THE MALAWI RIFT: BIOGEOGRAPHY, ECOLOGY AND COEXISTENCE OF HOMO AND PARANTHROPUS

ABSTRACT: Remains of earliest Homo and Paranthropus have been recovered from two contemporaneous sites (Uraka and Malemo) in the "Hominid Corridor" in northern Malawi (Chiwondo Beds). Faunal dating suggests an age of 2.5 – 2.3 Ma for both hominids. The associated bovid and said faunas show an overlap of a small amount of southern African with a great amount of eastern African faunal elements. Biogeographic variation in southern Africa may be linked to habitat change occurring due to climate change after 2.8 Ma. The Hominid taxa present in the Malawi Rift, Homo rudolfensis and Paranthropus boisei, both represent eastern African endemic elements originating from the eastern African australopithecine stem group. Their different lifestyles and survival strategies are linked to climate and habitat change as well as biogeographic variation and dispersal. A pan-african scenario of early hominin evolution is developed on this basis. This scenario suggests a single origin for the Paranthropus lineage but separate origins for Homo rudolfensis and Homo habilis from Australlopithecus anamensis/aferensis and Australopithecus africanus ancestors respectively.

KEYWORDS: Plio-Pleistocene – Climate Change – Palaeobiogeography – Homo – Paranthropus – Malawi Rift – Africa

INTRODUCTION

The ancient lake deposits of northern Malawi (Figure 1) were first described by Dixey (1927). He recognised Chiwondo Beds and Chitimwe Beds which he attributed to the Pliocene and Pleistocene, respectively. Determination of the Pliocene age of the Chiwondo Beds was based on fossil vertebrates collected by him. The first major contributions to our knowledge of the palaeoecology and palaeobiogeography of the Chiwondo Beds of the northern Malawi Rift were the result of pioneering interdisciplinary explorations into the prehistory of sub-Saharan Africa by J. Desmond Clark and colleagues (Clark et al. 1966, 1970, Clark, Haynes 1970, Croydon 1966, Mawby 1970). Clark led teams of researchers to conduct archaeological, palaeoentological and geological work on the Chiwondo Beds in 1963, 1965 and 1967. The deposits were re-investigated by Z. M. Kafulu and T. D. White in 1979 (Kafulu et al. 1981). Realising the specific potential for contributions to the understanding of the Plio-Pleistocene palaeobiogeography of continental Africa, the Hominid Corridor Research Project (HCRP) began a long-term study in 1983, focusing on the regional geology and the geographic role of south-east Africa on the origin and dispersion of Plio-Pleistocene faunas including early hominids (Bromage et al. 1985, Bromage, Schrenk 1987, Schrenk et al. 1993, Bromage, Schrenk 1995a).

The sedimentology and stratigraphy was described by Beitzler, Ring (1995), the tectonic development of the Malawi Rift was analyzed by Ring, Beitzler (1992, 1995). Lake beds and fluvialite deposits of palaeolake Malawi have been subdivided into five depositional units which are bounded by unconformities reflecting sedimentary breaks (Figure 2). Prior to the formation of a major perennial lake, the depositional area was characterised by extensive fluvialite deposits mainly formed by reworked material of Jurassic red beds. Formation of a major lake after this episode is reflected in widespread lacustrine silts
and sands with interbedded, mollusc-rich layers. Tectonic reorganization of the rift finally led to localized uplift resulting in an angular unconformity and exposure of the Plio-Pleistocene deposits. The fossil localities are concentrated in the area around Malena, referred to as the "northern localities", and around Uraha near Chiulumba, referred to as the "southern localities" (Figure 1).

Mammalian fauna of the Chiwondo-Beds

The sample of Plio-Pleistocene vertebrates recovered from the Chiwondo Beds in the Karonga District of northern Malawi, includes more than 1,000 identifiable fragmentary remains of fish, turtles, crocodiles and large mammals and a large number of invertebrate specimens from 131 fossil localities (Bromage et al. 1995a). Whereas the terrestrial vertebrate fossils are nearly all found in interbedded soft sand, the fresh water molluscs are contained in consolidated beds of carbonate cemented sandstone. Molluscan shell beds crop out as benches up to several meters thick and several hundred meters wide. Severe taphonomic processes due perhaps to the reworking of bones in beach environments and recent erosional processes leads to extinctions of fossil material. Micro-vertebrates and carnivores are virtually underrepresented in the bone assemblage.

Three-quarters of the vertebrate sample are of mammalian origin (Figure 3). Thereof ca. 150 postcranial elements have been collected, mostly high density elements – mainly fragments of long bones, vertebrae and foot bones of macro mammalian taxa. The remainder are 600 dental or cranial specimens which are taxonomically identifiable mostly to genus level. Of these the highest proportion representation show the bovids (43.3%), followed by equids (16.5%), hippopotamids (14.4%), suids (11.0%), proboscids (8.1%), giraffids (2.9%), primates (1.5%), and rhinocerotids (1.0%) (Schrenk et al. 1995).

Age of the Chiwondo Beds

An estimate of the age of the Chiwondo Beds must still rely on correlation with radiocarbon-dated biostratigraphic units in eastern Africa. In so doing, the first definitive study by Kafula et al. (1981) provided dates of approximately 2.4–2.6 Ma (based on suids) and 2.5–3.0 Ma (based on bovids) for the more northerly sites and 4.0 Ma or older for the southerly Uraha sites (based on suids). Most of the Late Pliocene fossil localities now are attributed to stratigraphic Unit 3A while older Middle Pliocene localities occur in stratigraphic Unit 2 in the north and the south. An age determination of older than 4.0 Ma to about 1.5 Ma is based on the faunal assemblages described by Bromage et al. (1995a).

Figure 3 presents a list of mammalian taxa from the Chiwondo Beds presently recognized by us and which provide broad age constraints for the deposits. These taxa are listed together with their age ranges. The age ranges are based on radiometric age determinations of volcanic tuffs and correlations between the Kooib Fora and Shungura Formations described by Brown et al. (1985) and Brown and Feibel (1986). These ages confirm a biogeographical consistent with the stratigraphy of the Chiwondo Beds as shown in Figure 2.

Mammalian biogeography

Many of the recovered faunal taxa confirm a certain degree of faunal continuity between the eastern and southern African Late Plioence. However, our research continues also to define a unique community assemblage. Kafula et al. (1981) characterized the faunal discontinuity of this assemblage by noting that the predominant bovid species at Makapanetse Member 3 – Redunca darti, Phanoceras vanhoepeni and Makapania broomi – do not occur in eastern African Late Pliocene sites. Furthermore, contemporaneous assemblages at Omo and Hadar, dominated by Aepyceros, reducine genera such as Kobus and Menelikia, and tragelaphines such as Tragelaphus nakawa, are absent from southern African sites.

The Malawi Rift faunas are partitioned between three geographically-based groups that give clues as regards palaeoecological domains and patterns of faunal dispersion between eastern and southern Africa (Figure 3). Five taxa occur in eastern as well as southern as African, 14 taxa are of eastern African origin and only three taxa are of southern African provenance.

The largest faunal group comprises eastern African endemics reflecting a regional African rift Valley corridor comprised of rift "chain" montane communities and associated lowlands and grasslands shared across eastern to south-east Africa (Kingdon 1989). Indeed, the North-South oriented structural evolution of the northern part of the African Rift Valley has been implicated as a "continuous rift corridor" related to rodent evolution and migration during the Pliocene (Denys et al. 1986, Denys 1996). Macromammalian distributions were certainly broader, however, and include east-west dispersions of savannah faunas across the Rift Valley at least as far as the Western Branch (cf. Boz et al. 1992), while its dense forest-adapted faunas were probably distributed even further west into the Zaire Basin. Thus the impression of a 'corridor per se is less one of passage along discrete faunal habitats than it is a broad melange of interconnected habitats stretching from north-east Africa to the Zambezian Ecoregion and the temperate zone transition in south-east Africa.

The southern African endemic group is very small (Figure 2). It transpires that this is most probably due to the equatorward dispersion of faunas keeping pace with the poleward migration belts due to the aridification of global climates ca. 2.5 Ma (southern endemics dispersing to eastern Africa diminish this category while contributing to the larger shared eastern plus southern faunal group; see Figure 3). How may these geographical groupings be interpreted? The answer to this question derives from the modern synthesis of biogeography and climate in
TABLE 1. African fossil Bovidae first appearances approximately 2.5 Ma, their geographic origin, and their dispersion direction. *Paranotoceros brauni*, *Tragelaphus priscus*, and *Syncerus sp.* have older origins (ca. 3.0 Ma) but dispersions around 2.5 Ma. Where the dispersion has occurred at some date other than ca. 2.5 Ma, an approximate date has been given. Data from Turner, Wood (1993a).

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taxa restricted to more specific habitats might have transgressed this region only when ecological extremities could afford latitudinal shifts in their appropriate vegetation zones. Such a latitudinal shift likely began approximately 2.8 Ma during which time cooler and dryer conditions prevailed (Bonnefille 1976, 1980, 1985, Prentice, Denton 1988, Vrba et al. 1985, 1989, Vrba 1995, deMenocal, Bloemendaal 1995, Dupont, Leroy 1995). These conditions are hypothesized to result in the equatorward shift of grassland and woodland biomes according to the "Habitat Theory" of Vrba (1992).

The Habitat Theory derives from seven hypotheses relating ecological conditions to faunal evolution and biogeography. Necessary features of this theory are that terrestrial vegetational habitat specificity is heritable and thus characteristic for clades, that terrestrial mammal biomes may be distinguished by their gross vegetational physiognomy, and that distribution movements (drift) occur in the context of physical environmental change. In order to test this proposition we have summarized the data provided by Turner, Wood (1993a) on the origin and dispersion of bovid taxa around 2.5 Ma (Table 1). *Paranotoceros brauni*, *Tragelaphus (jageri)* in the Early Pliocene in Africa, first appeared around 3 Ma. Indeed, we note that most taxa originating in southern Africa dispersed toward the equator around 2.5 Ma when aridity was increasing and biomes where shrubland shifted toward the equator. These taxa include both dispersing open/rid and closed/dry taxa, consistent with hypothetical north-south vegetation corridors propagating through the Zambezian Escuence when assuming 50-60% of present day rainfall (Cook 1962; see also Zinder Bakker 1969).

We also note that even amongst this small group of bovids originating about 2.5 Ma there are two taxa dispersing to southern Africa at 2.0 Ma and younger (Figure 3). This may represent average environmental conditions returning to more warm and humid conditions during this time (cf. Shackleton et al. 1984). This suggests to us that a model of bovid expansion away from the equatorial zone, during the terminal Pliocene or onset of the Early Pleistocene. This is compatible with early hominid biogeography and interpretations of the origins and distributions of Homo sapiens and Pananthropus (see below) as well as of Australopithecus africanus and Homo habilis (Broom, Schrenk 1959).

A second mammalian group which provides promising information about the context of climate and habitat change, as well as morphology change are the suids. The rapid evolution of several suid lineages during the African Plio-Pleistocene, and the discussion of this adaptive group as reaction to the proposed climate change between 2.8 and 2.5 Ma. During this time span the suid fauna was dominated by noutocerine species (*Notoceros eulaus, Notoceros capensis* and *Notoceros scotti*), although several other genera (*Pomatoceros, Metridiochoerus* and *Kolpocherus*) occurred in Africa at around 3 Ma. The first notocerines derived from a progressive form of Nyansarchoerus (Nyansarchoerus brauni), in the Early Pliocene in Africa, recorded in northern, eastern and southern Africa. Characteristic for this widely distributed suid is the elongation of the third molar, as well as an increase in crown height. Typical examples of *Ny. jageri* are described as a rare element from Hamada Damous, the Mursi Formation, Lothagam, Ater, Chemeron, Kanapoi, Ekkora and the Chiwondo Beds in northeastern Malawi. The specimens from Langebusch and Vial River Gravels in South Africa interpreted by Cooke, Hendey (1992) as *Ny. cf. jageri* probably are to conservative in their overall features to be the direct ancestors of the notocerines (Kullmer 1997). The proposed direct descendant of *Nyansarchoerus jageri*, *Notoceros eulaus* is unknown from southern Africa, while it is widespread in eastern African localities and in the south-east corridor, the Malawi rift valley. The first notocerines in southern Africa (Makapanstang and Vial River) described by Broom (1925) as *Notoceros capensis* represent an advanced form, more derived as *N. eulaus* from the Chiwondo Beds (Unit 3A). This evolutionary stage of notocerines is also common in the Chiwondo Beds (Unit 3A) and gave rise to the progressive *Notoceros scotti*, a suid species that developed high crowned and long third molars during the time *Homo* and *Paranthropus* occurred in eastern and south-eastern Africa around 2.5 Ma. Advanced *N. scotti* specimens are not known from southern African sites, although it is common in the Chiwondo Beds. The evolutionary trend in notocerines third molars towards an elongation and increase in crown height is obviously and can be interpreted as adaptation to more abrasive in soil fauna was dominating the modern earth containing mostly on grass (Kullmer, in print). Moreover, the suid dispersion and morphological changes are linked probably to habitat changes occurring due to climate change around 2.8 Ma.

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**Palaeoanthropology of the Malawi-Rift**

During the 1991 and 1992 field seasons the Hominid Corridor Research Project has recovered a mandibular corpus, UR 501, containing third and fourth premolars and first and second molars in variable states of preservation (Figure 4) (Schrenk et al. 1993). Many absolute and relative measures respecting molar and premolar crown shape indices, some relative cusp areas, and enamel microanatomical features, as well as fissure patterns and crown morphology, are within the sample range of early Homo. UR 501 corresponds closely to the subset of Late Pliocene fossils from east of Lake Turkana, Kenya, that have relatively large brains and robust jaws and teeth and that have been referred to *Homo rudolfensis* (Alexeev 1986), by Wood (1992), and to which we also referred UR 501 (Bromage et al. 1995).

During the field season 1996 the HCRP discovered a further hominid specimen, a maxillary fragment, CR 911, at the site Malema, approximately 50 km north of Uraba (Figure 5). The specimen CR 911 represents a part of the left processus alveolaris with M1 and a fragmentary crown of the M2. The fragment is broken mesially just in front of the M1 alveolus and distally of the M2 alveolus. Crown size, shape and micropattern on the occlusal surfaces together with the height of the alveolar process suggests a determination of *RC 911* as *Paranthropus boisei* (Kullmer et al. 1999)

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**South-eastern African Hominid biogeography**

The palaeobiogeographic significance of *Homo rudolfensis and Paranthropus boisei* of the Malawi Rift
lay in its association with an assemblage dominated by eastern African endemic faunas (Figure 3). This biogeographic pattern is most probably a reflection of the equatorial, tropical, and mountainous region of southern faunas, those with northward-drifting vegetation belts during the aridification of global climates ca 2.5 Ma (Bonneille 1976; 1988; Vauba 1989). During the 1980s, deMenocal, Bloemendaal 1995, Dupont, Leroi 1995). It may be surmised that equatorial lineages faced less the problem of latitudinal shifts in biome zonation than habitat fragmentation. Biogeographical lineages have a greater diversity of habitat choices, however, remained endemic to the tropical African ecological domain and experienced patterns of extinction and speciation. Thus the palaeoecological implications of the Climatic Implications of the Climatic and faunal assemblages may be that Homo rudolfensis arose during, and partly as a result of, the ca 2.5 Ma climatic cooling event in eastern Africa and remained endemic there in the face of prevailing equatorward dispersion tendencies in other taxa according to the Habitat Theory. This would be a demonstration of their ecosensitivities and some degree of niche-dependence in this taxon.

Homo rudolfensis was endemic to eastern Africa and conformal to the palaeobiogeographic response to environmental change exhibited by some boids (Bromage et al. 1988). This is probably also the case for the origins of the southern, geographically restricted eastern African faunas during the ascendency of cooler and dryer periods between ca 2.5 and 2.0 Ma. Paranthropus (= Australopithecus) aethopicus (cf. Teichert 1969; Walker et al. 1986; Walker et al. 1986; and Paranthropus boisei). It follows that the return to warmer and more humid conditions by 2.0 Ma would possibly have instituted or facilitated faunal dispersions away from the equatorial (boid dispersions between 2.0 and 1.5 Ma did just this, see Table 1). Consistent with this view is the later age of first appearance of Paranthropus in southern Africa between 2.0 and 1.5 Ma at Swartkrans. We may then characterize the evolution of Paranthropus robustus/ crassidens in southern Africa as including a moderation of the hypermasticatory trend of P. boisei with a diminution of the face and post-cranial dentition.

The same arguments may be applied to the origin and dispersal of Homo habilis. If one accepts the assignment of early Homo specimens from Sterkfontein Member 5 (ST5) (Hughes, Tobias 1977; Clarke 1985) and Swartkrans Member 1 (SK1) to Homo habilis (Brain et al. 1988), then we may attribute this taxon to the shared southern-plus-eastern African group. The earlier Late Pliocene presence of Homo habilis at Koobi Fora might suggest its origins in eastern Africa, increasing its distributional area into southern Africa sometime between 1.8 and 1.5 Ma during SK1 and ST5 times (Vauba 1982).

It is important to emerge from our palaeobiogeographic interpretations is that early hominids consistently arise in the eastern African ecological domain (which includes northern reaches of the Zambesian Eczone in the Malawi Rift). During favourable periods, some early hominids dispersed southward beyond the Zambesian Eczone, evolved there (perhaps due to relative isolation and/or differences associated with its temperate ecology), and then dispersed northward during periods more consistent with expectations that hominid diversity should be greater in tropical regions and, further, that speciation may at times be the consequence of dispersal and increasing for early hominids with an accompanying niche specialization (Foley 1991).

Early hominid evolution: a scenario
The geographic distribution of ancestral populations of the African ape and hominid clades was broadly constrained to tropical Africa and its lowland forests. This was largely due to the climatic conditions of the region as a whole, which was largely dominated by global cooling precipitated marked environmental change (cf. Brain 1981). These climatic conditions in eastern Africa, exacerbated by the regional environmental consequences of rifting (cf. Pickford 1991), led to a shrinking back of the forests. Indeed, significantly more open grasslands were featured in eastern Africa by 8.9 Ma (Cerling et al. 1991). At the same time, central African lowland forest habitats were itself fragmented or confined by forestation for differentiating hominoid subspecies and species (cf. Colyn et al. 1991, for a discussion of Late Pleistocene and Holocene environments).

Distribution drift of the tropical forests left more open wooded savannah in its wake (Andres 1981) and engendered increased habitat diversity (cf. Retallack et al. 1990). The latter became more extreme during the terminal Miocene, some 5-8 Ma (Brain 1988). This, in turn, led to the eventual expansion and northward migration of the hominid lineages. The particular lineages and ecosystems that the hominids would have used in their dispersal is beyond the scope of this chapter. However, it is clear that the lineages that dispersed northward during the terminal Miocene were sufficiently diverse to be able to colonize a variety of habitats.

During this period, the hominid clades dispersed southward and westward beyond the Zambesian Eczone, and evolved there (perhaps due to relative isolation and/or differences associated with its temperate ecology), and then dispersed northward during periods more consistent with expectations that hominid diversity should be greater in tropical regions and, further, that speciation may at times be the consequence of dispersal and increasing for early hominids with an accompanying niche specialization (Foley 1991).

As the terminal Miocene dry seasons became longer and more pronounced, ground-based foods resources included a proportionately higher diversity of underground perennial forbs while the rainy seasons would continue to supply the fruits, seeds, and pods of the woody species (cf. Peters et al. 1984). For over a million years the tundra and boreal habitats associated with a tundra environment is characterized by herbaceous and terrestrial niche were compromised during the Miocene to meet the demands of this mixed habitat and niche. Australopithecus anamensis and Australopithecus afarensis arose in eastern this in the African tropical ecological domain. Their behavioural inclination was to remain near the borders between broad riparian habitats and open woodlands during this time, and their dietary niche was more opportunistic than the most recent hominid taxon (Australopithecus afarensis) and the Homo lineage (Bromage et al. 1995a) permitted population dispersal into southern Africa by 3.0 Ma. This dispersal was self-sustained during the assembly of the South African clade, and the Malawian Rift and its associated rift habitats to temperate Africa and the riparian corridor (Bromage et al. 1995b).

The record of the Malawian Rift and its associated rift habitats to temperate Africa and the riparian corridor (Bromage et al. 1995b).

The record of the Malawian Rift and its associated rift habitats to temperate Africa and the riparian corridor (Bromage et al. 1995b).

The 1.5 MA ago, the fragmented habitat specificity to forested environments (cf. Rayner et al. 1993) through in more environmentally temperate climes and in relative geographical isolation at the extreme distal edge of its distribution, it would have been extraordinarily rare for hominids to have access to forested habitats, in part because of the long-term adaptations to those environments. This is reflected in the hominid fossils that have been recovered from the Malawian Rift, the oldest known hominid fossil from the area being an isolated tooth of Homo habilis from 1.8 Ma (Bonneille 1976, 1988; Prentice, Denton 1988; Vauba 1985, 1988; deMenocal, Bloemendaal 1995, Dupont, Leroi 1995). During this time Australopithecus afarensis and Australopithecus africanus were each subject to unique palaeoecological consequences of this global aridification, in accordance with the Habitat Theory of Vauba (1992). The rate of faunal turnover (including early hominids) in eastern Africa exceeded the southern African experience (Bromage et al. 1995a) because of the relative density of "habitable" alternatives in the tropics (a consequence of greater diversity). For Australopithecus afarensis, the extreme aridity caused by the drier climatic regime during this period was a direct consequence of its habitat and its distribution into more removed ecolonal riparian and closed lake margin environments. During the interregnum between ca 2.8 Ma and 2.5 Ma these changing conditions engendered more extensive open habitats comprising more resistant arid-tolerant vegetation around the remaining relatively lush but narrow "ribbons" of riparian habitats, the nature of which was further enhanced by the increasing aridity of the environment. This change in the environmental conditions resulting in the increased survival of more survived varieties capable of feeding on tougher fruit and open woodland/open savanna habitats, species capable of surviving in these more extreme conditions. As a result, the splitting of the Australopithecus afarensis into Paranthropus and Homo lineages after 2.8 Ma (Vauba 1988, Kimbel 1995, Bobe 1997).

The beginnings of the Malawi lineage, represented by Paranthropus (= Australopithecus) aethopicus (e.g. Walker et al. 1986, Kimbel et al. 1988), maintained a reliance on fruiting resources on the riverine side of its ecosystem, particularly during the dry season, but was equally adept at grading on the postcanine dentition those food items required from more open habitats during more pronounced times of the year. Over this time lineages adapted ecologically to the open habitat side of its ecosystem, becoming more facially robust and megadont in order to efficiently process the tougher, more durable, vegetation of the savannah. This evolved taxon, Paranthropus boisei, probably played a crucial role in the subsequent emergence of the closed features of its environment (cf. Shipman, Harris 1988), however, as these habitats would continue to provide essential protection, sleeping localities, and some foods that were either interesting if its enduring evolutionary history was the result of a biotic eccentricity in an otherwise so specialized a hominid). The beginnings of the Homo lineage, also ca 2.5 Ma, and represented by Homo rudolfensis, was an endorsement of its recency of common ancestry with Australopithecus afarensis, a distinction it shared with Paranthropus aethopicus (Bromage et al. 1995b). By this token Homo rudolfensis then shared with Paranthropus a number of masticatory-related cranial and dental adaptations (Wood 1992, 1993) to the tougher fruit and open savannah food items sought by early hominids. It need not concern us whether these similarities between Paranthropus and Homo rudolfensis were actually shared in a temporally fleeting post-Australopithecus afarensis ancestor or not. The intimacy of their shared genetic heritage closely dictates their sharing, also, numerous canalized developmental pathways commanding similar responses to specific selection pressures. Thus many or all uniquely derived similarities between Homo rudolfensis and Paranthropus may be homoplasies, but this is because of their relative recency of ancestry. These similarities, particularly as they relate to the vegetative responses to aridifying climate change, are considered to be our most important evolutionary evidence that Homo rudolfensis remained somewhat conservative in its feeding habits and depended still, and most of all, on plant resources.
REFERENCES


