



Deposited via The University of York.

White Rose Research Online URL for this paper:

<https://eprints.whiterose.ac.uk/id/eprint/1169/>

Book Section:

Bailey, G., Manighetti, I. and King, G. (2000) Tectonics, volcanism, landscape structure and human evolution in the African Rift. In: Bailey, G., Charles, R. and Winder, N., (eds.) Human Ecodynamics. Symposia of the Association for Environmental Archaeology. Oxbow Books, pp. 31-46.

Reuse

Items deposited in White Rose Research Online are protected by copyright, with all rights reserved unless indicated otherwise. They may be downloaded and/or printed for private study, or other acts as permitted by national copyright laws. The publisher or other rights holders may allow further reproduction and re-use of the full text version. This is indicated by the licence information on the White Rose Research Online record for the item.

Takedown

If you consider content in White Rose Research Online to be in breach of UK law, please notify us by emailing eprints@whiterose.ac.uk including the URL of the record and the reason for the withdrawal request.



5. Tectonics, Volcanism, Landscape Structure and Human Evolution in the African Rift

Geoff Bailey, Geoffrey King and Isabelle Manighetti

Tectonic movements and volcanism in the African Rift have usually been considered of relevance to human evolution only at very large geographical and chronological scales, principally in relation to long-term topographic and climatic variation at the continental scale. At the more local scale of catchment basins and individual sites, tectonic features are generally considered to be at worst disruptive and at best incidental features enhancing the preservation and exposure of early sites. We demonstrate that recent lava flows and fault scarps in a tectonically active region create a distinctive landscape structure with a complex and highly differentiated topography of enclosures, barriers and fertile basins. This landscape structure has an important potential impact on the co-evolution of prey-predator interactions and on interspecific relationships more generally. In particular, we suggest that it would have offered unique opportunities for the development of a hominid niche characterised by bipedalism, meat-eating and stone tool use. These landscape features are best appreciated by looking at areas which today have rapid rates of tectonic movement and frequent volcanic activity, as in eastern Afar and Djibouti. These provide a better analogy for the Plio-Pleistocene environments occupied by early hominids than the present-day landscapes where their fossil remains and artefacts have been discovered. The latter areas are now less active than was the case when the sites were formed. They have also been radically transformed by ongoing geomorphological processes in the intervening millennia. Thus, previous attempts to reconstruct the local landscape setting adjacent to these early hominid sites necessarily rely on limited geological windows into the ancient land surface and thus tend to filter out small-scale topographic detail because it cannot be reliably identified. It is precisely this local detail that we consider to be of importance in understanding the environmental contribution to co-evolutionary developments.

Keywords: NORMAL FAULTING; LAVA FLOWS; AFAR; AFRICAN RIFT; HOMINIDS.

INTRODUCTION

Our aim in this paper is to bring together two bodies of knowledge that have, for the most part, been pursued in isolation from each other. On the one hand is the geological investigation of the dynamics of rift formation using the new techniques of tectonic geomorphology. Considerable advances have been made during the past decade in our understanding of African tectonics both in terms of large-scale dynamics and, of particular relevance to this paper, their influence on local and regional changes of the physical environment (Stein *et al.* 1991; Manighetti

1993; Manighetti *et al.* 1997, 1998). These studies have, however, been largely pursued without reference to their potential impact on the course of human development.

On the other hand the palaeoanthropological and archaeological investigation of human evolution has focused on such issues as changes in the biological and cultural potential of early hominids, their intra-specific social interactions, and their inter-specific ecological interactions with prey and predator organisms. Discussion of the physical environment in relation to early hominids has mainly emphasised large-scale changes of climate,

vegetation and tectonics, and interactions between them (e.g. Foley 1994, *in press*; Partridge *et al.* 1995a; Vrba 1996; Vrba *et al.* 1995), or small-scale reconstructions of sedimentary environments, food and raw materials available within the vicinity of archaeological sites (e.g. Blumenshine & Peters 1998; Brown & Feibel 1991; Harris & Herbich 1978; Rapp & Vondra 1981). Tectonic factors have in general played very little role in interpretation except in indirect terms: as an ultimate cause of global climatic change (Ruddiman & Raymo 1988); as an indirect forcing agent on mammalian evolution through the impact on regional climatic variation (Partridge *et al.* 1995b); as a source of ecological diversity (Coppens 1994; Foley 1987; Gamble 1993); or simply as a mechanism for accelerating the protection and discovery of finds by rapid sedimentation and subsequent exposure by erosion.

Thus, the landscapes studied by geomorphologists, geologists and geophysicists are typically dominated by physical dynamics, and the human occupants are essentially out of sight or at best passive spectators. Conversely, an archaeological or palaeoanthropological perspective is one dominated by a foreground of biological and cultural dynamics with hominids as the centre of focus and an essentially passive and distant, albeit variable and changing, physical environment. The artist's reconstruction of an early hominid scene (Fig. 5.1) offers a graphic if somewhat exaggerated illustration of this point, with a foreground of active and indeed violent social interactions, and an environmental background composed, appropriately enough, of a volcanic mountain largely obscured by cloud.

Here we focus on the dynamic interactions that occur at the interface between the physical environment and human behaviour at the local scale. In particular we aim to show that the tectonics of the African Rift create a distinctive and complex topographic structure characterised by varying combinations of changing lake basins and river valleys, fault scarps and lava flows. We argue that a landscape structured in this way was highly attractive to early hominids, and may have exerted selective pressures favouring bipedalism, the exploitation of animal foods, and evolutionary divergence.

Discussion of interactions between humans and the physical environment tends to veer towards one of two extremes. Either humans are seen as passive tools of environmental change, or the environment is treated as essentially inert until acted on by human agency. Both are equally deterministic in their own way and both imply an essentially one-way relationship – either the physical environment is seen as determining behaviour, or behaviour is seen as determining what is significant in the physical environment. Intermediate interactions of varying strength can, however, be envisaged. In the hypothesis that we advance below, we do not imply that the course of human evolution was determined by the structure of tectonic landscapes. Our point is rather that

the interaction between hominids and tectonically active environments resulted in new configurations of hominid behaviour that would not otherwise have occurred. Early hominids selected certain sorts of environments, and these in turn selected for certain sorts of hominid behaviours in a process of reciprocal interaction that amplified some patterns of behaviour at the expense of others. This process is similar in some respects to that of a co-evolutionary relationship, commonly defined in biology as a situation in which two or more taxa undergo evolutionary change as a result of reciprocal selective pressures that each imposes on the other through their mutual ecological interaction (Pianka 1980). Recent examples of land use, where human activity is having a dramatic impact on the physical landscape and the changed physical landscape in its turn is further affecting human activity, could properly, in our view, be described as an example of a co-evolutionary process involving reciprocal interactions between physical, biological and cultural variables. The example that we describe below is not strictly a case of co-evolutionary development in that sense because the physical landscape was not (so far as we know) affected by the presence of hominid or other large-mammal activity. On the other hand, the distinctive landscapes that we describe below could have significantly altered or accelerated the pattern of co-evolutionary relationships between biological species, and cannot be treated as an essentially passive or uniform *tabula rasa* awaiting the imprint of ecological and evolutionary processes. We suggest that concepts of co-evolutionary behaviour and environmental selection provide a fruitful framework for examining interactions between variations of the physical environment and its biotic occupants including humans, and one that avoids the charge of determinism and the consequent dismissal of relevant factors – environmental, behavioural or cultural as the case may be.

TECTONIC ENVIRONMENTS AND PALAEOLITHIC SUBSISTENCE

We begin with a brief example from the Middle and Upper Palaeolithic of north-west Greece, an area which is subject to very high rates of tectonic activity as a consequence of its position at the boundary between the African and European plates (Bailey *et al.* 1993; King *et al.* 1994). It is also an area that has been the focus of detailed studies of Palaeolithic environment, economy and archaeology (Bailey 1997). We emphasise and elaborate on the following four points:

1. Tectonic activity accelerates processes of landscape change both directly by uplift and subsidence, and indirectly by amplifying or moderating the effect of climatic change and human land use, and it does so at a variety of chronological and geographical scales.



Figure 5.1 Artist's reconstruction of early hominid social interactions in a lake-edge setting.

2. Tectonic change can create and renew local landscape features that are attractive to human settlement. These features concentrate water supplies, plants and animal foods, or make them more easily accessible, and thus sustain local conditions of dynamic equilibrium and settlement stability for long periods.
3. The impact of underlying tectonic processes is not uniform across a regional landscape. The same forces that produce stability in one part of a region may be disruptive in other parts.
4. The overall effect of these tectonic processes is to greatly increase the *patchiness* of the environment, both spatially and chronologically. Such patchiness can have a significant impact on ecological and evolutionary processes.

Tectonic landscapes are highly dynamic and are liable to undergo relatively rapid and dramatic re-moulding of the physical surface. They are characterised by a complex topography with multiple series of uplifting mountain ranges and intervening valleys, rivers that cut across this ridge-and-valley pattern often carving deep-cut gorges, and more localised basins of subsidence which act as sediment and water traps and are often filled with lakes. They produce active erosion and sedimentation alternating over quite short distances and complex hydrological regimes, and these patterns may be further acted

on by changes in climate and vegetation or intensive human land-use practices.

Areas of the earth's surface primarily subjected to compression by convergent plate motions show a general trend towards regional uplift and mountain building, as is the case in north-west Greece. In extensional areas where the earth's crust is being stretched by subduction or plate separation, the general trend is towards subsidence, as in the Aegean basin. It is important to appreciate that this alternation of uplift and subsidence on sub-continental and larger geographical scales is also mirrored at a smaller scale. Reverse faulting in compressional environments and normal faulting in extensional ones both result in adjacent zones of uplift and subsidence at the local scale, such as fault-bounded lake basins, and similar patterns recur at the regional scale.

These changes can create and renew local environments that are attractive to human settlement. This attractiveness takes two forms. Localised subsidence focuses sediment accumulation and water supplies and thus creates a highly fertile environment that concentrates plant and animal life. At the same time the associated uplift creates a series of barriers that greatly facilitates the human prediction and manipulation of the movements of mobile animal resources. This makes potentially fast-moving or elusive prey species more easily accessible to an intelligent predator without the need for biological

abilities of rapid movement or elaborate technological means of killing at a distance such as spear throwers and guns. Repeated fault movements on the same axis continuously rejuvenate these features, sustaining a fertile environment and maintaining sharp topographic barriers, and can create a *climatically insensitive* local area that sustains attractive conditions for human existence regardless of external climatic changes.

The region of north-west Greece has been undergoing compression throughout the Tertiary and Quaternary periods, and continues to show rates of seismicity and tectonic activity which are amongst some of the highest in the world (King *et al.* 1993). The archaeological record extends back at least over the past 100,000 years, with long sequences of Middle and Upper Palaeolithic material in open air sites or limestone rockshelters associated with a subsistence economy in which large game animals (red deer, horse, cattle and ibex) were a major resource (Bailey 1997).

The archaeological sites are associated with tectonically created features such as fault-bounded lake basins and limestone gorges, and these appear to have favoured human habitation in a variety of ways and at a variety of geographical scales. At the regional scale, faulting and instability has created impressive NW-SE trending limestone mountain ridges, with softer younger flysch rocks on their lower flanks that create large-scale badlands erosion. These pose major barriers to animal movement and demarcate virtually enclosed large-scale grazing basins with limited entry and exit points that facilitate the control and prediction of seasonal animal migrations (Fig. 5.2).

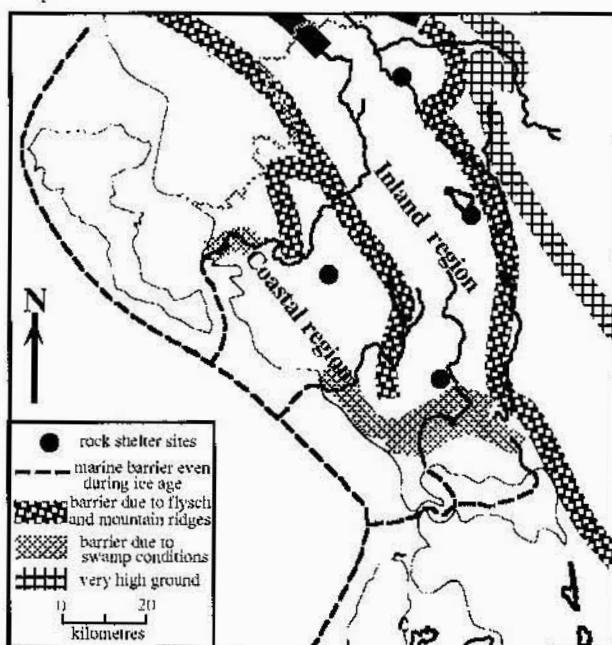


Figure 5.2 Map of Epirus showing basins and barriers at the regional scale.

At a more local scale, in the vicinity of individual sites, cumulative uplift on individual faults and associated subsidence has produced and maintained local lakes and sediment traps. At the local scale, as at the regional scale, active tectonics also creates physical barriers or *natural fences* and local enclosures. These can be used to control and predict the local movements of herd animals, and to trap or corral them. Such a local topography also provides secluded and protected locations from which people can observe animals without disturbing them (Fig. 5.3). These same locations also provide protection for the human group from predators or human competitors. Site sequences in these locations show rich and repeated human occupation over many millennia. Typically they span major episodes of climatic change from virtually fully glacial to fully interglacial conditions and persist throughout conditions of late glacial aridity.

Tectonic activity does not provide uniformly favourable conditions for human settlement throughout the region. In some areas continuing activity has transformed local

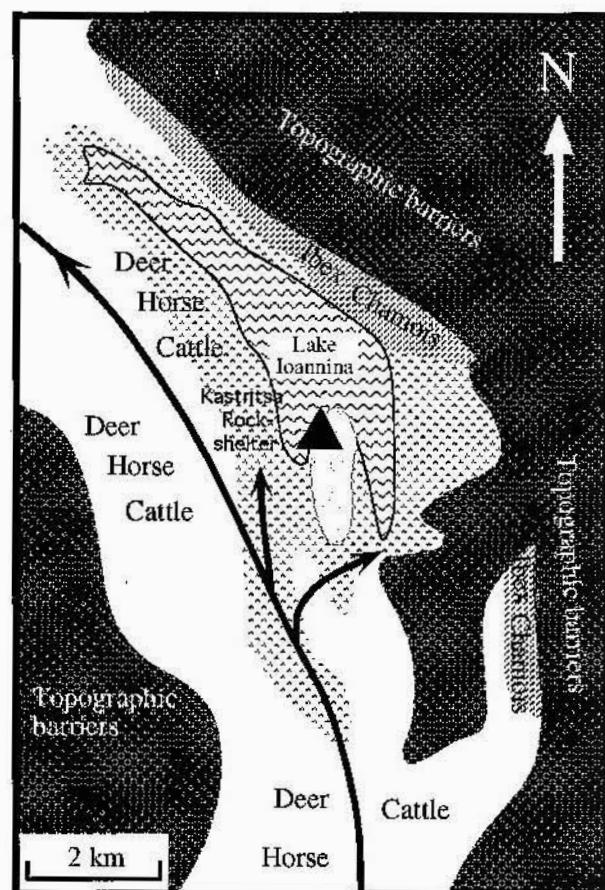


Figure 5.3 Map of local territory of the Kastritsa rockshelter, showing relationship to lake-edge environments, main routes of animal movement and local topographic barriers. The site was occupied from c. 21,000 to 11,000 BP.

environments which were once attractive basins and sediment traps into uplifted and eroded badlands landscapes. This is evidently so in the case of the Kokkinopilos red beds, which contain some of the earliest Palaeolithic artefacts of the region (Bailey *et al.* 1992; Runnels & Van Andel 1993). Here a once-fertile basin of sediment accumulation has been transformed into a zone of erosion. A similar transformation has also taken place in the Mazaraki basin in the north of the region. Conversely the Ioannina lake basin has remained in broadly its present form for at least the duration of the Pleistocene and probably much longer (Brousolis *et al.* 1999). Ongoing tectonic activity can, therefore, have disruptive as well as stabilising consequences for human settlement and subsistence, depending on the time span of interest, the rates of tectonic activity, and the nature of the local fault motions.

From the point of view of human hunters, the complex topography is something of a two-edged sword. For the same features that appear to facilitate human access to mobile or elusive prey can also provide means of escape or refuge for the prey species. In the long-run this may be of over-riding benefit to the human population by maintaining resilient relationships which reduce the risk of extinction to both animal-prey and human-predator populations alike (Winder 1997). By the time of the Upper Palaeolithic period, if not earlier, human populations were clearly skilful hunters who had established effective relationships with a variety of prey animals including both fast-moving (red deer and horse), defensive (cattle) and elusive (ibex and chamois) animals. The basis of that skill, according to our Greek case study, lies less in the use of technology, than in the intelligent manipulation of topographic features to monitor and control large areas of the landscape. We cannot of course assume that earlier hominids had the same sorts of technological and cognitive skills. But we see no reason why tectonic features such as we have described above should not have offered significant co-evolutionary opportunities arising out of a dynamic and 'patchy' topography at any period or in any biological context. Indeed, it is part of our argument that these features in the African context may have actively selected for emergent cognitive skills that we see in a more fully developed form in the later Pleistocene.

THE EAST AFRICAN RIFT

The East African Rift is a much larger and longer-lived structure than those we have described for Greece, and the archaeological record is much longer, thereby requiring us to think about the dynamic implications at a larger geographical and chronological scale. Nevertheless the initial focus here as in Greece is the local landscape structure.

In general the development of the East African Rift

involves processes of plate separation that have been underway for at least 12 million years, and exhibit extensional features, with normal fault scarps and volcanic activity. At present, much of the East African Rift is relatively inactive (extension rate of less than 5 mm/yr). However, although not yet well documented, earlier rates appear to have been greater, with the features we discuss below more widespread. Furthermore, the most intensive volcanic activity seems to have been associated with the inception of rifting and has become more subdued with time (Manighetti 1993; Tapponnier *et al.* 1990), a feature also observed for other continental rifts such as the Baikal Rift in Siberia. It is not surprising, then, that the features we emphasise have in general been overlooked or discounted in previous environmental reconstructions. In order to appreciate what local environments would have looked like to their early hominid occupants, we need to examine currently active areas of the Rift such as the Afar depression.

The tectonics of Afar

The Afar depression is a complex system of active features (faults, fissures and volcanoes) resulting from the interaction between the Red Sea and the Gulf of Aden rifts (Fig. 5.4) (De Chabalier & Avouac 1994; Deniel *et al.* 1994; Manighetti *et al.* 1997; Stein *et al.* 1991; Tapponnier *et al.* 1990). For many parts of the East African Rift, due south of the Afar depression, the geometry of opening seems simpler, with only a single, major active rift. Nonetheless similar processes recur. Activity causes the central part of the rift to subside and one or both of the adjacent sides to uplift and tilt away from the active axis. This typically means that earlier rift axes that form these flanks become perched at a higher level, from tens to hundreds of metres above the new rift.

Active volcanoes appear both within the active rift and on the rift flanks. Similar patterns to those found throughout the African Rift system are seen for other extensional regions: the Basin and Range of the USA; the Aegean region; North Island New Zealand; and Iceland. By the standards of some other continental rift systems (North Sea, Rhine, Rhone system, the Aegean system or the southern Basin and Range system), however, the volcanic activity of the African Rifts is high compared to the rate of extension (e.g. Ellis & King 1991).

The active central grabens commonly form internally draining basins, dotted with volcanoes and in many places covered by lava flows. Smaller or larger lakes are found everywhere. Contemporary sedimentation consists of slope wash, river and lake-deposits consisting of fine silt, reworked volcanic ash, and evaporites. The regions around the rivers and lakes have supported many African savannah animals in the past although hunting with automatic rifles has now greatly reduced their numbers.

Almost everywhere recent lava flows disrupt the *useful* land. They are not traversed by roads and represent formidable barriers to movement of any sort, with steep sides and jagged broken surfaces (Fig. 5.5). In time, especially in wet climates, they may become eroded and smoothed or reduced to boulder fields. In drier climates, lava fields with ages of many thousands of years remain impassable for domestic animals, or any large quadrupeds for that matter. Modern humans, in contrast, can cross lava flows but rarely do so unless there are good reasons.

Regions of volcanic activity are also associated with vertical faulting, resulting in impressive vertical barriers (Fig. 5.6). In contrast, the fault scarps in non-volcanic regions commonly have slope angles of 45° or less, which form less impressive obstacles to the movement of large mammals.

Volcanoes and lava fields

The lava flows and fault scarps associated with the areas around the Manda volcano (belonging to the Manda-Hararo rift) and the Gablaytu and Loma volcanoes (Fig. 5.4) create a complex and patchy local mosaic of barriers and small basins, with more open and extensive savannah regions beyond. The Manda volcano lies on the active rift axis and is cut by SSE-NNW oriented normal faults, the two largest of which have throws of some tens of metres. Smaller ones with throws of a few metres are not marked in Fig. 5.4. The lava flows are typically 3.5 m thick with steep sides (see Fig. 5.5), and the fault scarps are steep and very hard to climb, as is the case throughout the region (Fig. 5.6). An annotated aerial view of the Manda area showing the combined effect of these features on local landscape structure is shown in Fig. 5.7, and an oblique general view in Fig. 5.8.

The age of the visible part of the Manda volcanic system is thought to be between 20,000 and 40,000. This is partly derived from direct dating of the lavas (Y. Gillot *pers. comm.*) and partly deduced from the observed fault offsets and a rough knowledge of the vertical slip rates in the region (1–3 mm/year maximum on a fault).

Within the lava flows are numerous small sedimentary ponds completely isolated from their surroundings. Around the Manda volcano they are associated both with the volcanic cone and with the active faults. The present climate is arid, but both vegetation and water are present, and in a slightly wetter climate these would be quite fertile enclosures.

Although they are completely unused now (except for a camel track occasionally employed by smugglers en route to Djibouti) there is ample evidence of earlier human activity within the Manda flows. Particularly near their eastern and western edges close to large open (savannah-like) spaces, numerous worked artefacts were observed. These have not yet been subject to systematic study, nor are they dated. However, footprints of an adult and of an infant were found in water re-deposited

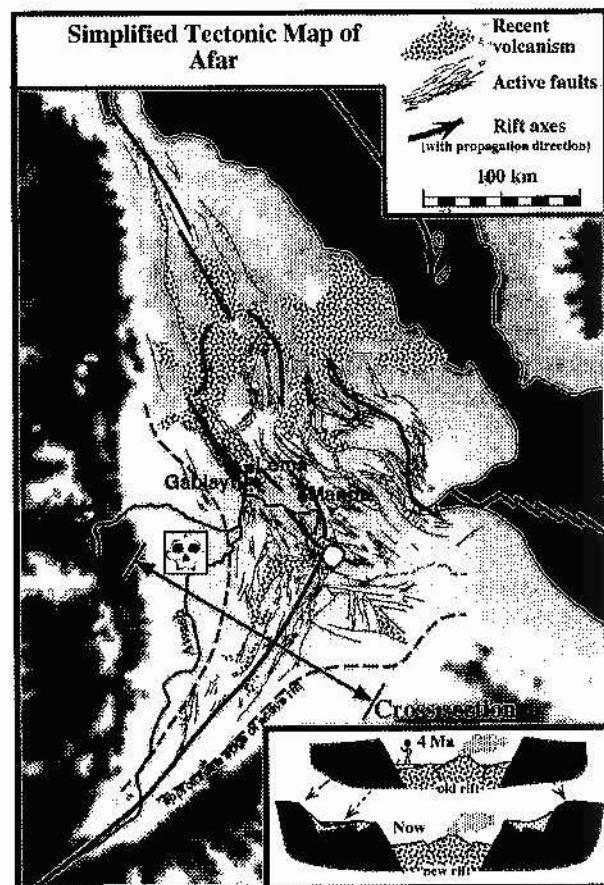


Figure 5.4 A simplified tectonic map of the Afar region, showing the distribution of main active faults and recent lava flows, and areas where we have undertaken more detailed examination of local landscapes. Thin lines mark active faults and solid lines indicate the centres of the active rifts. The faults and lava flows shown are sufficiently young to exhibit the features shown in Figs. 5.5–5.8. The location of Hadar where 'Lucy' was found is shown and today lies on the smoothed uplifted flank of the contemporary active East African rift in a setting quite different from 4 Ma.. The inset shows two cross-sections of the rift at 4 Ma ago and as it is today. Essentially the same cross-section can be drawn for other African Rift hominid sites.

volcanic ash, which lies within the period of *circa* 40,000 to 20,000 years ago according to our preliminary dating of the associated lava flows (Fig. 5.9 and inset of Fig. 5.7).

Two other volcanic systems were examined, Gablaytu and Loma, together with other basalt cliffs created by recent faulting. All of these volcanic systems and cliffs were associated with extensive stone-artefact scatters. Both the Gablaytu and Loma volcanoes have internal safe

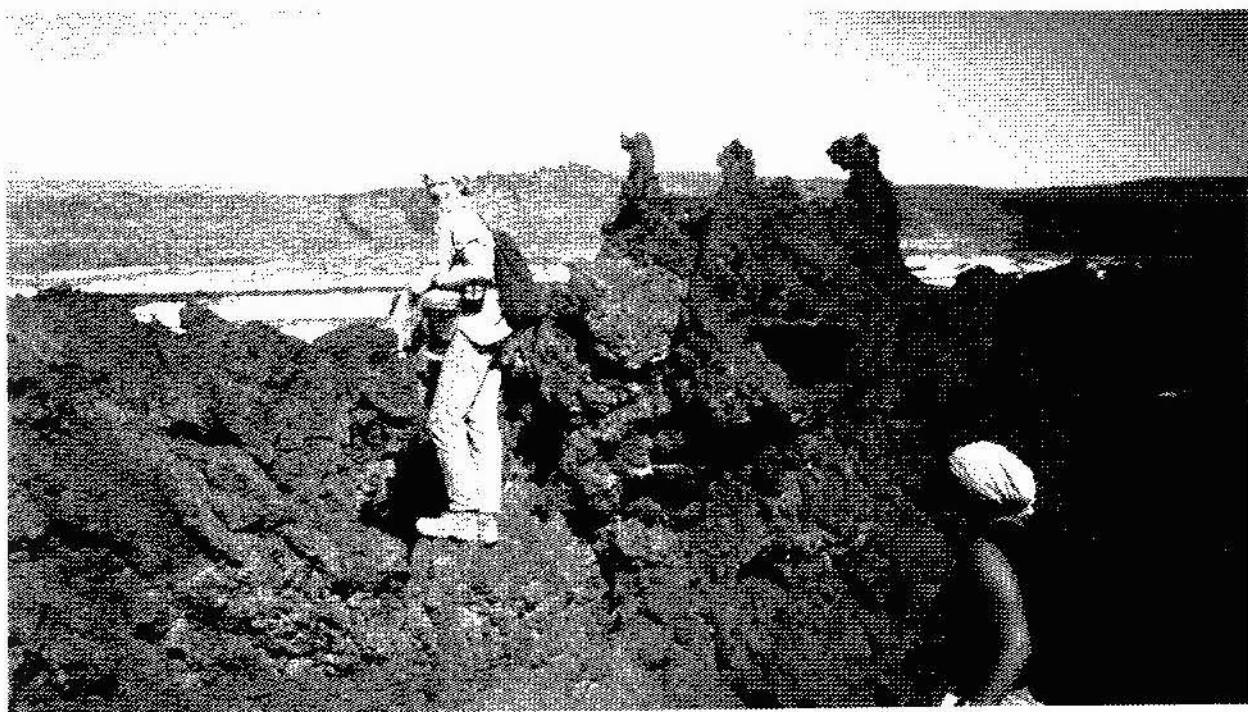


Figure 5.5 Lava flow in the Manda Volcanic system showing the typical height and jaggedness of a young feature. These pose a barrier to movement but are not insurmountable by bipeds.



Figure 5.6 Fault scarp in the Gablaysu region, demonstrating typical height and vertical face of fault displacement.

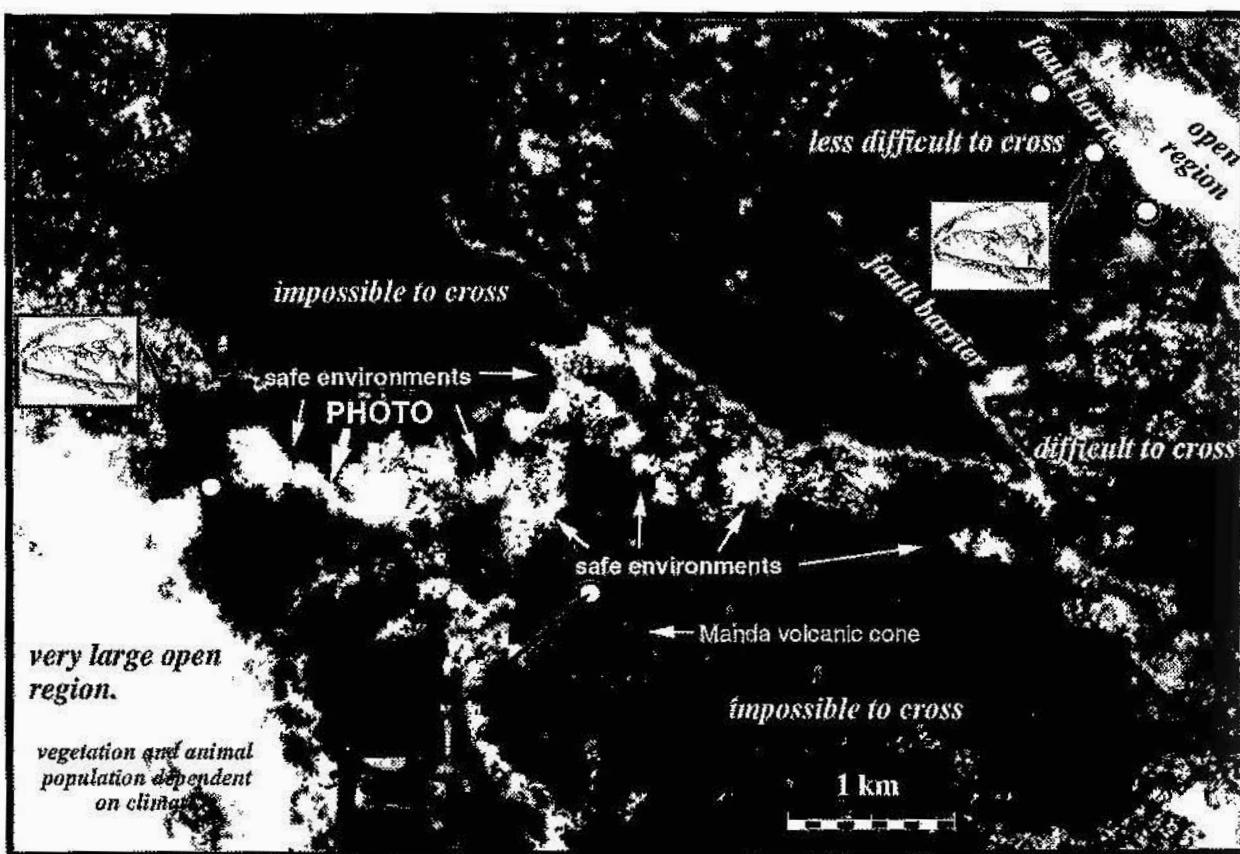


Figure 5.7 An annotated satellite photograph of faulted lava flows associated with the Manda Volcanic system. Part of the region is shown in an oblique photograph, Fig. 5.8, taken in the direction indicated by an arrow, from the summit of the southern Manda volcanic cone. The locations of extensive artefact scatters are shown, together with the location of the footprints described in the text. Internal safe areas are highlighted by a light shading.



Figure 5.8 Oblique photograph of the Manda region shown in Fig. 5.7. A lava flow with typical features is in the foreground and additional extensive lava flows appear as dark areas in the middle distance.



Figure 5.9 20,000 year-old footprints in water re-deposited volcanic ash deposits in the Manda region (see Fig. 5.7 for location).

areas. The Loma volcano has a crater lake with an obviously reliable water source and Gablaytu probably so. Some correlation between the location of artefact scatters and blind canyons appeared evident for all of the volcanoes, suggesting a hunting strategy involving entrapment.

There is evidence that the now contracted Lake Abbe (Fig. 5.3) has in the past reached and surrounded a nearby fault scarp. The enclosed spaces so created may also have played a role similar to those that we attribute to faulted volcanoes. Such lake-side environments would provide local barriers and enclosures that could be used in a similar way to faulted lava flows, and similar environments could also be produced by down-cutting rivers.

The region of Lake Asal in Djibouti provides another example of the way in which faults and lava flows may produce a complex series of barriers and partially enclosed areas of varying size adjacent to a lake-edge environment (Figs. 5.10 and 5.11). Today the climate here is very arid, and the local environments are fairly barren, being used only for brief seasonal stopovers by mobile pastoralists. Only small climatic changes, however, would convert this area into a more fertile region with a variety of plant and animal food supplies. The maze of lava flows and fault scarps visible today is not a transient feature of the landscape but a persistent feature that is constantly renewed by repeated volcanic activity and fault movement. Considering the 100 km length of rift in Djibouti as an example, several eruptions occur per century creating lava flows of 50 km² or more each time. At the same time, vertical fault scarps several kilometres in length can

increase in height by a metre. There is clearly a succession of local areas partially or totally enclosed by lava flows. The smaller areas are nested within larger enclosures defined by fault barriers and more extensive lavas, and these give way to more extensive areas of open terrain that would provide suitable habitat for larger game animals. It is this combination of enclosures at varying spatial scales that combines security with access to food supplies. And it is these sorts of features that are typically associated with lake basins in active areas of the African Rift, and which we would expect to have characterised many of the lake-edge environments inhabited by early hominids.

Figure 5.12 is a cartoon summarising many of the features that are actually observed in an active rift. To allow them to be shown in one picture the flat savannah areas are greatly reduced in size, as are the distances between volcanic centres. Important features shown are enclosed areas within lava flows, blind valleys created by faulted volcanic cones, and fault scarps that can extend for many tens of kilometres across otherwise featureless alluvial regions, and which potentially provide some security for travelling greater distances across the landscape.

Active tectonics and inward drainage

Although the centre of discussion in this paper is the role of lava flows and the vertical or near vertical faulting associated with active tectonics, it is worth noting that active extension also creates internal drainage systems.

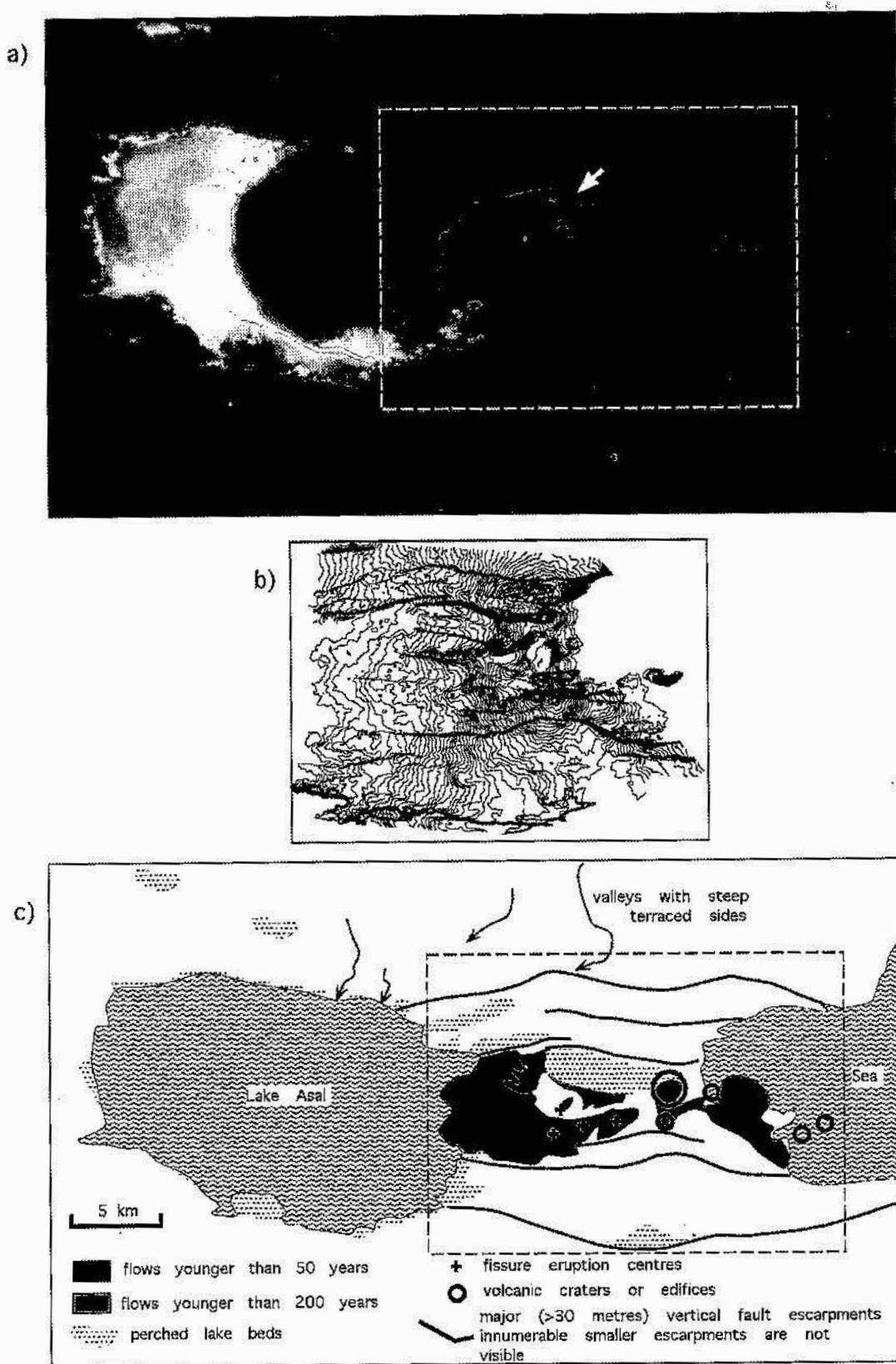


Figure 5.10 Map of Lake Asal region: (a) satellite photograph showing general features; (b) detailed mapping of faults and topography within the white box of (a); (c) simplified map of landscape features showing major faults, escarpments, volcanoes and lava flows.



Figure 5.11 Oblique photograph of Lake Asal region, taken from the top of one of the highest fault escarpments shown in Fig. 5.10 looking westwards towards Lake Asal. Lava flows and smaller faults create a series of partial and successively smaller enclosures as one moves from left to right of the picture and towards the lake shore in the right-hand corner.

For example all of the lakes between Lake Asal in Djibouti and Lake Turkana in Kenya currently have no outlet to the sea. Such inward draining systems are very sensitive to changes in precipitation and consequently to relatively rapid changes of water level. Some 6000 years ago Lake Asal was 200 metres higher and similar changes have occurred in other lakes. We have already noted the importance of interactions between lake shores and other features to create complex and partially enclosed environments. Rapidly varying lake levels, by controlling the erosional power of streams, also create steep-sided valleys and terraces which can exhibit similar features of partial enclosure and barriers to movement that we attribute to faults and lava flows.

EVOLUTIONARY OPPORTUNITIES AND CONSEQUENCES

Meat eating and bipedalism

As Davis (1987, 94) has noted, "The beginning of meat-eating, like the adoption of bipedalism, is shrouded in mystery", although both are considered to be critical factors in the development of human characteristics.

Current evidence suggests that both scavenging and hunting are likely to have played a significant role in hominid diets from at least as early as the first appearance of the *Homo* lineage (Bunn & Ezzo 1993). One puzzle, however, is how relatively defenceless and unspecialised early hominids descended from vegetarian tree dwellers

could have developed a meat-eating niche in the open savannah in competition with a number and variety of highly specialised carnivores and scavengers.

Scavenging offers one potential solution to the problem of gaining access to animal foods in the open savannah: that is reliance on specialised carnivores to do the hard work of running down the animal, and then moving in to take what is left. But in solving one problem, human scavengers are exposed to another, and that is the risk of themselves becoming prey victims. Studies of modern situations show that even today human groups, and especially women and children, are vulnerable to lethal attacks by carnivores (Treves & Naughton-Treves 1999). The problem of protection for hominid groups with dependent offspring has been discussed by a number of authors (e.g. Foley 1987, 183), and the usual solution has been to suggest the use of trees, which act as sources of food as well as shelter. Trees, however, also have disadvantages. Young chimpanzees, for example, are exposed to the risk of falls and require continuous protection (Goodall 1968). There is also the risk of exposure to tree-climbing predators.

Daytime foraging has been suggested by Wheeler (1984, 1985) as another tactic for avoiding carnivores, and one which might also have increased the selection pressure for bipedalism as a means of maximising heat loss. This hypothesis, however, leaves open the issue of protecting the young from predators, especially where there is an extended period of dependence on adult protection and food provisioning beyond weaning.

We suggest that a topography of fault scarps, lava

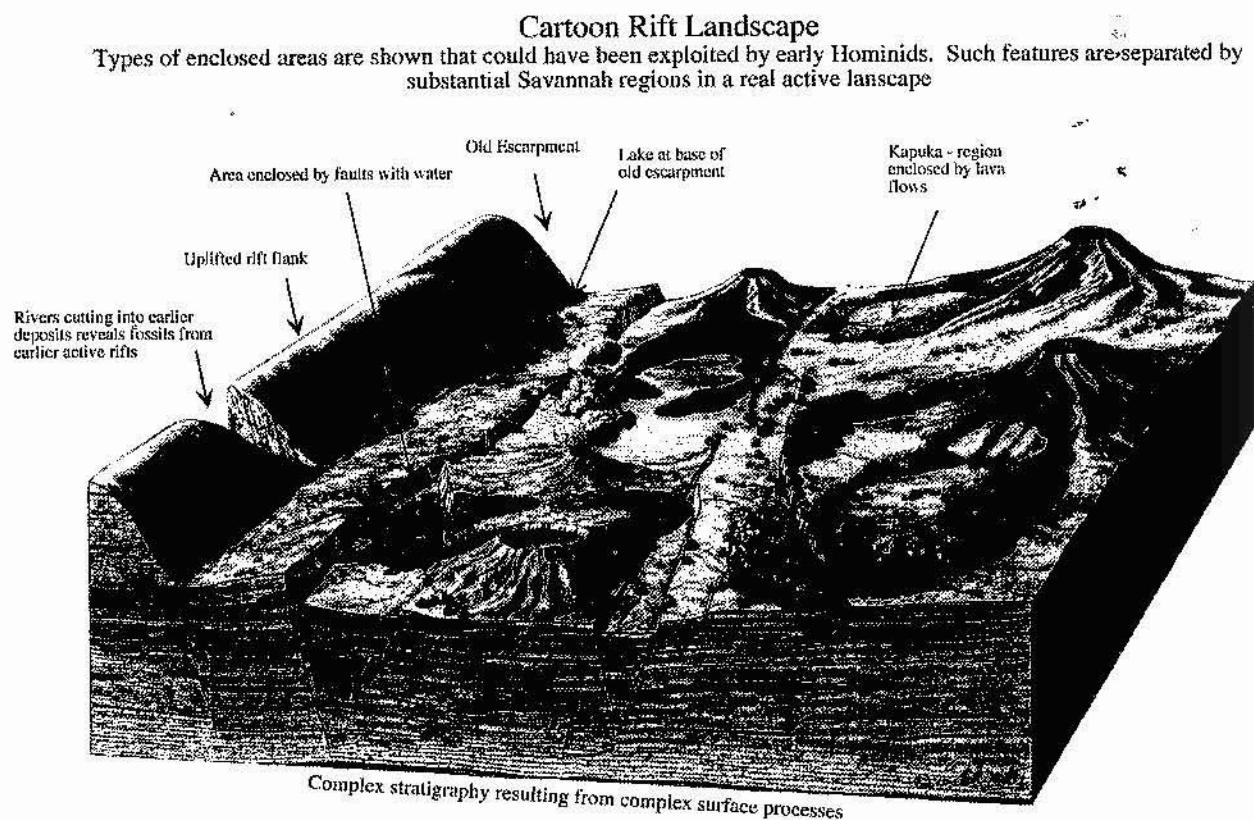


Figure 5.12 A cartoon representation of features within an active rift. An older smoothed escarpment is shown to the left and could have an age of 4 Ma. A river is shown cutting a narrow gorge into the escarpment. The same down-cutting is responsible for revealing fossils in earlier rift floor sediments. The view shows regions enclosed by lava flows (kapuka) or by near vertical faults or a combination of both. A lake is shown at the base of the older eroded escarpment in a similar position to the current Lake Gamarri. Distances between volcanic features have been contracted. They are commonly separated by 15 km or more. These regions have typical savannah characteristics although faults can extend all or part of the way between the regions and offer some temporary refuge for hominids moving between secure environments.

flows and steep sided valleys could have offered solutions to both issues, that of security and protection, and that of access to mobile and potentially elusive prey, while also accentuating selective pressures towards bipedalism.

Security

The unique feature of lava flows is the creation of totally secure environments. Basalt lava flows are remarkably difficult to cross. A traverse of 100 metres involves repeated climbing up and down jagged fragments. Such manoeuvres are possible for humans, as they would be for apes, but they are extremely difficult for quadrupedal mammals. Areas enclosed by lava flows provide protection from attack whether by speed or stealth without the need to depend on trees or the disadvantages of reliance on them. They also facilitate the protection of the vulnerable young while adult members of the group are engaged in subsistence practices elsewhere, and

would have created opportunities for extending the period of juvenile dependence.

Some modern ground-dwelling primates living in more open savannah are known to make sleeping nests on cliff faces or in caves, and the hamadryas baboons of Ethiopia frequently make use of fault scarps for protection (Kummer 1968). The idea of early hominids making use of lava flows and fault scarps as protective devices is thus entirely plausible.

Access to animal foods

Complex interlocking patterns of barriers and blind canyons composed of fault scarps and lava flows would have offered opportunities for diverting and trapping mobile animal species without the need for biological weapons of speed and attack. We cannot be sure that early hominids had the ability to behave like *predictive* hunters in the way we have described for Greece. Indeed

there is considerable controversy over the extent to which hunting was carried out at all in the earlier periods of human evolution. But the presence of topographic opportunities would certainly have created selective pressures for the development of such abilities, by offering important competitive advantages to a vulnerable hominid in otherwise relatively open savannah environments.

Food supplies

Unlike trees, lava flows, or small areas isolated within them, provide little or no food, which must be brought in from elsewhere. Animals brought down by hunting might conceivably have been diverted into topographic traps formed by lava flows before being killed, so as to minimise the distance over which the carcass had to be carried to a safe location. Even if hunting were not practised, meat acquired from scavenging would most probably have required transportation as would plant foods, if they were to be eaten at leisure in secure locations. As noted by numerous other authors bipedalism favours the transport of food by largely freeing the upper limbs (Lovejoy 1981). Limited modification leaves the same animal with the ability to negotiate cliffs and lava flows. We emphasise that food transportation in such a situation does not presuppose food sharing or a division of labour as envisaged by Isaac's (1978b) original food-sharing hypothesis, though such behaviours may be an outcome. It presupposes only the need to remove food from the point of capture or collection to a safe location for consumption.

Tools

Lava flows provide simple stone tools, sharp rock fragments are to hand everywhere and are usable without modification. The materials to create more sophisticated tools such as obsidian are also available.

Fire

Very early evidence for the use of fire remains controversial, but the association of early hominid activity with volcanically active areas would certainly have enhanced the possibilities for observing and making use of the benefits and effects of fire and heat (Gowlett *et al.* 1981). Fumaroles might have encouraged experiments with cooking.

Pressure towards change

Forested environments are essentially uniform in terms of the physical selection pressures they impose on species adapted to a forested habitat, except to the extent that areas of forest may expand or contract with climatic change. Such large-scale variations can alter

the patchiness of a landscape and thus the balance of predator-prey relationships, and the general contraction of forest in the late Tertiary is, of course, generally considered to be a key large-scale factor in opening up the hominid niche. At the smaller scales that are our focus here, however, landscapes characterised by faulting and volcanic lava flows may show greater variability than forests in the degree to which they provide enclosure and protection. Lava flows are not all the same. Although numerous completely enclosed areas exist, many more are partially enclosed or are in lava flows that are eroded sufficiently to be more readily traversed. Furthermore as climate changes, lava flows stay fixed. This offers a challenging environment to a species that inhabits them.

The existence of a range of niches that were similar in their general characteristics but different in detail would have provided an added incentive to evolutionary change, either through niche separation or by selecting for intra-species adaptability.

DISCUSSION

The modern equivalents of the sites of early hominid finds lie among the active faults and volcanoes of the currently active parts of the East African Rift. No reports of studies in these regions are to be found and they are generally regarded as inhospitable and inaccessible. Yet within them secure areas exist that could provide a refuge for an ape-like creature deprived of trees and an environment where bipedalism would confer advantages. Even a brief visit suggests that evidence for prehistoric occupation is strong, and that these seemingly inhospitable landscapes provided attractions for human settlement. Although not many sites have been identified, those that have are associated with the contemporaneous rift activity. Conversely, it is notable that scarcely any trace of stone tools was observed in the more open terrain on the Manda-Hararo rift flank, despite the fact that more than 60 locations similar in many respects to those we refer to in the central rift were visited for palaeomagnetic dating. By contrast, pastoral activity is now well developed on the rift flanks and rock paintings of domesticated camels suggest that this may have been so for some time. The implication is that, until the advent of animal domestication, human habitation of such regions was not practical. Although this is the savannah in which early hominids have commonly been placed, it appears that human occupation has only recently extended into it.

It also appears that at least some of the tribal people of the Kenyan Rift Valley were familiar with lava-flow environments. When deprived of firearms by the British in Kenya, the local people notoriously disappeared into a region of volcanoes and lava flows into which they could not be followed. Presumably they knew how to exploit the environment to survive. Thus it may be at

least as useful to examine how modern people have exploited the active regions of the East African Rift prior to the appearance of guns, as a source of insight and analogy for the sort of ecological niche that we have identified for early hominids, as to examine the behaviour of our nearest living relatives amongst the Great Apes, or the behaviour of carnivores with supposed functional similarities to hominid scavengers or hunters.

The environments that we have described for the present Manda Hararo rift are the exact conditions that will in due course create a future geological environment like that in which many early hominid remains have been found. Interbedded lacustrine and fine terrestrial sediments are associated with ash falls, water-reworked ash and basalt lava flows at Hadar (Taieb *et al.* 1976; Taieb & Tiercelin 1979), and at other classic Rift Valley sites such as Omo, Turkana and Olduvai (Feibel *et al.* 1989; Hay 1976; Rapp & Vondra 1981). Examining a contemporary example explains why geologists have such problems correlating strata between individual exposures in separate valleys. Lava flows and sediment traps simply do not correlate except over very short distances, and a layer cake stratigraphy misses an important insight into the nature of the original environment.

Indeed this geological issue is one of several factors that have obscured the role of tectonics at the local scale. Reconstructions of the landscape around early hominid sites tend to produce a picture of relatively smooth landscapes lacking in physical barriers and topographical detail (e.g. at Olorgesailie (Isaac 1978a; Shackleton 1978), at the Bed I Olduvai sites (Isaac 1981) and at Koobi Fora (Bunn *et al.* 1980; Isaac & Behrensmeyer 1997). This is an almost inevitable consequence of attempting reconstructions from a limited number of geological 'windows' into a landscape that has undergone radical alteration through ongoing rifting, tectonic activity and erosion since the time of hominid occupation. Such reconstructions inevitably arrive at a lowest common denominator in which local topographic detail is largely eliminated for the simple reason that it cannot be reconstructed with any confidence – or else has been smoothed away by erosion.

There are two other reasons, in our view, why the tectonic factors we have cited have been overlooked. Firstly, the role of the natural environment in evolutionary trends tends to be dealt with in very general terms, in relation to large-scale phenomena such as regional and global climatic and biotic changes (e.g. Vrba *et al.* 1995). Numerous studies of the more recent archaeological and palaeoenvironmental record, however, demonstrate that broad climatic and environmental changes can be significantly modified or moderated by local topographic features (e.g. Bailey 1997). Landscape structure, especially at the local scale, thus becomes a key focus for small-scale interactions between populations and environmental factors, and these small-scale interactions can have a significant if poorly understood impact on both

short-term ecological interactions and longer-term evolutionary trajectories.

Secondly, the African Rift where the best known early hominid sites occur was most probably more active tectonically and volcanically in the late Tertiary and early Quaternary than is the case today. The highest rates of activity at the present day are to be found in eastern Afar and Djibouti, and highly active areas such as these are rarely visited by modern observers and usually regarded as arid, inhospitable and inaccessible areas of lava flows. There is consequently a general lack of awareness about the physical structure of such active landscapes. However, as we have shown above, there is good evidence that these landscapes can be very attractive for human settlement under appropriate climatic conditions.

CONCLUSION

The hypothesis that we advance here is that lava flows and the young normal faults of tectonically active areas of the African Rift created a local landscape structure that was uniquely appropriate as an agent of environmental selection in the early stages of hominid evolution. We suggest that this process operated both directly, in selecting for and amplifying specific features such as bipedalism, meat-eating and cognitive development, and indirectly by controlling the pattern of interactions between species and their co-evolutionary development. In particular we emphasise the following features of tectonics in the African Rift:

- Unusually high rates of tectonic activity and volcanism, associated with a complex pattern of often impassable lava flows and vertical fault scarps.
- Complex patterns of enclosure at a variety of spatial scales that would have provided opportunities to hominids for the development of new niches as unspecialised predators, as well as protection to hominids as potential prey victims.
- The creation and maintenance of a rich and diverse mosaic of resources subject to varying degrees of patchiness.
- Topographic and environmental conditions that were locally variable in time as well as space, offering varying degrees of local isolation and/or regional mixing, and thus acting as an *environmental pace-maker* for evolutionary developments.

We suggest that this hypothesis has been overlooked both because of the difficulties of reconstructing Plio-Pleistocene topography and local environments in a highly active tectonic region, and because the classic sites of early hominid discoveries are in areas of the East African Rift which are now probably less active than when the sites were formed. Existing reconstructions which show early hominid sites surrounded by smooth alluvial plains are highly misleading because they are uninformed by a knowledge of topography in modern active environments,

and because the complex small-scale patterning of local faults and lava barriers that is so critical to an understanding of these environments cannot easily be recovered from the ancient landscape and has in consequence been erased from the reconstructions.

Finally, we acknowledge that the ideas presented above pose two sorts of challenges to future investigation, one practical, the other theoretical. On the practical side, systematic testing of our basic hypothesis will require two sorts of observations to be undertaken: the systematic archaeological investigation of those modern environments which provide contemporary analogies for the landscapes occupied by early hominids; and the reconstruction of past landscape structure with an eye to barriers and 'sharp' topographic features especially at the local scale. The need for the former arises from precisely the same set of factors which makes the latter so difficult, namely the large-scale transformation of local environmental features that has been effected by continued tectonic activity and environmental processes of erosion and sedimentation over hundreds of thousands of millennia. We do not underestimate the difficulties posed by both approaches, the dangers of extrapolation from modern analogues in the former case, and the uncertainties of reconstruction in the latter. But we suggest that both need to be attempted, and that in combination they should lead to a better understanding of the environmental context in which early hominid evolution took place, and a fuller integration of environmental factors into the understanding of co-evolutionary processes.

On the theoretical side, we observe that differences of scale continue to provide one of the most common sources of confusion and misunderstanding in the field of human evolution and human history, especially between specialists working in different disciplines or in different time periods. At the same time differences of scale also lie at the very heart of ecodynamic theory and present one of the most difficult challenges to theoretical understanding. Not the least part of that challenge is the forging of a common language that will allow communication across disciplinary and sub-disciplinary boundaries. However, a common conceptual framework that accommodates differences of scale is unlikely to emerge without a degree of co-evolutionary intellectual development, in which specialists emerge from behind barriers of isolation, old ideas are abandoned or modified, and new ones experimented with. That process of co-evolutionary intellectual development is not an easy or comfortable one, as anyone who has engaged in a large-scale multi-disciplinary project will know. Without it, however, there can be no prospect of understanding the co-evolutionary nature of the past.

ACKNOWLEDGEMENTS

We are grateful to John Coles for identifying the source of Fig. 5.1 and to Topham Picturepoint for permission

to reproduce it, to Nick Winder for highlighting the co-evolutionary significance of tectonic landscapes, to John Price for comments on fumaroles, and to Rob Foley and two anonymous assessors for critical readings of an earlier draft. The fieldwork which stimulated the observations and ideas reported here was undertaken during mapping and palaeomagnetic determination of deformation processes in Afar and Djibouti and field excursions and discussions associated with the Addis Ababa Conference of 1997 on Flood Basalts, Rifting and Palaeoclimates in the Ethiopian Rift and Afar depression. We thank C.N.R.S. and I.N.S.U., Paris, and the University of Newcastle-upon-Tyne for financial support.

REFERENCES

Bailey, G. N. (ed). 1997. *Klithi: Palaeolithic Settlement and Quaternary Landscapes in Northwest Greece*. Vol. 1: *Excavation and Intra-Site Analysis at Klithi*, Vol. 2: *Klithi in its Local and Regional Setting*. Cambridge: McDonald Institute for Archaeological Research.

Bailey, G. N., King, G. C. P. and Sturdy, D. A. 1993. Active tectonics and land use strategies: a Palaeolithic example from Northwest Greece. *Antiquity* 67, 292–312.

Bailey, G. N., Papaconstantinou, V. and Sturdy, D. A. 1992. Asprochaliko and Kokkinopilos: TL dating and reinterpretation of Middle Palaeolithic sites in Epirus, North-west Greece. *Cambridge Archaeological Journal* 2, 136–44.

Blumenschine, R.J. and Peters, C.R. 1998. Archaeological predictions for hominid land use in the paleo-Olduvai Basin, Tanzania, during lowermost Bed II times. *Journal of Human Evolution* 34, 565–607.

Broussoulis, J., Ioakim, C., Kolovos, G. and Papanikos, D. 1999. The Ioannina basin: geological and palaeoenvironmental evolution in Quaternary and historical times, pp. ?? in G.N. Bailey, E. Adam, E. Panagopoulou, C. Perls & K. Zachos (eds.), *The Palaeolithic Archaeology of Greece and Adjacent Areas*. London: British School at Athens.

Brown, F. H. and Feibel, C. S. 1991. Stratigraphy, depositional environments and palaeogeography of the Koobi Fora formation, pp. 1–30 in Harris, J.M. (ed), Koobi Fora Research Project, Volume 3, *The Fossil Ungulates: Geology, Fossil Artiodactyls, and Palaeoenvironments*. Oxford: Clarendon Press.

Bunn, H. T. and Ezzo, J. A. 1993. Hunting and scavenging by Plio-Pleistocene hominids: nutritional constraints, archaeological patterns, and behavioural implications. *Journal of Archaeological Science* 20, 365–98.

Bunn, H. T., Harris, J. W. K., Isaac, G. L., Kaufulu, Z., Kroll, E., Schick, K., Toth, N. and Behrensmeyer, A. K. 1980. FxJ 50: an early Pleistocene site in northern Kenya. *World Archaeology* 12, 109–36.

Coppens, Y. 1994. East side story: the origin of humankind. *Scientific American* 270, 62–9.

Davis, S. J. M. 1987. *The Archaeology of Animals*. London: Batsford.

De Chabrier, J.-B. and Avouac, J.-P. 1994. Kinematics of the Asal Rift Djibouti determined from the deformation of Fieale Volcano. *Science* 265, 1677–81.

Deniel C., Vidal, Ph., Coulon, C., Vellutini, P. J. and Piquet, P. 1994. Temporal evolution of mantle sources during continental rifting: the volcanism of Djibouti Afar. *Journal of Geophysical Research* 99(B2), 2853–69.

Ellis, M. and King, G. C. P. 1991. Structural control of flank volcanism in Continental Rifts. *Science* 254, 839–42.

Feibel, C. S., Brown, F. H. and McDougall, I. 1989. Stratigraphic context of fossil hominids from the Omo group deposits: Northern

Turkana basin, Kenya and Ethiopia. *American Journal of Physical Anthropology* 78, 595–622.

Foley, R. A. 1987. *Another Unique Species: Patterns in Human Evolutionary Ecology*. Harlow: Longman.

Foley, R. A. 1994. Speciation, extinction and climatic change in hominid evolution. *Journal of Human Evolution* 26, 27–89.

Foley, R. A. in press. Evolutionary geography of Pliocene African hominids, in Bromage, T. and Schrenk, F. (eds.), *African Biogeography, Climatic Change and Early Hominid Evolution*. Oxford: Oxford University Press.

Gamble, C. S. 1993. *Timewalkers: the prehistory of global colonization*. Stroud: Alan Sutton.

Goodall, J. 1968. *The Behaviour of Free-living Chimpanzees in the Gombe Stream Reserve*. (Animal behaviour Monographs; vol. 1(3)). London: Baillière, Tindall and Cassell.

Gowlett, J. A. J., Harris, J. W. K., Walton, D. and Wood, B. A. 1981. Early archaeological sites, hominid remains and traces of fire from Chesowanja, Kenya. *Nature* 294, 125–9.

Harris, J. K. and Herbich, Z. 1978. Aspects of early Pleistocene hominid behaviour of east Lake Turkana, pp. 529–47 in Bishop, W. W. (ed.), *Geological Background to Fossil Man*. Edinburgh: Scottish Academic Press.

Hay, R. L. 1976. *Geology of the Olduvai Gorge*. Berkeley: University of California Press.

Isaac, G. L. 1978a. The Olorgesailie formation: stratigraphy, tectonics and the palaeogeographic context of the Middle Pleistocene archaeological sites, pp. 173–206 in Bishop, W. W. (ed.), *Geological Background to Fossil Man*. Edinburgh: Scottish Academic Press.

Isaac, G. L. 1978b. The food-sharing behavior of protohuman hominids. *Scientific American* 238, 90–108.

Isaac, G. L. 1981. Stone Age visiting cards: approaches to the study of early land-use patterns, pp. 131–55 in Hodder, I., Isaac, G. and Hammond, N. (eds.), *Pattern of the Past*. Cambridge: Cambridge University Press.

Isaac, G. L. and Behrensmeyer, A. K. 1997. Geological context and palaeoenvironments, pp. 12–19 in Isaac, G. L. and Isaac, B. (eds.), *Koobi Fora Research Project, Vol. 5. Plio-Pleistocene Archaeology*. Oxford: Clarendon Press.

King, G. C. P., Sturdy, D. A. and Bailey, G. N. 1994. Active tectonics, complex topography and human survival strategies. *Journal of Geophysical Research* 99(B10), 20063–78.

Kummer, H. 1968. *Social Organization of the Hamadryas Baboon*. Chicago: University of Chicago Press.

Lovejoy, C. O. 1981. The origin of man. *Science* 211, 341–50.

Manighetti, I. 1993. *Dynamique des systèmes extensifs en Afar*. Unpublished PhD thesis, Institut de Physique du Globe de Paris.

Manighetti, I., Tappognier, P., Courtillot, V., Gruszow, S. and Gillot P. Y. 1997. Propagation of rifting along the Arabia-Somalia plate boundary: the gulfs of Aden and Tadjoura. *Journal of Geophysical Research* 102, 2681–710.

Manighetti, I., Tappognier, P., Gillot, P. Y., Jacques, E., Courtillot, V., Armijo, R., Ruegg, J. C. and King, G. 1998. Propagation of rifting along the Arabia-Somalia plate boundary into Afar. *Journal of Geophysical Research* 103, 4947–74.

Partridge, T. C., Bond, G. C., Hartnady, C. J. H., deMenocal, P. B. and Ruddiman, W. F. 1995a. Climatic effects of late Neogene tectonism and volcanism, pp. 8–23 in Vrba, E. S., Denton, G. H., Partridge, T. C. and Burckle, L. H. (eds.), *Paleoclimate and Evolution, with emphasis on Human Origins*. New Haven, CT: Yale University Press.

Partridge, T. C., Wood, B. A. and deMenocal, P. B. 1995b. The influence of global climatic change and regional uplift on large-mammalian evolution in east and southern Africa, pp. 331–55 in Vrba, E. S., Denton, G. H., Partridge, T. C. and Burckle, L. H. (eds.), *Paleoclimate and Evolution, with emphasis on Human Origins*. New Haven, CT: Yale University Press.

Pianka, E. R. 1978. *Evolutionary Ecology*. 2nd edition. New York: Harper & Row.

Rapp, G. and Vondra, C. F. (eds.) 1981. *Hominid Sites: their geologic settings*. American Association for the Advancement of Science, Selected symposium 63. Boulder, Colorado: Westview Press.

Ruddiman, W. F. and Raymo, M. E. 1988. Northern Hemisphere climate regimes during the past 3 Ma: possible tectonic connections, pp. 1–20 in Shackleton, N. J., West, R. W. and Bowen, D. Q. (eds.), *The Past Three Million Years: evolution of climatic variability in the North Atlantic region*. London: Royal Society.

Runnels, C. and Van Andel, T. J. H. 1993. A handaxe from Kokkinopilos, Epirus, and its implications for the Paleolithic of Greece. *Journal of Field Archaeology* 20, 91–103.

Shackleton, R. S. 1978. in Isaac, G. L. The Olorgesailie formation: stratigraphy, tectonics and the palaeogeographic context of the Middle Pleistocene archaeological sites, pp. 173–206 in Bishop, W. W. (ed.), *Geological Background to Fossil Man*. Edinburgh: Scottish Academic Press.

Stein, R. S., Briole, P., Ruegg, J. C., Tappognier, P. and Gasse, F. 1991. Contemporary, Holocene and Quaternary deformation of the Asal Rift, Djibouti: implications for the mechanics of slow spreading ridges. *Journal of Geophysical Research* 96, 21789–806.

Taieb, M., Johanson, D. C., Coppins, Y. and Aronson, J. L. 1976. Geological and palaeontological background of the Hadar hominid site, Afar, Ethiopia. *Nature* 260, 289–93.

Taieb, M. and Tiercelin, J.-J. 1979. Sédimentation Pliocène et Paléoenvironments de Rift: exemple de la Formation à Hominidés d'Hadar 5, Afar, Ethiopie. *Bulletin de la Société Géologique de France* 21, 243–53.

Tappognier P., Armijo R., Manighetti I. and Courtillot, V. 1990. Bookshelf faulting and horizontal block rotation between overlapping rifts in southern Afar. *Geophysical Research Letters* 17(1), 1–4.

Treves, A. and L. Naughton-Treves. 1999. Risk and opportunity for humans coexisting with large carnivores. *Journal of Human Evolution* 36, 275–82.

Vrba, E. 1996. *Paleoclimate and Neogene Evolution*. New Haven, CT: Yale University Press.

Vrba, E. S., Denton, G. H., Partridge, T. C. and Burckle, L. H. (eds) 1995. *Paleoclimate and Evolution, with emphasis on Human Origins*. New Haven, CT: Yale University Press.

Wheeler, P. E. 1984. The evolution of bipedality and loss of functional body hair in hominids. *Journal of Human Evolution* 13, 91–8.

Wheeler, P. E. 1985. The loss of functional body hair in man: the influence of thermal environment, body form and bipedality. *Journal of Human Evolution* 14, 23–8.

Winder, N. 1997. Dynamic modelling of an extinct ecosystem: refugia, resilience and the overkill hypothesis in Palaeolithic Epirus, pp. 625–36 in Bailey, G. N. (ed.), *Klithi: Palaeolithic Settlement and Quaternary Landscapes in Northwest Greece. Vol. 2: Klithi in its Local and Regional Setting*. Cambridge: McDonald Institute for Archaeological Research.