Paleoecology of Early Hominidae in Africa
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As Swedlund (1974:526) has noted, "the under-standing of how early man lived, where he lived, what he ate, and who ate him is exciting." As such, being both exciting and paleoanthropological, hominid paleoecology has been a fertile area for conjecture, hypothesis and model-building.

In this paper all of the African upper Neogene hominid sites are reviewed in terms of the geological, paleobotanical, invertebrate and vertebrate paleon-tological and archeological evidence relevent to recon-structing early hominid paleoenvironments. Past hypotheses on the major topics of hominid paleoecol-ogy are summarized and the current statuses of these are reviewed on the basis of the data now available.

Physical Environment

Determination of the physical environment in which early hominids lived is an essential starting point in paleoecological investigations. Unfortunately, until re-latively recently, concerted attention has not been paid to this aspect of hominid evolution and data relative to the reconstruction of temperature, rainfall, geomor-phology and flora were gathered as incidental to the main task of recovering hominid remains. ·

Dart (1925) in the first description of *Australopithecus africanus* from Taung, South Africa, considered its environmental context to have been an "open veldt" (p. 199). The basis for this contention was the site's geographic proximity to the Kalahari Desert and the extrapolation (from Rogers 1922) that then, as now, the region was "a vast open country with occasional wooded belts and a relative scarcity of water" (Dart, 1925:199). Rogers (1922) had concluded from primar-ily lithological, topographic, and floral and faunal evi-dence that during post-Cretaceous times "the climate of South Africa has fluctuated within rather narrow limits" (p. 21).

Dart's assessment of the environment at Taung did not go unquestioned. Keith (1931:114), who consi-dered the Taung specimen to represent a juvenile anthropoid not particularly closely related to man's ancestry, cited a Prof. Schwarz as having found "clear evidence of former fertility" after "a close study of the Kalahari." On this basis and on his firm belief that Taung was an ape, Keith (op. cit.) stated that at one time South Africa had been covered with "jungle," an environment "that suits anthropoid needs."[1]

Keith's (1931) critique was most systematically coun-tered by Broom and Schepers (1946) who: 1) reiter-ated the now prevalent view confirmed by finds at Sterkfontein that *Australopithecus* was a hominid and not an ape, 2) reviewed Schwarz's contention that Bechuanaland had had *slightly* greater rainfall (ca. 5" per year more than at present; see [1] below) and noted that no geologist had characterized the area as "forested," 3) stated that the evolution of indigenous South African desertic succulent plants indicated that the area had been "mainly desert for many millions of years," 4) adduced faunal evidence from Taung, un-available to Keith, to show that Taung had been "prac-tically desert." Fourteen faunal taxa were listed, in-cluding several species of desertic rodents (e.g. *Pet-romys, Thallomys*).

The monograph on the gracile australopithecines by Broom and Schepers (1946) did not discuss the paleoenvironments at Sterkfontein or Makapansgat. Treatment of the topic in the Broom and Robinson (1952) monograph on the Swartkrans robust aus-tralopithecines is limited to one paragraph, the conclu-sion of which is:

> "The countryside, even a million years ago, is not likely to have differed much from what it is to-day, though there was possibly a somewhat heavier rainfall and a little more vegetation. But of course anything like dense forest conditions were, we consider, very im-probable."

The data on which this statement rested is not pre-sented.

Bartholomew and Birdsell (1953), in an early impor-tant article, did not discuss the physical characteristics of the environment which they reconstructed for the "protohominids." However, the general opinion that the South African australopithecines lived in dry savanna or savanna-grasslands seems to have persisted (viz. Hewes 1961; Washburn and Howell 1960, and references cited therein).

Brain (1958) first examined the primary geological evidence for the paleoenvironmental conditions per-taining at the Sterkfontein Valley australopithecine cave sites at the time of their deposition. At the Sterkfontein site Brain interpreted a predominance of quartz grains in the middle cave breccia and the pre-sence of unweathered dolomite blocks (pp. 69-70) to indicated a dry phase. He hypothesized that rainfall dropped from 30 to 20 inches per annum. At Makapansgat, another site which yielded the gracile *Australopithecus africanus*, Brain found that the sand porosity indicated a "dry outside climate" although the cave environment itself was wet (p. 115).

The Swartkrans and Kromdraai sites, which yielded *Australopithecus ("Paranthropus") robustus* remains, were

interpreted as having accumulated during conditions wetter than today. Sand grains at Swartkrans were less angular, the measured porosity of the sand grains was larger and the few dolomite blocks were heavily eroded (pp. 84-85). Kromdraai was considered to have been deposited under rainfall conditions of around 40 inches per year on the basis of sand grain angularity (by comparison with modern day analogs) and the low occurrence of quartz grains in the breccia (p. 98). These environmental reconstructions were to prove of importance in initial attempts to reconstruct early hominid paleoecology and in larger questions of australopithecine systematics, to be discussed below.

Diet

Determination of diet is central to the construction of a model of early hominid paleoecology because it bears directly on hominid trophic levels and subsistence behavior. Dietary hypotheses have in fact played a large role in discussions of early hominid evolutionary ecology and interspecific relationships (Robinson 1954, and see below; Bartholomew and Birdsell 1953; Hewes 1961; Schaller and Lowther 1969; Todd and Blumenberg 1974; Cachel 1975) even though to date reliable data on actual early hominid diets have been virtually non-existent. Basically, three methods of proof have been used in support of dietary hypotheses: archeological, morphological and primatological.

Supposed archeological evidence in the form of bovid post-cranial bone "tools" with damaged condylar ends was considered by Dart (1949) to indicated the existence of a "predatory implemental technique" in South African australopithecines. Baboon crania with depressed fractures as well as other recovered animal remains were considered the prey of these early hominids (Dart op. cit.; Broom and Schepers 1946). Dart (1953, 1964) and others (e.g., Ardrey 1961, 1976) have continued to regard the australopithecines as carnivorous man-apes even though the evidence of the "osteodontokeratic" tools and preserved archeological bone remains has been shown convincingly to be spurious (Brain 1969, 1972; Sutcliffe 1972; Klein 1975) on both archeological and taphonomic grounds. Recent research by Brain (1976, 1977) and Vrba (1977) on the faunal remains of the South African cave infillings, however, indicates that only some of the later accumulations, such as Kromdraai B and Swartkrans Member 2, preserve small-sized prey suitable to have been hunted by hominids. Dart (1965:56-77) provides an interesting listing of possible components of australopithecine diet, based on a Bantu ethnological analogy and present South African biota.

Archeological evidence from East African early hominid sites relevant to diet comes from East Lake Turkana, Lower Member of the Koobi Fora Formation (FxJj3, Isaac 1971) and Olduvai sites FLK N (level 6, Bed 1) and FLK N, Bed II (M.D. Leakey 1971).

These occurrences date from approximately 1.8 to 1.5 m.y. BP and preserve stone tools in association with animal bone remains (a *Hippopotamus* skeleton at East Lake Turkana, and elephant and *Deinotherium* skeletons at the Olduvai sites). These data imply meat-eating with use of tools by at least one form of hominid at these sites. L. Leakey (1959) on the basis of broken bones of birds, snakes, frogs and juveniles of larger animals suggested that the robust *A. boisei* at Olduvai Bed I ate only small animals since he considered that it had not been a "skilled hunter."

Robinson (1954, 1956, 1961, 1962, 1963, 1969, 1972) has discussed two morphological adaptations in robust and gracile australopithecine cranial, mandibular and dental patterns, which he attributed to dietary differences, i.e. herbivorous diet in the former and carnivorous/omnivorous in the latter. On the basis of Brain's (1956) work the robust form was considered to have inhabited wetter, more vegetated environments than the gracile. Robinson initially applied his hypothesis to the South African australopithecines but similar robust and gracile morphological modes can be seen in East African early hominids (cf. Pilbeam and Zwell 1973; Howell 1977). The dietary hypothesis, if true, can be expected to apply equally to these populations. Groves and Napier (1968) compared mesio-distal measurements of molar and incisor rows in a number of extant and fossil (cast) hominoids. They conclude that molar length increases as fruit content in the diet increases and, in agreement with Robinson's findings, that the robust australopithecine "showed distinct adaptations to a coarser, more intensely vegetarian diet than other hominoids" (p. 274).

A more particularistic morphological approach has been used by Wallace (1974, 1975) to reconstruct early hominid diet based on microwear and striations of the dentition. Wallace (1973) first disproved an earlier contention put forward by Robinson (op. cit.) and modified by Tobias (1967) that gracile hominid teeth showed larger and less numerous pre-mortem chips than robust australopithecines. This pattern was interpreted to mean that the gracile forms had eaten meat and had accidentally cracked their molar enamel on bones, whereas the robust froms had suffered only minor chipping due to the grit in their mainly vegetarian diet. Wallace showed that the larger chips were post-depositional and that the supposed trend was not statistically significant. Approximal grooving of post-canine teeth, according to Wallace (1974), indicated substantial grit in the diet or drinking water and he found no wear of this type in South African australopithecines. The worn surface enamel of occluding teeth indicates the nature of the diet: shined and deeply sheared facets indicate soft food, and less deeply worn facets imply harder food which prevents opposing from meeting one another directly. Again Wallace (1975) found no difference in this respect in robust and gracile South African australopithecines,

though he did find wear differences in the incisors implying different diets of these two groups. Robust hominids have horizontal wear planes whereas gracile hominids show an upward bevel on the upper incisors.

In another morphological study stressing the total pattern of the early hominid dentition, Szalay (1975) considers the thickened molar crown enamel of hominids to be indicative of a bone crushing function. He further hypothesizes that the "strong, vertically implanted incisors plus incisiform canines become the tools which grasp and tear meat, tendon and fascia" (p. 423). Similar viewpoints on the function of the incisor region have been put forward by Gregory (1916) and Every (1970).

Various analogical studies have utilized primatological observations to extrapolate to early hominid dietary capabilities. Jolly (1970) proposed that early hominids had a feeding adaptation to seeds, a conclusion based on certain dental and morphological similarities to the extant *Theropithecus gelada*. Szalay (1975) pointed out that it is inconsistent to suggest that the anterior teeth of geladas and hominids are similar because of seed-eating while the molars of these two species, which actually process the food, are quite different. Wallace (1975) saw no evidence in tooth wear that any South African early hominid (and especially the robust species, Jolly's assumed early hominid morphotype) had eaten more "small, hard, solid objects" than any other.

Observations of meat-eating and a crude from of "hunting" by chimpanzees (Kawabe 1966; Teleki 1973, 1974; Suzuki 1971) and by baboons (Harding 1973; Strum 1975) have been cited as indications of a carnivorous proclivity in anthropoids which became intensified in early hominids.

Leopold and Ardrey (1972) have suggested that widespread toxins in plants may have resulted in many species being inaccessible to pre-fire-using hominids, and that meat-eating would have provided a more reliable and plentiful source of food. This suggestion seems extremely unlikey in view of the many modern and fossil African primate and other mammalian species which are or were herbivorous.

The interpretation of the archeological evidence cited above as indicative of meat-eating is convincing, but it only pertains to the lattermost segment of the time span of early hominid activity here under consideration.

The dietary hypothesis of Robinson (op. cit.) is still the best evolutionary explanation of the cranial, mandibular and dental morphological dichotomies between the robust and gracile hominid species. No later dental studies have discovered proof of different diets in these two groups with the exception of Wallace's (1975) finding that incisal wear differed. The consensus of Wallace's (1974, 1975), Every's (1970) and Szakay's (1975) works argues against the acceptance of a seed-eating phase in early hominid evolution as

proposed by Jolly (1970). Primatological observations noted above, in association with these morphological considerations, also make it improbable that an advanced hominoid such as *Australopithecus africanus,* or its immediate ancestor, had a diet more restricted in content or less diverse than modern *Pan* or *Papio.*

Definite answers on early hominid diet are elusive because of the nature of the data. As Dart (1965:53) has noted, "australopithecine diet and its relation to their dental characteristics have provoked the longest man-ape debate." Extrapolating backward from a tool-using/meat-eating phase for *Homo,* at between 1.5 to 1.8 m.y. BP, along the gracile hominid lineage it seems probable that *A. africanus* may have had a diet with a large component of meat. Morphological considerations seem to confirm this supposition and primatological data are not in disagreement with it. The diet of the robust australopithecine species is an enigma. Its large temporalis and masseter musculature, massive mandible and large molar occlusal area in relation to incisor size argue for an adaptation for processing large amounts of food, generally an indication of herbivory (Swindler and Sirianni 1976). Its molar wear does not indicate a diet of small hard objects such as seeds.

Intra- and Interspecific Relations

In an ideal ecological or paleoecological study (see Table 1) relations of the species in question with the other members of the community and of its own species in question with the other members of the community and of its own species are of paramount interest, even though these are frequently the most difficult data to obtain. Questions relating to intraspecific relations include how the species is divided into groups, and the reproduction and movement of these groups; effects of increased numbers on the species; population parameters such as natality, mortality and population growth; and spatial relationships of the populations such as space requirements and home range.

	Species A	Species B	Relation	
Todd and Blumenberg 1974	+	+	Mutualism	} Symbiosis
	+	0	Commensalism	
Robinson 1963, 1972; Cachel. 1975; Washburn 1976[1]	0	0	Neutrality	
(Weiss 1972)	0	–	Antibiosis	} Antagonism
(Wolpoff 1971; Swedlund 1974)	+	–	Exploitation	
	–	–	Competition	

[1]with later exclusion of *A. robustus* by *H. erectus*

(from Clarke 1954:364)

Table 1. A non-exhaustive chart of models proposed for gracile and robust early hominid interspecific interactions. Hypotheses are classified within a framework set forth by Clark (1954), similar to one figured by Swedlund (1974).

Mann's (1968, 1975) study on the paleodemography of the South African australopithecines is an attempt to ascertain some of the basic data needed to elucidate intraspecific relations. He determined numbers of individuals and constructed age distributions on the basis of analyses of the state of development and eruption of the dentition. The mean age at death for gracile australopithecines at Sterkfontein and Makapansgat was 22.2 years while at Swartkrans the robust australopithecine mean age was 17.2 years. Mann (op. cit.) was careful to state that these results applied to the sample in the caves and not to living australopithecine populations, implying that the taphonomic factors that resulted in deposition would have to be taken into account before conclusions relating to the population could be attempted.

McKinley (1971), however, uses Mann's (1968) data and age determinations of one additional Indonesian, and five additional East African hominids, and assuming equal preservation of both robust and gracile species and equal preservation of specimens of all ages, treats all aged hominids as a biological population. These assumptions are probably unwarranted because of the difference in manner of carcass accumulation by different predators of the South African caves (Brain 1970, 1977; Vrba 1977), as well as the entirely different taphonomic circumstances surrounding the deposition of the hominid remains in East Africa and Asia (cf. Behrensmeyer 1975; Jacob 1975). The treatment of widely separated samples as one population is also dubious. McKinley derives average ages at death for *A. africanus* as 22.9 years and *A. robustus* as 18.0 years, constructs survivorship curves for the two species, and determines that both had a human type of birth spacing.

Tobias (1968) also conducted an aging study of the South African early hominids by assigning specimens to developmental stages without inferred year ages. As Biggerstaff's (1967) article shows for the Taung specimen, the attribution of absolute ages to certain dental and skeletal developmental stages in fossil hominids is open to error if based on modern man equivalents. Tobias' (1968) age divisions are similar to those of Mann's (see Mann 1975, Table 13). 43% of robust australopithecines died and were preserved before reaching childbearing age while three out of four gracile hominids would have lived to procreate. This finding may indicate a real demographic difference or may reflect the competition of the robust form with an advanced "tool making hominine" at Swartkrans (Tobias 1968:26). Brain (1970) has noted that at Swartkrans Member 1 the bone accumulation likely was a result of leopard predation, and a preference for primates (and hominids) is shown by comparison with modern game park leopard kills.

Frazer (1973) calculated gestation periods for early hominids using estimates of fetal size in *A. africanus* and *A. boisei* from Leutenegger (1972), based on pelvic dimensions, and with a fetal growth rate factor of 0.06 for higher primates (Frazer and Huggett unpublished). His results were 257 days gestation for *A. africanus* and 300 days for *A. robustus*.

Data on other aspects of intraspecific relations of early hominids is minimal although speculation abounds. Archeological evidence has been adduced to indicate the habitation of "home bases" (Isaac 1971), population sizes have been estimated (e.g. Behrensmeyer 1976 b), territoriality has been widely assumed (e.g. Bartholomew and Birdsell 1953) and intraspecific competition and aggression between groups has been considered important, usually based on sub-human primate analogies (e.g. Washburn and Devore 1961). New evidence from East Africa on some of these aspects will be presented below.

Interspecific relations involve extragroup interactions between two or more different but sympatric species. Relations between sympatric zoological species can be schematized as in Table 1. Symbiosis occurs when two or more species co-exist to the competitive betterment of one or both. Antagonism comprises those interactions which are to the detriment of at least one species involved in the interaction. Neutrality is said to exist when species have no competitive effect on others.

The studies listed in Table 1 will not be treated in detail unless discussed elsewhere. Todd and Blumenberg (1974) present a model in which sympatric robust and gracile early hominid species lived in a mutualistic symbiotic relationship. The larger form scavenged from a hunting and meat-eating smaller form and, in turn, provided protection from predators.

Cachel (1975) proposed that both the gracile and robust hominid species were carnivores, but were specialized on smaller and larger prey, respectively. This study, along with Robinson's dietary hypothesis (op. cit.) and Washburn's (1975) brief paper on the mutual tolerance of the two lineages until *Homo erectus*, seems most appropriate under the heading of "neutrality," since the authors do not explicitly suggest a symbiotic relationship.

Weiss (1972), Wolpoff (1971) and Swedlund (1974) did not admit (less certainly in the latter) the presence of two lineages. Weiss considered, on the basis of a mathematical population ecology model, that the "total competitive effect" of an omnivorous gracile species would have had to have been 100 times greater than that of a closely related herbivorous robust species, for the two to co-exist. Weiss considered this impossible in nature, but if one accepts the now abundant evidence that two early hominid lineages did exist (cf. Leakey and Walker 1976), Weiss's conclusions would indicate that the robust form would have competitively excluded the gracile (antibiosis). Similarly, Wolpoff (1971, and elsewhere) in the "single species hypothesis" argued that all early hominids were adapted to a cultural ecological niche, an adaptation so

wide-ranging that only one early hominid taxon could have existed at one time because it would have competitively pre-empted any other (exploitation). Swedlund (1974) accepted Wolpoff's (1971) explanation as the best, although still imperfect, accounting of the known facts.

All of the above works make assumptions concerning early hominid behavior, diet and demography that simply cannot be made in the face of the present dearth of data. Several lines of evidence argue against acceptance of the models discussed above. It now appears, especially from East Africa discoveries, that the single species hypothesis is quite unlikely to be true; Weiss's (1971) estimate for a robust to gracile hominid population ratio is closer to 2.5 (a maximum) than to 10 (see below); and Cachel's (1975) suggestion for competition between gracile hominids and canids at Omo is untenable since the latter have not been discovered there (*See* Howell and Petter, 1976).

Recent Paleoecological Research

Much recent geological and paleontological work bearing directly on early hominid environments has been accomplished in the two main foci of hominid fossil occurrences, South Africa and East Africa. These new data provide a firmer empirical framework on which to base hypotheses relating to facets of hominid paleoecology.

Two main methods have been employed in empirical reconstructions of paleoecologies. Paleoenvironmental and -geomorphological data are primarily derived from geological, geophysical, sedimentological and stratigraphical studies. This basis is necessary before a comprehensive reconstruction is attempted.

Because all flora and fauna live under specific environmental conditions, any fossilized biotic remains have potential significance for paleoecological interpretation. In practice, however, due to depositional conditions, fossilization environments, collecting methods and research interests of investigators, attention has focused primarily on large mammals with a comparative disinterest shown, until recently, in paleobotanical, invertebrate, non-mammalian and microfaunal research. Consequently, many of the environmental reconstructions below are based to a large extent on remains of large mammals even though these animals frequently range into several habitats. The author's opinion is basically that of Ewer's (1963:344):

> "One swallow does not make a summer, nor does one bat-eared fox a desert, but a whole assemblage of typically desert-loving species is not likely to be found in dense bush or forest. If we do not rely on single species, but try to base our judgement on the characteristics of the fauna as a whole, then we are not likely to go seriously astray."

Hemmer (1965) used fossil remains of mammals to characterize environments of Upper Pleistocene hominids as wooded to bushy to grassland, and considered early hominid environments to have been similar. All relevent data in addition to large mammal remains will of course be presented when available.

The environments represented in a specific fossil locality or set of localities (as presented in Figure 1) are a reflection of the habitats sampled by its attendant depositional processes. Generally, sites deposited by fluviatile action preserve a wider range of habitats than do sites laid down by lacustrine or sub-aerial sedimentation or which are cave infillings. Streams and rivers, depending on their flow capacity, tend to transport certain skeletal parts, occasionally concentrate them and then deposit them in an aggrading or sediment-accumulating section of the fluviatile system such as a point or sand bar or on an overbank alluvial floodplain. This phenomenon was treated by Shotwell (1955, 1963) who suggested methods to discriminate the transported (allochthonous) segment of the fauna from the relatively untransported (autochthonous) segment based on body parts per individual.

South Africa

The dating of the South African cave breccias has been a long-standing paleoanthropological problem. However, on the basis of faunal comparisons with radiometrically dated East African sites these South African sites can be arranged from oldest to youngest. On the basis of the most recent reviews of the fauna (Vrba 1974, 1975; Brain 1976) it appears that the sites of Sterkfontein Type Site (STS) and Makapansgat (MLD), which have yielded specimens attributable to *Australopithecus africanus,* are the oldest, at dates of 2.0 to 3.0 m.y. BP or older. Swartkrans Member 1 (Butzer 1976a), which has yielded *Australopithecus robustus* and *Homo* sp., and Kromdraai B, with *A. robustus,* appear to post-date 2.0 m.y. BP Taung, the type site of *A. africanus,* has been ascribed a late date of some 0.5 m.y. BP by Partridge (1973) using a questionable (De Swardt 1974) geomorphological technique of stream nick-point migration. This dating has been accepted by Tobias (1973). Vrba (per. comm. 1976), however, in reassessing the bovid remains from Taung finds evidence for assemblages of multiple ages in the cave, so that the Taung hominid may in fact be as old as those from STS or Makapansgat.

In the present work the gracile *A. africanus* is considered the only hominid taxon represented in the early occurrences of the South African cave infillings. On the basis of present data, *A. robustus,* following Vrba (1975), is considered to appear at approximately 2.0 m.y. BP and is co-existent with a more advanced species of *Homo.*

It has become apparent in recent years that the means of accumulation of the bone remains in fossil sites must be understood before the fossils themselves can be justifiably related to the geological and chronological context of the site. The study of these

accumulating and burial processes is known as taphonomy. Brain (1969, 1970, 1976, 1977) and Vrba (1975, 1977) have shown that many of the South African sites represent carnivore accumulations, and not refuse of hominid hunters as was previously assumed (Dart 1949). STS, on the basis of the medium to large size of the faunal remains probably represents the lair of a large saber toothed felid such as *Megantereon* or *Dinofelis* (actually a dirk-toothed felid). SK Member 1 and Kromdraai A, the faunal site, contain the remains of prey from leopard kills as indicated by samples with high overall juvenile percentages and of low average weight. Sterkfontein Extension Site with its many stone artifacts and its broad distribution of weight classes may indicate hominid scavenging, while only later sites such as Kromdraai B, Sk Member 2, and Sterkfontein Rubble Dump 16 may preserve the remains of kills by hominids.

Within the limits of prey size selection the fauna of the Sterkfontein Valley cave sites can be considered as indicative of the animals living in the vicinity of the cave mouth at the time of deposition. On the basis of this deduction Vrba (1974, 1975) has used ratios of open country alcelaphine and antilopine bovids to other bovid tribes adapted to more bushy environments to reconstruct amount of bush cover at the time of deposition of the main sites. STS had significantly more bush cover than the other, later Sterkfontein Valley sites, SK Member 1, Kromdraai A, Sterkfontein Extension Site and perhaps also Kromdraai B. Vrba's conclusions vary from Brain's (1958) sedimentological study, which had reconstructed a wetter climate for the robust australopithecine accumulations, and from Ewer's (1963), Ewer and Cooke's (1964), Butzer's (1971) and Cooke's (1977) conclusions that the deposits of Sterkfontein, Swartkrans and Kromdraai had been of similar ecologies. Ewer (1963) had considered that the lack of species characteristic of thick bush, the lack of *Hippopotamus* and the presence of suids with a probable grazing adaptation indicated "moderately open country" at these three sties. Boné (1960) considered all the Transvaal sites (Sterkfontein Valley and Makapansgat), on the basis of the total fauna, to indicate open savanna or bush biotopes. However, he did suggest that the lack of large felids, *Panthera leo* and *Panthera pardus*, and the preponderance of smaller carnivores at Makapansgat probably indicated more bush cover at this site (Boné 1960:293).

Cartmill (1967) has reviewed the micromammalian fauna of the major early hominid sites in South Africa, with the exception of Swartkrans. He found that mean annual rainfall probably decreased west to east, from Taung to Sterkfontein to Makapansgat (this trend also corresponds to increasing altitude). Kromdraai (the faunal site and the hominid site were treated as one) was suggested to have had a higher rainfall than Sterkfontein even though all fossil taxa known from Kromdraai are present in the (semi-arid) area today

(Cartmill, 1967:194).

The cave site of Makapansgat has not recently been reviewed on a primary reappraisal of data. Wells and Cooke (1957) on the basis of the fauna and King's (1951) geological survey concluded that it represented a "moderately well watered, bushy valley opening on to nearby plains which, at no great distance, were decidedly dry." As noted above Cartmill's (1967) microfauna study indicated that Makapansgat received greater rainfall than the other South African sites under consideration. Boné's (1960) study, as well as others, considered Makapansgat to have been more bushy. Maier (1973) summarized the faunal evidence from this site and suggested paleoenvironmental conditions varying from open savanna and bush to woodland or perhaps forest conditions with perennial surface water. Cooke (1977) provides the most recent faunal list for the site and concludes, in accordance with former studies, that there was "rather more bush than at the other Transvaal sites, but the dominant impression is of grassland and thornscrub with water nearby."

Taung is not included in Figure 1 because of its unknown relative or absolute date. Initial paleoecological conclusions concerning the Taung site were summarized above. Ewer (1963:245) on the basis of the rodent fauna agreed with the assessment by Broom and Schepers (1946) and considered it "the most arid of the Australopithecine habitats." Cartmill (1967) reviewed the Taung microfauna and characterized the region in the Plio-Pleistocene as "definitely arid" with a mean annual rainfall of under 30 cm/yr. He disagreed with Broom and Schepers' (1946) assessment of a rainfall of less than 6 cm/yr.

Notwithstanding Butzer's (1974) recent geological survey Peabody (1954) has presented the best *a posteriori* geological summary of the site, which has been destroyed completely. Peabody (op. cit.:682) discerned on lithological grounds an earlier "dry-phase" sandy cave fill and a later "wet-phase" calcium carbonate ("pure lime") fill. He suggested that the Taung hominid derived from the latter wet phase deposit because the external surface of the cranial endocast was covered with a "clear, drusy calcite, a condition not observed in any of the numerous baboon skulls from the dry phase" (Peabody 1954:684). All of Butzer's (1974:382) conclusions, the primary of which are that the Taung hominid dates from later than the early Pleistocene and that it inhabited a moister environment than previously thought, depend on acceptance of Butzer's demonstration of the validity of Peabody's dry and wet phases. Butzer (1974:376) initially states that he has "analyzed samples of 'dry-' and 'wet-phase' deposits, and they are indeed quite distinctive," but in a rejoinder (p. 414), written after analyzing 9 matrix samples from baboon crania, he concluded that the "laboratory data did not bear out Peabody's macrostratigraphic dry- and wet-phase deposits."

Cooke (1977) has provided the most recent faunal list and environmental conclusions for Taung. He lists 10 more microfaunal species than does Cartmill (1967). Cooke (1977) considers that the overall Taung fauna does not suggest an arid environment but rather "one of dry grassland with rocky areas and scrub, or even localized bush in sheltered situations."

A synopsis of the probable environments of the South African cave sites with the exception of Taung which cannot at this time be dated, is presented in Figure 1.

East Africa

In contradistinction to the South African hominid-bearing sites none of the East African hominid localities are cave infillings. They instead occur in fluviatile, fluvio-lacustrine, fluvio-deltaic or, in one case, sub-aerial sediments. It is likely that many more taphonomically selective factors have influenced the compositon of the bone assemblages collected and excavated from East African sedimentary situations than in the case of the South African cave deposits where many of the faunal assemblages seem to be remains of carnivore or hominid prey. However, the occurrence of volcanic or volcano-clastic sediments in known stratigraphic relationships to fossiliferous horizons in East Africa has allowed the more precise dating of the hominid and associated faunal remains. A proliferation of multi-disciplinary studies in East Africa has also resulted in a wide body of geological, paleontological (invertebrate and vertebrate), paleobotanical and taphonomic data useful and necessary in reconstructing hominid environments.

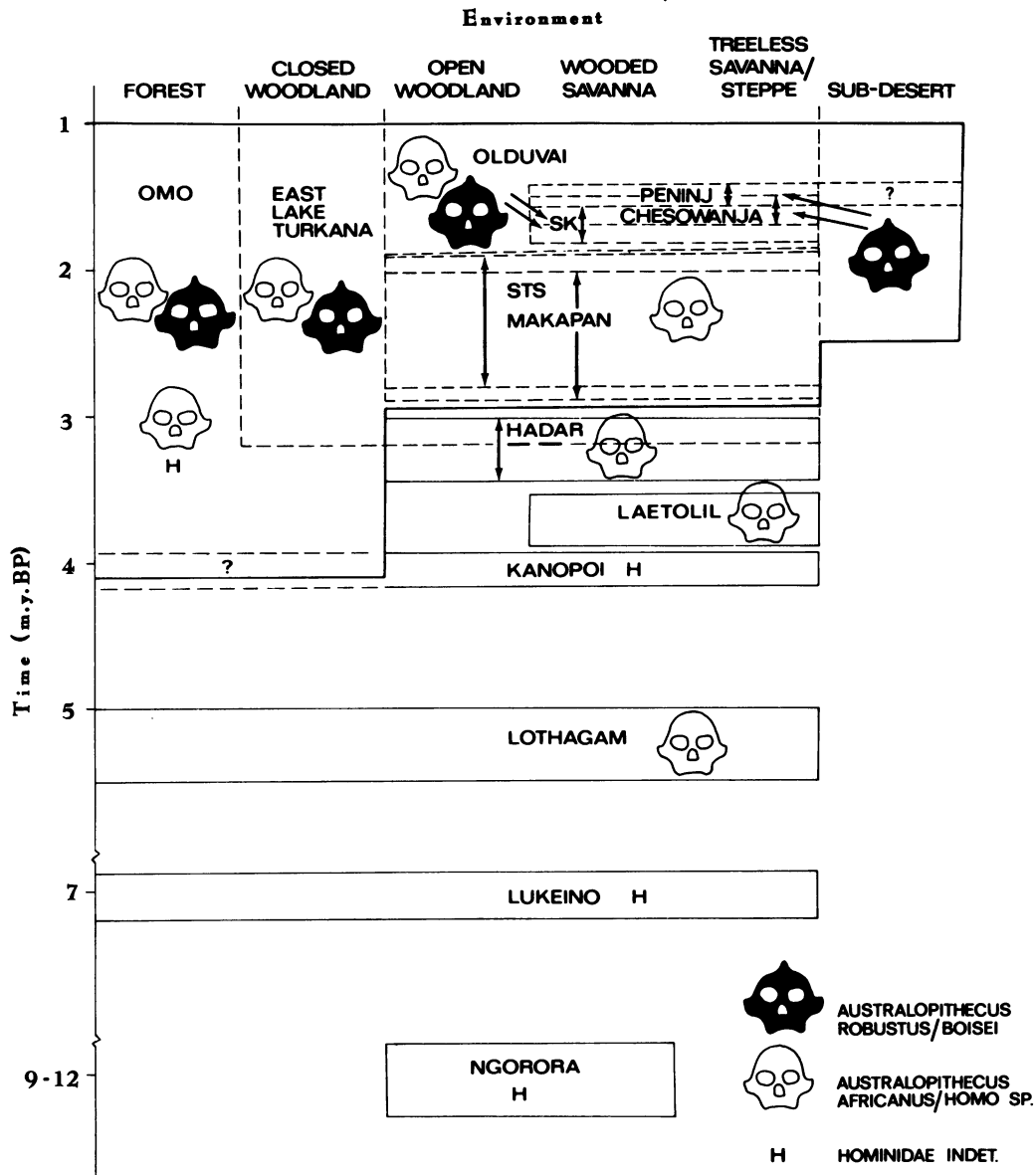The earliest known East African hominid sites have

Figure 1. Diagram indicating hominid taxa present, probable temporal spans and probable paleoenvironments (as deduced from geological, floral and faunal evidence) of Neogene early hominid sites in Africa. Environmental categories form a spectrum of increasingly open conditons from left to right.

yielded only isolated fossil documents: Ngorora and Lukeino, single teeth; Lothagam, one half-mandible; Kanapoi, a distal humerus. The taxonomic statuses of the Ngorora (Bishop and Pickford 1975) and Lukeino (Pickford 1975) molars and the Kanapoi humerus (Patterson 1966; Patterson and Howells 1967) are indeterminate although their morphologies closely approximate those of later gracile hominids. The Lothagam mandible has been referred to *Australopithecus* aff. *africanus* (Patterson, Behrensmeyer and Sill 1970).

The 13 known mandibles from the Laetolil Beds have been considered representative of the gracile *Australopithecus africanus-Homo* lineage (Leakey et al. 1976), here considered as *A. africanus*. The Hadar hominid specimens have been referred to the gracile *A. africanus* with the exception of one rather large proximal femur (AL 211-1), assigned to *A. boisei* (Johanson et al. 1976). Until further fossils, especially cranial and dental remains, confirm that this specimen did not belong to a large member of the *A. africanus* population and actually indicated the presence of *A. boisei;* the Hadar fossils will be considered here as belonging to one fossil taxon.

The remainder of the early hominid fossil sample from East African sites, Omo (primarily Howell and Coppens 1976), Olduvai (L. Leakey 1959, 1961, 1966; Leakey, Tobias and Napier 1964), East Lake Turkana (primarily R. Leakey 1976), Chesowanja (Bishop et al. 1975), Peninj (Leakey and Leakey 1964; Isaac 1967) dates from 2.9 m.y. (lower Member B, Omo) to the appearance of *Homo erectus* at approximately 1.3 to 1.5 m.y. BP [Member K, Omo (Howell and Coppens 1976); Bed II, Olduvai (L. Leakey 1961); Upper Member, Koobi Fora Formation (R. Leakey and Walker 1976)]). The *A. africanus-Homo* sp. lineage is present exclusively before about 2.1 m.y. BP when it is joined by *A. boisei* in Member E of the Shungura Formation. Both robust and gracile hominid lineages are known from East Lake Turkana, where hominid-bearing levels are no older than some 2.0 m.y. BP (Brown et al. 1976), and from Olduvai Bed I, at an age of 1.8 m.y. BP (Curtis and Hay 1972). Only robust hominid specimens are known from the small faunas collected from Chesowanja and Peninj but on the basis of the other contemporaneous sites a gracile hominid was certainly present in the general area at the time. The temporal spans of the East African sites and the hominid taxa empirically represented at them are depicted in Figure 1. Chemeron (Martyn 1967) and Koro Toro (Coppens 1965) have yielded probable early hominid fossils of indeterminate taxonomic attribution and with very incomplete data for paleoecological reconstruction, and they have been omitted from Figure 1.

Ngorora

The paleoecological conditons at Ngorora have been summarized by Bishop and Pickford, 1975. Deposition in Member C, from which the hominid was derived, occurred between two paleolakes. Lake Kabarsero was fresh, as indicated by the presence of fresh water potamid crabs and diatoms, while Lake Kapkiamu, some 8 km distant, was alkaline, as indicated by a stunted species of fish similar to *Tilapia grahami* now found in the very alkaline environment of Lake Magadi in Tanzania. The low-lying area between these two lakes was the site of abundant plant cover, as indicated by the presence of well-developed paleosols. A recovered specimen of fossil wood shows definite growth rings suggesting a fluctuating climate, probably between wet and dry seasons. The homin(o)id molar comes from a locality south of Lake Kabarsero. Floral remains include monocotyledons such as palms (unspecified species) and grasses, and dicotyledons, such as lianas, and a possible *Celtis*. The palm may be indicative of drier conditions in parts of the general area, as are the grasses, although if a doum palm it could have been part of a gallery forest of one of the feeding streams to one of the lakes. *Celtis,* a moderately-sized tree, and lianas, climbing plants usually found in forests, are indicative of wooded conditions.

Bishop and Pickford (1975:191) consider the ungulate fauna to represent "an open or lightly wooded grassland habitat." The presence of other mammalian fauna in Member C (p. 190, Figure 4), such as cercopithecoids, procaviids, hyaenids and cricetids (all identified to no lower taxonomic categories than families), neither supports nor detracts from this reconstruction, although the facts that rhinocerotids and giraffids are present would seem to suggest a more open and partially wooded environment.

Lukeino

The hominid lower molar from Lukeino derives from Member A of the Lukeino Formation, like Ngorora also a peri-lacustrine environment, as shown by the presence of deposits of algal mats on the margins of a lake and the presence of lacustrine bivalve molluscs (Pickford 1975). The diatoms, as well as the molluscs, algae and fish, none of which are identified taxonomically, are cited as indicative of a fresh or weakly saline lake (Ibid.:282). Fossil leaves, wood, grass and ferns have been found but no identifications of these are as yet available.

Hippopotamids and crocodilids comprise a large portion of the vertebrate faunal assemblage while bovids, suids and giraffids are scarce. A species of giant river otter, *Enhydriodon* cf. *iluecai*, is present, which probably indicates the proximity of riverine woodland or forest. Tragelaphine bovids suggest the presence of wooded savanna/thicket conditions, while antilopine (and gazelline) bovids and two species of aardvark, *Orycteropus,* definitely indicate more open savanna or grassland conditions. Pickford (op. cit.:281) states that

many of the fossils in Member A occur in sand- and grit-filled channels so it seems most accurate to describe the overall depositional environment at Lukeino as fluvio-lacustrine. On the basis of the fauna the range of sampled habitats was probably from open woodland to treeless savanna.

Lothagam

The hominid half-mandible reported by Patterson, Behrensmeyer and Sill (1970) derives from Lothagam 1, in Member C, which is comprised of fluviatile or fluvio-lacustrine sediments (Behrensmeyer 1976a). Smart (1976) has reviewed the vertebrate fauna and considered the remains of a non-gliding anomalurid rodent, cercopithecoids (*Cercocebus* and *Parapapio*), and proboscideans (*Deinotherium* and an anancine gomphothere) as indicative of forest conditions. Much of the rest of the fauna, which include *Ceratotherium*, *Hipparion* and bovid genera belonging to alcelaphine, hippotragine, reduncine and antilopine (but not tragelaphine) tribes indicates savanna. *Hippopotamus* is present. Smart (Ibid.:365) considered Lothagam to reflect "gallery forest fauna near the depositional sites grading through marginal bush into savanna." The site is here treated as encompassing forest to wooded savanna conditions.

Kanapoi

Kanapoi seems quite similar to the reconstructed environments for Lukeino and Ngorora. Patterson (1966:577) notes that the sediments were deposited around a shallow lake with lateral facies changes to scour-and-fill channels. Patterson, Behrensmeyer and Sill (1970) note that molluscs and fish remains were collected and that these are primarily of Nilotic affinities.

Carbonnel and Peypouquet (1976) have analyzed five samples of ostracods from Kanapoi. Stratigraphic levels corresponding to these samples are not clear but one sample yielding a diverse fauna, which may be the oldest, indicates fresh-water conditions in the paleolake at Kanapoi (perhaps part of paleo-Lake Turkana) at around 4 m.y. BP. The other four samples indicate, by the virtually monospecific predominance of the genus *Hemicypris*, a moderately deep lake or lakes subject to periods of rapid desiccation. This genus is known from modern temporary lakes in the Ngong Hills of Kenya. Due to similar sizes and thicknesses of the shells of the later to the earlier (?) ostracods Carbonel and Peypouquet (1976) consider the paleo-lake as non-saline and rich in Ca^{++} ions.

Behrensmeyer (1976a) has summarized the fauna. The exclusive presence of the low-crowned suid, *Nyanzachoerous*, and its higher crowned descendent *Notochoerus*, plus *Enhydriodon*, and tragelaphine and reducine bovids may indicate riverine woodland/forest to wooded savanna conditions, while *Ceratotherium praecox, Giraffa, Hipparion* and *Lepus* may indicate more

open conditions, perhaps to tree-less savanna. Wooded conditions probably extended to the lake margin.

Laetolil

The site of Laetolil comprises markedly different depositional and paleoenvironmental conditions compared to the other East African sites here discussed although similar in taphonomic features to the lower Miocene site of Napak in Uganda (Bishop 1968). It is of sub-aerial deposition with all of the faunal remains preserved under eolian volcanic ash falls (M.D. Leakey 1976). Laetolil is on a relatively high plateau and was so at the time of deposition. Features originally taken to be fossil root casts occuring in localized concentrations indicating "bush and small trees" (Hay 1976) have now been realized to represent casts of termite burrows in abundant collapsed termite mounds (Hay pers. comm.). Termite mounds occur in East Africa today only in semi-arid open savanna/ steppe. Geological work by Hay and Monahan (pers. comm. 1976) indicate stream channels draining to the west from an upland landscape. Clay deposits in one area indicate presence of a pond. Rain-drop markings and probably rain-held carbonatite tuffs indicate at seasonal rainfall. The extreme completeness of the fossil remains (M.D. Leakey et al. 1976) and the lack of water-laid fossiliferous sediment indicate that the fauna is virtually totally autochthonous and untransported by water action.

Urocyclid slugs suggest sub-humid conditions, probably within a microhabitat near water. Verdcourt (in Hay 1976) identifies three species of gastropods from Laetolil and suggests that they are indicative of "woodland, savanna or grassland with scattered thickets" (p.18).

The vertebrate fauna shows a complete absence of *Hippopotamus* and tragelaphine bovids and the presence of such dry-country-loving animals as rodents like *Pedetes*, the springhare, and *Saccostomus*, the pouched mouse; *Orycteropus*, the aardvark; *Diceros* and *Ceratotherium*; *Madoqua*, the dik-dik, which is predominant in the bovid fauna (M.D. Leakey et al. 1976). J.J. Jaegar (pers. comm. to Hay 1976) has identified *Heterocephalus*, the naked mole rat, characteristic of semi-arid areas with sandy substrates.

Overall the Laetolil deposits would seem to have preserved a wooded savanna/thicket to treeless savanna assemblage.

Hadar

The remains of some 12 hominid individuals from Hadar occur throughout a vertical section of several m, from nine distinct levels in the lower Sidi Hakoma Member to the lower Kada Hadar Member of the Hadar Formation (Johanson and Taieb 1976, and Johnson et al. 1976). Geological evidence indicates that easterly flowing streams from the Ethiopian

plateau, 10 to 20 km to the west of Hadar, emptied into a shallow lake (indicated by finds of ostracods) with a broad flat floodplain. The presence of fossil potamid crabs (Taieb et al. 1976) may indicate fresh water lacustrine conditions. A lignite coal deposit in Unit SH-3 (Johanson et al. 1976) would seem to indicate shallow lacustrine or marsh conditions, with abundant surrounding vegetation.

The fauna includes the rodents *Tachyoryctes, Oenomys* and *Mastomys,* indicative of open woodland or well-watered highland wooded savanna conditions (H.B. Wesselman pers. comm., cf. Kingdon 1971). Also suggestive of wooded savanna or open woodland conditions are the suid *Nyanzachoerus,* which possessed low-crowned molars and may have been similar in habits to the extant *Hylochoerus,* the African giant forest hog (see Cooke 1976), tragelaphine bovids and *Colobus* monkeys. Two species of *Giraffa, Aepyceros,* alcelaphine bovids, *Hipparion* and the two genera of rhinoceros, *Diceros* and *Ceratotherium,,* probably indicate more open habitats, wooded to treeless savanna.

In-depth paleoecological research is now underway at Hadar (B.T. Gray pers. comm.) but at present it seems possible to say that the Hadar localities sample low energy fluviatile and fluvio-deltaic depositional environments and represent paleoenvironments ranging from wooded savanna to treeless savanna.

Omo

Hominid fossils consisting primarily of teeth have been discovered in the Shungura and Usno Formations of the Omo Group in mainly fluviatile depositional environments. No hominids are as yet known from the Mursi Formation at a date of 4.2 m.y. BP.

Butzer (1976b) notes the presence of channel sands along with lacustrine, prodeltaic and deltaic clays and silts in the Mursi Formation Members I, II, and III. He considers the Mursi ("Yellow Sands") sediments overall to be analogous to fluviolittoral conditions in the modern Omo River delta (cf. Butzer 1971). The cyclic fluviatile fining-upwards sequences characteristic of the Shungura Formation are not present. The presence of evaporites indicates a period of desiccation of closed basins on the delta fringe, followed by littoral conditions (de Heinzelin et al. 1976).

Brown, Howell and Eck (1976), de Heinzelin (1971) and de Heinzelin, Haesaerts and Howell (1976) among other works, have dealt with the sedimentation and depositional environments of the Shungura Formation. A more detailed view of the geological evidence than is given here will be found in Boaz (1977).

De Heinzelin et al. (1976) have summarized some 17 time-successive sedimentary periods. Much of the Shungura Formation is composed of cyclic units coarse at the base (sands) grading to fine at the top (silts and/or clays). These are deposits largely laid down by the meandering paleo-Omo river in a subsiding basin. At two-times, during Unit F-1 and Units G-3 to G-5,

the meandering river system was apparently replaced by braided channels, as indicated by a less continuous floodplain, lower and broader banks and extensive sand bodies.

Lacustrine or deltaic conditions are known in the lowermost Basal Member (3.4 m.y. BP, Brown pers. comm.), in units G-14 to G-22 (1.85 to 1.9 m.y. BP), and upper Member L. Fluctuating lacustrine or deltaic fringe conditions are indicated in Units H-2 to J-1 and may be indicated in Unit C-7 (see Brown et al 1976) by the presence of supposed lacustrine molluscs. These genera, *Caelatura* and *Cleopatra,* however, also occur in East African rivers (see Verdcourt 1972).

Pollen data from primarily two levels in the Shungura Formation, upper Member C at 2.5 m.y. BP and upper Member E at just over 2.0 m.y. BP show an increase in predominance of grasses in the latter level. This has been interpreted as indicating drier climatic conditions with a greater degree of grass cover (Bonnefille 1976). Fossil wood determinations (see Figure 2) by Dechamps (1976) do not show the same clear difference in environments but instead the persistence through time of the riverine forest/woodland and the more distal and drier savanna habitats. It is probable, nevertheless, that the drying trend seen during Member E times is actual because it is based on a highly significant difference in pollen percentages (see Bonnefille's 1976, Table 1) whereas fossil wood taxa are based only on presence or absence. Woody taxa may well be represented because of their proximity to the depositional environment (the river).

Carbonel and Peypouquet (1975, 1976) and Carbonel, de Heinzelin and Peypouquet (1977) have analyzed samples of ostracods from several levels in the Omo Group. Basing their conclusions on the ecological tolerances of the some 22 taxa present, the diversity of species and the stages of development of the individuals preserved, they were able to reconstruct salinities of paleo-Lake Turkana. A complex pattern of salinity changes was indicated.

Van Damme and Gautier (1972) and Gautier (1976) have described the molluscan fauna from the Omo Group which now consists of 31 taxa. Gautier (1976: 382) notes that paleoenvironmental conclusions must be made with caution due to the presence of favorable (freshwater) microhabitats in otherwise unfavorable (saline) conditions. However, he suggests that since the Omo fossil fauna does not preserve stunted forms and molluscs always seem to occur in lacustrine littoral environments as expected, paleo-lake salinities were generally no less than Lake Turkana today. A comparison of the Omo molluscan fauna with biogeographical ranges provided by Verdcourt (1972) indicates that there are strong connections to the Nile drainage, as shown by *Caelatura, Etheria* and *Cleopatra,* and to the central African lakes, as shown by *Mutela, Corbicula, Eupera, Gabbiella* and *Bellamya.* An earlier report (Van Damme and Gautier 1972) of the pre-
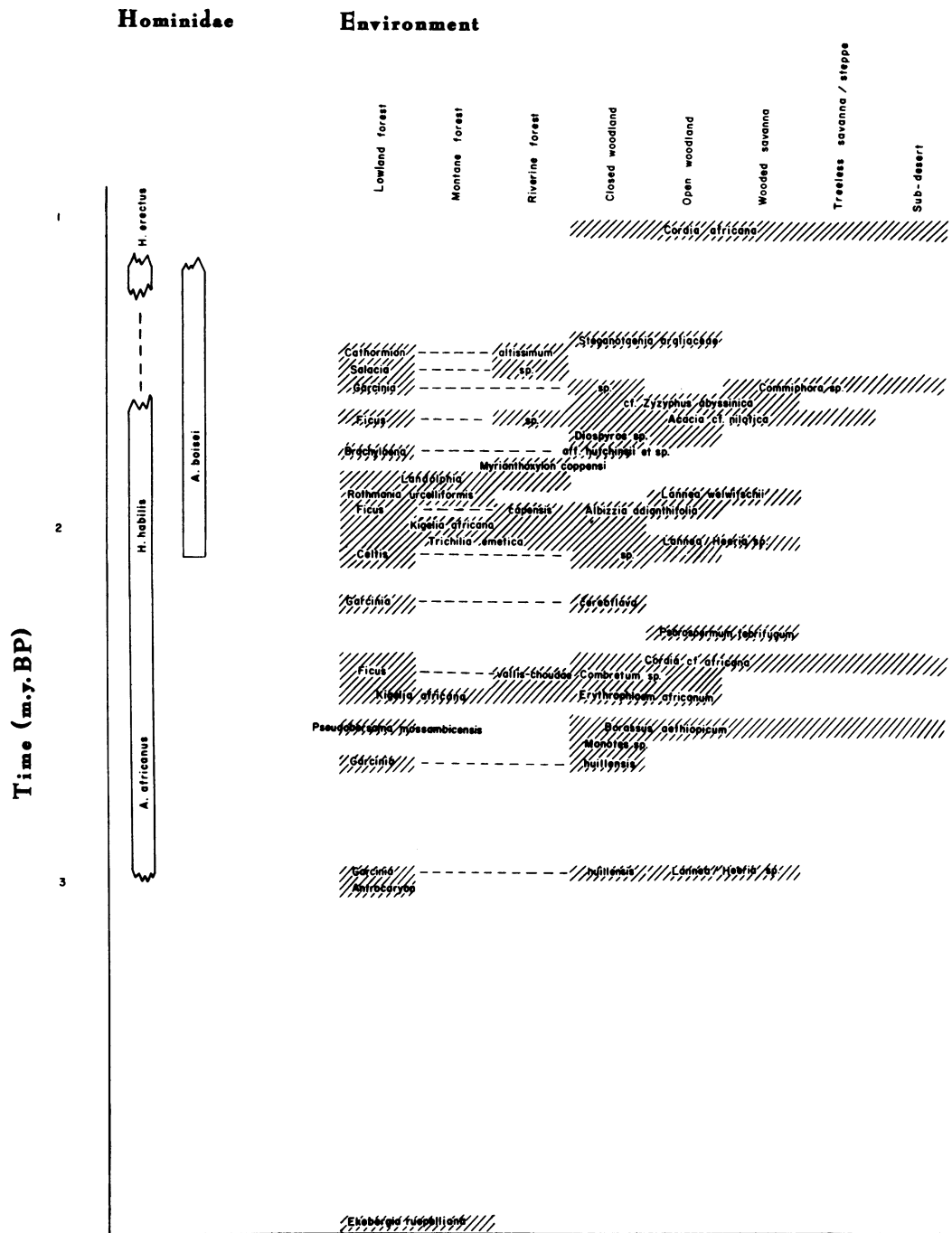
Figure 2. Woody taxa identified (by R. Dechamps) throughout the Mursi, Shungura and Usno Formation sequences with environmental tolerances indicated. These results indicate the persistence through time of the (riverine) forest community, even though palynological results show a significant increase in grassland at around 2.1 to 2.0 m.y. BP.

sence of *Mysorelloides*, an endemic form now known only from Lake Tanganyika, was revised to Gastropoda gen. et sp. indet. by Gautier (1976).

Tchernov (1976) suggests that hydrographic connections of the Turkana basin with the Nile drainage were not established until the late Neogene, based on the absence in eastern African waters of the North African Pliocene crocodilian genus *Tomistoma*. Greenwood (1976) notes that the fish genus *Sindacharax* from Shungura Unit G-24 resembles the

North African Pliocene form more closely than an upper Miocene species from Zaire, further suggesting Nilotic connections with the Omo.

Micromammal determinations primarily from the Shungura levels B-10 and F-1 show a fauna more adapted to drier conditions at the later level (2.0 m.y. BP; Jaeger and Wesselman 1976). The Member B fauna preserves three species of *Galago*, three species of bats and abundant rodents characteristic of "wooded savanna" and presence of a well-developed
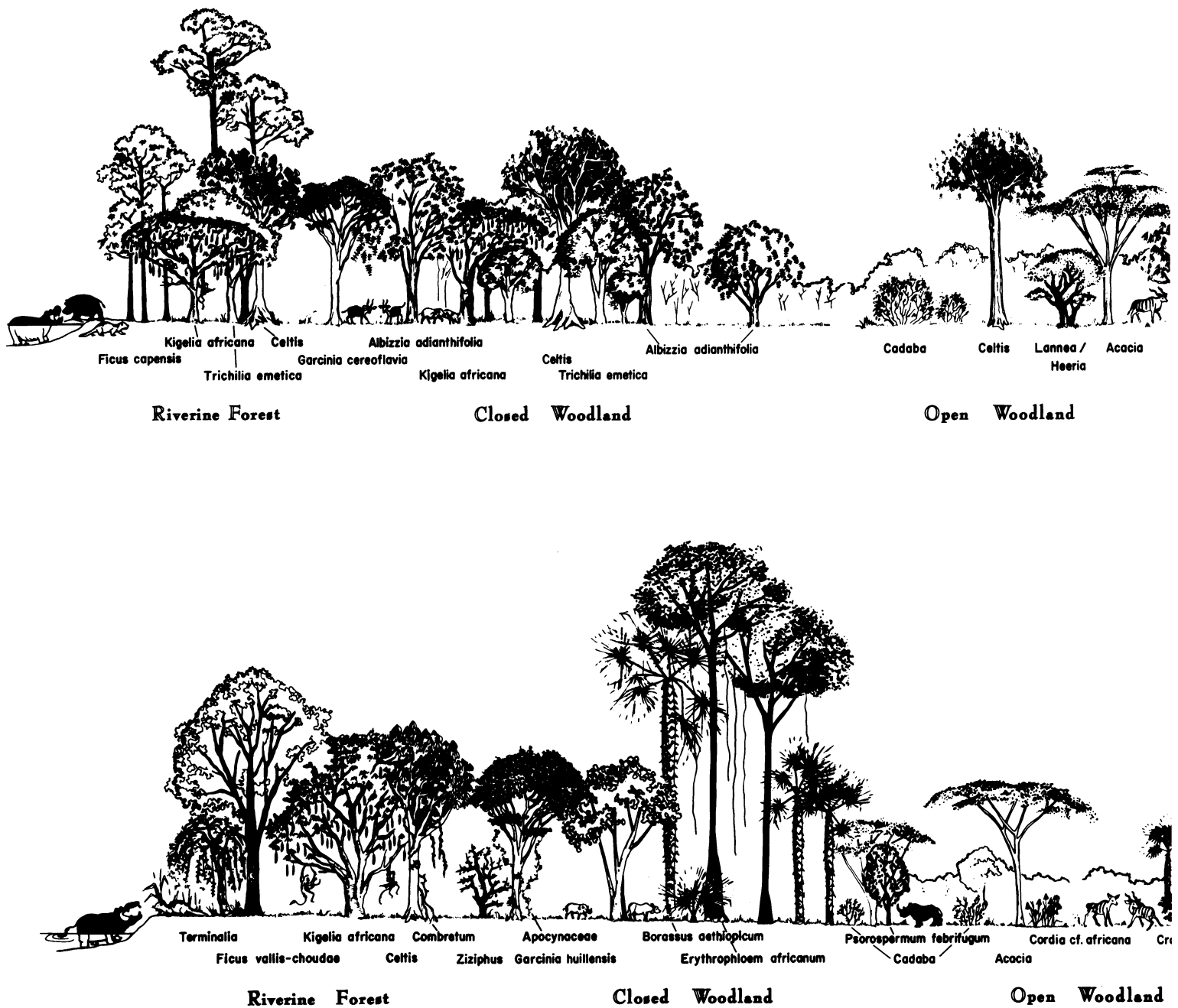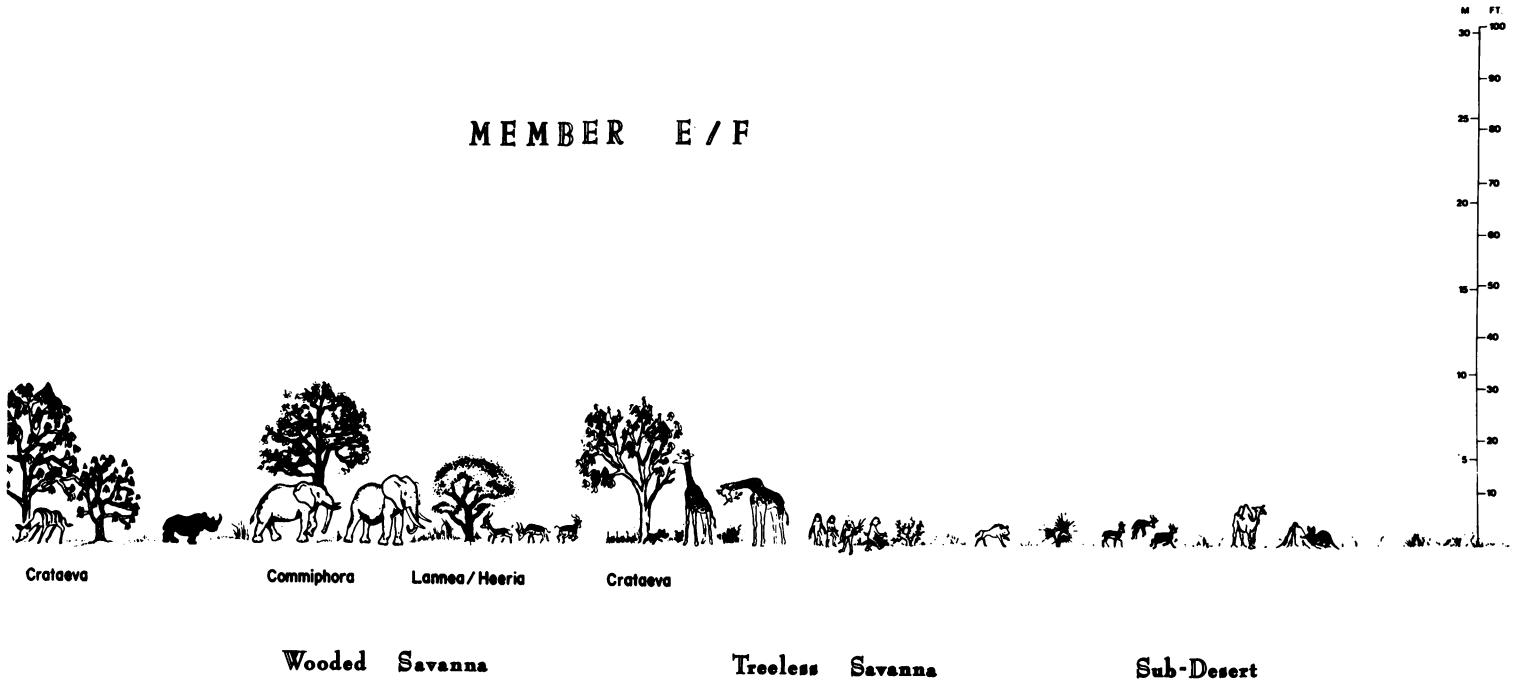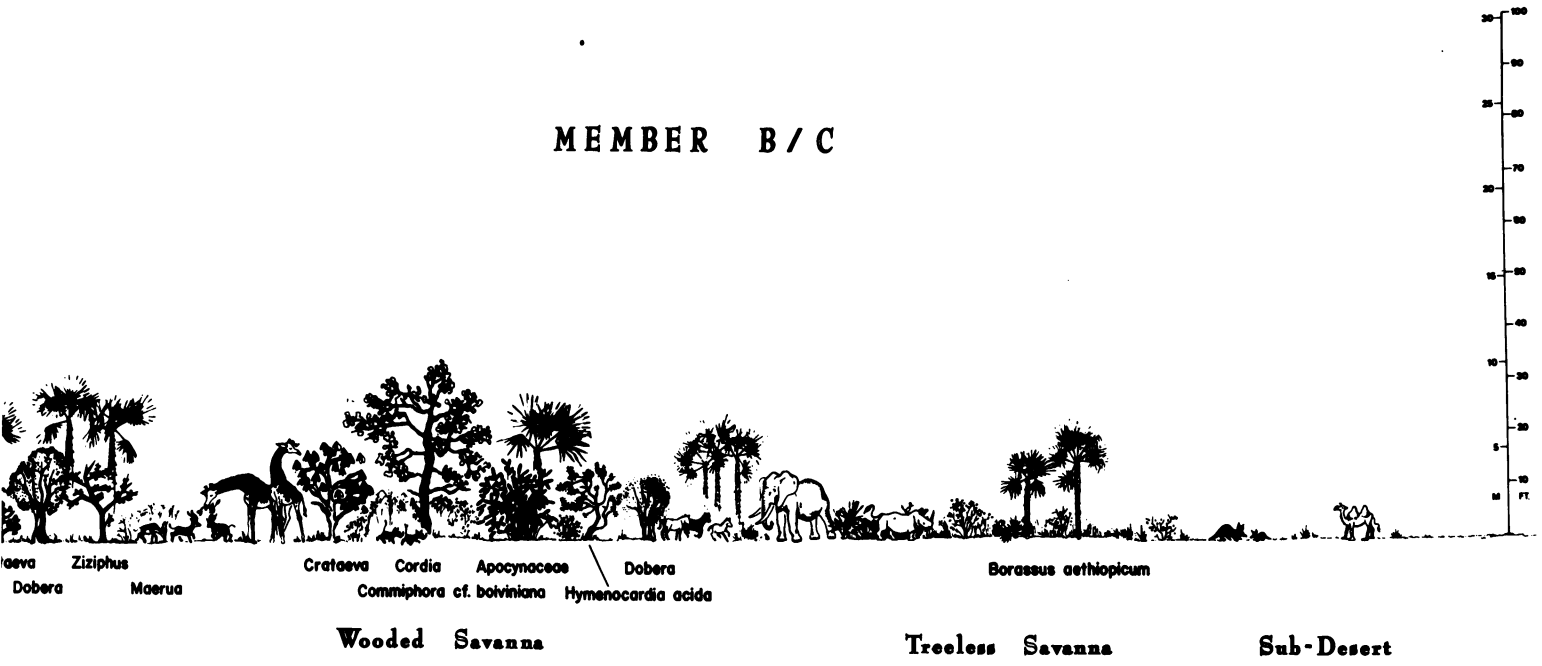
Figure 3. Semi-diagrammatic representations of identified flora from two levels (Members B-C, 2.9 to 2.5 m.y. BP; Members E-F, 2.1 to 2.0 m.y. BP) in the Shungura Formation (only vertical scale accurate) with fauna present in these levels and as used in this paper to be generally representative of habitats, included. Habitats and mammals depicted above are: riverine- *Hexaprotodon/ Hippopotamus;* riverine forest- *Enhydriodon,* Colobinae; closed woodland- *Tragelaphus nakuae, Metridiochoerus*/early *Mesochoerus limnetes, Syncerus* (?); open woodland-*Diceros, Tragelaphus gaudryi;* wooded savanna- *Ceratotherium, Elephas recki/Loxodonta, Aepyceros, Giraffa,* late *Mesochoerus limnetes/Phacochoerus, Hipparion;* treeless savanna- *Ceratotherium, Euryboas* (?), *Gazella, Australopithecus boisei* (?); sub-desert- *Orycteropus, Camelus.* (All these taxa certainly ranged into other habitats).

MEMBER E / F

Crataeva   Commiphora   Lannea/Heeria   Crataeva

Wooded Savanna   Treeless Savanna   Sub-Desert

MEMBER B / C

laeva Ziziphus
Dobera   Maerua
Crataeva   Cordia   Apocynaceae   Dobera
Commiphora cf. boiviniana   Hymenocardia acida
Borassus aethiopicum

Wooded Savanna   Treeless Savanna   Sub-Desert

forest. The Member F fauna in contrast shows fewer murid species and the presence of more open-habitat-preferring species such as *Gerbillurus, Jaculus, Heterocephalus*, a leporid and a savanna-adapted bat, *Coleura*. The murids present are more dry-adapted and no galagos are present. However, one *Hipposideros* bat indicates, as do the fossil wood determinations, that forest was still present, although reduced by Member F times.

The abundant large mammal fauna provides additional evidence for a drying trend in the Shungura Formation more by percentages of taxa than by presence and absence. *Camelus* and *Orycteropus* remains for example are known both from low in the sequence and higher (Figure 3; Grattard et al., 1976, Coppens and Howell 1976). Gentry (1975) notes that the probably forest dwelling bovid, *Tragelaphus nakuae*, decreases in abundance in relation to other species in Members F and G, and that the bovid fauna changes in Members E and G to more closely resemble the more arid Olduvai fauna. Ratios of numbers of alcelaphine plus antilopine dry-loving bovids compared to all other bovids (cf. Vrba 1976) indicates a more complex pattern of changes in relative bovid percentages (Figure 4). More research is needed to determine if this pattern is due to climatic change, increase in grasslands due to proximity of the lake or to taphonomic factors.
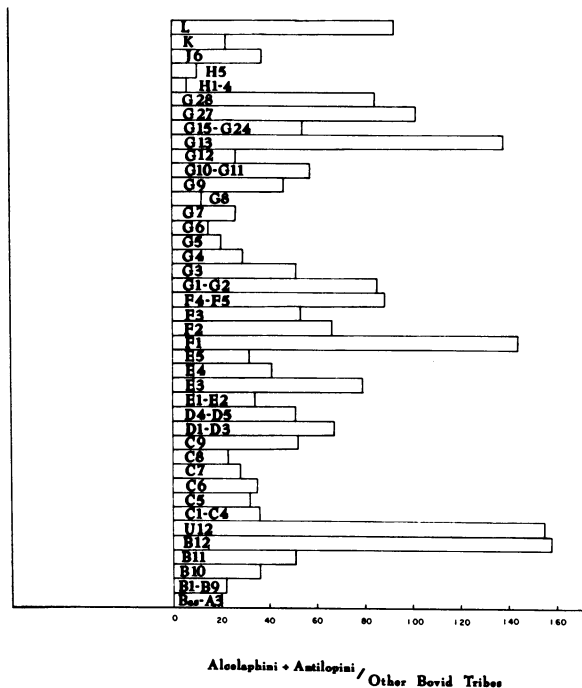

Figure 4. A comparison by unit of generally dry-preferring alcelaphine and antilopine bovids to other bovid specimens at Omo; as identified by A.W. Gentry. The interpretation of the four peaks apparent in this diagram is not clear but they are sugestive of a more complex climatic pattern of dry and wet phases than is indicated by other lines of evidence.

Other large mammals considered indicative of environmental habitats are shown in Figure 3.

The Shungura and Usno Formations have preserved fauna from a wide range of habitats (Figure 3) precisely because of the fluviatile nature of deposition. The paleobotanical and geological evidence themselves indicate habitats from riverine forest to treeless savanna/steppe or sub-desert. The microfauna and large vertebrate fauna confirm this. The palynological, geological, microfaunal and parts of the large mammal data equally well show a definite change toward a higher representation of more open environments in Member E (2.1 m.y. BP) and later.

Shungura Member E contains the first appearance of *Australopithecus boisei* in eastern Africa (Howell and Coppens 1976). Member E also contains the earliest evidence of manufactured stone tools *in situ* (Chavaillon pers. comm.) although it is likely that surface occurences indicate their presence as far back in time as Member B (de Heinzelin et al. 1976).

East Lake Turkana

Findlater (1976) has characterized the hominid-bearing sections of the Koobi Fora Formation as having been deposited by a main river flowing in a course similar to the Sagan River, from the northeast of Lake Turkana, smaller distributary streams, and a largely fresh-water paleo-Lake Turkana (formerly Rudolf; see also Bishop 1976). The lake was for the most part connected to the Nile drainage although drainage was intermittently internal to the basin. Findlater (1976) has also reconstructed a detailed paleogeographic history of the region through time.

Behrensmeyer (1975, 1976b, 1977) provides views of the paleoecology of the Koobi Fora Formation based on both geological and faunal grounds. She considers that the river systems at East Lake Turkana had smaller catchment areas than the Omo River to the north so that there were relatively great seasonal fluctuations in flow. This in turn indicates that seasonal migrations of mammals probably took place. Behrensmeyer (1977) suggests that the diversity of the fossil vertebrate fauna indicates "generally wetter conditions" in the Plio-Pleistocene compared to the semi-arid climate of the region today. Through analyzing three deltaic lake margin fossil assemblages and comparing them to two channel and one open mudflat samples, Behrensmeyer (1976a) concluded that lake margin deposits preserved more bush-preferring mammals while the fluvial situations generally preserved more grassland mammals. However, in later work on the hominid sites Behrensmeyer (1977, Table 6) found a predominance of the low-crowned suid *Mesochoerus*, probably a bush form, in the fluvially deposited localities, and an open-country alcelaphine bovid, *Megalotragus*, more highly represented in the lake margin habitats. These observations seem to vitiate earlier bush-lake margin and grassland-fluvial

correlations. Behrensmeyer's (1977) own paleo-environmental recontructions — lake margins "generally swampy, with extensive areas of mudflats which were seasonally covered with grass," and distributary systems with "coalescing gallery forests and interdistributary bush" — seem to contradict her environmental hypotheses based on the prior faunal data presented in the same paper (Behrensmeyer, 1977).

Bonnefille (1977) has identified in a pollen spectrum from the upper KBS Tuff and the lower-middle Tuff Complex (ca. 1.5 m.y. BP) species characteristic of dry woodland, perhaps an *Acacia/Commiphora* woodland. The hypothetical climate was neither excessively humid nor arid. Bonnefille has also discovered a surprisingly large proportion of montane forest pollen taxa in the Koobi Fora sample. These may have been transported from the highlands by the major paleo-Sagan River postulated by Findlater (1976) or montane forest may have existed at a lower altitude limit and thus may have been closer to the depositional environment.

Carbonel and Peypouquet (1976) report on seven ostracod species from the Upper Member of the Koobi Fora Formation, 71 m above the lower KBS Tuff. They suggest a lake with some alkaline tendency with a climate analogous to the present day. The fluctuations in paleo-Lake Turkana salinities derived from the ostracod sample from the Omo Group deposits (Carbonel and Peypouquet 1975, 1976) of course apply as well to the East Lake Turkana deposits.

Behrensmeyer (1976b, 1977) has reported that out of 65 hominid fossils she finds a predominance of the robust species in fluvial depositional environments whereas this species and the gracile occur in similar proportions in the lake margins. In view of the environmental ambiguities shown by the faunal evidence discussed above, this pattern would seem to have little paleoecological significance. Additionally, taxonomic assignations of several hominid specimens listed in Tables 1 and 8 of Behrensmeyer (1977) are no longer accurate reflections of current opinion. The point is mainly academic but it is possible that the pattern is not an overall trend, but an artifact caused by the exclusive presence of robust forms in an Area 105 channel deposit. This affects 5 robust specimens and if these are excluded from the sample (see Table 8, Behrensmeyer 1977) the deviation from a 50-50 representation is still statistically significant (Chi Square = 6.25, p$\leq$.025).

The large and diverse fauna from the Koobi Fora Formation (reported by various authors in Coppens et al. 1976) indicates a diversity of habitats ranging from perhaps closed or open woodland to treeless savanna or sub-desert. *Enhydriodon*, a giant, probably riverine-forest otter known from other East African sites, is absent at East Lake Turkana (M.G. Leakey 1976), while open-county canids are present, unlike the Omo succession (cf. Howell and Petter 1976). These faunal

characteristics, as well as the geological evidence, suggest that true riverine forests did not exist at East Lake Turkana.

Olduvai

Hay (1976) has summarized the geology and paleoenvironments at Olduvai Beds I and II, the levels from which early hominids are known. Bed I is composed primarily of lacustrine sediments deposited under saline and alkaline conditions as indicated by the presence of authigenic minerals (e.g. calcite, gaylussite and chert nodules). Streams also flowed into the southeastern and western borders of the lake as indicated by channels and alluvial sediments. The lake, which fluctuated between diameters of 7 and 25 km occupied a closed basin and was relatively shallow. The evidence of lake salinity and fluctuations, probably due to evaporation, indicates a climate that was "relatively dry over a long period" (Hay 1976:53). Fresh water emptied into the southeastern border of the lake by a stream and most of the faunal remains from Bed I derive from this environment.

Peri-lacustrine shore and swamp vegetation is indicated by vertical non-branching root casts and by identifications of *Cyperus papyrus* and cf. *Potamegeton*, typical marshland or shallow water plants.

Chrysophyte algae, characteristic of saline lacustrine conditions, are found near the same stratigraphic level in Bed I as freshwater gastropods. Urocyclid slugs almost anomalously suggest "damp conditions in evergreen forests" (Hay 1976:47). It is possible that these animals, as at Laetolil, lived in a damp microhabitat near water and were remnants of a former wider distribution when forests were more widespread over East Africa.

The Olduvai fauna has been published by L. Leakey (1965, 1970), M.D. Leakey (1971), Hooijer (1969), Petter (1973), Rage (1973), Jaeger (1976), Butler and Greenwood (1976), M.G. and R. Leakey (1973, 1976), and others. Hay (1976:47-48) summarizes some recent aspects of the fauna. On the basis of a change in bovid preponderance of water-tied reduncines in lower Bed I to a higher proportion of open-country alcelaphines, especially *Parmularius altidens*, and *Antidorcas recki*, an antilopine, in upper Bed I Gentry and Gentry (1973 pers. comm. to Hay 1976), suggest a drying trend. L. Leakey's (1965) faunal list shows such dry or open country taxa as *Saccostomus*, the pouched mouse, *Pedetes*, the spring hare, *Heterocephalus*, the naked mole rate (see also Jaeger 1976), 3 species of canids, *Diceros* and *Ceratotherium*, and hypsodont suids such as *Phacochoerus* and *Metridiochoerus* (following Cooke's 1976 taxonomy). More bush or wooded conditions are indicated by remains of soricids (shrews; see also Butler and Greenwood 1976), *Galago*, various murids (Jaeger 1976), *Potamochoerus*, the bush pig, and a low-crowned suid *Mesochoerus*. Jaeger (1976) has also noted a drying trend from lower Bed I (marsh-

land or moist savanna) to upper Bed I (drier savanna), indicated by increasing percentages of *Gerbillus*, bathyergids and sciurids. The avifauna, summarized by Brodkorb in Hay (1976:47) is abundant. Flamingoes indicate brackish water and seed-eaters suggest grasslands.

Bed II also preserves primarily peri-lacustrine depositional environments. Trona, a form of sodium carbonate formed under highly saline conditions, indicates a saline and alkaline lake with no outlet. Widespread aeolian sediment deposition indicates that vegetation cover at least seasonally was insufficient to prevent wind transport of sediment. Saline soils are indicated by the presence of zeolites (alumino-silicates). Coarse conglomerates and mudflows indicate rapid deposition of sediments during or following torrential rainfall in an arid or semi-arid climate with little ground cover. Deposits of caliche limestones and dolomite during Bed II times indicate that evapotranspiration exceeded rainfall.

Fauna from Bed II is summarized in L. Leakey (1965) and Hay (1976:93-94). Taxa overlap with Bed I forms. Alcelaphines and other bovids characteristic of dry savanna are dominant. *Ceratotherium*, a grazing rhinoceros, is more prevalent than *Diceros*, a browser. Urocyclid slugs are not present in Bed II. The faunal indications overall suggest drier savanna conditions than in Bed I.

All hominid remains from Bed I, both *Australopithecus boisei* and *Homo habilis*, occur at the southeastern border of the lake near a stream mouth and the incursion of fresh water. Here also are found most artifactual (Oldowan) occurrences (Hay 1976:180). In Bed II most of the hominid remains and Developed Oldowan tools occur within 1 km of the lake margin. Acheulian tool occurrences occur largely along stream courses greater than 1 km from the lake margin. Speth and Davis (1976) suggest that early hominid predation occurred primarily during the dry season as suggested by comparison with modern bushman prey percentages of bovids, carnivores and chelonians. Three of the four sites which appear to be rainy season occupation sites are the earliest at Olduvai. One of these, FLK NN, preserves a large percentage of *Pelusios castaneus*, the land tortoise, which probably hibernated during the dry season and thus would have been inaccessible to early hominids.

Cartmill (1967:191) suggests that the environment of the robust hominid (Old. Hom. 5) in Bed I was moister than that of the coeval *Homo habilis*. This statement is made on the basis that certain dry-preferring rodents such as *Gerbillus, Heterocephalus* and *Pedetes* are not present at FLK 1 (the Old. Hom. 5 site) but are present at sites FLK NI and FLK NNI, which have yielded *Homo habilis*. The suggestion seems unlikely in the absence of corroborating geological evidence, by the fact that other probable robust hominids (Old. Homs. 20 and 38) are known from the drier

(from Hay 1976) Bed II sediments, and in comparison with other East African sites.

Peninj

The *Australopithecus boisei* mandible from Lake Natron derived from the Humbu Formation of the Peninj Group, from directly under a transgressive phase of the lake (Isaac 1967). The transgression may be indicative of a slightly more humid climatic phase. Lake waters were fresh or only slightly saline, as indicated by abundant fish and the gastropod genus *Gabbia*. Isaac (Ibid.:251) concluded that in spite of small fluctuations, climatic conditions had been largely "very similar to those prevailing at present," cited as being "hot" and "dry" (p. 243).

The fauna as reported by Isaac (1967) contains few, if any, forest forms. Hypsodont suids, such as species of *Metridiochoerus* abd *Stylochoerus*, equids and rhinoceroses are predominant. Gentry (in Isaac 1967) reports a "rich diversity" of the generally dry-loving bovid family, the Alcelaphinae, and other open country genera. Only a "few" tragelaphine specimens and one reduncine specimen, with remains of *Elephas recki*, suggest wooded conditions.

The depositional environments were lacustrine or peri-lacustrine but the proto-Peninj River would not have been far distant. During accumulation of the sediments the site was some 600 m higher in elevation than it is now (Isaac, 1967:243). Dense masses of fossil root casts are suggestive of treeless savanna with shrubs and grasses while fossils of stem casts indicate the presence of bulrush swamps at the lake margin (Ibid.:251). Geological, faunal and floral indications suggest an environmental interpretation from wooded to treeless savanna.

Chesowanja

The two robust hominid individuals known from the Chemoigut Formation (KNM-CH 1 and KNM-CH 302) derive from a tuffaceous sand and a clay, respectively. Calcareous and calcrete horizons in this formation indicate that the lacustrine sediments were deposited under saline conditions (Bishop et al. 1975). The sediments indicate a depositional environment on the margin of a saline lake with a fluctuating water table (Ibid.:207).

The aquatic or semi-aquatic fauna includes a single gastropod species *(Bellamya* sp.) also known from the Omo sediments, a catfish, *Crocodylus* and *Hippopotamus*. Most of the mammalian fauna is indicative of open savanna: *Equus, Ceratotherium*, three species of hypsodont suids *(Metridiochoerus* and late *Mesochoerus)*, one species of antilopine and four species of alcelaphine bovids. But, as at Peninj, the presence of *Elephas* cf. *recki, Tragelaphus* and *Kobus* (a reduncine bovid) are suggestive of at least some wooded areas. The overall environmental indication is a treeless to wooded savanna, but probably unlike Peninj any trees

would have been distal to the lake margin due to the fluctuating water table and the saline lake water.

Stone artifacts such as cores, choppers and flakes, paralleling the "Developed Oldowan" from Olduvai and pre-dating higher Acheulian levels, are found in association with the two robust hominid specimens.

Overview and Conclusions

Table 3 lists hypothetical aspects important to the eventual elucidation of hominid paleoecology. It is analogous to a similar smaller table set forth by Behrensmeyer (1967b) but makes no assumptions on preferred habitats, behaviors or diets. Some of the parameters in Table 3 are more accessible to paleoanthropological proof than are others. No methodologies have yet been developed for investigation of many points not under physical environment. A brief and incomplete summary is offered below on the current status of research in these various areas. A more detailed discussion can be found in Boaz (1977).

Altitudinal reconstructions are complicated in East Africa by tectonic subsidence and uplift, but on the bases of geological and faunal evidence *Homo/Australopithecus africanus* sites range from lowlands, around 430 m above sea level (Omo, East Lake Turkana, Afar) to around 1300 m (Laetolil). All sites in South Africa yielding *A. africanus* are highland sites ranging from 1161 m above sea level at Taung (Peabody 1954:674), to 1478m at Sterkfontein, to over 1829 m at Makapansgat (Sampson 1974:18). *A. boisei* is known only from lowland sites in eastern Africa (Omo, Olduvai, East Lake Turkana, Peninj, Chesowanja), but there are no highland sites post-dating 2.1 m.y. BP. In South Africa the robust hominid, *A. robustus*, in known from Swartkrans and Kromdraai, both highland sites at 1478 m above sea level (Sampson 1974:18).

Temperature ranges are difficult to reconstruct but are probably similar for all known African Plio-Pleistocene sites. Temperatures varied between 22°C to 39°C, although mean temperature probably fluctuated by several degrees. There seems to be strong evidence for longterm vegetation change, especially in the Omo sequence, which is probably related to decreased precipitation from 3.0 to 2.1 m.y. BP. Rainfall today in the Omo is 320-380 mm/year and the upper range may have been greater in Members A to D. Mean annual rainfall at Taung may have been less than 300 mm (Cartmill 1967) and at Makapansgat over 500 mm (based on modern rainfall, Cartmill 1967). Boné (1960) suggested a rainfall as high as 711 mm/year (28 inches) for the Transvaal sites.

Gracile early hominid relationships to surface water seem to have been various: a river and lake margin environment was present at Lothagam and Hadar; small ephemeral channels and a single small pond were present at Laetolil; a meandering river in the Usno and lower Shungura Formations, with brief lacustrine phases; small streams at Makapansgat,

Sterkfontein and Taung. By contrast, robust australopithecines at least in East Africa occur where lake margin habitats are always present: Chesowanja and Olduvai Beds I and II (saline lake), Peninj, Omo and East Lake Turkana (slightly saline lake). Omo and East Lake Turkana also preserve riverine or channel environments. No robust hominids are known from more than 1 km distance from the Olduvai paleo-lake. However, at the highland Sterkfontein Valley sites, Swartkrans and Kromdraai, yielding robust hominids, streams were present. Hewes (1968) suggested a seashore locale as an optimal early (or "pre-") hominid environment. It is interesting to note that all coastal marine fossil localities dating from the upper Neogene, such as Langebaanweg (Southwest Africa), Sahabi (Libya) and Wadi Natrun (Egypt), lack hominids. The first hominid populations now known to have inhabited near-marine situations would belong to *Homo (erectus* or early *sapiens)*, e.g. Ternifine, Salé, Haua Fteah, Hopefield).

From what is known of paleosols at most hominid localities there seems to have been a wide range of soil conditions. Well developed and deeper soils (indicated by soil mulching and illuviation) tend to predominate in lower levels at Omo and less well developed soil horizons tend to be present later. No pattern is apparent, however, as *A. africanus* also occurs in regions with little or no soil development, such as at Laetolil.

Specific phytosocial aspects of early hominid habitats are not clear. Generally, it is true that greater tree and shrub density and greater herbaceous ground cover occur during Omo Members B through D, Sterkfontein and Makapansgat in relation to later sites in the same areas. But it is also true that *A. africanus* occurs in relatively open conditions at Laetolil. The robust hominid is associated with generally extensive grassland conditions but more mesic habitats were also present, at least at Omo, Olduvai and East Lake Turkana.

Determination of diet in early hominids is probably the most important aspect of paleoecology that needs to be elucidated. Elemental analysis of strontium content in fossil tooth enamel has proved inconclusive as a dietary indicator, at least on a large number of samples from Omo (Boaz and Hampel in preparation), and unpromising in South Africa (Wybenga and Wardale written comm. 1976; Vrba pers. comm.). Coprolite analysis may prove of use in determining dietary content if parasitological evidence can be adduced to show taxonomic affinities of the animals from which the coprolites derived. Samples from Omo are now being analyzed for this purpose.

The morphological studies discussed above suggest that at least gracile early hominids were adapted for a carnivorous or omnivorous diet, but as Garn (1976) has noted morphological indicators of diet are not conclusive.

Numbers of hominid individuals represented in

Omo excavated assemblages (Figure 5) and in surface collections (around or below 1%) are analogous to carnivore percentages. Comparable biomasses of hominids and carnivores suggest comparable positions in the food chain. A major assumption here is that hominids and represented carnivores (primarily felids, viverrids and lutrines), as relatively water-dependent forms had similar taphonomic probabilities of being preserved, while equids, rhinocerotids and giraffids were distal to the depositional environment and relatively taphonomically selected against.

Without basic data on the animal and plant contents of hominid diet the other dietary parameters cannot be dealt with. Basal hominid metabolism was probably in the range of 70kcal/kg$^{3⁄4}$ (based on Kleiber 1965) but actual energy requirements cannot be estimated. These values may exceed the basal metabolism by factors of 2 to 10 times (Hirst 1975). Water requirements of early hominids were certainly analogous to those of modern man and *Pan*, but solid food intake such as fruits may have supplied some of this need. Speth and Davis (1976) have suggested wet season hunting/food gathering behavior at Olduvai, but this is based on the assumption that the faunal remains there were actually accumulated primarily by hominids.

Population numbers can be estimated on the basis of excavation pyramids of numbers (Figure 5), taking taphonomic and biological variables into account. Ratios of excavated numbers of individuals of two taxa at L 398 at Omo are similar to ratios between the same two taxa in modern East African environments. For example, comparison of numbers of elephants to all bovids in a 600 km² short grass savanna area north of Lake Idi Amin Dada (ex-Edward; Bourlière 1965:203) is .07, and the elephant to bovid ratio in the L 398

excavation is .09. Hippopotamids are probably over-represented as fossils in the excavation because they are virtual total residents of the proximal community. This is reflected by higher ratios to bovid and elephant numbers in the fossil occurrence. L 398 suid numbers are also comparatively higher in comparison to these taxa. Only two suid taxa are present in the modern Lake Idi Amin Dada area compared to four relatively common suid taxa present during Member F time (Cooke 1976) and this accounts for their relatively higher numbers at L 398. Table 2 presents estimates of early hominid population densities calculated on the basis of modern mammalian densities for East Africa. The calculated values of hominid population densities are remarkably similar and range from .03 to 1.12 individuals per km² (Table 2). For the area covered by the Shungura exposures, approximately 200 square miles (518 km²), the hominid population would have been between 16 and 580 individuals.

Estimates of *Australopithecus africanus* heights range from 107 cm to 145 cm and estimates of weight, 18 kg to 27.6 kg (Lovejoy and Heiple 1970, 1972; Robinson 1972; McHenry 1974; Johanson and Taieb 1976). *Australopithecus robustus/boisei* heights have been estimated from 146 cm to 165 cm; weights from 43.2kg to 91kg (Burns 1971; Genet-Varcin 1969; Robinson 1972; McHenry 1976; see Thompkins, this volume, for further discussion).

Past research on early hominid paleodemography has been discussed above. Tobias' (1968, 1974) findings of differences in robust and gracile early hominid ages at death may reflect taphonomic differences in the deposition of the sites as much as real hominid populational differences. As discussed above Sterkfontein Type Site; with *A. africanus*, was probably the result of saber tooth felid accumulation, while
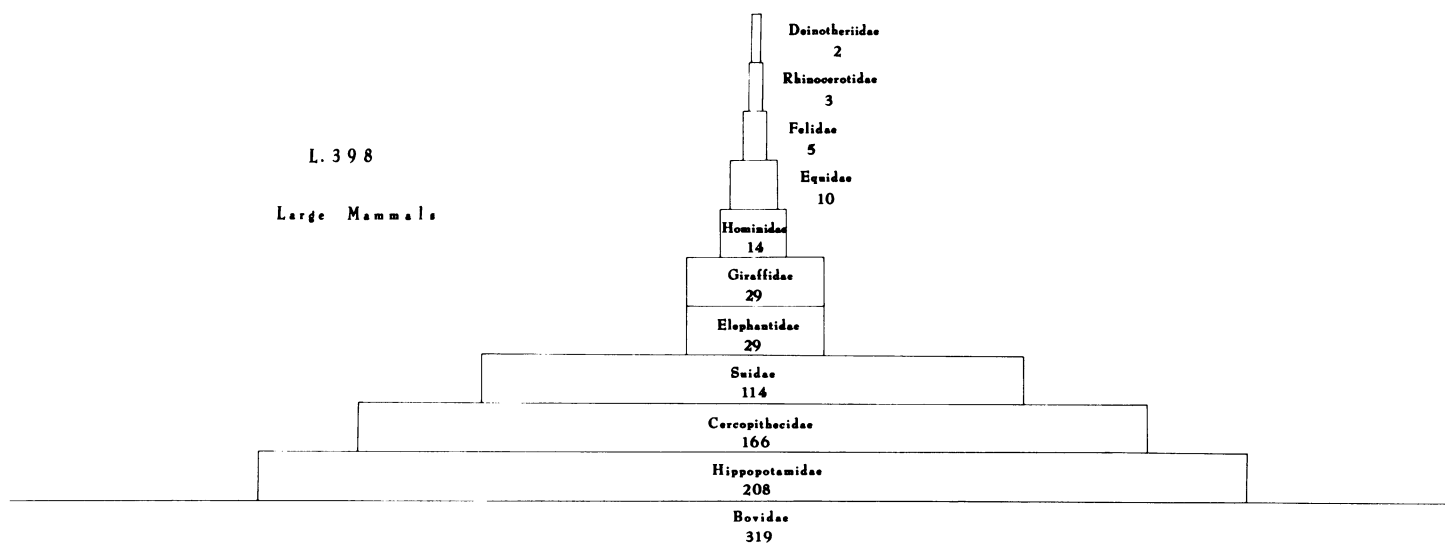

Figure 5. Pyramid of numbers of individual specimens (and probably of individuals) excavated at Locality 398, unit F-1 (ca. 2.0 m.y. BP) at Omo. If hominids were part of the "proximal community" their number indicates a carnivore-like position in the food chain.

L.398 Hominid Percentages of:			Modern Density Factor		Hominid Ind/km²
Cercopithecinae	.0843	X	1203/3261 km²	=	.03[1]
		X	374/114 km²	=	.28[2]
Bovidae	.0439	X	15265.5/600 km²	=	1.12[3]
Felidae	2.80	X	0.38/ind./km²	=	1.06[4]
		X	0.06 ind./km²	=	.17[5]
Elephantidae	.4828	X	1048.5/600 km²	=	.84[3]
Suidae	.1228	X	697.5/600 km²	=	.14[3]
Hippopotamidae	.0673	X	4800/600 km²	=	.54[3]

[1]Amboseli Park, Kenya; *Papio* population numbers from DeVore and Washburn 1963:338; area of park from Williams 1967:22.

[2]Nairobi Park, Kenya; *Papio* population numbers from DeVore and Washburn 1963:338; area of park from Williams 1967:54.

[3]South of Lake Idi Amin Dada (ex-Edward); Bourlière 1965:203. Densities are averages for two years.

[4]Lake Manyara Park, Tanzania; *Panthera leo* population density during period of high prey biomass(Schaller and Lowther 1969).

[5]Kruger National Park, South Africa; *Panthera leo* population density during period of low prey biomass (Schaller and Lowther 1969).

Table 2. Calculations of hominid population densities 2 m.y. BP in the lower Omo basin, on the basis of percentages that hominids comprise of various large mammalian taxa excavated from Locality 398. Comparative modern mammalian population data are from studies in East Africa, as cited.

Swartkrans Member 1 and Kromdraai B, with *A. robustus*, were accumulated by leopards and hominids, respectively, according to Vrba (op. cit) and Brain (op. cit.) The pattern observed by Tobias (1968, Table 2), that gracile hominids showed a greater proportion of child-bearing-age individuals, is caused primarily by the Sterkfontein sample (N=46; the 16 Makapansgat specimens, divided 6 and 10, do not significantly affect the result). The four-to-one ratio of child-bearing to pre-child-bearing age specimens at Sterkfontein could be due to a larger prey specialization of the large saber tooth felid hypothetically responsible for the assemblage. Aging of specimens from East African localities can be expected to clarify the paleodemographic patterns among early hominids. Since populational statistics by definition require large sample numbers further discoveries of hominid remains will also enable more definitive statements to be made.

Unfortunately, at this stage of investigation little if anything can be said concerning intra- and interspecific relations of early hominids. This situation can be expected to improve when more knowledge on habitat and diet has been gained. There is no dearth of "models" with which new data can be compared. A comparison of numbers of robust and gracile hominid specimens (reflecting numbers of individuals) from individual sites, taking taphonomic factors into consideration, would shed light on comparative biomasses of the two taxa in the same area. Using Howell's (1977) taxonomic assignments for hominids from Olduvai Beds I and II, the Koobi Fora Formation and Omo Member E and above, ratios of raw numbers of robust to gracile specimens are .47, 2.5 and .35, respectively. A numerical preponderance of robust hominids, as would be expected if these were herbivorous animals, is only seen at East Lake Turkana. If the "dietary hypothesis" is true, these results might be due to robust hominids inhabiting environments distal to the depositional site.

The earliest manufacture of stone tools is an important area of continuing research. At present, *in situ* stone tools appear first at Member E of the Shungura sequence (2.1 m.y. BP) at the same time that *A. boisei* appears. Bishop et al(1976) have noted that stone tools are present at Chesowanja where only *A. boisei* remains have been recognized and they have posed the question, "Who made the tools?" There are no early hominid occurrences in East or South Africa with tools without *A. boisei*, whereas *A. africanus*, without stone tools, is·known from pre-Member E, Shungura, and Usno Formations (Omo), Hadar, Laetolil and Sterkfontein Member 4. There is no hard evidence to point to either the robust or gracile hominid species as the maker of stone tools but if future research confirms the surface occurrences of artifacts in Member B of the Shungura Formation this would indicate stone tool manufacture before the appearance of the robust hominid in East or South Africa.

Many larger paleoecological questions, such as those concerning early hominid dispersion, hominid ecological relationships between East and South Africa, between these areas and other parts of Africa and between Africa and Eurasia, geographic origins of the gracile and robust early hominids and early hominid niche specializations, remain to be dealt with. The complete answers to these questions lie in the future but some suggestions based on data discussed above can be made.

Robust hominids appear in East and South Africa at around 2 m.y. BP, on the basis of radiometric and faunal ages, in environmental contexts that are decidedly dry. This observation prompts several questions, such as: 1) Where were the robust australopithecines prior to 2 m.y. BP?, 2) What environments did they live in?, 3) Why did they appear at around 2 m.y. BP?, 4) Why did they disappear around 1 m.y. BP?, 5) What was the relationship of the robust species to the gracile during this period of time?

It is doubtful that the robust australopithecine came from the West African forest. All of the known robust hominid sites occur where dry conditions were present in at least part of the environment. This would imply that these forms were savanna-adapted animals, but this argument is not overly convincing since there are no forested fossil sites for comparison. A more convincing argument is that the absence of these forms in sites earlier than 2 m.y. BP with environments similar to later robust hominid sites is due to an inability to disperse through large tracts of forest. Kingdon (1971:69-71) has shown the presence of two forest

routes from the West African forests into East Africa, accounting for mammalian distributions, and Bone (1960) has noted that even today Makapansgat lies on the southern limit of central African mammal ranges. Robust hominids therefore if they had been forest forms and if they had lived in West Africa, could be expected to have been present in eastern and southern Africa prior to 2 m.y. BP Even though claims have been made for Oldowan "pebble tools" in West Africa the oldest direct fossil evidence is Neolithic (Descamps 1968).

Hominid Paleoecology

Physical environment:
  Altitude   Mean wind speed
  Temperature   Degree of wind gusting
  Rainfall   Mean cloud cover
  Relative humidity   Surface water availability
  Insolation   Surface water salinity
  Soil:
    Development
    Physical composition
    Chemical composition
  Tree and shrub density   Habitat selectivity
  Shade cover   Herbaceous basal cover
  Degree of clumping of   Grass and forb height
    woody plants

Diet:
  Content: Metabolic energy
    Animal   requirements
    Vegetable   Energy intake
    Soil (geophagy)   Digestibility
  Manner obtained   Time of feeding
  Manner eaten   Season of feeding
  Drinking

Population:
  Numbers   Mortality
  Weights   Birth spacing
  Growth   Sexual maturity
  Natality

Intraspecific relations:
  Grouping   Division of labor
  Group interaction   Distances between group
  Sexual relations   sleeping sites
  Dominance interactions   Grooming

Interspecific interactions:
  Cooperation with other species   Prey
  Competition with other species   Predators
  Tolerance of other species

Other behavior:
  Extent of daily movement   Group activity at various
  Tool use and manufacture: times of the day:
    material, source, use   Feeding intensively
  Sleeping place   and/or moving rapidly
  Vocalizations   Feeding leisurely
  Diurnality/nocturnality   and/or resting
                              Resting

Table 3. Parameters of interest in hominid paleoecological studies, derived from a variety of modern ecological studies by Hirst (1975), Clark (1954), Bourlière (1965), Schaller and Lowther (1969) and others.

The suggestion made here is that robust australopithecines invaded East and South Africa from the north. Palynological evidence (Van Campo 1975) indicates that much of the Sahara in the Plio-Pleistocene was open woodland or savanna. Carcasson (1964) notes that the Sahara has acted as a barrier for sylvan but not savanna butterfly species. In respect to modern plant distribution, he states, "the scarcity of floral exchanges between tropical Africa and Mediterranean Africa suggests that whatever its past position, the Sahara has been an effective barrier for a very long time, possibly since the middle Miocene" (Carcasson 1964:127). If robust hominids were savanna forms intolerant of forest, and they inhabited North Africa, they would have been kept out of eastern and southern Africa by a line of forest known as the "Sclater Line" (Davis 1962) or the "northern forest route" (Kingdon 1971:79), stretching from the Congo basin to the Tana River basin in Kenya. Circumnavigation of this barrier would have been impossible in the west because of the lowland forest and in the east by the forests of the Ethiopian mountains, both of which are still present today. Entrance into eastern Africa would have been possible when forest thinned out and retreated in the lowland area north of Lake Turkana, during a time of decreased rainfall, as is indicated in the Shungura sediments by palynological, sedimentological and faunal data.

Interconnection of eastern and southern Africa seems probable on the basis of Kingdon's (1971:63) demonstration of an arid corridor from Southwest Africa to Somalia which served for the dispersal of dry-adapted animal and plant species now with disjunct distributions. This supposition would seem supported by the similar times of appearance of the robust hominid in East and South Africa. However, Kingdon's (1971:69-71) "southern forest route" across the African Ghats north of Lake Malawi may have had some disruptive effect.

Little definite can be said concerning the dispersal and origin of the gracile hominid. It may be an indigenous form evolved *in situ* in sub-Saharan Africa but the presence of gracile hominoids outside Africa in the Neogene makes this supposition unsupportable at present. There is definite co-existence of the gracile and the robust homind species for some one million years, but how they ecologically partitioned their shared environment is unknown.

Notes

[1]Although no reference is given, Keith is referring to E.H.L. Schwarz, whose cursory environmental reconstruction of the Kalahari region based on former presence of certain large mammal species, is summarized in Schwarz (1920). Rogers (1922:17) successfully refutes this argument by noting that such animals as hippopotamus, rhinoceros and quagga no longer occur in the area due to man's influence and not to climatic change.

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