
The Paleoclimatic Record and Plio-Pleistocene Paleoenvironments

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Abstract

New evidence from relatively recent methodological advances into hominin autecology presents interesting and often contradictory data. This article presents a broad overview of various paleoecological methods and summarizes what is known about the paleoecology of late Miocene hominins, through the hominin genera that begin to appear in the early Pleistocene, ~2.0 Ma. The use of taxon-free methods is emphasized in elucidating hominin habitats, and a more careful consideration of taphonomic and depositional biases that often result in “mosaic” reconstructions is advocated. Methods that focus on understanding the behavioral ecology of early hominin and other mammalian taxa are reviewed.

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Introduction

Paleoecology is concerned with understanding the ecology of organisms from the past, inasmuch as ecology can be reconstructed using the available evidence. The paleoecological evidence, whether biotic or abiotic, is then often compared with modern ecological patterns and processes to arrive at an understanding of the fossil taxon, taxa, or habitats of interest. Ecological patterns can be discerned in the past, but the processes that caused those patterns must be inferred. These can then be compared with modern ecological studies, wherein hypotheses about the processes are developed from observed patterns and subsequently linked to processes. For example, there are several hypotheses of community assembly processes, i.e., understanding why particular taxa co-occur in a circumscribed area, and these continue to be tested today (e.g., Hubbell 2001; Chase et al. 2005; Salisbury et al. 2012). There are many areas of inquiry that fall under the paleoecology rubric, including, but not limited to, geological depositional environments and paleosol analysis, habitat reconstruction, climate modeling, taphonomy, community ecology, biogeography, and autecology.

This chapter briefly outlines a variety of paleoecological methods that are used currently to develop reconstructions of the past habitat, climate, and behaviors of early hominins. What is currently known about early hominin ecology is synthesized, and those taxa recovered from the late Miocene, beginning at ~7 million years ago (Ma) to the end of the Pliocene, ~2.5 Ma, are included (Table 1).

Table 1 Habitat and dietary data for early hominin taxa

Taxon	Habitat	Isotopes	Microwear	References
<i>Sahelanthropus tchadensis</i>	savanna with some woody cover; semi-desert?	–	–	(Vignaud et al. 2002; Le Fur et al. 2009; Blondel et al. 2010)
<i>Orrorin tugenensis</i>	Forest-woodland mosaic	–	–	(Pickford and Senut 2001)
<i>Ardipithecus kadabba</i>	Riparian woodland	–	–	(Su et al. 2009)
<i>Ardipithecus ramidus</i>	Predominantly woodland; possibly bushland-grassland	C ₃ dominated	–	(White et al. 2009; Louchart et al. 2009; Cerling et al. 2011a)
<i>Australopithecus anamensis</i>	Woodland; Woodland with gallery forests	C ₃ dominated	Low complexity and anisotropy values; soft foods	(Leakey et al. 1995; White et al. 2006)

(continued)

Table 1 (continued)

Taxon	Habitat	Isotopes	Microwear	References
<i>Australopithecus afarensis</i>	Habitat generalist: riparian forest through bushland	Eurytopic; Individuals range from predominantly C ₃ to predominantly C ₄	Low complexity and anisotropy values; soft foods	(Reed 2008; Ungar and Sponheimer 2011; Wynn et al. 2013; Behrensmeier and Reed 2013)
<i>Australopithecus bahrelghazali</i>	Grassland around lake margins	Predominantly C ₄	–	(Brunet et al. 1996; Lee-Thorp et al. 2012)
<i>Australopithecus africanus</i>	Riparian woodlands, edaphic grasslands, dense to open woodland, and bushland	C ₃ /C ₄ mixed feeder	Low complexity and anisotropy values; soft foods	(Reed 1997; Sponheimer and Lee-Thorp 1999; Sponheimer et al. 2005)
<i>Australopithecus garhi</i>	Grassland around lake margins	–	–	(Asfaw et al. 1999; de Heinzelin et al. 1999)
<i>Australopithecus sediba</i>	Grassland to woodland	Predominantly C ₃	Moderate anisotropy, high complexity; some hard-object feeding	(Dirks et al. 2010; Henry et al. 2012)
<i>Paranthropus aethiopicus</i>	Wooded and wet in the Omo; dry and arid in the Ndolanya Beds, Laetoli	Predominantly C ₄	–	(Bobe and Eck 2001; Harrison 2011; Cerling et al. 2013)
<i>Paranthropus robustus</i>	Woodland and grassland near water sources	C ₃ /C ₄ mixed feeder	Hard-object feeding as evinced by pitting?	(Reed 1997; Ungar and Sponheimer 2011)
<i>Paranthropus boisei</i>	Mesic woodlands near lakes; grasslands at Konso, Ethiopia	Predominantly C ₄	Low complexity and anisotropy values; soft foods	(Cerling et al. 2011b, 2013; Ungar and Sponheimer 2011)

(continued)

Table 1 (continued)

Taxon	Habitat	Isotopes	Microwear	References
<i>Kenyanthropus platyops</i>	Woody, well-vegetated (although the Nachukui Formation is generally the most arid in Turkana Basin)	Eurytopic; Individuals range from predominantly C ₃ to predominantly C ₄	–	(Leakey et al. 2001; Cerling et al. 2013)
<i>Homo habilis</i>	Generally open and arid grasslands; possibly wooded environments	C ₃ /C ₄ mixed feeder	Low complexity and anisotropy values; soft foods	(Bobe and Behrensmeyer 2004; Ungar et al. 2006; Cerling et al. 2013; Kovarovic et al. 2013)

The Paleoclimatic Record

Research interest in the links between climate, ecology, and macroevolution has led to the advent of various proxies for paleoclimate during the African Plio-Pleistocene. While fauna has been historically used (e.g., Vrba 1985), new methods have come to the forefront of paleoclimatic studies, including records of terrigenous dust in marine drilling cores (e.g., deMenocal 1995), stable isotope analysis of paleosols (e.g., Cerling et al. 2011a), and stable isotope analysis of plant leaf wax (Feakins et al. 2013).

Vrba (1985, 1995) explored the interplay between paleoclimate and macroevolution using the fossil record of African mammals, primarily bovids, and such studies led to the formulation of the turnover pulse hypothesis (i.e., faunas “turn-over” in synchronous-like fashion as a response to perturbations of climate). She suggests that the radiation of cool and arid-adapted mammals over warm and moist-adapted mammals is evidence that Africa became increasingly cooler and more arid over the past 5 million years. Indeed, the origins of *Paranthropus* and *Homo* have been linked with the cooling event shortly after 2.8 Ma. Marine isotopic evidence (e.g., Zachos et al. 2001) also supports cooling in Africa during this time, along with intensification of glaciation at Northern Hemispheres.

Using records of continental dust derived from marine drilling projects in the Arabian Sea and Gulf of Aden, deMenocal (1995, 2004) has suggested three step-like increases in aridity, as evinced by an increase in dust, in East Africa over the last few million years. Dust production increased between 3.0–2.6 Ma, 1.8–1.6 Ma, and 1.2–0.8 Ma, all three of which are broadly consistent with periods of turnover in African faunas previously proposed by Vrba (1995).

Overall, it is clear that over the past 7 Ma in Africa, climate was becoming increasingly cooler, terrestrial ecosystems were becoming more arid, and the variability of climatic changes was becoming more dramatic. While various hypotheses have been proposed to explain key events in the human lineage (e.g., bipedalism and material technology), none is universally accepted although none are mutually exclusive. The remainder of this chapter will provide habitat descriptions for hominin species, but will refrain from speculating on the impetus for innovations in human evolution. For further reading, an in-depth review of paleoclimate and hypotheses regarding hominin evolution was recently provided by Potts (2013).

Paleoecological Methods

Faunas as Paleoenvironmental and Paleoecological Indicators

The remains of other fossil vertebrates, primarily mammals, have historically played a large role in the reconstruction of hominin habitats, and this method is still used today. The last few decades have witnessed a paradigm shift in paleoecology from taxon-based to taxon-free methods (i.e., analyses that do not rely on taxonomic or phylogenetic information). Traditional taxon-based methods, such as the relative abundance of grazing taxon x vs. browsing taxon y , rely on the assumption of taxonomic uniformitarianism. Under such an assumption it is supposed that fossil taxa share dietary and habitat preferences with their extant congeners and that these ecological traits can be used in paleoenvironmental reconstructions. This is problematic. For example, some lineages were diverse in the past and have only a single or few living representatives (e.g., *Theropithecus*), while others exhibit changes in their dietary ecology through time that would have been completely unforeseen under expectations of ecological continuity between fossil and extant taxa. For example, Bibi et al. (2012) recently showed that the suid *Kolpochoerus limnetes* and the tragelaphin bovid *Tragelaphus nakuae* from the Shungura Formation of southern Ethiopia increasingly consumed C_4 -based resources after 2.8 Ma, despite showing little craniodental change through time. The result was unexpected for both species, as modern analogs (*Potamochoerus* spp. and *Tragelaphus* spp.) are typically found in closed habitats, and C_3 plant sources make up the majority of their diet (Harris and Cerling 2002; Kingdon and Hoffmann 2013). This variation through time in lineages should caution future researchers wishing to reconstruct habitats based solely on taxonomic grounds. Unfortunately, taxonomically based methods remain pervasive in the hominin literature (e.g., Reynolds and Kibii 2011).

Bovids (antelope and their kin) are the most common mammalian family used in habitat reconstructions of the East and South African Plio-Pleistocene and provide a good model to explore the assumption of taxonomic uniformitarianism. Persistently, the relative distribution of bovid tribes in fossil deposits has been used as a proxy in habitat reconstructions and paleoenvironmental studies for sites of the

African Plio-Pleistocene (e.g., Vrba 1980; Shipman and Harris 1988; Harris and Leakey 1993). This methodology is based on the principle of taxonomic uniformitarianism, an idea itself based on the two postulates that (1) living representatives of bovid tribes collectively exhibit generalizable ecological preferences and that (2) these tribal preferences can be extended to their fossil representatives. However, there are notable difficulties with both of these assumptions.

With regard to living species, although members of a tribe may seem to collectively exhibit preferences for a certain habitat, the generalization is usually imprecise and there are always exceptions. For example, the sable antelope *Hippotragus niger* deviates from Hippotragini's generalized preference for open and arid grassland to semidesert habitats by instead preferring woodland and ecotones in the miombo (miombo is the Swahili word for the genus *Brachystegia*) woodland zone of southeastern Africa (Estes 2013). In Botswana, the southern limit of the sable's range happens to be limited by an annual rainfall isohyet of 500 mm, while fellow hippotragins *Oryx* and *Addax* persist, respectively, in habitats that receive much less than 500 and 100 mm of annual rainfall (Estes 2013; Knight 2013; Newby 2013). Similarly, the eland *Tragelaphus oryx* abandons its tragelaphin "tribal preference" for habitats with substantial woody cover and is found in habitats ranging from Kalahari semidesert scrub through Serengeti grassland to high-altitude alpine moorland on Mt Kilimanjaro (Thouless 2013). Through these examples, and there are many more, it is evident that homogenizing various habitat preferences of particular species into oversimplified habitat preferences for extant tribes, and then extrapolating this single homogenized tribal preference to fossil species living millions of years ago, is problematic without further explanation.

While the presence or absence of particular tribes might be of some paleoenvironmental significance, for example, the absence of reduncins at Laetoli (which indicates the lack of wetlands, lakes, or rivers (Gentry 2011)), paleoenvironmental and habitat inferences based on tribal relative abundance are subject to distortion by preservational, taphonomic, collection, and identification biases. For example, assemblages accumulated in fluvial systems may contain animals from multiple habitat types that often result in a "mosaic" reconstruction of early hominin habitats. Similar weaknesses characterize assemblages accumulated by carnivore activity, such as the size of prey that is accumulated and the resulting bias eliminating various size classes of animals that would be used in a paleoecological analysis.

In light of these issues, there has been a recent movement in paleoecology towards taxon-free methods of ecological and environmental reconstruction, based on fossil mammal specimens that do not rely on taxonomic or phylogenetic information. Such methods include isotopic analysis of herbivore enamel (Sponheimer et al. 2003; Cerling et al. 2011), mesowear of molar teeth (Fortelius and Solounias 2000; Kaiser 2011), craniodental ecomorphology (Spencer 1997), and postcranial ecomorphology (DeGusta and Vrba 2003, 2005a, b; Plummer and Bishop 1994). These taxon-free methods are used to re-create patterns of habitat use in mammals that existed with the early hominin taxa. Thus, the isotopic analysis of ungulate teeth from a particular site should provide an indication of the overall habitat from which the animals derived. Mesowear, craniodental, and postcranial

ecomorphology provide the same types of patterns, although an improved pattern is developed if all of the methods are used and compared at one locality as this may identify taphonomic biases in the information. Since many hominin habitats have been reconstructed on taxonomic grounds, the evidence is included here, but strong conclusions based on these data are not possible.

Dental Microwear

Microscopic examination of the enamel surfaces of molars and incisors provides data in the form of scratches and pits on the teeth that can be used to infer what members of a fossil taxon were actually eating. Microwear has been utilized to understand the diet of hyraxes, bovids, monkeys, carnivores, and hominins (e.g., Walker et al. 1978; Grine and Kay 1988; Merceron et al. 2004; Scott et al. 2005; Ungar et al. 2008, 2010b). Traditionally, microwear has been assumed to exhibit scratches on the teeth caused by ingestion of food in the last weeks of the animal's life (Teaford 1988). Recently, however, Lucas et al. (2013) have called this into question. They suggest that what the microwear is measuring is grit, since other foodstuffs do not, in an experimental setting, mar teeth to the extent that dirt does. This obviously needs further investigation, but considering these claims it is remarkable that browsing bovid teeth and grazing bovid teeth, as evinced by extant samples, show consistent differences between these groups (e.g., Schubert et al. 2006). This analysis of diagnostic wear patterns can be extended to primates, as monkeys that eat hard seeds and nuts show pitting on their teeth, while those that eat soft and abrasive foods do not. The results of microwear analyses of hominin taxa are included as paleobiological data in the section on hominin taxa, as are some interesting problems that arise when comparing these analyses with other methods of reconstructing hominin diets, such as stable isotope analysis.

Isotopes in Paleoecology

Of all skeletal tissues, dental enamel is ideal for isotopic studies because it is more highly mineralized than bone, and is thus unlikely to undergo postdepositional chemical alterations (i.e., diagenetic changes), and because changes in diet throughout ontogeny can be investigated since enamel is an incremental tissue (Ungar and Sponheimer 2011). For dietary information ^{13}C is the most suitable isotope for inferring the feeding ecology of extinct taxa, as its composition is directly related to the physiology and isotopic composition of the plants from which it was derived. Different terrestrial plants use different photosynthetic pathways, and this is reflected in their ^{12}C and ^{13}C ratios; these ratios are of interest to paleoecologists because, depending on which species of plant are consumed, a diagnostic ratio becomes incorporated into the enamel of herbivorous mammalian taxa. In tropical environments like Africa, browse vegetation such as woody trees, forbs, and shrubs exhibit the signature of a C_3 photosynthetic pathway. Conversely, savanna and

tropical grasslands are associated with a C_4 photosynthetic pathway. As previously stated, enamel has very low rates of diagenetic alteration and has proven to be a useful indicator for distinguishing between modern and fossil browsing (e.g., *Giraffa* spp.) and grazing species (e.g., *Equus* spp.). Quantitatively, browsers show ^{13}C values of $-8^0/00$ to $-10^0/00$, while grazers exhibit values greater than $-2^0/00$ to $1^0/00$. As would be expected, mixed feeders are characterized by intermediate values.

Stable isotopes of oxygen are useful for interpreting climatic conditions, as ^{18}O composition in organisms is largely determined by the ^{18}O composition of local drinking water (thus presenting a snapshot of altitude, aridity, precipitation, etc.). However, interpreting the results of stable isotope analyses of oxygen is confounded by the fact that organismal physiology and diet also influence oxygen ratios in mammals and must be taken into account when drawing conclusions from data. With mammals in particular, ^{18}O is strongly influenced by drinking behavior. Depleted levels of ^{18}O are observed in aquatic taxa and higher levels of ^{18}O are common in C_4 -adapted and arid taxa.

Carbon isotopes can also be used in chemical analyses of paleosols, if there are carbonate nodules (Cerling and Hay 1986; Sikes 1994; Wynn 2000). These nodules usually form under drying conditions and can give representation of the percentages of grasses and dicots (bushes and shrubs) that were present when the soil was formed. In addition, the soil carbon and carbonates can be used to estimate carbon dioxide in the atmosphere, which enables a better understanding of the paleoclimate (Cerling 1992).

Recently, Cerling and colleagues (2011a) have developed a method using soil carbon isotopes to evaluate the percentage of woody cover that was present on the landscape when the paleosols were formed. The percentage of woody cover is based on the amount of shrubs, bushes, and trees that had the C_3 pathway in the paleosol. The woody cover method is especially important in reconstructing environments for ancient African landscapes, as most hominin fossil localities in eastern and southern Africa are believed to have been deposited under “savanna environments.” A savanna is defined as having various amounts of woody cover (C_3) from 80 % to 20 % (Pratt and Gwynne 1977), with grasses (C_4) as ground cover. Reconstructions of past habitats and, in particular, hominin sites have suffered from the inaccuracy of the term “savanna” to describe what the habitat looked like, and indeed many people think of open grassland when they hear the term savanna, although 20 % woody cover is required. Cerling et al. (2011a) designed a formula to interpret exactly how much woody cover was present, although this method cannot differentiate between the types of woody cover. However, if methods are used in tandem a better depiction of the landscape is possible. For example, Cerling et al. (2011a) reconstruct the Dikika locality, where “Selam” was recovered, as a woodland, bushland, or shrubland, based on the fraction of woody cover. If one uses the fauna recovered from the Basal Member of the Hadar Formation to add to this interpretation, one would see many browsers and mixed feeders that independently indicate a bushland or medium density woodland. Using multiproxies to examine hominin ecology allows better understanding of the taxa and their relationship with their environments.

Finally, strontium isotopes have also been in play recently and have been used to investigate movement of hominin species on the landscape. Strontium isotopes are dependent upon the underlying composition of rocks and soil in any given area; for example, they have been used extensively in France to show that a particular wine grape was in fact grown in the area that is noted on a bottle of wine (Hodgkins 2012). In South Africa, Copeland et al. (2011) used these data to examine ranging patterns in early hominins and showed that the smaller hominins recovered in the Malmani dolomite region of South Africa had evidence of ingesting strontium outside of the range seen in that area. The authors suggested that this might reveal that male australopiths had relatively small home ranges and that females ranged widely. Thus, isotopic analyses permit inferences of social and reproductive behavior in the hominin fossil record.

Botanical Remains as Paleoenvironmental Indicators

Pollen, phytoliths, and wood have all been used to reconstruct the plant species that were present in ancient environments (Bonnefille and Riollot 1980; Bonnefille et al. 2004; Henry et al. 2011, 2012; Bamford 2005; Bamford et al. 2006). Fossilized plant material is subject to the same vagaries as fossilized animals, in that it is only preserved under certain conditions. Despite this, pollen has been recovered from many fossil localities, e.g., Hadar, Ethiopia, but only from particular strata, such as the Sidi Hakoma Tuff and in the base of the Denen Dora Member, and it has been noted that no pollen was preserved from the upper Kada Hadar Member. The conclusion is that reeds and grasses from the paleolake dominated Hadar, and through the section there were both increasing and decreasing proportions of tree and shrub species. Again, these data can be compared with the faunal data and isotope data, where available, to arrive at a better understanding of the habitat of *Australopithecus afarensis*. For example, there is a spike in the abundance of reduncin bovinds at the beginning of the Denen Dora Member, indicative of lacustrine and wetland deposits that are consistent with the pollen data.

The analysis of fossil woods allows identification of the actual tree species that existed in the region, and this often helps in determining the types of woody cover and the habitat. Bamford et al. (2006) used both macro-plant fossils and phytoliths to refine the habitats from the broad vegetation reconstruction previously done. At the HWKEE (Henrietta Wilfrida Korongo East East) site, they determined that the region was first dominated by palm trees and then a mixture of palms, grasses, and other dicot plants.

Phytoliths have come into the forefront in analyzing hominin diets. Henry et al. (2012) noted phytoliths of various plant materials in the calculus of *Au. sediba*. These included a fruit phytolith and a bark phytolith, consistent with the C₃ diet reconstructed using isotopic data. Phytolith analyses like that of Henry et al. (2012) offer a promising avenue of research for reconstructing hominin autecology.

The Ecology of Hominin Taxa

Sahelanthropus tchadensis

The earliest potential hominin comes from ~6 to 7 Ma perilacustrine sediments in Toros-Menalla, northern Chad. TM 266-01-060-1, “Toumai,” is the holotype of *Sahelanthropus tchadensis*, a distorted cranium possessing a thick supraorbital torus, small canines, and a cranial capacity of about 360 cc. The site was biochronologically dated as apparently older than the Lukeino Formation fauna (ca. 6 Ma), and the Toros-Menalla assemblage appears most similar to the Lower Nawata fauna of Lothagam (ca. 5.2-7 Ma) (Brunet et al. 2002).

Over ten species of fish, and abundant hippopotamid and crocodile remains, suggest a large and permanent lake, in concordance with the depositional evidence. The terrestrial habitat was reconstructed as a mosaic ranging from savanna to gallery forests at the edge of the watercourses, along with floodplain environments. Evidence for desert or semidesert conditions within the mosaic comes from fossil sand dunes, proposed by the authors as the earliest evidence for desert conditions in the southern Sahara (Vignaud et al. 2002).

Savanna conditions at Toros-Menalla seem to have been more prevalent than previously proposed, since a recent analysis of bovid mesowear implies the presence of extensive grasslands and open environments (Blondel et al. 2010). The dominance of Hippotragini and Reduncini at Toros-Menalla is also suggestive of open expanses of herbaceous vegetation, as extant representatives of both tribes are typically grazers (Kingdon and Hoffmann 2013). Gerbils and ground squirrels, along with fossorial genera like *Orycteropus* and *Serengetilagus*, also indicate dry savanna environments (Le Fur et al. 2009).

No isotopes or microwear studies have been published on *Sahelanthropus*.

Orrorin tugenensis

Senut et al. (2001) erected the genus *Orrorin* for late Miocene hominoid remains from the Lukeino Formation in the Tugen Hills of Kenya dated 6–5.7 Ma (Pickford and Senut 2001; Sawada et al. 2002). The hominin status of *Orrorin* is mainly supported by the morphology of the proximal femur in BAR 1002'00 which suggests that it may have been a biped (e.g., Richmond and Jungers 2008); but this view is not unanimous (e.g., Wood and Harrison 2011). Pickford and Senut (2001) described the associated fauna, but no isotope or microwear analyses have been performed. The late Miocene habitat of *Orrorin tugenensis* was reconstructed as a woodland mosaic based on the predominance of *Aepyceros*, a genus whose extant representative prefers ecotones between light woodland and savanna (Fritz and Bourgarel 2013). Colobine monkeys were interpreted as evidence for the presence of forests in close proximity to the depositional center, which alternates between fluvial and lacustrine throughout the Lukeino sequence. Crocodiles, hippos, fish, and freshwater snails suggest large, permanent bodies of water.

Ardipithecus kadabba

Ardipithecus kadabba is a late Miocene species of hominin recovered from sediments along the western margin of the Middle Awash, Ethiopia (Haile-Selassie and WoldeGabriel 2009). The hominin-bearing Asa Koma and Kuseralee Members of the Adu-Asa Formation have been dated to 5.54–5.77 Ma and ca. 5.2 Ma, respectively (WoldeGabriel et al. 2009). Su and colleagues (2009) associated *Ar. kadabba* with a densely wooded and well-watered landscape characterized by riparian woodland. The Asa Koma and Kuseralee Members are particularly rich in reduncin bovids, and this was taken as evidence for edaphic grasslands or swampy areas on the landscape. In contrast, Levin et al. (2008) interpret the habitat of *Ar. kadabba* at Gona as being predominantly bushland-grassland, based on carbon isotopes from herbivore tooth enamel suggesting diets dominated by C₄ grasses. This implies some habitat flexibility for early *Ardipithecus*.

Ardipithecus ramidus

The early Pliocene hominin *Ardipithecus ramidus* is best known from Aramis, a locality in the Middle Awash region of Ethiopia. The Lower Aramis Member of the Sagantole Formation is bracketed by two marker tuffs that constrain the age of Aramis to 4.4 Ma. The depositional environment has been characterized as a low-relief aggrading floodplain. White and colleagues (2009) recently published a comprehensive synthesis of the Aramis paleoenvironment using various lines of evidence (e.g., taxonomic abundance, mesowear, isotopes), and it is thus no surprise that the paleoenvironment of *Ar. ramidus* is the most completely known for all of the late Miocene-early Pliocene hominin taxa. The habitat evidence from Aramis is consistent with woodland exhibiting grassy and closed patches (although see Cerling et al. 2011a).

Carbon isotopes for *Ardipithecus ramidus* reveal a diet primarily comprised of C₃ plant products. The oxygen isotope data for *Ardipithecus* are slightly lower than the Aramis monkeys, suggesting that *Ar. ramidus* “obtained more water from fruits, bulbs, tubers, animals, and/or surface sources” (White et al. 2009). Dental morphology is broadly consistent with the isotopic data and indicates that the diet of *Ardipithecus* was generally derived from forest and woodland components. Suwa et al. (2009) showed that the enamel thickness of *Ar. ramidus* is intermediate between *Pan* and *Australopithecus* and suggested that the combined evidence indicates generalized omnivory and frugivory.

The community composition at Aramis is particularly interesting, being dominated by tragelaphin bovids and colobine monkeys. Cercopithecids in general are strikingly common at Aramis, as specimens attributable to *Pliopapio alemui* and *Kuseracolobus aramisi* comprise 30 % of the large mammal fauna, with the latter being the most common monkey in the assemblage. Conversely, equids are rare although the *Eurygnathohippus* species present at Aramis appears to be postcranially adapted to open-county running. *Tragelaphus* is the most common bovid, comprising 85 % of all antelope specimens collected. *Aepyceros* is also relatively common at Aramis, while Alcelaphini and Hippotragini are uncommon. Parrots and

the peafowl *Pavo* dominate the avifauna, and it was suggested by Louchart et al. (2009) that the relatively rare arid-adapted rodents of Aramis were transported by raptors, since woodland micromammals comprise most of the assemblage.

Ecomorphological analyses of postcrania investigated habitat-linked traits in cercopithecoid and bovid specimens, almost all of which were classified as “forest.” Mesowear analyses revealed browsing preferences for the Aramis giraffids, tragelaphins, and “neotragins,” while *Aepyceros* fell closer to the grazing end of the spectrum. Enamel isotopes reveal that grazing taxa were relatively uncommon and that browsing taxa dominated the assemblage. Notably, most fossil mammals at Aramis conformed to dietary expectations based on their extant congeners, which, in this case, supports the validity of taxon-based methods (e.g., relative taxonomic abundance) used to reconstruct the paleoenvironment of *Ardipithecus* at Aramis. The analysis of White and colleagues (2009) is a model example of the use of taxon-based methods, once independent lines of evidence have confirmed the supposed ecologies of indicator taxa.

Australopithecus anamensis

Australopithecus anamensis is the first species in the genus *Australopithecus* and has been found in sites in both Ethiopia and Kenya, appearing at Kanapoi, Allia Bay, Fejej, Aramis, Asa Issie, and Galili in roughly contemporaneous sediments indicating an origin of *Australopithecus* about 4.2 Ma. At Asa Issie, *Au. anamensis* is found in a woodland environment (White et al. 2006), while Kanapoi and Allia Bay were reconstructed as woodland mosaics with extensive gallery forests (Leakey et al. 1995).

Like *Ardipithecus*, the carbon isotopes of *Au. anamensis* reveal a narrow and C₃-based diet (Cerling et al. 2013). White et al. (2006) hypothesized niche expansion in early *Australopithecus* as the dentognathic morphology of *Au. anamensis* is indicative of consumption of tough, abrasive food resources relative to earlier hominins like *Ardipithecus*. Microwear analyses of *Au. anamensis* are notably similar to its descendant *Au. afarensis*, suggesting some dietary continuity between the lineages, although the evidence from isotope data contradicts this (Ungar and Spohnheimer 2011; Wynn et al. 2013).

Australopithecus afarensis

Australopithecus afarensis is the most completely known species of Pliocene hominin (Kimbel and Deleuzene 2009), likely due to its extensive geographic and temporal distribution. This species persists from roughly 3.8 to 2.95 Ma and is best documented by the well-constrained sediments in the Afar of Ethiopia and, to a lesser extent, the Upper Laetolil Beds of Laetoli, Tanzania (Harrison 2011). *Au. afarensis* is likely present 2,500 km west of the Rift Valley at Koro Toro, Chad (as *Au. bahrelghazali* sensu Brunet et al. 1996), but it is relatively rare in the Omo-Turkana Basin, represented by poorly preserved craniodental remains, despite the Basin’s close proximity to other East African sites (e.g., Suwa et al. 1996; Kimbel 1988).

The earliest well-documented specimens of *Au. afarensis* come from the Upper Laetolil Beds of Laetoli, Tanzania. The paleoenvironment of Laetoli has been

subject to debate. In the seminal 1987 volume on Laetoli edited by Mary Leakey and John Harris, most contributing authors concluded that past and present environments at Laetoli were effectively equal. This implied that the region must have been continuously characterized by savanna habitats, with some mixture of open woodland, since the mid-Pliocene when the Lower Laetolil Beds were deposited on bedrock. However, this view of habitat uniformity through time no longer appears to be true for Laetoli based on various lines of evidence including bovid ecomorphology (e.g., Kovarovic and Andrews 2007), vegetation structure (e.g., Andrews and Bamford 2008), and stable isotope analysis of herbivorous mammals (e.g., Kingston and Harrison 2007). These studies converge on the conclusion that Laetoli was wetter and more wooded during the deposition of the Laetolil Beds (3.8–3.5 Ma) than originally reconstructed. Ephemeral streams and ponds were likely present; however, the lack of aquatic taxa suggests permanent bodies of water were never present at Laetoli during this time. Hippopotamuses, crocodiles, and reduncin bovids are all absent from Laetoli, while they are common elsewhere in the East African Plio-Pleistocene. Despite this significant habitat difference, hominins are present at Laetoli and were probably more common than their relative abundance alone would suggest due to taphonomic biases related to body size (Su and Harrison 2008). Overall, the most recent data are in disagreement with original reconstructions of Laetoli, and the habitat of *Australopithecus afarensis* at Laetoli does not seem overtly anomalous with respect to other sites where the taxon is found, such as Hadar, which is discussed below.

The Hadar Formation of Hadar, Ethiopia, ca. 3.45–2.9 Ma, has produced the bulk of *Au. afarensis* specimens and permits longitudinal studies of this hominin's ecology since *Au. afarensis* is found throughout the entirety of the Hadar sequence (Campisano 2007). The paleoecology of the well-constrained Pliocene sediments at Hadar was recently reconstructed by Reed (2008). She provided habitat reconstructions for all members of the Hadar Formation by synthesizing faunal evidence with pollen and depositional data. In general, going up in the sequence, environments are wooded and closed during Sidi Hakoma times, transitioning to a wetter period in the Denen Dora when edaphic grasslands spread during the DD-2 submember and finally to more open and arid grasslands in the Kada Hadar Member (Reed 2008). *Au. afarensis* is most common in the Sidi Hakoma Member and, after declining in abundance, bounces back during the DD-2 submember when waterlogged grasslands dominate the landscape as evidenced by a substantial peak in reduncin bovids (Reed 2008). From the DD-2 submember on, the abundance of hominins stays relatively constant until they decline slightly in the KH-2 submember and then disappear from the Hadar fossil record roughly 2.95 Ma (Reed 2008; Kimbel and Deleuzene 2009). The evidence from Hadar supports the notion that *Australopithecus afarensis* was a habitat generalist as previously hypothesized (e.g., White et al. 1993).

Other habitat reconstructions are available for *Au. afarensis*. Woodland habitats dominate at Woranso-Mille, as the fauna is rich in Tragelaphini, *Aepyceros*, and *Theropithecus oswaldi* aff. *darti* (Geraads et al. 2009; Haile-Selassie et al. 2010). At Dikika, *Au. afarensis* is associated with woodlands around a delta, but grasslands may have also been present (Wynn et al. 2006). Two molars of *Au. afarensis* have

been recovered from a Ledi-Geraru site sampling the Denen Dora Member of the Hadar Formation that contains numerous reduncins, alcelaphins, and antilopins suggestive of areas containing wet and dry grasslands. White et al. (1993) reconstructed the environment at Maka in the Middle Awash as woodland-bushland using faunal evidence.

Microwear studies of *Au. afarensis* have revealed a lack of pitting and low complexity values, i.e., no evidence for hard-object feeding (Grine et al. 2006), despite the general robusticity of *Au. afarensis* craniodental architecture (e.g., Rak et al. 2007). Carbon isotopes imply that *Au. afarensis* was a dietary eurytope, as individuals throughout the Hadar Formation were consuming both C₃ and C₄ resources, with the latter being more common (Wynn et al. 2013). The isotopic evidence for *Au. afarensis* has broader implications for hominin evolution, as the time period ~3.5 Ma seems to represent a dietary shift among hominins to C₄-based resources, at least partially, as this trend is also seen in contemporaneous Chadian *Australopithecus* and *Kenyanthropus* (Lee-Thorp et al. 2012; Cerling et al. 2013; Wynn et al. 2013). The proposition that *Au. afarensis* was using stone tools and consuming meat by 3.4 Ma at Dikika, as evinced by purported cutmarked bones (McPherron et al. 2010), requires further evidence.

Australopithecus bahrelghazali

Brunet and colleagues (1996) erected a new species of *Australopithecus*, *Au. bahrelghazali*, for a fragmentary hominin mandible recovered in ca. 3.5 Ma sediments at Koro Toro, Chad. The validity of *Au. bahrelghazali* has been called into question since the mandible shares strong similarity with *Au. afarensis*, known from contemporary sediments at Hadar, Ethiopia (White et al. 2000). The fauna at Koro Toro is similar to that of Hadar, sharing some common elements (e.g., *Kolpochoerus afarensis* and *Parmularius pachyceras*) and hinting at potential faunal exchange across north-central Africa during or before this time (Brunet et al. 1996; Geraads et al. 2001, 2012). Evidence from the Koro Toro bovids suggests open environments as Reduncini and Alcelaphini dominate, while Tragelaphini and *Aepyceros* are notably absent. The absence of other primate taxa at Koro Toro may also point to a lack of canopy cover on the landscape.

Isotopic evidence reveals *Au. bahrelghazali* was incorporating large amounts of C₄ foodstuffs in its diet ca. 3.5 Ma, as evinced by its significantly high ¹³C values (Lee-Thorp et al. 2012). C₄ sedges with associated tubers and corms provide a potential explanation. The sedge genus *Cyperus* is widely distributed in tropical environments today and is often found around the margins of watercourses in Africa, including modern Lake Chad (White 1983; Lee-Thorp et al. 2012). It is possible that *Au. bahrelghazali* was exploiting sedges or similar plants around waterways, in a predominantly savanna environment. Thus, the dietary evidence would be in concordance with the faunally based habitat reconstruction and shows that Chadian *Australopithecus* lived and died in grasslands, suggestive of some degree of dietary and habitat flexibility in mid-Pliocene hominins considering that contemporaneous sites are typically wooded and well watered (e.g., Hadar).

Australopithecus africanus

Dart (1925) identified this taxon from the Taung mining dumps, and in the next several decades more individuals were discovered at the former cave sites of Sterkfontein and Makapansgat, although at first these hominins were referred to different species (Broom 1938; Dart 1958). Teeth were also recovered from the Gladysvale site in the 1990s (Berger and Tobias 1994). New paleomagnetic and uranium-lead dating of these cave sites suggests an age range of 3.0–2.0 Ma (Herries et al. 2013).

Habitat reconstructions differ for each of these sites. Makapansgat, considered the oldest of the localities, has been reconstructed as a mosaic of riparian woodlands, edaphic grasslands, and bushlands, with possible riverine forests (Dart 1925; Reed 1997). A study of bovid taxa, using both isotope values and ecomorphology of the masticatory apparatus, indicated that there were more browsing taxa than expected, and thus when the fauna was deposited, there may have been more closed woodland bushland than previously thought (Sponheimer et al. 1999). Taung has been reconstructed as dense woodland (Dart 1925; Berger and Clarke 1995); Sterkfontein has been reconstructed as open woodland, riparian forest, and bushland (Reed 1997; Clarke 2013). Finally, Gladysvale is considered to have ranged from closed to open vegetation (Berger and Tobias 1994).

Early works on both dental microwear and carbon isotopes were accomplished on this taxon. Grine (1986) and Grine and Kay (1988) suggested that the diet of *Au. africanus* was likely soft fruit and leaves, based on comparisons with chimpanzee microwear. However, later work on isotopes showed that this taxon had a very large range of carbon isotope values that included both C₃ and C₄ plants (Sponheimer and Lee-Thorp 1999; Sponheimer et al. 2005). Sponheimer et al. (2013) suggests that *Au. africanus* may have had greater population densities than forest-dwelling great apes due to their broad dietary patterns. Finally, Copeland et al. (2011) suggest that in *Au. africanus* females dispersed from their natal group, as evinced by strontium isotope analysis of the hominin teeth from Sterkfontein.

Australopithecus garhi

Australopithecus garhi is an enigmatic species of hominin known from a maxilla with complete dentition and postcranial remains from the Hata Member of Bouri, Ethiopia, ca. 2.5 Ma (Asfaw et al. 1999). The habitat of *Au. garhi* was reconstructed as grassy margins around a large freshwater lake, as evinced by high proportions of alcelaphin bovids and water-dependent taxa including hippos and crocodiles. If some Omo specimens are attributable to *Au. garhi*, as suggested by White (2002), this would place *Au. garhi* in a wetter and more heavily wooded environment than it is found in at Bouri (Bobe and Eck 2001; Bobe et al. 2007).

The remains of *Au. garhi* at Bouri are associated with zooarchaeological evidence for butchery and meat consumption. Cutmarks and percussion marks from stone tools were found on bovid and equid bones during the excavation of the BOU-VP-12/1 locality (de Heinzelin et al. 1999). The oldest stone tools occur at Gona about 2.6 Ma and are therefore roughly contemporaneous with the occurrence of cutmarked bones in the Hata Member (Semaw et al. 1997).

Australopithecus sediba

Discovered in August 2008 (Berger et al. 2010), this species appears to combine a more derived dentition with a primitive australopith body plan. Indeed, its generic attribution to *Australopithecus* was questioned during initial publication. Carbon isotopes indicate *Au. sediba* was feeding primarily on C₃ plant resources, and wood or bark has been suggested as a potential component of the diet, based on phytoliths recovered from dental calculus (Henry et al. 2013). It is interesting that *Au. sediba* incorporated no or very few C₄ food in its diet, as this is generally opposite the pattern observed in East Africa *Australopithecus*, with the exception of *Au. anamensis* (Sponheimer et al. 2013), although this may be an artifact of the small sample size of *Au. sediba*, as the Hadar hominins vary greatly in their isotopic signatures and thus the Malapa hominins could be sampling only the C₃-end of the spectrum.

Paranthropus aethiopicus

Arambourg and Coppens (1968) named a new species of hominin, *Paraustralopithecus aethiopicus*, and designated an edentulous mandible from Member C of the Shungura Formation as the holotype. The species was later realized to be the oldest member of the genus *Paranthropus* once the “Black Skull” KNM-WT 17000 was discovered (Walker et al. 1986).

The Omo habitat of *Paranthropus aethiopicus* was likely dry, closed, and wooded, since the lower part of the Shungura Formation shows a shift from wet woodlands in Member B to drier woodlands in Member C (Bobe and Eck 2001). *Paranthropus aethiopicus* has recently been reported from the Ndolanya Beds of Laetoli and is placed into the context of a savanna habitat with nearby woodland (Harrison 2011).

Cerling et al. (2013) found that Turkana Basin specimens of *P. aethiopicus* were characterized by diets high in C₄ content, as C₃ plant material comprised 50 % of the diet or less. Notably, 85 % of the diet of KNM-WT 17000 was found to derive from C₄ resources. This trend apparently continued in the eastern African *Paranthropus* lineage, as *P. boisei* typically exhibits the highest C₄ values of any hominin species for which we have isotopic data.

Paranthropus robustus

This taxon was discovered and named by Robert Broom (1938) at the Kromdraai mining site. Individuals have been recovered since that time at other cave locations in South Africa: Swartkrans, Drimolen, Gondolin, and Coopers D. Habitat reconstructions for these sites (except Drimolen) show them to be open woodland and grassland, although there always appears to be water in the form of rivers or wetlands in the vicinity as represented by the fauna (Brain 1993; Reed 1997; de Ruiter et al. 2009).

Robinson (1954) first suggested that *P. robustus* ate harder and different foodstuffs than *Au. africanus* because of the differences in the morphology of the masticatory apparatus in the two taxa. Grine (1986) tested this hypothesis by examining the microwear of both taxa, concluding that *P. robustus* had heavier

pitting on its molars, and therefore a harder diet. Isotopic data suggest that this species ate a broad range of plant material ranging from trees and shrubs to grasses, i.e., C₃ and C₄. Strontium isotopes also suggest that the female of this species was the sex to leave the natal group, if the smaller teeth represent female individuals (Copeland et al. 2011). Finally, a study by Grine et al. (2012a) suggests that extremely large males of this species may be missing from the fossil record, as a large molar from Gondolin exceeds the size specifications of most other males. These researchers propose that taphonomic biases against these larger individuals have underestimated sexual dimorphism in this species.

Paranthropus boisei

The paleobiology of *Paranthropus boisei* has been the subject of debate since its initial description as *Zinjanthropus boisei* by Louis Leakey (1959). Consequently, more research has been devoted to the dietary and habitat preferences of *P. boisei* than to virtually any other hominin. Leakey dubbed OH 5 “nutcracker man” because of its dished and buttressed face, prominent sagittal crest, huge postcanine dentition, and nubby anterior teeth. Everything about the craniodental morphology of OH 5 seemed adapted for crushing hard, brittle food items with powerful jaw muscles, and this view persisted until relatively recently (e.g., Wood and Strait 2004).

P. boisei has been often linked with a closed and mesic habitat preference (Shipman and Harris 1988) although specimens of *P. boisei* from Konso in southern Ethiopia are associated with an arid grassland fauna (Suwa et al. 2003), similar to the habitat of *P. boisei*'s presumed ancestor *P. aethiopicus* in the Upper Ndolanya Beds of Laetoli (Harrison 2011). Reed (1997) found that *P. boisei* was found in more open environments and that *P. aethiopicus* was associated with closed habitats. At Olduvai, *P. boisei* specimens from Bed I and lower Bed II are associated with woodland environments, although habitats tend to appear wetter in the latter due to the presence of the Olduvai paleolake (Sikes 1994; Kovarovic et al. 2013).

The occlusal microwear of *Paranthropus boisei* is low in complexity and anisotropy values, similar to *Au. anamensis* and *Au. afarensis* (Ungar et al. 2008; Ungar and Sponheimer 2011). The evidence from microwear throws doubt on the title of *P. boisei* as “nutcracker man” and is instead suggestive of a frugivorous diet. Fallback hypotheses have been put forth to explain the discrepancy between the hyper-robust craniodental morphology of *P. boisei* and the evidence from microwear studies. Was *P. boisei* preferentially eating soft and fleshy food resources (i.e., fruits), only consuming harder and more brittle foods during times of resource stress? More evidence is needed, and the carbon isotope data make the story even more puzzling.

Cerling et al. (2011b) revealed that the vast majority of *P. boisei*'s diet was derived from C₄ plant sources, using carbon isotope analysis. *P. boisei* was also a highly water-dependent taxon as evinced by low $\delta^{18}\text{O}$ values, second only to *Hippopotamus* (Cerling et al. 2011b), throwing support behind mesic habitat reconstructions for the species. C₄ sedges are a potential food source based on the carbon and oxygen evidence, as sedges are often found around the perimeter

of East African wetlands today and might also be characterized by relatively low $\delta^{18}\text{O}$ values as they are not subject to evapotranspiration pressures facing other terrestrial plant species (Lee-Thorp, 2011). Similarly, van der Merwe et al. (2008) hypothesized that *P. boisei* at Olduvai Gorge was consuming swampy C_4 vegetation, possibly papyrus.

Kenyanthropus platyops

Kenyanthropus platyops is a curious hominin of uncertain phylogenetic placement from mid-Pliocene sediments in West Turkana, Kenya (Leakey et al. 2001). High proportions of Alcelaphini and Antilopini in members of the Nachukui Formation in West Turkana suggest open and arid habitats throughout most of the sequence (Bobe et al. 2007). However, Leakey and colleagues (2001) reconstructed environments in localities LO4, LO5, LO6, and LO9 of the Lomekwi member as well vegetated and relatively wet in their initial publication of *Kenyanthropus platyops*. They report a high proportion of ecotonal (e.g., *Aepyceros*) and forest-dwelling (e.g., *Tragelaphus*) species relative to taxa of other bovid tribes. The synthetic picture of West Turkana during the mid-Pliocene emerges as relatively arid, with patches of woodland, while development of riverine forests was supported by small fluvial systems draining along the western margin of the basin (Leakey et al. 2001).

Carbon isotopes of *Kenyanthropus* dental specimens reveal a flexible diet similar to contemporaneous *Au. afarensis*, with diets spanning the C_3 to C_4 spectrum (Cerling et al. 2013).

Homo habilis

The Maka'amitalu Basin of Hadar is most notable for producing what is generally accepted as the earliest specimen of the genus *Homo*, a maxilla designated AL 666-1, with in situ Oldowan tools dated to 2.3 Ma (Kimbel et al. 1996). Earlier occurrences from Lake Baringo (ca. 2.3 Ma) and West Turkana (ca. 2.34 Ma) in Kenya have been proposed, but the evidence is fragmentary, consisting of a temporal bone and juvenile lower molar, respectively (Hill et al. 1992; Prat et al. 2005). The origin of the genus *Homo* has often been linked with environmental change, primarily in the form of increasing seasonality and aridification during the late Pliocene. It is thought that increasingly arid terrestrial environments and greater oscillations of climate imposed novel selective pressures on the human lineage during this time. For example, Bobe and Behrensmeyer (2004) note, "The fundamental importance of grasslands may lie in the complexity and heterogeneity they added to the range of habitats available to the early species of the genus *Homo*." Furthermore, Vrba (1985) proposed that an environmentally driven turnover in bovids between 2.7 and 2.5 Ma corresponded to the extinction of *Australopithecus* and the origin of *Homo* and *Paranthropus* in South Africa. Although savannas have been implicated as drivers for various events in human evolution (e.g., encephalization, toolmaking, and bipedalism), the expansion of grassland ecosystems in Africa has most often been implicated in the origin of *Homo*.

The paleoenvironment of AL 666-1 is under current study, but preliminary results suggest relatively open and arid conditions with the presence of nearby

thickets or woodland. Conversely, Reed and Geraads (2012) reconstructed the Busidima Formation locality AL 894 as a woodland-to-forest habitat that was well watered based on a rodent assemblage dated to ca. 2.4 Ma. Given that these two sites are separated by nearly 100,000 years of time, the results are not mutually exclusive. Throughout East Africa, Reed (1997) showed that *Homo* is often associated taxa indicative of open and arid environments. The Olduvai record of *H. habilis* occurs in more heavily wooded environments and the presence of the Olduvai paleolake in lower Bed II provided a permanent water source (Kovarovic et al. 2013).

Specimens of early *Homo* from the Turkana Basin exhibit dietary breadth and were apparently consuming both C₃ and C₄ resources (Cerling et al. 2013).

Conclusions

In his description of the Taung Child, Raymond Dart proposed savannas were a driving force in human evolution, stating that “. . . a vast open country with occasional wooded belts and a relative scarcity of water, together with a fierce and bitter mammalian competition, furnished a laboratory such as was essential to this penultimate phase of human evolution” (Dart 1925). Indeed, researchers have recognized the importance of environments in early human evolution ever since Darwin, traditionally focusing on the faunal context of hominin sites. Taxon-free methods like ecomorphology and isotopes have superseded such approaches and new methods are continually being developed, such as woody cover reconstructions based on carbon fractionation from paleosols (Cerling et al. 2011a).

The habitats of the earliest hominins are somewhat perplexing. Faunal evidence implies *Orrorin* existed in a forested habitat and both species of *Ardipithecus* are associated with fairly closed woodland habitats, while *Sahelanthropus* is purportedly associated with savanna and semidesert conditions along a lakeshore. The accumulating evidence for wooded habitat preferences during the early stages of human evolution is in stark contrast to decades of associating the origin of Hominini (and bipedalism) with the expansion of grasslands during the late Miocene. In contrast, Cerling et al. (2011a) recently resurrected the idea that savanna habitats played a large role throughout the course of human evolution and, in conjunction with growing dietary evidence, that some hominins shifted to C₄-dominated diets by 3.5 Ma.

Sites containing *Australopithecus* are often reconstructed as “mosaics,” but this could be due to time averaging and depositional processes or actually represent various habitats across the landscape. *Au. afarensis* persists at Hadar despite various environmental changes throughout the Hadar Formation (Reed 2008). *Au. afarensis*, and possibly all of *Australopithecus* species, were habitat generalists. The isotopic evidence supports a broad diet for four of these taxa, if one considers that eating both C₃ and C₄ plants indicates something bordering on a generalist diet. While both *Au. anamensis* and *Au. sediba* appear to have consumed only C₃ plant material, the specifics of those C₃ foods are not known, and indeed an impressive

range of plants and plant parts could have made them dietary generalists as well. The microwear evidence presents somewhat of a conundrum when these results are compared with the isotopic data in some species (Grine et al. 2012b; Ungar et al. 2010a). The South African taxa *Au. africanus* and *P. robustus* both exhibit variability in their dental microwear (Grine 1986) that matches the variation in C₃ and C₄ plant foods that they consumed, whereas the East African *Au. afarensis* exhibits extreme uniformity in the microwear scratches on teeth but included both plant types in its diet. It is possible that *Au. afarensis* ate the same types of foods, e.g., roots and tubers, from both C₃ and C₄ plants. In the future, if extraction of phytoliths from dental calculus in these species is possible, a better idea of the actual diet consumed may be available.

The impressive craniodental complex of *Paranthropus* is likely derived from an australopith ancestor ~2.6 Ma that began focusing on some different form of food. This is complicated further by the isotopic differences in the East and South African species. Repetitive loading, i.e., intensive chewing, could provide the adaptive explanation for such headgear. Conversely, various “fallback” explanations have been proposed to explain the discrepancy between microwear, isotopes, and the highly derived craniodental morphology of *Paranthropus* spp., but none is a particularly satisfying explanation. If the massive jaws of *Paranthropus* are in fact adaptations to fallback foods, then it seems likely that *P. robustus* engaged in this behavior more often than *P. boisei*, as the former exhibits pitting and high complexity values indicative of hard-object feeding (Ungar and Sponheimer 2011). As the jaws and teeth of *P. boisei* are even more robust, this is an obvious area for further study.

The role of environments in human evolution is as important as ever, and improving the accuracy of habitat reconstructions is critical as we delve deeper into the autecology of the earliest hominins with the refinement of microwear, isotopes, biomechanics, and other analyses. While it is true that most African habitats are somewhat mosaic in that they contain a diverse vegetation physiognomy, a more careful consideration of taphonomic and depositional biases, especially time averaging, is warranted. For faunal habitat reconstructions, the use of taxon-free methods (e.g., enamel isotopes) over taxon-based methods (e.g., tribal relative abundance) is encouraged because the latter involves considerable assumptions. In closing, while this chapter provided only a brief summary of methods and reconstructions of hominin habitats, the subject is worthy of a lengthier review. New methods are continually being developed and often contradict what we thought we knew about human evolution, and an in-depth synthesis of current lines of evidence would benefit all researchers in paleoanthropology.

Cross-References

- ▶ [Contribution of Stable Light Isotopes to Paleoenvironmental Reconstruction](#)
- ▶ [Geological Background of Early Hominid Sites in Africa](#)
- ▶ [Hominin Paleodiets: The Contribution of Stable Isotopes](#)

- ▶ [Paleoecology: An Adequate Window on the Past?](#)
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- ▶ [The Biotic Environments of the Late Miocene Hominoids](#)
- ▶ [Zoogeography: Primate and Early Hominin Distribution and Migration Patterns](#)

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