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Chapter 6

THE ORIGINAL ECONICHE OF THE GENUS *HOMO*: OPEN PLAIN OR WATERSIDE?

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ABSTRACT

That humans evolved as a result of a move from forests to more open plains is still the prevailing paradigm in anthropology, and researchers often assume that this transition influenced the origins of human bipedalism, omnivory, tool use, large brains, and even speech. Here, we argue that there are no scientific grounds on which to base such a hypothesis. While we agree that *Homo* may have evolved in more open (tree-poor) habitats than other apes (which could account for our relatively poor climbing skills), the suggestion that humans shifted to drier habitats away from water is, according to our research, unproven. We propose instead a more parsimonious model compatible with all known data and corroborated by a number of independent sources of evidence.

Comparisons of the locomotor styles and nutritional requirements of extant species and anatomical comparisons of fossil and extant species including *Homo sapiens*, especially in combination with palaeoecological data, strongly suggest that early *Homo* evolved at the water's edge (whether in savannahs or elsewhere) where resources essential for brain growth were both abundant and easily procurable by a thick-enameled tool-using omnivorous hominid.

INTRODUCTION

Many anthropologists still essentially follow the 20th-century view, exemplified by Dart (1925), that "a vast open country with occasional wooded belts and a relative scarcity of water" furnished the conditions that were necessary for the evolution of naked, bipedal, large-brained humans. Recent models, when taken together, suggest that *Homo* may have acquired a larger brain because, through endurance running, it was able to out-compete other savannah dwellers for scavenged carcass remains in open, semi-arid environments, thus providing access to the extra fats and proteins required for increased brain growth (e.g., Cordain *et al.* 2001, Bramble and Lieberman 2004).

The 'endurance running' model is one of the latest of a long list of anthropological models that conform to the idea that a shift in econiche from forests to more open landscapes was primarily responsible for the evolution of the genus *Homo*. These models have been collectively labelled 'open plain' hypotheses (Bender 1999). These hypotheses offer easy-to-understand scenarios for human origins, and were formulated well before most fossil hominid evidence had been discovered (Bender 1999). They were based from the very beginning on unproven assumptions rather than solid evidence, yet they today remain the dominant paradigm in human evolution in mainstream popular culture (see, e.g., the BBC productions *Walking with Cavemen*, and David Attenborough's *Life of Mammals* which, although acknowledging that human bipedalism may have evolved through wading, typifies *Homo* as long-distance 'persistence' hunters who run their prey down) and in respected peer-reviewed journals (e.g., Langdon 1997). Possibly, the strong (either implicit or explicit) tendency to regard humans as unique might explain why these 'open plain' ideas were never ecologically tested and methodically scrutinised. This tendency could also perhaps explain why traditional anthropology places remarkably little value on comparative biological data: if our species is ‘unique’, why would one expect to see parallels with other animals?

This anthropocentric perspective is contrary to the way we approach human evolution in this Chapter. We believe one of the key ways to understand human evolution is by comparing our species to other species: if something is true for other species, there is no *a priori* reason why this could not also be true for humans. We also believe that traditional human evolutionary models place too little emphasis on the broader topic of hominoid evolution (for instance, how the human–chimpanzee last common ancestor lived, and how the African apes evolved), whereas in our view this is essential. Although innumerous facts contradict the savannah and ‘endurance running’ models, it seems ‘open plain’ thinking is simply too traditional, widespread and ‘self-evident' to be easily dropped.

In this Chapter, we argue that ‘open plain’ models are incompatible with otherwise widely accepted concepts in evolutionary biology such as gradualism and convergence, and that they fail to take into account comparative biology. We present old and new scientific evidence contradicting ‘open plain’ interpretations and/or supporting more parsimonious ‘waterside’ models. Unlike ‘open plain’ models, the waterside models are based primarily on comparisons with other animals.

We present nutritional, behavioural, anatomical, locomotor and palaeoecological data that indicate that *Homo* populations have always (apparently at least until the late Pleistocene) lived at the water’s edge, where they could have collected a variety of foods from trees, from shores and from below the water’s surface. These waterside ecological niches could help explain peculiarities in which humans differ from other primates, such as loss of fur, abundant subcutaneous fat tissues, alined body posture, well-developed dexterity and a large brain – characteristics typical of mammals which inhabit aquatic and littoral habitats, but rare in cursorials and arid adapted animals.

‘OPEN PLAIN’ HYPOTHESES IN ANTHROPOLOGY

> “… It will appear to many a remarkable fact that an ultra-simian and pre-human stock should be discovered, in the first place, at this extreme southern point in Africa, and, secondly, in Bechuanaland, for one does not associate with the present fringe of the Kalahari desert an environment favourable to higher primate life. It is generally believed by geologists (*vide* A. W. Rogers, ‘Post-Cretaceous Climates of South Africa,’ *African Journal of Science*, vol. xix., 1922) that the climate has fluctuated within exceedingly narrow limits in this country since Cretaceous times. … For the production of man a different apprenticeship was needed to sharpen the wits and quicken the higher manifestations of intellect – a more open veldt country where competition was keener between swiftness and stealth, and where adroitness of thinking and movement played a preponderating role in the preservation of the species. Darwin has said, no other country in the world abounds in a greater degree with dangerous beasts than Southern Africa, and, in my opinion, South Africa, by providing a vast open country with occasional wooded belts and a relative scarcity of water, together with a fierce and bitter mammalian competition, furnished a laboratory such as was essential to this penultimate phase of human evolution. …”

This is an extract from Professor Raymond Dart’s (1925) famous paper, ‘*Australopithecus africanus*: the man-ape of South Africa’, published in *Nature* shortly after the discovery of the first australopithecine fossil, the 'Taung child'. Following the geological view of his time, Dart argued that the ancestors of man, for Dart saw the Taung child as a representative of early human ancestors, must have lived in treeless grasslands similar to the habitat in which the Taung skull was discovered. There is good evidence today, however, that the South African climate has changed drastically over time, and that the Taung child probably inhabited not treeless grasslands, but wet, tropical forests (e.g., Partridge 1985).

Dart was merely following the 'open plain' ideas that were particularly popular in the early 1900s ('*Freilandhypothesen*', see Bender 1999), and which go back almost two hundred years (e.g., Lamarck 1990: 261, Reinhardt 1906: 6, and Arldt 1907: 606). These hypotheses were based upon two facts and one subjective interpretation of these facts (see Figure 1).

The differences between humans and apes, the traditional story suggests, came about because humans left the forests and adapted to living on open plains (Bender and Oser 1997). The first primates were quadrupedal arboreals living in forests (most primates), and later they evolved into bipedal terrestrials living outside forests (humans), so therefore bipedalism must have evolved because human ancestors left the forests. But while this might seem an obvious conclusion, it is in fact a logical fallacy of the type: *post hoc, ergo propter hoc* ('after that, therefore because of that'), and our comparative research suggests to the contrary that there is no evidence that the two (leaving the trees and becoming bipedal) are causally related: in fact, ground-dwelling and savannah primates such as patas monkeys and hamadryas baboons are *more* quadrupedal than forest and arboreal primates such as indris, tarsiers, proboscis monkeys and gibbons.

'Out of Eden' hypotheses, which dominated thinking in the early 20th century, contrasted luxurious tropical forest econiches characterised by easy fruit-picking with a tough hunting life on open plains outside the forest, which required large brains, speech, and bipedality to 'free the hands' so that they could be used for holding tools and weapons. As Abel (1931: 369) pointed out, these early 'open plain' hypotheses were situated in many different locations, including India, Indonesia, Australia, Africa and Europe, and occurred anywhere between thirty million years ago to only a few hundred thousand years ago. As an historical analysis showed, the same sequence of events was always emphasised: the transition from a 'lower' apelike animal lifestyle towards the 'higher' human lifestyle characterised by mastering of the environment, whereever or whenever they were situated (Bender 1999: 75-79).

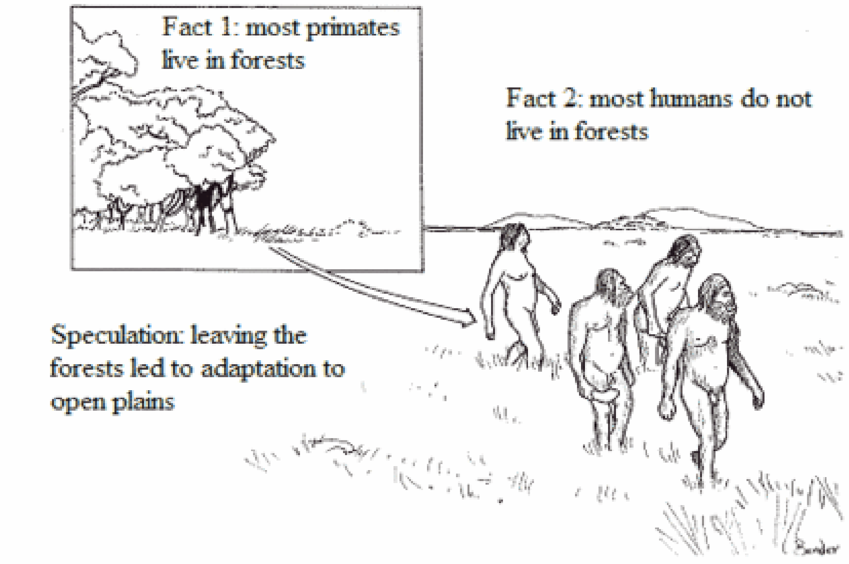

Figure 1. Origin of the ‘open plain’ hypotheses. Early scientists speculated from Fact 1 (“most primates live in forests”) and Fact 2 (“most humans do not live in forests”) that a transition from life in the woods to life on open plains was essential to the evolution of human characteristics such as bipedalism (adapted from Bender-Oser 2004).

Table 1. Four main episodes included in orthodox human evolutionary models (Landau 1984)

Episode	Description
Terrestriality	A shift from the trees to the ground
Bipedalism	The development of upright posture
Encephalisation	The development of the brain, intelligence, and language
Civilization	The development of technology, morals and society

Landau (1984), after studying texts on human evolution written by early 20th century scientists Arthur Keith, Grafton Elliot Smith, Frederick Wood Jones, Henry Fairfield Osborn, and William King Gregory, concluded that, “there appears to be some underlying agreement about what happens in human evolution. In constructing their theories, most anthropologists seem to have in mind a similar narrative pattern.” These narratives had four main episodes (Table 1), one of which was “a shift from the trees to the ground (terrestriality)” (1984: 264, see also Landau 1991).

The narrative style, Landau discovered, was overall most similar to popular folk-tales in which heroic characters, when faced with adversity, overcame great odds to prevail. While there was room within these narratives for different chronologies (bipedalism might have occurred before or after terrestriality, for example), the four key episodes were always included, thus forming a somewhat predictable framework. Perhaps this is why waterside models never made an impression in the minds of most anthropologists. In waterside models, there is no shift from the trees to the ground (episode of terrestriality), these models therefore fail to conform to the prevailing narrative framework, and are consequently considered unorthodox and 'impossible'.

Later in the 20th century, scenarios no longer based solely on the courage or initiative of early human ancestors were proposed, and these stressed instead the importance of external factors such as climatic changes, which led to shrinking forests and expanding open plains, notably, the dry and hot East-African savannahs (see especially Dart 1925, and for more recent discussion deMenocal 2004). This process of aridification more or less 'forced' our arboreal ancestors to leave the forests and expand into more open, arid habitats (discussion in Bender 1999: 56-59, see Figure 2).

Anthropologists often assume that this shift from 'internal' factors (human courage, curiosity, intelligence) to 'external' factors (climatic or geological changes which caused aridification and/or deforestation) came about because of the discovery of fossils and artefacts in areas that could only have been open savannah, but a survey of the literature shows that *Homo* sites are typically found near large water bodies including rivers, lakes, swamps and coasts, and not necessarily in open savannahs (see below).

Dart's version of the 'open plain' hypothesis eventually became widely accepted, mostly after the Piltdown debacle had been uncovered. The Piltdown hoax, in which an orangutan mandible and a modern human cranium were fraudulently buried and altered so that they appeared to belong to the same fossil species, was accepted as a genuine human ancestor for a number of years (1912–1940). Schematically, therefore, the consensus view at the time of Piltdown was that human ancestors had large canines and a large brain. When the hoax was becoming apparent, it also became clear that a new scheme was required, and eventually scientists supported the opposite view (Lewin 1987: 60-84, Le Gros Clark 1955), accepting Dart's Taung skull (small canines, small brain) as the intermediate step between apes (large canines, small brain) and humans (small canines, large brain).

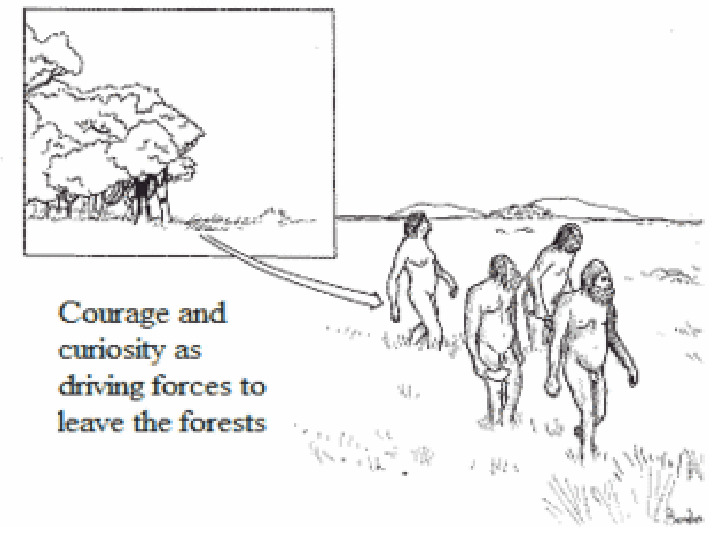

Figure 2a. Early 'open plain' hypotheses stressed mostly internal factors such as courage or curiosity to explain the transition from forests to open plains (adapted from Bender-Oser 2004).

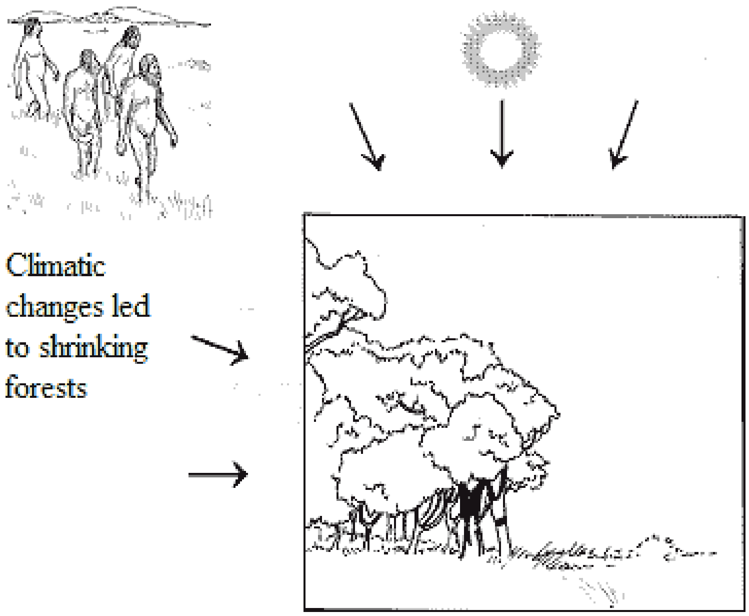

Figure 2b. Later, ‘modern’ versions began to stress more and more ‘external factors’ such as climatic factors and shrinking forests to explain this transition (adapted from Bender-Oser 2004).

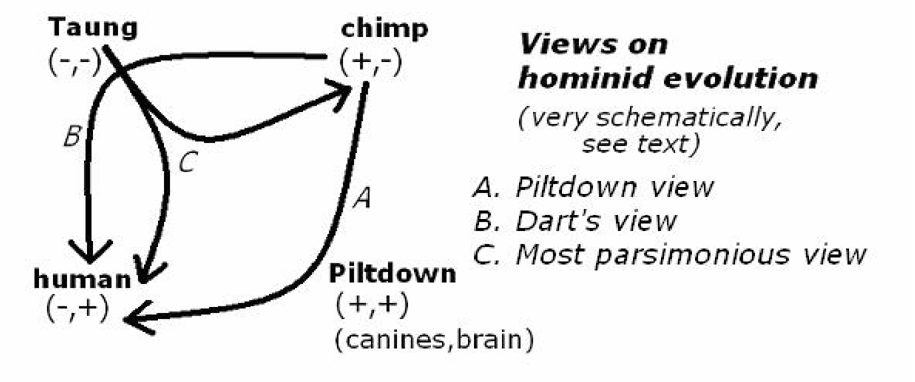

Figure 3. Different views on hominid evolution, very schematically (see text).
A. View based upon the fraudulous Piltdown skull. Large-toothed, small-brained apelike ancestors (+,-) evolved via large-toothed, large-brained Piltdown-like intermediates (+,+) into small-toothed, large-brained humans (-,+).
B. Traditional view after accepting the Taung fossil as a ‘hominid’, diametrically different from the Piltdown view. Apelike ancestors (+,-) evolved via australopithecines, exemplified by the Taung skull (-,-), into humans (-,+). In both tradiational views (A and B), ‘apelike’ equals ‘primitive’.
C. Alternative view incorporating temporal data: older specimens are more likely to have more primitive characteristics (Fox *et al*. 1999). It does not intend to say that both humans (-,+) and chimpanzees (+,-) descend from Taung, but rather that both evolved in different directions from more australopith-like ancestors (-,-) and that both humans and chimpanzees have several derived features (e.g., Drapeau and Ward 2007).

In the view of three of us (for the view of RB and NB, see Bender 1999), the Taung skull is not an intermediary between an ancestral apelike and an extant humanlike skull (the view that many palaeoanthropologists today tend to adopt). Instead, we prefer the more parsimonious views that evolutionary changes happened in both lineages (*Homo* as well as *Pan*) rather than that nearly all evolutionary changes happened in one lineage (*Homo*) and that the older skull is nearer to the ancestors of the living species (Fox *et al.* 1999), so that both chimpanzees and humans had more australopithecine-like ancestors (for detailed arguments, see Verhaegen 1994, 1996) (Figure 3).

Significantly, when, in the 1940s and 1950s, most palaeoanthropologists rejected Piltdown, not only did they accept Dart's ideas on Taung being ancestral to humans, but also his views on where it might have lived ("a vast open country with … a relative scarcity of water"), which we now know (e.g., Partridge 1985) were based on incorrect conclusions.

A Diversity of 'Open Plains' Ideas

The original 'open plain' ideas were obviously hypothetical, but soon the general impression of human ancestors coming out of the trees and colonizing the vast plains became set in the minds of most anthropologists, and different ideas – some more improbable than others – were put forward to explain how savannah-dwelling ancestors might have found enough food and water to survive on the open plains – as if the hypothesis had already been proven. Human characteristics were discussed in an evolutionary setting that involved a movement from the forests to the open plains, and reasons for these characteristics always tended to revolve around the 'open plain' theme (see Table 2). Even the most far-fetched of these ideas (for example, honey collection, liver consumption, or food collection at noon on open plains) have been seriously considered and published in scientific journals. Such *ad hoc* explanations are comparable to the hypothetical 'land bridges' between Africa and South-America that were popular in geology before the theory of Plate Tectonics became accepted.

What is striking about these hypotheses is their combined diversity. Some rely on hunting large game, others on small game, some on scavenging bone marrow, or brains, or livers, or collecting seeds, or tubers, or honey. Some of these 'open plain' models are more typical of slow-moving animals (feeding on belowground resources), others of fast-moving mammals ("bouts of strenuous activity"), and others rely on endurance (following migrating ungulates, or the dogged pursuit of prey). This diversity of theoretical models suggests that the 'open plain' scenarios are not the result of usual biological thinking. In evolutionary biology, hypotheses are not just 'possible scenarios', but normally the result of solid analyses of relationships between form and function. Biologists usually do not propose a scenario to explain the evolution of an animal without a careful comparison of different features of this animal with similar features (*convergences*) of other, not closely related species.

Table 2. Diverse savannah hypotheses of human origins.

Raymond Dart 1960	Osteodonto-keratic Culture – Savannah hunting
Robert Ardrey 1961	Man the Mighty Hunter – African Genesis – Adult men hunting large game
Mikhail Nesturkh 1967	Herd instinct developed along with bipedalism as our ancestors moved to more open territory.
Desmond Morris 1967	Mighty Hunter – The Naked Ape – Fur loss for easier sweating
Clifford Jolly 1970	The Seed Eaters – Savannah baboon model
John Napier 1971	Open grassy spaces provided 'arenas' where new locomotor skills could be safely practiced.
Hatley & Kappelman 1980	Belowground food resources
Walker, Zimmerman & Leakey 1982	High dietary intake of carnivore livers – Scavenger model
Hanna & Brown 1983	Bouts of strenous activity for hunting or digging outside the forest
Peter Wheeler 1984	Savannah foraging at noon, to minimise solar radiation
David Carrier 1984	Dogged pursuit of swifter animals over 1 or 2 days
Sinclair, Leakey & Norton-Griffiths 1986	Bipedal trekking after herds of migrating ungulates
Mark Skinner 1991	Savannah bee brood consumption – Tall grass savannah & tropical forest
Richard Wrangham *et al.* 1999	Cooking and bringing food to a processing area
Bramble & Lieberman 2004	Endurance Running over vaste plains
Dennell & Roebroeks 2005	Ability to ingest large amounts of meat – 'Savannahstan'
Richard Wrangham 2005	Delta hypothesis – Okavango-like savannah – Omnivory

Whereas modern biology sees evolution as a *sequence of overlapping niches* (Kemp 2007), the proposed 'open plain' lifestyles of these early human ancestors are discontinuous and have little or no overlap. Frequently they are incompatible with each other. Moreover, they suppose that humans collected foods without the typical adaptations that other mammals use when they collect the same foods. We have no large digging-claws, for example, we are slow runners (only some 36 km/hr over short, and some 20 km/hr over long distances), and we are very prone to dehydration by depletion of water and salts. We are heavily-built creatures with extensive fat tissues and (in archaic *Homo*) heavy bones, features that are not seen in cursorial species. Our cheekteeth lack the seed-grinding adaptations of baboons, while the human gastro-intestinal tract and digestive anatomy and physiology resemble frugi-omnivores such as suids, not carnivorous mammals (Stevens 1990). This contradiction has been labelled the 'baboon paradox', because we would expect humans to be more similar to baboons if we evolved on the savannah as they apparently did (Bender 1999).

The collection of waterside food resources, on the other hand, is compatible with the presumed lifestyle of early apes, and fits with modern human food-gathering strategies. Shifting from a fruit-based diet to a diet including more waterside foods such as coconuts and shellfish does not require significant behavioural modification. The use of tools to open hard-shelled nuts and fruits is easily transferable so that the meat of certain molluscs can also be procured (capuchin monkeys use tools to open fruit, nuts and shellfish), and shellfish, like fruits and nuts, are sessile food resources that need only be found and gathered, not chased or hunted. From such fruit, shellfish, plant and egg-gathering it is not difficult to envisage the incorporation of waterside catching of insects, frogs, fish or birds, and the butchering of turtles, crabs, whale or bovid carcasses found at the water's edge. We do not claim to know exactly how this waterside lifestyle evolved, but we are confident that the limited diving skills of humans came about as a result of increased time spent foraging under water. As to how frequently our ancestors may have dived or waded or collected fruit from trees or foods along the shore at low tide, or how long our ancestors' waterside phase or phases may have lasted, these are all questions requiring further investigation.

Questioning the Savannah Model

Although the savannah model still dominates anthropological thinking, many leading palaeoanthropologists no longer follow it automatically (Table 3). No other than professor Phillip Tobias, Dart's mental heir, already an emeritus himself, recently stated that "… All the former savannah supporters (including myself) must now swallow our earlier words in the light of the new results from the early hominid deposits ... Of course, if savannah is eliminated as a primary cause, or selective advantage of bipedalism, then we are back to square one. …" (Tobias 1995, 1998).

This questioning of the savannah model (Table 3) resulted from two lines of evidence: firstly, palaeoecological studies showed that the earliest bipedal hominids were associated not with open plains, but with wooded or forested environments (e.g., Tobias 1998); and secondly, anatomical studies showed that australopithecines and early *Homo* species such as *habilis* had good climbing abilities (e.g., Collard and Wood 1999) (some of which persisted into *Homo georgicus* and possibly even *Homo floresiensis*, see Lordkipanidze *et al.* 2007, and Tocheri *et al.* 2007). Rather than abandon the savannah theory, however, the chronology of events has been rearranged, with *Homo erectus* now seen as the first true savannah hominid, descending from earlier australopithecine and *habilis*-like species that are now seen as adapted to mosaic habitats including both forests and open plains (see Langdon 1997).

Table 3. Some quotes of leading palaeoanthropologists doubting savannah hypotheses

Tobias 1995	"We were all profoundly and unutterably wrong! … All the former savannah supporters (including myself) must now swallow our earlier words …"
Wood 1996	"the 'savannah' hypothesis of human origins, in which the cooling begat the savannah and the savannah begat humanity, is now discredited"
Stringer 1997	"One of the strong points about the aquatic theory is in explaining the origin of bipedality. If our ancestors did go into the water, that would forced them to walk upright …"
Tobias 1998	"Bamford identified fossil vines or lianas of *Dichapetalum* in the same Member 4: such vines hang from forest trees and would not be expected in open savannah. The team at Makapansgat found floral and faunal evidence that the layers containing *Australopithecus* reflected forest or forest margin conditions. From Hadar, in Ethiopia, where 'Lucy' was found, and from Aramis in Ethiopia, where Tim White's team found *Ardipithecus ramidus* … well-wooded and even forested conditions were inferred from the fauna accompanying the hominid fossils. All the fossil evidence adds up to the small-brained, bipedal hominids of four to 2.5 Ma having lived in a woodland or forest niche, not savannah." "… if ever our earliest ancestors were savannah dwellers, we must have been the worst, the most profligate urinators there"
Stringer 2001	"In the past I have agreed that we lack plausible models for the origins of bipedalism and have agreed that wading in water can facilitate bipedal locomotion (as observed in other normally quadrupedal primates). I have never said that this MUST have been the forcing mechanism in hominids, but I do consider it plausible. As for coastal colonisation, I argued in my *Nature News & Views* last year that this was an event in the late Pleistocene that may have facilitated the spread of modern humans."
Groves & Cameron 2004	"Nor can we exclude the Aquatic Ape Hypothesis. Elaine Morgan has long argued that many aspects of human anatomy are best explained as a legacy of a semiaquatic phase in the proto-human trajectory, and this includes upright posture to cope with increased water depth as our ancestors foraged farther and further from the lake or seashore."
Wrangham 2005	"Here I follow the conventional assumption that hominins began in the savanna." "… the composition of the Okavango as a network of islands could favor the evolution of bipedalism. For those who envisage bipedalism as facilitated by the need to traverse or exploit aquatic environments, an inland delta that generates low islands termitogenically or hydrodynamically offers rich scenarios."
Alemseged 2006	"I believe we should just put the savannah theory aside. I think they basically became biped while they were living in a wooded, covered environment …"
Thorpe *et al*. 2007	"… early hominins occupied woodland environments, not open or even bush-savannah environments (such as sites including Allia Bay, Aramis, Assa Issie and now Laetoli) ... they retained long grasping forelimbs, which are more obviously relevant in an arboreal context…"

Below we discuss anatomical, physiological, dietary and palaeoecological data indicating that a waterside lifestyle for our direct ancestors is many times more plausible as an explanation for our mental and physical characteristics than any 'open plain' or savannah-based hypotheses, and that *Homo erectus* was more likely to have been a waterside specialist than an arid savannah specialist. As an illustration, we compare the recently outlined 'endurance running' model with a model that includes part-time waterside dwelling as a prerequisite to later evolution of terrestrial bipedalism. Note that while Wrangham (2005) includes part-time waterside dwelling to explain the evolution of australopithecines, he still follows "the conventional assumption that hominins began in the savannah."

Endurance Running or Littoral Locomotion in Archaic *Homo*?

Bramble and Lieberman (2004), in a much-discussed review article in *Nature*, cite a number of derived *Homo* features they claim to be adaptations for more efficient endurance running in arid, open habitats. However, while some of these supposedly 'cursorial adaptations' appear first in the fossil record in *H. habilis*, others appear first in *H. erectus*, and others still in *H. sapiens*, suggesting a much more complex story than proposed by Bramble and Lieberman. Their conclusions are reached without systematic comparisons with other animals (including endurance runners) and with general comparisons restricted to fossil hominids and *Pan*. Since convergent traits are strong indicators of evolution in similar environments (Bender 1999), a systematic comparison with a broad range of animals with a variety of locomotor strategies would have been more informative.

In addition, discussion of possible locomotion styles is restricted to walking and running, with no consideration at all given to activities such as wading, swimming or underwater foraging, yet humans are regular waders and more accomplished swimmers and divers than other primates. Most of the list's 'adaptations' for walking could just as easily be explained by wading. One of the frequent 'explanations' in the list is "stress reduction", a reference to the vertical posture of humans with the weight resting on two legs. But this says nothing about endurance running, with standing, wading, walking or short distance running all using a similar posture, and therefore all requiring stress reduction. Other 'explanations' include "counter rotation", "thermoregulation" and "stabilization", but no comparative data to corroborate these interpretations are provided. In other words, their 'explanations' are *ad hoc* suppositions, applied to one example (human ancestors) without any consideration as to whether these supposed adaptations are seen in other animals, which means their 'explanations' are statistically invalid (n=1). Long legs, and possibly shortened forearms, could be seen as running adaptations, but these are just as typical of wading and swimming species compared with runners (Hildebrand 1974: 584, Bender 1999).

In a waterside scenario, wading and swimming would be preadaptative to the humanlike 'vertical' locomotion that Bramble and Lieberman (2004) believe to be a direct adaptation to endurance running. In our view, frequent terrestrial locomotion, whether for walking or for (relatively slow) running, was more recent (*Homo sapiens*) and could not be derived directly from an ancestral locomotion in forests, whether on the ground or in the branches, because in that case a more baboon-like locomotion would be expected (the 'baboon paradox').

Table 4. Bramble and Lieberman's (2004) list of supposedly derived features of the human skeleton with so-called cursorial functions

	Functional role in running & walking according to Bramble & Lieberman (2004)	W = walk R = run	Earliest evidence	Comparative data. More likely alternatives in our opinion. NSS = not seen in savannah animals. NSC = not seen in cursorial animals. NUL = not unexpected in littoral animals.
Enlarged posterior & anterior semicircular canals	Head/body stabilization	R	*H. erectus*	NSS as far as known. NUL, e.g., for equilibrium during descent & ascent in diving. Requires more comparative data.
Expanded venous circulation of neurocranium	Thermoregulation	R>W	*H. erectus*	NSS. NSC. NUL. Skull base & paravertebral venous networks are typical of diving species.
More balanced head	Head stabilization	R	*H. habilis*	NSS. NSC. Could be advantageous in frequent standing rather than running. Alined build NUL.
Nuchal ligament	Head stabilization	R	*H. habilis*	NUL, e.g., in pronograde swimming.
Short snout	Head stabilization	R>W	*H. habilis*	NSS. NSC. Snout shortening has to do with mastication rather than head stabilisation.
Tall, narrow body form	Thermoregulation	R>W	*H. erectus*	NUL: long legs are typical of wading species.
Decoupled head & pectoral girdle	Counter-rotation of trunk *vs* head	R	*H. erectus*?	NUL: waterside as well as a mosaic milieus require versatile locomotions.
Low, wide shoulders	Counter-rotation of trunk *vs* hips	R	*H. erectus*?	NUL: 'low' could be for wading as well as for underwater swimming. No relation to running.
Forearm shortening	Counter-rotation of trunk	-	*H. erectus*	NUL: typical of frequently swimming species.
Narrow thorax	Counter-rotation of trunk *vs* hips	R	*H. erectus*?	Dorso-ventrally narrow. NSS, NSC, NUL: typical of shallow water dwellers, e.g., platypus, hippo, beaver.
Narrow & tall waist between iliac crest & ribcage	Counter-rotation of trunk *vs* hips	R	*H. erectus*?	NUL: waterside as well as mosaic milieus require a wide range of locomotions.
Narrow pelvis	Counter-rotation of trunk *vs* hips Stress reduction	R R>W	*Homo*?	*H. erectus* had still flaring ilia, presumably for femoral abduction: NSS, NSC, NUL.

Expanded lumbar central surface area	Stress reduction	R>W	*H. erectus*	Suggests vertical body. NUL, e.g., for wading.
Enlarged iliac pillar	Stress reduction	R>W	*H. erectus*	Idem.
Stabilized sacroiliac joint	Trunk stabilization	R	*H. erectus*	Idem.
Expanded surface area for mm. erector spinae origin	Trunk stabilization	R	*H. erectus*	Idem.
Expanded surface area for m. gluteus maximus origin	Trunk stabilization	R	*H. erectus*	Idem.
Long legs	Stride length	R>W	*H. erectus*	NUL, typical of wading species.
Expanded hindlimb joint surface area	Stress reduction	R>W	*H. erectus*	Suggests vertical body. NUL, e.g., for wading.
Shorter femoral neck	Stress reduction	R>W	*H. sapiens*	Not seen in *H. erectus*. Presumably post-littoral.
Long Achilles tendon	Energy storage Shock absorption	R	*Homo*?	Comparative data are needed. Typical cursorial species are not plantigrade. NUL.
Plantar arch (passively stabilized)	Energy storage Shock absorbtion Powered plantar-flexion	R R>W R>W	*Homo*?	NSS. NSC. NUL: plantigrady for wading and swimming.
Enlarged tuber calcaneus	Stress reduction	R>W	*Homo*?	Cursorials do not have enlarged heels. NSS. NSC. NUL.
Close-packed calcaneo-cuboid joint	Energy storage Stability during plantarflexion	R>W	OH-8	Comparative data are needed. NUL.
Permanently adducted hallux	Stability during plantarflexion	R>W	OH-8	NUL: wading, swimming.
Short toes	Stability during plantarflexion Distal mass reduction	R>W	OH-8	NSS. NSC. NUL: metatarsal lengthening and toe shortening is to be expected in swimming & wading.

Most of Bramble and Lieberman's 'adaptations' are not what we would expect in a cursorial (running) animal. For example, their list includes "enlarged posterior and anterior semicircular canals", but there are no comparisons with, for instance, giraffes (heads high above the ground), gibbons (fast and versatile locomotion), kangaroos (cursorial bipeds), or swimming or diving species. It is conceivable in fact that the frequent change of posture seen when diving for seafood (descending and ascending) required a different labyrinth structure, and that the larger *Homo erectus* labyrinth was adapted to terrestrial walking and running as well as to wading, swimming and diving locomotions.

There is no indication that an "expanded venous circulation of neurocranium" had anything to do with thermoregulation, but there is long-standing evidence of expanded venous networks in diving species (Slijper 1936).

More balanced heads and short snouts are not seen in cursorial species, whether bi- or quadrupedal, and low shoulders are to be expected in wading and underwater swimming.

What Bramble and Lieberman refer to as "narrow body form", "narrow thorax" and "narrow pelvis" is not clear to us: compared to most primates, humans have a relatively broad thorax and pelvis (laterolaterally), and this was even more so in the case of australopithecines. In our opinion, the combination of 'flared' iliac blades and long and relatively horizontal femoral necks as seen in *Homo erectus* indicates well-developed ad- and abduction, which is obviously not an adaptation for running, but would not be unexpected and indeed would be advantageous for a species that had to regularly wade, tread water, swim or climb. In *Homo sapiens* the pelvis (bi-iliac diameter) did become narrower and the femoral necks shorter and more vertical, and we agree with Bramble and Lieberman that this could be related to more frequent terrestrial locomotion.

Plantar arches, enlarged tubera calcanei, close-packed calcaneo-cuboid joints and short toes are not seen in cursorials, whether bi- or quadruped, to the contrary: running species are typically unguli- or digiti-, not plantigrade, and typically have elongated toes.

In conclusion, comparative data suggest that none of the features described by Bramble and Lieberman (2004) are typical either of savannah dwellers or frequently running animals, whether slow or fast. Until the features are considered in the context of swimming and wading as well as terrestrial movement, their interpretations should be considered with extreme caution. As it is, there is no obvious reason why any of the features cited could not have been of advantage in a littoral environment. We do not deny that humans today are adapted to terrestrial locomotion including walking and moderate running, but in our opinion the peculiar human anatomy is *not directly* derivable from a typical primate ancestor who moved from closed to more open, arid habitats.

At least two conspicuous anatomical features of *Homo erectus* are notably not included in the list of features cited by Bramble and Lieberman (2004).

1) *Homo erectus* typically has a more robust, and therefore heavier, skeleton than all other (fossil and extant) primates, including *H. sapiens* and the other apes. One of its defining characteristics is the shape and size of the femoral bone, which shows cortex thickening and densening (*pachyostosis*) and a narrow cavity of the bone marrow (*medullary stenosis*). The cranial bones, especially the posterior part (the occiput), are also notably thicker than in other primates including *H. sapiens*. Unusually heavy bones would be a disadvantage for a species relying on endurance running, and are not seen in running mammals such as dogs or horses, whereas for a species collecting sessile food from the water's edge, including underwater foraging, they could have been a significant advantage. Human divers such as the Ama of Korea frequently use weights to help them descend (Hong and Rahn 1967). Slow-diving mammals for sessile foods typically have medullary stenosis and pachyostosis to a higher degree than in *H. erectus* (walruses, dugongs and fossil littoral species such as *Kolponomos*, *Odobenocetops* and some *Thalassocnus* species), while fast-diving mammals for mobile prey have light-weight bones (dolphins and sealions).

2) Archaic *Homo* had a lower and longer brain skull than *H. sapiens*, with generally less flexed cranial base and with the eyes somewhat more in front of the brain (requiring a supraorbital torus for eye protection) rather than fully below the frontal brain as in *H. sapiens*, meaning that the eyes would have been more naturally oriented towards the sky if they were standing with an upright posture, rather than directed more towards the horizon as is the case when *H. sapiens* stands upright. This would be a disadvantage for a species relying on endurance running because, among other things, more energy would be needed to look at where the feet were making contact with the ground. In a diving position, as well as in a more procumbent body position while wading for food, for example, this would have resulted in the eyes being more naturally oriented in the direction the individual was moving (i.e., in the case of swimming and diving, head first through the water). We are not aware of any models that suggest early *Homo* ran with a bent hip posture, but we do note that human sprinters generally run with the body leaning forward.

Within many contemporary *H. sapiens* populations there are individuals who are capable of long distance running, but compared to typical savannah species, humans are slow and inefficient (Figure 4). Moreover, recent research suggests that endurance training in athletes sometimes causes cardial arrhythmias and sudden death (Ector *et al.* 2007). Even Bramble and Lieberman (2004) admit that "humans are mediocre runners in several respects" and "running is more costly for humans than for most other mammals". And since *H. erectus* generally had, for instance, heavier bones than *H sapiens* and longer femoral necks, it must have been an even less efficient cursorial than extant *H. sapiens*.

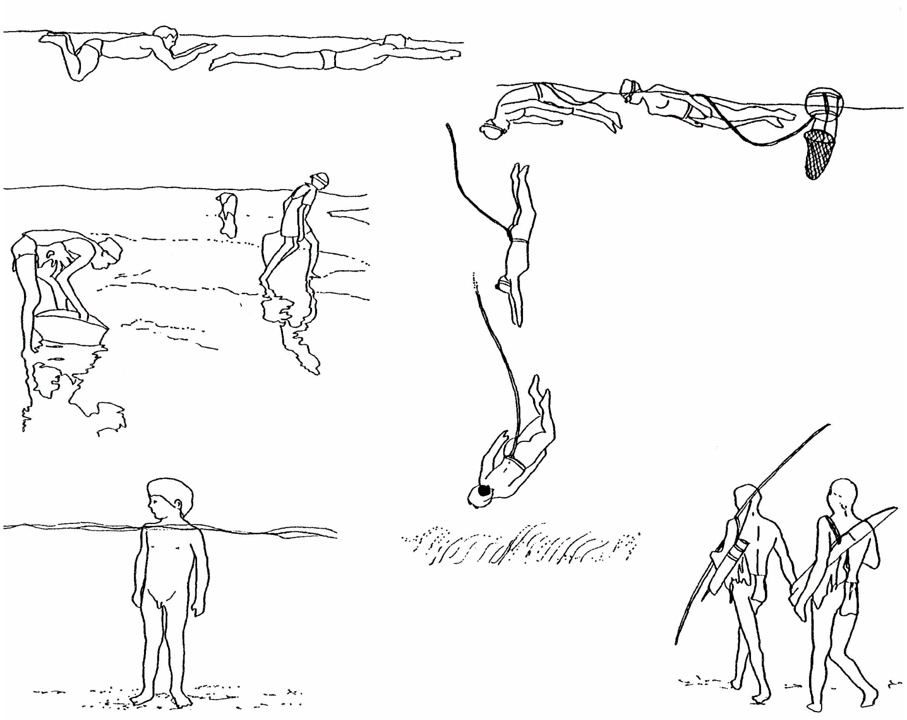

Figure 4. All available data suggest human locomotion *primarily* adapted to the waterside rather than to the open plains (from Bender *et al.* 1997).

FOOD COLLECTION AND PROCESSING IN HUMAN ANCESTORS

Finding and being able to procure adequate amounts of food are obviously essential for the survival of any population. Humans are more omnivorous than other apes, suggesting a shift in diet since our linage separated from chimpanzees. Traditionally, anthropologists have speculated that large savannah mammals (either hunted or scavenged) played an important role in this shift, but we consider it more likely that the initial shift in diet occurred with smaller, sessile prey, such as invertebrates, which could have been easily procured by our ancestors, even before they had diverged from the ancestral lineage leading to chimpanzees. A diet increasingly reliant on waterside invertebrates such as shellfish could help explain the evolution of a large brain, and would be compatible with many other features characteristic of the *Homo* genus.

Acquiring Adequate Brain Nutrition

Cordain *et al.* (2000), in the tradition of the ‘open plain’ ideas, have suggested that the brains of large terrestrial mammals may have provided the *Homo* genus with the extra docosahexaenoic acid (DHA) needed to help fuel a large brain. While we fully agree that the structural, cognitive and visual development of the brain requires adequate amounts of certain nutrients including DHA (Crawford and Sinclair 1972), we think the initial shift might have included more abundant and easily obtainable DHA-rich sources such as shellfish, crayfish, fish, turtles, birds and eggs (Broadhurst *et al.* 1998), although we admit that this alone is insufficient proof for a waterside past (Carlson and Kingston 2007, but Cunnane *et al.* 2007).

Brains and vision evolved in the animal kingdom more than five hundred million years ago, whereby the principle building-blocks were aquatic fatty acids (Crawford *et al.* 1999). DHA (22C:6ω3) is a poly-unsaturated fatty acid that has a chain of twenty-two carbon atoms and six unsaturated bonds (on the carbon atoms in the positions C3, C6, C9, C12, C15 and C18 starting from the omega-end of the carbon chain). It is the only omega-3 molecule used by fish, amphibia, reptiles, birds and mammals for both visual and neural signalling systems. Since the primary source of DHA is algae and plankton, it is abundant in the marine and lacustrine food chains, but almost absent in the meat, fats and offal associated with carnivore remains (Broadhurst *et al.* 2002). This might partially explain why some marine mammals which eat high DHA level foods have large brains (e.g., 1.8 kg for dolphins), whereas it is hard to find a land mammal except humans and elephants with brains that weigh more than about 1 kg. The rhinoceroses which inhabit African savannahs weigh more than a thousand kilograms, but have brain weights of about 400 grams, three times less than humans.

Other brain-selective nutrients are also more abundant in aquatic than in terrestrial milieus. This is notably the case for brain-selective minerals such as iron, copper, zinc, selenium, and iodine (Table 5). Of all the major food groups, shellfish requires the least amount (900 grams) to meet the minimum requirement for all five minerals, and is also the food group for which these requirements are most evenly distributed. Eggs (2500 grams) and fish (3500 grams), both more abundant at the waterside than in terrestrial environments, are next, while 5000 grams of meat, five times more than shellfish, would be needed to meet the minimum daily requirements for all five minerals (Table 5). Iodine especially is more abundant in littoral food chains than terrestrial food chains, and before the iodinisation of drinking-water and salt, hypothyroidy caused by iodine deficiency resulted in mental retardation and cretinism in millions of humans who lived away from the coasts.

Rather than running over open plains to gain adequate nutrition, women, children and the elderly could have collected all the brain food they required without expending nearly as much energy, by inhabiting the water's edge. A littoral existence does not preclude the hunting, scavenging or butchering of land animals (which often gather, drown and get bogged at the water's edge), nor the gathering of anti-oxidant rich plants, fruits and tubers that grow in abundance in moist regions besides estuaries, rivers, lakes and deltas (Wrangham 2005).

Table 5. Daily amount of major food groups (in kilograms), arranged from low to high, minimally required for five brain-selective minerals: iodine, iron, copper, zinc and selenium (I, Fe, Cu, Zn and Se), after Cunnane (2005)

	I	Fe	Cu	Zn	Se
shellfish	.7	.8	*.9*	.5	.3
eggs	.2	.6	*2.5*	.9	.9
fish	.2	*3.5*	3.1	2.7	.7
pulses	*3.7*	.4	.3	.5	3.0
cereals	3.2	3.1	*4.8*	1.9	2.2
meat	1.5	.8	1.7	.9	*5.0*
nuts	1.5	.8	.9	.5	*5.5*
vegetables	4.2	2.1	2.7	*8.7*	6.7
fruit	6.0	3.7	4.8	*9.3*	6.0
milk	6.7	24.0	12.5	*47.0*	5.5

The figure in *italic* is the most limiting factor in each food group.

Some other Considerations regarding Food Acquisition

a. Tool Use

Tool use is easily explained in a model where human ancestors foraged at the water's edge, where removing and open hard-shelled foods such as nuts, fruits and shellfish, would have been rewarding. Chimpanzees, capuchin monkeys and different otter species are all known to use tools to open hard-shelled foods. The *Homo*/*Pan* ancestral population was most likely at least partly arboreal, and early *Homo* ancestors might have lived in flooded forests where they could have collected fruit from the trees, and molluscs attached to tree roots, branches and trunks, as capuchin monkeys do today (Fernandes 1991).

b. Dental and Masticatory Reduction

Compared to australopithecines (large cheekteeth) and apes (large canine teeth), *Homo* typically has reduced dentition, and several archaic fossils (*H. georgicus*, *H. erectus* and *H. neanderthalensis*) show extensive tooth loss and bone resorption of tooth alveoli in older individuals, or even congenital generalised enamel dysplasia (Fischman 2005, Zilberman *et al*. 2004). Such dentitional atrophy is incompatible with an, even partial, dependence on carcass consumption on open plains, but is less of a problem or might even have been advantageous in a shore-based lifestyle where consumption of slippery foods such as shellfish might have been important. In the same way, hunting or scavenging lifestyles fail to explain the drastic and apparently abrupt reduction of human masticatory musculature (Stedman *et al*. 2004). Humans not only lack the sharp dentition of dogs and hyenas, but also their strong biting and chewing muscles.

c. Olfactory Reduction

Savannah-based large mammal consumption is hardly compatible with the drastically reduced olfactory capacity of humans compared to apes (Gilad *et al*. 2003). Dogs and hyenas rely on their superb olfactory abilities to detect carcasses, whereas to collect and consume water-side shellfish a sense of smell is unimportant. Underwater foragers have small (Pinnipedia) or absent (Cetacea) olfactory lobes in the brain compared to terrestrial mammals (Macdonald 2001).

d. Very Sensitive and Mobile Hands

Primates have more sensitive and mobile hands than most other mammals, especially cursorial and savannah-dwelling ones, but this is even more so the case in humans. Comparable trends are seen in waterside mammals such as racoons (*Procyon* species), marsh mongooses (*Atilax paludinosus*), and Cape clawless otters (*Aonyx capensis*), which have unwebbed and highly sensitive and mobile fingers used to forage for crabs and shellfish at the waterside (hence the term ‘Fingerotter’ in German). Such trends are not seen in savannah-dwelling mammals.

e. Subcutaneous Fat

Humans have about ten times as much subcutaneous fat as most terrestrial mammals and non-human primates including chimpanzees, and in this respect they approach ‘lean’ aquatics such as fin whales (Pond 1987). Greater distribution of subcutaneous fat is seen in all endothermic species that spend a lot of time in water, and could have been an advantage for humans in a waterside context (whether for energy storage, thermo-insulation in water, hydrodynamic streamlining, buoyancy, or other ‘purposes’). On the other hand, extra fat would be a disadvantage for an animal reliant on endurance running, which is clear when fat levels of marathon runners are compared with those of long-distance swimmers, who typically are three to five times fatter than long-distance runners (discussion and references in Verhaegen 1991).

PALAEOECOLOGICAL EVIDENCE

Overall, there are many different lines of evidence that point to the evolution of *Homo* at the water's edge. The waterside model is based in the first place on comparative anatomical data such as subcutaneous fat and lack of fur (Westenhöfer 1942, Hardy 1960), but nutritional, and comparative behavioural data are also compatible. It is often assumed the real 'hard evidence' (bones and stones) points to a savannah existence for early *Homo* species such as *erectus* and *ergaster*. Our research, however, suggests the earliest *Homo* fossils and artefacts and those throughout the Pleistocene are consistently associated with habitats in which water was apparently plentiful, and where underwater foraging would have been both possible for human ancestors and rewarding.

Although the fauna associated with early *Homo* sites is often cited as evidence in support of the open, semi-arid view (Reed 1997), these data are at best ambiguous when the waterside model is also taken into account. Palaeoecological evidence associated with *Homo* fossil and archaeological sites strongly suggests that *Homo* may well have been a waterside dweller (Munro 2004).

Although, due to taphonomic considerations, caution is required when interpreting fossil and archaeological data, the results of our preliminary survey reveal that, from its earliest appearance, all *Homo* sites (i.e., fossil *Homo* sites as well as archaeological sites presumed to be *Homo*) are typically and consistently associated with waterside contexts.

Homo *Sites Older than 0.2 Ma* (Mega-anni, Million Years Ago)

At Gona, Ethiopia, 2.5 Ma-old stone tools were deposited in "floodplain environments, close to margins of channels that carried the volcanic cobbles used as raw materials for tool manufacture" (Semaw *et al.* 1997: 333). Nearby, in the Hata Member of the Bouri Formation, hominid fossils of a similar age to the Gona deposits were discovered in sediments containing sandstone with bivalve and gastropod shells "deposited by fluvial processes associated with floodplains along distributary channels close to a shallow fluctuating lake" (de Heinzelin *et al.* 1999: 625). This Member also reveals evidence of cut and percussion marks on bones of medium and large-sized bovids, though stone tools have so far not been discovered.

The *Homo* maxilla AL 666, dated to 2.3 Ma, along with a stone tool assemblage (though no signs of butchering), was recovered from deposits of the Hadar Formation, suggesting a landscape which was "predominantly open, with wetlands and bushed or wooded grasslands, and with stands of trees close to the water source" (Kimbel *et al.* 1996: 559).

At Olduvai Gorge Plio-Pleistocene *Homo* remains are associated with deposits containing "cemented aggregates of the small benthic, freshwater clam *Corbicula*" as well as crocodiles, hippos and fish (Blumenschine *et al.* 2003: 1220). Cut and percussion marks are found on a percentage (4.2 and 8.3% respectively) of the long bones of larger mammals. Fish and gastropods, judging by the remains of 'living sites', might have been consumed at Olduvai Gorge, while the avian fauna included abundant waders (flamingoes, herons, storks, rails, jacanas, plovers, sandpipers and stilts), swimmers and divers (grebes, cormorants, pelicans and ducks) as well as marine birds (gulls, terns and skimmers) (Leakey 1979).

The earliest occurrence of the genus *Homo* in the Turkana Basin is associated with floodplain deposits in which gastropods, fish, crocodiles, bovids, equids, suids, cercopithecids and hippopotamids occur (Pratt *et al.* 2005). During Plio-Pleistocene times the Turkana Basin contained a large lake fringed by swampy wetlands as indicated by the numerous fossils of hippos, crocodiles, fish (including a stingray, suggesting a marine connection at the time), gastropods, bivalves, sponges and numerous ostracods. Lung fish, water bucks, cane rats, monkeys, giraffes, buffaloes, camels, rhinoceroses and elephants suggest a rich mosaic of wet, dry, open and closed habitats in the vicinity of an extensive lake, or large river (Feibel *et al.* 1991).

Table 6. Taxa found in Unit 2 at Nariokotome III (from Walker and Leakey 1993)

Taxa	Lifestyle and habitat
Pila ovata	Air-breathing, shallow-water swamp snail
Claria sp.	Shallow-water catfish
Clarotes sp.	Catfish
Hydrocynus sp.	Shallow- to deep-water fish predator
Synodontis sp.	Shallow-water spiny catfish
Varanus niloticus	Scavenging and often aquatic lizard
Trionyx sp.	Soft-shelled freshwater turtle
Pelomedusidae spp.	Smooth-shelled water tortoise
Homo erectus	Waterside hominid (this study)
Metridiochoerus sp.	Grazing pig
Hippopotamus aethiopicus	Aquatic herbivore
Hippopotamus gorgops	Aquatic herbivore
Bovidae spp. (duiker- to buffalo-sized)	Grazing and browsing herbivores
Lepus capensis	Grass and herb feeder

The most complete skeleton of an early *Homo* specimen, KNM-WT 15000, the so-called ‘Turkana Boy’ of Nariokotome, Kenya, was discovered on the western side of the Turkana Basin. It lay among reeds and hippopotamid footprints, and the most abundant faunal remains associated with it were water snails, fish and turtles (see Table 6).

The Plio-Pleistocene Shungara Formation in the Omo Basin contains an archaeological assemblage as well as molluscs (including freshwater oyster *Etheria* reefs), fish, crocodiles, hippopotamids, bovids, cercopithecids, turtles, suids and other vertebrates. The archaeological occurrences “are all in proximal river settings” (Clark Howell *et al.* 1987: 696).

In the Western Rift Valley, the Senga 5A site (2–2.3 Ma) contains artefacts associated with gastropods, bivalves, fish, hippopotamids, suids and bovids in a “low-energy littoral lacustrine setting” (Harris *et al*. 1987: 724).

The Plio-Pleistocene Chiwondo Beds of Malawi have yielded *Homo* fossils as well as fragmented remains of fish, turtles, crocodiles and large mammals. They also contain molluscs “in consolidated beds of carbonate cemented sandstone. Molluscan shell beds crop out as benches up to several meters thick and several hundred meters wide” (Schrenk *et al.* 1995: 59).

The late Pliocene Chemeron hominid (KNM-BC 1) was deposited in a lake filled basin where fish remains were abundant: “Molluscs also lived in the lake, and locally their remains accumulated to form shelly limestones. … There is little doubt that the fossil came from the Upper Fish Beds" (Martyn and Tobias 1967).

The Dmanisi *Homo* fossil site, dated to 1.8 Ma, is located at the confluence of two rivers, where at the time a lake or pond had formed due to the blocking of a river by a lava stream. "The hominid site itself was likely located near a lake or pond, rich in lacustrine resources. This biome, together with the adjacent forest-steppe formations, created a highly productive ecotone rich in animal and plant resources" (David Lordkipanidze, personal communication to MV). The inhabitants might have eaten hackberrys, since abundant seeds have been found at this site (Gabunia *et al*. 2000).

Early Pleistocene archaeological sites from the Jordan Valley include Erk-el-Ahmar and 'Ubeidiya. These sites are associated with lacustrine and fluvial deposits rich in fresh water gastropod and bivalve remains as well as fish, turtles, hippos and birds (Bar-Yosef and Tchernov 1972).

Aïn Hanech, an archaeological site in Algeria dated to about 1.8 Ma, was formed on an alluvial floodplain cut by a meandering river (an oxbow lake), and may indicate repeated activities by hominids at a shallow river embankment (Sahnouni *et al*. 2002).

At Pabbi Hills, Pakistan, artefacts of Pliocene age, about 2 Ma, have been discovered in deposits which also contain crocodiles, turtles, aquatic gastropods and bivalves. The molluscs suggest a large, slow-moving river with clean, shallow water less than five meters deep, analogous to unpolluted sections of the Ganges River (Dennell 2004).

The site of Mojokerto (Perning), on the Island of Java has been dated to between 1.5 and 1.8 Ma. This coastal deltaic environment (Huffman 2006) contained fresh water and marine molluscs, which would have been easily procured and consumed by early hominid inhabitants (Frank Wesselingh, personal communication to SM).

At Sangiran, also on Java, where *H. erectus* was found, "a thin layer of diatoms (unicellular marine phytoplankton) and dark clays with a marine musselfauna was deposited by the sea, as was noticed and described before by Professor Martin from Leiden" (von Koenigswald 1981).

Hominids on Java were using mollusc shells to butcher mammals, presumably to gain access to nutritious meats, as early as 1.5 Ma (Choi and Driwantoro 2007).

The archaeological site of Majuangou (Nihewan), in China, recently dated to 1.66 Ma, reveals that hominids inhabited a lake filled basin, where the remains of aquatic molluscs, and the leaves and fruits of aquatic plants have been discovered, indicating a low energy lakeshore or marsh environment (Zhu *et al*. 2004).

In the Middle Awash of Ethiopia, the Daka Member of the Bouri Formation, dated to 1 Ma, contains artefacts, *Homo erectus* cranial and post cranial bones, abundant hippo fossils, as well as gastropods and bivalves associated with alluvial, lakeside beaches or shallow water deposits in distributary channels (Asfaw *et al*. 2002).

Buia, in Ethiopia, contains *Homo erectus* fossils and artefacts dated to 1 Ma. These occur in deltaic deposits of the Alat Formation, which also contains fish and freshwater gastropod (*Melanoides*) remains (Abbate *et al*. 2004). Evidence that hominids butchered medium to large-sized bovids, hippos, and a crocodile, also come from these deposits (Fiore *et al*. 2004).

A partial *Homo* cranium from the same stratigraphic level as Acheulian artefacts from Olorgesailie, Kenya, has been dated to between 0.97 and 0.9 Ma. The sandy silt adhered to the frontal bone of this specimen contained amphibian bones and the tooth of the swamp rat

Otomys sp., which today inhabits thick grasses in and around the swamps, lakes and rivers of East Africa (Potts *et al*. 2004).

The Angolan site of Dungo V reveals evidence for the exploitation of a large whale (*Balaenoptera* sp.) on a former beach more than 0.35 Ma. Closely associated with the whale skeleton were numerous Lower Palaeolithic artefacts, together with numerous molluscs, other marine invertebrates and shark teeth (Gutierrez *et al*. 2001).

The earliest evidence for human activity in northern Europe comes from the site of Pakefield, England, about 0.7 Ma, where artefacts from estuarine silts containing marine fauna have been discovered. The majority of artefacts derive from '*Unio* bed' coastal river deposits (Parfitt *et al*. 2005).

Homo *Sites from 200 ka to 50 ka* (kilo-anni, Thousand Years Ago)

The earliest evidence for *H. sapiens* in the fossil record comes from the Ethiopian Kibish Formation in deposits dated to 195 ka. This formation consists of "flat-lying, tectonically undisturbed, unconsolidated sediments deposited mainly in deltaic environments over brief periods" (McDougal *et al*. 2005: 733). Human remains derive from essentially the same archeological level that remains of the fresh water oyster *Etheria* have been found.

Also in Ethiopia, *H. sapiens* and stone artefacts occur in the Herto Member of the Bouri Formation at 160 ka. This member contains gastropods, bivalves and (often butchered) hippopotamus bones, testifying to a waterside setting (Clark *et al*. 2003).

In Eritrea, the 125-ka-old Abdur Archaeological Site, on exposed Red Sea reefs, indicates that humans were using tools to "harvest shallow marine food resources and possibly to butcher large land mammals on the ancient shoreline" (Bruggemann *et al*. 2004: 180).

On the Mediterranean coast of Africa, the Haua Fteah site reveals evidence that *H. sapiens* were harvesting and consuming shellfish 80–100 ka (McBurney 1967), while at the coastal sites of Gibraltar (Barton *et al*. 1999) and Liguria (Stiner 1994) there is evidence that *H. neanderthalensis* was collecting and consuming shellfish.

Along the African Cape coasts there are many Middle Stone Age (MSA) sites with abundant shellfish and other marine food remains. The total number of sites may be in the hundreds. These sites are associated with some of the earliest modern human remains (see review in Broadhurst *et al*. 2002). The best known is Klasies River Mouth, where 20 meter deep shell middens occur, mostly dating to Oxygen Isotope Stage 5 (Grun *et al*. 1990, Deacon 1992). These deposits show "evidence for the exploitation of marine resources" (Thackeray 1988: 27). The shell middens associated with Blombos Cave, dated to 80–100 ka, indicate that marine molluscs were the "most abundant category of food waste" (Henshilwood *et al*. 2001: 441) and at Die Kelders the cave deposits contain "bones of seals, dolphins and marine birds" (Grine *et al*. 1991: 375).

On the Atlantic coast, the sites of Sea Harvest, Hoedjies Punt and Ysterfontein reveal evidence that the inhabitants were harvesting marine limpets and mussels (Volman 1978, Klein *et al*. 2004). Many more west coast MSA shell middens are known, but are as yet unexcavated.

The adipose tissue and organs of seals and sea birds, and the egg yolks of sea birds and turtles, which consume exclusively marine/littoral foods, are rich in DHA (Broadhurst *et al*. 1998, Speake *et al*. 1999). Cape penguins could have been scavenged or even hunted fairly easily, especially the eggs and nestlings. Collecting fresh eggs and live flightless nestling birds in a littoral environment could therefore have potentially provided the greatest amount of LC-PUFA (long-chain poly-unsaturated fatty acids) for the least amount of effort of any terrestrial food source known (Broadhurst *et al.* 2002).

Evidence from the Willandra Lakes in Australia confirms that at least by 50–46 ka (Bowler *et al.* 2003) and possibly as early as 63 ka (Thorne *et al.* 1999, but see also Bowler and Magee 2000, Gillespie and Roberts 2000, and Grun *et al.* 2000), humans were creating shell middens dominated by the fresh water mussel *Velesunio*, and hearths containing remains of the golden perch *Plectroplites* (Bowler *et al.* 1970). The earliest evidence of human occupation from New Guinea comes from uplifted coral reef terraces on the Huon Peninsula, which reveal some of the earliest (possibly 45–53 ka) examples of hafted axes known anywhere in the world (Groube *et al.* 1986).

Significantly, coastal fossil and archaeological sites older than about 125 ka are extremely rare because most coastal caves are younger than 125 ka, or have been flushed of older deposits by wave action or other erosion (Klein *et al.* 2004). Sea levels for much of the Pleistocene were lower than today, so the vast majority of Pleistocene coasts are now under water. Despite this, a number of *Homo* fossil sites older than 125 ka are known, such as the 1.5- or 1.8-Ma-old Indonesian site of Mojokerto, the whale butchering site of Angola, and the 700-ka-old Pakefield site from England. The non-coastal sites are generally associated with permanent water bodies such as rivers and lakes, that in most cases appear to have been connected, at least for a time, with the coast, for instance, Turkana, Dmanisi, Nihewan, Erq el-Ahmar, Aïn Hanech, and Pabbi Hills.

H. sapiens appears to have a strong correlation with shellfish, starting with its earliest appearance in the fossil record, and continuing throughout the Pleistocene and Holocene to modern times. Huge shell middens and evidence of aquatic exploitation are known from coasts, rivers and lakeside settings all over the world from recent times well back into the Pleistocene (see Fairbridge 1976, Meehan 1982, Shackleton and van Andel 1986, Waselkov 1987, Erlandson 2001).

The data presented here are far from complete and we acknowledge that a more detailed survey is necessary to provide a clearer picture. Yet, as far as we know, this is not an unrepresentative sketch of what is currently known about early fossil and archaeological *Homo* sites, and *H. sapiens* sites in particular from Africa prior to the last glacial. Even if there is a clear association between *Homo* remains, however, and permanent water and shellfish, this can not in itself be seen as proof that *Homo* was a water-side dweller. Other lines of evidence are important.

DISCUSSION

Several palaeontologists, adverse to the idea that part of our evolutionary history may be linked to an aquatic environment, claim that it is not parsimonious to go from land to water, and then back to land, in order to explain how we evolved running abilities.

First it should be noted that Bramble and Lieberman's (2004) idea that endurance running was a "major contributing factor" to the evolution of the human body form is not based on comparative biological evidence and is unclear in terms of the motivation and timing of key events. For example, nowhere is it detailed whether endurance running developed before or after large brains, and how these events relate to the need to obtain extra fats and proteins. It seems also unclear which *Homo* species may have been endurance runners. Despite the lack of these crucial details, the 'endurance running' model forms the basis for further research. For example, Arcadi (2006) compares wolf-like canids to Pleistocene hominids because he assumes they are "behaviourally similar" and that both are "adapted for endurance running."

In our opinion, the 'water's edge' hypothesis is backed by robust data, and is a more parsimonious model than 'open plain' models including the traditional savannah and 'endurance running' models. The waterside hypothesis is consistent with behavioural, comparative and nutritional data, as well as with evolutionary theory (natural selection, gradualism, mosaic evolution, parallelisms and convergences, and sequences of overlapping functions and niches). It helps explain typically human features that are rarely seen in open terrain cursorial mammals, such as tool use, breath-hold capacities, diving skills, nakedness and external nose.

Moreover, it provides an evolutionarily plausible explanation for our lineage's transition from arborealism to terrestrial bipedalism. Whereas comparative evidence suggests that a *direct* transition from the trees to the plains would induce a more quadrupedal form of locomotion (as seen in savannah baboons), an intermediary phase of vertical wading and climbing could plausibly explain a gradual evolution towards present-day human bipedalism (Stringer 2001, Kuliukas 2002). Other water-based scenarios, based on swimming and underwater foraging, are also conceivable, and are easily derived from climbing–wading lifestyles (Verhaegen *et al.* 2002). Although hypothetical, the wading–climbing scenario for bipedalism is not a 'just-so' construction of the kind that is used in 'open plain' arguments (Table 2), because there is comparative evidence of bipedal wading in arboreal species such as mangrove-dwelling proboscis monkeys (Figure 5) and in lowland gorillas dwelling in forest swamps (Doran and McNeilage 1997).

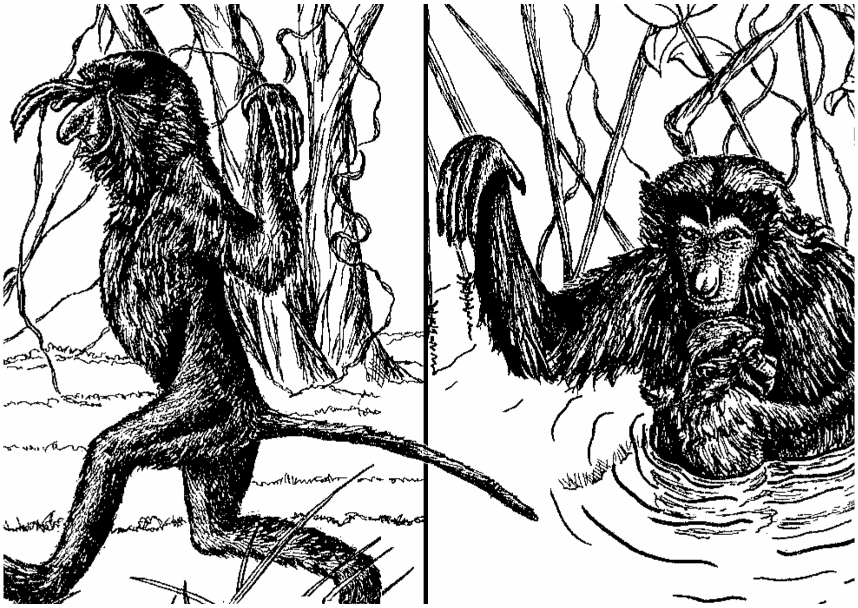

Figure 5. Proboscis monkeys (*Nasalis larvatus*) walking bipedally on land and wading bipedally in mangrove swamp (after an illustration of Amanda Williams in Morgan 1997: 65). “While wading, the monkey uses an upright posture, with the females carrying infants on their hip. Troops have been filmed continuing to walk upright, in single file, along forest trails when they emerge on land, the only non-human mammal, with the exception of gibbons and giant pangolins, known to use this form of locomotion for any length of time.” http://en.wikipedia.org/wiki/Proboscis_Monkey

Human waterside ancestors might have searched for and gathered foods from the shallow waters of flooded coastal, riverine, lacustrine, deltaic and swamp forests (Sauer 1962, Roede *et al.* 1992, Verhaegen *et al.* 2002, Wrangham 2005). They could have learnt to dip their heads under water to search for food, and could have gradually become more efficient swimmers and mobile underwater foragers (Hardy 1960, Morgan 1997, Vaneechoutte 2000).

In this scenario, ancestral human populations could have been increasingly capable of exploiting an increased range of foods from the shore and from under the water, becoming more omnivorous as they increasingly gained access to a rich source of easily obtainable nutritious foods such as insects, coconuts, shellfish, crabs, fish, frogs, eggs, as well as terrestrial, arboreal, aquatic, large and small reptiles, birds and mammals. Occasional or regular consumption of stranded whales (Gutierrez *et al.* 2001) or drowned or trampled bovids crossing major rivers could account for the instances where butchering of carcasses with shell (Choi and Driwantoro 2007) or stone tools have been described archaeologically.

In order to forage more efficiently underwater, a more alined body (with head, spine and legs all in one line) would have been an advantage, while relatively long legs could have been useful for wading, treading water, swimming, diving, terrestrial bipedalism and climbing, particularly palm trees. Present-day human running can therefore be parsimoniously derived from an ancestral body shape designed to perform a number of different activities at the water’s edge, not just at the forest–savannah interface.

And it should be emphasized again that, in order to acquire the minimum daily requirements for humans including brain-specific poly-unsaturated fatty acids, the resources associated with littoral habitats are much more easily accessible to primates than the brains of large mammals, which have to be removed from the skulls of dead animals and for which there is a fierce competition with large mammalian predators and scavengers, who are far better equipped for finding carcasses, cracking skulls and predation.

CONCLUSION

The 'endurance running' hypothesis of Bramble and Lieberman (2004) appears to have been accepted without discussion by many members of the scientific community and has largely remained unchallenged. It is one of the latest examples of the 'open plain' way of thinking, which can be traced back to the beginning of the 19th century. After the discovery of the first African fossil hominid by Raymond Dart (1925), this model was considered to be supported by hard evidence. This first australopithecine fossil was found in a region that is now a marginal desert habitat, but which was a much wetter habitat at the time of preservation. We have presented data showing that 'open plain' models are inconsistent with Darwin's theory that adaptation and analogies (convergences and parallelisms) as well as continuity and gradual functional shifts (*Natura non facit saltum*) are essential factors in evolutionary processes (e.g., Darwin 1903: 171, 82). There are a number of lines of evidence, including behavioural, biological, anatomical and nutritional data, inconsistent with 'open plain' models.

These same lines of evidence, on the other hand, fit remarkably well with the 'waterside' model. This model is consistent with all the available archaeological and fossil data. It explains much more satisfactorily the transition from tree-climbing to vertical terrestrial bipedalism, and helps explain otherwise unexpected traits such as our large brain, tool use, breath-hold diving abilities, protruding nose, alined body, subcutaneous fat deposits as well as other characteristics. These traits are often shared with waterside and aquatic mammals, but are not seen in plains- or savannah-dwelling mammals. The waterside model does not preclude the hunting, scavenging or butchering of large mammals, nor terrestrial bipedalism, but renders unnecessary endurance running over open, semi-arid plains.

Considering all we now know, the waterside model is the most parsimonious explanation for the evolution of many of the typical features in which the genus *Homo* differs from other primates. We predict that a more detailed and systematic study of the human features involved in locomotion, combined with an acceptance that wading, swimming and underwater foraging may have been important locomotor activities, will lead to a better understanding of our evolutionary past.

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