

# Environmental determinants in early hominid evolution: issues and evidence from the Tugen Hills, Kenya

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**Abstract:** Evidence of hominid/hominoid palaeoenvironments collected from the Tugen Hills succession has been key in appreciating the diversity of habitats that characterized the East African Rift Valley over the last 15.5 Ma. Isotopic analyses of fossil herbivore enamel, palaeosol carbonates and preserved organic matter from the Tugen Hills provide a means of reconstructing plant biomass based on differences in photosynthetic processes. In modern tropical ecosystems, carbon isotopic variation can be used to distinguish different physiognomic types of plant communities – in general differentiating ‘open’ vs ‘closed’ habitats. Isotopic data from palaeosol horizons in this sequence indicate that throughout this interval of time, at various locations in the Tugen Hills, slightly open woodland-like environments were available for hominoids and early hominids to exploit and that environments similar to modern East African grasslands at no time dominated this part of the rift valley. Analyses of a number of fossil herbivore taxa from the sequence indicate an increase in the dietary importance of C<sub>4</sub> grasses in the late Miocene. Cumulatively these data, in conjunction with palaeobotanical evidence, suggest that past environments in the Tugen Hills region were heterogeneous in both space and time from the middle Miocene through the Pleistocene.

When Darwin (1871) first suggested that hominid origins might be linked to environmental change he established a paradigm which remains central to most theories of human evolution. Many of the behavioural and morphological changes documented in the fossil hominid record have tentatively been linked to the general notion that forests were replaced by more open grassland and woodland habitats in East Africa during the late Miocene and Pliocene, presumably as a response to increasing aridity and cooler temperatures. The tempo and mode of this vegetational succession, informally referred to as the savanna hypothesis, has never been explicitly articulated but has nevertheless become entrenched as a theme in palaeoanthropological literature. This theoretical perception remains an attractive construct as it reconciles well with the traditional premise that major stages of human evolution unfolded as a response to increasingly open environments. In addition, directional global climatic change through the Neogene, well documented in the marine record, appears to support the possibility of progressively more arid and seasonal terrestrial conditions in Africa (Miller *et al.* 1987; Crowley & North 1991; deMenocal & Rind 1993; Kennett 1995). While most researchers interested in the role of environmental factors in hominid evolution recognize this scenario as probably somewhat simplistic

and generally unsubstantiated, they also appreciate that it potentially incorporates elements of truth. As such, the savanna hypothesis has endured to the extent that it is typically invoked in examining aspects of hominid evolution without reference to any supporting data. The circularity of linking early hominid traits interpreted as adaptations to open terrain with the concept of grasslands replacing forest in East Africa has been noted by previous researchers (such as Hill 1987) and recently there have been a number of discussions expressly challenging the hypothesis (Kingston *et al.* 1994; Hill 1995; Potts 1996; Shreeve 1996; Feibel 1997). Based on accumulating evidence, the emerging consensus is shifting to the view that the evolution of landscapes in East Africa relative to early hominids is complex. Simply invoking the directional development of open habitats as selective pressure for hominid speciation or extinction events is insufficient and possibly misleading. This perspective is also not novel. In 1962 after six years of field investigations in East Africa, Bill Bishop wrote:

‘It seems probable that with a combination of climatic variations and a diversified landscape containing a wide range of vegetation zones within a small compass, together with numerous lake basins of changing form, East Africa provided a patchwork of environmental niches

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which were ideally suited to man's development of varied techniques and ways of life.'

Although this comment was framed in the context of the Pleistocene, it is clear that the considerations that led to this deduction apply equally well to earlier periods in the Neogene.

### Nature of the fossil record

The difficulty in discussing early human evolution within the context of a palaeoecological framework is due primarily to the poor quality and resolution of the hominid/hominoid, faunal, floral and environmental fossil records available for study. While the course of human evolution was surely mediated by environmental change, empirical evidence from East Africa as yet remains too incomplete to support or refute these long-term directional environmental trends and potential correlations between evolutionary change and environmental shifts. In addition, distortions to the record related to taphonomic and collection biases further complicate interpretations.

A scrutiny of the assumptions underlying the notion that environmental factors direct the path of early hominid evolution reveals a number of fundamental, unresolved issues which need to be addressed in justifying this approach. One rudimentary question involves the relative significance of biotic and abiotic factors as driving mechanisms of evolution. Are physical changes in the environment necessary for speciation and extinction, or are biotic interactions such as competition, predation, parasitism and mutualism sufficient engines of evolution? Although a number of theoretical models advocating either biotic factors or perturbations in the physical environment as primary forces in evolution have been proposed (Van Valen 1973; Stenseth & Maynard Smith 1984; Vrba 1985*a*, 1995*a*), the fossil record, especially in the terrestrial realm, has yet to provide unequivocal support for any of these models. Alternatively, both biotic and abiotic factors are involved and the relative importance shifts depending on the specifics of intrinsic and extrinsic environmental and evolutionary factors.

Sidestepping the abiotic/biotic debate, a number of studies have implicated major global changes in climate and environment as the driving force in the evolution of early hominids (Bonnefille 1984; Prentice & Denton 1988; Stanley 1992, 1995; deMenocal 1995; Vrba *et al.* 1995). The underlying assumption in these hypotheses is that while biotic forces may have been factors, major physical perturbations of the

ecosystems were critical to what are perceived to be major adaptive shifts in our ancestry. The origin of Hominidae, provisionally defined by the advent of bipedality, has been linked to a shift to more open environments in East Africa which in turn has been linked to the Mediterranean Messinian salinity crisis between 5.6 and 5 Ma (Brain 1981; Laporte & Zihlman 1983; Ambrose 1995). Similarly, the apparent radiation of hominid species during the Pliocene has been linked to global cooling (Brain 1981; Bonnefille 1984; Grine 1986; Prentice & Denton 1988; Stanley 1992; deMenocal 1995; Vrba *et al.* 1989; Vrba 1995*a, b*). Although the specifics of hominid phylogeny are currently debated (e.g. Wood 1992; Wood *et al.* 1994; Suwa *et al.* 1996), the Plio-Pleistocene hominid fossil record of Africa indicates that there were at least four species within the genus *Australopithecus*, two or three species of *Paranthropus*, and up to four species of the genus *Homo*. Coincident with the earliest appearance of the genus *Homo* (Hill *et al.* 1992) is the oldest evidence for lithic artifacts dated 2.6–2.5 Ma (Semaw *et al.* 1997). In general, it has been assumed that the increase in species diversity and evidence of behavioural changes within the human lineage during this interval also reflect the replacement of forest environments by more open woodland and grassland environments. This increase in habitat diversity is linked in turn to the onset of northern hemisphere glacial cycling and resultant increase in low-latitude aridity.

While it is tempting to invoke global climatic change as a causal mechanism for hominid evolution, it is unclear how or if major climatic shifts detected in marine cores are reflected in the interior of continents. During the late Pleistocene, increased fluxes of aeolian dust to marine sediments off the African coast (deMenocal & Rind 1993), abrupt lowering of lake level in central and East Africa (Street-Perrott & Perrott 1990) and expansion of arid African vegetational zones (Pokras & Mix 1985) are coincident with high-latitude glacial advances. Recent analyses of terrestrial detritus in marine cores sampled off the African coast (deMenocal 1995; deMenocal & Bloemendal 1995) indicate that at 2.8 Ma the African climate became dependent on the rhythm of high-latitude glacial cycling, manifested by the onset and intensification of seasonally cooler and arid cycles in Africa. These changes are linked to ecological fragmentation and establishment of arid-adapted species in Africa. Although these data indicate that the African climate in general was tracking global shifts in the Pliocene and possibly earlier on in the Miocene, the effects on specific hominid

habitats and ecology remain unclear. Superimposed on the influence of global climatic change are alterations in local hominid habitats induced by crustal doming, volcanism and graben formation in East Africa. In addition to creating topographic and hence habitat heterogeneity, orographic effects probably had a significant influence on regional atmospheric circulation. Eruption of volcanic debris can have profound effects on a regional and even global scale, disrupting atmospheric circulation patterns and drastically altering ecosystems proximal and, in some cases, distal to the eruptive centre. Teasing apart the relative contribution of local, regional and global events to changes in East African environment remains extremely difficult given the complex interrelationships between these extrinsic factors as well as the fragmentary nature of the local palaeo-environmental record.

Fossil fauna associated with early hominid specimens potentially provides the most relevant and detailed information on possible habitat alteration and resulting ecological pressures on the various hominid species. Environmental shifts implicated in hominid evolution would mostly likely be detected in the evolutionary pathway of contemporaneous taxa. The difficulty in this approach, however, is controlling for all the interpretive, taphonomic and ecological factors that can either obscure or mimic true links between extrinsic factors and faunal turnover. Even recognition and characterization of faunal turnovers in general are problematic and require extensive temporal and geographic continuity in faunal data sets (Barry 1995; White 1995) as well as high resolution chronological control and uniform taxonomic classification. Typically raw palaeontological data from the terrestrial realm lack these attributes. Vrba (1985a) articulated a 'turnover pulse hypothesis' which proposes that faunal change resulting from climatic events should be synchronous in separate lineages. Turnovers in bovid taxa (Vrba 1985b) and micromammal taxa (Wesselman 1985) between 2.7 and 2.5 Ma in Africa have been cited as support for the turnover pulse hypothesis. The validity of this theory has been questioned (Hill 1987, 1995; Prothero 1995) and recently more specific biostratigraphic analyses by Bishop (1994), Bishop *et al.* (1999), White (1995) and Behrensmeyer *et al.* (1997) suggest that the speciation and extinction of East African fauna between 3 and 2 Ma does not track climatic change in any obvious way. A key element in understanding and interpreting potential links between environmental and evolutionary factors is resolving the specific timing of events.

Are environmental shifts abrupt or gradual? Is there a lag time required for communities to respond to changing abiotic conditions? Do different types of taxa or assemblages of taxa respond differentially? Are environmental shifts directional over the course of geological time or do they oscillate about a norm? Potts (1996) has suggested that hominid evolution is linked to a pattern of dramatic, episodic environmental oscillations rather than discrete events.

Assuming that the fossil taxa respond to environmental change induced by climatic shifts, it becomes necessary to differentiate faunal turnover due to *in situ* speciation and extinction from immigration, which may also correlate with climatic fluctuations. Faunal interchange is viewed as a significant process in the evolution and differentiation of terrestrial mammalian communities during the Neogene (Flynn *et al.* 1991; Janis 1993; Barry 1995; Opdyke 1995). The timing and location of these intercontinental migratory events are controlled to an extent by climatic events but also by tectonic change which can facilitate dispersal by the formation of 'corridors' in regions where interchange was previously restricted by geographical or ecological barriers. As barriers are transgressed, speciation and extinction occur as introduced faunas interact with novel ecosystems. Major faunal turnovers in terrestrial successions have been linked with the creation of 'corridors' formed by low sea level stands or by the tectonic reshuffling of land masses (Barry *et al.* 1985; Thomas 1985). Alternatively, the formation of barriers can separate previously continuous populations resulting in speciation by vicariance.

Correlating hominid evolution with environmental change ultimately requires developing a detailed palaeoecological perspective based on empirical data collected from terrestrial sequences in East Africa rather than relying on global climatic and tectonic events or habitat reconstructions documented elsewhere. Existing information for the late Miocene and Pliocene of East Africa is limited and interpretation of palaeohabitats based on different lines of evidence often appear incongruous (e.g. Fort Ternan: Andrews & Nesbit Evans 1979; Bonnefille 1984; Shipman 1986; Dugas & Retallack 1993; Cerling *et al.* 1997a). These apparent discrepancies most likely relate to the complex nature of past ecosystems as well as comparison of data from different stratigraphic levels rather than flawed analyses. These studies emphasize the need to develop and synthesize as many approaches to palaeoenvironmental reconstruction as possible. Within the past decade, stable isotopic analyses of fossil material which forms

in equilibrium with vegetation has been used to constrain interpretations of the vegetational physiognomy of palaeohabitats as well as aspects of palaeodiet. This technique provides an additional tool for semi-quantitative reconstruction of palaeoenvironments. Isotopic analyses of palaeosol components and fossil herbivore enamel collected from the Tugen Hills succession provide information on palaeohabitats in the Baringo Basin over the last 15.5 Ma.

### Tugen Hills

In the northern Kenya Rift Valley, the rift structure consists of a half-graben, characterized by marked asymmetry (Frostick 1997). In the Tugen Hills region of the rift, the Elgeyo Escarpment forms the main boundary (border) fault on the western escarpment while the eastern margin of the rift is characterized by antithetic and synthetic faults with much smaller throws which cut the structure into a series

of tilted fault blocks (Fig. 1). The Tugen Hills is a complex fault block uplifted along a synthetic fault (Saimo or Kamasia Fault) between the Elgeyo Escarpment and the axial Baringo–Suguta trench (Chapman *et al.* 1978). The rift in this area was initiated as a downwarped trough in the early to middle Miocene and served as a depositional basin for thick sedimentary sequences interbedded with intermittent phonolitic and basaltic lava flows. About 7 Ma, the ‘proto-Tugen Hills’ was formed by extensive normal faulting along the main Kamasia (Saimo) fault. After considerable erosion, late Miocene/Pliocene volcanics and sediments were deposited and then tilted and faulted in a second major rift-faulting episode (2–0.5 Ma). This event resulted in final uplift of the range and exposure of Miocene/Pliocene sequences in fault scarps along the eastern foothills of the Tugen Range.

As a result of its complex depositional and structural history, the Tugen Hills succession (Fig. 2) exists as a series of disjunct fault-bounded blocks. Sedimentation within each of

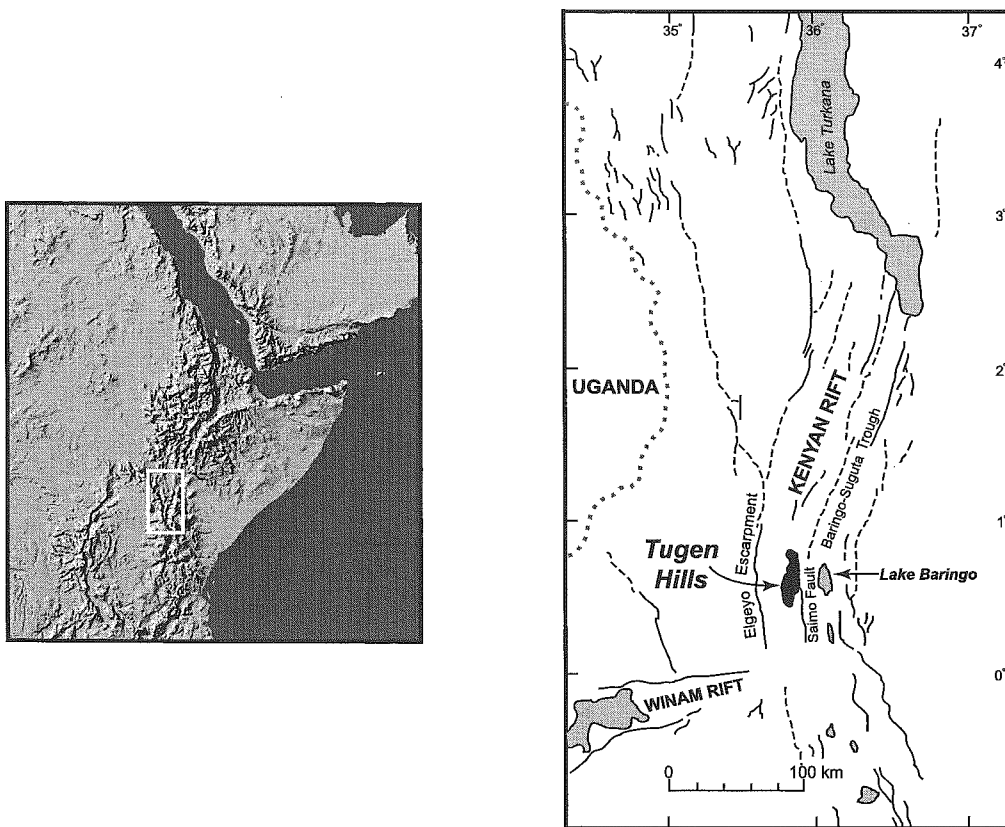


Fig. 1. Location of the Tugen Hills within the East African Rift Valley of Kenya.

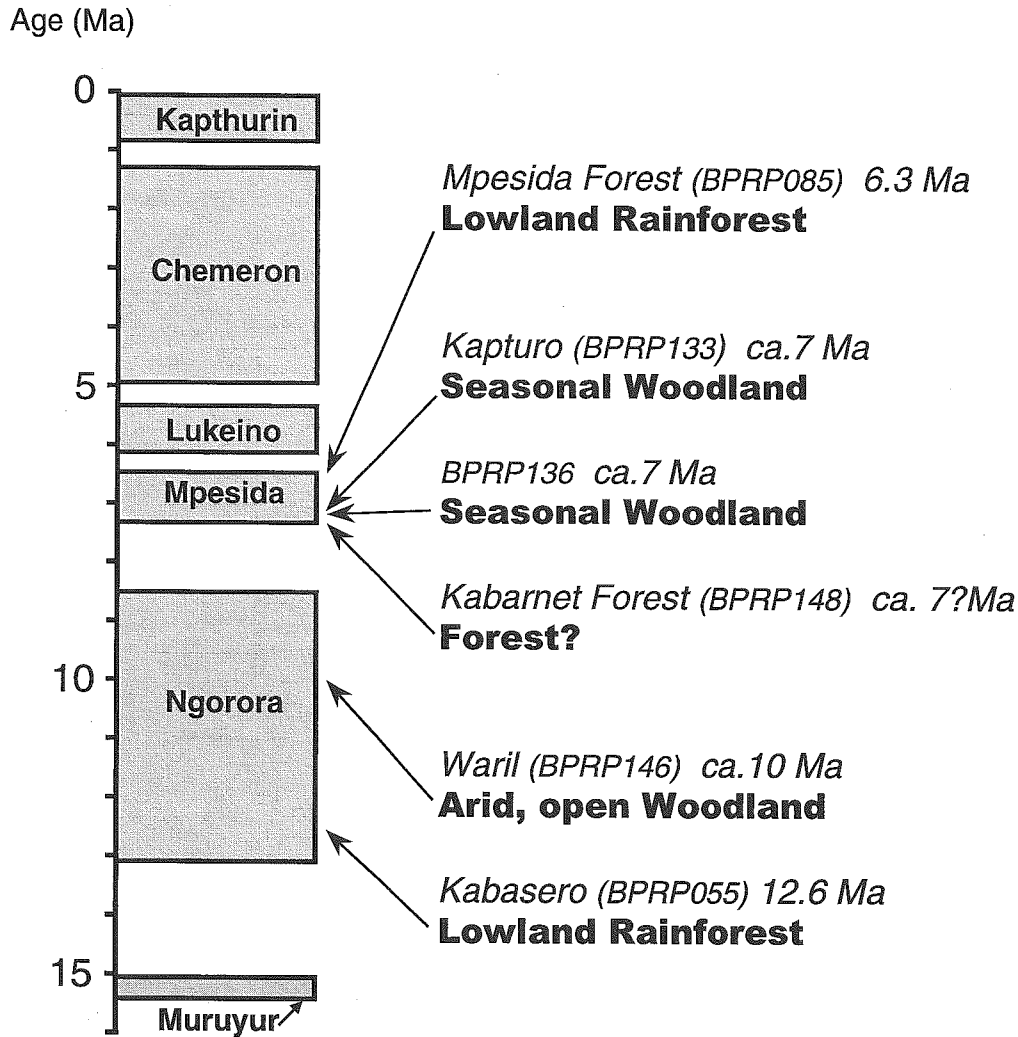


Fig. 2. Middle to late Miocene palaeohabitat reconstructions in the Tugen Hills succession based on palaeobotanical assemblages (Jacobs & Kabuye 1987, 1989; Jacobs & Winkler 1992; Jacobs & Deino 1996; Jacobs pers. comm.). Temporal span and formational designations of sedimentary units are depicted in the shaded rectangles. BPRP numbers refer to Baringo Paleontological Research Project site designations.

these blocks was localized and there is considerable lateral facies variation complicating direct correlation between structurally displaced sections. Establishment of a stratigraphic framework has relied on palaeomagnetic studies as well as geochemical analysis and radiometric dating of interbedded volcanic flows and associated volcanoclastic units (Chapman & Brook 1978; Dagley *et al.* 1978; Tauxe *et al.* 1985; Deino *et al.* 1990). Details of the 3000+m of intercalated Miocene and Pliocene sediments and volcanics exposed in fault scarps and eroded

surfaces along the eastern foothills of the Tugen Hills are described in Martyn (1969), Bishop *et al.* (1971), Chapman (1971), King & Chapman (1972), Pickford (1975, 1978*a, b*), Hill *et al.* (1986) and Hill (1994, 1995, 1999).

The long succession of fossiliferous sediments exposed in the Tugen Hills provides an opportunity to investigate the pattern of African Neogene faunal change in some detail, sampling intervals of time not well documented elsewhere in sub-Saharan Africa. The sequence has also yielded palaeofloral samples and biogeochemical

data that contribute to our understanding of the ecological context for the origin and development of the Ethiopian fauna including early hominids. Significantly, this sequence also provides the opportunity to document environmental change within a discrete portion of the rift, circumventing the confounding effects of splicing together a composite profile based on data collected from sites of different ages that are hundreds of kilometres apart. Faunal change can be detected between all five major formations and also within the duration of the Ngorora and Chemeron Formations (Fig. 2) (Barry *et al.* 1985; Hill *et al.* 1985, 1986; Hill 1987, 1994, 1995, 1999). The most notable interval of faunal change occurs between the Ngorora assemblages and the Mpesida Beds which includes the appearance of whole new families such as the Elephantidae and the first leporids in sub-Saharan Africa, the rhinoceros *Ceratotherium* and various new species in established genera.

### Isotopic evidence for palaeoecological reconstructions in the Tugen Hills

#### Theoretical background

Partitioning of two naturally occurring stable isotopes of carbon,  $^{12}\text{C}$  and  $^{13}\text{C}$ , in terrestrial plants, soil carbonates, soil and sediment organic matter, and ultimately herbivore tissue is in part a function of different ecophysiological adaptations of plants. During the first stage of photosynthesis (carboxylation), as plants assimilate carbon from the atmospheric  $\text{CO}_2$  reservoir, the lighter isotope ( $^{12}\text{C}$ ) is preferentially incorporated into the organic matrix, resulting in substantially lower ratios of  $^{13}\text{C}/^{12}\text{C}$  in the plant tissue relative to atmospheric  $\text{CO}_2$ . This discrimination against  $^{13}\text{C}$  (fractionation) is due to small differences in physical and chemical properties imparted by the difference in mass between  $^{12}\text{C}$  and  $^{13}\text{C}$ . The extent of this isotopic fractionation varies significantly depending on the photosynthetic pathway utilized by a plant (Craig 1953; Park & Epstein 1960; Smith & Epstein 1971; O'Leary 1981; Farquhar *et al.* 1982). There are three major photosynthetic types referred to as  $\text{C}_3$  (Calvin-Benson),  $\text{C}_4$  (Hatch-Slack or Kranz) and CAM (Crassulacian acid metabolism) pathways, each of which has a characteristic range of  $^{13}\text{C}/^{12}\text{C}$  values. These metabolic pathways represent adaptations to variable atmospheric and climatic conditions including  $p\text{CO}_2$ , moisture availability, temperature and irradiance.

Nearly all trees, shrubs, herbs and some sedges, as well as grasses growing in temperate,

high altitude or shaded habitats, fix carbon using the  $\text{C}_3$  photosynthetic pathway.  $\text{C}_3$  vegetation dominates terrestrial environments and accounts for approximately 85% of all plant species (Salisbury & Ross 1985). The isotopic composition of  $\text{C}_3$  flora, expressed as  $\delta^{13}\text{C}$ , ranges from  $-22\text{‰}$  to  $-3\text{‰}$  with a mean  $\delta^{13}\text{C}$  value of  $-27.1\text{‰}$  (O'Leary 1988). Isotopic ratios are expressed relative to the standard PDB (Pee Dee Belemnite) where

$$\begin{aligned} \delta^{13}\text{C} (\text{‰}) & \\ &= \left[ \left( \frac{^{13}\text{C}/^{12}\text{C}}{\text{sample}} / \left( \frac{^{13}\text{C}/^{12}\text{C}}{\text{standard}} - 1 \right) \right) \right] \\ &\quad \times 1000 \end{aligned}$$

The isotopic variation in  $\text{C}_3$  plants is due primarily to environmental influences, including water stress, nutrient availability, light intensity,  $\text{CO}_2$  partial pressure, temperature, and extent of forest canopy (Farquhar *et al.* 1982; van der Merwe & Medina 1989; Tieszen 1991).

$\text{C}_4$  physiology is linked almost exclusively to tropical and subtropical grasses. This pathway fixes  $\text{CO}_2$  more efficiently than  $\text{C}_3$  metabolism at lower atmospheric  $p\text{CO}_2$  levels ( $<c. 400 \text{ ppmV}$ ) and high temperatures ( $30\text{--}45^\circ\text{C}$ ) and  $\text{C}_4$  plants, in general, tolerate higher water stress. The  $\text{C}_4$  photosynthetic pathway represents a modification of the  $\text{C}_3$  mechanism and is considered to have evolved independently a number of times (Renvoize & Clayton 1992), possibly as a response to decreasing levels of  $\text{CO}_2$  relative to  $\text{O}_2$  in the atmosphere (Ehleringer 1991). A mean  $\delta^{13}\text{C}$  value of  $13.1\text{‰} \pm 1.2\text{‰}$  has been calculated for  $\text{C}_4$  plants (O'Leary 1988) with a range of  $-9$  to  $-15\text{‰}$ , about half that of  $\text{C}_3$  plants.

CAM plants are mostly succulents, including the cacti (Cactaceae) and stonecrops (Crassulaceae). Like  $\text{C}_4$  plants, they utilize both the  $\text{C}_3$  and  $\text{C}_4$  pathways but CAM plants differentially utilize the two pathways depending on environmental conditions resulting in  $\delta^{13}\text{C}$  values which span the range of values covered by  $\text{C}_3$  and  $\text{C}_4$  plants (Deines 1980; O'Leary 1981). The strategy of CAM plant physiology to endure extremely xeric conditions severely limits their ability to take in and fix  $\text{CO}_2$  and in general they compete poorly with  $\text{C}_3$  and  $\text{C}_4$  plants under less extreme conditions. It is unlikely that CAM plants constituted a significant portion of the plant biomass in palaeoenvironments supporting large vertebrate populations and CAM plants will not be considered further here.

Determining the relative proportions of  $\text{C}_3$  and  $\text{C}_4$  vegetation in the past provides a valuable tool for estimating aspects of environmental conditions and plant physiognomy in palaeohabitat reconstructions. Specifically, the link

between C<sub>4</sub> metabolism and grasses provides a means of identifying open woodland to grassland tropical/subtropical ecosystems in the past. After the evolution of C<sub>4</sub> plants, sometime in the middle to late Miocene, a greater C<sub>4</sub> component relative to C<sub>3</sub> potentially indicates more open habitats in low altitude/low latitude regions. However, the large variety of C<sub>3</sub>-dominated habitats, ranging from lowland rainforest to arid bushland to temperate grasslands, limits the resolving power of a C<sub>3</sub> isotopic signal in reconstructing vegetation. In addition, in adopting a uniformitarian approach, modern ecosystems typically provide the template for interpreting isotopic records of the past. Past habitats may in fact have no modern analogues. The possibility that C<sub>3</sub> grass-dominated tropical ecosystems existed before the evolution and spread of C<sub>4</sub> grasses, in particular, complicates interpretations of past landscapes.

A number of isotopic approaches have been developed to retrieve estimates of the relative proportions of plants using the C<sub>3</sub> and C<sub>4</sub> photosynthetic pathways in the past, including isotopic analyses of: (1) preserved organic plant matter in palaeosols (Ambrose & Sikes 1991; Kingston *et al.* 1994); (2) proxy material such as palaeosol carbonates which form in isotopic equilibrium with palaeovegetation (Cerling & Hay 1986; Quade *et al.* 1989a; Sikes 1994; Kingston *in press*); and (3) bone or enamel which reflects available dietary plants (Lee-Thorp & van der Merwe 1987; Morgan *et al.* 1994; Cerling *et al.* 1997b).

### *Palaeosols in the Tugen Hills*

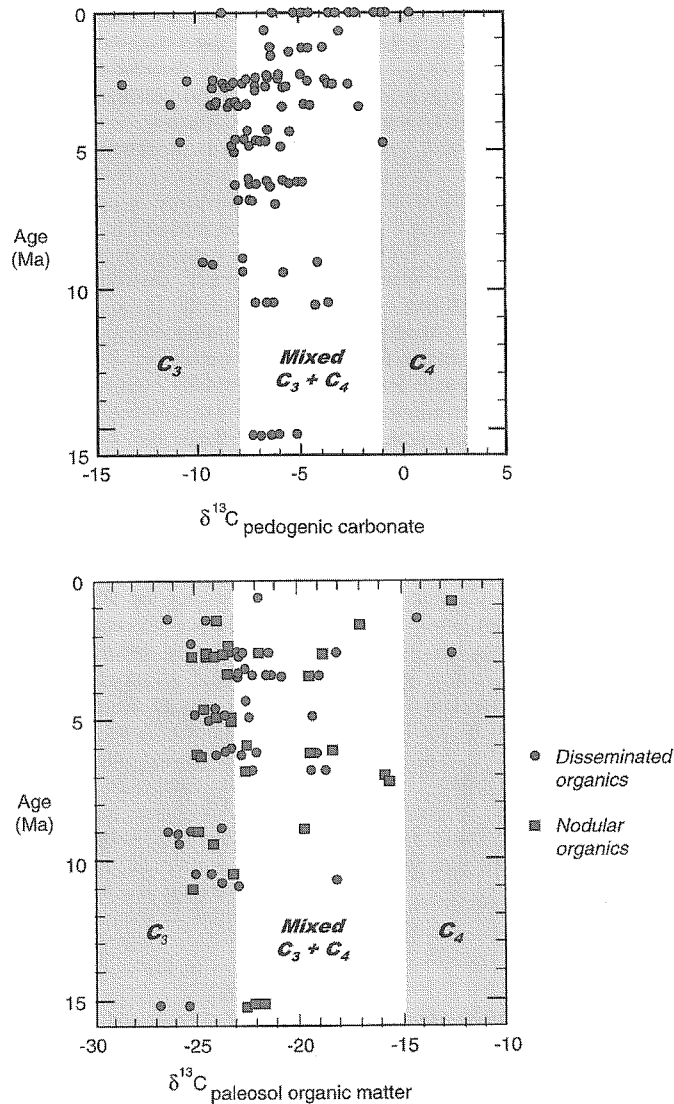
The isotopic composition of carbon in modern soils has been shown to closely reflect prevailing climatic and ecological conditions including the proportion of surface vegetation utilizing the C<sub>3</sub> or C<sub>4</sub> photosynthetic pathway (O'Brien & Stout 1978; Deines 1980; Cerling 1984; Amundson & Lund 1987; Quade *et al.* 1989b). These isotopic signals are retained in paleosols and have been retrieved from the fossil record to reconstruct aspects of the plant biomass in ancient landscapes (Kelly *et al.* 1991; Cerling 1992; Kingston *et al.* 1994; Sikes 1994; Quade & Cerling 1995). Although palaeosol components are not, in general, subjected to the types of taphonomic and sampling filters which can seriously bias interpretation of faunal and floral components, they may be subjected to differential preservation. For example, soils forming in high energy, non-stable environments such as on alluvial fans, hill sides or adjacent to major river channels

may be selectively destroyed and be underrepresented in the fossil record. If certain ecosystems are typically associated with these depositional settings, these settings may not be reflected in palaeosol studies.

Palaeosols, interbedded primarily with volcanoclastic alluvial fan, fluvial and lacustrine facies, constitute a conspicuous but in general minor component (<5%) of the sedimentary sequences exposed in the Tugen Hills. Palaeosols are unevenly distributed both laterally and vertically in the succession, most likely reflecting complex palaeotopography and the extremely localized nature of depositional regimes within the structurally complex inner rift. Intervals of time such as those represented by deposits of the Mpesida Beds and lower Ngorora Formation are characterized by significant influxes of volcanoclastic debris to the extent that soil development, preservation and recognition are generally poor.

$\delta^{13}\text{C}$  values of pedogenic carbonate nodules from the succession (Fig. 3a) record a complex distribution of C<sub>3</sub> and C<sub>4</sub> vegetation through time, indicating primarily a persisting mixed C<sub>3</sub>/C<sub>4</sub> mosaic. Most of the individual values fall within the range suggesting a contribution of carbon by both C<sub>3</sub> and C<sub>4</sub> vegetation, although values are heavily weighted towards the C<sub>3</sub> end of the spectrum. The lateral variation at any given level suggests a heterogeneous landscape although the  $\delta^{13}\text{C}$  ranges for all the fossil horizons are statistically more negative than the modern Baringo vegetation, indicating less of a C<sub>4</sub> component in the past. Excluding the modern data, only one palaeosol from the succession yielded carbonates with a  $\delta^{13}\text{C}$  value clearly indicating biomass composed almost exclusively of C<sub>4</sub> grasses. In general, the palaeosol carbonate isotopic values, where present, suggest woodland-type habitats although the specifics of these environments remain unknown.

Even though the isotopic variation in palaeosol carbonates is statistically consistent throughout the succession, there are a number of issues to be considered in evaluating this data set. First, the temporal resolution in sampling frequency is limited and it is conceivable that habitat shifts may have occurred during intervals not represented by the isotopic profile. In addition, palaeosols typically form over hundreds or even thousands of years and thus preserve a palaeoenvironmental record averaged over an interval spanning many generations of plants. Vegetational succession, however, can occur over time scales of only 100 to 1000 years as a result of fires, immigration or emigration of fauna, and climatic perturbations, all of which



**Fig. 3.** (a) Stable carbon isotopic composition ( $\delta^{13}\text{C}$ ) of paleosol carbonate sampled from horizons within the Tugen Hills succession. (b)  $\delta^{13}\text{C}$  of bulk paleosol organic matter from the Tugen Hills succession. Circles denote disseminated organics within the palaeosol matrix and the squares organic residue isolated from the carbonate matrix of pedogenic nodules. (c) Plot showing the  $\delta^{13}\text{C}$  values of the enamel apatite of various taxa sampled from the Tugen Hills succession.

can occur relatively rapidly (tens of years). In these cases environmental interpretations based on isotopic analyses of soil components may lack the resolution to distinguish perturbations in the ecosystem and would in effect average the relative proportion of  $\text{C}_3$  and  $\text{C}_4$  biomass, obscuring abrupt shifts in palaeovegetation. A further consideration in interpreting these data relates to assumptions that a consistent

isotopic signature of  $\text{C}_3$  relative to  $\text{C}_4$  plant biomass through time in the Baringo Basin implies static environmental conditions. A  $\text{C}_3$  component potentially reflects vegetation ranging from grasses to large trees and a persisting  $\text{C}_3/\text{C}_4$  signal would not necessarily record changes in the specific plants contributing a  $\text{C}_3$  isotopic signal. Finally, pedogenic carbonate was notably absent in palaeosols at a number of localities in



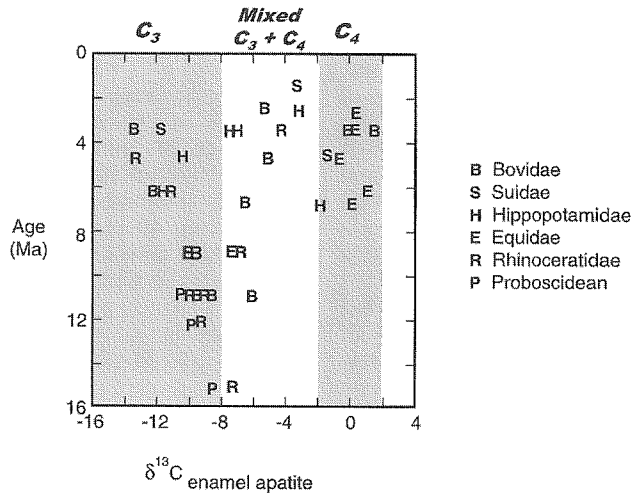


Fig. 3. (continued).

the Tugen Hills. These non-calcareous palaeosols may be indicative of environmental conditions which inhibit formation or preservation of pedogenic nodules such as forested habitats with acidic soils or heavy precipitation which leaches carbonates from the soil profiles. Such biomes would not be represented in this type of analysis. Interestingly, at sites in the Tugen Hills with fossil/macrofossil assemblages indicative of localized, if not widespread, forest environments, local palaeosols were devoid of pedogenic carbonate.

Although carbon isotopic analyses of associated palaeosol organic matter (disseminated and nodular) (Fig. 3b) also indicate lateral variation throughout the succession, there is significantly less evidence for a  $C_4$  component before *c.* 6.5 Ma.  $\delta^{13}C$  values of the organic matter from formational and subformational groups indicate ranges of up to 12‰ but, as with the palaeosol carbonates, the isotopic values cluster more toward the  $C_3$  endmember. Organic residue yielding isotopic signatures characteristic of essentially pure  $C_4$  vegetation occurs at three sites, all less than 2.3 Ma. The isotopic signatures of organic matter suggest an increase in the  $C_4$  component during an apparent gap in the fossil record between uppermost units of the Ngorora Formation (Ngeringerowa Beds at 8.5–9 Ma) and horizons within the Mpesida Beds (*c.* 6.5 Ma).

Theoretical models (Cerling 1984; Quade *et al.* 1989b) predict that differences in the isotopic signatures of carbonate nodules and associated organic residue ( $\Delta\delta$ ) are 14‰ and 15.5‰ at temperatures of 25°C and 15°C respectively.

Although the means for the  $\Delta\delta$  for both disseminated and nodular organics fall within this theoretical envelope (15.3‰ and 15.4‰), the standard deviation is significant (5.0‰ and 4.1‰). Discrepancies may relate to differential preservation of the various fossil records or to the way that each of these components records aspects of palaeoenvironments.

#### Fossil herbivore enamel from the Tugen Hills

An alternative and complementary method of documenting relative proportions of  $C_3$  and  $C_4$  vegetation in the past involves the isotopic analyses of the dietary carbonate preserved in the enamel of fossil herbivores. The carbon isotopic composition of modern herbivore tissue, including tooth enamel, is directly related to the  $\delta^{13}C$  value of the primary photosynthesizing plants in the food chain (DeNiro & Epstein 1978; Tieszen *et al.* 1983; Ambrose & DeNiro 1986). Unlike bone apatite, the mineral portion of enamel is highly resistant to diagenetic alteration and the biogenic dietary signal is preserved during fossilization (Lee-Thorp 1989). This signal can be used to reconstruct proportions of  $C_3$  and  $C_4$  vegetation in the diet of extinct taxa. Application of isotopic analyses to fossil enamel strictly for palaeodietary studies has been limited (Ericson *et al.* 1981; Lee-Thorp *et al.* 1989b), and instead its use has been primarily for palaeoecological reconstruction (Thackeray *et al.* 1990; Kingston 1992; Quade *et al.* 1992, 1994; Wang *et al.* 1993; Morgan *et al.* 1994; MacFadden *et al.* 1996; Cerling *et al.* 1997b).

The carbon isotopic composition of enamel carbonate from 58 fossil tooth samples collected from the Tugen Hills sequence was analysed. Sampling strategy emphasized collection of potential grazing forms such as equids, high-crowned bovids and hippopotamids which might provide constraints on the timing and nature of the introduction and continuity of  $C_4$  grasses into the Baringo Basin. The isotopic profile generated by analyses of fossil apatite represents a different type of record in that the environment is not sampled directly but rather through a dietary filter. The selectivity of animals, competitive exclusion, seasonal migrations and long-term biogeographic changes can all potentially complicate interpretation of fossil apatite for palaeovegetation reconstructions. With this in mind, analyses included a wide range of herbivore taxa through the succession with the assumption that dietary shifts associated with significant alteration of habitat might be detected.

During enamel formation, the lighter carbon ( $^{12}C$ ) is discriminated against and the isotopic signature of biological apatite is significantly heavier than dietary components (DeNiro & Epstein 1978). These physiological fractionation effects typically result in a 12–14‰ enrichment of enamel relative to diet (Sullivan & Kreuger 1981; Lee-Thorp *et al.* 1989a) although some researchers note less enrichment (DeNiro & Epstein 1978; Ambrose & Norr 1993). The  $\delta^{13}C$  of herbivore enamel from the Tugen Hills succession indicates that although there is a dietary  $C_4$  component as early as 15.5 Ma, there is no evidence for a significant  $C_4$  or an exclusive  $C_4$  component in diets until *c.* 6.5 Ma. Between 7 and 2 Ma, analysis of fossil enamel apatite records a wide range of  $\delta^{13}C$  values indicating dietary regimes ranging from pure  $C_3$  to pure  $C_4$ . In assessing the potential contribution of  $C_4$  vegetation to palaeodiets it is necessary to appreciate that the isotopic demarcation distinguishing essentially pure  $C_3$  diets from mixed  $C_3/C_4$  diets is actually represented by a range reflecting interpretive differences. The distinction between these dietary groups is dependent on assumptions made regarding: (1) a +1.5‰ correction for preindustrial atmospheric  $\delta^{13}C$  values (Marino & McElroy 1991); (2) the physiological fractionation of carbon in enamel formation (estimates range from 9.5‰ to 15‰); (3) environmental factors such as water stress or high irradiance which might cause an enrichment in  $C_3$  plants; and (4) differential fractionation in animals with different body sizes. Based on interpretations of these variables, estimates of this dietary boundary as detected isotopically

in enamel apatite range from –12‰ to –8‰ (Cerling *et al.* 1997b). In documenting early evidence for a  $C_4$  diet, a conservative approach would be to adopt a  $\delta^{13}C$  values of greater than –8‰ as reflecting a  $C_4$  dietary component. By these criteria, enamel samples from Muruyur and the Ngorora Formation horizons record a minor  $C_4$  component by as early as the middle Miocene. Alternatively, although less likely, these values may reflect a dietary reliance on CAM plants or  $C_3/C_4$  intermediates.

## Discussion

While the isotopic analyses of palaeosol carbonates indicate heterogeneous, mixed  $C_3/C_4$  environments throughout the 15.5 Ma spanned by sediments in the Tugen Hills succession, the isotopic signatures of associated organic matter and enamel carbonate suggest an increase in the  $C_4$  component during the late Miocene. These latter data sets provide support for a global increase in  $C_4$  biomass between 8 and 6 Ma possibly related to a decrease in atmospheric  $CO_2$  (Cerling *et al.* 1993) or intensification of monsoonal patterns (Quade *et al.* 1989a). The implications of this isotopic transition for late Miocene landscapes remain unclear as  $C_3$  grasses clearly were significant components of ecosystems before this shift and may have occupied the modern  $C_4$  niche, forming extensive temperate and tropical grasslands as well as grassy substrata in more wooded habitats. The earliest evidence for grasses in Africa is pollen contained in core sediments from coastal Cameroon in the early Eocene (Salard-Cheboldaef 1979, 1981). Grass pollen, however, is absent from this core during the middle Oligocene and into the early Miocene which marks the terminus of the core. Grass pollen and charred grass cuticle, interpreted to have formed as a result of savanna fires, are intermittently abundant in early Miocene to Pleistocene core samples taken from the Niger Delta (Morley & Richards 1993). Moderate rises in the relative abundance of these grassland components during the middle Miocene and a significant increase during the late Miocene are thought to indicate periods of marked aridity with strong seasonality of rainfall, with savanna habitats extending over most of the Niger delta region. In East Africa, autochthonous assemblages of grass blades (Dugas & Retallack 1993) and a pollen assemblage dominated by grass pollen (54%) (Bonnefille 1984) preserved in volcanic ash at the vertebrate-rich locality of Fort Ternan have been dated to about 14 Ma (Shipman *et al.* 1981). Although there has been

considerable debate concerning the habitat represented by the fossil record (Andrews & Nesbit Evans 1979; Shipman 1986; Cerling *et al.* 1992, 1997a; Retallack 1992; Dugas & Retallack 1993), the presence of abundant grass components in upper levels of the stratigraphic section exposed at Fort Ternan indicate that at some point in the middle Miocene, C<sub>3</sub> grasses constituted a significant portion of the Fort Ternan ecosystem, at least locally.

The apparent isotopic transition during the late Miocene may simply reflect the displacement of C<sub>3</sub> grasses in woodland/bushland or grassland biomes by C<sub>4</sub> grasses, requiring minimal perceptual change in the vegetational physiognomy of East African habitats. Alternatively, the transition involved the replacement of more forested habitats by grasslands. This latter interpretation would have significance for hominid evolution as it provides support for the savanna hypothesis. To attempt resolution of these potential interpretations, it becomes necessary to examine other data sets that provide information of palaeohabitats. Within the Tugen Hills, a number of macrofloral sites have been and are currently being investigated (summarized in Fig. 2). A fossil macrofloral assemblage from the Ngorora Formation dated to 12.6 Ma at the site of Kabasero records 57 taxa with affinities to lowland to submontane wet to moist rainforests (Jacobs & Kabuye 1987, 1989; Jacobs & Winkler 1992). Palaeobotanical evidence from the site of Waril, about 10–9 Ma based on stratigraphic position, suggests a seasonally dry wooded savanna habitat although no grass remains have been documented in the assemblage (Jacobs pers. comm.). Environmental reconstructions based on sedimentological and mineralogical evidence collected from lacustrine horizons penecontemporaneous to the Waril site in the Ngorora Formation also indicate that warm, arid conditions prevailed in this area *c.* 10 Ma (Renaut *et al.* 1999). Sediments of the Mpesida Beds at the site of Kapturo constrained to about 6.8 Ma contain numerous plants interpreted as representing a deciduous woodland (Jacobs & Deino 1996). Also within Mpesida sediments, about 10 km south-southwest of the Kapturo locality, are abundant fossil wood fragments preserved in an ash flow deposit exposed over an area >10 km<sup>2</sup>. Preliminary analyses of the fossil wood indicate affinities to central and West African forest (Jacobs pers. comm.). These data, especially when coupled with the isotopic data indicating significant C<sub>4</sub> grasses by the late Miocene, reflect a range of habitats suggesting a diverse, dynamic vegetative structure in the Baringo Basin from the middle Miocene onwards. Also significant,

the isotopic and palaeobotanical data indicate that at no time in the past was this portion of the rift valley dominated by C<sub>3</sub> or C<sub>4</sub> grasslands.

Exposures of the Tugen Hills succession are locally extensive (>800 km<sup>2</sup>) and palaeoecological data derived from the sequence have the potential to document local heterogeneity inherent in a rift valley setting. Based on the diverse landscapes present today in the rift valley, not only on a local but also on a regional scale, it would be unrealistic to extrapolate the type and range of habitat diversity documented in the Baringo Basin as representative of East Africa in general during the Neogene. Nevertheless, these data record the vegetation in an area of the rift where fossil evidence indicates that early hominids and hominoids ranged and as such are relevant to discussions of the role of shifting environments in the evolution of the human lineage. No obvious phytogeographical trend is revealed by the data and although globally, and to an extent locally, there is an isotopic shift indicating a spread of C<sub>4</sub> grasses during the late Miocene (8.5 to 6.5 Ma) (Cerling *et al.* 1997b), the effect of this transition on African hominid habitats is unknown. This interval also incorporates the establishment of vertebrate communities more similar to modern fauna but the timing and ecological basis of this faunal change during the late Miocene is also not well constrained.

### Summary

Environmental change has no doubt influenced the morphological and behavioural innovations characterizing early hominid evolution during the late Miocene and Pliocene in Africa. Basic questions of how and when and to what extent remain unanswered. Detailing the evolution of landscapes in Africa during this period is ultimately critical to addressing these questions yet at this point not much is known. This lack of data has forced us to adopt or accept simplified versions of environmental trends involving to some extent a monotonic replacement of forests by more open habitats during the Neogene. While data from late Miocene and Pliocene localities in Africa may ultimately in part support this scenario on a large-scale basis, emerging evidence implicates more heterogeneous, fluctuating landscapes during early hominid evolution. It is likely that the source of many of the selection pressures directing the course of human evolution lies in the specifics of African ecosystems and the complicated interrelationships between constituent faunas and floras as

well as with extrinsic climatic factors. Enhancing the resolution of the fossil record to a level at which we can address these issues remains one of the challenges of palaeoanthropology.

I am grateful to the organizers of the Bill Bishop Memorial Conference for inviting me to participate in the meeting and present some of my ongoing research in the Tugen Hills. By emphasizing a multidisciplinary approach, Bill Bishop helped establish the foundation for understanding the evolution of East African landscapes, which has proved essential to theories of human evolution. I thank the members of the Baringo Palaeontological Research Project, in particular A. Hill, for their collaboration and camaraderie. This work was funded by grants from National Science Foundation, L. B. S. Leakey Foundation, the Bill Bishop Memorial Trust and the Louise Brown Foundation.

## References

- AMBROSE, S. H. 1995. Paleocology and paleobiogeography of late Miocene hominoid/hominid cladogenesis: Was the trichotomy a reality. *4th Annual Meeting Paleoanthropological Society, Oakland, CA* (abstract).
- AMBROSE, S. H. & DENIRO, M. J. 1986. Reconstruction of African human diet using bone collagen carbon and nitrogen isotope ratios. *Nature*, **319**, 321–324.
- & NORR, L. 1993. Experimental evidence for the relationship of the carbon isotope ratios of whole diet and dietary protein to those of bone collagen and carbonate. In: LAMBERT, J. L. & GRUPE, G. (eds) *Prehistoric Human Bone: Archaeology at the Molecular Level*. Springer, Berlin, 1–13.
- & SIKES, N. E. 1991. Soil carbon isotope evidence for Holocene habitat change in the Kenya Rift Valley. *Science*, **253**, 1402–1405.
- AMUNDSON, R. G. & LUND, L. J. 1987. The stable isotope chemistry of a native and irrigated typical natrargid in the San Joaquin Valley of California. *Soil Science Society of America Journal*, **51**(3), 761–767.
- ANDREWS, P. & NESBIT EVANS, E. 1979. The environment of *Ramapithecus* in Africa. *Paleobiology*, **5**(1), 22–30.
- BARRY, J. C. 1995. Faunal turnover and diversity in the terrestrial Neogene of Pakistan. In: VRBA, E. S., DENTON, G. H., PARTRIDGE, T. C. & BURCKLE, L. H. (eds) *Paleoclimate and Evolution, with Emphasis on Human Origins*. Yale University Press, New Haven, 115–134.
- , JOHNSON, N. M., RAZA, S. M. & JACOBS, L. L. 1985. Neogene faunal change in southern Asia: Correlations with climatic, tectonic, and eustatic events. *Geology*, **13**, 637–640.
- BEHRENSMEYER, A. K., TODD, N. E., POTTS, R. & MCBRINN, G. E. 1997. Late Pliocene faunal turnover in the Turkana Basin, Kenya and Ethiopia. *Science*, **278**, 1589–1594.
- BISHOP, L. C. 1994. *Pigs and the ancestor: hominids, suids and environments during the Plio-Pleistocene of East Africa*. PhD Thesis, Yale University.
- , HILL, A. & KINGSTON, J. D. 1999. Palaeoecology of Suidae from the Tugen Hills, Baringo, Kenya. *This volume*.
- BISHOP, W. W. 1962. Pleistocene chronology in East Africa. *Advancement of Science*, January 1962.
- , CHAPMAN, G. R., HILL, A. & MILLER, J. A. 1971. Succession of Cainozoic vertebrate assemblages from the northern Kenya Rift Valley. *Nature*, **233**, 389–394.
- BONNEFILLE, R. 1984. Cenozoic vegetation and environments of early hominids in East Africa. In: WHYTE, R. O. (ed.) *The Evolution of the East Asian Environment. II Palaeobotany, Palaeozoology, and Palaeoanthropology*. University of Hong Kong, 579–612.
- BRAIN, C. K. 1981. The evolution of man in Africa: Was it a consequence of Cainozoic cooling? Alex L. du Toit Memorial Lecture 17. *Transactions of the Geological Society of South Africa*, annex **84**, 1–19.
- CERLING, T. E. 1984. The stable isotopic composition of modern soil carbonates and its relationship to climate. *Earth and Planetary Science Letters*, **71**, 229–240.
- & HAY, R. L. 1986. An isotopic study of paleosol carbonates from Olduvai Gorge. *Quaternary Research*, **25**, 63–78.
- 1992. Development of grasslands and savannas in East Africa during the Neogene. *Palaeogeography, Palaeoclimatology, Palaeoecology (Global and Planetary Change Section)*, **97**, 241–247.
- , KAPPELMAN, J., QUADE, J., AMBROSE, S. H., SIKES, N. E. & ANDREWS, P. 1992. Reply to comment on the paleoenvironment of *Kenyapithecus* at Fort Ternan. *Journal of Human Evolution*, **23**, 371–377.
- , WANG, Y. & QUADE, J. 1993. Expansion of C<sub>4</sub> ecosystems as an indicator of global ecological change in the late Miocene. *Nature*, **361**, 344–345.
- , HARRIS, J. M., AMBROSE, S. H., LEAKEY, M. G. & SOLOUNIAS, N. 1997a. Dietary and environmental reconstruction with stable isotope analyses of herbivore tooth enamel from the Miocene locality of Fort Ternan, Kenya. *Journal of Human Evolution*, **33**, 635–650.
- , —, MACFADDEN, B. J., LEAKEY, M. G., QUADE, J., EISENMANN, V. & EHLERINGER, J. R. 1997b. Global vegetation change through the Miocene/Pliocene boundary. *Nature*, **389**, 153–158.
- CHAPMAN, G. R. 1971. *The geological evolution of the northern Kamasia Hills, Baringo District, Kenya*. PhD Thesis, University of London.
- & BROOK, M. 1978. Chronostratigraphy of the Baringo Basin, Kenya. In: BISHOP, W. W. (ed.) *Geological Background to Fossil Man*. Scottish Academic, London, 207–223.
- , LIPPARD, S. J. & MARTYN, J. E. 1978. The stratigraphy and structure of the Kamasia Range, Kenya Rift Valley. *Journal of the Geological Society of London*, **135**, 265–281.

- CRAIG, H. 1953. The geochemistry of the stable carbon isotopes. *Geochimica et Cosmochimica Acta*, **3**, 53–92.
- CROWLEY, T. J. & NORTH, G. R. 1991. *Paleoclimatology*. Oxford University, New York.
- DAGLEY, P., MUSSETT, A. E. & PALMER, H. C. 1978. Preliminary observations on the paleomagnetic stratigraphy of the area west of Lake Baringo, Kenya. In: BISHOP, W. W. (ed.) *Geological Background to Fossil Man*. Scottish Academic, London, 225–235.
- DARWIN, C. 1871. *The Descent of Man, and Selection in Relation to Sex*. Murray, London.
- DEINES, P. 1980. The isotopic composition of reduced organic carbon. In: FRITZ, P. & FONTES, J. C. (eds) *Handbook of Environmental Isotope Geochemistry*. V. 1. *The Terrestrial Environment*. Elsevier, New York, 329–406.
- DEINO, A., TAUXE, L., MONOGHAN, M. & DRAKE, R. 1990.  $^{40}\text{Ar}/^{39}\text{Ar}$  age calibration of the litho- and paleomagnetic stratigraphies of the Ngorora Formation, Kenya. *Journal of Geology*, **98**, 567–587.
- DEMENOCAL, P. B. 1995. Plio-Pleistocene African climate and the paleoenvironment of human evolution. *Science*, **270**, 53–59.
- & BLOEMENDAL, J. 1995. Plio-Pleistocene climatic variability in subtropical Africa and the paleoenvironment of hominid evolution. In: VRBA, E. S., DENTON, G. H., PARTRIDGE, T. C. & BURCKLE, L. H. (eds) *Paleoclimate and Evolution, with Emphasis on Human Origins*. Yale University Press, New Haven, 262–288.
- & RIND, D. 1993. Sensitivity of Asian and African climate to variations in seasonal insolation, glacial ice cover, sea-surface temperature, and Asian orography. *Journal of Geophysical Research*, **98** (D4), 7265–7287.
- DENIRO, M. J. & EPSTEIN, S. 1978. Influence of diet on the distribution of carbon isotopes in animals. *Geochimica et Cosmochimica Acta*, **42**, 341–351.
- DUGAS, D. P. & RETALLACK, R. J. 1993. Middle Miocene fossil grasses from Fort Ternan, Kenya. *Journal of Paleontology*, **67**(1), 113–128.
- EHLERINGER, J. R. 1991. Climate change and the evolution of  $\text{C}_4$  photosynthesis. *Trends in Ecology and Evolution*, **6**, 95–99.
- ERICSON, J. E., SULLIVAN, C. H. & BOAZ, N. T. 1981. Diets of Pliocene mammals from Omo, Ethiopia, deduced from carbon isotope ratios in tooth apatite. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **36**, 69–73.
- FARQUHAR, G. D., O'LEARY, M. H. & BERRY, J. A. 1982. On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. *Australian Journal of Plant Physiology*, **9**, 121–137.
- FEIBEL, C. S. 1997. Debating the environmental factors in hominid evolution. *GSA Today*, **7**(3), 1–7.
- FLYNN, L. J., TEDFORD, R. H. & ZHANXIANG, Q. 1991. Enrichment and stability in the Pliocene mammalian fauna of North China. *Paleobiology*, **17**(3), 246–265.
- FROSTICK, L. E. 1997. The East African rift basins. In: SELLEY, R. C. (ed.) *African Basins. Sedimentary Basins of the World Vol. 3*. Elsevier Science, Amsterdam, 187–209.
- GRINE, F. E. 1986. Ecological causality and the pattern of Plio-Pleistocene hominid evolution in Africa. *South Africa Journal of Science*, **82**, 87–89.
- HILL, A. 1987. Causes of perceived faunal change in the later Neogene of East Africa. *Journal of Human Evolution*, **16**, 583–596.
- 1994. Late Miocene and Early Pliocene hominoids from Africa. In: CORRUCINI, R. S. & CIOCHON, R. L. (eds) *Integrative Paths to the Past*. Prentice Hall, Englewood Cliffs, 123–145.
- 1995. Faunal and environmental change in the Neogene of East Africa: evidence from the Tugen Hills Sequence, Baringo District, Kenya. In: VRBA, E. S., DENTON, G. H., PARTRIDGE, T. C. & BURCKLE, L. H. (eds) *Paleoclimate and Evolution, with Emphasis on Human Origins*. Yale University, New Haven, 178–193.
- 1999. The Baringo Basin, Kenya: from Bill Bishop to BPRP. *This volume*.
- (in press). Evidence for African vertebrate faunas and environments between 8 Ma and 4 Ma. In: WHYBROW, P. J. & HILL, A. (eds) *Fossil Vertebrates of Arabia*. Yale University, New Haven.
- , CURTIS, G. & DRAKE, R. 1986. Sedimentary stratigraphy of the Tugen Hills. In: FROSTICK, L. E. et al. (eds) *Sedimentation in the African Rifts*. Geological Society, London, Special Publications, **25**, 285–295.
- , DRAKE, R., TAUXE, L. et al. 1985. Neogene paleontology and geochronology of the Baringo Basin, Kenya. *Journal of Human Evolution*, **14**, 759–773.
- , WARD, S., DEINO, A., GARNISS, C. & DRAKE, R. 1992. Earliest *Homo*. *Nature*, **355**, 719–722.
- JACOBS, B. F. & DEINO, A. L. 1996. Test of climate-leaf physiognomy regression models, their application to two Miocene floras from Kenya, and  $^{40}\text{Ar}/^{39}\text{Ar}$  dating of the late Miocene Kapturo site. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **123**, 259–271.
- & KABUYE, C. H. S. 1987. A middle Miocene (12.2 Ma) forest in the East African Rift Valley, Kenya. *Journal of Human Evolution*, **6**, 147–155.
- & KABUYE, C. H. S. 1989. An extinct species of *Polliia* Thunberg (Commelinaceae) from the Miocene Ngorora Formation, Kenya. *Review of Paleobotany and Palynology*, **59**, 67–76.
- & WINKLER, D. A. 1992. Taphonomy of a middle Miocene autochthonous forest assemblage, Ngorora Formation, central Kenya. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **99**, 31–40.
- JANIS, C. M. 1993. Tertiary mammal evolution in the context of changing climates, vegetation, and tectonic events. *Annual Review of Ecology and Systematics*, **24**, 467–500.
- KELLY, E. F., AMUNDSON, R. G., MARINO, B. D. & DE NIRO, M. J. 1991. Stable carbon isotopic

- composition of carbonate in Holocene grassland soils. *Soil Science Society of America Journal*, **55**(6), 1651–1657.
- KENNETT, J. P. 1995. A review of polar climatic evolution during the Neogene, based on the Marine sediment record. In: VRBA, E. S., DENTON, G. H., PARTRIDGE, T. C. & BURCKLE, L. H. (eds) *Paleoclimate and Evolution, with Emphasis on Human Origins*. Yale University Press, New Haven, 49–64.
- KING, B. C. & CHAPMAN, G. R. 1972. Volcanics of the Kenya rift valley. *Philosophical Transactions of the Royal Society, London. Series A*, **271**, 185–208.
- KINGSTON, J. D. 1992. *Stable isotopic evidence for hominid paleoenvironments in East Africa*. PhD thesis, Harvard University.
- (in press). Isotopes and environments of the Baynunah Formation, Emirate of Abu Dhabi, United Arab Emirates. In: WHYBROW, P. J. & HILL, A. (eds) *Fossil Vertebrates of Arabia*. Yale University, New Haven.
- , MARINO, B. D. & HILL, A. 1994. Isotopic evidence for Neogene hominid paleoenvironments in the Kenya Rift Valley. *Science*, **264**, 955–959.
- LAPORTE, L. F. & ZHILMAN, A. L. 1983. Plates, climate and hominoid evolution. *South African Journal of Science*, **79**, 96–110.
- LEE-THORP, J. A. 1989. *Stable carbon isotopes in deep time: The diets of fossil fauna and hominids*. PhD thesis, University of Cape Town.
- & VAN DER MERWE, N. J. 1987. Carbon isotope analysis of fossil bone apatite. *South African Journal of Science*, **83**, 71–74.
- , SEALY, J. C. & VAN DER MERWE, N. J. 1989a. Stable carbon isotope ratio differences between bone collagen and bone apatite, and their relationship to diet. *Journal of Archaeological Science*, **16**, 585–599.
- , VAN DER MERWE, N. J. & BRAIN, C. K. 1989b. Isotopic evidence for dietary differences between two extinct baboon species from Swartkrans. *Journal of Human Evolution*, **18**, 183–190.
- MACFADDEN, B. J., CERLING, T. E. & PRADO, J. 1996. Cenozoic terrestrial evolution in Argentina: Evidence from carbon isotopes of fossil mammal teeth. *Palaeos*, **11**, 319–327.
- MARINO, B. D. & McELROY, M. B. 1991. Isotopic composition of atmospheric CO<sub>2</sub> inferred from carbon in C<sub>4</sub> plant cellulose. *Nature*, **349**, 127–131.
- MARTYN, J. E. 1969. *The geological history of the country between Lake Baringo and the Kerio River, Baringo District, Kenya*. PhD thesis, University of London.
- MILLER, K. G., FAIRBANKS, R. G. & MOUNTAIN, G. S. 1987. Tertiary oxygen isotope synthesis, sea level history, and continental margin erosion. *Paleoceanography*, **2**(1), 1–19.
- MORGAN, M. E., KINGSTON, J. D. & MARINO, B. D. 1994. Carbon isotopic evidence for the emergence of C<sub>4</sub> plants in the Neogene from Pakistan and Kenya. *Nature*, **367**, 162–165.
- MORLEY, R. J. & RICHARDS, K. 1993. Gramineae cuticle: a key indicator of Late Cenozoic climatic change in the Niger Delta. *Review of Palaeobotany and Palynology*, **77**, 119–127.
- O'BRIEN, B. J. & STOUT, J. D. 1978. Movement and turnover of soil organic matter as indicated by carbon isotope measurements. *Soil Biology and Biochemistry*, **10**, 309–317.
- O'LEARY, M. H. 1981. Carbon isotope fractionation in plants. *Phytochemistry*, **20**, 553–567.
- 1988. Carbon isotopes in photosynthesis. *Biochemistry*, **38**, 328–336.
- OPDYKE, N. D. 1995. Mammalian migration and climate over the last seven million years. In: VRBA, E. S., DENTON, G. H., PARTRIDGE, T. C. & BURCKLE, L. H. (eds) *Paleoclimate and Evolution, with Emphasis on Human Origins*. Yale University Press, New Haven, 109–114.
- PARK, R. & EPSTEIN, S. 1960. Carbon isotope fractionation during photosynthesis. *Geochimica et Cosmochimica Acta*, **21**, 110–126.
- PICKFORD, M. 1975. *Stratigraphy and palaeoecology of five late Cainozooid formations in the Kenya Rift Valley*. PhD thesis, University of London.
- 1978a. Geology, paleoenvironments and vertebrate faunas of the mid-Miocene Ngorora Formation, Kenya. In: BISHOP, W. W. (ed.) *Geological Background to Fossil Man*. Scottish Academic Press, London, 237–262.
- 1978b. Stratigraphy and mammalian paleontology of the late-Miocene Lukeino Formation, Kenya. In: BISHOP, W. W. (ed.) *Geological Background to Fossil Man*. Scottish Academic Press, London, 263–278.
- POKRAS, E. M. & MIX, A. C. 1985. Eolian evidence for spatial variability of late Quaternary climates in tropical Africa. *Quaternary Research*, **24**, 137–149.
- POTTS, R. 1996. Evolution and climate variability. *Science*, **273**, 922–923.
- PRENTICE, M. L. & DENTON, G. H. 1988. The deep-sea oxygen isotope record, the global ice sheet system and hominid evolution. In: GRINE, F. E. (ed.) *Evolutionary History of the "Robust" Australopithecines*. Aldine de Gruyter, New York, 383–403.
- PROTHERO, C. R. 1995. Faunal response to climatic events: Testing the turnover pulse hypothesis. *North American Paleontological Convention, 6th, Abstracts of Papers*. Paleontology Society, Special Publications, **8**, 314.
- QUADE, J. & CERLING, T. E. 1995. Expansion of C<sub>4</sub> grasses in the Late Miocene of Northern Pakistan: evidence from stable isotopes in paleosols. *Palaeo-geography, Palaeoclimatology, Palaeoecology*, **115**, 91–116.
- , —, BARRY, J. C. *et al.* 1992. A 16 Ma record of paleodiet using carbon and oxygen isotopes in fossil teeth from Pakistan. *Chemical Geology*, **94**, 183–192.
- , — & BOWMAN, J. R. 1989a. Development of Asian monsoon revealed by marked ecological shift during the latest Miocene in northern Pakistan. *Nature*, **342**, 163–166.
- , — & BOWMAN, J. R. 1989b. Systematic variations in the carbon and oxygen isotopic composition of pedogenic carbonate along elevation transects in the southern Great Basin, United States. *GSA Bulletin*, **101**, 464–475.

- , SOLOUNIAS, N. & CERLING, T. E. 1994. Stable isotopic evidence from paleosol carbonates and fossil teeth in Greece for forest or woodlands over the past 11 Ma. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **108**, 41–53.
- RENAUT, R., EGO, J., TIERCELIN, J. J., LE TURDU, C. & OWEN, R. B. 1999. Saline, alkaline palaeolakes of the Tugen Hills–Kerio Valley region, Kenya Rift Valley. *This volume*.
- RENOUVE, S. A. & CLAYTON, W. D. 1992. Classification and evolution of the grasses. In: CHAPMAN, G. P. (ed.) *Grass Evolution and Domestication*. Cambridge University, 3–37.
- RETALLACK, G. J. 1992. Comment on the paleoenvironment of Kenyapithecus at Fort Ternan. *Journal of Human Evolution*, **23**, 365–371.
- SALARD-CHEBOLDAEFF, M. 1979. Palynologie Maestrichtienne et Tertiaire du Cameroun. Etude qualitative et repartition verticale des principes especes. *Review of Palaeobotany and Palynology*, **28**, 365–388.
- 1981. Palynologie Maestrichtienne et Tertiaire du Cameroun. Resultats botaniques. *Review of Palaeobotany and Palynology*, **32**, 401–439.
- SALISBURY, F. B. & ROSS, C. W. 1985. *Plant Physiology*. Wadsworth, Belmont.
- SEMAW, S., HARRIS, J. W. K., FEIBEL, C. S., RENNE, P., BERNOR, T. L., FESSAHA, N. & MOWBRAY, K. 1997. The oldest archaeological sites with an early Oldowan Industry from the Gona River deposits of Ethiopia. *Nature*, **385**, 333–336.
- SHIPMAN, P. 1986. Paleocology of Fort Ternan reconsidered. *Journal of Human Evolution*, **15**, 193–204.
- , WALKER, A., VAN COUVERING, J. A., HOOKER, P. J. & MILLER, J. A. 1981. The Fort Ternan hominoid site, Kenya: geology, age, taphonomy, and paleocology. *Journal of Human Evolution*, **10**, 49–72.
- SHREEVE, J. 1996. Sunset on the savanna. *Discover*, **17**(7), 116–124.
- SIKES, N. E. 1994. Early hominid habitat preferences in East Africa: Paleosol carbon isotopic evidence. *Journal of Human Evolution*, **27**, 25–45.
- SMITH, B. N. & EPSTEIN, S. 1971. Two categories of  $^{13}\text{C}/^{12}\text{C}$  ratios for higher plants. *Plant Physiology*, **47**, 380–384.
- STANLEY, S. M. 1992. An ecological theory for the origin of *Homo*. *Paleobiology*, **18**, 237–257.
- 1995. Climatic forcing and the origin of the human genus. In: KENNETT, J. & STANLEY, S. M. (eds) *Effects of Past Global Change on Life*. Studies in Geophysics, National Academy, Washington DC, 233–243.
- STENSETH, N. C. & MAYNARD SMITH, J. 1984. Coevolution in ecosystems: Red Queen evolution or stasis? *Evolution*, **38**(4), 870–880.
- STREET-PERROTT, F. A. & PERROTT, R. A. 1990. Abrupt climate fluctuations in the tropics: the influence of Atlantic Ocean circulation. *Nature*, **343**, 607–612.
- SULLIVAN, C. H. & KRUEGER, H. W. 1981. Carbon isotope analysis of separate chemical phases in modern and fossil bone. *Nature*, **292**, 333–335.
- SUWA, G., WHITE, T. D. & HOWELL, F. C. 1996. Mandibular postcanine dentition from the Shungura Formation, Ethiopia: Crown morphology, taxonomic allocations, and Plio-Pleistocene hominid evolution. *American Journal of Physical Anthropology*, **101**, 247–282.
- TAUXE, L., MONAGHAN, M., DRAKE, R., CURTIS, G. & STAUDIGEL, H. 1985. Paleomagnetism of Miocene East African rift sediments and the calibration of the Geomagnetic Reversal Timescale. *Journal of Geophysical Research*, **90**, 4639–4646.
- THACKERAY, J. F., VAN DER MERWE, N. J., LEE-THORP, J. A., SILLEN, A., LANHAM, J. L., SMITH, R., KEYSER, A. & MONTEIRO, P. M. S. 1990. Changes in carbon isotope ratios in the late Permian recorded in therapsid tooth apatite. *Nature*, **347**, 751–753.
- THOMAS, H. 1985. The early and middle Miocene land connection of the Afro-Arabian plate and Asia: a major event for hominoid dispersal. In: DELSON, E. (ed.) *Ancestors: The Hard Evidence*. Liss, New York, 42–50.
- TIESZEN, L. L. 1991. Natural variations in the carbon isotope values of plants: Implications for archaeology, ecology, and paleoecology. *Journal of Archaeological Science*, **18**, 227–248.
- , BOUTTON, T. W., TESDAHL, K. G. & SLADE, N. A. 1983. Fractionation and turnover of stable carbon isotopes in animal tissues: implications for the  $^{13}\text{C}$  analysis of diet. *Oecologia (Berlin)*, **57**, 32–37.
- VAN DER MERWE, N. J. & MEDINA, E. 1989. Photosynthesis and  $^{13}\text{C}/^{12}\text{C}$  ratios in Amazonian rain forests. *Geochimica et Cosmochimica Acta*, **53**, 1091–1094.
- VAN VALEN, L. 1973. A new evolutionary law. *Evolutionary Theory*, **1**, 1–30.
- VRBA, E. S. 1985a. Environment and evolution: Alternative causes of the temporal distribution of evolutionary events. *South African Journal of Science*, **81**, 229–236.
- 1985b. African Bovidae: Evolutionary events since the Miocene. *South African Journal of Science*, **81**, 263–266.
- 1995a. On the connection between paleoclimate and evolution. In: VRBA, E. S., DENTON, G. H., PARTRIDGE, T. C. & BURCKLE, L. H. (eds) *Paleoclimate and Evolution, with Emphasis on Human Origins*. Yale University Press, New Haven, 24–45.
- 1995b. The fossil record of African Antelopes (Mammalia, Bovidae) in relation to human evolution and paleoclimate. In: VRBA, E. S., DENTON, G. H., PARTRIDGE, T. C. & BURCKLE, L. H. (eds) *Paleoclimate and Evolution, with Emphasis on Human Origins*. Yale University Press, New Haven, 385–411.
- , DENTON, G. H., PARTRIDGE, T. C. & BURCKLE, L. H. (eds) 1995. *Paleoclimate and Evolution, with Emphasis on Human Origins*. Yale University Press, New Haven.
- , — & PRENTICE, M. L. 1989. Climatic Influences on early hominid behavior. *OSSA*, **14**, 127–156.

- WANG, Y., CERLING, T. E., QUADE, J., BOWMAN, J. R., SMITH, G. A. & LINDSAY, E. H. 1993. Stable isotopes of paleosols and fossil teeth as paleoecology and paleoclimate indicators: An example from the St. David Formation, Arizona. *In*: SWART, P. K., LOHMANN, K. C., MCKENZIE, J. A. & SAVIN, S. (eds) *Climate Change in Continental Isotopic Records*. Geophysical Monograph, **78**, 241–248.
- WESSELMAN, H. B. 1985. Fossil micromammals as indicators of climatic change about 2.4 Myr ago in the Omo valley, Ethiopia. *South African Journal of Science*, **81**, 260–261.
- WHITE, T. D. 1995. African omnivores: Global climatic change and Plio-Pleistocene hominids and suids. *In*: VRBA, E. S., DENTON, G. H., PARTRIDGE, T. C. & BURCKLE, L. H. (eds) *Paleoclimate and Evolution, with Emphasis on Human Origins*. Yale University Press, New Haven, 369–384.
- WOOD, B. 1992. Origin and evolution of the genus *Homo*. *Nature*, **355**, 783–790.
- , WOOD, C. & KONIGSBERG, L. 1994. *Paranthropus boisei*: An example of evolutionary stasis? *American Journal of Physical Anthropology*, **95**, 117–136.