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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 (Uraha and Malema) 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 suid faunas show an overlap of a small amount of southern African with a great amount of eastern African faunal elements. Biogeographic variation in south-eastern 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 panafrican scenario of early hominid 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* Australopithecus anamensis/afarensis *and* Australopithecus africanus *ancestors respectively.*

KEY WORDS: 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 recognized 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, Coryndon 1966, Mawby 1970). Clark led teams of researchers to conduct archaeological, palaeontological and geological work on the Chiwondo Beds in 1963, 1965 and 1967. The deposits were re-investigated by Z. M. Kaufulu and T. D. White in 1979 (Kaufulu *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 longterm 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 Betzler, Ring (1995), the tectonic development of the Malawi Rift was analyzed by Ring, Betzler (1992, 1995). Lake beds and fluviatile 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 fluviatile deposits mainly formed by reworked material of Jurassic red beds. Formation of a major lake after this episode is reflected in widespread lacustrine silts

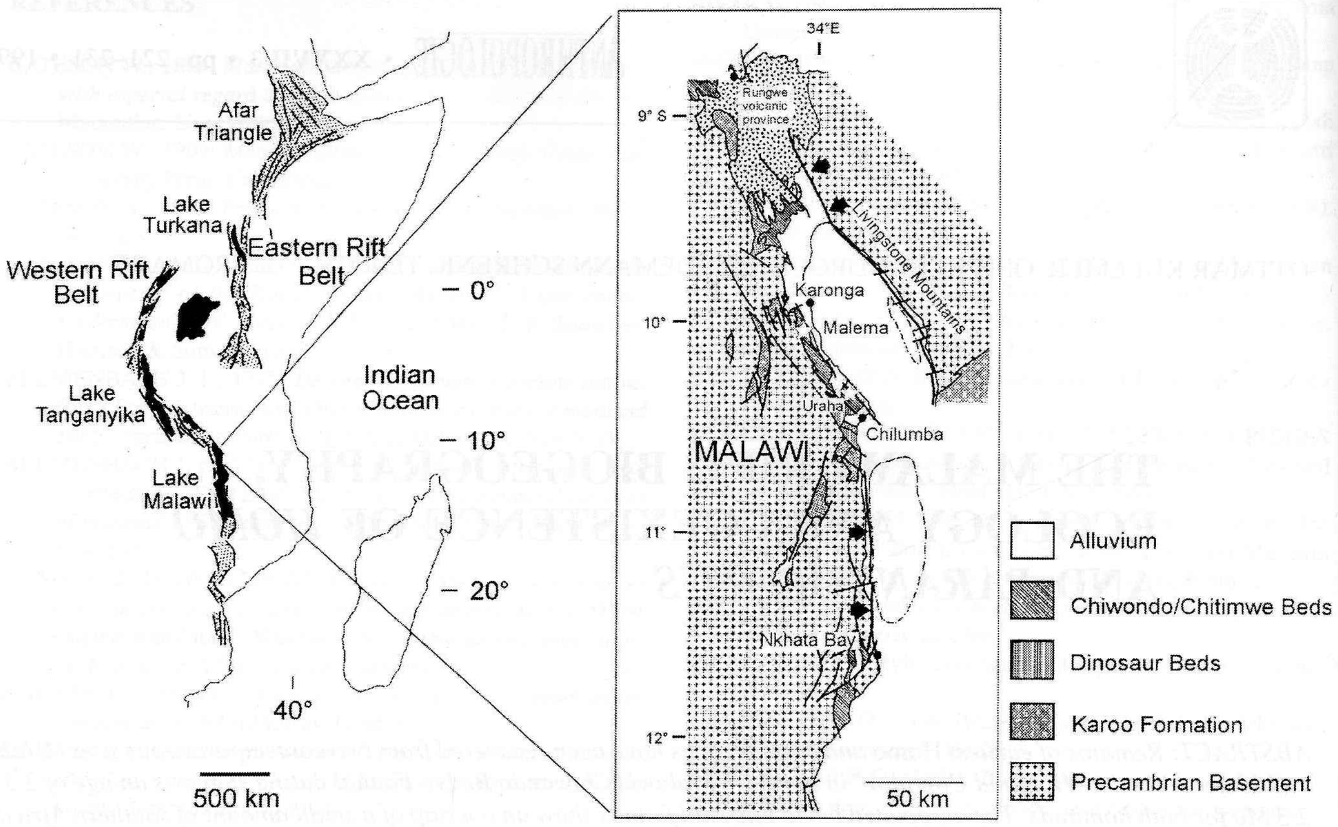

FIGURE 1. Position and geology of the Malawi Rift.

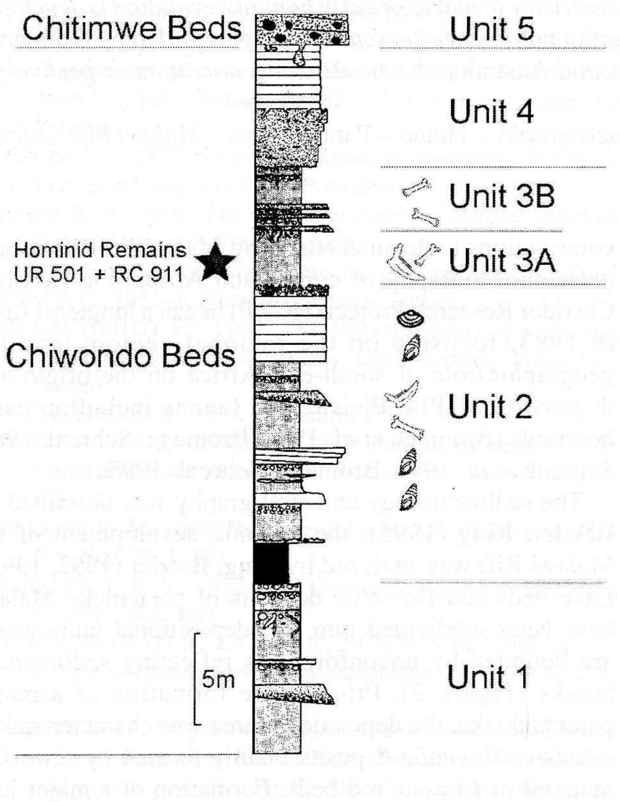

FIGURE 2. Stratigraphy of the Plio-Pleistocene Chiwondo Beds.

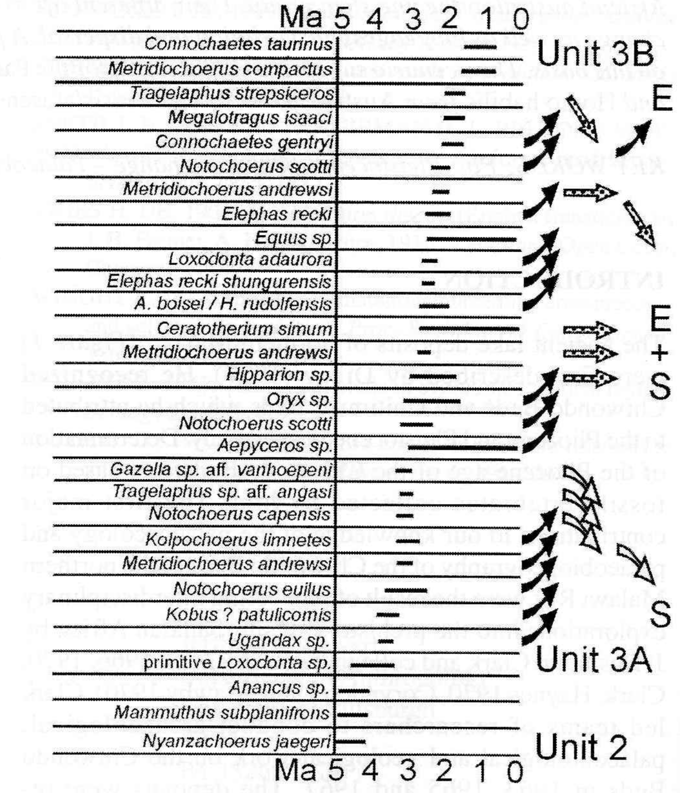

FIGURE 3. Biostratigraphy and biogeography of the Chiwondo Beds.

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 Malema, referred to as the "northern localities", and around Uraha near Chilumba, 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 fragmented 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 always 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 led to extensive destruction of fossil material. Micro-vertebrates and carnivores are veritably 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%), proboscidians (8.1%), giraffides (2.9%), primates (1.8%), rhinoceratids (1.0%) and camelids (0.3%)(Schrenk *et al.* 1995).

Age of the Chiwondo Beds

An estimate of the age of the Chiwondo Beds must still rely on correlation with radiometrically dated biostratigraphic units in eastern Africa. In so doing, the first definitive study by Kaufulu *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 Koobi Fora and Shungura Formations described by Brown *et al.* (1985) and Brown, Feibel (1986). These ages confirm a biochronology 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 Pliocene. However, our research continues also to define a unique community assemblage. Kaufulu *et al.* (1981) characterized the faunal discontinuity of this assemblage by noting that the predominant bovid species at Makapansgat Member 3 – *Redunca darti*, *Phenacotragus vanhoepeni* and *Makapania broomi* – do not occur in eastern African Late Pliocene sites. Furthermore, contemporaneous assemblages at Omo and Hadar, dominated by *Aepyceros*, reduncine genera such as *Kobus* and *Menelikia*, and tragelaphines such as *Tragelaphus nakuae*, 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 Africa, 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). Macromammal 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. Boaz *et al.* 1992), while its dense forest-adapted faunas were probably distributed even further west into the Zaire Basin woodlands. Thus the impression of a 'corridor' *per se* is less one of passage along discrete faunal habitat types than it is a broad melange of interconnected habitats stretching from north-eastern Africa to the Zambezian Ecozone 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 drifting vegetation belts during 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 geographic 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. *Parmularius braini*, *Tragelaphus pricei*, 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).

Habitat Preference	**Origin**		**Dispersion Direction**	
	SA	EA	S → E	E → S
OPEN/ARID				
Alcelaphini				
Beatragus antiquus		EA		
Connochaetes taurinus	SA		**S → E**	
Connochaetes gentryi		EA		
Damaliscus sp.	SEA			
Parmularius braini	SA		**S → E**	
Parmularius angusticornis		EA		
Hippotragini				
Oryx sp.		EA		
Antilopini				
Gazella praethomsoni		EA		
Antilope subtorta		EA		
Antidorcas recki	SA		**S → E**	
Antidorcas bondi	SA			
CLOSED/DRY				
Tragelaphini				
Tragelaphus gaudryi		EA		
Tragelaphus strepsiceros		EA		E → S 2-1.5
Tragelaphus pricei	SA		**S → E**	
Aepycerotini				
Aepyceros melampus		EA		E → S 0.5 Ma
CLOSED/WET				
Hippotragini				
Hippotragus equinus	SA		S → E 0.5 Ma	
Hippotragus gigas		EA		
Reduncini				
Kobus ellipsiprymnus		EA		E → S 2-1.5-
Menelika lyrocera		EA		
Redunca arundinum	SA			
Bovini				
Syncerus acoelotus		EA		
Syncerus sp.		EA		E → S
Pelorovis turkanensis		EA		

evolutionary biology (Matthew 1939). We note that continental position and climatic conditions are responsible for the tropical *versus* temperate zonation in Africa today (Griffiths 1984, Oliver, Crowder 1979). These conditions are our template against which Pliocene climate change may be interpreted and faunal distributions explained.

Situated as it is between climatic regimes, the south-east African region has most probably been the meeting point for endemic faunas from the north and south since the continents have been in their current positions. Eurybiomic taxa (i.e. those taxa able to acquire their resources in more than one biome; cf. Vrba 1987b) will have been shared between eastern and southern Africa, but taxa restricted to more specific habitats might have transgressed this region only when ecological extremes could affect 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, 1995, Prentice, Denton 1988, Vrba *et al.* 1985, 1989, Vrba 1995, deMenocal, Bloemedal 1995, Dupont, Leroy 1995). These conditions are hypothesized to result in the equatorward shift of grassland and woodland biomes accordant with 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's are 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*). *Parmularius braini*, *Tragelaphus pricei* und *Syncerus* sp. 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 shrinking towards the equator. These taxa include both dispersing open/arid and closed/dry taxa, consistent with hypothetical north-south vegetation corridors penetrating through the Zambezian Ecozone when assuming 50–60% of present day rainfall (Cooke 1962, see also Zinderen 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 a model of biome expansion away from the equator sometime during the terminal Pliocene or onset of the Early Pleistocene. This is compatible with early hominid biogeography and interpretations of the origins and dispersions of *Homo* and *Paranthropus* (see below) as well as of *Australopithecus africanus* and *Homo habilis* (Bromage, Schrenk 1995b).

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 summon us to discuss the dispersion 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 notochoerine species (*Notochoerus euilus*, *Notochoerus capensis* and *Notochoerus scotti*), although several other genera (*Potamochoeroides*, *Metridiochoerus* and *Kolpochoerus*) occurred in Africa at around 3 Ma. The first notochoerines derived from a progressive form of *Nyanzachoerus* (*Nyanzachoerus jaegeri*) 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. jaegeri* are described as a rare element from Hamada Damous, the Mursi Formation, Lothagam, Ateir, Chemeron, Kanapoi, Ekora and the Chiwondo Beds (Unit 2) in Malawi. The specimens from Langebaanweg and Vaal River Gravels in South Africa interpreted by Cooke, Hendey (1992) as *Ny.* cf. *jaegeri* probably are to conservative in their overall features to be the direct ancestors of the notochoerines (Kullmer 1997). The proposed direct descendant of *Nyanzachoerus jaegeri*, *Notochoerus euilus* 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 notochoerines in southern Africa (Makapansgat and Vaal River) described by Broom (1925) as *Notochoerus capensis* represent an advanced form, more derived as *N. euilus* from the Chiwondo Beds (Unit 3A). This evolutionary stage of notochoerines is also common in the Chiwondo Beds (Unit 3A) and gave rise to the progressive *Notochoerus scotti*, a suid species that developed high crowned and long third molars during the time when *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 notochoerines third molars towards an elongation and increase in crown height is obviously and can be interpreted as adaptation to more abrasive and harsher diet as we can find it in the modern warthog, feeding 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.

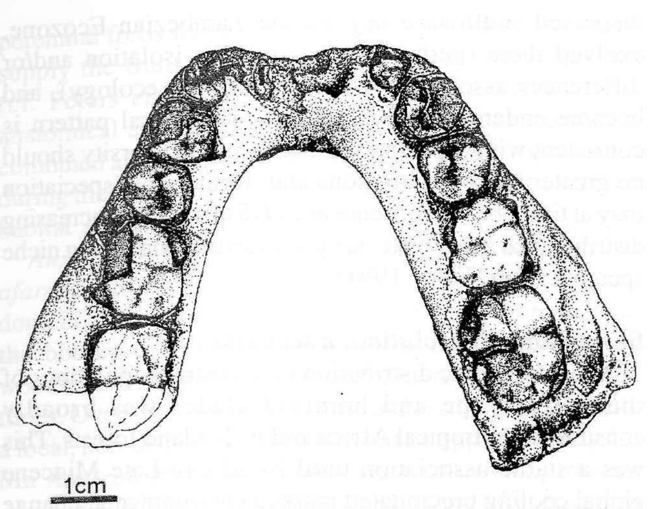

FIGURE 4. Mandible UR 501 (*Homo rudolfensis*) from Uraha (occlusal view).

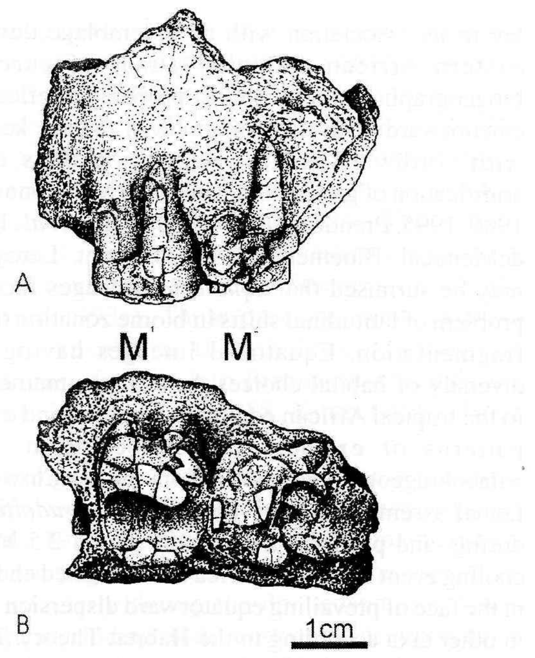

FIGURE 5. Maxillary Fragment RC 911 (*Paranthropus boisei*) from Malema, A) buccal view, B) occlusal view.

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.* 1995b).

During the field season 1996 the HCRP discovered a further hominid specimen, a maxillary fragment, RC 911, at the site Malema, approximately 50 km north of Uraha (*Figure 5*). The specimen RC 911 represents a part of the left *processus alveolaris* with M^1 and a fragmentary crown of the M^2. The fragment is broken mesially just in front of the M^1 alveolus and distally of the M^2 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)

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 equatorward dispersion of southern faunas, keeping pace with northward-drifting vegetation belts during the aridification of global climates *ca* 2.5 Ma (Bonnefille 1976, 1980, 1995, Prentice, Denton 1988, Vrba *et al.* 1985, 1989, deMenocal, Bloemendal 1995, Dupont, Leroy 1995). It may be surmised that *equatorial* lineages faced less the problem of latitudinal shifts in biome zonation than habitat fragmentation. Equatorial lineages having a greater diversity of habitat choices, however, remained endemic to the tropical African ecological domain and experienced patterns of extinction and speciation. Thus the palaeobiogeographic implications of the Chiwondo Beds 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 ecosensitivity and some degree of niche-dependence in this taxon.

Homo rudolfensis was endemic to eastern Africa and conformed to the palaeobiogeographic response to environmental change exhibited by some bovids (Bromage *et al.* 1995b). This reasoning applies also to the origins of other dento-facially robust eastern African endemics during the ascendancy of cooler and dryer times between *ca* 2.5 and 2.0 Ma; *Paranthropus* (=*Australopithecus*) *aethiopicus* (e.g. KNM-WT 17000; 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 equator (bovid 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-canine dentition.

The same arguments may be applied to the origin and dispersion 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 (Vrba 1982).

The pattern to emerge from our palaeobiogeographic interpretations is that early hominids consistently arise in the eastern African ecological domain (which includes northern reaches of the Zambezian Ecozone in the Malawi Rift). During favourable periods, some early hominids dispersed southward beyond the Zambezian Ecozone, evolved there (perhaps due to relative isolation and/or differences associated with its temperate ecology), and became endemic there. This spatio-temporal pattern is 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 distributional area particularly 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 a stable association until Middle-to-Late Miocene 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 featured in eastern Africa by 8–9 Ma (Cerling *et al.* 1991). At the same time, central African lowland forest refuges provided the allopatric conditions for differentiating hominoid subspecies and species (cf. Colyn *et al.* 1991, for a discussion of Late Pleistocene refuges).

Distribution drift of the tropical forests left more open wooded savannah in its wake (Andrews 1981) and engendered increased habitat diversity (cf. Retallack *et al.* 1990). As climatic conditions became their most extreme during the terminal Miocene, some populations of arboreal hominoids found themselves peripheralized to the east along the lush riparian habitats meandering across the rain shadows of the developing African Rift Valley. Vicariance of their habitat prompted evolutionary adjustments (i.e. speciation and extinction, pulses) amongst hominoids and other mammal groups (i.e. bovids; Vrba 1985, 1987a, 1995). The open woodland provided new niches for hominoids, but they occurred in resource patches separated by spans of non-arboreal terrain. Amongst the peripheralized populations natural selection favoured those with behavioural-morphological locomotor repertoires capable of more successfully traversing this ground and taking advantage of discontinuously distributed ground-based resources. Included amongst these repertoires was the advent of bipedalism – a more energetically efficient, albeit more upright, locomotory strategy at walking speeds (Rodman, McHenry 1980; see also Jablonski, Chaplin 1993, regarding a hypothesized role for the selective value of bipedal displays under these new resource conditions). This uprightness had also increased thermoregulatory advantages under conditions of intense incident solar and ground level radiation in open environments (Wheeler 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 anatomical and behavioural complexes associated with a combined arboreal and terrestrial niche were compromised during the Mio-Pliocene to meet the demands of this mixed habitat and niche.

Australopithecus anamensis and *Australopithecus afarensis* arose in this eastern African tropical ecological domain. Their behavioural inclination was to remain near the borders between broad riparian habitats and open woodlands during the ascendancy of more warm and humid times. Over short geological time scales, this was typically a local, non-dispersing tendency, but by approximately 4.0 Ma *Australopithecus anamensis* or *Australopithecus afarensis* successfully dispersed along the northern periphery of the tropical forests in order to give rise to *Australopithecus bahrelgazali*, known from Chad (Brunet *et al.* 1996). Over longer time frames this included dispersal through the riparian "corridor" connecting eastern and southern Africa (Bromage *et al.* 1995b) permitting population dispersal into southern Africa by 3.0 Ma. This dispersion was facilitated by the birth of palaeolake Malawi and the penetration of the Malawi Rift and its associated rift habitats into temperate Africa and the riparian corridor (Bromage *et al.* 1995b).

This dispersing unit maintained habitat specificity's to forested environments (cf. Rayner *et al.* 1993) though in more environmentally temperate climes and in relative geographical isolation at the extreme distal edge of its distribution. The dispersion along changing latitudinal circumstances co-varied with its transformation into, first, a geographic variant and, subsequently, into *Australopithecus africanus,* joining ranks with other southern African endemic faunas. Thus *Australopithecus afarensis* was essentially an eastern African endemic and it follows that no typical representatives are likely to be recovered from southern African deposits older than 3.0 Ma (e.g. within sub-Sterkfontein Member 4 levels).

By approximately 2.8 Ma the initiation of cooler and dryer conditions prevailed upon the African landscape, its vegetation, and its faunas, until climaxing *ca* 2.5 Ma (Bonnefille 1976, 1980, 1995, Prentice, Denton 1988, Vrba 1985, 1988, deMenocal, Bloemendal 1995, Dupont, Leroy 1995). During this time *Australopithecus afarensis* and *Australopithecus africanus* were each subject to unique palaeobiogeographic consequences of this global aridification, in accordance with the Habitat Theory of Vrba (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,* then, the changing climate meant vicariance of its habitat and its distribution into more removed ecotonal riparian and closed lake margin environs. During the interim 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 narrowed "ribbons" of tree-lined riverine forest. The selective pressures of this habitat change resulted in the increased survival of more megadont varieties capable of feeding on tougher fruit and open woodland-open savannah food items. This was so for early hominid as well as numerous eastern and southern African large terrestrial vertebrate lineages *ca* 2.5 Ma (Turner, Wood 1993a). These pressures were likewise sufficient to result in the phyletic splitting of *Australopithecus afarensis* into *Paranthropus* and *Homo* lineages after 2.8 Ma (Vrba 1988, Kimbel 1995, Bobe 1997).

The beginnings of the *Paranthropus* lineage, represented by *Paranthropus* (= *Australopithecus*) *aethiopicus* (e.g. Walker *et al.* 1986, Kimbel *et al.* 1988), maintained a reliance on fruiting resources on the riverine side of its ecotone, particularly during the dry season, but it was equally adept at grinding on the postcanine dentition those food items it required from more open habitats during more hospitable times of the year. Over time this lineage adapted itself more fully to the open habitat side of its ecotone, 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 never left its ancestral connection to the more closed features of its environment (cf. Shipman, Harris 1988), however, as these habitats would continue to provide essential protection, sleeping localities, and some foods (it would be rather interesting if its enduring evolutionary history was the result of a biomic eclecticism 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 aethiopicus* (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, embody our most impressive evidence to suggest that *Homo rudolfensis* remained somewhat conservative in its feeding habits and depended still, and most of all, on plant resources.

However, while *Paranthropus* was principally adapted by means of a robust masticatory system to its tough and abrasive diet, *Homo rudolfensis* exhibited an increased behavioural flexibility as its adaptation to climatic circumstances included a larger and more provoking, inquiring, and capable brain. This included a shift to proportionately less abrasive foodstuffs and more omnivorous habits (cf. Robinson 1962).

In the Malawi Rift there is evidence for the earliest co-existence of *Homo* and *Paranthropus*. It may therefore be concluded that an alternative to the development of hyperrobust and megadont constructions existed, which was equally suitable for coping with increasingly tougher food items: this alternative was the beginning of material culture. The oldest stone tools with an age of about 2.5 Ma are known from Ethiopia (Harris 1986, Kimbel *et al.* 1996). Material culture ameliorated the effects of climate change to the degree that it enabled *Homo rudolfensis* to take advantage of other resources more efficiently than was ever possible before.

Paranthropus boisei and *Homo rudolfensis* remained endemic to tropical latitudes during this time (Bromage, Schrenk 1995b). The eastern African tropical faunas, having habitable alternatives, remained within their biogeographical domain rather than brave the relative deterioration and paucity of habitats south of the African Rift Valley. It would not be for another half of a million years or so before *Paranthropus boisei*, at least, would disperse to more southern latitudes during an expansion of its biome sometime younger than 2.0 Ma.

The faunas of southern Africa were subject to a different set of environmental sequelae during the *ca* 2.5 Ma cooling event. Waning of the forests and woodlands in deference to more open arid grasslands invigorated not only evolutionary adaptations to savannah life in tropical eastern Africa, but also resulted in the distribution drift northward of faunas tracking the equatorward shift of grassland and woodland biomes into eastern Africa from the south ca 2.5 Ma (Bromage *et al.* 1995a). Until this time the Zambezian Ecozone was an environmental wedge between the tropic and temperate zones, maintaining high degrees of southern and eastern African faunal endemism (cf. Klein 1984, Sclater 1896). However, the temperate zone *ca* 2.5 Ma experienced more seasonal extremes, and many organisms unwittingly maintained their inherited preference for moderately seasonal climes and temperate vegetation physiognomy by moving northward with the shrinking of this biome toward the equator, effectively transgressing the Zambezian Ecozone. Amongst these migrants was *Australopithecus africanus* who, having been adapted to a modest temperate ecology, now found its suitable habitats shifted to the north toward the African Rift Valley.

During its tenure in southern Africa, *Australopithecus africanus* experienced the pressures of climate change related to increased seasonality. Some populations became peripheralized and adapted to the more open side of their woodland habitat. Indeed, selection favoured masticatory trends similar to those of *Paranthropus* in eastern Africa (cf. White *et al.* 1981). Other populations, however, by means of a dispersing strategy not available to their contemporaries in the north, endeavoured to maintain their habitat specificity's to the more closed side of their woodland habitat and so dispersed northward along the preserved riparian corridor. While dispersing toward the eastern African tropical domain, selection for increased behavioural flexibility was related to the habitat diversity of the tropics and the presence of other non-vegetative food resources available in their new region. This emerging taxon, *Homo habilis*, rapidly established itself as a categorical omnivore and found that it could buffer itself more resolutely from environmental changes. This enabled it to cross habitat boundaries more easily and also to advantage itself of more resources with its material culture. This ecogeographic perspective is consistent with one interpretation of polyphyly in *Homo* as it is currently beheld (Turner, Wood 1993b).

By approximately 2.0 Ma Africa was rebounding from its relatively cool and dry climate to return to slightly more warm and humid conditions (cf. Shackleton *et al.* 1984, Bromage *et al.* 1995a). A phase of biome expansion ensued that facilitated dispersions *away* from the equator, ending nearly one million years of relative endemism dominated by tropical equatorial speciations. *Paranthropus boisei* dispersed southward along re-established ecotonal habitats into southern Africa, varied there as a geographic variant under more temperate conditions, and evolved into *Paranthropus robustus/crassidens*. This view is consistent with a consideration of large mammal fauna biogeography and *Paranthropus* monophyly (Turner, Wood 1993a). *Homo rudolfensis*, however, remained endemic to the eastern African tropical domain due to its preference for more open habitats around the rain shadows of the African Rift Valley.

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