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Review

Brain-specific lipids from marine, lacustrine, or terrestrial food resources: potential impact on early African *Homo sapiens*[☆]C. Leigh Broadhurst^{a,b}, Yiqun Wang^c, Michael A. Crawford^{c,*}, Stephen C. Cunnane^d, John E. Parkington^e, Walter F. Schmidt^a^aUS Department of Agriculture, Environmental Chemistry Laboratory, Agricultural Research Service, Beltsville, MD 20705, USA^bUS Department of Agriculture, Human Nutrition Research Center, Agricultural Research Service, Beltsville, MD 20705, USA^cInstitute of Brain Chemistry and Human Nutrition, University of North London, 166-222 Holloway Road, London N7 8DB, UK^dDepartment of Nutritional Sciences, University of Toronto, 150 College Street, Toronto, Ont., Canada M5S 3E2^eArchaeology Department, University of Cape Town, Private Bag, Rondebosch, Cape 7700, Cape Town, South Africa

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Abstract

The polyunsaturated fatty acid (PUFA) composition of the mammalian central nervous system is almost wholly composed of two long-chain polyunsaturated fatty acids (LC-PUFA), docosahexaenoic acid (DHA) and arachidonic acid (AA). PUFA are dietarily essential, thus normal infant/neonatal brain, intellectual growth and development cannot be accomplished if they are deficient during pregnancy and lactation. Uniquely in the human species, the fetal brain consumes 70% of the energy delivered to it by mother. DHA and AA are needed to construct placental and fetal tissues for cell membrane growth, structure and function. Contemporary evidence shows that the maternal circulation is depleted of AA and DHA during fetal growth. Sustaining normal adult human brain function also requires LC-PUFA.

Homo sapiens is unlikely to have evolved a large, complex, metabolically expensive brain in an environment which did not provide abundant dietary LC-PUFA. Conversion of 18-carbon PUFA from vegetation to AA and DHA is considered quantitatively insufficient due to a combination of high rates of PUFA oxidation for energy, inefficient and rate limited enzymatic conversion and substrate recycling. The littoral marine and lacustrine food chains provide consistently greater amounts of pre-formed LC-PUFA than the terrestrial food chain. Dietary levels of DHA are 2.5–100 fold higher for equivalent weights of marine fish or shellfish vs. lean or fat terrestrial meats. Mammalian brain tissue and bird egg yolks, especially from marine birds, are the richest terrestrial sources of LC-PUFA. However, land animal adipose fats have been linked to vascular disease and mental ill-health, whereas marine lipids have been demonstrated to be protective. At South African Capesites, large shell middens and fish remains are associated with evidence for some of the earliest modern humans. Cape sites dating from 100 to 18 kya cluster within 200 km of the present coast. Evidence of early *H. sapiens* is also found around the Rift Valley lakes and up the Nile Corridor into the Middle East; in some cases there is an association with the use of littoral resources. Exploitation of river, estuarine, stranded and spawning fish, shellfish and sea bird nestlings and eggs by *Homo* could have provided essential dietary LC-PUFA for men, women, and children without requiring organized hunting/fishing, or sophisticated social behavior. It is however, predictable from the present evidence that exploitation of this food resource would have provided the advantage in multi-generational brain development which would have made possible the advent of *H. sapiens*. Restriction to land based foods as postulated by the savannah and other hypotheses would have led to degeneration of the brain and vascular system as happened without exception in all other land based apes and mammals as they evolved larger bodies. © 2002 Elsevier Science Inc. All rights reserved.

Keywords: Arachidonic acid; Brain nutrition; Coastal origin; Docosahexaenoic acid; Evolution; Savannah foods; Sea foods

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*Corresponding author. Tel.: +44-207-753-3165; fax: +44-207-753-3164.

E-mail address: michael@macrawf.demon.co.uk (M.A. Crawford).

1. Introduction

Many previous authors have considered human evolution from an ecological view point (Martin, 1983; Harvey and Clutton-Brock, 1985; Shipman and Walker, 1989; Blumenshine, 1991; Foley and Lee, 1991; McHenry, 1994; Aiello and Wheeler, 1995; Leonard and Robertson, 1997; Ambrose, 1998; Broadhurst et al., 1998). They have argued that the relatively large metabolic energy requirements of the *Homo* (mainly *H. sapiens*) brain require consistent access to higher quality food resources, both now and in the past. Regardless of the various selective pressures driving brain evolution of *H. sapiens*, sufficient dietary energy, protein, vitamins, and trace elements are strictly required. Particularly in tropical and sub-tropical climates, these nutrients can be obtained from many food resources that hominids could have accessed (Harris and Ross, 1987; O'Dea, 1991; Eaton et al., 1996, 1997). All land based mammals had access to this range of nutrients as is testified by the large body masses and fast growth rates they attained. The problem with this approach, is that despite achieving velocities of body growth approaching a ton in four years, the rule was a logarithmic decline in brain to body weight ratio with increase in body size.

Whilst proteins are important to body growth, 60% of the brain structural material (dry weight) is lipid. Different principles are required for body growth as opposed to brain growth. Dietary essential long-chain polyunsaturated fatty acids (LC-PUFA) are considered to be the most limiting nutrients for brain lipids and neural growth (Crawford and Sinclair, 1972; Hornstra et al., 1995; Crawford et al., 1993, 1997; Broadhurst, et al., 1998; Clandinin, 1999; Horrobin, 1999), and are not widely available in foods. Sustaining the comparatively large size, and the apparent unique complexity and high level of interconnectivity in the modern human brain require LC-PUFA (Mesulam, 1990; Fernstrom, 1999; Horrobin, 1999).

Very rapid brain growth characterizes the modern human fetus and neonate, who devote approximately 70% of their metabolic energy to fuel central nervous system (CNS) growth and development (Holliday, 1971; Cunnane et al., 2000). In the fetus and neonate both the quality and quantity of nutrients—especially LC-PUFA, iodine and other trace elements, are critically important. Normal intellectual growth cannot be accomplished if any

of these are lacking. Adult human brains require approximately 20% of metabolic energy, a large figure compared to other mammals of the same size (Leonard and Robertson, 1997; Crawford et al., 1993; Broadhurst et al., 1998; Dutta-Roy, 1997; Clandinin, 1999).

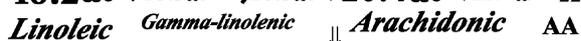
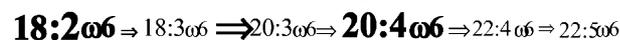
Due to these strict energetic constraints on *H. sapiens*, evolutionary models should consider quantitatively the sources of LC-PUFA in representative marine, lacustrine, riverine and terrestrial animal foods that may have been procured by hominids and delivered LC-PUFA. The archaeological evidence for the utilization of littoral resources by *Homo* during the period 20–200 kya is of increasing interest and significance.

2. Brain-specific nutrition must provide balanced dietary LC-PUFA

The lipid of the mammalian brain has a unique profile of LC-PUFA (Crawford and Sinclair, 1972; Crawford et al., 1976a). The highly unsaturated LC-PUFA is found in neuronal and retinal membranes at sites of high signal transfer activity. Membranes with higher amount of saturated fatty acids are found in more rigid structures such as those of the insulating myelin sheaths around nerves.

PUFA are 'essential', which means that they cannot be synthesized and must come from the diet. There are two PUFA series, $\omega 3$ and $\omega 6$ (Fig. 1). The $\omega 3$ and $\omega 6$ series are not interconverted in mammals; both are essential and intake needs to be balanced in the diet (Gerster, 1998; Sprecher, 1999). Fatty acids are referred to by numerical nomenclature: linoleic acid is 18:2 $\omega 6$. The number before the colon gives the number of carbon atoms in the molecule (18 in this case); and the number after the colon give the total number of methylene-interrupted double bonds (2 in this case). $\omega 6$ defines the position of the first double bond at carbon 6, starting from the terminal methyl group.

Precursor dietary essential PUFA *sensu stricto* are α -linolenic acid (LNA, 18:3 $\omega 3$) and linoleic acid (LA, 18:2 $\omega 6$). These 18 carbon PUFA are alternately desaturated and elongated to form mainly 20 and 22 carbon LC-PUFA with four or more double bonds. Docosahexaenoic acid (DHA, 22:6 $\omega 3$) and arachidonic acid (AA, 20:4 $\omega 6$) and are the main $\omega 3$ and $\omega 6$ series end-member LC-PUFA, respectively (Fig. 1). Due to the widespread development and food use of agricultural oil seeds,

SYNTHESIS OF AA & DHA from LINOLEIC & α -LINOLENIC ACIDS Δ -6 desaturase rate limiting**N-6 or OMEGA 6 Family**

SEEDS $\Delta 6$ prostaglandins & leukotrienes

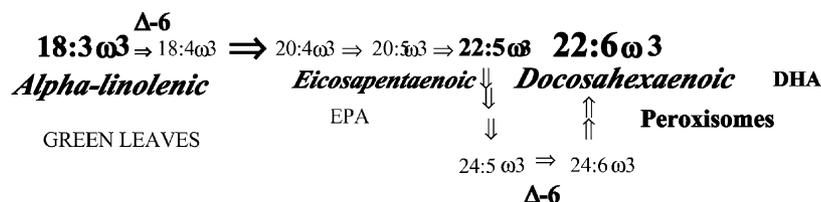
N-3 or OMEGA 3 Family

Fig. 1.

LA is far more prevalent in current diets than in the past (Broadhurst, 1997). Typical modern-day sources of LA are nuts (e.g. walnuts, peanuts, pistachios, almonds, pumpkin seeds) and seed oils (e.g. cotton, corn, sesame, sunflower, safflower, soybean). LNA is relatively uncommon in modern diets. It comprises 1% or less of the calories in green leaves and legumes, and is 7–45% by weight of walnut, flaxseed, mustard, rapeseed, perilla, and soybean oils. Foods richest in AA are egg yolk, organ meats, and muscle meats from land animals and tropical fish and shellfish. Foods richest in DHA and its precursor, eicosapentaenoic acid (EPA, 20:5 ω 3), are marine fish and shellfish from cold waters. Fish and shellfish from warmer marine or fresh water have ubiquitous DHA and EPA, however the AA content is generally higher (Table 1).

The CNS is unique compared to other tissues because it does not use LNA and LA but only their desaturated and elongated LC-PUFA. Polyunsaturates in the brain are over 90% DHA and AA and its elongation product, docosatetraenoic acid (22:4 ω 6), yet humans and other mammals are inefficient at synthesizing them from their respective 18-carbon precursors. The biosynthetic processes for LC-PUFA are complex and rate limited, particularly for humans and guinea pigs (Brenner, 1981; Weisinger et al., 1995; Gerster, 1998; Sinclair, 1975; Sprecher, 1999). In the developing rat brain, direct incorporation of AA and DHA into

neural tissue is an order of magnitude greater than is achieved by synthesis from LA and LNA. In rat radioisotope tracer studies, it was found that 30 times as many molecules of brain DHA came from pre-formed DHA as compared to biosynthesis from LNA (Sinclair and Crawford, 1972; Sinclair, 1975; Suzuki et al., 1997). ^{13}C nuclear magnetic resonance and isotopic studies have shown that more than 30 molecules of LNA within the rat brain are used to make brain cholesterol and the saturated fat palmitic acid (16:0) for every one used for DHA synthesis (Cunnane et al., 1994; Menard et al., 1998). The brain requires a large amount of cholesterol and synthesizes its own rather than importing it from the liver (Jurevics and Morell, 1995).

Part of the explanation for the low conversion of parent to LC-PUFAs, is that 50–70% of oral doses of either LA or LNA are oxidized (used for energy) in 24 h (Leyton et al., 1987). In growing or energy-deprived mammals, over 90% may be oxidized (Chen et al., 1995; Cunnane and Anderson, 1997; Cunnane et al., 1998). In comparison, DHA and AA are selectively incorporated into cell membranes, with only 15% oxidized in a 24-h period (Sinclair, 1975; Suzuki et al., 1997). During the rapid fetal and neonatal growth period, energy and CNS substrate material demands apparently outstrip LC-PUFA biosynthesis from 18 carbon PUFA, therefore LC-PUFA are considered conditionally essential for fetal and infant humans (Cun-

Table 1
Contents of fat, AA and DHA of some fishes and sea foods

Fish and habitat	Fat (g/100 g meat)	AA (mg/100 g meat)	DHA (mg/100 g meat)
<i>Tropical fish</i>			
Indian halibut	1.7	102	168
<i>Rift Valley Lake Nyasa, Tanzania</i>			
Mbebele (catfish)	10.3	421	842
Njenu (carp)	4.9	270	363
Mfui (local sp.)	1.1	84	200
Kambale (local sp.)	1.8	99	227
<i>Lake Turkana, Kenya</i>			
Tilapia species	2.3	184	343
Perch	2.6	190	447
<i>Closed-basin temperature marine (Black and Marmara Seas, Turkey)</i>			
Bluefish (mature)	31.3	1249	4103
Bluefish (immature)	42.9	2486	4931
Horse mackerel	12.8	170	803
Sardine	11.3	279	1578
Red mullet	8.8	385	1446
Sole	4.7	241	732
Garfish	4.2	184	970
Sand smelt	3.8	155	895
Whiting	2.7	90	1047
Emperor penguin egg yolk, 30–40% fat	3.3	16	172
Emperor penguin, maternal blubber	1.8	9	137
Penguin liver ^a	6.3	515	670
<i>Freshwater temperate</i>			
North American (unspec.)	(oil)	3135	7600
Rainbow trout, farm-raised ^b	6.7	204	1088
<i>Higher latitude marine</i>			
Atlantic salmon (skinless)	9.8 ^c	112	1601
Herring	(oil)	570	21 850
Menhaden	(oil)	855	6935
N. Atlantic mackerel	(oil)	380	7315
<i>Temperate invertebrates</i>			
Mussel (<i>Mytilus</i> spp.)	2	38–76	114–266
Surf clam (<i>Spisula</i> spp.)	2	76	209–228
Quahog clam ^d , –1 °C	3	46	373
Quahog clam ^d , 12 °C	3	20	390
American oyster ^e , –1°C	3	46	465
American oyster ^e , 12 °C	3	29	391
Moon snail (<i>Lunatia triseriata</i>)	3	145	219
Squid (various) ^f	2	19	475–684
Shrimp (various)	2	38–133	190–285

^a South Atlantic Rockhopper penguin; also contains 9.3% EPA. Data from Ackman and Hooper (1973), Ackman and McLeod (1988), Joseph (1989), Broadhurst et al. (1998), Gillis and Ballantyne (1999), Tanakol et al. (1999), Pauletto et al. (1996).

^b Due to farm feeding with fish chow, LA (18:2n–6) was 20.2%, compared to a range of 1.1–2.5% for wild fish.

^c Salmon with skin is up to 19.9% fat.

^d *Mercenaria mercenaria*; DHA and AA from membrane phospholipid only in winter/summer conditions.

^e *Crassostrea virginica*; DHA and AA from membrane phospholipid only winter/summer conditions.

^f Mantle and head, excluding viscera.

nane et al., 2000). In a stable isotope tracer study, neonatal baboons fed only LNA in formula were able to convert only 0.23% of ingested LNA to brain DHA (Su et al., 1999). This conversion

would supply only 9% of a human infant's DHA requirement.

With regard to neural connectivity, LC-PUFA are not only bulk and mechanical components of

CNS structure, but are also required for normal behavior of cell signalling systems which determine how neurones and sensory systems function (Horrobin, 1999). DHA is selectively incorporated into brain synaptosomes, and depletion is known to result in reduced cognitive ability (Messerli et al., 1975; Galli and Socini, 1983; Suzuki et al., 1997). In the human brain, quadrillions of neuronal microconnections are made between the dendritic extensions of the nerve cells. These microconnections are rows of tiny 'protrusions' made of phospholipids particularly rich in DHA.

There is a substantial body of evidence linking ω 3-LC-PUFA deficiency to attention-deficit and/or hyperactivity disorders, dyslexia, senile dementia, reduced visual and cognitive function, clinical depression, bipolar disorder, schizophrenia, and other problems of a dual psychological and physiological nature (Hibbeln and Salem, 1995; Adams et al., 1996; Peet et al., 1996; Stevens et al., 1995; Stordy, 1997; Birch et al., 1998; Hibbeln et al., 1998; Horrobin, 1998; Fernstrom, 1999; Hoffman et al., 1999; Stoll et al., 1999; Salem et al., 2000; see Peet et al., 1999 for a comprehensive overview). Many of these problems operate in a multi-generational manner, increasing in severity as successive generations continue to be deficient in LC-PUFA (Jensen et al., 1996; Greiner et al., 1999; Salem et al., 2000).

Coincidentally, Hibbeln et al. (1998) described the recent rise in mental ill health as similar in epidemiology of the previous rise, from country to country, in mortality from heart disease (Adams et al., 1996). The rise in mortality from heart disease last century is generally considered to be associated with the rise in dietary saturated fats and the biologically similar *trans* isomers. The introduction of unsaturated margarines and cooking oils starting in the 1960s resulted in a partial replacement of saturated fats by an ω 6 polyunsaturated fat, linoleic acid. The aim of reducing blood cholesterol levels and saturated fat intakes.

More recently it has become apparent that the highly unsaturated ω 3 fatty acids from fish and sea-foods are protective. Hibbeln et al. (1998) comment that the change in dietary fats has seriously reduced the ω 3/ ω 6 ratio. The epidemiology, supported by the experimental evidence, thus implies a change in balance and actual loss of ω 3 fatty acids, especially the ω 3 LC-PUFA. The cardinal epidemiological link is the inverse correlation of mental ill health and violence with fish

intake. That is, the lower the fish intake in the population, the higher the incidence of mental ill health. We believe that this evidence is not without relevance to the evolution of the human brain.

3. Maternal investment and fetal and neonatal growth determine intellectual capacity

Apart from the need for DHA, there is also a need for AA in the brain, placenta, internal organs, and blood vessels. AA is a major structural component of the endothelial cells that line blood vessels. The placenta is basically a very rapidly growing blood vessel matrix that processes great and increasing volumes of blood during pregnancy. High levels of AA are necessary to construct this blood vessel matrix. AA is also the substrate for the eicosanoid hormones that are involved in the blood flow regulation, the immune system and its response to injury, uterine smooth muscle contraction, and labor. The placental cell membranes selectively incorporate and are richer in AA than those of other organs, achieving fetal plasma choline phosphoglyceride (CPG) AA proportions at twice those of the mother (Al et al., 1995; Crawford et al., 1976a,b; Velzing-Aarts et al., 1999).

This substantial increment in AA and DHA across the placenta does not appear to be a function of placental conversion of precursor but of selective transfer. The placenta does not desaturate or elongate PUFA, but instead, selectively transfers LCPUFA to the fetus (Kuhn and Crawford, 1986; Crawford, 2000). This selective transfer is known as 'biomagnification' and results in high levels of LC-PUFA in fetal circulation, liver, and brain, whilst LA proportions are reduced to half of those in the maternal plasma CPG. The $n-3$ precursors are virtually absent from the fetal plasma (Crawford et al., 1976a,b, 1997; Dutta-Roy, 1997; Clandinin, 1999).

This situation where the blood plasma concentrations of LC-PUFA exceed those of the precursors is claimed to be exclusive to the fetus and neonate (Schouw et al., 1991; Dutta-Roy, 1997). However, this claim is not correct as the main, inner membrane phosphoglyceride, the ethanolamine phosphoglyceride (EPG) is dominated by higher levels of arachidonic and docosahexaenoic acid than any of the precursors. In the CPG, linoleic acid is usually present in higher proportions of than arachidonic acid whereas in the EPG the situation is reversed. The same is true of all

metabolically active cell membranes. The real difference lies in the lipid chemistry of the brain in which the precursor fatty acids are negligible in both CPG and EPG. The proportions of AA, DPA and DHA are consistently the same in the brain lipids of all species studied so far. This consistency holds true despite very wide variations in the concentrations of the different fatty acids in liver lipid stores. What is different is the size of the brain not its chemistry. This led us to postulate that arachidonic and docosahexaenoic acids were limiting factors in the evolution of the brain (Crawford and Sinclair, 1972; Crawford et al., 1976a,b).

The data on early human development support the above conclusion. After birth, infant blood AA levels are positively correlated to birthweight and growth in the first year postnatally (Leaf et al., 1992; Carlson et al., 1993). Despite these strict reproductive requirements, synthesis of AA from LA is not efficient, with only a few percent of LA actually being converted to AA in rat models and even less in humans (Cunnane et al., 1998; Lassere et al., 1985). Individuals eating vegan or mainly vegetarian diets have reduced plasma levels of both AA and DHA (Phinney et al., 1990; Adam et al., 1993; Pauletto et al., 1996).

Studies have consistently shown that most of the pre-formed DHA and AA provided in utero or during the first year of life is involved in the promotion of retinal and brain development with AA being particularly important for accompanying vascular growth (Farquarson et al., 1992; Makrides et al., 1994; Al et al., 1995; Hornstra, et al., 1995; Crawford et al., 1997; Dutta-Roy, 1997; Clandinin, 1999; Crawford, 2000). Deposition of LC-PUFA in the CNS is rapid during prenatal and postnatal brain growth (up to ~18 months in humans), and is dependent, in part, on the quantity and balance of fatty acids delivered by the placenta prenatally and in the diet postnatally. The stages of brain growth and maturation proceed in a fixed temporal sequence. In this sequence, LC-PUFA deficiency during critical growth periods results in irreversible failure to complete components of brain growth (Dutta-Roy, 1997; Clandinin, 1999; Fernstrom, 1999). Post-natally, human milk provides AA and DHA. There is consistent evidence that feeding preterm infants formulae without AA and DHA leads to loss of some mental development and visual acuity. The data has led to recommendations for the fortification of preterm and term infant

formulae with AA and DHA as is found in human milk (FAO/WHO, 1994). There is, however, less agreement about the same tests applied to term infants. One large study, which did not show any benefit, used the lowest, mean level (0.1% in Auestad et al., 1997) recorded for DHA in human milk. In contrast, the positive data emerged from studies using more than three times this amount and this is more consistent with experience across the world where mean DHA values are often higher (Birch et al., 2000; Willatts et al., 1998).

During the most active phase of fetal growth, human brain development consumes approximately 70% of the energy delivered to it by the mother; postnatally, the figure drops to 60% (Holliday, 1971). Consistent with previous authors, (Martin, 1983; Aiello and Wheeler, 1995), the maternal investment in synthesizing and maintaining healthy placental and mammary tissue is very large. This investment is telling us that (1), the priority of maternal energy investment in the next human generation is in the brain; and (2), the blood vessels also have a crucial role.

Without the *simultaneous* development of an efficient cardiovascular system to pump the blood and a cerebrovascular system to deliver glucose and essential nutrients to the brain, cerebral expansion would be strongly limited. One way this investment has been quantified is in terms of the potential LC-PUFA provided to each child during pregnancy and lactation, based on various international nutrition agency requirements for good health in modern humans.

Recommendations differ somewhat, but for normal adult humans, 0.5% of total dietary energy (en%) from $\omega 3$ and 3.0 en% from $\omega 6$ PUFA are typical (INFORM, 1998), with at least half the $\omega 3$ from EPA+DHA. Pregnant women and growing children may need up to twice as much. Term infants are estimated to require 20 mg/day DHA in first 6 months postnatally (Cunnane et al., 2000). Breast milk from women consuming omnivorous diets can easily supply 20 mg/day, but breast milk from mothers consuming vegan diets contains LNA but little DHA (Makrides et al., 1994; Gerster, 1998). Conversion of at least 5.2% of LNA intake is needed to provide the DHA requirement, however there is no research study to date in infant or adult humans demonstrating the actual, quantitative conversion of LNA to DHA (Cunnane et al., 2000).

These recommendations are for a largely sedentary modern, Western agriculture-based population. Under Paleolithic conditions with higher energy demands, and no ready source of refined fats or carbohydrates, the minimum PUFA requirements were at least ten times higher (Salem et al., 2000; Uauy et al., 2000). Prolonged physical activity increases significantly the amount of lipid used as an energy substrate, particularly in the absence of dietary sugars (Flatt, 1995; Brouns and van der Vusse, 1998). Strenuous and/or prolonged physical activity also raises protein requirements by 12–25%, (Lemon, 1997), but protein deficiency (especially animal protein) itself increases the requirements for PUFA, and may slow conversion to LC-PUFA (Decsi et al., 1995; Ratnayake et al., 1997). Further, under present Western dietary conditions, DHA levels in maternal blood and tissues decrease with increasing numbers of children, indicating that maternal DHA stores are stochastically depleted from successive pregnancies (Hornstra et al., 1995). Such depletion is even more severe with extended lactation, which was presumably the case in until fairly recently (Wright and Schwarcz, 1998). Under these circumstances (especially if older children did not survive), subsequent children would not have the same advantages for intellectual development if dietary LC-PUFA was not consistently available to the mother. The converse is the obvious advantage to the fetal and childhood brain development from a consistent supply of pre-formed AA and DHA to the mother. That is, a source of pre-formed AA and particularly DHA would have conferred a significant advantage in the context of neural and vascular development, the specific and unique requirement for the evolution of *H. sapiens*.

4. Marine and lacustrine sources of LC-PUFA

The evolution of the visual and nervous system occurred in the early proto-ocean environment some 600 million years ago. The first visual systems used what is now called vitamin A as the photon sensitive molecule with docosahexaenoic acid (DHA) as the main constituent of the lipid support for the protein and photo-transduction system. These molecules would have been present in abundance, having been produced by the algae which had dominated the proto-oceans for some 2.5 billion years previously. The algal and other photo-sensitive systems formerly had converted

sunlight into biochemicals. The new system powered by the high energy yielding oxidative metabolism derived from mitochondrial symbiosis, converted the photons not into chemicals but electricity.

As systems evolved differentiated functions, the electrical impulses would have been conducted by electron sensitive molecules and then by primitive nerves which evolved in different phyla into complex nervous systems. In some, nerve conduction was served by organising ganglia and in others by a central nervous system and ultimately a brain. The contact with the external environment through the visual systems used vitamin A as the photo-sensitive molecule and DHA as the major acyl component of the lipid membrane. Associated with cell differentiation of function, transmission of the electrical impulse to a specialised target was carried out at junctions or synapses utilising specialised neurotransmitting molecules. Like the photon receptor, the lipid architecture of the synaptic membrane used DHA. The key issue as far as the evidence of this paper is concerned is that throughout the subsequent 600 million years DHA was the common structural feature of the visual and neurotransmission functions. DHA has been found today as used in the dinoflagellate eye spot to fishes, reptiles and mammals.

Despite the greater ease of synthesis and the lower susceptibility to peroxidation, none of the DHA precursors appear to have been used in neuro-visual signal conduction systems. The immediate precursor used in cell membrane lipids is the docosapentaenoic acid. It is the major $\omega 3$ metabolite in large herbivorous mammals (Crawford et al., 1969, 1976a,b) yet even in these animals, it is the DHA which is found in the brain and photoreceptor. This high degree of exclusivity is the basis for evidence of the requirement for DHA in the ultimate evolution of the highest order, namely, the human brain.

5. Brain specific nutrient cluster includes iodine, vitamin A and anti-oxidants argues against an inland evolution of *H. sapiens*

It is evident that other nutrients occurred in the food chain quite specifically with DHA. These nutrients form a cluster which are at their richest in the marine food chain. They are vitamin A and trace elements. For example, iodine deficiency disease and mental retardation is found in high

prevalence amongst inland cultures. Dobson (1988) has discussed a plausible role for iodine in cerebral evolution and the separation of Cro-Magnon from the Neandertals. Dobson presents the case that the latter had skeletal structures 'identical to modern humans who suffer from cretinism'. In Indonesia, there were 1.5 million mentally retarded children; 60% of the school children had goitre. Iodine deficiency disease (IDD) was absent amongst the fishing villages (report to the Indonesian Ministry of Health, Crawford et al., 1993). This is a consistent finding. According to the World Health Organisation web site there are 1.6 billion people at risk to IDD; these people are all living today inland or on waterways and flood plains leached by rain.

On the assumption of the 'Out of Africa' postulate by Stringer (2000), humans evolved in Africa and populated the far East and the world by slow migration around the coastlines. An example of which can be found in The Solomons and Papua New Guinea. The high of population density in Papua New Guinea is associated with a high morbidity whereas morbidity and mortality in the Solomon Islands is low (Gebbie, personal comments). This mini, epidemiological gem is a reflection of the high mortality from other chronic diseases such as cardio-vascular disease associated with intensive land animal fat production and the protective marine lipids. What is evident is that the coastline populations expanded inland and it was the inland cultures in which degenerative disease emerged. Cerebral expansion demanded a different and stimulating environmental chemistry.

Deficiencies of the marine nutrients, are also simultaneously associated with some of the severest mental ill health issues today (Hibbeln et al., 1998). Mental ill health is predicted to be in the top three in the world-wide burden of ill health by the year 2020 (www.globalforumhealth.org). The highest incidence of vitamin A deficiency blindness is similarly found amongst the inland populations. It is likely that other trace elements are involved in this deficiency cluster as copper, zinc, selenium and manganese are constituents of the endogenous antioxidant systems¹ which protect the proteins and highly susceptible unsaturated fatty acids of the cellular membranes. It is no coincidence that the richest sources of this cluster of

brain-specific nutrition is found in the marine food chain. Deficiencies of other trace elements and DHA almost certainly co-exist with this problem. It is improbable that the cerebral expansion which led to *H. sapiens* would have occurred in such inland regions.

6. The wealth and ease of harvesting of the littoral food chain

The marine food chain consistently provided the DHA necessary for the origin and evolution of simple and then the advanced neural and visual systems. Fish and shellfish lipids from lower latitudes and/or fresh water are excellent sources brain-specific nutrition, since they provide a rich, balanced source of DHA. They also provide AA necessary for vascular development, which is essential for the provision of the disproportionately high energy requirement needed by the brain (Table 1, and Crawford et al., 1999). Both fish muscle meat and fat contain LC-PUFA; so fatter fish are richer in DHA, EPA, and AA than leaner fish. Moreover, the marine food chain is also the richest source of trace elements and vitamin A. Crabs, crayfish, lobsters, mussels, oysters, cockles, pippies, scallops, abalone and fish stranded in rocky pools, would have been abundant. This easily and readily gatherable food would have provided for women, even when pregnant, as well as for children.

Inland lacustrine regions would also have provided an abundance of food as is witnessed by contemporary lake coastal communities such as the El Molo living on the shore of Lake Turkana. The El Molo are dependent on the lake foods as the volcanic desert from Mount Loingalani reaches down a 800 m escarpment to the Lake shore (Brown et al., 1966). In the East African Rift Valley, freshwater fish and shellfish provide a major link in the food chain. They are consumed by birds, small mammals, reptiles and amphibians, all of which in turn could have been consumed with ease by hominids (Bailey and Parkington, 1988; Stiner et al., 1999). Marine plankton and algae are the primary sources of DHA, EPA, and AA; consequently, both herbivorous and carnivorous fish and shellfish contain LC-PUFA (Ackman, 1989). In addition, the adipose tissue, organs, and egg yolks of sea birds, which consume mainly marine foods, are rich in DHA (Table 2). Cape penguins, for example, could have been captured

¹ Cu/Zn and Mn superoxide dismutases, Se glutathione peroxidase, Fe catalase.

Table 2
Contents of fat, arachidonic acid (AA) and docosahexaenoic acid (DHA) of some animal meat, adipose tissue and organ tissue

Meat and habitat	Fat (g/100 g meat)	AA (mg/100 g meat)	DHA (mg/100 g meat)		
<i>Savannah meat</i>					
Wart hog	1.8	145	10		
African buffalo meat	1.75	116	7		
African buffalo liver	5.7	596	32		
African buffalo heart	2.3	179	13		
Eland	1.7	126	10		
Eland heart	2.0	158	17		
Zebra	2.6	74	6		
Topi	1.8	137	7		
Giraffe (liver)	4.8	547	36		
Elephant	2.0	190	11		
Uganda Kob liver	4.3	490	34		
<i>Canada</i>					
Goose flesh	7.6	210	40		
Goose leg/skin	26.4	150	20		
<i>South Africa</i>					
Ostrich	3.1	177	2		
<i>Adipose fat, game^a</i>					
		Linoleic (%)	α -Linolenic (%) (i.e. g/100 g fat)		
<i>Savannah</i>					
Buffalo fat (ruminant)	95	3.0	2.7		
Giraffe (ruminant)	95	3.67	2.30		
Zebra (non-ruminant)	95	7.88	47.5		
Warthog (non-ruminant)	95	17.0	17.0		
<i>Adipose fat, marine</i>					
		AA	EPA	DPA ω 3	DHA
Dolphin (<i>T. truncatus</i> , West Coast USA)	95	0.6	2.2	1.8	9.2

Data from Crawford et al. (1970a,b, 1976a,b), Williams and Crawford (1987), Sinclair (1992), Mann et al. (1995), Li et al. (1998), Speake et al. (1999).

^a Pericardial, perirenal, subcutaneous and omental adipose fat stores and liver triglycerides in ruminants generally contain little of no AA or DHA and no more than 2–4% linoleic and α -linolenic acids. Non-ruminant adipose fats are diet dependent. However, the composition of adipose fat does not adequately represent the nutritional or membrane status: viz. compare the dolphin fat and inner cell membrane lipid or the zebra high α -linolenic in the fat and low DHA in the liver.

quite easily with little effort required to take the eggs and nestlings.

Organized fishing with tackle would not have been necessary to regularly eat fish. Stewart (1989, 1994) describes procurement of fish in the East African Rift Valley without sophisticated technology. Hyenas, leopards, canids, and (anecdotally) baboons have been documented to pull fish from the water and eat them. During the spawning runs, catfish and cichlids move into very shallow waters and can be clubbed, speared, or picked up bare-handed. East African cichlids typically inhabit shallow, slow-moving waters, especially when spawning, and are very territorial (Riehl and Baensch, 1986; Loiselle, 1988). They often return to the same shallow water nesting areas year after

year. Modern fishers have been observed marking these spots for future reference and fish capture. During the dry season, as lake stream water levels recede, large numbers of fish become stranded in shallow pools or concentrated in lowland areas. Fish stranding is particularly common in the Rift Valley due to its unique, highly variable fault-controlled interior drainage system.

[It should be noted that the warm waters and high alkalinity of the Rift Valley Lakes has resulted in impoverished fish faunal diversity. Today, only a few families of 'hardy' fish are represented. Some Rift Valley cichlids have adapted to live in water nearly devoid of dissolved oxygen, and at pH up to 10.5 and temperatures of 40 °C (Riehl and

Table 3

Comparison of PUFA composition of inner cell membrane phospholipid from small and large savanna mammals and a marine mammal

Mammal/membrane	Weight (kg)	LA	LNA	AA	<i>n</i> -3 DPA	DHA
Rat liver	0.3	6.0	0.1	21	3.5	21
Capuchin ^a red cells	2.0	5.5	0.7	19	3.8	21
Hyrax liver	3.0	16	0.3	14	0.9	21
Patas ^b liver	9.0	9.0	2.3	18	4.0	8.9
Bush pig liver	80	24	3.8	10	6.2	1.8
Uganda kob ^c liver	90	10	4.0	11	8.5	1.0
Topi ^c liver	350	14	4.0	9.2	9.0	0.8
Giraffe ^c liver	1500	12	2.1	12	9.5	0.8
Dolphin <i>T. truncatus</i> (West Coast USA)	1200	0.23	0.32	16.8	3.55	11.2

Fatty acids in g/100 g phospholipid. Note also ox, lamb and kangaroo organs in Table 3.

^a New world primates.

^b Old world primates.

^c Ruminants; all others non-ruminants. Note body weights and DHA content.

Baensch, 1986; Loiselle, 1988; Johnson et al., 1996)].

Currently native Africans living on the shore of Lake Malawi eat 2196 kcal/day with 23 en% from fish and 12 en% from fat, most of which is from the fish (Pauletto et al., 1996). 12 en% equals 29 g fish oil. Half or even a quarter of this intake is still approximately 7–15 g fish oil per day. Fish intakes on the order of a half or quarter of 23 en% are 6–12 en% of the diet, easily within the 10–20 en% range for an evolutionary influence of high quality food proposed by Foley and Lee (1991).

7. Terrestrial sources of brain-specific nutrition

Brain-specific nutrition would have required a balanced source of both DHA and AA to provide the greatest advantage for cerebral expansion. Whilst the littoral food chain would have offered this advantage, the muscle meat and organs of large savannah herbivores would not (Crawford et al., 1976a,b). Small mammals are able to accumulate DHA consistent with their high brain to body weight ratios (which can be greater than the 2% of *H. sapiens* (Table 3). Thus, a small carnivorous or omnivorous primate would have had access to a source of AA and DHA. This would not have been the case with a large primate preying on the large herbivores as is postulated by the savannah hypothesis to be the stimulus for the advance to *H. sapiens*.

The meat and offal of the savannah species contains significant amounts of LA and LNA and some AA, but the DHA is replaced by its precursor, *n*-3 DPA (22:5 ω 3) (Crawford et al., 1969; Tables 2 and 3). This failure to complete the

desaturation process is consistent with the double rate limitation in the conversion process. Herbivores have access to LNA only, since DHA is absent from their primary source of the terrestrial food chain. This makes DHA a scarce nutrient for any large mammal using savannah herbivores as a primary food source. In Table 2, the LC-PUFA in terrestrial species are mainly present in small quantities as membrane phospholipids in lean tissue. LC-PUFA are not concentrated in adipose tissue; in the ruminant fats, there is very little LA or LNA. In addition, the fat content of game is exceedingly low (1–7%) compared to typical modern domestic meats (Crawford et al., 1970a,b, 1976a,b; Speth, 1989; O'Dea, 1991; Li et al., 1998). Bird eggs, and marine bird meat and fat are richer in LC-PUFA in both an absolute and relative sense than game meat (Tables 2 and 3; Speake et al., 1999).

Scavenging the remains of larger carnivore kills is a possibility for *Australopithecus* and *Homo*, and could have contributed protein, trace elements, and some essential lipids when the opportunity arose. Large cats have been observed to leave carcasses unattended for many hours at a stretch (Blumenschine, 1991; Blumenschine and Cavallo, 1992; Bunn and Ezzo 1993). The offal may be stripped with the carcass meat left untouched. The size of the carcass correlates positively with the length of time it is left unattended. Statistical evaluation of damage done to faunal remains recovered at or near hominid localities has found that in a small minority of cases, cut marks from stone tools can be identified (Blumenschine, 1991; Bunn and Ezzo, 1993; Selvaggio, 1994; Monahan,

1996). However, scavenging fresh kills with organ and CNS tissue intact was potentially dangerous, based on the number of carnivore attacks on modern unarmed native Africans (Treves and Naughton-Treves, 1999). Marean (1998) finds no reliable evidence for scavenging by early modern *H. sapiens* or *H. neandertalensis*, though it might be argued that these *Homo* had already mastered hunting, and thus relied less on scavenging.

In order to supply the DHA and AA found in a diet with only 10–20 en% as lacustrine/marine foods, a prodigious amount of muscle tissue of terrestrial game needs to be consumed, on the order of 100 en%. If a hominid were to find just one stranded bluefish (266 g with 31% fat as reported by Tanakol et al., 1999), this fish would provide 11.5 g DHA. An equivalent weight of lean beef as reported by Li et al. (1998) would supply only 0.11 g DHA. *This is a difference of two orders of magnitude.* Admittedly, high fat bluefish is an extreme example. At 3% fat, a dozen 20 g assorted molluscs (Table 2) would provide 1.2 g DHA. Warthog meat (240 g), also at 3% fat but twice as rich in DHA as the lean beef, provides 0.43 g DHA. The shellfish are 2.5 times richer in DHA than the non-ruminant meat, but the energy required to collect the sessile shellfish is minimal compared to hunting the notoriously ferocious wart hog.

If one considers scavenging terrestrial kills as the sole or primary source of dietary LC-PUFA, only the organs and brains of game could have provided consistent, concentrated sources of AA and especially DHA. Organs would need to be eaten along with their associated special fat tissue used for support (known as depot or 'caul' fat) as the organs themselves are fairly lean (Table 2). Internal organs and depot fat are parts of a carcass that are typically consumed first by carnivores and primary scavengers, and would not have been consistently available. Brain and bone marrow tissue are reasonable options for hominids with tool technology (Eaton et al., 1998; Cordain et al., 2000, 2002). However, even a very large herbivore such as the rhino has but 350 g brain tissue for one ton body weight. A carcass would need to be scavenged quickly, as brain, organ, and marrow tissues spoil very quickly. In fact, LC-PUFA is the most perishable component of organ and muscle foods (Erickson, 1998). If the 350-g brain of a rhino was divided amongst the hunting part, there would be little left to return to the women and

children even if it survived the transport in the tropical heat. Collecting fresh eggs, small mammals such as hyraxes or primates, live or nestling birds would have provided the greatest amount of LC-PUFA of any terrestrial food source, much more so than hunting the large species. Faced with the paucity of DHA in the food chain for large, land mammals, we contend that the considerable abundance of DHA as well as the essential trace elements in the estuarine, coastal and lacustrine food chains, would have conferred a significant advantage in brain nutrition over inland hominids.

8. Archaeological implications

8.1. Early modern humans in South Africa

The fossil and mitochondrial DNA evidence thus far supports an African origin for modern humans (Nitecki and Nitecki, 1994; Stringer and McKee, 1997). Lakeshore sites in the Rift Valley have yielded fairly sophisticated stone tools as old as 260 kyr associated with *H. sapiens* remains with varying mixes of archaic and modern traits (Clark, 1992). The Singa hominid (Sudan), considered to be postcranially robust but otherwise anatomically modern *H. sapiens* dates to circa 190 kyr (McDermott et al., 1996). Several of the earliest examples of anatomically modern human remains come from the Middle Stone Age (MSA) sites of South Africa — most notably Klasies River Mouth and Border Cave (Grun et al., 1990a,b; Rightmire and Deacon, 1991; Grun and Stringer, 1994; Pfeiffer and Zehr, 1996; Grine et al., 1998). Less persuasive examples come from Die Kelders, Sea Harvest, Cave of Hearths, Blombos, and Equus (Grine and Klein, 1993; Avery et al., 1997; Klein, 1999; Grine et al., 2000).

While human remains from the South African MSA are admittedly scarce, and the archaeological record far from perfect, components of the Howiesons Poort and Stillbay stone tool assemblages have been taken as evidence of early modern behavior (Deacon, 1992; Henshilwood and Sealy, 1997). Bone tools are reported from the MSA levels at Blombos (Henshilwood and Sealy, 1997; Grine et al., 2000) and at Klasies River Mouth (Singer and Wymer, 1982), but the unarguable widespread appearance of bone in Europe and the Near East does not appear until later. Sediments bearing bone harpoon-like points at the Katanda sites date to circa 90 kyr, suggesting that central

African MSA humans not only worked bone, but also systematically exploited fish (Brooks et al., 1995; Yellen et al., 1995). Apparently at least some of the MSA assemblages from South Africa and other areas of Africa were made by anatomically modern humans.

It is relevant to attempt to establish where people were on the Cape between 80 and 15 kya, the key time for appearance of the southern African people (Khoisan). South African MSA sites with Howiesons Poort (HP) or Stillbay (SB) assemblages, and sites dating to the last glacial maximum (LGM) are not randomly located, but instead occur almost wholly within a strip 100–200 km from the present coast (Fig. 2). The LGM (17–23 kyr) is within the ^{14}C dating window, so the site distribution data are better constrained. Examining the landscape between the exposed lowest sea level shore contour and the present continental escarpment, we find that well-dated Southern African LGM sites fall within a 200-km wide strip, the other half of which is presumably now submerged. During oxygen isotope stages 2–4, sea levels were lower and up to 150 km of continental shelf was exposed. These LGM sites are almost exclusively cave localities (Parkington, 1990), which further suggests there must have been other sites now lost by marine transgression.

Mapping HP and SB sites can be done based on the assumption that they are all more or less the same age, in the ranges 60–80 and 80–100 kyr, respectively. All HP sites fall within the strip, but are some are open sites close to the coast. During oxygen isotope stage 4, the best date estimate for HP (Deacon, 1992), people were apparently also restricted to near-shore environments. Tens of thousands of sites are recorded and, defined as inland of the escarpment, but none are LGM, HP or SB (Sampson, 1985). Some of the MSA sites from the surface of the interior could possibly be in the range between 80 and 13 kya, but so far are undated. (The sequences from this region range from regular MSA, which could easily be more than 80 kyr, to well-dated assemblages of approximately 13 kyr.) Evidently, for at least 70 kyr, people in southern Africa were living within 200 km (and often much less) of the coast. They may have been restricted to this area by the sea to the south and the arid, cold interior highlands to the north. At this point, dated MSA sites with apparently advanced patterns of tool manufacture are near the coast.

9. Shell middens in the Cape MSA

Along the Cape West and South coasts there are many MSA sites with abundant shellfish and other marine food remains; the total number of sites may be in the hundreds (Fig. 2). The best known of these coastal sites is at Klasies River Mouth, where over 20 m depth of shell midden has accumulated, much of it dating to oxygen isotope stage 5 (Grun et al., 1990b; Deacon, 1992). Recently the shell middens in a small cave at Blombos have been dated to 80–100 kyr (Henshilwood and Sealy, 1998). Some shell has been reported from the MSA levels at Die Kelders, although the quantity of marine food debris here may not be as substantial as at other now coastal sites (Avery et al., 1997). At Hoedjiespunt two shell midden sites are reliably dated to oxygen isotope stage 5 (most likely 5e) by luminescence dating (Jim Feathers, Seattle, WA, and Stephan Woodborne CSIR, Pretoria, RSA, personal communication JEP). A small shell midden in a cave at Boegoeberg near the mouth of the Orange River has radiocarbon and uranium-series dates that indicate an age of more than 50 kyr (Klein et al., 1999). Many more West Coast MSA shell middens are known but as yet unexcavated. Although most of these sites have so far not produced human remains, the association of modern humans and MSA artefacts at Klasies River Mouth, Blombos, and Die Kelders raises the question of the connection between early middens and early moderns.

Shellfish gathering is traditionally considered an archaeological indication of modern behavior because early anatomically modern people were clearly doing it (Parkington, 1998). It was considered that the awareness of the nutritional benefits of marine and lacustrine foods would have led to the creation of better tools and procedures for systematic exploitation of these resources (Volman, 1978). But while some fishing requires sophisticated tackle, shellfish gathering requires far less effort or creativity as we discussed above. Presumably humans and/or hominids had been gathering shellfish in earlier times, but perhaps not as systematically or in such a way as represented by the large shell middens that accumulated at particular locations. But at some Cape sites the earliest signs of shellfish middens piling up in coastal caves and dunes, coincides with the appearance of early modern humans.

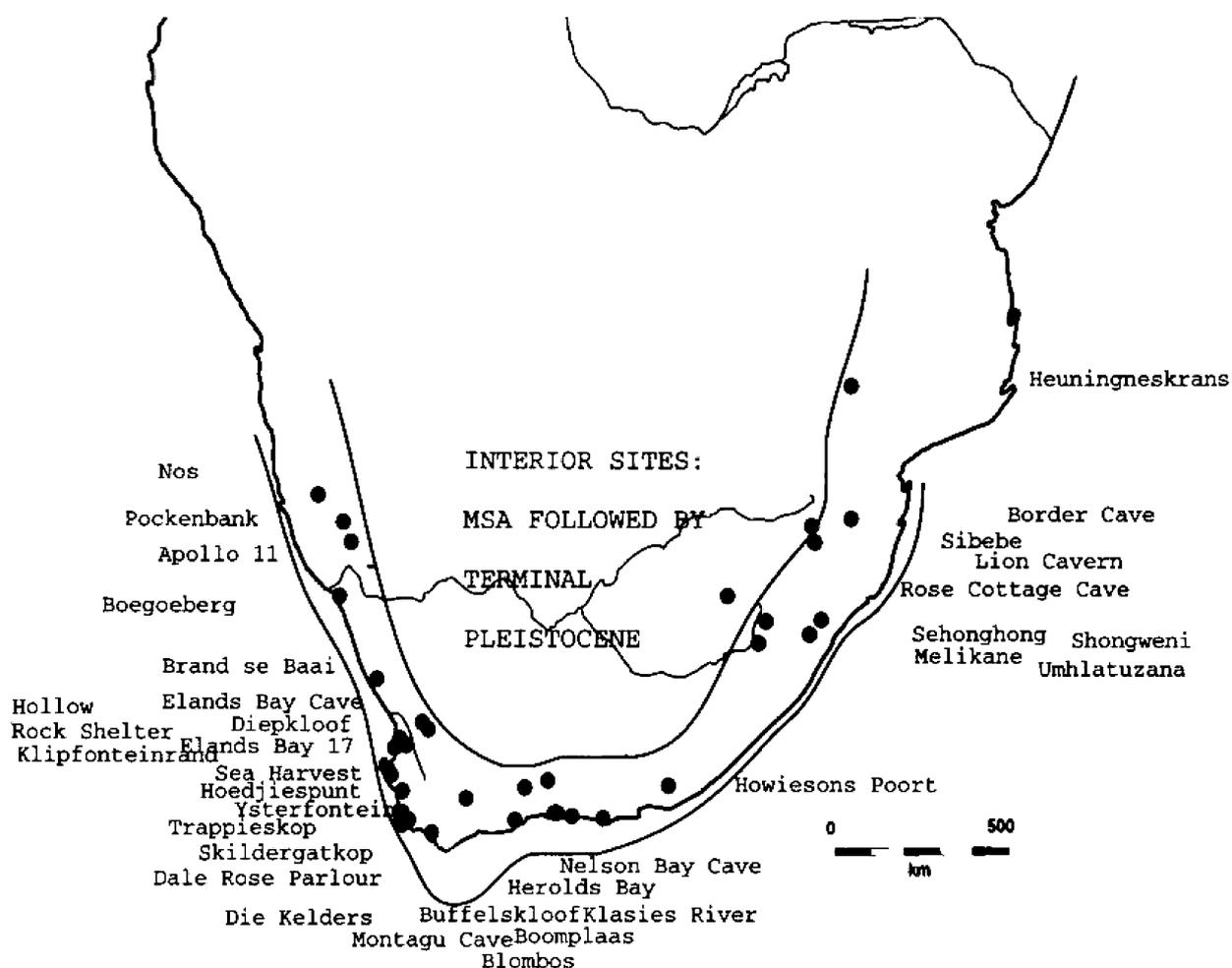


Fig. 2. Map of South African Cape showing dated Middle Stone Age (MSA) and Last Glacial Maximum (LGM) sites. The outer shoreline contour is the estimated coastline during LGM. The inner shoreline contour is the present coastline, and the heavy contour line inland is the present continental escarpment. Sites cluster in an approximately 200 km wide strip between the present coast and continental escarpment. Data from Sampson (1985) and Parkington (1990).

While the hard archaeological evidence at the Cape for shellfish consumption is incontrovertible, sea bird eggs, turtles, stranded fish, etc. would also have been collected (Stewart, 1989; Bailey and Parkington, 1988; Stiner et al., 1999). At Blombos fish up to 20 kg were apparently lured with bait to enter tidal inlets, where they were then speared (Grine et al., 2000). This fishing method requires an understanding of littoral cycles and advanced planning. Ethnographically, women and children collect shellfish in most parts of the world, snacking as they go, but return large collections to home bases for sharing with other group members (Bailey and Parkington, 1988; Claassen, 1991). Assuming that the near universality of this gen-

dering of behavior means that it has antiquity, it is likely that early modern women accessed the nutrients of the shoreline, rich in LC-PUFA, protein, and trace elements. This type of collecting is simple, even when pregnant, lactating, or accompanied by children, who would in all probability assist.

10. The Middle East

Shell and fish bone middens of phenomenal scale dating to 40 kyr are found at over 40 sites along the Nile River Valley leading out of Africa into the Middle East (Stewart, 1989, 1994). The remains provide evidence for seasonal fishing

camps that were frequented year after year. These archaeological data have been used to define modern human behavior at a site, but this corridor was in use long before 40 kya (Van Peer, 1998), and perhaps the fishing sites were, too. Walter et al. (2000) report MSA bifacial axes, and obsidian flake and blade tools found in association with mollusc and crustacean remains on Red Sea coast in Eritrea. The assemblage is dated at 125 kyr; no hominid remains were recovered, but the site is likely to be of early modern human origin.

A pattern of increased shellfish gathering is seen in Western coastal Italy (Liguria and Lazio) during oxygen isotope stage 5 (Stiner et al., 1999). Stiner et al. (1999) correlate exploitation of easily-caught shellfish and turtles with low population density in the early MP. Later MP and UP groups also exploited more fast-moving game such as partridges and hares presumably due to higher population densities. Coastal Italy and the South African Cape have the same warm but dry Mediterranean climate, with an ecological juxtaposition of rich coastal but relatively marginal inland resources (Bailey and Parkington, 1988; Parkington, 1998). Overall, a pattern of *Homo* littoral resource exploitation now stretches from one end to the other of the geologically unique extended East African/Arabian Rift System. Indeed, earlier fission track ageing of fossils on the island of Flores indicates that Hominids had 'acquired the capacity to make water crossings' 0.9 million years ago. Morwood et al. (1998) suggests that 'the cognitive capabilities of this species may be due for re-appraisal'. If these water crossings were made by boat or even as was suggested (Tobias, 2001) by elephant, a fairly high degree of social cohesion and probably language would have been essential for the design, motivation and execution of the boat making or elephant training. If language and social cohesion are characteristics of humans, it seems difficult to place a time at which human behaviour first appeared on the planet. We would therefore not wish to suggest any time at which humans first appeared. Our central theme is firstly that cerebral expansion could not have occurred on the savannahs of Africa and secondly that the land water interface provides the optimum nutritional conditions for cerebral expansion.

As the Flores evidence indicates established use of the marine environment in antiquity, it is plausible that the first exploration of the marine food chain might have occurred even further back in

time. The human genome is apparently only approximately 1.5% different from that of the chimpanzee. The genetic evidence suggests a separation took place 5 mya. This means that the line from which hominid and humans eventually descended was inhabiting a separate ecosystem 5 mya, as they were not interbreeding. They were therefore not in the forests or savannah/forest interface as they would still have had the opportunity for interbreeding. It is interesting to speculate that this separation which took place may have been linked to the discovery of the richness of the land water interface, probably starting through migration down a river to the estuary. This speculation would explain the separation and herald the exploitation of the land water interface. Continuous exploitation of the food chain in this uniquely rich, ecological niche would have prevented loss of brain capacity as happened in all land based mammals as they evolved larger bodies. The brain capacity of the chimpanzee as an example is approximately 0.5% but this falls to <0.3% in the larger gorilla which has a physically smaller brain, the brain capacity of the even larger savannah species falls to less than 0.1% of body mass (Crawford et al., 1993).

Regardless of when or where the separation from the great apes took place, the individual coastal African and Near Eastern sites can no longer be dismissed as representing localized rather than a generalized adaptive behavior. Indeed the opposite may have been the case. Inland exploitation may have led to an evolutionary dead-end and even cerebral loss of relative to brain size, as happened universally with all land based mammals and primates as they evolved larger bodies (Crawford et al., 1993).

11. Overview

All land based mammals, without exception, lost relative brain capacity logarithmically as they evolved larger bodies. The fast growth rate in these species outstrips their capacity to synthesise the LC-PUFA required for the brain and there is no significant source of these essential nutrients in the savannah food chain. There is no science-based evidence which would explain *H. sapiens* being an exception to this rule of brain capacity loss with increase in body size. The outstanding feature of *H. sapiens* was the evolution of the brain and its functions. It thus seems unlikely that *H. sapiens*

could have evolved and maintained a large, metabolically expensive brain in a land environment. The land-based ecology did not provide brain-specific nutrition which would have been a primary, long-term component of the resource base, in particular LC-PUFA. In a situation where dietary LC-PUFA are both restricted in quantity and unbalanced, the optimum levels and AA/DHA ratio in the fetal and infant brain could not have been maintained. If this experience is shared among most or all fetuses and infants of a hominid species or group, then LC-PUFA become limiting nutrients for the neural development of an entire population. Growth and maintenance of healthy placental tissues, and normal adult human brain function require LC-PUFA as well.

Conversion of 18-carbon PUFA from vegetation to AA and DHA is considered quantitatively insufficient due to a combination of high rates of PUFA oxidation for energy, inefficient enzymatic conversion, and substrate inhibition. The marine and lacustrine (littoral inclusive) food chains provide consistently greater amounts of pre-formed LC-PUFA than the terrestrial food chain. Dietary levels of DHA are 2.5–100-fold higher for equivalent weights of marine fish or shellfish versus lean or fat terrestrial meats. Mammalian brain tissue, very small mammals, primates and bird egg yolks, especially from marine birds, are the richest terrestrial sources of LC-PUFA. The large mammals alleged to be the prey for evolving *H. sapiens*, could not have provided the necessary DHA.

The archaeological record is a circumstantial opportunity to test ideas derived from elsewhere. A hypothesis based *solely* on the distribution of LC-PUFA in nature and the relationships between PUFA intake and fetal/neonatal development predicts there would be some coincidence in distribution with long shorelines (estuaries or in restricted coastal strips), of early shell middens, early anatomically modern fossil hominids, and evidence of behavior patterns such as bone working, production of blades, burins, and bifacially worked pieces. It also predicts a relative absence of such patterns elsewhere within the same frame. Although there are clearly inadequacies of dating and a dearth of human remains, the existing Cape, Nile Valley, and Near East archaeological record thus far may support it. We propose that shell middens, fish and shellfish remains are not simply a coincidental or circumstantial archaeological hallmark of modern human behavior, but perhaps

evidence for a sustained intake of brain-specific nutrition afforded by these littoral marine and lacustrine foods.

Early modern humans of the Rift Valley, Cape, and perhaps the Northern African MSA (Clark, 1992) are likely to be the ancestral population base of a substantial proportion of humans alive now (Stringer and McKee, 1997; Relethford, 1997; Relethford and Jorde, 1999). Richards et al. (2001) compared stable carbon and nitrogen isotopes in bone collagen from nine modern humans to previously published results for five Neandertals. All remains were from European Upper Paleolithic sites with dates ranging from 40 to 45 ka to approximately 20 ka. It is known that ^{15}N values for freshwater and marine fish (ca. 12‰) and carnivorous marine mammals (ca. 18‰) are much higher than those of terrestrial herbivores such as cattle and deer (ca. 4–6‰). Similar ^{15}N higher values are observed in waterfowl feeding on aquatic invertebrates and/or vertebrates. However, marine organisms are more enriched in ^{13}C than terrestrial organisms. ^{13}C values from marine mammals are less negative (ca. *12‰) than from terrestrial aquatic ecosystems (ca. *23‰) (Schoeninger and De Niro, 1984; Hare et al., 1991). Consistently higher ^{15}N values were observed in the human remains, indicating that 20–50% of dietary protein came from freshwater aquatic foods. One specimen (Kostenki 1, Russia) had an isotopic signature indicating that well over 50% of dietary protein came from freshwater resources. The Paviland 1 specimen (UK) came from a coastal environment, and results indicated that marine foods constituted 10–15% of dietary protein.

In contrast, despite living in close proximity to rivers and lakes, inland European Neandertals evidently ingested predominantly protein from terrestrial herbivores. Since ^{15}N can vary over time and geographic regions, ^{15}N values for herbivore and carnivore remains associated with the Neandertal remains were measured. Neandertal ^{15}N values were most similar to coextant top-level carnivores such as wolves, large felids, and hyenas. Neandertals from coastal Mediterranean sites are known to have exploited littoral resources on occasion, including fish, oysters, clams, mollusks, and mussels, however, this may have been opportunistic behavior (Stiner et al., 1999; Stringer et al., 2000). Results indicate that Upper Paleolithic humans had greater dietary breadth than Neandertals, which

may have allowed them to better adapt to natural pressures and increasing population densities of Late Pleistocene Europe.

Our case is the nutritional resources that available to the hominid line, which led to and included early *H. sapiens*, had significant bearing on how and why our modern intellects evolved in face of the universal collapse of brain EQ in land based mammals. It also has a bearing on the major problem of iodine deficiency and mental retardation which affects such a large proportion of today's inland or flood plain populations. It is relevant to recent, human history from the rise of civilisation to the exploration of the planet by sea, especially continued extensive marine explorations from the Minoans, Egyptians, Polynesians, Vikings, Columbus and the modern navies, which arose from the fishing experiences.

Moreover, with cardiovascular disease being greatest in populations based on land animal fats, it is germane to the present and future human health and the over exploitation and future of what was the planet's richest food resource. It bears mentioning that humans of the Cape MSA, for example, apparently accessed a resource base exceedingly rich and nutritious compared to the subsistence agriculture that most Africans practice today. We are not implying that all MSA people ate fish and/or shellfish only, but that the pool of people who make extensive use of it, did have the advantage of an increased LC-PUFA intake and fuel for brain development. This advantage would have had significant survival value in competition with other hominids living on the inland and/or dependent on the savannah food chain. It also needs to be emphasised that to maintain an advanced brain size today would be easier than to evolve from 450 g to 1.3 kg of brain.

Neither are we implying that humans *cannot* live in interior areas, just that living successfully in Central Eurasia during glacial oxygen isotope stage 4, for example, without the benefit of marine, lacustrine, or riverine foods would have required a heavy reliance on either (1) scavenged brains, organs, and bone marrow, or (2) modern behavior including big game hunting, social meal, and perhaps a rudimentary understanding of iodine, iron, and zinc deficiencies (Thilly et al., 1992; Horrobin, 1999). The high prevalence of iodine deficiency today amongst inland people to which 1.6 B are at risk, testifies to the significance and

advantage of the littoral cluster of brain specific nutrients.

12. Conclusion

In this paper we have attempted to discuss nutritional resources that could have contributed to an increase in intellectual capacity and creativity without relying on *pre-existing* modern behavior. Future excavations and resource modelling would benefit from quantitative treatment of the sources of brain-specific nutrition that hominids may have accessed. However, an evidence-based approach is essential. There is now robust evidence on the absolute requirements of brain growth for the omega three fatty acids and especially DHA. The present nutritional evidence makes a land ecology as an improbable basis for human evolution. The advantages of the littoral and lacustrine habitats are clearly supportive.

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