet broadening occurred far earlier, at the start of the Upper Palaeolithic. Stiner and colleagues (1999) noted an increased frequency of small fast-moving prey such as hares, which yield lean meat and are therefore low-ranked, at the start of the Upper Palaeolithic. This change came at the same time as a reduction of body size in hunted tortoises, which reflected the increased hunting pressure on this preferred, easy-to-acquire prey. This contrasted with the pattern of zooarchaeological remains seen among Middle Palaeolithic Neanderthals in the same geographic regions, which exhibited a rigid subsistence strategy centred on hunting the most high-ranked of resources prime-aged medium and large game (Stiner, 1994, 2013; Stiner and Kuhn, 2006).

Stiner (2013) argued the Neanderthal dietary niche changed little in the hundreds of thousands of years they occupied Eurasia and that it is far easier to find differences between the Middle Palaeolithic and other periods than within it. This largely static Middle Palaeolithic foraging niche, narrow and inflexible in most regions, placed a ceiling on the carrying capacity and ensured a very low population

density. In this perspective, as Upper Palaeolithic modern humans entered Eurasia their broader niche meant they would inevitably displace Neanderthals across all of their range through a gradual process of competitive exclusion (Stiner et al., 2000; Hockett and Haws, 2003; Kuhn and Stiner, 2006; O'Connell, 2006; Stiner and Kuhn, 2009).

Comparing plant consumption with the above animal food models is challenging due to the visibility bias in favour of animal foods. Plant remains are unlikely to survive on most Palaeolithic sites, thwarting attempts to extrapolate plant use with conventional approaches, despite being potentially essential for nutrition (see below) (Speth, 2010). The difficulties faced are exacerbated if data are viewed in isolation. The dissertation predicts that the contribution of plant foods to Palaeolithic diets breadth is masked by this taphonomic bias. It hypothesises that it may be possible to examine the plant contribution to dietary breadth by quantifying the variety of plant foods represented in dental calculus.

However, before this can take place, a synthesis is needed that re-evaluates the evidence of plant use in botanical, artefact, genetic and osteological studies to contextualise this information. This process requires that we first establish what plant food may have been available to Neanderthals and which were likely to have been most important from a behavioural ecology perspective.

2.3.3 A behavioural ecology model for Eurasian environments

Although edible energy-rich plants were present throughout western Eurasia (Sandgathe and Hayden, 2003; Hardy, 2010), there is a dearth of data on their availability. We can mathematically predict the total biomass of plants in Pleistocene environments, but not the total biomass of edible plants. Ethnographic data gives us the option of modelling Neanderthal plant use if they resembled recent foragers and if Pleistocene environments were similar. Assuming Neanderthals fell within the ecological gradient present in the economies of recent northern foraging people, plants would have been a significant part of their diet. Churchill (2014) used net primary productivity and effective temperature to predict Neanderthal dependence on plant consumption based on recent foragers. This model estimates that plant intake represented 11-25 % of diet in the coniferous forests north of the Alps, rising to 36-43 % in the temperate forest of the last interglacial MIS 5e.

Table 1: Energy yields of various food classes consumed by recent foragers. Reprinted from 'What's a Mother to Do? The Division of Labor among Neandertals and Modern Humans in Eurasia' by Kuhn and Stiner (2006).

	N cases	kJ/hr			kJ/kg	
		Mean	Min.	Max.	Mean	Sd
Large game	4	63,398[a]	36,000	75,115	6,980[b]	1,383
Small game	14	16,034[a]	1,672	56,317	6,980[b]	1,383
Reptiles	3	15,850[a]	17,556	12,435	4,489[b]	715
Birds	3	4,472[a]	961	8,255		
Roots and tubers	14	6,120[a]	418	26,133	2,926[c]	1,680
Roots and tubers	9	10412[a]	3,695	23,333	2,926[c]	1,680
Roots and tubers	13	1882[d]	1,045	2,300	3,136[d]	2,338
Seeds and nuts	34	3,520[a]	380	18,538	13,188[c]	9,334
Seeds and nuts	9	6,508[e]	1,203	24,933	13,188[c]	9,334
Seeds and nuts	6				19372[d]	6,250
Foliage					1,250[c]	819
Foliage	3				1,534[d]	186
Fruits					2,403[c]	1,463

[a] Data from Kelly (1995, table 3.3).

[b] Data from Hawkes et al.(1982), Hurtado and Hill (1987).

[c] Data from Pennington (1989)

[d] Data from Wiessner (2003 and personal communication); cases are from Nyae Nyae area minus those where elephant damage was severe for tubers.

[e] Data from Wright (1994, table 2).

There is also considerable ambiguity about candidate vegetal food staples and the types of low- and high-rank foods that we may expect in Pleistocene Eurasia. The diet-breadth model stipulates that abundance is no predictor of a resources' value, meaning that botanical surveys of species frequency are inadequate for extrapolating staples. There are few studies detailing the returns and costs of acquiring Eurasian plant foods that would allow us to develop a detailed set of predictions (Martinoli, 2005). Summaries of ethnographic data mostly from Great Basin foragers indicate that of all classes of plant foods, two categories offer the highest net energy per hour: seeds/nuts, and underground storage organs (Table 1). Underground storage organ returns exceed those from seeds/nuts, but they still return less energy than nearly all classes of animal foods (Kuhn and Stiner, 2006). Researchers have referred to USOs as a mainly African resource (Kuhn and Stiner, 2006), but this is based on anecdotal evidence and may not be reliable. Generalisations are inadequate for reconstructing Neanderthal dietary ecology because understanding plant use requires systematic data on plant and animal food variables. We know that in some cases prodigious amounts of USOs were available in Eurasia. For example, reedmace (*Typha* spp.) provides extensive and dense concentrations of edible USO biomass in marshes,

river and lake shores (Morton, 1975). Unfortunately, detailed ethnographic data of foragers that specialised in wetlands that we could use to model Pleistocene wetland foraging is unavailable, because such societies disappeared before they were studied in detail.

Although there is little information on how the edible plant food biomass varied in different Pleistocene habitats, we may presume that the availability of energy-rich plant foods was superior in southern regions. Open Mediterranean woodland and wetlands would have supported a greater diversity of plant foods than cold steppe or coniferous forest (Kelly, 1995). In northern areas, although winters were intensely cold, strong winds often blew away snow, thus exposing ground-based resources such as edible tubers (Guthrie, 2001). During glacial phases moisture loving edible plants were drastically limited by the intense aridity but edible plants tolerant of dry conditions may have been abundant in the rich often-alkaline steppe soils.

The use of plant foods by recent foragers makes it possible to suggest possible plant food staples. Diet breadth model criteria (Fig. 2) can indicate whether a food was high- or low-ranked (Haws, 2004). In Mediterranean woodlands, the high-ranked plants probably constituted nuts like pistachio (*Pistacia* sp.), olive (*Olea* spp.), chestnut (*Castanea sativa*), some aquatic plants such as water chestnut (*Trapa natans*) and certain underground storage organs including as burdock (*Arctium lappa*). Mid- or low-ranked foods likely included seeds of grasses (Poaceae), Madroños (*Arbutus* sp.), gum rockrose (*Cistus ladanifer*) seeds, acorns (*Quercus* spp.), legumes, and various woodland, coastal, and wetland underground storage organs (though some of these foods may have been relatively high-rank) such as honesty (*Lunaria annua*). In northern environments, high-ranked foods may have included reedmace, hazelnut (*Corylus avellana*), and sea kale (*Crambe martima*). Lower ranked foods probably included various underground storage organs like pignut (*Conopodium majus*), Asteraceae taproots such as dandelion (*Taraxacum)*, sea holly (*Eryngium maritimum*), silverweed (*Argentina anserine*), and lilies (*Lilium* spp.), as well as seeds such as grass grains, and acorns and perhaps pine bark (*Pinus* spp.). Most of these foods are relatively energy rich, though many have some processing costs. These species are far from a complete list of edible Eurasian plants but they are likely particularly important to Eurasia foragers. Across many of the environments Neanderthals occupied, a range of other less energy-dense foods were available, including mushrooms, leafy tissues, stems, drupes, berries, and seaweeds. In addition to the total energy content, food macro- and micro-nutritional qualities

influence forager selection (Hill, 1988). Unfortunately, micronutrient data from wild plants are extremely rarely compiled and most nutritional data that are available only covers a fraction of the whole nutritional spectrum So my project focuses on total energy and macro-nutrients rather than or micro-nutrients.

2.4 The nutritional requirements of Neanderthals

2.4.1 Neanderthal energetics

Distinctive cranial and postcranial morphology distinguishes Neanderthals from other hominins (Tattersall and Schwartz, 1999). Neanderthals' anatomy and inability to reduce the cost of mobility with technology presented energetic challenges, which may have limited their diet (Verpoorte, 2006; Churchill, 2014). Overall body proportions show the most resemblance to present-day cold-adapted populations (Trinkaus, 1981). Scientists interested in Neanderthal energetics have estimated their body mass range in order to calculate their energetic requirements, and though these estimates vary depending on the technique and skeletons used, all versions indicate that the body mass of Neanderthals was very high. Although Neanderthals stood at a comparable height to recent Arctic forgers, they could have weighed considerably more (Churchill, 2014). Well-developed muscular attachments demonstrate that they had heightened muscularity (Churchill and Rhodes, 2006). Overall, this indicates Neanderthals required increased amounts of energy compared with other hominins. Estimates of basic daily energy expenditure vary depending on supposed physical activity level but figures suggest a metabolic requirement far above the average of any human forager group (Sorensen and Leonard, 2001; Snodgrass and Leonard, 2009). To fulfil their energy requirements an ample energetic return from foraging would have been critical (Sorensen and Leonard, 2001). Recent studies have re-examined Neanderthal energy expenditure and suggest that although their locomotion required more energy than early modern humans, the difference is less than previously thought (Hora and Sladek, 2014). Heyes and MacDonald (2015) have pointed out that the error range in comparisons between European Neanderthals and Upper Palaeolithic early modern humans is too great to identify any differences in body mass. However, recent foragers differ substantially anatomically from early moderns. Our energetic model uses recent foragers rather than Upper Palaeolithic early moderns as an energetic yardstick.

Animal foods, such as muscle, fat, marrow, and organs, were the most calorie-rich foods available to Pleistocene foragers. However, there are physiological limits to animal food diets. If an animal-based diet contains insufficient fat, it can lead to protein poisoning. Consuming protein beyond a safe threshold leads to a progressive onset of nausea, wasting and eventual death (Speth, 2010; Butterworth et al., 2016). Unfortunately, many crucial details of this condition are unknown but nutritionists have gathered some information from ethnographic sources and small-scale trials (Stefansson, 1956; Speth, 2010). The notes of explorers and athletic studies show that people unaccustomed to a high protein intake may rapidly adjust in weeks to high protein ingestion but a protein ceiling remains (Phinney, 1995; Speth, 2010). Extant hunter-gatherers regularly consume vast amounts of lean protein when gorging on meat after kills. However, health records suggest that hunters who gorge in the dry season when game is thin lose weight (Speth, 2010). Recent Arctic foragers knew the dangers of consuming excessive lean meat and referred to protein poisoning as rabbit malaise (Stefansson, 1956). Although protein may have formed a large part of Neanderthals' dietary intake, a diet of mostly protein is improbable (Speth, 2010). Nutritionists argue that recent foragers who consume mostly animal foods overcome these problems by maximising their intake of fat. Neanderthal hunters must have relied especially on fatty meat to avoid this problem. Carbohydrates in mammal liver (absent elsewhere due to the effects of rigor mortis), shellfish and plants could have also played a role (Cordain et al., 2000).

The potential dangers of specialised animal food diets are highlighted in the case of pregnancy. Hockett (2012) has argued that given the formidable estimated daily energy expenditure, a diet consisting of only medium- and large-game would kill a pregnant Neanderthal due to excess protein, vitamin A, niacin, iron, zinc, and selenium in addition to a major calcium deficiency. This model attempted to take into account a variety of different levels of activity and thermoregulation, but in all cases, Hockett argued that a terrestrial animal-food-only diet was toxic to pregnant females.

2.4.2 Macronutrients provisioning

Along with total protein intake, specific amino acids must be consumed for maintaining health and ensuring correct development. These nutrients are an imperative for all mammals and Neanderthals must have acquired them. The body requires twenty amino acids and about nine must be directly sourced from food. A

meat-rich diet would have adequately provisioned Neanderthals with these nine amino acids (Churchill, 2014). In contrast, sourcing essential fatty acids may have been more difficult. The essential long-chain polyunsaturated fatty acids docosahexaenoic acid (DHA) and arachidonic acid (AA) are required for brain growth. Obtaining sufficient DHA would have been particularly crucial during pregnancy and lactation (Crawford et al., 2008). The body may synthesise them from linoleic acid (LA) and α-linolenic acid (LNA), but this is less efficient than acquiring them directly. Consumers can derive LA and LNA from some domesticated plants (e.g. flaxseed), but it is unclear if they occur abundantly in wild plant foods (Simopoulos, 2004). The highest DHA concentrations are found in marine foods. Foragers could also access this fatty acid through terrestrial mammals, but only in far lower concentrations, and only in certain tissues like the brain. AA is also present in terrestrial animals, especially in the viscera, but there are no highly concentrated sources of AA in large ungulates. Thus, AA deficiencies may have caused problems. Neanderthals, especially when pregnant, may have required additional AA or DHA. Supplementary intake of marine fish and mammal brains would be more important if they consumed a large amount of plant material low in these fatty acids. Neanderthals may have targeted smaller prey for DHA, as the ratio of brain size to body mass is larger in smaller mammals (Crawford et al., 2008). This selective feeding approach would also alleviate the particular risk of protein poisoning in late winter and early spring when prey had expended their stores of fat over the winter (Speth, 2010).

We can see that there is a need for a convincing energetic model for Neanderthals. It is possible that Neanderthals had adaptations that regulated their essential nutritional demands to what Pleistocene Eurasia could provide, but this is conjectural. Yet we can deduce without doubt that the large build, muscularity and large brain that Neanderthals evolved presented energetic and nutritional challenges although they must have offered some selective advantages. Neanderthal nutritional demands for fatty acids were the cost of their large and metabolically expensive brains. This has led Churchill (2014) to argue that the extent to which Neanderthals relied on plants was constrained by the sheer volume of meat they needed to obtain essential fatty acids in the absence of fish and shellfish consumption. This hypothesis is based on incomplete data of the nutritional opportunities of Pleistocene plant foods. Neanderthals may have alleviated nutritional deficiencies with selective use of certain resources including plants rich in fatty acids, mammal brains, and marine and freshwater fish.

2.5 Extant biological and technological traces of diet

Neanderthals were among the first hominins to spread into cold temperate and glacial environments (Hublin and Roebroeks, 2009), and by studying their dietary ecology, we may gain a better understanding of the strategies and adaptations that allowed them to thrive in these inimical environments. We may also find better explanations of how this close relative survived through 200,000 years of shifting climate, changing ecologies, and carnivore competition only to abruptly disappear as early modern humans entered Europe. The gradual expansion of research using macromammal remains allowed substantial insights into Neanderthal meat consumption, hunting techniques, and social cooperation (Stiner and Kuhn, 2006; Stiner, 2013; Churchill, 2014). There has been, however, limited ability to examine their complete dietary ecology. The recent advent and maturation of new approaches in archaeological sciences such as dental wear, isotope, biomarker, and dental calculus analyses has allowed considerable strides in building a more complete view of their dietary ecology. Although these advances have answered some questions, they have raised others. To explain diet, it is necessary to review and synthesise this evidence.

2.5.1 The implications Neanderthal technology for subsistence

Hunter-gatherer toolkits can have specialised functions for the collection of specific resources. Specialised toolkits can reveal resource use if the functional design can be identified by archaeologists. For instance, later Levantine foragers produced knapped sickle blades that reflect widespread harvesting of wild grasses (Bar-Yosef, 1998; Goodale et al., 2010). For these reasons, it is important to review Neanderthal technology and evaluate if it suggests gathering of plants for food.

Recent hunter-gatherers give us an approximate picture of the tools that Neanderthals may have used to gather plants. Implements such as stout digging sticks, folded bark containers, or seed and fruit beaters may have been used, but these organic items will seldom survive the vast periods of time that has passed. A handful of wooden implements have survived in special circumstances from 400-125 ka in present-day Germany and England (Thieme, 2000). Mostly these are interpreted as spears due to their length (1.8- 2.5 m) and pointed tips, however, digging sticks known from the ethnographic record reach up to 2 m (Nilles, 1942; Boesch, 2012). Thus, such wooden tools could plausibly have been used as digging

sticks, but they would be unusually long examples. Worked sticks resembling digging sticks in length have also been found at Schöningen (Schoch et al., 2015). Foraging tools are inclined to be made, used, and disposed over a short period, leaving few diagnostic markings or use-wear, and thus identification would be difficult. Furthermore, many of the plant collection tools in the repertoire of recent foragers are highly multifunctional, for example, foragers can use the same sticks for prying off edible inner tree bark as they use for dispatching game.

Unlike organic tools, stone tools are regularly preserved in the archaeological record. Knapped stone tools would have been extremely useful for preparing plant foods and shaping wood, despite being usually associated with animal butchery (Langejans, 2012; Hardy et al., 2013; Wadley and Langejans, 2014). Some Middle Palaeolithic flaked stone tools do preserve evidence of plant processing (Hardy et al., 2001; Hardy and Moncel, 2011). An alternative proxy line of evidence may be found in the stone technology used to process food (milling, scraping, and pounding); for instance, ground stone artefacts may be specialised implements for processing grass seed (Wright, 1994; de Beaune, 2004; Dubreuil and Nadel, 2015). Like other tools, they have a generalised function and are used for preparing minerals as well as processing plants. Ground stone tools for macerating and pulverising have been widely identified in early Upper Palaeolithic occupations although unequivocal verification that these ground stones were specifically used for plant processing is less forthcoming. Ground stones are known in African Middle Stone Age contexts (McBrearty and Brooks, 2000), but their prevalence is poorly known (Stiner, 2013). In contrast, ground stones are rarely present in Middle Palaeolithic deposits, but they are frequently found in Châtelperronian contexts (Straus, 1992; de Beaune, 1993; Churchill, 2014; Power et al., 2015a). One potential Middle Palaeolithic case was found associated with pine nuts at Gorham's Cave in Gibraltar (Barton et al., 1999). This has been interpreted as a tentative nutcracker. Middle Palaeolithic hominins may have used modest pieces of naturally shaped stone (manuports) to grind seeds and nuts, perhaps compatible with their highly mobile lifestyle. Likewise, the cobble hammers they used for knapping may have been serviceable for plant processing. Archaeologists might have overlooked such simple toolkits that used unmodified stones, while the same is not true if they used heavily modified specialised technology, like in the Epipalaeolithic of the eastern Mediterranean. In sum, we cannot infer plant use from their technology. Neanderthals could have widely used grinding stones, but they did not invest in unperishable specialised processing tools. This appears to be a reliable difference from the technology employed by early modern humans.

2.5.2 The genetic evidence of diet

The unfolding of genomic data from both living and fossil hominin specimens has opened a door to a vast array of data on nearly all aspects of hominin biology (Stoneking and Krause, 2011). With these data, we can test hypotheses about how hominins biologically adapted to varying diets. The process of piecing together Neanderthal genetic history has been an incremental undertaking but some insights into selection relating to diet are already available (Perry et al., 2007). Comparison of the genomes of contemporary humans, chimpanzees, Neanderthals and Denisovans has shown evidence that Neanderthals, Denisovans and present day humans all lost a masticatory myosin gene (*MYH16*) that helps develop powerful masticatory capabilities in chimpanzees. Changes in hominin social structure may have contributed to this but to a large extent this gracilisation is linked to the gradual adoption of a more energy-dense, softer diet, potentially around ~2 ma (Perry et al., 2015).

Research has also found that Neanderthals carried activated and deactivated variants of a gene for a bitter taste receptor- *TAS2R38* (Lalueza-Fox et al., 2009). *TAS2R38* detects a compound called PTC (phenylthiocarbamide). PTC does not occur in plants, but sensitivity to PTC reflects ability to experience bitter tastes in certain plants such as members of the cabbage (*Brassica*) genus (Kaplan et al., 1976). It seems Neanderthals may have experienced variable sensitivity to PTC, as do early modern humans. Early modern humans, Neanderthals and Denisovans have lost two genes rating to bitter taste (*TAS2R62* and *TAS2R64*) that are still operative in chimpanzees. Although in contemporary humans factors such as personal preference contribute to use of the plants (Niewind et al., 1988) this gene loss means that they experienced this taste variably as people do today (Perry et al., 2015). Some report that contemporary humans with the activated *TAS2R38* gene eat fewer plants, but bitter taste receptors may serve to protect against toxins and be quite useful for identifying plants that are safe to eat. It should be noted that in contemporary humans non-genetic factors such as personal preference contribute to use of the plants (Niewind et al., 1988). Low sensitivity to bitterness indicates that Neanderthals shared specific adaptations with early modern humans associated to the consumption of particular plant foods and more energy-dense diets. Yet these pseudogenising (gene loss) mutations occurred long before the divergence between Neanderthals and early modern humans, and they reflect selection in populations that predate Neanderthals (Perry et al., 2015). Though we currently have no way of

knowing if these adaptations were of dietary importance for Neanderthals, they probably were not.

Not all selection events that relate to diet predate the Neanderthal divergence from African populations. Like chimpanzees and humans, Neanderthals possess the salivary amylase gene (*AMY1*) enabling them to break down starch into more useable sugars in the mouth (Perry et al., 2015). Neanderthals, like chimpanzees and Denisovans, carried only one to two copies of the salivary amylase gene. However, the contemporary human lineage carries a higher number of copies depending on the population. Contemporary humans on an average have about six copies of the *AMY1* gene. This difference is thought to have emerged in Africa during the past 200,000 years, long after Neanderthals diverged roughly 600,000 years ago (Perry et al., 2015). We do not know why copies of *AMY1* were selected, since most starch digestion occurs in the gastrointestinal tract from pancreatic amylase activity (Lee et al., 2013). Some have proposed that oral starch digestion may have been lifesaving in infants, which have minimal pancreatic activity (Butterworth et al., 2011; Hardy et al., 2015a). Extra copies may have arisen to boost protection against death from diarrheal and intestinal disease in groups heavily reliant on starchy plant foods (Perry et al., 2007). The high number of copies of *AMY1* probably reflects the importance of starchy plant foods to early African humans. Some might argue that the fact that Neanderthals had few *AMY1* copies implies a low use of plants. However Neanderthal *AMY1* copy number reveals limited insight into their total intake of plants, because starch is absent in many nutritious plant foods. New World primates lack *AMY1* despite being obligate plant eaters (Perry et al., 2007).

2.5.3 Zoological traces of diet

The vast bulk of data concerning Middle Palaeolithic foraging stems from skeletal remains recovered from archaeological sites. Faunal remains are far the most numerous dataset available to researchers, even though many faunal assemblages are natural accumulations and not a product of hominin activity. This is due to fact that the karstic caves that dominate Palaeolithic archaeological research in Europe provide good environments for the preservation of skeletal remains, and act as landscape bone traps. Anthropogenic macromammal skeletal remains have been used to target a wealth of questions on meat provisioning capabilities, dietary breadth, and intensity of resource use. Faunal assemblages are frequently palimpsests, a sum of many unrelated episodes, such as hunting, scavenging, natural

death jumbled by unpredictable sedimentary processes, which leaves a complicated formation history (Lyman, 2003). Despite the difficulties in reconstructing economic strategies from skeletal remains, zooarchaeologists have accumulated much information about Neanderthal- animal interactions. Zooarchaeologists once argued that Neanderthals were primarily scavengers, due to presumed cognitive or technical limitations (Binford 1985) but zooarchaeological data have verified that Neanderthals were capable hunters who exploited a variety of game (e.g. Speth and Tchernov, 2001). Neanderthal hunting technology is distinct and appears to have centred on handheld hafted and unhafted spears used mainly for thrusting (Villa and Soriano, 2010). Specialists argue that Neanderthals' close range hunting technology and susceptibility to carnivores meant they may have depended on closed forests, ecotones, or brush-grass mosaic habitats for much of their kills, although they clearly ventured into open country to hunt at times (Churchill, 2014).

Neanderthal hunting strategies throughout their range focused on a handful of key mammals, typically prime-aged artiodactyls. However, Neanderthals were capable of exploiting most of the herbivorous taxa that they encountered (Churchill, 2014). The largest game available on the landscape is rare in Neanderthal sites, but there are traces of the consumption of some of these fauna including mammoths (e.g. Germonpré et al., 2014). They also hunted large, dangerous predators such as bears, leopards, and cave lions (e.g. Valensi and Psathi, 2004; Blasco et al., 2010). However, prey exploitation was heterogeneous across their range. Resource choice followed ecological gradients of the period. On the European Plain fauna that lived in open or mixed areas such as horse (*Equus* sp.), woolly rhino (*Coelodonta* sp.), ibex (*Capra* sp.), red deer (*Cervus elaphus*) and to a lesser extent reindeer (*Rangifer* sp.) were preferred (Patou-Mathis, 2000). Yet in Italy, Neanderthals seem to have favoured red, fallow (*Dama dama*) and roe deer (*Capreolus* sp.), suggesting a preference for closed habitats (Stiner, 1994). In Iberia, a pattern of red deer, horse, ibex, wild boar (*Sus* sp.) and bovine exploitation has emerged in the zoological reports although considerable variability is present. While these data seem to indicate a relatively static hunting pattern focused on ungulates, there are a few exceptional sites where other distinct varieties of animals were consumed. Some sites (Figueira Brava, Vanguard, Gorham's Caves and Grotta di Sant' Agostino) in Iberia and Italy have evidence for consumption of monk and ring seals (*Monachus monachus* and *Pusa hispida*), porpoises (*Phocoena phocoena*) and dolphins (*Tursiops truncate* and *Delphinus delphis)* (Antunes and Santinho-Cunha, 1992; Stiner, 1994; Stringer et al., 2008). Other sites (Bajondillo Cave, Bolomor Cave and Hayonim Cave) on the Mediterranean rim have abundant small game components (Cortés-Sánchez et al., 2011; Blasco and

Fernández Peris, 2012). Fauna analysts have studied Châtelperronian large-game fauna assemblages left by late Neanderthals and reported few differences from Aurignacian assemblages (Grayson and Delpech, 2008), but large game hunting practises are generally similar between the Middle and the Upper Palaeolithic (Stiner, 2013).

The role played by small animal prey is far more useful for distinguishing Neanderthal and early modern human subsistence, but it remains poorly understood (Fiorenza et al., 2015). The relative lack of information about small game is due in part to taphonomic problems. Small animals are less likely to be preserved, recovered, and identified (Yellen, 1991a; b). Foragers may consume small game in the field rather than bringing them to camp. Small game remains are harder to conclusively associate with hominin use, because they may be deposited in an archaeological site by carnivores or birds of prey, or the small animals may have simply lived, and died, in the site. Furthermore, small game can require less butchering to process and consume making them even harder to associate with hominin activity (Brown et al., 2011). Nonetheless, there is sufficient data to demonstrate that Neanderthals living in southern regions targeted some species of small game, including rabbits, birds and tortoise (Stiner et al., 2000; Blasco et al., 2013; Salazar-García et al., 2013). In some cases, such as Grotta dei Moscerini in central Italy and Hayonim Cave in Israel, small game like shellfish, tortoises, lizards, and ostrich eggs compromise 45 % or more of the faunal assemblage (Stiner, 1994). In central and northern Europe, Neanderthals also consumed small game during the MIS 5e interglacial. In Taubach (Germany) and Vindija (Croatia), there are many cut-marked beaver (*Castor fiber*) bones (Gaudzinski-Windheuser and Roebroeks, 2011).

Fish bones have been found in several sites in western Italy, France, and southern Iberia (Fiore et al., 2004; Fiorenza et al., 2015), as well as Vindija Cave in Croatia (Paunović and Smith, 2002) and at Raj Cave in Poland. Like small terrestrial game and shellfish, fish remains are rare in Mousterian levels of Palaeolithic sites. Even where fish remains are present, they are less frequent than in the contemporaneous Middle Stone Age sites in Africa (Klein and Steele, 2008), but this disparity may be related to sea level changes, as many western Middle Palaeolithic coastlines are currently under water and thus not available for study. In addition, fish remains are even less likely to be preserved than terrestrial small game (Szpak, 2011). A variety of shellfish species were found in Middle Palaeolithic sites in Iberia, Italy and Greece, but they are very rare (Stiner, 1994; Klein and Steele, 2008).

The use of small game and aquatic resources directly relates to dietary breadth. Zooarchaeologists usually consider small game a low-ranked prey item, because the costs are high relative to the amount of food each prey item provides. For example, a hunter may expend considerable energy to bag a fast-moving and agile hare with limited energetic returns, unless they use technology to assist the process. Dependence on low-ranked prey is often linked to the declining supply of high-ranked large and medium-sized game, population growth, and technological investments in energy capture (Stiner et al., 2000). However, regarding all small game as low-ranked prey is overly simplistic (Fiorenza et al., 2015). Some small prey, such as tortoises and eggs, may yield high returns with little foraging costs. In other cases, small prey may be low-return but may offer specific macronutrients (e.g. DHA in marine foods or small mammal brain) more important than total energy (Kelly, 1995; Winterhalder and Smith, 2000; Haws and Hockett, 2004). For these reasons, zooarchaeologists have attempted higher resolution approaches including sub classifying small game by ease of capture and species diversity (Stiner, 2001). These dietary breadth metrics have been used to argue that Neanderthals very rarely captured low-ranked small game, in contrast to recent hunter-gatherers, some Upper Palaeolithic foragers, and possibly some Middle Stone Age foragers (Stiner, 2013). However, there is still some apparent variability in Neanderthal behaviour. At Kebara Cave, Neanderthals increased their reliance on low-rank juvenile gazelle and fallow deer (low-rank due to their small body size and reduced adipose tissue), while the relative proportion of high-ranked aurochs, red deer, and boar decreased from 50 ka onwards. In this case, it appears that Neanderthals depleted large game supplies, and were forced to adapt through prey switching (Speth and Clark, 2006).

In sum, Neanderthals appear to have been capable hunters who favoured hunting medium and large game. The absence of small game, fish, and shellfish in their range in central and northern western Eurasia is due to a combination of bias in the archaeological signal and intentional hunting strategy. Although the Middle Palaeolithic predation niche varied considerably through time and space, the general pattern of Neanderthals as medium- and large-game hunters is to some extent correct. However, in some cases they were also consumers of other foods such as small mammals, fish, shellfish, bird eggs, lizards, and scavenged meat. Unfortunately, researchers have yet to describe full geographic and temporal variation in small-game procurement (Fiorenza et al., 2015). Nevertheless, the majority of studied faunal assemblages indicate most Neanderthals appear to have engaged in narrow spectrum foraging for most Neanderthal populations, with some

evidence for increased dietary breadth beginning about 50 ka (Speth and Clark, 2006; Stiner, 2013).

2.5.4 Indications of diet from macrobotanical plant remains

Evidence for the consumption of plant foods is sparse across the Neanderthal range in part because, unlike bones, most plant remains require a specific set of exceptional circumstances to preserve in archaeological deposits. In the western Eurasian context, this is typically carbonisation, though desiccation and waterlogging are also possible (Van der Veen, 2007). Carbonisation requires that the food plants are exposed to fire and typically best preserves seeds and nuts that benefit from cooking. The record of charred remains is biased in other ways too, because foragers frequently consume plant foods as they are collected, before returning to camp and encountering fire (Marlowe, 2010). In addition, macrobotanical assemblages poorly preserve tissue of some vegetal resources such as underground storage organs, leafy plant parts and oily plant foods (Pennington and Weber, 2004), rendering these foods largely invisible to archaeologists. Plant remains cannot be representatively recovered or even detected onsite without specialised archaeobotanical sampling, which the archaeobotanical community only commenced in the 1960s. Therefore, and unlike studies of fauna, literature so scarcely discussed botanical remains that some archaeologists may have avoided monitoring for them even after the techniques were available. In addition, even if plant remains are found, they may simply reflect plants growing near the site rather being a signal of food items. Neanderthal sites with plant remains are rare but this is a preservation bias.

Table 2: Neanderthal sites with evidence of macrobotanical plant remains.

Site	Macroremains	Region	Complex	Reference
Douara Cave	Hackberry	Syria	Mousterian	Matsutani, 1987; Griggo, 2004
Gorham's Cave	olive, stone pine	Iberia	Mousterian	Barton et al., 1999
Rabutz	hazelnut	Germany	Mousterian	Toepfer, 1958
Mas-des-Caves	hackberry	France	Mousterian	Barton et al., 1999
Kebara Cave	pistachio, grasses, lentil and other legumes	Israel	Mousterian	Lev et al., 2005
Theopetra Cave	lentil, chickpea and other legumes, grasses and nuts	Greece	Mousterian	Mangafa, 1998

The few existing Middle Palaeolithic sites with botanical remains provide a varied but are incomplete for all inhabited environments (Table 2). At Douara Cave in Syria, abundant deposits of hackberry (*Celtis* sp.) were identified dating to roughly 40 to 55 ka (Matsutani, 1987; Griggo, 2004) Barton and colleagues also reported this plant taxon from Mas-des-Caves in France (1999). Archaeobotanists have found macroremains from stone pine nut (*Pinus pinea*) and olive (*Oliva* spp.) dating to 51,700+3300 BP ^{14}C in the western Mediterranean at Gorham's Cave, Gibraltar. Charred hazelnut shells (*Corylus avellana*) have been identified at Rabutz in central Germany during the warm conditions of the MIS 5e interglacial (Toepfer, 1958), although these shells could have entered the archaeological site by natural processes. Lentil, chickpea, pea and vetchling are reported from Middle Palaeolithic deposits at Theopetra Cave (Mangafa, 1998). The most notable and diverse macrobotanical assemblage so far identified was located in Kebara Cave at Mt Carmel (Israel). This assemblage of charred seeds dates to 63-48 ka, and dwarfs in diversity and size all other Middle Palaeolithic as well as many Upper Palaeolithic macrobotanical assemblages so far recovered. The contents suggest a broad foraging strategy for potential staples, mostly legumes (Fabaceae) with some acorns (*Quercus* spp.), pistachio nuts (*Pistacia* spp.), and chenopods (Lev et al., 2005). Pistachio nuts are rich in lipids, proteins, and carbohydrates, and are therefore an excellent candidate high-rank food, although they would have been available only for a brief season (Dreher, 2012). However, the richness of the legume assemblage is unusual, although protein-rich, they are slow to collect and are arguably low-ranked foods and more usually associated with near-sedentary Epipalaeolithic groups of the Near East (Savard et al., 2006). Many plants were highly restricted by season and would have to be harvested from different habitats in windows from spring to autumn. Overall, the plant remains present evidence of plant use across a variety of Neanderthal habitats, and in at least one case, there are traces of particularly broad use of plants. Yet most macrobotanical examples cannot be unambiguously associated with diet. The collated macrobotanical evidence is promising but overall data are too fragmentary to explore the variation of plant use.

2.5.5 Sedimentological traces of microbotanical plant remains and diet

It is possible to collect data about subsistence patterns from particles in archaeological sediments. Phytoliths, also known as plant opal, are glassy bodies comprised of biogenic silica found in the aerial tissue of plants (Piperno, 2006). They

often preserve specific morphologies relating to the plant taxon or plant part that produced them. The decay of the plants releases the phytoliths and thus they enter the archaeological record. Phytoliths routinely survive for vast spans of time and can survive for hundreds of millions of years in certain conditions (Carter, 1999). Thus, they readily survive in the sheltered conditions of cave sediments (Albert et al., 1999). However, if stratigraphic levels are mixed and poorly associated with archaeological evidence it may be difficult link causality of phytoliths to hominin activity. Phytoliths can enter archaeological sites from windblown aerosols, colluvium, bird droppings and other animal activity. Phytolith studies may require well-preserved archaeological deposits examined collaboratively with FTIR and micromorphology. If properly performed, phytolith analyses can provide detailed information about the use of specific plants for many different uses. So far, it has been possible to infer food, bedding, or fuel using phytolith assemblages. Phytolith specialists have studied only a handful of Neanderthal sites for phytoliths. At 58-37 ka cal BP levels in Esquilleu Cave in Cantabria (Iberia), phytoliths indicate continuous deposition of grass leaves by a hearth, suggesting the presence of a bedding zone at this spot (Cabanes et al., 2010). Phytoliths at Amud cave in Israel also indicate plant bedding dating to 70-55 ka (Madella et al., 2002). In some cases, such as Kebara Cave, analysts have retrieved phytoliths from hearth deposits and inferred fuel choice (Albert et al., 2000). Even more interestingly, this site also contained high concentrations of the dendritic morphotype phytolith, which would usually be more familiar in agricultural contexts due to the abundance of domesticated grain. The authors interpreted this accumulation as evidence that Neanderthals repeatedly collected mature grass seed. This is a controversial interpretation because the same pattern could be the result of fauna burying caches of seed. If the anthropogenic interpretation is accepted, it may suggest that Neanderthals in one Levantine site made heavy use of a low-ranked food.

New studies have explored the potential for detecting other anthropogenic indicators in archaeological sediments. Researchers have highlighted that the products of biological processes (biomarkers) may yield insights into the dietary inputs of hominin metabolisms. Most analyses so far have focused on sterols and stanols as candidate faecal biomarkers, because they have the virtue of high stability through the food chains and are resistant to diagenesis (Peters et al., 2005). Only higher mammals form 5β-stanols, which they produce in their intestinal tracts during the metabolic breakdown of cholesterol and phytosterols. Their use as an anthropogenic indicator relies on identifying the source coprolite as hominin. Fortunately for archaeological science, the relative proportions of these stanols and

sterols are known to be indicative of dietary preferences although how this works is not understood (Floate, 1970; MacDonald et al., 1983). Sistiaga and colleagues (2014) took sediment samples from morphologically identified coprolites near combustion features in the open-air site of Abric d'El Salt (Alicante, Iberia) dated to 60.7 ± 8.9 and 45.2 ± 3.4 ka (Garralda et al., 2014). These samples were analysed with gas chromatography- multiple reaction monitoring-mass spectrometry. Some samples were dominated by coprostanol and its diagenetic product epicoprostanol, verifying that the samples represented coprolites. The ratio of coprostanol and phytosterol can indicate which taxa produced a coprolite. In all cases at El Salt the values were high, so the authors argued that the faecal residues are from suids or humans, and because no suids were found at the site, humans were the ostensible producers (Sistiaga et al., 2014). The authors report that they discovered from this find that Neanderthals have a high rate of conversion of cholesterol to coprostanol, yet in a fallacy of circularity, use this same trait to identify the coprolite as Neanderthal (Sistiaga et al., 2014). The faecal biomarkers almost certainly represent many separate events and thus cannot be identified to hominin without further biomarkers (i.e. bile acids) (Bull et al., 2002). Yet, although results from El Salt do not reveal diet, multi-pronged faecal biomarkers approaches will likely be highly useful, especially if coprolites deposits are discrete and can be unambiguously identified as Neanderthal.

2.5.6 Evidence of palaeodiet from pathologies

Health is deeply interrelated with diet and many disorders are a result of food choice. In some cases, details on health can be gleaned from surviving hominin skeletal material. Carious lesions are cavities that form on the surface of tooth enamel from the demineralising effects of oral microbiota (Selwitz et al., 2007). The intake of carbohydrates is one of several factors that are needed to form carious lesions (Selwitz et al., 2007) and thus carious lesions can be indirect evidence of diet in contemporary humans. The frequency of these lesions increases relative to the amount of carbohydrates consumed, leading many archaeologists to use this as a proxy for palaeodiet (e.g. Christophersen and Pedersen, 1939; Larsen et al., 1991; Flensborg, 2011). Compared with typical contemporary people, caries are rare in recent foragers (<10 %), but common in past agriculturalist groups (Lanfranco and Eggers, 2012). Dental caries are very rare in surviving Neanderthal teeth (Tillier et al., 1995; Walker et al., 2011b). Of the approximately 1250 Neanderthal teeth examined, just six (0.48 %) have been reported to display carious lesions. Of the six

cases, three occur in Iberia, two in France and one in Israel (Lanfranco and Eggers, 2012). Yet seldom do researchers identify caries in early modern humans, although their frequency is unclear. Nevertheless, the rarity of Neanderthals suffering from caries appears to reflect a reliance on animal foods. Not all agree, and the dearth of caries in Neanderthal teeth is taken by some to reflect absence of cariogenic bacterial species in Neanderthal oral flora (Sołtysiak, 2012). For example, molecular evidence suggests that cariogenic bacterial species *Streptococcus mutans* was not present in archaic humans. Yet microscopic examination of dental calculus identified these bacteria from the Kebara 2 and the Subalyuk 1 Neanderthals. In addition, caries may arise from the activities of other cariogenic bacteria species (Tomczyk, 2012).

Another example of a pathology demonstrating diet is dental calculus. The formation of dental calculus is a multicausal process (See 2.6.1), but some dietary factors are clearly involved. Protein consumption enhances calculus formation by increasing the pH of the mouth (Lieverse, 1999). Little effort has been made to extrapolate diet from the abundance of Neanderthal calculus deposits. This is unsurprising as interpreting diet from calculus abundance is challenging. Some agricultural populations with low protein intake have high calculus abundance while some forager populations with ample meat use have little calculus (Lieverse, 1999). This pattern has led some palaeopathologists to use high calculus abundance to trace a high use of carbohydrates instead of protein (Greene et al., 2005). Saliva flow, silicon intake, smoking and predisposition acerbate dental calculus formation in addition to diet explaining this contradiction (Bergström, 1999; Lieverse, 1999).

2.5.7 Evidence of diet from dental wear

Over the course of life, wear reduces the surfaces of teeth. Wear is heavily influenced by the mechanical properties of the food consumed and thus may reveal information on the characteristics of diet (Ungar, 1998). Food may have varied physical properties, such as abrasiveness, toughness, hardness, and brittleness, meaning different foods requires different masticatory processing (Cromton and Hiiemae, 1970; Fiorenza et al., 2011). Over time, attrition, abrasion, and erosion combine to gradually remove the enamel surface of teeth (Kaifu et al., 2003; Addy and Shellis, 2006; Kaidonis, 2008). Attrition is the mechanical force exerted from contact of opposing teeth. Abrasion is another physical wear caused by the rubbing of exogenous material pushed against teeth during mastication. Particles in food such as phytoliths that are softer than enamel are thought to still wear enamel

because they force apart the proteins that hold enamel crystallites together (Xia et al., 2015). In the context of Pleistocene foragers, this exogenous matter is predominantly hard and fibrous foods, foreign particles transported in food, and environmental dust carried in wind. Erosion is the chemical dissolution of the tooth surface, but its incidence in the teeth of foragers is insignificant, whereas abrasion and attrition are commonplace (Fiorenza, 2015). Thanks to the gradual advances in our knowledge of the mechanisms of how dental surfaces reform over life, dental wear has matured into a widely applicable means of dietary reconstruction. As the discipline has grown, dental wear has been used to broadly classify the diet of recent forager groups (e.g. El Zaatari, 2010) and the feeding niches of ancient hominins (e.g. Ungar and Sponheimer, 2011). The discipline comprises of two main fields based on the nature of the wear studied - microwear and macrowear.

Dental microwear analysis is the study of the microscopic damage on a tooth's surface as the result of its use. The surfaces of many Neanderthal teeth are highly worn, and this necessitated that early microwear research used the striation patterns on cheek side the buccal surface as a proxy for food masticated on the chewing surface (occlusal surface) (Pérez-Pérez, 1994; Lalueza et al., 1996; Puech, 1999). The buccal wear pattern in individuals consuming a high proportion of meat is characterised by a lower number of striations and a relatively high proportion of vertical ones, while individuals relying on a more vegetarian diet display an increased number of striations, with a greater proportion of horizontal ones (Fox and Pérez-Pérez 1993; Pérez-Pérez 1994). Using scanning electron microscopy, wear specialists (Lalueza et al., 1996) compared Neanderthals with archaic *Homo* specimens and with samples of recent people. Their samples of recent people represented strict vegetarians, tropical and subtropical foragers who consumed relatively high proportions of plant foods, and high-latitude foragers and horticulturalists who consume large amounts of meat. The eight sampled Neanderthals (La Quina V, Gibraltar 2, Tabun 1 and 2, Amud 1, Malarnaud, Saint Césaire and Les Pradelles) had different microwear patterns from those of vegetarians. Some Neanderthals were similar to living groups with high-meat diets, but most fell within the range of both high-meat and more mixed diets. Furthermore, the results taken as a whole showed no compelling chronological, climatic, or geographic patterns.

Buccal and occlusal wear both reflect diet but emerge in different patterns. The formation of occlusal wear is better-understood than buccal wear, making it a more informative approach for ancient hominins (El Zaatari, 2007). More recently,

wear studies have grown in sophistication with the integration of confocal microscopy with the advent of "occlusal microwear texture analysis". El Zaatari (2010) used this approach to analyse the occlusal microwear of recent foragers from known temperate, arctic, and other biomes. The groups had varying amounts of marine foods, large game, small game, and plant foods. These samples provided the baseline to which to compare 35 Neanderthal individuals from 23 European and Levantine sites. By grouping these sites by habitat type, El Zaatari showed that Neanderthals associated with mixed and wooded environments consumed plant foods, but in a lesser quantity than meat. Four Neanderthals deriving from open habitats (Spy, La Quina, Arcy-sur-Cure, and Subalyuk) most closely resembled recent groups who fed on fish, seals and guanaco (*Lama guanicoe*) with few plants (about <15 %) (El Zaatari, 2010; El Zaatari et al., 2011). The eight Neanderthals from mixed habitats (Saint Césaire, Petit-Puymoyen, Rochelot, La Chaise, Vindija, Kebara, and Tabun) more closely clustered with marine, small game and plant consuming foragers. The four Neanderthals from closed habitats (Amud, El Sidrón, Grotta Breuil and Zafarraya) had higher levels of molar occlusal complexity and heterogeneity indicating the highest levels of plant use of all the Neanderthal samples. Despite this, they did not cluster with the forest-dwelling recent foragers, tantalisingly suggesting they may not have been as reliant on plants.

The other main approach to wear-based dietary reconstruction is dental macrowear. Molar macrowear represents the cumulative impact of the mechanical properties of diet during an entire lifetime, unlike dental microwear which covers only a brief period just prior to death (Grine, 1986; Janis, 1990). Early efforts to document dental wear interpreted the generality of the abrasiveness of diet rather than the components of diet (Fiorenza et al., 2015). The effectiveness of macrowear studies for dietary interpretations has greatly grown in recent decades with the improved knowledge of how mastication reforms occlusal contact areas (Douglass and DeVreugd, 1997). These developments led Kullmer and colleagues (2009) to develop 3D virtual models to analyse wear patterns on the facets of teeth. By measuring perimeter, inclination, and orientation, it became possible to create a model of how food was chewed, in a method termed "occlusal fingerprint analysis" (Kay and Hiiemae, 1974; Janis, 1990). Fiorenza and colleagues (2011) analysed the occlusal fingerprints of 19 Neanderthals, which he grouped into a deciduous woodland group (Krapina), a steppe and coniferous forest group (Monsempron, Le Moustier and Vindija) and a Mediterranean evergreen woodland group (Amud, Tabun and Shanidar). Wear patterns of the deciduous woodland and Mediterranean evergreen woodland was suggestive of a mixed diet probably containing a

significant amount of plants. This group matched wear observed in several plant-reliant recent human reference populations. Neanderthals from steppe and coniferous forest regions exhibited patterns of cold dwelling groups that consume tough foods such as terrestrial mammal muscle or marine foods, though it was not possible to distinguish between these two (Fiorenza et al., 2011). More recently, occlusal fingerprint analysis has explored wear patterns of Neanderthal molars found on the Italian peninsula, Saccopastore 1 and 2, and Guattari 2 and 3 (Fiorenza, 2015). This study found wear suggestive of the use of animal and plant foods on all specimens, though the Saccopastore specimens were more suggestive of meat eating. Guattari 2 fell closer to the previous Mediterranean reference group and Guattari 3 clustered together with the deciduous woodland reference group. Fiorenza and colleagues (2015) interpreted these results as suggesting plant foods had a degree of importance in the warm interglacial MIS 5, while during warm phase MIS 3 Neanderthals appear to have relied more on animal foods.

Micro and macrowear provide a substantial amount of information of the mechanical characteristics of masticated food. From these data, inferences on the nature of diet can be made. However, interpreting these data presents significant problems relating to comparability of environments and differences in reference populations. For instance, the lumping of steppe with coniferous forest biomes makes comparison difficult (Fiorenza et al., 2011). Furthermore, some dental wear is derived not from diet but foreign mineral particles that come in to contact with the enamel, which can confound wear studies (Lucas et al., 2013). Nonetheless, wear-based approaches provide information about Middle Palaeolithic diets unavailable from other lines of evidence. These lines of evidence suggest that Neanderthals consumed plant foods as part of a diet rich in animal foods, and that there may have been more variability across habitats than isotope studies indicate.

2.5.8 Isotopic approaches to palaeodiet

The maturation of methods of dietary reconstruction borrowed from other fields has made major contributions to understanding Palaeolithic diets. The application of stable isotopic analysis to ancient hominins is one example that has become an important means for reconstructing diets and corroborating other lines of evidence (e.g. Codron et al., 2008). Stable isotopic palaeodietary analyses principally use carbon and nitrogen isotopes from collagen from bone and tooth dentine. Isotopes from other elements such as sulphur also can reveal dietary history (Privat

et al., 2007). Stable isotopes are analysed as the relative amount of a heavier isotope to a lighter isotope and expressed in δ notation in parts per mil (Schwarcz and Schoeninger, 1991). Carbon isotopes ($^{13}C/^{12}C$) can provide information about the consumption of plants and marine foods, and the nitrogen isotopes ($^{15}N/^{14}N$) reflect use of plants and animals and trophic level. Stable isotopes can sometimes provide detailed information on how much consumed protein was from terrestrial animals, marine animals, freshwater animals or plant foods. Comparison of values with contemporary fauna serves as a reliable means of quality control. The isotopic signal of hominin bone collagen reflects a variable amount of time but given its turnover rate it reflects years of diets in adults (Hedges et al., 2007).

Studies of Neanderthal diets using stable isotopes have garnered much attention. This analysis requires well-preserved collagen and thus is limited by chronology and the taphonomic conditions present at a site. Values have been published from at least 22 individual Neanderthals from 14 sites (See Table 3), and ambiguous values from two others. These sites date between 120 and 30 ka, and are located in France, the Netherlands, Belgium, Russia, Germany, and Croatia (Richards et al., 2000; Bocherens et al., 2005; Beauval et al., 2006; Krause et al., 2007; Richards and Schmitz, 2008; Hublin et al., 2009; Ecker et al., 2013; Wißing et al., 2015). Though isotope and fauna bone studies conflict on Neanderthal prey choice, both indicate that the protein in Neanderthal diets came predominately from terrestrial animals, likely medium and large herbivores (Dusseldorp, 2010, 2013). This isotopic signature has been interpreted as largely representing a consistent ecological niche at the apex of the Pleistocene terrestrial food chain. Isotope values from fauna bones from the same sites suggest that Neanderthals were higher on the food chain than even carnivores such as wolves and bears, but in some cases the comparative fauna was from different archaeological levels and thus may not provide a reliable baseline (Richards et al., 2000, 2008; Bocherens et al., 2005). Some researchers have gone as far to say that isotopically, Neanderthals mimic obligate carnivores (Churchill, 2014). Notably the Saint-Césaire Neanderthal associated with a Châtelperronian tool kit does not differ from the other Neanderthals despite the other indications from this technology that suggest more reliance on plant foods (See 2.5.1). Furthermore, the isotopic values give no indication that Neanderthals consumed aquatic resources like fish or shellfish. The sampled individuals were mostly from inland regions where marine foods are not expected, but the absence of freshwater fish is surprising. Similarly, the Neanderthal isotopic signature appears to leave little room for consumption of plant proteins. However, it cannot entirely rule out a regular intake of protein from plants, due to differences in absorbable

protein compared with meat. Plant nutrients such as protein and lipids are often less absorbed than animal equivalents (Baer et al., 2012). Plant foods are typically high in carbohydrates and often contain only moderate levels of protein.

Table 3: Neanderthal remains with published stable isotopic values ($\delta^{13}C$ and $\delta^{15}N$).

Site	N	Age	Region	Predominant diet	Source
Payre [a]	1	MIS 8-7	France	Terrestrial animal	Ecker et al., 2013
Scladina	2	MIS 5c-b	Belgium	Terrestrial animal	Bocherens et al., 1999, 2005
Les Pradelles [b]	5	MIS 4	France	Terrestrial animal	Beauval et al., 2006; Bocherens et al., 2005
Okladnikov	1	MIS 3	Russia	Terrestrial animal	Krause et al., 2007b
Vindija	2	MIS 3	Croatia	Terrestrial animal	Richards et al., 2000
Feldhofer	2	MIS 3	Germany	Terrestrial animal	Richards and Schmitz, 2008
Les Rochers-de-Villeneuve	1	MIS 3	France	Terrestrial animal	Beauval et al., 2006
Saint-Césaire	1	MIS 3	France	Terrestrial animal	Bocherens et al., 2005
Jonaz	1	MIS 3	France	Terrestrial animal	Richards et al., 2008c
Goyet	12 [c]	MIS 3	Belgium	Terrestrial animal	Wißing et al., 2015
Spy	1	MIS 3	Belgium	Terrestrial animal	Bocherens et al., 2001
Engis	1	MIS 3	Belgium	Terrestrial animal	Bocherens et al., 2001
Zeeland Ridge	1	MIS 3	Netherlands	Terrestrial animal	Hublin et al., 2009

[a] This sample derives from tooth enamel and thus has only carbon isotopic values.
[b] The reliability of the isotopic values has been questioned by Bocherens et al., 2005
[c] The twelve samples represents four or more individuals.

Neanderthals may have plausibly targeted vegetal foods low in protein and high in carbohydrates and lipids to ameliorate the risk of protein poisoning (See 2.4.1). We cannot quantitatively estimate contributions of each component of diet unless a mathematical model (mixing model) is used (Bocherens, 2009; Fernandes et al., 2014). Reliably fitting of such models requires the input of isotopic values of all the consumed foods, and this is not possible in a Palaeolithic context. Therefore, mixing models in these contexts might be misleading.

Some have challenged the view that Neanderthal protein intake was near exclusively animal-based. Specialists have explored various possibilities to assess if the nitrogen isotopic values reflect an extremely high trophic level. Speth (2010) noted that severe nutritional stress can lead to increases in $\delta^{15}N$ due to the effects of protein catabolism, and that this starvation signature may explain the elevated Neanderthal $\delta^{15}N$ signal. Bouts of starvation are a well-documented part of life for some foragers, particularly those in high latitudes such as Arctic foragers. Episodes of stress (nutritional or illness related) endured by Arctic foragers in childhood are visible with enamel defects such enamel hypoplasia on their teeth. Comparison of Arctic foragers and Neanderthal indicate comparable stress levels (Guatelli-Steinberg et al., 2004). However, given the slow turnover rates of bone, malnutrition

severe enough to elevate $\delta^{15}N$ is would normally be fatal before it could be recorded in bone (Beaumont et al., 2013), suggesting that malnutrition might not explain the Neanderthal signal.

Another source of confusion may come from the fauna used as a baseline for extrapolating Neanderthal trophic level. If prehistoric faunal diets differed from that of their present day counterparts, it may confuse our interpretation of Neanderthal diets. For example, if the herbivores that Neanderthals consumed had elevated $\delta^{15}N$, then the Neanderthal trophic level would appear high. This would mask consumption of plant protein if comparative fauna were unavailable. Usually ideal numbers of comparative fauna from the same levels are absent from isotopic studies. Furthermore Eurasian elephantids have unusually high $\delta^{15}N$ values unlike present day elephants (likely relating to consumption of faeces), and some have suggested that this explains the apparent trophic level of Neanderthals (Richards et al., 2000; Bocherens et al., 2005; Kuitems et al., 2012). However, elephantid consumption is unlikely to explain high $\delta^{15}N$ values for all individuals published. Neanderthals consumption of elephantids appears to have been rather limited (See 2.5.3), while the Neanderthal isotope values are remarkably consistent across samples. The consumption of high $\delta^{15}N$ nitrogen prey may have had an impact, but the potential to distort Neanderthal isotopic signals should not be overstated in this case. Although isotopic studies have given a powerful insight into protein consumption, these sampled Neanderthals are disproportionately from northern open environments and cold phases (Richards and Trinkaus, 2009; Salazar-García, 2012). Few southern Neanderthal isotopic values have been published, in part due to the poorer preservation of Neanderthal collagen in these warmer climates (e.g. Ambrose, 1990). Of the published 22 Neanderthals subject to collagen isotopic studies, only two individuals lived in the forested interglacial period (MIS 5), while others are derived from a range of environments from climatic phases. This biased sample should temper interpretations based on isotopic data and reveal little about dietary variation in different environments.

2.5.9 The contribution of dental calculus to understanding Middle Palaeolithic diets

One the most exciting emerging ways to learn about ancient diets is to use hominin dental calculus. Dental calculus along with dental enamel is the only tissue in the human body with no means of regulated shedding. This unique characteristic enables entrapment and preservation of food particles and other materials become

entrapped in this biomineral deposit following consumption. Such an approach could address how Neanderthals used plants. Dental calculus (tartar) is dental plaque that has become calcified by salivary calcium phosphate (Lieverse, 1999). It is a ubiquitous pathology of the mouth in humans and human relatives. Researchers have reported finding starch grains, phytoliths, pollen, diatoms and other particles relevant to life history entrapped in human dental calculus for extended periods of time (e.g. Dobney and Brothwell, 1988; Boyadjian, 2012). Dental calculus sampled from living or dead individuals is rapidly gaining recognition as an invaluable material for the reconstruction of life histories. The integration of dental calculus analyses to Palaeolithic hominin remains has made powerful contributions to our knowledge of Neanderthal diets. As dental calculus offers direct evidence of the plants that entered the mouth, this analysis can potentially give information of plant use that is invisible with other methods.

Henry and colleagues (2011) pioneered the application of this approach to the elucidation of Neanderthal diets. This study used dental calculus sampled from one individual from Shanidar Cave, Iraq, and from two Neanderthal individuals from Spy Cave, Belgium. These analyses recovered remains of phytoliths from date palms (*Phoenix* spp.) and starches from grass seeds (Triticeae), legumes (Faboideae) and potential indeterminate underground storage organs. Although the assemblages probably reflect consumed foods it is difficult to rule out the contribution of chyme (semi-digested stomach contents). Chyme is widely consumed by foraging societies and it probably was a feature of Middle Palaeolithic diets (Buck and Stringer, 2014). However, starches predominated in these samples, yet ungulate chyme would predominately contain phytolith not starches, arguing against chyme being the primary source of plant remains in dental calculus.

Some of the starch grains, including Triticeae starches, were apparently partially disrupted (semi gelatinised). Gelatinisation is a process where starch undergoes a breakdown of its intermolecular bonds when heated in the presence of water. Thus, semi gelatinisation was interpreted as evidence of the controlled boiling and cooking of these starches. Yet some have queried whether this process could occur spontaneously to starches trapped in calculus for tens of thousands of years (Collins and Copeland, 2011). Current research is investigating the tempo of spontaneous gelatinisation and it remains to be seen if we can ascertain if Neanderthals boiled Triticeae seeds.

Another study sampled dental calculus Neanderthals from El Sidrón in northern Iberia, where a rich assemblage of Neanderthal remains was found. Hardy

and colleagues (2012) analysed dental calculus from five Neanderthals dating to 51,100 ka. Notably, this sample is probably the only example from temperate woodland environment so far published. Hardy recovered moderate numbers of starches in four of the five samples and one grass phytolith in one of them using optical microscopy. In addition, the dental calculus samples were analysed with (thermal desorption and pyrolysis) gas chromatography-mass spectrometry to assess if compounds relating to diet could be present. This technique yielded molecular evidence of inhalation of wood smoke and naturally occurring bitumen. The presence of compounds such as chamazulene, dihydroazulene, and 4-methylherniarin suggested exposure to yarrow and chamomile herbs. Hardy interpreted this as traces of plants used for medicinal rather than for nutrition purposes. Critics have raised concerns that these herbs may enter diet in chyme (Buck and Stringer, 2014). Pleistocene ungulates probably commonly grazed on yarrow. In addition to undeliberate use in chyme, plants like yarrow and chamomile may have been gathered and consumed as a vegetable. Although bitter-tasting, Buck and Stringer (2014) point out that traditional Alaskan people consumed camomile as a food plant (Kuhnlein and Turner, 1991). All food types may enter the mouth in many alternative ways such as ritual uses, dental hygiene or accidental intake.

Later published research has attempted to address the lack of data on Neanderthals from Mediterranean environments. Within a multi-proxy research article about Neanderthal diets from eastern Iberia, the author analysed dental calculus from nine teeth and tools from Sima de las Palomas del Cabezo Gordo in southeast Iberia (Salazar-García et al., 2013). To control for contamination, wash samples of cave rock fall (éboulis) were collected, and these showed grass phytolith and some starch contamination traces. However, these control stones were selected from a unit balk exposed to atmospheric airborne microremains for an extended span of time. Calculus and sediment adhering to fauna teeth from the site were also examined, analysis found no starches and only three phytoliths, mostly coming from grasses. Unlike the controls Neanderthal calculus recovered microremains types included leafy matter indicated by polyhedral multi-cells, hard endosperm of seeds or nuts as well as grass seeds and possibly underground storage organs. The starch grains found in dental calculus samples largely overlapped with the types recovered on the stone tools, although this overlap may be overestimated due to the lack of universal starch classification types in the discipline.

These studies have provided some information on elements of Neanderthal foraging strategy and show that Neanderthals were capable of sourcing nutrients

from a variety of plant foods. However, these findings only constitute qualitative information from archaeological sites dispersed by space and time. More recent work by Henry and colleagues (2014) attempted to explore Neanderthal plant use by comparison to African Middle Stone Age and Near Eastern and Europe Upper Palaeolithic peoples. This research used both dental calculus samples and wash samples of the surfaces of stone tools from Neanderthals, African Middle and Later Stone Age, and Eurasian Upper Palaeolithic peoples. A Poisson mixed model was used to test if Middle Stone Age and Middle Palaeolithic groups used less plants than Upper Palaeolithic and Later Stone Age peoples, using number of plant types as a metric of diet breadth, and controlling for the effects of geographic region, stone tool type and sites. This model suggested that all of the considered groups consumed an approximately comparable array of plant foods and none of the expected parameters of variation (stone tool industry or geographic region) had a significant influence on the number of plant species consumed. There was also no apparent pattern in plant use through time. Fundamentally, the results failed to detect any difference between Neanderthals and any modern human group.

These studies have indicated the potential for dental calculus research to reveal foods, in particular the use of low-ranked underrepresented food sources (e.g. Triticeae) and details about the breadth of plants consumed. However, there are many aspects of the calculus record that must be considered when applying this method to Neanderthal samples. In the following two sections, I discuss issues faced when interpreting the dietary signal of dental calculus.

2.6 The state of the art in dental calculus research

2.6.1 A background

The study dental calculus has a long history in archaeological research. Archaeological dental calculus has been noted as a pathology in studies of health of past populations since early decades of the 20th century (Leigh, 1925; Hughes, 1963). It was long recognised that this pathology is intertwined with diet, and the incidence of dental calculus was studied as a proxy for the amount of carbohydrates or proteins ingested (See section 2.5.6). The potential of dental calculus to open a door to specific dietary choices of past populations was first noticed in the 1970-1980s. Dobney and Brothwell (1986; 1988) demonstrated that dental calculus could yield data on the diets of human populations. Today, analysis of plant and animal

microremains recovered from archaeological dental calculus has grown to become a widespread means of aiding dietary and health reconstruction (Boyadjian et al., 2007; Blondiaux and Charlier, 2008; Henry et al., 2011; Liu, 2012; Mickleburgh and Pagán-Jiménez, 2012; Warinner et al., 2014; Power et al., 2016). Microscopic plant remains preserved in dental calculus can inform us about the exploitation of plants otherwise invisible to us, thereby enabling us to obtain direct information on a wide variety of question on prehistoric societies. For example, plant microremains from dental calculus have indicated the use of beans in a complex plant diet in South America (Piperno and Dillehay, 2008), described early agricultural diets at Tell al-Raqā'i, Syria (Henry and Piperno, 2008), and recorded pre-Columbian Caribbean subsistence (Mickleburgh and Pagán-Jiménez, 2012). Dental calculus has also contributed to dietary studies of the early African hominin *Australopithecus sediba*. Phytoliths found in the dental calculus of the MH2 individual suggested a C_3 diet incorporating dicotyledons (tree leaves, fruits, wood and bark) and monocotyledons (grasses and sedges) (Henry et al., 2012). More recently, dental calculus has been used to examine characteristics of diet from Lower Palaeolithic hominins at Qesem Cave in Israel (420–200 ka). Hardy and colleagues (2015) used starch grains and specific chemical compounds recovered from dental calculus to infer the ingestion of plant foods. They interpreted pollen, fungal spores, microcharcoal and invertebrate remains as evidence of the inhalation of respiratory irritants.

2.6.2 Technical difficulties in current approaches in dental calculus research

Despite this growing interest in dental calculus as a source of ancient dietary information, dental calculus is still poorly understood. Dentistry research has paid scant attention to the mechanisms by which plant microremains become trapped and preserved within calculus. Native starch grains (i.e. starches in their original unaltered state) are the predominant focus of much of the microbotanical archaeology literature (Mickleburgh and Pagán-Jiménez, 2012; Leonard et al., 2015; Tao et al., 2015). Yet there has been a lag in explaining how starch grains and grain morphology persist in archaeological contexts (Haslam, 2004; Torrence and Barton, 2006; Hardy et al., 2009). Starch is a biodegradable molecule and it should rapidly degrade after burial (Hardy et al., 2009; Langejans, 2010; Henry, 2014). Starch does seem to survive in certain situations, as unambiguous ancient starch is found in archaeological contexts (Samuel, 1996). The survival of ancient starch presumably reflects protective qualities of its semi-crystalline polysaccharide structure and

specific microenvironment conditions that isolate starches from taphonomic processes (Hardy et al., 2009; Salazar-García et al., 2013; Henry et al., 2014). However, phytoliths are far more robust than are starches and routinely survive in most sediment types, yet they may dissolve when exposed to a high pH. It is poorly understood how the alkaline environment (pH ≤ 9) of dental calculus affects phytoliths (Kleinberg, 1970). Other botanical microremains that are useful for archaeobotanists have similar problems. Calcium oxalate crystals (calcium phytoliths) are a category of microremains found in energy-rich plants. Problematically, calcium oxalate crystals are susceptible to dissolution even in mild acids. The acidity of saliva may readily drop low enough to dissolve calcium oxalate present in the mouth (Tromp, 2012). The other types of microremains that may be present in dental calculus such as pollen, may well be subject to comparable problems.

Dental calculus could offer these microremains a secure mineralised matrix where they become embedded and entirely isolated from soil chemistry and microbial action (Warinner et al., 2014). Of course, to even reach this point, starches that have entered the mouth must first survive breakdown in the oral cavity. The mouth is a hostile environment for exposed starch grains because of the action of salivary digestive enzymes and bacterial metabolic activity that will rapidly attack and digest starches (Lukacs and Largaespada, 2006). Most digestion of starch occurs at a later point in the digestive system due to the effects of pancreatic amylase, but the high amounts of salivary amylase found in most human groups may still have an impact. We may only speculate that some starch avoids oral enzymatic digestion and is stochastically forced into protected niche areas of calculus. Alternatively, it could be explained in a slower model, where starch (resistant starch, higher in amylose content than typical starches) evades digestion and is gradually precipitated into dental calculus (Hardy et al., 2009).

There has been little attempt to examine mechanisms that may be involved. Regrettably, the conventional methodologies in dental calculus analysis rely on invasive sampling of calculus from the tooth, making this harder to study. They involve mechanically or chemically removing dental calculus from the enamel surface, grinding or dissolving it to break up the sample, and finally examining the particles using optical light microscopy (Henry and Piperno, 2008). Due to this extraction, microremains observed by the analyst are no longer in context in calculus. This is unfortunate, because the microenvironments that seem to preserve microremains in dental calculus may shed light on whether microremains are not lab

contamination, the mechanisms of microremain preservation, and if they are damaged in extraction. Due to this, Weyrich and colleagues have questioned reproducibility and accuracy of dental calculus studies using microremains, pointed to sedimentary contamination as undermining these studies (Weyrich et al., 2015).

2.6.3 The representativeness of the dental calculus dietary record

Perhaps the most serious problem in dental calculus dietary studies is the ambiguity of what can be inferred about diet from the plant microremain record found in dental calculus. Researchers can say surprisingly little about how representative this record is, despite the plethora of studies using dental calculus as a source of dietary information. Little research has attempted to quantitatively cross-validate the dietary material recovered in dental calculus with the organism's actual feeding ecology and life history. Detailed studies using controlled diets have not been pursued and there are few published studies using faunal dental calculus where diet may be reliably predicted (Armitage, 1975) . Many past studies have assumed that the plant matter preserved in dental calculus representatively reflects a long-term dietary average (Mickleburgh and Pagán-Jiménez, 2012). Yet we should question this assertion for many good reasons. Plant remains trapped in dental calculus could plausibly be derived from airborne particles, water, chewing of plant matter for health or fibre processing, amongst other possibilities. This raises the prospect that microremains found in dental calculus from the studied Neanderthal samples may not in fact reflect plant consumption at all.

Knowledge of the timing of the formation of the calculus dietary signal would greatly assist life-history based approaches. Dental calculus does not form and accumulate in a continuous and predicable way (Lieverse, 1999). Soft dental plaque can make the transformation into hard mineralised calculus over the course of weeks, but mineralization may be episodic and the rate it occurs varies among individuals according to age, oral hygiene, nutrient intake (Bergström, 1999; Lieverse, 1999; Jin and Yip, 2002) and possibly also genetic predisposition among other things. In addition to these complications, dental calculus deposits can become dislodged from the enamel at any point during life, resetting the dental calculus dietary record along with it.

Leonard and colleagues examined dietary representativeness using living Namibian Twe forager-horticulturists (2015). The Twe retain a partially traditional

diet in a mountainous arid habitat. Twe grow maize (*Zea mays*), pearl millet (*Pennisetum glaucum*), squash (*Cucurbita* sp.), melons (Cucurbitaceae spp.) and sugarcane (*Saccharum* sp.). Although they still collect a variety of wild plant foods, since 2006 an increasing proportion of their diet is from government-supplied maize meal. Leonard and colleagues established dietary patterns through interviewing and observing food choice during in short-term camp stays. Leonard and colleagues noted that older individuals and males had larger dental calculus deposits than young people (under 35 years old) and females, a potentially confounding affect. The number of microremains per individual poorly predicted the range of starch and phytolith producing plants consumed. Nineteen Twe vegetal foods contained starch and phytoliths, but no calculus sample contained more than six plant food types. A population approach was more successful, but Leonard and colleagues stressed that in her population, a sample of 50 individuals or more is needed to have 95 % confidence of observing several foods. Overall, their analysis suggested that starch grains and phytoliths in Twe dental calculus gave an incomplete picture of diet and significantly underrepresented vegetal foods (Leonard et al., 2015). It is unclear if these results can be applied to prehistoric hominin populations. It is unknown how many copies of *AMY1* the Twe people have so we cannot assess if this influenced the results. Despite this study's valuable contribution, this study lacked insight into the long-term dietary history of the studied individuals.

2.6.4 Outlining the findings for dental calculus research and Neanderthal diet

Sections 2.1 through 2.3.2 provide details why reconstructing diet is an essential part of studying both human origins and the life history of Neanderthals. A behavioural ecology framework is a very powerful means for achieving this task. By using diverse array of approaches, I have demonstrated what can be extrapolated from current evidence about the Neanderthal diets. I have assessed the crucial issues that must be resolved to move forward to a more complete palaeobiology of these hominins. This dissertation is based on using plant consumption to test how adaptable Neanderthal diets were. Dental calculus analysis was selected to provide a window on the plant use of Neanderthals. The unanswered questions highlighted by this introductory section form the basis of this PhD, which includes three main parts: are part of this PhD; a revision of how we obtain dietary data from dental calculus, a re-evaluation of the resolution of the dental calculus dietary record and a new measure of plant foods and dietary breadth for Neanderthal diets.

The first paper highlights the problems of conventional dental calculus research. It examines dental calculus from wild chimpanzees and archaeological specimens first with scanning electron microscopy–energy-dispersive X-ray spectroscopy, and then with conventional optical light microscopy to compare techniques. This allowed for the first time investigation of the microenvironment that traps starch and other microremains. Lastly, it developed a sequential workflow that maximises the amount of life history information extractable from dental calculus. The second paper focuses on associating debris of plants inside dental calculus to diet and behaviour. It aims to address the troubling gap between plants in dental calculus and dietary records by using calculus of chimpanzees with documented diets. Samples of chimpanzee dental calculus (Taï National Park, Côte d'Ivoire) showed that microremains accumulate as long-lived dietary markers. The paper found that phytoliths allow feeding preferences of the chimpanzees to be reconstructed, while starches do not. Microremains also implied that assemblages could record population information about other dietary behaviours, such as the age of weaning and learned food processing techniques like nut cracking. Finally, the third paper uses dental calculus from Neanderthal remains to provide new light on plant exploitation from a mix of environments. Dental calculus was analysed from five archaeological sites: Vindija (Croatia), Grotta Guattari (Italy), Grotta Fossellone (Italy), Sima de las Palomas del Cabezo Gordo (Spain) and Kalamakia (Greece). These sites represent a variety of regions and biomes across Europe. Starch, phytoliths and other microremains suggested Neanderthals used a wide variety of plants including low ranked plant foods. The findings were then combined with data from past studies to model if local vegetation, winter temperature or the age of the site account for variation in diet. The model found local vegetation and winter temperatures do not influence the patterns in the dental calculus data suggesting that although Neanderthal consumed they have had an inflexible but partially broad dietary adaptation.

3

Assessing use and suitability of scanning electron microscopy in the analysis of microremains in dental calculus

Robert C. Power,[1] Domingo C. Salazar-García,[1,2] Roman M. Wittig,[3] Amanda G. Henry[1]

[1]Max Planck Research Group on Plant Foods in Hominin Dietary Ecology, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103 Leipzig, Germany.
[2]Department of Human Evolution, Max-Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, Leipzig, Germany.
[3]Department of Primatology, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, Leipzig, Germany.

Published in the *Journal of Archaeological Science* (2014, Volume 49, 160-169).

Abstract

Dental calculus is increasingly recognised as a major reservoir of dietary information. Palaeodietary studies using plant and animal microremains (e.g. phytoliths, pollen, sponge spicules, and starch grains) trapped in calculus have the potential to revise our knowledge of the dietary role of plants in past populations. The conventional methods used to isolate and identify these microremains rely on removing them from their microenvironment in the calculus, thus the microenvironment that traps and preserves microremains is not understood. By using scanning electron microscopy and energy-dispersive X-ray spectroscopy (SEM-EDX) on modern chimpanzee calculus from the Taï Forest, Côte d'Ivoire, and human calculus from the Chalcolithic site of Camino del Molino, Spain, we present the first reported observations on characteristics of the matrix setting that are conducive to the survival of starch in dental calculus. We also assess the potential for SEM-EDX to detect starch and differentiate it from structurally and molecularly similar substrates. We demonstrate that SEM-EDX may offer a non-destructive technique for studying microremains in certain contexts. Finally, we compare traditional optical analytical techniques (OM) with less invasive electron microscopy. The results indicate that SEM-EDX and OM are both effective for

observing microremains in calculus, but differ in their analytical resolution to identify different microremains, and we therefore recommend a sequential use of both techniques.

3.1 Introduction

Dental calculus, or dental plaque calcified by salivary calcium phosphate, was first noticed as a reservoir of dietary information when Armitage (1975) recognised plant remains on the teeth of archaeological ungulates. Dobney and Brothwell (1986, 1988) later demonstrated the value of calculus in the study of human diets. Analysis of plant and animal microremains in archaeological dental calculus is a rapidly growing field in dietary reconstruction (e.g. Boyadjian et al., 2007; Henry et al., 2012; Liu, 2012; Mickleburgh and Pagán-Jiménez, 2012; Warinner et al., 2014). Researchers have reported starch, phytoliths, pollen, diatoms, chrysophycean cysts, sponge spicules, and mineral particles in human calculus up to tens of thousands of years old (e.g. Dobney and Brothwell, 1988; Boyadjian, 2012).

Despite this interest in dental calculus as a source of dietary information, there are still many questions about the mechanisms by which plant microremains, particularly starch grains, are preserved within the calculus. Native starch grains (i.e. starches in their original, unaltered state) are the major focus of many recent and ancient dietary studies. Starch is a foremost nutritional component in many human and non-human primate diets, and it can also survive in the archaeological record over long periods of time due to its semi-crystalline polysaccharide structure (Mercader et al., 2008; Hardy et al., 2009; Henry et al., 2011; Salazar-García et al., 2013; Leonard et al., 2015). The means by which starch embeds and preserves in calculus is still unclear. The mouth is a hostile environment for starch preservation because of the action of salivary digestive enzymes and bacterial metabolic activity (Lukacs and Largaespada, 2006). Calculus forms gradually as bacteria-rich plaque biofilms mineralise from calcium phosphate in the saliva over a period of days to years (Abraham et al., 2005). During this formation and mineralization process, the starch grains are exposed to α-amylase, which is present in the saliva of humans and several orders of mammals (Butterworth et al., 2011). Amylase quickly digests starch by breaking down the polysaccharide crystalline structure into various simple and complex sugars through hydrolysis (Lukacs and Largaespada, 2006). Theoretically,

starch may avoid oral digestion and survive in protected niche areas in calculus, but this has not yet been empirically confirmed.

In addition to the difficulties with starch preservation in the oral cavity, there is also the possibility that the starches that have been recovered from calculus are actually the result of modern contamination. Modern starches are abundant in the air, water, and working surfaces of most facilities, making environmental contamination a strong possibility. Archaeological and field site contexts suffer from sources of contamination such as airborne starch rain, but the greatest risk of contamination comes from excavation and post-excavation handling in the presence of food or due to the use of gloves powdered with corn or other starches (Newsom and Shaw, 1997; Loy and Barton, 2006; Laurence et al., 2011).

Currently, the standard methodology for starch grain recovery from calculus is too destructive to confirm whether observed starch came from the calculus or from contamination. This method involves mechanically or chemically removing calculus from the tooth, grinding or dissolution to break up the sample, and finally examining the particles using optical light microscopy (OM) (Henry and Piperno, 2008). Furthermore, to the untrained eye, several other calculus components, such as cysts, mineral grains, fungal spores, wood cells, and air bubbles may be confused with starch grains when viewed only under OM. Some have proposed confirming starch presence by measuring amylase activity on treated samples (Hardy et al., 2009), but this enzyme destroys the starch in the process. One common and reliable means to detect starch is to apply iodine potassium iodide (IKI) solution, which binds to the amylose molecule, and look for the characteristic blue-black stain. However, this temporarily obscures the starch's diagnostic surface features. Furthermore, it is impractical to apply a staining solution to an intact calculus matrix because objects within the mineralised matrix are protected from moisture. Accordingly, there is a great need for more sophisticated and non-destructive methods to confirm the successful detection of starch grains in dental calculus. Some researchers have suggested the possibility of using scanning electron microscopy (SEM) to study plant microremains in calculus (Dobney and Brothwell, 1986; Reinhard et al., 2001; Tromp, 2012). Despite the success of this method in locating phytoliths (Arensburg, 1996; Lalueza-Fox et al., 1996; Charlier et al., 2010; Kucera et al., 2011; Tromp, 2012; Tao et al., 2015), the detection of starch grains through SEM has not yet been attempted.

In this study, we present SEM coupled with energy-dispersive X-ray spectroscopy (EDX) as a novel means for identifying starch and other microremains in intact human and chimpanzee dental calculus. This system provides us with the ability to identify microremains, including starch grains, by their morphology and elemental composition *in situ* in the calculus, thus ruling out contamination. It also allows us to explore the kinds of environments within the calculus that may permit starch preservation. Furthermore, we examine the potential of EDX to detect starch by comparing the elemental makeup of native starch to those of saliva-hydrolysed starch and other non-starch saccharides to learn whether EDX distinguishes starch from other polymers of similar elemental makeup. This identification allows us to positively show that starch grains survive in calculus. Finally, we compare the results from SEM-EDX to those from OM on the same human calculus samples to determine whether these techniques offer comparable or complementary results. Due to time constraints, we were unable to conduct this portion of the analysis on the chimpanzee samples and instead only used human dental calculus samples.

3.2. Materials and methods

3.2.1 Study groups

The calculus samples were obtained from two groups, modern wild chimpanzees from the Taï Forest in Côte d'Ivoire and humans from the Chalcolithic collective burial of Camino del Molino in Spain (Table 4). We chose these two test groups for the following reasons: 1) individuals from both have abundant calculus on their teeth; 2) they represent modern (chimpanzee) and archaeological (Chalcolithic humans) timeframes; and 3) both groups maintained very different dietary strategies and should therefore have different microremain profiles.

The sample of chimpanzee calculus came from the Taï Chimpanzee Osteology Collection curated at the Max Planck Institute for Evolutionary Anthropology (MPI-EVA) in Leipzig, Germany. The behaviour of the wild chimpanzees living in the Taï Forest has been monitored and documented since the commencement of the Taï Chimpanzee Project in 1979 (Boesch and Boesch-Achermann, 2000). Taï Forest data collection complied with the requirements and guidelines of the Ministère de l'Enseignement Supérieure et de la Recherche Scientifique, and adhered to the legal requirements of Côte d'Ivoire. The osteology collection contains 77 chimpanzees. We chose calculus samples from individuals who had comprehensive observational

records documenting diet, sex and age. After their death, the remains of these individuals were interred for defleshing, later exhumed, and curated. We collected calculus from molars or canines of six individuals; two females and four males. The Taï Chimpanzees consume native starch from wild nuts and seeds such as the Gabon nut (*Coula edulis* Baill.) and Kola nut (*Cola nitida* (Vent) Schott et Endl.) (Hohmann et al., 2010; N'guessan, 2012), and unlike humans, they consume no cooked or processed foods. Our preliminary reference collection of Taï Forest chimpanzee foods shows that ten of the 82 foods we analysed are starch-rich. However, these 82 species represent less than a third of plants this population is known to consume, and we are still building this reference collection. Chimpanzees also produce salivary amylase, though purported at much lower quantities than do humans (Perry et al., 2007; Behringer et al., 2013).

Camino del Molino is a Chalcolithic collective burial pit found during construction work in the city of Caravaca de la Cruz (Murcia, southeast Spain). Radiocarbon dates from bone collagen samples spanning the burial sequence indicate that the site was in continual use over a span of 300- 400 years during the first half of the third millennium B.C. The site contained a minimum of 1,300 individuals, likely the remains of 16-20 generations of one population buried at one place (Lomba Maurandi et al., 2009). Approximately 30 % of the individuals are classified as juvenile (<14 yrs.), and the rest are adults spanning from young to old (Haber Uriarte et al., 2013). We collected dental calculus preferably from lower molars for standardisation from the teeth of six individuals; two females, two males, and two individual of unknown sex (Table 4). There are no archaeobotanical studies from Camino del Molino or from the broader region of Murcia contemporary to the site. However, studies of Late Neolithic and Chalcolithic deposits in neighbouring regions suggest that the number of cultivated species is low and consists mainly of naked wheat (*Triticum* sp.), barley (*Hordeum vulgare* L.), some lentil (*Lens culinaris* Medikus*)* and common vetch (*Vicia sativa* L.) (Pérez Jordà, 2005; Pérez Jordà and Carrión Marco, 2011). There is no published study from the site on culinary practices, in part because it is a necropolis and not a habitation site. Despite this, its Chalcolithic age indicates that this population consumed cooked food, because cooking is widespread across the European Neolithic and Bronze Age societies (Thissen et al., 2010; Halstead, 2012).

Table 4: Calculus samples analysed using SEM-EDX and OM. Sex and age classification of the Camino del Molino remains are preliminary (Haber Uriarte et al., 2013).

Lab identifier	Individual number	Type	Tooth	Sex	Age (years)	Weight
SJ-13-32	Sujeto 6	Camino del Molino	P1 mandible	F	26-28	1.76 mg
SJ-13-33	Sujeto 8	Camino del Molino	C maxilla	M	22-24	0.51 mg
SJ-13-36	Sujeto 11	Camino del Molino	I2 mandible	?	?	6.06 mg
SJ-13-37	Sujeto 17	Camino del Molino	M2 mandible	M?	43-55	10.0 mg
SJ-13-38	Sujeto 113	Camino del Molino	M2 mandible	F	24-28	1.88 mg
SJ-13-39	Sujeto 151	Camino del Molino	C mandible	M	30-35	1.09 mg
Venus	15001	Taï Chimpanzee	M3 maxilla	F	27	0.72 mg
Leo	15012	Taï Chimpanzee	M3 mandible	M	19	1.19 mg
Fanny	11780	Taï Chimpanzee	M3 mandible	F	25	3.34 mg
Goma	15004	Taï Chimpanzee	M3 mandible	F	28	2.40 mg
Rubra	15023	Taï Chimpanzee	M3 mandible	F	38?	3.88 mg
Castor	13439	Taï Chimpanzee	M3 mandible	F	22	2.25 mg

3.2.2 Calculus sampling

We selected teeth encrusted with a prominent band of calculus present on the enamel surface. We sampled only supragingival calculus (above the gum line), since it is unclear if subgingival calculus (below the gum line, on the neck of the tooth) preserves food remains. We photographed the calculus before sampling, and then brushed the sample tooth gently with a dry, sterile toothbrush to remove surface contaminants. We then used a dental scalar to remove small areas of supragingival calculus (~4 mm area), from the enamel. We conducted all calculus sampling in a positive pressure hood at the archaeological science laboratories at the MPI-EVA. We then weighed each of the samples and transferred them to microcentrifuge tubes for storage until further use. Following sampling, the teeth and surviving calculus were photographed again. Additionally, we collected control samples, including the packing material in which the teeth had been stored.

3.2.3 Electron microscopy analysis

We conducted the SEM-EDX analysis at University College Dublin's Nano-Imaging and Materials Analysis Centre (NIMAC) in Dublin, Ireland. The calculus samples were mounted on stubs using double-sided carbon tape, and sputter coated with gold for 20 seconds using an Emitech K575X Sputter Coating Unit, to prevent surface charging by the electron beam. We then examined the calculus using a FEI Quanta 3D FEG DualBeam (FEI Ltd, Hillsboro, USA) SEM with an attached EDAX ED APOLLO XV Silicon Drift Detector with a 5 – 10 kV accelerating voltage. EDX

detected and documented most elements of interest excluding hydrogen, which is non-detectable with this method. We omitted the gold elemental peak from each spectrum since the gold was added during sputter coating. We photographed and documented every tentative microremain and later described our observations.

3.2.4 Carbohydrate reference standards and partially hydrolysed controls

We used a variety of reference standards (see Table 5) to assess the accuracy of EDX reads on the experimental sample types of starch. Starches from a variety of plants were selected to represent major starch types such as corn starch, potato starch, and common dietary components for each population (Boesch and Boesch 1983): wheat (*Triticum aestivum* L.), Gabon nut (*Coula edulis* Baill.), Xylia (*Xylia evansii* Hutch.) and Kola nut (*Cola nitida* [Vent] Schott et Endl.). The nuts were ground, dried and weighed to derive nut flour suitable for use. Wheat, potato and corn were purchased from local distributers in Germany (see Table 5).

Table 5: List of reference samples analysed using EDX.

Reference sample	Part	Type	Source
Fructose	N/A	Lab-grade	Roth - 4981.1
Sucrose	N/A	Lab-grade	Roth - 4621.1
Maltose	N/A	Lab-grade	Roth - 8951.1
Glucose	N/A	Lab-grade	Sigma - G7528
Maize (*Zea mays* subsp. *Mays* L.)	Grain	Cornstarch	Speisestärke, RUF Lebensmittelwerk
Kola nut (*Cola nitida* (Vent) Schott et Endl.)	Nut	Bulk plant	Collected in Taï National Park
Xylia (*Xylia evansii* Hutch.)	Nut	Bulk plant	Collected in Taï National Park
Gabon nut (*Coula edulis* Baill.)	Nut	Bulk plant	Collected in Taï National Park
Potato (*Solanum tuberosum* L.)	Tuber	Flour	Kartoffelmehl, RUF Lebensmittelwerk KG
Wheat (*Triticum aestivum* L.)	Grain	wheatstarch	Weizella, Hermann Kröner GmbH

Laboratory-grade fructose, maltose, glucose and sucrose (Roth, Germany) were included as standards because they have nearly identical elemental compositions as starch but with structurally different molecular arrangements (e.g. sucrose has 2.1 wt % (mass fraction) more carbon than fructose, but 2.1 wt % less than starch).

To compare EDX element signatures for the different types of saccharides, we took EDX measurements from five individual grains of fructose, sucrose, maltose, glucose and wheat starch, corn starch, Kola nut starch, Xylia starch and potato starch. This allows the comparison of a monosaccharide, a disaccharide, and a polysaccharide (starch).

Finally, to assess whether EDX signatures and detection accuracy is affected by the salivary modification (hydrolysis) of starch, we experimentally hydrolysed the native starches from the wheat flour and both nut varieties using salivary amylase derived from human saliva – a simulation of the effects of oral digestion on starch that can occur. One of us (R.C.P.) provided the saliva used in all experiments, which was collected on a single occasion. We split each of the individual plant samples into nine subsamples of approximately 2 mg each: three subsample per plant remained untreated (control), three were exposed to amylase (35 μL of saliva) for 30 minutes, and three were exposed to amylase (35 μL of saliva) for 90 minutes. We also similarly partitioned the wheat flour into nine aliquots into three subsamples of 2 mg each for identical amylase treatment. We ceased hydrolysis by displacing the saliva with alcohol and centrifugation at 1691 x g to remove as much liquid from the sample as possible and stop hydrolysis. Then the remaining alcohol was evaporated at 35 º C in a drying oven. We performed measurements using SEM-EDX in triplicate on one starch grain from each subsample, creating nine readings per category (e.g. wheat 30 minute hydrolysed). A summary of these analyses is provided in Figs. 3 and 4.

3.2.5 Optical microscopy analysis

We performed optical microscopy on the ancient human remains at the Plants Working Group Laboratory in the MPI-EVA, Leipzig. We removed the gold plated calculus samples from the SEM mounting stubs, and then ground them in a 1.5 ml Eppendorf microcentrifuge tube with a micro pestle containing ~50 μl of a 25 % glycerine solution to reduce sample loss due to static electricity. Glycerine was chosen as its refractive index is lower than starch making it suitable for starch detection. The samples were then centrifuged at 1691 x g (Heraeus MEGAFUGE 16 with TX-400 Swinging Bucket Rotors) for 10 minutes. All of the resulting pellets were mounted on glass slides and examined under bright field and cross-polarised light on an A1 Zeiss Axioscope microscope at 400 × magnification. Larger samples were mounted on several slides. Each microremain was photographed and described (Table 6).

3.3. Results

3.3.1 Standards

The EDX spectrum of starch is distinct from other saccharides but not sufficiently to permit reliable identification (Fig. 3, Fig. 4; Appendix table 1, Appendix table 2). The EDX results from all the samples indicate that oxygen is underrepresented. Though carbon comprises roughly 40-50 wt % of these saccharides, the EDX spectra indicates carbon at 60-90 wt % (Fig. 3). Comparing the short-chain saccharides to the starches there is a difference but some types of starch overlaps with each short-chain saccharides. This indicates that some starch may be distinguishable from short-chain saccharides through EDX. There was far more variability in carbon values in starch than in short-chain saccharides. Starch is composed of oxygen, hydrogen and carbon $(C_6H_{10}O_5)_n$, where n ranges from 300 to 1000, so starch is approximately 42.1 %=carbon, 6.5 %=hydrogen, 51.4 %=oxygen (Newman et al., 1996). Thus, maize starch comes closest to the expected values of starch. This variability possibly reflects the heterogeneous nature of the starch. Starch varies in both proportion of amylose and amylopectin and minor compounds such as proteins and lipids (Belitz et al., 2009). We see further evidence of this elemental variability in the native starch samples in Fig. 4, which had a higher variability of both carbon and oxygen than the hydrolysed starches. The EDX profiles of hydrolysed starches fall within the range of their native counterparts, yet they show noticeable less variation and reduced oxygen values (Fig. 4). The reduction in variation and lower oxygen levels in these samples may be either from the result of the added ethanol reducing oxygen in the starch or the ethanol washed off debris on the starch surface. A few of the damaged starches have slightly increased oxygen percentages, but this is not consistent across all hydrolysed subsamples. We found no evidence that saliva-activated hydrolysis could obscure the starch EDX elemental signature. However, when large starch shaped objects are present under SEM, it is possible to test whether these particles have a molecular make-up that is similar to starch and other saccharides.

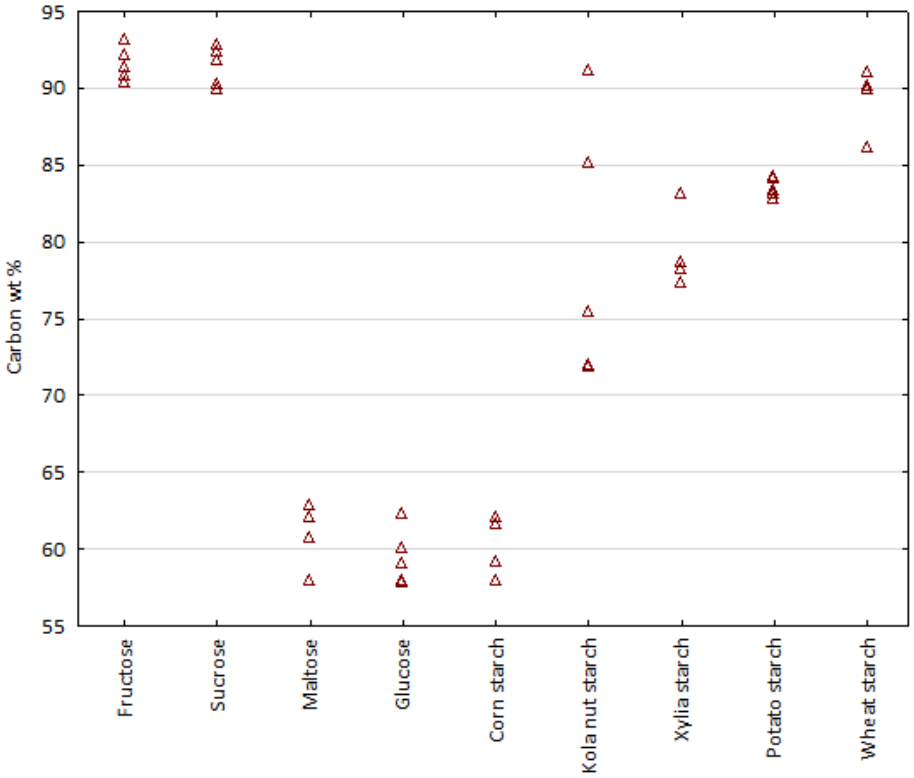


Fig. 3: Carbon wt % (mass fraction) of starch, sugars produced by hydrolysis and reference sugars. Plot shows five individual grains of starches, glucose, and maltose and out-group carbohydrates (fructose and sucrose) detected with EDX. Values exclude contaminating elements such as potassium from sweat (3.6.1).

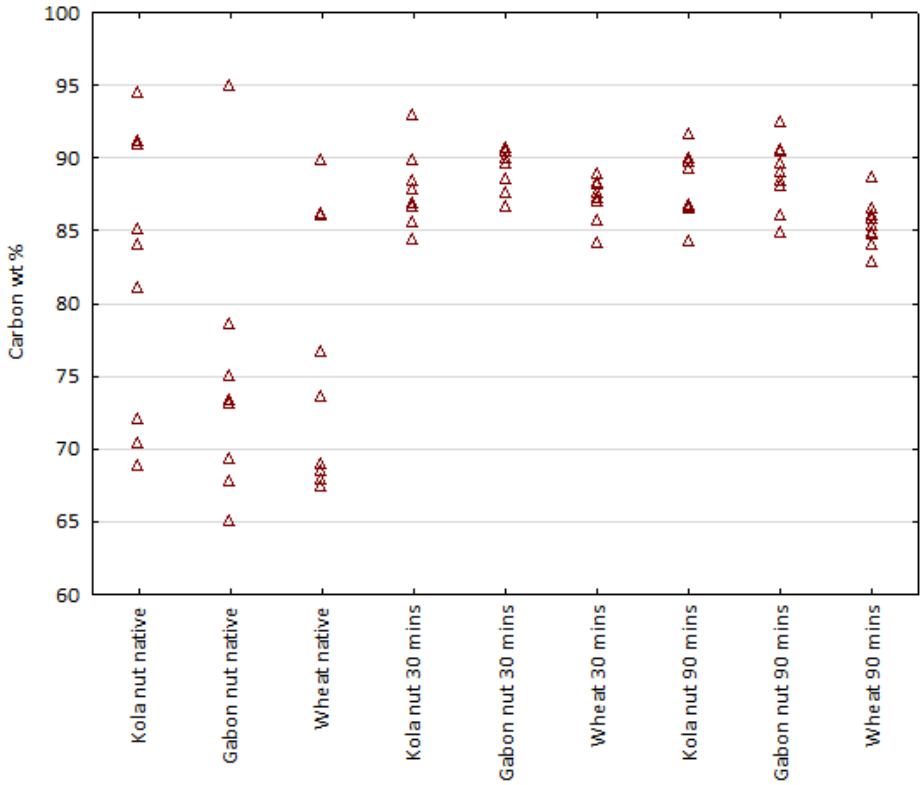


Fig. 4: Comparing native starch versus samples that were hydrolysed with amylase for 30 and 90 minutes at room temperature. Three starches were sampled with triplicate readings. Values exclude contaminating elements such as potassium such as potassium from sweat (3.6.2).

3.3.2 Calculus samples

Examination of the SEM images of the calculus confirmed that this matrix has a heterogeneous texture, with smooth surfaces as well as many pores, crack and crevices (Fig. 5, Fig. 6). Most of the pores appear to be the result of rod bacterial pseudomorphs, which are shallow and measure only between 0.3 -1 μm in width (bottom left in Fig. 5, and widely scattered in Fig. 6). These pores are too small to preserve microremains, but larger cracks and crevices had many microremains (Fig. 6). Further examination of the calculus revealed several types of inclusions within the matrix. In some cases, these inclusions were consistent with the overall size (15-40 μm) and shape (ovoid- pyriform) of certain starch grain types, and inconsistent with other microremains such as yeast and bacterial cells (Fig. 5). The supposed starch clusters were clearly embedded in the matrix, with grains occluded by overlying deposits of the matrix material. Interestingly, the starch grains were not evenly distributed in the matrix, and often appeared in clumps (Fig. 5). This could be explained in two ways; i) plant microremains are deposited in groups originating from clumps in food lumps, or ii) microremains are only preserved in localised niches, such as larger cracks and crevices, in the calculus matrix.

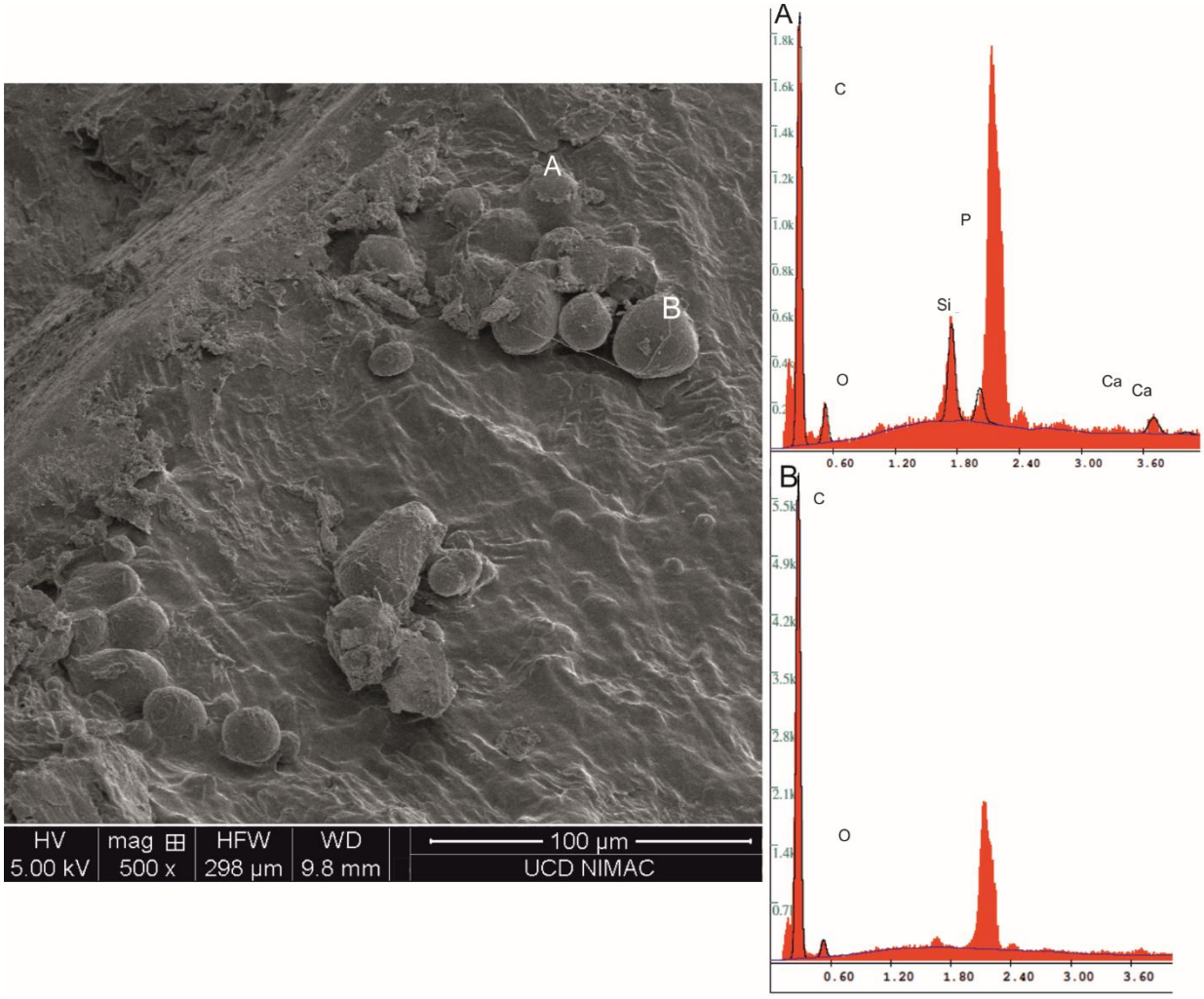


Fig. 5: Starch grains located *in-situ* on dental calculus surface. SEM image showing a group of starches trapped in the matrix of one of the chimpanzee dental calculus samples (Venus), with the corresponding EDX spectrum (right) showing a calcium phosphate and silicon mantle covering a carbon rich starch (A) and solely a carbon-rich starch (B).

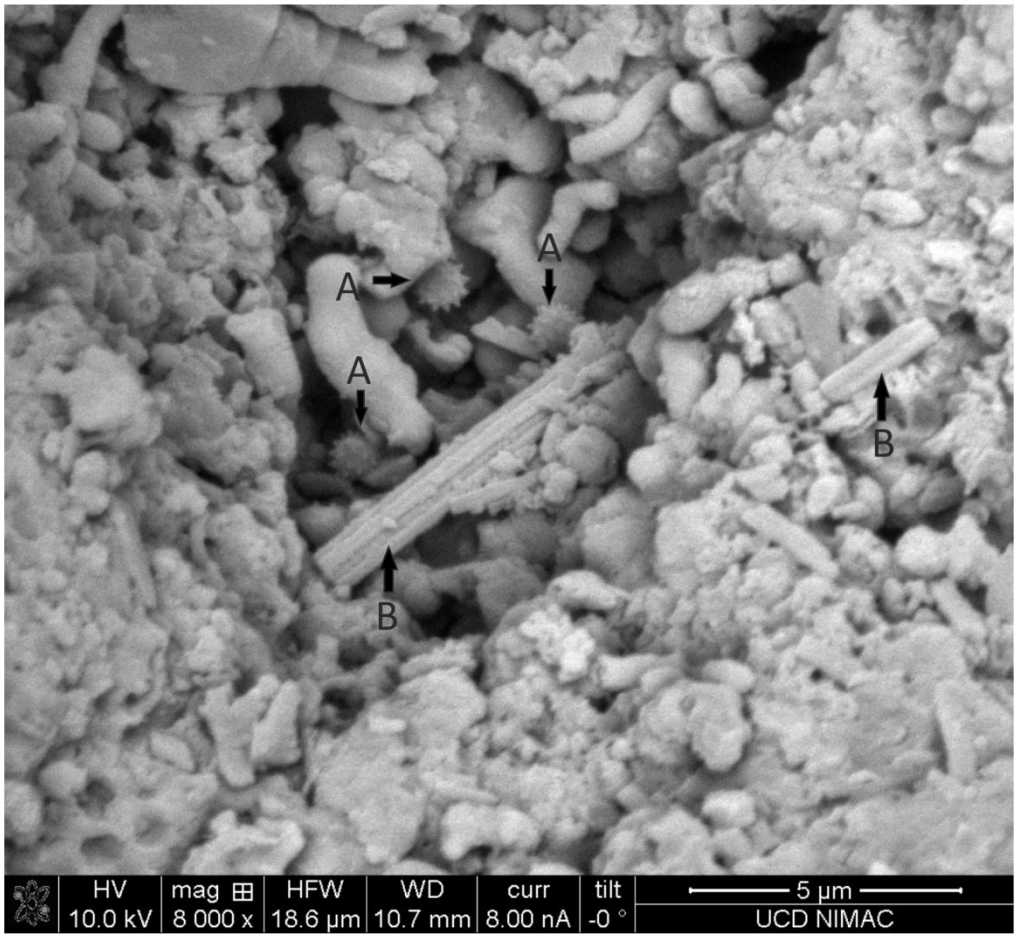


Fig. 6: SEM image showing microremain diversity. A concentration of pollen (A) and sponge spicules (B) in SJ-13-39 from Camino del Molino. Microremains were often found clustered.

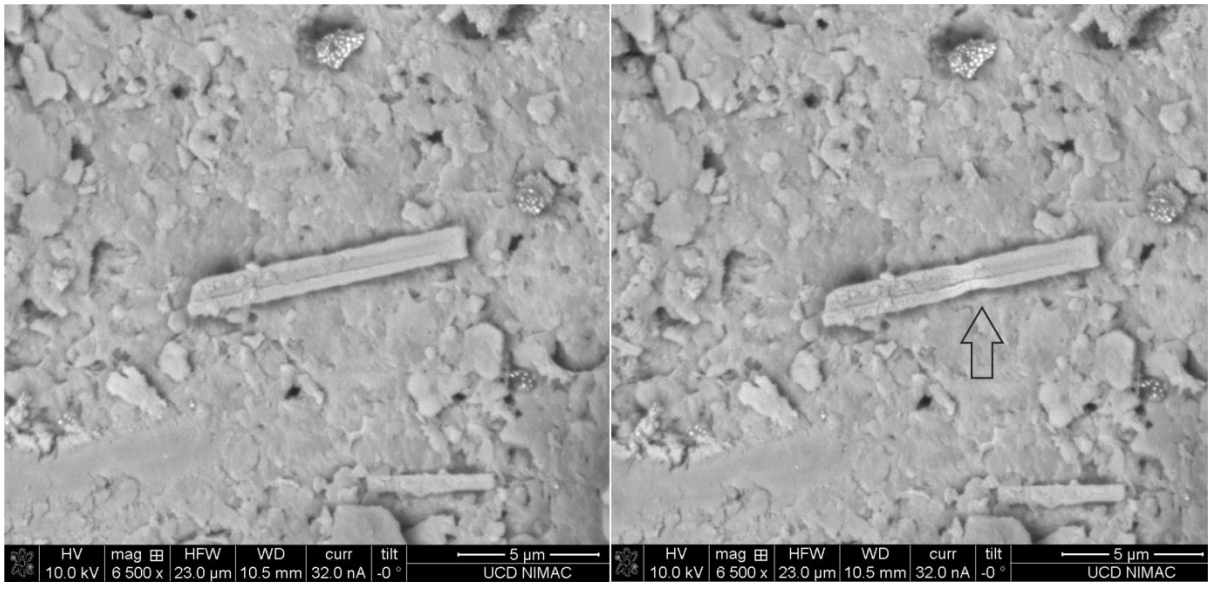


Fig. 7: SEM image showing localised damage that arises from higher primary voltage SEM (10 kV) and EDX on a spicule in calculus from Camino del Molino. Before (left); after (right).

The EDX spectra of the calculus matrix from all of our samples indicate that it is mostly composed of calcium and phosphorus, with trace amounts of aluminium, magnesium, silicon, sodium and manganese (Appendix table 3). These elements confirm our supposition that the majority of our samples consist of calculus, a mixture of hydroxyapatite and other minerals, rather than contaminating exogenous matter (Charlier et al., 2010; Salazar-García et al., 2014). In some instances, silicon was locally abundant in the calculus (Appendix table 3), which may be important for the preservation of starch grains. In contrast to the mineral matrix, the suspected starch clusters, such as on chimpanzees Venus and Castor had significant carbon peaks. Additionally, the starches often had calcium and phosphorus peaks, reinforcing visual observations that they were indeed embedded in calculus (Fig. 5). The combination of shape and elemental data (Fig. 5) is strongly suggestive of *in-situ* findings of microremains preserved in the dental calculus environment. This is possible as starch is morphologically distinct from other carbon rich particles such as fungal filaments, *Candida albicans* cells, cellulose and sugars. We also note that the starch we located with SEM-EDX was undamaged and we did not locate any semi gelatinised or hydrolysed starch. These were also not observed with optical microscopy but it is possible damaged starch was not visible with this approach.

In addition to the starches, we also identified a variety of other plant and animal microremains preserved in the calculus using SEM-EDX, including phytoliths, sponge spicules, diatoms and pollen (Table 6). These microremains were identified by their diagnostic morphology using conventional methods (Torrence and Barton, 2006; Nadel et al., 2013; Power et al., 2014a), and this identification was confirmed by their EDX spectra. For example, spicules were easily identified based on their long rectangular shape and high level of regularity (Fig. 6 and Fig. 7) unlike smooth long-cell phytoliths, and EDX readings confirmed their biogenic silica composition (7.1). OM also demonstrated the presence of a rich assemblage of plant microremains (Table 5). We noted some of these microremains during the SEM analysis, such as the abundant monaxon spicules (Fig. 6), but we only detected some, such as multi-cell long-cell phytoliths, unsilicified plant cells and calcium oxalate (Fig. 8), with OM.

Table 6: Recovered microremains using both microscopy approaches.

		Scanning electron microscopy												Optical microscopy					
		Taï chimpanzees						Camino del Molino						Camino del Molino					
		Venus	Leo	Fanny	Gema	Rubra	Castor	SJ-13-32	SJ-13-33	SJ-13-36	SJ-13-37	SJ-13-38	SJ-13-39	SJ-13-32	SJ-13-33	SJ-13-36	SJ-13-37	SJ-13-38	SJ-13-39
Starch		29	2	3	4	40	22	3		1		1	6	1		8	10	1	3
Phytoliths	Single-cell long-cell			1				1		1	1	2		3		5	10	1	3
	Multi-cellular Long-cell													1			11	1	
	Short-cell			1										3	1		2		3
	Parallelepipedal							1		1				1		1	6	1	
	Bulliform													1			2		
	Plate							1		1								1	
	Rugulose Spheroid		2			1													
	Smooth spheroid							3		2			1					1	1
	Hair										2	1			1	1		1	
	Unidentified							1			1		3	2					3
Unsilicified plant cell																	15		
Prism calcium oxalate																5	8		2
Annular ring															2				
Monaxon spicule								30	1	5	1	15	46	8	5	14	18	11	10
Quartz grain			1	2															
Pennate diatom						20													
Indet diatom				2														2	
Echinate pollen					1		1					1	3					3	
Other pollen										3		1	1	3	1	1	2		
Chrysophycean cyst				4															
Fungal filament			+	+															
Fibre		+						1											
Invertebrate		1																	
Other						2													

+ : a high but unquantified number

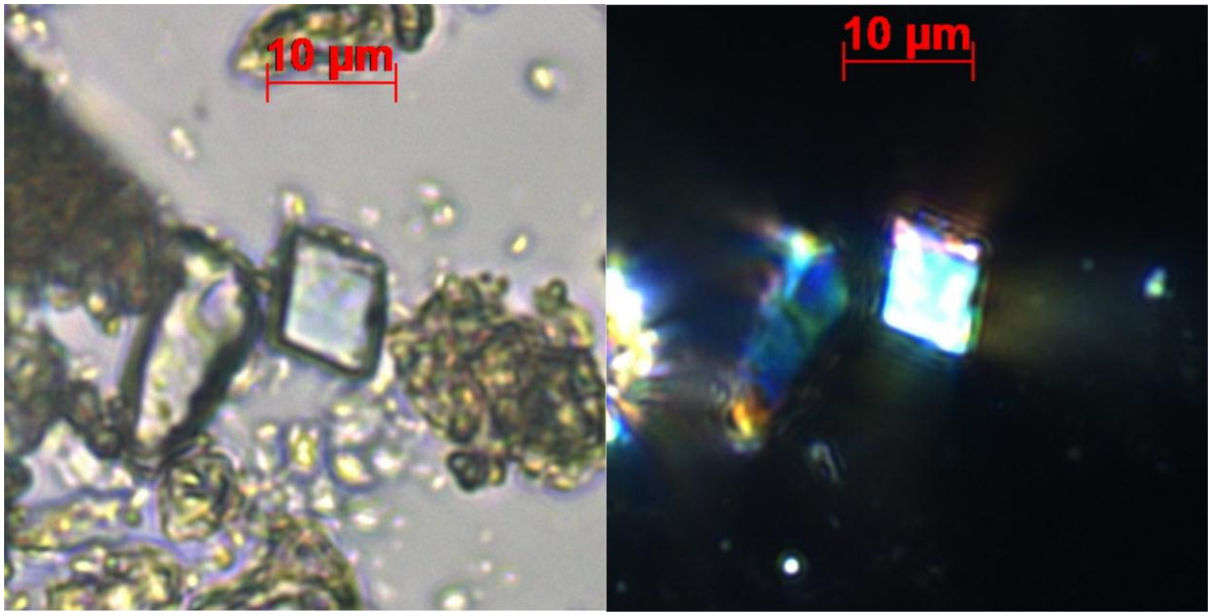


Fig. 8: A calcium oxalate prism observed with optical microscopy in SJ-13-37; under bright field optical microscopy (left), and cross-polarising optical microscopy (right).

A comparison of the microremains observed under SEM-EDX with those seen in OM revealed important differences (Table 6). We observed more starch microremains using OM than SEM-EDX. This is probably because the sample preparation for OM breaks down the calculus matrix, freeing starch microremains that were trapped in the middle of the calculus chunk. Yet paradoxically, other microremains, such as sponge spicules, were more commonly seen in SEM-EDX than in OM of the same samples.

Based solely on the SEM results (we did not perform OM on the chimpanzee samples), the two groups we studied did present some differences. The chimpanzee samples were rich in starch grains and diatoms, while the human samples had an abundance of unsilicified plant cells and sponge spicules (Table 6).

3.4. Discussion

Analysis of calculus samples by SEM-EDX and OM provides data that validates the study of microremains recovered from this biological material. By SEM-EDX, we were able to identify the elemental constituents of starch, and confirm its position *in situ* in calculus particles. This is the first time that starch has been identified by its elemental signature while still embedded within the calculus matrix,

and confirms that starch can be preserved in calculus, and can therefore be a useful source of dietary information.

The analysis suggests that certain features of the calculus may promote the preservation of microremains, and starch grains in particular. Food debris may trap around calculus rather than calculus growing around food debris. While the pores left from bacteria colonies were too small to provide a protected niche for starches, larger cracks and crevices were full of microremains, possibly because these areas provided a protected environment. Furthermore, the silicon we detected in the dental calculus may be significant. Silicic acid can induce spontaneous precipitation of calcium phosphate in the saliva, which is the precursor mineral necessary for calculus formation. Silicic acid may be consumed directly via water or indirectly via plants, as it enters plants along with groundwater. Consuming polysilicic acid and silica increases calculus formation, thereby regulating this process (Damen and Ten Cate, 1989; Roberts-Harry and Clerehugh, 2000; Jin and Yip, 2002). Our observations of silicon concentrations adjacent to embedded starch clusters (Fig. 5) corroborates these reports, suggesting that dietary exposure to silica or silicic acid enables enhanced calculus formation and thus the preservation of native starch in dental calculus.

By following the SEM analysis with an OM examination of the same samples, we are able to compare the effectiveness of each for specific microremain types. Sponge spicules were easily visualised under SEM, but were seen less with OM. This may be because the spicules are relatively fragile and are damaged when the calculus is processed, possibly explaining why spicules are rarely reported in dental calculus studies (Tromp, 2012; Dudgeon and Tromp, 2014). Because these particles, as well as diatoms and Chrysophycean cysts, are highly dependent upon water sources, they may indicate source type and provenance of consumed water, making them powerful potential ecological markers for primatology and archaeology studies (Dudgeon and Tromp, 2014). In contrast, calcium oxalate crystals were only visible under OM, and not SEM. These crystals, which may occur as druses, raphides or other similar forms, are a potentially useful marker of plants. They may be more visible using OM because they have high interference colours that are visible under cross polarised light (Fig. 8). For reasons that remain unclear, calcium oxalate is rarely reported or discussed in calculus literature. Some research indicates that calcium oxalate does not survive due to acidity in the mouth (Tromp, 2012), but given their sheer abundance in plants and the relatively neutral oral pH, it is likely that calcium oxalates do survive and are simply overlooked. On the other hand,

starch grains were clearly visible using both SEM and OM. However, we did note that within individuals, the starches that we observed under OM typically did not match the size and morphology of those seen in SEM-EDX. This contrasts with the spicules, which often matched size and shape. This is likely due to the small number of starches but high number of spicules. We also observed pollen grains embedded in the calculus using SEM (Fig. 6) and OM. Although this type of pollen grain were too small to analyse with the EDX, we do believe that SEM-EDX may be appropriate for identifying many larger types of pollen grains, since these plant remains are composed of potassium, magnesium, sodium and calcium (Szczęsna, 2007) and should be easily visible in the EDX spectra.

Finally, the SEM analysis accurately reflected some stark differences between our study groups. The differences in microremains number and types between the chimpanzee and humans likely reflect the dietary behaviour and the age of the remains. The chimpanzees consumed only raw plants, while the human group potentially cooked much of their food. The chimpanzees therefore consumed many more native, undamaged starch grains, and so there is greater opportunity for the preservation of native starch grains in dental calculus. Though the humans may have consumed more starch overall, many of these starches would have been semi gelatinised through cooking, disrupting the semi-crystalline structure and reducing the potential for starch preservation in the mouth (Holm et al., 1988). Cooking, combined with higher levels of salivary amylase in humans relative to chimpanzees (Perry et al., 2007; Behringer et al., 2013) may have greatly reduced the relative proportion of starch entering the human calculus matrix during its formation. Furthermore, the chimpanzee samples are modern and likely to be well-preserved while starch in the human calculus may have depleted due to digenesis over thousands of years.

Overall, SEM-EDX does allow us to visualise and identify microremains embedded in dental calculus, but this technique is not without limitations and constraints. Internal features of starch grains that are vital for identifying the taxonomic origin of the starch are not visible under SEM. We found that when using EDX combined with higher primary voltage (10 kV), the beam moved or damaged fragile microremains such as spicules (Fig. 7). EDX can only give reliable data on objects ≥4 μm due to the penetration of the beam, making it impossible to measure very small microremains including smaller starches. We found other techniques such as backscatter detection to be of little additional advantage in detecting starch, though this method may be useful in certain contexts such as examining calculus for

embedded phytoliths (Tromp, 2012). It is possible to examine only the surface portion of intact calculus matrix using SEM-EDX, and so this is not a viable method for visualising interior dental calculus structure and microremains. Sample preparation may also be destructive since samples must be gold-plated and mounted, but use of SEM without the plating may cause the sample image quality and identification power to deteriorate.

3.5. Conclusions

The visual identification and subsequent elemental testing of microremains embedded in the dental calculus of humans and chimpanzees suggests that these important dietary markers are indeed trapped and preserved in calculus during the lifetime of the individual. Clearly, this matrix has a protective quality that shields fragile and degradable components, namely starch, from the enzymatic oral environment.

SEM-EDX and OM have different sensitivity to different microremains. SEM-EDX offers a means to confirm the presence of starch by combining morphological and elemental information without having to destroy either the calculus, as required in processing for OM, or the starch grains themselves, as proposed when using enzymatic reactions. Even if starch is semi gelatinised it should preserve an elemental signature that is suggestive of starch. We applied SEM-EDX to intact calculus to witness microremains *in situ*, but this technique is equally viable for more finely processed calculus samples mounted on plates, or even to calculus still attached on the original tooth. However, it is important to note that diagnostic features of starch grains, such as the hilum and lamellae, are only visible using OM.

Our study indicates that SEM-EDX is a viable alternative to OM analysis of calculus, but researchers should choose their analytical method based on the questions they seek to answer, and the plant microremains that they intend to study. Furthermore, on very sensitive osteological remains, it may be possible to use SEM-EDX to study calculus using entirely non-destructive means to examine embedded microremains directly on the tooth; a useful technique if the tooth is not firmly attached in the mandible or maxilla. We prefer to consider SEM-EDX a complementary rather than replacement technique in the study of dental calculus microremains. A sequential workflow that first examines calculus under SEM-EDX and then under OM may be the optimal solution for highest resolution of microremains, though we recognise that this approach is time intensive and can be

costly. We believe that further exploration and experimentation of SEM techniques is important in the field of archaeological and palaeodietary reconstruction. The continued refinement and expansion of dental calculus analysis techniques is an important focus in order to optimise the information we can harvest from this ephemeral and fragile material.

4

Dental calculus evidence of Taï Forest Chimpanzee plant consumption and life history transitions

Robert C. Power,[1] Domingo C. Salazar-García,[2,3,4] Roman M. Wittig,[5,6] Martin Freiberg,[7] Amanda G. Henry[1]

[1]Max Planck Research Group on Plant Foods in Hominin Dietary Ecology, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103 Leipzig, Germany.
[2]Department of Archaeology, University of Cape Town, Cape Town, South Africa.
[3]Departament de Prehistòria y Arqueologia, Universitat de València, València, Spain.
[4]Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, Leipzig, Germany.
[5]Department of Primatology, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6 Leipzig, Germany.
[6]Taï Chimpanzee Project, Centre Suisse de Recherches Scientifiques, Abidjan, Cote d'Ivoire
[7]Institute of Botany, University of Leipzig, 04103 Leipzig, Germany.

Published in *Scientific Reports* (2015, Volume 5, 15161).

Abstract

Dental calculus (calcified dental plaque) is a source of multiple types of data on life history. Recent research has targeted the plant microremains preserved in this mineralised deposit as a source of dietary and health information for recent and past populations. However, it is unclear to what extent we can interpret behaviour from microremains. Few studies to date have directly compared the microremain record from dental calculus to dietary records and none with long-term observation dietary records thus limiting how we can interpret diet, food acquisition and behaviour. Here we present a high-resolution analysis of calculus microremains from wild chimpanzees (*Pan troglodytes verus*) of Taï National Park, Côte d'Ivoire. We test microremain assemblages against more than two decades of field behavioural observations to establish the ability of calculus to capture the composition of diet. Our results show that some microremain classes accumulate as long-lived dietary markers. Phytolith abundance in calculus can reflect the proportions of plants in the diet, yet this pattern is not true for starches. We also report microremains can record

information about other dietary behaviours, such as the age of weaning and learned food processing techniques like nut-cracking.

4.1 Introduction

Understanding feeding ecology is crucial for recognising the evolutionary pressures that shaped the great apes and humans. It is long recognised that factors such as dietary specialization, tool-assisted food acquisition and the weaning age of infants are important in great apes and humans, and differ significantly among species (Boesch et al., 1994; Ross, 1998; Boesch and Boesch-Achermann, 2000; Teaford and Ungar, 2000).

However, many approaches to dietary reconstruction leave unanswered specific questions on diet and related life history events, especially for fossil specimens. There is a need for new methods to reconstruct food acquisition from populations that can avoid some of the shortfalls of other techniques like direct observation, stable isotope analysis and microwear studies (Phillips and Lancelotti, 2014; Fiorenza et al., 2015). In some contexts, direct observation is simply not possible, for example with extinct great apes and human groups. Stable isotope analysis and dental microwear studies fail to provide total dietary data, and instead only give a picture of broad dietary patterns such as consumption of particular plant categories or mechanical properties of diet (Grine, 1986; Scott et al., 2012). Furthermore, even where direct observational data on food acquisition is available, data collection is frequently constrained because observation is only feasible over a short window of the lifetime of an individual that may live up to several decades.

Dental calculus sampled from living or dead individuals is rapidly gaining recognition as an invaluable material for the reconstruction of life history. Since Armitage (Armitage, 1975) first recognised plant remains from the teeth of ungulates, studies have reported starch grains, phytoliths, pollen grains, diatoms, mineral particles, proteins and DNA from diverse human and animal populations (Kucera et al., 2011; Adler et al., 2013; Salazar-García et al., 2013; Power et al., 2014b, 2015a; Warinner et al., 2014). Using dental calculus from present day forager-horticulturalists, Leonard (Leonard et al., 2015) showed for the first time that recovered microremains also occur in consumed foods verifying the link between microremains in calculus and diet. As demand grows for dietary history data, analysis of phytoliths and starches in dental calculus is been increasingly used to

reconstruct dietary ecology and ecological niches (Lalueza-Fox et al., 1996; Gobetz and Bozarth, 2001; Boyadjian et al., 2007; Henry et al., 2012; Mickleburgh and Pagán-Jiménez, 2012; Salazar-García et al., 2013; Buckley et al., 2014; Lazzati et al., 2015).

Despite the promise of calculus dietary studies, they are hindered by the lack of research that cross-validates the dietary material recovered in calculus with the organism's actual feeding ecology and life history. Until recently, our understanding of what the plant matter preserved in calculus precisely represents has been speculative. The initial effort to characterise the microremain record by Leonard (Leonard et al., 2015) reported that calculus captured only a limited proportion of dietary breadth. In this study many vegetable foods lacked phytoliths and starches, and cooking may have significantly reduced starch abundance even if present. Dietary patterns were established through interviewing and short-term camp stays by Leonard, and though the recovered microremains corresponded to the average diet of the population, the dietary records lacked insight into the long term life history of individuals. Without dietary records that cross intra- and inter-annual cycles, our knowledge of the nature of the calculus record and its potential for archaeological studies is incomplete. Furthermore, it is unclear if the calculus dietary record has input from non-dietary sources (e.g. preparation of plant-based tools and oral hygiene) as well as the consumption of stomach contents (Buck and Stringer, 2014; Dudgeon and Tromp, 2014; Tromp and Dudgeon, 2015), with bias from diagenetic and taphonomic factors rendering it ultimately purely stochastic.

In our study, we compare the plant microremains from the calculus of the chimpanzees of the Taï Forest to 22 years of group averaged dietary observation data in order to validate the calculus record and explore its potential as a source on information on life histories. For this purpose, the study of chimpanzees provides several strengths as a model. First, the chimpanzee mouth is analogous to humans, in that chimpanzees often accumulate large deposits of calculus unlike some mammals. Secondly, chimpanzees produce salivary amylase unlike some primates (Santos et al., 2012) although it is less abundant than in humans (Perry et al., 2007). Thirdly, Taï chimpanzees have a broad diet that includes nearly all food classes (e.g. fruits, piths, leaves, mammals, birds, invertebrates and honey) and is thus relevant to understanding hominin evolution in the African tropics and dietary ecology of hunter-gatherers living in other tropical regions. Fourthly, chimpanzees only consume raw foods meaning the microremains in their food are unaltered by cooking processes.

We sampled calculus from 24 individual chimpanzees using established methods (Dobney and Brothwell, 1986; Mickleburgh and Pagán-Jiménez, 2012), and built a random forest model in the R software environment (Breiman, 2001) to identify the microremains based on multivariate comparison to reference material (Fenwick et al., 2011; Saul et al., 2012; Out et al., 2014; Coster and Field, 2015; Out and Madella, 2015) (see detailed methods 7.2). We predict that if microremains reflect diet, they are accumulative in calculus and should increase with age of the individual. Chimpanzee sex might also influence the abundance of microremains, since male and female chimpanzee are known to vary in their time allocation to different food resources (Wrangham and Smuts, 1980; Boesch and Boesch-Achermann, 2000; N'guessan et al., 2009; Fahy et al., 2013). We also anticipate that the proportions of microremains from each plant will be determined by the frequency with which that plant is consumed and how abundant the microremains are in the plant tissue. Although we knew the taxonomic identity of the reference plants at the level of species, an important amount of dietary observation data was present only at the genus level. Therefore, we performed our analyses at the genus level in order to have a higher chance of capturing long term dietary averages for the group, and refer only to genera in the text. Except where otherwise noted, our analyses were done at the group level observational data, since the records for individual chimpanzees were not complete enough to provide a detailed overview of life history. We found the phytoliths in dental calculus to be an approximate record of diet, and furthermore that microremains can reflect important behaviour like nut-cracking and episodes of Taï Chimpanzee life history such as the age of weaning.

4.2 Materials

4.2.1 Taï Forest reference material

A reference collection with 91 genera (113 species) of the most frequently consumed chimpanzee plant foods in the Taï Forest was collected and examined for phytoliths and starch (Table 7; Appendix table 4) starches. Phytoliths and starches were isolated from reference plants using conventional approaches (Piperno, 2006). We selected thirteen starch- and seven phytolith-producing genera from the 91 we analysed for the identification model (Appendix table 4).

Table 7: Plant genera selected from reference collection species for the predictive identification model with the microremain content of the dried plant material provided as a percent of dried plant material, and the frequency of observed consumption provided as number of minutes eaten. We chose to use genus as the taxonomic rank as some dietary records only identify genus.

Plant category (Genus)	Type	Plant part	% Microremain/Dry Weight	Minutes eaten
Elaeis	Phytolith	Fruit and leaf	4.81	9379
Eremospatha	Phytolith	Pith	1.72	25,046
Laccosperma	Phytolith	Pith and seed	2.15	5311
Aframomum	Phytolith	Seed and leaf	2.13	1704
Sarcophrynium	Phytolith	Fruit	3.32	1847
Cola	Starch	Seed	40	35,778
Aframomum	Starch	Seed	54.58	1704
Piper	Starch	Seed	39.22	492
Sacoglottis	Starch	Fruit	2.46	258,225
Panda	Starch	Seed	0.85	17,299
Coula	Starch	Seed	31.15	118,095
Napoleona	Starch	Seed	20.79	51
Gilbertiodendron	Starch	Seed	23.87	11,808
Eremospatha	Starch	Pith	2.93	25,046
Calpocalyx	Starch	Fruit	9.1	49,074
Sarcophrynium	Starch	Fruit	23.83	1847
Xylia	Starch	Seed	19.58	46,587
Treculia	Starch	Seed	23.87	58,093

4.2.2 Calculus sampling

The calculus samples used for our analysis come from permanent and deciduous molars of 24 chimpanzees from the Taï Chimpanzee Osteology Collection at the Max Planck Institute for Evolutionary Anthropology (MPI-EVA) with varied life histories (4.6; Table 8, Appendix table 5). We selected only molars to standardise the sampling, and chose teeth that were encrusted with a prominent band of supragingival calculus (calculus present above the original gumline) on the enamel crown. Deposits of supragingival calculus were present on all individuals ≥ 1 years old. Subgingival calculus was also present but was not sampled since it occurs below the former gums and it is unclear if it preserves food remains. Calculus on the teeth was documented with photography before sampling, and the colour noted with how each skeleton as treated before our sampling (Appendix table 5). Packing material was sampled as a control. An unidentified adhesive used in the curation of some specimens was removed before sampling. A dental scalar was then used to remove small areas of calculus. The amount of calculus sampled had no relationship with the

amount of calculus present on the teeth except in the youngest chimpanzees (<5.3 years), where calculus was rare and almost entirely collected. We sampled in clean conditions in a laminar flow cabinet at positive-pressure at the MPI-EVA. We then weighed each of the samples and transferred them to microcentrifuge tubes. After sampling, the teeth and surviving calculus were photographed.

Some studies have highlighted the risks of laboratory contamination from modern plant microremains (Crowther et al., 2014; Barton and Torrence, 2015; Weyrich et al., 2015). To address the possibility of contamination, we conducted a regime of weekly laboratory cleaning to remove contamination. All work surfaces were wiped with hot water, washed with starch-free soap and wiped with 5 % sodium hydroxide (NaOH). We additionally performed wipe tests before and after weekly cleaning to quantify starch contamination and assess contaminating types. Wipe tests retrieved settled particles of the surface area (74 x 43 cm^2) of the laboratory positive-pressure laminar flow hood used for mounting. Results of these intensive contamination control tests are in Power and colleagues (2015b).

Table 8: All chimpanzee dental calculus samples analysed.

Name	ID	Tooth	Sex	Weight (mg)	Age at death	
					In years	In months
Ophelia	14993	Lower Left DM1	F	0.025	1	12
Leonardo	13432	Upper DM2	M	0.329	1.92	23
Bambou	11777	Lower Left DM1	M	0.135	2.08	25
Piment	11788	Lower Right DM1	F	0.27	3.58	43
Oreste	14995	Lower Left M1	M	0.536	5.25	63
Hector	12175	Upper Right M1	M	0.689	5.67	68
Noah	15011	Lower M1	M	1.165	7	84
Lefkas	13433	Upper Left M2	M	0.595	7.58	91
Tina	11790	Lower Right M1	F	1.36	9.08	109
Dorry	15020	Lower Right M2	F	0.742	11	132
Zerlina	11792	Lower Left M3	F	0.878	12.3	144
Clyde	11779	Lower Right M1	M	1.131	13	156
Agathe	11775	Lower Right M2	F	6.076	16	192
Leo	15012	Lower Right M3	M	1.085	19	228
Bijou	11778	Lower Left M2	F	5.041	19	228
Castor	13439	Lower Left M1	F	6.982	22	264
Kendo	11781	Lower Left M2	M	2.895	25	300
Fanny	11780	Lower Left M3	F	3.915	25	300
Venus	15001	Upper Right M1	F	1.133	27	324
Goma	15004	Upper Right M3	M	13.208	28	336
Rubra	15023	Lower Left M2	F	6.751	38	456
Ondine	11786	Lower Left M1	F	1.529	39	468
Mkubwa	13435	Lower Right M3	M	0.324	40	480
Brutus	15029	Upper Left M3	M	3.246	46	552

4.3 Methods

4.3.1 Optical microscopy

Optical microscopy was performed at the Plant Foods in Hominin Dietary Ecology laboratory in the MPI-EVA (for reference collection microscopy see 4.6 and Appendix table 6). We added 150 µl of 10 % hydrochloric acid to the calculus sample for one to three hours. The samples were then centrifuged at 1691 x g (Heraeus MEGAFUGE 16 with a microcentrifuge rotor) for 10 minutes and then about 100 µl of supernatant was decanted and replaced with distilled water. This was repeated three times to remove the hydrochloric acid. After the second decanting, it was refilled with a 25 % glycerine solution. The sample was then ground in the solution in the 1.5 ml Eppendorf microcentrifuge tube to reduce sample loss due to static

electricity. The samples then were centrifuged again at the same speed, and about 1 ml of supernatant was decanted. We mounted 20 µl per slide on as many slides as needed in order to examine the entire sample. Microscopy was used as in conventional phytolith and starch studies (Power et al., 2014a; b). We examined each slide under bright field and cross-polarized light on a Zeiss Axioscope microscope at 400 × magnification. We photographed each microremain and described each with the international microremain nomenclature including the International Code of Phytolith Nomenclature (Madella et al., 2005). In some cases, starch aggregates were identified in calculus. In this case, each component grain of each aggregate was counted as an individual starch.

4.3.2 Microremain identification

We identified microremains with a reference collection using multivariate analysis with a random forest algorithm. We collected five general microremain measurements and four specific to phytoliths and six specific to starches from a total of 900 reference microremains (Table 7). With the reference collection generated (Appendix table 6) we generated a certainty score that each matched each reference collection genus. The validity was tested through cross-validation with a subset of reference data. We identified the microremain as coming from the genus with the highest certainty score.

4.3.3 Behavioural records

The chimpanzees of the Taï Forest have been studied since the commencement of the Taï Chimpanzee Project in 1979 (Boesch and Boesch-Achermann, 2000). The detailed recorded behaviour of the group included observation of feeding time and food item consumed. The feeding records used in our study span the period between 1992 and 2014. The database includes 1,165,150 million behavioural observations of about 128 chimpanzees, with a total of 417,628 dietary observations (2,380,202 minutes). However, only roughly 30,000 observations come from chimpanzees available for sampling at the osteology collection. Furthermore, most of these chimpanzees have only sporadic coverage of their life history. Therefore, instead of using dietary records of individual chimpanzees or the

collated records of the 24 chimpanzees we sampled, we chose to combine dietary records from all 128 chimpanzees to best represent the average Taï Forest diet.

The feeding record includes the times when a chimpanzee started and finished eating, and the food consumed. We chose only those feeding records where the genus of the plant food eaten was documented, and calculated the total amount of time spent consuming each resource. Behavioural records do not account for variations in the volume of food consumed in given number of minutes. In addition, although some observations record the specific plant part that was eaten, most do not, so we do not include this information.

4.3.4 Statistical analysis

To test for the effects of age on microremains we used a negative binomial regression (log link) with a count of each microremain class treated as a response (phytoliths, starches and other unsilicified plant fragments) using a likelihood ratio test in R 3.1.0 (R Core Team, 2014). We ran the regression using the glm.nb function of R package MASS (Venables and Ripley, 2002). The full model included the fixed effects of age and sex (4.6). The mg weight of each calculus sample was used to weigh the model to account for larger samples likely being more representative of overall diet due to the potential of microremains to have a clustered distribution in the calculus matrix. Controlling for weight, heavier samples have less variable microremain counts (Compare Table 8 with Fig. 10). The full model was compared with a null model using an ANOVA. We used likelihood ratio tests comparing the full models with reduced models in which each fixed effect was dropped, one at a time. Model assumptions were met. Collinearity was not an issue (largest Variance Inflation Factor=1.001) and leverage values as well as DFBeta values indicated no obvious highly influential cases.

To explore the relationship between diet and the phytolith microremains found in dental calculus we tested an observational random effect Poisson model with likelihood ratio tests. We used counts of each genus predicted to be present with the total minutes spent consuming each genus. For this, we used the glmer function of the R package lme4 (Bates et al., 2013). If any genus was not predicted to be present in a chimpanzee sample, they were included as a 0 value. Our full model included minutes and chimpanzee age in months as fixed effects, and sex as a control predictor. The model included the weight of each calculus sample and the

successful identification rate of each type of genera as model weights, and used microremain content as an offset to factor in significant differences in content between different genera. To prepare the data, we z-transformed the minutes and age variables. The chimpanzee individual was included as a random slope term while year of death, tooth and food type were treated as random intercept terms. An id was assigned to each observation, and this was also included as a random intercept, thus reducing overdispersion to (x^2=13.369, df=116, dispersion parameter=0.115) in the phytolith model. To test the significance of the full model it was compared with a null model excluding fixed effects of minutes of observation and age. Variance inflation factors (VIF) were derived to assess collinearity using the function vif of the R-package car, from a standard linear model minus random effects, as offsets and weights (Fox and Weisberg, 2002; Field, 2005). Variance inflation factors indicated collinearity to not be an issue (largest VIF=1.02). We tested model stability by excluding each random effect one by one from the data set, running the full model and comparing the results with those from the original model that suggest no highly influential cases.

To explore the relationship between diet and the starch microremains we could not use the same approach due to high zero inflation present in the starch data. To overcome this, we implemented a mixed effects logistic regression using the same terms, random effects, weighs and offset as the phytolith Poisson model. This required the counts data (the response) to be treated as presence and absence data resulting in some loss of data. Variance inflation factors (Field, 2005) were derived to access collinearity using the function vif of the R-package car, from a standard linear model minus random effects as well as offsets and weights (Fox and Weisberg, 2002). Variance inflation factors indicated collinearity to not be an issue (largest VIF=1.018).

4.4 Results

4.4.1 Identification of the microremain assemblages

We were able to examine 91 of the 157 genera (113 of 230 species) of plants that the 128 Taï chimpanzees consumed during the observation period. After assessing these plants, we noted thirteen starch-producing genera that could be included in our identification model. Unlike starches, phytolith were abundant in most plants in many different morphotypes. Not all morphotypes could be included

in analysis, so we choose one morphotype (globular and spheroid) and identified the five genera that produces them (Table 7; Fig. 9). Most of these thirteen starch-producing and five-phytolith producing genera are major sources of food for these chimpanzees (Appendix fig. 2).

For each microremain-producing plant genus, we collected data from 50 microremains, to provide a range of measurements within each genus. We collected nine types of measurements for phytoliths and 11 for starches from 900 microremains using Zeiss AxioVision Microscopy Software (Appendix table 6). By using a subset of the reference collection to test the model, we assessed the success rate of identification of each genus with the model (Appendix table 8, Appendix table 9). Some genera were reliably identified, and others were more difficult to identify. For example, *Sarcophrynium* phytoliths were identified successfully 94 % of the time while *Panda* starch was only identified 22 % of the time. Generally, phytoliths were identified more reliably (Appendix table 8, Appendix table 9). Using this random forest model, we were able to proceed with identification of microremains recovered from the calculus.

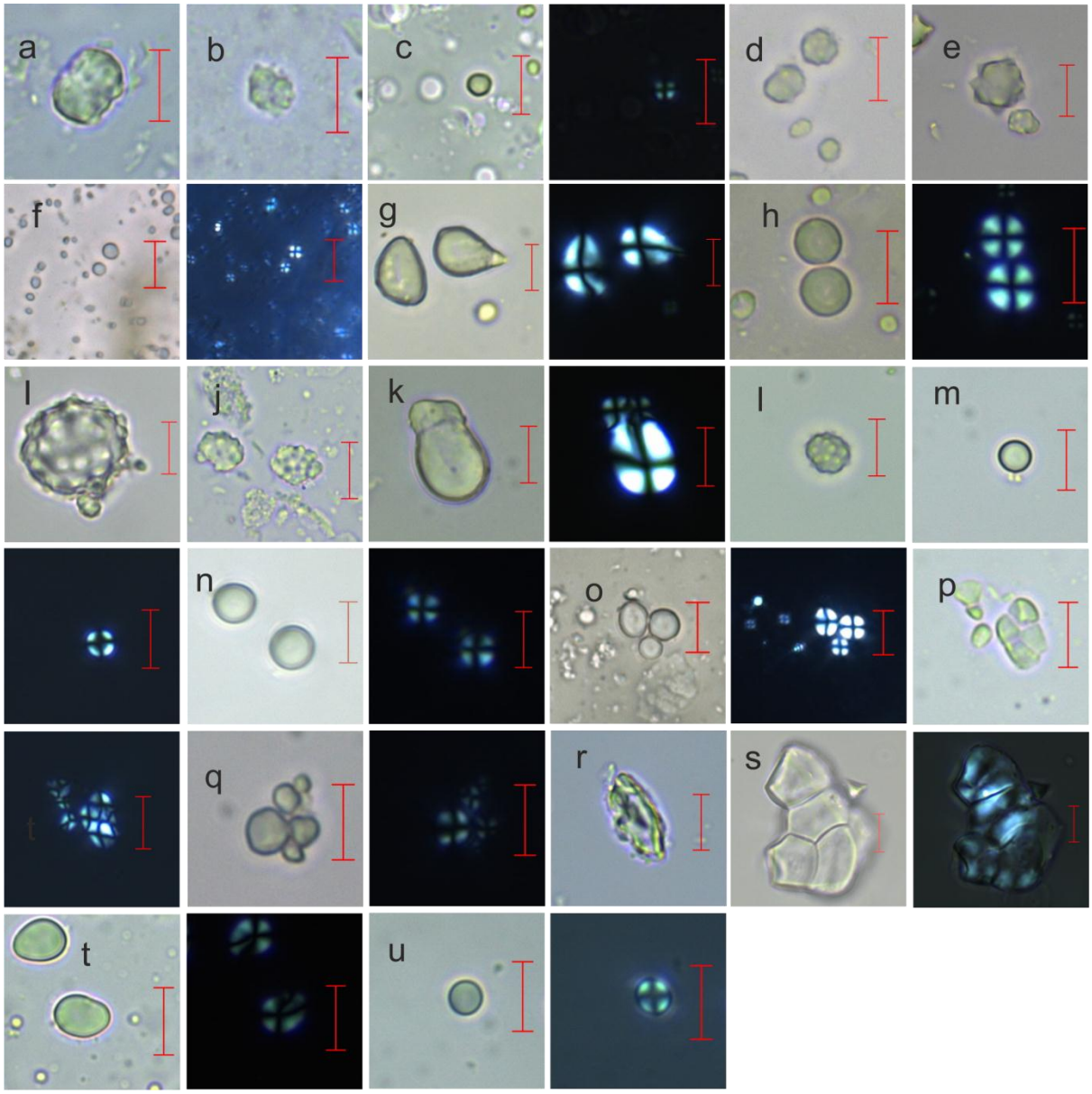


Fig. 9: Starch and phytolith morphotypes used in the identification model. Each scale bar represents 10 µm. (a) ***Aframomum sceptrum*** **seed phytolith, (b)** ***Aframomum excarpum*** **leaf (b)** ***Aframomum excarpum*** **leaf phytolith, (c)** ***Aframomum excarpum*** **seed starch under bright field (left) and cross polarized light (right), (d)** ***Laccosperma opacum*** **pith phytolith, (e)** ***Laccosperma secondiflorum*** **seed phytolith, (f)** ***Calpocalyx*** **sp. fruit starch under bright field (left) and cross polarized light (right), (g)** ***Cola nitida*** **seed starch under bright field (left) and cross polarized light (right), (h)** ***Coula edulis*** **seed starch under bright field (left) and cross polarized light (right), (i)** ***Elaeis guineensis*** **fruit phytolith, (j)** ***Elaeis guineensis*** **leaf phytolith, (k)** ***Gilbertiodendron splendidum*** **seed starch under bright field (left) and Cross polarized light (right), (l)** ***Eremospatha macrocarpa*** **pith phytolith, (m)** ***Eremospatha macrocarpa*** **pith starch under bright field (upper right) and cross polarized light (lower left), (n)** ***Napoleona leonensis*** **seed starch under bright field (left) and cross polarized light (right), (o)** ***Panda olesosa*** **seed starch, (p)** ***Piper guineense*** **seed starch under bright field (upper right) and cross polarized light (lower left), (q)** ***Sacoglottis gabonensis*** **fruit starch under bright field (left) and cross polarized light (right), (r) S*arcophrynium prionogonium*** **fruit phytolith, (s)** ***Sarcophrynium prionogonium*** **fruit starch under bright field (left) and cross polarized light (right), (t)** ***Treculia africana*** **seed starch under bright field (left) and cross polarized light (right), (u)** ***Xylia evansii*** **seed starch.**

Of the 24 chimpanzee calculus samples, we found starches in 17 of the samples, and phytoliths in 20 (Fig. 10, Fig. 11; Table 8, Appendix table 10). We also found unidentified phytoliths, unsilicified plant fragments, diatoms, pollen and insects, but these were not identified to taxon (Table 8). In ambiguous cases microremains were classified as possible starches and specifically stated, but were not used for statistical genera identification. Most definite starches and phytoliths that were free from damage (234 starches and 1035 phytoliths) were identified to genus using the random forest model, which assigned each unknown microremain to a genus and provided a certainty score that indicated the confidence with which that assignment was made. A microremain was considered to be damaged if it showed pitting, ruptured surfaces or other major irregularities. The highest certainty score for each individual microremain depended heavily on each genus identification rate (as described above), but generally ranged between 0.25 and 0.95.

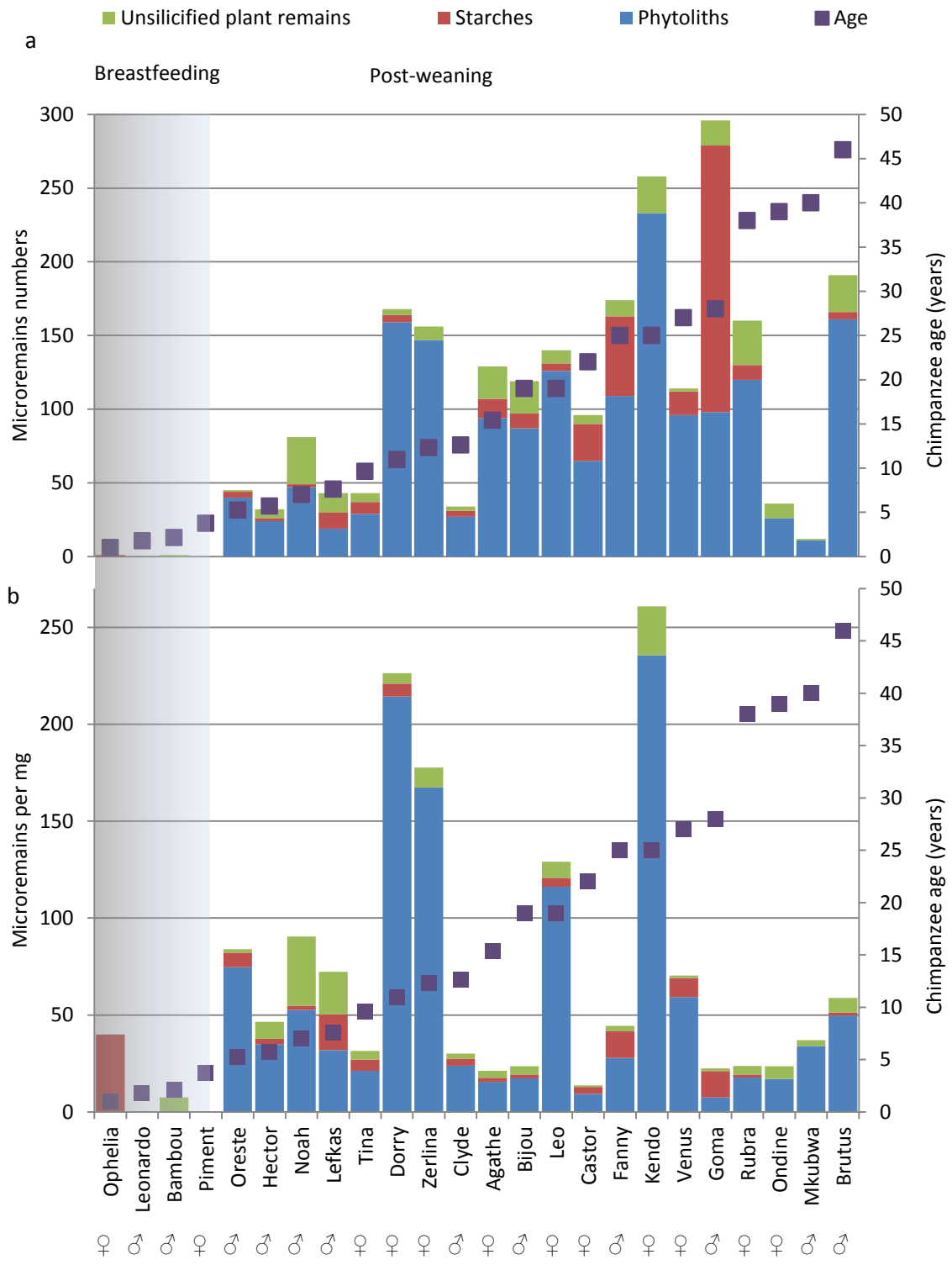


Fig. 10: Microremains recovered in calculus samples. Microremains include Unsilicified microremains, starches (definite and possible) and phytoliths recovered with chimpanzee age at death (in years) and approximate age of the cessation of weaning highlighted. a=total counts and b=counts per milligram of calculus. The number of microremains per mg in Ophelia was affected by an unusually small amount of calculus in the sample.

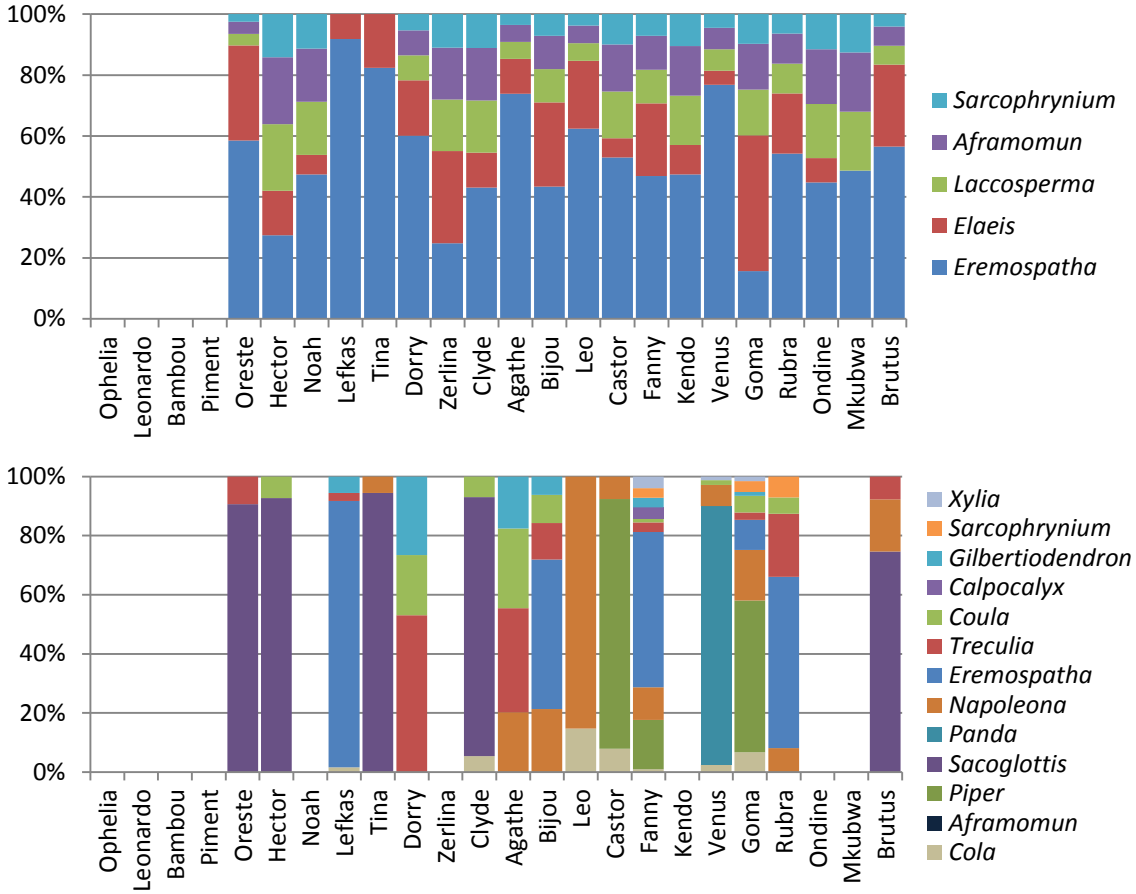


Fig. 11: Microremain assemblages recovered in calculus. (top) Bar chart of the composition of the phytolith assemblage recovered from calculus. (bottom) Bar chart of the composition of the starch assemblage recovered from calculus. The individuals are ordered by age from youngest to oldest.

4.4.2 Assessment of biases in our data

First of all, it was important to ascertain if the treatment of the skeletal material to prevent the spread of disease (including one year of burial, and various chemical treatments) had impacted microremain preservation in the calculus. After 2004 chorine and formalin was used to clean skeletal material. Boiling may have been used on some skeletons to clean them and remove Ebola pathogens between the Autumn of 1994 and the Spring of 1996 (Appendix table 10). To test if the three types of treatments significantly influenced starch preservation we used a Kruskal-Wallis test starch per mg on samples from each period (H=3.7633, df=2, p-value=0.1523). We included microremains classified as possible starches in the starch per mg count (Appendix fig. 1). Due to the small sample size we calculated a Kruskal-Wallis p-value based on 999 random permutations. This indicated no differences between the three groups (Permutation H=7.1215, df=2, p=0.159).

Previous studies of other organic material (bone collagen) in the Taï skeletal collection have indicated no significant post-mortem alteration (Fahy et al., 2013, 2014). While collagen does not necessarily behave in the same manner as plant microremains, it is likely that the comparable hydroxyapatite mineral matrices of bone and calculus have a similar protective effect on the organic materials trapped within them (Nicholson, 1996).

Before comparing the calculus results to the observational records, we wanted to see if there was excessive variation in plant representation among the calculus samples. Phytoliths from four of the five phytolith-producing genera were found on most, but not all, of the calculus samples, suggesting that there is not much variability among these calculus samples (Fig. 11, Appendix table 11). Some genera are found in each sample (*Eremospatha* and *Elaeis*) while others, like *Sarcophrynium,* were rare (Appendix table 12). However, the starch record varies significantly among individuals, with most of the thirteen starch-producing genera seldom found. This probably reflects the far lower numbers of starches compared with phytoliths. Several genera dominate the starch record, namely *Gilbertiodendron*, *Coula*, *Eremospatha*, *Treculia* and *Cola* (Fig. 11, Fig. 12). Most microremains were isolated, but three calculus samples had four starch aggregates from *Piper*; each starch in the aggregate was counted as an individual starch grain and thus constitutes a large proportion of the total number of the recovered starches. This potentially biases the starch assemblage's dietary representativeness (Fig. 11; Appendix table 12). In sum, it seems that there is not much variation in the phytolith record of our chimpanzee samples, but the starch record is less homogeneous. Another potential source of bias comes from the differential preservation of microremains relating to their inherent properties, like size and shape. We noted that our results were biased towards foods with larger sized microremains. *Elaeis* phytoliths and *Cola* starches, the largest microremains in the study (Fig. 11, Fig. 12), are disproportionately frequent across the assemblages even after controlling for the high concentration of microremains within these genera. They are frequently found, but are not dominant foods (Appendix fig. 2).

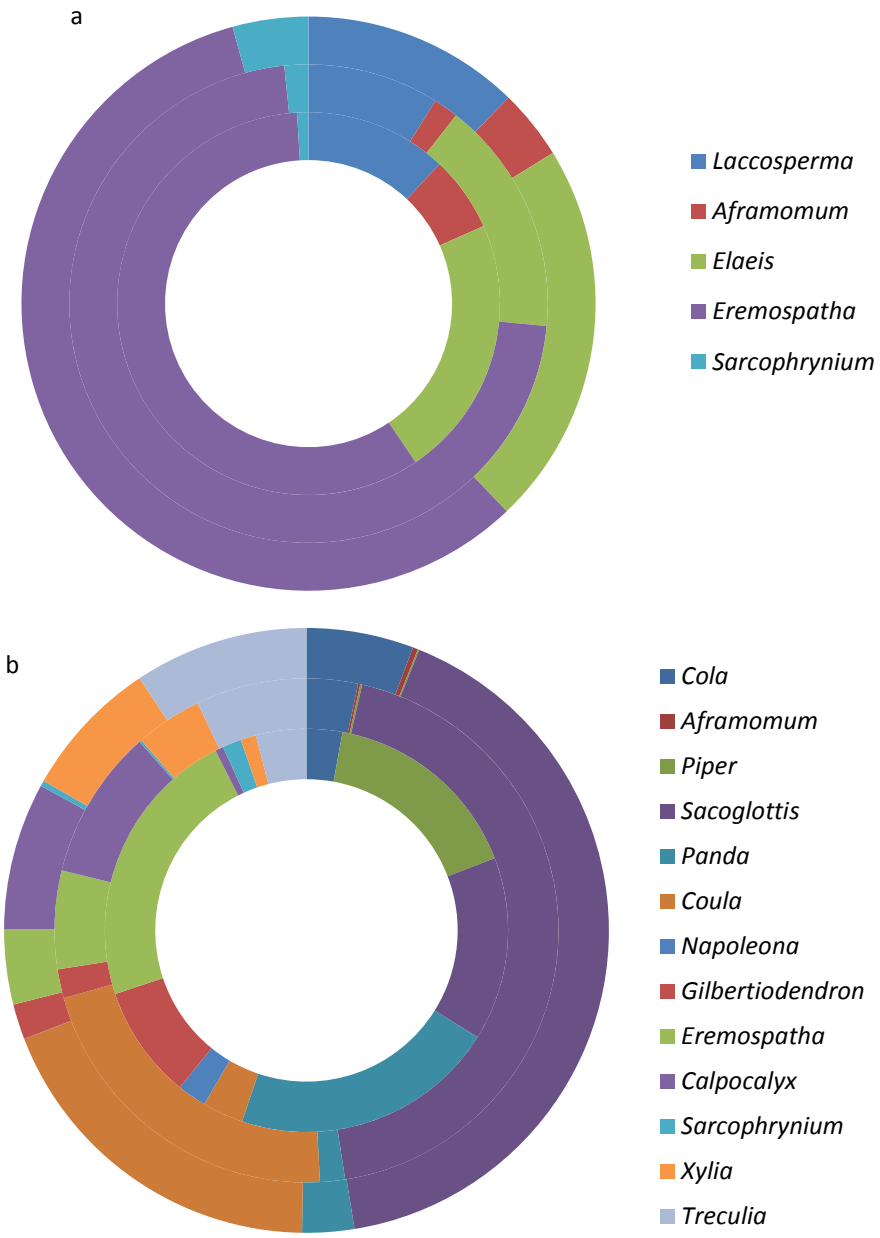


Fig. 12: Plant genera represented by microremain assemblages and Chimpanzees diet. Microremain counts are normalised by dividing counts by the percent content of by dry plant weight of starches and phytoliths among different genera. **(a) Phytolith counts compared with feeding records. Outermost ring=proportions of minutes spent consuming each genus averaged across the feeding records of sampled 24 chimpanzees, middle=proportions of minutes spent consuming each genus averaged across the feeding records of all 128 chimpanzees, innermost=phytolith counts from the sampled 24 chimpanzees. (b) Starch counts compared with feeding records outermost ring=proportions of minutes spent consuming each genus averaged across the feeding records of sampled 24 chimpanzees, middle=proportions of minutes spent consuming each genus averaged across the feeding records of all 128 chimpanzees, innermost=starch counts.**

4.4.3 Microremain accumulation, chimpanzee age and sex

If microremains reflect diet they should be more abundant in older chimpanzees, and might vary by sex. We tested this using (see detailed methods below). We ran separate tests for phytoliths, starches and unsilicified remains. For phytoliths, the full model of age and sex significantly influenced the count of phytoliths (x^2=11.794, df=2, P=0.0003), and the effect of age was also significant by itself (x^2=12.753, df=1, P=0.0004) (Appendix table 13). Older chimpanzees generally have a higher abundance of phytoliths. However, sex by itself did not explain the abundance of phytoliths we found (x^2=0.028, df=1, P=0.866). For unsilicified microremains, age and sex as the full model significantly influenced the microremain count (x^2=10.067, df=1, P=0.015), the effect of age alone was also significant (x^2=9.202, df=1, P=0.0015), but not sex by itself (x^2=0.59, df=1, P=0.806). Starch abundance was significantly determined by age and sex together (x^2=23.994, df=2, p=6.1622e-06). Older chimpanzees generally have a higher abundance of starches (x^2=3.559, df=1, p=0.0592). Unlike with phytoliths and unsilicified remains, sex strongly influenced the abundance of starch, with female chimpanzees having more starches (x^2=17.301, df=1, p=3.1897e-05) (Appendix table 13).

4.4.4 Microremain dietary picture and observational feeding records

We predicted that more frequently consumed plants should be highly represented in the chimpanzee calculus. To test this, we used an observational random effect Poisson model (4.3.4). The count of identified classes of microremains (phytoliths and starches) belonging to a particular genus was our response variable, and the fixed predictors were: (a) minutes spent consuming each genus, and (b) chimpanzee age in months. Sex was included as a control predictor, and both calculus sample weight and successful identification rate of each genus were included as weights. We used counts of each genus predicted to be present with the total minutes spent consuming each genus. The chimpanzee individual was included as a random slope term, while year of death, tooth and food type were treated as random intercept terms (see methods below for 7.2).

When comparing the genera proportions present in diet (calculated as the number of minutes spent foraging on a genus) with the recovered phytolith assemblages, we found a clear relationship. The number of minutes spent consuming a given plant genus influences its phytolith count in the calculus

assemblage even when accounting for the effects of sex, the tooth we sampled, variation in phytolith production between different plants, and the year the individual died. More specifically, an increased reliance on a genus leads to an increase in its representation in calculus (x^2=4.048, df=1, P=0.045; Appendix table 13; Fig. 13). The age of the chimpanzees was found to not influence how well it matches group diet (x^2=0.356, df=1, P=0.55; Appendix table 13).

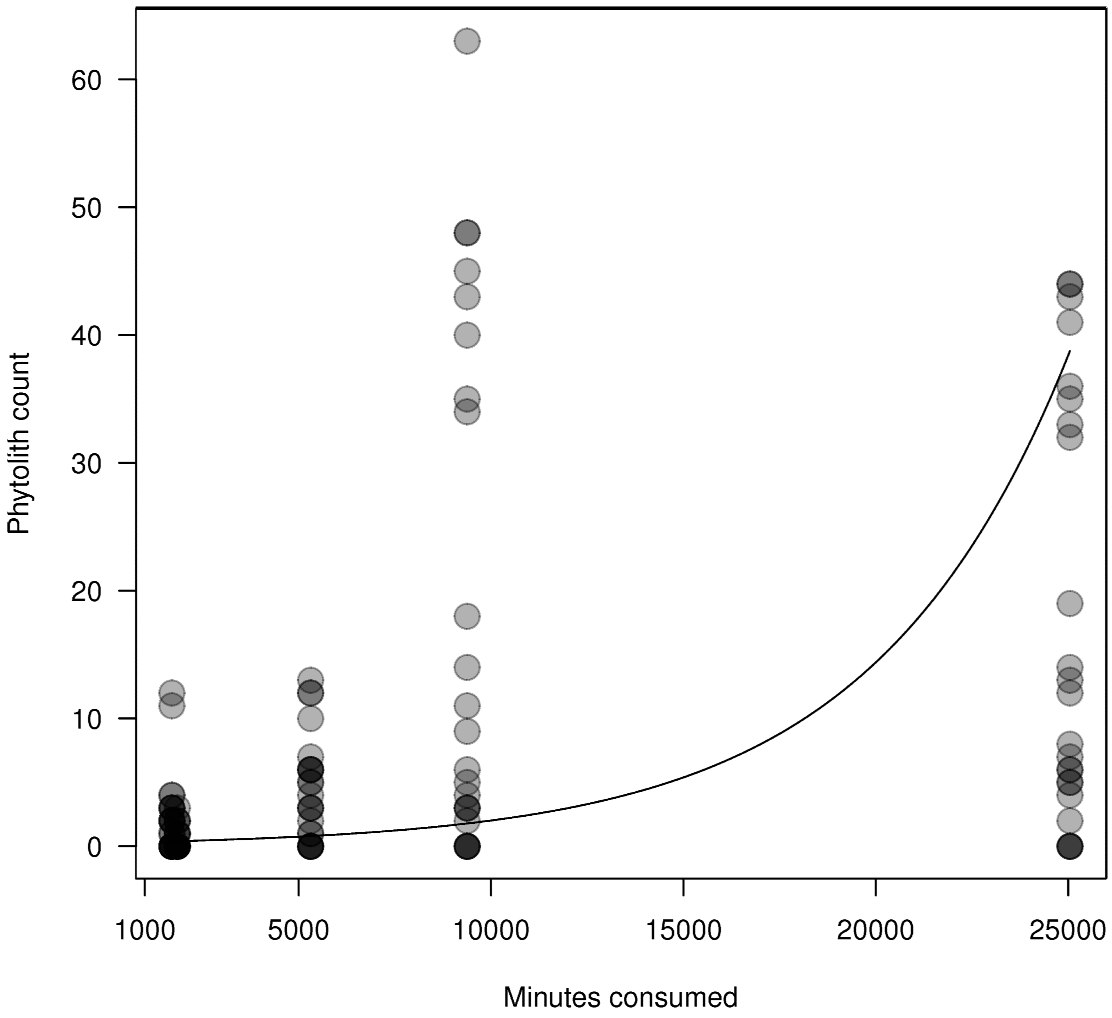


Fig. 13: Mixed Poisson regression model predicted values. The number of phytoliths from a genus increased as the minutes spent consuming this plant resource increased.

In contrast to phytoliths, there was no significant effect of consumption time on starch numbers (x^2=1.95, df=2, P=0.376). The number of minutes this group spent eating a specific genus of starchy foods does not influence its frequency in dental calculus. Yet there is an element of uncertainty because starches vary more among individuals than do phytoliths, as described above, and do not seem to be as good a record of dietary behaviour. Fig. 10 and Fig. 11 show the discrepancy between the

consistency of starch and phytolith results clearly. These results may be a product of post-mortem diagenesis that influenced our chimpanzee samples, including burial to deflesh the remains (Appendix table 5).

4.4.5 Weaning and other behavioural signatures in calculus

The microremains in the Taï calculus record other aspects of their behaviour. First, microremains were strikingly rare in samples from individuals less than 5.3 years old (Fig. 10, Fig. 11; Appendix table 5). The calculus deposits were sparse on these individuals, but despite the small volume of calculus, it was notable that only a single starch and an unsilicified plant fragment were found in these samples. Chimpanzees more than 5.3 years old typically show high numbers of microremains, regardless of the size of the calculus deposit.

Second, the exact plants that were recovered in the calculus provide an interesting view of an important learned behaviour. In our sample, many calculus samples had starches from the *Coula* nut, which is mainly consumed once chimpanzees learn to crack open these nuts. *Coula* nut starches were found in samples from individuals across all age ranges (except those under 5.7 years) (Fig. 14). Although common, *Coula* nut appears to be underrepresented in our sample. It was found only in nine calculus samples, despite this plant being a major food source, comprising of 4.7 % of the total Taï diet.

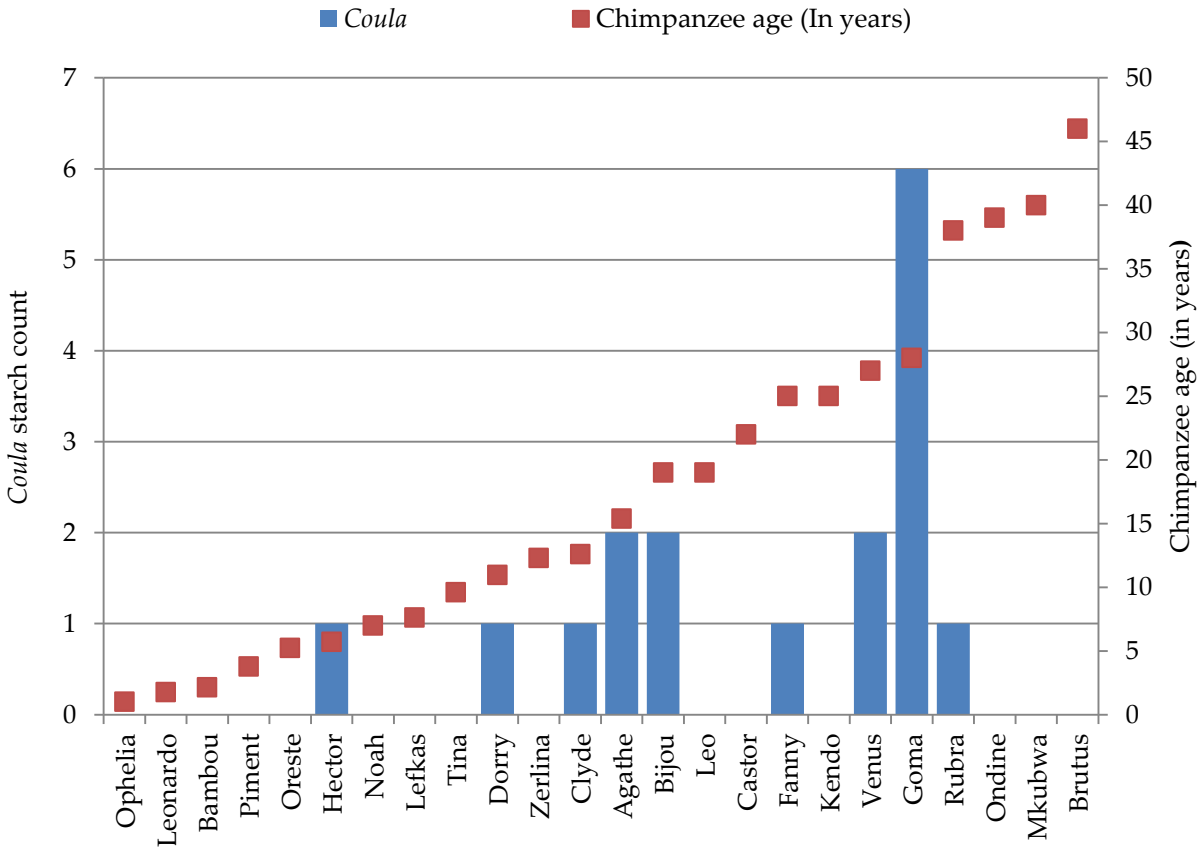


Fig. 14: Abundance of *Coula* nut starches with chimpanzee age at death. *Coula* nut consumption requires nut cracking and its presence implies nut cracking and tool use or food sharing. The individuals are ordered by age from youngest to oldest.

4.5 Discussion

Much of the chimpanzee calculus is relatively rich in plant microremains compared with what has been reported in previous studies of human calculus (Kucera et al., 2011; Mickleburgh and Pagán-Jiménez, 2012; Leonard et al., 2015). This is not entirely unexpected for several reasons. First, our samples are modern, and post-mortem microremain diagenesis is therefore less acute than in ancient remains. Secondly, Taï Chimpanzee diet is uncooked, plant-dominated and voluminous (Appendix fig. 1; Appendix fig. 2). Thirdly, and in contrast to humans, chimpanzees consume a large amount of phytolith-rich material. This richness in microremains is largely confined to phytoliths. Starch abundance falls within ranges observed elsewhere (Mickleburgh and Pagán-Jiménez, 2012; Power et al., 2014b; Leonard et al., 2015).

It is evident that starches are underrepresented and in some samples are even totally absent. In addition, phytoliths present a far more uniform picture of diet between different chimpanzees. This may be due to diagenesis occurring during the preparation of the skeletons for the osteology collection. It is known that all skeletons were buried for short periods of time during the defleshing process (Appendix table 5). These processes may preferentially alter or remove starches from the calculus record that are not sufficiently mineralised and sealed, while leaving the phytoliths relatively unaltered. Yet, our Kruskal-Wallis test indicates cleaning processes have not influenced starch numbers.

The comparison of microremains with diet was possible because our methodology generated a deep profile of dietary history. However, our metric of food use (minutes spent consuming a food) is not identical to the total volume of consumed food by each chimpanzee, or a food's total energetic value. Unfortunately, our analysis was not able to account for this.

Additionally, we found that the microremain record was likely biased by the differential survivability of microremain from different plants. The plants with the largest starches and phytoliths were overrepresented in our sample, possibly due to the larger surface area. This ties in with research that shows that phytolith and starch morphology and surface area is linked to long term stability (Haslam, 2004; Cabanes et al., 2011). Larger blocky microremains may be preferentially preserved. This is noteworthy given that their larger surface area would enhance their contact with bacterial and chemical process and alteration.

Overall, our results verify that the calculus record can be accumulative by showing that older individuals present more microremains. Sex may be a factor to take into consideration, and seems to influence the accumulation of starches but not phytoliths or unsilicified remains. It may reflect higher consumption of starches by female chimpanzees, or sex differences in amylase production or calculus formation, as has been suggested for humans (Monteiro da Silva et al., 1998). We do not currently have the ability to distinguish among these possibilities. The increase in microremains with age and possibly sex implies that microremain accumulation is bound up in aspects of diet that regulate calculus formation. Thus, microremain presence and proportions are likely effected or confounded by all the factors that influence plaque and calculus such as the intake of protein, smoking, polysilicic acid and silica (Damen and Ten Cate, 1989; Roberts-Harry and Clerehugh, 2000; Jin and

Yip, 2002). Calculus clearly can approach a long-term dietary signal, although the timespan involved is not yet clarified.

Our results strongly suggest that care must be taken when interpreting the microremains record preserved in dental calculus, particularly the starch grain record. However, our results also indicate that microremains in calculus can be used to recover important information about diet, behaviour and life history. For example, we observed a lack of microremains from individuals sampled from deciduous teeth of chimpanzees less than 5.3 years old. The microremain assemblages could indicate a rapid accumulation of microremains as solid food enters the diet (Fig. 10). This pattern matches what is generally reported for age of weaning using other measures. Much information on the age of chimpanzee weaning is estimated from inter-birth interval (Fahy et al., 2014). Inter-Birth Interval estimates of weaning ages vary from 4.5 years at Gombe to 5.75 years at Taï (Boesch, 1997), to 6 years at Mahale (Nishida and Hasegawa, 1992). Yet inter-Birth Interval is an indirect measure as it includes more than simply suckling duration. Isotopic based data indicates weaning at Taï commences at 2 years and ends at 3-4.5 years varying by factors such as sex of the offspring. If we combine this infant microremain signal together with the verification of the accumulative nature of the microremain assemblages, we can conclude calculus reflects information on the weaning transition that may be useful for studying unhabituated populations. Researchers should expand this research to infants from recent foragers and horticulturists to develop its applicability.

Furthermore, though the starch dietary record appears more stochastic than that of phytoliths, starches can still provide useful information about behaviour. Many of our starches come from the *Coula* nut (Fig. 11, Fig. 14). Among chimpanzees, *Coula* consumption requires a learned behaviour: nut cracking with a hammer and anvil. This behaviour is restricted to a limited area of the chimpanzee range in West Africa (Boesch et al., 1994). The presence of *Coula* starches (Fig. 11, Fig. 14) shows calculus can reveal nut-cracking behaviour in a group. The fact that tool-use in a group is discernible is relevant for dental calculus studies in both primatology and hominin evolution. The use of *Coula* nut is influenced by age and sex differences in nut cracking (Boesch and Boesch, 1984; Boesch and Boesch-Achermann, 2000), and, as expected, *Coula* starches are absent in youngest chimpanzees who are not yet weaned. Even after weaning infant nut consumption is low and is derived from nuts cracked by the mother as it takes years to learn how to crack nuts (Boesch and Boesch-Achermann, 2000). Beyond this, we do not have

enough calculus samples to examine if there are sex or age differences in the calculus record of nut cracking.

This profile of Taï Chimpanzee diet reflects high amount of contextual information available on a single population. Much research utilizing dental calculus is interested in reconstructing diet of collections of individuals and not contemporaneous populations from archaeological sites. Researchers using archaeological populations with small and even large samples must be aware of the unlikeness of being able to capture the full dietary breadth with dental calculus. The best strategy to account for this issue is to maximize the number of samples in a study.

In summary, the study verifies the relevance of dental calculus for investigations on diet, food acquisition behaviour and life history. It is the first to link dental calculus with foods that entered the oral cavity in quantified abundances but it also identifies clear weaknesses of this method. The data also provide valuable information on the commencement of plant food consumption in wild chimpanzees, and confirms the consumption of solid foodstuffs from at least 5.3 years in life. Our study suggests that calculus analysis provides a rich but wavering insight into complex dietary structure, and that phytoliths, when present in calculus and in diet, may provide a more reliable record of diet than starches.

5

Dental calculus indicates widespread plant use within the Neanderthal dietary niche

Robert C. Power,[1] Domingo C. Salazar-García,[2, 3, 4] Mauro Rubini,[5, 6] Katerina Harvati,[7] Andrea Darlas,[8] Michael Walker,[9] Jean-Jacques Hublin,[4] Amanda G. Henry[1]

[1]Max Planck Research Group on Plant Foods in Hominin Dietary Ecology, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103 Leipzig, Germany.
[2]Department of Archaeology, University of Cape Town, Cape Town, South Africa.
[3]Departament de Prehistòria i Arqueologia, Universitat de València, València, Spain.
[4]Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany.
[5]Department of Archaeology, University of Foggia, Italy.
[6]Anthropological Service of S.B.A.L. (Ministry of Culture Italy), v. Pompeo Magno 2, Rome, Italy.
[7]Paleoanthropology, Department of Early Prehistory and Quaternary Ecology, Senckenberg Center for Human Evolution and Paleoecology, Eberhard Karls University of Tübingen, Rümelinstrasse 23, Tübingen 72070, Germany.
[8]Ephoreia of Paleoanthropology and Speleology of Northern Greece, Greek Ministry of Culture, Navarinou 28, 55133 Kalamaria, Thessaloniki, Greece.
[9]Departamento de Zoología y Antropología Física, Universidad de Murcia, Murcia, Spain.

Submitted to the *Journal of Human Evolution.*

Abstract

The ecology of Neanderthals is a pressing question in the study of hominin evolution. Diet appears to have played a prominent role in their adaptation to Eurasia. Isotope and zooarchaeological studies indicate that Neanderthals ate large quantities of meat, and that there was little variation in their diet across Eurasia. However, we have only a fragmentary picture of their dietary ecology and how it may have varied among habitats, because we lack detailed information about their use of plants and other foods. To address the problem, we examined the plant microremains in Neanderthal dental calculus from five archaeological sites from the northern Balkans, and the western, central and eastern Mediterranean. The recovered microremains revealed the consumption of a variety of non-animal foods, including starchy plants. Using a modelling approach, we explored the relationships

among the diversity of microremains with chronological, climatological and ecological variation. We find no evidence that plant use is confined to the southern-most areas of Neanderthal geographic distribution. Although Neanderthals were predominately big game hunters, evidence of diet from dental calculus indicates that plant exploitation was a widespread and deeply rooted subsistence strategy. Given the limited dietary variation across Neanderthal range in time and space in both plant and animal food exploitation, we argue that vegetal consumption was part of a generally static dietary niche.

5.1 Introduction

Neanderthals occupied a variety of environments drastically different from those where hominins first evolved, earning them a special position in evolutionary history. The ability of this hominin to settle in environments as diverse as the Mediterranean margin and steppe as cold as present-day Arctic tundra implies that Neanderthals were successful at adapting to new conditions. In particular, their diets must have been flexible enough to allow them to thrive in these varied environments. However, some researchers have linked the displacement of Neanderthals at the end of the Middle Palaeolithic to narrower diets than those from Upper Palaeolithic peoples (Hockett and Haws, 2003, 2009; O'Connell, 2006). In this view, Neanderthal subsistence was reliant on a more restricted range of staples than that of modern humans, giving them a competitive disadvantage against Upper Palaeolithic peoples.

Dietary breadth models, borrowed from the framework of behavioural ecology, have provided a means to dissect Palaeolithic dietary adaptations. These models are predicated on the idea that foragers will select the foods that provide the most nutritional benefit at the lowest costs, within the constraints imposed by the environment. The costs and benefits of food are predominantly measured in calories (Winterhalder and Smith, 2000), or other currencies such as macro or micronutrients (Rothman et al., 2006). When the return rates for preferred foods decrease, due to climate change or hunting pressure caused by a population increase, then more food types are added to the diet. A broadening diet is therefore not an adoption of an improved diet; just a response to scarcity of preferred food types.

Neanderthals are often interpreted as narrow spectrum foragers (Kuhn and Stiner, 2006; O'Connell, 2006; Stiner and Kuhn, 2009; Stiner, 2013). Models of Middle

Palaeolithic dietary ecology suggest that they hunted predominantly medium and large prime-age fauna with only infrequent use of small mammals, and aquatic resources and plant foods (Hockett and Haws, 2005). Nitrogen stable isotope ratios indicate that they were at the top of the terrestrial food web and obtained most of their total dietary protein from animal sources, (Richards et al., 2000; Lee-Thorp and Sponheimer, 2006; Richards and Trinkaus, 2009; Salazar-García et al., 2013; Wißing et al., 2015). Some zooarchaeologists argue that this diet was stable over time, with little evidence of a chronological trend towards more diverse resource use (Stiner et al., 2000; Stiner, 2013). Surviving tool repertoires show scant evidence for the investment in specialised technology for collecting plants, fish, birds and small mammals (Kuhn and Stiner, 2006; O'Connell, 2006; Henry et al., 2014), indicating an unchanging and narrow dietary niche. A low diversification in food choice and high consumption of large and medium-sized game matches evidence from site density and their genetic history that imply sparse and, dispersed populations of Neanderthals that did not deplete high-ranked prey items (Stiner, 1999; Stiner and Munro, 2002; Macdonald et al., 2009; Verpoorte, 2009; Castellano et al., 2014).

This view of rigid Neanderthal diets is complicated by recent studies suggesting evidence for variation in diets. Prey selected by Neanderthals varies throughout their range, often along ecological gradients. In southern regions, there is evidence for the consumption of hard-to-catch, low-ranked small game (Stiner, 1994; Blasco and Fernández Peris, 2009; Stiner and Kuhn, 2009; Hardy et al., 2013; Salazar-García et al., 2013; Fiorenza, 2015). In southern Iberia and western Italy, there is also zooarchaeological evidence of a contribution of marine resources (Stiner, 1994; Stringer et al., 2008; Zilhão et al., 2010). A preponderance of low–ranked small game including shellfish and tortoise (*Testudo* spp.) is also known from sites in Greece, Italy, Spain and Israel (Stiner, 1994; Cortés-Sánchez et al., 2011; Blasco and Fernández Peris, 2012; Sanchis, 2012; Harvati et al., 2013). A study of tortoise remains at Nahal Meged showed a decrease in size due to hunting pressure and climate, beginning in the late Middle Palaeolithic, suggesting that Neanderthals were collecting these foods at significant enough rates to reduce their body size (Stiner et al., 2000). In Cova del Bolomor, tortoises, rabbits and birds appear to have been foraged during MIS 6 (Blasco and Fernández Peris, 2009; Salazar-García et al., 2013). In the warm MIS 5e interglacial, a greater proportion of small game is observed at several northern European sites despite the apparent continued dependence on large game (Gaudzinski-Windheuser and Roebroeks, 2011).

The current debate between a rigid, narrow diet and a more variable range of diets continues because most of our dietary evidence is fragmentary. Large parts of diet are poorly known, especially plant foods. Recent foragers in northern environments provide a poor reference for Pleistocene foragers, in part because the treeless biomes of the Pleistocene have no analogue in the modern era (Stewart, 2005). The biomass of Pleistocene grasslands far exceeded the biomass of present day Eurasian tundra, providing a greater number of available animals for Neanderthals. We know less about the productivity of plant foods in this ecological zone (Verpoorte, 2009), but energy-rich plants were available on the steppe-tundra and throughout western Eurasia (Sandgathe and Hayden, 2003; Hardy, 2010; Pryor et al., 2013; Power et al., 2016).

Relatively little evidence of plant use in this context is available. Most isotopic profiles conducted so far have been produced from collagen, and thus reveal little information on the consumed macronutrients other than proteins that could have been obtained from vegetable resources. Macrobotanical remains that survive in a number of archaeological sites alleviate the gap in the scholarship, but surviving traces of plant use have limited interpretative power due to taphonomic bias (Weiss et al., 2004). The most comprehensive studies of dietary variability that incorporate plant foods stem from indirect lines of evidence, in particular dental wear studies. Macro- and microwear studies of dental surfaces have revealed that Neanderthals predominantly consumed meat, with a possible increased use of plant foods in the southern wooded parts of their range (El Zaatari et al., 2011; Fiorenza et al., 2011). Microwear of Neanderthals who inhabited cold-steppe environments resembled that of recent historic Fuegians who inhabited Patagonian cold wet scrublands (Grine, 1986; Fiorenza et al., 2011). However, dental wear is silent on the number and types of plants consumed, or if low- ranked foods were consumed, meaning these studies create an incomplete picture of dietary ecology in different environments.

Neanderthals appear to have broader diets in southern regions possibly due to ecological variation (Stiner, 1999, 2001; Fiorenza, 2015). Factors other than ecological variation, such as demographic pressure and available technology, can determine the proportion of food classes consumed by foragers (Kelly, 1995). One way to examine the relative influence of these factors is to assess the extent that eco-geography accounted for variation in food acquisition. Resource choice is a product of the demands of the individual foraging society, and an increasing population requires additional energy capture from its territory. Increased energy capture can be achieved by more intensive use of costlier resources, often with technological

specialisation; this model is termed 'broad spectrum foraging'. Flannery (1969) envisaged that broad spectrum foraging emerged first at the end of the Pleistocene, laying a foundation for domestication. Broad spectrum foraging is now thought to have emerged in intervals that occurred throughout the Upper Palaeolithic in Eurasia and earlier in Africa (McBrearty and Brooks, 2000). The first appearance of this pattern has been proposed in the southern Levant and Europe by about 45-30 ka (Stiner, 1999; Revedin et al., 2010) and North China by the Late Glacial Maximum (Liu et al., 2013).

As increasing high-resolution methods reevaluate the adoption of broad spectrum subsistence strategies, Middle Palaeolithic subsistence has received more attention. The actual appearance of broad spectrum diets may long predate the point at which they are currently visible in the archaeological record. Some researchers have pointed to Neanderthal charred legume assemblages from Kebara Cave (63-45 ka) and grass seed phytoliths from Amud Cave (70-55 ka), arguing that the broad spectrum economy was present already in the Late Middle Palaeolithic (Madella et al., 2002; Lev et al., 2005). Others have studied starch and phytolith microremains trapped in dental calculus, and found that Neanderthal dental calculus from sites such as Spy and Shanidar indicate the use of date palm and grass seeds in the Levant, and water lily tubers in northern Europe (Henry et al., 2011). Despite these promising insights into Neanderthal use of plants, these samples are too widespread in time and space to give reasonable coverage of potential variation in Neanderthal diets. It is noteworthy that they, these studies tell us little about the longevity of the Middle Palaeolithic dietary niche. Thus, it is unknown if Neanderthal exploitation of plant foods broadened over the hundreds of thousands of years they occupied Eurasia in response to higher populations or milder climates, similar to what is observed for the Upper Palaeolithic and recent hunter-gatherers, or if variation is only linked to different ecologies.

To explore the flexibility and stability of Middle Palaeolithic dietary breadth through environmental variation, we investigated plant consumption as recorded in dental calculus from environments with varied vegetation and winter and summer temperatures. We analysed plant microremains trapped in dental calculus from Neanderthal teeth from five archaeological sites: Vindija (Croatia), Grotta Guattari (Italy), Grotta Fossellone (Italy), Sima de las Palomas del Cabezo Gordo (Spain) and Kalamakia (Greece). These samples derive from a variety of regions and biomes across Europe: The Northern Balkans, and the western, central and eastern Mediterranean (Fig. 15). We then identified microremains to examine the variety of

consumed types or taxa. Once complete we compared this data with previously published results (Henry et al., 2014; Appendix 7.3) and finally explored if Middle Palaeolithic dietary breadth varied in different climatic and ecological conditions. We predicted that if Neanderthal diet was flexible, the number of plant types represented in the calculus should be greater in warmer, more arboreal environments. Furthermore, if their population gradually increased dietary breadth, the number of plant types represented in calculus should be higher at sites that are more recent.

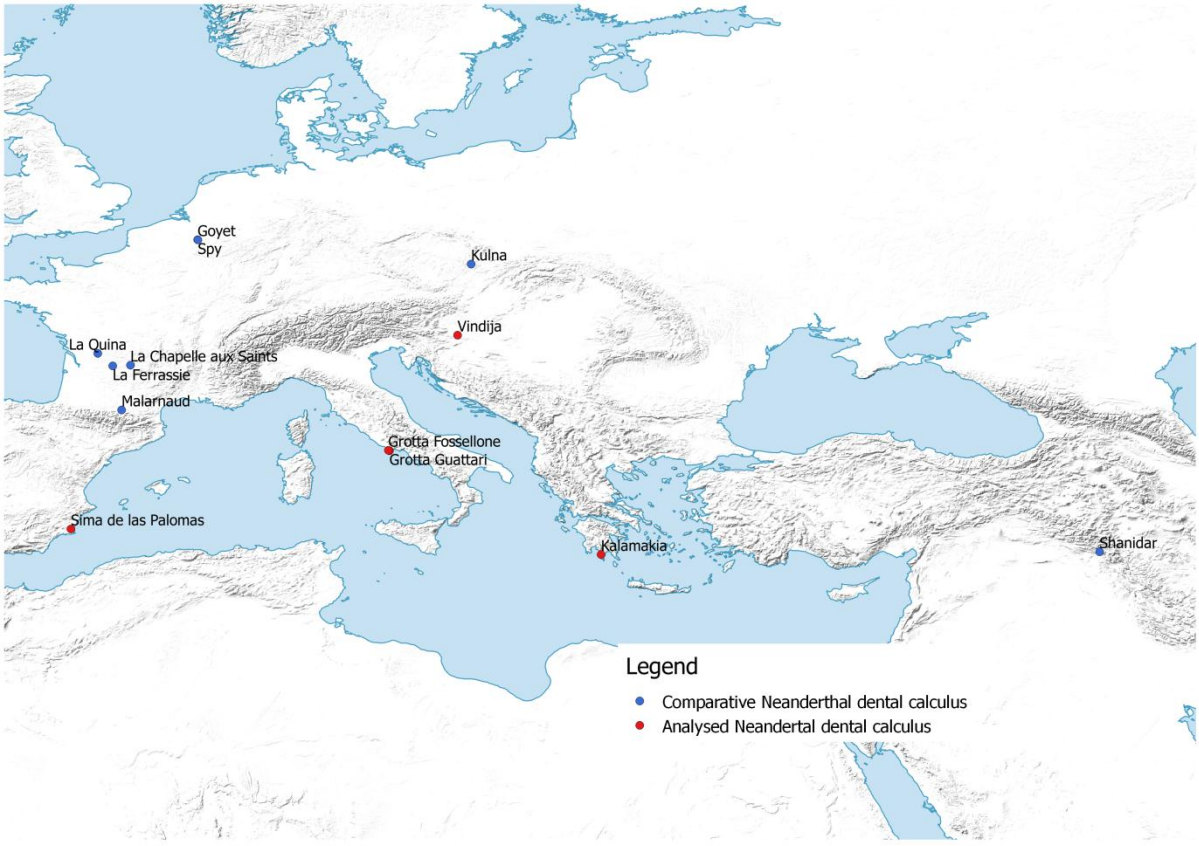


Fig. 15: Map of western Eurasia with the studied sites indicated.

5.2 Materials and Methods

5.2.1 Sites

Vindija Cave: this cave is situated on the southwest slopes of Kriznjak Peak in the Hrvatsko Zagorje region of northern Croatia (46°17'N, 16°6'E). Early exploration of the site began in 1928 with small-scale excavations. Malez and colleagues conducted large-scale archaeological excavations between 1974-1986 and 1993-1994.

These uncovered a complex of 10 m deep strata of 16 layers, with abundant palaeontological, archaeological and hominin material. A considerable number of hominin skeletal fragments was found in the cave deposits deriving from five or more individuals (Karavanić and Smith, 1998). A portion of this material was Mousterian-associated, and researchers identified the material as coming from Late Pleistocene Neanderthals due to its less pronounced archaic traits (Smith, Boyd, and Malez 1985). A radiocarbon date of >45.5 ka cal BP (Krings et al., 2000), and a U/Th date of a cave bear bone of 50.3 ka cal BP (Wild et al., 2001) have assigned layer G3 to MIS 3. Direct AMS ultrafiltration dating of hominin remains from layer G1 has assigned the most recent Neanderthals from this layer to 33,371 ± 399 - 35,382 ± 2224 ka cal BP (Higham et al., 2006). Archaeologists found Neanderthal material mostly in layers G1 and G3, but also four teeth in Layer F (of which we sampled two: 12.2 and 12.6). There was also modern human material in Layer D (MNI < 10). G3 is unambiguously Mousterian, while layers G1 and F contain some Aurignacian lithic material. However, dating and morphological evidence has firmly established the presence of Neanderthals in these layers, and cryoturbation is likely to have been responsible for bone displacement (Wolpoff et al., 1981; Higham et al., 2006; Frayer et al., 2010). Aurignacian lithic typology and early Upper Palaeolithic bone points are known in layers F and G1. The relatively low density of Aurignacian lithics, the mixing evident from contradictory dates, and the evidence of Neanderthal traits on the teeth (Frayer et al., 2010) suggest that the layer F teeth are in fact Neanderthal remains from layer G, so we feel comfortable including them also in our analyses. Excavators found red and giant deer (*Megaloceros giganteus*), elk (*Alces alces*), and aurochs (*Bos primigenius*) in layer G3, chamois (*Rupicapra* sp.), roe deer (*Capreolus capreolus)* and Merck's rhinoceros (*Stephanorhinus sp.*) in layer G1 and bison (*Bison sp.*), ibex and Merck's rhinoceros in layer F. Micromammals such as bank voles (*Myodes glareolus*) were found in layer G (Mauch Lenardić, 2014). These taxa are relatively unspecific but generally suggest continental conditions, and fauna such as roe deer and bank voles suggest at least a proportion of tree cover perhaps as parkland or riverine mosaics.

Grotta Guattari: this site is one of a complex of caves located in Monte Circeo, a limestone massif in Lazio, Central Italy (41°14'N, 13°05'E). The site was discovered in 1939 inadvertently when surface fauna and the remains of one Neanderthal (Guattari I) in layer G0 were discovered. Later explorations found more Neanderthals, firstly in a bone scatter (Guattari II) in layer G0, and subsequently in breccia (Guattari III) at the cave entrance (Sergi, 1954). Of the three Neanderthal

Guattari II and Guattari III were sampled. The cave has seven stratigraphic layers (G0-G5), but G0 is not vertically discrete partially due to carnivore disturbance (Stiner and Kuhn, 1992). Layers G1-G5 produced lithic artefacts and were deposited rapidly, but layers G6-G7 are beach deposits that accumulated more slowly (Stiner and Kuhn, 1992). Researchers identified the hominin remains as morphologically Neanderthal with a "classic" morphotype, suggesting they date to the Late Pleistocene (Howell, 1957). Stratigraphically below the fossils are the sequence's basal marine-influenced deposits (G7), which are thought to relate to the final high sea level event of oxygen isotope stage 5a [84-74 ka] (Martinson et al., 1987; Grün and Stringer, 1991). U-series and electron spin resonance dating of calcite encrustations on bones and mammal teeth from the stratum that produced Guattari I and II suggest a date of 60-50 ka, while Guattari III dates to the end of MIS 5, 74-60 ka (Grün and Stringer, 1991; Schwarcz and Schoeninger, 1991). Regional palynology studies indicate grasslands in cold periods and tree cover in warmer phases (Van Andel and Tzedakis, 1996; Follieri et al., 1998). A variety of fauna were found on site. Fauna such as ibex indicate mountainous open habitats, while boar (*Sus scrofa*) and roe deer, are thought to indicate tree cover or shrub. Other fauna may represent either open grasslands/parkland or mixed environments such as Merck's rhinoceros, aurochs and mammoth (*Elephas antiquus*). Extreme cold-adapted species like reindeer (*Rangifer tarandus*) or arctic fox (*Vulpes lagopus*) are absent on coastal sites in the region, demonstrating the absence of a bitter cold environment (Kuhn, 1991).

Sima de las Palomas del Cabezo Gordo: The site is a karstic vertical cave in the Permo-Triassic marble hill of Cabezo Gordo overlooking the Mediterranean Sea, in Torre Pacheco municipality, Murcia, SE Spain (37°47′59″ N, 0°53′45″ W). Much fossiliferous breccia was extracted from the 18-m-deep entrance shaft by 19th-century miners and discarded as rubble both on the hillside and inside the cave. Fortunately, inside the shaft there remained untouched a column of breccia in which was found a fossil (SP1) of a Neanderthal mandible fused to both maxillae. Subsequent sieving of rubble and systematic excavations by Walker and Gibert recovered Neanderthal skeletal elements, Late Pleistocene faunal remains, and Mousterian Middle Palaeolithic artefacts (Trinkaus and Walker; Walker et al., 2008, 2010, 2011a). The main in-situ archaeological layer has been dated using U-series and radiocarbon to between roughly 56 and 34 ka (Trinkaus and Walker). Three articulated Neanderthal skeletons were found in this layer: an adult woman (SP96; Walker et al., 1999, 2011a, 2012) lying over a child (SP97) below which lay another adult (SP92). The adult woman SP96 was directly dated using U-series to 54.1 ± 7.7

ka (APSLP1) (Walker and Ortega, 2011). Several taxa are typical of the Iberian Late Pleistocene (*Equus caballus, Bos primigenius*, *Capra pyrenaica, Cervus elaphus*, *Lynx lynx*, *Oryctolagus cuniculus* and *Testudo hermanni* etc.) whereas others occur that rapidly became extinct at the close of the early Late Pleistocene (*Panthera pardus, Crocuta crocuta, Stephanorhinus* sp., *Hippopotamus amphibius, Hystrix javanica*). Pollen from the uppermost sediments indicates presence of pines and moisture-dependent deciduous woodland (which is absent in the region today), and thermophylls characteristic of southeastern Iberian and North Africa that do not regenerate after frost (Carrión et al., 2003). Neanderthal teeth with carious lesions have been identified (Walker et al., 2011b). Teeth sampled for dental calculus come from excavated sediments except for one (SP50) recovered from the hillside rubble.

Kalamakia: this Middle Palaeolithic site is a cave on the western coast of the Mani peninsula in the Peloponnese in southern Greece (36°40'43.3"N 22°21'59.3"E). Archaeologists excavated Kalamakia from 1993 until 2006 (Harvati et al., 2009, 2013). Chronologists have dated basal deposits with U/Th radiometric dating to the MIS 5c transgression (109 + 14/−13 ka; De Lumley et al., 1994). Two of the five units produced substantial Middle Palaeolithic remains (Units III and IV). Excavation concentrated on Unit IV due to hard breccia in Unit III. Seventeen occupation levels were identified in the sedimentary deposits of Unit IV. In addition to fauna and Mousterian lithics, ten hominin teeth, crania and postcranial elements with diagnostic Neanderthal morphology were found, comprising of at least eight individuals, three of which we sampled for dental calculus (KAL 3, 5 and 8). Unit IV's youngest archaeological level has been dated to >39 ka (Harvati et al., 2013), placing KAL 5 and KAL 8 between MIS 5a (74 ka) and 39 ka. Excavators uncovered KAL 3 in Unit III, which overlies 5c beach rock and was truncated by sea transgressions in MIS 5a. Evidence of other truncations from sea transgressions from local caves implies that KAL 3 dates to the MIS 5b (Darlas, 2012). Faunal and palynological studies reveal that prevailing climatic local conditions were mild. Fallow deer (*Dama dama*) is particularly common in the assemblages, followed by ibex, wild boar, red deer, tortoise and some modified seashell. Maquis shrubland and Mediterranean pre-steppic forest species covered the peninsula (Lebreton et al., 2008). Extensive avian remains reveal evidence of tree cover in a predominantly open warm/temperate environment (Roger and Darlas, 2008).

From each site we collected a variety of control samples, including sediments from the sites, dust on the skeletal material, and samples of the material in which the

remains were stored (Appendix table 15, 16, 17, 18, 19). We also tried to sample dental calculus from the teeth of herbivorous and carnivorous fauna as an additional control and to explore if Neanderthals, like carnivores, consumed the stomach contents of herbivores (Buck and Stringer, 2014). Unfortunately, we were only able to access faunal material from Vindija and Sima de las Palomas del Cabezo Gordo. These samples included wolf (*Canis lupus*), which is mostly carnivorous but also known to consume some plant material; an unspecified feline (c.f. *Panthera*), which is nearly strictly carnivorous (Bocherens et al., 2011); and cave bear (*Ursus spelaeus*), which had a plant rich diet (Pacher and Stuart, 2009). In addition to the 30 Neanderthal calculus samples from the five sites that we processed for this study, we also included data from a variety of other northern European, Levantine, and southern European sites (Appendix 7.3.1) (Salazar-García et al., 2013; Henry et al., 2014).

In summary, our five sites represent a variety of environmental contexts. They range from more open temperate environment at Vindija to more Mediterranean mosaic woodland at Sima de las Palomas del Cabezo Gordo, and from cooler at Vindija to warmer at Kalamakia. This range reflects the bulk of environments Neanderthals occupied. We did not try to evenly represent different age classes or sexes, as often this information is not available.

5.2.2 Dental calculus and control sampling

Neanderthal teeth from each site were examined for deposits of dental calculus situated on the tooth surface in a cleaned lab of the institution where each specimen is curated. Deposits of dental calculus were common on teeth examined, but it was not present on all specimens. We documented the dental calculus deposits with photography before sampling. We then collected 14 samples of dental calculus from the Vindija Neanderthal teeth (levels F, G1 and G3), five from the Grotta Guattari teeth (levels G0), two from the Grotta Fossellone teeth (level 4), six from Sima de las Palomas del Cabezo Gordo teeth (Upper Cutting level 2 and I), and three from the Kalamakia teeth (Unit III and Lower IV) (Table 9). Many of the sampled teeth had a visible band of hard supragingival dental calculus, except the Iberian teeth that were encrusted in calcium carbonate. In these samples, we therefore took 'deep' and 'shallow' samples. "Shallow" samples were closer to the surface and likely to represent the sediment while "deep" ones were more likely calculus.

The sampling surface was gently dry brushed with a disposable toothbrush to dislodge contaminants at the sampling locations. We then used a dental scalar to remove small areas of dental calculus onto creased weighing paper underlain by aluminium foil. The material collected in the paper was then transferred to a microcentrifuge tube. After sampling, we photographed the teeth and the remaining unsampled dental calculus. We then transported the samples to the Plant Foods lab at the Max Planck Institute for Evolutionary Anthropology (MPI-EVA).

To minimize risk of contamination from airborne modern plant material and lab supplies (Langejans, 2011; Crowther et al., 2014; Henry, 2014), we conducted a regime of weekly laboratory cleaning. All lab work surfaces were cleaned with hot water, washed with starch-free soap and with 5 % sodium hydroxide (NaOH). To assess contamination types, we additionally performed wipe tests before and after weekly cleaning to quantify starch and other contaminants. Wipe tests retrieved settled particles of the surface area (74 x 43 cm^2) of the laboratory positive-pressure laminar flow hood used for mounting.

Table 9: Neanderthal dental calculus Grotta Guattari, Grotta Fossellone, Sima de las Palomas del Cabezo Gordo and Vindija analysed. Dates are ka cal BP.

Sample	Site	Specimen	Tooth	Weight (mg)
FON1	Grotta Fossellone	Fossellone 3	LL M1	0.067
FON2	Grotta Fossellone	Fossellone 3	LL M2	0.1
GTN1	Grotta Guattari	Guattari II	RL M3	0.654
GTN2	Grotta Guattari	Guattari III	RL M1	0.871
GTN3	Grotta Guattari	Guattari III	LL I2	0.654
GTN4	Grotta Guattari	Guattari III	RL I2	0.258
GTN5	Grotta Guattari	Guattari III	LL M1	0.289
KAL_3	Kalamakia	KAL 3	UL M3	2.866
KAL_5	Kalamakia	KAL 5	UR P2	0.05
KAL_8	Kalamakia	KAL 8	UR M2	N/A
Vja-13	Vindija	12.1	UR M2	0.393
Vja-14	Vindija	12.2	LR I2	0.046
Vja-16	Vindija	12.4	UR I1	0.046
Vja-17	Vindija	12.5	UR C	0.045
Vja-18	Vindija	12.6	LL C	0.02
Vja-19	Vindija	12.7	LL I2	0.89
Vja-20	Vindija	11.39	LR C	0.446
Vja-21b	Vindija	11.39	LR M1	0.408
Vja-21a	Vindija	11.39	LR M1	0.502
Vja-24	Vindija	11.45	LL M3	0.672
Vja-26	Vindija	11.46	UL M2	0.865
Vja-51	Vindija	11.4	LL M1	0.19
Vja-54	Vindija	11.4	LL M1	0.046
Vja-55	Vindija	11.4	LL M1	0.085
SP45	Sima de las Palomas del Cabezo Gordo	SP45	LR P3	0.08
SP54	Sima de las Palomas del Cabezo Gordo	SP54	LR C	0.102
SP78a	Sima de las Palomas del Cabezo Gordo	SP78	P4	0.415
SP79	Sima de las Palomas del Cabezo Gordo	SP79	I1	N/A
SP83	Sima de las Palomas del Cabezo Gordo	SP83	LR DM2	0.09
SP84	Sima de las Palomas del Cabezo Gordo	SP84	M2	N/A

5.2.3 Sample preparation and mounting

Using standard procedures (Power et al., 2014b) each sample was weighed and transferred to microcentrifuge tubes while in a clean laminar flow hood at the Plant Food Group Laboratories at the MPI-EVA. We then ground the samples with a micropestle in a 1.5 ml Eppendorf microcentrifuge tube containing ~30 µl of a 25 % glycerine solution to reduce sample loss due to static electricity. The samples were then centrifuged at 1691 x g (Heraeus MEGAFUGE 16 with TX-400 Swinging Bucket

Rotors) for 10 minutes. These samples were mounted on glass slides and examined under bright field and cross-polarized light on a Zeiss Axioscope microscope at 400 × magnification.

5.2.4 Identification and classification

We photographed and described recovered microremains using the international nomenclature codes (Madella et al., 2005; ICSN, 2011). Phytoliths were classified into conventional morphotypes, while we developed types to classify other microremains based on shared morphology. Starches were classified according to shape, the presence and prominence of lamellae, hilum morphology, formation type (i.e. simple or compound), cross features, cracks and other surface features. Some types are unique to a single plant taxon, but in other cases, several types may all have originated from a single taxon, or one type may be common to several taxa. For example, several phytolith types (short-cell, bulliform and psilate) may all represent a single species of grass. When possible, we identified the types to the lowest taxonomic level possible, usually family or genus (Appendix 7.3). Many categories of plant foods that could have been important have few or no microremains. These include lipid-, sugar-, and inulin-rich plants, like olives, walnuts, and Asteraceae tap roots. Images of all microremains are deposited on the Archaeological Microremain Database of the Plant Foods in Hominin Dietary Ecology Research Group in Leipzig.

Once we classified the microremains, we calculated ratios that may provide quantitative information about the assemblage. These included Menhinick's index, a richness metric common in ecological studies, which is the ratio of the number of taxa to the square root of sample size (Magurran, 2004). We used this index to compare samples to test breadth in each assemblage. We calculated total number of unique starch and phytoliths types. We also prepared ratios that are phytolith-specific such as the monocot: dicot phytolith ratio, which may indicate contribution of grasses, sedges and other monocots versus the contribution of flowering plants; and the variable: consistent morphology (v/c) phytolith ratio, which indicates taxon.

5.2.5 Palaeotemperature reconstruction

In order to best approximate the climatic conditions of each site, we used detailed climate simulations for western Eurasia created as part of the Stage 3 Project

(Van Andel and Davies, 2003). This project quantified climatic variables during much of the range of the last glaciation from 59 up to 24 ka, and generated four regional model simulations: a MIS 3 warm climatic event, a MIS 3 cold climatic event, the extremely cold Last Glacial Maximum (LGM), and finally a modern climatic model. These simulations are also created to model conditions in other periods such as Stage 4 (e.g. Aiello and Wheeler, 1995; Wales, 2012). Unfortunately, these models cannot account for third order climate fluctuations that occurred within these phases. However, when each simulation is examined for each Neanderthal site, we see that the variation in temperatures is driven more by the latitude and longitude of the site than by the specific climatic period. Therefore, despite being somewhat coarse-grained, these models allow us to quantify much temperature variation.

These simulations of temperature can be made more ecologically relevant by calculating effective temperature, a climatic predictor that evens out yearly temperature variation. Binford used this powerful measure to explain why recent forager subsistence varies latitudinally (Bailey 1960; Binford 2001). The necessary data to calculate effective temperature was unavailable so we developed modified effective temperature (MET) to adapt effective temperature for available palaeotemperature data. This differs from effective temperature in that it uses the mean of the three warmest and three coldest months instead of the warmest and coldest month. Modified effective temperature is identical to effective temperature in all other ways. Effective temperature is based on three constants- the minimum mean temperature (18°C) that supports tropical plant communities (a 365 day growing season), the minimum temperature (10°C) at the start of the growing season at the zonal boundary of polar and boreal environments and the minimum temperature (8°C) at the beginning of the growing season (Binford 1980, 2001). Modified effective temperature (MET) is as follows

$$MET=\{18* MST)-(10*MWT)\}/(MST-MWT+8)$$

where

MST is mean summer temperature (June, July and August)

MWT is mean winter temperature (December, January and February)

The Stage Three Project supplied mean temperature (ºC) 2 m above ground level from June through August and December through February for each climate

simulation. We matched plots of each simulation to the climatic phases covered in our sample set (Table 10, Table 11), and we collected relevant values from each simulation plot and then calculated modified effective temperature for each hominin sample (Table 11; Appendix 7.2).

Table 10: Stage 3 Project simulations used to predict average summer and winter temperatures experienced by each Neanderthal. Dates are ka cal BP. See Table 11 for the actual predicted temperatures per specimen.

Interval	Phase	Simulation model used	Date
MIS 5e	Eemian Interglacial	Modern	130-117
MIS 5d	Early Glacial Stadial Phase	Warm	117-105
MIS 5c	Early Glacial Interstadial Phase	Warm	105-95
MIS 5b	Early Glacial Stadial Phase	Warm	94-85
MIS 5a	Early Glacial Warm Phase	Warm	85-74
MIS 4	Transitional Phase	Warm	74-66
MIS 4	First Glacial Maximum	Last Glacial Maximum	66-59
MIS 3	Stable Warm Phase	Warm	59-44
MIS 3	Transitional Phase	Warm	44-37
MIS 3	Early Cold Phase	Cold	37-27
MIS 2	Last Glacial Maximum	Last Glacial Maximum	27-16

Table 11: Palaeoenvironment reconstructions for each specimen used in this study. Tree cover: O=open, C=closed, M=mixed. P=publication, 1=this study, 2=Henry et al., 2014, 3=Salazar-García et al., 2013. Dates are ka cal BP.

Specimen	Site	Date	Tree cover	Palaeotemperature		MET	P
				Dec- Feb	June- Aug		
Fossello 3	Grotta Fossellone	70	O	-6	16	11.6	1
Guatt II	Grotta Guattari	55	O	-4	16	11.71	1
Guatt III	Grotta Guattari	67	O	-6	16	11.6	1
KAL 3	Kalamakia	91	O	4	20	13.33	1
KAL 5	Kalamakia	63	O	4	20	13.33	1
KAL 8	Kalamakia	63	O	4	20	13.33	1
12.1	Vindija	34.3	O	-8	20	12.22	1
12.2	Vindija	34.3	O	-8	20	12.22	1
12.4	Vindija	34.3	O	-8	20	12.22	1
12.5	Vindija	34.3	O	-8	20	12.22	1
12.6	Vindija	34.3	O	-8	20	12.22	1
12.7	Vindija	34.3	O	-8	20	12.22	1
11.39	Vindija	45.5	O	-8	20	12.22	1
11.45	Vindija	45.5	O	-8	20	12.22	1
11.46	Vindija	45.5	O	-8	20	12.22	1
11.4	Vindija	45.5	O	-8	20	12.22	1
SP45	Sima de las Palomas del Cabezo Gordo	50	C	4	16	12.4	1
SP50	Sima de las Palomas del Cabezo Gordo	50	C	4	16	12.4	3
SP53	Sima de las Palomas del Cabezo Gordo	50	C	4	16	12.4	3
SP54	Sima de las Palomas del Cabezo Gordo	50	C	4	16	12.4	1
SP58	Sima de las Palomas del Cabezo Gordo	50	C	4	16	12.4	1
SP60	Sima de las Palomas del Cabezo Gordo	50	C	4	16	12.4	3
SP68	Sima de las Palomas del Cabezo Gordo	50	C	4	16	12.4	3
SP74	Sima de las Palomas del Cabezo Gordo	50	C	4	16	12.4	3
SP78	Sima de las Palomas del Cabezo Gordo	50	C	4	16	12.4	1
SP79	Sima de las Palomas del Cabezo Gordo	50	C	4	16	12.4	1
SP83	Sima de las Palomas del Cabezo Gordo	50	C	4	16	12.4	1
SP84	Sima de las Palomas del Cabezo Gordo	50	C	4	16	12.4	1
SP88	Sima de las Palomas del Cabezo Gordo	50	C	4	16	12.4	3
SP100	Sima de las Palomas del Cabezo Gordo	50	C	4	16	12.4	3
Kůlna 1	Kůlna	45	O	-8	16	11.5	2
GoyetVII	Goyet	40.5	O	-8	12	11.5	2
Chapel 1	La Chapelle-aux-Saints	57	O	-4	12	10.57	2
Malarn 1	Malarnaud	75	M	-4	12	10.57	2
LFI	La Ferrassie	39	M	0	12	10.8	2
LFII	La Ferrassie	39	M	0	12	10.8	2
Quina V	La Quina	64	M	-4	12	10.68	2

5.2.6 Palaeoenvironmental reconstruction

In contrast to temperature, we assessed tree cover using all published data on the habitats that existed at each site. We used investigations of macromammals, micromammals and pollen that record palaeovegetation at different scales from local and regional studies to classify each environment. Based on the prevalence of tree cover we assigned each sample as coming from open, mixed or closed habitats (Table 11).

5.2.7 Statistical analysis

To explore the relationships among environment, trends in foraging breadth, and microremains found in our samples and those from previous studies (Salazar-García et al., 2013; Henry et al., 2014) we fitted an Observational random effect Poisson model with likelihood ratio tests, using the glmer function of the R package lme4 (Bates et al., 2013). We chose this Observational model because it is appropriate for count data, like ours, which is not normally distributed, and instead is skewed towards zero. We only included those samples that had been weighed prior to processing, and for which the recovered microremains were assigned to specific types. If any dental calculus samples produced no microremains, they were included as zero values. Our full model included modified effective temperature, the chronological time period in which the age of the Neanderthal lived and tree cover (open, mixed or closed) as fixed effects. It also included the weight of each dental calculus sample as model offset to factor in significant differences of sample dental calculus. We prepared the data by z-transforming age and modified effective temperature. The site and analyst were treated as random intercept terms. The weight of the dental calculus sample in mg was included as an offset. An id was assigned to each observation, and this was also included as a random intercept, thus removing overdispersion (x^2=30.62, df=44, dispersion parameter=0.696). To test the significance of the full model, it was compared with a null model excluding fixed effects of modified effective temperature, age of each fossil specimen and tree cover. Variance inflation factors (VIF) were derived to assess collinearity, from a standard linear model minus random effects and offsets. Variance inflation factors indicated collinearity to not be an issue (largest VIF=1.27). We tested model stability by excluding levels of random effect one by one from the data set, running the full model and comparing the results with those from the original model that suggest no highly influential cases. To allow for the possibility of mixing between layers F, G1

and G3 in Vindija Cave we built an identical model except that samples from F and G1 derive from G3. We performed similar checks on this alternative model as the previous model. We removed overdispersion on this model (x2=32.90, df=0.89, dispersion parameter=0.748) and ensured VIF was not an issue (largest VIF=1.371).

5.3 Results

5.3.1 Contamination controls

Vindija Cave: We collected some samples of faunal calculus, as well as adhesives used to hold Vindija tooth 11.39 (Appendix 7.3.4). Bear, wolf and felid samples from Vindija yielded 81 plant microremains, but these were disproportionally more common on bear than wolf samples, consistent with the expected diets of these species (Pacher and Stuart, 2009).

38 phytoliths were found in bear and wolf samples. Multicellular polyhedrons were abundant in one bear sample, reflecting rich consumption of dicot fruit and leaves. Multicellular polyhedrons are rare or absent in most wolf samples except Vja-12-31. We found a small number of dicot phytoliths in a few other wolf samples. Present-day wolves consume plant matter, and plants may comprise up to 40 % of their food intake in certain seasons (Meriggi et al., 1991). European wolves especially favour fruit, but wolves may also consume plants in stomach contents or intentionally consume grass to smooth digestion or ease parasites (Murie, 1944; Stahler et al., 2006).

Starches were particularly uncommon in these fauna samples. Most were small nondiagnostic types. A Triticeae grass aggregate was found in a wolf control sample (Vja-30). Total numbers of starches found and the number of starches per milligram were lower than in Neanderthal samples (Appendix 7.3.4). Furthermore, the faunal samples appear to share similar starch types (1-7 types), while the Neanderthal calculus had more varied starches (1-15 types). Two control samples of mandible adhesive revealed 56 contaminant starches but nearly all of these were heavily damaged potato starch. These starch are morphological distinct from those in the Neanderthal dental calculus samples (Appendix table 15, Appendix table 16, Appendix table 17, Appendix table 18, Appendix table 19).

Grotta Guattari and Grotta Fossellone: We took a variety of control samples, though not all preferred control types (e.g. faunal teeth) were available. Most controls were samples of adhesives used to bond bone, or washes of distilled water

taken from the surfaces of the sampled mandibles. These contamination assays produced no or few microremains, and where microremains were found they showed a narrow range of types (Fig. 16; Appendix 7.3.4). We found that these samples contained few types of starch, and contaminating grains appeared distinctly fresh and usually occurred as starch aggregates unlike more damaged and isolated starch in dental calculus samples. A Triticeae grass seed starch aggregate was found in controls 2e and Fon3. None of this type of aggregates were found in hominin samples.

Sima de las Palomas del Cabezo Gordo: In addition to controls (non-worked stone from archaeological strata, carnivore dental calculus and packing cotton) published in Salazar-García et al., 2013, we sampled carnivore dental calculus and sediment found attached to hominin teeth. One sediment sample produced a single isolated subspherical starch. These results show a very low rate of background starch and phytoliths.

Kalamakia: We did not have access to any contamination control materials for Kalamakia.

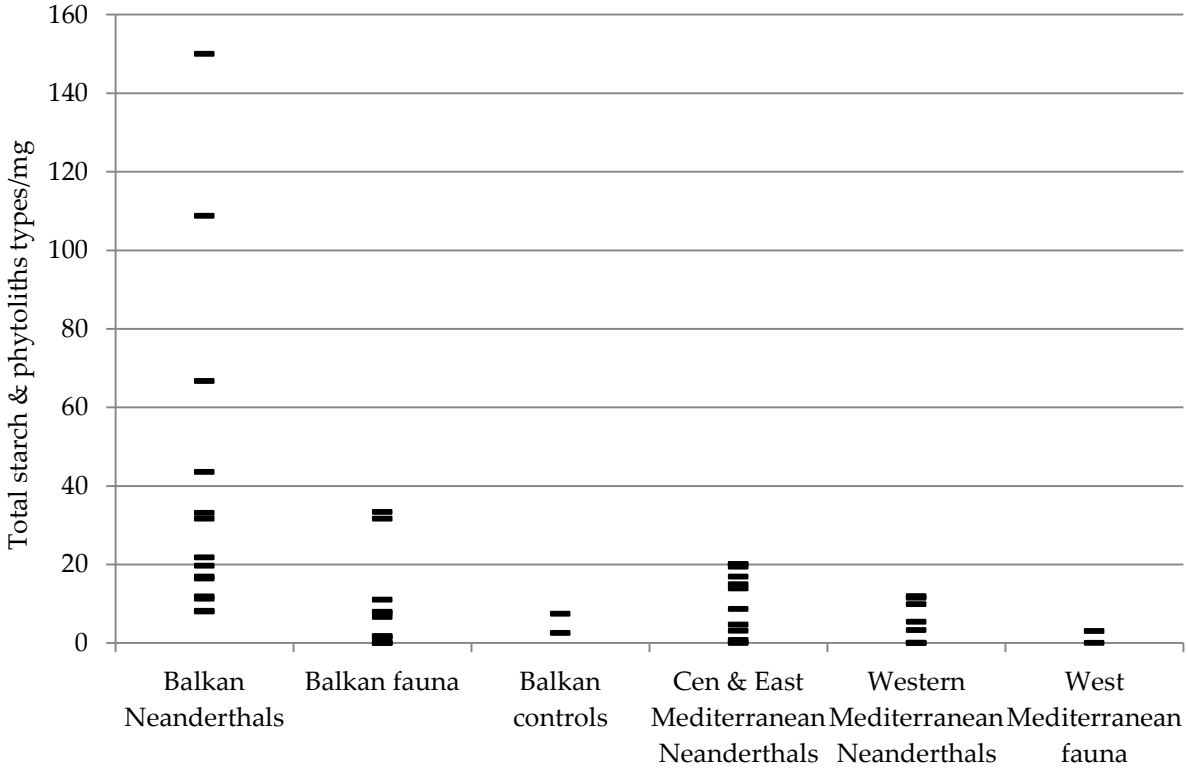


Fig. 16: Starch and phytoliths from Neanderthal calculus, fauna calculus and controls show that Neanderthal dental calculus samples show a distinct signal indicating they reflect hominin diet.

5.3.2 Dental calculus microremain assemblages and dietary breadth

Vindija Cave: We collected calculus from six isolated teeth and five *in situ* teeth (Table 9). Isolated teeth included a right second molar, a lower second incisor, upper first incisor, upper canine, lower canine, and lower second incisor. Our sample of *in situ* teeth included a lower canine, a lower third molar, an upper second molar, and a lower first molar. Microremains were recovered in all Neanderthal dental calculus samples but there was major variation in the numbers and classes present. The plant microremain assemblages found on the Vindija samples is considerably more diverse than what was reported in the previous studies of Neanderthal calculus (Hardy et al., 2012; Henry et al., 2012, 2014; Salazar-García et al., 2013).

229 microremains were found in Vindija dental calculus samples, including 87 starch microremains (Appendix 7.3.4). 15 starches displayed a lenticular cross-section, circular or subcircular plane view, a hilum exhibiting a thin line, and distinctive surface dimples and lamellae, clearly representing starches from Triticeae grass seeds (Fig. 5). Although grass leaf microremains may arise from non-edible resources such as bedding, this seems unlikely to be the case for grass seeds.

Two of the starches are likely to derive from a legume based on their characteristics: circular, oval, ovoid shape, the presence of lamellae, and the characteristic longitudinal cleft fissure. We have observed these traits in peas (*Pisum* sp.), vetches (*Vicia* sp.), and sweet peas/vetchlings (*Lathyrus* sp.). Three other starches (Fig. 17) displayed the size, highly faceted surface and polyhedral shape consistent with those of starches from hard endosperm (Eliasson and Larsson, 1993). Plants that produce this starch morphology include nuts, hard seeds, seeds from grasses not in the Triticeae tribe, and seeds of sedges like *Schoenoplectus*. Two starches from underground storage organs were evident from large elongated shapes and highly eccentric polarisation crosses. None of these legume, hard endosperm, or underground storage organ starches had specific enough morphological characteristics to identify them to a lower taxonomic category. The remaining starches fall into nine groupings, probably reflecting several taxa, but due to starch damage, redundant types and a limited reference collection, they cannot be identified. Five starch types also found in Neanderthal samples were also found in cave bear samples, but these were nondiagnostic types.

We recovered 91 phytoliths from the Vindija dental calculus samples (Appendix 7.3.4). Thirty-two of the 91 were long cell morphotypes, which are

common in the leaves of monocots. However, because monocots produce more phytoliths than dicots per gramme (Tsartsidou et al., 2007), they are more visible in the archaeological record. Phytolith production between the two categories varies from 80:1 to 20:1 (Tsartsidou et al., 2007). Ratios of monocot to dicot in our sample of Vindija Neanderthal dental calculus vary from 5:1 to 0.67:1, which suggests an abundance of dicot types such as fruits, nuts and leaves rather than grasses and sedges.

Twenty-five spores were also found, representing approximately five types of fungus. However, these are nondiagnostic and could represent mushroom-bearing higher fungi or lower fungi such as moulds. Pollen was rare and only one Betulaceae pollen was found. Ten unsilicified plant tissue fragments were recovered, two reflecting grass and one an unspecific monocot, but others were indeterminate.

Grotta Guattari and Grotta Fossellone: We examined the calculus from the right lower third molar of Grotta Guattari II and the lower first molars (right and left) and lower second incisors (right and left) of Grotta Guattari III. Calculus samples from the five teeth from Grotta Guattari produced high numbers of microremains and high levels of diversity per mg. A total of 151 microremains were found in the dental calculus of the five teeth (Appendix 7.3.4).

Starch grains were found on four of the five teeth and totalled to 69 grains. Six starches found in an amyloplast cell were elongate ovoid in plane-view and oval in cross-section, with an eccentric polarisation cross, all characteristics matching *Lilium* type starches (Fig. 3). One starch clearly represented a Triticeae grass seed starch. Further evidence of grass use is evident from intact grass leaf tissue found in one sample. The other detected starches represented five unknown types.

Thirty-nine phytoliths were recovered, 31 of which originated in monocot tissue and eight from dicot plants. Nine short cell rondel phytoliths were identified. One phytolith was a multicellular epidermal jigsaw morphotype, indicating dicot leafy or fruit matter. We also note the presence of a tracheid vessel, which is another dicot marker.

Other microremains were numerous. Ten spores were observed, some of which exhibited features that enabled us to identify them as coming from bracken (*Pteridium* sp.). We also noted the presence of spores from *Nigrospora* sp. We also identified other spores such as fusiform spores, indicative of boletoid fungi. Many bolete fungi are edible and widely consumed, while *Nigrospora* is a diverse genus of

fungi that are mostly agents of decay. Five pollen grains were found including two Betulaceae pollens. In total 14 other cellular plant tissue fragments were noted, including vascular bundles reflecting plants that entered the mouth. Also recovered were a number of stellate hairs and a pennate diatom.

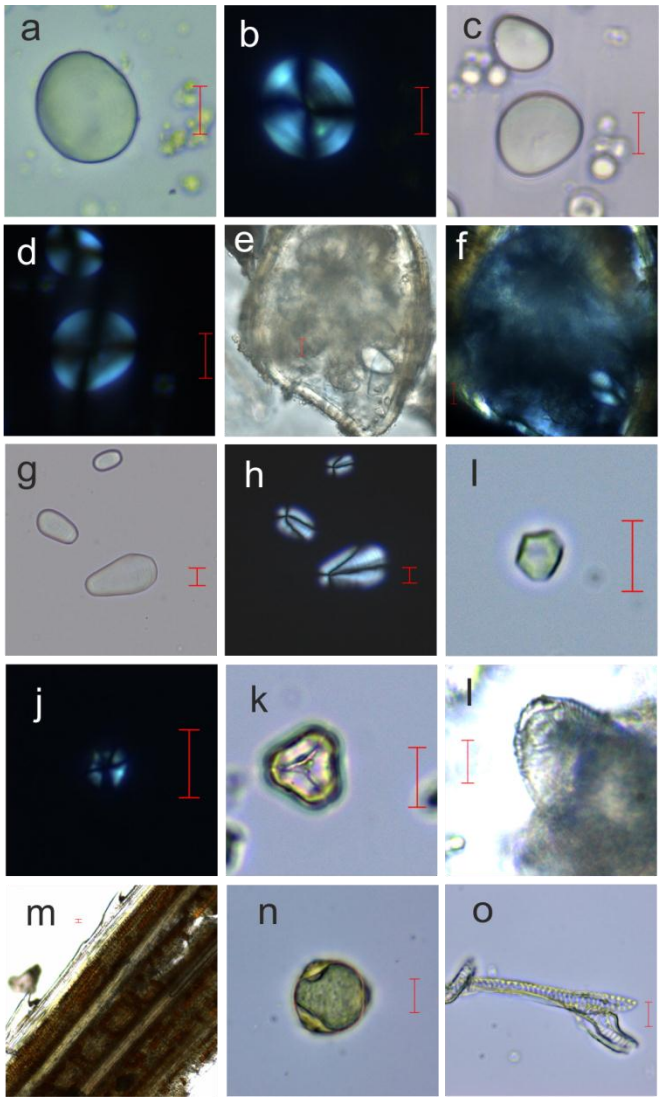


Fig. 17: Mosaic of microremains and comparative modern reference plant matter. Each scale bar represents 10 µm. (a) Starch from Vindija Neanderthal identified as Triticeae under bright field and (b) cross polarized light, (c) a reference Triticeae starch (*Triticum turgidum* sp.) under bright field and (d) cross polarized, (e) Amyloplast with several ovoid starches resembling *Lilium* bulb starches under bright field and (f) cross polarized light, (g) reference *Lilium* sp. bulb starches under bright field and (h) cross polarized light, (i) polyhedral starch under bright field and (j) cross polarized light, (k) *Pteridium* sp. spore, (l) diatom embedded in calculus, (m) fragment of grass leaf, (n) triporate Betulaceae pollen, (o) Unsilicified tracheid plant tissue.

Grotta Fossellone: We sampled dental calculus from the left lower first molar and second molar of Grotta Fossellone III. Eleven starches were found in the two

Grotta Fossellone dental calculus samples. These comprised of indeterminate starches that cannot yet be matched to reference material. Only one phytolith was found in the assemblage: a rondel phytolith from a grass. Additionally, one piece of monocot and one piece of unidentified plant tissue were found.

Sima de las Palomas del Cabezo Gordo: For this study, we sampled dental calculus from six hominin teeth, including a lower third premolar, lower canine, lower deciduous second molar, a lower forth premolar, an upper first incisor, and a lower first molar. We found relatively few microremains in these samples, reflecting the very small amount of dental calculus in each sample. We recovered only five starches and phytoliths, and one diatom. None could be identified to plant taxon.

Kalamakia: We sampled dental calculus from three Kalamakia teeth - an upper molar (KAL 3), an upper fourth premolar (KAL 5) and an upper molar (KAL 8). Only five starch grains were found on the three teeth. Two phytoliths were also found: one from a grass and one from a non-monocotyledon plant. Sixteen possible calcium oxalate forms were found. Calcium oxalate represents consumed plant matter, but it is readily soluble and occurs in most plants, and is therefore not assignable to taxon. Lastly, we found one fragmented sponge spicule. This last microremain likely entered the mouth through accidental consumption.

5.3.3 Dietary flexibility and dietary niche stability

We predicted that if the breadth of Neanderthal plant use was driven by ecological conditions, then the number of consumed types should be influenced by temperature and tree cover. We produced a Menhinick's index comparison of all available samples, including all previously published data and the new samples from this study. Although there is no distinct trend among Neanderthals from different periods or chronologies (Fig. 18; Appendix 7.3.4), there is a possible curvilinear relationship, with the Menhinick's index /mg increasing with temperature until a peak is reached, at which point the index drops again. It is possible this pattern reflects the degradation of starches in the warmest environments (Langejans, 2010).

We condensed the list of samples to include only those with documented weights (Wt column, Appendix 7.3.4). We then used an observational random effect Poisson model to test dietary breadth patterns (described above). We find no relationship between the number of microremain types found in calculus and the

chronological age or environmental conditions of the sample, even when accounting for the effects of variation between tree cover, sites, analyst, age, and weight of the dental calculus sample (Appendix table 20). More specifically, an increase in temperature did not lead to an increase in the number of types represented in dental calculus and younger sites did not show an increase in the number of types represented in dental calculus (x^2=5.148, df=4, P=0.273; Appendix fig. 3; Appendix table 20). Even in the alternative model, which assumed bones in Vindija Cave layer G1 are older than thought and derive from G3, there was still no relationship (x^2=2.683, df=4, P=0.612; Appendix fig. 3; Appendix table 20).

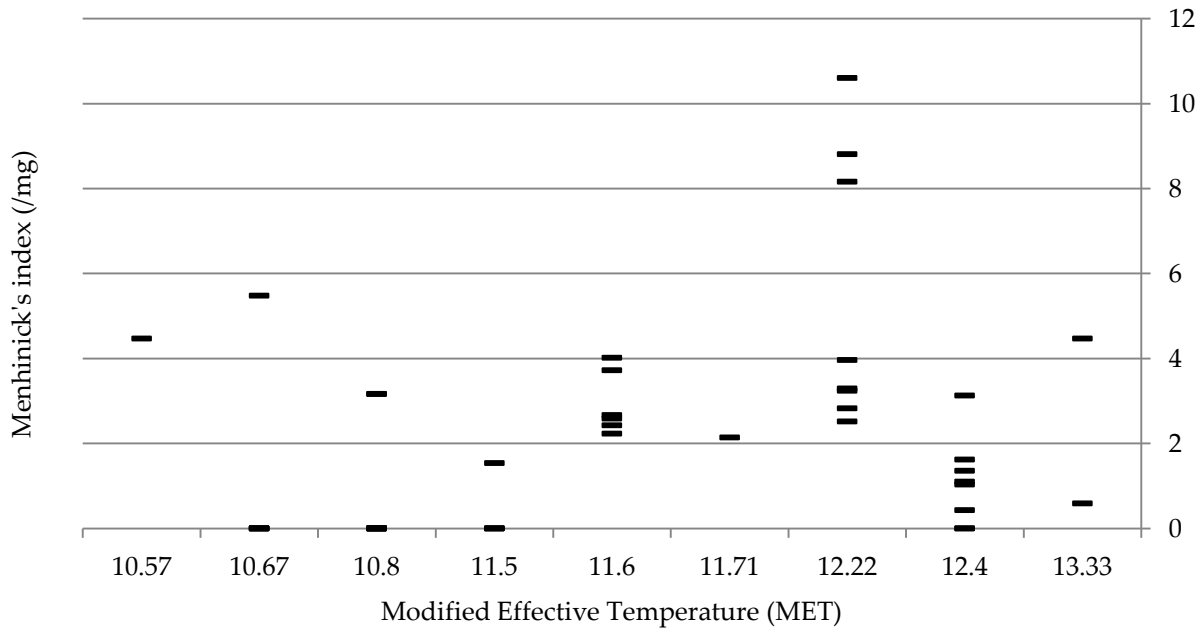


Fig. 18: A Menhinick's index of types of starch and phytolith from Neanderthal dental calculus shows that warmer climates are not associated with increased diversity. Samples are from Neanderthal remains presented in this study and Salazar-García, et al., 2013 and Henry et al., 2014. Each dash represents an individual sample.

5.4 Discussion

Microscopy revealed starch and phytoliths in most samples but many samples were highly variable. Fig. 16 and Appendix fig. 3 shows that many dental calculus samples from Grotta Fossellone, Sima de las Palomas del Cabezo Gordo and Kalamakia yielded few microremains. Previous work that established baselines with chimpanzee (Power et al., 2015b) and living human (Leonard et al., 2015) populations indicates that this stochastic pattern is normal. These studies also

emphasize that we have not recovered information on the majority of consumed plants when using this approach.

Our previous work with chimpanzees indicated that age influences the microremain record, with older individuals having more microremains and more plant types represented. Though we do not have precise age estimates for the individuals in this study, all of the teeth were from adults. Furthermore, we have no reason to expect that any site was biased towards individuals from one particular age class. Taken together, these data suggest that the differences among the sites do not reflect simple age differences within our sample.

By using this metric of dietary breadth we were able to show that Neanderthals in warmer environments who had better access to arboreal edible resources might not have used a broader range of plant foods than Neanderthals from colder environments, and in some cases they even show less diversity than cool climate ones. This picture could arise by methodological limitations of this approach, since it is possible that plant remains such as starches are underrepresented in samples from warmer environments due to worsened taphonomic conditions (Smith et al., 2001). However, the phytoliths follow a similar pattern in our results, despite being insensitive to temperature, suggesting that the observed pattern in our study samples is due to dietary, not post-depositional, trends. Our results on microremain diversity do not negate occlusal dental wear findings that link tree cover to plant use, as occlusal wear only approximates classes of the total diet and not its composition. The availability of Pleistocene plant foods, however, likely reflects forest type (Mediterranean or Boreal) far more than tree cover alone. Open and mixed environments have less primary biomass than closed canopy environments, but they may offer significantly more edible plant biomass, as much of the biomass in forests consists of tree trunks, and is thus unavailable to hominin consumers (Odum, 1975). Pleistocene aridity may also have encouraged plant use; amongst recent foragers at a given latitude plant consumption usually increased in more open environments, largely because aquatic animal foods are less available in these dryer habitats (Keeley, 1992).

The plants used indicate how Neanderthals sourced nutrition from their environment. We find evidence of the use of grass seeds, true lily tubers, legumes and other starchy plants that leave no taxon-attributable types. Other microremains types included pollen and spores. Spores from Guattari III suggest interaction with fungi but these spores are too rare to ascertain the presence of deliberate interaction

with fungi such as the consumption of mushrooms (Power et al., 2015a). Not all recovered microremains reflect intentionally consumed food. Recovery of Betulaceae pollen and bracken spores may highlight use of birch, or hazel and bracken, but as these particles are excellent dispersers, they probably simply reflect characteristics of the airborne suspensions and aerosols in the Pleistocene airborne environment.

Some of the types we were able to identify also tell us about Neanderthal dietary behaviour. In particular, many of the microremains come from low-ranked foods, like grass seeds and tubers (Simms, 1985). Grass seeds are widely used by recent foragers in warm and cool environments (Lothrop, 1928; Simms, 1985; Harlan, 1989; Brand-Miller and Holt, 1998). Grass seeds used at Vindija and at Guattari demonstrate an investment in a low-rank plant food in cool habitats of the northern Balkans and coastal Italy. The use of grass seeds is often linked to terminal Pleistocene Southwest Asian foragers invested in broad spectrum diets because grass seeds are usually costly to harvest and prepare for consumption (Simms, 1985). On the other hand, there is abundant evidence that groups like the Vindija Neanderthals were big game hunters and that energetic contribution from plants is not likely to have rivalled meat. Middle Palaeolithic foragers probably only used grass seed as a limited component of the broader plant diet as this resource offers limited nutritional return (Simms, 1985). This is the same pattern observed in Upper Palaeolithic human foragers of Southwest Asia where grass seed use is most prominent (Savard et al., 2006; Rosen, 2010).

Overall, there is no indication that Neanderthals gradually used a more diverse array of plants, despite some evidence of a modest increase in population from 70 ka onwards (Foley and Lahr, 2003; Van Andel and Davies, 2003; Speth and Clark, 2006). The possible absence of a chronological trend in vegetal dietary breadth agrees with the lack of a trend in their predation niche prior to 55 ka. Yet dental calculus may hint that Neanderthal vegetal dietary breadth diverged from the narrow spectrum hunting economy. While the exploitation of small, fast and hard-to-catch game necessitated a costly increase in technology, some plants can be harvested and processed without technological investment. Although this may contradict conventional expectations of glacial period foragers in Central Europe, the cold temperatures of Pleistocene Eurasia may mislead us on the ecological productivity of this region. The pattern is better explained by decoupling seed and nut use from the dietary expectations of broad spectrum diets. Low intensity use of plants outside broad spectrum diets is possible (Hockett and Haws, 2003; Revedin et

al., 2010). Although an expanding plant food niche may be a sign of demographic packing population increase, its presence need not signify a total investment in complex foraging/broad spectrum foraging if such plant exploitation was possible without costly plant harvesting and processing technology (Hockett and Haws, 2003). Non-intensive use of these plants was possible with the technology available to Neanderthals.

Neanderthals could have reduced their processing costs by making use of caches of USOs and seeds, such as rodent stores (underground winter food stores), and by choosing to harvest the plants during seasons when they were easiest to prepare. The raiding of rodent stores requires little technology, though it often requires considerable ecological knowledge (Jones, 2009). For example, Siberian peoples raided rodent stores to obtain *Lilium* tubers all year round (Ståhlberg and Svanberg, 2010, 2012), but they had to be able to discern edible tubers from toxic USOs. Neanderthals ecological knowledge may have also been useful for the consumption of grass seeds. As Neanderthals exhibit no evidence of plant processing or food storage, we propose Neanderthals collected these seeds without laborious and expensive processing costs. One of the few ways this is possible is by plucking green grain from spikelets before they ripen and harden (Rosner, 2011). Unlike ripe grain, green grain requires no grinding or pulverising and may be consumed once dehusked, which can be done by hand. Green grain starch grains are smaller than those of ripe grain but they share most morphological characteristics and are likely to be identified as Triticeae with our methodology (Evers, 1971). Green grain is a resource that is only available in a narrow window before the grain ripens into a hard dry grain (Rosner, 2011). This collection of green grain would be suggestive of precisely seasonally organized Neanderthal foraging. Unfortunately, there is insufficient data to reconstruct a seasonal round of plant food gathering, but gathering during at least the spring is evident

5.5 Conclusions

The dental calculus microremain assemblages present strong evidence of Neanderthal use of various plants as foods, and complement our understanding of Neanderthal subsistence. This suggests that plant-harvesting strategies existed alongside their hunting economy. Plant foods were likely valued for their micro- or macronutrient profiles rather than caloric energy alone. Hominin physiology limits the total dietary protein intake, impeding an absolute reliance on protein-rich foods

such as terrestrial mammals lean meats (Cordain et al., 2000; Speth, 2010; Hockett, 2012). Recent foragers have avoided the effects of protein overconsumption by incorporating other macronutrients in diet. Foragers often source animal fat as the preeminent strategy for offsetting risk of protein poisoning (Speth and Spielmann, 1983; Cordain et al., 2000). However, animal fat from a diet of terrestrial ungulates may have been insufficient. Triticeae, Fabaceae and Liliaceae offer rich sources of carbohydrates that may have offset the problems of lean protein consumption.

The incorporation of diverse plant foods including those with low- or middle–ranking returns into the human diet probably predates Neanderthal diets, has a long history in the human lineage, and is likely that such diets persisted throughout hominin evolution mediated by energetic ecological necessity and labour availability. Similarly, resource depletion-driven subsistence changes may have occurred at many points in hominin evolution. Indeed it is observed elsewhere in Homininae, in present day chimpanzees, where increases in chimpanzee populations have been linked to increased use of low ranked prey (Watts and Mitani, 2015).

Regarding Neanderthal subsistence, we find no evidence of variation throughout the final 60,000 years they occupied Eurasia. Our model also finds no indication that plant use was confined to certain parts of their range. Surprisingly we did not find that a more diverse range of types were consumed in southern areas. Although this may suggest dietary inflexibility, it could also reflect relatively unchanging strategies, stable thanks to their success. While past research has revealed unappreciated variability in Neanderthal animal food use (Stiner, 1994; Speth and Clark, 2006), as a whole animal food provision centred on hunting of large and medium-sized game and thus Neanderthals exhibit lower intensity of diverse resources than early modern counterparts in Eurasia (Richards et al., 2000, 2001). A large- and medium-sized game hunting economy supplemented with plant foods may have evolved as a specialisation strategy in response to Eurasian environments (Stiner, 2013).

6

Discussion: A pathway for reconstructing Neanderthal Dietary Ecology

This dissertation opened with the great conundrum of Neanderthal ecology. How can Neanderthal diet be defined and its apparent distinctiveness explained when surviving evidence is so incomplete? By now, it is observable that most of the surviving evidence illustrates diets that are unrealistically carnivorous. Instead of relying solely on evidence that is intractable, it is necessary to extrapolate diet from indirect lines of evidence, ethnographic analogy and alternative methodologies such as dental calculus analysis, which is the focus of this work. The work presented above aimed to improve the method of analysing plant microremains trapped in dental calculus as a means to reconstruct diet, and then apply the lessons learned from methodological exploration to a study of the diets of Neanderthals. Each of the individual research projects contributed to the greater whole, while simultaneously raising its own issues and concerns; some of which will be discussed below.

6.1 Developments in dental calculus analysis and dietary reconstructions

The publication of applications of dental calculus analysis has greatly outpaced the progress of its theoretically and methodologically driven justification. There is a shortage of data on the extent that dental calculus analysis methodologies retrieve dietary debris that is present in dental calculus (Hardy et al., 2009; Henry, 2014; Leonard et al., 2015). This problem implied that a central part of the dissertation needed to bridge the increasing use of dental calculus for dietary inferences and the characteristics of dental calculus that allow it to trap foods; necessitating. One outcome is that this dissertation built a practical framework that allows reliable analysis of the dental calculus record in spite of its variability.

Improving the methodology available for dental calculus research has broadened the role that dental calculus can play in reconstructing the life history of Palaeolithic hominins. These validation studies enhance our ability to make inferences about Neanderthal diet because they provided information on the limitations of dietary interpretation from microremains preserved in dental calculus.

The methods appraisal undertaken with chimpanzee calculus from the Taï Forest in Côte d'Ivoire, and human dental calculus from the Chalcolithic site of Camino del Molino in southeastern Iberia (Power et al., 2014b), revealed insights to the microenvironments and structures in dental calculus that preserve food debris and other markers of life history. High-resolution analysis identified numerous microremains *in-situ* on the outer extents of dental calculus matrices. The identification of these remains shows how dental calculus preserves complex and diverse assemblages of plant, animal, and fungal microremains, all of which are useful for studying life histories of our ancestors. The comparative approach established that microremain types retrieved are a product of chosen sample preparation and microscopy technique. In particular, I noted that a combined SEM-OM approach was most useful for researchers interested in a variety of microremains, but that OM alone was a swifter and better technology for identifying the taxonomic origins of starch grains, which can be important in reconstructing diet. The study showed that researchers must customise their analytical technique to the desired suite of microremains (Power et al., 2014b). A sequential workflow translated these findings into an effective means of revealing underrepresented types relating to consumed food and water as well as the local environment (See 3.4).

The dissertation has built upon this exploration by investigating the representativeness of dental calculus as a dietary record. My work accomplished this by closely matching recorded diet to the plant microremain assemblages in dental calculus, using wild chimpanzees from the Taï Forest as a validation population (Power et al., 2015b). The project was able to compare over two decades of dietary data from 128 chimpanzees observed by primatologists to the selected group of 24 chimpanzees (only 24 of the available skeletons were from known individuals with documented age and sex). After building an extensive reference collection of Taï Chimpanzee plant foods, my study predicted how microremains in dental calculus would record diet. I then cross-validated the calculus record with the dietary observations. In the process of carrying out the analysis of this reference sample, the research pioneered machine learning identification of botanical remains in dental calculus. This technique matched each microremain to the most likely source plant genus. In addition, it yielded a score of confidence to each identified microremain. This reduced some of the subjectivity and biases commonly present in conventional identification approaches.

With this comparison, the analysis quantified the resolution of the dental dietary record. It showed that there is a relationship between the number of starches,

phytoliths and other microremains with diet. However, diagnostic-starch-producing plants represented only 25 % of total feeding time in the dietary records, whereas diagnostic-phytolith-producing plants represented just 2 % of feeding time. Many of the plants that chimpanzees eat produce few or unidentifiable microremains. However, a more extensive study of the Taï chimpanzee diet would plausibly be able to cover a substantially larger portion of diet as the time restrictions on my project prevented examination of many food plants. A large portion of unidentified diet likely was reflected in the dental calculus by non-starch and non-phytolith microremains, some of which may once become identifiable. Only 49.56% of microremains (starches and phytoliths) in the dental calculus were analysed and the remaining (plant fragments, calcium oxalate, and pollen) were not. Microremain patterns showed that starch, phytoliths, and other microremains accumulate in dental calculus over the lifetime of an individual, yet it was apparent that this process is subject to a number of factors that are hard to account for. A number of non-dietary factors may influence microremains in chimpanzee calculus, such as sex, but this remains to be confirmed. My statistical analysis found that the frequency of phytolith a genus correctly predicted the time spent consuming that plant genus. Yet with starches, the proportion of each genus poorly predicted its actual dietary importance, as it is probably thwarted by uncontrolled taphonomic factors. The record provides only a minimum estimate of the number of plant types consumed. However, even starch microremains provided details on specific chimpanzee resource choices that are unavailable with all other methods. It can record the presence of key resources important for specific behaviours, in my case the first introduction of foods as a result of weaning, and the consumption of hard to open nuts, which are linked to social attributes including learned behaviour.

When applied to the plant microremain record more generally, the results of these studies suggest several patterns. First, the relative quality of plant microremains depends on the microremain type. Phytoliths are far more likely to survive taphonomic processes and have no known preservation limit owning to their molecular make-up. Unlike phytoliths, starches are not robust and microbial breakdown often underrepresents these microremains. Starches are often damaged, and degrade beyond a certain age (Collins and Copeland, 2011), although this starch half-life is not yet known. It is reasonable that local conditions may preserve starch and phytolith contrastingly (Langejans, 2010). It is clear from our Chalcolithic group and Neanderthal samples that starches tend to be more abundant than phytoliths in human calculus. This reflects the fact that starch, unlike phytoliths, is a sought after nutrient among human groups.

Microremain analysis on dental calculus is one of the few methods to explore the taxonomy of foods that have entered the mouth. Documenting specific types of exploited plants is a window on how important plant foods were to Neanderthals. If taphonomic conditions have not degraded calculus dietary data, microremains can preserve some of the lifetime diversity of vegetal diet. Diversity may be a useful metric of the vegetal component to diet in itself. It is also valuable for assessing the ability of foragers to identify diet- related ecological knowledge. This is the knowledge of the useful properties of specific plant taxa and the proficiency in extracting in varied complex sequences according to the correct growth cycle stage (Jones, 2009).

There would be no ambiguity in stating that calculus analysis will not detect the majority of Neanderthal foods. Fortunately, dental calculus can preserve details about food plants correspondently absent from macrobotanical studies. If used in isolation dental calculus analysis would build a misleading picture of Neanderthal subsistence strategies. A dental calculus approach is suited to multi-disciplinary research using dental wear, isotopic analysis, ideally with large collections of fossil individuals along with macrobotanical screening on archaeological sites.

6.2 New information on Neanderthal diets revealed by microremains

The Neanderthal microremain assemblages showed evidence of the use of grass seeds, lilies, legumes, and other starchy plants that do not leave taxon-attributable types. Of these plants, legumes and grass seeds have also been identified in Middle Palaeolithic macrobotanical assemblages at Kebara Cave. At this site, legumes were overwhelmingly dominant, whereas grass seed was only a minor component, the opposite pattern to the one observed across the samples I examined. Likewise, the plant taxa recovered from Middle Palaeolithic sites found at Douara Cave, Gorham's Cave, Mas-des-Caves and Rabutz did not overlap with my results. However, all of these assemblages contain few taxa and low number of individual seeds and thus are not representative. Furthermore, most of the charred and desiccated botanical remains so far found on these sites are lipid-rich nuts (e.g. olive and hazelnut) that produce no or few starch or phytoliths. Thus, these plants are unlikely to be represented in dental calculus. In addition, my results agree with sediment-based phytolith studies at Amud Cave, which also reported significant use of grass seeds (2.5.5). This study was based on dendritic phytoliths and thus reflects deposited grass seed husks rather than edible endosperm matter represented by

starch. Grass seed husks identified at sites such Amud Cave may be accidental inclusions, but when combined with the starch record found in calculus in this and other studies, which is unlikely to be accidentally introduced, these results provide strong support to the idea that Neanderthals consumed grass seeds. This is one example of how different types of microremains reveal varied and complementary information.

Our rigorous contamination controls and weekly tests confirmed that the large majority of microremains in the Neanderthal samples were endogenous, however, a few remains, particularly the fibres (numerous in Vindija dental calculus; Appendix table 15), could be contaminants. The microremains that I was able to distinguish from contamination and identify as ancient markers of life history included starch grains, phytoliths, plant and fungi spores, other plant tissues, diatoms and mineral particles. These were not present in all samples and some whole sites such as Kalamakia exhibited very few microremains. I did not try to infer the total vegetal contribution to diet because my chimpanzee findings demonstrate that it is not yet possible to interpret the total dietary contribution of plants from the total microremain numbers. The feasibility of this is not established because the dental calculus record appears too stochastic. This might be further confounded if Neanderthals cooked starch-containing foods, or if they removed phytoliths from food plants before use. Although my study of chimpanzees used a population approach, this is not possible in these Palaeolithic sample as very few Neanderthal remains are available and due to the impossibility of knowing if remains are contemporaneous. Our studied Neanderthals are a collection of individuals rather than a population sample. Neanderthal diet may have exhibited considerable variation according to sex and age like recent hunter-gatherers, but this cannot to examined as so few samples are available.

The resources with evidence of consumption include plants whose roles to Late Pleistocene foragers are usually overlooked by archaeologists. Diet breadth models and the ethno-historic record contextualise the significance of these food plants. Foods such as grass seeds and legumes are likely to have been low-rank for central European Neanderthals (Simms, 1985; Kelly, 1995; Savard et al., 2006). In more recent societies, these foods are often hallmarks of commitment to low-rank plant foods because of the high amount of processing used to access their energy dense nutrients For example, as such plants grew in importance in terminal Pleistocene societies, processing of these plants began to dominate life and restrict mobility (Wright, 1994; Molleson, 2000). One problem of these foods is they occur as

small packages of nutrients, which are dwarfed by nuts and underground storage organs. Yet these foods offer the advantage of occurring predictably annually, while nuts often occur periodically in three to five year cycles, which occur synchronously over geographic regions (Vander Wall, 2001). Section 5.4 proposed Neanderthals collected these plants without laborious and expensive processing costs. This purported collection of green grain would be suggestive of highly seasonal Neanderthal foraging. Even if harvested outside of this window, the use of these resources indicate there was a seasonal round that allowed exploitation of resources unavailable for most of the year. One alterative way to source high search cost foods is to raid rodent caches of tubers and seeds. These caches may store many kilograms of edible and nutritious plant foods throughout the year (Nabhan, 2009; Ståhlberg and Svanberg, 2010).

In mild and humid parts of Neanderthal range, a broader range of plant foods including leafy greens, drupes and berries as well as USOs occurred for a large part of the year but elsewhere they were more restricted. In cool dry regions some plant foods such as USOs are always present in the environment, for recent foragers they become less accessible in winter. In northern winters, plant foods become locked in frozen soils, buried in snow, or trapped under lake ice. However, the animal food supply also diminishes over winter as the condition of prey deteriorates as they expend body fat. These factors result in long winters depleting energy supply in northern foraging diets. The extent to which plant foods became inaccessible to Neanderthals during winter months is unclear, and if they used them to bridge this period of scarcity. When plant foods took a marginal role for acquiring energy, they may have been sourced for micronutrients, as well as macronutrients as emergency fallback foods, when high-ranked winter resources failed. Hunting medium and large game unusually produces an irregular food supply, and due to their reliance on hunting Neanderthals may have suffered from being in an ecologically precarious position. Regular plant consumption possibly alleviated some of this risk but the regularity that fallback foods may have been required should not be understated. The archaeological record suggests plant use and other fallback foods were insufficient to avoid frequent local extinctions (Hublin and Roebroeks, 2009; Snodgrass and Leonard, 2009).

The range of consumed plants is unlikely to be explained by opportunistic Neanderthal foragers who only occasionally used plants. It is notable that this study shows that Neanderthals used plant foods (grass seeds and legumes) outside of the traditional period of food scarcity in the northern hemisphere (late winter to early

spring). This pattern signifies regular use of plant foods. Isotopic and microwear demonstrate Neanderthals were predominantly consuming meat but microremains indicate that Neanderthals were not the Pleistocene equivalents of the near carnivorous recent Arctic foragers. However, due to the absence of habitats equivalent to Pleistocene Eurasia, there is no ethnographic analogy for Neanderthals (Stringer et al., 2000; Stewart, 2005; Zimov et al., 2012). This is especially troublesome for Neanderthals in open environments because the rarity of ethnographic analogies compounds the lack of a recent habitat parallels (Kelly, 1995). This issue may also influence or distort sister studies of Neanderthal diet using recent foragers as analogies (e.g. dental wear). Anthropologists documented few temperate grassland foragers aside from horse cultures of the American Plains. However, in recent forager societies occupation of cooler climates correlates with reliance on aquatic resources and food storage (Kelly, 1995; Cordain et al., 2000). The scarcity of Neanderthal examples for either of these dietary resources and techniques implies a unique dietary niche with potential oversupply of protein and undersupply of certain fatty acids in certain seasons (Section 2.4.2). The risk of these problems was mediated by plant gathering. Carbohydrates offered energy to offset or defray the potential costs of excessive reliance on muscle issue, which could otherwise lead to protein poisoning (Cordain et al., 2000; Speth, 2010). It is also possible that essential fatty acids vital for development were available in certain wild plant foods (Simopoulos, 2004). Plant consumption must have been crucial element of Neanderthal ecology.

6.3 The response of Neanderthal subsistence to varied environments

Neanderthals are the evolutionary outcome of the reproductive isolation from African populations in the environments of northern Eurasia for hundreds of thousands of years. In this period, Neanderthals and their ancestors persisted through severe climatic change due to glacial cycles. These cooling and drying events transformed Eurasian fauna and flora, affecting the habitability of the region itself. Neanderthals reacted to events in various ways, and in much of their distribution, their range contracted (See 2.2.2). Given that, Neanderthals inhabited a plethora of different environments from arid steppe to boreal forest to warm coastal Mediterranean woodland, it is possible that they possessed sufficient cultural knowledge to accommodate glacial cycle environment change. Microwear analysts have proposed that Neanderthals altered their diet in periods of climatic fluctuation (El Zaatari et al., 2016).

My dissertation attempted to identify the dietary signal of glacial phases and climate by testing microremain diversity. Contrary to expectations, the model of plant consumption revealed that plant use breadth appears relatively static across their range in time and space (See 5.4). This possibly argues that Neanderthal plant use shows a limit to their behavioural flexibility. Not all plants produce distinct microremains, therefore some dietary variation in plant use may not be visible with this method. In modern environments, edible wild plants provide subtly different suites of macro and micronutrients across varying habitats. If we assume, as is suggested by evidence, that Neanderthals were not solely seeking energy, then they may have foraged for different plant foods in the different habitats they occupied. However, the model does indicate local adaptations were limited. Perhaps this conservatism mirrors the limited cultural evolution in Neanderthal technology (Stiner, 2013). The failure of Neanderthals to acquire more regional foraging repertoires is not necessarily maladaptive, or reflective of their cognitive abilities. It is clear they were a successful species, having dominated western Eurasia for hundreds of thousands of years without interruption. Simply put, they had a very different suite of behaviours than those seen among modern or recent historical humans.

6.4 Archaic hominin diet and social structure

The choice of resources used by this hominin has implications for Neanderthal socioeconomics. The specialisation of labour by sex in recent foraging cultures is deeply intertwined with how edible plants are available (See section 2.3.1). Previously researchers have taken Neanderthal hunting and lack of highly specialised technological investment to infer far less division of labour compared with recent foragers (Kuhn and Stiner, 2006). The breadth of plant use indicated by past dental calculus analysis has been interpreted as suggestive of a sexual division of labour closer to recent foragers than previously thought (Henry, 2010). Unfortunately, the dissertation data cannot confirm this level of sociality, but the observed diversity of plant exploitation does agree with the idea that a specialisation of labour was present. It is probable that, if it existed, a plant gathering specialisation was adopted by females due to nursing. Sexual division of labour and food sharing are likely to have been essential for pregnant and nursing females to overcome seasonal shortfalls of food supply.

6.5 The use of palaeoecological models for inferring subsistence

In this dissertation, I made inferences on the environments Neanderthals occupied in order to model their plant use. The parameters used were palaeotemperature and dominant local vegetation. By using the outputs of the Stage Three Project, the dissertation had a rich insight into climate but the palaeotemperature simulations used have a limited resolution, which is inevitable given that climate is an enormously variable system. Combining this with the thousands of years of climate change in Late Pleistocene Europe adds further complexity. Even if the simulations are accurate, they are averages of second order events that lasted thousands of years. If a Neanderthal specimen was from a climatic phase affected by an anomalous third order temperature variation, our estimates may be incorrect. Furthermore, I had to rely on matching the map graduations from each temperature simulation to the coordinates of each archaeological site. This approach potentially lost fine detail of each simulation that is not visible on the project output maps. If this approach were to be used in the future, it would be improved by developing an algorithm to match each archaeological site to each simulation. Other useful available climatic parameters are annual temperature range, precipitation and snow depth and these may have refined the model if sample size was large enough to permit their conclusion.

The project also calculated if the localities of these sites were forested, mixed or devoid of trees. In contrast to the regional level temperature reconstruction, this vegetation reconstruction used proxies (pollen and mammal assemblages) for local, or mesoscale environmental reconstruction. Undoubtedly, more regional level or megascale environmental models would enrich the interpretative power of the study. However, for this extra variable to allow further dissecting of Neanderthal habitats a greater calculus sample size would be required.

6.6 Future directions

In spite of the rise of knowledge on Middle Palaeolithic dietary ecology, diet in this period remains poorly comprehended. An exploration of eco-geography and plant consumption is required to address this. Increasing scale by increasing sample size will make it possible to catalogue dietary variation. The expansion of dental calculus, dental wear, and stable isotopic research is needed, particularly in the large spans of their northern, southern and eastern range that remain underrepresented in

dietary studies. If larger sample sizes are available, scientists may be able to estimate the majority of starch- and phytolith-rich plants they consumed. If data becomes available on the other Pleistocene archaic hominins that existed contemporary to Neanderthals in Eurasia and Africa it would be possible to contextualise Neanderthal resource use.

Future research will also need to interpret implications of plant use in Pleistocene ecologies. This requires exploring the energy returns of plant and animal foods in Pleistocene environments with models of Neanderthal demographics. Nutritional returns and processing costs would allow us to analyse food choice with diet breadth models. It would allow us to predict the rank of specific plant taxa and consider if Neanderthals were targeting bulk energy, specific nutrients or other traits. In no case is there a robust sequence of the steps of use of different taxa - a chaîne opératoire - that follows gathering through processing to consumption. Some of the plants identified in this dissertation could be explored with historical and experimental archaeological studies (Haws, 2004). Studies of the costs and returns of harvesting, processing and consumption of identified plant foods with Middle Palaeolithic technology would assist this. Yet ultimately, experimental archaeology is chained by the limited span of the ethnographic record and Neanderthals may have used these plants in ways unintelligible with the ethnographic record.

Most of what is known about the diet of this Pleistocene relative of our species only describes their last 40,000 years. Researchers have inadequate details about plant foods and subsistence over the approximate preceding 150,000 years they occupied Eurasia. How stable their plant food niche was during their earlier history is a fundamental question. Presumably, diet varied between the warm interglacial and cold glacial phases. Information is also needed to assess if the ancestors of Neanderthals who colonised Eurasia used the same taxa as Neanderthals. Did adapting to Eurasia involve a changing reliance on plant foods? Perhaps inherited gathering strategies receded and new hunting strategies emerged as these hominins moved to colder climes. The higher environmental productivity in southern regions tells us that these hominins probably used more plants than Neanderthals (Kelly, 1995). However, this may not be the case if they originated in a more arid climate as less plant biomass is available in arid areas (Kelly, 1995).

This dissertation highlights some of the problems in the current techniques used to study microremains in dental calculus. It is recommended that further investigations be carried out to continue to investigate these issues. By performing an appraisal of methodology in the discipline, my research has built a platform of

approaches that anthropological and archaeological scientists can use to advance dental calculus for dietary research. Scientists can now test how variability in the formation history of dental calculus in other groups and regions may influence assemblages of plant microremains. Now researchers know more clearly that dental calculus is highly variable in composition and in abundance, so analysts need to account for this in the interpretation of diet.

However, researchers still know little about the stimulus and tempo of biomineralisation of dental calculus in the mouth. The community needs to consider the process of biomineralisation and its ability to preserve long-term dental calculus dietary histories. This may be possible using a more multifaceted approach that combines methods used in this work with Raman and micro-Fourier Transform Infrared spectrometry. Momentum is already substantially increasing in avenues such as mass spectrometry, genetic and proteomic approaches. Further research that integrates these technologies on contemporary reference samples and as well as ancient sample could overcome some of these unaddressed obstacles (Charlier et al., 2010; Adler et al., 2013; Warinner et al., 2014). One recent study (Warinner et al., 2014) has attempted to bring several of these techniques together but only on an archaeological sample where there are major uncontrolled confounding effects. Researchers have not yet combined these techniques on a reference group with a known diet. Such an attempt would offer to resolve questions on the temporal span represented by calculus. These approaches may directly examine diet too. In some cases, these techniques, such as genetic and lipid studies, could be used on dental calculus to find traces of food evident from microremains and cross validate microremain evidence of Neanderthal diet.

One of the observations of the project is that particles in dental calculus cannot simply reflect diet. Microremains in dental calculus must also reflect the environment that the individual occupied. Some microremain types included pollen and spores, which are often found in airborne suspensions and aerosols. This topic is of concern for the question of respiratory health of Pleistocene foragers as some of these airborne particles are environmental irritants. Little is known about air or other types of pollution that Neanderthals must have endured (Hardy et al., 2015b; Monge et al., 2015). Further studies may be able to quantify air-carried microremains, perhaps as a way to extrapolate Pleistocene suspensions and aerosols.

All dental calculus dietary studies are dependent on the sedimentary processes that alter and breakdown the archaeological record (taphonomy). These processes are increasingly relevant as investigators attempt dental calculus analysis

on hominin fossils. Extending dental calculus research to earlier Middle Palaeolithic hominins samples will be valuable for acquiring information about the diets of these archaic humans. Researchers have reported starches on sites as early 420–200 ka at Qesem Cave (Israel). Yet there is no hard data on the chronological and environmental limits of preservation of degradable plant debris in dental calculus. The study of taphonomy of dental calculus remains in its infancy. Most dental calculus studies rely on major assumptions about taphonomy, and downplay its potential to influence results. Yet it seems unwise to underestimate the complex and variable impact that taphonomy may have. Chemical, fungal and microbial processes all play a part in breaking down food debris particles in dental calculus. With starches, there is also the potential risk of spontaneous decay over long periods of time (Collins and Copeland, 2011). To account for taphonomy future research could prioritise assessing if dental calculus is sealed from external agents. Much work is needed to combine elemental composition assays using thin sections of archaeological dental calculus to clarify the factors contributing to preservation.

6.7 Conclusions

Until relatively recently hunting dominated Palaeolithic literature, but plant foraging was either ignored or received minimal attention. This occurred even though plants were almost certainly the primary food source for most of the history of the Hominidae family (Butterworth et al., 2016). Fortunately, the emergence of new methodologies has awoken interest addressing this discrepancy. Particularly dental calculus analysis, the focus of this research, has encouraged examination of Palaeolithic and especially Neanderthal foraging.

In evaluating the role of dental calculus analysis for reconstructing Neanderthal foraging, this dissertation with high-resolution approaches helped to explain how dietary microremains are preserved in dental calculus. However, since microremains in dental calculus are not useful without contextualisation, Chapter Two quantified the reliability of dietary phytoliths and starches in a Taï Chimpanzee population. The representativeness of these assemblages varies considerably and sometimes according to factors that are challenging to control, but the findings do establish that these assemblages can mirror diet. Although no technique offers a high-precision reconstruction of diet composition, dental calculus can make a unique contribution to dietary studies when it is combined with other techniques. These insights affirm the value of dental calculus for gaining an insight into ancient diet.

Past studies have highlighted that the use of plant resources is not a hallmark of modern humans, and that they may be common feature of Neanderthal subsistence (Hardy et al., 2012; Henry et al., 2014). Not only do the samples in this study support these findings, many also exhibit a diversity in microremain types that exceeds that of past Neanderthal dental calculus studies (Henry et al., 2011, 2014; Hardy et al., 2012). This was an unexpected pattern as it was undocumented in other calculus studies. Yet, my research was able to detect this diversity thanks to the observations from the Camino del Molino and the Taï Chimpanzee samples.

Evidence of plant consumption from many different lines of evidence has left a powerful impression that Neanderthal diets cannot be defined by hunting alone. The identification of plant use has provoked a wave of discussion on Palaeolithic dietary ecology. The new direction that researchers have taken has kindled a new paradigm in dietary ecology that is far more aware of the potential breadth of hominin diets and how frequently plants play an important role (Barton et al., 1999; Lev et al., 2005; Henry et al., 2011; Sołtysiak, 2012). The findings of my dissertation hint at how widespread plant use may have been. However, there has been a lag in translating this evidence into sufficiently nuanced subsistence models. Some research has interpreted any level of Neanderthal plant use as suggestive of broad spectrum foraging, but this model fits empirical data poorly. The broad spectrum foraging concept emerged to describe specific characteristics of pre-agricultural societies in southwest Asia, and other regions where agriculture emerged. Attempts to identify broad spectrum foraging in other regions (Jones, 2016) have been in in vain. Arguably, this model is unsuited to foragers who occupied habitats with differing climate and technology. In cooler climates, the broad-spectrum framework may not be readily applicable due to habitat and other differences. Narrow spectrum foraging, with a marked emphasis on large game hunting as well as fishing, continued by some inland northern foragers late into the Holocene (e.g. Yesner, 1989). Researchers must find a more appropriate set of concepts for foragers in cooler climates where trajectories of change were expressed in different ways.

Ethnographic evidence and dental wear studies unequivocally convey that plants were more important in southern regions (2.3.3; 2.5.7) but this eco-geographic variation is undetectable in the series of isotopic studies so far conducted. Now with the dental calculus data, we can infer that eco-geographic variation is also not apparent with the range of resources used. Although my work's diet model is not a full model of dietary breadth, it documents a degree of plant diet breadth. The results show that the number of plant foods consumed did not vary detectably

between climates (5.3.6). Although this finding is unexpected, it parallels the relative dietary homogeneity between different regions that is indicated by multiple isotopic studies (2.5.8) and the slow pace of technological development in the Middle Palaeolithic. During the Upper Palaeolithic, plant use increased over time (El Zaatari and Hublin, 2014). However, Neanderthal plant use appears homogenous through the tens of thousands of years represented by our sample, reinforcing the picture of Neanderthal dietary staticity.

My thesis argues that this evidence of Neanderthal plant use suggests plants were an essential feature of subsistence but does not contradict evidence of a Neanderthal economy centred on medium and large game. Nor does this imply that Neanderthal dietary ecology was necessarily identical or similar to that of the modern humans who colonised Eurasia during the Upper Palaeolithic. The variability of Neanderthal diets is clearly less than modern human diets in Eurasia (Richards et al., 2000, 2001). Yet it is possible that both Neanderthals and modern humans had optimal diets from a diet breadth perspective, which maximised the nutritional opportunity available with their respective technology. However, Neanderthals differ from moderns by exhibiting lower levels of variability. Although to a certain extent Neanderthal diet may have been rigid from region to region, this does not imply a shortfall in Neanderthal adaptability. Neanderthal dietary ecology was specialised to the specific fauna and flora conditions to Eurasia. The reliance on terrestrial mammals and plant foods should be seen as interaction with the hyper-arid Pleistocene climates. Further work will find the temporal and geographic boundaries of their unique adaptation to Eurasia.

References

Abraham J, Grenón M, Sánchez HJ, Pérez C, Barrea R. 2005. A case study of elemental and structural composition of dental calculus during several stages of maturation using SRXRF. J Biomed Mater Res A 75:623–8.

Ackerknecht EH. 1948. Medicine and disease among Eskimos. Eskimo, Ciba Symp 10:916–21.

Addy M, Shellis RP. 2006. Interaction between attrition, abrasion and erosion in tooth wear. In: Lussi A, editor. Dental Erosion: From Diagnosis to Therapy. Vol. 20. Basel: Monographs in Oral Science, Karger Publishers. p 17–31.

Adler CJ, Dobney K, Weyrich LS, Kaidonis J, Walker AW, Haak W, Bradshaw CJA, Townsend G, Sołtysiak A, Alt KW, Parkhill J, Cooper A. 2013. Sequencing ancient calcified dental plaque shows changes in oral microbiota with dietary shifts of the Neolithic and Industrial revolutions. Nat Genet 45:450–455.

Aiello LC, Wheeler P. 1995. The Expensive-Tissue Hypothesis: The Brain and the Digestive System in Human and Primate Evolution. Curr Anthropol 36:199–221.

Albert RM, Lavi O, Estroff L, Weiner S, Tsatskin A, Ronen A, Lev-Yadun S. 1999. Mode of Occupation of Tabun Cave, Mt Carmel, Israel During the Mousterian Period: A Study of the Sediments and Phytoliths. J Archaeol Sci 26:1249–1260.

Albert RM, Ruíz JA, Sans A. 2016. PhytCore ODB: A new tool to improve efficiency in the management and exchange of information on phytoliths. J Archaeol Sci 68:98–105.

Albert RM, Weiner S, Bar-Yosef O, Meignen L. 2000. Phytoliths in the Middle Palaeolithic Deposits of Kebara Cave, Mt Carmel, Israel: Study of the Plant Materials used for Fuel and Other Purposes. J Archaeol Sci 27:931–947.

Ambrose SH. 1990. Preparation and characterization of bone and tooth collagen for isotopic analysis. J Archaeol Sci 17:431–451.

Van Andel TH, Davies W. 2003. Neanderthals and modern humans in the European landscape during the last glaciation: archaeological results of the Stage 3 Project. Cambridge: McDonald Institute for Archaeological Research.

Van Andel TH, Davies W, Weninger B. 2004. The human presence in Europe during the last glacial period I: human migrations and the changing climate. In: Neanderthals and modern human in the European Landscape during the Last Glaciation. Cambridge: McDonald Insititute Monographs. p 31–56.

Van Andel TH, Tzedakis PC. 1996. Palaeolithic landscapes of Europe and environs, 150,000-25,000 years ago: An overview. Quat Sci Rev 15:481–500.

Anderson JP. 1939. Plants Used by the Eskimo of the Northern Bering Sea and Arctic Regions of Alaska. Am J Bot 26:714–716.

Antunes MT, Santinho-Cunha A. 1992. Neanderthalian remains from Figueira Brava cave, Portugal. Geobios 25:681–692.

Arensburg B. 1996. Ancient dental calculus and diet. Hum Evol 11:139–145.

Armitage PL. 1975. The extraction and identification of opal phytoliths from the teeth of ungulates. J Archaeol Sci 2:450–455.

Armstrong RA, McGehee R. 1980. Competitive exclusion. Am Nat 115:151–170.

Baer DJ, Gebauer SK, Novotny JA. 2012. Measured energy value of pistachios in the human diet. Br J Nutr 107:120–125.

Bailey HP. 1960. A method of determining the warmth and temperateness of climate. Geogr Ann 42:1–16.

Bank RA, Hettema EH, Muijs MA, Pals G, Arwert F, Boomsma DI, Pronk JC. 1992. Variation in gene copy number and polymorphism of the human salivary amylase isoenzyme system in Caucasians. Hum Genet 89:213–222.

Barton H, Torrence R. 2015. Cooking up recipes for ancient starch: assessing current methodologies and looking to the future. J Archaeol Sci 56:194–201.

Barton RNE, Currant AP, Fernández-Jalvo Y, Finlayson JC, Goldberg P, MacPhail R, Pettitt PB, Stringer CB. 1999. Gibraltar Neanderthals and results of recent excavations in Gorham's, Vanguard and Ibex Caves. Antiquity 73:13–23.

Bar-Yosef O. 1998. The Natufian culture in the Levant, threshold to the origins of agriculture. Evol Anthropol Issues, News, Rev 6:159–177.

Bates D, Maechler M, Bolker B. 2013. lme4: Linear mixed-effects models using S4 classes. R Packag version 0999999-2:999999.

Beaumont J, Geber J, Powers N, Wilson A, Lee-Thorp JA, Montgomery J. 2013. Victims and survivors: stable isotopes used to identify migrants from the Great Irish Famine to 19th century London. Am J Phys Anthropol 150:87–98.

de Beaune SA. 1993. Nonflint stone tools of the Early Upper Paleolithic. In: Knecht H, Pike-Tay A, White R, editors. Before Lascaux: The Complex Record of the Early Upper Paleolithic. Boca Raton: CRC Press. p 163–191.

de Beaune SA. 2004. The invention of technology. Curr Anthropol 45:139–162.

Beauval C, Lacrampe-Cuyaubère F, Maureille B, Trinkaus E. 2006. Direct radiocarbon dating and stable isotopes of the neandertal femur from Les Rochers-de-Villeneuve (Lussac-les-Châteaux, Vienne). Bull Mémoires la Société d'anthropologie Paris 18:35–42.

Behringer V, Borchers C, Deschner T, Möstl E, Selzer D, Hohmann G. 2013. Measurements of Salivary Alpha Amylase and Salivary Cortisol in Hominoid Primates Reveal Within-Species Consistency and Between-Species Differences. PLoS One 8.

Belitz HD, Grosch W, Schieberle P. 2009. Food chemistry. Berlin: Springer-Verlag.

Berbesque JC, Marlowe FW. 2009. Sex differences in food preferences of Hadza hunter-gatherers. Evol Psychol 7:601–616.

Bergström J. 1999. Tobacco smoking and supragingival dental calculus. J Clin Periodontol 26:541–547.

Bermúdez de Castro JM. 1997. A Hominid from the Lower Pleistocene of Atapuerca, Spain: Possible Ancestor to Neandertals and Modern Humans. Science (80-) 276:1392–1395.

Binford LR. 1968. Post-Pleistocene adaptations. In: Binford SR, Binford LR, editors. New Perspectives in Archaeology. Chicago: Aldine. p 314–341.

Binford LR. 1980. Willow Smoke and Dogs' Tails: Hunter-Gatherer Settlement Systems and Archaeological Site Formation. Am Antiq 45:4–20.

Binford LR. 1985. Human ancestors: Changing views of their behavior. J Anthropol Archaeol 4:292–327.

Binford LR. 2001. Constructing frames of reference: an analytical method for archaeological theory building using hunter-gatherer and environmental data sets. Berkeley: University of California Press.

Bird DW, O'Connell JF. 2006. Behavioral ecology and archaeology. J Archaeol Res 14:143–188.

Blasco R, Fernández Peris J. 2009. Middle Pleistocene bird consumption at Level XI of Bolomor Cave (Valencia, Spain). J Archaeol Sci 36:2213–2223.

Blasco R, Fernández Peris J. 2012. A uniquely broad spectrum diet during the Middle Pleistocene at Bolomor Cave (Valencia, Spain). Quat Int 252:16–31.

Blasco R, Rosell J, Arsuaga JL, Bermúdez de Castro JM, Carbonell E. 2010. The hunted hunter: the capture of a lion (*Panthera leo fossilis*) at the Gran Dolina site, Sierra de Atapuerca, Spain. J Archaeol Sci 37:2051–2060.

Blasco R, Rosell J, Fernández Peris J, Arsuaga JL, Bermúdez de Castro JM, Carbonell E. 2013. Environmental availability, behavioural diversity and diet: a zooarchaeological approach from the TD10-1 sublevel of Gran Dolina (Sierra de Atapuerca, Burgos, Spain) and Bolomor Cave (Valencia, Spain). Quat Sci Rev 70:124–144.

Blondiaux J, Charlier P. 2008. Palaeocytology in skeletal remains: microscopic examination of putrefaction fluid deposits and dental calculus of skeletal remains from French archaeological sites. Int J Osteoarchaeol 18:1–10.

Bocherens H. 2009. Neanderthal Dietary Habits: Review of the Isotopic Evidence. In: Hublin J-J, Richards MP, editors. The Evolution of Hominin Diets: Integrating Approaches to the Study of Palaeolithic Subsistence. Dordrecht: Springer Netherlands. p 241–250.

Bocherens H, Drucker DG, Billiou D, Patou-Mathis M, Vandermeersch B. 2005. Isotopic evidence for diet and subsistence pattern of the Saint-Césaire I Neanderthal: review and use of a multi-source mixing model. J Hum Evol 49:71–87.

Bocherens H, Drucker DG, Bonjean D, Bridault A, Conard NJ, Cupillard C, Germonpré M, Höneisen M, Münzel SC, Napierala H, Patou-Mathis M, Stephan E, Uerpmann H-P, Ziegler R. 2011. Isotopic evidence for dietary ecology of cave lion (*Panthera spelaea*) in North-Western Europe: Prey choice, competition and implications for extinction. Quat Int 245:249–261.

Boesch C. 1997. Evidence for dominant wild female chimpanzees investing more in sons. Anim Behav 54:811–815.

Boesch C. 2012. Wild Cultures: A Comparison between Chimpanzee and Human Cultures. Cambridge, UK: Cambridge University Press.

Boesch C, Boesch H. 1983. Optimisation of Nut-Cracking with Natural Hammers by Wild Chimpanzees. Behaviour 86:265–286.

Boesch C, Boesch H. 1984. Possible causes of sex differences in the use of natural hammers by wild chimpanzees. J Hum Evol 13:415–440.

Boesch C, Boesch-Achermann H. 2000. The Chimpanzees of the Taï Forest: Behavioural Ecology and Evolution. Oxford, UK: Oxford University Press.

Boesch C, Marchesi P, Marchesi N, Fruth B, Joulian F. 1994. Is nut cracking in wild chimpanzees a cultural behaviour? J Hum Evol 26:325–338.

Boule M. 1889. La caverne de Malarnaud, près Montseron (Ariège). Bull la Société Philomath Paris 8th 1:83–86.

Boule M. 1911. L'Homme fossile de La Chapelle-aux-Saints. Ann Paléontologie 6:106–172.

Bouyssonie A, Bouyssonie J, Bardon L. 1913. La station Moustérienne de la "Bouffia" Bonneval a la Chapelle-aux-Saints. Anthropologie 24:609–640.

Boyadjian CHC. 2012. Análise e identificação de microvestígios vegetais de cálculo dentário para a reconstrução de dieta sambaquieira: estudo de caso de Jabuticabeira II, SC.

Boyadjian CHC, Eggers S, Reinhard K. 2007. Dental wash: a problematic method for extracting microfossils from teeth. J Archaeol Sci 34:1622–1628.

Brand-Miller JC, Holt SH. 1998. Australian aboriginal plant foods: a consideration of their nutritional composition and health implications. Nutr Res Rev 11:5–23.

Breiman L. 2001. Random forests. Mach Learn 45:5–32.

Brown JK. 1970. A Note on the Division of Labor by Sex. Am Anthropol 72:1073–1078.

Brown K, Fa DA, Finlayson G, Finlayson C. 2011. Small game and marine resource exploitation by Neanderthals: the evidence from Gibraltar. In: Trekking the Shore. New York, NY: Springer. p 247–268.

Buck LT, Stringer CB. 2014. Having the stomach for it: a contribution to Neanderthal diets? Quat Sci Rev 96:161–167.

Buckley S, Usai D, Jakob T, Radini A, Hardy K. 2014. Dental calculus reveals unique insights into food items, cooking and plant processing in prehistoric central Sudan. PLoS One 9:e100808.

Bull ID, Matthew J. Lockheart, Mohamed M. Elhmmali, David J. Roberts, Richard P. Evershed. 2002. , Evershed RP (2002) The Origin of Faeces by Means of Biomarker Detection. Environ Int - Google Scholar. Environ Int 27:647–654.

Butterworth PJ, Ellis PR, Wollstonecroft M. 2016. Why protein is not enough: the role of plants and plant processing in delivering the dietary requirements of modern and early Homo. In: Hardy K, Kubiak-Martens L, editors. Wild harvest: plants in the Hominin and pre-agrarian human worlds. Oxbow. p 31–55.

Butterworth PJ, Warren FJ, Ellis PR. 2011. Human α-amylase and starch digestion: An interesting marriage. Starch - Stärke 63:395–405.

Cabanes D, Mallol C, Expósito I, Baena J. 2010. Phytolith evidence for hearths and beds in the late Mousterian occupations of Esquilleu cave (Cantabria, Spain). J Archaeol Sci 37:2947–2957.

Cabanes D, Weiner S, Shahack-Gross R. 2011. Stability of phytoliths in the archaeological record: a dissolution study of modern and fossil phytoliths. J Archaeol Sci 38:2480–2490.

Capitan L, Peyrony D. 1912a. Station préhistorique de La Ferrassie, commune de Savignac-du-Bugue (Dordogne). Rev Anthropol:29–50.

Capitan L, Peyrony D. 1912b. Station préhistorique de La Ferrassie, commune de Savignac-du-Bugue (Dordogne). Rev Anthropol:76–99.

Capitan L, Peyrony D. 1912c. Trois nouveaux squelettes humains fossiles. Rev Anthropol:439–442.

Carpenter D, Dhar S, Mitchell LM, Fu B, Tyson J, Shwan NAA, Yang F, Thomas MG, Armour JAL. 2015. Obesity, starch digestion and amylase: association between copy number variants at human salivary (*AMY1*) and pancreatic (*AMY2*) amylase genes. Hum Mol Genet 24:3472–80.

Carrión JS, Yll EI, Walker MJ, Legaz AJ, Chain C, Lopez A. 2003. Glacial refugia of temperate, Mediterranean and Ibero-North African flora in south-eastern Spain: new evidence from cave pollen at two Neanderthal man sites. Glob Ecol Biogeogr 12:119–129.

Carter JA. 1999. Late devonian, permian and triassic phytoliths from antarctica. Micropaleontology 45:56–61.

Castellano S, Parra G, Sánchez-Quinto FA, Racimo F, Kuhlwilm M, Kircher M, Sawyer S, Fu Q, Heinze A, Nickel B, Dabney J, Siebauer M, White L, Burbano HA, Renaud G, Stenzel U, Lalueza-Fox C, de la Rasilla M, Rosas A, Rudan P, Brajković D, Kucan Ž, Gušic I, Shunkov M V., Derevianko AP, Viola B, Meyer M, Kelso J, Andrés AM, Pääbo S. 2014. Patterns of coding variation in the complete exomes of three Neandertals. Proc Natl

Acad Sci U S A 111:6666–71.

Cerling TE, Mbua E, Kirera FM, Manthi FK, Grine FE, Leakey MG, Sponheimer M, Uno KT. 2011. Diet of Paranthropus boisei in the early Pleistocene of East Africa. Proc Natl Acad Sci U S A 108:9337–41.

Charlier P, Huynh-Charlier I, Munoz O, Billard M, Brun L, de la Grandmaison GL. 2010. The microscopic (optical and SEM) examination of dental calculus deposits (DCD). Potential interest in forensic anthropology of a bio-archaeological method. Leg Med 12:163–71.

Christophersen KM, Pedersen PO. 1939. Investigations into dental conditions in the neolithic period and in the bronze age in Denmark. Dent Rec (London) 59:575.

Churchill SE. 2014. Thin on the Ground: Neandertal Biology, Archeology and Ecology. Oxford, UK: John Wiley & Sons.

Churchill SE, Rhodes JA. 2006. How strong were the Neandertals? Leverage and muscularity at the shoulder and elbow in mousterian foragers. Period Biol 108:457–470.

Codron D, Lee-Thorp JA, Sponheimer M, de Ruiter D j., Codron J. 2008. What Insights Can Baboon Feeding Ecology Provide for Early Hominin Niche Differentiation? Int J Primatol 29:757–772.

Collins MJ, Copeland L. 2011. Ancient starch: Cooked or just old? Proc Natl Acad Sci U S A 108:E145, author reply E146.

Colliot G, Anderson Patricia C., Bonnet N. 1997. Preliminary classification of phytolith shapes using computerized image analysis and pattern recognition. In: The State-of-the-Art of Phytoliths in Soils and Plants. . p 275.

Constantino PJ, Lee JJ-W, Chai H, Zipfel B, Ziscovici C, Lawn BR, Lucas PW. 2010. Tooth chipping can reveal the diet and bite forces of fossil hominins. Biol Lett 6:826–9.

Cordain L, Miller JB, Eaton SB, Mann N, Holt SH, Speth JD. 2000. Plant-animal subsistence ratios and macronutrient energy estimations in worldwide hunter-gatherer diets. Am J Clin Nutr 71:682–92.

Cortés-Sánchez M, Morales-Muñiz A, Simón-Vallejo MD, Lozano-Francisco MC, Vera-Peláez JL, Finlayson C, Rodríguez-Vidal J, Delgado-Huertas A, Jiménez-Espejo FJ, Martínez-Ruiz F, Martínez-Aguirre MA, Pascual-Granged AJ, Bergadà-Zapata MM, Gibaja-Bao JF, Riquelme-Cantal JA, López-Sáez JA, Rodrigo-Gámiz M, Sakai S, Sugisaki S, Finlayson G, Fa DA, Bicho NF. 2011. Earliest known use of marine resources by Neanderthals. PLoS One 6:e24026.

Coster ACF, Field JH. 2015. What starch grain is that? – A geometric morphometric approach to determining plant species origin. J Archaeol Sci 58:9–25.

Crawford MA, Broadhurst CL, Ghebremeskel K, Sinclair AJ, Saugstad LF, Schmidt WF, Cunnane SC, Galli C, Holmsen H. 2008. The role of docosahexaenoic and arachidonic acids as determinants of evolution and hominid brain development. In: Tsukamoto K, Kawamura T, Takeuchi T, T. D. Beard J, M. J. Kaiser, editors. Fisheries for Global

Welfare and Environment, 5th World Fisheries Congress. Tokyo: Terrapub. p 57–76.

Crevecoeur I, Bayle P, Rougier H, Maureille B, Higham T, van der Plicht J, De Clerck N, Semal P. 2010. The Spy VI child: A newly discovered Neandertal infant. J Hum Evol 59:641–656.

Cromton AW, Hiiemae K. 1970. Molar occlusion and mandibular movements during occlusion in the American opossum, Didelphis marsupialis L. Zool J Linn Soc 49:21–47.

Crowther A, Haslam M, Oakden N, Walde D, Mercader J. 2014. Documenting contamination in ancient starch laboratories. J Archaeol Sci 49:90–104.

Damen JJM, Ten Cate JM. 1989. The effect of silicic acid on calcium phosphate precipitation. J Dent Res 68:1355–1359.

Darlas A. 2012. Geomorphologic evolution and occupation of the caves of the western Mani peninsula during the Upper Pleistocene and the Holocene. Proc 5th Symp Hell Soc Archaeom:237–253.

Debénath A, Jelinek AJ. 1998. Nouvelles fouilles à La Quina (Charente) : Résultats préliminaires. Gall Préhistoire 40:29–74.

Dobney K, Brothwell D. 1986. Dental calculus: its relevance to ancient diet and oral ecology. In: Cruwys E, Foley RA, editors. Teeth and anthropology. Oxford: BAR International Series 291. p 55–81.

Dobney K, Brothwell D. 1988. A scanning electron microscope study of archaeological dental calculus. In: Olsen SL, editor. Scanning electron microscopy in archaeology. Oxford: BAR International Series. p 372–385.

Douglass GD, DeVreugd RT. 1997. The dynamics of occlusal relationships. In: McNeill C, editor. Science and practice of occlusion. Berlin: Quintessence. p 69–78.

Dreher ML. 2012. Pistachio nuts: composition and potential health benefits. Nutr Rev 70:234–240.

Dubreuil L, Nadel D. 2015. The development of plant food processing in the Levant: insights from use-wear analysis of Early Epipalaeolithic ground stone tools. Philos Trans R Soc London B Biol Sci 370:20140357-.

Dudgeon J V, Tromp M. 2014. Diet, Geography and Drinking Water in Polynesia: Microfossil Research from Archaeological Human Dental Calculus, Rapa Nui (Easter Island). Int J Osteoarchaeol 24:634–648.

Dupont E. 1872. Les temps préhistoriques en Belgique: L'homme pendant les âges de la pierre dans les environs de Dinant-sur-Meuse. Brussels: Murquardt.

Dusseldorp GL. 2010. Studying Pleistocene Neanderthal and cave hyena Dietary Habits: Combining Isotopic and Archaeozoological Analyses. J Archaeol Method Theory 18:224–255.

Dusseldorp GL. 2013. Neanderthals and Cave Hyenas: Co-existence, Competition or Conflict? In: Clark JL, Speth JD, editors. Zooarchaeology and Modern Human Origins. Springer. p 191–208.

Ecker M, Bocherens H, Julien M-A, Rivals F, Raynal J-P, Moncel M-H. 2013. Middle Pleistocene ecology and Neanderthal subsistence: insights from stable isotope analyses in Payre (Ardèche, southeastern France). J Hum Evol 65:363–73.

Eliasson AC, Larsson K. 1993. Cereals in breadmaking: a molecular colloidal approach. New York: CRC Press.

Evers AD. 1971. Scanning electron microscopy of wheat starch. III. Granule development in the endosperm. Starch - Stärke 5:157–192.

Evins MA. 1982. The fauna from Shanidar Cave: Mousterian wild goat exploitation in northeastern Iraq. Paléorient 8:37–58.

Fahy GE, Richards MP, Fuller BT, Deschner T, Hublin J-J, Boesch C. 2014. Stable nitrogen isotope analysis of dentine serial sections elucidate sex differences in weaning patterns of wild chimpanzees (*Pan troglodytes*). Am J Phys Anthropol 153:635–642.

Fahy GE, Richards MP, Riedel J, Hublin J-J, Boesch C. 2013. Stable isotope evidence of meat eating and hunting specialization in adult male chimpanzees. Proc Natl Acad Sci U S A 110:5829–33.

Falchi M, El-Sayed Moustafa JS, Takousis P, Pesce F, Bonnefond A, Andersson-Assarsson JC, Sudmant PH, Dorajoo R, Al-Shafai MN, Bottolo L, Ozdemir E, So H-C, Davies RW, Patrice A, Dent R, Mangino M, Hysi PG, Dechaume A, Huyvaert M, Skinner J, Pigeyre M, Caiazzo R, Raverdy V, Vaillant E, Field S, Balkau B, Marre M, Visvikis-Siest S, Weill J, Poulain-Godefroy O, Jacobson P, Sjostrom L, Hammond CJ, Deloukas P, Sham PC, McPherson R, Lee J, Tai ES, Sladek R, Carlsson LMS, Walley A, Eichler EE, Pattou F, Spector TD, Froguel P. 2014. Low copy number of the salivary amylase gene predisposes to obesity. Nat Genet 46:492–7.

Fenwick RSH, Lentfer CJ, Weisler MI. 2011. Palm reading: A pilot study to discriminate phytoliths of four Arecaceae (Palmae) taxa. J Archaeol Sci 38:2190–2199.

Fernandes R, Millard AR, Brabec M, Nadeau M-J, Grootes P. 2014. Food Reconstruction Using Isotopic Transferred Signals (FRUITS): A Bayesian Model for Diet Reconstruction. PLoS One 9:e87436.

Field A. 2005. Discovering Statistics Using SPSS. Sage Publications Ltd.

Filhol MH. 1889. Note sur une machoire humaine trouvée dans la caverne de Malarnaud près de Montseron (Ariège). Bull la Société Philomath Paris 8th 1:69–82.

Finlayson C. 2008. On the importance of coastal areas in the survival of Neanderthal populations during the Late Pleistocene. Quat Sci Rev 27:2246–2252.

Finlayson C, Pacheco FG, Rodríguez-Vidal J, Fa DA, Gutierrez López JM, Santiago Pérez A, Finlayson G, Allue E, Baena Preysler J, Cáceres I, Carrión JS, Fernández Jalvo Y, Gleed-

Owen CP, Jiménez-Espejo FJ, López P, López Sáez JA, Riquelme Cantal JA, Sánchez Marco A, Guzman FG, Brown K, Fuentes N, Valarino CA, Villalpando A, Stringer CB, Martinez Ruiz F, Sakamoto T. 2006. Late survival of Neanderthals at the southernmost extreme of Europe. Nature 443:850–3.

Fiore I, Gala M, Tagliacozzo A. 2004. Ecology and subsistence strategies in the eastern Italian Alps during the Middle Palaeolithic. Int J Osteoarchaeol 14:273–286.

Fiorenza L. 2015. Reconstructing diet and behaviour of Neanderthals from Central Italy through dental macrowear analysis. J Anthropol Sci 93:1–15.

Fiorenza L, Benazzi S, Henry AG, Salazar-García DC, Blasco R, Picin A, Wroe S, Kullmer O. 2015. To meat or not to meat? New perspectives on Neanderthal ecology. Am J Phys Anthropol 156 Suppl:43–71.

Fiorenza L, Benazzi S, Tausch J, Kullmer O, Bromage TG, Schrenk F. 2011. Molar macrowear reveals Neanderthal eco-geographic dietary variation. PLoS One 6:e14769.

Flannery K V. 1969. Origins and ecological effects of early domestication in Iran and the Near East. In: Ucko PJ, Dimbleby GW, editors. The domestication and exploitation of plants and animals. Chicago, IL: Gerald Duckworth and Co. p 73–100.

Flensborg G. 2011. Dento-alveolar lesions and palaeodietary inferences from the Paso Alsina 1 site (eastern Pampean-Patagonian transition, Argentina). Homo Int Zeitschrift für die vergleichende Forsch am Menschen 62:335–50.

Floate MJS. 1970. Decomposition of organic materials from hill soils and pastures. Soil Biol Biochem 2:173–185.

Foley R, Lahr MM. 2003. On stony ground: Lithic technology, human evolution, and the emergence of culture. Evol Anthropol Issues, News, Rev 12:109–122.

Follieri M, Giardini M, Magri D, Sadori L. 1998. Palynostratigraphy of the Last Glacial period in the volcanic region of central Italy. Quat Int 47–48:3–20.

Fox CL, Pérez-Pérez A. 1993. The diet of the Neanderthal Child Gibraltar 2 (Devil's Tower) through the study of the vestibular striation pattern. J Hum Evol 24:29–41.

Fox J, Weisberg S. 2002. An R Companion to Applied Regression. SAGE Publications.

Frayer DW, Fiore I, Lalueza-Fox C, Radovčić J, Bondioli L. 2010. Right handed Neandertals: Vindija and beyond. J Anthropol Sci 88:113–127.

Fu Q, Hajdinjak M, Moldovan OT, Constantin S, Mallick S, Skoglund P, Patterson N, Rohland N, Lazaridis I, Nickel B, Viola B, Prüfer K, Meyer M, Kelso J, Reich D, Pääbo S. 2015. An early modern human from Romania with a recent Neanderthal ancestor. Nature 524:216–219.

Galván Santos B, Hernández CM, Ortega F. 2006. Territorio y producción lítica en los valles de Alcoy (Alicante) durante el Paleolítico Medio. In: Martínez G, Morgado A, Alfonso JA, editors. Sociedades prehistóricas, recursos abióticos y territorio. Granada:

Fundación Ibn al-Jatib de Estudios de Cooperación Cultural. p 135–158.

Garralda MD, Galván B, Hernández CM, Mallol C, Gómez JA, Maureille B. 2014. Neanderthals from El Salt (Alcoy, Spain) in the context of the latest Middle Palaeolithic populations from the southeast of the Iberian Peninsula. J Hum Evol 75:1–15.

Gaudzinski-Windheuser S, Roebroeks W. 2011. On Neanderthal Subsistence in Last Interglacial Forested Environments in Northern Europe. In: Conard NJ, Richter J, editors. Neanderthal lifeways, subsistence and technology: one hundred fifty years of Neanderthal study. Dordrecht: Springer Science & Business Media. p 61–71.

Germonpré M, Udrescu M, Fiers E. 2014. Possible evidence of mammoth hunting at the Neanderthal site of Spy (Belgium). Quat Int 337:28–42.

Gobetz KE, Bozarth SR. 2001. Implications for Late Pleistocene mastodon diet from opal phytoliths in tooth calculus. Quat Res 55:115–122.

Gomez-Robles A, Bermúdez de Castro JM, Arsuaga JL, Carbonell E, Polly PD. 2013. No known hominin species matches the expected dental morphology of the last common ancestor of Neanderthals and modern humans. Proc Natl Acad Sci U S A 110:18196–18201.

Goodale N, Otis H, Andrefsky W, Kuijt I, Finlayson B, Bart K. 2010. Sickle blade life-history and the transition to agriculture: an early Neolithic case study from Southwest Asia. J Archaeol Sci 37:1192–1201.

Goodman MJ, Griffin PB, Estioko-Griffin AA, Grove JS. 1985. The compatibility of hunting and mothering among the agta hunter-gatherers of the Philippines. Sex Roles 12:1199–1209.

Granger J-M, Lévêque F. 1997. Parure castelperronienne et aurignacienne: étude de trois séries inédites de dents percées et comparaisons. Comptes Rendus l'Académie des Sci - Ser IIA - Earth Planet Sci 325:537–543.

Grayson DK, Delpech F. 2008. The large mammals of Roc de Combe (Lot, France): The Châtelperronian and Aurignacian assemblages. J Anthropol Archaeol 27:338–362.

Greene TR, Kuba CL, Irish JD. 2005. Quantifying calculus: A suggested new approach for recording an important indicator of diet and dental health. HOMO - J Comp Hum Biol 56:119–132.

Griggo C. 2004. Mousterian fauna from Dederiyeh Cave and comparisons with fauna from Umm el Tlel and Douara Cave. Paléorient 30:149–162.

Grine FE. 1986. Dental evidence for dietary differences in *Australopithecus* and *Paranthropus*: a quantitative analysis of permanent molar microwear. J Hum Evol 15:783–822.

Grün R, Stringer CB. 1991. Electron Spin Resonance Dating and the Evolution of Modern Humans. Archaeometry 33:153–199.

Guatelli-Steinberg D, Larsen CS, Hutchinson DL. 2004. Prevalence and the duration of linear

enamel hypoplasia: a comparative study of Neandertals and Inuit foragers. J Hum Evol 47:65–84.

Guérin G, Frouin M, Talamo S, Aldeias V, Bruxelles L, Chiotti L, Dibble HL, Goldberg P, Hublin J-J, Jain M, Lahaye C, Madelaine S, Maureille B, McPherron SJP, Mercier N, Murray AS, Sandgathe D, Steele TE, Thomsen KJ, Turq A. 2015. A multi-method luminescence dating of the Palaeolithic sequence of La Ferrassie based on new excavations adjacent to the La Ferrassie 1 and 2 skeletons. J Archaeol Sci 58:147–166.

Gunz P, Neubauer S, Maureille B, Hublin J-J. 2010. Brain development after birth differs between Neanderthals and modern humans. Curr Biol 20:R921–R922.

Gurven M, Allen-Arave W, Hill K, Hurtado AM. 2001. Reservation food sharing among the Ache of Paraguay. Hum Nat 12:273–297.

Guthrie DR. 2001. Origin and causes of the mammoth steppe: a story of cloud cover, woolly mammal tooth pits, buckles, and inside-out Beringia. Quat Sci Rev 20:549–574.

Haber Uriarte M, Avilés Fernández A, Lomba Maurandi J. 2013. Estudio antropológico preliminar de los restos humanos calcolíticos del enterramiento múltiple de Camino del Molino (Caravaca de la Cruz, Murcia). In: Turbón D, Fañanás L, Rissech C, Rosa A, editors. Biodiversidad humana y evolución. Barcelona: Universidad de Barcelona. p 236–242.

Halstead P. 2012. Feast, Food and Fodder in Neolithic-Bronze Age Greece: Commensality and the Construction of Value. eTopoi J Anc Stud 2:21–51.

Hardy BL. 2010. Climatic variability and plant food distribution in Pleistocene Europe: Implications for Neanderthal diet and subsistence. Quat Sci Rev 29:662–679.

Hardy BL, Kay M, Marks AE, Monigal K. 2001. Stone tool function at the paleolithic sites of Starosele and Buran Kaya III, Crimea: Behavioral implications. Proc Natl Acad Sci U S A 98:10972–10977.

Hardy BL, Moncel M-H. 2011. Neanderthal use of fish, mammals, birds, starchy plants and wood 125-250,000 years ago. PLoS One 6:e23768.

Hardy BL, Moncel M-H, Daujeard C, Fernandes P, Béarez P, Desclaux E, Chacon Navarro MG, Puaud S, Gallotti R. 2013. Impossible Neanderthals? Making string, throwing projectiles and catching small game during Marine Isotope Stage 4 (Abri du Maras, France). Quat Sci Rev 82:23–40.

Hardy K, Blakeney T, Copeland L, Kirkham J, Wrangham RW, Collins MJ. 2009. Starch granules, dental calculus and new perspectives on ancient diet. J Archaeol Sci 36:248–255.

Hardy K, Brand-Miller J, Brown KD, Thomas MG, Copeland L. 2015a. The Importance of Dietary Carbohydrate in Human Evolution. Q Rev Biol 90:251–268.

Hardy K, Buckley S, Collins MJ, Estalrrich A, Brothwell D, Copeland L, García-Tabernero A, García-Vargas S, de la Rasilla M, Lalueza-Fox C, Huguet R, Bastir M, Santamaría D,

Madella M, Wilson J, Cortés AF, Rosas A. 2012. Neanderthal medics? Evidence for food, cooking, and medicinal plants entrapped in dental calculus. Naturwissenschaften 99:617–26.

Hardy K, Radini A, Buckley S, Sarig R, Copeland L, Gopher A, Barkai R. 2015b. Dental calculus reveals potential respiratory irritants and ingestion of essential plant-based nutrients at Lower Palaeolithic Qesem Cave Israel. Quat Int.

Harlan JR. 1989. Wild-grass seed harvesting in the Sahara and sub-Sahara of Africa. In: Harris DR, Hillman GC, editors. Foraging and farming: the evolution of plant exploitation. London: Unwin Hyman. p 79–98.

Harvati K, Darlas A, Bailey SE, Rein TR, El Zaatari S, Fiorenza L, Kullmer O, Psathi E. 2013. New Neanderthal remains from Mani peninsula, Southern Greece: the Kalamakia Middle Paleolithic cave site. J Hum Evol 64:486–99.

Harvati K, Panagopoulou E, Runnels C. 2009. The Paleoanthropology of Greece. Evol Anthropol 18:131–143.

Haslam M. 2004. The decomposition of starch grains in soils: implications for archaeological residue analyses. J Archaeol Sci 31:1715–1734.

Hawkes K, Bird RB. 2002. Showing Off, Handicap Signaling, and the Evolution of Men's Work. Evol Anthropol 11:58–67.

Hawkes K, Hill K, O'Connell JF. 1982. Why hunters gather: optimal foraging and the Ache of eastern Paraguay. Am Ethnol 9:379–398.

Haws JA. 2004. An Iberian perspective on Upper Paleolithic plant consumption. Promontoria 2:49–105.

Haws JA, Hockett BS. 2004. Theoretical perspectives on the dietary role of small animals in human evolution. Petits Animaux Soc Hum:173–184.

Hedges REM, Clement JG, Thomas CDL, O'Connell TC. 2007. Collagen turnover in the adult femoral mid-shaft: modeled from anthropogenic radiocarbon tracer measurements. Am J Phys Anthropol 133:808–16.

Henri-Martin G. 1961. Le niveau de Chatelperron a la Quina (Charente). Bull la Société Préhistorique Française 58:796–808.

Henry AG. 2010. Plant Foods and The Dietary Ecology of Neandertals and Modern Humans.

Henry AG. 2014. Formation and taphonomic processes affecting starch grains. In: Marston JM, Guedes JD, Warinner C, editors. Current Methods in Paleoethnobotany. Boulder: University of Colorado Press. p 35–50.

Henry AG, Brooks AS, Piperno DR. 2011. Microfossils in calculus demonstrate consumption of plants and cooked foods in Neanderthal diets (Shanidar III, Iraq; Spy I and II, Belgium). Proc Natl Acad Sci U S A 108:486–491.

Henry AG, Brooks AS, Piperno DR. 2014. Plant foods and the dietary ecology of Neanderthals and early modern humans. J Hum Evol 69:44–54.

Henry AG, Piperno DR. 2008. Using plant microfossils from dental calculus to recover human diet: a case study from Tell al-Raqā'i, Syria. J Archaeol Sci 35:1943–1950.

Henry AG, Ungar PS, Passey BH, Sponheimer M, Rossouw L, Bamford M, Sandberg P, de Ruiter DJ, Berger L. 2012. The diet of *Australopithecus sediba*. Nature 487:90–3.

Heyes P, MacDonald K. 2015. Neandertal energetics: Uncertainty in body mass estimation limits comparisons with Homo sapiens. J Hum Evol 85:193–7.

Higham TFG. 2011. European Middle and Upper Palaeolithic radiocarbon dates are often older than they look: problems with previous dates and some remedies. Antiquity 85:235–249.

Higham TFG, Douka K, Wood RE, Ramsey CB, Brock F, Basell L, Camps M, Arrizabalaga A, Baena J, Barroso-Ruíz C, Bergman C, Boitard C, Boscato P, Caparrós M, Conard NJ, Draily C, Froment A, Galván B, Gambassini P, Garcia-Moreno A, Grimaldi S, Haesaerts P, Holt B, Iriarte-Chiapusso M-J, Jelinek AJ, Jordá Pardo JF, Maíllo-Fernández J-M, Marom A, Maroto J, Menéndez M, Metz L, Morin E, Moroni A, Negrino F, Panagopoulou E, Peresani M, Pirson S, de la Rasilla M, Riel-Salvatore J, Ronchitelli A, Santamaría D, Semal P, Slimak L, Soler J, Soler N, Villaluenga A, Pinhasi R, Jacobi R. 2014. The timing and spatiotemporal patterning of Neanderthal disappearance. Nature 512:306–9.

Higham TFG, Jacobi R, Julien M, David F, Basell L, Wood RE, Davies W, Ramsey CB. 2010. Chronology of the Grotte du Renne (France) and implications for the context of ornaments and human remains within the Châtelperronian. Proc Natl Acad Sci U S A 107:20234–9.

Higham TFG, Ramsey CB, Karavanić I, Smith FH, Trinkaus E. 2006. Revised direct radiocarbon dating of the Vindija G1 Upper Paleolithic Neandertals. Proc Natl Acad Sci U S A 103:553–7.

Hill K. 1988. Macronutrient modifications of optimal foraging theory: An approach using indifference curves applied to some modern foragers. Hum Ecol 16:157–197.

Hockett BS. 2012. The consequences of Middle Paleolithic diets on pregnant Neanderthal women. Quat Int 264:78–82.

Hockett BS, Haws JA. 2003. Nutritional Ecology and Diachronic Trends in Paleolithic Diet and Health. Evol Anthropol 12:211–216.

Hockett BS, Haws JA. 2005. Nutritional ecology and the human demography of Neandertal extinction. Quat Int 137:21–34.

Hockett BS, Haws JA. 2009. Continuity in animal resource diversity in the Late Pleistocene human diet of Central Portugal. Before Farming 2009:1–14.

Hohmann G, Potts K, N'Guessan A, Fowler A, Mundry R, Ganzhorn JU, Ortmann S. 2010.

Plant foods consumed by Pan: exploring the variation of nutritional ecology across Africa. Am J Phys Anthropol 141:476–85.

Holm G. 1911. Ethnological sketch of the Angmagssalik Eskimo. In: Thalbitzer W, editor. The Ammassalik Eskimo : contributions to the Ethnology of the East Greenland Natives. Copenhagen: Meddelelser om Grønland. p 1–147.

Holm J, Lundquist I, Björck I, Eliasson AC, Asp NG. 1988. Degree of starch gelatinization, digestion rate of starch in vitro, and metabolic response in rats. Am J Clin Nutr 47:1010–6.

Hora M, Sladek V. 2014. Influence of lower limb configuration on walking cost in Late Pleistocene humans. J Hum Evol 67:19–32.

Howell FC. 1957. The Evolutionary Significance of Variation and Varieties of "Neanderthal" Man. Q Rev Biol 32:330–347.

Hublin J-J. 1998. Climatic changes, paleogeography, and the evolution of the Neandertals. In: Akazawa T, Aoki K, Bar-Yosef O, editors. Neandertals and modern humans in Western Asia. New York, NY: Kluwer Academic Publishers. p 295–310.

Hublin J-J. 2009. The origin of Neandertals. Proc Natl Acad Sci U S A 106:16022–7.

Hublin J-J. 2015. The modern human colonization of western Eurasia: when and where? Quat Sci Rev 118:194–210.

Hublin J-J, Roebroeks W. 2009. Ebb and flow or regional extinctions? On the character of Neandertal occupation of northern environments. Comptes Rendus Palevol 8:503–509.

Hublin J-J, Spoor F, Braun M, Zonneveld F, Condemi S. 1996. A late Neanderthal associated with Upper Palaeolithic artefacts. Nature 381:224–6.

Hublin J-J, Talamo S, Julien M, David F, Connet N, Bodu P, Vandermeersch B, Richards MP. 2012. Radiocarbon dates from the Grotte du Renne and Saint-Césaire support a Neandertal origin for the Châtelperronian. Proc Natl Acad Sci U S A 109:18743–8.

Hublin J-J, Weston D, Gunz P, Richards M, Roebroeks W, Glimmerveen J, Anthonis L. 2009. Out of the North Sea: the Zeeland ridges Neandertal. J Hum Evol 57:777–85.

Hughes DR. 1963. A study of a series of mandibles from the Mulu cave, Sarawak. J Anthropol Inst Gt Britain Irel 93:235–249.

Hurtado MA, Hill KR. 1987. Early dry season subsistence ecology of Cuiva (Hiwi) foragers of Venezuela. Hum Ecol 15:163–187.

Hutchinson GE. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? Am Nat 93:145–159.

ICSN. 2011. The International Code for Starch Nomenclature. Available from: http://fossilfarm.org/ICSN/Code.html

Janis CM. 1990. The correlation between diet and dental wear in herbivorous mammals, and

its relationship to the determination of diets of extinct species. In: Boucot AJ, editor. Evolutionary paleobiology of behavior and coevolution. Amsterdam: Elsevier. p 241–259.

Jin Y, Yip H-K. 2002. Supragingival calculus: formation and control. Crit Rev Oral Biol Med 13:426–441.

Jones EL. 2016. In Search of the Broad Spectrum Revolution in Paleolithic Southwest Europe. Cham: Springer International Publishing.

Jones M. 2009. Moving North: Archaeobotanical Evidence for Plant Diet in Middle and Upper Paleolithic Europe. In: Hublin J-J, Richards MP, editors. The Evolution of Human Diets: Integrating Approaches to the Study of Paleolithic Subsistence. Springer. p 171–180.

Kaidonis JA. 2008. Tooth wear: the view of the anthropologist. Clin Oral Investig 12 Suppl 1:S21-6.

Kaifu Y, Kasai K, Townsend GC, Richards LC. 2003. Tooth Wear and the "Design" of the Human Dentition: A Perspective from Evolutionary Medicine. Am J Phys Anthropol 122:47–61.

Kaplan AR, Powell WE, Moorhouse AB, Hinko EN. 1976. Taste sensitivity and human variation: some biological and clinical implications. In: Kaplan AR, editor. Human Behaviour Genetics. Springfield: Charles C. Thomas. p 401–423.

Karavanić I, Smith FH. 1998. The Middle/Upper Paleolithic interface and the relationship of Neanderthals and early modern humans in the Hrvatsko Zagorje, Croatia. J Hum Evol 34:223–248.

Kay RF, Hiiemae KM. 1974. Jaw movement and tooth use in recent and fossil primates. Am J Phys Anthropol 40:227–56.

Keeley LH. 1992. The Use of Plant Foods among Hunter-Gatherers : A Cross-Cultural Survey. In: Anderson PC, editor. Prehistoire de l'Agriculture. Nouvelles Approches Experimentales et Ethnographiques. Paris: National Center for Scientific Research. Monographie du CRA. p 29–38.

Kelly RL. 1995. The Foraging Spectrum: Diversity in Hunter-Gatherer Lifeways. New York: Eliot Werner Publications.

Klein RG. 2009. The human career: human biological and cultural origins. Chicago: University of Chicago Press.

Klein RG, Steele TE. 2008. Gibraltar data are too sparse to inform on Neanderthal exploitation of coastal resources. Proc Natl Acad Sci U S A 105:E115; author reply E116.

Kleinberg I. 1970. Biochemistry of the Dental Plaque. In: Staple PH, editor. Advances in Oral Biology, Volume 4. New York: Elsevier Science. p 40–93.

Krause J, Orlando L, Serre D, Viola B, Prüfer K, Richards MP, Hublin J-J, Hänni C,

Derevianko AP, Pääbo S. 2007. Neanderthals in central Asia and Siberia. Nature 449:902–4.

Krings M, Capelli C, Tschentscher F, Geisert H, Meyer S, von Haeseler A, Grossschmidt K, Possnert G, Paunović M, Pääbo S. 2000. A view of Neandertal genetic diversity. Nat Genet 26:144–146.

Kucera M, Pany-Kucera D, Boyadjian CHC, Reinhard K, Eggers S. 2011. Efficient but destructive: A test of the dental wash technique using secondary electron microscopy. J Archaeol Sci 38:129–135.

Kuhn SL. 1991. "Unpacking" reduction: Lithic raw material economy in the mousterian of west-central Italy. J Anthropol Archaeol 10:76–106.

Kuhn SL, Stiner MC. 2006. What's a Mother to Do? The Division of Labor among Neandertals and Modern Humans in Eurasia. Curr Anthropol 47:953–981.

Kuhnlein H V., Turner NJ. 1991. Traditional plant foods of Canadian indigenous peoples: nutrition, botany, and use v8. Amsterdam: Taylor & Francis.

Kuitems M, van Kolfschoten T, van der Plicht J. 2012. Elevated δ15N values in mammoths: a comparison with modern elephants. Archaeol Anthropol Sci 7:289–295.

Kullmer O, Benazzi S, Fiorenza L, Schulz D, Bacso S, Winzen O. 2009. Technical note: Occlusal fingerprint analysis: Quantification of tooth wear pattern. Am J Phys Anthropol 139:600–605.

Laden G, Wrangham RW. 2005. The rise of the hominids as an adaptive shift in fallback foods: plant underground storage organs (USOs) and australopith origins. J Hum Evol 49:482–498.

Lalueza C, Pérez-Pérez A, Turbón D. 1996. Dietary inferences through buccal microwear analysis of middle and upper Pleistocene human fossils. Am J Phys Anthropol 100:367–87.

Lalueza-Fox C, Gigli E, de la Rasilla M, Fortea J, Rosas A. 2009. Bitter taste perception in Neanderthals through the analysis of the *TAS2R38* gene. Biol Lett 5:809–11.

Lalueza-Fox C, Juan J, Albert RM. 1996. Phytolith analysis on dental calculus, enamel surface, and burial soil: Information about diet and paleoenvironment. Am J Phys Anthropol 101:101–113.

Lanfranco LP, Eggers S. 2012. Caries through time: an anthropological overview. In: Li M-Y, editor. Contemporary Approach to Dental Caries. InTech. p 3–34.

Langejans GHJ. 2010. Remains of the day-preservation of organic micro-residues on stone tools. J Archaeol Sci 37:971–985.

Langejans GHJ. 2011. Discerning use-related micro-residues on tools: testing the multi-stranded approach for archaeological studies. J Archaeol Sci 38:985–1000.

Langejans GHJ. 2012. Middle Stone Age pièces esquillées from Sibudu Cave, South Africa: an initial micro-residue study. J Archaeol Sci 39:1694–1704.

Larsen CS, Shavit R, Griffin MC. 1991. Dental caries evidence for dietary change: an archaeological context. In: Kelley M, Larsen C, editors. Advances in Dental Anthropology. New York, NY: Wiley-Liss. p 179–202.

Laurence AR, Thoms A V., Bryant VM, McDonough C. 2011. Airborne Starch Granules as a Potential Contamination Source at Archaeological Sites. J Ethnobiol 31:213–232.

Lazzati AMB, Levrini L, Rampazzi L, Dossi C, Castelletti L, Licata M, Corti C. 2015. The Diet of Three Medieval Individuals from Caravate (Varese, Italy). Combined Results of ICP-MS Analysis of Trace Elements and Phytolith Analysis Conducted on Their Dental Calculus. Int J Osteoarchaeol.

Lebreton V, Psathi E, Darlas A. 2008. Environnement vegetal des neandertaliens de la Grotte deKalamakia (Aréopolis, Grèce). In: Darlas A, Mihailovi D, editors. The Palaeolithic of the Balkan. Proceedings of the XV UISPP World Congress. Oxford: BAR International Series 1819. p 61–68.

Lee B-H, Bello-Pérez LA, Lin AH-M, Kim CY, Hamaker BR. 2013. Importance of Location of Digestion and Colonic Fermentation of Starch Related to Its Quality. Cereal Chem 90:335–343.

Lee-Thorp JA, van der Merwe NJ, Brain CK. 1994. Diet of Australopithecus robustus at Swartkrans from stable carbon isotopic analysis. J Hum Evol 27:361–372.

Lee-Thorp J, Sponheimer M. 2006. Contributions of biogeochemistry to understanding hominin dietary ecology. Yearb Phys Anthropol 43:131–148.

Leigh RW. 1925. Dental pathology of Indian tribes of varied environmental and food conditions. Am J Phys Anthropol 8:179–199.

Leonard C, Vashro L, O'Connell JF, Henry AG. 2015. Plant microremains in dental calculus as a record of plant consumption: A test with Twe forager-horticulturalists. J Archaeol Sci Reports 2:449–457.

Leroi-Gourhan A. 1968. Le Neanderthalien IV de Shanidar. Bull la Société Préhistorique Française LXV:79–83.

Leroi-Gourhan A. 1969. Pollen grains of Graminae and Cerealia from Shanidar and Zawi Chemi. In: Ucko PJ, Dimbleby GW, editors. The domestication and exploitation of plants and animals. Chicago: Aldine Transaction. p 141–148.

Leroi-Gourhan A. 1975. The Flowers Found with Shanidar IV, a Neanderthal Burial in Iraq. Science (80-) 190:562–564.

Lev E, Kislev ME, Bar-Yosef O. 2005. Mousterian vegetal food in Kebara Cave, Mt. Carmel. J Archaeol Sci 32:475–484.

Lieverse AR. 1999. Diet and the Aetiology of Dental Calculus. Int J Osteoarchaeol 232:219–

232.

Liu H. 2012. Research of plant remains of some sites in Shaanxi and Henan and their implication for the two millets of China.

Liu L, Bestel S, Shi J, Song Y, Chen X. 2013. Paleolithic human exploitation of plant foods during the last glacial maximum in North China. Proc Natl Acad Sci U S A 110:5380–5385.

Lomba Maurandi J, López Martínez M, Ramos Martínez F, Avilés Fernández A. 2009. El enterramiento múltiple, calcolítico, de Camino del Molino (Caravaca, Murcia). Metodología y primeros resultados de un yacimiento exepcional. Trab Prehist 66:143–159.

Loring Brace C, Rosenberg KR, Hunt KD. 1987. Gradual change in human tooth size in the late Pleistocene and post-Pleistocene. Evolution (N Y) 41:705–720.

Lothrop SK. 1928. The Indians of Tierra del Fuego. New York: Museum of the American Indian.

Loy T, Barton H. 2006. Post-excavation contamination and measures for prevention. In: Torrence R, Barton H, editors. Ancient Starch Research. Walnut Creek: Left Coast Press. p 165.

Lucas PW, Omar R, Al-Fadhalah K, Almusallam AS, Henry AG, Michael S, Thai LA, Watzke J, Strait DS, Atkins AG. 2013. Mechanisms and causes of wear in tooth enamel: implications for hominin diets. J R Soc Interface 10:20120923.

Lukacs JR, Largaespada LL. 2006. Explaining sex differences in dental caries prevalence: saliva, hormones, and "life-history" etiologies. Am J Hum Biol 18:540–55.

De Lumley H, Darlas A, Anglada R, Cataliotti-Valdina J, Desclaux E, Dubar M, Falguères C, Keraudren B, Lecervoisier B, Mestour B, Renault-Miskovsky J, Trantalidou K, Vernet JL. 1994. Grotte de Kalamakia (Aréopolis, Péloponnèse). Bull Corresp héllénique 118:535–559.

Lyman RL. 2003. The influence of time averaging and space averaging on the application of foraging theory in zooarchaeology. J Archaeol Sci 30:595–610.

MacArthur RH, Pianka ER. 1966. On Optimal Use of a Patchy Environment. Am Nat 100:603.

MacDonald IA, Bokkenheuser VD, Winter J, McLernon AM, Mosbach EH. 1983. Degradation of steroids in the human gut. J Lipid Res 24:675–700.

Macdonald K, Roebroeks W, Verpoorte A. 2009. An Energetics Perspective on the Neandertal Record. In: Hublin J-J, Richards MP, editors. The Evolution of Hominin Diets: Integrating Approaches to the Study of Palaeolithic Subsistence. Dordrecht: Springer. p 211–220.

Madella M, Alexandre A, Ball T. 2005. International code for phytolith nomenclature 1.0.

Ann Bot 96:253–260.

Madella M, Jones MK, Goldberg P, Goren Y, Hovers E. 2002. The Exploitation of Plant Resources by Neanderthals in Amud Cave (Israel): The Evidence from Phytolith Studies. J Archaeol Sci 29:703–719.

Magurran AE. 2004. Measuring biological diversity. Oxford: Blackwell Publishing.

Mangafa M. 1998. Plant exploitation from the Middle Paleolithic to the Neolithic: from food gathering to farming. Archaeobotanical study of Theopetra cave. Theopetra Cave Proc Int Conf Trkala:6–7.

Marlowe FW. 2010. The Hadza: hunter-gatherers of Tanzania. London: University of California Press.

Martinoli DC. 2005. Plant food economy and environment during the epipalaeolithic in southwest Anatolia : an investigation of the botanical macroremains from Öküzini and Karain B.

Martinson DG, Pisias NG, Hays JD, Imbrie J, Moore TC, Shackleton NJ. 1987. Age dating and the orbital theory of the ice ages: Development of a high-resolution 0 to 300,000-year chronostratigraphy. Quat Res 27:1–29.

Matsutani A. 1987. Plant remains from the 1984 excavations at Douara Cave. In: Akazawa T, Sakaguchi Y, editors. Paleolithic Site of Douara Cave and Paleogeography of Palmyra Basin in Syria: Part IV: 1984 Excavations. Tokyo: The University of Tokyo Press.

Mauch Lenardić J. 2014. Bank vole Myodes (=Clethrionomys) glareolus (Schreber, 1780): Rare species in the Late Pleistocene fauna of Croatia. Quat Int 328–329:167–178.

McBrearty S, Brooks AS. 2000. The revolution that wasn't: a new interpretation of the origin of modern human behavior. J Hum Evol 39:453–563.

Mellars P. 1986. A new chronology for the French Mousterian period. Nature 322:410–411.

Mercader J, Bennett T, Raja M. 2008. Middle Stone Age starch acquisition in the Niassa Rift, Mozambique. Quat Res 70:283–300.

Meriggi A, Rosa P, Brangi A, Matteucci C. 1991. Habitat use and diet of the wolf in northern Italy. Acta Theriol (Warsz) 36:141–151.

Meyer M, Fu Q, Aximu-Petri A, Glocke I, Nickel B, Arsuaga J-L, Martinez I, Gracia A, de Castro JMB, Carbonell E, Paabo S. 2014. A mitochondrial genome sequence of a hominin from Sima de los Huesos. Nature 505:403–406.

Mickleburgh HL, Pagán-Jiménez JR. 2012. New insights into the consumption of maize and other food plants in the pre-Columbian Caribbean from starch grains trapped in human dental calculus. J Archaeol Sci 39:2468–2478.

Molleson TI. 2000. The People of Abu Hureyra. In: Moore AMT, Hillman CC, Legge AJ, editors. Village on the Euphrates from Foraging to Farming at Abu Hureyra. Oxford:

Oxford University Press. p 301–34.

Monge G, Jiménez-Espejo FJ, García-Alix A, Martínez-Ruiz F, Mattielli N, Finlayson C, Ohkouchi N, Sánchez MC, de Castro JMB, Blasco R, Rosell J, Carrión JS, Rodríguez-Vidal J, Finlayson G. 2015. Earliest evidence of pollution by heavy metals in archaeological sites. Sci Rep 5:14252.

Monteiro da Silva A. M, Newman HN, Oakley DA, O'Leary R. 1998. Psychosocial factors, dental plaque levels and smoking in periodontitis patients. J Clin Periodontol 25:517–523.

Morton JF. 1975. Cattails (*Typha* spp.) — Weed Problem or Potential Crop? Econ Bot 29:7–29.

Mulder MB, Schacht R. 2012. Human Behavioural Ecology. eLS.

Murie A. 1944. The wolves of Mount McKinley. Fauna of the National Parks of the U. S. Fauna Series No. 5. Fauna Series No. 5.

Murray J, Nasheuer HP, Seoighe C, McCormack GP, Williams DM, Harper DAT. 2015. The Contribution of William King to the Early Development of Palaeoanthropology. Irish J Earth Sci 33:1–16.

N'guessan AK. 2012. Aspects quantitatifs et qualitatifs du régime alimentaire des chimpanzés au parc national de Taï, Côte d'Ivoire.

N'guessan AK, Ortmann S, Boesch C. 2009. Daily energy balance and protein gain among *Pan troglodytes verus* in the Taï National Park, Côte d'Ivoire. Int J Primatol 30:481–496.

Nabhan GP. 2009. Ethnoecology: Bridging Disciplines, Cultures and Species. J Ethnobiol 29:3–7.

Nadel D, Danin A, Power RC, Rosen AM, Bocquentin F, Tsatskin A, Rosenberg D, Yeshurun R, Weissbrod L, Rebollo NR, Barzilai O, Boaretto E. 2013. Earliest floral grave lining from 13,700-11,700-y-old Natufian burials at Raqefet Cave, Mt. Carmel, Israel. Proc Natl Acad Sci U S A 110:1–5.

Newman AW, Vitez IM, Kiesnowski C, Mueller RL. 1996. Starches and starch derivatives. In: Swarbrick J, Boylan JC, editors. Encyclopedia of pharmaceutical technology. New York: Marcel Dekker Inc. p 223–248.

Newsom SWB, Shaw M. 1997. A survey of starch particle counts in the hospital environment in relation to the use of powdered latex gloves. Occup Med (Chic Ill) 47:155–158.

Nicholson RA. 1996. Bone Degradation, Burial Medium and Species Representation: Debunking the Myths, an Experiment-based Approach. J Archaeol Sci 23:513–533.

Niewind A, Krondl M, Shrott M. 1988. Genetic influences on the selection of brassica vegetables by elderly individuals. Nutr Res 8:13–20.

Nilles J. 1942. Digging-Sticks, Spades, Hoes, Axes, and Adzes of the Kuman People in the Bismarck Mountains of East-Central New Guinea. Anthropos 37/40:205–212.

Nishida T, Hasegawa T. 1992. Meat-sharing as a coalition strategy by an alpha male chimpanzee. In: Nishida T, Mcgrew WC, Marler P, Pickford M, de Waal MFB, editors. Topics in primatology. Tokyo: University of Tokyo Press. p 159–174.

O'Connell JF. 2006. How did modern humans displace Neanderthals? Insights from hunter-gatherer ethnography and archaeology. In: Conard NJ, editor. When Neanderthals and modern humans met. Tübingen: Kerns Verlag. p 43–64.

O'Connell JF, Hawkes K, Blurton Jones NG. 1999. Grandmothering and the evolution of homo erectus. J Hum Evol 36:461–85.

Odum EP. 1975. Ecology. 2nd Editio. New York: Holt, Rinehart and Winston.

Otte M. 1979. Le Paléolithique supérieur ancien en Belgique. Bruxelles: Musees Royaux d'art et d'histoire.

Out WA, Madella M. 2015. Morphometric distinction between bilobate phytoliths from Panicum miliaceum and Setaria italica leaves. Archaeol Anthropol Sci.

Out WA, Pertusa Grau JF, Madella M. 2014. A new method for morphometric analysis of opal phytoliths from plants. Microsc Microanal 20:1876–87.

Ovchinnikov I V., Götherström A, Romanova GP, Kharitonov VM, Lidén K, Goodwin W. 2000. Molecular analysis of Neanderthal DNA from the northern Caucasus. Nature 404:490–3.

Oyebade T. 1973. Some aspects of developmental physiology of the Nigerian kola (*Cola nitida*) fruit. Econ Bot 27:417–422.

Pacher M, Stuart AJ. 2009. Extinction chronology and palaeobiology of the cave bear (*Ursus spelaeus*). Boreas 38:189–206.

Patou-Mathis M. 2000. Neanderthal subsistence behaviours in Europe. Int J Osteoarchaeol 10:379–395.

Paunović M, Smith FH. 2002. Taphonomy of lower vertebrates from Vindija cave (Croatia): delicacy on Neandertal table of animal prey? J Hum Evol 42:A27–A27.

Pennington HL, Weber SA. 2004. Paleoethnobotany: Modern Research Connecting Ancient Plants and Ancient Peoples. CRC Crit Rev Plant Sci 23:13–20.

Pennington L. 1989. Bowes and Church's Food values of portions commonly used. New York: Harper and Row.

Pérez Jordà G. 2005. Nuevos datos paleocarpológicos en niveles neolíticos del País Valenciano. In: Arias Cabal P, Ontañón Peredo R, García-Moncó Piñeiro C, editors. III Congreso del Neolítico en la Península Ibérica. Universidad de Cantabria. p 103–114.

Pérez Jordà G, Carrión Marco Y. 2011. Los recursos vegetales. In: Pérez Jordà G, Bernabeu Aubán J, Carrión Marco Y, García Puchol O, Molina Balaguer LL, Gómez Puche M, editors. La Vital (Gandia, Valencia). Vida y muerte en la desembocadura del Serpis

durante el III y el I milenio a.C. Museo de Prehistòria de València-Diputación de Valencia.

Pérez-Pérez A. 1994. Intraindividual and intragroup variability of buccal tooth striation pattern. Am J Phys Anthropol 94:175–187.

Perkins D. 1964. Prehistoric Fauna From Shanidar, Iraq. Science (80-) 144:1565–1566.

Perry GH, Dominy NJ, Claw KG, Lee AS, Fiegler H, Redon R, Werner J, Villanea FA, Mountain JL, Misra R, Carter NP, Lee C, Stone AC. 2007. Diet and the evolution of human amylase gene copy number variation. Nat Genet 39:1256–1260.

Perry GH, Kistler L, Kelaita MA, Sams AJ. 2015. Insights into hominin phenotypic and dietary evolution from ancient DNA sequence data. J Hum Evol 79:55–63.

Peters KE, Walters CC, Moldowan JM. 2005. The Biomarker Guide. Volume 1: Biomarkers and Isotopes in the Environment and Human History. Cambridge University Press.

Phillips C, Lancelotti C. 2014. Chimpanzee diet: phytolithic analysis of feces. Am J Primatol 76:757–73.

Phinney SD. 1995. The functional effects of carbohydrate and energy underconsumption. In: Bernadette MM, editor. Not Eating Enough: Overcoming Underconsumption of Military Operational Rations. Washington, DC: National Academy Press. p 303–315.

Pinhasi R, Higham TFG, Golovanova L V., Doronichev VB. 2011. Revised age of late Neanderthal occupation and the end of the Middle Paleolithic in the northern Caucasus. Proc Natl Acad Sci U S A 108:8611–6.

Piperno DR. 2006. Phytoliths: A Comprehensive Guide for Archaeologists and Paleoecologists. Lanham: AltaMira.

Piperno DR, Dillehay TD. 2008. Starch grains on human teeth reveal early broad crop diet in northern Peru. Proc Natl Acad Sci U S A 105:19622–7.

Power RC, Rosen AM, Nadel D. 2014a. The economic and ritual utilization of plants at the Raqefet Cave Natufian site: The evidence from phytoliths. J Anthropol Archaeol 33:49–65.

Power RC, Salazar-García DC, Henry, Amanda G. 2016. Dental calculus evidence of Gravettian diet and behaviour at Dolní Věstonice and Pavlov. In: Svoboda J, editor. Dolní Věstonice II: Chronostratigraphy, Paleoethnology, Paleoanthropology. Brno: Academy of Sciences of the Czech Republic, Institute of Archeology,. p 345–352.

Power RC, Salazar-García DC, Straus LG, González Morales MR, Henry AG. 2015a. Microremains from El Mirón on Cave human dental calculus suggest a mixed plant-animal subsistence economy during the Magdalenian in Northern Iberia. J Archaeol Sci 60:39–46.

Power RC, Salazar-García DC, Wittig RM, Freiberg M, Henry AG. 2015b. Dental calculus evidence of Taï Forest Chimpanzee plant consumption and life history transitions. Sci

Rep 5:15161.

Power RC, Salazar-García DC, Wittig RM, Henry AG. 2014b. Assessing use and suitability of scanning electron microscopy in the analysis of micro remains in dental calculus. J Archaeol Sci 49:160–169.

Privat KL, O'Connell TC, Hedges REM. 2007. The distinction between freshwater- and terrestrial-based diets: methodological concerns and archaeological applications of sulphur stable isotope analysis. J Archaeol Sci 34:1197–1204.

Prüfer K, Racimo F, Patterson N, Jay F, Sankararaman S, Sawyer S, Heinze A, Renaud G, Sudmant PH, de Filippo C, Li H, Mallick S, Dannemann M, Fu Q, Kircher M, Kuhlwilm M, Lachmann M, Meyer M, Ongyerth M, Siebauer M, Theunert C, Tandon A, Moorjani P, Pickrell J, Mullikin JC, Vohr SH, Green RE, Hellmann I, Johnson PLF, Blanche H, Cann H, Kitzman JO, Shendure J, Eichler EE, Lein ES, Bakken TE, Golovanova L V., Doronichev VB, Shunkov M V., Derevianko AP, Viola B, Slatkin M, Reich D, Kelso J, Pääbo S. 2014. The complete genome sequence of a Neanderthal from the Altai Mountains. Nature 505:43–9.

Pryor AJE, Steele M, Jones MK, Svoboda J, Beresford-Jones DG. 2013. Plant foods in the Upper Palaeolithic at Dolní Věstonice? Parenchyma redux. Antiquity 87:971–984.

Puech PF. 1999. Usures des dents et sédentarisation? Doss Pour la Sci 22:90.

de Puydt M, Lohest M. 1887. L'homme contemporain du Mammouth à Spy (Namur). In: de Radiguès de Chennevière H, editor. Fédération archéologique et historique de Belgique. Namur. p 205–240.

R Core Team. 2014. R: A language and environment for statistical computing. R Found Stat Comput Vienna, Austria:URL http://www.R-project.org/.

Reinhard KJ, Mendonça de Souza SMF, Rodrigues C, Kimmerle E, Dorsey-Vinton S. 2001. Microfossils in dental calculus: a new perspective on diet and dental disease. In: Williams E, editor. Human Remains: Conservation, Retrieval and Analysis. London: British Archaeology Research Council. p 113–118.

Revedin A, Aranguren B, Becattini R, Longo L, Marconi E, Lippi MM, Skakun N, Sinitsyn A, Spiridonova E, Svoboda J. 2010. Thirty thousand-year-old evidence of plant food processing. Proc Natl Acad Sci U S A 107:18815–9.

Richards MP, Pettitt PB, Stiner MC, Trinkaus E. 2001. Stable isotope evidence for increasing dietary breadth in the European mid-Upper Paleolithic. Proc Natl Acad Sci U S A 98:6528–6532.

Richards MP, Pettitt PB, Trinkaus E, Smith FH, Paunović M, Karavanić I. 2000. Neanderthal diet at Vindija and Neanderthal predation: the evidence from stable isotopes. Proc Natl Acad Sci U S A 97:7663–7666.

Richards MP, Schmitz RW. 2008. Isotope evidence for the diet of the Neanderthal type specimen. Antiquity 82:553–559.

Richards MP, Taylor G, Steele TE, McPherron SP, Soressi M, Jaubert J, Orschiedt J, Mallye JB, Rendu W, Hublin J-J. 2008. Isotopic dietary analysis of a Neanderthal and associated fauna from the site of Jonzac (Charente-Maritime), France. J Hum Evol 55:179–185.

Richards MP, Trinkaus E. 2009. Out of Africa: modern human origins special feature: isotopic evidence for the diets of European Neanderthals and early modern humans. Proc Natl Acad Sci U S A 106:16034–9.

Rink WJ, Schwarcz HP, Valoch K, Seitl L, Stringer CB. 1996. ESR Dating of Micoquian Industry and Neanderthal Remains at Kůlna Cave, Czech Republic. J Archaeol Sci 23:889–901.

Roberts-Harry EA, Clerehugh V. 2000. Subgingival calculus: where are we now? A comparative review. J Dent 28:93–102.

Roebroeks W, Hublin J-J, Macdonald K. 2011. Continuities and Discontinuities in Neandertal Presence: A Closer Look at Northwestern Europe.

Roger T, Darlas A. 2008. Upper-Pleistocene bird remains from Kalamakia Cave. In: Darlas A, Milhailović D, editors. The Palaeolithic of the Balkans. Proceedings of the XV UISPP World Congress. Oxford: BAR International Series 1819. p 69–76.

Rosen A. 2010. Natufian plant exploitation: Managing risk and stability in an environment of change. Eurasian Prehistory 7:117–131.

Rosner A. 2011. Roasting Green Wheat in Galilee. Gastronomica 11:60–68.

Ross C. 1998. Primate Life Histories. Evol Anthropol 6:54–63.

Rothman JM, Van Soest PJ, Pell AN. 2006. Decaying wood is a sodium source for mountain gorillas. Biol Lett 2:321–4.

Rougier H, Crevecoeur I, Beauval C, Bocherens H, Flas D, Germonpré M, Semal P, Van der Plicht J. 2012. New data from an old site : Neandertals at Goyet (Belgium) and their mortuary behavior. Am J Phys Anthropol 147:252–253.

Rougier H, Crevecoeur I, Beauval C, Flas D, Bocherens H, Wißing C, Germonpré M, Semal P, van der Plicht J. 2014. New fossils at the "Troisième Caverne" of Goyet (Belgium) and the mortuary practises of late Neandertals. In: Middle Palaeolithic in North West Europe: Multidisciplinary Approaches. Namur. p 35.

Ruebens K, McPherron SJP, Hublin J-J. 2015. On the local Mousterian origin of the Châtelperronian: Integrating typo-technological, chronostratigraphic and contextual data. J Hum Evol.

Salazar-García DC. 2012. Isótopos, dieta y movilidad en el País Valenciano. Aplicación a restos humanos del Paleolítico medio al Neolítico final.

Salazar-García DC, Power RC, Sanchis Serra A, Villaverde V, Walker MJ, Henry AG. 2013. Neanderthal diets in central and southeastern Mediterranean Iberia. Quat Int 318:3–18.

Salazar-García DC, Richards MP, Nehlich O, Henry AG. 2014. Dental calculus is not equivalent to bone collagen for isotope analysis: a comparison between carbon and nitrogen stable isotope analysis of bulk dental calculus, bone and dentine collagen from same individuals from the Medieval site of El Raval (Alicante. J Archaeol Sci 47:70–77.

Samuel D. 1996. Investigation of Ancient Egyptian Baking and Brewing Methods by Correlative Microscopy. Science (80-) 273:488–490.

Sanchis A. 2012. Los lagomorfos del Paleolítico medio en la vertiente mediterránea ibérica. Diputación De Valencia.

Sandgathe DM, Hayden B. 2003. Did Neanderthals eat inner bark? Antiquity 77:709–718.

Sankararaman S, Patterson N, Li H, Pääbo S, Reich D. 2012. The date of interbreeding between Neandertals and modern humans. PLoS Genet 8:e1002947.

Santos JL, Saus E, Smalley S V., Cataldo LR, Alberti G, Parada J, Gratacòs M, Estivill X. 2012. Copy number polymorphism of the salivary amylase gene: implications in human nutrition research. J Nutrigenet Nutrigenomics 5:117–31.

Saul H, Wilson J, Heron CP, Glykou A, Hartz S, Craig OE. 2012. A systematic approach to the recovery and identification of starches from carbonised deposits on ceramic vessels. J Archaeol Sci 39:3483–3492.

Savard M, Nesbitt M, Jones MK. 2006. The role of wild grasses in subsistence and sedentism: new evidence from the northern Fertile Crescent. World Archaeol 38:179–196.

Schoch WH, Bigga G, Böhner U, Richter P, Terberger T. 2015. New insights on the wooden weapons from the Paleolithic site of Schöningen. J Hum Evol 89:214–225.

Schwarcz HP, Schoeninger MJ. 1991. Stable isotope analyses in human nutritional ecology. Am J Phys Anthropol 34:283–321.

Scott RS, Teaford MF, Ungar PS. 2012. Dental microwear texture and anthropoid diets. Am J Phys Anthropol 147:551–79.

Selwitz RH, Ismail AI, Pitts NB. 2007. Dental caries. Lancet 369:51–9.

Semal P, Rougier H, Crevecoeur I, Jungels C, Flas D, Hauzeur A, Maureille B, Germonpré M, Bocherens H, Pirson S, Cammaert L, De Clerck N, Hambucken A, Higham T, Toussaint M, Van der Plicht J. 2009. New data on the late Neandertals: Direct dating of the Belgian Spy fossils. Am J Phys Anthropol 138:421–428.

Sergi S. 1954. La mandibola neandertaliana Circeo II. Riv Di Antropol 41:305–344.

Simms SR. 1985. Acquisition Cost and Nutritional Data on Great Basin Resources. J Calif Gt Basin Anthropol 7:117–126.

Simopoulos AP. 2004. Omega-3 Fatty Acids and Antioxidants in Edible Wild Plants. Biol Res 37:263–277.

Sistiaga A, Mallol C, Galván B, Summons RE. 2014. The Neanderthal meal: a new

perspective using faecal biomarkers. PLoS One 9:e101045.

Slimak L, Svendsen JI, Mangerud J, Plisson H, Heggen HP, Brugere A, Pavlov PY. 2011. Late Mousterian Persistence near the Arctic Circle. Science (80-) 332:841–845.

Smith CI, Chamberlain AT, Riley MS, Cooper A, Stringer CB, Collins MJ. 2001. Neanderthal DNA: Not just old but old and cold? Nature 410:771–772.

Smith EA. 2011. Endless forms: human behavioural diversity and evolved universals. Philos Trans R Soc London B Biol Sci 366:325–332.

Smith FH, Boyd DC, Malez M. 1985. Additional upper pleistocene human remains from Vindija cave, Croatia, Yugoslavia. Am J Phys Anthropol 68:375–383.

Smith TM, Toussaint M, Reid DJ, Olejniczak AJ, Hublin J-J. 2007. Rapid dental development in a Middle Paleolithic Belgian Neanderthal. Proc Natl Acad Sci U S A 104:20220–5.

Snodgrass JJ, Leonard WR. 2009. Neandertal energetics revisited: insights into population dynamics and life history evolution. PaleoAnthropology:220–237.

Solecki RS. 1960. Three adult Neanderthal skeletons from Shanidar cave, northern Iraq. Annu Rep Board Regents Smithson Inst:603–635.

Solecki RS. 1961. New anthropological discoveries at Shanidar, northern Iraq. Trans N Y Acad Sci 23:690–699.

Sołtysiak A. 2012. Comment: low dental caries rate in Neandertals: the result of diet or the oral flora composition? Homo Int Zeitschrift für die vergleichende Forsch am Menschen 63:110–3.

Sorensen M V., Leonard WR. 2001. Neandertal energetics and foraging efficiency. J Hum Evol 40:483–95.

Speth JD. 2010. The Paleoanthropology and Archaeology of Big-Game Hunting. New York, NY: Springer New York.

Speth JD, Clark JL. 2006. Hunting and overhunting in the Levantine Late Middle Palaeolithic. Before Farming 3:1–42.

Speth JD, Spielmann KA. 1983. Energy source, protein metabolism, and hunter-gatherer subsistence strategies. J Anthropol Archaeol 2:1–31.

Speth JD, Tchernov E. 2001. Neandertal hunting and meat processing in the Near East, Evidence from Kebara cave (Israel). In: Stanford C, Bunn H, editors. Meat-eating and Human evolution. Oxford: Oxford University Press. p 52–72.

Spoor F, Hublin J-J, Braun M, Zonneveld F. 2003. The bony labyrinth of Neanderthals. J Hum Evol 44:141–165.

Squires BT. 1953. Human salivary amylase secretion in relation to diet. J Physiol 119:153–156.

Sroubek P, Diehl JF, Kadlec J, Valoch K. 2001. A Late Pleistocene palaeoclimate record based

on mineral magnetic properties of the entrance facies sediments of Kulna Cave, Czech Republic. Geophys J Int 147:247–262.

Ståhlberg S, Svanberg I. 2010. Gathering Food from Rodent Nests in Siberia. J Ethnobiol 30:184–202.

Ståhlberg S, Svanberg I. 2012. Gathering dog's tooth violet (*Erythronium sibiricum*) in Siberia. J la Soc Finno-Ougrienne 91:349–351.

Stahler DR, Smith DW, Guernsey DS. 2006. Foraging and feeding ecology of the gray wolf (*Canis lupus*): lessons from Yellowstone National Park, Wyoming, USA. J Nutr 136:1923S–1926S.

Stefansson V. 1956. The Fat of the Land. New York: The Macmillan Company.

Stewart JR. 2005. The ecology and adaptation of Neanderthals during the non-analogue environment of Oxygen Isotope Stage 3. Quat Int 137:35–46.

Stiner MC. 1994. Honor among thieves: a zooarchaeological study of Neandertal ecology. Princeton: Princeton University Press.

Stiner MC. 1999. Paleolithic Population Growth Pulses Evidenced by Small Animal Exploitation. Science (80-) 283:190–194.

Stiner MC. 2001. Thirty years on the "Broad Spectrum Revolution" and paleolithic demography. Proc Natl Acad Sci U S A 98:6993–6996.

Stiner MC. 2013. An Unshakable Middle Paleolithic? Trends versus Conservatism in the Predatory Niche and Their Social Ramifications. Curr Anthropol 54:S288–S304.

Stiner MC, Kuhn SL. 1992. Subsistence, Technology, and Adaptive Variation in Middle Paleolithic Italy. Am Anthropol 94:306–339.

Stiner MC, Kuhn SL. 2006. Changes in the "Connectedness" and Resilience of Paleolithic Societies in Mediterranean Ecosystems. Hum Ecol 34:693–712.

Stiner MC, Kuhn SL. 2009. Paleolithic Diet and the Division of Labor in Mediterranean Eurasia. In: Hublin J-J, Richards MP, editors. The Evolution of Hominin Diets: Integrating Approaches to the Study of Palaeolithic Subsistence. Dordrecht: Springer. p 155–168.

Stiner MC, Munro ND. 2002. Approaches to Prehistoric Diet Breadth, Demography, and Prey Ranking Systems in Time and Space. J Archaeol Method Theory 9:181–214.

Stiner MC, Munro ND, Surovell TA. 2000. The Tortoise and the Hare: Small Game Use, the Broad Spectrum Revolution, and Paleolithic Demography. Curr Anthropol 41:39–79.

Stoneking M, Krause J. 2011. Learning about human population history from ancient and modern genomes. Nat Rev Genet 12:603–14.

Straus LG. 1992. Iberia Before the Iberians: The Stone Age Prehistory of Cantabrian Spain. Albuquerque: University of New Mexico Press.

Stringer CB, Barton RNE, Finlayson JC. 2000. Neanderthals on the edge: papers presented at the conference marking the 150th anniversary of the Forbes' Quarry discovery, Gibralta. (Stringer CB, Barton RNE, Finlayson JC, editors.). Oxford: Oxbow.

Stringer CB, Finlayson JC, Barton RNE, Fernández-Jalvo Y, Cáceres I, Sabin RC, Rhodes EJ, Currant AP, Rodríguez-Vidal J, Giles Pacheco F, Riquelme-Cantal JA. 2008. Neanderthal exploitation of marine mammals in Gibraltar. Proc Natl Acad Sci U S A 105:14319–14324.

Szczęsna T. 2007. Concentration of selected elements in honeybee-collected pollen. J Apic Sci 51:5–13.

Szpak P. 2011. Fish bone chemistry and ultrastructure: implications for taphonomy and stable isotope analysis. J Archaeol Sci 38:3358–3372.

Tao D, Zhang J, Zheng W, Cao Y, Sun K, Jin S. 2015. Starch grain analysis of human dental calculus to investigate Neolithic consumption of plants in the middle Yellow River Valley, China: A case study on Gouwan site. J Archaeol Sci Reports 2:485–491.

Tattersall I, Schwartz JH. 1999. Hominids and hybrids: The place of Neanderthals in human evolution. Proc Natl Acad Sci U S A 96:7117–7119.

Teaford MF, Ungar PS. 2000. Diet and the evolution of the earliest human ancestors. Proc Natl Acad Sci U S A 97:13506–13511.

Thieme H. 2000. Lower Palaeolithic Hunting Weapons From Schöningen, Germany - The Oldest Spears in the World. Acta Anthropol Sin 19:136–143.

Thissen L, Özbal H, Türkekul Bıyık A, Gerritsen F, Özbal R. 2010. The land of milk? Approaching dietary preferences of Late Neolithic communities in NW Anatolia. Leiden J Pottery Stud 26:157–172.

Tillier A, Arensburg B, Rak Y, Vandermeersch B. 1995. Middle Palaeolithic dental caries: new evidence from Kebara (Mount Carmel, Israel). J Hum Evol 29:189–192.

Toepfer V. 1958. Steingeräte und Palökologie der mittelpaläolithischen Fundstelle Rabutz bei Halle (Saale). Jahresschrift für Mitteldeutsche Vor 41/42:140–177.

Tomczyk J. 2012. Comments on Soltysiak's paper: "Comment: Low dental caries rate in Neandertals: The result of diet or the oral flora compositions?" HOMO - J Comp Hum Biol 63:311–314.

Torrence R, Barton H. 2006. Ancient Starch Research. (Torrence R, Barton H, editors.). Walnut Creek: Left Coast Press.

Torrence R, Wright R, Conway R. 2004. Identification of starch granules using image analysis and multivariate techniques. J Archaeol Sci 31:519–532.

Toussaint M. 2006. Research in the caves of Goyet (Gesves, Province of Namur, Belgium). In: Demarsin B, Otte M, editors. Neanderthals in Europe. Liege. p 115–134.

Trinkaus E. 1981. Neanderthal limb proportions and cold adaptation. In: Stringer CB, editor. Aspects of Human Evolution. London: Taylor and Francis. p 187–224.

Trinkaus E, Walker MJ. The People of Palomas: The Neandertals from the Sima de las Palomas del Cabezo Gordo, Southeastern Spain. College Station: Texas A & M University Press.

Tromp M. 2012. Large-scale Analysis of Microfossils Extracted from Human Rapanui Dental Calculus: a Dual-Method Approach Using SEMEDS and Light Microscopy to Address Ancient Dietary Hypotheses.

Tromp M, Dudgeon J V. 2015. Differentiating dietary and non-dietary microfossils extracted from human dental calculus: the importance of sweet potato to ancient diet on Rapa Nui. J Archaeol Sci 54:54–63.

Tsartsidou G, Lev-Yadun S, Albert RM, Miller-Rosen A, Efstratiou N, Weiner S. 2007. The phytolith archaeological record: strengths and weaknesses evaluated based on a quantitative modern reference collection from Greece. J Archaeol Sci 34:1262–1275.

Ungar PS. 1998. Dental allometry, morphology, and wear as evidence for diet in fossil primates. Evol Anthropol Issues, News, Rev 6:205–217.

Ungar PS, Grine FE, Teaford MF. 2008. Dental microwear and diet of the Plio-Pleistocene hominin Paranthropus boisei. PLoS One 3:e2044.

Ungar PS, Sponheimer M. 2011. The Diets of Early Hominins. Science (80-) 334:190–193.

Valensi P, Psathi E. 2004. Faunal Exploitation duringtheMiddle Palaeolithic in South-eastern France and North-western Italy. Int J Osteoarchaeol 14:256–272.

Valoch K. 1970. Early Middle Palaeolithic (Stratum 14) in the Kulna Cave near Sloup in the Moravian Karst (Czechoslovakia). World Archaeol 2:28–38.

Van der Veen M. 2007. Formation processes of desiccated and carbonized plant remains – the identification of routine practice. J Archaeol Sci 34:968–990.

Venables WN, Ripley BD. 2002. Modern Applied Statistics with S. 4th Editio. New York: Springer.

Vernot B, Akey JM. 2015. Complex History of Admixture between Modern Humans and Neandertals. Am J Hum Genet 96:448–453.

Verpoorte A. 2006. Neanderthal energetics and spatial behaviour. Before Farming 3:1–6.

Verpoorte A. 2009. Limiting factors on early modern human dispersals: The human biogeography of late Pleniglacial Europe. Quat Int 201:77–85.

Villa P, Soriano S. 2010. Hunting weapons of Neanderthals and early modern humans in South Africa: similarities and differences. J Anthropol Res 66:5–38.

Wadley L, Langejans GH. 2014. Preliminary Study Of Scrapers Around Combustion Features In Layer Ss, Sibudu, 58000 Years Ago. South African Archaeol Bull 69:19–33.

Wales N. 2012. Modeling Neanderthal clothing using ethnographic analogues. J Hum Evol 63:781–95.

Walker M, Ortega J. 2011. Morphology, body proportions, and postcranial hypertrophy of a female Neandertal from the Sima de las Palomas, southeastern Spain. Proc Natl Acad Sci 108:10087–10091.

Walker MJ, Gibert J, López M V., Lombardi AV, Pérez-Pérez A, Zapata J, Ortega J, Higham T, Pike A, Schwenninger J-L, Zilhão J, Trinkaus E. 2008. Late neandertals in southeastern Iberia: Sima de las Palomas del Cabezo Gordo, Murcia, Spain. Proc Natl Acad Sci U S A 105:20631–6.

Walker MJ, Gibert J, Sánchez F, Lombardi AV, Serrano I, Gómez A, Eastham A, Ribot F, Arribas A, Cuenca A, Gibert L, Albadalejo S, Andreu JA. 1999. Excavations at new sites of early man in Murcia: Sima de las Palomas del Cabezo Gordo and Cueva Negra del Estrecho del Río Quípar de la Encarnación. Hum Evol 14:99–123.

Walker MJ, Lombardi AV, Zapata J, Trinkaus E. 2010. Neandertal mandibles from the Sima de las Palomas del Cabezo Gordo, Murcia, southeastern Spain. Am J Phys Anthropol 142:261–72.

Walker MJ, López-Martínez, M. V., Ortega-Rodrigáñez, J. Haber-Uriarte M, López-Jiménez A, Avilés-Fernández A, Polo-Camacho, J. L., Campillo-Boj M, García-Torres J, Carrión-García JS, San Nicolás del Toro, M., Rodríguez-Estrella T. 2012. The excavation of buried articulated Neanderthal skeletons at Sima de las Palomas (Murcia, SE Spain),. Quat Int 259:7–21.

Walker MJ, Ortega J, López M V., Parmová K, Trinkaus E. 2011a. Neandertal postcranial remains from the Sima de las Palomas del Cabezo Gordo, Murcia, southeastern Spain. Am J Phys Anthropol 144:505–15.

Walker MJ, Zapata J, Lombardi A V., Trinkaus E. 2011b. New evidence of dental pathology in 40,000-year-old Neandertals. J Dent Res 90:428–32.

Vander Wall SB. 2001. The evolutionary ecology of nut dispersal. Bot Rev 67:74–117.

Warinner C, Rodrigues JFM, Vyas R, Trachsel C, Shved N, Grossmann J, Radini A, Hancock Y, Tito RY, Fiddyment S, Speller C, Hendy J, Charlton S, Luder HU, Salazar-García DC, Eppler E, Seiler R, Hansen LH, Castruita JAS, Barkow-Oesterreicher S, Teoh KY, Kelstrup CD, Olsen J V., Nanni P, Kawai T, Willerslev E, von Mering C, Lewis CM, Collins MJ, Gilbert MTP, Rühli F, Cappellini E. 2014. Pathogens and host immunity in the ancient human oral cavity. Nat Genet 46:336–44.

Watts DP, Mitani JC. 2015. Hunting and Prey Switching by Chimpanzees (*Pan troglodytes schweinfurthii*) at Ngogo. Int J Primatol 36:728–748.

Weiss E, Wetterstrom W, Nadel D, Bar-Yosef O. 2004. The broad spectrum revisited: evidence from plant remains. Proc Natl Acad Sci U S A 101:9551–5.

Weyrich LS, Dobney K, Cooper A. 2015. Ancient DNA analysis of dental calculus. J Hum

Evol 79:119–124.

Wiessner P. 2003. Owners of the future: Calories, cash, and self-sufficiency in the Nyae Nyae area between 1996 and 2003. Vis Anthropol Rev 19:149–159.

Wild EM, Paunović M, Rabeder G, Steffan I, Steier P. 2001. Age determination of fossil bones from the Vindija Neanderthal site in Croatia. Radiocarbon 43:1021–1028.

Wilson J, Hardy K, Allen R, Copeland L, Wrangham RW, Collins MJ. 2010. Automated classification of starch granules using supervised pattern recognition of morphological properties. J Archaeol Sci 37:594–604.

Winterhalder B. 1986. Diet choice, risk, and food sharing in a stochastic environment. J Anthropol Archaeol 5:369–392.

Winterhalder B, Smith EA. 2000. Analyzing adaptive strategies: Human behavioral ecology at twenty-five. Evol Anthropol 9:51–72.

Wißing C, Rougier H, Crevecoeur I, Germonpré M, Naito YI, Semal P, Bocherens H. 2015. Isotopic evidence for dietary ecology of late Neandertals in North-Western Europe. Quat Int.

Wolpoff MH, Smith FH, Malez M, Radovčić J, Rukavina D. 1981. Upper pleistocene human remains from Vindija cave, Croatia, Yugoslavia. Am J Phys Anthropol 54:499–545.

Wood RE, Barroso-Ruíz C, Caparrós M, Jordá Pardo JF, Galván Santos B, Higham TFG. 2013a. Radiocarbon dating casts doubt on the late chronology of the Middle to Upper Palaeolithic transition in southern Iberia. Proc Natl Acad Sci U S A 110:2781–6.

Wood RE, Higham TFG, De Torres T, Tisnérat-Laborde N, Valladas H, Ortiz JE, Lalueza-Fox C, Sánchez-Moral S, Cañaveras JC, Rosas A, Santamaría D, de la Rasilla M. 2013b. A New Date for the Neanderthals from El Sidrón Cave (Asturias, Northern Spain). Archaeometry 55:148–158.

Wrangham RW. 2000. Why are male chimpanzees more gregarious than mothers? In: Kappeler P, editor. Primate Males: Causes and Consequences of Variation in Group Composition. Cambridge: Cambridge University Press. p 248–258.

Wrangham RW, Smuts BB. 1980. Sex differences in the behavioural ecology of chimpanzees in the Gombe National Park, Tanzania. J Reprod Fertil Suppl Suppl 28:13–31.

Wright KI. 1994. Ground-Stone Tools and Hunter-Gatherer Subsistence in Southwest Asia: Implications for the Transition to Farming. Am Antiq 59:238–263.

Xia J, Zheng J, Huang D, Tian ZR, Chen L, Zhou Z, Ungar PS, Qian L. 2015. New model to explain tooth wear with implications for microwear formation and diet reconstruction. Proc Natl Acad Sci U S A 112:10669–10672.

Yellen JE. 1991a. Small mammals: !Kung San utilization and the production of faunal assemblages. J Anthropol Archaeol 10:1–26.

Yellen JE. 1991b. Small mammals: Post-discard patterning of !Kung San faunal remains. J Anthropol Archaeol 10:152–192.

Yesner DR. 1989. Moose hunters of the boreal forest? A re-examination of subsistence patterns in the western subarctic. Arctic 42:97–108.

Young TK. 1996. Obesity, Central Fat Patterning, and Their Metabolic Correlates among the Inuit of the Central Canadian Arctic. Hum Biol 68:245–263.

El Zaatari S. 2007. Ecogeographic variation in Neandertal dietary habits: evidence from microwear texture analysis.

El Zaatari S. 2010. Occlusal microwear texture analysis and the diets of historical/prehistoric hunter-gatherers. Int J Osteoarchaeol 20:67–87.

El Zaatari S, Grine FE, Ungar PS, Hublin J-J. 2011. Ecogeographic variation in Neandertal dietary habits: evidence from occlusal molar microwear texture analysis. J Hum Evol 61:411–24.

El Zaatari S, Grine FE, Ungar PS, Hublin J-J. 2016. Neandertal versus Modern Human Dietary Responses to Climatic Fluctuations. PLoS One 11:e0153277.

El Zaatari S, Hublin J-J. 2014. Diet of upper paleolithic modern humans: evidence from microwear texture analysis. Am J Phys Anthropol 153:570–81.

Zeder MA. 2012. The Broad Spectrum Revolution at 40: Resource diversity, intensification, and an alternative to optimal foraging explanations. J Anthropol Archaeol 31:241–264.

Zhang J, Lu H, Huang L. 2014. Calciphytoliths (calcium oxalate crystals) analysis for the identification of decayed tea plants (*Camellia sinensis* L.). Sci Rep 4:6703.

Zilhão J, Angelucci DE, Badal-García E, D'Errico F, Daniel F, Dayet L, Douka K, Higham TFG, Martínez-Sánchez MJ, Montes-Bernárdez R, Murcia-Mascarós S, Pérez-Sirvent C, Roldán-García C, Vanhaeren M, Villaverde V, Wood RE, Zapata J. 2010. Symbolic use of marine shells and mineral pigments by Iberian Neandertals. Proc Natl Acad Sci U S A 107:1023–8.

Zilhão J, d'Errico F, Bordes J-G, Lenoble A, Texier J-P, Rigaud J-P. 2006. Analysis of Aurignacian interstratification at the Chatelperronian-type site and implications for the behavioral modernity of Neandertals. Proc Natl Acad Sci U S A 103:12643–8.

Zimov SA, Zimov NS, Tikhonov AN, Chapin FS. 2012. Mammoth steppe: a high-productivity phenomenon. Quat Sci Rev 57:26–45.

Zwyns N, Roebroeks W, McPherron SP, Jagich A, Hublin J-J. 2012. Comment on "Late Mousterian Persistence near the Arctic Circle." Science (80-) 335:167–167.

7

Appendixes

7.1 Chapter three appendix

Appendix tables

Appendix table 1: Elemental composition of standards from EDX.

No.	Grouping	C	O	Na	Mg	Al	Si	P	Ca	F	N	K	S	Cl	Cr	Mn
Fru.1	Fructose	90.8	9.17													
Fru. 2	Fructose	92.2	7.78													
Fru. 3	Fructose	90.4	9.58													
Fru. 4	Fructose	91.4	8.62													
Fru 5	Fructose	93.2	6.8													
Suc. 1	Sucrose	90.3	9.75													
Suc. 2	Sucrose	91.8	8.21													
Suc. 3	Sucrose	89.9	10.1													
Suc. 4	Sucrose	92.9	7.15													
Suc. 5	Sucrose	92.4	7.58													
Mal. 1	Maltose	60.7	39.3													
Mal. 2	Maltose	62	38													
Mal. 3	Maltose	58	42													
Mal. 4	Maltose	62.8	37.2													
Mal. 5	Maltose	58	42													
Glu. 1	Glucose	62.3	37.7													
Glu. 2	Glucose	57.9	42.1													
Glu. 3	Glucose	57.9	42.1													
Glu. 4	Glucose	59.1	40.9													
Glu. 5	Glucose	60.1	39.9													
Corn 1	Corn starch	58	42													
Corn 2	Corn starch	61.7	38.3													
Corn 3	Corn starch	61.6	38.4													
Corn 4	Corn starch	59.2	40.8													
Corn 5	Corn starch	62.1	37.9													
Cola 3.2	Kola starch	81.8	14.3	14.9	0.3	0.5	0.2	0.17	0.3	0.67		1.4		0	0.25	
Cafr-2	Kola starch	54.8	5.28	1.51	2.02							23		4	5	4.7
Cola 2.3	Kola starch	67.5	26.2	0.24	0.88	0.4	0.2	0.67		0.51		2.4	0.59	0		
Cola 2.4	Kola starch	70	22.8	0.16	0.61	0.5	0.5	0.86		1.4		1.9	0.75	1		
Cola 2.5	Kola starch	66.1	25.9		0.7	0.2	0.3	0.76		0.13			0.7	0		
Xylia 1	Xylia starch	76.8	21.4	0.17	0.21	0.5	0.1	0.11		0.1		0.2	0.24	0		
Xylia 2	Xylia starch	78.1	21.1				0.8									
Xylia 3	Xylia starch	74.7	20.2		0.42	0.4		0.94				2.5	0.89			

Xylia 4	Xylia starch	79.7	16.2	0.62	1	0.8			0.7	0.92			
Xylia 5	Xylia starch	75.8	22.2	0.43	0.6	0.18			0.5	0.25			
Pot. 1	Potato starch	82.8	17.2										
Pot. 2	Potato starch	83.1	16.9										
Pot. 3	Potato starch	84.3	15.7										
Pot. 4	Potato starch	84.1	15.9										
Pot. 5	Potato starch	82.1	16.5				1.4						
wtfr-1	Wheat starch	86.2	13.8					6.9					
wtfr-2	Wheat starch	86.1	13.9										
wtfr-3	Wheat starch	89.9	10.1										
wheat n	Wheat starch	91	8.97										
wheat n2	Wheat starch	90.2	9.81										

Appendix table 2: Elemental composition of degraded and native starch.

No.	Grouping	C	O	Na	Mg	Al	Si	P	F	K	S	Cl	Cr	Mn
Cafr-1	Kola native	64.7	3.8	1.46	0.91					18		4.44	3.03	3.97
Cafr-2	Kola native	54.8	5.3	1.51	2.02					23		3.92	4.97	4.67
Cafr-3	Kola native	60.1	6.0	1.47	1.66					17		5.25	3.81	5.03
Cola 2 1	Kola native	65.3	29.6							5.1				
Cola 2 2	Kola native	67.8	28.5							3.7				
Cola 2 3	Kola native	67.5	26.2	0.24	0.88	0.35	0.24	0.67	0.51	2.4	0.59	0.46		
Cola 3 1	Kola native	80.8	15.3	0.32	0.56	0.3	0.08	0.21	0.55	1.5				
Cola 3 2	Kola native	81.8	14.3	0.3	0.51	0.15	0.17	0.27	0.67	1.4	0.35	0.15		
Cola 3 3	Kola native	77.5	18.0	0.28	0.62	0.26	0.18	0.43	0.47	1.8	0.3	0.13		
Csfr-1 1	Gabon nut native	75.1	24.9											
Csfr-1 2	Gabon nut native	94.9	5.1											
Csfr-1 3	Gabon nut native	94.9	5.1											
Csfr-2 1	Gabon nut native	74.5	20.3											
Csfr-2 2	Gabon nut native	69.2	25.4											
Csfr-2 3	Gabon nut native	68.4	24.8											
Csfr-3 1	Gabon nut native	65.4	28.9											
Csfr-3 2	Gabon nut native	62.6	33.7											
Csfr-3 3	Gabon nut native	65.1	30.9											
Wtfr-1 1	Wheat native	86.2	13.8											
Wtfr-1 2	Wheat native	86.1	13.9											
Wtfr-1 3	Wheat native	89.9	10.1											
Wtfr-2 1	Wheat native	67.4	32.6											
Wtfr-2 2	Wheat native	76.7	23.3											
Wtfr-2 3	Wheat native	73.1	26.2											
Wtfr-3 1	Wheat native	67.9	32.1											
Wtfr-3 2	Wheat native	68.5	31.5											
Wtfr-3 3	Wheat native	68.9	31.1											
Ca301-1	Kola 30 mins	84.4	15.6											
Ca301-2	Kola 30 mins	85.6	14.4											
Ca301-3	Kola 30 mins	86.6	13.4											

Ca302-1	Kola 30 mins	86.9	13.1
Ca302-2	Kola 30 mins	88.4	11.6
Ca302-3	Kola 30 mins	89.9	10.1
Ca303-1	Kola 30 mins	88.5	11.6
Ca303-2	Kola 30 mins	87.8	12.2
Ca303-3	Kola 30 mins	92.9	7.1
Cs301-1	Gabon nut 30 mins	90.5	9.5
Cs301-2	Gabon nut 30 mins	90.7	9.3
Cs301-3	Gabon nut 30 mins	86.7	13.3
Cs302-1	Gabon nut 30 mins	88.6	11.4
Cs302-2	Gabon nut 30 mins	87.6	12.4
Cs302-3	Gabon nut 30 mins	89.6	10.4
Cs303-1	Gabon nut 30 mins	90.0	10.0
Cs303-2	Gabon nut 30 mins	87.6	12.4
Cs303-3	Gabon nut 30 mins	89.6	10.4
Wt301-1	Wheat 30 mins	88.9	11.1
Wt301-2	Wheat 30 mins	85.7	14.3
Wt301-3	Wheat 30 mins	87.3	12.7
Wt302-1	Wheat 30 mins	84.2	15.9
Wt302-2	Wheat 30 mins	84.2	15.8
Wt302-3	Wheat 30 mins	87.6	12.4
Wt303-1	Wheat 30 mins	88.3	11.7
Wt303-2	Wheat 30 mins	87.0	13.0
Wt303-3	Wheat 30 mins	88.3	11.8
Ca901-1	Kola 90 mins	86.7	13.3
Ca901-2	Kola 90 mins	86.8	13.2
Ca901-3	Kola 90 mins	89.7	10.3
Ca902-1	Kola 90 mins	86.6	13.5
Ca902-2	Kola 90 mins	91.6	8.4
Ca902-3	Kola 90 mins	90.0	10.0
Ca903-1	Kola 90 mins	84.3	15.7
Ca903-2	Kola 90 mins	90.0	10.0
Ca903-3	Kola 90 mins	89.3	10.7
Cs901-1	Gabon nut 90 mins	90.6	9.4
Cs901-2	Gabon nut 90 mins	89.0	11.0
Cs901-3	Gabon nut 90 mins	84.9	15.1
Cs902-1	Gabon nut 90 mins	88.0	12.0
Cs902-2	Gabon nut 90 mins	89.6	10.4
Cs902-3	Gabon nut 90 mins	92.5	7.5
Cs903-1	Gabon nut 90 mins	86.0	14.0
Cs903-2	Gabon nut 90 mins	88.4	11.6
Cs903-3	Gabon nut 90 mins	90.5	9.5
Wt901-1	Wheat 90 mins	86.5	13.5
Wt901-2	Wheat 90 mins	86.1	13.9
Wt901-3	Wheat 90 mins	85.8	14.2
Wt902-1	Wheat 90 mins	82.8	17.2

Wt902-2	Wheat 90 mins	85.4	14.6
Wt902-3	Wheat 90 mins	88.7	11.3
Wt903-1	Wheat 90 mins	84.0	16.0
Wt903-2	Wheat 90 mins	84.8	15.3
Wt903-3	Wheat 90 mins	84.93	15.07

Appendix table 3: Elemental composition of calculus and microremains in calculus from EDX. T=Taï Forest Chimpanzee, C=Camino de Molino.

No.	Type	Category	C	O	Na	Mg	Al	Si	P	Ca	F	N	K	Ba	La	T
	T	Venus exposed starch clump	95.1	5.0												
	T	Venus starch clump mantel	61.5	5.0				16.3	7.1	10.2						
	T	Castor calculus matrix	14.2	9.9	0.5	0.63	0.5	0.8	22.8	50.6						
1a	T	Castor starch cluster	63.1	8.2	1.4	1.87	0.8	0.7	12.3	11.7						
1b	T	Castor starch cluster	60.1	6.4	1.4	1.62	1.2	2.3	13.4	13.8						
3	T	Castor unknown microf	13.0	14.4	0.7	0.61	0.2	0.1	25.4	45.6						
4	T	Castor unknown microf	16.1	10.4	0.7	0.78	0.4	0.3	24.1	47.3						
5	T	Castor unknown microf	25.3	10.9	0.6	0.71	0.5	0.6	19.8	41.6						
1	T	Fanny unknown microf	13.7	10.2	0.4	0.59	1.0	1.1	22.7	50.3						
2	T	Fanny unknown particle	5.1	19.2	0.2	7.12	17.9	35.1	4.8	10.6						
3	T	Fanny unknown particle	9.4	8.7	0.5	0.63	0.6	0.6	24.3	55.2						
4	T	Fanny unknown particle	26.2	9.0	0.7	0.67	1.2	0.5	18.5	42.9						
5	T	Fanny unknown particle	6.4	15.5		0.15	0.5	71.2	2.0	4.3						
6	T	Fanny unknown microf	61.3	4.3	0.2	0.29	11	2.7	9.9	21.3						
7	T	Fanny unknown microf	79.9	7.1	0.6	0.1	0.2	3.9	2.6	5.6						
8	T	Fanny unknown microf	10.4	3.3	0.2	0.61	0.4	0.1	23.5	61.5						
9	T	Fanny unknown microf	47.3	7.8	0.4	0.8	0.4	0.5	11	31.8						
12	T	Fanny phytolith	16.3	14.2	1.2	1	0.4	31.1	11.8	23.9						
16	T	Fanny unknown microf	46.2	8.0	0.7	1.13	1.3	1.5	17.2	24.0						
17	T	Fanny unknown microf	7.2	4.5		0.47	3.2	6.3	13.7	64.7						
	T	Goma calculus matrix	6.8	9.9	0.3	1.16	2.0	2.6	24.0	51.2	0.1	1.6	0.5			
1	T	Goma phytolith	6.3	15.9	0.6	3.88	7.8	15	17.0	27.0	0.7	1.0	5			
2	T	Goma microremain	44.4	5.3	1	1.16	0.3	1	19.7	22.6		3.2	1.4			
3	T	Goma diatom	3.4	9.7	0.1	0.28	2.3	79.3	0.7	2.4		1.1	0.7			
5	T	Goma microremain	3.5	5.8	0.4	1.66	6.8	8.2	11.0	59.0	0.2	2.2	1.4			
11	T	Goma microremain	7.7	15.1	0.7	2.45		0.4	36.5	34.8		0.8	1.6			
	T	Leo calculus matrix	6.9	11.0	0.4	1.53	0.6	1.2	26.4	51.9						
1	T	Leo microremain	38	9.3	0.4	0.62	12.1	18.1	8.0	13.5						

3	T	Leo palm phytolith	7.1	20.1				7.8						
11	T	Leo invertebrate	91.7	8.3										
15	T	Leo microremain	8.0	9.5	0.8	2.21	2.3	3.7	9.5	61.0			1	2
18	T	Leo unknown		21.6				78.4						
	T	Rubra unknown	13.4	17.2	0.4	1.74			26.4	41.0				
1	T	Rubra unknown	8.7	18.1		0.54	26.2	39.8		6.7				
2	T	Rubra unknown	5.1	13.8	0.7	2.35			28.6	48.7				
4	T	Rubra diatom	41.0	11.9	0.1	0.28	0.9	20.5	7.7	17.6				
14	T	Rubra starch cluster	5.0	14.7	0.4	1.15	0.9	35.6	15.8	26.6				
15	T	Rubra diatom	4.3	12.4	0.1	0.38	19.9	57.6	1.9	3.5				
20	T	Rubra diatom	4	21.5	0.1	0.11	28.5	43.1	0.7	2.0				
	C	SJ-13-32_1 rectangle	5.6	12.1	0.8	0.76	1.8	4.6	17.1	57.9				
	C	SJ-13-32_2 unknown	7.1	13.1		9.62	16.9	41.9	1.7	4.5	3.4			2
	C	SJ-13-32_7 unknown	7.8	5.2	0.4		2.8	3	3.1	77.8				
	C	SJ-13-32_10 unknown	3.0	7.1		0.7	1			88.2				
	C	SJ-13-32_12 spicule	2.3	5.0		0.46	1.4	4.3		85.8	0.9			
	C	SJ-13-32_16 unknown	1.8	9.2		1.08	3.4	8.8		75.4	0.4			
	C	SJ-13-32_18 unknown	6.9	17.2		0.61	5.5	18.8	2.7	44.3	4.1			
	C	SJ-13-33 unknown	4.4	10.0	0.2	0.35	0.3	1	21.2	62.5				
	C	SJ-13-36 phytolith	4.1	11.6		0.27	19.9	31.2	1.4	31.6				
	C	SJ-13-39 -3 unknown	3.6	7.5			0.9	2.3	9.4	76.2				
	C	SJ-13-39 -7 spicule	2.5	9.0		0.46	0.6	1.5	6.5	79.5				
	C	SJ-13-39 -11 unknown	5.4	14.5		1.3	4.8	13.2	14.7	46.1				

7.2 Chapter four appendix

7.2.1 Study population

The chimpanzee calculus samples derive from the Taï Chimpanzee osteology collection of 77 chimpanzees curated at the Max Planck Institute for Evolutionary Anthropology (MPI-EVA) in Leipzig, Germany. The remains were collected with as many details as possible on sex, age and cause of death. All Taï Forest material and data collected complied with the requirements and guidelines of the Ministère de l'Enseignement Supérieure et de la Recherche Scientifique of Côte d'Ivoire, and adhered to its legal requirements. When possible we sampled chimpanzees who had known life histories, and ideally with comprehensive dietary records. Much of the observational data relate to chimpanzees that are not part of this osteology collection. Dietary records vary from thousands of observations over a decade to a limited number over the course of a single day. After death, these individuals were interred for defleshing and then later exhumed. Some of the skeletal material was cleaned using strong disinfectants before storage to minimise the risk of disease transmission.

It has been noted that chimpanzees produce less salivary α-amylase than humans, especially humans from agricultural societies that consume high levels of starch (Perry et al., 2007). Thus, starch entering the chimpanzee mouth may be less readily hydrolysed than in human groups, which may make it more likely for starches to enter and preserve in chimpanzee dental calculus than in human dental calculus. However, if this patterns occurs in our samples it is unclear and it cannot testable with our data.

7.2.2 Collection of calculus samples

Occasionally, chimpanzee calculus showed substantial flecks of dark material that did not resemble calculus and appeared to be sediment contamination. Chimpanzee samples where sediment contamination was suspected were omitted. All chimpanzee remains sampled are curated at the Max Planck Institute for Evolutionary Anthropology in Leipzig, Germany. Samples from two chimpanzees (Vanessa and 13438) were omitted from analysis because their age at death was not recorded. A sample from a further chimpanzee (Loukoum) was omitted due to surface adherents on the calculus. The calculus we chose for the final complete

analysis came from molars of 24 individuals (12 males and 12 females) ranging in age from between 12 and 552 months (1 and 46 years) old (Table 8).

7.2.3 Taï Forest plant reference collection

A microremain reference collection with 119 plant species was built using the most frequently consumed chimpanzee plant foods in the Taï forest (Appendix table 4). Taï Chimpanzees consume a particularly diverse range of foods. We collected plant parts that were documented as a specific component of the diet (fruits, seeds, piths, leaves, stems, bark, flowers, and roots.) We also include fungal fruiting bodies known to be consumed. Effort was made to include other rainforest edible plants not recorded as chimpanzee foods. Although our reference collection is not exhaustive, it incorporates the most important plants foods of the Taï Chimps, achieving coverage of 89 % of the total dietary observations. Plants collected in the Taï Forest were immediately preserved onsite either by freezing or by drying in 15 or 50 ml centrifuge tubes with silica gel (Roth- T858.1 and P077.1, Karlsruhe, Germany). Additionally, we collected some plant material from the University of Leipzig Botanical Garden (marked as fresh in Appendix table 4) and analysed this material fresh for starch or dried for phytoliths. We did not make a reference collection for unsilicified plant microremains, as these microremains are unlikely to be nondiagnostic.

Starch was analysed by directly mounting finely sliced dry plant material on slides with approximately 10 µl of distilled water and 10 µl of a 25 % glycerol solution. Starches were observed at 200-640 x magnification using a Zeiss Axioscope. Phytoliths were isolated from plant material by dissolving weighed dried plant material in ≥65 % nitric acid with a heating block to expedite the reaction. Small quantities of the oxidiser potassium chlorate were added to encourage the process.

In most chimpanzee foods we observed either very few starch grains or none at all, suggesting quantities too negligible to be detected or a complete lack of starch in the plant. Plants that produced negligible numbers of starches were not analysed for the identification model, because they did not have enough starch grains to build a reference set of 50 starches. We found phytoliths were common in many species, but many morphotypes are poorly studied in morphometric studies and cannot be easily described using the variables we chose for our model (e.g. hair cells, epidermal, cylindroids, plates and tracheid phytoliths). These morphotypes were

found in a number of genera in the reference collection plant but only in low numbers.

Plants that had few phytoliths were not included. Furthermore, if microremains were found in parts of a plant that chimpanzees do not eat, the plants were not included (e.g. starch from *Beilschmedia mannii* seed). Thirteen starch- and seven phytolith-producing plants were selected for developing identification criteria. We chose to measure or quantify several variables on 50 microremains per species, focusing on variables that past studies have shown to be effective in distinguishing among starches and phytoliths (Torrence et al., 2004; Fenwick et al., 2011). Our variables include max length, max width, area, shape, surface regularity, the number of echinate spines, length of longest cross axis, type, number and length of cracks, number of facets and lamellae (Appendix table 6). If abundant starches or phytoliths were recovered, their abundance was analysed in order to assess the expected starch and phytolith contribution to dental calculus. Starch content was established by combining previous nutritional content studies (Oyebade, 1973; N'guessan, 2012). For species where this data was not available we assessed starch content per gram dried plant material colourimetrically using an Amyloglucosidase/α-amylase method with a Megazyme Total Assay Kit (AA/AMG 11/01, AOAC Method 996.11, AACC Method 76.13, ICC Standard Method No. 168). Phytolith content was estimated by calculating the total weight of sample left after nitric acid digestion.

7.2.4 Identification of microremains by classification

Statistical approaches are increasingly used for the study and classification of microremains (Wilson et al., 2010; Fenwick et al., 2011; Saul et al., 2012; Zhang et al., 2014; Coster and Field, 2015). A variety of approaches have been implemented in past studies such as image analysis (Colliot et al., 1997), linear discrimination (Torrence et al., 2004), and factor regression analysis by principal components (Fenwick et al., 2011). We used random forest-based classification because it is robust, non-parametric and easily accommodates both large number of variables and categorical data. Using this approach, we can easily see the most important variables that drive the differences among the microremain types. The most important variables in our phytolith model include length and the number of spines (Appendix table 14). In the starch random forest model, area and length were the most important variables (Appendix table 14).

7.2.5 Model design and formulae

We predicted that number of microremains should increase with age, and might vary by sex. We tested this using a negative binomial regression, with microremain count as the response, and age and sex as predictors, weighting each observation by the weight of the calculus sample (see detailed methods below). We ran separate tests for phytoliths, unsilicified remains and starches.

The models described in R terminology are as follows:

Microremain type count~ chimpanzee age + chimpanzee sex, weights=calculus sample weight

Expressed as a mathematical formula, this analysis is written as follows:

$$y_i = Negbin(\mu_i, k)$$

$$log(\mu_j) = \beta_0 + X_j\beta_j + \varepsilon$$

where $\beta_0 = 0$

$$log(\mu_j) = \beta_0 + \sum_{j=1}^{p} [\beta_{11j}\text{chimp\_age}_j + \beta_{12j}\text{chimpanzee sex}_j] + \varepsilon_j$$

where $\beta_0 = 0$

We predicted that more frequently consumed plants should be highly represented in the chimpanzee calculus. To test this, we used an observational random effect Poisson model. The count of microremains (starches or phytoliths) belonging to a particular genus was our response variable, and the fixed predictors were: (a) minutes spent consuming each genus, and (b) chimpanzee age in months. Sex was included as a control predictor, and both calculus sample weight and successful identification rate of each genus were included as weights. We accounted for the variation in production of microremains in different genera by using microremains content as an offset. We used counts of each genus predicted to be present with the total minutes spent consuming each genus. The chimpanzee

individual was included as a random slope term, while year of death, tooth and food type were treated as random intercept terms

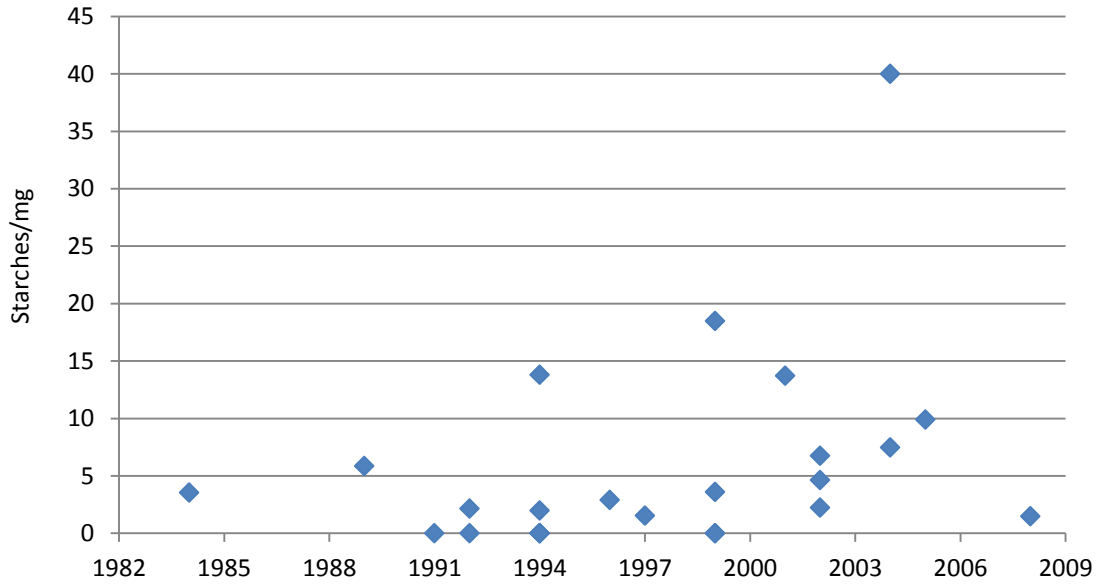
The models described in R terminology are as follows:

The observational feeding records model. Key: obs_id=observation id, plant_id=Plant genus, death_year=year that chimpanzee died, mr_content=Prevalence of starch in each plant species, wt=Milligrams in each sample, class_rate=Rate of successful identification in this species.

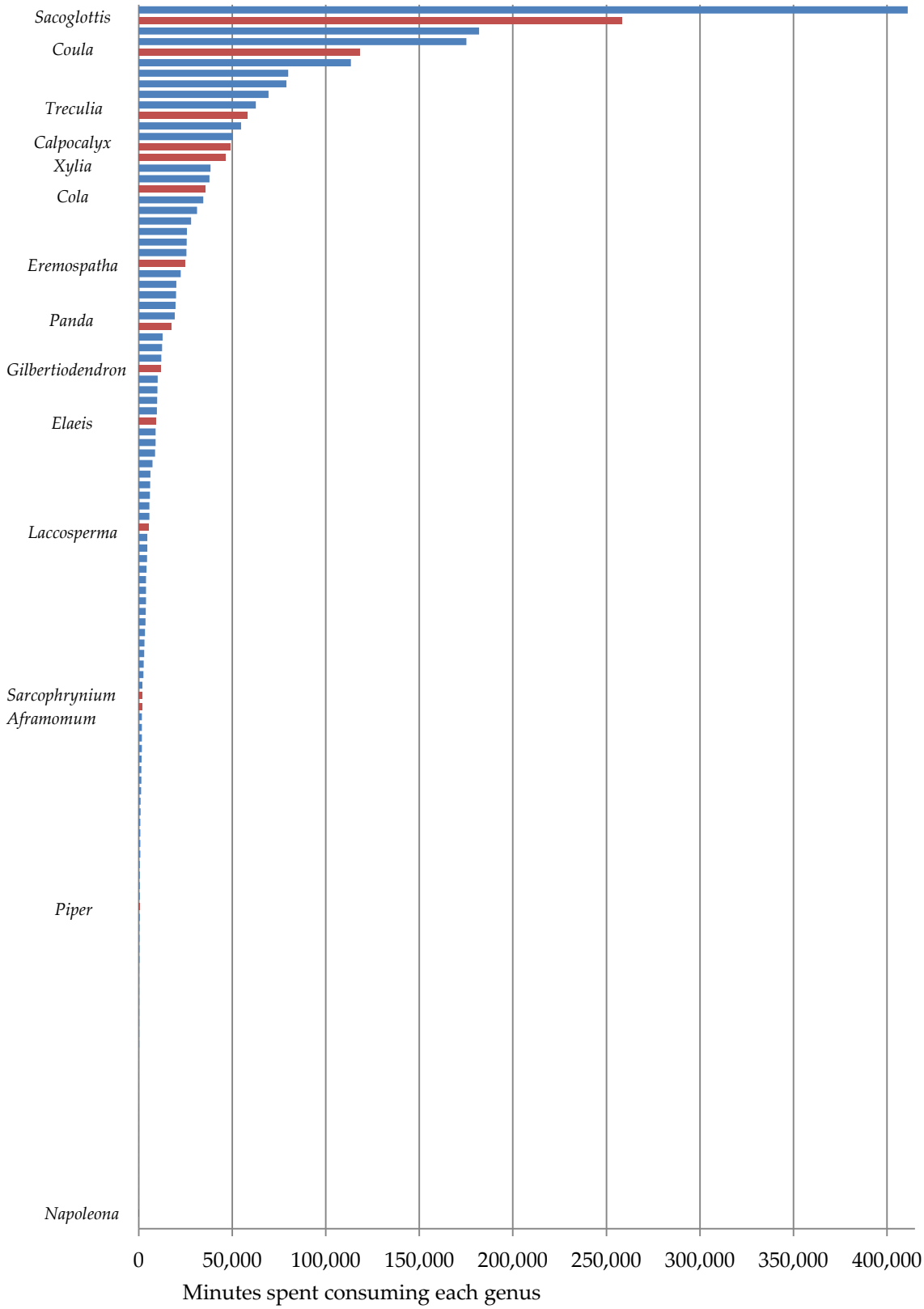
Count of each plant species~mins+age+sex+(1|obs_id)+(1|plant_id)+(1|tooth)+(1|chimp_name)+(1|death_year)+(0+mins|chimp_name)+(0+mins|tooth)+(0+mins|death_year)+(0+age|plant_id)+(0+age|tooth)+offset(log(mr_content)),
weight=class_rate+ calculus samples weight

In mathematical notation, the models are written as follows:

$$
\begin{aligned}
log_e(\lambda) = -n\lambda + log_e(\lambda) \sum_{j=1}^{p} [\, & \beta_{11j}\text{mins}_j + \beta_{12j}\text{age}_j + \beta_{13j}\text{sex}_j) + \beta_{21j} + u_{11j})\text{tooth}_j \\
& + (\beta_{22j} + u_{12j})\text{death\_year}_j + (\beta_{23j} + u_{13j})\text{plant\_id}_j + (\beta_{24j} + u_{14j})\text{age}_j \\
& - \sum_{j=1}^{p} \ln[\beta_{11j}\text{mins}_j + \beta_{12j}\text{age}_j + \beta_{13j}\text{sex}_j) + \beta_{21j} + u_{11j})\text{tooth}_j \\
& + (\beta_{22j} + u_{12j})\text{death\_year}_j + (\beta_{23j} + u_{13j})\text{plant\_id}_j + (\beta_{24j} + u_{14j})\text{age}_j] \,! \\
& + u_{01} + u_{02} + u_{03} + u_{04} + u_{05} + \varepsilon_j
\end{aligned}
$$



Appendix fig. 1: Starches per mg in each chimpanzee calculus sample and year of death. Starches/mg incudes the possible starch microremain category. Treatment of the skeletal remains and year of chimpanzee death does not predict variation of starches per mg.



Appendix fig. 2: Chimpanzee plant foods, ranked by minutes consumed. Plants in random forest model are in red and those that are not are in blue. Chart omits foods eaten for <40 minutes. Our sample includes plants that are frequently consumed (e.g. *Sacoglottis* and *Coula*) as well as those less often eaten (e.g. *Piper* and *Napoleona*).

Tables

Appendix table 4: Inventory of plants and fungi analysed in reference collection. x=no microremain found. o=microremains found and used for identification model. 1=found but not used in classification model due to their complex morphology, 2=found but not included as they are very rare, 3=found but only in parts that are not eaten. Prep=preparation. d=dried, fn=frozen and fh=fresh.

		Leaf	Fruit pulp	Seed	Stem	Pith	Shell	Flower	USO	Bark	Leaf	Fruit pulp	Seed	Stem	Pith	Shell	Flower	USO	Bark	Prep
Plant genus	Plant species	Starch									Phytoliths									
Aframomum	*exscapum* (Sims) Hepper	x		x																d
Aframomum	*cereum* (Hook.f.) K.Schum.										X		x							d
Afzelia	*bella* Harms										1									d
Agaricus	*bispourus* (J.E.Lange) Emil J. Imbach				x															d
Anchomanes	*difformis* (Bl.) Engl.													x						fn
Antiaris	*toxicaria subsp. welwitschii* (Engl.) C.C.Berg		x	2																d
Auricularia	*auricula-judae.* (Bull.) J.Schröt.				x									x						d
Beilschmiedia	*mannii* (Meisn.) Benth. & Hook.f.			2																d
Bombax	*buonopozense* P.Beauv.			x																d
Bombax	*ceiba* L.	x									2									fh
Calpocalyx	Sp.		o																	d
Calpocalyx	*aubrevillei* Pellegr.	x									X									d
Canarium	*schweinfurtii* Engl.		x	x																fn
Castanola	*paradoxa* (Gilg) Schellenb.											x	x							d
Chrysophyllum	*taiense* Aubrév. & Pellegr.	x	x	x							X	x	x							d
Cola	*nitida* (Vent) Schott & Endl.	x	x	x							1	x	x							d, fh
Cola	*heterophylla* (P Beauv.) Schott. & Endl.	x	x	x							1	x	x							d
Cola	*laterita* K Schum.											x	x							d
Cordia	*platythyrsa* Baker		x	x								x	x							d
Coula	*edulis* Baill.	x		x			x				1		x			1				d
Dacryodes	*klainaea* (Pierre) H.J.Lam		x									x								fn
Desplatsia	*chrysochlamys* (Mildbr. & Burret) Mildbr. & Burret	x									X									d
Detarium	*senegalense* J.F.Gmel.											x	x							d

Dialium	*aubrevillei* Pellegr.	x	x							X	x							d
Dialium	*dinklagei* Harms		x	x														d
Dichapetalum	*heudelotii* (Planch.) Baill.	x								X								d
Dioscorea	*burkilliana* J.Miège																x	d
Diospyros	*chevalieri* De Wild.										x							d
Diospyros	*manii Hiern*		x							X	1							d
Diospyros	*sanza minika* A Chev.										x							d
Diospyros	*soubreana* F.White									X								d
Drypetes	*aubrevillei* Léandri					x						x		x				d
Duboscia	*viridifolia* (K.Schum.) Mildbr.		x															d
Duguetia	*staudtii* (Engl. & Diels) Chatrou		3	3														d
Elaeis	*guineenis* Jacq.	x	x							O	o		o					d, fh
Entandrophragma	*angolense* (Welw.) C. DC.		x	x														d
Eremospatha	*macrocarpa* H.Wendl.				o									o				d
Erythrophleum	*ivorensis* A.Chev											x						fn
Ficus	*barteri* Sprague									1								d
Ficus	*elastica* Roxb.		x							1								fh
Ficus	*elasticoides* De Wild		x															d
Ficus	*lutea* Vahl		x															d
Ficus	*polita* Vahl									1								d
Gilbertiodendron	*splendidum* (Hutch. & Diels) J. Léonard		o	o							x	x						d
Glyphaea	*brevis* (Spreng.) Monach.	x								3								d
Grewia	*biloba* (Bunge.)Hand. Mazz.		x	x							x	x						d
Grewia	*malacocarpa* Mast.		x	x														d
Guibourtia	*tessmannii* (Harms) J.Léonard															x		d
Halopegia	*azurea* (K.Schum.) K.Schum.				x		x			X	x			x		x		d
Harungana	*madagascariensis* Lam. ex Poir.		x	x														fn
Heisteria	*parvifolia* Sm.			x														d
Hexalobus	*crispiflorus* A.Rich			x														fn
Hypselodelphys	*violacea* (Ridl.) Milne-Redh				x									1				d
Irvingia	*gabonensis* (Aubry-Lecomte ex O'Rorke) Baill.		x	x														d
Irvingia	*grandifolia* (Engl.) Engl.		x															d
Keayodendron	*bridelioides*		x															d

	(Gilg & Mildbr. ex Hutch. & Dalziel) Leandri															
Klainedoxa	*gabonensis* Pierre		3													fn, d
Laccosperma	*secundiflorum* (P.Beauv.) Kuntze				x							x				d
Laccosperma	*opacum* Drude				x							x				d
Landolphia	*dulcis* (Sabine ex G.Don) Pichon		x							x					x	fn
Magnistipula	*butayei* DeWild		x													d
Mammea	*africana* Sabine		x							x						d
Manilkara	*obovata* (Sabine & G.Don) J.H.Hemsl.		x	x												fn
Manniophyton	*fulvum* Müll.Arg.	x														d
Memecylon	Sp.		x													fn
Musanga	Sp.		x							1	1					d
Myrianthus	Sp.							x								fn
Myrianthus	*arboreus* P.Beauv.		x													fn
Napoleona	*leonensis*			o												d
Napoleonaea	*vogelii* Hook. & Planch	x							X		x					fh
Nauclea	*diderrichii* (De Wild. & T.Durand) Merr.ill		x													d
Nauclea	*xanthoxylon*		x							x						d
Pachira	*cubensis* (A.Robyns) Fern.Alonso	x														fh
Palisota	*barteri* Hook.f.		2	2						x	x	x				d
Palisota	*bracteosa* C.B.Clarke		x	x												d
Palisota	*hirsuta* (Thunb.) K.Schum.											x				d
Panda	*oleosa* Pierre	x		o					X		x					d
Parinari	*excelsea* Sabine	x	x						1	x						fn
Parkia	*bicolor* A.Chev.		x							x						fn
Pentaclethra	*macrophylla* Benth					x										d
Pentaclethra	*macrophylla* Benth					x							x			d
Pentadesma	*butyracea* Sabine		x													fn, d
Piper	*betle* L.	x				x			1				1			fh
Piper	*guineense* Schumach. & Thonn.		o	o												d
Piper	*longum* L.		x	x												d
Piper	*arboreum* Aubl.	x							1							fh
Piper	*ornatum* N.E.Br.	x														fh
Pouteria	*pierrei* (A.Chev.)		x	x						x	x					d

	Baehni														
Pseudospondias	Sp.		x	x											fn
Pseudospondias	*microcarpa* Engl		x	x											d
Psychotria	*bacteriophila Va*leton		x	x											d
Pycnanthus	*angolensis* (Welw.) Warb.		x												d
Raphia	*sudanica* A.Chev.												x		d
Rhodognaphalon	*brevicuspe* (Sprague) Roberty		x	x											d
Rudgea	*ciliata* (Ruiz & Pav.) Spreng.	x	x	x					X						d
Sacoglottis	*gabonensis* (Baill.) Urb.	x	o						1	1					d
Sarcocephalus	*pobeguinii* Hua ex Pobég		x												d
Sarcophrynium	*prionogonium* (K.Schum.) K.Schum.		o	o						o	x				d
Scottellia	*coriacea* A.Chev. & al.		x												d
Scytopetalum	*tieghemii* Hutch. & Dalziel	x													d
Strombosia	*glaucescens* Engl.									x					d
Strychnos	*aculeata* Soler.	x	x						X	x	x				d
Syzygium	*guineensis* (Willd.) DC.			3											fh
Syzygium	*paniculatum* Gaertn.	x	2	2			x		1		1				fh
Tamitia	*utilis*								X						d
Treculia	*africana* Decne. ex Trécul	x	x						X	2	x				d
Trichophyton	*Sp.*						x								d
Trichoscypha	*arborea* (A.Chev.) A.Chev.		x	3											d
Triclisia	*macrophylla* (Baill.) Diels		x							1					d
Tristemma	*hirtum* P.Beauv.		x												d
Uapaca	*corbisieri* DeWild.	x	x						X	x					d
Uapaca	*guineensis* Müll.Arg.									x					fn
Uvariastrum	*pierreanum* Engl. & Diels		x	x						1					d
Vitex	*doniana* Sweet		x	x											fn
Xylia	*evansii Hu*tch.	x		o					1						d
Xylopia	*quintas*		x	x											d
Xylopia	*villosa* Chipp							x							d
Zanha	*golungensis* Hiern		x	x											d
Fungus															
Agaricus	*bispourus* (J.E.Lange)				x										d
Auricularia	*auricula-judae.* (Bull.) J.Schröt.				x							x			d

Appendix table 5: Additional details of Chimpanzee calculus samples. Recovered plant microremains, both in the full sample and per milligram of calculus with cause of death of the sampled chimpanzees, colour and condition of their dental calculus and skeleton treatment during curation. Cur: Curation a) Buried for unknown duration, cleaned and dried (1984-1994, 1996-2004 b) Necropsy, burial for 1 year, possible boiling and dried (1994-1996) and c) Necropsy, burial for 1 year, disinfection with chlorine, 10 % formalin and dried (2004- onwards).

Name	Phytolith		Starch		Unsilicified Remains		Cause of death	Colour	Cur
	Total	/mg	Total	/mg	Total	/mg			
Ophelia	0	0	1	40	0	0	Pneumonia	White	C
Leonardo	0	0	0	0	0	0	Starvation	White/grey	A
Bambou	0	0	0	0	1	7.41	Tree fall	White	A
Piment	0	0	0	0	0	0	Ebola	White	B
Oreste	40	74.63	4	7.46	1	1.87	Pneumonia	Grey	C
Hector	24	34.83	2	2.9	6	8.71	Anthrax	Orange	A
Noah	47	52.51	2	2.23	32	35.75	Unknown	Brownish	A
Lefkas	19	31.93	11	18.49	13	21.85	Pneumonia	White	A
Tina	29	21.21	8	5.85	6	4.39	Leopard	Brownish	A
Dorry	159	214.29	5	6.74	4	5.39	Unknown	White	A
Zerlina	147	167.43	0	0	9	10.25	Ebola?	Moderate	B
Clyde	27	23.87	4	3.54	3	2.65	Poacher	White	A
Agathe	94	15.47	13	2.14	22	3.62	Ebola?	Brown/creamy	A
Bijou	87	17.26	10	1.98	22	4.36	Unknown disease	Brownish	A
Leo	126	116.13	5	4.61	9	8.29	Unknown	Brownish	A
Castor	65	9.31	25	3.58	6	0.86	Pneumonia	White	A
Fanny	109	27.84	54	13.79	11	2.81	Ebola?	White brown	B
Kendo	233	235.59	0	0	25	25.28	Ebola?	Grey	B
Venus	96	59.26	16	9.88	2	1.23	Unknown	Brownish	C
Goma	98	7.42	181	13.7	17	1.29	Anthrax	White	A
Rubra	120	17.78	10	1.48	30	4.44	Anthrax?	Mixed/white	C
Ondine	26	17	0	0	10	6.54	Ebola?	Brown/ green	A
Mkubwa	11	33.95	0	0	1	3.09	Unknown	Whitish green	A
Brutus	161	49.6	5	1.54	25	7.7	Unknown	Brownish	A

Appendix table 6: Metrics of reference phytoliths and starches. Phytoliths=first part of table. Starches=second part of table.

Species	Length	Width	LW Ratio	Brea	Area	Irregular	Spinelen	Spineno	Spineang	Shape	Conjoined
Elaeis	13.0	10.9	1.2	10.9	108.3	1	0.96	24	81	prolate	1
Elaeis	8.5	6.1	1.4	6.1	35.7	1	0.76	13	80	ovoid	1
Elaeis	10.4	9.2	1.1	9.2	71.4	2	1.2	17	98	prolate	1
Elaeis	9.3	8.6	1.1	8.6	50.8	3	0.9	14	75	spherical	1
Elaeis	12.5	10.3	1.2	10.3	105.8	2	0.95	16	80	spherical	1
Elaeis	13.3	10.5	1.3	10.5	115.5	2	1.2	19	78	prolate	1
Elaeis	8.4	7.7	1.1	7.7	45.8	1	0.68	18	83	spherical	1
Elaeis	12.7	10.0	1.3	10.0	100.0	4	1	16	95	spherical	1
Elaeis	17.8	16.7	1.1	16.7	246.0	3	1.74	18	96.25	spherical	1
Elaeis	15.5	15.0	1.0	15.0	210.1	2	2	13	94	spherical	1
Elaeis	8.6	8.6	1.0	8.6	59.0	3	1.05	14	85	spherical	1
Elaeis	11.7	8.1	1.4	8.1	75.7	4	1.2	20	90	ovoid	1
Elaeis	10.8	7.9	1.4	7.9	70.2	4	1.02	14	80.59	ovoid	1
elaeis	12.1	11.2	1.1	11.2	125.6	4	1.33	24	83	spherical	1
elaeis	7.3	6.5	1.1	6.5	46.0	4	1.13	11	103	ovoid	1
elaeis	11.0	8.3	1.3	8.3	84.6	3	1.23	17	84.43	prolate	1
elaeis	13.2	11.5	1.1	11.5	107.4	2	1.74	11	103	prolate	1
elaeis	7.8	7.2	1.1	7.2	47.1	4	1.74	10	64	spherical	1
elaeis	6.5	5.6	1.1	5.6	29.8	8	0.63	10	85	ovoid	1
elaeis	11.2	8.4	1.3	8.4	82.0	3	1.19	13	80.86	prolate	1
elaeis	13.2	11.4	1.2	11.4	125.4	3	1.17	11	82	prolate	1
elaeis	11.2	9.5	1.2	9.5	87.8	4	1.23	20	83.97	prolate	1
elaeis	8.6	7.1	1.2	7.1	45.6	5	0.92	13	99.37	ovoid	1
elaeis	9.3	6.9	1.4	6.9	49.5	4	0.79	12	69.05	prolate	1
elaeis	10.6	9.0	1.2	9.0	75.6	3	1.3	14	75.56	spherical	1
elaeis	7.8	6.2	1.2	6.2	33.0	4	0.89	14	102	ovoid	1
elaeis	5.4	5.3	1.0	5.3	22.5	4	1.1	6	96	polygon	1
elaeis	7.8	5.9	1.3	5.9	33.4	2	1.03	14	85	ovoid	1
elaeis	7.1	4.8	1.5	4.8	20.0	4	0.8	11	93	polygon	1
elaeis	7.3	3.5	2.1	3.5	17.2	4	0.84	3	50	elongate	1
elaeis	3.3	2.2	1.5	2.2	5.4	4	0.37	3	94	polygon	1
elaeis	5.7	4.1	1.4	4.1	18.4	5	0	0	0	polygon	1
elaeis	7.5	5.6	1.3	5.6	29.6	3	0.94	8	84.36	polygon	1
elaeis	6.7	4.2	1.6	4.2	20.7	4	0.6	10	70	polygon	1
elaeis	6.3	4.5	1.4	4.5	15.5	4	0.9	12	93	elongate	1
elaeis	6.5	5.8	1.1	5.8	34.4	2	0.89	12	110	polygon	1
elaeis	5.5	3.1	1.8	3.1	12.6	2	0.77	14	80	elongate	1
elaeis	7.4	3.1	2.4	3.1	16.4	3	0.78	7	81	elongate	1
elaeis	11.0	8.6	1.3	8.6	66.6	4	1.28	8	71	polygon	1
elaeis	7.4	4.1	1.8	4.1	21.3	2	0.63	10	95	prolate	1

elaeis	7.4	5.0	1.5	5.0	24.9	4	0.92	10	86	polygon	1
elaeis	9.4	8.0	1.2	8.0	54.6	1	1.1	16	108	prolate	1
elaeis	8.0	6.1	1.3	6.1	34.2	3	0.6	13	115	prolate	1
elaeis	7.5	5.5	1.4	5.5	30.7	3	0.72	13	98	ovoid	1
elaeis	9.1	6.3	1.4	6.3	41.8	4	0.94	12	75.83	elongate	1
elaeis	5.7	4.0	1.4	4.0	16.0	5	0.87	11	77	polygon	1
elaeis	8.3	6.4	1.3	6.4	36.4	4	0.7	11	102	polygon	1
elaeis	8.7	7.1	1.2	7.1	54.1	4	0.87	19	101	ovoid	1
elaeis	8.3	7.3	1.1	7.3	51.0	4	0.62	9	101	polygon	1
elaeis	6.8	6.2	1.1	6.2	33.0	4	0.92	15	82.61	ovoid	1
eremo	7.8	7.6	1.0	7.6	41.4	1	1	9	70	spherical	1
eremo	6.9	6.5	1.1	6.5	36.2	2	0.7	10	115	spherical	1
eremo	6.3	5.6	1.1	5.6	25.1	3	0.7	6	96	prolate	1
eremo	7.5	7.2	1.0	7.2	37.2	1	0.87	10	90	spherical	1
eremo	8.2	6.1	1.3	6.1	40.7	2	0.78	8	82	ovoid	1
eremo	7.5	7.3	1.0	7.3	42.6	1	0.87	9	78	prolate	1
eremo	6.2	6.1	1.0	6.1	27.5	4	0.82	5	86	spherical	1
eremo	5.5	5.1	1.1	5.1	22.4	2	0.5	6	90	spherical	1
eremo	8.1	6.3	1.3	6.3	38.1	3	0.6	9	81	prolate	1
eremo	7.0	6.0	1.2	6.0	35.0	2	0.94	10	70	prolate	1
eremo	7.8	7.6	1.0	7.6	40.1	2	1.7	8	90	spherical	1
eremo	5.9	4.4	1.3	4.4	23.1	4	0.88	6	89	ovoid	1
eremo	6.7	6.6	1.0	6.6	31.0	2	0.92	9	79	spherical	1
eremo	5.4	4.3	1.3	4.3	17.9	2	0.5	2	112	prolate	1
eremo	6.6	6.2	1.1	6.2	25.0	2	0.64	7	110	spherical	1
eremo	6.6	5.4	1.2	5.4	27.0	2	0.68	12	0.96	spherical	1
eremo	6.2	5.4	1.1	5.4	24.2	1	0.79	8	109	spherical	1
eremo	6.2	4.9	1.3	4.9	21.3	2	0.63	8	99	triangular	1
eremo	4.9	4.1	1.2	4.1	12.6	5	0.51	4	104	triangular	1
eremo	7.6	7.1	1.1	7.1	33.8	1	1.6	8	80	spherical	1
eremo	7.1	6.3	1.1	6.3	36.0	2	0.88	9	99	spherical	1
eremo	4.5	4.2	1.0	4.2	16.3	1	0.41	7	110	spherical	1
eremo	7.4	6.1	1.2	6.1	34.3	3	0.68	10	105	polygon	1
eremo	5.5	5.2	1.1	5.2	22.8	2	0.61	5	86	spherical	1
eremo	7.5	7.5	1.0	7.5	38.2	2	0.94	8	62.81	spherical	1
eremo	5.9	5.6	1.1	5.6	27.6	2	1.02	8	91	spherical	1
eremo	6.5	4.8	1.3	4.8	21.1	4	0.83	9	114	ovoid	1
eremo	5.6	5.1	1.1	5.1	22.1	3	0.72	3	111	spherical	1
eremo	6.0	5.0	1.2	5.0	25.6	4	0.94	9	91	spherical	1
eremo	5.9	5.9	1.0	5.9	26.2	3	0.92	9	99	spherical	1
eremo	3.7	3.6	1.0	3.6	12.6	3	0.61	4	127	spherical	1
eremo	6.2	6.2	1.0	6.2	34.7	3	1.02	12	99.69	spherical	1
eremo	6.5	4.8	1.4	4.8	28.1	3	0.83	8	95	prolate	1
eremo	7.9	6.7	1.2	6.7	44.2	3	0.94	13	84.53	spherical	1
eremo	6.1	4.0	1.5	4.0	19.2	3	0.69	8	122.88	prolate	1
eremo	6.8	6.1	1.1	6.1	33.5	4	1.02	6	110	polygon	1

eremo	5.6	5.1	1.1	5.1	21.9	3	0.74	6	92	spherical	1
eremo	4.9	4.4	1.1	4.4	17.5	2	0.5	8	89	spherical	1
eremo	4.6	4.4	1.0	4.4	20.2	5	0.83	5	95	polygon	1
eremo	7.9	6.2	1.3	6.2	35.6	4	0.83	10	102	polygon	1
eremo	5.5	5.2	1.1	5.2	22.1	3	0.52	7	124	spherical	1
eremo	6.1	5.5	1.1	5.5	30.9	4	0.95	7	92	polygon	1
eremo	3.9	3.3	1.2	3.3	10.1	3	0.74	2	94	prolate	1
eremo	6.9	6.7	1.0	6.7	38.8	4	1.17	10	90.68	spherical	1
eremo	5.8	4.7	1.2	4.7	26.1	4	0.83	6	75	polygon	1
eremo	3.9	3.3	1.2	3.3	10.6	5	0.62	7	85	polygon	1
eremo	4.5	3.4	1.3	3.4	13.7	4	0.66	2	107	polygon	1
eremo	6.2	5.3	1.2	5.3	27.1	3	0.66	8	87.47	prolate	1
eremo	6.5	6.1	1.1	6.1	36.2	3	0.8	11	36.22	spherical	1
eremo	6.5	4.1	1.6	4.1	24.4	5	0.72	6	91.39	polygon	1
aframomum	10.9	9.9	1.1	9.9	85.0	3	0.6	6	0	ovoid	1
aframomum	11.4	10.2	1.1	10.2	86.6	3	0	0	0	spherical	1
aframomum	10.5	7.6	1.4	7.6	66.5	4	0.55	5	0	ovoid	1
aframomum	8.4	7.5	1.1	7.5	70.7	4	0	0	0	quadrangular	1
aframomum	9.1	6.0	1.5	6.0	50.0	3	0	0	0	prolate	1
aframomum	10.0	6.1	1.6	6.1	48.6	3	0	0	0	prolate concave-convex	1
aframomum	11.4	10.4	1.1	10.4	94.5	4	0	0	0	spherical	1
aframomum	10.1	9.5	1.1	9.5	83.7	3	0	0	0	spherical	1
aframomum	14.2	9.7	1.5	9.7	14.2	4	0.5	10	0	ovoid	1
aframomum	9.9	6.6	1.5	6.6	52.5	3	0	0	0	quadrangular	1
aframomum	10.4	6.1	1.7	6.1	53.9	3	0	0	0	quadrangular	1
aframomum	11.9	10.2	1.2	10.2	96.3	3	0.55	14	0	spherical	2
aframomum	12.5	7.4	1.7	7.4	82.7	4	0.6	11	0	prolate	1
aframomum	8.5	5.5	1.5	5.5	47.8	4	0	0	0	polygon	2
aframomum	9.5	7.3	1.3	7.3	62.0	4	0	0	0	prolate concave-convex	1
aframomum	10.5	5.2	2.0	5.2	53.4	5	0	0	0	prolate concave-convex	1
aframomum	7.2	3.5	2.1	3.5	28.2	2	0	0	0	polygon concave	1
aframomum	9.6	6.3	1.5	6.3	43.1	4	0.75	9	0	prolate	1
aframomum	8.8	6.6	1.3	6.6	54.4	0	0	0	0	polygon concave	1
aframomum	7.4	4.7	1.6	4.7	31.0	0	0	0	0	polygon	1
aframomum	8.1	6.3	1.3	6.3	39.7	0	0	0	0	polygon	1
aframomum	11.0	9.6	1.1	9.6	83.5	4	0.5	15	0	spherical	1
aframomum	9.1	6.6	1.4	6.6	48.2	5	0.6	5	0	prolate concave-convex	1
aframomum	9.1	7.9	1.2	7.9	55.0	5	0.7	7	0	ovoid	1
aframomum	9.0	8.1	1.1	8.1	52.4	5	0	0	0	ovoid	1
aframomum	5.7	4.9	1.1	4.9	20.7	3	0.6	3	47	spherical	1
aframomum	7.3	6.1	1.2	6.1	35.4	3	1	11	41	spherical	1
aframomum	7.2	6.3	1.1	6.3	37.3	4	0.9	8	59	spherical	1
aframomum	6.0	6.0	1.0	6.0	30.2	3	1	6	64.88	spherical	1
aframomum	7.0	5.0	1.4	5.0	22.2	4	0.4	6	99	spherical	1
aframomum	5.3	4.1	1.3	4.1	20.4	4	0.4	3	47	spherical	1
aframomum	5.2	5.1	1.0	5.1	22.6	4	0.4	2	41	quadrangular	1

aframomum	5.5	4.7	1.2	4.7	20.7	1	0.26	1	54	spherical	1
aframomum	6.0	5.7	1.0	5.7	26.2	3	0.5	5	89	spherical	1
aframomum	5.8	4.6	1.3	4.6	23.5	4	0	0	0	spherical	1
aframomum	5.6	4.2	1.3	4.2	12.9	3	0.6	4	47	spherical	1
aframomum	5.5	5.0	1.1	5.0	28.8	4	0.72	8	64	spherical	1
aframomum	9.4	7.1	1.3	7.1	44.4	3	0	0	0	angularpoint	1
aframomum	6.0	5.1	1.2	5.1	20.2	0	0	0	0	spherical	1
aframomum	6.9	4.4	1.6	4.4	26.2	5	0	0	0	spherical	1
aframomum	6.4	4.3	1.5	4.3	21.6	4	0.55	6	66	spherical	1
aframomum	6.0	5.6	1.1	5.6	28.3	3	0.6	6	82	spherical	1
aframomum	5.9	5.4	1.1	5.4	28.0	3	0.4	7	70	spherical	1
aframomum	6.1	3.5	1.7	3.5	34.5	4	0.7	10	53	spherical	1
aframomum	6.8	6.0	1.1	6.0	33.0	3	0.7	8	82	spherical	1
aframomum	6.6	5.8	1.1	5.8	30.0	3	0.52	7	77	spherical	1
aframomum	5.8	4.9	1.2	4.9	22.2	5	0.83	5	41	spherical	1
aframomum	6.4	5.7	1.1	5.7	22.1	5	0.83	4	42	polygon	1
aframomum	6.5	5.5	1.2	5.5	30.2	3	0.9	8	78	spherical	1
aframomum	7.2	6.3	1.1	6.3	40.0	4	0.5	6	100	ovoid	1
ancistrophy	6.0	6.0	1.0	6.0	27.8	2	0.7	7	116	spherical	1
ancistrophy	5.4	4.2	1.3	4.2	18.9	4	0.55	4	105	ovoid	1
ancistrophy	4.9	4.8	1.0	4.8	21.2	2	0.58	4	116	spherical	1
ancistrophy	3.7	3.2	1.2	3.2	10.2	2	0	0	0	polygon	1
ancistrophy	5.9	4.4	1.3	4.4	19.8	4	0.46	3	191	ovoid	1
ancistrophy	3.2	2.5	1.3	2.5	7.2	4	0	0	0	polygon	1
ancistrophy	4.8	4.5	1.1	4.5	18.0	3	0.51	3	90	polygon	1
ancistrophy	5.8	5.7	1.0	5.7	22.9	4	0.75	4	108.06	polygon	1
ancistrophy	5.0	4.1	1.2	4.1	15.4	3	0.52	3	120.35	polygon	1
ancistrophy	4.9	2.9	1.7	2.9	12.4	5	0	0	0	elongate	1
ancistrophy	3.5	2.8	1.3	2.8	8.2	5	0	0	0	polygon	1
ancistrophy	3.2	2.3	1.4	2.3	5.3	5	0	0	0	polygon	1
ancistrophy	5.8	5.0	1.2	5.0	18.8	4	0.51	7	0	spherical	1
ancistrophy	4.9	4.2	1.2	4.2	16.8	3	0.32	3	95.28	prolate	1
ancistrophy	4.1	3.3	1.2	3.3	11.7	5	0.5	4	91	polygon	1
ancistrophy	4.7	3.7	1.3	3.7	13.3	4	0	0	0	prolate	1
ancistrophy	4.5	3.6	1.2	3.6	11.5	3	0.4	3	118	polygon	1
ancistrophy	5.2	3.5	1.5	3.5	16.3	5	0.62	4	87	ovoid	1
ancistrophy	3.6	2.8	1.3	2.8	8.1	4	0	0	0	ovoid	1
ancistrophy	3.4	2.8	1.2	2.8	7.5	4	0	0	0	spherical	1
ancistrophy	5.1	3.9	1.3	3.9	15.3	4	0.55	3	109	polygon	1
ancistrophy	4.3	3.9	1.1	3.9	13.4	3	0.4	3	116	spherical	1
ancistrophy	3.6	2.9	1.3	2.9	8.0	5	0	0	0	polygon	1
ancistrophy	3.8	2.9	1.3	2.9	9.6	5	0	0	0	polygon	1
ancistrophy	4.9	3.8	1.3	3.8	13.5	5	0.3	4	111	polygon	1
ancistrophy	7.2	4.2	1.7	4.2	27.3	4	0.62	9	27.27	prolate	1
ancistrophy	5.6	5.3	1.0	5.3	24.0	2	1.07	5	61.83	spherical	1
ancistrophy	7.3	6.5	1.1	6.5	43.5	1	1.2	8	83.46	spherical	1

ancistrophy	8.9	7.6	1.2	7.6	53.5	1	1.1	12	85.57	spherical	1
ancistrophy	6.1	5.8	1.0	5.8	29.5	3	1.27	8	82	spherical	1
ancistrophy	5.3	4.3	1.2	4.3	20.2	4	1.25	8	76.85	spherical	1
ancistrophy	7.2	5.2	1.4	5.2	34.2	2	1.05	9	79.57	prolate	1
ancistrophy	7.5	5.0	1.5	5.0	29.1	4	0.88	6	73.5	ovoid	1
ancistrophy	8.5	7.2	1.2	7.2	44.5	1	1.11	10	86.09	spherical	1
ancistrophy	5.8	5.4	1.1	5.4	24.9	3	0.88	9	106	spherical	1
ancistrophy	7.5	5.9	1.3	5.9	38.1	3	1.23	9	85	spherical	1
ancistrophy	7.5	6.5	1.2	6.5	36.8	3	1.2	7	81	spherical	1
ancistrophy	6.3	5.8	1.1	5.8	32.5	3	1.11	7	84.33	spherical	1
ancistrophy	5.9	5.4	1.1	5.4	27.4	3	0.97	9	69.85	ovoid	1
ancistrophy	7.0	4.9	1.4	4.9	31.0	5	0.65	7	96	spherical	1
ancistrophy	9.7	8.8	1.1	8.8	82.7	2	1.64	11	92	spherical	1
ancistrophy	7.6	7.1	1.1	7.1	47.5	2	1.25	9	86.23	spherical	1
ancistrophy	8.8	6.2	1.4	6.2	49.3	3	1.33	10	82.53	prolate	1
ancistrophy	6.5	6.2	1.0	6.2	35.8	3	1.02	8	84.17	spherical	1
ancistrophy	7.0	6.6	1.1	6.6	35.3	4	1.24	6	88.91	spherical	1
ancistrophy	6.8	5.8	1.2	5.8	30.9	3	0.97	6	97	spherical	1
ancistrophy	5.6	5.6	1.0	5.6	24.5	3	0.55	7	115	spherical	1
ancistrophy	5.4	3.8	1.4	3.8	17.9	4	0.92	5	77	prolate	1
ancistrophy	8.9	6.9	1.3	6.9	57.3	3	1.2	2	72	prolate	1
ancistrophy	7.9	5.8	1.4	5.8	37.5	4	1.5	10	84	spherical	1
sarcoph	17.5	6.6	2.7	6.6	87.8	4	0	0	0	angularpoint	1
sarcoph	15.5	6.1	2.6	6.1	63.0	3	0	0	0	angularpoint	1
sarcoph	16.5	6.3	2.6	6.3	81.6	3	0	0	0	angularpoint	1
sarcoph	16.3	7.6	2.2	7.6	82.0	3	0	0	0	angularpoint	1
sarcoph	14.4	7.2	2.0	7.2	55.6	4	0	0	0	angularpoint	1
sarcoph	14.7	7.4	2.0	7.4	73.3	5	0	0	0	angularelongate	1
sarcoph	19.8	7.5	2.6	7.5	108.6	5	0	0	0	angularpoint	1
sarcoph	19.4	7.2	2.7	7.2	70.0	4	0	0	0	angularpoint	1
sarcoph	19.3	7.3	2.6	7.3	92.5	4	0	0	0	angularpoint	1
sarcoph	14.3	5.3	2.7	5.3	66.5	3	0	0	0	angularpoint	1
sarcoph	14.2	6.7	2.1	6.7	83.5	3	0	0	0	quadrangular	1
sarcoph	14.8	12.9	1.1	12.9	133.9	5	0	0	0	triangular	1
sarcoph	15.9	5.7	2.8	5.7	76.7	4	0	0	0	angularpoint	1
sarcoph	14.1	8.7	1.6	8.7	89.1	4	0	0	0	angularpoint	1
sarcoph	16.1	6.2	2.6	6.2	87.1	4	1.68	1	40	angularpoint	1
sarcoph	16.7	6.4	2.6	6.4	92.0	4	0	0	0	angularpoint	1
sarcoph	15.0	7.8	1.9	7.8	82.2	4	0	0	0	angularpoint	1
sarcoph	11.8	7.6	1.6	7.6	57.4	5	0	0	0	angularpoint	1
sarcoph	16.2	6.3	2.6	6.3	80.8	5	0	0	0	angularelongate	1
sarcoph	11.6	5.1	2.3	5.1	56.8	4	0	0	0	angularpoint	1
sarcoph	10.3	7.6	1.3	7.6	49.5	4	0	0	0	angularpoint	1
sarcoph	16.4	6.6	2.5	6.6	95.1	4	0	0	0	angularelongate	1
sarcoph	19.3	6.3	3.1	6.3	74.7	4	0	0	0	angularelongate	1
sarcoph	20.4	7.6	2.7	7.6	136.4	4	0	0	0	angularelongate	1

sarcoph	14.4	6.8	2.1	6.8	81.0	3	0	0	0	angularelongate	1
sarcoph	14.7	8.6	1.7	8.6	87.8	3	0	0	0	angularelongate	1
sarcoph	14.7	8.6	1.7	8.6	71.7	4	0	0	0	angularelongate	1
sarcoph	23.6	21.7	1.1	21.7	294.8	3	5	12	40.2	spherical	1
sarcoph	14.0	6.9	2.0	6.9	89.5	3	0	0	0	quadrangular	1
sarcoph	21.3	8.8	2.4	8.8	130.9	4	0	0	0	angularpoint	1
sarcoph	13.3	7.2	1.8	7.2	75.9	5	0	0	0	angularelongate	1
sarcoph	19.5	8.4	2.3	8.4	114.5	5	0	0	0	angularpoint	1
sarcoph	11.5	4.6	2.5	4.6	37.9	3	0	0	0	angularpoint	1
sarcoph	13.8	7.6	1.8	7.6	71.4	4	0	0	0	angularpoint	1
sarcoph	15.2	6.5	2.3	6.5	84.9	4	0	0	0	quadrangular	1
sarcoph	15.3	9.3	1.6	9.3	127.6	3	0	0	0	quadrangular	1
sarcoph	11.5	6.6	1.8	6.6	51.2	4	0	0	0	angularpoint	1
sarcoph	13.8	6.2	2.2	6.2	56.3	4	0	0	0	angularpoint	1
sarcoph	11.4	6.6	1.7	6.6	56.1	3	0	0	0	quadrangular	1
sarcoph	16.8	6.0	2.8	6.0	78.3	4	0	0	0	angularpoint	1
sarcoph	19.7	6.2	3.2	6.2	94.7	4	0	0	0	angularpoint	1
sarcoph	13.8	6.7	2.0	6.7	74.2	5	0	0	0	angularpoint	1
sarcoph	17.6	9.4	1.9	9.4	94.9	4	0	0	0	angularpoint	1
sarcoph	13.8	8.4	1.6	8.4	105.4	3	0	0	0	quadrangular	1
sarcoph	17.3	6.6	2.6	6.6	70.2	4	0	0	0	angularpoint	1
sarcoph	16.6	9.3	1.8	9.3	91.9	4	2.3	1	58	angularpoint	1
sarcoph	15.2	7.5	2.0	7.5	89.7	3	0	0	0	angularpoint	1
sarcoph	16.5	7.7	2.1	7.7	101.4	5	0	0	0	angularpoint	1
sarcoph	20.2	7.8	2.6	7.8	118.8	5	0	0	0	angularpoint	1
sarcoph	12.2	6.5	1.9	6.5	57.2	5	0	0	0	angularpoint	1

Metrics of reference starches.

Species	Length	Width	LW Ratio	Brea	Area	Shape	Facets	Striaelen	Striaeno	Type	Lam	Dist
cola	27.82	23.59	1.18	18.9	515	ovoid	0	6.48	1	1	3	12.19
cola	21.85	20.68	1.06	13	396.24	elongate conovoid	0	5.86	2	2	3	10.24
cola	13.13	8.4	1.56	8.4	70.65	pyriform	0	0	0	1	2	6.56
cola	11.87	8.54	1.39	8.54	82.8	elongate conovoid	0	0	0	2	2	6.04
cola	11.16	8.61	1.3	8.61	75.1	elongate conovoid	0	0	0	2	2	4.72
cola	3.42	3.42	1	2.39	7.52	oblate conovoid	0	0	0	2	0	1.13
cola	22.39	17.83	1.26	12.3	300.88	ovoid	0	4.36	1	1	2	8.33
cola	9.19	7.6	1.21	7.6	61.36	prolate	1	0	0	1	0	3.25
cola	8.41	6.67	1.26	6.67	42.84	prolate	1	0	0	1	0	2.59
cola	11.68	8.94	1.31	7.65	79.98	triangular	0	0	0	1	0	4.65
cola	12.73	9.8	1.3	9.8	88.7	prolate	1	2.62	1	1	0	5.02
cola	5.86	4.51	1.3	4.51	20.95	oblate conovoid	2	0	0	2	0	2.06
cola	13.18	9.99	1.32	9.99	105.93	ovoid	0	0	0	1	0	5.88

cola	6.04	4.92	1.23	4.92	25.57	ovoid	1	0	0	1	0	2.62
cola	4.18	3.21	1.3	3.21	15.26	ovoid	1	0	0	1	0	1.23
cola	7.62	7.62	1	6.69	103.45	oblate	2	0	0	2	0	4.09
cola	4.75	3.69	1.29	3.69	21.38	conovoid prolate	1	0	0	1	0	1.79
cola	3.57	3.57	1	2.7	9.79	oblate	1	0	0	2	0	1.35
cola	11.59	9.34	1.24	9.34	83.96	conovoid ovoid	0	0	0	1	0	4.61
cola	8.78	7.92	1.11	7.92	58.53	ovoid	0	0	0	1	0	3.71
cola	4.85	4.08	1.19	4.08	18.63	polygon	3	0	0	2	0	1.33
cola	6.4	4.42	1.45	4.42	22.9	ovoid	2	0	0	1	0	1.85
cola	27.23	19.54	1.39	18	402	ovoid	0	8	4	1	2	11.84
cola	26.46	17.45	1.52	17.5	346.76	ovoid	0	7	5	1	0	15.59
cola	14.34	12.99	1.1	12.99	143.36	prolate	0	0	0	1	2	6.18
cola	20.34	14.36	1.42	14.4	226.29	ovoid	0	7.8	4	1	0	9.62
cola	26.75	19.64	1.36	19.64	408.6	ovoid	0	9.87	3	1	3	15.02
cola	14.7	11.69	1.26	11.69	144.5	elongate	0	2.27	1	2	2	7.62
cola	10.22	8.71	1.17	8.71	68.55	conovoid prolate	0	0	0	1	0	2.91
cola	9.52	7.2	1.32	7.2	64.07	ovoid	0	0	0	1	2	2.97
cola	8.26	6.45	1.28	6.45	42.47	ovoid	0	0	0	1	0	2.46
cola	10.59	7.91	1.34	7.91	76.69	ovoid	0	0	0	1	2	4.12
cola	11.43	8.14	1.4	8.14	73.02	pyriform	0	0	0	1	0	4.16
cola	8.91	6.6	1.35	6.6	48.02	ovoid	1	0	0	1	0	2.69
cola	7.45	5.73	1.3	5.73	39.98	ovoid	0	0	0	1	0	2.67
cola	5.6	3.7	1.51	3.7	18.25	prolate	0	0	0	1	0	1.37
cola	6.52	4.86	1.34	4.86	45	polygon	3	0	0	2	0	1.83
cola	14.55	14.55	1	10.4	119.07	elongate	0	2.9	2	2	2	7.89
cola	8.7	6.15	1.41	6.15	39.45	conovoid ovoid	0	0	0	1	0	3.8
cola	12.24	9.38	1.3	9.38	89.29	ovoid	0	1.62	2	1	0	1.85
cola	12.82	10.55	1.22	10.55	120.54	prolate	0	0	0	1	0	4.51
cola	6.6	5.03	1.31	5.03	25.85	ovoid	0	0	0	1	0	2.46
cola	6.65	5.36	1.24	5.36	50.82	triangular	0	0	0	1	0	1.84
cola	15.39	9.32	1.65	9.32	99.78	pyriform	0	0	0	1	0	3.69
cola	4.5	3.69	1.22	3.69	16.32	spherical	0	0	0	1	0	2.15
cola	14.47	12.81	1.13	12.81	130.47	prolate	0	0	0	1	0	3.07
cola	3.6	3.08	1.17	3.08	11.8	spherical	0	0	0	1	0	1.45
cola	7.32	5.32	1.38	5.32	33.19	oblate	2	0	0	1	0	1.65
cola	13.82	10.61	1.3	10.61	104.83	conovoid ovoid	0	0	0	1	0	2.97
cola	16.98	11.45	1.48	11.45	128.62	triangular	0	0	0	1	0	2.46
aframomum	2.86	2.73	1.05	2.73	4.95	hemispherical	1	0	0	3	0	1.43
aframomum	2.36	2.1	1.12	2.1	3.87	spherical	0	0	0	3	0	1.18
aframomum	2.39	2.18	1.1	2.18	3.71	spherical	1	0	0	3	0	1.195
aframomum	2.32	1.99	1.17	1.99	4.08	spherical	0	0	0	3	0	1.16
aframomum	3.13	2.83	1.11	2.83	4.7	spherical	0	0	0	3	0	1.565
aframomum	2.47	2.18	1.13	2.18	4.1	spherical	0	0	0	3	0	1.235
aframomum	3.26	2.85	1.14	2.85	7.5	spherical	1	0	0	3	0	1.63
aframomum	2.88	2.57	1.12	2.57	5.59	spherical	1	0	0	3	0	1.44

aframomum	4.81	4.45	1.08	4.45	16	spherical	2	0	0	3	0	2.405
aframomum	3.52	3.4	1.04	3.4	7.18	spherical	2	0	0	3	0	1.76
aframomum	2.57	2.46	1.04	2.46	4.36	spherical	1	0	0	3	0	1.285
aframomum	2.46	2.15	1.14	2.15	3.5	spherical	1	0	0	3	0	1.23
aframomum	3.25	2.4	1.35	2.4	5.67	ovoid	0	0	0	3	0	1.625
aframomum	2.9	2.1	1.38	2.1	4.91	spherical	1	0	0	3	0	1.45
aframomum	2.54	2.21	1.15	2.21	4.31	spherical	2	0	0	3	0	1.27
aframomum	2.73	2.63	1.04	2.63	5.54	spherical	2	0	0	3	0	1.365
aframomum	2.5	2.2	1.14	2.2	5.99	spherical	3	0	0	3	0	1.25
aframomum	2.15	2.02	1.06	2.02	3.8	spherical	2	0	0	3	0	1.075
aframomum	2.95	2.16	1.37	2.16	5.55	spherical	1	0	0	3	0	1.475
aframomum	3.71	3.56	1.04	3.56	10	spherical	2	0	0	3	0	1.855
aframomum	3.49	2.98	1.17	2.98	6.23	spherical	2	0	0	3	0	1.745
aframomum	3.69	3.69	1	3.69	9.25	spherical	1	0	0	3	0	1.845
aframomum	3.49	3.19	1.09	3.19	9.97	spherical	2	0	0	3	0	1.745
aframomum	1.99	1.87	1.06	1.87	2.71	spherical	1	0	0	3	0	0.995
aframomum	3.04	2.58	1.18	2.58	5.08	spherical	0	0	0	3	0	1.52
aframomum	5.65	5.45	1.04	5.45	21.99	spherical	2	0	0	3	0	2.825
aframomum	3.85	2.82	1.37	2.82	8.69	spherical	2	0	0	3	0	1.925
aframomum	2.66	2.05	1.3	2.05	4.82	hemispherical	1	0	0	3	0	1.33
aframomum	2.86	2.21	1.29	2.21	4.96	hemispherical	2	0	0	3	0	1.43
aframomum	2.83	2.53	1.12	2.53	6.78	spherical	2	0	0	3	0	1.415
aframomum	3.11	2.88	1.08	2.88	9.42	spherical	3	0	0	3	0	1.555
aframomum	1.9	1.68	1.13	1.68	3	spherical	3	0	0	3	0	0.95
aframomum	3.58	3.38	1.06	3.38	9.45	spherical	1	0	0	3	0	1.79
aframomum	1.78	1.54	1.16	1.54	1.8	spherical	1	0	0	3	0	0.89
aframomum	2.05	1.64	1.25	1.64	2.22	spherical	2	0	0	3	0	1.025
aframomum	2.78	2.36	1.18	2.36	3.99	spherical	2	0	0	3	0	1.39
aframomum	1.81	1.69	1.07	1.69	2.57	spherical	0	0	0	3	0	0.905
aframomum	5.12	4.5	1.14	4.5	16.4	spherical	1	0	0	3	0	2.56
aframomum	2.57	1.96	1.31	1.96	3.89	spherical	1	0	0	3	0	1.285
aframomum	2.73	2.32	1.18	2.32	5.95	polygon	4	0	0	3	0	1.365
aframomum	4.27	4.08	1.05	4.08	14	polygon	4	0	0	3	0	2.135
aframomum	2.02	1.7	1.19	1.7	3.5	hemispherical	1	0	0	3	0	1.01
aframomum	2.82	2.67	1.06	2.67	6.37	spherical	1	0	0	3	0	1.41
aframomum	3.09	2.15	1.06	2.15	5.59	polygon	4	0	0	3	0	1.02
aframomum	3.49	2.87	1.06	2.87	8.31	polygon	4	0	0	3	0	1.45
aframomum	3.18	3.08	1.06	3.08	8.34	spherical	0	0	0	1	0	1.13
aframomum	4.3	3.28	1.06	3.28	11.5	spherical	1	0	0	1	0	1.13
aframomum	2.27	1.64	1.06	1.64	3.4	spherical	1	0	0	1	0	1.21
aframomum	5.03	3.18	1.06	3.18	12.83	polygon	3	0	0	3	0	1.5
aframomum	3.41	3.24	1.06	3.24	7.96	polygon	4	0	0	3	0	1.6
piper	5.15	3.8	1.36	3.8	14.67	polygon	7	0	0	3	0	2.36
piper	2.58	2.25	1.15	2.25	3.61	polygon	6	0	0	3	0	1.3
piper	4.18	2.84	1.47	2.84	9.52	polygon	5	0	0	3	0	2
piper	3.86	3.4	1.14	3.4	7.37	hemispherical	4	0	0	3	0	1.9

piper	3.4	2.7	1.26	2.7	7.49	polygon	7	0	0	3	0	1.7
piper	3.21	2.79	1.15	2.79	8.9	polygon	6	0	0	3	0	1.6
piper	3	2	1.5	2	10	polygon	6	0	0	3	0	1.5
piper	3.98	3.28	1.21	3.28	15	polygon	7	0	0	3	0	1.49
piper	3.95	3.58	1.1	3.58	13.99	polygon	7	0	0	3	0	1.49
piper	3.18	2.9	1.1	2.9	10.17	polygon	6	0	0	3	0	1.64
piper	3.32	3.11	1.07	3.11	9.15	polygon	6	0	0	3	0	1.67
piper	3.04	2.58	1.18	2.58	6.68	polygon	7	0	0	3	0	1.52
piper	3.25	2.27	1.43	2.27	9.73	polygon	7	0	0	3	0	1.63
piper	4.98	3.92	1.27	3.92	14.44	polygon	6	0	0	3	0	2.5
piper	4.87	4.82	1.01	4.87	17.68	hemispherical	5	0	0	3	0	2.3
piper	5.94	3.62	1.64	3.62	11.91	polygon	7	0	0	3	0	2.8
piper	4.45	3.98	1.12	3.98	16	oblate conovoid	4	0	0	3	0	2.2
piper	4.33	3.9	1.11	3.9	12.22	oblate conovoid	4	0	0	3	0	2.15
piper	2.84	2.17	1.31	2.17	5.07	polygon	6	0	0	3	0	1.4
piper	5.33	5.24	1.02	3	19	hemispherical	3	0	0	3	0	2.6
piper	4.66	3.92	1.19	3	16.72	hemispherical	3	0	0	3	0	2.33
piper	3.7	2.56	1.45	2.56	10.55	polygon	5	0	0	3	0	1.8
piper	2.95	2.25	1.31	2.25	8.38	oblate conovoid	3	0	0	3	0	1.8
piper	4.23	3.11	1.36	3.11	18.74	polygon	6	0	0	3	0	2.1
piper	4.41	3.75	1.18	3.75	10.84	oblate conovoid	5	0	0	3	0	2.2
piper	3.52	2.62	1.34	2.62	18	polygon	6	0	0	3	0	1.75
piper	4.17	3.12	1.34	3.12	11.77	polygon	6	0	0	3	0	1.07
piper	3.15	2.43	1.3	2.43	18.55	quadrangular	6	0	0	3	0	1.6
piper	3.49	2.93	1.19	2.93	10.6	polygon	7	0	0	3	0	1.7
piper	2.98	2.53	1.18	2.53	7.22	polygon	7	0	0	3	0	1.5
piper	3.71	3.41	1.09	3.41	10.94	polygon	7	0	0	3	0	1.87
piper	3.47	2.33	1.49	2.33	8.52	oblate conovoid	3	0	0	3	0	1.72
piper	4.03	3.33	1.21	3.33	8.55	polygon	6	0	0	3	0	2
piper	5.82	5.82	1	3.62	16.57	hemispherical	2	0	0	3	0	2.8
piper	5.41	5.41	1	3.91	18.7	hemispherical	2	0	0	3	0	2.7
piper	6.01	6.01	1	5.07	18.37	oblate conovoid	3	0	0	3	0	3
piper	3.92	3.85	1.02	3.85	11.54	polygon	7	0	0	3	0	1.95
piper	5	3.85	1.3	3.85	15.22	polygon	7	0	0	3	0	1.65
piper	3.39	3.12	1.09	3.12	13.91	quadrangular	6	0	0	3	0	2.9
piper	3.82	2.07	1.85	2.07	6.73	oblate conovoid	5	0	0	3	0	1.35
piper	2.71	2.27	1.19	2.27	4.84	oblate conovoid	5	0	0	3	0	1.35
piper	3.58	2.76	1.3	2.76	7.99	polygon	7	0	0	3	0	1.79
piper	2.27	2.05	1.11	2.05	6.1	polygon	6	0	0	3	0	1.13
piper	4.16	3.75	1.11	3.75	15.12	polygon	4	0	0	1	0	1.64
piper	4.23	3.85	1.1	3.85	14.17	polygon	4	0	0	3	0	2.15
piper	2.77	2.13	1.3	2.13	4.12	polygon	2	0	0	3	0	0.87
piper	4.57	3.27	1.4	3.27	15.01	polygon	4	0	0	3	0	1.85
piper	3.84	3.61	1.06	3.61	14.88	polygon	6	0	0	3	0	1.88

piper	3.34	3.25	1.03	3.25	7.88	polygon	5	0	0	3	0	1.54
piper	2.25	2.06	1.09	2.06	4.78	polygon	4	0	0	3	0	1.13
sacog	5.99	4.77	1.26	3	21.57	polygon	3	0	0	2	0	1.77
sacog	5.55	4.03	1.38	2	18.73	polygon	2	0	0	2	0	1.74
sacog	6.96	5.88	1.18	3.4	36.03	oblate conovoid	3	0	0	2	0	1.71
sacog	5.03	4.18	1.2	3	16.51	quadrangular	3	0	0	1	0	1.77
sacog	5.74	5.3	1.08	5.3	32.7	polygon	3	0	0	1	0	1.77
sacog	6.06	5.69	1.07	5.69	34	polygon	3	0	0	1	0	2.46
sacog	6.93	6.02	1.15	6.02	30.27	polygon	2	0	0	1	0	2.79
sacog	6.49	6.49	1	4.57	25.49	oblate conovoid	2	0	0	2	0	2.63
sacog	6.23	6.23	1	4.37	18.06	oblate conovoid	2	0	0	2	0	2.39
sacog	6.81	6.81	1	3.92	19.054	oblate conovoid	2	0	0	2	0	2.15
sacog	5.37	5.37	1	4.23	19.02	oblate conovoid	2	0	0	2	0	1.33
sacog	4.82	4.42	1.09	3	18.94	oblate conovoid	2	0	0	2	0	1.43
sacog	6.72	6.72	1	4.3	22.45	oblate conovoid	2	0	0	2	0	1.64
sacog	7.41	7.25	1.02	7.25	37.49	oblate conovoid	2	0	0	2	0	2.46
sacog	7.8	7.01	1.11	3	41.67	oblate conovoid	2	0	0	2	0	2.36
sacog	6.51	6.51	1	5.44	24.12	oblate conovoid	2	0	0	2	0	1.96
sacog	8.7	6.65	1.31	6.65	56.62	oblate conovoid	2	0	0	2	0	3.08
sacog	7.75	7.7	1.01	5.21	33.52	oblate conovoid	2	0	0	2	0	2.36
sacog	5.96	5.96	1	4.02	18.37	oblate conovoid	2	0	0	2	0	1.96
sacog	4.92	3.82	1.29	3.82	23	quadrangular	3	0	0	1	0	1.96
sacog	3.7	3.7	1	2.9	10.5	oblate conovoid	3	0	0	2	0	1.75
sacog	6.29	5.49	1.15	5.49	27.54	polygon	3	0	0	1	0	2.25
sacog	5.22	4.21	1.24	4.21	20.85	polygon	4	0	0	1	0	2.16
sacog	3.69	3.07	1.2	3.07	8.21	oblate conovoid	2	0	0	2	0	1.03
sacog	4.88	4.27	1.14	4	14.7	oblate conovoid	3	0	0	2	0	1.75
sacog	6.97	6.97	1	5.2	34.78	polygon	4	0	0	1	0	2.05
sacog	7.77	6.45	1.2	5.12	37.23	polygon	4	0	0	1	0	2.61
sacog	4.28	4.02	1.06	3.28	31.28	polygon	4	0	0	1	0	2.35
sacog	6.8	5.88	1.16	4.6	31.59	polygon	2	0	0	1	0	2.36
sacog	4.69	4.69	1	3.33	14.7	polygon	2	0	0	1	0	1.59
sacog	7.07	5.68	1.24	4.67	34.16	polygon	2	0	0	1	0	1.97
sacog	6.78	6.45	1.05	6.41	40.39	ovoid	1	0	0	1	0	2.17
sacog	6.35	6.13	1.04	5.68	24.12	polygon	3	0	0	1	0	3.01
sacog	6.74	6.26	1.08	3.98	19.55	polygon	3	0	0	1	0	2.27
sacog	6.23	4.9	1.27	4.51	19.3	polygon	2	0	0	1	0	1.81
sacog	7.63	7.63	1	4.13	27.61	hemispherical	1	0	0	2	0	2.01
sacog	7.77	7.77	1	5.15	32.7	hemispherical	1	0	0	2	0	2.05
sacog	6.79	6.1	1.11	6.1	33.09	quadrangular	1	0	0	1	0	2.05
sacog	6.99	5.79	1.21	5.79	28.54	hemispherical	2	0	0	2	0	2.15
sacog	5.37	2.88	1.86	2.88	15.25	hemispherical	1	0	0	2	0	2.97

sacog	4.77	3.26	1.46	3.26	14.97	hemispherical	1	0	0	2	0	2.65
sacog	5.77	3.48	1.66	3.48	14.77	hemispherical	2	0	0	2	0	2.35
sacog	5.25	4.47	1.17	4.47	21.11	hemispherical	1	0	0	2	0	1.99
sacog	5.41	4.31	1.26	4.31	17.58	hemispherical	1	0	0	2	0	1.95
sacog	5.92	5.07	1.17	5.07	22.21	hemispherical	1	0	0	2	0	2.05
sacog	5.34	5	1.07	5	18.45	polygon	5	0	0	1	0	2.59
sacog	6.04	6.04	1	6.04	27.63	spherical	1	0	0	1	0	2.14
sacog	6.18	3.95	1.56	3.95	17.37	hemispherical	1	0	0	2	0	2.98
sacog	4.66	3.16	1.47	3.16	9.24	oblate	2	0	0	2	0	2.27
sacog	5.14	3.79	1.36	3.79	18.35	conovoid oblate	2	0	0	2	0	1.59
panda	4.86	3.61	1.35	3.89	15.37	conovoid ovoid	0	1.96	2	1	0	2.76
panda	5.39	4.36	1.24	4.36	15.11	spherical	0	0	0	1	0	1.75
panda	6.88	5.37	1.28	5.37	31.25	ovoid	0	0	0	1	0	3.92
panda	4.6	4.6	1	4.6	16.17	ovoid	1	0	0	1	0	2.31
panda	5.32	5.02	1.06	5.02	22.8	spherical	0	0	0	1	0	2.66
panda	4.86	3.11	1.56	3.11	12.53	elongate ovoid	1	0	0	1	0	2.48
panda	6.92	5.62	1.23	5.62	37.39	ovoid	1	0	0	1	0	3.18
panda	7.68	5.05	1.52	5.05	29.8	pyriform	0	0	0	1	0	4.42
panda	7.02	5.65	1.24	5.62	29.65	prolate	0	2.69	2	1	0	3.29
panda	7.18	6.15	1.17	6.15	36.33	ovoid	0	1.6	2	1	0	3.39
panda	4.67	3.89	1.2	3.89	15.91	ovoid	0	0	0	1	0	2.61
panda	2.51	2.16	1.16	2.16	4.54	ovoid	0	0	0	1	0	1.5
panda	4.06	4.06	1	4.06	12.13	spherical	0	0	0	1	0	1.85
panda	6.49	6.49	1	6.49	33.53	spherical	0	1.01	3	1	0	2.77
panda	4.35	3.7	1.18	3.7	12.09	ovoid	0	0	0	1	0	1.3
panda	4.18	3.8	1.1	3.76	11.66	ovoid	2	0	0	1	0	1.44
panda	6.76	5.32	1.27	5.32	30.13	prolate	0	2.05	2	1	0	3.05
panda	4.52	3.69	1.22	3.69	15.1	prolate	0	1.24	2	1	0	2.06
panda	5.09	5.09	1	5.09	21.11	spherical	1	0	0	1	0	1.13
panda	3.03	2.88	1.05	2.88	8.12	ovoid	0	0	0	1	0	1.74
panda	4.94	4.23	1.17	4.23	17.6	prolate	0	0	0	1	0	1.85
panda	4.5	3.79	1.19	3.79	14.45	prolate	0	0	0	1	0	1.85
panda	7.47	6.09	1.23	6.09	39.18	prolate	0	0	0	1	0	3.55
panda	3.55	2.66	1.33	2.66	7.22	prolate	0	0	0	1	0	1.55
panda	4.1	3.69	1.11	3.69	13.07	prolate	0	0	0	1	0	1.54
panda	5.4	5.4	1	5.4	22.07	spherical	0	0	0	1	0	2.4
panda	3.17	3.17	1	3.17	8.09	spherical	0	0	0	1	0	1.33
panda	3.13	3.13	1	3.13	8.63	spherical	1	0	0	1	0	1.43
panda	5.59	4.12	1.36	4.12	19.12	prolate	0	0	0	1	0	2.76
panda	4.73	4.73	1	4.73	18.62	spherical	0	0	0	1	0	2.15
panda	4.18	3.47	1.2	3.47	12.87	prolate	1	0	0	1	0	2.29
panda	4.93	3.5	1.41	3.5	16.27	prolate	0	0	0	1	0	2.05
panda	3.18	2.67	1.19	2.67	7.8	prolate	1	0	0	1	0	1.02
panda	7.72	7.04	1.1	7.04	47.48	prolate	0	0	0	1	0	3.17
panda	4.4	3.39	1.3	3.39	15.43	prolate	0	0	0	1	0	2.09

panda	4.45	3.18	1.4	3.18	14.18	prolate	0	0	0	1	0	1.54
panda	4.85	4.69	1.03	4.69	18.14	spherical	0	0	0	1	0	1.65
panda	5.06	2.81	1.8	2.81	18.96	pyriform	0	0	0	1	0	1.14
panda	4	3.81	1.05	3.81	10.25	spherical	0	0	0	1	0	1.85
panda	5.02	3.17	1.58	3.17	26.04	prolate	0	0	0	1	0	2.79
panda	4.2	2.35	1.79	2.35	10.04	ovoid	0	0	0	1	0	1.54
panda	2.16	2.15	1	2.15	5	spherical	0	0	0	1	0	1.07
panda	2.87	1.84	1.56	1.84	5.7	prolate	0	0	0	1	0	1.23
panda	4.3	3.89	1.11	3.89	16.75	spherical	0	0	0	1	0	2.15
panda	2.97	2.77	1.07	2.77	7.5	spherical	0	0	0	1	0	1.33
panda	5.59	3.9	1.43	3.9	20.94	ovoid	0	2.34	1	1	0	2.11
panda	4.97	4.11	1.21	4.97	15.6	ovoid	0	0	0	1	0	2.3
panda	3.38	2.87	1.18	2.87	16.75	prolate	1	0	0	1	0	1.13
panda	3.07	2.66	1.15	2.66	7.19	spherical	0	0	0	1	0	1.13
panda	5.33	5.12	1.04	5.12	24	spherical	0	0	0	1	0	2.16
coula	7.6	7.6	1	7.6	36	spherical	0	0	0	1	2	4.5
coula	7.7	7.7	1	7.7	48	spherical	0	2.25	1	1	2	3.38
coula	2.5	2.5	1	2.5	8.27	spherical	0	0	0	1	0	1.54
coula	6.7	6.7	1	6.7	36	spherical	0	0	0	1	2	2.97
coula	7.36	7.36	1	7.36	48	spherical	0	0	0	1	2	3.45
coula	2.88	2.88	1	2.88	7.2	spherical	0	0	0	1	0	1.45
coula	6.15	6.15	1	6.15	27.39	spherical	0	0	0	1	2	2.79
coula	4	4	1	4	13	spherical	0	0	0	1	2	1.74
coula	4.41	4.41	1	4.41	14.55	spherical	1	0	0	1	2	2.15
coula	5.54	5.54	1	5.54	23.23	spherical	0	0	0	1	2	3.79
coula	8.53	8.53	1	8.53	57.11	spherical	0	0	0	1	2	4
coula	10.98	10.98	1	10.98	87.4	spherical	0	0	0	1	2	5.86
coula	8.76	8.76	1	8.76	61.12	spherical	0	0	0	1	2	4.31
coula	7.55	7.55	1	7.55	40.68	spherical	0	0	0	1	2	2.98
coula	5.12	5.12	1	5.12	40	spherical	0	0	0	1	2	3.29
coula	11.34	11.34	1	11.34	90.41	spherical	0	0	0	1	2	5.43
coula	4.73	4.73	1	4.73	18.5	spherical	0	0	0	1	2	2.35
coula	6.35	6.35	1	6.35	33.19	spherical	0	0	0	1	2	3.28
coula	5.09	5.09	1	5.09	30.3	spherical	0	0	0	1	2	2.56
coula	5.81	5.81	1	5.81	24	spherical	1	0	0	1	2	3.15
coula	6.76	6.76	1	6.76	32.16	spherical	1	0	0	1	2	3.28
coula	5.43	5.43	1	5.43	22.79	spherical	0	0	0	1	2	2.56
coula	4.71	4.71	1	4.71	19.28	spherical	0	0	0	1	2	2.07
coula	5.18	5.18	1	5.18	22.92	spherical	0	0	0	1	2	2.47
coula	7.58	7.58	1	7.58	42.52	spherical	0	0	0	1	2	4.13
coula	3.29	3.29	1	3.29	14.59	spherical	0	0	0	1	2	1.69
coula	6.35	6.35	1	6.35	37.24	spherical	0	0	0	1	2	2.97
coula	5.36	5.36	1	5.36	25.06	spherical	0	0	0	1	2	2.66
coula	5.23	5.23	1	5.23	18.26	spherical	1	0	0	1	2	2
coula	5.45	5.45	1	5.45	25.54	spherical	1	0	0	1	2	2.67
coula	4.13	4.13	1	4.13	15.29	spherical	0	0	0	1	2	1.54

coula	7.88	7.88	1	7.88	46.8	spherical	0	0	0	1	2	3.38
coula	9.34	9.34	1	9.34	66.9	spherical	0	0	0	1	2	4.9
coula	6.64	6.64	1	6.64	30.14	spherical	1	0	0	1	2	2.56
coula	7.81	7.81	1	7.81	44.41	spherical	0	1.14	1	1	2	3.6
coula	3.44	3.44	1	3.44	9.67	spherical	0	0	0	1	0	1.44
coula	6.47	6.47	1	6.47	30.62	spherical	0	0	0	1	2	3.19
coula	6.88	6.88	1	6.88	32.11	spherical	0	1.14	1	1	2	2.76
coula	6.66	6.66	1	6.66	34.56	spherical	0	1.14	1	1	2	3.69
coula	4.15	4.15	1	4.15	13.52	spherical	0	1.62	2	1	2	1.85
coula	7.91	7.91	1	7.91	46.31	spherical	0	0	0	1	2	4.51
coula	5.92	5.92	1	5.92	24.25	spherical	1	0	0	1	2	2.46
coula	3.75	3.75	1	3.75	16.7	spherical	1	0	0	1	2	1.84
coula	9.5	8.18	1.16	8.18	64.16	spherical	1	0	0	1	2	3.69
coula	6.45	6.14	1.05	6.14	30.29	spherical	1	0	0	1	1	2.15
coula	8.88	8.51	1.04	8.51	55.31	spherical	0	0	0	1	2	3.07
coula	5.73	5.16	1.11	5.16	21.69	spherical	2	0	0	1	1	1.45
coula	3.9	3.43	1.14	3.43	9.36	oblate	2	0	0	1	0	1.65
coula	8.66	8.41	1.03	8.41	56.62	conovoid spherical	0	0	0	1	2	2.97
coula	6.63	6.51	1.02	6.51	32.19	spherical	0	0	0	1	2	2.46
napoleona	6.32	4.17	1.52	4.17	23.45	ovoid	0	0	0	1	1	2.26
napoleona	5.44	3.66	1.49	3.66	12	elongate ovoid	0	0	0	1	0	1.97
napoleona	5.84	5.64	1.04	5.64	20.17	spherical	0	0	0	1	0	2.06
napoleona	5.08	4.65	1.09	4.65	16.55	ovoid	0	0	0	1	0	1.85
napoleona	4.92	4.53	1.09	4.53	17.7	spherical	0	0	0	1	0	2.25
napoleona	4.76	4.63	1.03	4.63	15.39	spherical	2	0	0	1	0	1.81
napoleona	7.12	5.65	1.26	5.65	32.47	spherical	0	0	0	1	0	3.08
napoleona	6.36	4.71	1.35	4.71	22.32	spherical	0	0	0	1	0	2.11
napoleona	4.72	3.28	1.44	3.28	15.57	spherical	0	0	0	1	0	1.99
napoleona	3.55	2.69	1.32	2.69	7.14	spherical	1	0	0	1	0	1.54
napoleona	5.15	5.08	1.01	5.08	22.96	prolate	0	0	0	1	0	2.56
napoleona	4.75	3.41	1.39	3.41	11.63	ovoid	1	0	0	1	0	1.88
napoleona	4.22	4.17	1.01	4.17	15.78	ovoid	1	0	0	1	0	1.55
napoleona	3.53	3.16	1.12	3.16	7.8	polygon	0	0	0	1	0	2.44
napoleona	5.51	5.34	1.03	5.34	25.52	spherical	0	0	0	1	0	2.61
napoleona	4.35	3.44	1.26	3.44	13.89	ovoid	0	0	0	1	0	1.54
napoleona	4.96	3.73	1.33	3.73	18.9	triangular	1	0	0	2	0	2.25
napoleona	5.31	4.1	1.3	4.1	16.47	triangular	1	0	0	2	0	2.21
napoleona	3.79	3.5	1.08	3.5	12	prolate	0	0	0	1	0	2.39
napoleona	6.66	5.32	1.25	5.32	25.8	prolate	0	0	0	1	0	2.66
napoleona	5.71	5.26	1.09	5.26	23.09	ovoid	1	0	0	1	0	2.25
napoleona	5.31	4.86	1.09	4.86	20.11	spherical	0	0	0	1	0	1.98
napoleona	4.78	4.71	1.01	4.71	19.64	spherical	1	0	0	1	0	2.09
napoleona	6.27	4.61	1.36	4.61	22.13	elongate ovoid	0	0	0	1	0	2.41
napoleona	6.49	6.07	1.07	6.07	31.17	spherical	0	0	0	1	0	2.76
napoleona	4.61	4.53	1.02	4.53	14.91	spherical	1	0	0	1	0	2.19
napoleona	5.07	4.63	1.1	4.63	20.34	spherical	0	0	0	1	0	1.96

napoleona	4.51	3.69	1.22	3.69	13.93	spherical	0	0	0	1	0	1.64
napoleona	4.49	3.77	1.19	3.77	12.72	spherical	1	0	0	1	0	1.69
napoleona	3.99	3.89	1.03	3.89	12.09	spherical	0	0	0	1	0	1.54
napoleona	6.14	4	1.54	4	19.5	prolate	0	0	0	1	1	2.77
napoleona	5.02	4.61	1.09	4.61	19.58	prolate	0	0	0	1	0	2.66
napoleona	5.53	5.22	1.06	5.22	22.7	spherical	1	0	0	1	0	1.74
napoleona	7.2	2.9	2.48	2.9	15.98	triangular	1	0	0	2	0	2.36
napoleona	6.45	3.71	1.74	3.71	18.98	quadrangular	2	0	0	2	0	3.11
napoleona	6.96	4.29	1.62	4.29	22.36	quadrangular	2	0	0	2	0	3.52
napoleona	5.04	4.05	1.24	4.05	16.02	polygon	2	0	0	1	0	1.85
napoleona	7.71	5.43	1.42	5.43	33.27	elongate ovoid	0	0	0	1	0	4.03
napoleona	7.56	5.69	1.33	5.69	31.76	ovoid	1	0	0	1	0	4.2
napoleona	3.88	3.27	1.19	3.27	9.22	prolate	0	0	0	1	0	1.47
napoleona	2.67	2.46	1.09	2.46	6.5	spherical	0	0	0	1	0	1.13
napoleona	2.66	2.56	1.04	2.56	5.5	spherical	0	0	0	1	0	1.13
napoleona	2.66	2.56	1.04	2.56	2.89	spherical	1	0	0	1	0	0.72
napoleona	8.79	6.74	1.3	6.74	47.3	ovoid	2	0	0	1	0	3.28
napoleona	8.35	4.75	1.76	4.75	31.01	elongate ovoid	0	0	0	1	0	3.63
napoleona	7.25	6.25	1.76	6.25	32.95	ovoid	0	0	0	1	0	3.13
napoleona	5.37	4.75	1.76	4.75	18.86	ovoid	0	0	0	1	0	18.86
napoleona	9.06	7.09	1.76	7.09	40.33	ovoid	0	0	0	1	0	4.85
napoleona	11.06	5.14	1.76	5.14	38.99	elongate ovoid	0	0	0	1	0	4.82
napoleona	11.03	4.5	1.76	4.5	38.99	elongate ovoid	0	0	0	1	0	5.79
gilbert	10.26	7.78	1.32	7.78	70.17	ovoid	1	0	0	1	0	3.99
gilbert	9	8.12	1.11	8.12	59.98	ovoid	1	0	0	1	0	2.47
gilbert	13.48	13.05	1.03	13.1	142.87	ovoid	1	0	0	1	0	4.51
gilbert	7.75	7.74	1	5.04	32.76	hemispherical	1	0	0	2	0	2.93
gilbert	14.555	14.33	1.02	1.33	163.84	spherical	1	0	0	1	0	5.44
gilbert	7.27	7.27	1	5.94	39.5	oblate conovoid	0	0	0	2	0	1.99
gilbert	8.4	8.08	1.04	8.08	62.07	hemispherical	1	0	0	2	0	3.79
gilbert	8.01	6.69	1.2	6.69	49.65	hemispherical	1	0	0	2	0	2.83
gilbert	12.79	10.98	1.16	10.98	119.09	ovoid	1	0	0	1	0	4.51
gilbert	7.18	7.18	1	5.02	29.29	hemispherical	1	0	0	2	0	2.63
gilbert	5.94	5.94	1	5.21	30.51	hemispherical	1	0	0	2	0	2.98
gilbert	4.56	4.56	1	2.42	8.18	hemispherical	1	0	0	2	0	1.19
gilbert	8.7	8.39	1.04	8.39	34.95	hemispherical	1	0	0	2	0	3.73
gilbert	7.34	7.34	1	5.72	65.33	hemispherical	1	0	0	2	0	2.81
gilbert	14.25	11.89	1.2	11.89	133.04	ovoid	2	0	0	1	0	6.04
gilbert	6.78	6	1.13	5.51	30.9	oblate conovoid	2	0	0	2	0	3.11
gilbert	13.72	11.68	1.17	11.68	131.85	ovoid	2	0	0	1	0	5.14
gilbert	16.01	12.44	1.29	12.4	167.1	ovoid	0	0	0	1	0	7.29
gilbert	10.25	9.22	1.11	9.22	84.46	ovoid	1	0	0	1	0	3.59
gilbert	17	14.56	1.17	14.56	166.92	ovoid	0	0	0	1	0	8.34
gilbert	15.12	13.58	1.11	13.58	154.6	ovoid	1	0	0	1	0	7.76
gilbert	7.74	7.74	1	5.42	30.66	hemispherical	1	0	0	2	0	2.63

gilbert	12.54	10.08	1.24	10.08	96.89	prolate	0	4.32	2	1	0	4.22
gilbert	8.31	8.16	1.02	8.16	51.53	oblate	2	0	0	2	0	4.1
gilbert	7.16	5.08	1.41	5.08	20.2	conovoid oblate	2	0	0	2	0	1.88
gilbert	7.62	7.62	1	6.88	34.42	conovoid oblate	2	0	0	2	0	3.79
gilbert	10.02	9.38	1.07	9.38	75.18	conovoid ovoid	1	0	0	1	0	5.03
gilbert	9.44	9.38	1.01	9.38	83.58	ovoid	1	0	0	1	0	5.39
gilbert	12.13	10.86	1.12	10.86	95.93	ovoid	1	0	0	1	0	5.53
gilbert	4.75	4.53	1.05	3	24.19	oblate	2	0	0	2	0	2.34
gilbert	9.76	8.54	1.14	8.54	67.71	conovoid ovoid	1	0	0	1	0	3.17
gilbert	5.44	5.44	1	2.06	12.16	hemispherical	1	0	0	2	0	1.65
gilbert	10.04	8.57	1.17	8.57	68.53	ovoid	1	0	0	1	0	4.1
gilbert	17.26	14.72	1.17	14.72	205.35	ovoid	2	2.63	1	1	0	7.87
gilbert	18.2	14	1.3	14	196.58	ovoid	1	5	3	1	0	9.74
gilbert	13.08	11.6	1.13	11.6	124.23	ovoid	1	0	0	1	0	6.06
gilbert	8.15	4.45	1.83	4.45	27	hemispherical	1	0	0	2	0	2.7
gilbert	5.49	5.46	1.01	5.46	25.01	spherical	0	0	0	1	0	2.05
gilbert	11.23	9.05	1.24	9.05	89	spherical	0	0	0	1	0	4.73
gilbert	7.84	7.76	1.01	7.76	46.55	oblate	1	0	0	2	0	2.61
gilbert	7.18	6.74	1.07	6.74	35.18	conovoid oblate	2	0	0	2	0	2.71
gilbert	6.64	5.95	1.12	5.95	33.45	conovoid spherical	2	0	0	1	0	2.49
gilbert	10.67	10.34	1.03	10.34	99.27	spherical	2	0	0	1	0	5.16
gilbert	7.07	6.37	1.11	6.37	32.19	spherical	2	0	0	1	0	1.97
gilbert	6.86	5.63	1.22	5.63	26.39	spherical	2	0	0	1	0	1.95
gilbert	7.66	6.78	1.13	6.78	41.03	spherical	1	0	0	1	0	1.95
gilbert	6.8	6.74	1.01	6.74	38.36	spherical	1	0	0	1	0	1.57
gilbert	9.13	8.34	1.09	8.34	68.58	hemispherical	1	0	0	2	0	3.07
gilbert	6.83	6.1	1.12	6.1	34.08	hemispherical	1	0	0	2	0	2.1
gilbert	5.29	5.09	1.04	5.09	22.94	hemispherical	1	0	0	2	0	1.54
eremo	3.99	3.99	1	3.99	12.61	spherical	0	0	0	1	0	1.64
eremo	2	2	1	2	3.39	spherical	0	0	0	1	0	0.7
eremo	1.88	1.88	1	1.88	4.2	spherical	0	0	0	1	0	0.74
eremo	4.73	4.73	1	4.73	18.9	spherical	0	0	0	1	0	2.05
eremo	4.65	3.91	1.19	3.91	14.46	prolate	0	0	0	1	0	1.35
eremo	3.89	3.89	1	3.89	11.09	spherical	0	0	0	1	0	1.17
eremo	4.63	4.63	1	4.63	16.53	spherical	0	0	0	1	1	2.05
eremo	3.1	3.1	1	3.1	9	spherical	0	0	0	1	0	1.25
eremo	4.9	4.9	1	4.9	20.14	spherical	0	0	0	1	0	2.65
eremo	2.76	2.76	1	2.76	6.57	spherical	0	0	0	1	0	1.74
eremo	3.38	3.38	1	3.38	9.97	spherical	0	0	0	1	0	1.44
eremo	2.63	2.63	1	2.63	5.17	spherical	0	0	0	1	0	1.13
eremo	4.13	4.13	1	4.13	13.66	spherical	0	0	0	1	0	2.67
eremo	2.58	2.58	1	2.58	5.1	spherical	0	0	0	1	0	1.3
eremo	4.5	4.1	1.1	4.1	14.31	prolate	0	0	0	1	0	1.74
eremo	4.05	3.96	1.02	3.96	12.67	prolate	1	0	0	1	1	2.07

eremo	3.05	3.05	1	3.05	9	spherical	0	0	0	1	0	1.65
eremo	4.06	3.83	1.06	3.83	13.63	prolate	0	0	0	1	0	1.85
eremo	3.42	3.42	1	3.42	11	spherical	0	0	0	1	0	1.14
eremo	4.32	4.32	1	4.32	15	spherical	0	0	0	1	0	1.81
eremo	4.12	4.12	1	4.12	14.91	spherical	0	0	0	1	1	1.7
eremo	3.15	3.15	1	3.15	9.46	spherical	0	0	0	1	0	1.43
eremo	3.43	3.43	1	3.43	10.89	spherical	1	0	0	1	0	1.95
eremo	3.89	3.89	1	3.89	12.97	spherical	0	0	0	1	1	1.79
eremo	3.36	3.36	1	3.36	9.65	spherical	1	0	0	1	0	1.45
eremo	2.77	2.77	1	2.77	7.88	spherical	1	0	0	1	0	1.44
eremo	4.43	4.43	1	4.43	15	spherical	0	0	0	1	0	2.06
eremo	2.78	2.78	1	2.78	7.15	spherical	0	0	0	1	0	1.55
eremo	2.58	2.58	1	2.58	5.78	spherical	0	0	0	1	0	0.93
eremo	4.11	4.11	1	4.11	12.89	spherical	1	0	0	1	1	2.05
eremo	2.4	2.4	1	2.4	4.68	spherical	0	0	0	1	0	0.83
eremo	2.89	2.89	1	2.89	7.61	spherical	1	0	0	1	0	1.14
eremo	3.07	3.07	1	3.07	7.23	spherical	0	0	0	1	0	1.44
eremo	2.39	2.39	1	2.39	4.55	spherical	0	0	0	1	0	1.13
eremo	2.47	2.47	1	2.47	5.08	spherical	0	0	0	1	0	1.02
eremo	4.58	3.86	1.19	3.86	14	prolate	0	0	0	1	0	2.46
eremo	5.14	5.14	1	5.14	21	spherical	0	0	0	1	0	2.25
eremo	2.7	2.7	1	2.7	7	spherical	0	0	0	1	0	1.54
eremo	3.89	3.89	1	3.89	12	spherical	0	0	0	1	0	1.64
eremo	3.69	3.69	1	3.69	10.55	spherical	0	0	0	1	0	1.74
eremo	3.49	3.49	1	3.49	7.6	spherical	0	0	0	1	0	1.55
eremo	3.07	2.17	1.41	2.17	5.64	hemispherical	1	0	0	2	0	1.62
eremo	2.17	2.17	1	2.17	3.43	spherical	0	0	0	1	0	1.03
eremo	7.07	6.37	1.11	6.37	17.69	spherical	0	0	0	1	0	1.95
eremo	6.86	5.63	1.22	5.63	8.51	spherical	0	0	0	1	0	1.23
eremo	7.66	6.78	1.13	6.78	6.27	spherical	0	0	0	1	0	0.92
eremo	6.8	6.74	1.01	6.74	12.3	spherical	0	0	0	1	0	2.15
eremo	9.13	8.34	1.09	8.34	12.35	spherical	0	0	0	1	0	1.84
eremo	6.83	6.1	1.12	6.1	6	spherical	0	0	0	1	0	0.92
eremo	5.29	5.09	1.04	5.09	6.28	spherical	0	0	0	1	0	1.13
calpo	2.6	2.6	1	2.6	5.33	spherical	0	0	0	1	0	1.25
calpo	2.16	1.75	1.23	1.75	3.49	ovoid	0	0	0	1	0	0.72
calpo	2.36	2.36	1	2.36	4.13	spherical	0	0	0	1	0	0.83
calpo	2.66	2.66	1	2.66	6	spherical	0	0	0	1	0	1.52
calpo	1.84	1.84	1	1.84	3.13	spherical	0	0	0	1	0	1.33
calpo	2.29	2.29	1	2.29	4.4	spherical	0	0	0	1	0	1.33
calpo	2.27	2.27	1	2.27	4	spherical	0	0	0	1	0	0.7
calpo	1.81	1.81	1	1.81	3.34	spherical	0	0	0	1	0	0.93
calpo	1.69	1.69	1	1.69	2.3	spherical	0	0	0	1	0	0.94
calpo	2.15	2.15	1	2.15	3.12	spherical	0	0	0	1	0	0.93
calpo	2.66	2.66	1	2.66	3.52	spherical	0	0	0	1	0	1.59
calpo	2.43	2.43	1	2.43	3.51	spherical	0	0	0	1	0	0.93

calpo	1.92	1.92	1	1.92	3.29	spherical	0	0	0	1	0	1.23
calpo	2.16	2.16	1	2.16	4.6	spherical	0	0	0	1	0	1.13
calpo	2.05	2.05	1	2.05	3.31	spherical	1	0	0	1	0	1.05
calpo	2.87	2.87	1	2.87	6.4	spherical	0	0	0	1	0	1.33
calpo	2.05	2.05	1	2.05	4	spherical	0	0	0	1	0	0.92
calpo	1.96	1.96	1	1.96	3.43	spherical	0	0	0	1	0	0.61
calpo	2.35	2.35	1	2.35	4.35	spherical	0	0	0	1	0	0.92
calpo	2.15	2.15	1	2.15	5.1	spherical	0	0	0	1	0	0.83
calpo	1.95	1.95	1	1.95	4.08	spherical	0	0	0	1	0	0.72
calpo	2.25	2.25	1	2.25	6.11	spherical	0	0	0	1	0	1.11
calpo	2.25	2.25	1	2.25	4.91	spherical	0	0	0	1	0	1.03
calpo	2.46	2.46	1	2.46	4.59	spherical	0	0	0	1	0	1.03
calpo	1.95	1.95	1	1.95	3.78	spherical	0	0	0	1	0	0.93
calpo	2.35	2.35	1	2.35	4.23	spherical	0	0	0	1	0	0.92
calpo	2.85	2.85	1	2.85	8.51	spherical	0	0	0	1	0	1.85
calpo	2.36	2.36	1	2.36	4.51	spherical	0	0	0	1	0	1.23
calpo	1.95	1.95	1	1.95	4.3	spherical	1	0	0	1	0	0.72
calpo	1.65	1.65	1	1.65	2.28	spherical	0	0	0	1	0	0.72
calpo	2.57	2.57	1	2.57	5.33	spherical	0	0	0	1	0	1.2
calpo	2.76	2.76	1	2.76	6.52	spherical	0	0	0	1	0	1.33
calpo	2.77	2.77	1	2.77	6.09	spherical	0	0	0	1	0	1.57
calpo	1.45	1.45	1	1.45	1.98	spherical	0	0	0	1	0	0.72
calpo	2.46	2.46	1	2.46	5.3	spherical	0	0	0	1	0	0.92
calpo	1.95	1.95	1	1.95	2.6	spherical	0	0	0	1	0	0.82
calpo	2.15	2.15	1	2.15	3.52	spherical	0	0	0	1	0	0.83
calpo	1.74	1.74	1	1.74	2.46	spherical	0	0	0	1	0	0.61
calpo	2.98	2.98	1	2.98	5.44	spherical	0	0	0	1	0	1.02
calpo	1.95	1.95	1	1.95	4.11	spherical	0	0	0	1	0	1.2
calpo	2.07	2.07	1	2.07	3.96	spherical	0	0	0	1	0	1.04
calpo	2.46	2.05	1.2	2.05	5.87	hemispherical	1	0	0	2	0	1.02
calpo	2.53	2.05	1.23	2.05	6.1	ovoid	0	0	0	1	0	1
calpo	2.96	2.38	1.24	2.38	5.72	prolate	0	0	0	1	0	1.39
calpo	2.82	2.82	1	2.82	6.15	spherical	0	0	0	1	0	1.41
calpo	2.31	2.24	1.03	2.24	5.34	hemispherical	1	0	0	1	0	1.15
calpo	2.76	1.94	1.42	1.94	4.03	hemispherical	1	0	0	1	0	1.38
calpo	2.68	2.46	1.09	2.46	3.86	hemispherical	1	0	0	1	0	1.34
calpo	2.96	2.1	1.41	2.1	4.45	ovoid	0	0	0	1	0	1.48
calpo	2.5	2.5	1	2.5	4.84	spherical	0	0	0	1	0	1.25
sarcoph	14.16	14.16	1	12.57	143.83	quadrangular	6	0	0	3	0	5.92
sarcoph	20.9	13.71	1.52	13.71	192.11	polygon	7	0	0	3	0	5.64
sarcoph	17.49	12.45	1.4	12.45	153.67	polygon	8	0	0	3	0	4.4
sarcoph	21.84	15.25	1.43	15.25	294.44	polygon	9	0	0	3	0	6.45
sarcoph	12.56	11.14	1.13	11.14	136.42	polygon	6	0	0	3	0	6.63
sarcoph	14.14	11.62	1.22	11.62	141.63	polygon	4	0	0	3	0	5.94
sarcoph	11.87	9.98	1.19	9.98	113.99	quadrangular	6	0	0	3	0	5.5
sarcoph	11.27	9.98	1.13	9.88	125.26	polygon	7	0	0	3	0	4.66

sarcoph	12.47	12.21	1.02	12.21	137.97	polygon	6	0	0	3	0	5.76
sarcoph	11.2	11.1	1.01	11.1	104	polygon	7	0	0	3	0	4.73
sarcoph	7.96	5.83	1.37	5	42.99	quadrangular	6	0	0	3	0	3
sarcoph	5.48	5.04	1.09	4.55	25	quadrangular	5	0	0	3	0	2.3
sarcoph	18.22	12.52	1.46	12.5	176	quadrangular	6	0	0	3	0	5.08
sarcoph	14.68	14.68	1	14.68	147	polygon	7	0	0	3	0	4.03
sarcoph	10.92	9.43	1.16	9.43	72	polygon	7	0	0	3	0	4.45
sarcoph	10.08	8.76	1.15	8.76	82	quadrangular	6	0	0	3	0	2.91
sarcoph	11.45	10.45	1.1	10.45	116	quadrangular	6	0	0	3	0	6.38
sarcoph	13.56	11.33	1.2	11.33	135.67	polygon	7	0	0	3	0	3.69
sarcoph	16.49	9.73	1.69	9.73	148	polygon concaveconvex	6	0	0	3	0	5.45
sarcoph	12.58	12.23	1.03	12.23	120.81	polygon	7	0	0	3	0	6
sarcoph	12.23	10	1.22	10	96.81	polygon	7	0	0	3	0	7.44
sarcoph	14.37	11.21	1.28	11.21	119.21	polygon	6	0	0	3	0	10.01
sarcoph	12.36	11.77	1.05	11.77	117.06	hemispherical	1	0	0	2	0	6.24
sarcoph	12.5	10.85	1.15	10.85	10.85	hemispherical	3	5.03	4	2	0	5.16
sarcoph	17	10.04	1.69	10.4	131.55	polygon	9	0	0	3	0	6.1
sarcoph	14.87	10.67	1.39	10.67	141.83	polygon	7	0	0	3	0	5.52
sarcoph	9.88	8.25	1.2	8.25	85.73	polygon	7	0	0	3	0	4.92
sarcoph	10.04	6.69	1.5	6.69	70.08	polygon	7	0	0	3	0	4.85
sarcoph	10.82	9.14	1.18	9.14	85.49	polygon	7	0	0	3	0	4.2
sarcoph	9.91	8.44	1.17	8.44	88.71	polygon	7	0	0	3	0	4.9
sarcoph	10.86	9.58	1.13	9.58	91.81	polygon	7	0	0	3	0	4.72
sarcoph	10.2	9.13	1.12	9.13	91.65	polygon	6	0	0	3	0	5.27
sarcoph	15.69	9.65	1.63	9.65	130.79	polygon concaveconvex	7	0	0	3	0	6.16
sarcoph	10.7	8.03	1.33	8.03	79.75	polygon	6	0	0	3	0	4.64
sarcoph	10.86	9.73	1.12	9.76	85.53	polygon	7	0	0	3	0	5.754
sarcoph	8.78	5.57	1.58	5.57	51.99	polygon	6	0	0	3	0	4.45
sarcoph	20.15	15.79	1.28	5.57	308.59	polygon	6	0	0	3	0	9.24
sarcoph	20.81	16.35	1.27	5.57	232.32	polygon	7	0	0	3	0	6.96
sarcoph	23.75	12.01	1.98	5.57	181.22	polygon	7	0	0	3	0	6.07
sarcoph	17.1	14.59	1.17	5.57	205.63	polygon	9	0	0	3	0	13.16
sarcoph	19.99	13.95	1.43	5.57	163.25	polygon	9	0	0	3	0	5.95
sarcoph	16.41	12.4	1.32	5.57	193.32	polygon	6	0	0	3	0	9.76
sarcoph	17.72	15	1.18	5.57	275.54	polygon	7	0	0	3	0	9.31
sarcoph	18.26	16.95	1.08	7.53	61.53	polygon	6	0	0	3	0	3.58
sarcoph	11	9.09	1.21	9.09	69.42	polygon	6	0	0	3	0	3.62
sarcoph	9.63	9.45	1.02	9.45	82.19	polygon	7	0	0	3	0	4.92
sarcoph	12.47	10.5	1.19	10.5	102.83	polygon	7	0	0	3	0	4.7
sarcoph	9.01	8.87	1.02	8.87	55.17	polygon	7	0	0	3	0	4.83
sarcoph	9.41	7.81	1.2	7.81	60.64	polygon	5	0	0	3	0	4.5
sarcoph	20.15	15.79	1.28	10	258.38	polygon	9	0	0	3	0	9.77
xylia	6.27	5.27	1.19	5.27	26.26	prolate	0	0	0	1	0	1.77
xylia	2.98	2.7	1.1	2.7	6.67	prolate	0	0	0	1	0	0.93

xylia	4.27	3.69	1.16	3.69	13.63	prolate	0	0	0	1	0	1.23
xylia	2.9	2.26	1.28	2.69	5.15	hemispherical	1	0	0	2	0	1.13
xylia	2.81	2.59	1.08	2.59	5.35	hemispherical	1	0	0	2	0	1.3
xylia	4.05	2.7	1.5	2.7	8.46	ovoid	0	0	0	1	0	1.47
xylia	3.38	3.07	1.1	3.07	8.27	prolate	1	0	0	1	0	2.27
xylia	2.87	2.87	1	2.87	7	spherical	0	0	0	1	0	1.03
xylia	4.15	3.69	1.12	3.69	11.74	ovoid	0	0	0	1	0	1.79
xylia	2.77	2.66	1.04	2.66	5	prolate	0	0	0	1	0	0.93
xylia	5.34	3.62	1.48	3.62	14.56	ovoid	0	0	0	1	0	1.96
xylia	3.38	3.28	1.03	3.28	10.53	spherical	0	0	0	1	0	1.62
xylia	5.2	5.2	1	5.2	19	spherical	0	0	0	1	0	2.32
xylia	5.25	4.49	1.17	4.49	16.75	ovoid	0	0	0	1	0	1.64
xylia	4.78	4.78	1	4.78	20	spherical	1	0	0	1	0	1.85
xylia	3.38	3.07	1.1	3.07	8.9	prolate	0	0	0	1	0	1.64
xylia	4.76	3.71	1.28	3.71	14.12	prolate	1	0	0	1	0	1.89
xylia	4.22	4.13	1.02	4.13	15.62	ovoid	2	0	0	1	0	2.17
xylia	3.4	3.18	1.07	3.18	9.08	spherical	1	0	0	1	0	1.65
xylia	5.6	4.65	1.2	4.65	21.12	prolate	1	0	0	1	0	2.29
xylia	4.45	3.44	1.29	3.44	11.84	ovoid	1	0	0	1	0	1.42
xylia	4.18	4.18	1	4.18	13.66	spherical	0	0	0	1	0	1.44
xylia	2.99	2.64	1.13	2.64	6.71	prolate	1	0	0	1	0	1.02
xylia	3.2	3.2	1	3.2	8.57	spherical	1	0	0	1	0	1.85
xylia	3.83	2.11	1.82	2.11	10.05	hemispherical	1	0	0	2	0	1.45
xylia	4.06	3.21	1.26	3.21	10.82	hemispherical	1	0	0	2	0	2.25
xylia	5.31	4.12	1.29	4.12	15.35	prolate	1	0	0	1	0	1.59
xylia	5.77	5.04	1.14	5.04	23.53	prolate	1	0	0	1	0	2.16
xylia	4.22	3.21	1.31	3.21	10.42	ovoid	0	0	0	1	0	1.64
xylia	6	4.51	1.33	4.51	20.11	ovoid	1	0	0	1	0	2.11
xylia	5.13	2.98	1.72	2.98	15.29	hemispherical	1	0	0	2	0	1.74
xylia	5.45	4.18	1.3	4.18	17.82	prolate	1	0	0	1	0	3.18
xylia	2.62	2.62	1	2.62	5.76	spherical	0	0	0	1	0	0.82
xylia	2.2	2.2	1	2.2	4	spherical	0	0	0	1	0	1
xylia	4.93	4.43	1.11	4.43	17	spherical	1	0	0	1	0	2.11
xylia	6.21	5.51	1.13	5.51	29.98	prolate	1	0	0	1	0	2.05
xylia	4.64	3.55	1.31	3.55	11.17	ovoid	1	0	0	1	0	0.72
xylia	5.45	4.03	1.35	4.03	16.51	ovoid	1	0	0	1	0	1.13
xylia	3.84	3.26	1.18	3.26	11.71	prolate	1	0	0	1	0	1.55
xylia	6.56	3.43	1.91	3.43	6.56	prolate	2	0	0	2	0	1.3
xylia	4.6	4.34	1.06	4.34	17.95	prolate	1	0	0	1	0	1.95
xylia	4.61	3.78	1.22	3.78	14.33	prolate	0	0	0	1	0	1.74
xylia	3.92	3.13	1.25	3.13	10.24	ovoid	2	0	0	1	0	1.39
xylia	5.62	5.43	1.03	5.43	25.45	ovoid	1	0	0	1	0	1.84
xylia	4.5	3.33	1.35	3.33	10	ovoid	0	0	0	1	0	0.94
xylia	5.02	4.7	1.07	4.7	22.2	spherical	2	0	0	1	0	1.55
xylia	2.78	2.36	1.18	2.36	8.15	spherical	2	0	0	1	0	1.33
xylia	2.97	2.46	1.21	2.46	6	spherical	1	0	0	1	0	1.33

xylia	3.09	2.87	1.08	2.87	7.75	spherical	1	0	0	1	0	1.57
xylia	3.85	3.25	1.18	3.25	11.43	spherical	1	0	0	1	0	1.25
treculia	8.91	5.07	1.76	5.07	39.15	ovoid	0	0	0	1	0	3.63
treculia	7.5	4.92	1.52	4.92	25.04	oblate	0	0	0	1	0	3.4
treculia	8.38	6.99	1.2	6.99	38.74	conovoid ovoid	1	0	0	1	0	3.42
treculia	4.81	4.31	1.12	4.31	12.82	triangular	3	0	0	2	0	1.9
treculia	6.97	5.21	1.34	5.21	29.15	ovoid	0	0	0	1	0	2.53
treculia	11.6	8.22	1.41	8.22	66.6	ovoid	0	0	0	1	0	4.1
treculia	7.83	5.74	1.36	5.74	30.67	oblate	0	0	0	1	0	3.04
treculia	4.94	4.18	1.18	4.18	14.95	conovoid oblate	0	0	0	1	0	2.47
treculia	6.91	6.11	1.13	6.11	36.2	conovoid ovoid	0	0	0	1	0	2.75
treculia	7.91	5.86	1.35	5.86	29	ovoid	0	0	0	1	0	3.21
treculia	6.52	4.92	1.33	4.92	27.78	ovoid	1	0	0	1	0	2.49
treculia	5.78	4.57	1.26	4.57	23.98	ovoid	1	0	0	1	0	1.65
treculia	8.43	5.91	1.43	5.91	34.9	ovoid	0	0	0	1	0	3.19
treculia	5.93	5.03	1.18	5.03	27.5	ovoid	1	0	0	1	0	2.97
treculia	6.16	4.97	1.24	4.97	22.8	ovoid	0	0	0	1	0	1.95
treculia	5.12	4.81	1.06	4.81	18.45	ovoid	0	0	0	1	0	2.05
treculia	7.41	5.74	1.29	5.74	35.56	ovoid	0	0	0	1	0	2.95
treculia	6.96	5.65	1.23	5.65	31.28	ovoid	0	0	0	1	0	1.87
treculia	15.73	8.65	1.82	8.65	112.17	pyriform	0	0	0	1	0	6.65
treculia	6.69	4.57	1.46	4.57	21.49	oblate	0	0	0	1	0	2.66
treculia	7.36	5	1.47	5	29.18	conovoid pyriform	0	0	0	1	0	2.9
treculia	4.99	4.36	1.14	4.36	20.12	spherical	1	0	0	1	0	1.88
treculia	6.7	6.42	1.04	6.42	33.52	ovoid	0	0	0	1	0	3.08
treculia	6.92	5.28	1.31	5.28	28.34	ovoid	0	0	0	1	0	2.66
treculia	9.03	7.33	1.23	7.33	50.23	ovoid	0	2.03	2	1	0	2.82
treculia	9.42	7.99	1.18	7.99	59.23	plano-convex	0	1.85	1	1	0	3.66
treculia	11.27	7.33	1.54	7.33	67.5	ovoid	0	0	0	1	0	4.77
treculia	6.7	6.05	1.11	6.05	31.26	ovoid	0	0	0	1	0	3.35
treculia	8.46	6.53	1.3	6.53	39.46	ovoid	0	0	0	1	0	2.25
treculia	7.67	6.64	1.16	6.64	35.62	prolate	0	0	0	1	0	2.77
treculia	6.65	5.32	1.25	5.32	28.98	ovoid	1	0	0	1	0	2.66
treculia	10.58	7.47	1.42	7.47	60.42	ovoid	0	0	0	1	0	4.55
treculia	5.68	5.31	1.07	5.31	23.85	hemispherical	1	0	0	1	0	2.07
treculia	6.43	5.09	1.26	5.09	24.92	ovoid	0	0	0	1	0	1.85
treculia	8.99	6.33	1.42	6.33	46.95	ovoid	0	0	0	1	0	4.54
treculia	7.97	5.58	1.43	5.58	33.01	prolate	0	0	0	1	0	2.44
treculia	6.11	5.74	1.06	5.74	28.51	hemispherical	0	0	0	1	1	2.93
treculia	7.15	5.47	1.31	5.47	31.15	ovoid	1	0	0	1	0	3.21
treculia	7.34	5.6	1.31	5.6	32.68	ovoid	0	0	0	1	0	3.2
treculia	8.17	4.98	1.64	4.98	33.67	plano-convex	0	0	0	1	0	3.98
treculia	3.08	2.97	1.04	2.97	7.5	spherical	0	0	0	1	0	1.23
treculia	3.29	2.97	1.11	2.97	8.41	spherical	0	0	0	1	0	1.43
treculia	7.17	5.19	1.38	5.19	26.68	ovoid	0	7.7	5.84	1	0	2.83

treculia	12.47	10.07	1.24	10.07	89.85	ovoid	0	0	0	1	0	5.85
treculia	7.23	7.06	1.02	7.06	37.1	spherical	0	0	0	1	1	3.48
treculia	13.32	10.14	1.31	10.14	93.77	ovoid	0	0	0	1	0	6.33
treculia	5.96	4.1	1.45	4.1	20.23	hemispherical	0	0	0	1	0	2.98
treculia	5.04	4.42	1.14	4.42	18.39	hemispherical	0	0	0	1	0	2.52
treculia	9.73	6.58	1.48	6.58	47.73	ovoid	0	0	0	1	0	3.91
treculia	9.63	8.5	1.13	8.5	58.52	prolate	1	0	0	1	0	4.1

Appendix table 7: Microremain variables used for identification model.

Variable	Description	Metric
Shared variables		
Length	Maximum diameter (μm), measured from spine tip to spine tip	Numeric (μm)
Width	Maximum diameter (μm) perpendicular to the maximum diameter	Numeric (μm)
LW Ratio	Length to width ratio	Numeric (μm)
Area	Total observable area in a 2D plane	Numeric (μm^2)
Shape	Ovoid, elongate ovoid, pyriform, oblate conovoid, elongate conovoid, hemispherical, triangular, quadrangular, polygon, polygon concave-convex, angularpoint, angulate elongate, ovoid concave-convex, prolate concave	16 descriptors
Starch specific		
Facets	Total number of maximum observable facets	Counts
Lam	Lamellae presence and distinctness	0-3 scale
Dist	Distance of longest arm of cross observed on cross-polarised light	Numeric
Striaelen	Average length of radial striae/cracks visible on the starch	Numeric
Striaeno	Number of radial striae/cracks visible on the starch	Counts
Type	simple, semi-compound or compound classification	3 descriptors
Phytolith specific		
Irregul	Measure of phytolith surface irregularity	0-4 scale
Spinelen	Estimated mean spine length: the mean length of spines approximately parallel with the viewing plane	Numeric (μm)
Spineno	Number of spines visible in entirety in the viewing field. Spines were counted value if their base was not obscured by the phytolith.	Numeric
Conjoined	Score of phytolith attachment to other phytoliths	1-2 scale

Appendix table 8: Random forest phytolith identification model. Using spheroid, globular morphotypes only. Identification rate=rate of successful identification per genus.

Number of variables tried at each split (mtry)						15
Tune length						3
Tree number						500
Out of bag estimate of error rate						25.75 %
Confusion matrix						
	Aframomum	*Ancistrophyllum*	*Elaeis*	*Eremospatha*	*Sarcophrynium*	Identification rate
Aframomum	39	3	1	5	2	0.78
Ancistrophyllum	3	32	3	12	0	0.64
Elaeis	2	3	40	5	0	0.8

Eremospatha	5	11	1	33	0	0.66
Sarcophrynium	2	0	1	0	47	0.94

Appendix table 9: Random forest starch identification model. Identification rate=rate of successful identification per genus.

Number of variables tried at each split (mtry)														14
Tune length														3
Tree number														500
Out of bag estimate of error rate														32.77 %
Confusion matrix	*Aframomum*	*Calpocalyx*	*Cola*	*Coula*	*Eremospatha*	*Gilbertiodendron*	*Napoleona*	*Panda*	*Piper*	*Sacoglottis*	*Sarcophrynium*	*Treculia*	*Xylia*	Identification rate
Aframomum	45	1	0	0	0	0	0	0	2	0	0	1	1	0.9
Calpocalyx	0	40	0	0	7	0	0	2	0	0	0	0	1	0.8
Cola	0	0	26	0	0	3	0	2	0	5	0	11	3	0.52
Coula	0	0	0	44	3	0	0	0	0	2	0	0	1	0.88
Eremospatha	0	10	0	0	31	0	0	7	0	0	0	0	2	0.62
Gilbertiodendron	0	0	4	0	0	38	1	0	0	7	0	0	0	0.76
Napoleona	0	2	0	0	1	1	18	7	0	2	0	8	11	0.36
Panda	0	3	1	0	6	0	11	11	0	0	0	6	12	0.22
Piper	2	0	0	0	0	0	0	0	47	1	0	0	0	0.94
Sacoglottis	0	0	0	0	0	6	0	0	0	43	0	0	1	0.86
Sarcophrynium	0	0	0	0	0	2	0	0	1	0	47	0	0	0.94
Treculia	0	0	7	0	0	2	4	6	0	1	0	26	4	0.52
Xylia	0	3	0	0	6	0	7	7	0	3	0	3	21	0.42

Appendix table 10: All recovered microremains in each dental calculus sample. M=many.

	Chimp	Tina	Agathe	Rubra	Mkubwa	Clyde	Kendo	Leo	Lefkas	Zerlina	Castor	Fanny	Goma	Hector	Brutus	Noah	Ondine	Venus	Bijou	Dorry	Oreste	13438	Loukou	Piment	Leonard	Bambou	Ophelia
Starches		4	9	7	-	4	-	5	11	-	25	54	167	2	3	5	-	16	10	4	2	15	1	-	-	-	-
Possible starches		4	4	3	-	-	-	-	-	-	-	-	14	0	11	1	-	2	-	1	2	-	2	-	-	-	1
Phytoliths	Spheroid echinate	14	71	90	4	18	18	100	10	110	55	98	70	21	12	30	15	58	72	11	34	69	8	-	-	-	-
	Long cell	3	3	10	1	2	12	9	3	17	-	3	14	-	4	2	1	4	1	9	2	3	3	-	-	-	-
	Cylindroid	1	-	1	-	-	2	1	-	-	2	-	-	-	1	-	1	4	2	1	-	-	4	-	-	-	-
	Grass short cell	-	3	2	-	3	2	1	-	-	1	-	1	-	7	2	-	3	-	2	-	-	1	-	-	-	-
	Hair cell	-	2	3	3	-	6	1	-	3	3	1	3	1	6	6	4	7	4	6	-	3	3	-	-	-	-
	Acicular hair cell	1	-	-	-	-	-	-	-	1	-	1	2	-	-	1	-	3	1	-	2	-	-	-	-	-	-
	Bulliform	3	3	3	-	-	10	3	1	1	-	5	3	1	4	1	2	4	2	4	1	1	1	-	-	-	-
	Parallepipedal	-	2	3	1	2	11	5	2	6	-	-	1	-	4	2	1	5	3	7	-	2	-	-	-	-	-
	Plate	1	-	1	-	-	2	1	1	1	-	-	1	-	2	-	-	1	-	2	-	-	-	-	-	-	-
	Undenti. phytolith	6	9	7	2	1	7	5	2	7	4	-	2	1	3	3	1	7	2	15	1	2	2	-	-	-	-
	Tracheid	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-
	Ellipsoid	-	-	-	-	-	-	-	-	1	-	1	1	-	1	-	1	1	-	-	-	1	-	-	-	-	-
Unsilicified plants cells	Monocot	-	1	1	-	-	-	-	-	3	1	-	2	1	3	-	-	-	-	-	-	-	-	-	-	-	-
	Dicot	-	3	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	1	-	-	2	-	-	-	-	-
	Unclear	6	10	13	-	-	6	1	6	3	3	7	4	2	14	14	1	2	12	3	1	4	1	-	-	1	-
	Stoma	-	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
	Dicot stoma	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	9	-	-	-	-	-	1	-	-	-	-
	Palm	-	-	-	-	-	-	-	-	-	-	2	-	-	2	-	-	-	-	1	-	-	-	-	-	-	-
	Spiral thickening	-	-	13	-	-	-	-	-	-	-	-	3	-	-	-	-	-	1	-	-	2	-	-	-	-	-
	Honeycomb sheet	-	-	-	-	-	2	-	-	-	-	-	2	-	3	2	-	-	1	-	-	1	-	-	-	-	-
	Stellate hair	-	-	-	-	-	1	-	-	-	-	-	-	-	2	-	-	-	-	-	-	1	-	-	-	-	-
	Hairs	-	8	1	1	3	14	8	7	1	2	1	2	2	1	6	-	-	2	-	-	3	-	-	-	-	-

	Jigsaw	-	-	2	-	-	-	-	-	-	-	-	3	-	-	9	-	-	4	-	-	-	-	-	-	-	-
	Tracheid	-	-	-	-	-	1	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Fungal spore		1	-	M	-	-	-	-	M	M	M	-	M	M	M	M	-	-	-	-	-	M	M	-	-	-	1
Diatom		-	-	-	1	-	-	1	1	-	5	1	1	1	1	-	-	1	2	-	-	1	-	-	-	-	-
Pollen		-	-	-	-	-	-	1	-	-	-	5	1	3	-	-	-	2	5	2	-	2	-	-	-	-	-
Cystolith		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	1	-	-	-	-	-
Barbule		-	-	-	-	-	-	-	-	-	-	2	-	-	-	1	-	-	-	-	-	2	-	-	-	-	-
Indeterminate rod		1	-	-	-	-	-	-	-	-	-	-	8	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Possible starch amyloplast (Aframomum?)		-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Oxalate																						15	-				
Falcates		-	-	-	-	-	-	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cup hair		-	-	-	-	-	9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Feather hair		-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mammal hair		-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Insects		-	-	-	-	-	-	-	-	1	7	2	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-
Insect hairs		-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
insect scale		-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Unknown		4	5	7	2	-	-	4	3	-	5	3	2	2	5	4	-	1	2	1	1	2	-	-	-	-	-
Phytoliths included in identification model		3	6	7	-	3	-	5	8	-	22	38	103	2	4	-	-	16	9	4	2	N/A	N/A	-	-	-	-
Starches included in identification model		9	52	104	3	9	16	94	11	76	69	124	129	21	93	27	9	47	63	86	35	N/A	N/A	-	-	-	-

Appendix table 11: Counts of identified genera in Taï Chimpanzee calculus samples.

Name	Phytolith Genera count	% of total genera	Starch Genera count	% of total genera
Ophelia	0	0	0	0
Leonardo	0	0	0	0
Bambou	0	0	0	0
Piment	0	0	0	0
Oreste	5	100	2	15.38
Hector	3	60	2	15.38
Noah	5	100	0	0
Lefkas	2	40	4	30.77
Tina	3	60	2	15.38
Dorry	4	80	3	23.08
Zerlina	4	80	0	0
Clyde	3	60	3	23.08
Agathe	4	80	4	30.77
Bijou	5	100	5	38.46
Leo	4	80	2	15.38
Castor	5	100	3	23.08
Fanny	4	80	10	76.92
Kendo	5	100	0	0
Venus	4	80	5	38.46
Goma	5	100	9	69.23
Rubra	5	100	5	38.46
Ondine	3	60	0	0
Mkubwa	2	40	0	0
Brutus	5	100	3	23.08

Appendix table 12: Measurements of phytoliths from calculus. ER=*Eremospatha*, AF=*Aframomum*, AN=*Laccosperma*, EL=*Elaeis*, SA=*Sarcophrynium*.

Chimpanzee name	Length	Width	LW Ratio	Brea	Area	Irregul	Spinelen	Spineno	Spineang	Shape	Conjoined	Plant genera	Certainty score
Leo	7.89	7.68	1.03	7.68	48.0	3	0.92	6	99	spherical	1	ER	0.53
Leo	9.74	9.43	1.03	9.43	79.6	3	0.92	10	91	spherical	1	ER	0.49
Leo	6.59	4.18	1.58	4.18	21.7	3	0.65	8	94	ovoid	1	ER	0.60
Leo	8.5	6.41	1.33	6.41	46.2	4	0.51	9	110	ovoid	1	AF	0.42
Leo	6.67	6.39	1.04	6.39	36.6	3	0.88	8	98	spherical	1	ER	0.77
Leo	3.1	2.71	1.14	2.71	7.4	2	0.4	5	88	polygon	1	ER	0.56
Leo	6.84	5.74	1.19	5.74	33.0	2	0.75	6	110	spherical	1	ER	0.77
Leo	4.72	4.72	1	4.72	19.2	4	0.91	8	82	polygon	1	ER	0.40
Leo	10.49	9.08	1.16	9.08	76.6	3	1.04	6	77	spherical	1	AN	0.56

Leo	12.01	8.71	1.38	8.71	87.6	2	0.8	7	131	prolate	1	EL	0.41
Leo	13.63	13.42	1.02	13.42	140.7	3	1.33	13	95.81	spherical	1	EL	0.77
Leo	5.51	4.58	1.2	4.58	22.8	2	0.4	5	113	spherical	1	ER	0.61
Leo	7.97	3.42	2.33	3.42	28.1	4	0.7	10	80	prolate	1	EL	0.69
Leo	9.56	7.17	1.33	7.17	45.6	4	0.87	8	90	ovoid	1	ER	0.53
Leo	6.4	4.92	1.3	4.92	28.8	2	0.55	7	106	spherical	1	ER	0.53
Leo	5.03	4.22	1.19	4.22	16.8	2	0.66	7	113	spherical	1	ER	0.94
Leo	17.86	11.05	1.62	11.05	147.0	2	0.58	14	103	ovoid	1	EL	0.65
Leo	11.28	10.86	1.04	10.86	98.2	2	0.88	15	88	spherical	1	EL	0.77
Leo	8.64	6.45	1.34	6.45	50.3	3	0.92	7	92	ovoid	1	ER	0.42
Leo	8.55	7.5	1.14	7.5	61.2	4	0.66	7	93	spherical	1	EL	0.39
Leo	5.97	5.07	1.18	5.07	23.8	4	0.9	8	126	polygon	1	ER	0.74
Leo	8.47	7.65	1.11	7.65	52.5	3	0.78	8	89	spherical	1	ER	0.44
Leo	7.93	7.39	1.07	7.39	48.9	2	0.78	11	116	spherical	1	ER	0.39
Leo	10.07	9.63	1.05	9.63	87.8	3	1.28	12	101	spherical	1	EL	0.51
Leo	7.08	5.77	1.23	5.77	34.6	3	0	0	0	polygon	1	AF	0.99
Leo	8.48	6.69	1.27	6.69	44.5	2	0.51	11	94	prolate	1	EL	0.90
Leo	8.76	5.03	1.74	5.03	33.5	3	0.7	10	83	prolate	1	EL	0.56
Leo	8.39	7.79	1.08	7.79	59.0	3	0.87	9	107	spherical	1	ER	0.46
Leo	8.8	8.55	1.03	8.55	62.6	3	0.94	8	98	spherical	1	ER	0.42
Leo	8.66	8.06	1.07	8.06	56.0	3	0.87	8	80	spherical	1	ER	0.38
Leo	11.77	8.89	1.32	8.89	73.0	3	0.97	16	125	prolate	1	EL	0.95
Leo	6.19	5.34	1.16	5.34	28.8	4	0.78	7	72.46	spherical	1	AF	0.52
Leo	9.33	9.02	1.03	9.02	64.5	3	0.87	12	82	spherical	1	EL	0.48
Leo	8.6	8.52	1.01	8.52	58.7	4	0.52	15	81	prolate	1	EL	0.83
Leo	16.1	15.56	1.03	15.56	220.0	2	1	19	87	spherical	1	EL	0.91
Leo	11.98	11.01	1.09	11.01	109.0	2	0.83	15	104	spherical	1	EL	0.94
Leo	10.76	6.92	1.55	6.92	62.0	3	0.83	13	119	ovoid	1	EL	0.97
Leo	10.31	9.78	1.05	9.78	80.2	3	0.75	10	80	spherical	1	ER	0.41
Leo	16.43	15.22	1.08	15.22	283.3	2	1.34	22	98	prolate	1	EL	0.89
Leo	6.52	5.63	1.16	5.63	28.2	3	0.6	9	88	polygon	1	ER	0.56
Leo	9.57	8.5	1.13	8.5	67.8	3	0.94	15	105	prolate	1	EL	0.98
Leo	4.81	4.61	1.04	4.61	101.5	4	0.88	9	101	spherical	1	ER	0.53
Leo	8.95	5.73	1.56	5.73	44.3	3	0.71	11	126	ovoid	1	EL	0.93
Leo	5.13	4.71	1.09	4.71	19.5	4	0.87	8	90.78	spherical	1	ER	0.86
Leo	9.79	9.26	1.06	9.26	69.3	3	0.83	14	96	spherical	1	EL	0.85
Leo	11.23	9.41	1.19	9.41	97.8	3	1.24	11	86	prolate	1	EL	0.92
Leo	19.42	18.77	1.03	18.77	305.0	2	1.44	11	111	spherical	1	EL	0.67
Leo	7.6	5.68	1.34	5.68	34.6	4	0.83	14	97	ovoid	1	EL	0.99
Leo	10.89	8.71	1.25	8.71	98.8	4	0.8	16	87	ovoid	1	EL	0.99
Leo	10.43	8.09	1.29	8.09	60.3	4	0.92	6	82	prolate	1	ER	0.38
Leo	8.93	8.24	1.08	8.24	60.9	3	0.96	7	90	spherical	1	ER	0.40
Leo	11.82	9.68	1.22	9.68	97.5	4	1.43	19	78	quadrangular	1	EL	0.95
Leo	6.24	5.23	1.19	5.23	27.3	3	0.8	7	81	ovoid	1	ER	0.60

Leo	6.44	5.36	1.2	5.36	28.1	3	0.78	6	116	spherical	1	ER	0.74
Leo	5.04	4.34	1.16	4.34	15.2	4	0.72	6	96	polygon	1	ER	0.87
Leo	11.57	11.38	1.02	11.38	100.8	3	0.87	14	121	spherical	1	EL	0.81
Leo	7.44	5.48	1.36	5.48	29.4	3	0.65	9	110	prolate	1	ER	0.63
Leo	14.66	12.68	1.16	12.68	155.9	3	1.33	16	75	prolate	1	EL	0.76
Leo	13.27	9.34	1.42	9.34	94.7	4	0.93	16	96	ovoid	1	EL	0.86
Leo	10.67	8.36	1.28	8.36	71.0	2	1.05	11	81	prolate	1	EL	0.91
Leo	4.77	3.43	1.39	3.43	10.4	3	0.6	6	94	polygon	1	ER	0.56
Leo	5.1	3.67	1.39	3.67	14.6	3	0.6	5	112	ovoid	1	AN	0.48
Leo	6.79	5.43	1.25	5.43	27.0	3	0.75	9	108	spherical	1	ER	0.72
Leo	7.98	7.02	1.14	7.02	44.5	3	0.74	9	96	prolate	1	ER	0.71
Leo	12.85	10.82	1.19	10.82	104.6	3	1.02	12	84	ovoid	1	EL	0.96
Leo	8.05	5.07	1.59	5.07	32.9	4	1.02	12	86	ovoid	1	EL	0.95
Leo	9	7.73	1.16	7.73	54.9	3	1.07	7	98	ovoid	1	AN	0.45
Leo	4.63	3.53	1.31	3.53	14.4	4	0.7	3	91	polygon	1	ER	0.57
Leo	6.31	5.3	1.19	5.3	26.3	2	1	8	117	prolate	1	ER	0.58
Leo	9.47	9.27	1.02	9.27	65.2	2	1.02	15	115	spherical	1	EL	0.73
Leo	9.8	9.66	1.01	9.66	75.7	2	0.92	13	91	spherical	1	EL	0.51
Leo	9.66	9.54	1.01	9.54	77.6	2	1.09	12	107	spherical	1	EL	0.41
Leo	4.3	4.1	1.05	4.1	13.1	4	0.72	7	92.3	polygon	1	ER	0.87
Leo	4.29	4.27	1	4.27	15.4	4	0.65	7	103	polygon	1	ER	0.50
Leo	4.52	4.36	1.04	4.36	17.7	4	0.52	5	110	spherical	1	ER	0.46
Leo	14.83	13.66	1.09	13.66	155.7	3	1.1	19	81	ovoid	1	EL	0.79
Leo	8.58	5.74	1.49	5.74	40.1	4	0.6	12	78	prolate concave-convex	1	EL	0.95
Leo	6.76	5.78	1.17	5.78	39.1	3	0.66	8	94	spherical	1	ER	0.67
Leo	9.02	7.48	1.21	7.48	52.7	4	0.94	10	95	polygon	1	EL	0.53
Leo	5.46	4.38	1.25	4.38	21.2	2	0.5	8	110	spherical	1	ER	0.86
Leo	10.38	6.79	1.53	6.79	66.9	2	0.84	11	78	ovoid	1	EL	0.93
Leo	7.08	6.36	1.11	6.36	40.8	3	0.62	8	119	spherical	1	ER	0.60
Leo	10.21	9.64	1.06	9.64	81.9	1	1.14	10	96	spherical	1	AN	0.42
Leo	24.12	20.27	1.19	20.27	435.5	3	1.8	20	111	prolate	1	EL	0.81
Leo	4.41	3.81	1.16	3.81	14.4	3	0.51	4	110	polygon	1	AN	0.79
Leo	7.76	6.26	1.24	6.26	39.1	3	0.78	16	100	spherical	1	EL	0.58
Leo	7.28	7.17	1.02	7.17	38.1	4	0.7	7	98	polygon	1	ER	0.69
Leo	11.4	10.34	1.1	10.34	96.8	3	1.07	16	89	prolate	1	EL	0.97
Leo	10.4	9.31	1.12	9.31	84.2	4	1.01	13	121	ovoid	1	EL	0.95
Leo	6.99	4.85	1.44	4.85	35.7	4	0.8	9	85	polygon	1	ER	0.37
Leo	13.33	12.72	1.05	12.72	128.6	3	0.92	16	116	spherical	1	EL	0.89
Leo	6.9	5.64	1.22	5.64	35.3	3	0.7	8	100	spherical	1	ER	0.67
Leo	10.67	10.03	1.06	10.03	94.2	2	1	13	105	spherical	1	EL	0.61
Leo	10.89	8.81	1.24	8.81	99.7	3	0.84	10	93	spherical	1	ER	0.44
Rubra	5.03	3.99	1.26	3.99	21.2	4	0.75	9	71	polygon	1	ER	0.52
Rubra	4.32	3.9	1.11	3.9	12.2	3	0.5	5	86	spherical	1	ER	0.44
Rubra	5.14	4.23	1.22	4.23	25.7	3	0.7	6	88	polygon	1	ER	0.86

Rubra	11.14	9.56	1.17	9.56	87.5	4	1.3	7	120	ovoid	1	AN	0.42
Rubra	5.65	5.49	1.03	5.49	27.2	3	0.72	6	110	polygon	1	ER	0.66
Rubra	20.7	13.04	1.59	13.04	210.3	4	0.97	19	102	ovoid	1	EL	0.73
Rubra	5.04	3.44	1.47	3.44	13.8	4	0.8	7	72	spherical	1	AN	0.43
Rubra	4.4	3.83	1.15	3.83	12.1	3	0.66	4	114	polygon	1	ER	0.62
Rubra	6.59	3.85	1.71	3.85	19.3	3	0.82	6	70	ovoid	1	EL	0.40
Rubra	9.41	8.54	1.1	8.54	66.2	3	0.87	12	87	spherical	1	EL	0.56
Rubra	13.29	12.04	1.1	12.04	130.2	4	0.75	16	110	ovoid	1	EL	0.86
Rubra	6.04	4.88	1.24	4.88	27.8	4	1.04	7	82.83	polygon	1	AN	0.50
Rubra	11.37	10.36	1.1	10.36	106.3	3	0.6	12	111.16	spherical	1	EL	0.58
Rubra	4.87	4.58	1.06	4.58	17.5	3	0.83	4	100	spherical	1	ER	0.65
Rubra	5.43	5.23	1.04	5.23	23.9	4	0.7	7	110	spherical	1	ER	0.74
Rubra	5.47	4.2	1.3	4.2	15.4	5	0.58	5	99.57	polygon	1	AN	0.47
Rubra	9.63	9.14	1.05	9.14	68.4	3	0.84	7	80	ovoid	1	ER	0.45
Rubra	6.03	5.52	1.09	5.52	26.7	3	0.75	8	56	spherical	1	AF	0.84
Rubra	8.01	6.54	1.22	6.54	39.9	3	0.84	8	86	prolate	1	ER	0.75
Rubra	8.09	7.32	1.11	7.32	49.7	4	0.69	9	95	spherical	1	ER	0.56
Rubra	6.45	4.94	1.31	4.94	26.1	4	0.82	8	91	spherical	1	ER	0.92
Rubra	7.39	4.72	1.57	4.72	32.7	3	0.66	5	89	ovoid	1	ER	0.40
Rubra	6.04	4.64	1.3	4.64	22.0	4	0.85	8	76.18	prolate	1	ER	0.60
Rubra	10.08	7.87	1.28	7.87	63.6	4	0.84	15	86	ovoid	1	EL	1
Rubra	6.29	6.19	1.02	6.19	34.7	3	0.88	5	90	prolate	1	ER	0.74
Rubra	22.19	14.79	1.5	14.79	237.3	2	0.83	15	94	ovoid	1	EL	0.74
Rubra	8.12	6.37	1.27	6.37	45.6	3	0.83	10	99	prolate	1	ER	0.66
Rubra	9.13	8.81	1.04	8.81	65.9	3	0.92	14	104	spherical	1	EL	0.77
Rubra	6.45	4.71	1.37	4.71	23.0	4	0.82	7	92	ovoid	1	ER	0.93
Rubra	10.46	8.45	1.24	8.45	76.9	3	0.84	11	99	ovoid	1	EL	0.95
Rubra	10.67	8.59	1.24	8.59	65.2	4	0.65	7	98	ovoid	1	EL	0.43
Rubra	10.15	8.46	1.2	8.46	83.1	4	1	12	80	ovoid	1	EL	0.97
Rubra	10.55	10.44	1.01	10.44	89.4	4	0.84	16	79.01	spherical	1	EL	0.80
Rubra	12.13	11.81	1.03	11.81	87.4	3	1.17	10	87.43	spherical	1	EL	0.41
Rubra	17.4	12.93	1.35	12.93	180.7	4	0.66	11	107	ovoid	1	EL	0.61
Rubra	12.17	11.04	1.1	11.04	119.0	3	1	17	117	spherical	1	EL	0.95
Rubra	6.42	4.5	1.43	4.5	20.1	4	0.8	7	92	polygon	1	ER	0.71
Rubra	11.8	11.71	1.01	11.71	123.0	4	1.5	12	99	spherical	1	EL	0.55
Rubra	5.74	2.87	2	2.87	20.6	5	2	4	64.16	polygon	1	EL	0.37
Rubra	6.23	6.1	1.02	6.1	35.9	3	0.5	6	101	spherical	1	AF	0.67
Rubra	9.4	7.24	1.3	7.24	56.0	4	0.8	9	107	ovoid	1	ER	0.46
Rubra	28.67	18.76	1.53	18.76	381.8	4	2.4	15	98	ovoid	1	EL	0.71
Rubra	10.63	9.06	1.17	9.06	68.6	4	1.13	11	87	ovoid	1	EL	0.93
Rubra	6.88	5.57	1.24	5.57	31.3	3	0.7	9	110	ovoid	1	ER	0.73
Rubra	10.2	6.57	1.55	6.57	60.5	4	0.92	9	84	ovoid	1	EL	0.36
Rubra	23.9	23.45	1.02	23.45	445.4	3	1.37	15	113	spherical	1	EL	0.82
Rubra	17.74	16.73	1.06	16.73	217.1	3	1.2	17	97	spherical	1	EL	0.89

Rubra	5.59	3.62	1.54	3.62	14.0	3	0.8	5	78	polygon	1	ER	0.36
Rubra	16.66	12.46	1.34	12.46	160.8	3	0.72	18	103	ovoid	1	EL	0.75
Rubra	5.49	5.14	1.07	5.14	25.0	4	0.87	10	93	polygon	1	ER	0.67
Rubra	4.45	3.8	1.17	3.8	19.1	4	0.75	6	93	spherical	1	ER	0.92
Rubra	6.25	5.17	1.21	5.17	23.8	3	0.6	9	102	prolate	1	ER	0.72
Rubra	6.6	6.3	1.05	6.3	27.6	3	0.72	6	0.72	spherical	1	AF	0.84
Rubra	17.82	16.19	1.1	16.19	229.1	2	2.3	11	90	spherical	1	EL	0.61
Rubra	13.42	11.74	1.14	11.74	119.4	3	1.11	3	127	prolate	1	EL	0.31
Rubra	14.11	9.72	1.45	9.72	134.1	4	0.7	20	93	prolate	1	EL	0.73
Rubra	12.12	8.93	1.36	8.93	82.4	2	0.9	14	95	prolate	1	EL	0.96
Rubra	12.43	9.34	1.33	9.34	104.8	4	1	14	100	prolate	1	EL	0.98
Rubra	9.32	6.24	1.49	6.24	49.0	3	0.87	15	103	ovoid	1	EL	0.99
Rubra	6.66	5.65	1.18	5.65	33.2	4	0.75	13	95	ovoid	1	EL	0.95
Rubra	11.06	8.74	1.27	8.74	76.1	4	1	15	105	ovoid	1	EL	0.98
Rubra	8.91	8.29	1.07	8.29	58.0	4	0.9	6	111	spherical	1	ER	0.38
Rubra	8.16	6.05	1.35	6.05	35.7	3	0.6	13	95	ovoid	1	EL	0.96
Rubra	6.21	4.21	1.48	4.21	24.9	4	0.65	9	110	polygon	1	ER	0.60
Rubra	14.52	14.44	1.01	14.44	170.7	4	1.23	15	107	ovoid	1	EL	0.77
Rubra	7.85	6.4	1.23	6.4	42.0	4	1	7	87	prolate	1	AN	0.54
Rubra	5.81	5.76	1.01	5.76	27.5	3	0.5	9	115	spherical	1	AN	0.42
Rubra	5.18	3.94	1.31	3.94	16.5	3	0.82	6	92	polygon	1	ER	0.86
Rubra	6.57	6.45	1.02	6.45	33.1	2	0.7	8	90	spherical	1	ER	0.89
Rubra	4	3.5	1.14	3.5	11.9	3	0.5	9	93	spherical	1	ER	0.57
Rubra	6.64	4.69	1.42	4.69	21.4	4	0.7	9	99	polygon	1	ER	0.62
Rubra	8	5.85	1.37	5.85	37.8	4	0.5	11	103	ovoid	1	EL	0.90
Rubra	12.62	11.65	1.08	11.65	107.8	3	0.84	13	122	spherical	1	EL	0.77
Rubra	3.99	3.62	1.1	3.62	13.9	4	0.92	4	99	polygon	1	ER	0.57
Rubra	10.9	10.13	1.08	10.13	91.8	3	0.8	16	86	spherical	1	EL	0.89
Rubra	6.61	6.33	1.04	6.33	35.5	4	0.9	8	97	spherical	1	ER	0.77
Rubra	3.91	3.6	1.09	3.6	12.9	4	0.72	6	98	polygon	1	ER	0.88
Rubra	4.78	4.35	1.1	4.35	19.9	3	0.72	8	101	spherical	1	ER	0.91
Rubra	10.35	8.91	1.16	8.91	81.5	3	0.87	17	88	prolate	1	EL	0.99
Rubra	4.29	3.69	1.16	3.69	13.9	4	0.6	10	90	prolate	1	ER	0.57
Rubra	8.85	5.68	1.56	5.68	33.2	4	0.61	17	80	ovoid	1	EL	0.97
Rubra	6.39	5.84	1.09	5.84	33.0	4	0.82	7	127	polygon	1	ER	0.72
Rubra	6.37	6.01	1.06	6.01	31.7	4	0.93	9	79	spherical	1	ER	0.44
Rubra	4.21	3.19	1.32	3.19	12.8	4	0.6	8	120	ovoid	1	ER	0.62
Rubra	4.61	4.46	1.03	4.46	15.8	4	0.7	4	115	polygon	1	AN	0.50
Rubra	11.29	9.98	1.13	9.98	95.0	5	1.02	20	90	polygon	1	EL	0.98
Rubra	11.28	10.28	1.1	10.28	84.6	3	0.75	15	106	polygon	1	EL	0.96
Rubra	13.8	7.07	1.95	7.07	96.3	5	0.75	11	83	quadrangular	1	SA	0.46
Rubra	9.25	8.91	1.04	8.91	90.2	5	0.75	6	111	ovoid	1	ER	0.39
Rubra	8.3	7.49	1.11	7.49	58.6	3	0.65	17	99	spherical	1	EL	0.75
Rubra	11.23	8.04	1.4	8.04	80.0	3	0.72	9	110	prolate	1	ER	0.39

Rubra	3.49	2.39	1.46	2.39	6.2	3	0.6	6	100	polygon	1	ER	0.49
Rubra	5.75	4.55	1.26	4.55	21.5	4	0.65	11	74	polygon	1	EL	0.87
Rubra	12.09	9.11	1.33	9.11	91.6	2	0.65	19	100	ovoid	1	EL	0.94
Rubra	10.04	7.89	1.27	7.89	55.0	4	0.65	7	61	ovoid	1	AF	0.74
Rubra	11.51	9.43	1.22	9.43	90.7	3	0.9	9	119	prolate	1	EL	0.47
Rubra	12.37	11.13	1.11	11.13	124.4	3	1	13	98	ovoid	1	EL	0.96
Rubra	4.73	4.56	1.04	4.56	17.2	4	0.8	6	70	polygon	1	ER	0.49
Rubra	3.72	3.15	1.18	3.15	10.7	3	0.9	7	63	prolate	1	AN	0.71
Rubra	3.86	3.33	1.16	3.33	11.8	3	0.53	6	90	spherical	1	ER	0.62
Rubra	5.89	4.1	1.44	4.1	19.2	4	0.55	9	100	ovoid	1	ER	0.37
Rubra	5.65	4.73	1.19	4.73	26.0	4	0.97	7	100	polygon	1	ER	0.58
Rubra	3.55	2.79	1.27	2.79	8.2	3	0.4	4	85	ovoid	1	AN	0.50
Rubra	5.08	4.12	1.23	4.12	6.5	3	0.51	5	95	ovoid	1	AN	0.47
Noah	3.72	3.39	1.1	3.39	12.2	3	0.6	8	70	polygon	1	ER	0.42
Noah	11.17	9.66	1.16	9.66	83.6	3	0.87	11	97	ovoid	1	EL	0.94
Noah	8.3	7.06	1.18	7.06	50.4	3	0.88	3	99	polygon	1	AN	0.37
Noah	18.72	11.19	1.67	11.19	149.6	3	0.7	20	85	triangular	1	EL	0.67
Noah	7.95	7.11	1.12	7.11	41.5	3	0.8	5	107	spherical	1	ER	0.67
Noah	8.04	8.01	1	8.01	53.8	2	0.92	12	92	spherical	1	ER	0.37
Noah	6.48	5.96	1.09	5.96	28.5	5	1.03	6	0.6	polygon	1	AF	0.79
Noah	14.38	9.27	1.55	9.27	124.1	3	0	0	0	polygon	1	SA	0.92
Noah	2.85	2.8	1.02	2.8	8.6	3	0.43	3	116	polygon	1	AN	0.57
Noah	6.14	5.63	1.09	5.63	32.0	3	0.78	7	101	ovoid	1	ER	0.79
Noah	7.58	7.48	1.01	7.48	36.1	3	0.75	6	89	ovoid	1	ER	0.63
Noah	3.8	3.75	1.01	3.75	12.1	4	0.69	6	111	polygon	1	ER	0.73
Noah	3.01	2.66	1.13	2.66	5.1	3	0.4	5	107	polygon	1	AN	0.37
Noah	12.02	11.19	1.07	11.19	114.4	4	1	16	95	spherical	1	EL	0.95
Noah	9.32	8.7	1.07	8.7	66.7	4	0.9	12	96	spherical	1	EL	0.55
Noah	4.73	4.43	1.07	4.43	15.1	3	0.62	6	80	spherical	1	ER	0.50
Noah	6.32	4.32	1.46	4.32	21.2	4	1	5	74	polygon	1	AN	0.49
Noah	5.39	4.2	1.28	4.2	17.5	4	0.55	5	100	spherical	1	AN	0.55
Noah	7.64	7.52	1.02	7.52	45.0	3	0.7	13	92	spherical	1	ER	0.59
Noah	7.17	6.74	1.06	6.74	46.7	4	0.88	11	56	spherical	1	ER	0.47
Noah	7.37	7.21	1.02	7.21	45.8	4	1	10	106	spherical	1	ER	0.66
Noah	5.12	4.4	1.16	4.4	17.8	9	0.84	11	100	polygon	1	EL	0.86
Noah	7.49	6.83	1.1	6.83	47.9	3	0.78	6	89	polygon	1	ER	0.55
Noah	4.93	4.06	1.21	4.06	18.1	3	0.74	8	99	ovoid	1	ER	0.86
Noah	6.32	6.09	1.04	6.09	31.7	3	0.5	8	102	spherical	1	AF	0.64
Noah	4.74	4.37	1.08	4.37	21.3	4	0.52	4	98	polygon	1	AN	0.77
Noah	7.29	4.45	1.64	4.45	31.7	5	0.94	9	92	polygon	1	ER	0.40
hector	6.32	6.04	1.05	6.04	30.5	4	0.83	7	80	polygon	1	ER	0.60
hector	7.17	4.82	1.49	4.82	30.3	4	0.7	9	101	ovoid	1	ER	0.46
hector	6.59	4.76	1.38	4.76	25.8	4	0.8	7	115	ovoid	1	ER	0.79
hector	5.95	3.79	1.57	3.79	18.5	3	0.72	5	97	prolate	1	ER	0.65

hector	11.66	10.63	1.1	10.63	110.0	4	0.97	6	95	spherical	1	EL	0.44
hector	19.32	15.84	1.22	15.84	281.6	1	2.4	15	77.5	prolate	1	EL	0.78
hector	8.24	8.12	1.01	8.12	53.4	2	0.7	12	90	spherical	1	EL	0.41
hector	5.92	5.91	1	5.91	27.9	3	0.72	9	98	spherical	1	ER	0.49
hector	7.65	4.95	1.55	4.95	32.6	4	0.72	4	70	prolate	1	AN	0.42
hector	6.03	3.98	1.52	3.98	27.3	4	0.94	4	77	polygon	1	AN	0.47
hector	4.02	3.5	1.15	3.5	11.4	4	0.83	4	80	polygon	1	ER	0.52
hector	20.32	14.28	1.42	14.28	228.7	3	0.9	30	78	prolate	1	EL	0.81
hector	7.97	7.03	1.13	7.03	43.6	3	1	7	87	ovoid	1	AN	0.52
hector	5.14	4.15	1.24	4.15	16.6	4	0.52	4	100	ovoid	1	AN	0.85
hector	12.98	10.1	1.29	10.1	119.1	4	1.3	8	80.41	ovoid	1	EL	0.47
hector	16.7	13.62	1.23	13.62	198.1	3	1.14	17	71	ovoid	1	EL	0.74
hector	12.6	11.75	1.07	11.75	114.4	3	1	4	120	spherical	1	AN	0.31
hector	12	9.68	1.24	9.68	107.0	4	1	5	100	spherical	1	EL	0.37
hector	19.7	16.43	1.2	16.43	254.7	3	1.44	9	102	ovoid	1	EL	0.47
hector	8.15	7.37	1.11	7.37	53.5	4	1.13	4	84	polygon	1	AN	0.55
hector	12.76	10.63	1.2	10.63	102.6	4	0.87	9	100	spherical	1	EL	0.53
castor	4.52	3.91	1.16	3.91	14.3	3	0.5	5	104	polygon	1	AN	0.51
castor	13.34	11.74	1.14	11.74	112.8	3	0.9	15	116	spherical	1	EL	0.86
castor	6.02	5.47	1.1	5.47	30.0	2	0.65	8	108	spherical	1	ER	0.86
castor	5.63	5.12	1.1	5.12	24.6	2	0.55	7	101	spherical	1	ER	0.80
castor	6.56	5.05	1.3	5.05	31.2	4	0.83	8	59.11	polygon	1	AF	0.86
castor	5.2	4.5	1.16	4.5	20.4	3	0.42	7	108	ovoid	1	ER	0.50
castor	7.31	5.54	1.32	5.54	30.4	4	0.75	11	84.33	polygon	1	EL	0.96
castor	3.77	2.69	1.4	2.69	8.6	3	0.51	3	85	ovoid	1	AN	0.48
castor	6.04	4.3	1.4	4.3	20.7	3	0.4	5	116	prolate	1	AF	0.41
castor	5.95	5.54	1.07	5.54	24.8	2	0.4	7	123	spherical	1	AF	0.39
castor	9.94	6.86	1.45	6.86	48.0	4	0.55	11	90	ovoid	1	EL	0.94
castor	4.53	4.13	1.1	4.13	15.2	4	0.61	6	68	polygon	1	AN	0.39
castor	5.47	5.45	1	5.45	23.0	3	0.46	8	100	spherical	1	AN	0.46
castor	10.56	9.02	1.17	9.02	88.1	4	1.25	6	88.06	spherical	1	AN	0.60
castor	8.29	5.73	1.45	5.73	45.9	5	0.82	5	103	polygon	1	AN	0.35
castor	9.1	6.45	1.41	6.45	47.2	3	1	7	109	polygon	1	ER	0.38
castor	7	6.67	1.05	6.67	32.4	3	0.72	14	68	spherical	1	EL	0.50
castor	6.45	5.6	1.15	5.6	30.0	3	1	8	92.67	spherical	1	ER	0.51
castor	4.54	3.53	1.29	3.53	14.2	3	0.72	3	94	polygon	1	ER	0.58
castor	7.53	5.8	1.3	5.8	28.1	5	0.88	4	77	polygon	1	AN	0.39
castor	2.46	2.35	1.05	2.35	4.7	2	0.42	4	82	polygon	1	ER	0.41
castor	3.58	3.39	1.06	3.39	8.3	4	0.83	2	41	spherical	1	AN	0.79
castor	4.22	3.74	1.13	3.74	14.4	3	0.72	6	71	spherical	1	ER	0.40
castor	5.59	5.45	1.03	5.45	25.6	4	0.6	5	91.25	spherical	1	ER	0.54
castor	13.71	11.85	1.16	11.85	126.0	4	1.25	4	99	spherical	1	SA	0.45
castor	4.74	4.32	1.1	4.32	18.1	2	0.74	8	94.06	spherical	1	ER	0.97
castor	8.76	6.82	1.28	6.82	51.7	3	0.61	17	117.95	ovoid	1	EL	0.96

castor	7.54	5.44	1.39	5.44	34.5	3	0.69	6	100	prolate	1	ER	0.50
castor	4.53	3.12	1.45	3.12	13.9	3	0.65	5	78	polygon	2	AN	0.47
castor	6.25	5.96	1.05	5.96	26.5	3	0.72	9	102.89	triangular	2	ER	0.85
castor	6.18	5.34	1.16	5.34	25.9	3	0.46	8	97.41	prolate	1	AF	0.51
castor	6.86	6.25	1.1	6.25	36.7	3	0.88	6	75	ovoid	1	ER	0.46
castor	6.15	4.72	1.3	4.72	23.0	2	0.72	1	65.35	spherical	1	AF	0.73
castor	10.68	8.65	1.23	8.65	65.1	3	0.83	17	88.44	prolate	1	EL	0.99
castor	6.64	4.63	1.43	4.63	26.2	3	0.6	9	90	ovoid	1	ER	0.45
castor	5.22	5	1.04	5	18.8	2	0.75	5	126	spherical	1	ER	0.69
castor	7.18	5.68	1.26	5.68	34.1	4	0.92	7	92	ovoid	1	ER	0.63
castor	5.2	4.72	1.1	4.72	19.9	3	0	0	0	spherical	1	AF	0.90
castor	4.49	3.77	1.19	3.77	12.9	3	0.83	8	89.85	spherical	1	ER	0.91
castor	5.22	5.12	1.02	5.12	21.4	4	0.75	7	85	polygon	1	ER	0.75
castor	7.81	6.09	1.28	6.09	27.7	5	0.83	8	129	polygon	1	ER	0.66
castor	4.06	3.74	1.09	3.74	12.8	4	0.58	5	89	polygon	1	ER	0.53
castor	6.97	5.79	1.2	5.79	33.7	4	0.52	7	88	spherical	1	AF	0.67
castor	5.79	4.71	1.23	4.71	23.1	3	0.61	8	65	spherical	1	AF	0.77
castor	8.93	8.56	1.04	8.56	61.6	3	0.72	9	62	ovoid	1	AF	0.49
castor	4.72	4.24	1.11	4.24	15.9	4	0.97	5	81	polygon	1	AN	0.46
castor	12.18	11.27	1.08	11.27	101.5	3	0.87	5	128.5	ovoid	1	EL	0.38
castor	13.93	11.06	1.26	11.06	128.6	3	1.37	13	55.37	ovoid	1	SA	0.39
castor	5.31	4.96	1.07	4.96	24.1	4	1.01	7	91.91	spherical	1	ER	0.57
castor	4.66	3.99	1.17	3.99	13.9	2	0.52	4	1	prolate	1	AN	0.81
castor	14.06	11.57	1.22	11.57	123.8	2	1.19	14	105	spherical	1	EL	0.78
castor	13.94	11.69	1.19	11.69	119.8	2	0.94	20	75	ovoid	1	EL	0.76
castor	7.29	7.01	1.04	7.01	38.9	3	0.69	7	88	spherical	1	ER	0.66
castor	5.47	4.37	1.25	4.37	17.0	4	0.62	9	84.58	polygon	1	ER	0.62
castor	5.07	4.52	1.12	4.52	18.2	2	0.61	6	85	spherical	1	ER	0.83
castor	5.03	3.54	1.42	3.54	17.9	3	0.75	4	82.1	prolate	1	AN	0.61
castor	10.59	6.86	1.54	6.86	51.3	2	0.83	8	72.34	ovoid	1	ER	0.38
castor	4.1	3.08	1.33	3.08	10.8	3	0.72	6	70	ovoid	1	ER	0.40
castor	5.53	4.82	1.15	4.82	19.3	2	0.61	6	64.66	prolate	1	AF	0.42
castor	9.54	8.72	1.09	8.72	65.2	3	0.94	11	91	prolate	1	EL	0.92
castor	7.05	6.01	1.17	6.01	38.3	3	0.7	9	75	spherical	1	AF	0.50
castor	7.84	5.19	1.51	5.19	34.7	3	0.8	8	96	ovoid	1	ER	0.45
castor	5.33	5.23	1.02	5.23	24.5	4	0.51	7	104	ovoid	1	ER	0.47
castor	4.2	3.9	1.08	3.9	13.9	4	0.52	6	95.19	spherical	1	ER	0.59
castor	9.03	8.81	1.02	8.81	67.7	3	0.83	16	104	spherical	1	EL	0.75
castor	3.9	3.5	1.11	3.5	12.3	3	0.7	7	87	polygon	1	ER	0.87
castor	5.86	4.24	1.38	4.24	19.4	5	0.82	7	90	polygon	1	ER	0.83
castor	6.23	6.06	1.03	6.06	33.8	3	0.72	6	92	ovoid	1	ER	0.75
castor	5.43	4.51	1.2	4.51	19.0	3	0.69	5	95	spherical	1	ER	0.86
bijou	11.52	9.87	1.17	9.87	98.7	3	0.78	13	119.07	prolate	1	EL	0.93
bijou	11.91	9.09	1.31	9.09	80.9	4	0.7	8	130	quadrangular	1	EL	0.48

bijou	6.82	6.29	1.08	6.29	34.0	2	0.65	8	96.97	spherical	1	ER	0.87
bijou	8.27	8.23	1	8.23	138.3	5	0.52	7	138.28	polygon	1	AF	0.39
bijou	15.35	9.54	1.61	9.54	125.5	3	0.8	6	125.54	prolate	1	EL	0.40
bijou	9.83	9.73	1.01	9.73	80.8	2	0.65	8	125.06	spherical	1	ER	0.37
bijou	13.78	10.79	1.28	10.79	107.8	3	1.14	15	93.49	spherical	1	EL	0.75
bijou	5.14	4.35	1.18	4.35	19.0	4	0.6	6	123	polygon	1	ER	0.66
bijou	6.02	4.69	1.28	4.69	21.8	3	0.5	4	111.1	polygon	1	AN	0.56
bijou	18.14	13.74	1.32	13.74	225.6	4	1.65	26	97.83	prolate	1	EL	0.79
bijou	10.62	7.8	1.36	7.8	60.0	4	0.93	9	135	polygon	1	EL	0.46
bijou	6.33	5.14	1.23	5.14	36.5	3	0.83	10	104	polygon	1	ER	0.82
bijou	8.81	7.78	1.13	7.78	49.9	3	0.7	9	112.01	spherical	1	ER	0.45
bijou	5.02	4.66	1.08	4.66	21.8	4	0.82	6	98.98	spherical	1	ER	0.90
bijou	6.87	6.66	1.03	6.66	36.7	4	1.03	9	92.28	polygon	1	ER	0.73
bijou	10.58	8.9	1.19	8.9	75.1	3	0.83	12	135.35	spherical	1	EL	0.54
bijou	7.97	6.74	1.18	6.74	43.7	2	0.52	7	107.33	spherical	1	ER	0.43
bijou	19.89	15.17	1.31	15.17	245.6	2	1.33	28	116.95	ovoid	1	EL	0.81
bijou	7.96	5.61	1.42	5.61	41.5	5	1.38	6	94.45	polygon	1	AN	0.50
bijou	8.33	7.18	1.16	7.18	43.9	4	0.9	5	109.88	polygon	1	ER	0.48
bijou	9.55	7.4	1.29	7.4	55.4	4	0.66	6	119.19	ovoid	1	ER	0.39
bijou	6.86	6.07	1.13	6.07	39.1	3	0.6	8	114.04	polygon	1	ER	0.52
bijou	5.91	5.37	1.1	5.37	26.5	5	0.66	7	105.53	spherical	1	ER	0.77
bijou	12.59	11.48	1.1	11.48	108.4	3	1.2	7	107.62	spherical	1	EL	0.42
bijou	9.42	8.42	1.12	8.42	81.4	5	1.47	17	88.21	prolate	1	EL	0.93
bijou	10.09	9.14	1.1	9.14	67.8	3	1.13	11	67.75	prolate	1	EL	0.79
bijou	10.05	9.96	1.01	9.96	85.4	3	0.69	10	84.61	spherical	1	ER	0.39
bijou	10.83	8.3	1.3	8.3	72.4	3	0.6	14	115.75	ovoid	1	EL	0.96
bijou	11.22	10.87	1.03	10.87	100.8	2	0.84	14	123.01	prolate	2	EL	0.84
bijou	19.87	13.21	1.5	13.21	209.9	5	0.97	5	131.4	ovoid	2	SA	0.40
bijou	12.3	9.82	1.25	9.82	96.5	4	0.93	11	108.2	polygon	1	EL	0.91
bijou	11.48	10.24	1.12	10.24	97.3	3	1.01	15	119	ovoid	1	EL	0.96
bijou	7.82	7.2	1.09	7.2	112.3	3	0.55	10	112	spherical	1	ER	0.33
bijou	8.7	7.58	1.15	7.58	49.5	3	0.41	2	134	spherical	1	AF	0.35
bijou	10.92	8.22	1.33	8.22	72.6	4	1.1	8	92.45	prolate	1	AN	0.38
bijou	12.89	11.02	1.17	11.02	119.7	4	1.17	11	122	spherical	1	EL	0.68
bijou	16.28	10.44	1.56	10.44	137.3	3	1.35	6	96.39	ovoid	1	EL	0.38
bijou	10.85	8.37	1.3	8.37	71.2	4	0.92	4	103.66	polygon	1	AN	0.37
bijou	9.11	8.91	1.02	8.91	64.4	2	1.1	12	96.04	spherical	1	EL	0.40
bijou	14.53	14.45	1.01	14.45	172.5	3	1.25	17	114.06	spherical	1	EL	0.86
bijou	9.85	7.73	1.27	7.73	68.6	3	1.23	13	95.02	prolate	1	EL	0.98
bijou	7.69	7.2	1.07	7.2	47.0	4	0.83	14	118.89	polygon	1	EL	0.89
bijou	11.44	9.36	1.22	9.36	81.0	4	0.87	10	114	prolate	1	EL	0.52
bijou	22.53	21.32	1.06	21.32	364.3	2	1.45	15	106.07	ovoid	1	EL	0.84
bijou	7.37	6.46	1.14	6.46	133.6	2	0.43	3	133.55	spherical	1	AN	0.43
bijou	10.69	10.03	1.07	10.03	90.9	3	0.5	16	119.15	spherical	1	EL	0.83

bijou	11.42	9.63	1.19	9.63	90.3	4	0.8	6	106	spherical	1	EL	0.46
bijou	8.65	7.37	1.17	7.37	51.5	3	0.92	9	92	spherical	1	ER	0.44
bijou	9.83	9.74	1.01	9.74	74.0	3	0.8	8	95.94	spherical	1	ER	0.44
bijou	11.45	11.13	1.03	11.13	93.3	4	0.72	10	78.76	ovoid	1	EL	0.47
bijou	19.32	17.24	1.12	17.24	256.9	2	0.93	15	116.31	prolate	1	EL	0.80
bijou	11.42	9.29	1.23	9.29	84.1	2	0.4	13	88	ovoid	1	EL	0.90
bijou	6.32	5.93	1.07	5.93	29.7	4	0.78	9	110	polygon	1	ER	0.74
bijou	13.4	11.6	1.16	11.6	136.7	5	1.33	12	104.18	polygon	1	EL	0.80
bijou	14.18	11.63	1.22	11.63	152.9	3	0.9	8	116	polygon	1	EL	0.51
bijou	7.56	6.82	1.11	6.82	43.3	2	0.4	18	82	prolate	1	EL	0.89
bijou	10.31	7.27	1.42	7.27	51.2	2	1.1	8	110	ovoid	1	AN	0.48
bijou	14.13	13.53	1.04	13.53	155.1	5	1.3	15	108.1	polygon	1	EL	0.80
bijou	11.37	10.21	1.11	10.21	89.4	2	0.95	17	83	spherical	1	EL	0.92
bijou	10.79	9.75	1.11	9.75	83.0	3	0.94	9	94	polygon	1	EL	0.51
bijou	7.93	6.62	1.2	6.62	41.9	3	0.97	6	110	polygon	1	ER	0.53
bijou	10.72	9.79	1.09	9.79	78.4	2	0.88	3	66	ovoid	1	AF	0.57
bijou	10.21	9.18	1.11	9.18	73.6	2	0.75	10	90	spherical	1	ER	0.46
Goma	7.82	6.04	1.29	6.04	37.9	2	0	0	0	spherical	1	AF	0.99
Goma	6.77	6.24	1.08	6.24	33.2	2	0.51	10	100	spherical	1	ER	0.59
Goma	11.87	6.68	1.78	6.68	54.7	0	0	0	0	spherical	1	SA	0.74
Goma	20.04	18.05	1.11	18.05	303.1	2	1.42	19	91	spherical	1	EL	0.85
Goma	11.59	8.57	1.35	8.57	75.2	3	1.2	13	103	ovoid	1	EL	0.95
Goma	6.65	5.86	1.13	5.86	30.8	5	0	0	0	quadrangular	1	AF	0.98
Goma	8.44	6.95	1.21	6.95	49.3	4	1.01	14	95.03	ovoid	1	EL	1
Goma	5.43	4.51	1.2	4.51	19.0	4	0	0	0	polygon	1	AN	0.51
Goma	23.45	21.32	1.1	21.32	398.3	3	1.43	20	111	spherical	1	EL	0.82
Goma	10.35	8.7	1.19	8.7	66.2	3	1.74	7	66.17	spherical	1	EL	0.40
Goma	17.63	14.66	1.2	14.66	220.2	2	1.62	22	124.85	spherical	1	EL	0.84
Goma	17.3	13.53	1.28	13.53	215.0	3	1.44	16	101.93	prolate	1	EL	0.81
Goma	15.01	13.01	1.15	13.01	143.6	1	1.04	8	123.41	spherical	1	EL	0.49
Goma	8.7	7.92	1.1	7.92	57.5	3	1.17	10	57.51	spherical	1	AF	0.44
Goma	6.58	4.82	1.37	4.82	25.0	4	0.7	7	24.95	prolate	1	AF	0.77
Goma	6.38	5.8	1.1	5.8	38.2	3	0	0	38.2	quadrangular	1	AF	0.98
Goma	19.45	15.59	1.25	15.59	243.7	4	1.33	16	243.69	spherical	1	EL	0.81
Goma	6.72	5.87	1.14	5.87	36.0	2	0.7	6	36.02	spherical	1	AF	0.94
Goma	17.93	12.92	1.39	12.92	191.2	2	1.27	11	80.54	ovoid	1	EL	0.67
Goma	16.05	13.33	1.2	13.33	167.2	4	1.1	8	94	ovoid	1	EL	0.47
Goma	10.73	9.49	1.13	9.49	76.3	5	0.75	8	117.27	spherical	1	ER	0.38
Goma	11.77	8.81	1.34	8.81	88.9	5	0.7	5	11.97	polygon	1	AF	0.54
Goma	15.02	12.36	1.22	12.36	155.1	3	1.3	13	100.25	prolate	1	EL	0.75
Goma	20.3	18.26	1.11	18.26	303.7	3	1.69	24	89.34	spherical	1	EL	0.81
Goma	15	11.29	1.33	11.29	133.1	2	1.14	11	91.53	prolate	1	EL	0.68
Goma	17.58	16.61	1.06	16.61	118.6	4	1.23	11	118.55	spherical	1	EL	0.64
Goma	11.38	8.86	1.28	8.86	88.9	3	1.11	5	105	spherical	1	AN	0.42

Goma	9.9	8.76	1.13	8.76	68.6	4	0.88	18	110	ovoid	1	EL	0.98
Goma	10.08	8.46	1.19	8.46	56.6	4	1.02	15	118.21	prolate	2	EL	0.98
Goma	10.26	6.6	1.55	6.6	66.8	4	1.02	15	103	spherical	2	EL	0.72
Goma	19.89	16.12	1.23	16.12	270.4	4	1.96	18	92.42	polygon	1	EL	0.80
Goma	10.4	8.47	1.23	8.47	77.0	2	0.93	19	84.4	ovoid	1	EL	0.99
Goma	19.39	14.23	1.36	14.23	220.1	4	1.33	24	112.26	ovoid	1	EL	0.78
Goma	19.03	18.8	1.01	18.8	167.1	3	1.74	13	267.06	spherical	1	EL	0.78
Goma	22.73	20.08	1.13	20.08	360.2	3	1.33	11	118.62	spherical	1	EL	0.59
Goma	15.72	14.09	1.12	14.09	177.5	4	1.43	8	177.49	spherical	1	EL	0.47
Goma	17.72	15.08	1.18	15.08	198.7	4	0.94	13	110.35	spherical	1	EL	0.73
Goma	7.47	6.86	1.09	6.86	43.5	4	0.6	15	113.87	spherical	1	EL	0.53
Goma	13.92	13.01	1.07	13.01	159.4	3	1.33	11	120.31	spherical	1	EL	0.62
Goma	14.35	13.62	1.05	14.35	164.4	4	1.33	12	109	spherical	1	EL	0.65
Goma	9.23	8.5	1.09	8.5	65.7	2	0.6	9	106	spherical	1	ER	0.44
Goma	7.3	6.04	1.21	6.04	34.5	5	0.55	7	102	ovoid	1	AF	0.58
Goma	8.33	6.87	1.21	6.87	50.3	4	0.74	13	106.54	spherical	1	EL	0.48
Goma	10.11	7.91	1.28	7.91	69.5	3	0.52	4	114.23	ovoid	1	AN	0.39
Goma	9.85	8.27	1.19	8.27	65.9	4	1.01	9	105.36	polygon	1	EL	0.43
Goma	21.3	16.08	1.32	16.08	263.6	5	1.07	22	110.99	polygon	1	EL	0.79
Goma	9.41	7.37	1.28	7.37	60.6	5	0	0	0	polygon	1	AF	0.99
Goma	16.73	13.74	1.22	13.74	186.0	3	0.75	4	99	ovoid	1	SA	0.40
Goma	18.85	13.74	1.37	13.74	190.9	5	1.07	17	99	ovoid	1	EL	0.78
Goma	18.98	9.32	2.04	9.32	144.8	5	0	0	0	angular point	1	SA	1
Goma	14.96	14.44	1.04	14.44	172.8	1	1.13	18	91	spherical	1	EL	0.88
Goma	16.21	13.09	1.24	13.09	165.4	4	1.25	16	101	ovoid	1	EL	0.77
Goma	11.53	9.88	1.17	9.88	82.8	3	0.88	5	113	spherical	1	EL	0.38
Goma	10.38	9.82	1.06	9.82	82.5	5	0.92	7	106	polygon	1	EL	0.43
Goma	10.71	10.59	1.01	10.59	100.2	3	0.97	8	99.67	spherical	1	ER	0.43
Goma	12.15	10.2	1.19	10.2	93.2	3	1.03	4	104.17	ovoid	1	EL	0.32
Goma	9.06	8.11	1.12	8.11	58.8	3	0.88	10	103.67	ovoid	1	ER	0.44
Goma	11.26	8.65	1.3	8.65	79.3	4	1.31	10	103.89	spherical	1	AN	0.45
Goma	13.34	13.19	1.01	13.19	144.8	2	1.11	8	92.68	spherical	1	EL	0.47
Goma	8.13	7.68	1.06	7.68	49.8	3	0	0	0	polygon	1	AF	0.90
Goma	18.91	16.33	1.16	16.33	265.9	2	0.9	17	99	ovoid	1	EL	0.82
Goma	9.55	8.57	1.11	8.57	71.1	4	1.38	3	75	ovoid	1	AN	0.59
Goma	8.87	6.77	1.31	6.77	47.4	5	0	0	0	ovoid	1	AF	1
Goma	8.66	7.28	1.19	7.28	54.3	4	0.6	5	100	spherical	1	EL	0.31
Goma	7.24	6.23	1.16	6.23	35.4	3	0.5	4	87.1	spherical	1	AF	0.51
Goma	10.4	7.27	1.43	7.27	64.5	3	1	5	104	prolate	1	AN	0.42
Zerlina	7.95	7.14	1.11	7.14	38.2	3	0.75	8	111	spherical	1	ER	0.74
Zerlina	12.24	12.04	1.02	12.04	124.2	3	0.84	6	98	spherical	1	EL	0.48
Zerlina	8.98	8.26	1.09	8.26	69.8	4	1.02	9	89	polygon	1	EL	0.43
Zerlina	6.31	5.74	1.1	5.74	27.7	4	1.23	8	90	spherical	1	AN	0.65
Zerlina	3.99	3.58	1.11	3.58	12.1	4	0.8	5	92	spherical	1	ER	0.88

Zerlina	6.69	5.07	1.32	5.07	34.8	3	0.97	9	78	ovoid	1	AN	0.59
Zerlina	20.79	16.53	1.26	16.53	267.0	4	1.23	15	118.71	prolate	1	EL	0.76
Zerlina	4.11	3.69	1.11	3.69	12.0	3	0.6	7	83	spherical	1	ER	0.50
Zerlina	22.42	21.32	1.05	21.32	386.9	3	1.75	17	93	spherical	1	EL	0.89
Zerlina	16.93	15.06	1.12	15.06	243.0	3	0.83	18	101	spherical	1	EL	0.81
Zerlina	12.88	9.43	1.37	9.43	100.0	3	0.97	8	116	prolate	1	EL	0.44
Zerlina	12.72	11.34	1.12	11.34	98.5	3	0.94	12	98	prolate	1	EL	0.95
Zerlina	8.64	6.55	1.32	6.55	37.9	4	1.23	6	86	polygon	1	AN	0.63
Zerlina	14.65	13.51	1.08	13.51	175.5	4	1.17	14	82	spherical	1	EL	0.81
Zerlina	7.23	6.99	1.03	6.99	42.1	4	1.11	7	88	spherical	1	AN	0.53
Zerlina	15.67	15.08	1.04	15.08	196.2	4	0.97	14	114	spherical	1	EL	0.82
Zerlina	17.38	14.84	1.17	14.84	200.9	3	1.25	19	106	spherical	1	EL	0.82
Zerlina	3.88	3.42	1.13	3.42	12.0	3	0.72	3	91	polygon	1	ER	0.72
Zerlina	10.79	8.97	1.2	8.97	78.9	3	1.11	14	116	prolate	1	EL	0.98
Zerlina	12.26	11.27	1.09	11.27	118.3	2	0.84	16	109	spherical	1	EL	0.95
Zerlina	9.43	8.1	1.16	8.1	61.7	4	0.97	11	103	ovoid	1	EL	0.93
Zerlina	8.12	5.83	1.39	5.83	37.3	3	0.51	7	120	prolate	1	AF	0.45
Zerlina	6.56	5.84	1.12	5.84	32.9	3	0.55	10	99	spherical	1	AF	0.39
Zerlina	15.96	12.03	1.33	12.03	167.6	3	1.37	17	97	ovoid	1	EL	0.77
Zerlina	17.85	17.92	1	17.92	257.0	3	1.5	17	84	ovoid	1	EL	0.83
Zerlina	6.9	5.71	1.21	5.71	32.3	3	0.83	6	98	spherical	1	ER	0.63
Zerlina	10.88	10.17	1.07	10.17	85.0	4	0.92	8	88	polygon	1	EL	0.49
Zerlina	9.69	6.64	1.46	6.64	112.4	4	1.31	10	112	ovoid	1	AN	0.54
Zerlina	11.53	9.26	1.25	9.26	91.0	4	0.8	8	121	ovoid	1	EL	0.48
Zerlina	6.38	4.43	1.44	4.43	26.0	4	0.62	9	100	polygon	1	ER	0.53
Zerlina	9.82	7	1.4	7	58.0	4	1.11	7	79	polygon	1	AN	0.53
Zerlina	5.49	4.32	1.27	4.32	20.3	4	0.78	5	93	polygon	1	ER	0.82
Zerlina	9.52	8.4	1.13	8.4	54.7	4	0.7	11	89	ovoid	1	EL	0.96
Zerlina	4.3	4.32	1	4.32	13.8	4	0.52	6	115	polygon	1	AN	0.59
Zerlina	12.24	11.42	1.07	11.42	110.6	2	1.17	11	89	prolate	1	EL	0.90
Zerlina	9.52	5.95	1.6	5.95	45.9	4	0.72	9	99.74	ovoid	1	EL	0.43
Zerlina	7.9	6.03	1.31	6.03	40.5	4	0.8	5	93.7	ovoid	1	ER	0.64
Zerlina	4.93	3.98	1.24	3.98	15.6	3	0.5	4	90	polygon	1	AN	0.86
Zerlina	17.35	12.7	1.37	12.7	167.6	3	1.17	18	93	prolate	1	EL	0.80
Zerlina	9.81	7.9	1.24	7.9	57.1	3	1.07	17	95	ovoid	1	EL	1
Zerlina	10.51	9.36	1.12	9.36	65.6	3	1.23	7	107	spherical	1	AN	0.45
Zerlina	15.19	13.32	1.14	13.32	159.0	3	1.28	14	104	spherical	1	EL	0.76
Zerlina	9.83	7.39	1.33	7.39	56.2	4	1.44	2	86	spherical	1	AN	0.67
Zerlina	6.71	5.91	1.14	5.91	32.5	4	0.83	11	88	polygon	1	EL	0.91
Zerlina	4.92	4.69	1.05	4.69	20.0	3	0.83	6	81	spherical	1	ER	0.53
Zerlina	11.8	10.66	1.11	10.66	101.4	3	0.97	12	102	spherical	1	EL	0.68
Zerlina	6.36	4.1	1.55	4.1	24.9	3	0.61	5	107	ovoid	1	ER	0.52
Zerlina	9.21	8.92	1.03	8.92	71.6	2	0.92	13	95.76	spherical	1	EL	0.52
Zerlina	9.71	8.03	1.21	8.03	75.8	3	1.17	11	81	prolate	1	EL	0.91

Zerlina	7.42	5.5	1.35	5.5	34.5	3	0.75	10	75	prolate	1	ER	0.42
Zerlina	12.39	11.18	1.11	11.18	112.9	2	0.83	19	110	spherical	1	EL	0.94
Zerlina	11.95	7.82	1.53	7.82	76.6	3	1.09	14	108	ovoid	1	EL	0.94
Zerlina	8.39	8.33	1.01	8.33	60.9	4	1.1	6	115	polygon	1	EL	0.47
Zerlina	13.4	12.85	1.04	12.85	139.6	3	1.13	17	103	prolate concave-convex	1	EL	0.89
Zerlina	13.58	12.68	1.07	12.68	130.8	3	1.11	15	105	spherical	1	EL	0.82
Zerlina	15.75	15.57	1.01	15.57	178.5	3	1.02	20	115	ovoid	1	EL	0.82
Zerlina	16.36	12.5	1.31	12.5	163.0	3	1.7	13	86	ovoid	1	EL	0.73
Zerlina	8.81	7.71	1.14	7.71	63.3	4	0.97	8	87	polygon	1	EL	0.43
Zerlina	10.72	10.61	1.01	10.61	93.8	3	1.09	18	94	spherical	1	EL	0.76
Zerlina	11.15	10.58	1.05	10.58	104.7	3	1.14	16	96	spherical	1	EL	0.85
Zerlina	7.03	6.38	1.1	6.38	36.1	4	0.88	7	87	prolate	1	ER	0.72
Zerlina	11.13	9.49	1.17	9.49	86.9	4	0.88	17	90.79	ovoid	1	EL	0.98
Zerlina	7.17	6.86	1.05	6.86	44.2	4	0.84	9	111	spherical	1	ER	0.72
Zerlina	9.52	8.6	1.11	8.6	69.8	3	0.94	10	76	spherical	1	ER	0.37
Zerlina	16.37	11.61	1.41	11.61	146.2	3	1.23	19	101	ovoid	1	EL	0.77
Zerlina	15.09	12.89	1.17	12.89	145.6	4	1.3	11	106	ovoid	1	EL	0.63
Zerlina	9.34	7.45	1.25	7.45	55.1	5	1.33	7	97	polygon	1	EL	0.42
Zerlina	11.98	9.72	1.23	9.72	108.2	4	1.01	9	119	ovoid	1	EL	0.46
Zerlina	11.37	9.22	1.23	9.22	90.2	3	1.23	13	107	spherical	1	EL	0.69
Zerlina	21.3	18.12	1.18	18.12	311.0	2	1.17	18	101	ovoid	1	EL	0.82
Zerlina	7.9	5.51	1.43	5.51	37.3	2	0.75	12	89	ovoid	1	EL	0.95
Zerlina	12.02	7.25	1.66	7.25	61.7	3	0.83	7	106	ovoid	1	EL	0.47
Zerlina	17.2	15.46	1.11	15.46	219.0	3	1.36	18	106	spherical	1	EL	0.82
Zerlina	17.47	13.35	1.31	13.35	165.4	3	1.37	17	92	ovoid	1	EL	0.79
Zerlina	5.73	5.43	1.06	5.43	26.0	3	0.6	4	75	prolate concave-convex	1	AN	0.43
Zerlina	3.79	3.58	1.06	3.58	11.0	3	0.42	3	108	polygon	1	AN	0.69
Dorry	6.41	4.61	1.39	4.61	21.0	2	0.69	13	74	prolate	1	EL	0.95
Dorry	7.77	5.72	1.36	5.72	40.2	3	0.9	13	77	prolate	1	EL	0.96
Dorry	7.69	7.07	1.09	7.07	43.8	4	0.55	15	97	spherical	1	EL	0.54
Dorry	7.17	6.76	1.06	6.76	36.7	3	1.09	11	89	spherical	1	ER	0.51
Dorry	6.04	5.77	1.05	5.77	25.7	3	0.65	8	93	spherical	1	ER	0.77
Dorry	7.03	5.29	1.33	5.29	31.6	4	0.72	7	94	ovoid	1	ER	0.71
Dorry	10.49	9.32	1.13	9.32	67.0	3	0.83	12	108	spherical	1	EL	0.55
Dorry	5.98	5.74	1.04	5.74	33.6	3	0.65	15	82	prolate	1	EL	0.74
Dorry	5.66	5	1.13	5	26.5	2	0.83	8	92	spherical	1	ER	0.95
Dorry	6.99	5.55	1.26	5.55	31.0	3	0.83	8	105	spherical	1	ER	0.70
Dorry	9.88	8.26	1.2	8.26	69.4	4	1.1	13	97	ovoid	1	EL	0.98
Dorry	8.73	8.13	1.07	8.13	56.6	4	0.88	12	105	spherical	1	EL	0.54
Dorry	6.17	4.95	1.25	4.95	22.4	3	0.74	7	90	prolate	1	ER	0.98
Dorry	10.09	8.34	1.21	8.34	68.0	4	0.78	16	90	spherical	1	EL	0.87
Dorry	9.67	7.47	1.29	7.47	62.1	4	1.35	14	76	spherical	1	EL	0.80
Dorry	9.96	9.27	1.07	9.27	71.0	3	0.8	10	111	spherical	1	ER	0.46

Dorry	8.91	6.15	1.45	6.15	43.6	4	0.88	9	89	ovoid	1	ER	0.39
Dorry	7.52	5.14	1.46	5.14	31.7	5	0.52	6	107	prolate	1	AF	0.45
Dorry	5.41	4.73	1.14	4.73	21.9	2	0.87	8	85	spherical	1	ER	0.78
Dorry	7.78	5.8	1.34	5.8	45.5	5	1.13	9	76	ovoid	1	AN	0.84
Dorry	10.78	7.32	1.47	7.32	55.0	3	0.62	15	98	ovoid	1	EL	0.98
Dorry	10.03	9.63	1.04	9.63	75.0	3	0.9	13	79	spherical	1	EL	0.60
Dorry	5.62	3.71	1.51	3.71	21.9	3	0.6	7	100	prolate	1	ER	0.51
Dorry	5.53	5.43	1.02	5.43	22.3	3	0.83	9	62	spherical	1	AF	0.54
Dorry	12	10.81	1.11	10.81	124.9	3	0.94	15	91	spherical	1	EL	0.94
Dorry	5.33	4.4	1.21	4.4	20.3	4	0.74	7	89	prolate	1	ER	0.93
Dorry	10.86	8.18	1.33	8.18	65.9	4	1.14	9	96	ovoid	1	AN	0.40
Dorry	4.87	4.36	1.12	4.36	21.5	3	0.83	6	83	spherical	1	ER	0.57
Dorry	4.92	3.92	1.26	3.92	16.6	4	0.51	7	95	ovoid	1	ER	0.49
Dorry	9.5	8.36	1.14	8.36	55.7	4	0.61	9	118	ovoid	1	EL	0.46
Dorry	6.29	3.52	1.79	3.52	22.3	5	1.19	9	89	prolate	1	AN	0.55
Dorry	5.77	4.54	1.27	4.54	24.1	3	0.74	6	82	spherical	1	ER	0.53
Dorry	24.69	21.2	1.16	21.2	353.3	1	2.7	19	79	spherical	1	EL	0.82
Dorry	10.65	9.65	1.1	9.65	86.3	3	0.82	11	106	spherical	1	EL	0.51
Dorry	10.31	8.01	1.29	8.01	61.6	3	0.87	16	86	ovoid	1	EL	1
Dorry	6.14	5.45	1.13	5.45	26.2	4	0.92	9	94	spherical	1	ER	0.84
Dorry	5.43	5.22	1.04	5.22	34.4	3	0.84	10	91	spherical	1	ER	0.79
Dorry	6.45	5.63	1.15	5.63	31.8	3	0.66	10	95	spherical	1	ER	0.76
Dorry	9.85	6.85	1.44	6.85	46.0	5	1.1	8	94	triangular	1	AN	0.56
Dorry	10.85	10.44	1.04	10.44	87.9	3	0.93	9	100	spherical	1	ER	0.45
Dorry	7.78	6.27	1.24	6.27	38.8	3	0.8	7	89	spherical	1	ER	0.70
Dorry	11.64	10.42	1.12	10.42	105.9	4	1.14	13	113	spherical	1	EL	0.77
Dorry	10.36	8.8	1.18	8.8	74.0	3	0.78	12	111	prolate	1	EL	0.95
Dorry	4.83	4.37	1.11	4.37	16.3	3	0.65	5	100	spherical	1	ER	0.80
Dorry	8.3	5.63	1.47	5.63	34.8	4	0.82	8	88	ovoid	1	ER	0.36
Dorry	7.83	6.25	1.25	6.25	39.2	4	0.72	10	93	ovoid	1	ER	0.71
Dorry	3.53	2.42	1.46	2.42	7.8	3	0.52	5	93	prolate	1	ER	0.37
Dorry	4.61	4.61	1	4.61	13.5	5	0.51	8	75	spherical	1	AN	0.43
Dorry	3.67	3.02	1.22	3.02	12.2	4	0.55	6	111	spherical	1	ER	0.54
Dorry	5.94	4.49	1.32	4.49	25.9	3	0.75	11	102	spherical	1	ER	0.59
Dorry	10.15	7.19	1.41	7.19	65.1	3	0.74	13	89	prolate	1	EL	0.99
Dorry	7.07	5.73	1.23	5.73	28.1	2	0.75	14	90	prolate	1	EL	0.98
Dorry	6.86	5.86	1.17	5.86	31.2	5	0.94	12	87	ovoid	1	EL	0.92
Dorry	7.69	6.17	1.25	6.17	42.8	3	0.78	12	102	prolate	1	EL	0.92
Dorry	5.46	4.29	1.27	4.29	20.3	4	0.61	7	106	ovoid	1	ER	0.71
Dorry	5.42	4.92	1.1	4.92	22.5	3	0.82	3	105	spherical	1	ER	0.68
Dorry	15.05	14.44	1.04	14.44	175.6	2	0.78	12	105	spherical	1	EL	0.66
Dorry	6.74	5.99	1.13	5.99	29.4	3	0.88	7	90	spherical	1	ER	0.70
Dorry	4.41	3.71	1.19	3.71	14.1	3	0.51	8	85	spherical	1	ER	0.55
Dorry	7.16	6.04	1.19	6.04	50.1	3	0.66	10	107	spherical	1	ER	0.64

Dorry	7.07	6.56	1.08	6.56	42.3	2	0.93	11	81	spherical	1	ER	0.55
Dorry	5.33	4.81	1.11	4.81	19.0	3	0.84	9	93.33	spherical	1	ER	0.85
Dorry	7.66	5.68	1.35	5.68	36.6	3	1.05	11	83	spherical	1	ER	0.45
Dorry	7.28	5.53	1.32	5.53	30.4	3	0.97	14	103	prolate	1	EL	0.97
Dorry	5.94	5.33	1.11	5.33	29.7	3	0.87	11	108	spherical	1	ER	0.59
Dorry	7.17	4.98	1.44	4.98	33.9	2	0.72	11	87	prolate	1	EL	0.94
Dorry	9.17	8.91	1.03	8.91	67.1	2	0.87	13	120	spherical	1	EL	0.52
Dorry	10.46	10.03	1.04	10.03	77.9	4	0.97	19	99	spherical	1	EL	0.78
Dorry	6.79	5.4	1.26	5.4	27.1	3	0.65	13	91	ovoid	1	EL	0.96
Dorry	18.76	14.9	1.26	14.9	236.0	1	1.88	32	60	ovoid	1	EL	0.50
Dorry	19.78	17.67	1.12	17.67	271.0	3	1.48	11	99	spherical	1	EL	0.59
Dorry	5.63	5.33	1.06	5.33	22.6	3	0.61	7	97	spherical	1	ER	0.71
Dorry	6.81	5.58	1.22	5.58	28.3	3	0.51	9	106	prolate	1	AF	0.44
Dorry	7.37	5.73	1.29	5.73	34.9	4	0.88	16	97	spherical	1	EL	0.59
Dorry	11.81	10.41	1.13	10.41	100.0	5	1.13	7	90	spherical	1	EL	0.42
Dorry	5.26	4.1	1.28	4.1	20.0	3	0.75	6	91	polygon	1	ER	0.88
Dorry	6.37	5.07	1.26	5.07	27.8	5	0.72	12	95	polygon	1	EL	0.93
Dorry	5.09	4.67	1.09	4.67	19.6	3	0.62	7	80	ovoid	1	ER	0.55
Dorry	5.61	5.29	1.06	5.29	21.7	3	0.61	5	98	polygon	1	ER	0.68
Dorry	8.5	8	1.06	8	54.1	2	1.01	11	83	spherical	1	EL	0.48
Dorry	7.48	7.18	1.04	7.18	35.6	3	0.93	7	95	spherical	1	ER	0.66
Dorry	8.16	6.47	1.26	6.47	38.8	2	1.25	9	100	spherical	1	AN	0.61
Dorry	6.12	4.6	1.33	4.6	25.8	3	1	9	70	prolate	1	AN	0.62
Dorry	3.7	2.97	1.25	2.97	7.0	3	0.61	4	91	spherical	1	ER	0.65
Dorry	8.55	8.13	1.05	8.13	59.4	3	0.8	13	92	ovoid	1	EL	0.92
Dorry	5.37	3.3	1.63	3.3	13.1	5	0.72	7	90	polygon	1	ER	0.61
Venus	5.07	4.49	1.13	4.49	17.2	3	0.55	6	99	spherical	1	ER	0.57
Venus	7.42	2.73	2.72	2.73	19.0	5	0	0	0	angular point	1	EL	0.43
Venus	5.23	4.3	1.22	4.3	19.2	3	0.61	9	70	spherical	1	ER	0.33
Venus	4.56	3.33	1.37	3.33	11.7	3	0.75	7	70	spherical	1	ER	0.36
Venus	6.16	4.25	1.45	4.25	22.4	3	0.8	7	88	spherical	1	ER	0.61
Venus	5.07	3.79	1.34	3.79	16.4	3	0.6	7	84	prolate	1	ER	0.55
Venus	5.77	4.22	1.37	4.22	19.5	4	0.83	6	101	spherical	1	ER	0.84
Venus	8.32	7.31	1.14	7.31	50.9	3	0.75	10	100	spherical	1	ER	0.43
Venus	6.54	4.74	1.38	4.74	26.5	5	0.88	6	94	prolate	1	ER	0.77
Venus	6.83	4.5	1.52	4.5	34.1	4	0.63	8	85	prolate	1	ER	0.32
Venus	4.3	3.28	1.31	3.28	12.9	4	0.51	5	100	polygon	1	AN	0.49
Venus	5.54	4.81	1.15	4.81	18.3	3	0.78	8	85	spherical	1	ER	0.74
Venus	7.07	5.63	1.26	5.63	34.5	3	1	7	88	spherical	1	AN	0.64
Venus	3.72	3.66	1.02	3.66	10.5	4	0.72	5	85	polygon	1	ER	0.73
Venus	6.59	4.99	1.32	4.99	25.0	3	0.72	8	88	polygon	1	ER	0.85
Venus	7.08	5.12	1.38	5.12	28.4	4	0.62	5	98	polygon	1	ER	0.47
Venus	7.16	5.45	1.31	5.45	36.1	3	0.69	10	78	prolate	1	ER	0.42
Venus	2.82	2.53	1.11	2.82	5.9	4	0.75	4	101	polygon	1	ER	0.68

Venus	5.45	4.95	1.1	5.45	27.1	4	0.8	9	89	ovoid	1	ER	0.81
Venus	5.33	3.49	1.53	3.49	14.2	5	0.75	7	95	ovoid	1	ER	0.61
Venus	12.7	7.89	1.61	7.89	72.0	2	0.8	12	107	ovoid	1	EL	0.87
Venus	6.14	4.64	1.32	4.64	30.6	5	1.24	5	78.06	polygon	1	AN	0.65
Venus	9.24	7.7	1.2	7.7	55.6	4	0.87	8	55.6	spherical	1	AF	0.85
Venus	9.27	8.47	1.09	8.47	67.0	5	1.64	4	68	polygon	1	EL	0.43
Venus	5.36	4.13	1.3	4.13	18.4	3	0.7	7	87	spherical	1	ER	0.80
Venus	4.71	3.69	1.28	3.69	12.0	4	0.6	5	79	polygon	1	ER	0.45
Venus	7.58	5.53	1.37	5.53	31.5	3	0.4	8	110	ovoid	1	AF	0.59
Venus	8.31	3.18	2.61	3.18	8.3	4	0.75	4	75	polygon	1	EL	0.56
Venus	4.6	4	1.15	4	16.1	2	0.6	7	100	prolate	1	ER	0.87
Venus	7.62	5.73	1.33	5.73	34.3	3	0.69	6	80	ovoid	1	ER	0.38
Venus	10.35	7.95	1.30	7.95	63.9	4	0.87	9	99	spherical	1	ER	0.44
Venus	4.8	4.56	1.05	4.56	17.9	4	0.62	5	77	polygon	1	ER	0.48
Venus	5.9	3.41	1.73	3.41	16.5	5	0.62	8	82	polygon	1	EL	0.46
Venus	5.14	4.22	1.22	4.22	15.7	3	0.72	7	97	ovoid	1	ER	0.83
Venus	6.53	4.92	1.33	4.92	25.1	3	0.62	7	82.14	prolate	1	ER	0.53
Venus	12.32	10.32	1.19	10.32	97.7	3	1	9	91	ovoid	1	EL	0.46
Venus	4.51	4.1	1.1	4.1	16.6	4	0.58	5	95	polygon	1	ER	0.51
Venus	5.92	4.72	1.26	4.72	24.2	4	0.65	9	102	polygon	1	ER	0.84
Venus	7.8	5.74	1.36	5.74	31.7	5	1.44	4	61	polygon	1	AN	0.41
Venus	7.69	6.36	1.21	6.36	35.3	3	0.78	8	98	spherical	1	ER	0.75
Venus	5.8	5.08	1.141	5.08	25.3	3	0.66	8	92	spherical	1	ER	0.89
Venus	4.1	3.99	1.03	3.99	13.8	3	0.6	7	88	polygon	1	ER	0.70
Venus	4.51	4.4	1.03	4.4	13.5	3	0.61	7	91	polygon	1	ER	0.75
Venus	6.86	5.84	1.17	5.84	32.1	3	0.72	9	96	polygon	1	ER	0.75
Venus	3.1	2.78	1.12	2.78	9.0	4	0.74	5	80	polygon	1	ER	0.60
Venus	4.34	3.72	1.17	3.72	14.2	4	0.84	7	89	polygon	1	ER	0.90
Venus	6.15	5.84	1.05	5.84	30.8	5	0.97	7	88	polygon	1	ER	0.50
fanny	5.24	4.12	1.27	4.12	15.3	3	0.82	11	95	spherical	1	ER	0.58
fanny	7.11	6.6	1.08	6.6	39.2	3	0.7	9	119	spherical	1	ER	0.72
fanny	9.56	8	1.2	8	66.3	3	1.15	10	65	spherical	1	EL	0.32
fanny	8.61	6.65	1.29	6.65	41.9	4	0.85	15	98	spherical	1	EL	0.67
fanny	10.08	8.94	1.13	8.94	73.2	3	1	15	92	spherical	1	EL	0.86
fanny	6.97	6.45	1.08	6.45	38.7	3	0.72	8	80	spherical	1	ER	0.48
fanny	10.46	7.24	1.44	7.24	67.5	3	0.85	14	80	ovoid	1	EL	1
fanny	9.83	6.65	1.48	6.65	55.1	4	0.61	7	112	ovoid	1	EL	0.31
fanny	5.8	5.36	1.08	5.36	25.0	4	0.69	6	97	polygon	1	ER	0.80
fanny	5.8	4.95	1.17	4.95	27.0	4	1.17	4	113	polygon	1	AN	0.52
fanny	7.33	4.69	1.56	4.69	107.0	5	0.6	9	107	polygon	1	EL	0.38
fanny	8.5	6.55	1.3	6.55	41.2	4	1.33	1	55.58	polygon	1	AF	0.54
fanny	12.59	11.88	1.06	11.88	117.5	3	1.23	12	104.46	spherical	1	EL	0.66
fanny	12.51	8.94	1.4	8.94	97.0	4	0.92	19	88.6	spherical	1	EL	0.93
fanny	4.18	3.92	1.07	3.92	15.3	4	0.7	5	85	polygon	1	ER	0.70

fanny	7.07	5.54	1.28	5.54	30.2	4	1.1	6	105	ovoid	1	AN	0.56
fanny	10.96	9.91	1.11	9.91	85.3	4	1.35	5	91.89	spherical	1	AN	0.47
fanny	9.77	8.43	1.16	8.43	61.6	3	0.74	8	94.15	spherical	1	ER	0.42
fanny	12.8	11.27	1.14	11.27	117.1	4	1.09	10	106	spherical	1	EL	0.48
fanny	8.5	7.25	1.17	7.25	59.9	4	0.94	15	73	spherical	1	EL	0.79
fanny	10.85	9.12	1.19	9.12	80.3	3	0.69	8	84	spherical	1	ER	0.33
fanny	11.7	9.09	1.29	9.09	90.3	4	0.94	9	96	polygon	1	EL	0.61
fanny	5.41	4.17	1.3	4.17	16.7	4	1.13	5	102	polygon	1	AN	0.44
fanny	8.49	6.85	1.24	6.85	49.0	3	0.88	8	88.08	polygon	1	EL	0.44
fanny	8.52	8.5	1	8.5	68.6	2	0.83	17	94.22	spherical	1	EL	0.75
fanny	8.98	8.9	1.01	8.9	63.3	2	0.92	8	72.47	spherical	1	ER	0.56
fanny	9.1	8.92	1.02	8.92	61.7	3	0.84	13	119	spherical	1	EL	0.51
fanny	12.92	10.41	1.24	10.41	98.1	3	1.02	21	103.14	ovoid	1	EL	0.99
fanny	8.32	7.2	1.16	7.2	49.2	3	0.83	5	97.88	polygon	2	ER	0.43
fanny	9.34	8.91	1.05	8.91	59.5	4	1.02	8	100	spherical	2	ER	0.40
fanny	13.92	13.83	1.01	13.83	137.4	4	1.14	19	112.56	ovoid	1	EL	0.80
fanny	13.93	13.11	1.06	13.11	144.2	2	1.19	17	56	spherical	1	EL	0.50
fanny	7.75	6.87	1.13	6.87	39.3	3	0.75	16	91.79	spherical	1	EL	0.55
fanny	10.9	8.08	1.35	8.08	67.4	3	0.88	8	101	spherical	1	ER	0.40
fanny	9.69	8.32	1.16	8.32	58.8	3	0.82	9	92	prolate	1	ER	0.50
fanny	14.74	13.03	1.13	13.03	85.6	4	0.92	6	85	spherical	1	EL	0.43
fanny	8.96	8.22	1.09	8.22	67.9	4	0.52	8	137	polygon	1	AF	0.39
fanny	17.98	15.2	1.18	15.2	234.6	3	1	14	97.16	spherical	1	EL	0.77
fanny	10.07	9.01	1.12	9.01	72.9	3	0.72	5	88.97	spherical	1	ER	0.41
fanny	13.4	9.02	1.49	9.02	96.4	4	0.66	8	116	ovoid	1	EL	0.41
fanny	9.69	8.74	1.11	8.74	72.8	3	0.78	13	111	spherical	1	EL	0.63
fanny	10.72	10.53	1.02	10.53	98.2	3	1.16	11	99	spherical	1	EL	0.43
fanny	5.4	4.72	1.14	4.72	19.6	3	0.6	6	83	spherical	1	ER	0.46
fanny	13.12	12.84	1.02	12.84	142.0	3	1.16	11	89.24	spherical	1	EL	0.58
fanny	4.95	4.27	1.16	4.27	17.3	3	0.7	4	17.3	spherical	1	AN	0.71
fanny	5.32	4.6	1.16	4.6	72.3	3	0.5	6	101	polygon	1	ER	0.39
fanny	6.38	3.33	1.92	3.33	17.9	3	0.42	7	102	ovoid	1	EL	0.35
fanny	10.4	9.45	1.1	9.45	73.0	4	0.72	13	92	ovoid	1	EL	0.96
fanny	10.89	9.04	1.2	9.04	77.2	3	0.6	11	81	ovoid	1	EL	0.92
fanny	4.67	3.76	1.24	3.76	11.8	3	0.47	8	96	spherical	1	ER	0.54
fanny	9.93	9.01	1.1	9.01	71.6	3	0.78	14	94	ovoid	1	EL	0.99
fanny	12.1	10.49	1.15	10.49	103.3	4	0.88	17	90.25	prolate	1	EL	0.99
fanny	9.04	8.85	1.02	8.85	59.4	2	0.84	8	97	spherical	1	ER	0.53
fanny	6.15	4.53	1.36	4.53	19.3	3	0.66	3	82	polygon	1	ER	0.39
fanny	10.21	9.21	1.11	9.21	76.4	2	0.74	18	110	spherical	1	EL	0.84
fanny	5.98	5.08	1.18	5.08	27.9	4	1	2	74	polygon	1	AN	0.44
fanny	11.06	10.44	1.06	10.44	90.5	3	0.82	10	117	spherical	1	ER	0.46
fanny	11.17	8.4	1.33	8.4	75.8	3	0.8	17	66	ovoid	1	EL	0.64
fanny	15.56	14.57	1.07	14.57	170.4	2	1.25	15	81.61	spherical	1	EL	0.85

fanny	7.62	6.31	1.21	6.31	40.4	3	0.72	12	89.9	prolate	1	EL	0.92
fanny	6.8	6.22	1.09	6.22	34.3	4	0.88	10	95.29	spherical	1	ER	0.82
fanny	8.77	7.89	1.11	7.89	55.2	3	0.87	9	99	spherical	1	ER	0.46
fanny	3.6	3.38	1.07	3.38	9.2	3	0.84	6	100	polygon	1	ER	0.86
fanny	5.22	4.92	1.06	4.92	19.5	3	0.7	5	93	spherical	1	ER	0.83
fanny	2.93	2.33	1.26	2.33	5.3	3	0.55	3	92	polygon	1	AN	0.45
fanny	4.31	3.89	1.11	3.89	12.0	3	0.55	3	99	spherical	1	AN	0.68
fanny	15	12.55	1.2	12.55	128.2	3	1.01	19	87	ovoid	1	EL	0.78
fanny	8.47	6.86	1.23	6.86	40.7	3	0.72	8	118	prolate	1	ER	0.58
fanny	6.88	4.59	1.5	4.59	33.4	4	0.97	6	105.71	polygon	1	ER	0.47
fanny	15.07	10.98	1.37	10.98	129.3	3	0.94	12	104.33	ovoid	1	EL	0.65
fanny	7.01	5.77	1.21	5.77	31.3	4	0.78	4	93	polygon	1	ER	0.48
fanny	15.18	14.77	1.03	14.77	186.3	3	1.14	7	97	spherical	1	EL	0.55
fanny	6.46	5.43	1.19	5.43	30.0	3	0.88	6	100	spherical	1	ER	0.68
fanny	9.06	8.09	1.12	8.09	61.4	3	0.88	8	82.57	spherical	1	ER	0.36
fanny	8.71	8.4	1.04	8.4	52.1	4	0.94	7	52.14	polygon	1	AF	0.61
fanny	6.25	4.52	1.38	4.52	22.7	3	0.8	9	94	ovoid	1	ER	0.86
fanny	10.71	6.96	1.54	6.96	66.6	3	1.1	12	95	prolate	1	EL	0.97
fanny	8.19	7.79	1.05	7.79	48.8	4	0.8	6	96	polygon	1	ER	0.50
fanny	8.48	8.41	1.01	8.41	57.6	3	0.93	7	86.42	spherical	1	ER	0.39
fanny	11.04	10.44	1.06	10.44	92.9	3	0.84	6	92.86	spherical	1	ER	0.44
fanny	18.84	16.9	1.11	16.9	261.6	4	1.05	7	124	spherical	1	EL	0.47
fanny	13.57	12.85	1.06	12.85	121.1	3	1	10	93.74	spherical	1	EL	0.56
fanny	13.26	12.89	1.03	12.89	149.9	3	1.6	12	92	polygon	1	EL	0.75
fanny	17.8	14.9	1.19	14.9	223.3	3	1.33	14	95	ovoid	1	EL	0.76
fanny	14.64	14.54	1.01	14.54	160.8	3	0.8	16	77	spherical	1	EL	0.83
fanny	6.1	6.05	1.01	6.05	31.4	4	0.65	6	114	spherical	1	ER	0.56
fanny	9.56	8.63	1.11	8.63	72.9	4	0.78	10	85.67	polygon	1	EL	0.50
fanny	8.5	8.09	1.05	8.09	52.3	4	1.1	7	101	polygon	1	EL	0.43
fanny	12.77	12.25	1.04	12.25	136.1	3	0.93	20	100	spherical	1	EL	0.86
fanny	12.69	12.09	1.05	12.09	120.8	3	0.94	12	98	spherical	1	EL	0.65
fanny	9.85	9.52	1.03	9.52	78.8	3	0.85	12	91	spherical	1	EL	0.46
fanny	10.32	9.45	1.09	9.45	67.7	5	0.75	11	112	polygon	1	EL	0.92
fanny	13.47	11.01	1.22	11.01	115.1	3	0.83	13	100	ovoid	1	EL	0.85
fanny	16.29	14.48	1.13	14.48	191.3	3	1	11	95	ovoid	1	EL	0.67
fanny	11.11	9.11	1.22	9.11	86.5	3	0.8	11	90	ovoid	1	EL	0.94
fanny	6.86	4.24	1.62	4.24	25.8	4	0.9	6	81	ovoid	1	AN	0.36
fanny	12.91	11.99	1.08	11.99	133.4	3	1.1	9	109	spherical	1	EL	0.44
fanny	5.4	4.2	1.29	4.2	16.2	4	0.72	5	76.85	spherical	1	ER	0.39
fanny	7.38	4.92	1.5	4.92	31.2	4	1	5	79	polygon	1	AN	0.45
fanny	4.06	3.98	1.02	3.98	15.0	4	0.72	5	65	spherical	1	AN	0.59
fanny	7.61	6.91	1.1	6.91	42.4	4	0.93	7	75	polygon	1	ER	0.52
fanny	6.45	5.25	1.23	5.25	31.2	4	0.92	9	108	ovoid	1	ER	0.72
fanny	10.3	9.39	1.1	9.39	79.1	3	0.92	12	93	ovoid	1	EL	0.95

fanny	5.02	4.41	1.14	4.41	17.7	3	1.05	4	71	spherical	1	AN	0.83
fanny	13.64	10.14	1.35	10.14	99.9	2	0.93	12	89	spherical	1	EL	0.59
fanny	9.36	8.61	1.09	8.61	63.7	3	0.51	9	120	ovoid	1	AF	0.38
fanny	5.61	4.54	1.24	4.54	16.2	4	0.8	6	102	polygon	1	ER	0.89
fanny	17.26	12.84	1.34	12.84	178.8	5	1.43	14	102	polygon	1	EL	0.74
fanny	17.55	13.1	1.34	13.1	190.7	3	1.3	12	100	prolate	1	EL	0.68
fanny	8.89	7.48	1.19	7.48	49.1	2	0.7	9	108	prolate	1	ER	0.54
fanny	3.38	3.28	1.03	3.28	11.7	3	0.46	6	75	polygon	1	ER	0.40
fanny	9.68	8.18	1.18	8.18	61.7	3	0.88	8	77	spherical	1	ER	0.34
fanny	13.95	12.1	1.15	12.1	126.8	3	0.87	17	95	ovoid	1	EL	0.77
fanny	11.27	10.36	1.09	10.36	93.0	2	0.87	9	112	spherical	1	ER	0.53
fanny	8.25	8.1	1.02	8.1	52.1	3	0.51	14	109	spherical	1	EL	0.71
fanny	5.04	4.3	1.17	4.3	15.7	3	0.62	4	113	spherical	1	ER	0.56
fanny	9.41	8.16	1.15	8.16	79.4	3	0.94	15	115	ovoid	1	EL	0.98
fanny	9.12	8.4	1.09	8.4	63.8	3	0.7	11	120	spherical	1	EL	0.53
fanny	9.22	7.47	1.23	7.47	59.0	4	1	8	92	spherical	1	AN	0.36
fanny	6.93	4.78	1.45	4.78	27.6	4	0.66	7	96	prolate	1	ER	0.51
fanny	9.22	7.88	1.17	7.88	57.8	4	0.58	9	103	ovoid	1	EL	0.41
fanny	15.86	15.72	1.01	15.72	215.0	4	1.17	24	90	ovoid	1	EL	0.82
fanny	8.55	6.95	1.23	6.95	52.7	4	0.8	10	83	prolate	1	ER	0.45
fanny	12.31	8.13	1.51	8.13	76.6	4	0.9	11	94	ovoid	1	EL	0.92
Brutus	5.92	5.78	1.02	5.78	33.0	3	0.66	6	91	polygon	1	ER	0.69
Brutus	5.08	4.81	1.06	4.81	19.2	3	0.69	9	90	spherical	1	ER	0.81
Brutus	6.46	5.36	1.21	5.36	31.1	4	0.75	10	85	polygon	1	ER	0.57
Brutus	6.86	5.23	1.31	5.23	26.0	4	0.72	5	118	ovoid	1	ER	0.68
Brutus	13.01	11.28	1.15	11.28	130.1	3	1.17	15	93	prolate	1	EL	0.99
Brutus	6.47	4.71	1.37	4.71	25.5	3	1.13	9	107	spherical	1	AN	0.58
Brutus	3.58	3.28	1.09	3.28	11.0	4	0.51	5	103	polygon	1	ER	0.48
Brutus	11.9	11.67	1.02	11.67	11.5	3	1.17	16	85	spherical	1	EL	0.81
Brutus	14.02	10.79	1.3	10.79	123.0	4	1.03	12	123	prolate	1	EL	0.65
Brutus	7.17	6.55	1.09	6.55	36.3	4	0.74	8	105	polygon	1	ER	0.79
Brutus	5.95	4.52	1.32	4.52	21.1	4	0.93	5	100	polygon	1	ER	0.74
Brutus	10.67	9.88	1.08	9.88	96.1	3	0.94	14	94	prolate	1	EL	0.98
Brutus	6.69	6.15	1.09	6.15	32.7	2	0.84	13	70	spherical	1	ER	0.51
Brutus	5.97	5.13	1.16	5.13	22.2	3	0.78	12	70	spherical	1	ER	0.54
Brutus	18.45	16.46	1.12	16.46	240.0	4	1.16	15	92	ovoid	1	EL	0.75
Brutus	11.22	9.11	1.23	9.11	81.2	4	0.75	15	111	prolate	1	EL	0.97
Brutus	24.76	17.74	1.4	17.74	341.7	3	1.7	19	102	ovoid	1	EL	0.78
Brutus	13.63	13.38	1.02	13.38	153.4	3	0.93	16	105	spherical	1	EL	0.84
Brutus	17.54	11.72	1.5	11.72	180.6	5	1.1	11	111	ovoid	1	EL	0.62
Brutus	13.98	11.82	1.18	11.82	140.7	3	0.94	10	90	spherical	1	EL	0.50
Brutus	18.93	13.04	1.45	13.04	205.1	3	1	19	86	prolate	1	EL	0.80
Brutus	7.18	6.16	1.17	6.16	40.0	3	0.8	10	89	spherical	1	ER	0.80
Brutus	9.45	6.78	1.39	6.78	48.8	4	0.8	11	88	prolate	1	EL	0.96

Brutus	18.62	14.62	1.27	14.62	208.0	3	1.05	14	105	ovoid	1	EL	0.75
Brutus	13.64	13.12	1.04	13.12	133.4	2	1.03	13	92	spherical	1	EL	0.82
Brutus	4.75	4.06	1.17	4.06	16.5	4	0.6	6	95	polygon	1	ER	0.71
Brutus	10.54	9.48	1.11	9.48	85.6	3	0.97	7	101	spherical	1	AN	0.35
Brutus	6.13	4.94	1.24	4.94	28.3	3	0.65	10	88	polygon	1	ER	0.67
Brutus	13.43	11.47	1.17	11.47	120.4	3	0.92	13	110	spherical	1	EL	0.75
Brutus	18.23	15.67	1.16	15.67	230.7	4	1.4	14	105	spherical	1	EL	0.76
Brutus	6.32	4.66	1.36	4.66	21.3	3	0.65	7	100	ovoid	1	ER	0.85
Brutus	13.26	9.86	1.34	9.86	113.3	4	1.14	10	113	prolate	1	EL	0.50
Brutus	12.95	9.75	1.33	9.75	86.2	3	1.17	10	91	spherical	1	EL	0.42
Brutus	7.85	7.81	1.01	7.81	42.3	5	0.66	8	113	ovoid	1	ER	0.55
Brutus	9.5	7.12	1.33	7.12	51.0	4	0.72	8	100	prolate	1	ER	0.45
Brutus	21	18	1.17	18	309.0	3	1.23	18	120	spherical	1	EL	0.82
Brutus	5.79	5.36	1.08	5.36	23.7	4	0.78	7	90	polygon	1	ER	0.84
Brutus	19.59	11.59	1.69	11.59	119.8	3	0.84	19	90	spherical	1	EL	0.70
Brutus	19	18.03	1.05	18.03	283.0	3	1.09	13	94	spherical	1	EL	0.81
Brutus	13.5	8.52	1.58	8.52	90.6	3	0.94	9	77.25	ovoid	1	EL	0.42
Brutus	5.94	5.43	1.09	5.43	23.3	3	0.72	6	86	polygon	1	ER	0.84
Brutus	6.35	3.38	1.88	3.38	16.8	4	0.72	7	89	quadrangular	1	ER	0.45
Brutus	5.57	5.37	1.04	5.37	26.6	3	0.78	7	86	polygon	1	ER	0.77
Brutus	11.9	10.66	1.12	10.66	105.0	4	0.9	13	100	ovoid	1	EL	0.97
Brutus	5.96	5.41	1.1	5.41	28.8	3	0.66	12	102	spherical	1	ER	0.60
Brutus	17.82	13.64	1.31	13.64	193.3	3	1.2	16	93	ovoid	1	EL	0.79
Brutus	9.43	7.62	1.24	7.62	56.0	3	0.77	11	97	prolate	1	EL	0.95
Brutus	7.75	5.69	1.36	5.69	33.2	4	0.92	9	99	polygon	1	ER	0.55
Brutus	5.04	4.45	1.13	4.45	18.9	4	0.6	7	78	polygon	1	ER	0.53
Brutus	9.45	7.25	1.3	7.25	47.0	3	0.78	12	88	ovoid	1	EL	0.98
Brutus	10.44	6.43	1.62	6.43	45.8	5	0.78	6	100	ovoid	1	ER	0.35
Brutus	6.7	4.8	1.4	4.8	25.2	3	0.65	8	101	prolate	1	ER	0.62
Brutus	12.08	7.07	1.71	7.07	68.8	3	1.2	7	57	prolate concave-convex	1	SA	0.39
Brutus	8.45	6.91	1.22	6.91	43.1	4	0.5	10	93.6	triangular	1	AF	0.36
Brutus	13.57	9.16	1.48	9.16	101.6	4	1.03	9	111	elongate	1	EL	0.43
Brutus	25.24	11.43	2.21	11.43	139.4	3	1.37	8	119	prolate	1	SA	0.46
Brutus	6.16	4.05	1.52	4.05	20.7	3	1	7	73.26	prolate	1	AN	0.58
Brutus	6.5	5.32	1.22	5.32	28.0	3	0.69	8	94	spherical	1	ER	0.84
Brutus	5.87	5.69	1.03	5.69	27.2	3	0.65	5	96	spherical	1	ER	0.66
Brutus	4.56	3.19	1.43	3.19	14.1	4	0.61	6	78	polygon	1	AN	0.42
Brutus	6.78	5.45	1.24	5.45	29.9	5	1.03	5	82	polygon	1	AN	0.45
Brutus	5.39	3.67	1.47	3.67	17.2	4	0.94	6	89	polygon	1	ER	0.48
Brutus	6.19	5.18	1.19	5.18	27.7	4	0.8	7	78	polygon	1	ER	0.62
Brutus	7.06	5.85	1.21	5.85	35.6	3	0.8	12	93	prolate	1	EL	0.93
Brutus	5.43	4.31	1.26	4.31	18.1	4	0.85	9	94	prolate	1	ER	0.86
Brutus	9.11	7.83	1.16	7.83	57.1	2	0.93	13	94	spherical	1	EL	0.58
Brutus	10.28	9.56	1.08	9.56	74.7	4	1.13	17	113	ovoid	1	EL	0.97

Brutus	10.78	9.75	1.11	9.75	90.0	3	0.92	11	97	spherical	1	EL	0.53
Brutus	10.86	9.85	1.1	9.85	84.5	4	0.84	14	108	ovoid	1	EL	0.97
Brutus	15.01	14.76	1.02	14.76	185.8	3	0.97	15	107	spherical	1	EL	0.81
Brutus	8.3	6.09	1.36	6.09	90.8	4	1.01	9	90	polygon	1	EL	0.39
Brutus	14.17	14.01	1.01	14.01	150.5	4	1.01	13	85.85	spherical	1	EL	0.76
Brutus	16.81	14.98	1.12	14.98	194.0	3	0.88	14	101.75	spherical	1	EL	0.77
Brutus	16.35	15.4	1.06	15.4	202.0	2	1.4	13	110	spherical	1	EL	0.85
Brutus	8.15	7.3	1.12	7.3	43.0	3	0.66	10	99	spherical	1	ER	0.65
Brutus	5.82	5.69	1.02	5.69	31.4	3	0.64	7	97	polygon	1	ER	0.53
Brutus	14.8	14.2	1.04	14.2	165.7	3	1.19	10	115.7	spherical	1	EL	0.54
Brutus	6.33	5.71	1.11	5.71	25.7	3	0.6	9	110	spherical	1	ER	0.57
Brutus	5.68	4.95	1.15	4.95	26.5	4	0.74	6	92.7	polygon	1	ER	0.90
Brutus	6.95	5.95	1.17	5.95	34.6	3	0.66	10	100	polygon	1	ER	0.79
Brutus	8.66	8.32	1.04	8.32	56.0	3	0.83	10	102	polygon	1	ER	0.48
Brutus	17.72	13.52	1.31	13.52	159.0	3	1.02	15	120	ovoid	1	EL	0.74
Brutus	8.37	6.22	1.35	6.22	34.2	4	0.55	8	120	ovoid	1	AF	0.38
Brutus	10.27	6.71	1.53	6.71	60.1	4	0.94	9	97	prolate concave-convex	1	EL	0.42
Brutus	11.95	8.36	1.43	8.36	82.0	3	1.14	12	85	ovoid	1	EL	0.92
Brutus	11.43	10.58	1.08	10.58	103.7	3	1.03	15	87	spherical	1	EL	0.95
Brutus	10.14	9.01	1.13	9.01	75.0	5	1.02	9	96.6	polygon	1	EL	0.44
Brutus	9.02	7.79	1.16	7.79	58.5	3	0.83	11	100	spherical	1	EL	0.50
Brutus	14.24	11.86	1.2	11.86	123.8	3	0.92	17	81	prolate	1	EL	0.80
Brutus	11.39	10.21	1.12	10.21	91.5	3	0.82	19	86	ovoid	1	EL	0.97
Brutus	14.57	14.01	1.04	14.01	169.3	3	1.14	15	116	spherical	1	EL	0.83
Brutus	12.44	9.75	1.28	9.75	99.7	3	1.13	10	97	ovoid	1	EL	0.49
Brutus	5.86	4.52	1.3	4.52	26.3	4	0.6	6	109.4	polygon	1	ER	0.59
hector	6.32	6.04	1.05	6.04	30.5	4	0.83	7	80	polygon	1	ER	0.60
hector	7.17	4.82	1.49	4.82	30.3	4	0.7	9	101	ovoid	1	ER	0.46
hector	6.59	4.76	1.38	4.76	25.8	4	0.8	7	115	ovoid	1	ER	0.79
hector	5.95	3.79	1.57	3.79	18.5	3	0.72	5	97	prolate	1	ER	0.65
hector	11.66	10.63	1.1	10.63	110.0	4	0.97	6	95	spherical	1	EL	0.44
hector	19.32	15.84	1.22	15.84	281.6	1	2.4	15	77.5	prolate	1	EL	0.78
hector	8.24	8.12	1.01	8.12	53.4	2	0.7	12	90	spherical	1	EL	0.41
hector	5.92	5.91	1	5.91	27.9	3	0.72	9	98	spherical	1	ER	0.49
hector	7.65	4.95	1.55	4.95	32.6	4	0.72	4	70	prolate	1	AN	0.42
hector	6.03	3.98	1.52	3.98	27.3	4	0.94	4	77	polygon	1	AN	0.47
hector	4.02	3.5	1.15	3.5	11.4	4	0.83	4	80	polygon	1	ER	0.52
hector	20.32	14.28	1.42	14.28	228.7	3	0.9	30	78	prolate	1	EL	0.81
hector	7.97	7.03	1.13	7.03	43.6	3	1	7	87	ovoid	1	AN	0.52
hector	5.14	4.15	1.24	4.15	16.6	4	0.52	4	100	ovoid	1	AN	0.85
hector	12.98	10.1	1.29	10.1	119.1	4	1.3	8	80.41	ovoid	1	EL	0.47
hector	16.7	13.62	1.23	13.62	198.1	3	1.14	17	71	ovoid	1	EL	0.74
hector	12.6	11.75	1.07	11.75	114.4	3	1	4	120	spherical	1	AN	0.31
hector	12	9.68	1.24	9.68	107.0	4	1	5	100	spherical	1	EL	0.37

hector	19.7	16.43	1.2	16.43	254.7	3	1.44	9	102	ovoid	1	EL	0.47
hector	8.15	7.37	1.11	7.37	53.5	4	1.13	4	84	polygon	1	AN	0.55
hector	12.76	10.63	1.2	10.63	102.6	4	0.87	9	100	spherical	1	EL	0.53
kendo	6.31	4.69	1.35	4.69	23.0	5	0.72	5	88	polygon	1	ER	0.82
kendo	6.45	5.43	1.19	5.43	29.5	3	0.94	7	82.55	spherical	1	AF	0.36
kendo	7.72	5.05	1.53	5.05	42.5	2	1.17	11	96.81	prolate	1	EL	0.90
kendo	15.35	13.95	1.1	13.95	191.8	4	1.49	5	84.4	polygon	1	SA	0.45
kendo	4.37	4.04	1.08	4.04	16.4	5	0.5	5	88	polygon	1	AN	0.48
kendo	7.59	6.16	1.23	6.16	34.0	3	0.72	13	83.68	spherical	1	ER	0.55
kendo	3.88	3.2	1.21	3.2	9.4	3	0.81	6	92.55	polygon	1	ER	0.91
kendo	16.78	14.13	1.19	14.13	175.7	3	1.03	12	107	ovoid	1	EL	0.68
kendo	4.2	4.04	1.04	4.04	23.6	4	0.98	6	0.81	polygon	1	AN	0.50
kendo	11.01	10.42	1.06	10.42	98.0	3	0.9	14	94	spherical	1	EL	0.85
kendo	6.67	6.31	1.06	6.31	39.4	4	0.74	9	94	polygon	1	ER	0.81
kendo	5.7	5.02	1.14	5.02	26.0	3	0.9	7	98	spherical	1	ER	0.73
kendo	14.84	13.38	1.11	13.38	161.6	3	1.03	8	111	spherical	1	EL	0.48
kendo	7.1	6.77	1.05	6.77	41.4	4	1.17	8	97	polygon	1	ER	0.39
kendo	5.18	4.68	1.11	4.68	23.7	3	0.98	4	102	polygon	1	AN	0.51
kendo	7.85	7.1	1.11	7.1	42.4	3	0.81	8	91	polygon	1	ER	0.72
Ondine	4.85	4.5	1.08	4.5	16.4	2	0.55	7	110	spherical	1	ER	0.85
Ondine	4.43	3.19	1.39	3.19	12.0	4	0.46	7	90	polygon	1	ER	0.41
Ondine	8.23	7.7	1.07	7.7	55.2	3	0.66	10	90	spherical	1	ER	0.49
Ondine	7.17	6.56	1.09	6.56	39.1	3	1.05	15	70	spherical	1	EL	0.56
Ondine	5.18	4.24	1.22	4.24	18.2	2	0.62	5	102	prolate	1	ER	0.83
Ondine	8.92	7.23	1.23	7.23	52.7	2	0.8	14	85	ovoid	1	EL	0.99
Ondine	6.96	3.69	1.89	3.69	22.2	3	0.72	7	99	polygon	1	EL	0.47
Ondine	6.34	4.67	1.36	4.67	29.5	3	0.66	6	120	prolate concave-convex	1	ER	0.75
Ondine	4.57	3.1	1.47	3.1	12.0	5	0.72	7	106	polygon	1	ER	0.60
Lefkas	5.53	4.27	1.3	4.27	21.7	4	0.78	6	118	spherical	1	ER	0.78
Lefkas	4.71	4.3	1.1	4.3	15.5	3	0.51	9	87	polygon	1	ER	0.56
Lefkas	7.56	6.06	1.25	6.06	38.2	4	0.81	11	105	spherical	1	ER	0.55
Lefkas	6.19	4.64	1.33	4.64	26.9	4	0.75	9	94	polygon	1	ER	0.91
Lefkas	6.41	5.34	1.2	5.34	24.1	4	0.58	9	75	ovoid	1	AF	0.38
Lefkas	4.64	2.79	1.66	2.79	9.8	5	0.72	6	93	polygon	1	ER	0.58
Lefkas	6.46	5.85	1.1	5.85	24.8	3	0.62	6	99	spherical	1	ER	0.68
Lefkas	6.5	5.18	1.25	5.18	25.0	3	0.66	14	96	spherical	1	EL	0.58
Lefkas	5.76	4.95	1.16	4.95	24.9	4	0.88	8	71	polygon	1	ER	0.44
Lefkas	5.84	4.81	1.21	4.81	22.3	3	0.94	8	100	spherical	1	ER	0.80
Lefkas	14.44	14.14	1.02	14.14	173.3	2	0.97	11	116	spherical	1	EL	0.64
Agathe	9.99	8.36	1.19	8.36	67.6	3	0.66	11	101	ovoid	1	EL	0.95
Agathe	6.79	5.14	1.32	5.14	29.0	3	0.51	7	93	prolate	1	AF	0.54
Agathe	7.3	6.09	1.2	6.09	34.6	5	0.92	5	92	polygon	1	ER	0.66
Agathe	5.43	5.07	1.07	5.07	23.3	4	0.58	10	93	polygon	1	ER	0.52
Agathe	7.2	5.67	1.27	5.67	27.7	4	0.92	7	95	ovoid	1	ER	0.61

Agathe	14.45	9.62	1.5	9.62	108.9	3	1.09	9	109	ovoid	1	EL	0.42
Agathe	8.33	7.35	1.13	7.35	44.6	4	0.8	10	96	polygon	1	ER	0.50
Agathe	12.27	11.67	1.05	11.67	127.7	4	1.09	24	88	ovoid	1	EL	0.96
Agathe	4.6	3.94	1.17	3.94	16.0	3	0.72	8	85	spherical	1	ER	0.73
Agathe	7.36	5.13	1.43	5.13	32.2	4	0.83	8	104	prolate	1	ER	0.53
Agathe	13.39	11.78	1.14	11.78	129.8	2	0.92	9	125	prolate	1	EL	0.51
Agathe	5.84	5.02	1.16	5.02	29.9	3	0.58	8	110	polygon	1	ER	0.49
Agathe	3.94	3.86	1.02	3.86	14.5	4	0.58	9	79	polygon	1	ER	0.49
Agathe	4.66	4.64	1	4.64	16.8	3	0.8	9	92	spherical	1	ER	0.56
Agathe	7.58	6.46	1.17	6.46	43.2	3	0.65	6	110	spherical	1	ER	0.58
Agathe	18.04	16.72	1.08	16.72	241.0	2	1.23	16	88	ovoid	1	EL	0.86
Agathe	9.85	6.25	1.58	6.25	45.7	4	0.94	9	98	prolate	1	EL	0.37
Agathe	5.16	5.02	1.03	5.02	23.6	3	0.51	8	91	polygon	1	ER	0.52
Agathe	8.71	6.36	1.37	6.36	49.0	3	0.72	9	117	ovoid	1	ER	0.48
Agathe	9.88	8.61	1.15	8.61	76.8	3	1.09	13	81.75	spherical	1	EL	0.68
Agathe	3.79	3.69	1.03	3.69	12.9	4	0.72	5	114	polygon	1	ER	0.75
Agathe	6.37	4.32	1.47	4.32	22.2	4	0.65	10	93	ovoid	1	ER	0.44
Agathe	4.64	3.13	1.48	3.13	14.4	4	0.46	5	106	polygon	1	AN	0.45
Agathe	4.03	3.87	1.04	3.87	14.5	4	0.78	6	95	polygon	1	ER	0.84
Agathe	10.78	9.49	1.14	9.49	78.7	2	0.72	9	105	spherical	1	ER	0.50
Agathe	4.82	3.49	1.38	3.49	16.2	4	0.8	5	87	polygon	1	ER	0.66
Agathe	12.37	7.33	1.69	7.33	76.5	2	1.85	11	76	prolate	1	EL	0.73
Agathe	4.24	3.62	1.17	3.62	11.9	4	0.62	6	73	polygon	1	ER	0.56
Agathe	2.81	2.48	1.13	2.48	4.9	3	0.5	4	86	polygon	1	AN	0.39
Agathe	4.61	3.28	1.41	3.28	13.1	3	0.62	7	92	polygon	1	ER	0.58
Agathe	6.49	5.87	1.11	5.87	29.8	2	0.92	8	92.35	spherical	1	ER	0.86
Agathe	5.24	5.23	1	5.23	20.8	4	0.69	8	100	polygon	1	ER	0.49
Agathe	3.71	3.67	1.01	3.67	10.4	3	0.8	4	82	spherical	1	ER	0.58
Agathe	14.06	8.63	1.63	8.63	99.9	2	1.03	11	70	ovoid	1	EL	0.51
Agathe	13.98	11.8	1.18	11.8	121.5	4	1.3	10	100	prolate	1	EL	0.47
Agathe	3.08	2.67	1.15	2.67	6.6	3	0.55	9	82	spherical	1	ER	0.43
Agathe	6.76	5.23	1.29	5.23	30.6	3	0.84	6	108	prolate	1	ER	0.79
Agathe	9.87	5.92	1.67	5.92	49.1	4	0.69	10	100	ovoid	1	EL	0.51
Agathe	9.91	8.01	1.24	8.01	61.0	3	0.62	8	86	ovoid	1	EL	0.40
Agathe	5.74	4.12	1.39	4.12	21.4	4	0.87	7	93.61	polygon	1	ER	0.67
Agathe	8.35	5.53	1.51	5.53	39.5	4	0.83	8	107	ovoid	1	ER	0.39
Agathe	6.54	5	1.31	5	75.5	3	0.84	7	75.5	spherical	1	AF	0.43
Agathe	10.96	7.11	1.54	7.11	55.1	3	0.92	9	66.1	prolate	1	AF	0.42
Agathe	9.85	7.58	1.3	7.58	61.3	3	0.94	7	91.53	spherical	1	ER	0.38
Agathe	5.59	5.1	1.1	5.1	24.2	4	0.72	9	86	spherical	1	ER	0.76
Agathe	5.24	4.31	1.22	4.31	17.9	3	0.6	7	87	spherical	1	ER	0.67
Agathe	4.61	4.3	1.07	4.3	17.6	4	0.72	5	103.17	polygon	1	ER	0.77
Agathe	8.92	8.5	1.05	8.5	55.3	2	0.84	9	97.72	spherical	1	ER	0.55
Agathe	10.01	5.95	1.68	5.95	48.2	5	1.02	8	90.1	ovoid	1	AN	0.41

Agathe	11.26	10.14	1.11	10.14	98.3	3	1.47	14	71.23	spherical	1	EL	0.88
Agathe	5.23	3.38	1.55	3.38	14.8	4	0.83	7	99.55	polygon	1	ER	0.62
Agathe	11.04	7	1.58	7	68.6	4	0.74	10	94.7	ovoid	1	EL	0.49
Clyde	8.54	7.26	1.18	7.26	47.3	3	0.74	11	87.78	prolate	1	EL	0.93
Clyde	7.1	5	1.42	5	31.1	2	0.51	12	113.61	prolate	1	EL	0.91
Clyde	3.65	3.23	1.13	3.23	9.4	3	0.51	5	91	polygon	1	ER	0.47
Clyde	4.77	4.17	1.14	4.17	16.9	3	0.55	8	93	polygon	1	ER	0.59
Clyde	4.85	3.4	1.43	3.4	14.8	3	0.74	6	93	polygon	1	ER	0.64
Clyde	7.79	6.96	1.12	6.96	47.5	4	0.69	10	88	ovoid	1	ER	0.52
Clyde	5.43	3.5	1.55	3.5	16.2	3	0.72	6	74	prolate	1	AN	0.35
Clyde	3.94	2.47	1.6	2.47	8.1	4	0.51	6	77	polygon	1	EL	0.38
Clyde	3.99	3.16	1.26	3.16	7.8	4	0.51	4	79	polygon	1	AN	0.58
Tina	8.42	5.14	1.64	5.14	43.1	4	0.82	11	96.75	ovoid	1	EL	0.93
Tina	3.69	2.46	1.5	2.46	7.6	3	0.6	6	91	polygon	1	ER	0.49
Tina	6.64	5.67	1.17	5.67	31.6	4	0.72	13	85.65	spherical	1	ER	0.55
Tina	8.7	7.79	1.12	7.79	45.2	4	0.72	8	45.22	polygon	1	AF	0.92
Tina	9.11	7.68	1.19	7.68	54.6	5	1.31	6	68.12	polygon	1	EL	0.46
Tina	8.85	4.92	1.8	4.92	37.9	4	0.87	5	98.19	prolate	1	EL	0.37
Tina	5.94	3.38	1.76	3.38	18.7	4	0.69	4	108.59	polygon	1	ER	0.35
Tina	4.05	2.66	1.52	2.66	11.2	4	0.61	8	100	prolate	1	ER	0.55
Tina	7.58	7.28	1.04	7.28	44.5	3	0.94	11	89.22	spherical	1	ER	0.61
Mkubwa	3.49	3.18	1.1	3.18	8.7	3	0.5	6	100	spherical	1	ER	0.57
Mkubwa	7.84	6.24	1.26	6.24	46.6	3	1.02	9	91.05	spherical	1	AN	0.45
Mkubwa	2.88	2.34	1.23	2.34	6.1	3	0.58	5	102	spherical	1	ER	0.53
Oreste	8.7	7.17	1.21	7.17	57.1	3	0.72	9	94.11	quadrangular	1	ER	0.47
Oreste	11.58	9.44	1.23	9.44	89.0	3	1.04	14	97.62	ovoid	1	EL	0.96
Oreste	5.97	5.34	1.12	5.34	24.9	4	0.61	8	101	polygon	1	ER	0.75
Oreste	4.04	3.01	1.34	3.01	16.0	4	0.82	6	75.75	polygon	1	ER	0.55
Oreste	7.2	6.57	1.1	6.57	35.4	2	0.6	6	105	spherical	1	ER	0.62
Oreste	9.4	9.32	1.01	9.32	73.7	2	0.85	7	97.79	spherical	1	ER	0.48
Oreste	14.64	12.05	1.21	12.05	133.2	2	0.83	13	114.75	prolate	1	EL	0.75
Oreste	13.37	10.73	1.25	10.73	115.5	3	0.9	12	128	prolate	1	EL	0.81
Oreste	8.11	6.5	1.25	6.5	42.4	4	0.6	7	95	prolate	1	ER	0.50
Oreste	12.89	11.2	1.15	11.2	118.4	3	0.52	13	87	prolate	1	EL	0.92
Oreste	12.42	7.79	1.59	7.79	74.2	4	0.94	12	102	ovoid	1	EL	0.91
Oreste	7.85	6.66	1.18	6.66	40.0	2	0.62	10	123	prolate	1	ER	0.67
Oreste	14.42	12.09	1.19	12.09	139.2	2	0.72	17	122	prolate	1	EL	0.79
Oreste	6.97	6.82	1.02	6.82	39.7	4	0.8	6	87	spherical	1	ER	0.70
Oreste	12.98	12.46	1.04	12.46	138.3	5	1.16	20	90	polygon	1	EL	0.89
Oreste	5.17	3.95	1.31	3.95	21.4	3	0	0	0	polygon	1	AF	0.71
Oreste	9.21	7.01	1.31	7.01	50.5	4	0.75	9	99	polygon	1	EL	0.48
Oreste	6.26	5.86	1.07	5.86	26.7	1	0.4	6	117	spherical	1	AF	0.46
Oreste	6.56	6.24	1.05	6.24	30.5	3	0.72	8	117	polygon	1	ER	0.70
Oreste	7.07	6.99	1.01	6.99	40.1	2	0.46	11	124	spherical	1	ER	0.63

Oreste	13.75	11.53	1.19	11.53	133.8	4	0.94	20	92.32	spherical	1	EL	0.79
Oreste	18.6	14.65	1.27	14.65	219.9	3	0.74	23	115	prolate	1	EL	0.78
Oreste	11.39	9.26	1.23	9.26	86.8	4	2.1	4	70	polygon	1	EL	0.51
Oreste	9.32	8.19	1.14	8.19	64.2	5	1.33	8	91	polygon	1	EL	0.43
Oreste	11.63	9.53	1.22	9.53	81.6	4	0.9	11	116	ovoid	1	EL	0.91
Oreste	9.91	7.01	1.41	7.01	64.1	4	0.91	10	89.35	quadrangular	1	EL	0.42
Oreste	5.06	4.03	1.26	4.03	16.1	4	0.62	7	81	polygon	1	ER	0.60
Oreste	18.34	14.28	1.28	14.28	165.9	5	0.72	8	97	polygon	1	EL	0.49
Oreste	9.32	7.38	1.26	7.38	60.0	4	0.72	15	89	polygon	2	EL	0.99
Oreste	10.52	9.54	1.1	9.54	81.6	3	0.92	13	91.63	prolate	2	EL	0.96
Oreste	10.51	9.49	1.11	9.49	87.4	3	1.1	9	112.25	ovoid	1	AN	0.35
Oreste	12.72	7.12	1.79	7.12	52.6	3	0	0	0	angular point	1	SA	0.98
Oreste	13.62	11.74	1.16	11.74	131.7	3	1.1	6	58	polygon	1	SA	0.65
Oreste	6.35	5.43	1.17	5.43	29.2	5	0.7	8	95	polygon	1	ER	0.81
Oreste	14.65	11.98	1.22	11.98	155.4	3	2.36	6	91	polygon	1	EL	0.48

Starch microremains from calculus. ER=*Eremospatha*, AF=*Aframomum*, AN=*Laccosperma*, GI=*Gilbertiodendron*, CO=*Cola*, NA=*Napoleona*, TR=*Treculia*, CU=*Coula*, XY=*Xylia*, PI=*Piper*, PA=*Panda*, SG=*Sacoglottis*, CL=*Calpocalyx*.

Chimpanzee name	Length	Width	LW Ratio	Brea	Area	Shape	Facets	Striaelen	Striaeno	Type	Lam	Dist	Genus with highest certainty score	Certainty score
castor	13.21	12.67	1.0	12.7	131.22	spherical	0	0	0	1	1	6.16	GI	0.31
castor	16.89	14.11	1.2	14.1	191.72	ovoid	0	0	0	1	2	10.78	CO	0.45
bijou	6.02	4.98	1.2	5.0	24.77	spherical	0	0	0	1	0	3.01	NA	0.30
bijou	12.38	10.67	1.2	10.7	113.42	spherical	0	0	0	1	0	7.3	GI	0.32
bijou	11.67	11.16	1.0	11.2	103.46	spherical	0	2.2	2	1	0	5.12	GI	0.28
bijou	11.14	7.47	1.5	7.5	69.21	ovoid	0	0	0	1	0	6.45	TR	0.51
bijou	8.64	6.53	1.3	6.5	59.32	ovoid	0	0	0	1	1	3.98	TR	0.66
bijou	5.63	4.92	1.1	4.9	23.65	spherical	1	0	0	1	1	2.78	CU	0.28
bijou	5.12	5.12	1.0	5.0	20.55	spherical	1	0	0	1	1	1.96	ER	0.33
bijou	9.76	9.11	1.1	9.1	81.09	spherical	1	1.27	2	1	0	4.88	GI	0.39
bijou	10.26	10.26	1.0	10.2	82.18	spherical	0	0	0	1	0	5.13	CU	0.35
fanny	10.03	8.08	1.2	8.1	56.48	ovoid	0	0	0	1	0	5.32	TR	0.50
fanny	5.01	4.9	1.0	4.9	19.72	polygon	7	0	0	3	0	1.95	PI	0.53
fanny	3.71	3.5	1.1	3.5	10.52	hemispherical	1	0	0	1	0	1.24	XY	0.31
fanny	5.25	5.25	1.0	5.0	26.12	spherical	0	0	0	1	0	1.85	ER	0.31
fanny	4.83	4.32	1.1	4.3	16.57	spherical	1	0	0	1	0	1.74	NA	0.24
fanny	11.38	11.18	1.0	11.2	108.01	oblate conovoid	2	1.59	1	2	0	5.69	GI	0.41
fanny	3.62	3.33	1.1	3.3	10.84	hemispherical	1	0	0	1	0	1.54	XY	0.32
fanny	12.18	11.48	1.1	11.5	115.41	spherical	0	0	0	1	0	5.47	GI	0.34
fanny	20.04	16.43	1.2	16.4	242.33	polygon	6	0	0	1	1	8.47	SA	0.63
fanny	8.82	8.69	1.0	8.7	56.17	oblate conovoid	3	0	0	2	0	2.77	GI	0.45
fanny	5.99	5.51	1.1	5.5	26.15	spherical	0	0	0	1	1	2.15	NA	0.25

fanny	15.52	11.89	1.3	11.9	132.17	ovoid	0	3.2	2	1	0	6.06	CO	0.40
fanny	9.35	8.4	1.1	8.4	62.36	oblate conovoid	3	0	0	1	0	4.675	GI	0.43
fanny	6.06	5.73	1.1	5.7	33.11	hemispherical	1	0	0	1	0	2.36	GI	0.27
fanny	7.7	7.08	1.1	7.1	43.67	spherical	0	0	0	1	0	2.1	ER	0.21
fanny	2.43	2.14	1.1	2.1	5.09	oblate conovoid	1	0	0	1	0	1.04	CL	0.33
fanny	10.14	9.14	1.1	9.1	81.11	spherical	0	4.5	3	1	0	4.71	GI	0.27
fanny	4.94	4.51	1.1	4.5	18.28	spherical	0	0	0	1	0	1.44	ER	0.26
fanny	8.43	6.48	1.3	6.5	37.77	prolate	0	0	0	1	0	3.8	TR	0.32
fanny	4.86	4.22	1.2	4.2	18.97	polygon	7	0	0	3	0	2.63	PI	0.55
fanny	6.02	4.78	1.3	4.8	20.54	polygon	7	0	0	3	0	3.01	PI	0.46
fanny	4.86	3.5	1.4	3.5	16.57	polygon	7	0	0	3	0	2	PI	0.72
fanny	4.36	3.25	1.3	3.3	18.98	polygon	7	0	0	3	0	1.75	PI	0.70
fanny	6.22	5.18	1.2	5.2	31.03	polygon	5	0	0	3	0	2.19	PI	0.40
fanny	6.36	3.48	1.8	3.5	27.6	polygon	8	0	0	3	0	2.87	PI	0.51
fanny	5.04	3.75	1.3	3.8	35.22	polygon	7	0	0	3	0	2.52	PI	0.54
fanny	7.6	6.78	1.1	6.8	36.75	polygon	8	0	0	3	0	3.58	SA	0.57
fanny	4.61	4.61	1.0	4.6	18.18	spherical	0	0	0	1	1	1.23	ER	0.47
fanny	9.3	9.3	1.0	8.4	64.03	spherical	0	0	0	1	0	4.31	CU	0.41
fanny	4.86	4.4	1.1	4.4	17.47	polygon	7	0	0	3	0	2.43	PI	0.60
fanny	5.22	4.61	1.1	4.6	19.72	polygon	5	0	0	3	0	2.31	PI	0.52
fanny	4.74	4.64	1.0	4.6	14.72	polygon	8	0	0	3	0	2.14	PI	0.58
fanny	4.32	4.14	1.0	4.1	18.99	polygon	6	0	0	3	0	1.85	PI	0.58
fanny	3.53	3.18	1.1	3.2	15.66	polygon	3	0	0	3	0	2.15	PI	0.53
fanny	6.51	4.12	1.6	4.1	18.44	polygon	5	0	0	3	0	3.255	PI	0.39
fanny	5.2	3.69	1.4	3.7	17.72	concaveconvex polygon	7	0	0	3	0	2.6	PI	0.67
fanny	3.67	3.13	1.2	3.1	10.76	polygon	7	0	0	3	0	1.835	PI	0.74
fanny	4.67	4.46	1.0	4.5	20.97	polygon	7	0	0	3	0	2.335	PI	0.53
Leo	14.23	12.29	1.2	12.3	130.05	spherical	2	0	0	1	1	7.43	GI	0.46
Leo	15.02	14.2	1.1	14.2	178	spherical	0	2.03	1	1	0	7.99	GI	0.29
Leo	22.91	18.17	1.3	18.2	346	prolate	0	9.44	2	1	3	7.95	CO	0.73
Leo	19.42	13.85	1.4	13.9	218	ovoid	0	0	0	1	0	9.5	GI	0.39
Leo	6.73	6.12	1.1	6.1	38.18	spherical	0	0	0	1	0	2.56	NA	0.23
castor	5.5	5.08	1.1	5.1	24.45	polygon	8	0	0	3	0	2.19	PI	0.42
castor	5.5	5.08	1.1	5.1	24.45	polygon	8	0	0	3	0	2.19	PI	0.42
castor	5.5	5.08	1.1	5.1	24.45	polygon	8	0	0	3	0	2.19	PI	0.42
castor	5.5	5.08	1.1	5.1	24.45	polygon	8	0	0	3	0	2.19	PI	0.42
castor	5.5	5.08	1.1	5.1	24.45	polygon	8	0	0	3	0	2.19	PI	0.42
castor	5.5	5.08	1.1	5.1	24.45	polygon	8	0	0	3	0	2.19	PI	0.42
castor	5.5	5.08	1.1	5.1	24.45	polygon	8	0	0	3	0	2.19	PI	0.42
castor	5.5	5.08	1.1	5.1	24.45	polygon	8	0	0	3	0	2.19	PI	0.42
castor	5.5	5.08	1.1	5.1	24.45	polygon	8	0	0	3	0	2.19	PI	0.42
castor	5.5	5.08	1.1	5.1	24.45	polygon	8	0	0	3	0	2.19	PI	0.42
castor	5.5	5.08	1.1	5.1	24.45	polygon	8	0	0	3	0	2.19	PI	0.42
castor	5.5	5.08	1.1	5.1	24.45	polygon	8	0	0	3	0	2.19	PI	0.42
castor	5.5	5.08	1.1	5.1	24.45	polygon	8	0	0	3	0	2.19	PI	0.42
castor	5.5	5.08	1.1	5.1	24.45	polygon	8	0	0	3	0	2.19	PI	0.42

castor	5.5	5.08	1.1	5.1	24.45	polygon	8	0	0	3	0	2.19	PI	0.42
castor	5.5	5.08	1.1	5.1	24.45	polygon	8	0	0	3	0	2.19	PI	0.42
castor	5.5	5.08	1.1	5.1	24.45	polygon	8	0	0	3	0	2.19	PI	0.42
castor	5.5	5.08	1.1	5.1	24.45	polygon	8	0	0	3	0	2.19	PI	0.42
castor	5.5	5.08	1.1	5.1	24.45	polygon	8	0	0	3	0	2.19	PI	0.42
castor	5.5	5.08	1.1	5.1	24.45	polygon	8	0	0	3	0	2.19	PI	0.42
castor	6.41	4.36	1.5	4.4	24.45	polygon concave convex	8	0	0	3	0	2.19	PI	0.36
castor	13.83	11.75	1.2	11.8	113.82	triangular	0	0	0	1	1	6	CO	0.45
Goma	24.38	19.47	1.3	19.5	342	ovoid	0	0	0	1	2	17.96	CO	0.57
Goma	5.32	4.92	1.1	4.9	25.84	spherical	0	0	0	1	0	2.61	NA	0.34
Goma	4.38	3.67	1.2	3.7	14.85	spherical	0	0	0	1	0	1.95	ER	0.29
Goma	29.37	20.49	1.4	20.5	432	ovoid	0	0	0	1	2	20	CO	0.58
Goma	12.42	11.61	1.1	11.6	107	spherical	0	3	2	1	1	4.82	GI	0.27
Goma	16.72	15.6	1.1	15.6	212	quadrangular	1	2	4.86	1	2	6.56	CO	0.50
Goma	9.35	8.83	1.1	8.8	60.53	spherical	0	0	0	1	1	4.675	CU	0.30
Goma	14.5	13.95	1.0	14.0	154	spherical	0	0	0	1	1	6.79	GI	0.33
Goma	14.63	13.13	1.1	13.1	129.55	spherical	0	0	0	1	1	6.97	GI	0.31
Goma	20.31	18.43	1.1	18.4	304.94	polygon	6	3.36	9	1	0	7.76	SA	0.53
Goma	24.12	19.79	1.2	19.8	368.42	ovoid	0	4	1	1	2	12	CO	0.75
Goma	7.38	5.08	1.5	5.1	32.32	ovoid	1	0	0	1	0	3.65	TR	0.72
Goma	29.31	20.18	1.5	20.2	463	ovoid	1	0	0	1	1	20.86	GI	0.45
Goma	17.47	16.82	1.0	16.8	215	ovoid	1	0	0	1	0	8.5	GI	0.72
Goma	11.99	11.99	1.0	12.0	106	spherical	1	3.2	1	1	0	4.84	GI	0.30
Goma	11.57	9.93	1.2	9.9	90.26	spherical	0	0	0	1	0	2.95	GI	0.25
Goma	14.06	11.38	1.2	11.4	129.31	ovoid	0	0	0	1	3	9.76	CO	0.52
Goma	30.68	21.71	1.4	21.7	493.67	ovoid	0	0	0	1	2	10	CO	0.59
Goma	11.33	11.33	1.0	11.0	103.43	spherical	0	0	0	1	0	5.5	CU	0.34
Goma	16.15	15.79	1.0	15.8	201.29	spherical	0	0	0	1	1	8	GI	0.33
Goma	30.27	25.27	1.2	25.3	568.1	triangular	0	0	0	1	2	19	CO	0.65
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38

Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38

Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	5.32	5.12	1.0	5.1	20.16	polygon	8	0	0	3	0	3.81	PI	0.38
Goma	20.17	20.17	1.0	20.0	312.77	spherical	0	0	0	1	1	6.3	CU	0.32
Goma	23.46	11.8	2.0	11.8	213.82	elongate ovoid	0	0	0	1	2	9.54	CO	0.52
Goma	10.44	10.44	1.0	10.2	80.19	spherical	0	0	0	1	1	9.76	CU	0.38
Goma	9.04	8.36	1.1	8.4	60.76	spherical	0	0	0	1	1	4.5	CU	0.32
Goma	11.05	10.06	1.1	10.1	84.6	spherical	0	0	0	1	1	5	GI	0.30
Goma	6.74	4.71	1.4	4.7	23.52	prolate	0	0	0	1	1	1.95	XY	0.23
Goma	14.35	12.35	1.2	12.4	180	polygon	6	0	0	1	1	5.87	SA	0.62
Goma	21.41	15.77	1.4	15.8	261	ovoid	0	0	0	1	1	14.55	GI	0.37
Goma	9.42	7.68	1.2	7.7	63.58	hemispherical	1	0	0	2	1	4.89	GI	0.51
Goma	8.63	6.06	1.4	6.1	40.83	hemispherical	1	0	0	2	0	4.5	GI	0.46
Goma	15.43	12.53	1.2	12.5	166.28	polygon	4	0	0	1	0	6.75	SA	0.47
Goma	7.99	7.17	1.1	7.2	46.48	ovoid	0	0	0	1	0	4.2	TR	0.62
Goma	12.46	12.46	1.0	11.7	111.51	spherical	0	0	0	1	2	6.81	CU	0.62
Goma	25	18	1.4	18.0	372	ovoid	0	0	0	1	0	13	CO	0.34
Rubra	9.84	12.34	0.8	12.3	95.74	hemispherical	3	0	0	2	0	5.08	GI	0.47
Rubra	5.29	4.37	1.2	4.4	16.86	spherical	0	0	0	1	0	1.79	ER	0.27
Rubra	7.39	5.59	1.3	5.6	30.21	ovoid	0	0	0	1	0	1.87	TR	0.71
Rubra	9.95	9.95	1.0	9.7	72.27	spherical	0	0	0	1	0	4.17	CU	0.36
Rubra	6.9	5.55	1.2	5.6	28.27	prolate	0	0	0	1	0	2.89	TR	0.31
Rubra	7.97	6.41	1.2	6.4	43.34	elongate conovoid	2	0	0	1	0	4.61	TR	0.26
Rubra	16.52	12.95	1.3	13.0	182.78	polygon	7	0	0	1	0	7.23	SA	0.64
Dorry	8.81	7.6	1.2	7.6	51.33	ovoid	0	0	0	1	0	3.34	TR	0.58
Dorry	8.61	6.05	1.4	6.1	38.2	prolate	0	0	0	1	0	3.6	TR	0.34
Dorry	5.84	5.22	1.1	5.2	26.04	spherical	0	0	0	1	0	2.07	NA	0.32
Dorry	6.96	6.48	1.1	6.5	35.5	spherical	0	0	0	1	1	3.48	CU	0.28
Venus	9.43	7.9	1.2	7.9	65.51	spherical	1	0	0	1	0	4.3	GI	0.33
Venus	9.93	9.01	1.1	9.0	73.23	spherical	0	0	0	1	0	6.59	GI	0.32
Venus	17.91	14.01	1.3	14.0	185.85	ovoid	0	0	0	1	1	11.17	GI	0.46
Venus	8.4	7.79	1.1	7.8	53.82	spherical	0	0	0	1	0	3.38	CU	0.25
Venus	4.53	4.12	1.1	4.1	15.04	hemispherical	1	0	0	1	0	1.91	XY	0.23
Venus	15.97	11.92	1.3	11.9	134.03	pyriform	0	0	0	1	1	8.2	CO	0.44
Venus	7.48	6.16	1.2	6.2	33.17	prolate	1	0.5	2	1	1	3.18	PA	0.33
Venus	6.04	4.22	1.4	4.2	23.28	prolate	0	0	0	1	0	2.11	PA	0.31
Venus	12.17	10.44	1.2	10.4	93.68	prolate	0	0	0	1	0	5.64	CO	0.48
Venus	15.61	12.87	1.2	12.9	150.5	prolate	0	0.7	2	1	0	8.2	CO	0.44
Venus	26.95	20.72	1.3	20.7	435	ovoid	0	0	0	1	2	20	CO	0.58
Venus	9.56	8.69	1.1	8.7	65.62	hemispherical	0	0	0	2	0	5.49	GI	0.47
Venus	10.79	10.72	1.0	10.7	93.61	hemispherical	0	0	0	2	0	6.04	GI	0.42
Venus	14.25	12.7	1.1	12.7	143.15	spherical	0	0	0	1	1	8	GI	0.32
Venus	8.43	7.16	1.2	7.2	44.74	spherical	0	0	0	1	1	4.15	CU	0.27
Venus	4.89	3.26	1.5	3.3	12.52	prolate	0	0	0	1	0	1.77	PA	0.42

Brutus	6.41	5.65	1.1	5.7	34.96	hemispherical	2	0	0	2	0	3.32	GI	0.40
Brutus	6.02	5.06	1.2	5.1	24.28	hemispherical	2	0	0	2	0	2.87	SG	0.38
Brutus	4.73	4.35	1.1	4.4	17.12	ovoid	0	0	0	1	0	2.35	TR	0.28
Brutus	21.56	16.95	1.3	17.0	181	ovoid	0	0	0	1	0	15.88	GI	0.43
hector	8.19	8.19	1.0	8.0	50.66	spherical	0	1.02	1	1	0	3.38	CU	0.47
hector	5.95	5.39	1.1	5.4	25.88	oblate conovoid	2	0	0	2	0	2.61	SG	0.57
Lefkas	6.48	5.63	1.2	5.6	27.02	spherical	0	0	0	1	0	3.24	NA	0.28
Lefkas	4.35	4.13	1.1	4.5	18.23	spherical	1	0	0	1	0	2.175	NA	0.27
Lefkas	19.67	18.32	1.1	18.3	276.13	ovoid	1	0	0	1	3	11.29	CO	0.41
Lefkas	3.61	3.61	1.0	3.6	9.81	spherical	0	0	0	1	0	1.805	ER	0.62
Lefkas	4.53	3.35	1.4	3.4	11.13	spherical	0	0	0	1	1	1.65	ER	0.34
Lefkas	5.18	5.18	1.0	4.4	18.33	spherical	0	0	0	1	0	1.65	ER	0.41
Lefkas	3.98	3.98	1.0	3.9	14.39	spherical	0	0	0	1	0	1.99	ER	0.57
Lefkas	7.48	4.4	1.7	4.4	29.47	ovoid	0	0	0	1	0	3.74	TR	0.70
Agathe	12.37	7.81	1.6	7.8	77.7	ovoid	0	0	0	1	0	6.185	TR	0.39
Agathe	7.82	6.97	1.1	7.0	42.71	spherical	2	0	0	1	0	3.88	GI	0.30
Agathe	7.85	6.65	1.2	6.7	39.78	spherical	1	0	0	1	1	2.31	CU	0.26
Agathe	5.8	5.25	1.1	5.3	24.04	spherical	1	0	0	1	1	2.9	CU	0.31
Agathe	8.23	6.03	1.4	6.0	37.76	prolate	0	0	0	1	0	3.62	TR	0.34
Agathe	4.58	4.22	1.1	4.2	15.2	spherical	0	0	0	1	0	2.29	NA	0.31
Clyde	12.65	10.84	1.2	10.8	106	spherical	2	0	0	1	0	4.75	GI	0.49
Clyde	6.01	4.5	1.3	4.5	21.7	spherical	0	0	0	1	2	3.005	CU	0.50
Clyde	13.31	12.49	1.1	12.5	133	polygon	8	1.7	2	3	0	4.93	SA	0.78
Tina	5.34	4.72	1.1	4.7	20.45	oblate conovoid	2	0	0	2	0	2.39	SG	0.65
Tina	4.92	3.98	1.2	4.0	15.51	hemispherical	1	0	0	1	0	1.85	SG	0.25
Tina	8.92	8.64	1.0	8.6	68.1	spherical	0	0	0	1	0	4.32	GI	0.27
Oreste	6.5	4.81	1.4	4.8	27.18	ovoid	1	0	0	1	0	2.44	TR	0.65
Oreste	6.16	5	1.2	5.0	25.54	oblate conovoid	2	0	0	2	0	2.47	SG	0.57
Vanessa	8.65	7.85	1.1	7.9	48.29	spherical	0	0	0	1	0	3.94	CU	0.25
Vanessa	9.37	8.2	1.1	8.2	62.79	prolate	0	0	0	1	0	3.65	CO	0.35

Appendix table 13: Coefficients of the statistical models.

Model	Term	Estimate	Std. Err.	Z value	P
Tests of effect of age and sex on microremain numbers					
Phytolith Negative binomial	Intercept	3.969	0.160	24.790	1.1398e-135
	Age	0.002	0.0005	3.833	1.2616e-04
	Sex	-0.027	0.157	-0.170	8.6469e-01
Starch Negative binomial	Intercept	3.009	0.426	7.052	1.7575e-12
	Age	0.003	0.001	2.661	7.7805e-03
	Sex	-2.569	0.437	-5.873	4.2665e-09
Unsilicified remains	Intercept	2.210	0.202	10.904	1.0978e-27
Negative binomial	Age	0.001	0.0006	3.093	1.9775e-03
	Sex	-0.048	0.199	-0.245	8.0594e-01
Tests of effect of consumption frequency on microremain numbers					

Phytolith Poisson model	Intercept	-0.231	0.876	-0.263	0.791
	z.min	1.707	0.680	2.509	0.012
	z.age	3.612	2.075	1.740	0.081
	sex	-0.801	0.934	-0.858	0.390
Starch logistic regression model	Intercept	-14.218	0.870	-6.325	6.4911e-60
	z.min	0.591	0.505	1.169	2.4224e-01
	z.age	0.489	0.442	1.105	2.6885e-01
	sex	-1.266	0.996	-1.271	2.0372e-01

Appendix table 14: Variable importance in phytolith and starch classification random forest.

Phytolith model		Starch model	
Variable	Importance	Variable	Importance
Length	100	Area	100
Spine number	75.301	Length	75.8434
Spine ang	74.109	Width	67.5876
LW Ratio	43.996	Dist	61.1718
Spine length	42.854	Facets	60.4963
Area	29.581	LW Ratio	56.2298
Width	22.056	Type	55.9587
Irregul	10.236	Lam	35.8372
Spherical	6.667	Spherical	31.833
Angularpoint	6.575	Prolate	8.2554
Polygon	4.590	Ovoid	7.157
Ovoid	1.663	Polygon	5.8693
Prolate	1.620	Hemispherical	4.9279
Triangular	1.447	Oblate conovoid	4.6926
Elongate	0.440	Striaelen	2.4395
Quadrangular	0.228	Elongate ovoid	2.4011
Facets	0.184	Striae no	2.1051
Conjoined	0.106	Triangular	1.8956
Prolate concave-convex	0.043	Quadrangular	0.9141
Polygon concave	0.042	Pyriform	0.4986

7.3 Chapter five appendix

7.3.1 Comparative data for model

We prepared data from past dental calculus studies for a comparative analysis (Salazar-García et al., 2013; Henry et al., 2014). This dataset included starch and phytolith counts from nine other Middle Palaeolithic sites. As other microremains are not included in previous published studies, we only included starch and phytoliths in our model. Although our samples were weighed in mg, weights for all eight sites are not available. Similarly, in the datasets presented in this paper we treated starches of the same type that occurred as lumps as one starch as

accurately counting each starch in a lump is not possible. We collected the most to date estimated date range for each site and used the median value.

Goyet: this archaeological site comprises several caves near Gesves, in the Namur Province of Belgium. The cave system has seen several campaigns of excavation in the 19th and 20th century. Early explorers found hominin remains (Goyet VIII) in 1868 in the largest of the caves. Dupont found the studied mandible in the second of five fauna-rich levels (Dupont, 1872; Toussaint, 2006). Originally, the fossil was thought to be modern human due to its stratigraphic proximity to Aurignacian artefacts, but this has been re-evaluated and it now is accepted to be a Neanderthal (Rougier et al., 2012, 2014). In addition, in the Aurignacian phase there is an upper Magdalenian level dated to 13 ka (Toussaint, 2006). Mixing is present in all levels and its date was long ambiguous but this has recently been re-evaluated as dating to 44-45.5 ka cal BP (Rougier et al., 2014). This date places the hominin in a transitional period. Regional vegetation reconstructions suggest the surrounding environment was generally tundra-steppe.

La Chapelle-aux-Saints: this Middle Palaeolithic site is located in the Corrèze region of southern France. Researchers have excavated La Chapelle-aux-Saints since 1905, and this has recovered evidence of Mousterian sediments and a complete Neanderthal in 1908. The chronological history of this site has been studied with electron spin resonance (ESR), suggesting dates of 56 ka or 47 ka depending on the radiation uptake model used (Grün and Stringer, 1991). The ESR may suggest the remains belongs to the warm parts of MIS 3, but this contradicts correlation with the Combe-Grenal sequence which would put the remains at the end of MIS 4 and beginning of MIS 3. The associated fauna profile is predominately reindeer (*Rangifer tarandus*), with some bovines (*Bos*/*Bison* sp.), horse (*Equus* sp.), ibex, wolf (*Canis lupus*), fox (*Canis vulpes*), *Rhinoceros*, cave hyena (*Crocuta spelaeaus*), boar (*Sus scrofa*) and marmot (*Arctomys* sp.) (Boule, 1911; Bouyssonie et al., 1913). The fauna is clearly a cold phase profile indicating a date during the late MIS 4 (Mellars, 1986). In addition, fauna shows the surrounding environment was a cold open biome.

La Ferrassie: this site is located in the Vézère Valley, in the Dordogne region of France. La Ferrassie is a large deep cave with an adjoining long rock-shelter and small rock-shelter. The site has a plethora of levels of different periods in various sections of the cave. Mousterian levels below the long rock-shelter produced remains of six Neanderthals in excavations during 1909 and 1921. The bison, auroch and red deer that dominate the Mousterian fauna imply a moderate temperate environment.

These fauna suggest tree cover and a closed, forested environment (Capitan and Peyrony, 1912a; b; c; Guérin et al., 2015). Mousterian deposits at La Ferrassie has been recently dated with OSL and radiocarbon dating, suggesting that the Neanderthal remains La Ferrassie 1 is most likely 39 ±5 ka and 2 skeletons 43 ±3 ka (Guérin et al., 2015).

La Quina: La Quina is a series of rock shelters in the Charente region of Central France. Remains used in this study were found in 1911 in one of two sub-sections of Station Amont, a deposit extending below the upper rock shelter base. This deposit was studied over the course of several excavations. Excavations revealed Mousterian remains, faunal debris and the remains of many Neanderthals (Henri-Martin, 1961). The upper deposits of the sequence at Station Amont are considered to date to 48-43 ka. This, combined with cold phase fauna, indicates a date for the fossil of MIS 4, probably 71-57 ka (Debénath and Jelinek, 1998). Fauna found was mostly bovines, horse and reindeer, with few other species represented (Debénath and Jelinek, 1998). These faunas also suggest a cold and dry environment that was devoid of trees.

Malarnaud: this site is a cave in the Ariège region of Southern France. There has been scientific interest in the cave since 1883. Deposits dated to Mousterian, Aurignacian and Magdalenian have been found onsite. Investigators found a juvenile Neanderthal mandible during 1888 in the lower of two layers in a side chamber of this cave complex. However, it is possible that the mandible was moved by carnivores in this chamber as it is removed from much the archaeological material. Unfortunately, the site has not been radiometrically dated. Faunal profiles indicate the mandible dates to Riss-Würm interglacial, 130-117 ka or the beginning of the Würm, 100-50 ka. Fauna in the layer of the mandibles include cave lion (*Panthera leo*), cave hyena, fox, and wolf, mammoth and rhinoceros (Rhinocerotidae) (Boule, 1889; Filhol, 1889). This fauna is suggestive of tree cover in the early glacial warm or transitional phase, and thus we classify the environment as of mixed openness.

Spy: this archaeological site is located in Jemeppe-sur-Sambre, Namur in Belgium. The site was excavated from 1879 onwards, and the Neanderthal remains were found in a bone rich layer. Later excavations have clarified the stratigraphy of the cave. Faunal profiles from excavation of this layer have suggested an intensely cold climate (Otte, 1979). Some studies found misclassified Neanderthal remains in faunal bags (Crevecoeur et al., 2010). These teeth were directly radiocarbon dated to about 36 ka (Semal et al., 2009). De Puydt and Lohest recovered fauna from this

level, including horse and hyena, with some mammoth, wholly rhinoceros, reindeer, red deer, aurochs, cave bear, cave lion, wolf, wolverine (*Gulo gulo*) and badger (*Meles meles*). However, palaeoenvironment reconstructions may be questioned due to the poor stratigraphic integrity of this layer (de Puydt and Lohest, 1887). The direct data of the hominin remains firmly places the occupation in a cold phase when dry tree landscapes dominated much of Europe. We consider the environment as open for our model.

Kůlna Cave: this Middle Palaeolithic site is located in the Moravian Karst, in the eastern part of the Czech Republic in Central Europe. The cave saw first investigations in 1880 when stone tools and bones of extinct animals were noticed (Sroubek et al., 2001). Karel Valoch conducted the first modern archaeological investigation in 1961 and 1976. He identified 14 sedimentary complexes covering the last interglacial to the Holocene. Neanderthal remains were found in strata 7a and 7c of but specimens in this study come from stratum 7a only. Radiocarbon dating has suggested a data of >45 ka BP ^{14}C, and electron spin resonance on layer 7a shows it dates to 50 ± 5 ka BP (Rink et al., 1996). The character of the fauna from this layer matches this age (Rink et al., 1996). Layer 7a contained reindeer, with mammoth and a few elk, the presence of reindeer clearly indicate cold conditions of central Europe in the MIS 3 (Valoch, 1970).

Shanidar Cave: This site is located in the Zagros Mountains in Northwest Iraq. Solecki and colleagues excavated the cave between 1952 and 1957. Excavators described four archaeological strata (A, B, C and D). The Shanidar III fossils were found in Mousterian level D (Solecki, 1960). A radiocarbon date near the Shanidar I fossil indicates that Shanidar III is >46 ka BP, possibly as old as 50 ka BP (Solecki, 1960). Goat (*Capra* sp.) and sheep (*Ovis* sp.) dominate fauna found on site. This reflects the local mountainous topography (Perkins, 1964; Evins, 1982). Pollen analysis indicated the presence of date palms (*Phoenix dactylifera*), walnuts (*Juglans* sp.), chestnuts (*Castanea* sp.), oaks (*Quercus* spp.) and herbs (Solecki, 1961; Leroi-Gourhan, 1968, 1969, 1975). These plant taxa indicate a mild moist environment with at least some level of tree cover. For our model, we classified this habitat as closed.

7.3.2 Reference collection

Microremain identification was based on a reference collection of modern plant samples, including >2,000 global species. Our reference collection has extensive

coverage of edible western Eurasian species. From these species, we identified over 54 species that produced starches, and thus that might be represented in our samples (Appendix table 21). More information is available for phytoliths produced by different taxa so; we instead identified phytoliths using available literature including PhyCore database (Albert et al., 2016). We did not make a reference collection for unsilicified plant microremains, as its unclear if these microremains are diagnostic, nor do we currently have a sufficient reference collection for identifying this types of microremains (Power et al., 2015b).

7.3.3 Classification of microremain taxa

We identified microremains to plant taxon, usually at the family or tribe level. When this was not possible, we assigned microremains to a type based on shared diagnostic morphology that indicates that the morphology likely represents a single plant taxon. We then used the summed number of types to derive a metric of breadth of plant use.

7.3.4 Microremain results

See following tables.

Appendix table 15: Total recovered microremains from Vindija Cave Neanderthal and control samples.

					Starches															Phytoliths										
Identifier	Specimen	Species	Tooth	Wt	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6	Type 7	Type 8	Type 9	Type 10	Type 11	Type 12	Type 13	Type 14	Type 15	partially disrupted	Pes/Dmg	Long-cell	Rondel	Hair	unknown phyto hair	Globular sinuate?	Bulliform	Parallelepipedal	Long-cell multi-cell	Brachiform	Multicellular polyhedrons
Vja-12-13	12.1/229	Neanderthal	URM2	0.39	3	3	5	1	3		1			8	3		3	1			4	3					1	2			
Vja-12-14	12.2/286	Neanderthal	LRI2	0.05			1				1	1									2	1						1			
Vja-12-16	12.4/ 290	Neanderthal	URI1	0.05																								2			
Vja-12-17	12.5/287	Neanderthal	URC	0.05		1		1																				1			
Vja-12-18	12.6/288	Neanderthal	LLC	0.02			1														1	1					1				
Vja-12-19	12.7/201	Neanderthal	LLI2	0.89		4	4	1			2		1					1			8	3	3	5	2			3			
Vja-12-20	11.39/206	Neanderthal	LRC	0.45						1				1								3						2			
Vja-12-21b	11.39/206	Neanderthal	LRM1	0.41		1		1			1			1								4						1	1		
Vja-12-21a	11.39/206	Neanderthal	LRM1	0.50	1	1			1				1																		
Vja-12-24	11.45/231	Neanderthal	LLM3	0.67							1											1	1	4		4	1	3		1	
Vja-12-26	11.46/259	Neanderthal	ULM2	0.87				3										2			1	1					5	3			
Vja-12-51	11.40+11.40a – Vi76/226+265	Neanderthal	LLM1	0.19										1	1					1	1		1	1			2	1			
Vja-12-54	11.40+11.40a – Vi76/226+265	Neanderthal	LLM1	0.05			1																				1				
Vja-12-55	11.40+11.40a – Vi76/226+265	Neanderthal	LLM1	0.09																											
Vindija fauna calculus samples																															
Vja-12-28	1639/car Vi-87	*Panthera*	C	0.63																											
Vja-12-29	555/car 78	*Canis*		0.79																1											
Vja-12-30	735/car Vi-83	*Canis*		0.53			7							3								1						1			
Vja-12-31	335/car Vi-78	*Canis*	P1	0.10							1			1															1		
Vja-12-34	637/car Vi-76	*Canis*		0.40																											
Vja-12-35	714/car Vi-1976	*Canis*		0.58																								1			
Vja-12-37	2/car Vi-76	*Ursus spelaeus*	M2	1.04																											
Vja-12-38	nova 3/car Vi-76	*U.spelaeus*	M2	0.46																		1	1								8
Vja-12-45	nova 1/car Vi-76	*U.spelaeus*	M2	1.248																		2									
Vja-12-46		*U.spelaeus*	M2	0.88	1	4									1						1	3				1		3			
Vja-12-47		*U.spelaeus*	M2	0.18																	1	2	1				2	5			
Vja-12-48		*U.spelaeus*	M2	0.30																							1	3			
Vja-12-53	599 Vi-78	*Canis*		0.43																											

Controls									
Vja-12-43	adhesive used to hold teeth, sampled on Vi-11.39	0.796		1			1		2
Vja-12-44	adhesive used to hold teeth, sampled on Vi-11.40	0.54	1		7	11		4	30

	Phytoliths (continued)				Calcium oxalates			Spores							Pollens				Spicule	Hair	Unsilicified plant microremains											
Identifier	Ellipsoid rugulate	Epidermis	Plate	Indet. phytolith	Prism	Styloid	Irreg oxalate	Very small round dark	Ellipsoidal, single-walled spore	Unknown spore	Clear fusiform	Cluster	Tube of spheres	Unidentified	Pollen indet.	Pollen (Betulaceae)	Algae?	Yellow pollen/spore?	Unknown spicule	Hair	Monocot unsilicified	Unknown unsilicified	Vascular bundle	Grass unsilicified	Indet. animal cells	spherulite	Nematode??	Cellouse type fibre	Fibre	Total starch & phytoliths	Total starch & phytoliths types	Menhinick's index
Vja-12-13					2	1				2								2			1									37	13	2.1
Vja-12-14						1	3					1																		5	5	2.2
Vja-12-16														1						1								1		2	1	0.7
Vja-12-17					2					2										1									2	3	3	1.7
Vja-12-18					3									1			1					2								3	3	1.7
Vja-12-19	2		1		1					2				2		1			1							1	1			32	13	2.3
Vja-12-20																														7	4	1.5
Vja-12-21b					1	2	3	1				1																		10	7	2.2
Vja-12-21a																														4	4	2
Vja-12-24			1							1				1								1						1	3	17	9	2.2
Vja-12-26			1			3		1	1	2	1		1	1						1			1	3						15	6	1.5
Vja-12-51														3				1				2						3	2	7	6	2.3
Vja-12-54																												2		2	2	1.4
Vja-12-55				1																								2			1	
Vindija fauna calculus samples																																
Vja-12-28																			1									2				
Vja-12-29																												1			1	
Vja-12-30														4						4									1	12	4	1.2
Vja-12-31																														3	3	1.7

Vja-12-34				1										1	1											
Vja-12-35				1																				1	1	1
Vja-12-37														1												
Vja-12-38	1	1												2					1	1		1	2	12	5	1.4
Vja-12-45		1											2									1	1	3	2	1.2
Vja-12-46		1							1	1												3		14	7	1.9
Vja-12-47		1								1												4	3	11	5	1.5
Vja-12-48										1					1		1					5		4	2	1
Vja-12-53									2													3	3			
Controls																										
Vja-12-43																								2	2	
Vja-12-44																								23	4	

Starch key	
Type 1	Moderate size, spherical-subspherical, with thick lamellae, some show yellow colouration, diameter is 10-22 μm.
Type 2	Large circular-subcircular in 2D, spherical-lenticular-subspherical 3D, diameter is 20->μm.
Type 3	Small round, constrained facets may be present, diameter is <10 μm.
Type 4	Sub-polyhedral, 2 or more facets but more of surface is not covered by facets, facets often are less sharply defined, no lamellae.
Type 5	Slightly eccentric starch.
Type 6	Faceted, generic type.
Type 7	Ovoid starch, with or without surface features, some have damaged central cavity but this is not a classification trait.
Type 8	Triangular-elliptical, may have central fissure, other surface features can include lamellae.
Type 9	Very eccentric and partially disrupted starch.
Type 10	Lenticular or subelliptical in 3D, equatorial groove may be visible, some show signs of gelatinisation, distinguished from type 8 by poorly defined longitude crack.
Type 11	Small oval or slight ovoid, subspherical (5-10 μm), 1-2 facets may be apparent, little surface features but a central aperture may be present.
Type 12	Large ovoid, routinely eccentric, often with lamellae, diameter is >40 μm.
Type 13	Large spherical/subspherical
Type 14	Polyhedral, distinct facets surface on ≥50 %, no lamellae present.
Type 15	Very small polyhedral, highly facets surface on ≥50 %, no lamellae present.

Appendix table 16: Total recovered microremains from Grotta Guattari Neanderthal and control samples. Specimen column uses Circeo numbering.

				Starches												Phytoliths												Spores			Other microremains										
Identifier	Specimen	Tooth	Wt	Type 1	Type 2.	Type 3	Type 4	Type 5	Type 6	Type 7	Type 8	Type 9	Type 11	Other	Dmg/indet.	Long Cell	Rondel	Bulliform Parallelepipedal	Trichome	Parallelepipedal	Spheroid granulate	Cylindroid psilate	hair	Mesophyll	Multicellular indet.	Prism & sub calcium oxalate	Cystolith	cf Pteridium spore	Nigrospora	fusiform (boletoid)	Indet. spore	Triporate pollen	Pollen with airsacs	Indeterm. pollen	Diatom	Faunal Hair	Grass cells	Stellate hair	Vascular budle	Indet. plant cell	Menhinick's
Neanderthal samples																																									
GTN1	2	RLM3	0.65														1						1		1				2						1						2.1
GTN2	3	RLM1	0.87			1		1	1			7			6	5	4	1	2	1			1	1	2	1								2	1		2	1		1	2.5
GTN3	3	LLI2	0.65			2			1	1	2				4	5	3	2			2	2	2			2	1	1	1	1	4	2		1	4	1			1	8	2.6
GTN4	3	RLI2/M1	0.26	1	1	2	1										1									2		1													4.0
GTN5	3	LLM1/PM 1	0.29				1	1									1			1						2															3.7
Guattari Control samples																																									
2a	2	Wash	n/a												7															4											
2b	2	Wash	n/a												1	1																									
2c	2	Wash	n/a										1	1	1																								1		
2d	2	Wash	n/a											1																7		1	1							
2e	2	Adhesive	1.30	2				104					1	1																										0.3
2g	2	Bone dust	0.34																																					
3a	3	Filler	####	4																																				0.1
3b	3	Adhesive residue	n/a											2																2		1								

Starch key

Type 1: Polyhedral with centric extinction cross oval with no fissures, cross arms are clear and straight, diameter is 17 μm.

Type 2: Unknown shape, partially disrupted (semi gelatinised) eccentric starch, diameter is 90 μm.

Type 3: Spherical starch, typically with cross arms that are clear and straight or near straight. No discernible surface features. Diameter is 6-9 μm.

Type 4: Sub-polyhedral, cross arms are faint and straight.

Type 5: lenticular, cross arms clear and straight. Faint lamellae present. Diameter is 17 μm. (Possible Triticeae).

Type 6: large sub polyhedral. 15 μm or above.

Type 7: Very small polyhedral, no lamellae or fissures (Possible *Avena or* bogbean).

Type 8: slightly eccentric.

Type 9: Highly eccentric.

Type 10: Very small starch with centric cross.

Type 11: with think lamellae, diameter is 10-20 μm.

Appendix table 17: Total recovered microremains from Grotta Fossellone Neanderthal remains and control samples.

					Starches						Phytoliths		Unsilicified plant microremains									
Identifier	Specimen	Tooth	Wt	Sampling date	Type 2	Type 5	Type 6	Type 7	Type 10	Other	Rondel	Indet. monocot	Grass cell	Stellate hair	Xylem	Vascular bundle	Indet. plant cells	Total numbers/mg	Total starch & phytoliths	Total starch & phytolith types	Menhinick's	Menhinick's/mg
Fossellone Neanderthal samples																						
FON1	Fossellone 3	LLM1	0.07	16th Mar 13					3						1			59.70	3	1	0.58	2.2
FON2	Fossellone 3	LLM2	0.1	16th Mar 13	4		1	1	1	1	1	1					1		9	6	2.00	2.6
Fossellone Control samples																						
FON3	Fossellone 3	Wash		16th Mar 13		17*																

Starch key

Type 1: Polyhedral with centric extinction cross oval with no fissures, cross arms are clear and straight. Diameter is 17 μm.

Type 2: Unknown shape, possible semi gelatinised eccentric starch, diameter is 90 μm.

Type 3: Spherical starch, typically with cross arms that are clear and straight or near straight. No discernible surface features. Diameter is 6-9 μm.

Type 4: Sub-polyhedral, cross arms are faint and straight.

Type 5: lenticular, cross arms clear and straight. Faint lamellae present. Diameter is 17 μm, (Possible Triticeae).

Type 6: large sub polyhedral. 15 μm or above.

Type 7: Very small polyhedral, no lamellae or fissures (Possible *Avena* sp. or bogbean).

Type 8: slightly eccentric.

Type 9: Highly eccentric.

Type 10: Very small starch with centric cross.

Appendix table 18: Total recovered microremains from Sima de las Palomas del Cabezo Gordo Neanderthal and control samples.

						Starches				Phytoliths				Other microremains											
Identifier	Specimen	Species	Tooth	Wt.	Sampling date	Type 1	Type 2	Other	Dmg/indet	Polyhedral multicell	Psilate	Shortcell	Bulliform	Parallelepiped	Indet. phytolith	Indet. particle	Possible fibre	Possible algae	Degraded glove starch	Total starch & phytoliths	Total starch & phytoliths types	Menhinick's index	Total starch & phytoliths/mg	Total starch & phytoliths types/mg	Menhinick's index/mg
SP45	SP45	Neanderthal	LRP3	0.08	25.July.15																		0	0	0
SP54	SP54	Neanderthal	LRC	0.10	20.July.15										1					1	1	1	9.8	9.8	3.1
SP83	SP83	Neanderthal	LRdm2	0.09	25.July.15																			0	0
SP78	SP78	Neanderthal	LLP4	n/a	30.June.11						1									1	1	1			
SP79	SP79	Neanderthal	ULI1	n/a	30.June.11																				
SP84	SP84	Neanderthal	LLM1	n/a	1.July.11									1	1	6			1	2	2	1.4			
SP84	SP84	Sediment on SP84	LLM1	n/a	1.July.11																				
SP1	SP1	Teeth consolidant	LRM3	n/a	22.Mar.12	44														44	1	0.2			
		Packing cotton		n/a	1.July.11											1	3	1	2	0	0				
SPF1S	SPF1S	Lagomorph		n/a	27.Mar.12			1				2		1		1				4	3	1.5			
SPF1D	SPF1D	Lagomorph		0.33	19.Jul.13											1				0	0				0
SPF2S	SPF2S	Carnivore	P	n/a	26.Mar.12															0	0				
SPF3	SPF3	Carnivore	M	n/a																0	0				
SPF4	SPF4	Carnivore	M	n/a	25.Mar.12												1		1	0	0				
SPF5D	SPF5D	Carnivore	M	n/a	8.Apr.12										1	1				1	1	1			
SPF5S	SPF5S	Carnivore	M	n/a	5th Apr 12				1											1	1	1			
SPF7	SPF7	Horse	LRM3	n/a	8th Apr 12						1	1							1	2	2	1.4			

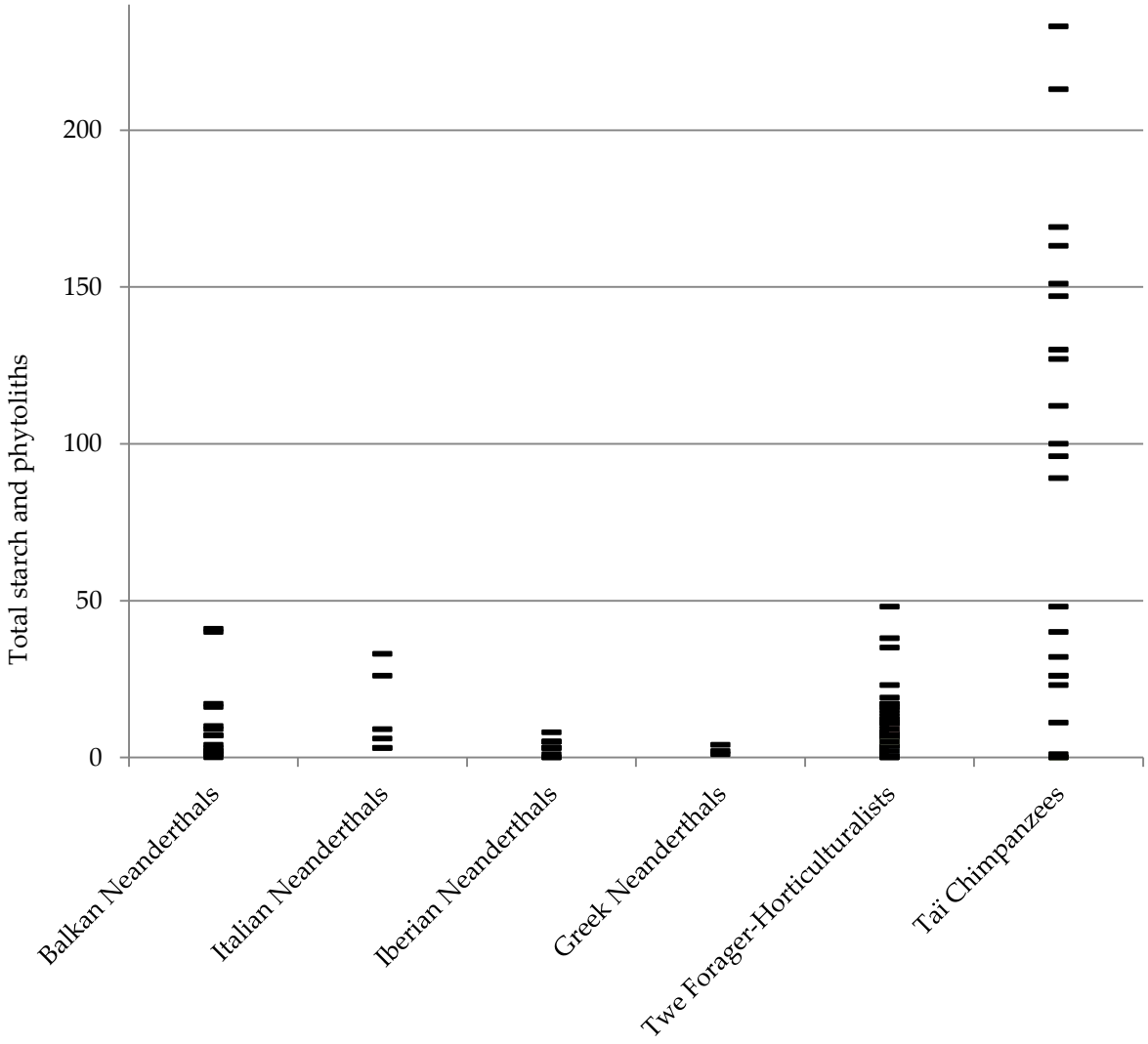
Starch key

Type 1 Polyhedral, moderate size, aggregating type, diameter is 8-25 μm.

Type 2 Lenticular.

Appendix table 19: Total recovered microremains from Kalamakia Cave Neanderthal remains samples.

						Starches				Phytoliths			Calcium oxalates									
Identifier	Specimen	Type	Tooth	Wt	Sampling date	Type 1	Type 2	Dmg/indet.	Possible starch	Rondel	Tabular	Indet.	block & sub	5 face	Irregular	Spicules	Total starch & phytoliths	Total starch & phytoliths types	Menhinick's index	Total starch & phytoliths/mg	Total starch & phytoliths types/mg	Menhinick's index/mg
KAL 3	KAL 3	Neanderthal	UlM3	2.87	12.Feb.13				3	1			1	1			4	2	1	1.40	0.70	0.59
KAL 5	KAL 5	Neanderthal	URP2	0.05	29.Jan.13						1				14		1	1	1	20	20	4.47
KAL 8	KAL 8	Neanderthal	URM2	n/a	26.Jan.13	1	1									1	2	2	1.41			
Starch key																						
Type 1		Lamellae, faint cross on cross polarization.																				
Type 2		Faceted.																				



Appendix fig. 3: Total numbers of starch and phytoliths in each Neanderthals site with reference groups (Twe forager-horticulturalists from Namibia and Taï Forest Chimpanzees) from Leonard et al., 2015 and Power et al., 2015.

Appendix table 20: Coefficients of statistical models.

Model	Term	Estimate	Std. Err.	Z value	P
Tests of effect of openness, MET and age on microremain diversity					
Random effect Poisson model	Intercept	0.918	0.756	1.205	0.228
	Openness mixed	1.189	1.259	0.945	0.345
	Openness open	1.241	0.500	2.481	0.013
	MET	-0.464	0.708	-0.656	0.512
	Age of fossil specimen	-0.432	0.278	-1.553	0.121
Random effect Poisson model with alternative chronology	Intercept	1.039	0.496	2.094	0.036
	Openness mixed	0.429	1.223	0.351	0.726
	Openness open	1.200	0.636	1.886	0.059
	MET	-0.017	0.445	-0.037	0.970
	Alternative age of fossil specimen	-0.198	0.241	-0.824	0.410

Appendix table 21: Western Eurasian economic plants that we identified as starch-rich plants. These plants are candidate plant food staples.

Family	Species	Common name
Anacardiaceae	*Pistacia* sp.	pistachio
Amaryllidaceae	*Allium ursinum*	ramson
Apiaceae	*Pastinaca sativa*	wild parsnip
Apiaceae	*Conopodium majus*	pignut
Alismataceae	*Sagittaria sagittifolia*	arrowhead
Alismataceae	*Alisma plantago-aquatica*	water plantain
Araceae	*Arum maculatum*	arum
Butomaceae	*Butomus umbellatus*	flowering rush
Brassicaceae	*Crambe maritima*	seakale
Dioscoreaceae	*Dioscorea communis*	black bryony
Fabaceae	*Pisum sativa*	common pea
Fabaceae	*Vicia sativa*	common vetch
Fabaceae	*V. sepium*	bush vetch
Fabaceae	*V. cracca*	tufted vetch
Fabaceae	*Lathyrus sylvestris*	everlasting pea
Fabaceae	*Lathyrus latifolius*	bitter pea
Fabaceae	*Lathyrus sativus*	grass pea
Fabaceae	*Lathyrus ochrus*	cyprus pea
Fabaceae	*Lathyrus cicera*	red pea
Fabaceae	*Lathyrus aphaca*	yellow pea
Fabaceae	*Vicia ervilia*	bitter vetch
Fabaceae	*Vicia hirsuta*	hairy tare
Fabaceae	*Vicia narbonensis*	purple broad vetch
Cyperaceae	*Cyperus longus*	sweet flag
Cyperaceae	*Cyperus esculentus*	tigernut

Cyperaceae	*Schoenoplectum* spp.	common clubrush
Corylaceae	*Corylus cf. avellana*	hazel
Liliaceae	*Lilium martagon*	turk's cap lily
Liliaceae	*Erythronium*	dog's tooth violet
Rosaceae	*Potentilla anserina*	silverweed
Rosaceae	*Sanguisorba officinalis*	great burnet
Papaveraceae	*Corydalis cava*	corydalis
Polygonaceae	*Bistorta officinalis*	european bistort
Equisetaceae	*Equisetum palustre*	marsh horsetail
Menyanthaceae	*Menyanthes trifoliata*	bogbean
Typhaceae	*Typha latifolia*	reedmace
Poaceae	*Avena elatior*	false oat-grass
Poaceae	*Avena sativa*	common oats
Poaceae	*Brachypodium pinnatum*	false brome
Poaceae	*Festuca* sp.	fescue
Poaceae	*Deschampsia cespitosa*	hair grass
Poaceae	*Echinochloa crus -galli*	barnyard grass
Poaceae	*Dactylis glomerata*	cocksfoot grass
Poaceae	*Elymus repens*	couchgrass
Poaceae	*Hordeum murinum*	wall barley
Poaceae	*Hordeum bulbosum*	bulbous barley
Fagaceae	*Castanea sativa*	sweet chestnut
Fagaceae	*Quercus ilex subsp. rotundifolia*	holm oak
Fagaceae	*Quercus coccifera*	kemes oak
Fagaceae	*Quercus faginea*	portugese oak
Smilacaceae	*Smilax aspera*	rough bindweed
Dennstaedtiaceae	*Pteridium* sp.	bracken
Ranunculaceae	*Ficaria verna*	lesser celandine
Nymphaea	*Nuphar lutea*	yellow waterlily
Nymphaea	*Nymphaea alba*	white waterlily
Trapaceae	*Trapa natans*	water caltrop

Summary

Dietary studies have transformed our understanding of hominin palaeobiology. Establishing the diet of Neanderthals has been crucial for understanding the basis of their ecology. The gradual expansion of research using macromammal remains has allowed substantial insights into Neanderthal meat consumption, hunting techniques, and social cooperation. More recent approaches in archaeological sciences such as dental wear, isotope, biomarker, and dental calculus analyses have allowed considerable strides to be made in building a more complete view of their dietary ecology, as they have raised further questions.

Zooarchaeological and isotopic research has shown that Neanderthals widely hunted large- and medium-size game. Further evidence of the importance of animal-based foods is also apparent from analysis of wear on teeth, which suggest that across their range Neanderthals relied heavily on animal foods. Recent foragers from northern environments, purportedly analogous to those in which some Neanderthal populations lived, have shown that staples other than animal foods may provide up to half of total dietary energy. However, researchers still debate the role of non-animal foods in Neanderthal subsistence. Palaeodiet studies have so far allowed only partial recovery of the Neanderthal diet, as there are biases against the survival of many foods particularly plants. An alternative means of exploring plant use is to retrieve microbotanical particles that become trapped in dental plaque as it calcifies into hard dental calculus. Some of this debris can be identified to specific plant taxa and plant parts. This methodology can provide direct evidence of foods and other substances that have entered the mouth. Yet it is still unclear whether the data generated does represent diet and other behavioural activities, because it could possibly be merely a product of background plant debris, which is unrelated to diet. To test the impact of these potential problems so that a working methodology could be applied to Neanderthals, my project assessed the reliability of dental calculus in reconstructing diets of individuals in two different populations. The first is an archaeological sample from southeastern Iberia, and the second is a skeletal population of West African chimpanzees. Using a comparative analysis, my project was able to identify the utility of dental calculus to shed light not only on diet, but also on other life history traits. The results from the Iberian assemblage prompted me to question whether dietary reconstructions based on traditional dental calculus studies can stand alone. Microremains from these populations exhibited evidence for behaviours such as water intake and inhalation of airborne suspensions, as well as

diet. This work also characterised some of the microenvironments that likely shield plant microremains from degradation. In the next stage of analysis, I assessed how accurately dental calculus can record long-term diet by examining plant microremains preserved in chimpanzees from a population with over two decades of documented dietary history. The project then built an extensive reference collection of Côte d'Ivoire forest plants for microremain identification, and compared the calculus microremains to the expected presence of plants based on examination of the feeding records. The results indicate that microremains accumulate as long-lived dietary markers and some can reflect the proportions of plants in the diet.

After consolidating dietary inferences obtained from the study of plant microremains in dental calculus, my dissertation analysed Neanderthal dental calculus from five archaeological sites to document variation in Neanderthal plant consumption. This identified reliable evidence of plant use across different regions. Observed remains were positively identified as Neanderthal foods by comparing plant microremains retrieved from calculus to a control dataset. We then used published literature and databanks with a substantial database of Eurasian plants to identify food plants across Neanderthal range. Contrary to expectations, when the results were compared with data from previous studies, we found the breadth of food plants with evidence of consumption was unrelated to Eurasian eco-geography. This suggests that although southern Neanderthals relied on plants considerably more than northern populations, Neanderthals in central and northern Europe still consumed a diversity of plants that are comparable with Neanderthals from southern territories. These findings open new perspectives on Neanderthal dietary ecology. Overall, Neanderthals were foragers that combined plant use with large-scale mammal hunting as part of a unique dietary niche adapted to Eurasia.

Samenvatting

Dieetstudies hebben ons begrip van de biologie van vroege mensachtigen getransformeerd. Vaststelling van het dieet van de Neanderthalers is van cruciaal belang geweest voor het begrijpen van hun ecologie. De geleidelijke ontwikkeling van onderzoek aan zoogdierresten heeft substantiële inzichten geleverd in de vleesconsumptie, jachttechnieken en sociale samenwerking van Neanderthalers. Hoewel recente benaderingen in de archeologische wetenschappen zoals tandslijtage, isotopen-, biomarker- en tandsteen-onderzoek hebben geleid tot aanzienlijke vooruitgang bij het verkrijgen van een meer compleet beeld van hun dieetecologie, hebben ze ook nieuwe vragen opgeworpen.

Zooarcheologisch en isotopenonderzoek heeft aangetoond dat Neanderthalers wijdverbreid jaagden op groot en middelgroot wild. Verder bewijs voor het belang van dierlijke voedingsmiddelen blijkt uit de analyse van tandslijtage, dat suggereert dat Neanderthalers over hun gehele verspreidingsgebied zeer afhankelijk van dierlijk voedsel waren. Recente jager-verzamelaars uit noordelijke gebieden, die onder ogenschijnlijk analoge omstandigheden leefden als sommige Neanderthalerpopulaties, hebben laten zien dat tot maximaal de helft van hun totale energie opname afkomstig is van niet-dierlijk voedsel. Desondanks bediscussiëren onderzoekers de rol van niet-dierlijk voedsel in het levensonderhoud van Neanderthalers nog altijd. Palaeodiëtaire studies hebben tot nu toe een incompleet beeld gegeven van het dieet van Neanderthalers vanwege een negatief effect op de preservering van sommige voedselresten, in het bijzonder dat van plantaardig voedsel.

Een alternatieve methode om het gebruik van planten te onderzoeken is door het bestuderen van microbotanische deeltjes die vast komen te zitten in tandplak als dit calcificeert tot tandsteen. Een deel daarvan kan geïdentificeerd worden tot specifieke plantentaxa en plantendelen. Deze methode verschaft direct bewijs voor voedsel en andere substanties die de mond binnen gekomen zijn. Echter, het is nog altijd onduidelijk of de data dieet en andere gedragsactiviteiten vertegenwoordigen omdat ze ook het gevolg kunnen zijn van plantendelen die ongerelateerd zijn aan dieet. Om de impact van deze potentiële problemen te testen, zodat een werkende methode kan worden toegepast op de Neanderthalers, onderzocht ik in mijn project de betrouwbaarheid van tandsteen in het reconstrueren van diëten van individuen in twee verschillende populaties. De eerste is een archeologische populatie uit Zuidoost-Iberië, en de tweede een populatie van West-Afrikaanse chimpanzees. Door vergelijkend onderzoek in mijn projects was het mogelijk het nut van tandsteenonderzoek voor diëtaire studies aan te tonen, maar ook met betrekking tot andere levensgeschiedeniskenmerken. De resultaten van de Iberische populatie

leidden me ertoe me af te vragen of dieetreconstructies gebaseerd op traditioneel tandsteenonderzoek op zichzelf kunnen staan. Microresten van deze populaties vertegenwoordigen bewijs voor de consumptie van water en de inhalatie van luchtdeeltjes , naast dieet. Verder karakteriseert dit onderzoek enkele micro-omgevingen die waarschijnlijk plantaardige microresten beschermden tegen degradatie. In de volgende fase onderzocht ik hoe nauwkeurig tandsteen het dieet kan reflecteren op de lange termijn door microresten te onderzoeken bij chimpansees uit een populatie met meer dan twee decennia aan gedocumenteerde dieetgeschiedenis. Vervolgens verzamelde het project een uitgebreide referentiecollectie van bosplanten uit Ivoorkust voor de identificatie van microresten, en vergeleek de geobserveerde microresten uit tandsteen met de verwachtte aanwezigheid van planten op basis van de dieetgeschiedenis. De resultaten geven aan dat microresten uit tandsteen accumuleren als dieetindicatoren over de lange termijn en dat sommigen het aandeel van planten in het dieet reflecteren.

Na het bevestigen van dieetreconstructies op basis van het onderzoek aan microresten uit tandsteen, analyseerde ik Neanderthalertandsteen van vijf archeologische vindplaatsen om variatie in het gebruik van plantaardig voedsel in Neanderthalers te documenteren. Dit resulteerde in betrouwbaar bewijs voor het gebruik van planten in verschillende gebieden. Waargenomen overblijfselen werden positief geïdentificeerd als Neanderthaler voedsel door het vergelijken van de plantenmicroresten uit tandplak met een controledataset. Vervolgens gebruikten we gepubliceerde literatuur en databases die een substantieel deel van de Euraziatische planten bevatten om plantaardig voedsel te identificeren voor het gehele verspreidingsgebied van de Neanderthalers. In tegenstelling tot onze verwachingen vinden we, als we onze resultaten combineren met data van voorgaande studies, dat de diversiteit van plantaardig voedsel met bewijs voor consumptie ongerelateerd is aan de Euraziatische ecogeografie. Dit suggereert dat hoewel zuidelijke Neanderthalers meer afhankelijk waren van plantaardig voedsel dan noordelijke populaties, Neanderthalers in Centraal en Noord-Europa wel een diversiteit aan planten consumeerden die vergelijkbaar was met die van Neanderthalers in zuidelijke gebieden. Deze resultaten geven een nieuw perspectief op de dieetecologie van Neanderthalers. In het algemeen waren Neanderthalers jager-verzamelaars die het gebruik van planten combineerden met het jagen op groot wild als onderdeel van een unieke niche aangepast aan Eurazië.

Acknowledgements

I am deeply grateful to my supervisor and group leader Amanda Henry. During my studies in the group, Amanda Henry supported my work and ensured my development, patiently to a fault. In no way could the project have advanced as smoothly without her foresight, expertise and generosity, even letting me use lab resources after my dissertation submission. I am in appreciate not just for giving me the opportunity to write a doctorate in the Plant Group but for sharing four years of formation. I am grateful to second supervisor, Domingo C. Salazar-García for who guided me through the PhD process. He always selflessly gave time to ensure every spontaneous deadline could be met. His contributions to my doctoral thesis and my formation are not easily summarised or quantified. Jean-Jacques Hublin deserves thanks for his insightful comments through my studies. He always made me feel welcome as a Research Group member hosted by the Department of Human Evolution. Wil Roebroeks, for his tips and mentoring along the way.

Aside from my supervisory team, many others contributed to the progress of the PhD. Fellow PhD candidate Stephanie who deeply enriched my perspectives on the evolution of nutrition. Chelsea Leonard on many occasions kindly gave her time to critique and develop my ideas and papers. Shira Gur-Arieh, for her grounding comments and pharmacological support.

This project was carried forward immeasurably by the support of the Department of Primatology and the Taï Forest Project staff. Roman Wittig's openness to arrange the collection of plants in the Taï Forest made the convoluted task of building a reference collection possible. I am indebted to Roger Kami Nabo and the other staff in the forest who took the time to collect the reference plants, dry fresh plants and return them to Leipzig. I also wish to note the support of the Ministère de la Recherche Scientifique and the Ministère de l'Environnement et des Eaux et Forêts of Côte d'Ivoire, Centre Suisse de Recherches Scientifiques at Abidjan, Côte d'Ivoire, the Office Ivorien des Parcs et Reserves, the Director of the Taï National Park for authorisation of this research. Utah Schwarz sorted out all the practicalities of sampling the chimpanzee skeletal collection. Julia Riedel answered many questions on working with Taï Chimpanzee observational data. Loki du Toit made it possible for me to use these observation records. Geraldine Fahy, Gottfried Hohmann and Tobias Deschner took the time to fill me in with much essential

background information and providing valuable plant samples. I am also thankful to the Head of Primatology Christophe Boesch who kindly allowed my sampling of the Taï Skeletal Collection.

Many helpful archaeological scientists assisted the project by advising on microremain and material identifications such as Marco Madella, Paschal Verdin, Sanjay Eksambekar, Arlene M. Rosen, Irwin Rovner Linda Perry, Angela Perri, Vera Aldeias, and Dan Cabanes. The extensive statistics and programming support from Colleen Stephens and Roger Mundry without whom I would not have complete the projects data analysis. Maria Bendžuchová helped by providing spectroscopy technical advice. I am also grateful to Philip Gunz, Layne Vashro, and Andre Strauss who also helped on data analysis and programming.

I am keen to mention Ian Reid of Nano Imaging and Material Analysis Centre at the University College Dublin for SEM-EDX analysis of many dental calculus samples. Pat O'Reilly of Nature First, genially identified spores that were found in certain dental calculus samples. A great number of people provided the archaeological contexts of the many sites where I sourced dental calculus. Authorities such as Bence Viola, Ivor Karavanić, Julià Maroto Genover, Philip Nigst and Fred Smith kindly gave the time to give all the background information the project required.

The diligence, professionalism and kindness of the group's technical staff Antje Hutschenreuther, Joerg Watzke, Simone Schmidt, Thomas Büdel, Annabell Reiner and Steffi Hess deserve a lot of credit. Their work unfailingly kept the labs and protocols running when other events took my attention. For the time spent outside the laboratories, I thank Victor Weiler, Silke Streiber, and Conny Schicke for administrative assistance and helping me adapt to Germany and Lukas Westphal for superb ICT support. Also helpful were, Roswitha Manning and Anneke Hendriks for Leiden University assistance. Marie Soressi, for support at the Faculty of Archaeology in Leiden University. Frido Welker, for translating my doctorate summary into Dutch and Karen Ruebens for QGIS advice.

I appreciate the archaeologists and curators who saw the value of this project and provided access to skeletal material for sampling. Michael J. Walker (University of Murcia, Spain) permitted access to the Sima de las Palomas del Cabezo Gordo material, and Mariano López helped to make our collaboration happen. Jadranka Lenardić, Dejana Brajkovic and Ivan Gusic (Croatian Academy of the Sciences, Croatia) allowed me to sample the Vindija hominin remains. Rosa Alsius (Farmàcia

Rosa Alisus in Banyolas, Spain) allowed me to access to the Banyolas mandible. Raffaele Sardell and Mauro Rubini (Servizio di Antropologia, Italy) permitted access to Grotta Guattari and Grotta Fossellone. Andreas Darlas (Greek Ministry of Culture) and Katerina Harvati-Papatheodorou (Eberhard-Karls-Universität Tübingen, Germany) permitted access to the Kalamakia remains. Joaquín Lomba, María Haber and Azucena Avilés for kindly allowed access to the Camino del Molino calculus samples. In addition, the project benefited from plant samples provided by Martin Freiberg from the Leipzig Botanical Gardens. The doctorate required drawing approaches and data from many different disciplines outside my training such as palaeoclimatology to take into account all the factors that affected Neanderthals. It is due to the advice of Dave Pollard, Robert Foley, Kathryn Fitzsimmons and William Davies that integrating palaeoclimatology approaches was successful.

A word of acknowledgement is needed for my friends and fellow Max Planck students and colleagues; Nicole Antonette del Rosario for helping me develop my thoughts thoroughly and for diligently proofreading my work, Cynthianne Debono Spiteri, Mariska Carvalho, Nadia Scott, Sylvio Tüpke, Liu Huan, Tao Chen, Marcello Mannino, Zewdi Tsegai, Collin Moore, Nina Doerschner, Dawit Desta, Nick Stephens, Viktoria Oelze, Stefanie Stelzer, Will Archer, Adeline Le Cabec, Sahra Talamo, and Vaidas Suncovas at the Max Planck Institute for Evolutionary Anthropology, who raised my spirits during the hard slog of the doctorate. Each made the institute a uniquely enriching place to work.

My family played a large role in writing this dissertation. I am appreciative to my brother John for proof reading many drafts along the way and Eunhee for her kindness. At this point I must acknowledge my parents John and Julie Power, whose endless encouragement above all motivated me. Their personal sacrifices for me not only made it all happen but have been an inspiration.

Contributions

Robert C. Power has designed the research with input from Dr Amanda G. Henry and Dr Domingo C. Salazar-García, done all lab work, data analysis, written the papers and interpreted results. Dr Amanda G. Henry and Dr Domingo C. Salazar-García have supervised this PhD. Both gave feedback and guidance along all steps of the process to Robert C. Power.

Contributions to each paper

Paper 1:

Assessing use and suitability of scanning electron microscopy in the analysis of micro remains in dental calculus

This paper was written following analysis of the dental calculus from two populations with multiple means of microscopy. As author, I developed the concept of comparing microremain data gathered from different methods of microscopy (optical microscopy/scanning electron microscopy and energy-dispersive X-ray spectroscopy). It allowed me to develop an approach to assess the potential of energy-dispersive X-ray spectroscopy to detect starch exposed to salivary amylase. I performed all sampling of dental calculus and all microscopy and spectroscopy, but scanning electron microscopy and spectroscopy was conducted with assistance of Ian Reid for SEM–EDX analysis (NIMAC UCD). Roman Wittig and Domingo C. Salazar-García provided materials. I prepared and wrote the manuscript, with input from all authors and guidance of my supervisors (A.G.H and D.C.S.G.).

Paper 2:

Dental calculus evidence of Taï Forest Chimpanzee plant consumption and life history transitions

This project was conducted in four steps- initially I employed Taï observational records to develop a chimpanzee diet profile. This was used to build an extensive reference collection of the microremains present in Taï Chimpanzee diet, allowing me to create a replicable method to classify microremains frequent in their diet. Lastly, I analysed chimpanzee dental calculus and matched identified starch and phytoliths to dietary records. I sampled calculus and conducted microscopy of all dental calculus and plant reference material. Roman Wittig

advised on using Taï Forest data to meet research goals, and organised the collection of plant reference samples from the Taï Forest National Park. This reference collection was supplemented with plants from the Institute of Botany that were supplied by Martin Freiberg. Geraldine Fahy supplied some useful additional plant reference samples. I conceptualised the statistical approach to identifying microremains found in dental calculus with input from Amanda G. Henry, Colleen Stephens and Roger Mundry, these last two helped me to design the statistical analysis methodology. I performed all of the analysis required for the project. This was completed in a framework devised in with liaison with Amanda G. Henry, Roman Wittig and Domingo C. Salazar-García. I compiled the findings, wrote the paper, and edited it along with all authors. Amanda G. Henry and Domingo C. Salazar-García, supervised the process.

Paper 3:

Dental calculus indicates widespread plant use within the Neanderthal dietary niche

My contribution to this paper involved designing and leading the project at all stages with support of Amanda G. Henry and Domingo C. Salazar-García. This study of Neanderthal dental calculus required traveling for sampling to a variety of museums and research institutions that curated Neanderthal and fauna remains. The Kalamakia teeth were sampled in Leipzig by Amanda G. Henry, and the Sima de las Palomas del Cabezo Gordo samples were taken in the University of Murcia by Amanda G. Henry and Domingo C. Salazar-García. I examined each sample of dental calculus using microscopy. I identified all finds with plant reference material and prepared the results. Drs. Domingo C. Salazar-García, Mauro Rubini and Jadranka Lenardic assisted with interpreting archaeological site data. I then accompanied pollen, charcoal and fauna with palaeotemperature simulations from the Stage Three Project, and used it to build a model of dietary breadth with the guidance of Colleen Stephens and Roger Mundry. I wrote the article with the guidance of Amanda G. Henry, Domingo C. Salazar-García. Amanda G. Henry and Domingo C. Salazar-García helped me revise and finalised the article.

Curriculum vitae

The author of this dissertation, Robert C. F. Power, was born in Waterford in Ireland. After receiving his Leaving Certificate at Waterpark College in 2007, he read for a Single Honours Bachelor in Arts (Archaeology) in University College Cork, National University of Ireland. In Cork he began his interest in ancient diets by studying macro and microbotanical research. During this time participated in archaeological excavations of prehistoric and historic sites in Ireland and Canada. In addition, he has carried out post-excavation analysis as an archaeobotanical research assistant at the Discovery Programme in Dublin, Ireland. He was also an officer in the University's Medieval and Renaissance Society. His interest in the complexity of human interactions with the natural world led him to specialise in Environmental Archaeology. He pursued this in 2010 with a Master of Science in Environmental Archaeology from the Institute of Archaeology, University College London in the University of London. He received his Master of Science in 2011 with a dissertation on using phytoliths from Raqefet Cave in Israel to infer plant use by Natufian foragers. After the Master of Science, he started his PhD in 2011, focusing on dental calculus in dietary studies and reconstructing Neanderthal plant use in the Plant Foods in Hominin Dietary Ecology Research Group at the Max Planck Institute for Evolutionary Anthropology. In addition to the doctorate research, he has presented his work at international conferences and published his work in several peer-reviewed, international journals such as the Journal of Anthropological Archaeology, Quaternary International and the Proceedings of the National Academy of Sciences. He is now employed as a research fellow at the Max Planck Institute for the Science of Human History in Jena in Germany.