



## A fish is not a fish: Patterns in fatty acid composition of aquatic food may have had implications for hominin evolution



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### ABSTRACT

From c. 2 Ma (millions of years ago) onwards, hominin brain size and cognition increased in an unprecedented fashion. The exploitation of high-quality food resources, notably from aquatic ecosystems, may have been a facilitator or driver of this phenomenon. The aim of this study is to contribute to the ongoing debate on the possible role of aquatic resources in hominin evolution by providing a more detailed nutritional context. So far, the debate has focused on the relative importance of terrestrial versus aquatic resources while no distinction has been made between different types of aquatic resources. Here we show that Indian Ocean reef fish and eastern African lake fish yield on average similarly high amounts of eicosapentaenoic acid (EPA), docosahexaenoic acid (DHA), and arachidonic acid (AA). Hence a shift from exploiting tropical marine to freshwater ecosystems (or vice versa) would entail no material difference in dietary long-chain polyunsaturated fatty acid (LC-PUFA) availability. However, a shift to marine ecosystems would likely mean a major increase in access to brain-selective micronutrients such as iodine. Fatty fish from marine temperate/cold waters yield twice as much DHA and four times as much EPA as tropical fish, demonstrating that a latitudinal shift in exploitation of African coastal ecosystems could constitute a significant difference in LC-PUFA availability with possible implications for brain development and functioning. We conclude that exploitation of aquatic food resources could have facilitated the initial moderate hominin brain increase as observed in fossils dated to c. 2 Ma, but not the exceptional brain increase in later stages of hominin evolution. We propose that the significant expansion in hominin brain size and cognition later on may have been aided by strong directional selecting forces such as runaway sexual selection of intelligence, and nutritionally supported by exploitation of high-quality food resources in stable and productive aquatic ecosystems.

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### Introduction

Before c. 2 Ma (millions of years ago), the cranial capacity of hominins (*Paranthropus* and *Australopithecus*) averaged below or around 500 cm<sup>3</sup>, in the same range as that of recent African apes (Carlson et al., 2011). At 2.06 Ma, as shown by the well-dated early *Homo* cranium KNM-ER 1470, hominin cranial capacity had increased to 752 cm<sup>3</sup> (Holloway et al., 2004; Joordens et al., 2013). In general, with some striking exceptions (Falk et al., 2005; Spoor et al., 2007), hominin cranial capacity kept rising over time to an

average of 1500 cm<sup>3</sup> (Holloway et al., 2004; Potts, 2011). The modern human brain stands out among mammals by its relative size and its energy-expenditure: the brain consumes about 20–25% of the basal energy needs of an adult human (Navarrete et al., 2011; Potts, 2011). A key question in paleoanthropology is therefore: what drove the striking brain growth in the hominin lineage over time, and how was it ‘paid for’ in nutritional terms? In this paper we aim to address the second part of the question, and will discuss the implications of our findings for the first part of the question.

There is growing consensus that the normal development of the modern human brain and its cognitive functioning are constrained by several requirements: availability of ‘brain-selective’ micronutrients such as iodine and selenium (Delange, 2000; Cunnane, 2010), and most notably the availability of the long-chain

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polyunsaturated fatty acids (LC-PUFA) docosahexaenoic acid (DHA), eicosapentaenoic acid (EPA) and arachidonic acid (AA) (e.g., Kitajka et al., 2004; Muskiet et al., 2004; Kawakita et al., 2006; Gómez-Pinilla, 2008; Muskiet, 2010; Tattersall, 2010; Martin et al., 2012; Kuipers et al., 2012a; Hussain et al., 2013). All extant animals need sufficient DHA, EPA and AA to build their brains and to maintain brain functioning; this must also have been the case for our extinct hominin ancestors and relatives (e.g., Broadhurst et al., 2002; Kuipers et al., 2010; Muskiet and Kuipers, 2010). Animals, including humans and hominins, can obtain these LC-PUFA by synthesis in their body through desaturation and elongation of the plant-based precursor fatty acids  $\alpha$ -linolenic acid (ALA) and linoleic acid (LA) (Fig. 1), and through direct uptake from dietary sources rich in pre-formed DHA, EPA and AA.

Aquatic food sources contain relatively large amounts of EPA and DHA (e.g., Broadhurst et al., 2002; Kuipers et al., 2005; Cunnane and Stewart, 2010). In contrast, these fatty acids are rarely available (except in mammal brain tissue; Cordain et al., 2002) or occur in low amounts (e.g., eggs) in foods from terrestrial ecosystems (Broadhurst et al., 2002; Carlson and Kingston, 2007). The reason for this substantial difference between terrestrial and aquatic food sources stems from the fact that phytoplankton, the primary producer base of freshwater and marine aquatic foodchains, produce EPA and DHA (and AA) that are progressively bio-accumulated by other aquatic organisms (e.g., zooplankton, molluscs, fish) higher up in the food chain (Sargent et al., 1995; Kainz et al., 2004). Recent research has shown that not only early modern humans (Marean et al., 2007) but also other hominin species such as Neandertals and *Homo erectus* collected and consumed aquatic resources (e.g., Stiner, 1994; Stringer et al., 2008; Alperson-Afil et al., 2009; Joordens et al., 2009; Hardy and Moncel, 2011). Moreover, Stewart (1994) and Braun et al. (2010) have demonstrated, based on cut-mark evidence, that as early as 1.95 Ma the hominin diet in the Turkana Basin (eastern Africa) included freshwater catfish, turtle and crocodile (see also Archer et al., 2014; Stewart, 2014). These findings demonstrate that the earliest evidence for consumption of

aquatic food is largely contemporaneous with, and found in the same area as, the observed initial onset of hominin brain growth in early *Homo* (Holloway et al., 2004), implying that a causal link between the two occurrences is possible (Braun et al., 2010).

However, this issue remains unresolved. At present, researchers still debate the relative importance of an aquatic versus a terrestrial diet to cause or facilitate hominin brain development and cognition (Muskiet et al., 2004, 2007; Langdon, 2006; Carlson and Kingston, 2007; Cunnane et al., 2007; Joordens et al., 2007; Cunnane and Stewart, 2010; Steele, 2010; Kuipers et al., 2012a). The aim of this study is to contribute to the ongoing debate on the possible role of aquatic resources in hominin evolution by providing a more detailed nutritional context, building on that of Broadhurst et al. (2002). In short, no distinction has been made, thus far, between different types of aquatic resources. This is despite the fact that it is well known that aquatic organisms within one ecosystem differ in LC-PUFA composition, depending on their ecology and diet, and that there are also differences in typical LC-PUFA composition between organisms from different ecosystems, e.g., in tropical versus temperate and freshwater versus marine fish (e.g., Piché et al., 2010 and references therein). Therefore, we hypothesize that in terms of nutritional impact 'a fish is not a fish' and that variation in fatty acid composition in aquatic food resources may have played a role in hominin evolution. Our objectives are: 1) to compare the LC-PUFA composition and absolute amounts of EPA, DHA and AA in fish from different possible hominin habitats in Africa (inland lake shores, Indian Ocean coast) to those of temperate ecosystems; and 2) to explore implications of shifts in aquatic exploitation (e.g., from marine to freshwater, or from tropical to cold/temperate) for hominin evolution, notably brain growth and development. Finally, we will also address the more fundamental question of whether the consumption of aquatic food sources may have played a role in causing the remarkable brain expansion in the hominin lineage.

## Materials and methods

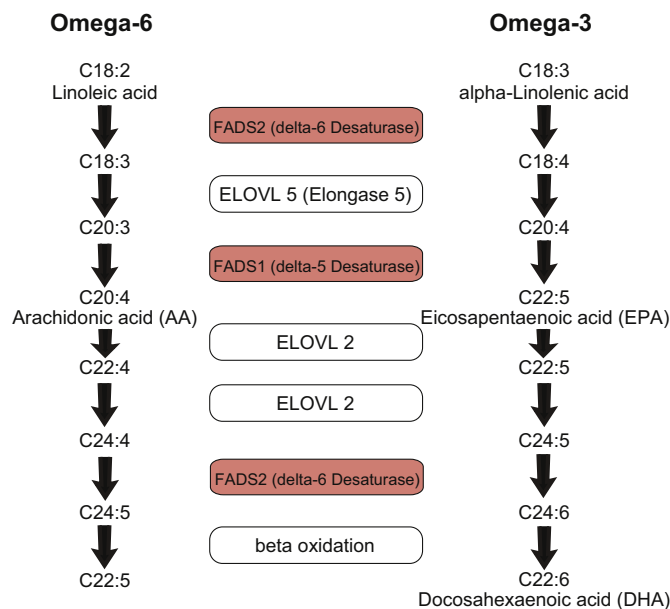
In total, 59 fish species were analyzed in this study: 24 from the western Indian Ocean coral reef (Tanzanian coast), 14 from the tropical freshwater lakes Victoria and Malawi, six from Dutch freshwater, and 15 from the Dutch part of the North Sea. The fish were caught by line or by bottom trawling, and purchased from local fishermen or bought at local markets in Kenya, Malawi, Tanzania, and in the Netherlands by two of us (RSK and JHW).

### Fish sampling

An initial sample (100–500 mg) was cut from a well-defined part of the dorsal muscle between the dorsal fin and the head; a second 100–500 mg sample was taken from between the pectoral fin and the anal fin. Skin was included as it is always eaten. Very small sardine-like fish were stored whole. Sampling was performed by the same person and thus highly reproducible. In some cases, tissue was accurately weighted on a calibrated Accurate Professional Mini scale (Max 10 g;  $d = 0.001$  g). Dissected samples were added to a vial containing 2 ml of a methanol-hydrochloric acid solution (methanol-6 mol/L HCl (5:1 v/v) containing 1 mg butylated hydroxytoluene (BHT).

### Fatty acid analysis

The dissolved tissue was homogenized (Potter apparatus) in its original solution and adjusted to 10.0 ml with chloroform-methanol (volume ratio 2:1). With a calibrated pipette, 1.0 or 2.0 ml of this solution was taken, dried under nitrogen and taken up in 2.0 ml methanol-hydrochloric acid (5:1 v/v). After addition of



**Figure 1.** Overview of metabolism of omega-3 and omega-6 PUFA pathways, adapted from Mathias et al. (2012). The figure illustrates the desaturation and elongation steps necessary to transform linoleic acid to AA (omega-6 pathway) and  $\alpha$ -linolenic acid to EPA and DHA (omega-3 pathway). The desaturation and elongation steps are mediated by the genes FADS1 and FADS2 (producing desaturase enzymes), and the genes ELOVL5 and ELOVL2 (producing elongase enzymes).

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