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## OUT OF AFRICA

**ABSTRACT:** *Humans were not forced, squeezed, or starved out of Africa. It was a matter of opportunity and the evolving human ability to take advantage of it. Necessary prerequisites evolved with the changing anatomical adaptations to diurnal activities, including large body size, long legs and a number of physiological changes, and what was at the time, sophisticated tool use. Key innovations include flakes used for cutting and dismembering, digging sticks, and containers. Yet the human approach to adaptation is and has been a social one as well as technological. The mobility-related morphological peculiarities of early *H. sapiens* played an important role, but their behavioural consequences took some time to emerge. It is in the organization of society, at least as much as in the evolution of technology, that we can hope to understand how the evolving human brain was the ultimate cause of that first sweep out of Africa. As humans began the colonization of the Old World tropics, they evolved a trellis of interrelationships across a broad geographical range, contrasting a centre and an edge pattern of variation.*

**KEY WORDS:** *Colonizing Species – Homo sapiens – Centre and Edge – Early Technology*

### INTRODUCTION

A number of years ago I was quoted in *National Geographic* as explaining that people first left Africa when they did "because they wanted to, because they had to, and especially because they could" (cited in Weaver 1985: 609). When this quip ended up in the magazine I began to wish I had given the comment a bit more thought. Yet, on reflection, the last part, "when they could", still rings true. It is, after all, people who became colonizers, not some Pliocene hominid species of the genus *Australopithecus* victimized by its life circumstances and limitations and a slave to environmental changes. These people, earlier members of our taxon *Homo sapiens*, were quite revolutionary in adaptation and anatomy when they appeared some 2 million years ago. Yet the best evidence is that they first left Africa more than a half-million years later. Their evolution, in other words, was necessary but not sufficient to turn humans into a colonizing species. What else was necessary but not sufficient? Why did colonization finally become a human characteristic? How

did this Diaspora affect the human species? These are the questions I hope to address here.

### WHO?

The people who first left Africa and began to spread throughout the tropics of the Old World are widely referred to as "*Homo erectus*", but is this correct? A number of scientists including this author have come to believe that *H. erectus* is not a valid species name (Hublin 1986, Jelinek 1978, Thoma 1973, Weidenreich 1943, Wolpoff *et al.* 1994). There are several reasons for this. Like its descendant *H. sapiens*, *H. erectus* is a polytypic species, continuously varying but with geographic differences that show continuity in certain characteristics over time. Within the geographic range of the polytypic species *H. sapiens* different combinations of morphological features appear commonly in different regions, but these only reflect isolation by distance and do not imply reproductive isolation (Templeton 1998). This means the internal



subdivisions of one human species, its subspecies or races, can never extend from an ancestral species to its descendant: regional continuity across a speciation involving different features in different regions, is simply impossible. So if there is reality to the observations of continuity, as I believe there is (Wolpoff 1989, 1998, Wolpoff *et al.* 1984), it follows there was no speciation.

There is another point. No region inhabited by both of these time successive species has a distinct or abrupt boundary between them. Unlike the unique events at the origin of *H. erectus*, there is nothing to mark the beginning of *H. sapiens*. New combinations of features separating earlier and later populations do not appear, as they must in every inhabited area if *H. sapiens* had a single populational origin. Instead, the characteristics of *H. erectus* and *H. sapiens* are mixed in transitional samples that are found in the later Middle Pleistocene of every region where there are human remains, but different features are mixed in different regions.

Finally, no single definition has been found that distinguishes *H. sapiens* from *H. erectus* in all regions where the fossils of both are found. Criteria that apply to one area of the world are demonstrably invalid for other regions.

The meaning of these details is that there is no speciation involved in the emergence of *H. sapiens* from *H. erectus*. No valid definition is possible because there is not a single region of origin from the preceding polytypic species. With neither clear distinctions nor a definition possible nor a recognizable beginning for *H. sapiens* as narrowly defined, these reasons combine to require that the full *H. erectus* – *H. sapiens* lineage be regarded as a single evolutionary species: *H. sapiens*.

Or at least it should be. Yet in an article by R. Flanagan (1996), I. Tattersall is cited as saying that merging the two reflects the bias and emotions we have in studying ourselves. He disagrees with the "penchant for linking everything from *Homo erectus* to *Homo sapiens* into 'one big happy family'. ... Paleontologists do not give other animals such special treatment," he notes. Perhaps this is a reflection of a paleontological versus evolutionary genetics outlook, because the highly respected evolutionist A. Templeton thinks just the opposite. He is cited as saying "we make far too much of our anatomical differences, as our fixation on trivial racial differences so often tragically demonstrates. Biologists who study, say, fruit flies know that each population can look quite distinct ... and yet they are not tempted to hastily split them into separate species. Why must we look at ourselves any differently?"

But for the question of *H. erectus* and *H. sapiens* there is something wrong in both sets of comparisons, because this issue is not about ranges of variation or about the interpretation of evolution, but rather concerns how we name species in accordance with evolutionary species criteria. The important fact is that there is no distinct beginning for *H. sapiens* as long as *H. erectus* is recognized. The earlier species can be seen merging into

the later one everywhere they both are found, and because each has some of the morphology of the other there is continued and unresolvable confusion about whether they overlap in time. Such a pattern would be unexpected if there was cladogenesis, with subsequent expansion of the daughter species and replacement of the mother one. The best solution that recognizes these facts is to cease distinguishing the earlier specimens on the lineage as *H. erectus*, and instead include them in *H. sapiens*.

Africa is the only place from which the earliest *H. sapiens* remains are known, and indeed Africa was the sole continent inhabited by the species for at least its first half million years of existence. The first African *H. sapiens*, of course, must have appeared even earlier than the first specimens that have been found, or at least identified. It is

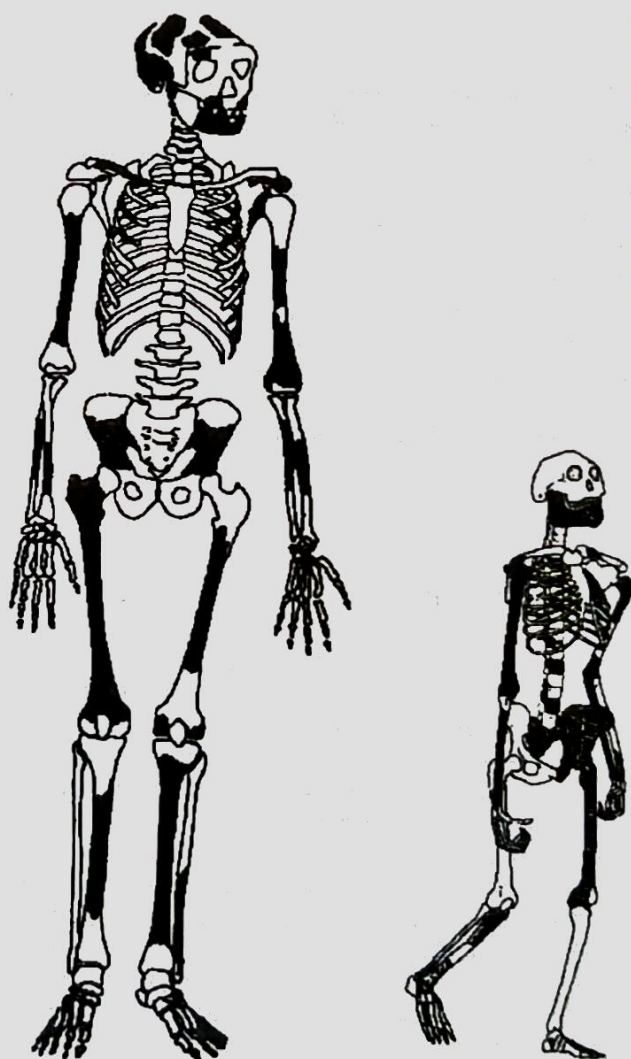


FIGURE 1. Early *Homo sapiens* is really quite distinct from its australopithecine predecessors and contemporaries. Shown here is perhaps the most fundamental dissimilarity, the dramatic size difference, in this correctly scaled comparison of the reconstructed skeletons of the two women: "Lucy", after Wood (1992), and ER 1808, after Walker *et al.* (1982).



possible that some of the Omo dental remains spanning 2.25–1.90 Myr may belong to it as well, but this cannot be determined because teeth alone are insufficient to resolve taxonomic issues within *Homo*. Other possible early examples include the Chemeron temporal (Hill *et al.* 1992), the Hadar (AL 666) maxilla (Kimbel *et al.* 1997), and the Uraha mandible (Bromage *et al.* 1995). These are interesting although incomplete specimens, and could possibly be in populations ancestral to *H. sapiens* – the species surely had ancestors. But for various reasons they are similar to australopithecines and are not diagnostically transitional between them and *H. sapiens* (Tobias 1993, Wolpoff 1998).

While speculation abounds over the number and relationships of habiline species, the hard fact is no habiline species is demonstrably earlier than *H. sapiens* (Feibel *et al.* 1989, Wolpoff 1998, Wood 1991).

## IT TOOK LONG LEGS TO WALK LONG DISTANCE

The earliest members of our species are anatomically and behaviourally unique and distinct. Brain size, for instance, was greatly expanded compared to earlier australopithecines and contemporary habilines (Begun, Walker 1993). Even the earliest *H. sapiens* are the first individuals to have a brain size relative to body size that is significantly greater than other primates of similar body size (Wolpoff 1999). But, expanded body size is their calling card and *modus operandi*.

## BODY SIZE

In fact, I believe that the most spectacular distinction of the earliest *H. sapiens* is the increase in body size (Figure 1) and change in limb proportions. The body height estimates for the earliest individuals, East Africans in the 2.0–1.5 million-year span, are close to double those of the smaller habiline variety. Weight differences are even greater. Weight should vary with the cube of height, all other things being equal. All other things are not equal, however, as early *H. sapiens* is more linear in body build:

- C. Ruff (1991) shows that pelvic widths are more constant in a given environment than limb lengths, so taller individuals have relatively narrower trunks and therefore relatively less body mass.
- Limb elongation is an allometric consequence of increased body size – heavier individuals will tend to change disproportionately and have relatively longer limbs (Ruff 1991).
- Within these constraints the maximization of body surface area relative to mass (heat adaptation) is accomplished by limb elongation (Brues 1959).

The increased linearity has implications beyond heat adaptation, which is to say that the body size changes were

for more reasons than to adapt to the tropics. After all, hominids had adapted to the tropics for a long time, and the very small bodies of the australopithecines and habilines are an effective alternative to maximizing the surface area-to-volume ratio and thereby adapt to tropical conditions. The question is “why size increase then?”

A number of scientists have suggested that the reason for the body size increase and limb elongation is a behavioural rather than a habitat change (c.f. R. Foley 1987, and others). This contention makes sense since early *H. sapiens* is found in the same habitats as much smaller habiline species. A. Sinclair and colleagues (1986) note that limb elongation would improve stride length and make it easier to follow migratory herds. P. Wheeler (1991a, 1991b, 1993) shows that even if similar limb proportions are assumed, larger bipeds are more efficient in hot and arid conditions when water resources are limited. Water resources became an important constraint, as human populations were increasingly active during the daytime – one of the behavioural changes seemingly underway at this time. Comparing two of the body sizes that Wheeler analyzed, that happened to approximate the mean weights of *A. africanus* (or *H. habilis*) and early *H. sapiens*, relative surface area decreases at the larger (e.g. early *H. sapiens*) size. The body proportions at all sizes are the same in his analysis; holding proportions constant, smaller body sizes have higher relative surface areas. However in spite of this decrease the relative sweat loss goes down, as does the total water requirement relative to body weight. Wheeler estimates the maximum daily range; this almost doubles at the approximate early *H. sapiens* size, even though body weight is only 76% greater for the sizes compared in this analysis.

If larger sized bodies of the same proportions are more efficient in water usage and have markedly greater ranges, the reader can imagine that the actual situation in which the larger bodies of early *H. sapiens* are disproportionate. Relatively longer legs in the larger bodies would make an even greater difference. Wheeler contends that a diurnal arid grasslands-activity adaptation requires proportional changes as well as increased body size because they:

- lengthen stride (more distance for the same energy),
- increase surface area/mass ratio (with increased efficiencies discussed above),
- make the whole body more linear, improving both radiation and evaporation heat loss,
- place more of the trunk in a microhabitat away from the ground, minimizing plant cover and exposing the naked skin to more breezes and cooler air.

In modelling the affects of the proportional changes, Wheeler shows (Table 1) that at the extremes, comparing the body build of early *H. sapiens* and australopithecines, water loss in early *H. sapiens* is reduced to 70–80% the value for a similarly behaving australopithecine (or habiline) of the same weight.

Wheeler's contention is that bipedalism is a necessary exaptation (c.f. Gould, Vrba 1982) for a diurnal mobility



TABLE 1. Water loss parameters relative to body size for active sweating hominids in a 35–40°C environment.<sup>1</sup>

Weight (kg)	Surface area relative to weight (m <sup>2</sup> /kg)	Sweat loss relative to weight	Total water loss relative to weight	Water consumption (kg/12hr)	Range (km. at 4% dehydration tolerance)
35 <sup>2</sup>	0.034	2.36%	3.71%	1.30	11.5
61 <sup>3</sup>	0.028	1.90%	3.10%	1.88	22.0

<sup>1</sup> From Wheeler (1993).<sup>2</sup> Middle sex *A. africanus* weight is 35.5 kg, mean weight of the smaller habiline variety is slightly less.<sup>3</sup> Mean for the earliest *H. sapiens* male and female (ER 15000 adult estimate and ER 1808) is 63.5 kg.

in an arid tropical setting. What Wheeler clearly shows is that the postcranial changes in early *H. sapiens* greatly increase mobility and the efficiency of diurnal activity in arid habitats.

There is one other aspect of the body size increase that can be explored. Hunting has only rarely been observed in primates. When the adaptation appears in a primate species, the particular characteristics shared by primates are used to develop a pattern of both behaviour and morphology that is unlike most other hunting animals. Since early hominid hunting and confrontational scavenging was almost certainly diurnal (Blumenschine, Cavallo 1992), this would accrue another advantage because most carnivores hunt at dawn or dusk and therefore would provide little direct competition (if not danger). In addition, there is every reason to believe that the early hominids were extraordinarily social, even for primates. Thus the inference is that hominid hunting was a social activity. In Africa today, the only diurnal social hunters besides us are wild dogs. These carnivores prefer game weighing approximately 55 kg or less. Therefore, it is possible that a niche for a social diurnal hunter and confrontational scavenger focused on larger prey was open in the earliest Pleistocene, and that the first hominid hunters-scavengers occupied it.

## THE RESPIRATORY SYSTEM

Independent evidence of behavioural changes derive from the fact that early *H. sapiens* faces are distinguished by broad, prominent noses, with the base of the nasal aperture greatly expanded and the nasal bone breath increased in size even relative to the base. The noses markedly project in front of the maxillary pillars surrounding them and the pillars themselves project in front of the rest of the middle face. Combined, these changes reflect a much more voluminous nasal chamber in early *H. sapiens*. R. Franciscus and E. Trinkaus (1988) relate this to important changes in nasal respiratory physiology. The changes have two functions:

– increasing the volume of inspired air,

– helping retain internal humidity by retrieving moisture during expiration.

A large nasal chamber encourages nasal inhalation and provides for the possibility of humidifying the air. The most efficient lung function requires virtually 100% internal humidity, and high activity levels in arid environments would rapidly dry the nose and have serious metabolic consequences if the air is not moistened. Franciscus and Trinkaus argue that a large nasal chamber with downward facing nostrils creates turbulence in air that is expired through the nose because it must change the direction of its flow and thereby slow significantly. Promoted by the turbulence, and by the fact that the internal nose is cool relative to the body core (where the air was at 100% humidity), moisture condenses on the inner surface, where it is used for humidifying the next breath of dry air. Franciscus and Trinkaus regard these as adaptations to high activity levels in an arid environment.

These respiratory changes can be related to the requirements of high levels of diurnal activity, and there are others. D. Carrier (1984) notes that an adaptation to efficient running required some energy-effective changes, both respiratory-related and others. While both slow and fast walking are energy efficient in terms of oxygen consumption, the energy cost of human running is relatively high in comparison with other mammals. Carrier reports that a running mammal of human size would be expected to consume about 0.10 millilitres of oxygen per gram of body mass per kilometre travelled, but running humans actually use more than twice as much. In spite of this humans are particularly good long distance runners and there are numerous reports of hunters running down animals until they are slowed from overheating or exhaustion and can be killed. Six things combined to make humans energy-effective long distance runners:

1. Breathing that is independent of locomotion. Bipedalism releases the lungs from the dictation of the expanding and contracting chest cavity during quadrupedal running, so that breathing can be faster or slower than the rate of forelimb motion.
2. Long legs. These provide more than long stride length, they maximize the amount of distance that energy is



- translated into, at the expense of speed (or acceleration).
3. Arched foot. The elastic tendons that maintain the arch in the human foot also store energy: strain energy created at foot fall is briefly stored and returned as elastic recoil during toe off, likening the foot during running to a rubber ball bouncing.
  4. Sweating. Sweat evaporation is the most efficient mechanism for dissipating metabolic heat, as many calories are used in changing the physical state of sweat from liquid to vapour.
  5. Large thyroid and adrenal glands. These glands produce some of the hormones that mobilize and control the rate of muscular utilization of carbohydrates and fatty acids. Large body stores of these, used over the period of running, extend the time before the depletion of muscle glycogen leads to fatigue.
  6. Larger lung size, reflected in a large chest cavity. In fact, the expansion by broadening of the upper part of the thoracic cage creates the barrel-shape characteristic of *Homo sapiens* but not of earlier hominid species or of any other hominoid.

## LAND USE

S. Cachel and J. Harris (1995) argue that the dramatic body size increase in early *H. sapiens* populations had immediate and important consequences in the pattern of land use. Their ideas are reinforced by the physiological and respiratory related heat adaptations discussed above. They focus on an interrelated complex of changes that include:

- much larger range, especially home range but also emerging seasonality in total range,
- expanded populations,
- the emergence of K-strategies as true dietary diversity emerges (sexual division of labour and food sharing is important here),
- reliance on technology in food acquisition and processing.

They posit that the change from a basic *r* to a *K* strategy reflects dietary diversity developing as the technology of hunting/gathering/scavenging, and of food preparation makes food more available and predictable over the course of a year. Sexual division of labour allows different food sources to be exploited at the same time. Their contention is that food becomes a limiting resource for these human populations because:

- expanded population sizes make populations more dependent on local fluctuations in the food supply,
- body fat is increasingly important in controlling female fertility.

These changes are directly reflected in the land-use pattern of the early humans. Their sites occur over broader ecological ranges and are often located farther from water sources.

## THE ROLE OF TECHNOLOGY

Ironically, one very successful adaptive innovation of early *H. sapiens* may have been the replacement of dry season use of animal protein by underground resources made possible by the invention of digging sticks. Binford's (1985) insistence that one main focus of Oldowan technology was to obtain marrow and fats by smashing bones is significant in this context, because it represents another alternative strategy to solve the problems of seasonality in resource abundance. Both of these, underground resources and bone smashing, are dependent on a simple technology that it is increasingly clear all early hominid species did not share. Even at this earliest time, and in this simplest sense, some hominids had become increasingly dependent on technology. Many, including this author, believe that a hominid dependence on technology presages a dependence on culture because, as Gamble (1993) and others argue, human technology is a social behaviour.

The important technological innovations were not wholly or perhaps even significantly related to hunting and scavenging. The technology required for effective gathering and mutual provisioning is much more complex. The use of digging sticks is a case in point, extending the range of critical resources during the season when most foods (perhaps except for fat-poor animal protein) are difficult to obtain. Some 68 bone tools were found in the three members of the Swartkrans Cave, South Africa. They are mostly made of large flakes from animal limb shafts and horn core pieces. According to C.K. Brain and colleagues (1988) three categories of tools have been recognized:

- bones whose pattern of wear and details of scratching suggest they were used as digging tools,
- similar bones whose worn areas are as described above but also covered with a fine polish,
- awl-like tools only showing wear on their tips.

The digging tools taper to a smooth point, where the wear is rounded. They are covered with numerous long scratches, with occasional prominent cross-striations. Two aspects of their use were established by Brain in a series of experiments (see Brain 1993). Similar tools were systematically used to dig up edible lily bulbs on the stony Swartkrans hillside. It was found that the longitudinal scratching and end wear came from repeatedly plunging the tool into the ground and the cross-stria from its encounters with stones. A full day of digging failed to reproduce the number of longitudinal scratches usually found on these tools and Brain and colleagues concluded that the tools were curated in that they were kept and used for several days before being discarded. Supporting this interpretation are the tools covered with fine polish. In discussing a similar bone tool from Sterkfontein Member 5, J. T. Robinson had suggested the polish might have come from rubbing the tool with a soft substance such as leather. Again relying on experiment, Brain and colleagues found they could replicate the polish by carrying the tools in



leather bags, and they suggest this was their means of transporting and curating the objects. They further posit that the awl-like tools may have been used in punching holes in soft material like leather. Finally, the persistent, unchanging tool collections in each of the three members suggests even given the shortest Swartkrans chronology, digging on this hillside was a long-lasting, seasonally specific, tradition for hominids.

Planning, the ability to project and organize future action, is an outgrowth of the hominid facility in mental mapping and can be linked to various aspects of cognition and perhaps communication in the context of culture (in the sense of Parker, Milbrath 1993). Some Swartkrans hominid left behind three elements that reflect on its cultural capacity:

- a bone and horn core culture based on the carrying and curation, perhaps in leather bags, of digging tools that were used for several days before being discarded,
- indirect evidence that this culture encoded a regular seasonal activity as a long-lasting tradition,
- the application of stone tools in defleshing animals.

The question is "which one?" A. Sillen and colleagues proposed a solution to the question about who owns the Swartkrans tools that seems most satisfactory (1995). In his ongoing Strontium/Calcium research Sillen analyzed a fragment of bone attributed to *Homo*, from the SK 847 composite skull. This specimen has a much higher Sr/Ca ratio than any of the eight *A. robustus* specimens. The geophytes (lily bulbs) that grow on the Swartkrans hillside have a very high Sr/Ca ratio. Although it is the robust australopithecines who are supposed to be vegetarians, Sillen posits that at least some of the *Homo* populations were using the bone points for digging tools to obtain these roots. They were expanding their niche to intensely collect enough of these underground resources to leave a distinct chemical marker. This reconstruction also fits data developed for the molar crown enamel thickness pattern, as the geophytes are greasy and chewy, rather than hard. The requirements for chewing them would account for the combination of thick enamel cap and thin walls on a Swartkrans *Homo* tooth reported by G. Macho and J. F. Thackeray (1990).

The idea that an omnivore might reduce its meat input and successfully expand its niche to encompass significant underground plant resources turns some of the assumptions of "Man the Hunter" upside down, but makes good sense in a seasonally dry environment. During dry seasons, when most aboveground plant resources have disappeared, is when omnivory might have been most important during the hominid yearly cycle. Yet, J. Speth (1989) has shown that the use of animal protein toward the ends of dry seasons is prohibited by the fact that fats or carbohydrates are required to digest it. The problem is that the available fat or carbohydrate resources for both hominids and their potential prey are minimal at this time in strongly seasonal environments. Early hominids shifting to hunting, or more likely to scavenging, would encounter the strongest

potential for food resource limitations on population size during this time of the year. These are the lack of predictability, the fluctuating uncontrolled supply of scavengable foods, and the danger of spending more than is gained by eating fat-depleted meats. The invention of digging sticks to obtain the nutritionally rich underground tubers and roots, the structures plants use to store their resources, would be particularly advantageous. Bone and antler artifacts that were used in digging have been identified at some Oldowan sites, but only the teeth of some *Homo* specimens show the gouged microwear that suggests grit was getting into the mouth.

If it is true that only *Homo*, and not one of the australopithecines, was able to invent this simple Oldowan technology, it reflects significant limits to the adaptability and depth of australopithecine mental processes in spite of the brain size increases shown in several australopithecine clades.

- It would imply that this seemingly simple Oldowan technology was beyond the mental capabilities of australopithecines to learn or copy.
- It would support C. Gamble's contention that hominid technology became a social behaviour when larger brained, socially more complex, *Homo* evolved.
- It would strongly suggest that the Oldowan technology from East African sites (in contrast to the pre-Oldowan) was the product of *Homo* populations.

Thus there is reason to believe that the capacity for tool use, and the adaptive functions of this behaviour, may not have been the same in all of the hominid species. The differences are not clearly apparent in the technology or tool types, but the Swartkrans evidence suggests that curation and traditions might have differed and we can look at land use patterning and other related behavioural reflections in the archaeological record as well.

This, the other important changes appearing in the evolution of technology for food preparation (and in the improvement of stone tool manufacturing skills) may also be attributed to early *H. sapiens*. These were probably causal factors in the increasing number recognizable, repeated tool types within the Olduvai sequence. Developed Oldowan tool kits include crudely pointed chopper-like tools and small scraping tools. A roughly circular tool usually showing evidence of battering greatly increases in frequency. The battering on these spheroids is thought to result from pounding foods to make them easier to chew. If so, this was a marked improvement in food preparation, the beginning of shifting it from inside to outside of the mouth.

Problems much more formidable than food preparation are met when the object of gathering shifts from snacking to food sharing, as collected foods that are very difficult to carry such as small grains, roots and tubers, insects, and so on must be separated, cleaned, and transported. Technology played a more critical role in the evolution of these and related activities than in the evolution of hunting and confrontational scavenging *per se*. Implements are



extremely important in both obtaining and preparing plant foods, while containers are important for carrying them once the pattern of eating all foods at their source is left behind. The three decisive inventions of the Lower Palaeolithic are, in my opinion:

- flakes for cutting,
- digging sticks,
- containers for carrying.

We view early hominids through our modern eyes, and have almost certainly incorrect expectations that they are little different from simply adapted modern hunter/gatherers and that the ancestral condition, as represented by chimpanzees, is near-humanity in any event. In doing so we tend to forget that these three were perhaps the most difficult of all hominid inventions. They are not part of the chimpanzee behavioural repertoire, and the best evidence suggests that hominids attained the intellectual capacity and behavioural complexity to invent and effectively use them only for the last third of their evolution. Big deal? They are a much bigger deal than one might have supposed, and in my opinion the combination is a unique behavioural hallmark of early *H. sapiens*.

The containers are ever so more complex than the other two, but absolutely critical for collecting and transporting foods that are small or time-intensive to obtain in large numbers. Containers play another role in this adaptation. The innovation of containers may have been one of the key factors resulting in the dramatic body size increases that characterized the earliest *H. sapiens* populations. Carrying a water supply provided the opportunity for long distance diurnal walking, an important element in many hunting strategies as well as in landscape scanning for scavenging possibilities. This is because of the hominid emphasis on sweating as the major heat-loss mechanism. Moreover, it is possible that by providing sufficient water during daily activities, containers helped remove the earlier small-size limitation on hominids adapted to arid or semi-arid regions. By allowing activities that are best accomplished by long legged hominids, and removing one of the factors limiting body size, the invention of containers may be the earliest case in which a technological innovation affects behavioural adaptations and ultimately leads to morphological change.

In fact, *without containers there would be no hunting, scavenging, and gathering adaptation*. Their early invention, however, is not just speculation. It is almost astonishing that there is evidence for containers at this early time. This evidence is provided by:

- The polish on the Swartkrans digging sticks – they almost certainly had to have been curated as their scratches represent several days of digging activity and Brain and colleagues (1988) suggest the polish covering many of the scratches comes from being carried in a leather bag.
- The cutmarks on some Olduvai bones which Potts and Shipman (1981) claim is in positions denoting the detachment of skin tendons.

This adaptive complex was clearly a necessary but not sufficient prerequisite for colonizations to begin.

## ACHEULEAN ADAPTATIONS

Habitat expansion is perhaps the most important consequence of the adaptive shift involved in *H. sapiens* origins. Hominids, in a phrase, became a colonizing species during the last quarter of their career, as populations expanded their ecological range into arid and highland-to-mountainous habitats, and eventually moved out of Africa to spread across the tropical and subtropical regions of the Old World (see Table 2). During this time many regional differences appeared, and populations at the edges of the human range developed regional features that in some cases have persisted into the Late Pleistocene and even recent and modern times.

Some half million years or more after the human species appeared, a recognizable change in hominid adaptation was underway, in part reflected in their stone tool industries. These changes had clear adaptive consequences and, more indirectly, helped orient the direction of morphological evolution. They can be best documented in East Africa, where the archaeological record has enough time depth for us to trace their origin and subsequent development. By the time of middle Bed II at Olduvai, a more complex, better-made tool set was being manufactured. The Acheulean Industrial Complex begins at this time and spans more than a million years, it is ultimately found across the inhabited world. It is, in the words of the late L. S. B. Leakey (speaking to a different question), the first attempt to produce decently made artifacts in "a set and regular pattern". Often lumped together with the Oldowan as the "Early Stone Age", or "Lower Palaeolithic", the Acheulean is quite unlike the Oldowan. Forms of Acheulean tools appear to have been clearly preconceived and executed with some skill by their makers, and the concept of "tool types" can be validly applied to some of the artifacts. Many Acheulean tools were made from large flakes that were first struck from cores. It has been suggested that it was this innovation of producing large flakes to be worked into tools that underlay the technological developments that followed (Klein 1990). One tool type, the biface, is the defining characteristic of the Acheulean. The most common tools, however, are the amorphous, ubiquitous utilized flakes.

The handaxe is a mirror to help understand the mind of early *H. sapiens*. Its form underwent considerable change and refinement over its long history and even the technology of its manufacture changes dramatically. These refinements are probably tied to the evolution of hand-and-eye coordination in hominids, and provide a clear reflection of its evolution. G. Isaac (1983) suggests that the complexity of its design and the precision with which it is executed can help indicate both the level of technological capability and the complexity of rule



TABLE 2. Hominid stratigraphic positions at the diaspora.

Date (Myr)	Africa	Indonesia	Eastern Asia	Western Asia
			†	
0.7	Lainyamok (0.70–0.56)	†	Jianshi	
	OH 28 (0.78–0.70), ?Yayo?	Ardjuna 9		
	Tighenif	Hanoman 13		
0.8		↓	Yuanmou	
		Sangiran 10	↓	
0.9	OH 12,22 (0.90–0.78),	S2,3,12,17, Trinil		
1.0	Bouri (Lower Dalca Beds)	S4,13a,27,31	Gongwangling	
	Buia 31	S1,5,6,9,22		
		?↓?		
1.1				†
1.2	Gomboré II (1.20–0.78)			Dmanisi
				↓
1.3	OH 34			
1.4	OH 9, Konso-Gardula			
1.5				
	ER 3883			
1.6	WT 15000			
1.7	ER 1808			
	ER 3733			
1.8				
	earliest <i>H. sapiens</i> crania			
1.9				
	earliest <i>H. sapiens</i> (ER 3228)			
2.0				

systems. T. Wynn (1993) finds importance in the two concepts that he believes to distinguish handaxes and other Acheulean implements from Oldowan tools, symmetry and what he calls spacial quantity (identification of geometric properties such as diameters and parallel sides). These are important, in his view, because they are not coincidental consequences of the reduction process but clearly indicate the intent of the toolmaker. If these ideas are valid, the modelling in the minds of the toolmakers (perhaps an extension of the earlier hominid capabilities for mental mapping) and their skill in translating this modelling into forms that can be replicated, underwent considerable change and refinement during the Acheulean span. It was at this time that humans began to expand their range and colonize other habitats and regions. There is much to be said for the ideas of workers such as Wynn who believe

that handaxe evolution is a reflection of significant mental changes incorporating generalization and conceptualization into the realm of human abilities.

The Acheulean is characterized by far more than the development and increasing frequency of handaxes. New types of tools appear, and most importantly they are treated quite differently over a much longer functional life. In the earlier assemblages, the vast majority of the tools are unmodified flakes; retouch (or reworking) becomes much more common later. Many Acheulean tools reflect more concentrated periods of workmanship during their manufacture, and were resharpened after being used. H. Dibble (1992) points out that the resharpening, the object of the retouch process, can significantly alter the shape of tools and make them seem to change from one "tool type" into another (I have seen him do this quite



forcefully, on a stage as he resharpened an elongated blade into a spheroid-shaped artifact, and coincidentally left a large scatter of debris for the next speaker to deal with). The continued retouch is a sure sign of curation. Perhaps most importantly, the retouch process shows that people were insightful about the characteristics that tools needed to have to work effectively, and recognized the advantages of taking care of and curating the tools that they made. Gamble (1993) argues that tools kept and curated attain an importance that gives them symbolic as well as functional significance. As such, they become social markers akin to language, and he contends that this marks a series of social changes that reflect the development of wide regional networks. The importance of these in colonization is described below.

The relationship of the early *H. sapiens* specimens and the Acheulean industry has long plagued east African prehistory. It is quite likely that the evolving abilities of early *H. sapiens* led to the changes in behaviour, technology-related anatomical developments, and increasingly efficient use of resources that combined to characterize the Acheulean culture. Critical to this idea is the age of the Acheulean's beginning. According to B. Asfaw and colleagues (1993), the earliest clearly dated Acheulean is from the Konso-Gardula site in Ethiopia, where its age is 1.4 Myr. This is *more than a half million years later* than the first appearance of *H. sapiens*, and these authors therefore suggest the two are not linked. They comment on the sudden appearance of the industry in east Africa, and the "surprising control over raw material and tool form" shown by its earliest manifestation there.

Therefore, the possibility of a link between the beginning of the colonizing phase of human evolution and the sudden appearance of the Acheulean in east Africa is suggestive. This is because habitat expansion within Africa was an immediate consequence of the adaptive changes that were occurring.

But why, then, did hominids finally leave Africa? Explanations that have been proposed range from the ultimate consequences of population size increases that follow from the evolving hunting/scavenging/gathering adaptation (Klein 1990), to the idea that the Sahara acted like a pump, drawing in populations when it was wet and fertile and spitting them out (presumably right out of Africa) when the climate returned to the aridity of today (Baker 1982). Yet, these mechanisms functioned long before hominid colonizations began. The difference, C. Gamble (1993) suggests, lies in the changes in human social behaviour. What we *do* know is that some half million years or more after the species appeared, there were significant adaptive changes that were associated with the spread of the Acheulean. These include:

- more effective habitat utilization,
- food resources available through organized hunting and confrontational scavenging,
- improved techniques for collecting and preparing gathered foodstuffs.

A sexual division of labour, if it was established by this time, would have allowed organized groups to simultaneously use different resources, thereby increasing the carrying capacity of the regions they inhabited and allowing expansion into new and more difficult habitats (this is a form of K selection).

Adapting by hunting, scavenging, and gathering required a wider yearly home range to take best advantage of seasonal resources. These increased ranges brought groups into contact in regular, predictable manners and from these contacts and the mate exchanges that must surely have followed, broad social networks developed. Combined, these improved the knowledge base necessary for populations to incorporate new habitats, and made them less dependent on the distribution of particular resources. Gamble argues that the new opportunities could be advantaged with fewer risks, and range expansions for *H. sapiens* was the result. It is at this time that the drier peripheries of the East African lake basins were utilized for the first time, according to J. D. Clark and H. Kurashina (1979), with highland occupations soon following. The occupied range expanded into the southernmost and northernmost parts of Africa, and as R. Klein (1990) points out, the first dispersals out of Africa may have been an inevitable consequence. Human populations had begun to successfully colonize other regions in significant enough numbers to leave archaeological and fossil records by this time. Populations spread through the tropics of South and Southeast Asia (including Indonesia, connected to the continent during periods of low sea level), and ranged eastward into central China and as far west as the western edge of Asia.

## WHY NOT EARLIER?

There is some evidence of habitation outside Africa earlier than the African Acheulean. Data from Israel are particularly convincing, but Israel is ecologically part of Africa, and of course geographically adjacent. Pliocene and Early Pleistocene (1.6–1.9 myr) dates have also been suggested for the Yuanmou incisors from China (Qing Fang 1985), the Dmanisi mandible from Georgia (Gabunia, Vekua 1995), and the earliest Indonesian hominid crania (Swisher *et al.* 1994). Yet, the Yuanmou teeth were surface finds, and subsequent biostratigraphic and geological analysis led to questioning their initial late Pliocene date estimate that was based on the paleomagnetism of nearby but unassociated sediments (Liu, Ding 1983). It is now thought they may be as young as 600–500 Kyr (Wu, Poirier 1995). Dmanisi is separated from the 1.6 myr radiometric date attributed to it by an unconformity of unknown duration. The early Indonesian dates for Mojokerto and Sangiran crania 27 and 31 may well be valid dates, but according to geologists such as Brown or paleoanthropologists such as Potts (cited in Shipman 1994) there is no reason to believe that they pertain to the



hominids that are said to be dated. For instance, DeVos (1985) noted that the earliest of the specimens, Mojokerto, was discovered in 1936 at a locality that can no longer be found and in fact was attributed to four different places only a short time after it was first reported. Its discoverer "reidentified" the site in 1975, but credibility was lost when 10 years later he returned to identify it again and associated the skull with a different layer (Shipman 1994). Moreover, according to DeVos, the *Leptobos* said to be associated with this child's head is from the Middle Pleistocene, which is half the age attributed to the cranium. The relationships of the dates to the other specimens are, if anything, even more problematic (Hyodo *et al.* 1993). The provenience of neither Sangiran 27 nor 31 is known with certainty. Scientists did not recover them and they can only be related to the dated tuffs on the basis of their colour or the matrix adhering to each, but according to White (cited in Lewin 1994) the matrix has not yet been analyzed. Without these dates, the earliest habitations out of Africa cluster in a period between 1.4 and 1.2 Myr, and postdate the earliest Acheulean.

## A PATTERN OF EVOLUTION OUT OF AFRICA

To some extent, the geographical distribution of human variation reflects the immediate consequences of the dispersals and population movements toward the end of the Early Pleistocene. It has long been recognized that differences between populations are inevitable when a species is widespread, especially when populations occupy different habitats. This is a consequence of isolation by distance (Wright 1942). E. Mayr (1963) noted that the amount of polytypism decreases towards a species border. A. Thorne (1981) suggested that this pattern applies to human populations from the Early Pleistocene, after the first colonizations out of Africa. He noted that:

- The human fossil populations sampled at what were the peripheries of the range at that time, places where many remains have been found such as Central Java, were far more homogeneous than samples from the center (eastern Africa where *H. sapiens* first was successful).
- Early populations in various peripheral regions had quite different combinations of relatively homogeneous features, often different character states of the same anatomy.
- Some of the homogeneous features at the peripheries that differed from place to place could be linked to common characteristics found in populations from the same areas today.

How did this happen? It is mainly because central populations are larger and more anatomically diverse. Since central populations have relatively higher population densities than peripheral populations and therefore often live closer together, they have less drift loss and are more often in contact and exchange genes, thereby increase the heterogeneity within them. Gene flow from other regions will be multidirectional at a species' geographic centre,

but from the centre it will be mostly outward. Peripheral populations contrast with the central ones in more:

- differences between populations in different regions,
- relative homogeneity within them.

This is the primary basis for the observation that in peripheral regions some of the features that mark modern geographic variation have been found to appear in the initial immigrants (Wolpoff, Wu, Thorne 1984, Wolpoff 1989). The first colonizing populations were probably small (Birdsell 1972, Wobst 1976). The characteristics of their gene pools were initially established by the partial isolation of numerous populations with different histories of drift and bottlenecking (Wolpoff 1989). As the more peripheral regions were colonized, populations were subject to harsher conditions and climatic fluctuations of greater magnitudes than at the centre. Numerous local extinctions and recolonizations from nearby created a population structure in which broad regional continuity could be expected. Yet, as small populations regularly became extinct, drift continued to play a significant role in regional evolution (Maryuma, Kimura 1980, Takahata 1994). The consequence was relative morphological homogeneity. This can be observed in human crania from peripheral sites with large sample sizes such as Sangiran, Zhoukoudian and later Ngandong.

An example of the homogeneity found *within* peripheral samples is in the forehead shape of the Early Pleistocene Indonesian hominids from Sangiran and Trinil. Virtually all of the specimens have a low, flat forehead with the sagittal keel on the parietal join extending onto it. There is only poor frontal boss expression and therefore a shallow supratatorial sulcus between the front of the forehead and the top of the supraorbitals. These tori are continuous and fairly straight across the top of the face, and are usually well developed at the centre over the nose. Not every specimen is identical and each of these features varies in the sample, but most of the *combination* of features characterizes all of the specimens. Most of these features appear in the African early *H. sapiens* remains as well, but the sample is much more variable in each of them and they are never found all together.

An example of the heterogeneity found *between* peripheral samples is in the face. The Sangiran faces have cheeks beginning well to the rear of the upper jaw, their base positioned over the anterior molars, and their sides angle backwards so that they do not face anteriorly. The Gongwangling (Chinese Early Pleistocene) face is quite different, the base of the cheeks being much more anterior, just behind the nose, and their angulation quite forward, producing extreme facial flatness. These are alternative character states that probably have no adaptive significance, although their anatomy was subsequently exapted into local adaptations. Thus flat Asian faces have been explained as cold adaptations and as adaptations to maximize the leverage of vertical muscle forces through the incisors, as they are most strongly expressed in living Eskimos. Yet, European Neandertal faces have been explained exactly



the same way and these are as anatomically different as possible. The point is that both Eskimo and Neandertal anatomies are used in the adaptations suggested, but these are exaptations based on pre-existing morphology whose initial variation was established by the "centre and edge" process described above.

## CONCLUSIONS

Humans were not forced, squeezed, or starved out of Africa. It was a matter of opportunity and the evolving human ability to take advantage of it. Necessary prerequisites evolved with the changing anatomical adaptations to diurnal activities, including large body size, long legs, and a number of physiological changes, and what was at the time, sophisticated tool use. Yet the human approach to adaptation is and has been a social one as well. The mobility-related morphological peculiarities of early *H. sapiens* played an important role, but their behavioural consequences took some time to emerge. It is in the organization of society, at least as much as in the evolution of technology, that we can hope to understand how the evolving human brain was the ultimate cause of that first sweep out of Africa—beginning the trellis of relationships, the evolving complex inter-regional association of populations, in the expanding polytypic species that became us.

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