Karl W. Butzer

Environment, Culture, and Human Evolution

Hominids first evolved in mosaic environments, but stone toolmaking accelerated the emergence of Homo, *and both culture and environment subsequently served as catalysts for evolution*

The social sciences were profoundly affected by the discovery of the "Zinjanthropus" skull by Mary Leakey in 1959 and the subsequent potassium-argon dating of this fossil to a hoary age of 1.75 million years. Scientific interest in human evolution took a quantum jump, and unprecedented public and private funding was made available to human paleontology and prehistoric archeology. By the late 1960s, fossil sessions drew capacity crowds at annual meetings, even though human paleontologists represent only a small minority of the American anthropology profession. The $2 million invested in the Rudolf Basin of East Africa provided an ample return in tangible evidence of early hominids, and discoveries continue with predictable certainty.

Cutbacks in funding and an apparent ebb of public interest during the past few years have resulted in part from media saturation and the often sensational and sometimes irresponsible claims made in premature press releases. More detrimental has been the preeminent concern with finding, rather than studying, fossils. Few discoveries have been usefully described in interim reports, and only one fossil recovered since 1959 has been given proper monographic treatment. Similar criticism can be voiced of the exponential increase in archeological excavations, involving

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uncounted dollars, months of volunteer labor, and numbers of sites. The net result has been material objects that are additive but that seem to provide little new information for cumulative understanding of past human activities. An overall preoccupation with classification and taxonomy, whether of stone or bone, may be attributed to the indirect and fragmentary nature of the evidence; but the resulting interpretations of prehistoric people are little more than guesswork and are focused on objects rather than dynamic communities.

The fossils and sites now available will probably still require a generation to study and evaluate. This may seem encouraging, but the nature of the recorded evidence is often inadequate to justify such an investment, and agencies willing to support fieldwork are often reluctant to finance the less spectacular but equally essential follow-up research. These two sobering facts must be remedied before interest in the human past begins to wane seriously. First, there is great need for research strategies that involve not rhetoric but implementation of multidisciplinary perspectives in all stages of a project. Second, there must be a greater share of reflection by the very people who know the materials and the sites best. Repeated assessments of the state of the art are essential if interrelationships are to be perceived and persistent problems isolated. Only then can research strategies be redesigned and better field returns achieved.

The purpose of this essay is to take another look at hominization and the human career from an unusual vantage point: context and environment. Instead of taxonomy, I shall emphasize the interrelationships between nature and culture, exploring potential environmental factors in biological evolution and cultural innovation.

Temporal frameworks

The great spans of time in the prehistoric past are difficult to imagine. The time depth of major European groups, such as the Celts, Germans, and Slavs, is generally less than 3,000 years. Earlier Bronze Age or Neolithic cultures also had a time depth of several millennia. But the Paleolithic spanned 2 million years—approximately 100,000 generations. The beginnings of prehistoric art, as witnessed by cave walls of western Europe or *art mobilier* in central and eastern Europe, probably do not go back beyond 35,000 years, and the earliest deliberate burials in certain French caves may be no older than 70,000 years. This places in perspective the incredible lengths of time over which man evolved biologically prior to the major cultural innovations that raised man to an intellectual level comparable to our own.

The first primates began to evolve as much as 90 million years ago. Higher primates underwent rapid diversification during the Miocene, ca. 23 to 5 million years ago. The Pliocene, about 5 to 1.8 million years ago, saw the dramatic evolution of two or more lineages of hominids. Archeological evidence for toolmaking *Homo* comes from the close of this period. From the viewpoint of biological evolution, the late Tertiary is of paramount significance for the adaptive radiation that led to the emergence of the hominids.

The second stage in human evolution encompasses most of the Pleistocene, often called the Ice Age. This period of strongly fluctuating climate, characterized by repeated glaciation in higher latitudes, is now widely considered to have begun 1.8 million years ago. At present, we are probably midway in an interglacial, known as the Holocene, that began about 10,000 years ago. The last glaciation,

or Würm-Wisconsin, began about 65,000 B.P. (Before Present), and anatomically modern man—*Homo sapiens sapiens*—replaced a variety of more archaic populations, including Neandertal Man, possibly as early as 115,000 B.P. in southern Africa and as late as 33,000 B.P. in Europe.

This second stage of human evolution spans the period between the first evidence of toolmaking *Homo,* ca. 2 million B.P., and the ascendance of *Homo sapiens sapiens* in Europe ca. 35,000 B.P. Biological evolution during the course of the Pleistocene involved an intricate feedback between evolution of the brain, cultural innovation, and improved skills in dextral manipulation, as well as more complex verbal communication and social organization. Changes at first were very slow, but they accelerated markedly after 200,000 B.P.

The third stage of human evolution proceeded from the intellectual plateau achieved during the course of the Pleistocene. Specifically, by 35,000 B.P., *Homo sapiens sapiens* had acquired the linguistic and social skills essential to the increasingly rapid evolution of our overall cultural heritage. Specialized and efficient hunting was now possible in adverse northern environments; new continents such as the Americas and Australia were colonized; brilliant artistic expression emerged from the darkness of prehistory; manipulation of plants and animals led eventually to their domestication; agriculture and pastoralism began to provide supplementary, then alternative, modes of subsistence; intensified agriculture allowed the creation of villages settled for a whole generation and sometimes permanently; highly intensive agriculture, supplemented by artificial irrigation, began to support multitiered economies and increasingly urbanized centers; and, finally, stratified societies allowed the development of industry and industrialization as we know it today. During the course of these 1,750 generations there developed the plethora of increasingly complex cultures and the social systems that provided the background for the political, economic, and intellectual events recorded in historical times. This historical record begins 5,000 B.P. in Mesopotamia and Egypt, 2,500 B.P. in southern Europe, and as late as the nineteenth century A.D. in some parts of the world. From the perspective of
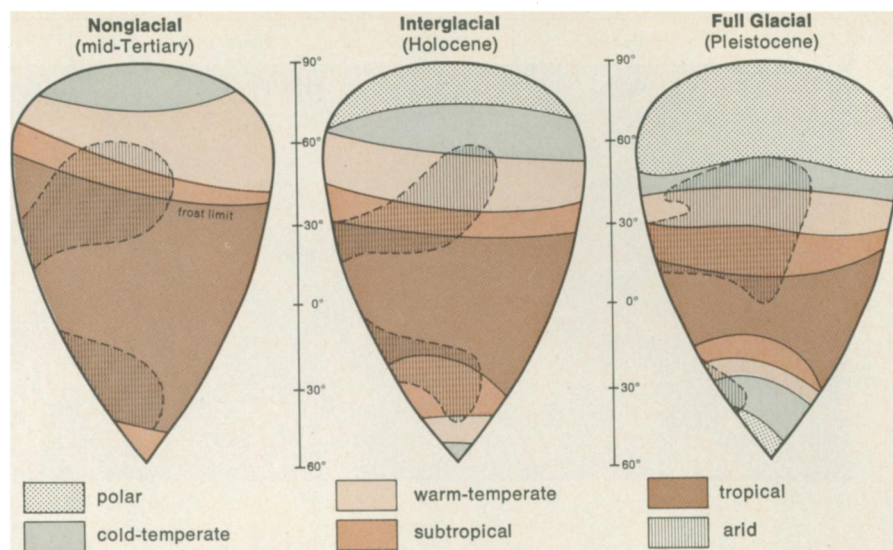

Figure 1. Descriptive models of generalized planetary climatic zonation during nonglacial (mid-Tertiary), interglacial (Holocene), and full glacial (Pleistocene) periods. Latitudinal temperature gradients were weak during the warmer Tertiary, but greatly accentuated during the Pleistocene glacials, when hot and temperate woodlands were constricted in area; modern and interglacial conditions are intermediate. (After Butzer, 1976a.)

the human past, prehistory encompasses almost 99.8 percent of the existence of mankind.

Tertiary adaptive radiation

In general, the Tertiary was a time of warm and little-differentiated climate (Fig. 1). During the Eocene, for example, subtropical or semitropical environments prevailed in middle latitudes, and even the high Arctic was temperate; glaciers were absent from the planet. Under such conditions, modern summer weather patterns prevailed even in the winter hemispheres. But cooling trends gathered momentum during the later Tertiary. Two key factors favored such cooling. The large Antarctic landmass shifted fully into polar position, where mountain ranges—the highest ones, at least—were prone to glaciation. Furthermore, the Tertiary saw repeated mountain-building, increasing the low, average continental relief of the Cretaceous.

By mid-Miocene times great mountain belts ran along the margins of the geotectonic plates, creating large zones with cool, montane climates and in many instances restricting access of maritime airmasses to the increasingly dry and winter-cold continental interiors. In this way, the planet was gradually preconditioned to mountain glaciation in high latitudes and, by the end of the Miocene or early Pliocene, to full-scale glaciation of Antarctica. Winter tempera-

tures in middle and high latitudes dropped progressively between 15 and 2 million B.P. (Fig. 2), creating a world climatic zonation substantially similar to that of today (see Fig. 1).

The warm climate prevailing in middle latitudes during much of the Tertiary favored primate dispersal at comparatively high latitudes, e.g. in the northern Great Plains of the United States during the Eocene, and in western Europe during the Miocene. However, the evolution of Tertiary higher primates can hardly be discussed in terms of generalities at a global scale. Instead, different primates probably favored different meso- or microenvironments within comparable macroenvironments. It is, therefore, at the local habitat level that paleoecological studies must be focused. In geological terms these are sedimentary microenvironments, such as a lakeshore, a sandy torrential riverbed, or an open cave. The geoecology of the major Tertiary primate localities is outlined and discussed in Butzer (in press). The geological contexts as well as the composition of the associated assemblages of nonprimate bone suggest complex mosaic environments that included a variety of ecological opportunities.

The ancestral apes found in mid-Oligocene rocks (35–30 million B.P.) of northern Egypt probably lived in a mosaic of forest and parkland, seasonally flooded by a great river, the primeval Nile, and its delta, but with open savanna vegetation on the
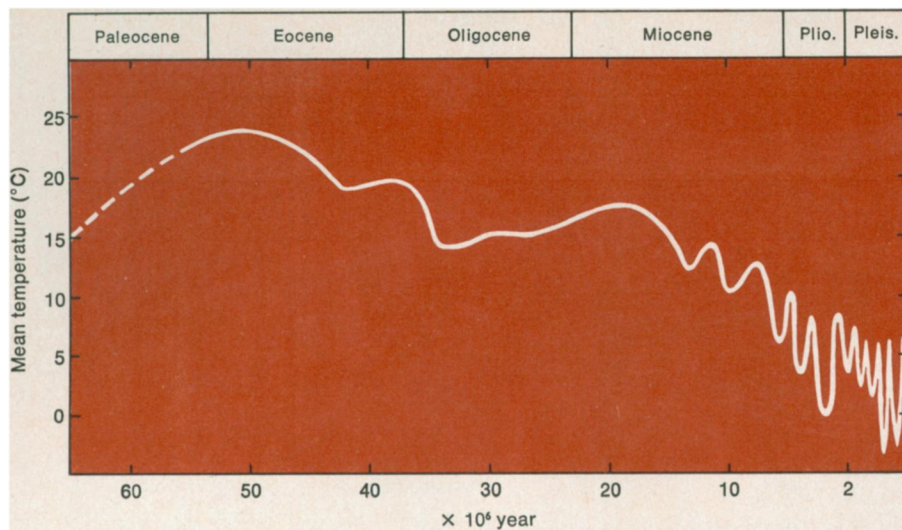
Figure 2. The trend of mean Tertiary to Pleistocene temperatures (Celsius) in middle latitudes has been generally downward, with an increasing number and amplitude of fluctuations. The scale of the Pliocene and the Pleistocene is distorted to allow for schematic representation of the rapid oscillations of temperature. (After Butzer, 1976a.)

higher land surfaces beyond the floodplain (Fig. 3). The hominoid (*hominoids* include humans, apes, and their ancestors; *hominids* include humans and their ancestors, not apes) fossils from the early Miocene (23–17 million B.P.) of East Africa come from humid drainage basins that included tropical forests and mosaics of forest and savanna, as well as perennial streams (Fig. 4). Most of the higher primates were probably drowned in or washed into flooded rivers moving through dense woodland.

In middle Miocene times (17–12 million B.P.) East Africa was significantly modified by rift-faulting. High active volcanoes lined the watersheds, and deep grabens compartmentalized the drainage into a number of closed lakes; vegetation ranged from montane tropical forests to dry grassland and bush in the rift lowlands. Rivers were highly seasonal in regime, and the lakes increasingly alkaline. Some of the higher primate fossils come from airborne volcanic ash (tuffs) interbedded with stream deposits; others come from sands or gravels laid down where streams debouched into lakes; still others are associated with abundant fish bones and were evidently carried into lakes, where they came to rest in lake-bottom muds or sands (Fig. 5). Similarly, mid-Miocene hominoids (dryopithecines) of western and central Europe were mainly recovered from sandy to gravelly river deposits of small lakes that probably were lined with abundant vegetation.

The critical late Miocene primate record from 12 to 5 million B.P. un-

fortunately is relatively fragmentary in most areas. In East Africa, for example, it is limited to isolated teeth found in deposits laid down in lakes or in the proximity of lakes in semiarid graben settings. The rocks on the Siwalik Hills of northwestern India and Pakistan record multiple rivers draining southward from the newly rising Himalaya ranges. The late Miocene Nagri beds are particularly important for the fossil record and pertain to shifting sandy channels with marked seasonality of waterflow. The associated biota speak for fringing forests and mosaics of open woodlands and savanna.

The Oligocene and Miocene witnessed the differentiation of the anthropoid apes into a number of larger- and smaller-bodied lineages, some of which may have been arboreal in their adaptations, others primarily terrestrial. The still controversial segregation of the hominid line in relation to this background of rapid and diversified evolution presumably had specific ecological determinants. Yet the fossil record, by itself, is inadequate to allow a reconstruction of this adaptive radiation: there are insufficient fossils, dietary inferences from dentitions are relatively generalized, the limb and pelvic bones are too few and incomplete, and biomechanical interpretation of the postcranial skeletal remains difficult.

Studies of modern locomotory and dietary behavior by living primates is certainly very helpful, but such analogs do not really disentangle the morass of Miocene fossils. Biomolecular investigation of living pri-

mates also provides a valuable complementary approach (e.g. Sarich and Cronin 1977) to phylogenetic reconstruction by the fragmentary fossil record and its not always exact isotopic dating. Finally, the associated faunal assemblages include a high number of extinct genera or families, and interpretation is complicated by relatively late evolution and dispersal, during the second half of the Miocene, of those cursorial forms now so prominent in the savannas.

For these reasons the adaptive radiation of Tertiary primates has been subject to much speculation, and often unwarranted inferences have been drawn from the overall geological context. Many authors, for example, propose a general arboreal adaptation for the primates, with a progressive sequence to semiarboreal and ultimately ground-dwelling adaptation for the evolving Hominoidea (see Simons, in press). Others prefer to seek hominid origins among brachiating or knuckle-walking forms. The preceding paleoenvironmental evaluation, focused on one category of evidence, does not lend support to any one theory. The geoecological data show that early and mid-Miocene hominoids were all found in complex mosaic environments. This should have generally favored ecological diversification and adaptive radiation among the rapidly evolving higher primates that shared overlapping geographical ranges.

Significantly, the dental adaptations of *Ramapithecus,* a hominoid found in southern Eurasia and East Africa, argue for grinding mastication. The association with mixed faunas, including grazers, and geological evidence for a seasonally dry, if not semiarid, environment is probably not fortuitous. This, and the preferred setting of later hominid fossils of Pliocene age (5–1.8 million B.P.) within the semiarid grabens of East Africa or the plateau grasslands of South Africa, suggests that nonleafy plant foods (such as seeds, fruits, tubers) and open habitats represented a part, however small, of the activity range of the evolving hominoids as much as 14 million years ago.

The Plio-Pleistocene: Human emergence

The Pliocene and early Pleistocene, between 5 and 1 million B.P., saw Earth cross a critical climatic

threshold. Glaciation was now commonplace, not only across most of the Antarctic continent, but in the high mountain ranges of middle latitudes as well. The botanical record from several areas, such as the Netherlands, shows that repeated long intervals of cold climate—each lasting tens of thousands of years—punctuated the overall cooling trend (see Fig. 2). Each cold interval decimated the warm temperate forests, favoring cool, steppic conditions in central and eastern Europe. At the same time, the deep-sea record of ocean surface temperature and salinity changes suggests that during each of these Plio-Pleistocene cool intervals ice caps had already developed in Scandinavia and parts of Canada. In short, the Pliocene and early Pleistocene saw impressive fluctuations of climate, accompanied by significant ecological changes, in middle and higher latitudes.

The Plio-Pleistocene record of tropical Africa does not imply cyclic climatic changes. Admittedly, lake levels or spring discharge fluctuated with considerable amplitude, and periods of humid soil development alternated with periods of reduced vegetation cover and soil erosion. There is, however, little evidence concerning temperature changes, and the wavelength of the hydrological changes is difficult to quantify and generalize. In East Africa tectonic events were of a magnitude and frequency that often overshadowed regional climatic changes. These factors help make the geological record of tropical Africa difficult to synthesize into systematic "events" that can be correlated between regions, let alone with hemispheric trends in high latitudes.

It is perhaps not fortuitous that the key focus of hominid evolution during the Pliocene and early Pleistocene was eastern and southern Africa, an area least affected by the large-scale environmental dislocations of the end-Tertiary. Here we find increasingly large populations of taxonomically diverse hominids in overlapping geographical ranges, at present documented between 27°S and 9°N latitude. These early hominids (australopithecines) occur well within the modern tropical distribution of the larger primates—in terms of climatic parameters such as radiation, temperature, and precipitation. At the time in question, these environments appear to have represented a specific
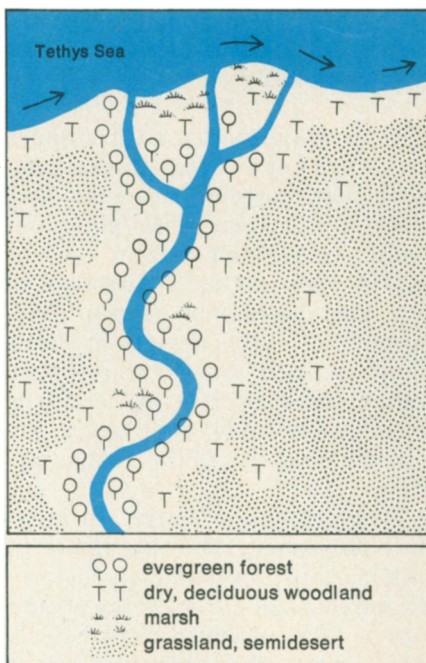

Figure 3. In this paleoenvironmental model for key Oligocene primate localities of the Fayum, main and delta channels of the primeval Nile floodplain were fringed by evergreen forest. Dry deciduous woodland and semidesert grassland lie farther removed from the channels. Fossils were recovered from channel sands and beach and longshore sands, redistributed by prevailing currents (*arrows*). (Based in part on Bowen and Vondra, 1974.)
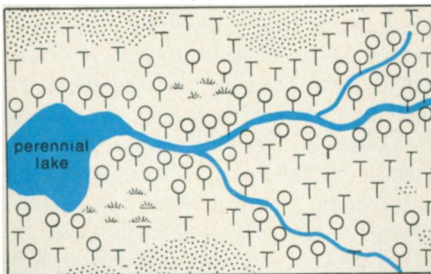

Figure 4. This model of a part of East Africa in the early Miocene can be compared with Figure 5, a model for the same area in the mid-Miocene, when grasslands were more extensive. Fossils were mainly preserved in lake and stream beds. (Based in part on Bishop, 1963, and Andrews and Van Couvering, 1975.)
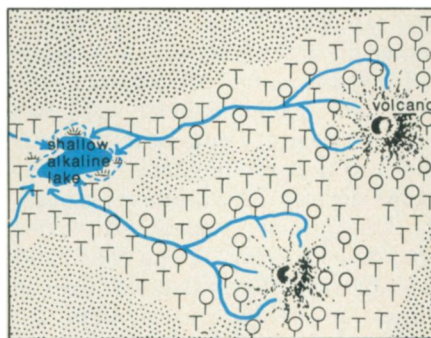

Figure 5. The shore of the lake (*dashed line*) fluctuated in mid-Miocene times. Fossils were preserved in lake beds, in former shore zones (mixed stream and lake beds), and among volcanic foothills in ash deposits partly reworked by streams. Dashed arrow indicates seasonal stream. (Based in part on Bishop, 1963, and Andrews and Van Couvering, 1975.)

segment of the tropical world to which the hominids of the late Tertiary were adapted.

Large parts of southwestern Ethiopia and northern Kenya drain into Lake Rudolf—an international body of water now called "Turkana" by Kenya, but not by Ethiopia. This basin provides an excellent record of Pliocene hominids (see Coppens, Howell, Isaac, and Leakey 1976). The oldest, rather fragmentary, fossils come from Lothagam and Kanapoi, west and southwest of the lake, from sandy channel or nearshore deposits dated 6–4 million B.P.

The most spectacular finds, from northeast of the lake (East Turkana), are widely held to fall into two basic types: one or several very robust forms of hominid, and a more gracile form, probably an early hominine. Dating of these specimens has recently been revised. The robust forms span a range greater than 2.0 million to 1.2 million B.P. The gracile forms (? *Homo* sp.) are now dated from 2.3 to 1.2 million B.P. and are widely assumed to be responsible for the important early archeological site of Koobi Fora, originally thought to be 2.6 million B.P. but now set at between 1.8 and 2.0 million B.P. by revised potassium-argon dates and new paleomagnetic cross-correlations.

The East Turkana hominids and archeological sites come from delta and stream deposits, mainly silty or sandy channels of ephemeral character, as well as from extensive delta-mouth marshes, mudflats, and shore zones that probably were seasonally dry (Fig. 6). Gracile and robust forms are not restricted to distinct microsedimentary environments. This by itself probably is significant, in the sense that the differences among hominids in the 2–3 million year time range may well have been far less important than their similarities.

Behrensmeyer (in press) makes a probable but not unequivocal case that there are many more robust australopithecines in the stream deposits than there are gracile forms, while both types occur in similar proportions in lake-margin deposits. This would suggest that robust hominids may have preferentially exploited food resources in the fringing forests of stream valleys, whereas both the robust and gracile forms favored the more open vegetation of the

shore and delta plains in equal measure. This suggests different microenvironmental adaptations, the exact nature of which remain to be determined.

Along the lower Omo River, emptying into Lake Rudolf from the north, there is a major sequence of deltaic and riverine deposits. Here the robust and gracile forms not only overlap temporally but may occasionally be found at the same sites. However, the robust forms are frequently found as partial mandibles and are primarily dated 2.4 to 2.0 million B.P., whereas the gracile forms begin between 3.0 and 2.7 million B.P. and are restricted to isolated teeth. The majority of the fossil sites are related to channels or delta distributaries of the ancient Omo (see Fig. 6), and the preponderance of robust forms appears to correspond with that from comparable situations in East Turkana. Indisputably man-made stone artifacts have been found in reasonable quantity within deposits dating 2 million B.P. or slightly older.

New fossil discoveries, of comparable age to those of the Omo, in the Afar lowlands of east-central Ethiopia, are promising. They come from lakeshore and stream deposits, similar to fossiliferous beds of the Rudolf Basin. The well-known hominid and artifact-bearing sites of Olduvai Gorge, in the Eastern Rift of Tanzania, were found in Bed I, a suite of interdigitated lake and stream deposits laid down 1.8 to 1.7 million B.P. Both robust australopithecines and an early form of *Homo* were found near the fluctuating shoreline of a large alkaline lake or along the intermittent streams emptying onto the margins of the lake basin from nearby volcanic peaks (Fig. 7). The archeological sites represent occupation loci of early humans, who not only made stone artifacts (Oldowan industry) but collected or killed a large variety of animal and aquatic foods and probably bagged an occasional robust australopithecine.

Also of importance are the similar Laetolil deposits from the adjacent Eyasi Basin, where studies suggest that relatively advanced hominids may possibly be as old as 3.5 million B.P. (Leakey et al. 1976). Another locality is Peninj, in the Natron Basin, where beds dating approximately 1.5 to 1.0 million years ago include archeological sites pertaining to the early handax technocomplex, as well as lingering australopithecines (Isaac and Curtis 1974).

The australopithecine sites of South Africa are not situated in compartmentalized tectonic lowlands, like those of the Great Rift Valley, but mainly come from ancient caverns and fissures originally dissolved in dolomitic limestones (Brain 1958; Butzer 1974, 1976b, in press, in prep.). They are, then, karst features; such "caves" first formed in relation to the groundwater table, well below the rolling high plains of the Transvaal.

In the Sterkfontein Valley, northeast of Johannesburg, the site of Sterkfontein proper represents the bottom of a former sinkhole below the upland surface. The nearby site of Swartkrans, on the other hand, was part of a complex sinkhole gradually exposed on a hillside. The third site in this area, Kromdraai, originally was a solution fissure opening below a bedrock platform. The other major site, Makapansgat, is found farther north, near Pietersburg, in a large double sinkhole then situated below the floor of a stream valley (Fig. 8). None of these sites was a typical cave and none was used as a hominid shelter. Instead, the fossils come from soil or alluvium washed into the cave from the outside, through near-vertical shafts or, laterally, through interconnecting underground passages. Study of the many subvarieties of these sediments indicates ongoing environmental change in the Transvaal. However, in each case it is likely that open grasslands were prevalent, with some trees inside the sinkholes and along the floor of the river valleys.

The age of the Transvaal breccias is known in a general way only, since isotopic dating has proved impracticable, and paleomagnetic work has only just begun. Tenuous faunal correlations that can be made with East Africa suggest three temporal groups: (1) the gracile australopithecines from Sterkfontein "Type Site" and Makapansgat "Gray Breccia" are the oldest—probably greater than 2.5 million B.P.; (2) the robust australopithecines from Swartkrans "Lower Member" and Kromdraai may be in the order of 2 million years old; (3) the *Homo* and associated early artifacts from Swartkrans "Upper Member" and Sterkfontein "Extension Site" are substantially younger than 1.5 million B.P. and in part are even Middle Pleistocene.

At Taung-Norlim, in the northern Cape Province, successive sheets of calcareous tufa were laid down in front of a major dolomitic escarpment (see Fig. 9) during the course of the last several million years. After each such travertinelike layer had been deposited, corrosion repeatedly formed deep underground fissures that were filled in, redissolved, and then refilled on several occasions. One such secondary filling that may be as young as 1.1 million B.P. contained the very first australopithecine ever discovered, the Taung "baby." The associated calcareous matrix argues that massive tufas were accumulating at this time, in response to a climate somewhat wetter than that prevalent today on the margin of the Kalahari Desert. A proliferation of baboon bones found nearby came from an older sandy deposit, reflecting somewhat drier conditions outside.

As a general conclusion it can be inferred that the South African australopithecine deposits were related to open, grassy environments with only local or scattered tree growth and to a uniform precipitation range of 600–800 mm. Despite some environmental differentiation, there is no correlation between different types of australopithecines and drier or wetter settings. Neither is there any external evidence to support the notion that gracile and robust lineages had different diets.

Thus we see that African australopithecines and the earliest hominines lived in a wide range of contexts from Ethiopia to South Africa: lakeshores, deltaic marshes, minor stream channels, river banks, upland sinkholes, and karstic fissures below valley floors or at the foot of escarpments. In East Africa most of the sites are in the deep grabens of rift valleys; in South Africa most are in the upland plains of a rolling plateau landscape. The unifying themes are that (1) the sites share a single macroenvironment— what was then a semiarid or subhumid climate, characterized by alternating wet and dry seasons and by what is generally referred to as "savanna" vegetation; (2) the sites were all at mesoenvironmental interfaces or in ecotones—between open and closed vegetation—whether along a lakeshore or a stream, or around a sinkhole; and (3) the sites would all

have been located in complex mosaics of meso- and microenvironmental opportunities— essentially potential econiches. These geoecological conclusions find explicit support in the associated faunal assemblages.

The location of all early hominid sites in mosaic environments along ecotones of the seasonally dry African "savanna" is highly interesting. It shows, for example, that the Plio-Pleistocene hominids were to a large degree sympatric, and the Miocene evidence further suggests that sympatric distributions were typical for higher primates as early as 14 million B.P. or beyond. Whatever phylogenetic lineages are recognized, hominid radiation took place rapidly during Plio-Pleistocene times but within similar overall environments.

There was, then, progressive speciation, or at least character displacement, whether behavioral, ecological, or morphological (see Brown and Wilson 1956), within a sympatric range. This implies that hominid evolution during the late Tertiary and early Pleistocene took place mainly in relation to multiple interfingering ecological opportunities. Although selective grazing by an increasing number of specialized ungulates appears to have favored the evolution of grassland or savanna ecosystems during the Miocene, there is no basis for the now time-honored hypothesis that adaptive radiation was a response to progressive environmental change. Specifically, there is no supporting evidence for a shift from a herbivorous to an omnivorous diet among any one more precocious lineage in the wake of increasing aridity and reduced arboreal vegetation during the critical period between the late Miocene and early Pleistocene. Instead, the evidence points strongly to mosaic evolution and ecological speciation of the hominids.

Presumably the cultural innovations, reflected in early stone toolmaking and animal butchery at sites such as Olduvai and Koobi Fora, would have laid the foundations (see Zihlman and Tanner, in press) for unprecedented species success, greatly accelerating character displacement. At such a point, perhaps about 2 million B.P., a polymorphic group of more evolved hominids began to diverge rapidly from other hominids of the time. By one million years ago, at the latest, these early humans had increased in
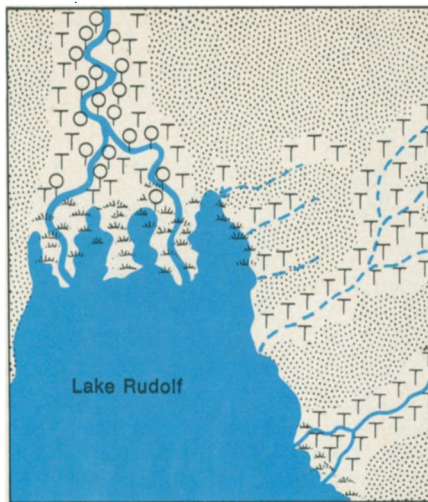

Figure 6. This model of key Pliocene localities in the Rudolf Basin of East Africa suggests conditions in the Lower Omo Valley (*top*) and East Turkana (*right*). The key fossil contexts are channel sands and flood silts of rivers or intermittent streams, delta channels and related overbank deposits, delta marsh and lagoon, low wave-energy beaches and marshy alluvium (eastern shore), and high wave-energy beaches (western shore). (Based in part on Behrensmeyer, Butzer, de Heinzelin, and Isaac, in Coppens et al., 1976.)

Figure 7. In this model for Olduvai Gorge and other lacustrine basins of the Eastern Rift, the dashed lines suggest the fluctuating shore zone and seasonal streams. The key archeological sites were originally situated on seasonally dry mudflats around the lake and in channels or on the overbank deposits of intermittent streams. (Based in part on Hay, 1976.)
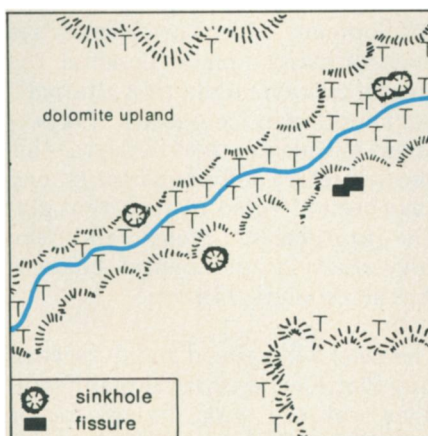

Figure 8. In a model for Plio-Pleistocene australopithecine site contexts in the Transvaal, hominid and other bone is preserved among soil washed into dolomite sinkholes and fissures. Dry deciduous woodland is found on the valley floor, where springs emerge, as well as inside the sink-holes.

numbers and had completely displaced their closest relatives, the remaining lineages of australopithecines. Whether this disappearance, during an uncertain span of time after 1.5 million B.P., was due to direct or indirect competition for resources, or even to outright aggression or predation, is at present unknown.

What exactly was the ecological differentiation between the Plio-Pleistocene hominid lineages? Here, too, the information is inconclusive. The fact that geographical distributions and even site locales were sympatric makes microenvironmental differentiation particularly difficult. The East Turkana information provides some clues that the gracile australopithecines may have preferred more open habitats than their robust relatives. But most nonarcheological, early hominid sites represent places of natural burial, or of death and burial. So, for example, isolated hominid bones found within lake beds imply an individual swept into that lake by a flooded stream, or someone bemired or drowned near the lakeshore. Hominid bone fragments in a stream channel could represent the remains of a corpse left behind on a dry stream bed or an individual grabbed from the bank by a crocodile during flood stage.

The bulk of the South African breccias were washed into deep underground caverns and the bones found in them may well represent unlucky hominids taken by leopards that ate their prey in the branches of a tree growing in or around such a doline (Brain, in press). A burial site may therefore be very near or relatively distant from the setting of most day-to-day activities of the living populations. Most nonartifactual hominid occurrences also include remains of other mammals and represent "bone traps" rather than habitation sites. With proper reservations, the information such bone traps provide is highly valuable. Strictly geological studies of such occurrences, no matter how detailed, are limited in their potential. They must be complemented by equally detailed study of the exact composition and disposition of other fossil remains, including the nature of the animal communities and those conditions determining the composition and distribution of the bones preserved in death.

At the same time, more systematic

and objective investigations must continue to be directed to interpretation of dietary and locomotory adaptations of the fossil materials themselves. Here, again, the available information is interesting but inconclusive. The basic locomotory functions inferred from the limb and pelvic bones preserved from Plio-Pleistocene contexts are more similar than they are different, although there are indeed some differences (Lovejoy, in press; Zihlman, in press).

Similarly, dental wear (i.e. abrasion and chipping) differs considerably from one specimen to another, quite apart from the age of individuals at death (see Wallace 1975). However, such differential wear does not seem to be identical for any one taxonomic grouping: instead, there appear to be more similarities among all teeth from one site and from a similar time range. As we begin to understand the theme better, the dental evidence may imply that early hominids utilized a considerable variety of food types, differing according to seasonal and regional opportunities. This is, of course, exactly what some early archeological sites such as those in Olduvai Bed I (Leakey 1971) demonstrate. The very versatility of early hominid diets makes the interpretation of dental wear difficult and may well obscure significant differences in overall dietary preferences, food-procurement activities, and foraging or hunting abilities.

The Mid-Pleistocene: Toward *Homo sapiens*

Repeated episodes of cold climate, beginning about 1.8 million B.P., are recorded in Europe by severe soil frost, by recurrent episodes of open, tundralike vegetation, and by the repeated accumulation of wind-borne dust or loess (see Butzer and Isaac 1975). By 700,000 B.P. ice-wedges began to develop in the subsoil, a process indicative of arctic permafrost conditions and implying periodic "glacial" conditions and mean annual temperatures at least 17°C colder than those of today. On a more worldwide scale, ocean surface water temperatures and salinities, as calculated from deep-sea cores, indicate that a total of 10 or more cycles of northern hemisphere glaciation began about 800,000 B.P.

Despite the indisputable significance of these glacial–interglacial cycles of
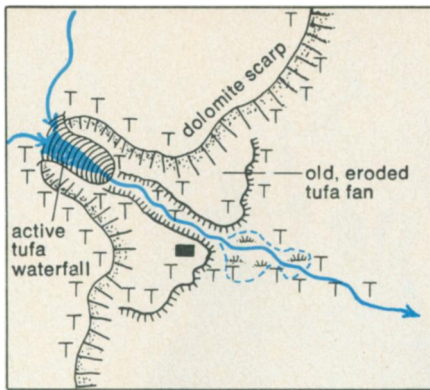
Figure 9. At a dolomite escarpment site, such as Taung, fissures erode in limestone tufa and later fill in with soil wash, travertine, and fossils. Deciduous woodland is on the escarpment and below the slopes; marsh and dense bush are downstream from the active tufa waterfall.

the last million years or so, their chronology is only imperfectly understood and their correlation with the complex range of geological imprints worldwide is generally difficult and sometimes impossible. What we can say is that the "last glacial" began at least 65,000 B.P., terminating about 10,000 B.P. An earlier major glacial terminated about 130,000 B.P., beginning as much as 200,000 years ago. These are the Last and the Penultimate Glacials, respectively. The mainly warm-to-temperate phase that began 130,000 B.P. is the Last Interglacial; that which began 10,000 B.P. is the Holocene; and that which occurred roughly 200,000 years ago is the Penultimate Interglacial.

The million years preceding the Last Glacial saw the disappearance of the very last australopithecines, the evolution of *Homo erectus,* and the first appearance of *Homo sapiens.* This same span of time also saw a very slow development of cultural capacities that ultimately made possible the human achievements first dramatically verified in Ice Age art. It is pertinent to consider to what degree this long trajectory of human history may have been affected by recurrent glacial–interglacial cycles and the large-scale environmental changes that accompanied them.

The most widespread and durable of mid-Pleistocene cultural manifestations was the early Paleolithic or Acheulian (see Butzer 1971, chap. 26; Butzer and Isaac 1975). Strictly speaking, the Acheulian is a stone-tool assemblage in which large, bifacially worked tools, especially hand-axes and cleavers, are present. In a broader sense, the Acheulian repre-

sents the material culture of prehistoric men already living near Olduvai by 1.5 million B.P. and inhabiting much of the three Old World continents by 500,000 B.P. In subsaharan Africa, the Acheulian was displaced by the "Middle Stone Age" about 200,000 B.P. (Butzer and Cooke, in press), whereas in western Europe the Acheulian progresses with few sharp breaks into material cultures such as the "Mousterian of Acheulian Tradition A," possibly as late as 100,000 B.P. The Acheulian thus represents a fundamental way of life that persisted for well over a million years and that allowed durable adaptations to a variety of tropical, temperate, and even cold environments.

The basic Acheulian toolkit includes a simple but versatile range of cutting, scraping, piercing, chopping, and pounding tools that were presumably used primarily for the butchery of animals killed or for the preparation of unsophisticated animal and vegetable products. Bones were also broken and trimmed for use as tools, and wood was worked into spears or analogous offensive weapons. Those sites that preserve animal bone indicate a heavy emphasis on large game, but chance preservation of plant remains argues that vegetable foods also were very important. The overall range of bone remains argues that hunting was still opportunistic rather than specialized, but in contrast to the record of the earlier Oldowan, there is evidence that larger and often adult animals were hunted, that hunters favored the most readily bagged forms of big game in any one area, and that dietary preferences focused attention on a generally smaller range of food sources.

It is therefore apparent that the Acheulians, who for most of the time in question were biological representatives of *Homo erectus,* were culturally distinct from the earlier australopithecines and the earliest bearers of human culture. They dispersed over much larger geographical ranges and the repetitiveness of their archeological residues suggests a strongly patterned if rudimentary human way of life. It is probable that food preferences required larger territories, and thus far fewer Acheulians could be supported in any one area than had been the case for the australopithecines. Mobility and the periodicity of seasonal activities may also have been significantly greater.

The cultural complex of the Acheulians was remarkably stable in both time and space. So, for example, the kinds of lithic innovations achieved in a few millennia by *Homo sapiens sapiens* some 15,000 B.P. took hundreds of thousands of years for the Acheulians; differences between coeval Acheulian toolkits from tropical East Africa and temperate France were less than the differences between the toolkits of any two adjacent European river valleys 10,000 B.P. A cultural heritage with so little dynamism is inconceivable among contemporary human populations. It argues for a self-regulating mechanism akin to (biological) homeostatic equilibrium (see Lerner 1954, p. 6). But it also implies a very low level of manipulative, cognitive, and organizational skills, presumably related to biological and intellectual limitations and also to the very small store of cumulative experience upon which early humans had to build.

Another aspect of the material culture is noteworthy: stone-tool assemblages do not show a unilinear progression to more varied, sophisticated, or artistic forms through time. Overall, Acheulian toolkits from 500,000 to 200,000 B.P. may include some items that are more refined than any dating from 1.5 to 0.5 million B.P.; yet, in any one area, a range of sites spanning a few hundred thousand years will as often as not show a deterioration rather than an improvement in artifactual skills. This can be best explained by small population groups (of 20 to 50 people?) that included only one or two competent stoneworkers and that were widely dispersed in space. A single group might not encounter another group for as much as a generation. Thus, if the best stone craftsman was prematurely killed in a hunting accident, the stoneknapping skills of the group would be diminished for several generations or more. Similarly, such very small and almost isolated breeding populations would favor genetic drift and the persistence of considerable polymorphism among the *Homo erectus* populations dispersed across Africa and parts of Eurasia.

It is therefore imperative to envisage Acheulian populations as hunters and gatherers, with a very simple, flexible, and self-adjusting culture system and a comparably rudimentary range of intellectual capacities, living in small groups that were relatively mobile
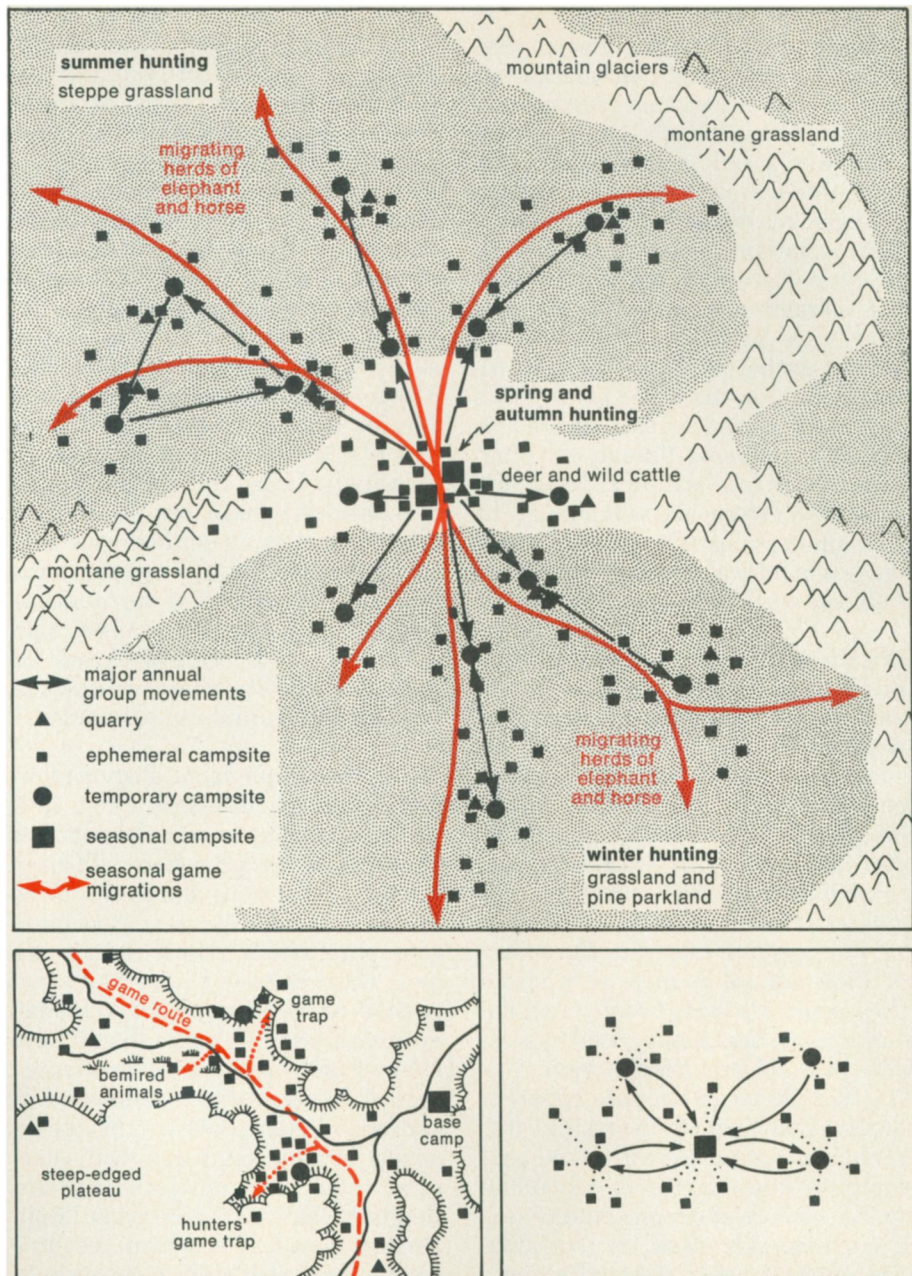

Figure 10. A seasonal mobility model for Acheulian hunter-gatherers in mid-Pleistocene Spain, based in part on information from Torralba and Ambrona. During spring and autumn the hunters preyed systematically on migrating herds forced to pass through the mountain routes (see lower left detail map),

while during winter and summer the hunters subdivided into smaller groups and fanned out into a succession of temporary sites and ephemeral camps, related to water, the whereabouts of the animal herds, and availability of flint and quarzite quarries. The mobility model is abstracted in the lower right.

and widely dispersed. Change was more often random than cumulative, and the transition to *Homo sapiens* and the progressive cultures of the Ice Age artists was painfully circuitous and slow. The price in human suffering of such an inefficient evolutionary trajectory must have been high: in the course of 1.5 million years it is probable that many thousands of Acheulian isolates disappeared without issue in marginal environments or in the face of natural events beyond their capacity to cope.

The different environmental adap-

tations of the Acheulians cannot be discerned from the surviving material culture, which exhibits little geographical variation of a functional rather than stylistic nature. A survey of the known sites from Africa, Europe, and Asia instead shows an underlying preference for open, grassy environments, with large herds of gregarious herbivores. The modern environments of such sites range from deserts to forests, but study of their geological context indicates that semiarid or subhumid macroenvironments prevailed at the time of occupancy. Such sites range from

what were tropical savannas in equatorial East Africa to what were montane grasslands in glacial-age Spain. This argues that temperature conditions were much less important than was a rich and relatively dependable supply of game. Thus the cold glacials opened up large areas of light woodland or parkland in mid-latitude Europe, greatly increasing the biomass of the large herbivores that were attractive to Acheulian hunter-gatherers. The warmer interglacials, on the other hand, saw a return of closed forests and a low biomass, reducing human carrying-capacity. In low latitudes, desert and rainforest were unfavorable. The Acheulian perspective of an optimal environment was predicated on open habitats with high animal biomass.

Within the wide macroenvironmental range of such open grassland or savanna vegetation it appears that sites were preferentially located with respect to water sources—stream channels, springs, karstic caves, lakeshores, and coasts—and suitable stone for working. It is still uncertain to what degree Acheulian groups circulated through a number of temporary or seasonal camps in the course of their annual rounds, or whether they favored a cycle based on an advantageous base camp, used repeatedly at a specific time of year (Fig. 10). Both kinds of sites are apparent in the archeological record, but it is probable that persistently used base camps were advantageous only under special ecological circumstances—e.g. a site complex such as Torralba-Ambrona in Spain, located along a marshy, low-level animal migration route through mountains separating Old and New Castille (Fig. 10).

The picture given here of small bands of technologically simple hunter-gatherers, scattered at wide intervals across the open landscapes of Africa and Eurasia, is quite compatible with the osteological evidence for considerable biological variability (especially cranial polymorphism) of *Homo erectus* in time and space. Eventually, it should be expected that if sufficiently numerous populations were isolated in a peripheral continental area or by surrounding unattractive biomes, spurts of biological evolution or cultural innovation (or both) would be increasingly likely.

Such progressive regional centers with accelerated change become evi-

dent during the last phases of the Acheulian, in the form of increasingly polytypic biological populations (representing early forms of *Homo sapiens,* according to many authors), and as a multitude of transitional material cultures. These appear to be represented by industries such as the Fauresmith, Sangoan, or Mousterian of Acheulian Tradition "A," which preceded the first appearance of increasingly complex and distinctive stone industries, such as the Middle Stone Age in subsaharan Africa and the Mousterian complex in Europe and the Mediterranean area. As increasingly large and differentiated populations spread out from their original centers, major biological and cultural discontinuities appear in the archeological record of surrounding areas where population numbers were very low or in central areas of Acheulian activity where homeostatic equilibrium had inhibited change.

Given the simple technology and organization of the Acheulians, it is probable that aperiodic fluctuations of the food resource base will have caused recurrent hardship. The question is whether repeated environmental stress or long-term ecological changes would have had a net positive or negative impact on human evolution. Overall, stress should have favored survival of the better adapted groups. In areas with diffuse concentrations of Acheulian groups, alternating sets of good and bad years may, in fact, have accelerated evolution (see Clark 1960; Hiernaux 1963). During decades in which resource productivity was high, groups would tend to multiply and disperse, at least initially favoring isolation of breeding populations, with random loss of genes (genetic drift). During decades of declining productivity, groups would abandon marginal areas and a centripetal movement, focused on the most reliable sources of food and water, would set in. At such times the remnants of temporarily isolated breeding populations would be drawn into larger regional aggregates, favoring gene flow. At a sufficiently large scale, environmental fluctuations could stimulate biological evolution through a feedback mechanism involving continued selection for ability to manipulate culture, on the one hand, and alternating genetic drift and gene flow, on the other.

It is, therefore, probable that environmental factors played a basic role

in the Pleistocene biological evolution that led to the emergence of *Homo sapiens.* In this writer's view, one prerequisite to such evolution is an unequal distribution of resources at the subcontinental scale, so that subcontinental regions will include several areas of intermediate size with a sufficient density and productivity of resource opportunities to support sizeable clusters of population groups while large intervening areas are incompletely occupied. The second prerequisite is long-term cyclic variation of resource productivity that both creates sufficient ecological stress to promote natural selection and also sets into motion alternating centrifugal and centripetal movements of dispersed breeding populations (Fig. 11), to favor genetic drift and gene flow. Such circumstances would provide potentials for rapid local change in peripheral settings (punctuated equilibrium in the sense of Eldredge and Gould 1972).

Late Pleistocene innovations

The traditional picture of late Pleistocene prehistory involves a European scenario in which proto-Neandertalers were biologically isolated in western Europe at the beginning of the Last Glacial; they evolved a number of aberrant, perhaps archaic, physical traits in the isolation and the rigorous wet-cold climate of the early Last Glacial; then, under somewhat mysterious circumstances, these "classic" Neandertalers and their Mousterian material culture disappeared, to be totally replaced ca. 37,000 B.P. by large populations of essentially modern, Cro-Magnon type coming in from the east; these new, Upper Paleolithic peoples, superior in their technological and organizational skills, developed the first cave art as early as 35,000 B.P.; this Ice Age art reached its zenith during the Magdalenian, perhaps 16,000 B.P., then withered away after 10,000 B.P. as European populations readapted their material culture to the new postglacial forest environments.

Much of this picture still applies, but the research of the last decade requires that some significant modifications be made. Some concern dating and interpretation of the European materials; others, of a more fundamental nature, concern the overall evolution of *Homo sapiens sapiens.* outside of Europe. On

present information, the Mousterian is the only Middle Paleolithic industrial complex that appears to derive without *major* discontinuities from the preceding Acheulian. In fact, classification of a number of essentially transitional industries found in France ("Pre-Mousterian," "Mousterian of Acheulian Tradition A"), which mainly date to the Penultimate Glacial and Last Interglacial, is somewhat arbitrary. The Mousterian *sensu strictu* represents a set of stone-tool assemblages suggesting greater versatility and sophistication in applying an overall technology already mastered in late Acheulian times. Handaxes were no longer important and were generally rendered in much smaller versions. Instead, a wide range of new tools, made on prepared flakes, were now produced. At their best, most of these new tools were very carefully prepared and trimmed, suggesting special purpose rather than multiple functions.

Although the stone craftsmanship exhibited at some sites is shoddy, the artifact assemblages at the major caves, rock overhangs, and open-air sites that served as seasonal or base camps are more often than not characterized by careful workmanship. This suggests an increasing number of good craftsmen who were producing new artifactual types to accommodate a wider range of activities than had been the case with their Acheulian forebears. Similar tool forms are found in northern Africa and the Near East at about the same time, but the true Mousterian of Europe includes a greater proportion and diversity of highly refined tools. The classical range of Mousterian industries is in fact restricted to Europe, and, according to some authors, to only a small part thereof: southern France and northern Spain.

The basic continuity of the Acheulian and Mousterian, on the one hand, and the archaic biological traits of the Neandertalers, on the other, could be cited as evidence of conservatism in Europe. However, the sophisticated toolkits and elaborate burial practices suggest otherwise. The Mousterians were successful hunters in the tundras and forest-tundras of the then subarctic environments. They built large tentlike structures and appear to have repeatedly used many favored sites for months at a time.

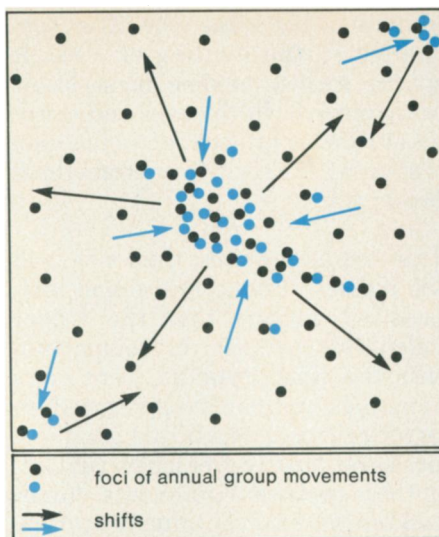In parts of France and Spain, at least

foci of annual group movements

shifts

Figure 11. Settlement patterns readjusting to Pleistocene environmental changes. The impact of *positive,* long-term climatic anomalies is reflected in the movement pattern shown in *black* and includes outward dispersal of groups to secondary resource centers, reduced pressure on local resources, more groups (with increased overall population), and linkage among distant group clusters. The effect of *negative,* long-term climatic anomalies (*blue*) includes convergence of groups to primary resources, greater pressure on remaining resources, group decimation, and isolation of group clusters.

four types of stone-tool assemblages interchange in space and time, between about 60,000 B.P. and the end of the Mousterian. They are attributed to ethnic groups ("tribes") by some authors (e.g. Bordes 1972) or assigned to distinctive seasonal or special-purpose toolkits by others. Recent studies in northern Spain show that these particular assemblages are not fundamentally discrete (Freeman, in press), but microstratigraphic sequences demonstrate that they often occur repeatedly in a cave, in both "cold" and "warm" deposits, with identical assemblages often coeval in adjacent caves (Butzer, in prep). These findings argue against an "ethnic" interpretation and also indicate that little progressive change took place over a period of 20–25 thousand years, unlike the brief 2–5 thousand-year spans characteristic of artifact assemblages during the Upper Paleolithic.

Besides the differential rates of innovation, there were other differences, too, between the Mousterian and Upper Paleolithic: there is no evidence of art, and the animal remains found in Mousterian cave middens and other coeval sites seldom include nimble-footed alpine and hillside forms, dangerous animals such as wild pigs, or fish and birds. These substantive points underscore

that the Mousterian capacity for culture was not yet comparable to that shared by all world populations since the demise of the Neandertalers (Freeman 1973; Klein 1977). There also is osteological evidence for rheumatism, inflamed sinuses, and dental abcesses. Some authors have suggested that the Neandertalers represented a breeding isolate evolving aberrantly in response to a particularly harsh physical environment (e.g. Howell 1957), but Acheulians had already confronted comparable environments successfully (Butzer 1971, pp. 460–61), and there can be no question that Mousterian technology was superior. Dispassionate analysis of the Neandertalers, their distribution and environment, and their culture deserves greater attention, since here is a tangible test case for assessing the potential systemic interplay of the critical ingredients of the prehistoric record. It would, for example, be interesting to determine whether or not the peculiar facial adaptations (large nose, enlarged facial sinuses, prognathism) represent morphological adaptations to the cold (see Howells 1974).

Modern-looking *Homo sapiens sapiens* at Border Cave in South Africa (De Villiers 1976) can be dated by extrapolation of radiocarbon-dated sedimentation rates and correlation of cold-climate roof spall horizons, and so assigned to the cold episode occurring ca. 90,000 B.P. (Butzer, in prep.). A similar physical type is represented in the Mousterian levels of Jebel Qafzeh Cave, in Israel, where it may be as early as 50,000 B.P. These fossils imply that rapid biological evolution was going on in Africa, and perhaps also in Asia, at a time when traditional Middle Paleolithic industries continued to dominate the Old World. Further archeological resolution of the center of this accelerated evolution should receive priority in future research strategies.

In Europe the Mousterian–Upper Paleolithic interface appears to date earlier in the east than in the west: greater than 44,000 B.P. in parts of the Balkans (Klein 1973), compared with as late as 33,000 B.P. in northern Spain. When and if these dates and geological correlations can be confirmed, a strong argument could be made that replacement of the Neandertalers in Europe was by no mean sudden. It is even possible that, as more precise information becomes

available, the cultural and biological discontinuities may no longer show a one-to-one correlation in Europe, in that a degree of cultural continuity may be confirmed for some areas.

Outside of Europe, the Middle/Upper Paleolithic contact still remains difficult to define with chronometric precision, but it appears to be no younger than 38,000 B.P. in the Near East and Libya, and probably older still in the case of Northwest Africa. The Middle/Late Stone Age interface in eastern and southern Africa, representing a similar but not identical phenomenon, possibly is earlier than 38,000 B.P. in Tanzania and varies from greater than 35,000 to younger than 16,000 B.P. in South Africa.

Artifactually, the early Upper Paleolithic of northern Africa is not as precocious as its age: older technological traits were preserved to a high degree, and complex, sophisticated toolkits in this region do not generally appear until after 20,000 B.P. Similarly, the Later Stone Age of subsaharan Africa was ushered in by artifactual assemblages that include few formal tool categories of any refinement; only later, about 12,000 B.P., do these industries begin to exhibit greater tool-type diversity as well as standardization. A seeming lack of sophistication among late Upper Pleistocene lithic industries also appears to be suggested for southeastern Asia. What this means in terms of environmental adaptations and human groups in tropical and subtropical environments is unclear. It may represent a shift of emphasis from lithic processing-tools to a range of hunting weapons made preeminently of perishable materials, including hafted wood-and-stone tools.

Of particular interest during the 35,000 to 10,000 B.P. time span are two phenomena: (1) the dramatic cultural advances of Upper Paleolithic peoples in Eurasia, culminating in the Ice Age art, and (2) the first colonization of the Americas and Australia (Fig. 12). The Upper Paleolithic in its classic form dates to the second half of the Last Glacial and belongs to a group of peoples ranging across a belt of cool to very cold, mainly grassy environments, from Spain and France in the west, across central and eastern Europe, eastward beyond Lake Baikal, and southward into southwest Asia. More than anything else, these people were

hunters of big game who often specialized in the hunting of a single species, such as reindeer, horse, bison, or mammoth. Both caves and open-air sites were utilized, and elaborate tent or hutlike shelters are sometimes preserved.

The number of sites, their size, and the masses of bone refuse and artifacts all suggest that the Upper Paleolithic peoples, in comparison with the Neandertalers, were more numerous, probably aggregated in larger groups, and utilized good site locales repeatedly over longer periods. In these cooler environments, stone-tool innovations continue to appear, suggesting unusual stylistic and technological sophistication, while the cave art, primarily associated with the Magdalenian (ca. 19,000–13,000 B.P.), speaks eloquently for artistic competence and esthetic values in no way inferior to ours. The turnover of stone industries was relatively rapid—a few millennia only, comparable to the half-life of late prehistoric to historical European cultures. This all argues for intellectual capacities and cultural systems similar to those of modern peoples.

It is probable that the Upper Paleolithic hunters lived well at the expense of the high game biomass of the subarctic to cold-temperate grassland belt then spanning Eurasia. It is also likely that a degree of biological microevolution continued during these 25 millennia of ongoing cultural innovation, e.g. reduced face size linked to better food processing. Nonetheless, life continued to be as precarious as it had always been for Pleistocene hunters: less than half of 76 related skeletons studied from Eurasia had reached the age of 21, and only 12 percent had passed the age of 40.

The adaptational capacities of *Homo sapiens sapiens* during the late Upper Pleistocene can be inferred from the successful colonization of the New World continents. By 33,000 B.P. some groups coming from the tropical rainforest islands of central Indonesia had already adapted themselves to lakeshores in the semidesert of interior Australia. Whether they came directly across the Timor Straits or indirectly, via the Banda Sea and New Guinea, the ancestors of the first Australians had to navigate long stretches of open water.

In the case of the Americas, the first

human settlers had to traverse the harsh and rugged environment of northeastern Siberia, crossing the exposed Beringian shelf dryshod or via the winter pack ice, to regroup on the Alaskan-Beringian tundras (prior to 27,000 B.P.), and then penetrate southward between the glacier front and the Rocky Mountains. The very first colonists may well have completed such a slow migration by 25,000 B.P., although the rapid dispersal of the Paleo-Indians across the United States and down the mountainous spine of the Americas to Tierra del Fuego that began about 12,500 B.P. took less than four millennia. The rapidity and apparent success of the Paleo-Indian movements, across almost the full range of available world environments, was perhaps the most impressive feat of Pleistocene man. It argues not only for viable subsistence modes but also for organizational talents, initiative, and a flexibility in no way inferior to those displayed by the western European nations during that other great Age of Discovery that began during the fifteenth century A.D.

In the last decade or so, a number of authors have raised the question whether Upper Paleolithic peoples were in fact too successful—whether they may, in fact, have hunted some animals so intensively as to bring about their local or total extinction. It is a well-known fact that, depending on the area, many genera or species, such as the mammoth, woolly rhinoceros, bison, horses, and several antelopes, as well as some archaic forms (in North America), died out during the late Last Glacial or during the first millennium or two of the Holocene. No reasonable proof can yet be devised that human predation was responsible for the demise of any one species, although there is a close correlation between significant environmental changes at the close of the Pleistocene and the disappearance of certain animals. Nonetheless, it is important not to underestimate the possible role of man in accelerating or implementing the extinction of forms whose population levels were already precarious as a result of environmental stress (Butzer 1971, pp. 503–12). Study of this theme continues not only in the northern hemisphere but also in other areas such as South Africa (Klein 1977). The question of man-animal relationships signals a first case where reciprocal man-land interactions assume potential importance.
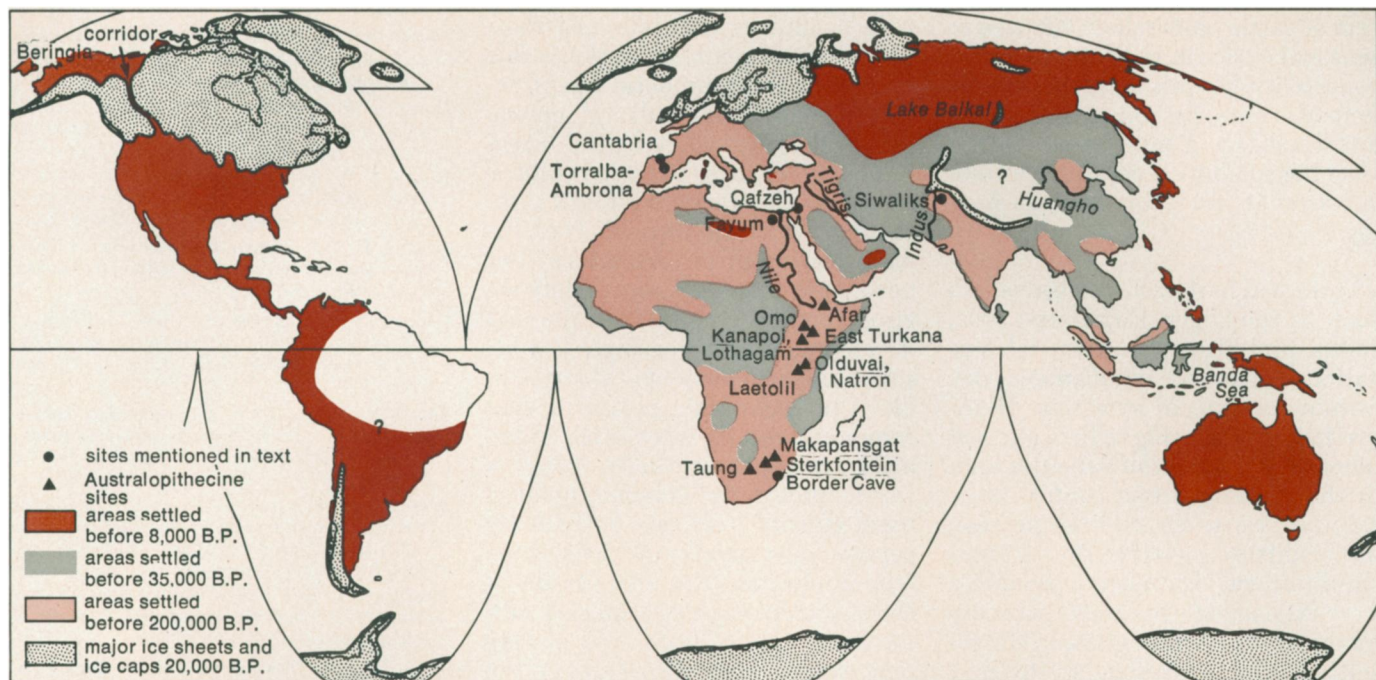
Figure 12. Expansion of the inhabited world during the course of the Pleistocene.

Postglacial adaptations

The postglacial—or Holocene interglacial—has so far lasted some 10,000 years. Oscillations toward a warmer climate were already apparent during the late Last Glacial: the continental glaciers began a gradual retreat, thermophile vegetation moved into higher latitudes or altitudes, and ocean surface waters warmed up. The temperate Alleröd oscillation ca. 11,500 B.P. gave a glimpse of the new interglacial to come, only to be cut short by a last millennium of cold and glacial readvances ca. 11,000 B.P. By 10,300 B.P. glaciers everywhere began their final retreat, with the Scandinavian ice sheet disappearing ca. 8,500 B.P., and the residual Canadian ice caps some 2,500 years later.

Two major cultural phenomena deserve to be singled out during the Holocene. One is the readaptation of hunting peoples to the significant expansion of woodland, in both high and low latitudes, as interglacial conditions returned and created warmer environments in Eurasia and North America, or wetter environments in the inner-tropical zone. The other major event was the first domestication of plants and animals, a process leading to a sequence of comparatively rapid cultural evolution from sedentary agriculture to intensive irrigation-farming, urbanization, and, ultimately, industrialization. The cumulative impact of both changes in basic lifeways was

dramatic, but both the environmental and cultural changes were gradual and evolutionary, not revolutionary.

In Europe, the readvance of the woodlands began early in the Late Glacial, leading to a reduction in the carrying capacity of large areas for grassland-adapted forms. Overall, the biomass of large herbivores was sharply reduced when closed woodlands became firmly established. However, like the warm-up of the North Atlantic Ocean or the retreat of the ice sheets, this vegetation shift across the European continent took 4,000 years or more, ample time to allow for satisfactory readaptations by hunting groups that had the basic ability to cope with the range of North and South American environments. The evidence suggests that aquatic and vegetable food resources now received specialized attention, with a gradual concentration of settlements along seashores, rivers, and lakes. Whether or not overall population densities were reduced, it is reasonable to assume that smaller groups would be more successful, now that the large herds of open-country grazers had disappeared.

In Africa it is possible that woodland adaptations were first made during the Last Interglacial. However, high lake levels and accelerated spring activity from about 10,000 B.P. saw the rapid rise of aquatic cultures, with prominent archeological traces, in the lake basins of East Africa and along

ponds and seasonal streams across the Sahara. Both in Europe and Africa these aquatic cultures, and their parallels in the woodlands of eastern North America, maintained themselves successfully until displaced by advancing farmers or pastoralists many millennia later.

The origins and dispersals of agriculture are beyond the scope of this paper, but some basic implications deserve to be enumerated. Archeologically definable agricultural societies were probably established in much of southwest Asia and the Aegean sphere during the tenth millennium B.P. By 7,500 B.P. the new subsistence system, based on crop-planting and livestock-raising around essentially permanent village settlements, had been successfully developed to the point that long-term population increases were possible and a major wave of migration and colonization was set in motion. Farmers spread rapidly from Greece into the forest-steppe of southeastern Europe and northward into the temperate forest belt. Resident hunting groups were displaced, absorbed, or acculturated. Significant landscape change resulted as native faunas and floras began to be replaced by domesticated stock and cultigens. The hydrologic cycle was disturbed and soil erosion initiated. The heavy hand of civilization had been laid on the environment.

Even in the arid environments of North Africa herders began to move

along the desert valleys into the less barren highlands, developing a system of cattle pastoralism adapted to seasonal cycles in pasture and water availability. Surprisingly, these cattle nomads were established prior to 8,000 B.P., i.e. a millennium earlier than the adaptation of an agricultural subsistence mode in the Nile Valley.

The die had been cast. In river valleys such as the Tigris-Euphrates, Nile, Indus, and Huangho, artificial irrigation began to supplement dry farming or natural irrigation. High-productivity farming in turn allowed increasing population densities and, in the growing urban centers, specialized craftsmen such as potters, metalsmiths, woodworkers, and shipbuilders. Industrial products were exchanged over great distances by the new merchant class. In the resulting urban societies, multitiered economies and complex social stratification were the rule, not the exception. These in turn supported the increasingly large political superstructures that dominated ancient history.

The bulk of the world's population was now sedentary and concentrated in high-density areas and large cities made possible by intensive agriculture, industry, or commerce. The diet of the mass of the people consisted of agricultural products—starches and grain proteins—and it appears that a new trend of microevolution favored smaller teeth with less complex cusp patterns more resistant to caries. At the same time, poor sanitation and overcrowding created endemic centers of contagious disease, the long-term result of which was selection for populations better-adapted to high-density settlement. In this way cultural innovations have continued to favor microevolution, up to the industrial revolution and into the twentieth century.

In the perspective of the last two million years, culture and biological evolution have been inextricably interwoven. This interrelationship is a logical one, since culture serves to mediate between society and environment. Our Acheulian ancestors already attempted to circumvent environmental limitations, via culture, in expressing different dietary preferences than the australopithecines and in colonizing both drier and colder environments. Culture, instead of obviating the role of biological ev-

olution, acted as a catalyst.

In the general context of the Pleistocene it appears that adaptations to new environments, or periodic and long-term environmental stress, involved concomitant cultural innovation and biological evolution. Environmental changes triggered cultural responses that favored biological evolution, which in turn affected the biological capacity for culture. The peculiar human tendency to defy environmental constraints saw the slow development of increasingly flexible subsistence settlement systems. Unlike the ecological speciation that commonly results when other mammals expand their ranges into new environments, the common bond of basic culture has been sufficiently pervasive to maintain the unity of the human species. The ascendance of *Homo sapiens sapiens* coincided with the perfection of a cultural system that, despite many variations on the theme, has been shared by all peoples since. Macroevolution has been overshadowed by microevolution while this cultural system was rapidly elaborated in its details. But the system itself has proved as durable in human terms as the internal combustion engine has in automotive engineering.

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