



Landscapes and their relation to hominin habitats: Case studies from *Australopithecus* sites in eastern and southern Africa

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ABSTRACT

We examine the links between geomorphological processes, specific landscape features, surface water drainage, and the creation of suitable habitats for hominins. The existence of mosaic (i.e., heterogeneous) habitats within hominin site landscape reconstructions is typically explained using models of the riverine and gallery forest settings, or the pan or lake setting. We propose a different model: the Tectonic Landscape Model (TLM), where tectonic faulting and volcanism disrupts existing pan or river settings at small-scales (~10–25 km). Our model encompasses the interpretation of the landscape features, the role of tectonics in creating these landscapes, and the implications for hominins. In particular, the model explains the underlying mechanism for the creation and maintenance of heterogeneous habitats in regions of active tectonics. We illustrate how areas with faulting and disturbed drainage patterns would have been attractive habitats for hominins, such as *Australopithecus*, and other fauna. Wetland areas are an important characteristic of surface water disturbance by fault activity; therefore we examine the tectonically-controlled Okavango Delta (Botswana) and the Nylsvley wetland (South Africa) as modern examples of how tectonics in a riverine setting significantly enhance the faunal and floral biodiversity. While tectonic landscapes may not have been the only type of attractive habitats to hominins, we propose a suite of landscape, faunal, and floral indicators, which when recovered together suggest that site environments may have been influenced by tectonic and/or volcanic activity while hominins were present. For the fossil sites, we interpret the faulting and landscapes around australopithecine-bearing sites of the Middle Awash (Ethiopia) and Makapansgat, Taung, and Sterkfontein (South Africa) to illustrate these relationships between landscape features and surface water bodies. Exploitation of tectonically active landscapes may explain why the paleoenvironmental signals, anatomy, diets, as well as the fauna associated with *Australopithecus* appear largely heterogeneous through time and space. This hypothesis is discussed in light of potential preservation and time-averaging effects which may affect patterns visible in the fossil record. The model, however, offers insight into the landscape processes of how such habitats are formed. The landscape features and range of habitat conditions, specifically the wetter, down-dropped plains and drier, uplifted flanks persist in close proximity for as long as the fault motion continues. The Tectonic Landscape Model provides an alternative explanation of why mixed habitats may be represented at certain sites over longer timescales.

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Introduction

The effect of large-scale Pliocene climate shifts on vegetation changes and mammalian evolution has been used to construct a framework within which hominin evolutionary changes have been interpreted (deMenocal, 1995, 2004; deMenocal and

Bloemendal, 1995; Vrba, 1995; Campisano and Feibel, 2007; Kingston et al., 2007;). A key part of this framework is the reconstruction of habitats at hominin sites, using both faunal and floral indicators (e.g., Vrba, 1982; Reed, 1997; Spencer, 1997; Bamford, 1999; Avery, 2001; Bobe and Eck, 2001; Bonnefille et al., 2004; Hernández-Fernández and Vrba, 2006; Reynolds, 2007). Reconstructions for hominin sites typically identify 'habitat mosaic' environments: lakeside or riverside gallery forest, with a close proximity to open grassland or woodland habitats. These features are used to reconstruct the likely landscape use by the hominins

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across their foraging range (e.g., Peters and Blumenshine, 1995; Blumenshine et al., 2003). Habitat reconstructions often mention the presence of certain physical landscape features, such as lakes and rivers, which are important determinants of the surrounding vegetation (e.g., Peters and O'Brien, 2001). We examine the landscape processes which create specific landscape features and habitats at the sites; in particular, we present illustrations of how geomorphological processes can create certain combinations of landscape and surface features. This in turn provides new perspectives on how habitats exploited by hominins may have originated and been sustained in specific regions.

Volcanism and tectonic faulting are two processes that act on landscapes in specific and predictable ways (Bailey et al., 2011) and can also indirectly enhance the habitat diversity of a region (Ramberg et al., 2006; Havenga et al., 2007). We use the wealth of site, habitat, and dietary reconstructions for the genus *Australopithecus* as a case-study to evaluate the possible impact of small-scale tectonics on landscapes and human evolution. *Australopithecus* is suitable for several reasons: 1) it is known from geographically and temporally widespread localities, which differ quite substantially in depositional contexts, geology, and the degrees of volcanism and tectonism (e.g., Partridge et al., 1995a, b), 2) *Australopithecus* paleoenvironmental reconstructions range from wooded, forested conditions to more open, grassland-dominated conditions, and also varying combinations of these habitat categories (e.g., Clarke and Tobias, 1995; Brunet et al., 1995; Reed, 1997; Bamford, 1999; Avery, 2001; Bonnefille et al., 2004), and finally 3) it is a relatively long-lived genus by hominin standards, spanning approximately two million years. The earliest occurrence is from Asa Issie, Ethiopia, dating to around 4.1 Ma (White et al., 2006), while the youngest *Australopithecus* dates to approximately 2.1 Ma from the upper Sterkfontein Member 4 of South African deposits (Partridge, 2005).

We assume that the site regions of Ethiopia and South Africa offered suitable habitats for *Australopithecus* at the time that they were present there, although the present-day landscapes of these regions differ from each other. Here we define 'suitable habitats' as comprising three basic elements, or resources: a range of C₄ and C₃ foods within foraging distance of the group, access to drinking water, and relatively safe sleeping and nesting areas or so-called 'predator refuge' opportunities (Durant, 1998). Even large modern primates such as gorillas and chimpanzees are vulnerable to predation by leopards (Hart, 2007), and hominins would have required strategies for avoiding predators. The use of cliffs for shelter and safety could have played an important role in reducing the risk of predation by large, cursorial predators. Several extant species utilize landscape features extensively for this reason (e.g., the gelada, *Theropithecus gelada*; Gippoliti and Hunter, 2008).

We investigate how geomorphological processes in eastern and southern Africa could have created homologous (or analogous) landscape features and habitats to accommodate hominins such as *Australopithecus*. To illustrate the models of the tectonically-altered landscape, we examine the site regions of Makapansgat, Taung, and the Sterkfontein Valley (South Africa) and compare these landscape features to our reconstructions of how Ethiopian fossil sites could have looked at the time of hominin occupation. We also discuss the advantages and disadvantages of using analogous sites closer to the Rift margin, rather than attempting to reconstruct the landscapes of the fossil sites in the Middle Awash in their present location and eroded condition (Bailey et al., 2011).

Australopithecus habitats and diets

Numerous studies have addressed the question of what types of habitats were preferred by hominins. A characteristic mix of

environments is commonly identified from hominin sites across Africa and through time, from the site of Koro Toro, Chad (Brunet et al., 1995) to the latest site of upper Member 4 at Sterkfontein in South Africa (Bamford, 1999; Sponheimer and Lee-Thorp, 1999; Kuman and Clarke, 2000). Various paleoenvironmental proxies indicate a wide range of vegetation types, ranging from wooded, forested conditions to more open, grassland-dominated conditions at *Australopithecus*-bearing Members of Sterkfontein and Makapansgat (e.g., Wells and Cooke, 1956; Vrba, 1982; Cadman and Rayner, 1989; Rayner et al., 1993; Clarke and Tobias, 1995; Reed, 1997; Bamford, 1999; Avery, 2001). High resolution palynological studies from Hadar (Ethiopia) show that *Australopithecus afarensis* is associated with a range of habitats, including forest and grassland, between 3.4–2.9 million years ago (Bonnefille et al., 2004). Studies of *Australopithecus* microwear from a large geographic sample of *Australopithecus* (referred to *Praeanthropus afarensis*) in eastern Africa indicate a stable but varied diet through space and time (Grine et al., 2006), while stable carbon isotopes from *Australopithecus africanus* enamel at Sterkfontein Member 4 suggest that variable proportions of C₃ and C₄ foods were consumed (van der Merwe et al., 2003). The range of habitats have led authors to suggest that *Australopithecus* may have been a eurytopic genus capable of surviving in a range of different habitats (Potts, 1996, 1998) or that certain *Australopithecus* species were adapted to specific local niches. We approach the vegetation question from the known landscape processes of that region and the effect these would have had on habitat diversity.

Examining the landscapes around hominin sites

This study focuses on four *Australopithecus*-bearing sites and their surrounding regions, specifically Makapansgat, Taung, and Sterkfontein (South Africa) and the Middle Awash region (Ethiopia), as specific examples of how landscapes can be modified by tectonic activity, and the implications of these processes for habitat creation. But before this, we must address a series of potentially confounding issues:

- 1) What did these ancient sites look like at the time that hominins were present?
- 2) Are the distributions of *Australopithecus* sites in Africa a pattern created by preferential preservation and intensive prospection in certain regions for hominins and other fossils?
- 3) Did sites possess suitable habitats, or were australopithecines more prone to die there?
- 4) How would time-averaging and large-scale climate shifts affect our ability to see evidence of tectonically-controlled environments in the fossil record?
- 5) How does the Tectonic Landscape Model apply more broadly to other *Australopithecus* sites which we do not directly address here?

Hominin landscape site models

We consider three simple landscape models of the regions around *Australopithecus*-bearing sites and the abilities of each to meet the suitable habitat requirements of *Australopithecus* (Fig. 1). As general landscape models, however, they cannot represent all possible combinations of landscape features at every fossil locality. Each scenario offers suitable habitat opportunities, but the first two landscape models have very little variable surface topography and are profoundly influenced by the level of the water table, and this in turn is affected by large-scale climate changes (deMenocal, 1995,

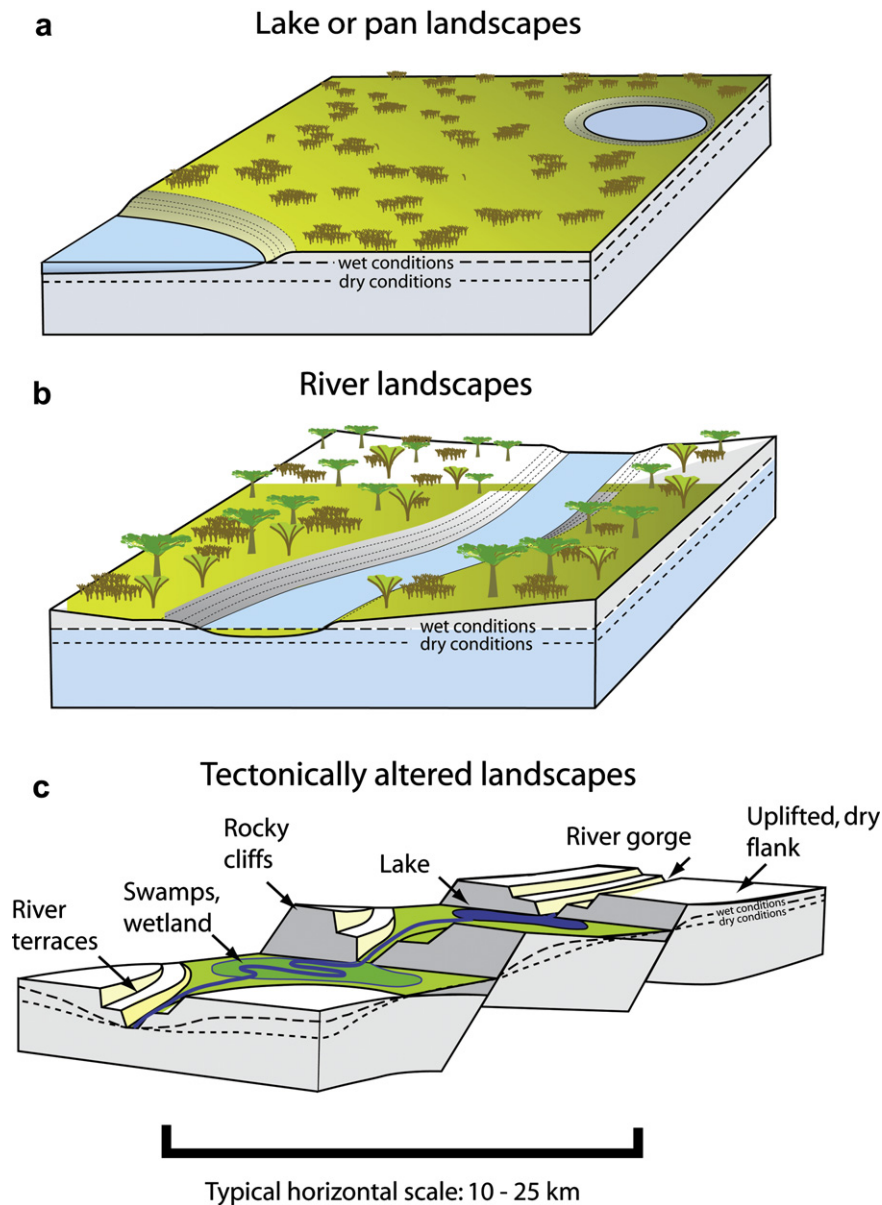


Figure 1. Topographically flat settings of lakes (a) and rivers (b) as landscape supporting environments suitable for hominins. (c) illustrates landscapes altered by small-scale tectonic activity, at a range of 10–25 km. Each landscape possesses different topographic features and associated capacities to support tree cover, and plant and animal biodiversity.

2004) and the interaction between local topographic and climatic effects (Sepulchre et al., 2006).

The first two scenarios (Fig. 1a and b) are the most often inferred landscape scenarios for hominin habitats, particularly on the banks of shallow lakes and ancient rivers but also in close proximity to open plains and grasslands (e.g., White et al., 1993; WoldeGabriel et al., 1994, 2001; Peters and Blumenschine, 1995; de Heinzelin et al., 1999; Haile-Selassie, 2001; Blumenschine et al., 2003). The pan or lake setting (Koro Toro, Middle Awash sites, shown in Fig. 1a) and the riverine and gallery forest scenario (e.g., Makapansgat, Sterkfontein, indicated in Fig. 1b) are well-established landscape scenarios for hominin sites (de Heinzelin et al., 1999; Kuman and Clarke, 2000). Where such habitats occurred, these would certainly have offered attractive habitats for hominins, for as long as these features lasted. However, our emphasis for this paper falls on the third type of landscape, that which is altered by small-scale tectonic faulting and volcanism (ca. 10–25 km, indicated in Fig. 1c).

Pans, lakes, and waterhole environments Waterholes, oases, or billabongs result where the water table intersects the surface in flatter landscapes (Fig. 1a). These surface bodies of water, and dramatic changes to them, are likely to have been a significant determinant of local vegetation (O'Brien and Peters, 1999; Peters and O'Brien, 2001). However, the availability of surface water in flat landscapes is closely linked to variation in elevation and is vulnerable to climate change. A drop in the water table caused by a variety of large-scale-climatic variables will cause fluctuations in water levels, as documented for Lake Chad and Lake Turkana. In some cases these changes resulted in these surface water bodies drying up altogether, as with paleolakes Ologesailie, Olduvai, and in the late Pleistocene, Lake Tana (Lamb et al., 2007). This type of flat landscape would have provided suitable habitats for hominins as long as the surface water and the level of the water table did not drop.

Riverine environments The second model is a riverine landscape which supports a gallery forest (Fig. 1b). Unless these rivers



Figure 2. Location of Okavango and Nylsvley wetlands and the major southern African *Australopithecus* hominin sites for which we reconstruct the landscape features. The region of the Okavango Delta falls within the 'semi-desert' classification, yet the faulting activity and disruption of the Okavango River creates and maintains habitat heterogeneity and high levels of biodiversity (Ramberg et al., 2006).

have headwaters that lie in upland regions of high rainfall, the river water levels are closely linked to variation in elevation and are, again, vulnerable to climate change. In areas of low relief even the most reliable rivers or lakes may dry up under extreme conditions of climatic aridity, and, unless the landscape intersects with the lower level of the water table or significant increases in rainfall occur, these areas will become arid. Therefore, this type of landscape would have been attractive to hominins and other faunas as long as surface water remained available.

Landscapes altered by small-scale tectonic activity (ca. 10–25 km) Tectonically active areas are where faulting activity creates characteristic landscape features, including steep, rocky escarpments, disruption of water flow where rivers intersect with the faulting, and finally, sedimentation into fertile valleys (see also Bailey et al., 2011). Such features will remain present as long as fault motion persists (regardless of magnitude or frequency). If faults become inactive, or quiescent, erosion becomes the predominant geomorphological process. Then uplifted areas are liable to erode, subsided regions fill with sediment, which flattens the landscape topography. Additionally, the water table drops and surface water becomes scarcer. However, continued tectonic activity rejuvenates these favorable conditions of sediment and water supply in down-dropped regions (Fig. 1c).

We examine two wetland ecosystems, namely the Okavango Delta (Botswana) and the Nylsvley wetland (Limpopo Province, South Africa) to demonstrate the effect of tectonics on modern drainage and surrounding ecosystems (Fig. 1c). Our examples are hosted in differing geological areas and climatic regimes (Fig. 2),

but the similarity between them is that they are both riverine landscapes where surface water has been disturbed by fault activity (Fig. 3). As a result, they both possess habitat heterogeneity with high biodiversity of plants, reptiles, and mammals. Our purpose for highlighting the existence of known faults and features such as down-dropped, sedimented plains and wetlands is to show that the faults in these regions are active. The interpretation of the landscape and the presence of the suite of features is geomorphological evidence that fault motions are occurring.

Whereas the two other models previously discussed (pan and rivers) are observations of characteristics of a landscape (i.e., 'there was a river close by'), we concentrate on geomorphological processes which sustain these habitats through time and provide a different interpretation to the origins of the 'mosaic environments' which are commonly inferred for hominin site habitats. This is an important distinction, as the Tectonic Landscape Model acknowledges the dynamic nature of the landscape and considers the processes acting on the landscape features, which can be identified, studied, and whose effects can be predicted within a broad framework.

Confounding factors

How can ancient landscapes be accurately reconstructed? For the Middle Awash sites, but also more generally in the eastern African region, the area in which hominins were living would have been closer to the active African Rift floor (King and Bailey, 2006; Bailey et al., 2011). Faunal analysis from the Middle Awash sites indicates that present site conditions are very different from those when hominins were present (Table 1). Sites have steadily been uplifted and moved away from the Rift axis over the last few millions of years and are now situated at higher elevations and in drier conditions, relative to their original position. Sites now lie in areas where erosional down-cutting is the predominant geological process, and so it is difficult to reconstruct the landscape features of the sites using the features of their present location. Instead, we use an analogy with areas that are presently closer to the active Rift margin (King and Bailey, 2006; Bailey et al., 2011).

Southern African geology and tectonics are quite different from eastern Africa. The South African rocks are metamorphosed and consequently very hard and erosion-resistant. These landscapes tend to maintain vertical cliffs and fissures, instead of becoming rounded and flattened by erosion. The region has only modest levels of tectonic activity and no recent volcanism. However, when infrequent faulting does occur, the landscapes are likely to preserve the diagnostic features of these geomorphological processes which have created them (cliffs, sedimented basins, as are shown in Fig. 1c). We can therefore examine the southern African sites in the context of their present landscapes, using existing features as a base model for how the landscape would have looked during *Australopithecus* occupation of the area.

Is this an artificial pattern created by preferential preservation and intensive prospection? The spatial distribution of hominin and fossil localities across Africa is not random and may partly reflect active exploration aided by political and historical factors and developed infrastructures for prospection. Other possible underlying causes, such as collagen preservation, which could influence bone preservation and indirectly site patterning in Africa have been examined (Holmes et al., 2005). The Holmes study utilized a predictive model of African sites as a function of temperature and bone collagen degradation and compared this to an exhaustive database of cave and open localities in all areas of Africa. No significant difference between preservation in caves versus open sites was found, nor do site distributions follow the

Table 1

Middle Awash Valley paleoenvironmental reconstructions for several genera and species of hominins, dating from 5.77–0.15 Ma.

| Locality | Species | Age | Vegetation and topographic reconstruction for locality | Type of data and reference |
|-------------------------------------|-------------------------------------|---------------|--|---|
| Sangatole and Asa Koma Members | <i>Ardipithecus ramidus kadabba</i> | 5.54–5.77 Ma | “Predominantly wet and closed woodland/forest” combined with “wooded grasslands around lake margins” | Macro-, micromammalian taxa (WoldeGabriel et al., 2001: 177), (Haile-Selassie, 2001) |
| Aramis Locality | <i>Ardipithecus ramidus</i> | 4.4 Ma | Wooded habitats, within a “Flat plain, with little topography” | Sedimentological, botanical and faunal data (WoldeGabriel et al., 1994: 332) |
| Sangatole Formation | <i>Australopithecus anamensis</i> | 4.1–4.2 Ma | Closed to grassy woodland | Macro-, micromammalian taxa (White et al., 2006) |
| Maka | <i>Australopithecus afarensis</i> | 3.4 Ma | “Ecologically intermediate between...open, dry...and the more closed, mesic” conditions | (White et al., 1993: 263) |
| Bouri Formation, Hata Member | <i>Australopithecus garhi</i> | 2.5 Ma | Open, lake margin habitat | Faunal and sedimentological data (De Heinzelin et al., 1999) |
| Bouri Formation, Daka Member | <i>Homo erectus</i> | ~1.0 Ma | “Widespread open grassland habitats...(a)djacent water-margin habitats” | Faunal data (Asfaw et al., 2002: 317) |
| Upper Bodo Beds | ‘archaic’ <i>Homo sapiens</i> | 0.64 Ma | Fluvial deposits, with combination of aquatic, grazing and browsing taxa represented | Sedimentology, macromammalian species list (Conroy et al., 1978), (Kalb et al., 1982a,b:26) |
| Bouri Formation, Upper Herto Member | <i>Homo sapiens</i> | 0.16–0.154 Ma | “Proximity of both aquatic and grassland habitats” and “margin of freshwater lake” | Macro-, micromammalian taxa (White et al., 2003), (Clark et al., 2003:750, 751) |

predictive collagen degradation model. Instead, hominin site distribution “is not a reflection of bias in excavation history, but is a real phenomenon reflecting hominin habitat choice” (Holmes et al., 2005:157).

King and Bailey (2006) suggest that a potential landscape pattern underlies this habitat choice (Fig. 4). Specifically, hominin sites are more common in areas of tectonically active landscapes relative to inactive regions (King and Bailey, 2006; Bailey et al., 2011). There are exceptions to this observed pattern: there are regions with rough topography and active tectonics that lack early hominin sites (no *Australopithecus* species from North Africa, for instance) and there are hominin sites in regions of apparently smooth topography with little or no presently known tectonic activity (e.g., *Australopithecus bahrelghazali* from Chad). Other

regions have few sites, but this probably reflects lack of exploration, notably in the western Rift, along parts of the West African littoral, and in the central Sahara. The reverse is also true; there are other areas which have been intensively explored and that preserve abundant cave assemblages containing mammal species common to the rest of Africa, but that do not contain hominin species geologically older than *Homo erectus* (e.g., Ahl al Oughlam, Morocco; Geraads, 1997). We accept that the fossil hominin record is incomplete and so confine our investigations to regions where sizeable samples of *Australopithecus* have been found. Our aim is not to speculate on the potential gaps in the fossil record but rather to examine regions where they have been preserved (where hominins were definitely, not only hypothetically, present) and treat these locations as indicative of a real pattern of hominin habitat choice.

Were sites good *Australopithecus* habitats? Various taphonomic factors affect the preservation of carcasses, and these agents vary between regions. The dearth of *A. afarensis* at Laetoli (Tanzania) relative to other, hominin-rich assemblages, as at Hadar (Ethiopia), is explained as due to preferential deletion by carnivore destruction of hominin carcasses and other mammals of similar body mass (Su and Harrison, 2008). Our focus remains on the regions where evidence of hominin presence has been recovered, even though such gaps exist. However, where hominins died and were discovered within the site catchment areas of the fossil sites, their presence in these areas is necessarily implied. We infer that hominins used the surrounding habitats as part of their normal foraging regions.

How do climatic shifts and time-averaging affect habitat signals in the fossil record? Climatic shifts over the Plio-Pleistocene had profound influence on mammalian species evolution, range changes, extinction, and adaptation (e.g., Reynolds, 2007). There are numerous studies suggesting correlations between orbital forcing, large-scale tectonic uplift, and paleoenvironmental datasets in Africa (e.g., Vrba et al., 1995; Sepulchre et al., 2006; Maslin and Christensen, 2007). According to such studies, areas inhabited by hominins would have become increasingly drier, colder, and grassland-dominated beginning in the Miocene and continuing into the Pliocene (Cerling, 1992; Cerling et al., 1997; deMenocal, 1995, 2004; deMenocal and Bloemendal, 1995; Denton, 1999). In particular, for the temporal period of the genus *Australopithecus*, the presence of grassland and savanna vegetation appears to have been well-established in southern Africa (e.g., Hopley et al., 2006).

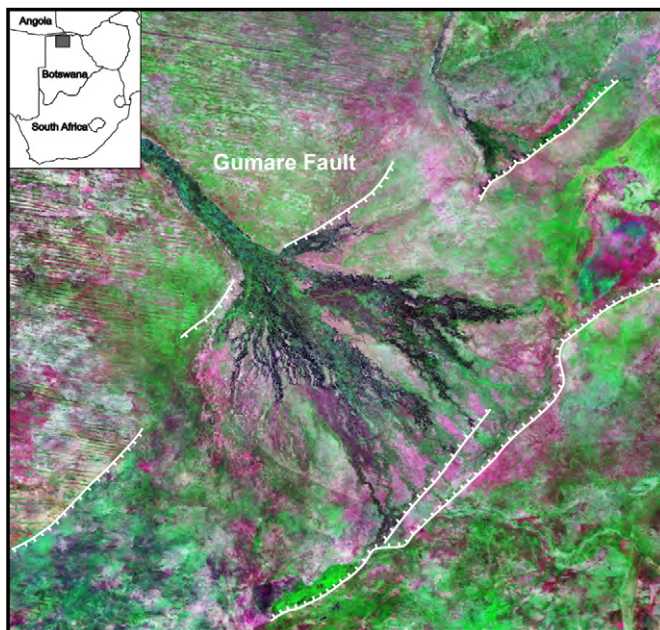


Figure 3. Landsat image of the Okavango Delta (Botswana). The Gumare Fault is indicated, which intersects with the Okavango River and causes the wetland region in the down-dropped flank of the normal fault. Reverse faulting bounds this basin and prevents sediment and water from escaping from the basin.

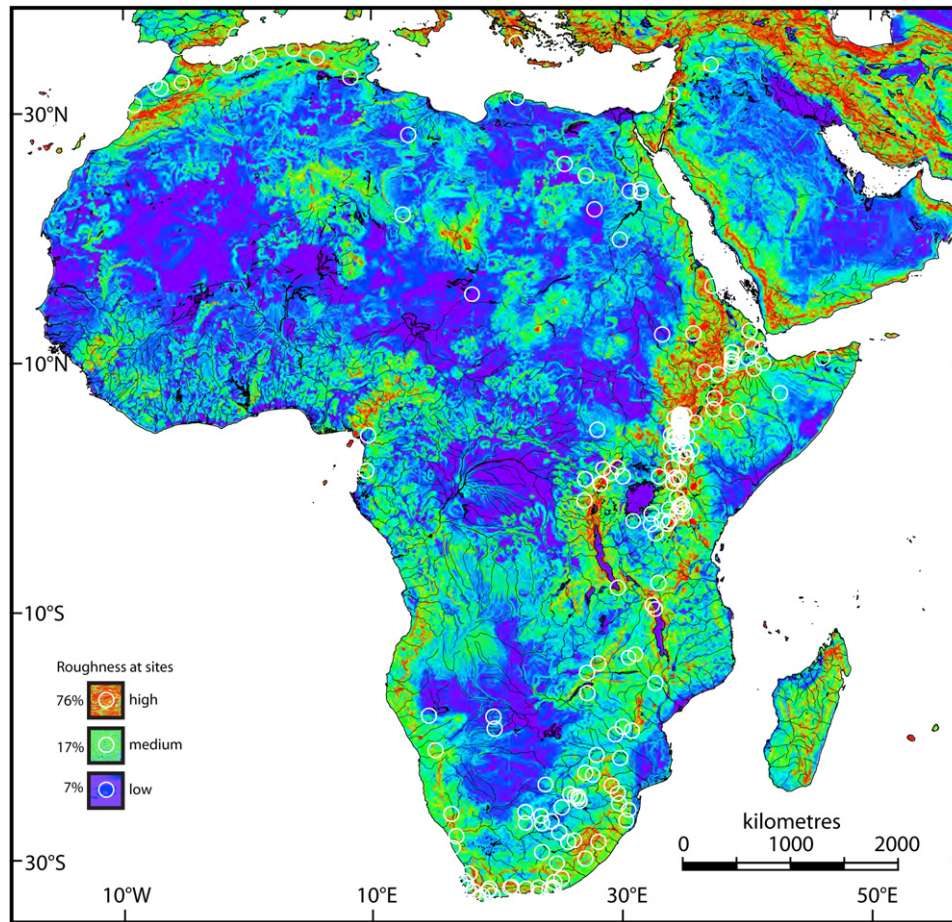


Figure 4. Regions characterized by tectonic roughness, as explained in Bailey et al. (2011), and the location of early hominin sites appear closely correlated.

Unfortunately, purely environmental signals can be complicated both by time-averaging and climate-averaging in the fossil record, especially from depositionally-complex karstic deposits, such as at the *Australopithecus*-bearing Sterkfontein Member 4 deposit (O'Regan and Reynolds, 2009; Hopley and Maslin, 2010).

The deposits may therefore contain fossil fauna and other paleoenvironmental indicators of a range of environmental conditions, as has been proposed by Bonnefille et al. (2004) for eastern African sites. However, differentiating between scenarios of time-averaging of a range of environmental conditions versus a stable, mosaic environment rests instead on the identification of landscape features around the sites in question, rather than simply the evidence contained *within* the deposits. Of the three landscape models, two showing flatter topography and one landscape which shows topographic variability due to tectonic fault motions (Fig. 1), only the Tectonic Landscape Model addresses the underlying geomorphological processes which create a signature suite of landscape features, including cliffs, sedimented plains, and wetlands. The identification of such features and the re-interpretation of existing faunal and floral evidence are illustrated in our case studies.

How does the Tectonic Landscape Model apply to other sites not discussed here? Although *Australopithecus* specimens are known from several other important site regions, such as Laetoli (Tanzania) and Koro Toro (Chad), we here confine our landscape reconstructions only to regions where we have observed the landscape features in the field. However, the implications of habitat creation in tectonically-altered landscapes can be more widely

applied and the tectonic model tested against other fossil landscapes from different regions (e.g., Dmanisi, Georgia, or North Africa). Our goal here is to highlight the relation between tectonics, volcanism, and the creation of habitats which would be attractive to hominins.

Elsewhere we have proposed that hominin sites in eastern Africa would have looked very different and far closer to the active African rift floor during the time that hominins were living there (King and Bailey, 2006; Bailey et al., 2011). We suggest that this hypothesis could be tested by reviewing a range of habitat reconstructions based on fossil and living faunal and floral material and reinterpreting these in the light of the tectonic landscape model. For example, reconstructions of paleoenvironments for Laetoli, northern Tanzania (e.g., Kingston and Harrison, 2007; Andrews and Bamford, 2008) offer excellent opportunities to attempt to correlate the types of flora and fauna recovered there with the landscape features as they may have been when the material was deposited. While we have not undertaken fieldwork in this region, some landscape features discussed can be interpreted in the light of the Tectonic Landscape Model. These deposits span the period from approximately 4–2.0 Ma, while the site itself is unusual in that it is not directly associated with a lake or river setting (i.e., as in our Fig. 1a). The Laetoli fauna include the giraffids, an obligate browsing group, as well as grazers such as equids, but the remaining herbivore fauna indicate mixed C₃/C₄ feeding behaviors (Kingston and Harrison, 2007). Herbivore stable isotopes from the site give insights into the type of environments that *A. afarensis* would have had access to: “heterogeneous vegetation, that probably included

grasslands, open woodlands, more closed woodlands, and possibly forest” (Kingston and Harrison, 2007:286).

The site is associated with large-scale rifting, being located on the western side of a central graben which hosts Lake Eyasi today (illustrated in Fig. 1 in Kingston and Harrison, 2007). The site is on the uplifted Eyasi Plateau, and it is the erosion of the uplifted sediments which is causing the surface exposure of the fossils, over an approximate area of 100 km². The absence of river or lacustrine environments, combined with the full spectrum of grazers, mixed feeders, and browsers suggests that there must have been sufficient surface moisture to support obligate drinkers, especially grazing mammal species. We therefore hypothesize that small-scale rifting in and around the region may have disrupted surface drainage during site formation, thus enabling a range of mosaic habitats to emerge, without obvious signs of river or lake presence.

Methods

Statistical comparison of site types in South Africa and Ethiopia

As we examine fossil site regions in South Africa and Ethiopia, we confine our statistical comparisons to sites found in these two countries (but see Holmes et al. (2005) for a pan-African study of site preservation). An extensive dataset of site localities from the Miocene to the present is used ($n = 320$), grouped into seven categories: 1) fauna (non-hominin) only; 2) hominins only; 3) lithic artifacts only; 4) lithic artifacts and hominins; 5) hominins, lithic artifacts, and fauna; 6) lithic artifacts and non-hominin fauna, and finally 7) hominins and other fauna (Table 2). These data derive primarily from two databases: the Paleobiology database (www.paleodb.org) and the database created by Holmes et al. (2005), available on the Arts and Humanities Research website (<http://ads.ahds.ac.uk/catalogue/>). Additional literature sources were also used (Berger and Brink, n.d.; McBrearty and Brooks, 2000; Partridge and Maud, 2000; d’Errico and Backwell, 2005).

In particular, we addressed two questions using this statistical analysis: first, do the distributions of categories differ between Ethiopia and South Africa (i.e., are the proportions of the site categories broadly similar between regions)? Secondly, are there regions where certain types of sites predominate? In other words, could preservation biases create the pattern of site categories observed in the fossil record? Statistical comparisons of different site categories were performed using PAST software (Hammer et al., 2001). When we compared all categories of sites in Ethiopia to those in South Africa, we found that the category distributions do not significantly differ (Table 2; Mann–Whitney U test, $p > 0.05$). The numbers of each site category were then tested separately between the Ethiopian and South African samples (as 2×2 tables), using the Chi-Square test of association. The category of lithic artifacts and hominins was excluded from further analysis, since there are zero cases in both groups. We are able to establish that there are no significant differences between the number of faunal only assemblages (i.e., non-hominin-bearing) in Ethiopia and South Africa ($\chi^2 p > 0.05$; Table 3). If we take this category of site as a general proxy for preservation, then there is no significant

difference in the preservation potential between Ethiopia and South Africa. In contrast, isolated finds of hominin fossils are rare in both regions ($\chi^2 p > 0.05$; Table 3). The majority of site categories show differences between countries, but the reasons for the differences are discernable. Theoretically, stone tool survivorship should be higher than that of more easily eroded bone (Holmes et al., 2005). While this may be the case, the number of known lithic artifact scatters and lithic-related assemblages nevertheless shows significant differences between regions. Although the oldest lithic tools are known from Ethiopia (approximately 2.5 Ma), there are more Middle Stone (MSA) and Later Stone Age (LSA) shelters and coastal long-occupation sites known from South Africa (Sibudu Cave, Blombos Cave, and Klasies River, among others) relative to Ethiopia ($\chi^2 p > 0.001$; Table 3). Lithic artifact recovery is possibly affected by the predominantly erosional and destructive processes of the active Africa Rift, relative to the quiescence of South African cave shelters. For the site category of hominins, fauna, and lithic artifacts, South Africa contains significantly more of these types of sites than does Ethiopia ($\chi^2 p > 0.01$; Table 3). This could reflect the abundance of MSA and LSA shelters in South Africa, as mentioned previously, but could also be related to the depositional environments within karstic caves that would tend to preserve lithic, faunal, and hominin material together.

The category of hominins and fauna together shows very highly significant differences ($\chi^2 p > 0.001$) between Ethiopia and South Africa (Tables 2 and 3). For this type of site, the many localities of early, pre-stone tool using localities from the Middle and Lower Awash regions far exceeds the number of australopithecine sites known in southern Africa. Cave deposits in South Africa generally begin accumulating at approximately 3.3 Ma, with no known older hominin fossil record at present. In contrast, the Ethiopian sites date from closer to 4.4 Ma and younger (Table 1), and this longer fossil record is a likely reason for the marked disparity between regions for this category.

No significant difference between the number of fauna-only sites in South Africa and Ethiopia suggests that preservation is not a potential biasing factor, and this result is in agreement with those reported by Holmes et al. (2005). However, there are significantly more sites with hominins and fauna in Ethiopia, which may reflect the present predominantly erosional regimes in the Middle Awash region. While total numbers of sites with and without hominins in both regions suggest that there is no differential hominin preservation, the influence of active prospecting cannot be eliminated as a possible source of bias.

Reconstruction of site landscape features in South Africa and Ethiopia

We reconstruct the Makapan and Taung hominin sites in southern Africa based on satellite imaging techniques and on-site observations of these regions. We combine high resolution satellite images (Landsat ETM + and Shuttle Radar Topographic Mission: SRTM-3), which are draped on vertically exaggerated digital topography to study the landscape features. A fuller account of this method is provided in an accompanying paper (Bailey et al., 2011).

Table 2

The sample of 320 sites is divided according to seven site categories, but the category 'lithic artifacts and hominins' is not subjected to further analysis^a

| Country | Total sites | Fauna only | Hominins only | Lithic artifacts only | Lithic artifacts and hominins | Hominins, lithic artifacts, and fauna | Lithic artifacts and fauna | Hominins and fauna |
|--------------|-------------|------------|---------------|-----------------------|-------------------------------|---------------------------------------|----------------------------|--------------------|
| Ethiopia | 145 | 47 | 9 | 4 | 0 | 9 | 8 | 68 |
| South Africa | 175 | 61 | 4 | 25 | 0 | 28 | 38 | 19 |
| Totals | 320 | 108 | 13 | 29 | 0 | 37 | 46 | 87 |

^a Mann–Whitney U test of the distributions of site categories in Ethiopia and South Africa indicates no significant difference ($p > 0.05$).

Table 3
Site categories and numbers of incidences recorded for Ethiopia and South Africa^a

| Assemblage category | Country | n | χ^2 p-value |
|---------------------------------------|--------------|-----|-------------------|
| Fauna only | Ethiopia | 47 | $p > 0.05$ (n.s.) |
| | South Africa | 61 | |
| | Total | 108 | |
| Hominins only | Ethiopia | 9 | $p > 0.05$ (n.s.) |
| | South Africa | 4 | |
| | Total | 13 | |
| Lithic artifacts only | Ethiopia | 4 | $p < 0.001$ |
| | South Africa | 25 | |
| | Total | 29 | |
| Lithic artifacts, hominins, and fauna | Ethiopia | 9 | $p < 0.01$ |
| | South Africa | 28 | |
| | Total | 37 | |
| Lithic artifacts and fauna only | Ethiopia | 8 | $p < 0.0001$ |
| | South Africa | 38 | |
| | Total | 46 | |
| Hominins and fauna | Ethiopia | 68 | $p < 0.001$ |
| | South Africa | 19 | |
| | Total | 87 | |

^a The Chi-squared test of association p-value is also indicated.

For the Ethiopian sites, we employ a similar technique, but use the landscape features of an analog region nearer the active Rift margin (Fig. 5). This analog site should be representative of typical landscape features in this region.

Results

Before presenting the fossil landscape interpretations, we discuss two important facets of tectonic influence on a given landscape. The first is the influence of the faulting on the surface water and the formation of wetlands, which is illustrated by two modern tectonically-controlled wetlands. Second, since we suggest that *Australopithecus* was attracted to tectonically active environments, we examine three species of mammals that utilize habitats likewise modified by volcanism and faulting. These species, the extinct reedbeak (*Redunca darti*), the klipspringer (*Oreotragus oreotragus*), and the gelada (*Theropithecus gelada*), use certain features modified by the geomorphological processes we discuss.

Modern wetlands

The Okavango Delta in Botswana is an extensive inland wetland habitat (28,000 km²) in an area of semi-desert and arid conditions in the Kalahari Desert. Whilst it is not a region where hominin fossils are recovered, the faulting in this region has a dramatic influence on the landscape features and facilitates the existence of a high biodiversity of plants, invertebrates, birds, fish, and mammals (Ramberg et al., 2006). Climatic variations and seasonal flooding have led to the creation of several different habitat types, namely perennial and seasonal swamps, flooded grasslands, and drylands, which together support approximately 122 mammal species, 444 species of birds, and 1078 plant species (including aquatic, semi-aquatic, and non-aquatic plant species; see Ramberg et al. [2006] for a detailed review). The area around the delta and much of southern Africa falls into the modern climatic category of 'semi-desert,' with an average annual rainfall of between 250–500 mm (Fig. 2). The Okavango (also spelled Kavango) River originates in the central Angolan highlands and flows south into the Kalahari Basin. In the northern reaches of Botswana, the river course is altered by a series of tectonic faults, which are inferred to be south-westward extensions of the East African Rift system. The upper reaches of the river are controlled by two lateral faults

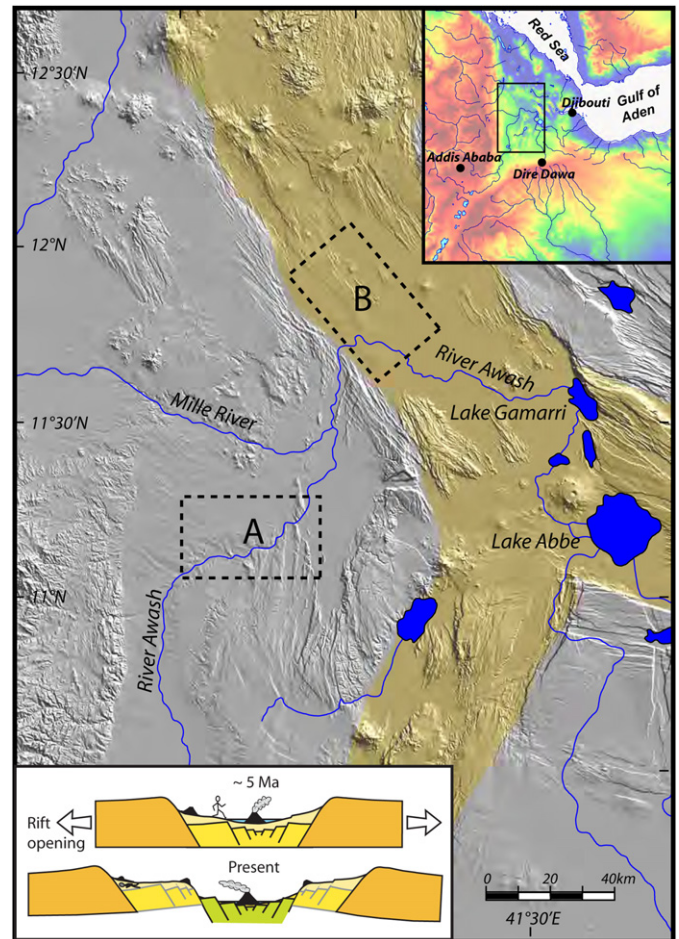


Figure 5. The Afar region of Ethiopia, where the locations of the fossil sites of the Middle Awash river are indicated in the lower rectangle, and the region chosen as our analog region is in the second rectangle lying closer to the present active Rift margin (after Bailey et al., 2011).

(forming a graben, or rift valley) which, although present, simply channel the river, but do not disrupt the drainage. However, when the river is intersected by the Gumare (or Gomare) Fault (shown in Fig. 3), the down-dropped section becomes the flooded, sedimented plain which creates the wetland. Further smaller faults are also indicated in the region (McCarthy and Hancox, 2000). The delta is a sedimented basin with the Gumare (normal) Fault down-dropping the sediment into the basin, but there are several smaller reverse faults (or alternatively, rising footwalls of normal faults) that uplift and bound the basin, thus trapping the sediment and water and preventing it from being eroded or drained away (Fig. 3). If this fault activity were absent, the delta would probably look like other late-stage meandering rivers, as indicated in the riverine landscape scenario (Fig. 1b). In that case, it would support a variety of gallery forest species and aquatic faunas, but not to the extent that it does today. It is the tectonically-altered nature of the river that has created, and which sustains, this wetland. Although smaller than the Okovango Delta, the 240 km² Nylsvley wetland in the semi-arid region of the Limpopo province of South Africa is considered a 'Wetland of International Importance,' (Fig. 2; Havenga et al., 2007). The ecosystem possesses very high levels of avifaunal biodiversity, hosting a total of 420 bird species, of which 102 are waterbird species. Mammals are represented by 70 species, and reptile, fish, and insect diversity is also very high. There are two main dominant plant species in the broad-leaved savanna: the wild

seringa tree species (*Burkea africana*) and the broom grass (*Eragrostis pallens*; Laio et al., 2001).

This wetland is fed by the Nyl River, which has its headwaters in the Waterberg mountain range, at approximately 1500 m elevation (Tooth and McCarthy, 2007). The Nylsvley wetland is also tectonically-controlled (McCarthy and Hancox, 2000) by several smaller normal faults that control the flooding. The Nylsvley wetland is also very close to the Makapan Valley and the fossil site of Makapansgat Limeworks, as discussed below.

The biodiversity of mammal, avifauna, and reptile species in these wetland areas is considerably enhanced by the action of the small-scale faulting that creates the potential for a more diverse range of habitats. Several species of mammals and invertebrates are almost exclusively found in such wetland habitats, including mole rats (*Cryptomys hottentotus*), the clawless otter (*Aonyx capensis*), and the marsh mongoose (*Atilax paludinosus*). The Okavango Delta supports a high biomass of large grazing mammal species, including the African elephant (*Loxodonta africana*), the Plains zebra (*Equus burchellii*), the hippopotamus (*Hippopotamus amphibius*), and the giraffe (*Giraffa camelopardalis*; Ramberg et al., 2006).

Swampy areas and sedimented plains are not the only features that can be created by small-scale tectonics. The presence of

associated features, such as cliffs, river terraces, and river gorges can also be used to identify fault activity, although these features are not present in our Okavango wetland example (Fig. 1c). Our emphasis is therefore on the geomorphology of the landscape as a whole, rather than the presence or absence of isolated features. Taken together, tectonically-altered landscapes can create rough topography and habitat heterogeneity, two features that may have been attractive to hominins. Although the exact diet of *Australopithecus* is unknown, stable carbon isotope studies from Sterkfontein Member 4 indicate a mix of C₃ and C₄ food sources were consumed (van der Merwe et al., 2003).

Modern non-hominin faunal habitat and landscape preferences

Fauna are important indicators of paleoenvironmental conditions at hominin sites (e.g., Plummer and Bishop, 1994; Kappelman et al., 1997; Bishop, 1999; Sponheimer et al., 1999). The relationships between species and their habitats (as indicated by stable carbon isotopes or ecomorphological signals) are used to reconstruct aspects of the vegetation, but here we examine whether or not species can be related to different types of landscape features.

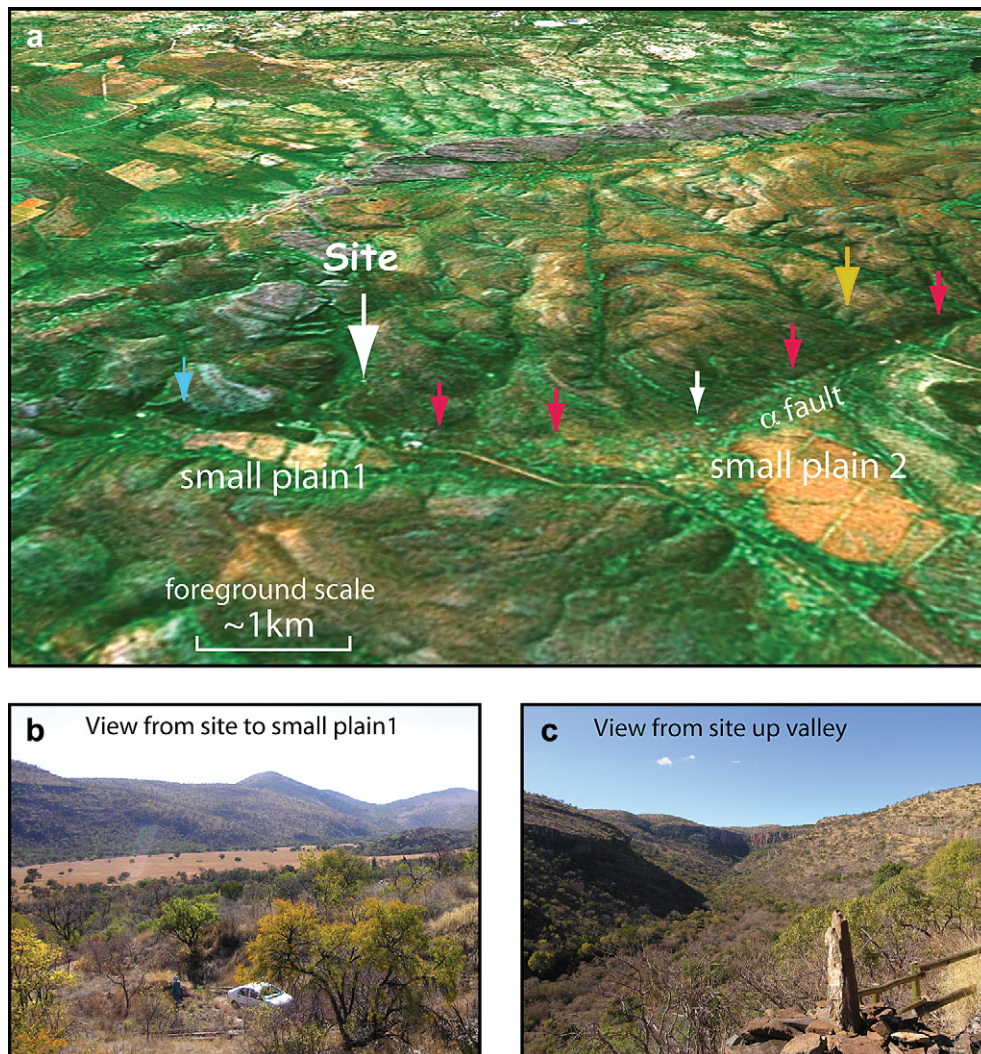


Figure 6. Region around the Makapan Valley, Northern Province, South Africa. Landsat images draped over the exaggerated digital elevation data indicate topographic roughness (see Bailey et al. [2011] for more detail on this method). Around the site is a suite of landscape features including the presence of rocky cliffs, sedimented plains, and marshy areas, specifically the Nylsvley wetland.

Extant mammals exploit the landscapes of their habitats in specific ways. The klipspringer (*O. oreotragus*) is a small antelope that inhabits rocky outcrops across a wide geographic range in sub-Saharan Africa. It occurs in regions of high and low elevation, and in areas of both high and low rainfall (Estes, 1991). In eastern Africa, the modern klipspringer is closely associated with lava flows and craters, while it is common on the rough cliffs and river gorges of southern Africa. Although mostly confined to rocky shelters, the klipspringer will travel short distances (500 m) to graze.

The fossil klipspringer is common in southern African sites but not in the eastern African fossil record. Where present, this genus is inferred to indicate rocky outcrops (e.g., Reed, 1996). It is known from Makapansgat, and within the Cradle of Humankind at

Gladysvale (Berger et al., 1993), Drimolen (Keyser et al., 2000), Sterkfontein, Swartkrans, and Haasgat (Watson, 2004). The modern habitat distribution of the klipspringer is a good faunal proxy for areas of rough topography in eastern and southern Africa, as defined in Bailey et al. (2011).

The extant gelada (*T. gelada*) has a small geographic range compared to that exploited by extinct members of this genus. It inhabits high grassland plateaus between 1800–4400 m above sea level, which are created by the uplifting of the flanks of the Rift Valley in Ethiopia (Gippoliti and Hunter, 2008). The extent of the modern range of this species is affected by the tectonic movement and spreading of the Rift Valley. The gelada use steep cliffs of this landscape as sleeping roosts and troops stay within 2 km of the escarpments for safety (Gippoliti and Hunter, 2008).

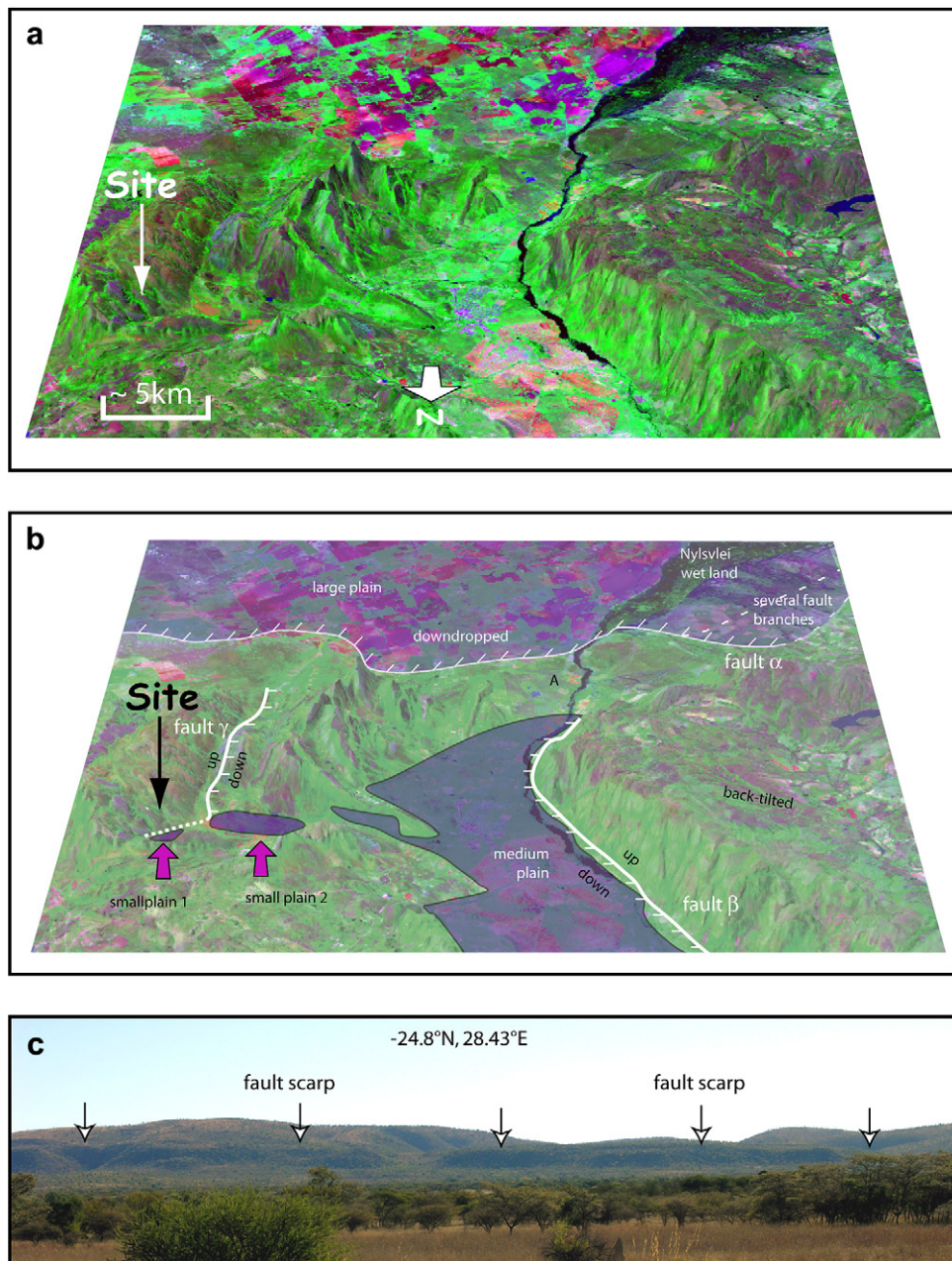


Figure 7. A: Closer view of the topography of the Makapan Valley sites, showing the combination of low lying sedimented plains and rocky cliffs in close proximity. B shows the interpreted landscape features (after Bailey et al., 2011).

Although the modern gelada range does not extend into southern Africa, fossil species of *Theropithecus* are abundant in the Plio-Pleistocene sites of South Africa. Two species occur: *Theropithecus darti* is known from the Makapansgat site, dating from 3.0 Ma, and in the Sterkfontein Valley, the larger-sized, more terrestrial, grassland-adapted species, *Theropithecus oswaldi* is known from deposits of approximately 1.7–1.5 Ma (Kuman and Clarke, 2000). *T. darti* is common from Makapansgat Member 2, 3, and 4, as well as from Hadar in Ethiopia (Reed, 1996). It is plausible that the extinct relatives of the gelada may have used the landscape features in similar ways, for security and places to roost. The presence of these species may therefore indicate the existence of similar landscape features during deposition of the fossil record.

The extinct reedbuck (*R. darti*) is abundant in the Makapansgat Limeworks deposit, which suggests the close proximity of water and wetlands, since extant members of the Reduncini are closely associated with such habitats (Reed, 1996, 1997). The association of *R. darti* with wetland habitats has been confirmed by stable carbon isotope studies (Sponheimer et al., 1999).

These three genera indicate the possible presence of features (wetlands, fault scarps, cliffs, and lava flows) associated with tectonically-controlled environments. We turn our attention to the landscape reconstructions of fossil sites and the possible faunal indicators that suggest these sites were affected by faulting and/or volcanism during the time that they were inhabited by *Australopithecus*.

Southern African landscapes

The Makapan valley Excavation for the Makapansgat Limeworks caves (Northern Province, South Africa) commenced in 1946, and Members 3 and 4 yielded a sample of 27 hominin specimens (Fig. 2). These *A. africanus* specimens represent a minimum number of ten individuals, and the dates for these deposits are between 3.2 and 2.7 Ma (Reed, 1997; Tobias, 2000). For this time period, reconstructions of the habitats for the site have been variously reconstructed as woodland, or dense forest (Vrba, 1982; Cadman and Rayner, 1989), or possibly representing a mosaic habitat of woodland and grassland, or open savannah woodland habitats (Wells and Cooke, 1956; Reed, 1997). Although other younger fossil-bearing caves are present in this valley, such as the Buffalo Cave and the Cave of Hearths, our emphasis is only on the *Australopithecus*-bearing members and their habitat reconstructions.

The geomorphology of the Makapan Valley region and the cave sites is shown in Figs. 6 and 7. This plain hosts the tectonically-controlled Nylsvley wetland, as discussed earlier (Wagner, 1927; McCarthy and Hancox, 2000). The river Nyl runs close to its base, a feature that could indicate continued activity or which may simply be the result of sediment that reaches the valley from sources predominantly to the east (left), pushing the river course to the west (Bailey et al., 2011). The present habitat conditions resemble the previous habitat reconstructions proposed for Members 3 and 4 (Reed, 1997; Sponheimer and Lee-Thorp, 1999). The high diversity of fossil species (McKee, 1999) may indicate that the full range of proposed habitats could have been present simultaneously during Member 3/Member 4 times. Stable isotope studies of *A. africanus* from Limeworks Cave reveal a significant C₄ (grass and sedge) signal, suggesting these were nearby and relatively easy to exploit (Sponheimer and Lee-Thorp, 1999).

The landscape topography provides a combination of water, food, and safety, which would have been attractive to *Australopithecus*. The river and the sedimentary plains would have offered foraging areas close to the relative safety of the river gorges, caves, and the characteristic cliffs of the Makapan Valley (Figs. 6 and 7a, b). The wider landscape contains plains of varying sizes and wetlands within ranging distance of the valley itself.

Taung rift valley The geomorphology of the Taung Valley region, in the North-West Province of South Africa, and the location of the Buxton Limeworks site are shown as a vertically exaggerated topography onto which a Landsat image is draped (Fig. 8). The type specimen of *A. africanus* was recovered from the lime-mining quarry in 1924, and published by Dart in 1925. Faunal dating suggests an approximate age of between 2.6–2.4 Ma (McKee, 1993; Partridge, 2000). The Taung child was the first and only hominin specimen discovered from this site. Lime-mining activities destroyed large portions of fossil-bearing deposits, and later excavations did not find further hominin material (Partridge, 2000; Tobias, 2000). Although the child's fossil is the only one recovered to date, it is reasonable to assume that it must have formed part of a larger population of *A. africanus* that foraged in the area during the time when the child was killed by a bird of prey, possibly a large African eagle (Berger and Clarke, 1995).

The mining activities may have destroyed the deposits and other fauna which could have provided information on the habitats associated with the Taung Child, but the wider landscape features of the region remain largely unchanged. Our emphasis is on the landscape features around the site, which are still discernable. The Taung valley is currently used for agriculture, and this valley section is the down-dropped plain, between two parallel faults on either side. Essentially, the two faults and the down-dropped plain form a rift valley (also called a graben). As in the other examples, the flanks are uplifted and drier regions, relative to the fertile, wetter section in the centre of the valley (Fig. 8; discussed in Bailey et al., 2011). Two rivers are shown on either flank and both incise into the uplifted sediments. The Thabaseek River runs next to the Taung site, on the uplifted Ghaap escarpment (Partridge, 2000). Agriculture in the valley is now aided by irrigation because the natural water flow has been substantially reduced by the Wentzel and Taung dams upstream. The character is very different from adjacent regions in the same province that lack the advantages of being a former wetland. Despite these recent human modifications to the

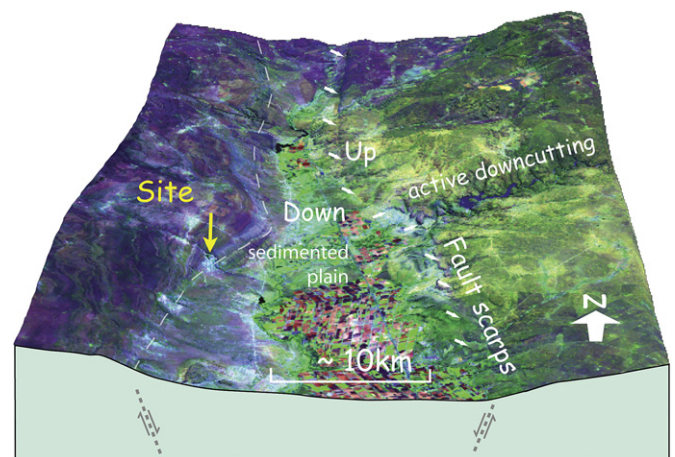


Figure 8. Region around the Taung Valley, North-West Province, South Africa. Landsat images draped over the exaggerated digital elevation data in relation to the site are shown. Two faults on either side of the Taung region create a rift valley (graben) with uplifted, drier flanks on each side and a down-dropped, sedimented plain in the centre. As can be seen in the foreground, this fertile, sedimented plain is today being used for agriculture but has been substantially modified. The river upstream has been dammed (including Wentzel and Taung dams) in several places, reducing the natural supply of water, and there is now irrigation to permit water intensive agriculture in the fertile sediments. Two rivers are shown on either flank, and the river on the right flank is actively cutting down into the uplifted sediments. The Thabaseek River can be seen running next to the Taung site on the uplifted Ghaap escarpment (Partridge, 2000). On each side of the uplifted rift flanks, the rivers experience drainage disturbances when they intersect with the faults.

drainage, the landscape features and mosaic habitats at Taung are similar to those identified at Makapan.

Sterkfontein and the Cradle of Humankind The Sterkfontein Valley contains several sites with gracile australopithecines, but here we focus the discussion on the paleoenvironmental evidence

from the Sterkfontein site itself. The Blaaubank River would have supported several aquatic or amphibious species, such as hippos (*Hippopotamus amphibius*) and crocodiles, as well as a forest fringe along the river. Wetter, riverine environments are indicated by fossil pieces of liana vines in *Australopithecus*-bearing Member 4

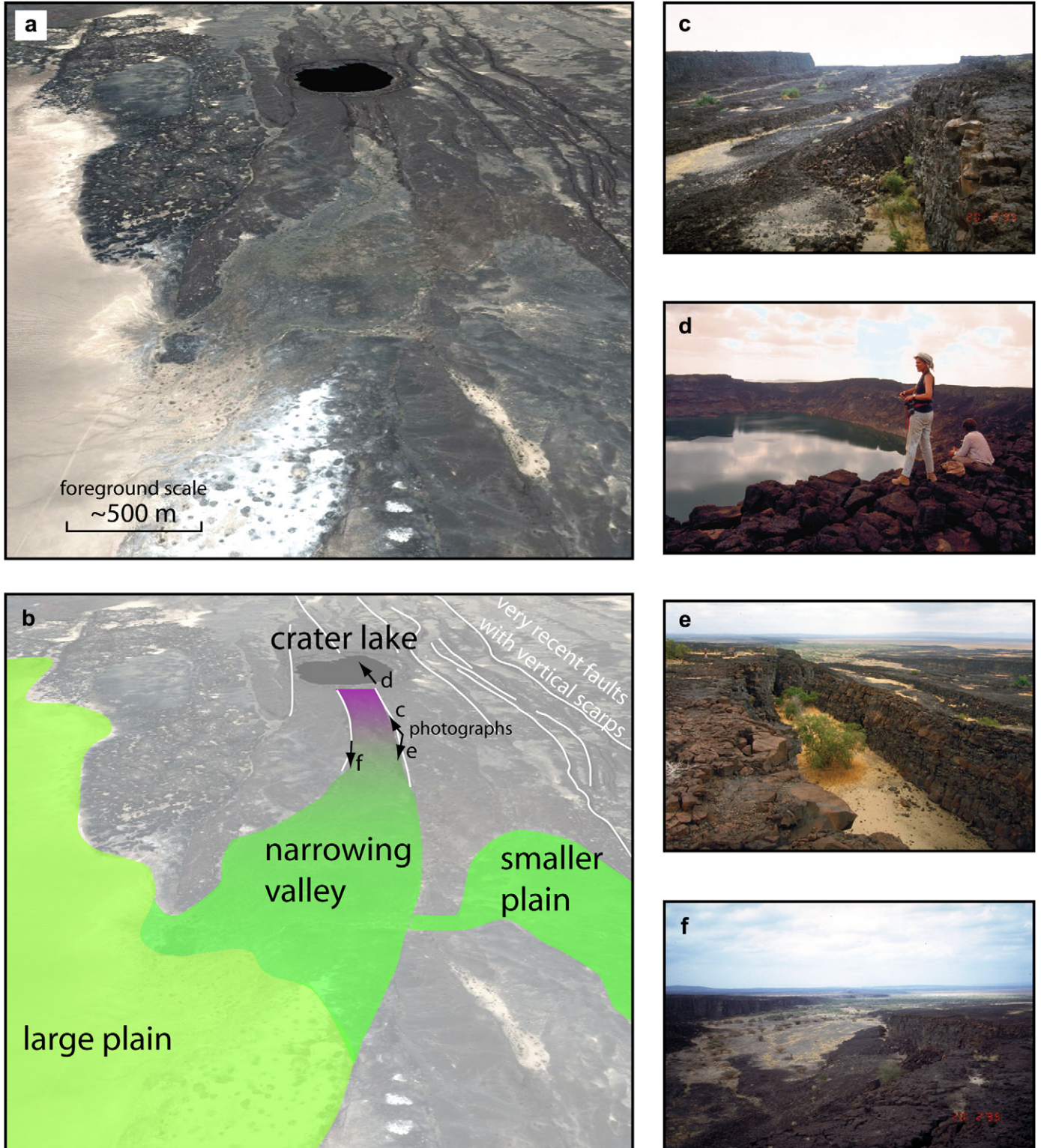


Figure 9. Close up of analog region indicated in black rectangle B in Fig. 5. Various landscape features found in this region include lava flows, fault scarps, and crater lakes, all of which could have been utilized by hominins as part of their habitats.

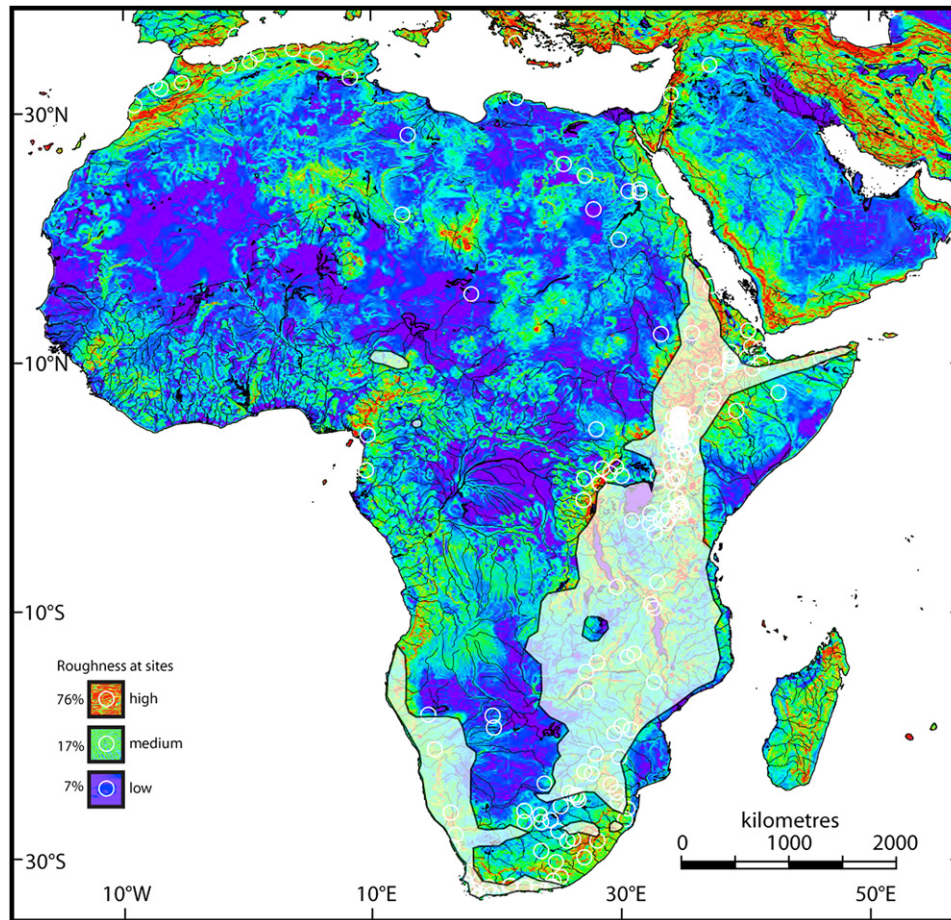


Figure 10. Topographic roughness, as indicated in Fig. 4, but here the lighter areas indicate the present-day habitat of the klipspringer (*Oreotragus oreotragus*). This species prefers rocky outcrops in southern Africa and utilizes lava flows for safety in volcanically active regions (Estes, 1991). In this respect, the present distribution follows the pattern of topographic roughness in Africa proposed in King and Bailey (2006) and Bailey et al. (2011).

(Bamford, 1999), while grassland environments are indicated by certain micromammal species from Sterkfontein Member 4 and Member 5 (see Avery [2001] for a complete discussion). The geomorphological evidence indicates faulting and sedimentation within this riverine environment and is illustrated in-depth in Bailey et al. (2011).

Makapan, Taung, and Sterkfontein site regions share several landscape features: each is set in a riverine landscape, which has been further modified by faulting activity. Although fault scarps are more easily recognized at Makapansgat and Taung, the down-cutting of the river and sedimentation in the Sterkfontein Valley indicate earthquake activity has been responsible for modifying the landscapes (Bailey et al., 2011). All three sites would have contained the heterogeneous wetter, down-dropped fault scarps, combined with drier, uplifted flanks characteristic of the Tectonic Landscape Model (Fig. 1c).

Eastern African site landscapes and analogs with the presently active Rift margin

Middle Awash region, Afar region (Ethiopia) The second region we examine in detail contains the sites along the modern day Awash River in the Afar region of Ethiopia. Various fossil hominin and archeological localities suggest that the landscapes of this region have provided attractive habitats for hominins for millions of years. In particular, the Gona region of Afar has yielded the oldest

stone tools, dating to between 2.6–2.5 Ma (Semaw et al., 1997), as well as a sample of cut-marked bones, suggesting that hominins employing scavenging and butchery behaviors were already present in this region around 2.58–2.1 Ma (de Heinzelin et al., 1999; Dominguez-Rodrigo et al., 2005). Several habitat reconstructions for the sites of this region (Table 1) indicate that a range of vegetation types was probably present during the time of hominin occupation, including swamps, seasonal pans (or ‘playas,’ Partridge and Scott, 2000), and more closed, wooded regions (WoldeGabriel et al., 1994; Semaw et al., 2005). This is similar to habitat reconstructions for Sterkfontein and Makapansgat, suggesting that a range of foraging opportunities would have been available.

The Landsat image of the analog region is draped on digital topography (Fig. 9a), with the important landscape features indicated in Fig. 9b. The important features of this region include a Kurub Volcano lying on the active rift, as well as an annual lake, and wet- and swamp-land. The lighter colored region probably contained a fresh water or slightly brackish lake >6000 years ago, as there is evidence to suggest that the Afar region was more humid in the past (Gasse, 2001). The Gablytu Volcano shows that, in an uneroded landscape, active faults have dissected the volcano and resulted in vertical cliffs, enclosed fertile valleys, and blocky lava flows (King and Bailey, 2006). Together, these features would have offered a measure of cursorial predator refuge for hominins and for other mammal species (Hart, 2007).

Discussion

Similarities between *Australopithecus* landscapes across Africa

Small-scale tectonic processes have created similar, but not identical, suites of landscape features in southern and eastern Africa, specifically a combination of steep uplifted escarpments and down-dropped, sedimented fertile plains (Fig. 1c; Table 4). The volcanism in eastern Africa further modifies the geomorphology of the region, creating different types of landscape features, such as blocky lava flows and crater lakes, but these would have presented similar habitat opportunities for the hominins to exploit. In the case of other faunas, the rocky outcrop dwelling klipspringer (*Oreotragus oreotragus*) is able to use the rocky terrain of southern Africa, as well as the lava flows in eastern Africa interchangeably over its geographic range, as shown in Fig. 10 (Estes, 1991).

A key feature of tectonic activity is the disruption of the river drainage, causing marshes, edaphic grasslands and wetlands. Many of the paleovegetation reconstructions in several regions make mention of such swampy, marshy conditions (e.g., Reed, 1997; McCarthy and Hancox, 2000; Semaw et al., 2005). Although the modern measured levels of tectonic activity are low in southern Africa, they have been enough to preserve and maintain these

landscape features, including the continued disturbed drainage of the present Nyslvley wetland, close to the Makapan Valley.

Tectonic landscapes and hominin diets, limb morphology, and behavior

A number of longstanding problems in paleoanthropology can be reinterpreted in the light of hominin exploitation of variable topography sustained by small-scale tectonic activity. Although we do not suggest that all hominins exploited *only* tectonically-modified landscapes, the application of the TLM may provide new insight into morphological and dietary evidence, deriving from studies of several different hominin genera (*Australopithecus*, *Paranthropus*, and *Homo*). Morphological variability in the *Australopithecus* postcrania has received much study and review, and has been best described as “a strange mélange” of ape-like and human-like traits (Tobias, 1998:51). Habitual bipedalism in hominins appears early and well before the appearance of *Australopithecus*, but highly variable foot bone morphologies identified in fossil specimens led Harcourt-Smith and Aiello (2004) to suggest that there may have been more than one type of bipedalism. The derived morphology of the pelvis, femur, and the metatarsals appears to suggest that the primary adaptation of early hominins is to upright locomotion. Yet, the

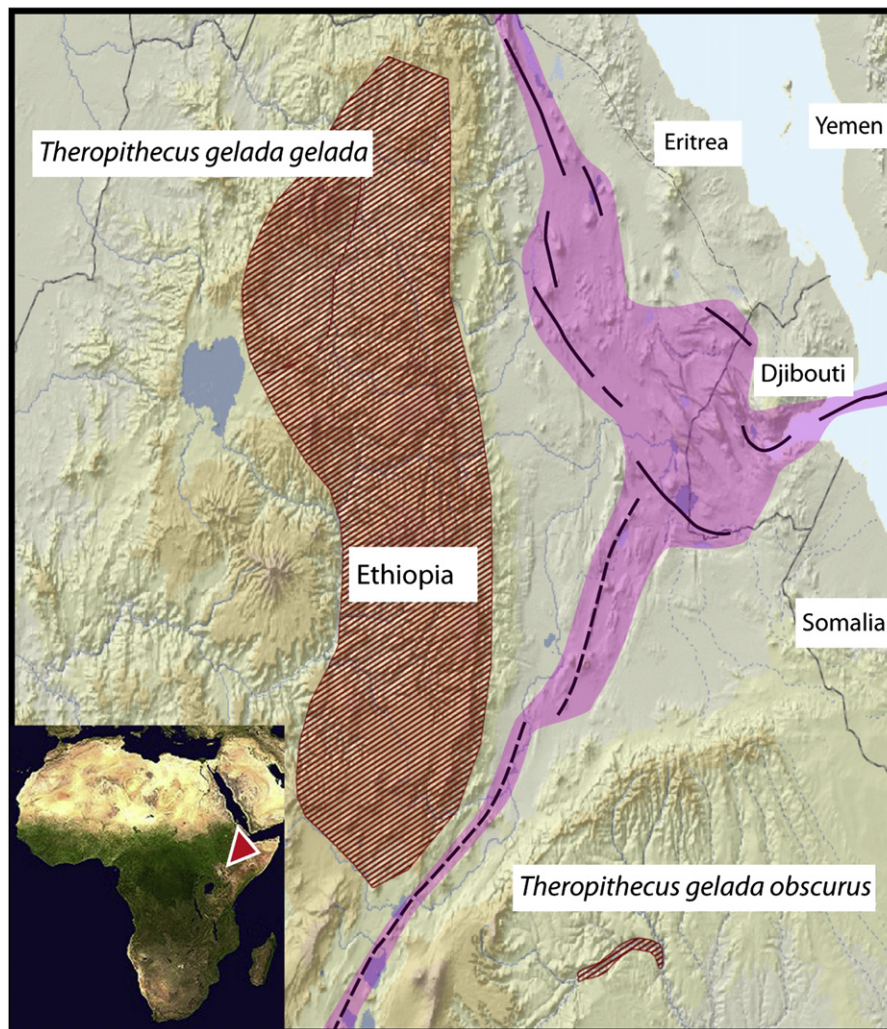


Figure 11. Present range of the gelada baboon (*Theropithecus gelada*) in Ethiopia. Two subspecies are recognised, over a discontinuous region. The Rift has separated these two subspecies, recognised on the basis of mtDNA differences (Belay and Mori, 2006). Base map from IUCN website. Shaded area and lines within this area indicate major active fault structures in the Afar triangle.

retention of traits related to arboreal locomotion such as divergent, prehensile big toes suitable for grasping branches has been noted in australopithecine specimens such as StW 573 from Member 2, Sterkfontein (Clarke and Tobias, 1995; Clarke, 2002). Other authors have noted the remarkable similarities of hominin upper and lower forelimb traits to those of arboreal apes (e.g., Senut, 1980; Drapeau et al., 2005). In particular, Olduvai Gorge Upper Bed II (Tanzania) ulna specimen (OH 36) has been assigned to the presumably grassland-adapted *Paranthropus boisei* by two different studies (Aiello et al., 1999; McHenry et al., 2007), despite its marked similarities to that of chimpanzees (illustrated in Drapeau et al., 2005). More puzzling still is that the Olduvai ulna is very different from *Paranthropus robustus* ulnae from the southern African sites of Swartkrans and Sterkfontein, suggesting high levels of morphological variability within the genus *Paranthropus* (McHenry et al., 2007).

The morphology of hand bones of *Australopithecus* and *Paranthropus* indicates a degree of manual dexterity and the capability for a precision grip (Susman, 1988; Panger et al., 2002; Drapeau et al., 2005). The observed combination of both well-adapted arboreal and bipedal features in hominins has provoked much debate (reviewed in Stern, 2000) and has been argued by some researchers to suggest that tree climbing was still an important part of the hominin locomotory repertoire (e.g., Clarke, 2002). The tectonically-altered landscape model suggests an alternative explanation for this pattern. We propose that effective exploitation of tectonically-altered environments would have required both well-developed climbing (hill and rock climbing) and walking abilities, as well as a certain degree of manual dexterity to negotiate barriers (such as steep, rocky cliffs or blocky lava flows) which predators would find more difficult, but not impossible, to negotiate. Such climbing abilities may have enabled hominins to find relative safety from predators within the landscape features of the region without being wholly dependent on tree cover. Likewise, the geladas intensively exploit the tectonic features of their environment for refuge from predators (Fig. 11).

Variable proportions of C₃ and C₄ food sources in hominin diets

Variable C₃/C₄ diet signals have been identified in several hominin genera (*Australopithecus*, *Paranthropus*, and *Homo*) at

varying sites and at different time-periods. Stable isotope studies of tooth enamel of various hominin species confirm that their diets show a mix of C₃ (trees, shrubs) and C₄ (grasses, sedges) foods (Sponheimer and Lee-Thorp, 1999, 2003). Surprisingly, this is also the case for *Paranthropus robustus*, a species assumed to have been adapted to exploiting drier and more grassland-dominated environments based on their specialized grinding dentition (Sponheimer et al., 2006). Likewise, *A. africanus* specimens from Sterkfontein Member 4 show highly diverse proportions of C₃ and C₄ food sources, which may be interpreted as a diet comprising a mix of vegetation types (van der Merwe et al., 2003). Elsewhere, Member 4 habitat reconstructions suggest more wooded environments (Bamford, 1999), but this paleoenvironmental signal has probably been affected by time-averaging of different climatic conditions (O'Regan and Reynolds, 2009; Hopley and Maslin, 2010).

The mixed C₃/C₄ diet signal has led authors to propose possible hominin foraging strategies, such as the exploitation of underground storage organs, sedges, termites, and other 'fallback' foods (Backwell and d'Errico, 2001; Laden and Wrangham, 2005; Peters and Vogel, 2005; Sponheimer et al., 2005). Together, these studies suggest hominins favored living and foraging conditions in regions where a range of C₄ and C₃ types of foods were locally available. Since tectonic activity can create zones of wetter and drier areas in close proximity, this landscape model predicts that sources of C₃ and C₄ foods would have remained reliable, and in close proximity, for as long as these features were maintained.

Role of tectonically active landscapes in understanding wider patterns of evolution and extinction

If the exploitation of tectonically active habitats was the single defining factor in promoting the survival of a species, then all species exploiting such habitats should theoretically be successful. However, the role of large-scale and small-scale climate changes and their effects on these regions cannot be dismissed (deMenocal, 1995, 2004). Several very successful taxa at sites associated with *Australopithecus* have become extinct, while *Theropithecus* is presently an IUCN Red List endangered species (Gippoliti and Hunter, 2008). In the case of the klipspringer (*O. oreotragus*), this species is thriving and has expanded its former range. What we aim to

Table 4
Landscape processes, resulting landscape features, and potential implications for how hominins may have exploited these environments

| Processes | Resulting landscape features | Modern fauna associated with these features | Potential fossil evidence | Hominin habitat implications |
|--|--|--|---|--|
| East Africa: Volcanism and tectonic faulting | Lava flows, crater lakes | Mole rats (Family Bathygeridae), Klipspringer (<i>Oreotragus oreotragus</i>) | Lacustrine fauna and flora | Safety from predation, water (not potable in all cases) |
| | Uplifted fault flank | Grazing equids and Bovidae, Subfamily Alcelaphini | Dry grassland flora and fauna | Foraging in drier grasslands |
| | Cliffs and escarpments | Klipspringer (<i>Oreotragus oreotragus</i>); Gelada baboons (<i>Theropithecus</i> sp.) | Fauna preferring rocky outcrops | Safety from predation, drinking water |
| | Sedimented plains Wetlands, marshes | Gelada baboons (<i>Theropithecus</i> sp.) Waterbuck (<i>Kobus ellipsiprymnus</i>), Crocodiles (<i>Crocodylus</i> sp). Family Rodentia: Vlei Rat <i>Otomys</i> sp. Cape clawless otter (<i>Aonyx capensis</i>); Marsh mongoose (<i>Atilax paludinosus</i>) | Edaphic grasslands, grazing faunas Aquatic and amphibious faunas | Foraging in edaphic grasslands Foraging in wetland, marshy habitats |
| South Africa Tectonic faulting | Uplifted fault flank | Grazing equids and Bovidae, Subfamily Alcelaphini | Dry grassland flora and fauna | Foraging in drier grasslands |
| | Cliffs and escarpments | Klipspringer (<i>Oreotragus oreotragus</i>); Gelada baboons (<i>Theropithecus</i> sp.) | Fauna preferring rocky outcrops | Safety from predation, drinking water |
| | Sedimented plains Wetlands, marshes | Gelada baboons (<i>Theropithecus</i> sp.) Waterbuck (<i>Kobus ellipsiprymnus</i>), Crocodiles (<i>Crocodylus</i> sp). Family Rodentia: Vlei Rat <i>Otomys</i> sp. Cape clawless otter (<i>Aonyx capensis</i>), Marsh mongoose (<i>Atilax paludinosus</i>) | Edaphic grasslands, grazing faunas Aquatic and amphibious faunas | Foraging in edaphic grasslands Foraging in wetland, marshy habitats |

highlight is that landscapes affected by geomorphological processes are dynamic, not static, and to stress that these processes are relevant at both spatial and temporal scales for the evolution of hominins and other faunas. If certain animals were drawn to the landscape features of cliffs, sedimented plains, and wetlands, as we propose, then the knowledge of where and why such habitats existed in the past can aid the broader understanding of population movements through the corridor of the Rift between southern and eastern Africa. The Tectonic Landscape Model is not only relevant to the topography of site regions, but has also been proposed as a key determinant of the routes chosen by early *H. erectus*, as this species dispersed out of Africa (King and Bailey, 2006).

Conclusions

We have illustrated the effect that tectonics has on landscapes and the suite of features created by ongoing fault motion and/or volcanic activity. This is the basis of our argument for suggesting that these sites were, and probably still are, active. This data is qualitative, as is the nature of landscape interpretations done by geomorphological studies. We do not, however, suggest that classic models (river, pans) do not apply, only that areas of long hominin occupations can be understood in the light of the changes and rejuvenation of landscapes that tectonic activity brings. Our aim is to highlight the geomorphological processes which created aspects of the hominin habitat and to explain the effects of tectonism and volcanism on a variety of landscapes, both modern (i.e., wetlands) and past.

We have illustrated specific features associated with tectonically-altered landscapes in eastern and southern Africa. The tectonic disruption of drainage patterns and the subsequent creation of wetlands (such as the Okavango Delta and the Nylsvley wetland) have important beneficial consequences, by creating habitats with high faunal and floral biodiversity. According to the three basic habitat requirements for hominins such as *Australopithecus*—food, safety, and drinking water—the tectonic model provides landscape features which meet all three requirements, although the types of landscape features differ between South Africa and Ethiopia. While riverine and lacustrine habitats unaltered by tectonic activity would also have presented attractive habitats, our emphasis is on the geomorphological processes that sustain habitats with variable topography through time. Exploitation of tectonic landscapes by hominins may illuminate our understanding of two aspects of hominin site distributions. Firstly, hominins and other fauna were most likely drawn to highly heterogeneous habitats (whether riverine, lacustrine, or tectonic, as we propose here), which is why the reconstructions of *Australopithecus* diets, paleovegetation, and the faunal communities they are associated with appear to be mosaic or mixed. Secondly, high concentrations of hominin sites in certain areas are not a simple artifact of preservation but rather are related to habitat choice and active utilization of these regions by hominins and other fauna. Our statistical analysis indicates that preservation factors alone cannot account for the distribution of different categories of sites in Ethiopia and South Africa. We concur with Holmes et al. (2005) that hominin site distribution therefore reflects aspects of their habitat choice. However, active prospection has led to certain areas being better investigated than others. Large-scale-climatic variations and time-averaging have been proposed as an explanation for a range of habitat conditions visible in the fossil record (e.g., deMenocal, 1995, 2004; Bonnefille et al., 2004; Hopley, 2004). The model, however, offers insight into the underlying mechanism for the creation and maintenance of mosaic habitats through time. The landscape features and range of habitat conditions, specifically the wetter, down-dropped plains and drier, uplifted flanks, persist in close

proximity for as long as the fault motion continues. The Tectonic Landscape Model provides an alternative and equally powerful explanation of the time-averaging and climatic-averaging effects on the preservation of diverse habitats through time.

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