Review article

Rift Valley lake fish and shellfish provided brain-specific nutrition for early Homo

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An abundant, balanced dietary intake of long-chain polyunsaturated fatty acids is an absolute requirement for sustaining the very rapid expansion of the hominid cerebral cortex during the last one to two million years. The brain contains 600 g lipid/kg, with a long-chain polyunsaturated fatty acid profile containing approximately equal proportions of arachidonic acid and docosahexaenoic acid. Long-chain polyunsaturated fatty acid deficiency at any stage of fetal and/or infant development can result in irreversible failure to accomplish specific components of brain growth. For the past fifteen million years, the East African Rift Valley has been a unique geological environment which contains many enormous freshwater lakes. Paleoanthropological evidence clearly indicates that hominids evolved in East Africa, and that early Homo inhabited the Rift Valley lake shores. Although earlier hominid species migrated to Eurasia, modern *Homo sapiens* is believed to have originated in Africa between 100 and 200 thousand years ago, and subsequently migrated throughout the world. A shift in the hominid resource base towards more high-quality foods occurred approximately two million years ago; this was accompanied by an increase in relative brain size and a shift towards modern patterns of fetal and infant development. There is evidence for both meat and fish scavenging, although sophisticated tool industries and organized hunting had not yet developed. The earliest occurrences of modern *H. sapiens* and sophisticated tool technology are associated with aquatic resource bases. Tropical freshwater fish and shellfish have long-chain polyunsaturated lipid ratios more similar to that of the human brain than any other food source known. Consistent consumption of lacustrine foods could have provided a means of initiating and sustaining cerebral cortex growth without an attendant increase in body mass. A modest intake of fish and shellfish (6–12 % total dietary energy intake) can provide more arachidonic acid and especially more docosahexaenoic acid than most diets contain today. Hence, 'brain-specific' nutrition had and still has significant potential to affect hominid brain evolution.

Fish: Brain-specific nutrition: Long-chain PUFA: East Africa Rift Valley Lakes

Marked expansion of the hominid cerebral cortex took place only in the last one to two million years. During this small evolutionary window, genus Australopithecus became extinct while Homo greatly expanded. Sophisticated tool manufacture, organized hunting, culture, and speech followed rapidly. We hypothesize that the unique geological and ecological environment of the East African Rift Valley provided an equally unique nutritional resource base for the enlargement of the Homo brain, culminating in *Homo sapiens*. How in this remarkably short stretch of evolutionary history did our intelligence arise? While many physical (i.e. development of bipedalism, speech), ecolo-

gical (adaptation to omnivorous diet, drier climatic conditions) and cultural adaptations (use of tools, living in groups) have roles, these adaptations alone are apparently not sufficient to account for the unique intelligence and culture we have today. If these adaptations alone were sufficient, then in all cases we must ask ourselves why no other primates developed as such.

Previous authors (Martin, 1983; Harvey & Clutton-Brock, 1985; Blumenschine, 1991; Foley & Lee, 1991; McHenry, 1994) have considered an ecological approach to human evolution. In these arguments, the high metabolic energy requirements of the brain require that hominids must have accessed relatively-high-quality and abundant food resources. Various selective pressures affecting hominid evolution might be necessary, but are not sufficient conditions for cerebral expansion. Whatever the selective pressures, they can only be satisfied in a context where sufficient dietary energy and essential nutrients are available to fuel the added brain growth. Sufficient protein, vitamins, and trace elements are certainly required, but dietary essential polyunsaturated fatty acids (PUFA) are probably the most limiting nutrients for neural growth (Crawford & Sinclair, 1972). If hominid diets were consistently deficient in long-chain (LC-) PUFA, the uniquely complex human neurological system could not have developed, regardless of the diverse stimuli that may have been involved.

We are in agreement with the ecological approach to evolution of human intelligence, and propose that nutrition played a more crucial role in the rapid neural development of genus Homo than has been considered previously. We concentrate specifically on the nutrition provided by the unique ecosystem of the East African Rift Valley lakes. The fossil evidence clearly indicates that Homo arose in the vicinity of these lakes, which are geologically better classified as 'proto-oceans'. The diverse alkaline-freshwater fish species within those lakes provided, either directly or indirectly, a source of both protein and PUFA. In particular, the freshwater-fish lipid profile has a docosahexaenoic acid (DHA) : arachidonic acid (AA) value that is closer to that in our brain phospholipids than any other food source known. We hypothesize that consistent consumption of fish, crustaceans, molluscs, and other lacustrine species from the lake margins provided a facile means of both initiating and sustaining growth of the cerebral cortex without an attendant increase in body mass.

We are aware that the origin of human intelligence is one of the most fundamental questions ever posed by man, and we do not propose to answer it completely in this brief discourse. Many genetic, environmental and climatic conditions almost certainly conspired to allow for the selection and expansion of our large, complex brains. We discuss some of these relevant conditions in the following sections. However, we are not fully satisfied with the slow pace and passivity of evolutionary models based entirely on selective pressures. For example, we can hypothesize two end-member conditions for the eventual occurrence of *H. sapiens*: Did hominids 'become' intelligent enough to begin fishing, or did they fish and then become intelligent? Since these two end-members are not mutually exclusive, and would in fact reinforce each other, the answer is likely

to lie between. We envision something such as: hominids scavenged fish and/or fished opportunistically, which helped increase intelligence enough for them to fish more often and more successfully. We aim to bring attention to the fact that the latter end-member, in which nutrition plays a crucial role in the origin and maintenance of intelligence, has not been given adequate consideration.

Encephalization quotients (EQ): quantifying cerebral expansion

The term EQ was introduced in the 1970s to account for the influence of body size on brain size, thereby permitting a scale of comparison between species that would identify relatively larger-brained species independent of body size (Martin, 1983). The EQ compares brain weight : overall body weight for all species of interest, and is scaled so that the comparison among brains is in effect done for constant body size. It has become a valuable tool for quantifying the remarkably larger brain size in *H. sapiens v.* other extant primate and extinct hominoid species (Table 1). By providing a quantitative and reproducible scale, the EQ has helped evolutionists focus on developing an adequate explanation for the enlargement of the evolving human brain. Exact EQ values vary among sources, depending on the method of calculation and the database used; however, all sources consistently show that adult *H. sapiens* has an EQ about 2·4–2·7 times larger than adult *Pan troglodytes* (modern chimpanzee). They also consistently show that as hominids evolved, EQ increased from about 1·4 in *Australopithecus africanus* to about 2·4 in *Homo erectus*.

EQ values are not as different between neonates of various primate species as they are between adults, suggesting that both brain and body growth postnatally have an influence on the resultant EQ of adults. It should be noted that overall body weight is still a key reference point for establishing EQ values, and modern-day primates are significantly leaner than humans. Hence, the presence of 15–30 % body fat in humans actually reduces the EQ difference between primates (or hominids) and *H. sapiens*. This is especially true for neonates, since human infants have much more body fat than infants of other primate species.

Table 1. Mean brain volumes and encephalization quotients (brain weight : overall body weight; EQ) for selected hominoid species

Species	Brain volume (ml)	EQ1*	EQ2†
Australopithecus:			
afarensis	384	1·23	1·45
africanus	420	1·31	1·62
boisei	488	1·37	1·72
robustus	502	1·49	1·92
Homo:			
habilis	579–597	1·74–1·79	2·10–2·29
rudolfensis	709	1·41	2·11
erectus	820–844	1·59–1·63	2·38–2·44
sapiens	1250	3·05	4·26
Pan troglodytes	410	1·25	1·57

* From calculations of Martin (1983).
† From calculations of Harvey & Clutton-Brock (1985).

East African Rift Valley geological summary

The Red Sea, Gulf of Aden, and East African Rift Valley are the only current examples of what is termed geologically as a 'failed ocean'. Rifting began about thirty million years ago, thinning and stretching the continental crust, but significant uplift did not begin until fifteen million years ago. Bohannon et al. (1989) proposed that rifting was passive, doming postdated rather than preceded uplift, and was caused by adjacent asthenosphere (plastic, flowing mantle) and deep continental lithosphere (partially rigid mantle) flowing into the area of thinned crust. The Red Sea axis has thin longitudinal strips of oceanic crust that are only approximately five million years old; 2·5–4 km of uplift has occurred in the continental areas adjacent to the Red Sea in the past 13·8 million years.

In East Africa, faulting related to the crustal extension and uplift formed a series of half-graben basins which link together to form the Rift Valley (Fig. 1). Large lakes formed in the basins, with inputs from both interior drainage and river systems. On the border fault side of the lakes, cliffs may rise to > 2 km above the lake level. Some of the lakes were so extensive during Cenozoic (sixty-five million years ago to present) highstands that they are termed proto-oceans. Lakes Malawi and Tanganyika presently have water depths up to 1500 and 600 m respectively. Many of the deep water channels in Lakes Malawi and Tanganyika are similar in form and scale to those observed in the deep ocean (Scholz et al. 1990).

Lakes with interior drainage have little or no input from major rivers, the water levels are highly dependent on the geology and climate. For example, Lake Victoria currently loses 90 % of its water input by evaporation; therefore the lake level is very sensitive to regional temperature and rainfall (Leeder, 1995). During the Miocene and Early Pliocene, lakes covered > 1 000 000 km^2 that are now desert or savanna. By comparison, Lake Victoria is presently 69 000 km^2, and is the world's largest tropical lake (Stager et al. 1997).

Permanent lake levels fluctuated widely during the Middle to Late Pliocene and Pleistocene between shallow, alkaline and saline, and deep and stratified. Smaller lakes tended to become more alkaline and saline, or even ephemeral. Associated with the lakes are fine-grained lacustrine, shoreline sand, coarse-grained fluvial or channel, and alluvial-fan or delta deposits. These sedimentation patterns indicate prolonged lowstands in the Pleistocene (Baker et al. 1972; Scholz & Rosendahl, 1988; Scholz et al. 1990). Lake Victoria, for example, is at least 0·8–1·6 million years old, but its level has fluctuated greatly. The lake was completely dry in the Late Pleistocene, until 12·4 thousand years ago (Johnson et al. 1996).

Even in a passive rifting model, there is broad agreement that the Afar area (Ethiopia; Fig. 1) overlies a mantle plume. Extensive alkalic volcanism and plutonism (molten rock intruded into the crust, not erupted) along the East African Rift has occurred in the past twenty-six million years (Dawson, 1992). The Rift is the largest peralkaline volcanic province in the world, and has the only volcano known to have erupted carbonatite tephra and lava in historic times (Dawson et al. 1996).

Carbonatite/peralkaline magmas (magma is molten rock below surface, actual or hypothetical) are very unusual in that they are relatively poor in SiO_2, and water, but relatively rich in CO_2, halogens, Na, Ca, and trace elements. They are associated with continental rifting or oceanic islands over mantle plumes. Large stratovolcanoes (typical cone-shaped volcanoes with alternating layers of lava, ash and pyroclastic flows) are common, and much of the Cenozoic strata in the Rift Valley consists of lava, tufa and pyroclastic flows, or ash fall. These carbonatite-type volcanic rocks are rich in alkali and incompatible (i.e. rare earth elements, Zr, Rb, halogens) elements (Bailey & Macdonald, 1987; Bestland et al. 1995). In summary, the East African Rift Valley, with its extensive proto-oceanic lakes and intracontinental volcanic activity, is a unique tectonic province unmatched elsewhere on Earth in both type and extent.

Divergence of hominids from hominoids

The phylogenetic designation 'hominoid' refers to the Superfamily Hominoidae, which contains the extinct common ancestors of apes and humans, as well as extinct precursors to, and extant genera of both apes and humans. The designation 'hominid' refers to the Family Hominidea, including only bipedal primates considered to be in the lineage leading to modern humans. Combined geological and environmental conditions are thought to have initiated the divergence of Hominidae from Hominoidae.

Before divergence, protosavanna (evergreen woodland with some open patches) appeared in Southwest Africa, Arabia, and North Africa 17 million years ago, but did not appear in equatorial Africa until 14 million years ago (Harris, 1993), roughly coincident with the onset of continental uplift. Protosavanna existed until the Late Miocene, although there was a mosaic of environments, with at least some rainforest present in the Eastern Rift 12·2 million years ago (Jacobs & Kabuye, 1987).

Extensive uplift and faulting occurred along the rift axis starting at eight to nine million years ago. The tectonic activity may have geographically isolated two groups of the common ancestor of Ponginae (great apes) and Hominidae (Coppens, 1994). The population on the eastern, more arid and open side of the rift evolved into the hominids. Those on the western side remained in a more humid, arboreal environment and continued along their evolutionary track to great apes (e.g. Pan, Gorilla, Pongo).

Near the end of the Miocene, Africa became cooler and drier. Savanna appeared in equatorial Africa seven million years ago. Between four and seven million years ago, 75 % of fifty-nine known land mammal genera were new, including the first leporids and hominids, new felids, extant hyaenids, new hippopotamids, extant giraffids, extant and diverse elephantids, and diverse extant bovids (Harris, 1993; Vrba et al. 1995). Growth of the Antarctic ice sheet lowered sea levels, and was a fairly major factor in a complete dehydration of the Mediterranean Sea approximately six million years ago. With these major changes in local oceanic circulation, cold Antarctic ocean currents flowed along the west coast of Africa and drew moisture-
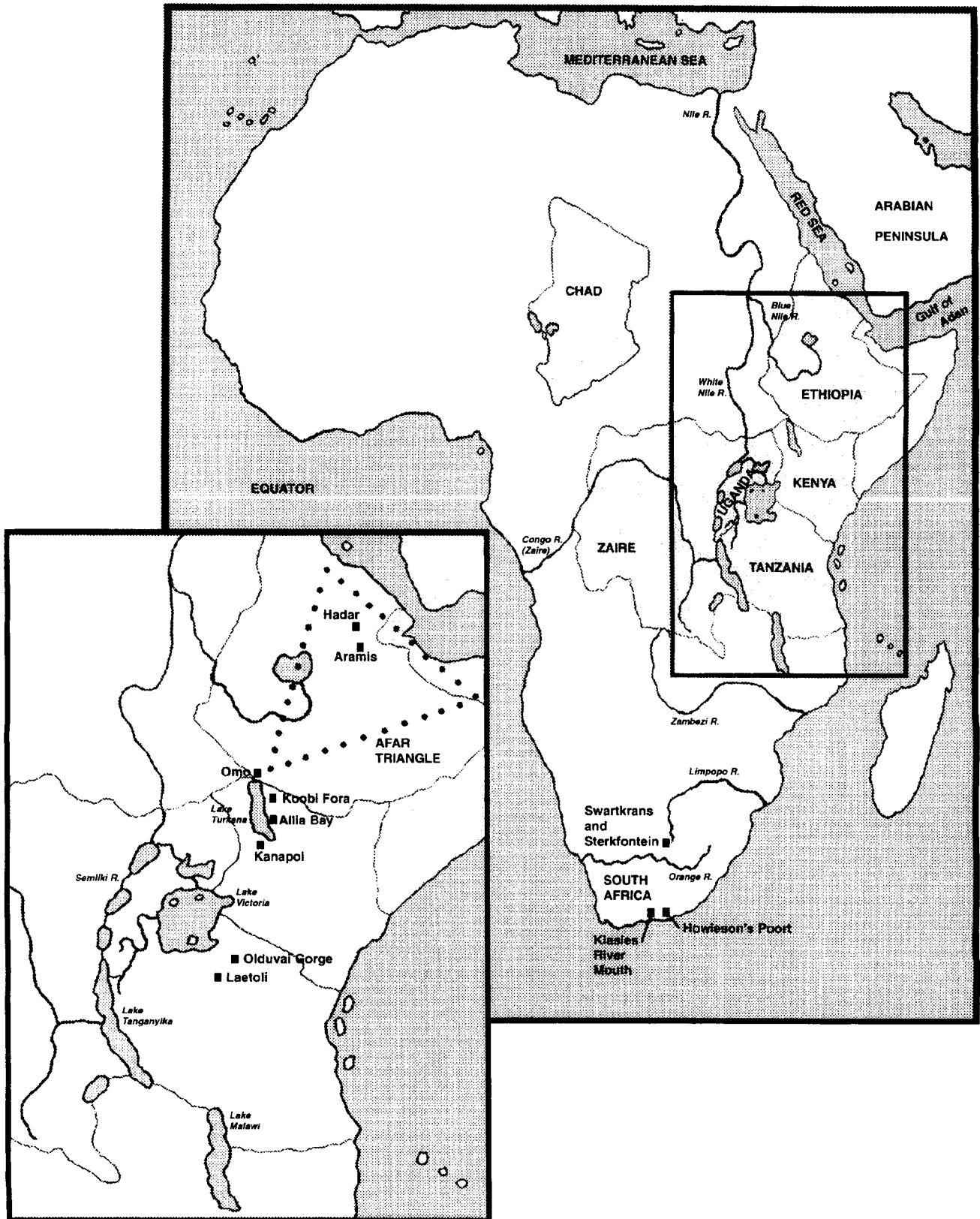
Fig. 1. Map of East Africa and South Africa giving major hominid fossil localities and lakes discussed in text. The Red Sea and the Gulf of Aden are considered to be two 'arms' of a tectonic plate triple junction (i.e. the intersection of three tectonic plates). The third 'arm' is the East African Rift Valley, extending from the Afar area of Ethiopia (see inset) to near the eastern Zambezi River, below Lake Malawi. Lake Victoria is the world's largest tropical lake; many other lakes are present in the Rift Valley which are not shown on this scale.

laden air from the land, increasing the aridity of coastal southern Africa. The equatorial forest began to shrink, and more drought-resistant flora spread. The transitional ecological zone between forest and adjacent savanna increased in extent (Conroy, 1990; Sikes, 1994; Vrba et al. 1995).

This phenomenon was intensified in the Eastern Rift due to the combined effects of global climatic changes, rainshadow and altitude effects from the continued uplift, and periodic volcanic eruptions which temporarily reduced surrounding areas to wastelands. Several authors have hypothesized that adapting to these transitional zones, neither forest nor savanna, drove the shift from arboreal quadrupedalism to terrestrial bipedalism in the Late Miocene primates (Lovejoy, 1981; Conroy, 1990; Coppens, 1994). As noted in the previous section, the first oceanic crust appeared in the Red Sea Rift approximately five million years ago. Oceanic crust appearance indicates near-maximum lithospheric attenuation (thinning of the uppermost brittle layer of crust plus mantle), and in response volcanic activity in both Africa and Arabia increased.

Australopithecus afarensis and precursors

About four million years ago, the land mammal generic diversity nearly tripled (Harris, 1993). Included in this expansion are the oldest hominids known (Fig. 2).
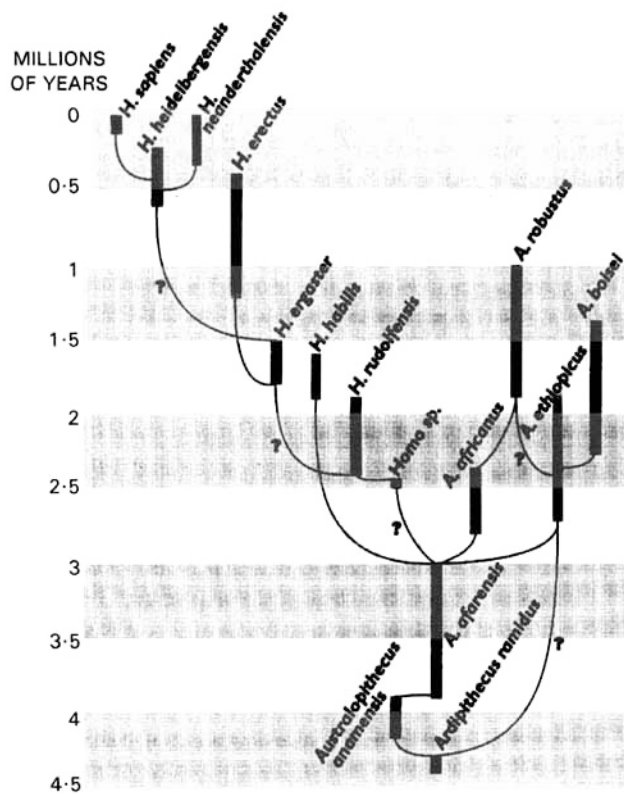

Fig. 2. Proposed phylogenetic tree for hominid evolution. Questionable lineages represent differing opinions among researchers as well as incomplete fossil records. (Adapted from Wood, 1993 and Johansen & Edgar, 1996.)

Currently *Ardipithecus ramidus* is recognized as the oldest hominid, dating to 4·4 million years ago (White et al. 1995; fossils from Aramis, Ethiopia only). It cannot be determined conclusively from the fossils recovered whether this hominid was bipedal. The oldest bipedal hominid *Australopithecus anamensis* dates to 3·9–4·2 million years ago (Leakey et al. 1995; fossils from Allia Bay and Kanapoi, Lake Turkana, Kenya). *Australopithecus afarensis*, the oldest undisputedly widespread hominid, is found in many localities dating to 3·8–3·9 million years ago. (One recent fossil has been dated to 4·18 million years ago, which if confirmed may make this species contemporaneous with *A. anamensis* (Kappelman et al. 1996).)

Australopithecine fossils are confined to Africa, and collectively demonstrate that bipedalism preceded dramatic enlargement of cranial capacity by over 2 million years. *A. afarensis* was primitive, with a brain volume of approximately 400 ml, well within the size for extant apes (Table 1). AL-288 'Lucy' had a birth canal which was not designed to allow the passage of an enlarged fetal cranium (Lovejoy, 1981; Rak, 1991; Rosenberg, 1992). Major dentition differences between pongids and *A. afarensis* are indicative of a shift towards an omnivorous diet, including: (1) decrease in canines and loss of canine gap; (2) increase in premolar and molar size; (3) overall more gracile dentition (Rak, 1983; Kimbel et al. 1984; Suwa et al. 1994). Dental wear indicates that *A. afarensis* ate mostly plant foods, but occasional small vertebrates and insects are not ruled out; neither would be eggs and invertebrates such as molluscs (Johansen & Edgar, 1996).

Australopithecus africanus

A. afarensis remains have not been found in any strata younger than three million years. The next hominid to appear in the fossil record is *A. africanus* at 2·8 million years. *A. africanus* was about the same height and weight, and is thought to have eaten a similar vegetarian or omnivorous diet (Skelton & McHenry, 1992; Wood, 1992; Sikes, 1994; Johansen & Edgar, 1996). *A. africanus* shows no evidence for the delayed maturation characteristic of human infants, or selection for a pelvic structure designed to accommodate an enlarged fetal cranium (Rak, 1991; Rosenberg, 1992; Conroy & Kuykendall, 1995; this would be true for *A. aethiopicus* also, but this species is very poorly represented in the fossil collections). For example, it is estimated that Australopithecine young erupted their first adult molars at about 3–4 years of age, similar to pongids, and dissimilar to human children, who erupt these teeth at 6 years (Smith et al. 1995).

In general, *A. afarensis* is thought to be ancestral to two distinct lineages, one Australopithecine and one Homo (Fig. 2), but there is no agreement on the detailed phylogeny, and discussion of such is both beyond the present scope, and subject to change each time a new fossil discovery is made. It is agreed that *A. boisei*, *A. robustus*, and *Homo* spp. share a common ancestor, which is likely to be *A. afarensis*, but may also be a hominid as yet unknown (Skelton & McHenry, 1992; Foley, 1994).

Further evolution of hominids: an overview

Three million years ago the Northern hemisphere climate was generally warmer, with sea levels at least 25 m higher than present levels. The most significant warming was in the high latitudes. Equatorial East Africa was actually cooler than at present, but was wetter (Dowsett *et al.* 1994), and had evergreen forests (Bonnefille *et al.* 1987). From 2·5 to 2 million years ago, coincident with the onset of major northern hemisphere glaciation (mostly growth of polar ice caps), the climate became cooler and drier (Shackleton *et al.* 1984; Versteegh *et al.* 1996). The environment was more similar to that of the present (Bonnefille, 1983), but was not yet dominated by savanna grassland (Cerling, 1992). There was a mosaic of forest, bush, savanna and patchy wooded grassland, with a general trend towards a more open, arid, grassland-dominated environment (Vrba *et al.* 1995). Mammalian generic diversity remained high and relatively unchanged, but guilds deepened (a guild being a group of closely related but distinct species that have very similar ecological requirements and also occur together in particular habitats; deepening of a guild indicating that the number of species in the guild is generally increasing), and some extant genera appeared for the first time (Harris 1993; Vrba *et al.* 1995; including especially grazers such as Equus and Oryx (horse, oryx), carnivore–omnivores such as Vulpes and Ichneumia (fox, mongoose), and the browser *Loxodonta adaurora* (modern elephant)).

Australopithecus robustus, A. boisei *and* Homo habilis

Homo was one of these new genera, appearing in East African deposits dating to 2·3–2·5 million years ago, and South African deposits dating to approximately two million years ago (Conroy, 1990; Wood, 1993; Foley, 1994; Schwarz *et al.* 1994; Johansen & Edgar, 1996). Also approximately 2·3 to 2 million years ago, the gracile Australopithecines *A. africanus* and *A. aethiopicus* were replaced by the robust species *A. robustus* and *A. boisei*. Robust australopithecines coexisted with *H. habilis*, and later *H. erectus*, for over one million years, so there must have been subtle ecological differences between genera (Conroy 1990; Wood, 1992; Johansen & Edgar, 1996).

Fossils in South Africa are confined to cave breccia (an accumulation of angular rocks from cave roof falls that are loosely cemented with $CaCO_3$; since the breccia accumulates over time by numerous cave collapses and cementing episodes, it cannot be accurately dated) formed in Precambrian (older than 580 million years) limestone, and are not generally used to directly infer phylogenetic, paleoenvironmental, or chronometric relationships, but rather to support or repudiate inferences made from East African fossil localities. Fossils from these limestone caves are not *in situ*, and are considered to have accumulated via accidental deposition by predators and/or other hominids, which makes sample dating very difficult (Conroy, 1990; Schwarz *et al.* 1994). In addition, the rock types in which the fossils are found are not amenable to K:Ar or U:Th radiometric dating. Schwarz *et al.* (1994) reported an electron-spin-resonance date for bovid teeth recovered at

the Australopithecine site at Sterkfontein, South Africa of 2·1 million years ago, but this is an average of dates from 1·72 to 2·37 million years ago. Further confusing the South African fossils in the past was a one million years radiometric date for the Dart 'Taung baby'; *A. africanus* skull, which has recently been revised to 2·3 million years, a date consistent with faunal evidence (Tobias *et al.* 1993).

In contrast, East African early hominid sites are contemporaneous with the geological strata. Numerous stratigraphically coherent layers of lava and volcanic ash allow for K:Ar dating of many East African localities, and cross-referencing between localities. East African sites are associated with watercourses, mostly ancient lake margins, but also riverene forests (for discussion, see below). Every site contains both sedimentary and igneous strata which record continual uplift, faulting, and volcanic activity (Baker *et al.* 1972; Dawson, 1992; Sikes, 1994). The Miocene to Pleistocene lakes were typically 10 000–100 000 km^2 in area.

Hominid localities and paleoenvironments

As depicted in Fig. 1, numerous hominid fossils have been recovered in Ethiopia (e.g. Hadar and Omo River), Kenya (e.g. Lake Turkana Basin) and Tanzania (e.g. Olduvai and Laetoli). *H. habilis* and *H. erectus* have been found at Omo, Turkana and Olduvai. (Fossils from Koobi Fora, Turkana, classified as *H. habilis* may represent another species *H. rudolfensis*, but this is not generally accepted (Wood, 1993).) The Hadar locality was mainly a marshy lake margin with rivers flowing in from the Ethiopian escarpment; Paleo Lake Hadar periodically filled the whole basin. However, there was a mosaic of microenvironments, including bush, grassland and wooded areas. The Omo River locality had both riverene fluvial environments and swampy lakes. Allia Bay records evidence of the proto-Omo river system flowing into the Turkana basin, with bordering gallery forest (Bonnefille *et al.* 1987; Leakey *et al.* 1995; Vrba *et al.* 1995). Overall, Turkana was an enormous (> 15 000 km^2) lake basin with wide marshy lake margins, and extensive mud flats which were covered with grasses in the dry season. Lake levels fluctuated significantly during the Plio-Pleistocene and Lake Turkana was a closed, alkaline lake for at least part of the time (Abell, 1982).

The Olduvai locality was also on the margins of a fluctuating lake, probably with no outlet. The perennial lake was alkaline and saline, but there was periodic flooding of the lake basin. Alluvial-fan and plain deposits are also present, indicating significant sedimentation derived from continual Rift fault uplift and associated river downcutting (Leakey, 1971, 1979; Plummer & Bishop, 1994; Behrensmeyer *et al.* 1995). Lateoli was more arid, upland savanna, not necessarily near a permanent water course (Leakey & Harris, 1987; Andrews, 1989; Cerling, 1992). *A. afarensis* fossils are the only species found at Lateoli and Hadar. Localities under development include Manoga Valley, Tanzania (Harrison, 1994), and Semliki Valley, Zaire (Boaz *et al.* 1994) both of which were also large lake basins. At 2500 km west of the Rift Valley, *A. afarensis*

fossils dating to 3 to 3·4 million years have been found in Chad (Brunet *et al.* 1995). The paleoenvironment was also lakeside, with both perennial and permanent streams and a mosaic of gallery forest, wooded savanna, and open grassland.

Although Australopithecines were evidently widespread and existed for two to three million years, their EQ increased little (Table 1). In an analysis of *A. boisei*, Wood *et al.* (1994) found little evidence for gradual modification of this species. They remarked that 'evolutionary stasis is the predominant signal coming from the masticatory morphometric data . . . and is the predominant signal throughout the time span of the lineage'. How did *H. habilis* and *H. erectus* gain an adaptive and/or intellectual edge over *A. boisei* and *A. robustus* that resulted in the dominance of the former, and the extinction of the latter? The answer may lie in the adaptation of Homo to the lake margin environment. Clearly all hominids would benefit from proximity to permanent water courses, especially since the overall climate pattern was one of progressive drying and seasonal precipitation. However, certain lines of evidence indicate that Homo was more likely to inhabit areas that were relatively open and arid, but that were near the lake shores.

Behrensmeyer (1975) was one of the first to propose that *H. habilis* may have been more restricted ecologically to the lake margin than was *A. boisei*. At Turkana, Behrensmeyer (1975) assigned eighty-four hominids to major depositional environments, thirty-nine to fluvial, and forty-five to lake-margin deposits. *A. boisei* was more abundant in fluvial environments, while *H. habilis* was rare there. Both are represented in comparable numbers in lake-margin environments; however *A. boisei* fossils are more common than Homo in both channel and flood-plain deposits. The fluvial channels were probably bordered with gallery forest, as is the case today, while the lake margins had wide mudflats, swampy in the rainy season and grass-covered in the dry season.

Sikes (1994) reviewed over seventy studies concerning the reconstruction of Plio-Pleistocene hominid paleoenvironments. While there was no strong consensus regarding habitats, reflecting perhaps the overall generalistic and opportunistic nature of Hominidae, trends can be recognized. An overall preference for more closed habitats as opposed to open savanna was characteristic of all Australopithecus and Homo species. Very few hominid localities are reconstructed as open grasslands, with Laetoli and Swartkrans being the major exceptions. *A. robustus* and *A. boisei* were found in montane, riverene, and closed forest localities, while Homo was not. In contrast, only *H. erectus* and *H. sapiens* were found on the lake margins per se, but they also utilized open arid and closed wet habitats. Almost all species were found in localities featuring patchy woodland. Both *A. boisei* and *H. habilis* had among the widest diversity of habitats, from savanna to riverine forest. These two species are contemporaneous at Olduvai, the most investigated hominid locality, and evidence indicates that hominids in general accessed a full range of habitats around Paleo Lake Olduvai (Plummer & Bishop, 1994).

Arguments related not to archaeology but to the change in skeletal morphology between Australopithecus and

Homo provide support for the general paleoenvironmental trends. Ruff (1991, 1994) considered the relationship between body morphology and ambient climate. In the past, ambient climate was a more powerful selective force, since we now modify our microenvironments considerably. Briefly, there are adjustments that can be made in body morphology in order to conserve or dissipate heat in different environments. In hot climates such as tropical East Africa, it is desirable to dissipate heat and to keep the body surface area : mass value constant as overall body mass increases. Body breadth cannot change much, so the alternative is an increase in height. Compared with *A. robustus* and *A. boisei*, *H. erectus* was taller and had a narrower pelvis, the implications of which will be discussed further (see pp. 10–11). *H. erectus* is considered to have a morphology that was adapted to drier, more open environments, while Australopithecus could have inhibited open dry or closed wet environments. A modern analogy can be drawn by comparing East African natives such as the tall, slender Masai with the small, stocky 'pygmy' natives of the Central African rainforest. Ruff (1991) comments: 'It is clear that *H. erectus* would not have inhabited a forested environment, whether or not Australopithecus did'. A change towards a higher-quality nutritional base may also have a role in this change in body shape, since it was accompanied by an increase in EQ (Table 1).

The skull and dental morphology of Australopithecus provide good evidence that these hominids adapted early to more arboreal niches, and that this adaptation was reinforced with time. *A. boisei* is at least 2·3 million years old, and thus must have diverged from a more gracile Australopithecine ancestor relatively early (Skelton & McHenry, 1992). Australopithecus species from *A. afarensis* to *A. boisei* have an increasing level of post-canine megadontia; along with this comes larger jaws and stronger muscles to move the jaw. The robust Australopithecines developed prominent sagittal and nuchal crests for the attachment of powerful chewing and neck muscles respectively. They had bony struts in the face to withstand the powerful chewing stresses set up through the massive jaws and teeth. This type of molar enlargement and jaw structure indicates that the robust Australopithecines were chewing tough, fibrous vegetation (Rak, 1983; Ramirez-Rozzi, 1993; Suwa *et al.* 1994; Johansen & Edgar, 1996). In particular, *A. boisei* fossils found contemporaneously with *H. habilis* are the most 'robust', with extremely large jaws, teeth, zygomatic arches, and lateral ptyeroid plates. Both molars and premolars are enormous compared with incisors and canines, providing good evidence for a diet including a high percentage of tough plant foods, with seed crushing and nut cracking, etc. (Rak, 1983; Kimbel & Rak, 1993).

However, stable-isotope studies of remains from Swartkrans indicate that *A. robustus* was not completely vegetarian (Lee-Thorp *et al.* 1994). About 25–30 % of plants consumed by *A. robustus* were from C_4 (initial product of photosynthesis is a C_4 molecule; grass) plants, and the remaining 70–75 % were from C_3 (woody, broadleaf) plants. (C_3 plants are the source of tubers, roots, corms, leaves, nuts and fruit that provide the majority of plant foods in the diet of hunter–gatherers observed

ethnographically.) It could not be determined whether 25–30 % of C_4 grass-type plants were consumed directly, or whether the flesh of grass-eating animals was eaten instead. Overall, dental morphology and a lack of grass phytolith microwear on the fossil teeth support the latter case. Bone Sr : Ca values provide independent evidence for the latter case, as they fall between those for leopards and baboons, and are unlike those of grazers (Schwarz & Schoeninger, 1991; Sillen *et al.* 1995). It is noted also that Hominoidea is generally omnivorous and adaptable, as even chimpanzees will occasionally hunt in groups, and often eat insects, small mammals, and reptiles. Stable isotope studies are just beginning to be a major tool for investigating the diets of hominids and other extinct fauna, and may in the future provide some insight into the proportion of aquatic foods consumed by hominids.

Fish remains are associated with many early homind sites, but since these sites tend to be near watercourses, the fish bones have mostly been considered as background noise. Stewart (1994) found that most fish faunal assemblages were natural. Statistical evidence of fish-bone size and frequency at Olduvai Beds I and II did yield some discrepancies from natural scatter, which appear to indicate sites where large numbers of fish were stranded and then consumed by carnivores and/or hominids. The beds with discrepancies are associated with *H. habilis* and *A. boisei* (contemporaneous species) and *H. erectus* fossils and/or artifacts.

Homo erectus

Homo erectus first appears approximately 1·2 million years ago, and a lesser-know transitional species *H. ergaster* dates from 1·8 million years ago. This time frame is coincident with the first major continental glaciation in the northern hemisphere (Shackelton *et al.* 1984). Due to polar ice build up, the East African climate became significantly hotter and drier, and there were massive local East African extinctions. Those hardest hit were the wetter and more-closed-habitat species, but the extinctions were not due entirely to an increase in dry habitat. A number of open, dry habitat genera did become extinct or locally extinct, so the ecological change appears to be more complex (Harris, 1993; examples of dry open habitat genera reduction between the Turkanan (2·5–1·0 million years ago) and Natronian (1·0–0·15 million years ago) are as follows: medium to very large herbivores dropped from thirty to twenty-two, very small to small primarily-herbaceous omnivores from twenty-nine to ten, and carnivores from sixteen to eight).

H. erectus has been considered to have originated in Africa, but the most recent interpretation of the fossil record hints at an alternative explanation. *H. ergaster* may have been the common African ancestor of *H. erectus* and *H. heidelbergensis*. *H. ergaster* migrated from Africa to Eurasia, and subsequently evolved into *H. erectus*, which was then an evolutionary 'dead end' (Tattersall, 1997). African *H. erectus* fossils are then reclassified as *H. ergaster*, and possibly other transitional species.

A. boisei and *A. robustus* did not become extinct until about 0·4 million years later, but neither did they undergo speciation events (or gradual change c.f. Wood *et al.* 1994) as did Homo. Like others who have investigated this period of prehistory, we consider this to be very significant, transcending arguments based mainly on selective pressures. As discussed by Foley (1994) and Vrba *et al.* (1995), climatic changes during the period of hominid evolution can be fairly clearly and consistently related to extinction events, but not necessarily to speciation events. Speciation triggers in higher mammals are more complex than climatic changes, and we believe that the role of brain-specific nutrition is one of these complexities.

The time period about 1·6–1·7 million years ago saw dramatic changes in hominid anthropometry. Female body size increased dramatically, thus the marked sexual dimorphism that characterized previous hominid species diminished (McHenry, 1994). Birth canal enlargement and related changes in the pelvic–femoral anatomy had not been initiated or had not proceeded very far. However, the modern pattern of infant secondary altriciality (extended neonatal helplessness) and fetal growth was almost as fully derived as that for modern humans (Ruff, 1991; Rosenberg, 1992).

McHenry (1994) recognized that a major change in the hominid food supply must have been occurring: 'Given the energetic costs of brain size increases, this remarkable change in brain size implies a major alteration in subsistence'. However, McHenry (1994) did not suggest specific food types, but rather hypothesized that greater mobility by *H. erectus* and *H. ergaster* allowed access to a wider range of environments and food sources. Similarly, Foley & Lee (1991) concluded that about two million years ago, the energetic costs imposed by increasing encephalization would require both substantial quantities of higher-quality foods and increased foraging efficiency. Foley & Lee (1991) note that the incorporation of 100–200 g meat/kg in the hominid diet could have had a profound evolutionary influence. We propose that at least some of this 'meat', either scavenged or hunted, could have been from fish and shellfish. Stewart (1994) found possible cut marks on fish bones associated with *H. erectus*, which makes 'a strong but not absolute case of early hominid fish procurement'.

Homo sapiens

Periodic advances of continental glaciers continued throughout the Middle and Upper Pleistocene (1·6 million years to 10 thousand years ago), and severely affected climate in the tropics as well as in higher latitudes. For example, the tropical deep Atlantic Ocean cooled 4° on average during the last glacial maximum (Schrag *et al.* 1996), and the cold ocean currents drew moisture-laden air off the African continent, as was the case at the end of the Miocene. As the climate became more arid, lake basins shrank, rivers dried, and forest diminished. Paleosol carbonate isotope data indicate that relatively pure savanna grasslands similar to present conditions became established about one million years ago (Cerling, 1992), just after the last appearance of Australopithecus. The Rift Valley lakes became virtually the only permanent sources of fresh water.

In another geological setting, without the deep and numerous Rift fault basins to retain water, a climate of such aridity would not have permanent lakes (Leeder, 1995; Stager *et al.* 1997).

Despite the climate, around the lake margins Homo not only survived, but again underwent a speciation event, which featured astonishing cerebral expansion (Table 1). During the period 500 thousand–200 thousand years ago, cranial capacity expanded greatly, and the pelvic–femoral complex characteristic of early Homo was replaced by the modern anatomical complex, confirming that large fetal crania, relatively difficult childbirth, and infant secondary altriciality were present (Rosenberg 1992; Ruff, 1995; Smith *et al.* 1995).

H. erectus appears in Europe, China, Java, and possibly Siberia (Waters *et al.* 1997) by 800 thousand years ago. Nevertheless, the new species *H. sapiens* is thought to have originated in Africa between 100 and 300 thousand years ago (Stringer, 1992; Foley, 1994; Johansen & Edgar, 1996; Swisher *et al.* 1996; Tishkoff *et al.* 1996). *H. sapiens* populations then migrated out of Africa to the rest of the world about 120 thousand years ago, rather than independent evolution of separate *H. erectus* or other ancestral populations (Harrison 1993; Lahr, 1994; Tishkoff *et al.* 1996). In addition, a very young date of 27 thousand to 53 thousand years ago for *H. erectus* in Java was recently reported (Swisher *et al.* 1996). If confirmed, this would require coexistence of *H. erectus*, *H. neanderthalensis*, and *H. sapiens* and would preclude independent evolution of disparate *H. erectus* populations into *H. sapiens*.

Fully anatomically modern humans may have migrated to the Middle East before 100 thousand years ago, but were definitely widespread throughout Africa, Europe, and Asia by forty thousand years ago (Schwarz & Grun, 1992). The many controversies surrounding *H. neanderthalensis* cannot be discussed here (for a review, see Shreeve, 1995), but there is general agreement that *H. neanderthalensis* is a different species which lived between 300 thousand and 30 thousand years ago. *H. neanderthalenesis* coexisted with *H. sapiens* for about 50 thousand years (Mercier *et al.* 1991; Stringer, 1992; Shreeve, 1995; Johansen & Edgar, 1996). *H. neanderthalensis* apparently never developed the sophisticated types of tools that *H. sapiens* utilized, including Aurignacian Industry stone tools, bone points, projectile weapons, harpoon-type spear points, and fish-hooks. The origin of *H. neanderthalensis* may be analogous with that of *H. erectus* (Tattersall, 1997). *H. heidelbergensis* may have been the common African ancestor of *H. neanderthalensis* and *H. sapiens*. *H. heidelbergensis* migrated out of Africa to Europe and there evolved into *H. neanderthalensis*, who also became an evolutionary 'dead end'.

The earliest evidence for modern *H. sapiens* is found in Africa. Lake-shore sites in the Rift Valley have yielded fairly sophisticated stone tools as old as 260 thousand years ago associated with *H. sapiens* remains. These Homo skeletons have varying mixes of archaic and modern traits (Clark, 1992). Two other African localities have yielded early modern human remains associated with tools which have not been found elsewhere until the Upper Paleolithic

(40 thousand to 10 thousand years ago). In both of these cases, the 'precocious' cultures are associated with the consumption of fish and shellfish.

At the Klasies River Mouth area, along the southern coast of South Africa (Fig. 1), a record of hominid occupation for 60 thousand years beginning 120 thousand years ago is recorded. Modern human fossils dating to about 100 thousand years ago have been recovered in Klasies River Mouth and Border Caves in the area. The numerous occupation sites are littered with the shells of mussels, turbans, and periwinkles (molluscs that can still be picked up in abundance today). Some of the shells are burnt, indicating the shellfish were cooked. The remains of penguins, fur seals, eland, and small terrestrial mammals have also been recovered; these relatively docile animals were either hunted or scavenged (Deacon, 1992; Shreeve, 1995). Klein & Cruz-Oribe (1996) found that large, dangerous game was not typically utilized. However, the most recent analysis of Klasies River Mouth faunal remains found that nearly one in five bones bears incisions from butchery. Animal remains from heavily-fleshed body parts are found in the caves with few signs of carnivore tooth marks. In addition, a broken spear point tip was found in the neck of an extinct giant buffalo, one of the largest game animals in southern Africa at the time. Evidently these Middle Stone Age humans could hunt efficiently and collectively, perhaps driving game over cliffs or into pits (Milo, 1997).

About 70 thousand years ago, a remarkably advanced Upper Paleolithic-type tool technology (Howiesons Poort Industry) emerged. The Howiesons Poort Industry features sharp blades and projectile points which were hafted onto shafts. Material for the points was not local, but came from nearby areas with more suitable stone. Also about 70 thousand years ago, glaciers were advancing; the climate became cooler and drier and the coastline receded several miles. One explanation for the Howiesons Poort Industry is that superior tool technology was invented in order to adapt to the harsher environment, which had less available for scavenging and gathering, and required more hunting. Shellfish remains are scarcer during this time (Deacon, 1992; Shreeve, 1995).

We would consider that regardless of the deteriorating climate, the effects of 30 thousand to 50 thousand years of brain-specific nutrition on the emergence of the technology should not be ignored, especially since (1) the modern human remains predate the Howiesons Poort Industry, and (2) there is general agreement that the hominids must have been travelling around and 'taking note' of superior stone deposits before adopting the technology. Despite its advancement, this culture was evidently not successful. As time passed, the Howiesons Poort Industry petered out, and was actually replaced by a less-sophisticated technology more typical of elsewhere in the world. The area was then abandoned 10 thousand years later until 50 thousand years ago, when Upper Paleolithic hunters arrived and began exploiting both marine and terrestrial food resources with sophisticated hunting and fishing techniques (Shreeve, 1995; Klein & Cruz-Oribe, 1996).

At Katanda, in the Semliki River Valley, Zaire, there is evidence that bone harpoon points were made as early as

100 thousand years ago, but such tools have not been observed at other sites until 18 thousand years ago. The harpoon points are associated with catfish and mollusc remains, and one fragment of a human skull (Boaz *et al.* 1992; Shreeve, 1995; Johansen & Edgar, 1996). It again appears that a 'precocious' culture developed on an aquatic (riverene and lakeshore) resource base, but remained isolated for at least 40 thousand years. The explanations for the precocious Katanda culture also invoke a response to deteriorating climate, but could just as well incorporate the influence of the aquatic brain-specific diet. Unlike the Klasies River Mouth area, Katanda is a single site, so the isolated culture remains anachronistic until confirmed at other localities. Since archaeological exploration of the general area is practically non-existent, the future may hold some answers.

Upper Paleolithic *H. sapiens* in the East African Rift Valley definitely utilized fish. Stewart (1989, 1994) describes numerous sites with vast fish faunal assemblages dating from 40 thousand years ago to the present. Barbed spear points, and evidence for fish-trapping dams and weirs have also been recovered. The huge numbers of bones and their distribution profiles provide evidence that foraging *H. sapiens* groups returned to certain areas year after year, probably to take advantage of spawning runs or dry-season fish stranding. Extensive use of diverse fish, shellfish, and marine mammal and bird food resources is also recorded in the Upper Paleolithic of South Africa (Buchanan, 1988). In the following sections, we present research data indicating that freshwater fish, shellfish, and similar lacustrine or marine foods can and do provide brain-specific nutrition. Finally, we will discuss the procurement of fish and other animal food resources with limited technology, and summarize our ideas.

Long-chain polyunsaturated fatty acid composition of mammalian neural tissue

Unlike the protein- and mineral-rich musculo-skeletal system, the major structural component of mammalian neural tissue is lipid. The dry weight of the brain comprises about 600 g lipid/kg, and has a unique profile of LC-PUFA. PUFA are 'essential', which means that a portion of the lipids which comprise the mammalian central nervous system (CNS) cannot be synthesized and must come from dietary sources. Precursor dietary essential PUFA in the strict sense are linoleic acid (LA; $18:2n$-6) and α-linolenic acid (LNA; $18:3n$-3; Fig. 3). These C_{18} PUFA are alternately desaturated and elongated to form mainly C_{20} and C_{22} LC-PUFA with four or more double bonds. AA ($20:4n$-6) and DHA ($22:6n$-3) are the main n-6 and n-3 series end-member LC-PUFA respectively.

Good modern-day sources of LA are nuts (e.g. walnuts, peanuts, pistachios, almonds, pumpkin seeds) and seed oils (e.g. cotton, maize, sesame, sunflower, safflower, soyabean). Due to the widespread food use of agricultural oil seeds, LA is far more prevalent in current diets than in the past (Broadhurst, 1997). LNA is relatively uncommon in modern diets, and is found in green leaves and walnuts as well as flaxseed, mustard, rapeseed, and soyabean oils. Foods richest in AA are egg yolk and organ meats and muscle meats from land animals and tropical fish. Foods richest in DHA and its precursor, eicosapentaenoic acid (EPA; $20:5n$-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 content of AA can also be high (Table 2).

In the forty-two mammalian species studied so far (Crawford *et al.* 1976, 1992; Armstrong, 1983), the PUFA
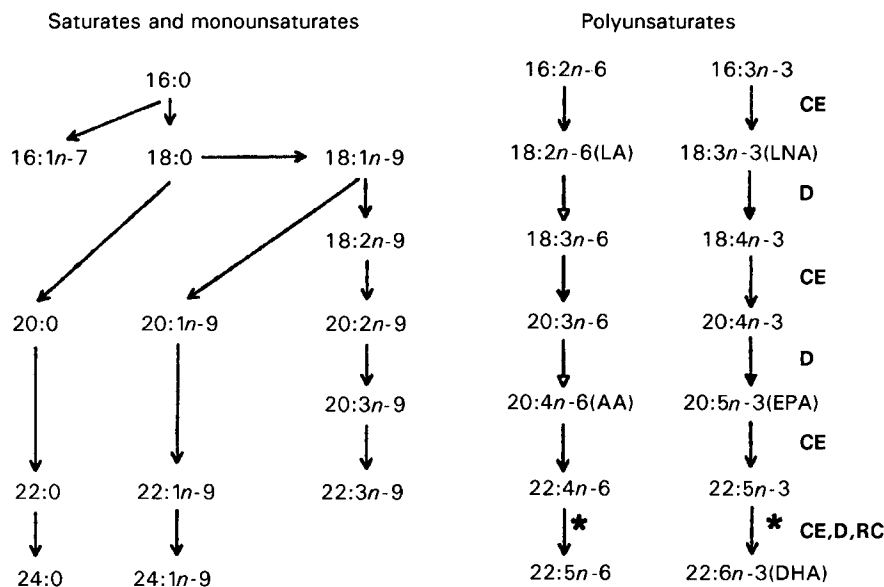

Fig. 3. Long-chain fatty acid pathways in mammals. Palmitic acid (16:0) is the starting point for saturates (18:0–24:0) and monounsaturates (16:1n-7–24:1n-9). Linoleic acid (18:2n-6; LA) and α-linolenic acid (18:3n-3; LNA) are the main precursors to the polyunsaturates (n-3 and n-6 polyunsaturated fatty acid series). Note also that the C_{16} n-6 and n-3 polyunsaturated fatty acids are present in the human diet (i.e. selected green vegetables) and can be metabolized to 18:2n-6 and 18:3n-3. Pathways proceed through chain elongation (CE) and desaturation (D). The final step in polyunsaturated fatty acid metabolism involves retroconversion (RC) from C_{24} intermediates (*not shown). Preference by desaturase enzymes is also shown ⟶▸> ⟶▷> →. EPA, eicosapentaenoic acid; DHA, docosahexaenoic acid.

Table 2. Total fat content (g/kg) of representative fish and invertebrates, and arachidonic acid (AA) and docosahexaenoic acid (DHA) in total lipid (g/100 g). These fat ratios are typically not present in the terrestrial food chain.

Fish and habitat	Fat (g/kg)	AA (g/100 g)	DHA (g/100 g)	Reference
Lake Malawi African freshwater				
Mbelele (catfish)	103	4·3	8·6	Pauletto *et al.* (1996*a*)
Njenu (carp)	49	1·8	7·8	
Mfui (local sp.)	11	8·0	19·1	
Kambale (local sp.)	18	5·9	13·3	
Australian tropical freshwater				
Bream meat	16	5·3	5·6	Sinclair (1992)
Bream fat	910	2·0	1·5	
Tropical marine				
Australian barramundi	3	14·5	16·2	Mann *et al.* (1995)
Indian halibut	17	6·3	10·4	Pauletto *et al.* (1996*a*)
Freshwater temperate				
Unspecified	(Oil)	3·3	8·0	Innis *et al.* (1995)
Higher-latitude marine				
Atlantic salmon (skinless)	98*	1·2	17·2	Mann *et al.* (1995)
Herring	(Oil)	0·6	23·0	Cunnane *et al.* (1993)
Menhaden	(Oil)	0·9	7·3	Innis *et al.* (1995)
N. Atlantic mackerel	(Oil)	0·4	7·7	Pauletto *et al.* (1996*a*)
Temperate invertebrates				
Mollusc	>10	2·3	22·0	Cunnane *et al.* (1993)
Squid	>10	5·8	21·3	

*Salmon with skin contains up to 199 g fat/kg.

content of brain ethanolamine phosphoglycerols is fairly similar, and consistently dominated by AA, docosatetraenoic acid (22:4n-6), and DHA, with a n-6:n-3 PUFA value of 1–2:1 (Table 3). The n-6:n-3 PUFA value in most other cells is 3–5:1 (Horrobin, 1995), and is variable, depending on dietary intake and metabolic factors. Mammalian brains all contain similar proportions of the same basic phosphoglycerols; hence, the human brain differs from the other mammalian species in a quantitative rather than a qualitative sense (human brains are relatively much larger, especially the frontal lobes, and have a more sophisticated and diverse regional organization). While the interspecies brain compositions are similar, the human EQ is much larger (Table 1), and humans devote a significantly greater proportion of metabolic energy to the brain,

especially neonatally (Martin, 1983; Foley & Lee, 1991; Cunnane *et al.* 1993).

The CNS is unique in not using the C_{18} precursors LA and LNA, only the desaturated and chain-elongated LC-PUFA. Thus, the mechanisms and efficiency of chain elongation and desaturation as well as the dietary intake are crucial for neural development. In humans, the intake of preformed AA is a significant source of tissue AA, because very little AA appears to be formed from LA in normal individuals consuming mixed diets (Emken *et al.* 1992; Mann *et al.* 1994). This conversion is slow, especially when compared with rats and mice, and can be impaired by many physiological and pathological processes. When AA is consumed it is readily incorporated into tissues (Whelan *et al.* 1992, 1993; Mann *et al.* 1994). Adam *et al.* (1993) found that at intakes normal for Western diets, LA does not contribute to the formation of AA. Subjects on vegetarian diets very low in preformed AA but with abundant LA show correspondingly low AA levels in erythrocyte lipids.

Similarly, the conversion of LNA to EPA and finally to DHA is slow and inefficient in many species (Cunnane, 1992; Gerster, 1995). LNA desaturation and chain elongation is especially weak in humans, and subject to competition from n-6 and n-9 fatty acids (Fig. 3). LNA may not be converted to DHA and EPA in any significant amount unless there has been a long-term deficiency of n-3 PUFA, or if LNA levels are consistently low (Lands *et al.* 1991; Sprecher, 1991; Cunnane, 1992, 1995). Caughey *et al.* (1996) found that 4 weeks of flaxseed oil supplementation increased plasma mononuclear cell LNA by 3-fold and EPA by 2·3-fold, but did not raise DHA levels. However,

Table 3. Mean polyunsaturated fatty acid composition of ethanolamine phosphoglycerols (g/100 g) in brain motor cortex grey matter of thirty-two mammalian species (Data from Crawford *et al.* 1968, 1969, 1976)

Fatty acid	%
18:2 n-6	0·9
20:3 n-6	1·7
20:4 n-6	15
22:4 n-6	8
18:3 n-3	0·3
20:5 n-3	0·9
22:5 n-3	2·3
22:6 n-3	21

fish-oil supplementation for the following 4 weeks dramatically increased both EPA and DHA. It must be noted that although conversion of LA and LNA is thought to be inefficient, it is variable among populations, and its control is not fully understood. The majority of dietary LA and LNA is likely to be oxidized or stored, not converted (Cunnane & Anderson, 1997).

Abundant LC-PUFA is an absolute requirement for advanced neural growth, and it is unlikely to be accidental that the nutrient base of the Rift Valley lakes is an excellent example of a rich dietary source of balanced, preformed LC-PUFA (Table 2).

Long-chain polyunsaturated fatty acids during neural growth and development

Research concerning fetal and infant growth and development is relevant in considering the origin of human intelligence overall. In order to sustain the rapid expansion of the cerebral cortex, generation after generation of early Homo must have had access to sources of abundant, balanced PUFA, mostly probably in the form of AA and DHA at a ratio of about 1:1. In the sequential neural development of infants, LC-PUFA deficiency during critical growth periods results in irreversible failure to complete components of brain growth. If LC-PUFA are the limiting nutrients for the neural development of a population, then EQ cannot increase much beyond that observed in Ponginae, who have largely vegetarian diets. Research with small mammals has also shown that with increasing demands on maternal lactation, such as increasing the number of pups in a litter, AA and DHA in the milk are depleted faster than LA and LNA, which remain fairly stable (Crawford *et al.* 1986). Primates are noted for their relative infrequence of multiple births, which may be a prerequisite for brain expansion.

In some nutritional or ecological niches (i.e. savanna, patchy woodland) LC-PUFA are greatly limited while protein and minerals are not; subsequently body mass increases greatly as compared with brain mass (Foley & Lee, 1991; Cunnane *et al.* 1993). This is the case in herbivores, whose dietary PUFA consists entirely of LNA and limited LA. The herbivore devotes a large proportion of metabolic energy to grazing and digestion as opposed to brain function. For example, a young rhino grows very fast, reaching 1 tonne at age 4 years. The milk provided by its mother has sufficient protein, minerals, LA and LNA, but very little DHA and AA. The food supply onto which the rhino is weaned also has no DHA or AA (Crawford *et al.* 1986; Crawford & Marsh, 1995). The rhino's diet is associated with a brain:body weight value (g/100 g) 0·04, as compared with 0·4 for the gorilla, and approximately 2 for *H. sapiens*.

Deposition of LC-PUFA in the CNS is rapid during mammalian prenatal and postnatal brain growth (up to approximately 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 (Innis, 1991). The placenta does not desaturate or chain elongate PUFA, but instead actively concentrates and transfers to the fetus more AA and DHA than LA or LNA. During the most active phase of fetal growth, human brain development uses as much as 70 % of the energy delivered to it by the mother; postnatally, this figure drops to 60 %, and in adults is about 20 % (Crawford, 1993).

Polyunsaturated fatty acid balance and long-chain polyunsaturated fatty acid requirements

Maternal PUFA intake should be both adequate (4–8 % total dietary energy intake) and balanced in order to ensure a child's normal CNS development. At a minimum, it is considered that the n-6:n-3 PUFA value should be kept in the range 5:1–1:1 from conception to age 2 years. Human milk normally contains both precursor and LC-PUFA with a n-6:n-3 value of 4–5:1. However, human milk contains less LC-PUFA if they are chronically deficient in the maternal diet (i.e. vegetarians; Holman *et al.* 1991; Simopoulos, 1996).

The lack of LC-PUFA in infant formulas is of deep concern, because the infant has a restricted ability to utilize LA and LNA (Carlson *et al.* 1993*a*; Nettleton, 1995). Adult humans differ greatly in their ability to elongate and desaturate LA and LNA, and although full-term infants can synthesize AA and DHA (Carnielli *et al.* 1996), it is not known whether this occurs efficiently enough to accommodate their rapid brain growth (Farquharson *et al.* 1992). The presence of quantitatively significant amounts of preformed LC-PUFA in breast milk and in the CNS suggests that these metabolites are indeed essential for the neonate. Preterm infants are in effect still dependent on the placenta and definitely cannot utilize LA and LNA effectively (Crawford, 1993; Simopoulos, 1996).

An imbalance favouring n-6 or n-3 PUFA, or lack of LC-PUFA is a potentially serious problem for fetuses, infants, and growing children. Infant formulas are supplemented with significant LA (from several vegetable oils), and lesser amounts of LNA (usually from soyabean oil). Infant formulas in some countries such as Japan now contain supplemental n-3 LC-PUFA, particularly to provide DHA. The decision to supplement all formulas with AA and DHA is still under heated scientific scrutiny (Makrides, 1997); however, it is generally agreed that formulas for premature neonates need such supplementation (Crawford, 1993; Simopoulos, 1996; Hansen *et al.* 1997).

Formulas supplemented with marine fish oil have been utilized in animal studies and for preterm human infants, and do significantly increase plasma and tissue DHA (Arbuckle *et al.* 1991; Carlson *et al.* 1992; Clandinin *et al.* 1992; Innis *et al.* 1994). However, the very high EPA and DHA and low AA contents of marine fish oils (Table 2) pose a risk for infants, because AA levels in tissues decline to the point where development is affected (Carlson *et al.* 1992, 1993*a*). AA requirements are highest during early postnatal growth, and EPA in particular competes with n-6 PUFA for desaturation and chain elongation, thereby interfering with AA production.

In a situation where dietary PUFA are both restricted in quantity and unbalanced, the optimum AA:DHA in the infant brain cannot be maintained (Farquharson *et al.* 1992). Supplementing formulas with both AA and DHA normalizes neurodevelopment in full-term infants (Agostoni *et al.* 1995; Makrides *et al.* 1995; Gibson *et al.* 1997) and eicosanoid production in neonatal pigs (Huang & Craig-Schmidt, 1996), and has no reported negative effects on growth or neurocognitive development. Innis *et al.* (1995) compared the effect of freshwater-fish oil (EPA:AA 1·8) on growing rats as compared with cold-water marine fish oil (EPA:AA 16·8). In the brain and other organs, the freshwater-fish oil generally increased *n*-6 PUFA (including AA) while slightly decreasing but still maintaining *n*-3 PUFA levels. Both AA and DHA were high, indicating that freshwater-fish oil can prevent the decline in AA imposed by marine-fish-oil feeding.

Tropical fish diets: current examples

Modern analogues for pre-agricultural diets based on tropical marine and lacustrine resource bases exist, and have been shown to be exceptionally healthy. Stewart (1989, 1994) describes modern ethnographic and personal observations of East African traditional fishers. As the dry season ends and the rainy season begins, some hunter–gatherer groups follow the fish spawning migrations. During the dry season, fish became stranded in progressively smaller pools as waters recede, and hunter–gatherers will camp for extended periods near swampy lowlands to take advantage of the naturally-high fish concentration. These fishing societies have been observed personally by one of us while working as a 'bush doctor' in East Africa (M.A.C; c.f. Crawford & Marsh, 1995), and their habits and excellent health noted.

Fish rich in fat, especially catfish, are highly prized by these traditional fishers. Most of the fish caught today are catfish, with the remainder mainly cichlids. Like other tropical freshwater and marine fish, catfish have a relatively high AA:DHA, which would favour brain expansion (Table 2). Catfish also comprise over 90% of the fish fauna recovered from over forty Late Pleistocene Nile River sites described by Stewart (1989, 1994). Other sites have more equal proportions of catfish, cichlids (known as *Tilapia* spp.), and a large minnow-like fish, *Barbus*.

Near the end of the dry season, game is relatively scarce, and the fat content of game is exceedingly low (10–40 g/kg; Crawford *et al.* 1976; Speth, 1989; O'Dea, 1991; Crawford & Marsh, 1995). Plant foods are scarcest during this time also. Fish are preparing to spawn at the first rains of the season, and may actually have an increase in fat content at the end of the dry season. A diet based on scarce, lean game may be severely deficient in both protein and fat (Speth, 1989). As will be discussed further (see p. 16), scavenged mammalian bone marrow and brain tissue have been proposed as options for fat procurement, especially during times of climatic stress (Blumenschine, 1991; Blumenschine & Cavallo, 1992; Bunn & Ezzo, 1993). Similarly, Cunnane *et al.* (1993) and Stewart (1994)

proposed that fish and shellfish may have served as an important source of protein, trace minerals and fat.

Pauletto *et al.* (1996*a*,*b*) investigated two groups of genetically-homogeneous native Bantus near Lake Malawi (Nyasa), Tanzania. One group lives on the lakeshore and consumes a fish-based mixed diet (FD, *n* 622). The other group lives approximately 75 km from the lake, and consumes a grain-based vegetarian diet (VD, *n* 686). Both FD and VD eat strictly locally-available foods, as processed foods are not available.

The proportions of plasma *n*-3 LC-PUFA were three to four times higher in FD *v*. VD. Plasma AA was higher in FD *v*. VD, despite the fact that VD had overall higher levels of *n*-6 PUFA. Most of the VD dietary and plasma *n*-6 PUFA was in the form of LA. The FD Bantus consume 300–600 g freshwater fish daily throughout most of their lives; however, the percentage of total dietary energy intake from fat is approximately 12, the majority of which is derived from the fish (see Table 2). Despite a higher cholesterol and saturated fat intake, their blood cholesterol and triacylglycerols were lower than those of the VD consuming an exceedingly-low-fat (approximately 7% total dietary energy from fat) vegetarian diet. Overall, FD had significantly lower mean blood pressure, total cholesterol, triacylglycerols and lipoprotein than VD. Before the very recent introduction of agriculture, these two groups would have existed on wild plants alone or on wild plants plus fish. The lakeside group has a clear advantage in terms of cardiovascular fitness, high-quality protein intake, and brain-specific nutrition. If we imagine the isolation of these groups from one another for one million years or so, perhaps we may gain a glimpse of the divergent pathways taken by coexisting *Homo* and *Australopithecus*.

Aborigines in northwestern Australia traditionally consume a diet rich in tropical coastal fish. Typical marine-fish diets lower plasma AA significantly; however, this tropical-fish diet increased AA by 3-fold and EPA and DHA by 2-fold as compared with controls (O'Dea & Sinclair, 1982). Although tropical and subtropical fish species have ubiquitous DHA and EPA, the content of AA can also be high (Table 2).

In order to investigate the aetiology of type II diabetes in native populations, diabetic and non-diabetic Aborigines were put on three diet trials (Sinclair, 1993): (1) 40% total dietary energy from fat with 75% total dietary energy from beef; (2) 20% total dietary energy from fat with 80% total dietary energy from coastal tropical seafood; (3) 13% total dietary energy from fat, with 85–87% total dietary energy from kangaroo meat, freshwater fish, and yams. The kangaroo meat consumed was only 10–20 g fat/kg wet weight since it was wild game. Most of the fat in wild game is structural phospholipid, containing significant LC-PUFA but quantitatively low amounts of saturated fat. Diets 2 and 3 were traditional diets, low in LA and saturated fatty acids, and produced marked improvements in the metabolic abnormalities associated with diabetes, and a reduction in cardiovascular disease risk factors, including hyperlipidaemia and blood pressure. Plasma phospholipids in diets 2 and 3 had roughly equal values for AA:EPA:DHA. Prostacyclin activity was estimated *in vivo*, and tropical-fish and kangaroo diets had evidence for high activity. High

activity was not seen, in comparison, in the cold-water-marine-fish (plasma AA being approximately one-fifth of EPA plus DHA) or vegetarian (AA, DHA and especially EPA much lower) diets.

In summary, the lipid profile of tropical and subtropical freshwater fish and other aquatic species have a DHA:AA that is closer to that in brain phospholipids than any other food source known. These edible species are found in the East African Rift Valley Lakes around which *H. sapiens* arose and eventually dominated. This food source also provides abundant protein, and is known to be a healthy diet for humans. Humans in the Rift Valley have a tradition of utilizing the lake resources, especially as a source of dietary fat.

Soils and surface rocks in the Rift Valley area were and still remain relatively rich in trace elements due to the constant volcanism and uplift (Baker *et al.* 1972; Bailey & Macdonald, 1987; Dawson, 1992). Although the details are beyond the scope of the present discussion, we note particularly that the Rift Valley environment provides abundant Zn, Cu, and I, trace elements necessary for PUFA metabolism and for normal brain development and function (Cunnane *et al.* 1993). Hence, the enormous proto-oceanic lakes provided a plentiful, protected source of brain-specific nutrition, even as the climate in the area changed dramatically in the Pleistocene. As discussed later (below), accessing the lake resource base was not strictly dependent on the seasons or the intellectual status of the evolving hominids.

Cultural considerations, scavenging, and 'low-tech' fishing

It is not necessary to invoke organized fishing or hunting by early Homo; in fact the origin of our intellect was probably the more humble occupation of grabbing small cold-blooded creatures and scavenging. While hominids may have eaten some fish directly, it is important to realize that the freshwater fish and shellfish provide a major link in the broader food chain. They are consumed by birds, small mammals, reptiles, amphibians, etc. all of which in turn could have been consumed by hominids (although perhaps in the form of eggs). For example, Leakey (1971) postulated that tortoise shells found without other skeletal pieces in bed at Olduvai were evidence for consumption by hominids.

Stewart (1989, 1994) described procurement of fish 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 *Barbus* 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 & 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 and 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. Stranded fish may be scavenged after death, or again, clubbed, speared, or picked up live; fishing tackle is not required. Fish in the central, deeper waters of major rivers are difficult to procure without sophisticated equipment, including hooks, lines, baskets, weirs, dams, and nets, and were probably not a nutritional option until 40 thousand years ago. (It should be noted that the present warm waters and high alkalinity of the Rift Valley Lakes has resulted in impoverished fish faunal diversity. Only a few families of 'hardy' fish are represented. Some Rift Valley cichlids have adapted to live in water nearly devoid of dissolved O_2, and at pH up to 10·5 and temperatures of 40° (Riehl & Baensch, 1986; Loiselle, 1988; Johnson *et al.* 1996).)

Scavenging of the remains of larger carnivore kills is also a logical possibility for hominids, and could also have provided protein and some AA and DHA if the opportunity arose. The initiation of meat scavenging has been proposed as a causative factor of the dramatic increase in EQ about two million years ago (Speth, 1989; Foley & Lee, 1991). We would agree that scavenging played a role, but would broaden the scavenging resource base to include fish, shellfish, reptiles, etc. in addition to game, particularly since the proportion of fat in game meat is low.

Cheetahs and leopards often leave ample meat on their kills which is then available for both primary and secondary scavengers. Large cats have been observed to leave carcasses unattended for many hours at a time (Blumenschine, 1991; Blumenschine & Cavallo, 1992; Bunn & Ezzo, 1993). The size of the carcass correlates positively with the length of time it is left unattended. Scavenging hyenas typically leave a carcass stripped, but prefer open or lightly-wooded habitats. Carnivore kills in densely-wooded areas, such as lake and river margins, were found to be less likely to be scavenged by hyenas than were open-land kills (Blumenschine, 1987). Scavenging was likely to have been more prevalent in the dry season, when other resources are scarcest, and dietary fat is at a premium. Scavenging kills brought down by the savanna pursuit carnivores is not as difficult as hunting, but is still fairly dangerous, and requires skillful, intelligent observation of the environment and the behaviour patterns of other animals (Blumenschine & Cavallo, 1992).

Scavenging hominids could have used bone-crushing tools to extract bone marrow and brains. There is no absolute proof of tool making by Australopithecus, but they probably utilized opportunistic tools such as crushers and digging sticks. The Oldowan tradition (2·4 to two million years ago) of simple flaked tools first appears in strata where *H. habilis* and *A. boisei* remains are contemporaneous. There are no Oldowan sites with *A. boisei* fossils alone. After 1·8 to two million years, the Oldowan tradition continued to develop, and the Aechulian tradition (approximately 1·4 million years ago) arose, but between 1·5 and one million years ago, Australopithecus became extinct. The Aechulian tradition is clearly associated with *H. erectus*, although it has also been found with *H. habilis* in Olduvai and Sterkfontein (Clark, 1985, 1992; Conroy, 1990; Shreeve, 1995). Oldowan and Early Aechulian tools

are sufficient for extracting brains and marrow, and crude butchering of carrion, but probably not for organized hunting.

Culture, speech, and tool use are not prerequisites for the expansion of the cerebral cortex, but rather result from expansion. Based on the EQ evidence, it cannot be assumed that early hominids possessed the creativity and hand–eye coordination to manufacture or use a variety of tools which have yet to be discovered. Organized hunting with effective weapons is mainly an Upper Paleolithic phenomenon (forty to ten thousand years ago), but rather than postulate a vegetarian diet until this time, it is considered that scavenging occurred, despite a lack of compelling archaeological evidence. 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. Most marks on the bones are from carnivore teeth (Blumenschine, 1991; Bunn & Ezzo, 1993; Selvaggio, 1994). An analysis of faunal remains from Olduvai Bed II also found that most bone cuts were done by carnivores; however, when hominids were involved, it appeared they were acquiring scavenged carcasses long before all the meat was gone, and had a preference for larger game. They were evidently eating more than just bone marrow, irrespective of their ability to actively hunt (Monahan, 1996).

However, the logic applied to terrestrial fauna has not been transferred to aquatic foods. Since sophisticated fishing tackle, harpoons, and fishhooks are usually not found up to eighteen thousand years ago, it has been assumed that earlier humans and hominids did not eat fish. While they may not have actively fished, they may well have eaten fish. Fish scavenging, shellfish gathering, etc., is not possible in every environment, but is very plausible in the unique East African Rift Valley, and in other areas of Africa with long histories of hominid occupation.

Homo proceeded from an opportunistic tool user to a premeditated tool maker, and ultimately to a fine craftsman and organized hunter, with astonishing rapidity. EQ increased significantly in *H. habilis*, and even more dramatically in *H. erectus* (Table 1). It is difficult to account for this in an evolutionary sense without at least considering the sources of brain-specific nutrients available to early Homo (Cunnane *et al.* 1993). Grabbing or trapping fish and crustaceans by hand, and smashing mollusc shells requires less sophistication than either hunting or scavenging game, yet yields a far greater amount of preformed DHA and AA for the effort. Modern fishers often smash fish crania with rocks or sticks in order to extract the brains. Based on the large number of fish cranial fragments found in Olduvai Level 3, fish-skull crushing could have been done by hominids also (Stewart, 1994).

It is not suggested by the relatively crude nature of the archaeological evidence that *H. habilis* or *H. erectus* posed a serious threat to the subsistence base of the existing savanna pursuit carnivores. While early Homo may have scavenged meat and bones, it is only the internal organs and their associated fat depots, and brains of game that could have provided a consistent, concentrated source of preformed LC-PUFA on a par with freshwater fish. The organs and depot fat are parts of a carcass that are likely to be consumed first by carnivores and primary scavengers, and may not have been consistently available. We note also that high consumption of internal organs can have a price; a *H. erectus* skeleton shows pathological changes indicative of retinol hypervitaminosis, probably caused by too much animal liver (Walker *et al.* 1982), or possibly honeybee larvae (Skinner, 1991), although fish liver is an equally plausible source. This leaves only brains and bone marrow, which require the use of tools to extract. Since tool use is a result of cerebral cortex expansion rather than a cause, this begs the question of which factors were most responsible for the initiation and expansion of the hominid intellect.

The Lake Malawi Bantu eat 9188 kJ/d with 23 % dietary energy from fish and 12 % dietary energy from fat, most of which is from the fish (Pauletto *et al.* 1996*a,b*); 12 % dietary energy equals 29 g fish oil. Half or even one-quarter of this intake is still about 7–15 g fish oil/d, a much higher intake than the majority of the population obtains today. Fish intakes of the order of half or one-quarter of 23 % dietary energy intake are 6–12 % of the diet, easily within the 10–20 % range for evolutionary influence proposed by Foley & Lee (1991). Working within the framework of known ecological influences on evolution and prodigious expansion of the cerebral cortex, it is in fact difficult to argue that very moderate freshwater-fish intakes could not have affected hominid evolution.

Conclusions

African Rift Valley lake margins provided a unique source of brain-specific nutrition, namely abundant freshwater fish and shellfish providing LC-PUFA. If this resource base was consistently exploited by hominids, it could have helped provide a means for rapid, sustained cerebral cortex enlargement without an attendant increase in body mass. We recognize that this enlargement is based on a pre-existing primate genetic capacity for relatively high intelligence, and is subject to numerous selective pressures and cultural reinforcements. However, we believe that the role of abundant brain-specific nutrient deserves consideration in the past and current evolution of Homo. Although *H. erectus* evidently migrated to Eurasia, the weight of evidence from very diverse anthropological arguments points to a single speciation event in Africa which produced *H. sapiens*. *H. sapiens* populations then migrated out of Africa to the world approximately 120 thousand years ago, rather than independent evolution of separate *H. erectus* populations (Harrison, 1993; Lahr, 1994; Tishkoff *et al.* 1996; Tattersall, 1997).

In this case we suggest that the same basic lacustrine environment was responsible for the successful evolution from *H. habilis* to *H. sapiens*. Perhaps we could not successfully emerge from the African Lake Cradle until we became intelligent enough to adapt to very diverse environments. We hypothesize that part of this adaptation to diverse environments involves ensuring that the food supply for males, females, and children contains adequate PUFA. Accessing rich sources of dietary fat, especially LC-PUFA, may have been unconscious or opportunistic at first, but eventually became conscious and desirable.

Additionally, faunal evidence from Lainyamok, Kenya indicates that in some areas of East Africa, extant mammalian taxa were present as far back as 390 thousand years ago (Potts & Deino, 1995). Foley (1994) and Vrba *et al.* (1995) concluded that while climatic change may be clearly related to extinction, it is rarely if ever clearly related to the creation of species. This indicates that climatic changes alone 120 thousand years ago may be too simplistic an explanation for migration out of Africa, and the origin of modern *H. sapiens*. However, we would agree that increasing population, coupled with deteriorating climate and extreme lake lowstands in the Pleistocene almost certainly influenced migration from the Rift Valley, and the adoption of organized hunting.

Postulating that LC-PUFA are limiting nutrients for human brain evolution leads to the prediction that chronically-inadequate LC-PUFA nutrition will result in suboptimal brain development in both individual cases and in populations as a whole. There is good evidence today that lack of abundant, balanced DHA and AA *in utero* and infancy leads to lower intelligence quotient and visual acuity (Crawford *et al.* 1992; Carlson *et al.* 1993*b*; Cunnane *et al.* 1993; Nettleton, 1995; Simopoulos 1996), and in the longer-term contributes to clinical depression (Hibbeln & Salem, 1995; Adams *et al.* 1996) and attention-deficit hyperactivity disorder (Stevens *et al.* 1995). We are not so far removed from our Paleolithic ancestors that we can expect our present agricultural, processed-food-based diet to provide indefinitely for our continued intellectual development.

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