



Contents lists available at ScienceDirect

Journal of Archaeological Science

journal homepage: <http://www.elsevier.com/locate/jas>

The missing mushrooms: Searching for fungi in ancient human dietary analysis

Hannah J. O'Regan^{a,*}, Angela L. Lamb^{b,c}, David M. Wilkinson^d

^a Department of Archaeology, Humanities Building, University Park, University of Nottingham, Nottingham, NG7 2RD, UK

^b NERC Isotope Geosciences Facility, British Geological Survey, Nottingham, NG12 5GG, UK

^c Centre for Environmental Geochemistry, University of Nottingham, NG7 2RD, UK

^d Natural Science and Psychology, Liverpool John Moores University, Byrom Street, Liverpool, L3 3AF, UK

ARTICLE INFO

Article history:

Received 28 November 2015

Received in revised form

29 September 2016

Accepted 30 September 2016

Available online xxx

Keywords:

Diet

Fungus

Carbon

Nitrogen

Sulphur

Stable isotope

Protein

ABSTRACT

Fungi are a common part of modern human diets, but are rarely discussed in an archaeological context. Power et al. (2015) published data on bolete spores in human tooth calculus, suggesting that Upper Palaeolithic peoples ate mushrooms. Here we briefly consider the likelihood of mushroom consumption in the past, and examine whether or not stable isotopes may provide a way of seeing this in archaeological populations. We also consider the complexities of fungal stable isotopes using our own data and that from the literature. We conclude that fungi are highly variable isotopically, and are an additional dietary factor that should be considered when trying to interpret 'terrestrial' carbon isotope signatures combined with relatively high nitrogen isotope values in humans and other animals. Substantial mushroom ingestion could, in some cases, result in isotope values that may be interpreted as considerable meat consumption.

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1. Introduction

In April 2015 Power et al. (2015) published a paper on micro-remains in Palaeolithic human tooth calculus from El Mirón cave, Spain. The press release that accompanied the paper emphasised the finding of bolete mushroom spores, and postulated that Palaeolithic hunter-gatherers could have been eating fungi under the title 'the oldest evidence for mushrooms used as a food source' (Anon, 2015). Fungal fruitbodies (sporocarps) are the macro-structure of a fungus that produces the reproductive structures (Spooner and Roberts, 2005), and are here referred to as mushrooms. They are a common food item in many modern human diets, yet they are rarely included when archaeological foodstuffs are being discussed. Here we highlight that mushrooms should be included in such discussions and examine another potential line of evidence for mushroom eating – that of stable isotope analysis of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ from bone collagen in archaeological skeletons. Anomalous bone collagen stable isotope values with apparently

terrestrial $\delta^{13}\text{C}$ and relatively high $\delta^{15}\text{N}$ have been reported from a number of sites and species, and we suggest that fungus may play a part in explaining these results.

1.1. The potential importance of mushrooms

Mushrooms are consumed by modern *Homo sapiens* throughout the world. Different cultures favour different species, and the quantity of mushrooms eaten can vary enormously, e.g. in 2007 estimated consumption of mushrooms in China was 1,226,551 metric tons, while in Belarus it was 6800 tons (McCarty, 2010), equating to 0.93 kg and 0.71 kg per person respectively (population data from Worldbank.org). The quantity of fresh and processed mushrooms consumed by any single individual will vary according to taste, but in America it has been estimated to be 1.36 kg per person per year (Hoyle, 2014) and in Germany 3.2 kg per person (Lelley, 2014). Mushrooms are proteinaceous, low in fat and ergosterol (the functional equivalent of cholesterol), and contain useful dietary nutrients (McCarty, 2010), such as sulphur (see Supplementary Information). Ancient texts mention mushrooms (e.g. Theophrastus c.371–c.287 BCE (Sharples and Minter, 1983)) and their hallucinogenic and poisonous properties are also widely

* Corresponding author.

E-mail address: hannah.oregan@nottingham.ac.uk (H.J. O'Regan).

known from ethnographic studies (Stephenson, 2010). As soft-bodied organisms mushrooms are very rarely found on archaeological sites and those taxa that have been recovered are often woodier and may or may not have been collected to be eaten (e.g. bracket fungi from the Neolithic Italian village of 'La Marmotta' (Berniccia et al., 2006)). However, a few examples do suggest consumption, in addition to the spores identified as those from bolete and agaric mushrooms by Power et al. (2015). Oetzi the Copper Age 'iceman' from the European Alps was carrying the birch polypore *Piptoporus betulinus* (Peintner and Pöder, 2000), which could have been ingested as a vermifuge (Carpasso, 1998). Puffballs *Bovista nigrescens* and *Calvatia utriformis* have been found on UK archaeological sites and may have been used for culinary or medicinal purposes (Watling and Seaward, 1976). These are rare exceptions to the archaeological invisibility of mushrooms and there is little tangible evidence of the edible mushrooms that people are much more likely to have encountered and eaten. In the temperate zone mushrooms are often available from early summer through into the winter, although peak occurrence of fungal fruiting bodies is during the autumn and some animals may become mushroom specialists at this time of year (e.g. Avila et al., 1999) – however the extent of this 'fungi season' is in part controlled by changes in climate, and this season is currently lengthening in Europe (Kausrud et al., 2012). Indeed in Europe some species 'fruit' all year round (such as truffles and many bracket fungi). Mushrooms can yield between 160 and 250 g protein from a dried kg of fruiting bodies (De Román et al., 2006), and dried mushrooms can last for several seasons, potentially extending their dietary impact over a much longer period. The drying of mushrooms is not exclusive to humans, for example several North American squirrel species are known to dry and cache fungi for later consumption (Stephenson, 2010). Mushrooms are likely to have been a frequent component in past human diets, but as yet they are not often included in such discussions. Stable isotope analysis provides one way of investigating the role of such invisible foods, although in the case of fungi their potential impact on $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values may be highly complex.

2. Mushrooms and stable isotopes

As mushrooms are highly proteinaceous (e.g. crude protein ranging from 16.5 to 59.4% dry matter (Kalač, 2009)) they have considerable potential to affect body $\delta^{15}\text{N}$ values in their consumers. Recent work has demonstrated that dietary $\delta^{15}\text{N}$ systems are complex with many possible contributors to the results seen in archaeological material (e.g. Müldner and Richards, 2007; Szpak, 2014). Here we encourage researchers to consider mushrooms as another factor within this complexity. Mushrooms have a wide range of isotope values as illustrated by nearly 1000 stable isotope values for worldwide fungi plotted in Fig. 1. This shows that worldwide nitrogen values range from $\delta^{15}\text{N}$ -7.1‰ to $+21.8\text{‰}$ and $\delta^{13}\text{C}$ values range from -31.7‰ to -19.0‰ . However, not all species will be present in a single region (although many taxa have a very wide geographic distribution) and more importantly, not all taxa are edible, although only a small minority of mushrooms are really poisonous to humans (Ramsbottom, 1953). Few studies of fungal stable isotopes have been undertaken in Europe, with the exception of work in the Scandinavian forests (e.g. Taylor et al., 1997), in France (e.g. Zeller et al., 2007) and on UK waxcaps (*Hygrocybe* spp., Griffith, 2004). Almost no studies, with the exception of the truffle analyses of Zeller et al. (2008), have focussed on taxa that are edible to humans. To illustrate this, Fig. 2 plots data for some common European edible mushrooms. These data are from the same sources as Fig. 1 but also include our own data from North West England – mainly sampled from Mere Sands Wood nature reserve during

October 2013 (see Supplementary Information for full details of these previously unpublished analyses). Fig. 2 demonstrates that there is very wide variation, with $\delta^{15}\text{N}$ values ranging from -1.1‰ to 12.5‰ and $\delta^{13}\text{C}$ from -28.6‰ to -21.1‰ . Six species have values $\delta^{15}\text{N} > 8\text{‰}$, ceps, wood hedgehog, horse mushroom and the truffles. There are replicate data for several species: notably the chanterelle has a very narrow range of carbon values, but nitrogen values that differ by 7‰ ($\delta^{15}\text{N}$ 0.7‰ – 7.7‰ , and $\delta^{13}\text{C}$ from -26.6‰ to -25.2‰ , $n = 5$), while the wood hedgehog has only a 0.6‰ difference in nitrogen, but a 3.2‰ difference in carbon values ($\delta^{15}\text{N}$ 8.6‰ to 9.2‰ and $\delta^{13}\text{C}$ from -28.6‰ to -24.5‰ , $n = 3$).

2.1. Archaeological examples

Typically, the trophic level effect for $\delta^{15}\text{N}$ is expected to be between $+3$ and $+5\text{‰}$ (Bocherens and Drucker, 2003). The highest $\delta^{15}\text{N}$ values recorded from human bone collagen are typically around the $+20\text{‰}$ range but values over $+15\text{‰}$ are usually interpreted as relatively high and evidence for marine mammal intake. Such consumption would also result in relatively high $\delta^{13}\text{C}$ values, but interpretation of diet is more difficult when relatively high $\delta^{15}\text{N}$ values are accompanied by relatively low $\delta^{13}\text{C}$ values. Müldner and Richards (2007) examined a number of reasons for high $\delta^{15}\text{N}$ values (but relatively low $\delta^{13}\text{C}$) in human bone collagen from Roman and Medieval York, concluding that omnivore meat, bird eggs, marine molluscs, freshwater fish and/or manuring could have contributed to this profile. However, mushrooms, a food source that may be ^{15}N enriched but with a 'terrestrial' (i.e. relatively low) $\delta^{13}\text{C}$ signal were not considered, yet Figs. 1 and 2 demonstrate that mushrooms can also fall into this isotopic range. In addition to humans, individuals of several herbivore taxa such as red deer, *Cervus elaphus* (Stevens et al., 2006) and woolly mammoths, *Mammuthus primigenius* (Fox-Dobbs et al., 2008) have been found to have higher than predicted $\delta^{15}\text{N}$ values when compared to their assumed diet of vegetation, and mushrooms may also have a role here.

A rare example of fungal stable isotopes being considered in an archaeological context is work by Hamilton et al. (2009) which attempted to model the potential input of mushrooms into pig diets in the Neolithic – but the evidence base for the fungal data was very limited. While the work focussed on the contribution of mushrooms to $\delta^{13}\text{C}$, the model also included $\delta^{15}\text{N}$. This was based on mushrooms being 1‰ – 3‰ higher in $\delta^{15}\text{N}$ than plant foods, which may be realistic if animals do not discriminate between fungal taxa. However humans and other animals will target mushrooms that are palatable, including some taxa that have particularly high $\delta^{15}\text{N}$ (e.g. truffles), and the means of the edible fungi shown in Fig. 2 are 7.9‰ for $\delta^{15}\text{N}$ ($n = 43$) and -25.4‰ for $\delta^{13}\text{C}$ ($n = 43$). Later work (Hamilton and Thomas, 2012; Millard et al., 2013) has also focussed on the effect of fungi on $\delta^{13}\text{C}$ values rather than $\delta^{15}\text{N}$ in pigs. Here we emphasise that $\delta^{15}\text{N}$ values may also be influenced by mushrooms, and indeed this may lead to a trophic effect if people are consuming animals such as pigs and deer which eat large quantities of mushrooms at certain times of year (Hohmann and Huckschlag, 2005; Pokorny et al., 2004). Overall, the data shown in Fig. 2 suggests that nitrogen isotope values in edible mushrooms vary between those expected of legumes up to those present in freshwater fish (Schoeninger and DeNiro, 1984).

2.2. Isotopic complexity in fungi

In parallel to science-based archaeology, there has been a significant increase in the application of stable isotopes within fungal ecology over the last few decades (Griffith, 2004). This has focussed largely, but not exclusively, around the fields of ecosystem ecology and food web studies. Stable isotopes have the potential to quantify

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