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Part I **Modern Africa and Overview of Late Cenozoic Paleoenvironments**

1

Introduction: African Paleoecology and Human Evolution

René Bobe and Sally C. Reynolds

Early hominins were not limited to particular sites or localities in a paleontological or archeological sense, but lived and died in complex and dynamic landscapes and ecosystems of which we have partial, incomplete records. The fossil evidence of early hominin paleoenvironments is always limited, sometimes providing brief snapshots of small areas, other times affording very coarse chronological and spatial resolution over large distances. Taphonomic conditions typically vary within any one locality over time, and from one locality to another. And yet, it is these partial and biased records that we use to build an understanding of the forces that have shaped our evolution.

We think that to gain a better understanding of our evolution and its ecological context it is necessary to take a broad view. As in the pioneering volume by Clark Howell and François Bourlière, *African Ecology and Human Evolution* (1963), here we aim to consider the whole continent of Africa during the time when our lineage emerged and dispersed across the continent. The focus of this volume is on the paleoenvironmental conditions and paleoecological relationships that are likely to have shaped the evolution of our ancestors as well as closely related species during the past 7 million years. We aim to discuss regions with a rich fossil record as well as regions with a sparse record, from north to south and from east to west (Figure 1.1).

This volume bears witness to decades of painstaking work by numerous researchers at hundreds of different sites. The research presented in the following chapters is necessarily interdisciplinary and builds on the efforts of scholars like Jean de Heinzelin, Bill Bishop, Maurice Taieb, Frank Brown, and Richard Hay, who, among others, laid a solid geological foundation for studies of hominin paleoenvironments. Likewise, the taphonomic approaches of Kay Behrensmeyer in East Africa, among others, continue to shape paleoecological studies across the continent.

This volume is organized into four main parts. In Part I, we present a review of key methods of paleoecological reconstruction, discuss biases in the hominin fossil record, and provide two synthetic chapters on the paleoenvironments of the continent. Part II is focused on southern Africa (Figure 1.2), with an overview chapter followed by site-specific contributions on Makapansgat, Kromdraai, Cooper's Cave, Sterkfontein, Swartkrans, Cornelia-Uitzoek, Taung, and Wonderwerk Cave.

Part III begins with an overview of eastern, central, and western African paleoenvironments during the late Miocene to the early Pleistocene, followed by site-specific chapters on Buia, Gona, Hadar, Dikika, Galili, Melka Kunture, Konso, the lower Omo Valley, West Turkana, East Turkana, Tugen Hills, the Homa Peninsula, Olorgesailie, Peninj, Olduvai, Laetoli, and the Karonga Basin (Figure 1.3a, 1.3b). Part IV provides a discussion of North African paleoenvironments in the Pliocene and Pleistocene, with site-specific contributions on Ahl al Oughlam, Tighenif, Thomas Quarry, and Oulad Hamida Quarry (Figure 1.4).

As currently understood, hominin evolution spans the period from nearly 7 Ma (million years) to the present (Figure 1.5). This time frame is based on the earliest records of possible hominins, including the species *Ardipithecus kadabba* (Haile-Selassie, 2001; Haile-Selassie et al., 2004a, 2009a), *Orrorin tugenensis* (Senut et al., 2001), and *Sahelanthropus tchadensis* (Brunet et al., 2002). Thus, current evidence indicates that the earliest hominins lived in eastern and central Africa. The earliest evidence of the genus *Australopithecus* dates to about 4.2 Ma, and by about 3.4 Ma there is some evidence of phylogenetic diversification with a few species of *Australopithecus* occurring in eastern, central, and possibly southern Africa (Haile-Selassie et al., 2016a). *Homo* and *Paranthropus* appear in the fossil records of eastern Africa toward the end of the Pliocene, about 2.8–2.7 Ma (Wood and Leakey, 2011; Villmoare et al., 2015), and diversify during the early Pleistocene (Antón et al., 2014). By the end of the early Pleistocene, ~0.8 Ma, only species of the genus *Homo* remain in Africa and elsewhere (Rightmire, 2013; Schroeder et al., 2017).

Hominid evolution takes place in the late Cenozoic during a time of important climatic, tectonic, and environmental changes. After the Mid-Miocene Climatic Optimum, 17–15 Ma, high-latitude global temperatures as measured by oxygen isotopes in marine Foraminifera began to decline (Figure 1.6; Zachos et al., 2001). This cooling trend resulted in the establishment of the East Antarctica ice sheets in the middle Miocene (Lewis et al., 2007) and the West Antarctic ice sheets in the late Miocene (Zachos et al., 2001). The late Miocene climatic cooling culminated in ephemeral glaciation in the northern hemisphere between 6 and 5.5 Ma (Holbourn et al., 2018) coincident with the Messinian salinity crisis (Krijgsman et al., 1999; Garcia-Castellanos and Villaseñor, 2011). The early Pliocene (4.5–3.0 Ma) saw a return to warmer temperatures (Wara et al., 2005; Ravelo et al., 2006; Fedorov et al., 2013) with generally wetter conditions in much of Africa (Feakins and deMenocal, 2010;

Supplementary resources for this chapter are available on www.cambridge.org/africanpaleoecology

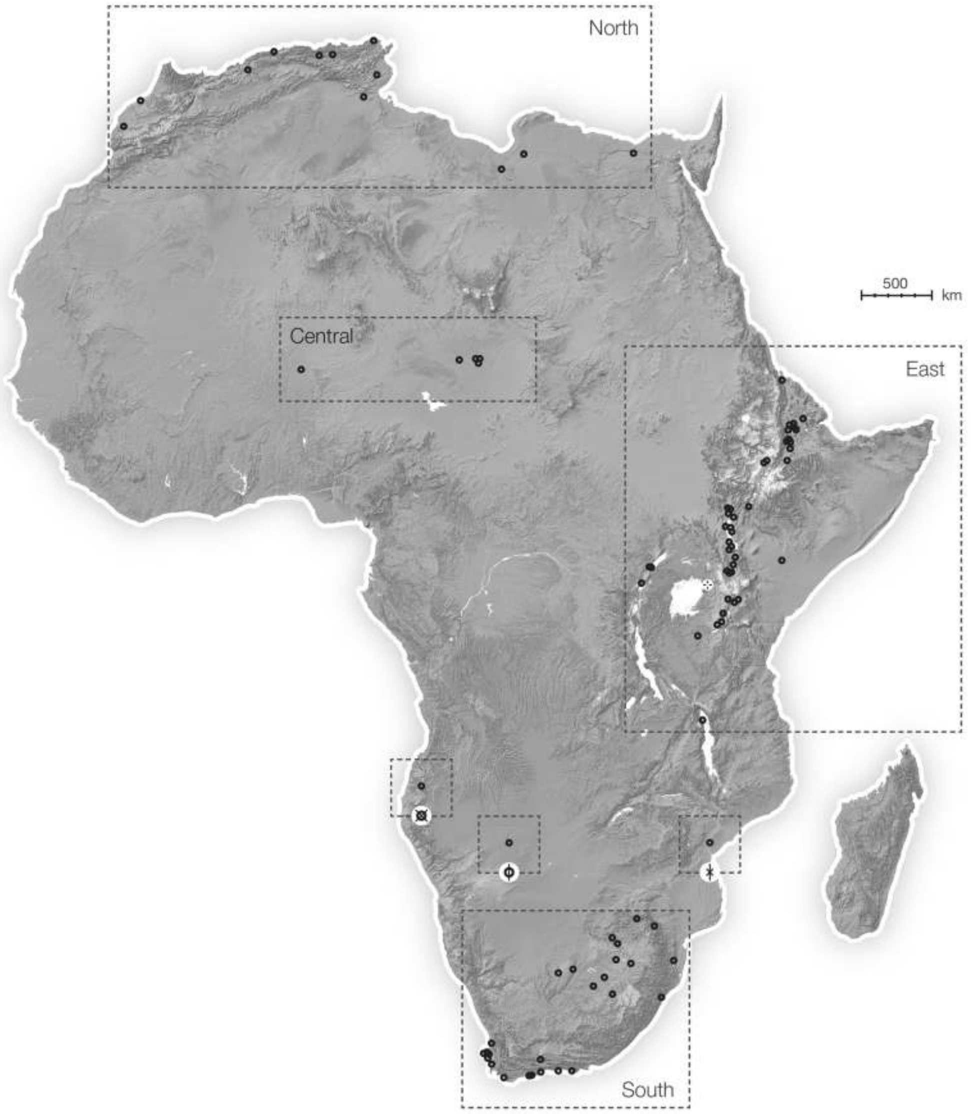

Figure 1.1 Continental map of Africa, with dashed boxes showing the geographic extent of the smaller regional maps. Individual sites (or site regions) are indicated with open circles and are labelled in the regional maps and discussed in the text.

Salzmann et al., 2011). The late Pliocene and Pleistocene was a time of further global cooling, with the onset of Northern Hemisphere glaciation between 3 and 2.6 Ma (Ravelo et al., 2004), and increasing amplitude of climatic oscillations during the Pleistocene ice ages (Raymo and Huybers, 2008). The mid-Pleistocene transition at ~0.95 Ma was marked by increased ice volume in northern latitudes and an increase in the amplitude of climatic oscillations (Larrasoaña et al., 2003). Dust records off the coast of Africa indicate that there were peaks of aridity at 2.8, 1.7, and 1.0 Ma (deMenocal, 1995). Alongside these major trends, climate cycles resulting from orbital forcing, i.e., changes in the Earth's orbital precession, axial obliquity, and orbital eccentricity (Milankovitch cycles; Hays et al., 1976; Shackleton, 2000; Philander and Fedorov, 2003; Lisiecki and Raymo, 2007; Bajo et al., 2020), may have played an important role in environmental and ecological changes in Africa (Kingston et al., 2007; Lupien et al., 2019). Cycles of ~21 ky (orbital precession) were dominant during the Miocene and most of the Pliocene, shifting to 41 ky (obliquity) dominant cyclicity at ~2.8 Ma, and 100–400 ky cycles (eccentricity modulating orbital precession) after 1 Ma (Tiedemann et al., 1994; deMenocal, 1995). Orbital forcing interacts with monsoon cycles to modulate levels and distribution of precipitation across eastern Africa, where the Intertropical Convergence Zone plays a key role (Feakins and deMenocal, 2010). Some of the high-eccentricity intervals coincided with periods of high precipitation in eastern Africa and expansion of rift valley lakes (Trauth et al., 2005, 2009). However, it remains a major challenge to relate the fine-scale resolution of many climatic records from the oceans to the coarser and more discontinuous records of hominins and their environments on land (Behrensmeyer, 2006).

The climatic changes discussed above are manifested in Africa through their influence on precipitation and vegetation. In modern African savannas, the proportion of woody vs. grassy

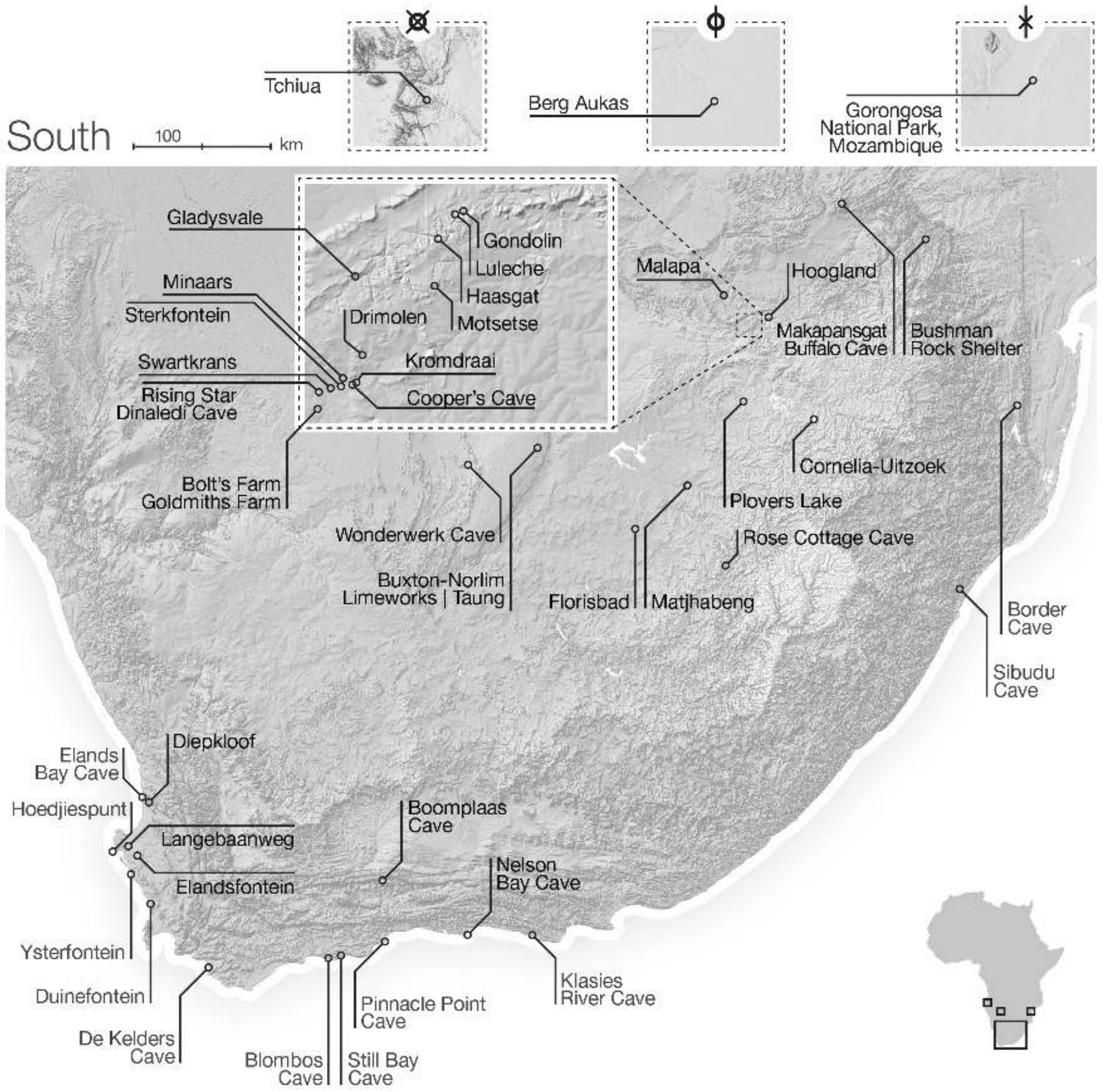

Figure 1.2 Regional map of southern Africa, including site regions in Angola, Namibia, and Mozambique. The very dense cluster of sites in the Cradle of Humankind World Heritage Site are indicated in the dashed inset box.

vegetation is primarily determined by mean annual precipitation. Regions which receive <650 mm of rain per year tend to have constrained woody cover but with significant grasses (Sankaran et al., 2005). Regions with more than 650 mm of rainfall have woody cover that tends to become dominant, unless constrained by fires or herbivores, with megaherbivores playing an important role in opening up wooded areas (Western, 1989). It is not only the amount of rainfall that's important in structuring vegetation: the seasonal distribution of rainfall and the severity and length of dry seasons also play a key role (Shorrocks, 2007). Furthermore, topography and soil types modify the effects of rainfall.

In our environmental descriptions, we rely on Frank White's African main vegetation types (White, 1983). *Forests* consist of continuous stands of trees with interdigitating crowns in multiple layers, frequently with lianas. Canopy height ranges from 10 to 50 m or more. The ground layer may include shrubs, bryophytes, and localized grasses. Rainforests are most widespread in the Guineo-Congolian region, with drier forests in this region classified as semi-evergreen. Dry forests, which may experience several months of dry season, are most common in the Zambezian and Sudanian regions. Riparian or gallery forests bordering fluvial channels and floodplains provide shade, refuge, and arboreal resources in areas that may otherwise have sparse arboreal vegetation. Afromontane forests typically occur at elevations above 1500 m and are composed of shorter trees than in lowland rainforests. *Woodlands* consist of widely spaced stands of trees with canopies covering at least 40 percent of the ground surface. Canopy height ranges from 8 to 20 m, and heliophilous grasses dominate the ground layer. Deciduous and semideciduous woodlands are common in the Sudanian and Zambezian regions. *Bushland* consists of areas dominated by woody plants usually 3–7 m in height, and covering at least 40 percent of the ground surface. Bushland is

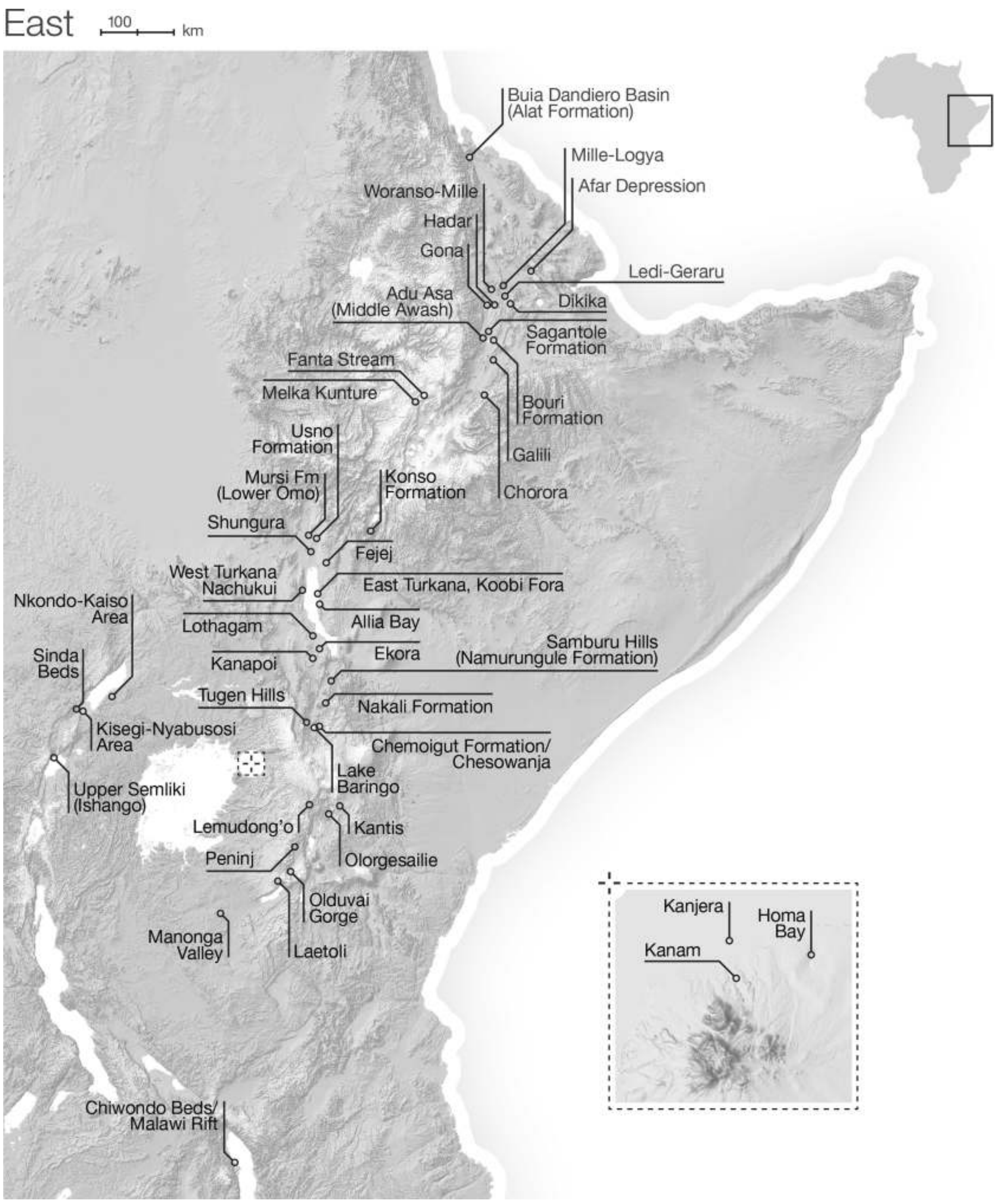

Figure 1.3a The dense clustering of sites in eastern Africa is closely associated with the East African Rift System, which contains two main rift branches: the Eastern (Gregory) Branch, which extends from the Afar region in Ethiopia through Kenya and Tanzania, and the Western (Albertine) Branch from Uganda and the DRC to Malawi and Mozambique.

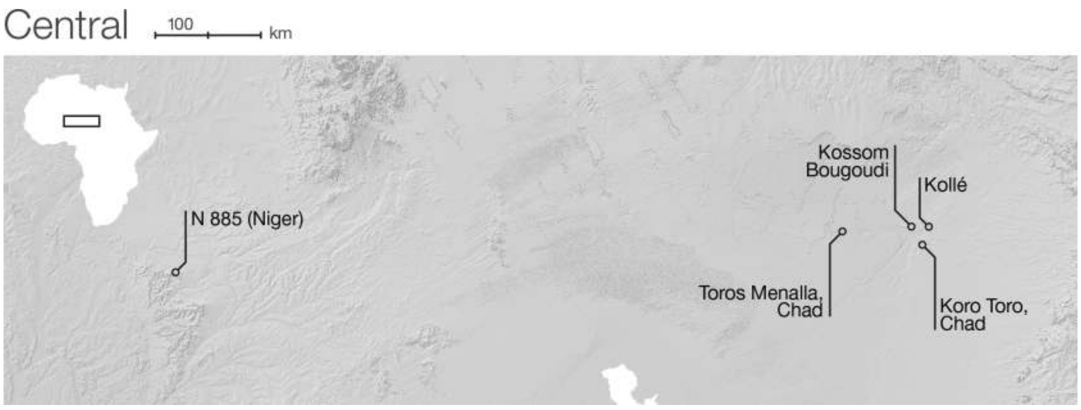

Figure 1.3b The central African region comprises few sites but includes the oldest hominin material currently known from Africa, namely *Sahelanthropus tchadensis* (Vignaud et al., 2002).

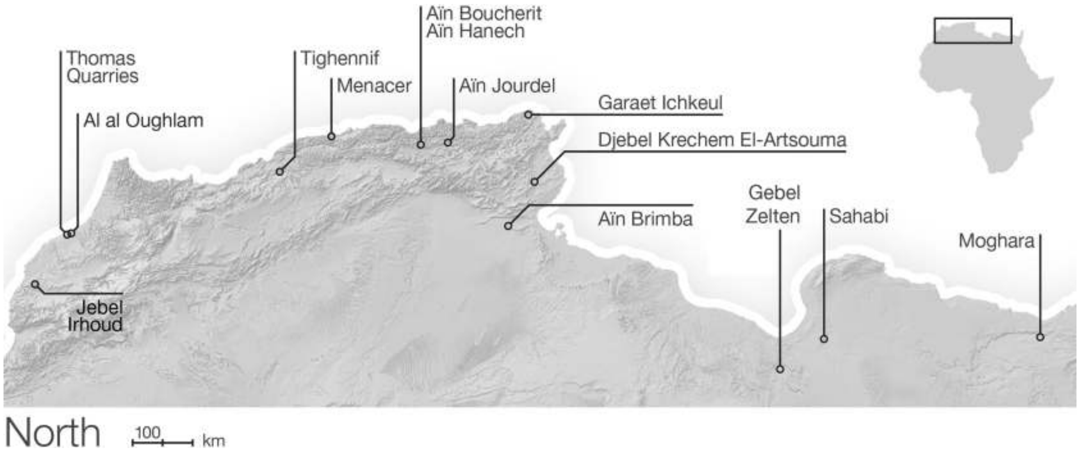

Figure 1.4 The important sites of northern Africa, including Jebel Irhoud, which has yielded the oldest remains of *Homo sapiens* (Hublin et al., 2017).

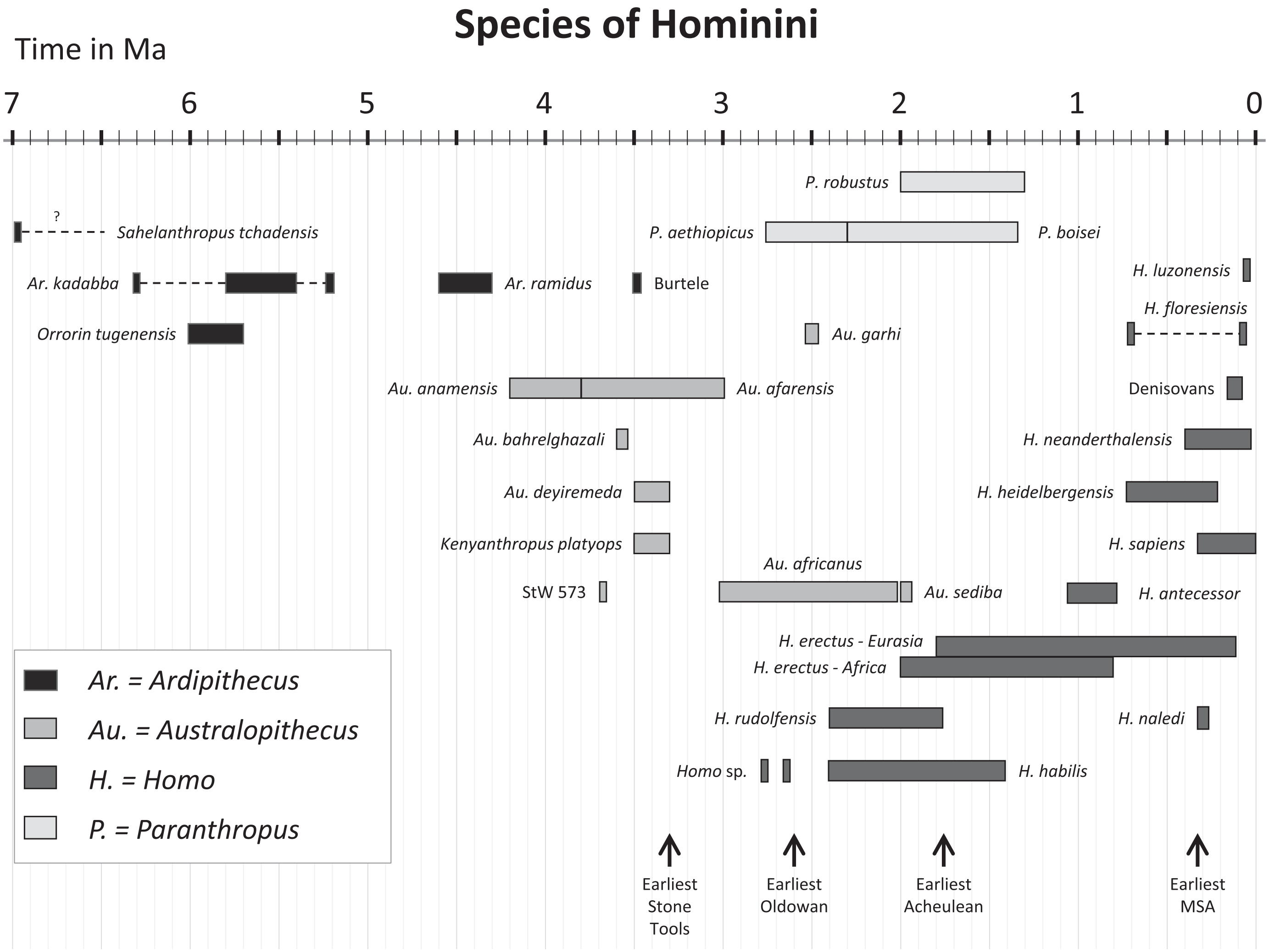

Figure 1.5 Chronology of hominin species. There are alternative interpretations to the hominin taxa depicted here. (A black and white version of this figure will appear in some formats. For the color version, please refer to the plate section.)

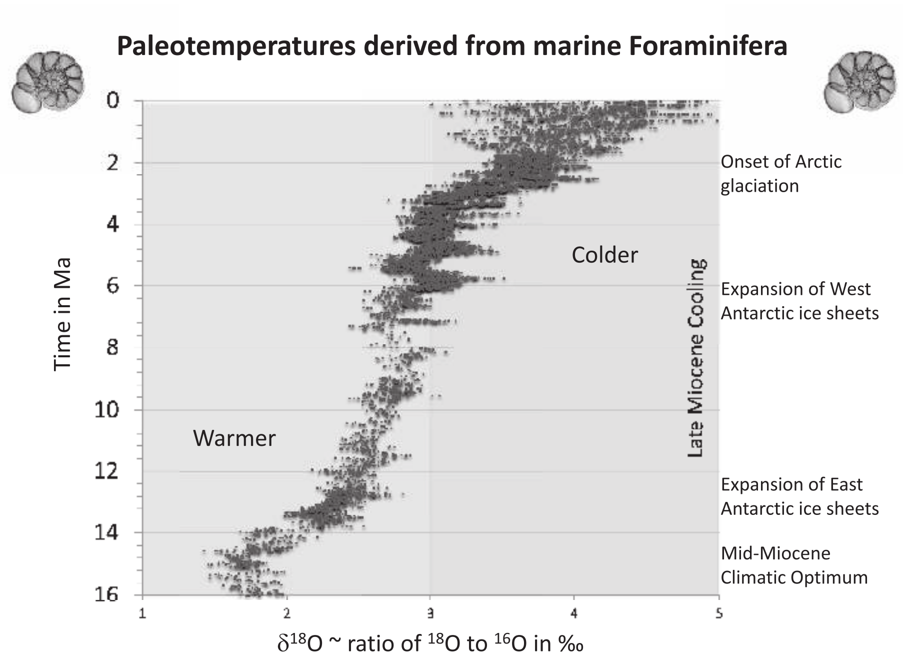

Figure 1.6 Paleotemperatures derived from benthic Foraminifera with $\delta^{18}O$ values in ‰ on the horizontal axis and time in Ma (million years) on the vertical axis. Graph drawn with data from the Deep Sea Drilling Project and the Ocean Drilling Project summarized in Zachos et al. (2001). This graph provides a view of global temperatures during the past 16 million years as a general background to understanding evolution in Africa. (A black and white version of this figure will appear in some formats. For the color version, please refer to the plate section.)

common in the Somalia–Masai region. *Wooded grasslands* are areas in which woody plants cover from 10 percent to 40 percent of the surface area, with grasses predominating. *Grasslands* are areas covered primarily by grasses with up to 10 percent cover of woody plants. Sedges (Cyperaceae) may be very common in edaphic grasslands associated with waterlogged conditions, which are widespread in the Sudanian, Zambezian, Somalia–Masai, and coastal regions. The term *savanna* refers to tropical and subtropical grasslands with scattered bushes and trees where the dominant grasses tend to be C_4 plants (Shorrocks, 2007). These vegetation types usually grade into one another and may be interdigitated in complex ways depending on various factors (topography, hydrology, and soils).

We use the term *environment* to refer broadly to the supporting matrices of life that surround living organisms (Calow, 1999). An environment may be more or less heterogeneous depending on the organism sensing it (Begon et al., 2006). Paleoenvironments are the inferred matrices of life surrounding organisms in the past. The term *habitat* refers to the place where a species or population lives. Species favor some habitats over others, evidenced by their abundance and distribution. An assemblage of species that interact with one another in a given area is called a *community* (Levin et al., 2009). Fossil assemblages rarely constitute past communities in an ecological sense. Time-averaging, bone durability, and transport tend to mix individuals from different communities at different times (Behrensmeyer et al., 2000). On a broader scale, the term *ecosystem* refers to the integrated biological and physical components of a landscape with a range of community types (Levin et al., 2009).

The chapters that follow provide a rich source of primary and synthetic data on hominin paleoenvironments and paleoecology in Africa, with most contributions focusing on the Pliocene and early Pleistocene, but also with contributions spanning from the late Miocene to the late Pleistocene and Holocene. Several chapters present primary data on the mammalian fauna, but also discuss other available paleoenvironmental and paleoecological sources of evidence. We hope that these contributions will generate further synthetic work, exploration of unknown areas, and generate new ideas and approaches to the study of our African origins.

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2

Approaches to the Study of Past Environments

Peter Andrews, Sally C. Reynolds, and René Bobe

Introduction

In a book on African paleoecology and human evolution, it is important to define several key themes, including biomes, vegetation formations and associations, as well as plant physiognomy. We first define these terms, before examining the sources of data employed in paleoenvironmental reconstructions. Finally, we provide an overview of the approaches used to understand past habitats, which underpin the chapters on the specific sites which make use of these approaches to refine our understanding of African paleoenvironments and the place of hominins within them.

Biome – A major regional ecological community of plants and animals extending over large natural areas, for example, tropical forest, or subtropical grassland (Figure 2.1). The plants of terrestrial biomes consist of Formations. We are concerned here with the forest, savanna, grassland, and desert biomes, particularly with the first two, which are key habitats associated with early hominin activity.

Vegetation Formation – A climax community of plants extending over large areas and their nature determined by climate, for example, tropical rainforest. Plant formations form the main natural vegetation types of the world.

Vegetation Association – These are the natural units of vegetation within a Vegetation Formation. There might be many plant associations in a single forest, savanna, or grassland, the variations resulting from variations in soil, topography, and altitude. Soil catenas have a succession of plant associations dependent on the different soils.

Plant physiognomy – This term covers all aspects of the structure of vegetation, for example, height, density, thorniness, evergreen, or deciduous plants.

Catena – A grouping of soil–vegetation types in relation to topography (Milne, 1935). Catenas form when soils change along a gradient, usually down a slope, and this relationship is repeated wherever the same topographic and geological conditions occur. They form within single rainfall, temperature, and altitudinal zones and the nature of the vegetation associations is affected by the combination of soil types and topography (Milne, 1935). Several catenas have been described for Laetoli (Tanzania) environments (Andrews and Bamford, 2008; see also Harrison et al., Chapter 34), e.g., downslope from broad-leaved woodland association on hill slopes with shallow soil → low *Acacia* woodland association on lower slopes with deep clay soils and impeded drainage → riverine woodland association where erosion has cut through the deep soils. Milne (1947) gives another example from the Uyansi plateau, Tanzania: upper slopes, deciduous thicket → middle to lower slopes, open woodland → lowest slopes, transition open woodland → bottom flats, hard pan vegetation of low trees and grass.

Mosaic vegetation – A soil–vegetation patchwork following topography and relief (modified from Morison et al., 1948). Landscape heterogeneity leading to heterogeneous habitats promotes the coexistence of a wide range of species and greater biodiversity (Reynolds et al., 2015). Fossil faunal assemblages may accumulate over enough time for climate changes between wetter and drier habitats to give the appearance of mosaic habitats. Mosaic vegetation associations follow topography within a single climatic zone, in which case it is based on catenas, or it may be related to altitude, with precipitation and temperature varying with altitude. Variations in climate occur over a minimum distance of 100 km (Griffiths, 1976), i.e., within areas of at least 10,000 km^2, and mosaic vegetation would normally occur within these distances. It is, therefore, a local effect at the landscape level, rather than a regional effect.

Habitat heterogeneity is assumed to be the major driving force behind continental and global biodiversity (Kerr and Packer, 1997), but within Africa the correlation between mammal species richness and variations in topography has low significance. Multiple regression models of 17 climate and topography variables in southern Africa showed that the one-variable and two-variable models most highly correlated with mammal species richness were measures of seasonality (temperature and precipitation), and only with the three-variable model did topography play a part (Andrews and O'Brien, 2000). Habitat heterogeneity is important at the local and landscape level and therefore also for fossil faunas.

Spatial mosaics are common wherever there are variations in soil, topographic relief, or water availability. Several recent soil/vegetation catenas have been described for the Laetoli region (Andrews et al., 2011) and their presence has been inferred for the Pliocene deposits based on the geomorphology of the region (Hay, 1987). Modern vegetation mosaics are typically transient stages in a vegetation succession, both spatial and temporal. For example, there is evidence for temporal mosaic variation

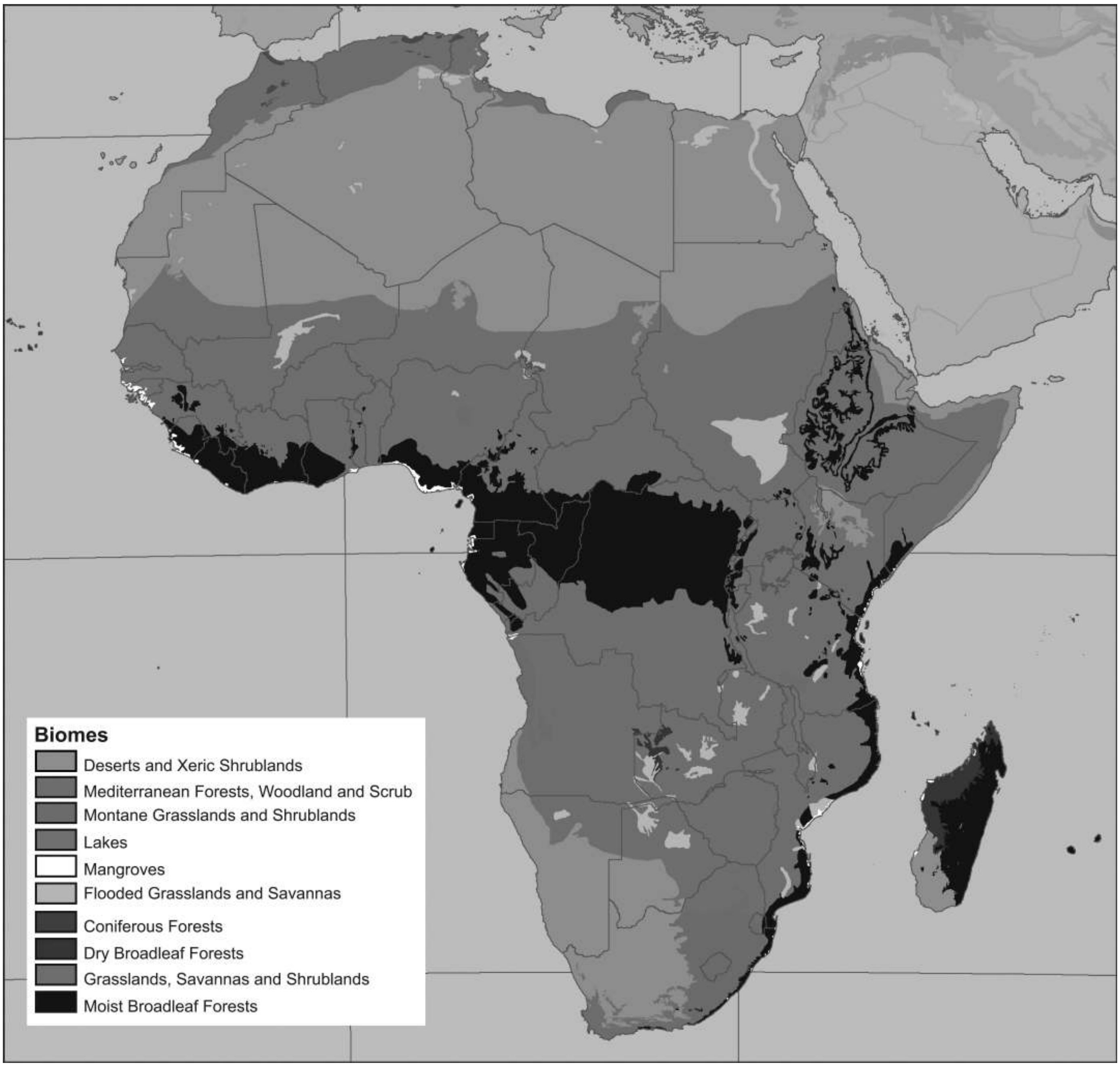

Figure 2.1 Simplified biome map of Africa, with emphasis on the major biomes of interest in the fossil record, namely forest, savanna, grassland, and desert. (*Source*: Modified from https://sedac.ciesin.columbia.edu/data/set/nagdc-population-landscape-climate-estimates-v3/maps based on WWF (2006) World Biomes Data set, www.worldwildlife.org/biome-categories/terrestrial-ecoregions). (A black and white version of this figure will appear in some formats. For the color version, please refer to the plate section.)

for the Masai Mara: it was observed to be open grassland in the nineteenth century (White, 1915) and was heavily grazed by wild and domestic livestock, but it reverted to dense woodland thicket during the rinderpest outbreak in the late nineteeth century when there was ~95 percent mortality of large mammals, including almost all domestic stock (Sinclair, 1979a, 1979b). With European expansion into the region, much of the area was mechanically cleared to eradicate the tsetse fly, and bush-clearing was facilitated by the reintroduction of elephants in the 1970s, so that the area is now once again open grassland.

Sources of Evidence

In this section we describe several sources of evidence and analytical methods to infer past environments.

Sediments and Soils

Soils may be formed in the past and preserved as paleosols, and may be regarded as trace fossils representing past ecosystems (Retallack, 1991; Retallack et al., 1995). The different stages of soil formation can often be identified in preserved paleosols, indicating how mature the soil was, and soil horizons may still be identifiable. In exceptional cases, the uppermost layer, the humus horizon may still be preserved. Paleosols are a key feature found at many hominin-bearing sites in Africa, such as Taung, South Africa (Parker et al., 2016; Hopley and Kuhn, Chapter 13). Fossil sand dunes, for example, are key ancient features associated with the other southern African sites of Langebaanweg, Elandsfontein, and Still Bay (Reynolds, Chapter 6). There is a close relationship between aeolian processes and climatic aridity, and at its most extreme this may be seen in the formation of fossil sand dunes. The presence of tropical forest in Central Africa growing on old sand dunes shows the existence of a former arid period affecting the region, and the structure of the aeolian deposits may indicate wind strength and direction. The formation of soil calcretes is another indicator of aridity, coupled with highly seasonal rainfall, for both are requisites for the formation of calcareous nodules in soil and calcretes.

The presence of lakes and their expansion and contraction is shown by past shorelines and the formation of shoreline terraces, providing information on changes in past rainfall. The chemical composition of the sediments themselves may indicate if the lakes had drainage outlets or were closed systems with consequent build-up of minerals. The taxonomic distribution of aquatic organisms such as diatoms or ostracods can indicate water temperature or salinity. Many key hominin sites were based around paleo-lakes, such as Olduvai Gorge, Tanzania (see Peters et al., Chapter 33; Farrugia and Njau, Chapter 32), Hadar, Ethiopia (Campisano et al., Chapter 18), Konso, Ethiopia (Suwa et al., Chapter 22), Olorgesailie, Kenya (Potts and Faith, Chapter 30), and the Chad Basin, Chad (Vignaud et al., 2002; Bobe and Reynolds, Chapter 15).

Structures in the immediate vicinity of fossil sites provide evidence on the local environment. For example, evidence of rivers or channels may be present, or there may be drainage features in the sediments, outflow or spring deposits. Both the soil formation processes and the nature of weathering processes in the soils provide evidence on past climates. Well-aerated soils may have a reddish color indicating the presence of oxidized iron compounds, or waterlogged soils may be deprived of oxygen and be gleyed, giving a gray color. Lignites and black clays may form in waterlogged soils, and calcareous horizons in the soil profiles may form under conditions of seasonal drying of the soil. As the rain penetrates the soil, it carries down dissolved minerals from the upper part of the soil, and if the rain is heavy and prolonged, these minerals may be carried to great depths through the soil, but when it is sparse and seasonal, the minerals may only be carried down a few tens of centimeters. When the rain stops and no more water is passing down the soil, the soil dries out and the minerals in the water are deposited at the lowest point the water has reached. Repetitions of this process over hundreds or thousands of years result in calcretes or hard pans in the soil, sometimes so thick that they impede further drainage of water through them, resulting in local flooding.

The integration of local and regional sedimentary features is therefore a primary source of evidence on past environments. Landscape reconstruction at Olduvai Gorge showed that the sediments at FLK 22 accumulated as a 100 m wide and half-meter high peninsula between a river to the south and a freshwater marsh to the north (Blumenschine et al., 2012b). Recent minor uplift of the FLK Fault appears to have played a role in deflecting the river channel and containing the wetland's flood basin. Good drainage on the peninsula permitted the establishment of woody vegetation. Short mixed sedge/grassland occurred in open areas on the peninsula and lower-lying channel (Bamford et al., 2006, 2008; Peters et al., Chapter 33), while mixed-species marshland occurred in the wetland. The trees on the peninsula within this landscape mosaic provided repeated activity foci for hominins and carnivores, and arboreal refuge in the vicinity that allowed hominins to acquire resources at the more open ecotone between the peninsula and wetland. In this way, the dense and diverse paleoanthropological assemblages from FLK 22 and elsewhere on and immediately north of the peninsula are predicted by a model of Oldowan hominin land use (Blumenschine et al., 2012b). This example shows just how valuable the landscape approach is and how much it adds to interpretations based on single sites.

Geomorphology on the landscape level may also provide insights into habitat variability (Bailey et al., 2011; Reynolds et al., 2011). This is a function of variations in geology, soils, and topography rather than climate, and if these features can be reconstructed for a fossil site it may then be possible to reconstruct the structure of plant communities that were present in the past. For example, the geomorphology of the Laetoli area in northern Tanzania (Hay, 1987) showed that the Pliocene sediments at Laetoli were deposited on an uplifted peneplain of basement rocks that had an uneven surface with low relief, dissected by shallow valleys for the most part and with drainage to the west and southwest. Compared with today, there was less topographic relief over most of the area during the Pliocene. The development of paleosols on the surfaces of the sediment and the presence of fossilized termite nests, which have been found in some abundance in some levels, indicate stable land surfaces with good drainage and well-established vegetation over several thousands of years (Leakey and Harris, 1987; Harrison et al., Chapter 34).

Relating present-day vegetation to existing geomorphological structures showed great variability of woodland types related to different topographical and edaphic features (Andrews and Bamford, 2008; Andrews et al., 2011): several types of riverine woodlands and gallery forest, broad-leaved deciduous woodlands on thin, well-drained soils, *Acacia* woodlands on valley bottoms with impeded drainage; limited areas of grassland on soils with well-developed calcretes; and increasing forest elements in the flora to the east with increasing altitude (and rainfall). All these associations exist today under one climatic regime, semi-arid with rainfall 500–700 mm. Comparing this distribution of existing vegetation to geomorphology and then extending this comparison to the Pliocene geomorphology of the Laetoli area, it was possible to reconstruct the distributions of past mixed woodlands at the site. For some levels it was possible to check predictions against fossil plant remains; for example, fossil wood, grass and sedges, and pollen (Bamford, 2011a, 2011b).

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Stable Isotopes

The analysis of stable isotopes in soil carbonates and organic matter measures proportions of C_3 to C_4 plants present. In tropical environments, C_3 plants include nearly all trees, shrubs, and herbs, together with grasses where there is a cool growing season, while C_4 grasses grow in open, unshaded places. The carbon isotope composition of carbonates in fossil soils shows that C_4 vegetation was present in Africa by about 9 Ma, but it began to expand only after about 7 Ma (Cerling, 1992). In other words, Miocene vegetation was mainly trees and shrubs, with little evidence of open grassland until the Pleistocene, after the emergence of *Homo*.

The paleogeographic reconstruction mentioned previously for landscape analysis of Olduvai Bed I has also been tested for carbon isotopes, and this confirms the existence of open wooded grassland for upper Bed I, the level associated with the earliest member of the genus *Homo*, *H. habilis*. Analyses of micromammals confirms this, and it contrasts with the results for middle Bed I, for which the small mammals indicate the presence of dense closed woodland (Fernandez-Jalvo et al., 1998; Harrison et al., Chapter 34).

The carbon isotope proportions can also be investigated in the enamel of herbivorous mammals, which provides an indication of the vegetation the animals were eating while the tooth enamel was forming. For example, 500 specimens from the Pliocene deposits at Laetoli had a mix of C_3 and C_4 signals on the teeth from 23 large mammal species (Kingston and Harrison, 2007; Kingston, 2011; Harrison et al., Chapter 34): suids had mixed and C_4 diets; giraffes had only C_3 diets; equids had mainly C_4 diets; different bovid tribes ranged from C_3 to C_4; and monkeys, proboscideans, and rhinos had mixed diets. Ostrich eggshells had an exclusively C_3 signal. The results indicate environmental variability at Laetoli, with vegetation varied enough to support both grazers and browsers. Oxygen isotopes were used to calculate an aridity index for the site derived from the water deficit (WD) calculated for different groups of mammals, and the range of values for WD at Laetoli indicated mean annual precipitation nearly the same as it is today.

Isotopic analysis of herbivore teeth from Dikika, Ethiopia (Bedaso et al., 2013; see also Bobe et al., Chapter 19) show that a range of wooded savanna habitats was present at the site, but there was no indication of forest or closed canopy woodland and C_4 grasses made up nearly 75% of herbivore diets. The relative proportions of wooded versus grassed habitats changed through time, and the oxygen isotope values suggest that the climate was wetter than earlier in the Pliocene and at present. In a similar vein, Wynn and colleagues (2020) have used hominin stable carbon isotope values to reconstruct changing diets of *Paranthropus* within the Shungura and Usno Formations (Ethiopia), which complements the findings of Negash and colleagues (2020; Chapter 24) on the herbivore isotopes of the same deposits.

The oxygen isotope composition of bone is largely determined by the $\delta^{18}O$ value of environmental water, although this is affected by the different species' metabolic processes. Plant foliage can be enriched in ^{18}O by evaporation from the leaves, so that an animal feeding on leaves exposed to the sun has enriched $\delta^{18}O$ values. This is the case with giraffes, which feed high up on the tree canopies, and for arboreal monkeys such as the seven arboreal monkeys living in closed canopy forest in the Taï Forest, Côte d'Ivoire (Krigbaum et al., 2013). Differences in $\delta^{18}O$ values between species correlated with the different canopy levels and suggest that it might be possible to identify the canopy levels occupied by fossil species.

Nitrogen isotopes are used to investigate differences in trophic level, which may indicate the presence of meat in the diets of fossil animals or the consumption by herbivores of aquatic plants (Palmqvist et al., 2008). The $\delta^{15}N$ levels distinguish meat-eaters and herbivores, but as many carnivorous species also eat vegetation, the evidence can be debatable, and meat-eating populations of chimpanzees show no difference in isotope values between males and females although males have been observed to eat six or seven times more meat (Smith et al., 2010). The explanation may be that the tooth enamel is formed during infancy, when infants and juveniles have little access to meat, or that adults do not eat enough meat to influence their isotopic signal.

Trace Fossils and Taphonomy

Trace fossils are the imprint left by living organisms in sediment where the organisms themselves have disappeared, such as footprints. Commonly found trace fossils are burrows in the sediment that have later been infilled with sediment of different colors or textures. Rarely, the organism is found in association with the burrow. Also trace fossils are the impressions made by plant roots, which form both in the sediment and on the surfaces of bones preserved in the sediment, which are visible as branching grooves with rounded profiles on the surfaces of the bones. Occasionally, whole trees are preserved as infilled cavities, for example the fossil ape site of Rusinga Island, Kenya (Walker and Teaford, 1988).

The presence of footprints preserved in the Footprint Tuff at Laetoli, described by Mary Leakey (Leakey and Harris, 1987), was the first and earliest unequivocal evidence for hominin bipedalism just over 3.6 Ma. Tracks, trails and footprints of many species of mammals and birds preserve evidence of the movements of animals across the Pliocene land surface (Bennett and Reynolds, 2021).

Traces of carnivore activity such as chew marks or digested bones and teeth may show the presence of a predator species even if body fossils are absent (Brain, 1981; Andrews, 1990; Su and Harrison, 2008). Other traces may be present, such as rodent gnawing, weathering, and rounding by water or wind abrasion. These traces are considered as the focus of taphonomic studies, but can also be environmental indicators.

Trace fossils also include pellets and scats left by all types of animals, which are referred to as coprolites if preserved (Andrews, 1990). In some cases, it is possible to infer the presence of a specific predator in a fossil assemblage even without body fossils. If the actual pellet or scat is present, this may be informative, but even in their absence the degrees of breakage and digestion of the prey remains is often enough to identify the predator. At Laetoli, many coprolites retain enough of their original shape for them to be identified at least to family (Harrison, 2011i).