



Having the stomach for it: a contribution to Neanderthal diets?



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ABSTRACT

Due to the central position of diet in determining ecology and behaviour, much research has been devoted to uncovering Neanderthal subsistence strategies. This has included indirect studies inferring diet from habitat reconstruction, ethnographic analogy, or faunal assemblages, and direct methods, such as dental wear and isotope analyses. Recently, studies of dental calculus have provided another rich source of dietary evidence, with much potential. One of the most interesting results to come out of calculus analyses so far is the suggestion that Neanderthals may have been eating non-nutritionally valuable plants for medicinal reasons. Here we offer an alternative hypothesis for the occurrence of non-food plants in Neanderthal calculus based on the modern human ethnographic literature: the consumption of herbivore stomach contents.

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1. Introduction

Diet is one of the most fundamental determinants of any animal's ecology and behaviour. The nature and availability of resources has an impact on activity pattern, time budgets, locomotion, predation risk, group size and organization, population density, and may even play a role in the development of cognitive abilities (Fleagle, 1982; Martin, 1982; Rose, 1982; Kinzey and Cunningham, 1994; Fleagle, 1999). This centrality of diet has long been recognized in zoology, and to a lesser extent appreciated in palaeoanthropology (Grine, 1982; Hockett and Haws, 2003; Gamble and Boismier, 2012), resulting in a considerable body of research devoted to reconstructing the diets of extinct hominins. Given the relative abundance of archaeological and palaeoanthropological evidence, and our enduring fascination with our closest relatives, nowhere is this more truer than for Neanderthals. The most recent addition to the suite of methods used to reconstruct hominin diet is the analysis of dental calculus (see below). The preservation of plant remains in the mineralized plaque of Neanderthals has been interpreted as evidence of the consumption of vegetable foods (Henry et al., 2011; Hardy et al., 2012), and also for self-medication (Hardy et al., 2012). Whilst the former assertion is highly probable, and the latter certainly possible, we suggest another potential reason for the presence of these remains. Ethnographic accounts of

traditional subsistence strategies in a wide variety of cultural groups document the practice of consuming stomach contents (chyme). The potential nutritional benefits of chyme consumption are clear, especially in high latitude populations living in vegetable-poor environments, to say nothing of possible taste and cultural factors. Chyme consumption could lead to the preservation of plant remains within dental calculus. We therefore suggest that caution is required in the interpretation of such remains in the fossil record.

2. Methods of reconstructing Neanderthal diets

Historically, hominin diets have been inferred indirectly from reconstructions of local environments (e.g. Shipman and Harris, 1988; Vrba, 1988). Palaeoecological reconstructions can be problematic as it has been suggested that the environment inhabited by Neanderthals may have no modern analogue (Stewart, 2005). Nevertheless, it is possible to make broad statements such as that, in the cold environments in which many Neanderthals lived, animals would have been the key food source (Richards et al., 2000). This assumption has led to the use of dietary analogies based on recent hunter-gatherers from high latitudes, for whom the same is true (e.g. Marean and Yeun Kim, 1998; Speth, 2010; Hockett, 2011; Gamble and Boismier, 2012; Speth, 2012). Potential diet does not necessarily translate directly to actual diet, however, since we know from optimal foraging theory that hunter-gatherers tend to favour a small number of the edible foodstuffs in their environments, based on decisions balancing energetic and social costs and benefits (Berbesque and Marlowe, 2009; Marlowe and Berbesque, 2009;

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Gamble and Boismier, 2012). Furthermore, these decisions may differ between groups in similar environments, something likely to be exacerbated when comparisons are between species. For example, dental microwear analyses have shown that the Tigara from Alaska have very different wear profiles to Neanderthals, due to abrasives used in the former group's food preparation (El Zaatari et al., 2011).

Faunal remains from archaeological sites have been analysed in an attempt to assess diet more directly. This approach encompasses analyses of species presence in assemblages, the frequency and distribution of body parts, and also signs of human modification such as cut-marks or burning (e.g. Marean and Yeun Kim, 1998; Stringer et al., 2008; Braun et al., 2010). This suite of methods has been very influential, but the presence of a species in an assemblage does not necessarily require hominin agency. Bones may be brought in by other carnivores, washed in by water, or may simply be the remains of animals that once inhabited the site. In some cases anthropogenic, but non-dietary reasons, have been posited for the presence of faunal remains in sites, for example bird material from Gibraltar and Italy (Peresani et al., 2011; Finlayson et al., 2012). Transport decisions may bias accumulations towards smaller animals, as large animals may be preferentially butchered at the kill site, and only their meat brought back to the home base (Rabinovich and Hovers, 2004). If this is an important issue for hominins, it may create or exacerbate differences between species, since it is likely that Neanderthals were stronger on average than modern humans (De Groote, 2011). Therefore, in the absence of additional technology, they might have been more likely to transport large prey back to living sites, confounding evidence as to whether there is a difference between species in terms of exploitation of small game. Head and foot dominated assemblages have been used to infer scavenging, but it has been argued that these may sometimes be the result of biased collecting or analysis (Marean and Yeun Kim, 1998).

In addition to these issues with faunal remains, all dietary reconstructions based on remains from living sites are unavoidably biased in one major respect: plant remains generally survive less well in the fossil record, and may also not be targeted in archaeological retrieval. Fragments of plants (especially the tougher elements, such as phytoliths and seeds) are sometimes found in sediments (Madella et al., 2002; Lev et al., 2005; Devos et al., 2009), but it is impossible to reliably infer what these may have been used for, or if they are even the result of hominin agency. The pollen in the famous Shanidar IV Neanderthal burial, initially taken as evidence for grave goods and subsequently shown to be most likely the result of rodent caching (Gargett, 1989; Sommer, 1999), is a case in point.

In recent years, an increased appreciation of the importance of vegetable foods in hominin diets (Hardy et al., 2001; El Zaatari et al., 2011; Fiorenza et al., 2011; Hardy and Moncel, 2011; Hardy et al., 2012) has led to the development of methods aimed at detecting the consumption of plants. Microscopic use-wear, and even plant residues, can be found on stone tools, indicating activity that involved vegetable material (Hardy et al., 2001; Hardy and Moncel, 2011), but it does not necessarily follow that this is evidence of food processing. In a mixed residue and use-wear analysis of tools from Starosele and Buran Kaya III in the Ukraine (Middle and early Upper Palaeolithic) evidence of processing woody and non-woody plants was found (Hardy et al., 2001). However, the authors pointed out that, not only can non-food related plant processing not be ruled out, but also that some of the starch grains seem to have been used as glue in a hafted tool, rather than pointing to plant processing using the finished tool (Hardy et al., 2001).

In order to overcome the problem of whether plant processing is for dietary or non-dietary purposes, hominin remains themselves have been analysed. Teeth survive well in the fossil record and can

hold evidence of an individual's life across multiple timescales. Dental macrowear accumulates over an individual's lifetime and thus provides a longitudinal sample of diet (Fiorenza et al., 2011). Analyses using optical 3D topometry have been used to show ecogeographic dietary variation between different groups of Neanderthals, and Upper Palaeolithic *Homo sapiens*. Both species showed a tendency towards more varied diets in warmer climates and more protein-based diets at higher latitudes (Fiorenza et al., 2011). Similar results were obtained by researchers examining dental microwear signatures, which change very quickly and reflect a snapshot of diet over a short period before death (El Zaatari et al., 2011). Neanderthal microwear patterns were compared to recent hunter-gatherers with known diets. As a group, Neanderthals were found to be most similar to populations subsisting mainly on meat, but Neanderthals from wooded environments were found to have a more mixed diet, with a higher plant component than those from mixed or open environments (El Zaatari et al., 2011).

One should be wary of assuming that all tooth wear is dietary; it has long been hypothesized that the severe anterior tooth wear seen in many Neanderthals is the result of paramastication, using the teeth as tools (Smith, 1983; Rak, 1986; Demes, 1987; Spencer and Demes, 1993). Furthermore, a recent study by Lucas et al. (2013) has shown that accidentally consumed quartz dust may in fact be a major contributor to tooth wear, confusing links between wear patterns and inferred diet. These authors propose that the case of the robust australopithecine *Paranthropus boisei*, with its heavy macroscopic tooth wear, yet shallow scratched microwear, is an example of the effect of quartz rather than vegetation. They suggest that there may be many other examples where dental adaptations thought to be dietary in nature may instead result from a high volume of dust ingested with food.

Animal matter, seeds, pollen and phytoliths recovered from coprolites (fossilized faeces) have been used to reconstruct diet (Callen, 1963; Holloway and Bryant, 1986; Devos et al., 2009). Coprolite analyses might be thought to avoid some of the problems of tooth-wear analysis; it seems fairly safe to conclude that if something is in faeces it must have been eaten and passed through the digestive system, but this is not necessarily the case. Wind-borne pollen, as well as pollen from food plants, is usually present in coprolites. Consequently it is generally judged to be safe to infer consumption from pollen only when the species in question is zoophilous. This makes inferences about the consumption of windborne species problematic (Bryant, 1974; Holloway and Bryant, 1986). Phytoliths may also adhere to faeces after excretion, rather than originating in food, but the removal of the outer layer of a coprolite generally overcomes this problem (Bamford et al., 2010). Despite these issues, coprolite-based dietary reconstruction has been profitable in reconstructing diets of later periods (e.g. Bryant, 1974; Horrocks et al., 2004). Notwithstanding the existence of a number of coprolites from as far back as the Middle Palaeolithic (Jouy-Avantin et al., 2003), however, this method is rarely used in reconstructing diet from extinct hominin sites because their age means that methods normally used to distinguish the originator of the coprolite are unreliable (Trevor-Deutsch and Bryant, 1978; Jouy-Avantin et al., 2003).

Stable isotopes are a record of what an individual actually ate over a period of time, obtained from measuring the ratios of isotopes of carbon and nitrogen incorporated into the collagen of bones and teeth from food (Richards et al., 2000; Bocherens et al., 2005; Richards and Trinkaus, 2009). Isotope analysis from Neanderthal sites such as Saint-Césaire, (Bocherens et al., 2005), Vindija (Richards et al., 2000), Les Pradelles (Bocherens et al., 2005), Engis, and Spy (Bocherens et al., 2001) indicate a high protein, high trophic level diet, similar to or even exceeding that of a wolf or hyaena. This has been interpreted as evidence that Neanderthals were top

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