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Oldest *Homo* and Pliocene biogeography of the Malawi Rift

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THE Malawi Rift and Pliocene palaeofaunas, which include a hominid mandible attributed to *Homo rudolfensis*, provide a biogeographical link between the better known Plio–Pleistocene faunal records of East and Southern Africa. The Malawi Rift is in a latitudinal position suitable for recording any hominid and faunal dispersion towards the Equator that was brought on by increased aridity of the Late Pliocene African landscape. The evidence suggests that Pliocene hominids originated in the eastern African tropical domain and dispersed to southern Africa only during more favourable ecological circumstances.

Formation of the Malawi Rift began about 8 Myr ago. Subsequent rifting and faulting led to subsidence which created a riverine system and eventually a rift lake (palaeolake Malawi) 5–4 Myr ago (Fig. 1)[1]. The Plio–Pleistocene Chiwondo Beds include fluviatile, palaeosol, swamp, beach, and foreshore and offshore lacustrine deposits (Fig. 2)[2], and so provide the southernmost African Rift Valley occurrences.

After the pioneering surveys of Malawi Rift faunas[3–6], the Hominid Corridor Research Project (HCRP) began a long-term study in 1983 which focused on the role of southeastern Africa in the origin and dispersion of Plio–Pleistocene faunas and early hominids.

The HCRP has identified 131 fossil localities in the Karonga and Uraha areas (Fig. 1), representing two biochronological zones (Fig. 2). The faunal assemblages indicate an age of 4 Myr and older for unit 2 and of 3–1.5 Myr for unit 3 (see Fig. 2 legend).

An early hominid mandibular corpus in two joining parts (UR 501; Fig. 3) was recovered from stratigraphic unit 3A (Fig. 2). The two halves are broken behind the roots of the rami posterior to the RM_2 and through the LM_2. The superior lateral tori fade quickly off the roots of the anterior borders of the rami, and the inferior marginal tori are only weakly developed. A broad jugum incorporates the C and P_3 roots. Mental tubercles and a mental trigone are distinct. An inferior transverse torus is weakly developed at the level of mesial P_4. The mental foramen is situated about 4 mm below corpus midline. P_3s are intact lingually, oval in shape, and with a small distolingually placed talonid. P_4s are well preserved, with a lingual cusp distal to the larger buccal cusp; the large talonid projects distolingually. The five cusps of

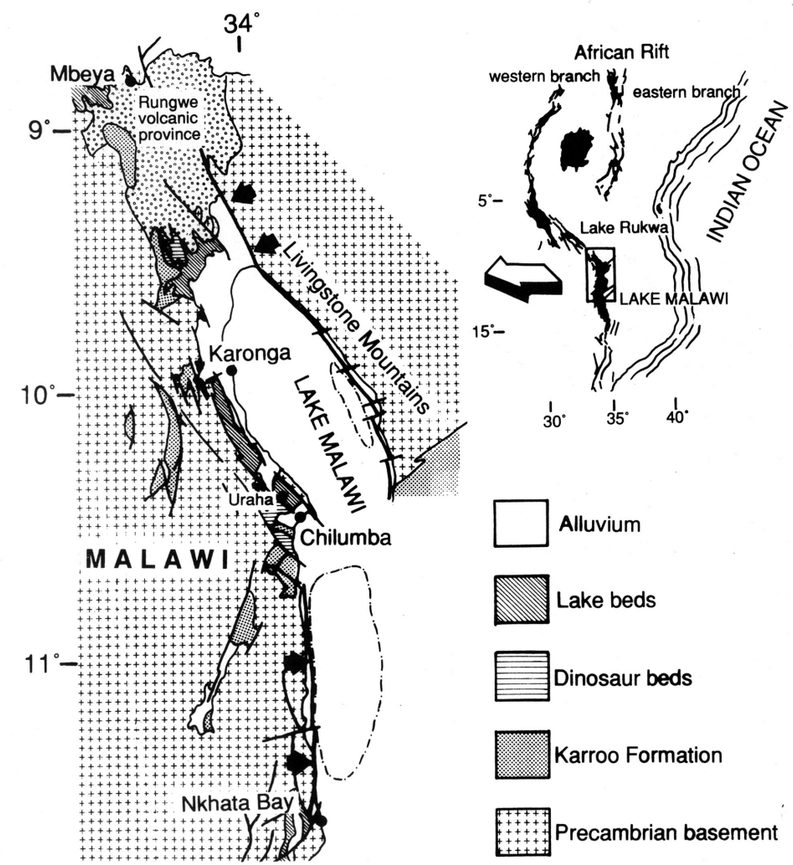

FIG. 1 Lithology and structure of the northern Malawi Rift. Right: Tectonic studies of the western[19,20] and eastern[21] branches of the East African Rift Valley system show that initial rifting is older in the eastern branch. Malawi rifting (western branch) began ~8.0 Myr ago. An early phase of normal faulting was followed by a strike-slip dominated system. The western side of the Karonga-Chilumba basin was susceptible to localized uplift and thus Cenozoic Lake sediments were exposed. Left: Lithology and structural elements of the northern Malawi Rift, showing border fault segments (arrows) adjacent to lake depocentres (dashed line represents 550 m depth); opposite border fault segments are en-echelon step faults and flexures. Plio–Pleistocene deposits ('Lake Beds' indicates Chiwondo Beds, Chitimwe Beds) occur south of Karonga and north of Chilumba (Uraha).

TABLE 1 Mammalian taxa recovered from unit 3A of the Chiwondo Beds, northern Malawi, grouped according to geographic distribution

Southern Africa only
Artiodactyla
Notochoerus capensis
Potamochoeroides shawi
Gazella sp. aff. *vanhoepeni*
Tragelaphus aff. *angasi*
Shared southern and eastern Africa
Primates
Theropithecus sp.
Parapapio sp.
Proboscidea
Elephas recki
Mammuthus subplanifrons
Perissodactyla
Equus sp.
Hipparion sp.
Ceratotherium aff. *simum*
Diceros bicornis
Artiodactyla
Metridiochoerus andrewsi
Phacochoerus sp.
Hippopotamus sp.
Tragelaphus aff. *strepsiceros*
Megalotragus kattwinkeli
Syncerus sp.
Connochaetes aff. *taurinus*
Giraffa camelopardalis
Camelus sp.
Eastern Africa only
Primates
Homo rudolfensis
Proboscidea
Elephas ekorensis
Loxodonta adaurora
Deinotherium bozasi
Artiodactyla
Notochoerus euilus
Kolpochoerus limnetes
Metridiochoerus compactus
Ugandax sp.
Kobus sigmoidalis
Kobus aff. *patulicornis*
Oryx aff. *gazella*
Damaliscus sp.
Aepyceros sp.
Madoqua sp.
Giraffa stillei
Giraffa pygmaea
Camelus sp.

the M_1s are separated by Y-shaped fissure patterns and are worn flat. A low distal marginal ridge surrounds a relatively large talonid. The RM_2 is nearly complete, but only a sheared dentine surface of the left mesial M_2 is preserved. Fissuring demarcates a tuberculum intermedium (C7) platform. The distal longitudinal fissure meets a posterior fovea delimited by a marginal ridge adorned with at least two tubercles of the tuberculum sextum (C6). A distal wear facet indicates that the RM_3 was in occlusion, suggesting that the individual was a young adult.

Many absolute and relative molar and premolar crown shape indices, relative cusp areas, enamel microanatomical features, fissure patterns and crown morphology are within the range of early *Homo*, though some may be as well subsumed within the limits of variation represented by *Australopithecus* (*A. afarensis* and *A. africanus*)[7]. However, UR 501 is similar to specimens from Koobi Fora, Kenya, such as KNM-ER 1802, in overall corpus dimensions, strength and the morphology of the 'chin' region. These specimens also share absolutely large molar crown areas together with diminished M_2 protoconid relative cusp area, P_3 molarization (that is, relative talonid expansion), plate-like P_3 and P_4 roots, and some enamel microanatomical features that correspond more closely to the *Paranthropus* condition[7]. Taken together, UR 501 corresponds closely to the subset of Late Pliocene fossils from Koobi Fora with relatively large brains and robust jaws and teeth that have been referred to *Homo rudolfensis*[8], and to which we also refer UR 501.

UR 501 is biochronologically aged at 2.4 Myr (see Fig. 2 legend for unit 3A). Hill *et al.*[9] have reported the occurrence of an early *Homo* temporal bone (KNM-BC1) traced to radiometrically dated 2.4 Myr deposits from the Chemeron Formation, Kenya. Wood[10] suggests that this specimen may be an early representative of *Homo rudolfensis*, whereas other specimens assigned to this taxon[8] derive from just below and above the KBS Tuff of the Koobi Fora Formation and date to approximately 1.9–1.8 Myr. Thus a date of 2.4–1.8 Myr is at present indicated for *Homo rudolfensis*.

The significance of UR 501 lies in the context of its temporal origin and its biogeographical relationships. These are demonstrated by placing the mammalian assemblage of unit 3A into three geographically based groups (Table 1). *Homo rudolfensis* is associated with an assemblage dominated by eastern African endemic faunas, whereas the group of southern African endemics of the Malawi Rift is strikingly small. This pattern reflects the equatorward dispersion of southern African faunas, which is in accord with the northward-drifting of vegetation belts during the aridification of global climates at about 2.5 Myr[11–13]. Evidence for this resides in patterns of extinction and speciation among Pliocene Bovids[14,15]. Southern African endemics dispersing to eastern Africa contribute to the larger shared 'southern and eastern' faunal group in Table 1. Equatorial lineages faced not so much the problem of latitudinal shifts in biome zonation as habitat fragmentation, and, having a greater diversity in habitat choices, remained endemic to the tropical African ecological domain and experienced either extinction or speciation. We therefore suggest that *Homo rudolfensis* arose during, and partly as a result of, the 2.5 Myr 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'[16].

In southern Africa the supposed time-aggregated deposits of Sterkfontein member 4 (ref. 17) overlap the age of Chiwondo Beds unit 3A but do not represent *Homo rudolfensis*; instead they represent a southern African endemic, *Australopithecus africanus*. As *H. habilis* is present in the Late Pliocene at Koobi Fora, the possibility remains that *A. africanus* dispersed to eastern Africa around 2.5 Myr ago and evolved into *H. habilis* during this phase of equatorward biome constriction. If the assignment is accepted of early *Homo* specimens from Sterkfontein member 5 (ST5) and Swartkrans member 1 (SK1) to *Homo habilis*, then we can attribute this taxon to a shared 'southern + eastern' African group, which according to our ecological model, later expanded its distribution deeper into southern Africa between 1.8–1.5 Myr ago[18] during a period of biome expansion[13].

The pattern emerging from our biogeographical interpretation is that early hominids persistently arose in the tropical ecological domain of eastern Africa, a pattern that also dominates speciation events of the Bovidae 2.5 Myr ago. Only during more favourable periods did early hominids disperse southwards, evolve and become established in an environmentally temperate ecological domain. □

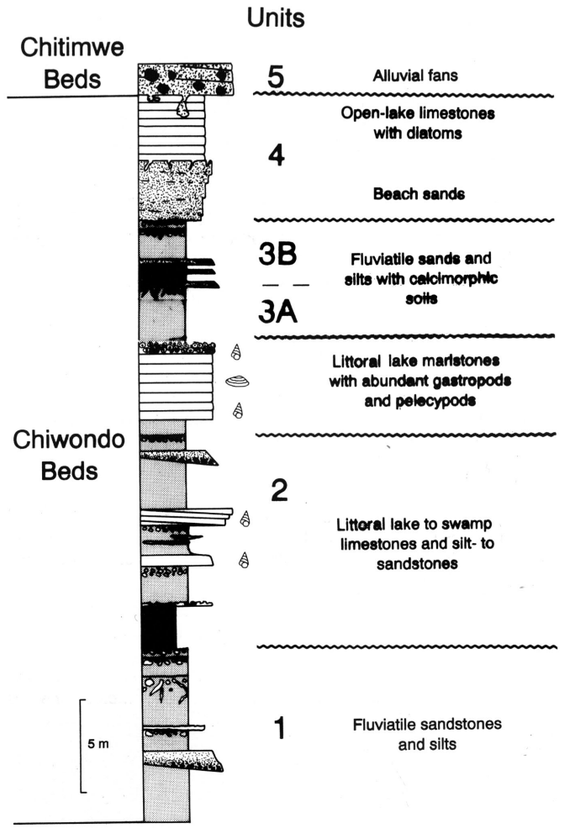

FIG. 2 Sedimentary succession in the southern part of the Karonga-Chilumba basin at Uraha. The Plio–Pleistocene Chiwondo Beds[22], overly the Jurassic–Cretaceous dinosaur beds unconformably and are partially covered and eroded by late Pleistocene alluvial fan deposits (Chitimwe Beds). The large-scale transgressive–regressive cycle represents a highly dynamic depositional system in a nearshore to backshore position. Facies elements are fluviatile, palaeosol, swamp, beach, and foreshore and offshore lacustrine deposits. Maximum thickness is 125 m and five depositional sequences (units 1–5) are limited by unconformities (palaeosols, angular unconformities) reflecting lake level changes or tectonic activity. An endemic gastropod species *Bellamya* cf. *pagodiformis* in upper unit 2 abets the relative ordering and correlating of sedimentary Units and fossil localities that are distant from one another[23]. Age estimates rely on correlation with radiometrically dated biochronological units in eastern Africa[13,24]. Unit 1 consists of reddish- to -greyish braided stream deposits. No vertebrate fossils occur and no age attribution is possible. Unit 2 reflects the flooding of the depositional area; wave-accumulated bioclastic beaches show an aggrading to strongly prograding stacking pattern. Distally, silts and sands with abundant pelecypods were deposited. Marls with oncoids around gastropod shells characterized the low-energy depositional ramps. The vertebrate fauna indicates an Early Pliocene age; a primitive proboscidean *Anancus kenyensis* and the suid *Nyanzachoerus jaegeri* indicate an age of about 4.0 Myr or older[25]. Of the Hippotragini, there are specimens similar to those from the Laetoli Beds at 3.6–3.8 Myr[5]. Unit 3, marked at the base by an angular unconformity in the Karonga area and a major palaeosol horizon in the Chilumba area (Uraha Hill), contains two subunits: Unit 3A, meandering river and deltaic deposits, is strongly condensed at Uraha Hill, as reflected by a major ferrugineous calcimorphic palaeosol. The hominid lower jaw UR 501 was found within this condensed section. Faunas associated with UR 501 are[13]: *Notochoerus euilus* (3.35–2.5 Myr), *Tragelaphus* sp. aff. *angasi* (3.0 Myr), an early *Notochoerus scotti* (3.0–2.3 Myr), a mid–late Pliocene *Hipparion* (2.9 Myr or younger), *Ceratotherium simum* (2.5 Myr or younger), *Oryx* (3.0–1.64 Myr) and a late Pliocene representative of *Metridiochoerus andrewsi* (2.3–1.9 Myr). This assemblage is similar to that reported from the Chemeron Formation[9] in association with purported early *Homo* (KNM-BC1), except that *Notochoerus euilus* of unit 3A points to an older age, whereas KNM-BC1 is associated with a younger suid (*N. scotti*) not represented in unit 3A. Although the associated faunas represent a time-transgressive deposit, either an older (~2.5 Myr) or, more conservatively, an age closer to 2.3 Myr is suggested. Thus 2.4 Myr for UR 501 remains a consensus date until further studies can determine an absolute age. Unit 3B, restricted to Uraha Hill, consists of a series of stacked ferrugineous calcimorphic palaeosol horizons. A late Pliocene to early Pleistocene date (2 to 1.5 Myr) is indicated by *Tragelaphus* aff. *strepsiceros*, *Connochaetes* aff. *taurinus* and *Metridiochoerus compactus*[26]. Unit 4, restricted to the southernmost part of the Karonga-Chilumba Basin (Uraha), consists of a transgressive part with well-sorted, unconsolidated beach sands overlain by open lake limestones with abundant diatoms. No date has been proposed. Unit 5 (Chitimwe Beds) overlies the Chiwondo Beds (units 1–4) with an erosional unconformity. The formation of the alluvial fans is related to a major lowering of lake level after deposition of unit 4. No reliable age has been proposed.

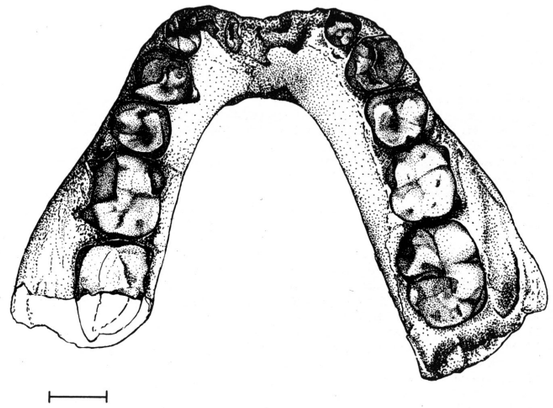

FIG. 3 Early hominid mandible UR 501 (*Homo rudolfensis*) from Uraha in occlusal view. Scale bar, 1 cm. Selected dental measurements (corrected) of UR 501 are compared with KNM-ER 1802 (ref. 27):

	UR 501		KNM-ER 1802	
	Buccal–lingual	Mesial–distal	Buccal–lingual	Mesial–distal
LP_4	11.4 mm	9.8 mm	11.8 mm	12.1 mm
LM_1	13.2 mm	14 mm	13.2 mm	14.9 mm
RP_3	11.4 mm	9.7 mm	11.5 mm	10.7 mm
RP_4	11.5 mm	9.5 mm	12.0 mm	11.4 mm
RM_1	13.3 mm	14 mm	13.0 mm	14.8 mm
RM_2	14.6 mm	17.3 mm	14.2 mm	16.6 mm

Selected corpus measurements of UR 501 are compared with KNM-ER 1802 (ref. 27):

	UR 501	KNM-ER 1802
Symphyseal height	34 mm (estimate)	36 mm
Symphyseal depth (max.)	16.8 mm	24.5 mm
Corpus height at RM_1	34 mm	38 mm
Corpus width at RM_1	21 mm	23 mm