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Buck, LT and Stringer, C (2013) Having the stomach for it: a contribution to Neanderthal diets? Quaternary Science Reviews, 96. pp. 161-167. ISSN 0277-3791

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

Laura T. Buck[a, b, *] and Chris B. Stringer[a]
[a]Earth Sciences Department, Natural History Museum, Cromwell Road, London, SW7 5BD.
[b]Centre for Evolutionary and Ecological Anthropology, University of Roehampton, Holybourne Avenue, London, SW15 4JD.

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 consider this argument and the benefits of calculus analysis in the context of the current state of Neanderthal dietary research, and 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.

* Corresponding author. Email: l.buck@nhm.ac.uk. Tel: 00 44 207 942 7004

1. Reconstructing Neanderthal diets
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 relatively large body of archaeological and palaeoanthropolgical evidence, and our enduring fascination with our closest relatives, nowhere is this more true than for Neanderthals.

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 exact 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 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, 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; 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. Animal bones may be brought in by other carnivores, washed in by water, or simply be the remains of animals that once inhabited the site. In some cases anthropological, but non-dietary reasons, have been posited for the presence of faunal remains, for example bird remains 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 than modern humans (De Groote, 2011). Therefore, in the absence of additional technology, they would 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.

Over the last few decades, an increased appreciation of the importance of plant 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 vegetable remains. 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 II in the Ukraine (Middle and early Upper Palaeolithic) evidence of processing of 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 found seem to have been used as glue in producing 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 a record 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 within different groups of Neanderthals, and Upper Palaeolithic *H. 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 with 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 closed environments (El Zaatari *et al.*, 2011).

One should be wary of assuming that all toothwear is dietary; it has long been hypothesized that the severe anterior toothwear seen in many Neanderthals is the result of paramastication, or 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 toothwear, confusing links between wear patterns and inferred diet. These authors propose that the case of the robust australopithecine *Paranthropus boisei*, with its heavy macroscopic toothwear, 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 all 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 toothwear 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. Windborne 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 of pollen found is zoophilous, rather than wind-pollinated, making 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 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) 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 predators, skilled at hunting large mammals (Richards *et al.*, 2000; Bocherens *et al.*, 2001; Bocherens *et al.*, 2005; Richards and Trinkaus, 2009).

Nitrogen and carbon analyses are only informative about proteins, therefore plant signatures (and other high-calorie, low protein food sources) are unlikely to be detected (Bocherens *et al.*, 2005; Richards and Trinkaus, 2009). Additionally, such studies are limited by the fossil samples analysed; Neanderthals in more temperate regions, or climatic phases, seem to have had different diets to those living in colder environments with a necessary focus on carnivory during severe winters (El Zaatari *et al.*, 2011; Fiorenza *et al.*, 2011). Climate change may also confound isotope analysis; carbon and nitrogen values vary with temperature and aridity, and so different climatic conditions associated with different fossils may complicate comparison of isotope results (Richards and Trinkaus, 2009). This may be exacerbated by the abrupt climate changes in the Pleistocene (Schmidt and Hertzberg, 2011) and imprecise dating for some fossils from this period. Ratios of C^{12} to C^{13} isotopes can be used to distinguish between ingestion of plants using C3 and C4 pathways for photosynthesis (or between prey animals that have fed on grasses or woody plants in the case of carnivores), but C4 plants generally inhabit warm, arid environments, so this distinction is not very useful in the case of Neanderthal dietary reconstruction (Richards and Trinkaus, 2009).

2. Calculus studies

In the most recent innovation in fossil hominin dietary research, food particles from calculus (mineralized dental plaque that often survives well on fossilized remains) have been analysed (Henry *et al.*, 2011; Hardy *et al.*, 2012). Starch grains and phytoliths were recovered from Neanderthal remains from Shanidar (Iraq) and Spy (Belgium), which were identified as belonging to grasses related to the barley family, legumes, date palms, and underground storage organs (Henry *et al.*, 2011). A second study found starch grains, phytoliths, and chemical compounds indicative of plant foods and fire smoke in calculus from Neanderthals from El Sidrón in Spain (Hardy *et al.*, 2012). As with dental wear, Henry *et al.* note that calculus would preserve evidence of non-dietary plants put into the individual's mouth, as well as food (2011), and Hardy *et al.* (2012) show evidence for oil shale or bitumen as well as evidence for vegetable foods, which they relate to hafting. This demonstrates again that not all evidence found in the mouth should be considered to represent food. Despite this possible limitation however, the results from this new source of data are exciting.

Calculus studies have had an important impact on the understanding of Neanderthal diets. Evidence of diet obtained from the very teeth of an individual is more likely to be an accurate record of what was consumed than some of the more traditional methods described above. We can at least say that remains in calculus come from something put into the individual's mouth, and greater accuracy in plant identification is possible than for dental wear and isotope studies, with phytoliths, organic compounds, and starch grains enabling reasonable inferences about species presence (Henry *et al.*, 2011; Hardy *et al.*, 2012). Furthermore, calculus is likely to be preserved on many fossils already in collections, offering a wealth of untapped potential evidence for dietary composition.

Calculus studies have contributed to a growing body of evidence against the distinction in dietary breadth between Neanderthals and modern humans, by presenting evidence of the importance of vegetable foods to Neanderthals (Hardy, 2010; Henry *et al.*, 2011). This area continues to be subject to heated debate (e.g. Hardy *et al.*, 2001; Hockett and Haws, 2003, 2005; Richards and Trinkaus, 2009; Hardy, 2010; El Zaatari *et al.*, 2011; Fiorenza *et al.*, 2011; Hardy and Moncel, 2011). The isotope data (as discussed in Section 1) suggest Neanderthals were top predators, and some very recent papers have continued to suggest that a failure to exploit small game, resulting in a less diverse diet, could have been instrumental in Neanderthal extinction (Fa *et al.*, 2013). However, some sites do preserve substantial evidence of small game and marine resource exploitation (e.g. Stringer *et al.*, 2008; Gaudzinski-Windheuser and Roebroeks, 2011), and there is much to suggest considerable plant use in Neanderthal sites (Madella *et al.*, 2002; Hockett and Haws, 2003; Lev *et al.*, 2005; Hardy, 2010; Fiorenza *et al.*, 2011; Hardy and Moncel, 2011; Henry *et al.*, 2011; Hardy *et al.*, 2012). Furthermore, it seems likely that protein consumption to the levels suggested by some analyses would have been injurious to Neanderthal health (see Section 5).

Implications from calculus studies for levels of meat consumption are equivocal; the evidence for fat and protein from meat is low in the El Sidrón sample (K. Hardy *et al.*, 2012). This is surprising, given nitrogen values (Wood *et al.*, 2013) that are similar to those which have been interpreted as showing high levels of carnivory at other sites (see Bocherens *et al.*, 2005). There is evidence of methylation (cooking) of lipids in one individual, but no evidence that those lipids were of animal origin. Another specimen shows organic compounds indicative of protein, but these are not accompanied by lipids, as would be expected from the consumption of meat (Hardy *et al.*, 2012).

The evidence for cooked plants preserved in calculus from smoke-related compounds, methylated lipids, and heat-cracked starch grains indicates a level of sophistication in the Neanderthal diet beyond what is often considered (Henry *et al.*, 2011; Hardy *et al.*, 2012). Henry *et al.* (2011) also point out that several of the plants they identified from the calculus would require relatively complex processing before consumption. Thus this new method provides support for planning and breadth in dietary practices, which run counter to many ideas about Neanderthal diet and cognition. Perhaps most intriguing of all the results from calculus analyses to date, however, is the suggestion by Hardy et al. (2012) that some of the evidence from El Sidrón points to medicinal plant use.

3. Remains of "medicinal" plants in calculus?

In the calculus of one individual from El Sidrón, Hardy *et al.* (2012) found evidence for the ingestion of "medicinal" plants, suggested to be yarrow and chamomile, based on carbohydrate compounds. The authors propose that these plants were not simply food, due to their bitter flavour and lack of nutritional value. This is an interesting suggestion in light of the fact it is known that at least one of the Neanderthals from El Sidrón had the gene which in *Homo sapiens* allows us to taste bitter flavours (Lalueza-Fox *et al.*, 2009).

Yarrow and chamomile both have long histories of medicinal use in *H. sapiens.* Chamomile is renowned today for its calming and mild analgesic properties, and it has also been used to treat common complaints such as stomach pain, asthma, bites and stings, diarrhoea, and skin inflammations (Hatfield, 2004; van Wyk and Wink, 2004). Yarrow's main use is clear from its common name ("soldiers' wound-wort"), but as well as being antiseptic and anti-inflammatory it has long been used to treat indigestion, toothache, fevers, and has been taken as a general tonic (Hatfield, 2004; van Wyk and Wink, 2004). As Hardy *et al.* (2012) point out, other primate species are known to self-medicate (e.g. Huffman, 2003), so it would not be surprising if Neanderthals were also capable of this kind of botanical knowledge. This is not the only explanation, however.

We suggest instead that plants of no nutritional value to hominins (and perhaps also those that needed processing to be rendered edible) could have been ingested indirectly via the consumption of the stomach contents of herbivorous prey. This is not the first time it has been suggested that Neanderthals may have consumed the stomachs of their prey (Speth, 2010; Hockett, 2011; Speth, 2012), but to our knowledge, the possibility of this practice confounding dietary reconstructions has not been acknowledged. It is known however, that phytoliths occur in the coprolites of carnivores with herbivorous prey due to the consumption of the digestive system of the herbivore (Bamford *et al.*, 2010), which could confuse dietary analyses if this source of plant matter was not considered.

4. The ethnographic evidence

The consumption of prey stomach contents was historically widespread amongst non-agricultural peoples following traditional subsistence strategies. Ethnographic accounts come from high latitudes (the Inuit [Nansen, 1893; Sollas, 1911; Fediuk, 2000; Andersen, 2005], the Cree [Corrigan, 1946]), temperate regions (Blackfoot [Lee and Daly, 2004] and Lakota [Lame Deer and Erdoes, 1972]), and hot, arid regions (Australian Aborigines [O'Dea *et al.*, 1991], the Damara and KhoeSan [Low, 2009], and the Kuria [Peterson and Walhof, 2002]). Although this is a practice most associated with hunter-gatherers, it is also recorded amongst pastoralists (such as the Kuria, from Kenya and Tanzania [Peterson and Walhof, 2002]). A wide range of species' stomachs are consumed, reindeer is the most reported (Nansen, 1893; Sollas, 1911; Fediuk, 2000; Andersen, 2005), but ringed seal, ptarmigan, arctic hare, beluga, bearded seal, narwhal, and walrus are also recorded as being part of the traditional Inuit diet (Fediuk, 2000; Andersen, 2005; Speth, 2012). The Damara and KhoeSan of the Kalahari consume the stomach contents of ostrich, kori bustard, and porcupine (Low, 2009) and Native American groups who depended on buffalo ate stomach and stomach contents as part of their sacred use of the entire body (Lame Deer and Erdoes, 1972; Lee and Daly, 2004). Thus it is not only ruminants, nor even herbivores, which are favoured.

The following quote describes the practice in the group who are most famous for it, the Inuit (previously referred to as Eskimo):

> "One of their greatest delicacies is the contents of a reindeer's stomach. If a Greenlander kills a reindeer, and is unable to convey much of it home with him, he will, I believe, secure the stomach first of all; and the last thing an Eskimo lady enjoins upon her lover, when he sets off reindeer-hunting, is that he must reserve for her the stomach of his prey. It is no doubt because they stand in need of vegetable food that they prize this so highly, and also because it is in reality a very choice collection of the finest moss and grasses which that *gourmet*, the reindeer, picks out for himself. It has undergone a sort of stewing in the process of semi-digestion, while the gastric juice provides a somewhat sharp and aromatic sauce. Many will no doubt make a wry face at the thought of this dish, but they really need not do so. I have tasted it, and found it not uneatable, though somewhat sour, like fermented milk. As a dish for very special occasions, it is served up with pieces of blubber and crowberries." (Nansen, 1893).

This illustrates several of the key reasons people may have for consuming the stomachs of prey animals: reasons of taste, culture, or nutrition.

5. Why eat stomachs and their contents?

Strange as it might seem to modern Western palates, stomach contents are often described in ethnographic accounts as a delicacy, something sought after. It seems that the piquant taste of the digestive juices was prized as enlivening every day diet (Lame Deer and Erdoes, 1972; Fediuk, 2000; Speth, 2010, 2012). Thus bitterness does not preclude an item from being favoured as food. An elderly Greenland Inuit informant of Fediuk's vividly illustrates that stomachs and stomach contents were traditionally eaten for more than their nutritional value, and are missed even when other foods are available: "Today, when she craves one of her favourite foods, ringed seal pup stomach, she purchases Philadelphia cream cheese instead."(Fediuk, 2000). In such cases, the consumption of such traditional foods may play a part in reinforcing cultural identity as well as being sought after for taste, as described by Lame Deer, a Lakota medicine man (Lame Deer and Erdoes, 1972).

The consumption of stomach contents is ascribed a ritual or spiritual value in several cultures. This may be related to how the animal is butchered and eaten:

> "…The chyme [partly digested food from the stomach] is then eaten by other elders or sprinkled over a person who has been rendered unpropitious by some misfortune. For the Kuria, eating the chyme is eating the life of the animal; it transfers to the taker the vital force of the slaughtered animal" (Peterson and Walhof, 2002).

Or it may be bound up in why the stomach contents are eaten: the Damara consume the stomach contents (and dung, which may also preserve plant fragments) of ostrich and kori bustard in the treatment of various ailments, including dehydration, malaria, and burns. These birds are perceived to have medicinal power drawn from their size and eating habits. Similarly, porcupine stomach is prized for its potency amongst KhoeSan because of the animal's diet of medicinal plants (Low, 2009).

Lame Deer also describes the perceived health benefits of eating stomach contents:

> "In the old days we used to eat the guts of the buffalo, making a contest of it, two fellows getting hold of a long piece of intestines from opposite ends, starting chewing toward the middle, seeing who can get there first; that's eating. Those buffalo guts, full of half-fermented, half-digested grass and herbs, you didn't need pills and vitamins when you swallowed those."(Lame Deer and Erdoes, 1972).

There are in fact very good nutritional reasons for eating stomach contents, particularly for populations living at high latitude, where plant food is scarce. More than 50 organic (vitamins) and non-organic (minerals) non-caloric nutrients are necessary for optimal maintenance and growth in humans. Vitamins and minerals are both essential for human metabolism, and minerals also play a vital role in cell structure (Hockett and Haws, 2003). Vegetable foods are a source of important nutrients, including vitamin E, C, and the precursor to vitamin A, which are not present or are present in low concentrations in animal foods. Some of these nutrients may be obtained from raw liver, but consuming sufficient amounts of liver to maintain adequate vitamin C and E carries the risk of hypervitamintosis from potentially toxic levels of vitamin A (Hockett and Haws, 2003). Thus, alternative sources of nutrients must be sought, and vegetable matter predigested by herbivores (reindeer stomach contents) is a key source of vitamin C (Fediuk, 2000; Andersen, 2005) and minerals, particularly manganese (Andersen, 2005), for the Inuit, who inhabit an environment with very little plant life.

Another potentially crucial reason for the consumption of herbivore stomach contents is that it is a rich source of carbohydrates. Reindeer stomach is the best source of carbohydrates (with the exception of berries, which are equally rich in carbohydrates, but more seasonal) in the Greenland Inuit diet (Andersen, 2005). Humans cannot live healthily on a diet of more than approximately 40% protein, and therefore the availability of carbohydrates and/or fat can be a limiting factor in energy intake (Cordain *et al.*, 2000; Hardy, 2010; Speth, 2012). This physiological 'protein ceiling' results from the inability of the liver to synthesise infinite amounts of urea. Excess protein leads to a build-up of amino acids and ammonia, probably causing symptoms of what has been anecdotally referred to as "rabbit starvation" (Cordain *et al.*, 2000). Part-digested vegetation in stomach contents also contains some fat (O'Dea *et al.*, 1991), and although this is not high compared to other food items in the Inuit diet (Andersen, 2005), it may have been of greater importance to a species which relied less heavily on marine mammals than the Inuit. We cannot be sure that Neanderthal metabolism functioned in the same way as that of modern humans, but given how closely related the two species are (able to interbreed to at least some extent [Green *et al.*, 2010]), it seems likely that it would be very similar.

These ethnographic accounts demonstrate how common the practice of consuming the stomach of prey has been in recent human history; this is not an unusual dietary item in terms of global food practices. Given the demonstrable benefits of consuming stomach contents, it seems likely that Neanderthals would have eaten this, at least on occasion. Even if the contents of the stomach are not eaten intentionally, part-digested plant material may often remain in the stomach and tripe, and be eaten along with it. From this description of kangaroo butchery in Australia, one can imagine how food ingested by the animal might come to be eaten by the human hunter, and so how plant remains from this source might end up in human calculus.

> "A short incision, some 60-100mm is then made down the length of the lower stomach and the intestines are pulled out and heaped onto the bushes…The stomach is opened and the contents emptied out…the tripe is roughly cleaned with the fingers" (Palmer and Brady, 1991).

Similarly, many groups use the stomach and intestines as vessels, particularly for water-carrying and cooking (Tannahill, 1988; Speth, 2012), and the level of cleaning which is used is likely to leave traces of stomach contents inside the vessel, which could then be secondarily ingested:

> "Long before the advent of pottery and bronze there was one kind of container that was widely distributed, naturally waterproof, and heatproof enough to be hung over, if not in, the fire. This was an animal stomach." (Tannahill, 1988: 14-16).

6. Impact of secondary ingestion on plant material in calculus

The vegetable remains found in carnivore calculus that derived from herbivorous prey would depend on the species of herbivore consumed, and the stage of digestion at which the prey was caught. However, it is reasonable to assume that the more resistant plant components would withstand the digestive processes of the herbivore, enabling them to be indentified after secondary ingestion by a carnivore. Phytoliths (Bamford *et al.*, 2010) and starch grains (Horrocks *et al.*, 2004) are still identifiable after having passed entirely through an animal's digestive system (being found in a coprolite). In fact, it is even possible to identify phytoliths (to at least order level) eaten by herbivorous prey in carnivore coprolites (Bamford *et al.*, 2010). This may be taken as evidence that phytoliths or starch grains that had been part-digested by a herbivore, which was then consumed by a Neanderthal, would be identifiable if recovered from the Neanderthal's calculus. Other structures and compounds (such as the particular carbohydrate compounds used as the basis for the suggestion of yarrow and chamomile in the diet of the El Sidrón Neanderthal) may be less resistant, but would likely still be identifiable if the prey was consumed soon after it had eaten.

7. Concluding comments:

We suggest that the remains of medicinal (and other) plants found in Neanderthal calculus could have come from stomach contents rather than being evidence for self-medication. Very little fauna has been found at El Sidrón (Rosas *et al.*, 2006; Rosas *et al.*, 2012; Rosas Gonzalez *et al.*, 2012). What remains, however, includes chamois, bovid, deer, and rabbit (Rosas *et al.*, 2006; Rosas Gonzalez *et al.*, 2012). There is ethnographic evidence that the Inuit eat lagomorph (Arctic and snow hare) stomach contents (Andersen, 2005), and given the wide range of other species enumerated above (especially that pertaining to cervids), there is no reason to believe that the stomach contents of those species for which there is evidence at El Sidrón would not have made a profitable meal. We are not proposing that Neanderthals would not have eaten plant foods, nor are we discounting the possibility of Neanderthal self-medication. However we suggest that, given the evidence for widespread consumption of stomach contents in recent human groups, and the likely benefits of a rich source of vitamin C and carbohydrates, this behaviour should be taken into account as a possible source of plant foods, including 'medicinal' ones, in the archaeological and fossil record.

Acknowledgements

We would like to thank Mark Lewis, Adrian Lister, and Collette Berbesque for sharing their expertise, and the Human Origins Research Fund of the Natural History Museum and the Calleva Foundation for funding. We would like to thank Sarah Elton, Hannah O'Regan, and Danielle Schreve for the opportunity to contribute to this memorial volume in honour of Alan Turner. CBS would also like to acknowledge his many years of friendship with Alan, and thank him for all the information he passed on to so many in the field regarding carnivores and their evolution.

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