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

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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.