

Vertebrate Paleobiology and Paleoanthropology Series



Kaye E. Reed
John G. Fleagle
Richard E. Leakey
Editors

The Paleobiology of *Australopithecus*

 Springer

Vertebrate Paleobiology and Paleoanthropology Series

Edited by

Eric Delson

Vertebrate Paleontology, American Museum of Natural History,
New York, NY 10024, USA
delson@amnh.org

Eric J. Sargis

Anthropology, Yale University
New Haven, CT 06520, USA
eric.sargis@yale.edu

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The Paleobiology of *Australopithecus*

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Edited by

Kaye E. Reed

*School of Human Evolution and Social Change, Institute of Human Origins,
Arizona State University, Tempe, AZ 85287, USA*

John G. Fleagle

*Department of Anatomical Sciences, Stony Brook University, Stony Brook, NY
11794, USA*

Richard E. Leakey

*Department of Anthropology and Turkana Basin Institute, Stony Brook
University, Stony Brook, NY 11794, USA*

Editors

Kaye E. Reed
School of Human Evolution and Social Change
Institute of Human Origins
Arizona State University
Tempe, AZ
USA

Richard E. Leakey
Department of Anthropology and Turkana Basin
Institute
Stony Brook University
Stony Brook, NY
USA

John G. Fleagle
Department of Anatomical Sciences
Health Sciences Center
Stony Brook University
Stony Brook, NY
USA

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Chapter 4

Reconstructing the Habitats of *Australopithecus*: Paleoenvironments, Site Taphonomy, and Faunas

Anna K. Behrensmeyer and Kaye E. Reed

Abstract Hominin paleoecology is reconstructed using many types of evidence from fossils and their geological context. This evidence is limited by vagaries of the fossil and geological record. What questions can be asked regarding *Australopithecus* ecology given these limitations? We address this topic by reviewing the major issues concerning hominin synecology and taphonomy and discuss methods for deriving ecological information from fossil assemblages and their geological context. We provide basic information about the context of the six *Australopithecus* species known from 22 collecting sites and review their environment of deposition and other paleoecological evidence. Using this information we attempt to answer a series of questions, such as whether we can determine the habitat preferences of the different species, and whether more than one *Australopithecus* species shared an ecosystem at any given place and time. We conclude that *Australopithecus* as a genus was eurytopic because of the wide range of well-documented habitat reconstructions, but only *Australopithecus afarensis*, and possibly *Australopithecus anamensis*, have enough time range and fossil material to support the interpretation that these species were eurytopic. The dietary differences between east and south African species are intriguing given microwear analyses differentiating the two groups, although the carbon isotope data are similar. Further evidence of the ecological context of these species is needed and should be standardized using an appropriate scale of evidence (temporal and spatial) for the desired scale of habitat reconstruction.

A. K. Behrensmeyer (✉)
National Museum of Natural History, Department of
Paleobiology and Evolution of Terrestrial Ecosystems Program,
Smithsonian Institution, P.O. Box 37012NHB MRC 121,
Washington, DC 20013-7012, USA
e-mail: behrensa@si.edu

K. E. Reed
School of Human Evolution and Social Change, Institute of
Human Origins, Arizona State University, Box 874101
Tempe, AZ 85287-4101, USA
e-mail: kreed@asu.edu

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Introduction

Ecological adaptations of early hominins and how these changed over time are fundamental to understanding human evolution. Hominin paleoecology can be reconstructed through various types of evidence contained in fossils and their geological context. Basic information about hominin autecology—diet, locomotion, body size dimorphism, etc.—can be inferred from their anatomy and the isotope geochemistry of the fossils themselves. Hominin synecology, i.e., reconstructions of population structure and abundance, habitat preferences and associations with other organisms in natural communities, is more elusive, in large part because hominins are rare components of most fossil assemblages. Much effort has been devoted to inferring hominin habitats based on evidence from associated organisms (e.g., co-occurrence with arboreal mammals indicating that they lived in a forest community) and geological evidence for the physical environments and climatic conditions. Fewer attempts have been made to assess other aspects of hominin paleoecology, such as population structure or abundance relative to other taxa.

What do we want to know about the ecology of *Australopithecus*, and how much of what we would like to know is actually possible, given the limitations of the geological and paleontological record? These two questions provide the framework for this paper, which focuses primarily on synecology and approaches to reconstructing the habitats in which *Australopithecus* lived. We review the major issues regarding hominin paleo-synecology and taphonomy and discuss methods for distilling ecological information from fossil assemblages and their geological context. We draw upon examples from the East African record showing how researchers address various aspects of the ecological life and times of *Australopithecus*, and we also review current interpretations of paleohabitats at

African *Australopithecus* sites. Using different scales of information ranging from documentation of paleoecological features at individual sites to global-scale climate records provide a secondary theme for this paper.

The study of *Australopithecus* synecology draws heavily upon inferred ecological characteristics of animals, particularly mammals that were preserved with these hominins. Information on the sedimentary environments of the sites and taphonomic attributes of these fossil assemblages also is necessary for credible interpretations of the associated fauna. This three-component approach can be applied to habitat reconstructions for particular fossil assemblages and also to document habitat variation relating to mammalian turnover patterns and adaptive shifts associated with different types of habitats. An apparent change in faunal composition through time can be caused by a shift in depositional environment or a change in taphonomic processes that select for or against certain types of organisms and skeletal parts. If these confounding variables can be addressed and corrected for, then it is possible to assess biological processes that caused turnover, such as the dispersal of species out of a region or into a region from elsewhere, by local speciation and extinction events, and changes in the relative abundance of persistent lineages. Conversely, long temporal ranges, broad geographic distributions of species, or stable patterns of relative abundance are useful for identifying the persistence of similar habitats through time or across the landscape. Examination of such patterns in the fossil record can lead to testable hypotheses regarding the interaction of climate change, local and regional tectonic processes, and the living communities of plants and animals, thereby providing ecological information necessary for understanding large-scale processes driving hominin evolution.

We begin by outlining major questions regarding *Australopithecus* paleoecology that, ideally, we would like to answer. We then introduce what is known about the *Australopithecus* fossil record, and present three major integrated approaches to inferring hominin habitats—taphonomy, paleoenvironmental (geological) context, and faunas. This is followed by summaries of current interpretations of *Australopithecus* paleoecology and recommendations for future research to refine and test these interpretations.

Questions About *Australopithecus* Paleoecology

1. What was the range of habitats associated with the genus *Australopithecus*, and is it possible to discern each species' preferred habitat? Did this genus initially live in forests, woodlands, or other types of closed habitats, or was it adapted to a mix of open and closed habitats from its beginnings?
2. What were the important limiting ecological variables (e.g., food, water, shelter, competition with other species, predator avoidance, intra-species interactions) for *Australopithecus*?
3. Did the habitats occupied by *Australopithecus* species vary across different regions? Was there more than one *Australopithecus* species sharing an ecosystem at any one place and time? How did the later species of *Australopithecus* co-exist with *Paranthropus* and early *Homo*?
4. Was *Australopithecus* a maker and user of stone tools? Did any *Australopithecus* species incorporate significant meat into its diet?
5. Is there evidence of change through time in a habitat where the same species continued to exist? Did niche breadth increase or decrease within the genus *Australopithecus* as it evolved?
6. How might global or continental-scale climate change between 4.5 and 2.0 Ma have affected the paleoecology of *Australopithecus*? What was happening in the environments of southern versus eastern versus central Africa, and how do these regional variations compare with later African climate changes associated with northern hemisphere glaciation?

These questions represent both possible and impossible goals for what we can expect to learn from the fossil record. Answers to many of them depend on both autecological and synecological evidence. Anatomical data, dental microwear, and isotopic readings from the hominin fossils themselves address some of the critical questions regarding australopithec autecology—i.e., what these hominins were functionally capable of (morphology) and what they actually did in terms of substrate use, resource use, and other behaviors (microwear, isotopes, etc.). We do not attempt to review the vast array of such autecological evidence in this paper. Instead, we focus on geological context, taphonomic analysis, and associated fauna, which provide evidence for: (1) the physical environments and vegetation habitats occupied by *Australopithecus*, (2) taphonomic processes that affected their skeletal remains in the transition from biosphere to lithosphere, and (3) their distribution through time relative to changes in paleoenvironments and other organisms. Sampling biases, especially those relating to differential preservation of species and time-averaging, limit what we can know about synecology (see examples below). One of taphonomy's important contributions is to indicate what questions can be realistically pursued with the

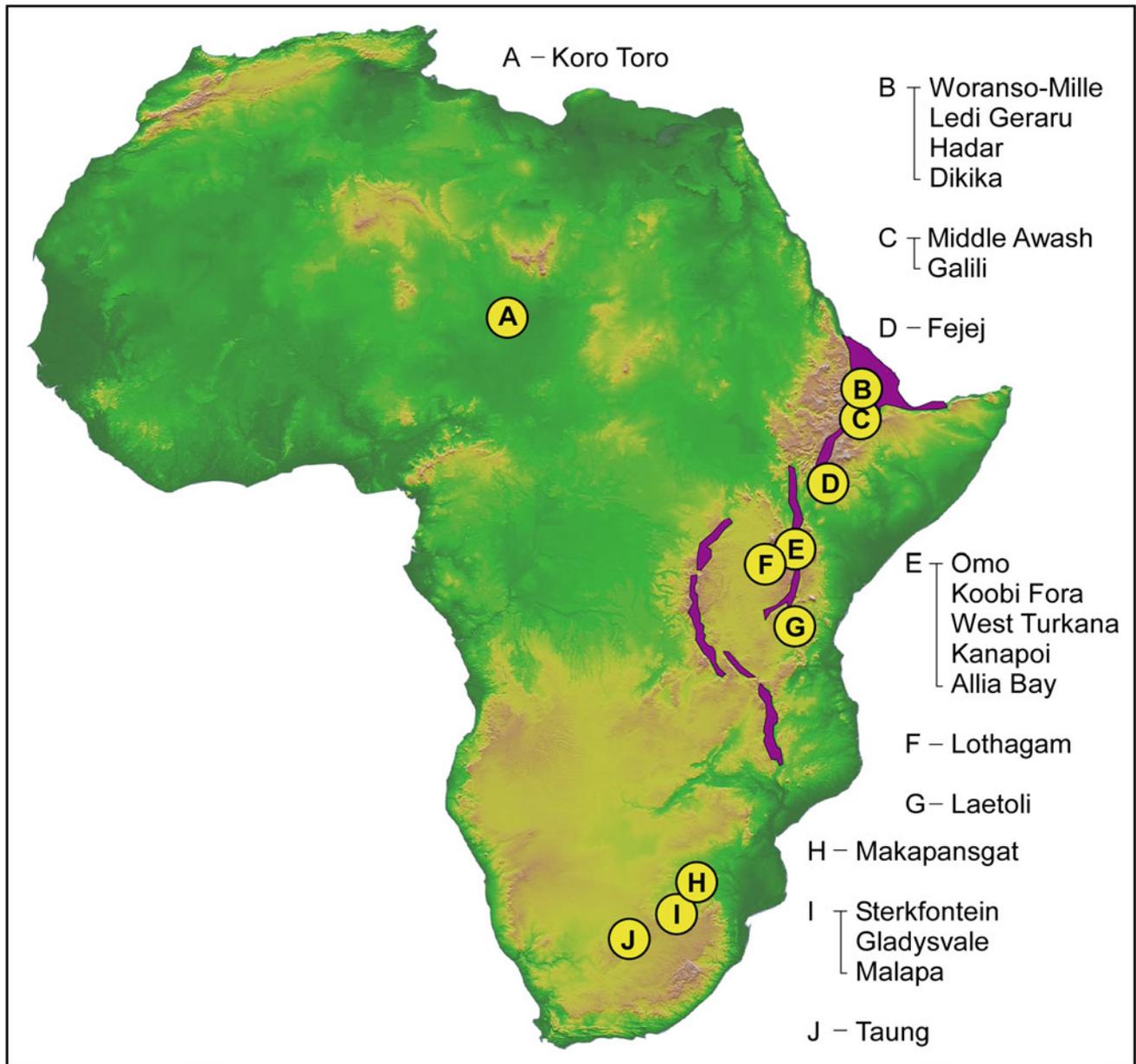


Fig. 4.1 Map of Africa showing regions and sites in Table 4.1

evidence we have, or are likely to have, from multi-disciplinary field and laboratory research.

What We Know: The Basics

At present, six species of early *Australopithecus* have been named from three sub-continental regions and ~22 collecting sites on the African continent (Figs. 4.1, 4.2; Table 4.1). Remains are relatively abundant in some of these sites, including Hadar (Ethiopia) and Sterkfontein

(South Africa), fewer but relatively complete in some such as Malapa (South Africa), and sparse and fragmentary in many others. In some cases, fragmentary hominin remains from the currently documented range of *Australopithecus*, i.e., between ~4.2 and ~2.0 Ma, cannot be certainly identified as belonging to this genus (see Table 4.1). Much of what we currently know about the site taphonomy and paleoecology of *Australopithecus* is based on a sub-sample of these sites, including the greater Awash Basin (Hadar, Maka, Asa Issie, Dikika, Woranso-Mille, Bouri), Laetoli, and the South African cave sites (Makapansgat, Sterkfontein).

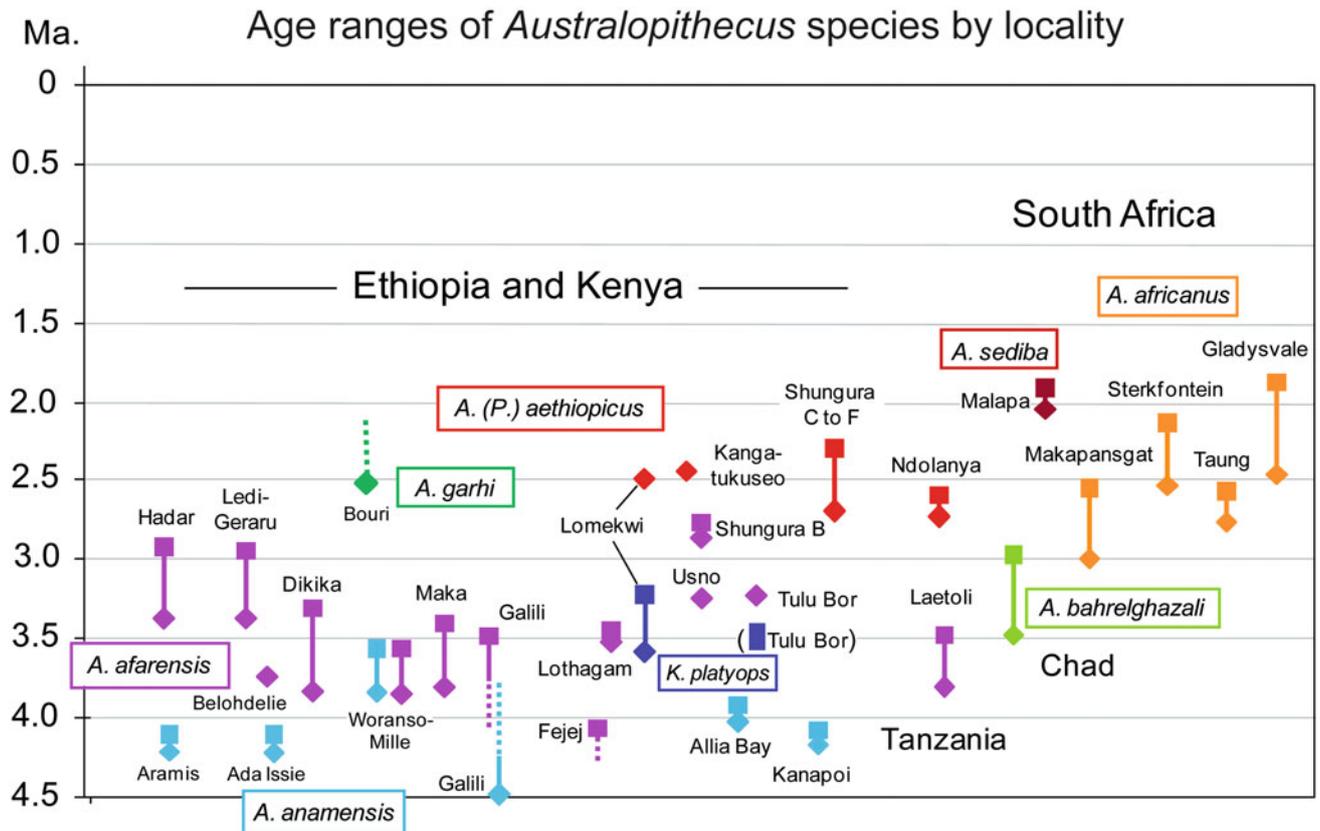


Fig. 4.2 Chronostratigraphic ranges of species of the genus *Australopithecus* (color coded) based on information from published hominin-bearing deposits. Dashed lines indicate uncertainty in range limit. See Table 4.1 for references

Documented Depositional Contexts for *Australopithecus*

- Volcaniclastic plains and paleosols (Laetoli)
- Fluvial channels and floodplains (Lothagam, Kanapoi, East and West Turkana, Omo Shungura Formation, Hadar, Dikika, Middle Awash)
- Lake margins (East and West Turkana, Hadar, Middle Awash, Chad)
- Karst terrain and cave deposits (Makapansgat, Sterkfontein, Taung, Gladysvale, Malapa).

Scales and Types of Evidence for *Australopithecus* Ecology

The evidence from geological and fossil records includes a wide range of temporal and spatial scales, each of which can provide different types of information bearing on hominin paleoecology (see also Table 4.2):

- *Footprints* preserve an instant in time, evidence for hominin behavior such as foraging and social behavior,

and ecological characteristics of contemporaneous (i.e., within hours to days) flora and fauna.

- *Partial skeleton(s)* anatomically informative, represents the life span of an individual, and if associated in a contemporaneous death assemblage may provide information on group structure.
- *Excavation* (10^{1-4} m²) provides detailed evidence of the burial environment and circumstances of the hominin and any contemporaneous associated fauna and flora, usually within a short period of time-averaging ($\sim 10^1-10^3$ years).
- *Surface assemblage* Fragmentary bones and teeth of single individuals collected from a surface fossil assemblage derived from one or more eroding sedimentary layers; each specimen represents the life and death of a single individual but the combined (time-averaged) faunal assemblage may represent $\sim 10^2-10^5$ years.
- *Locality* (e.g., 10^4-10^6 m²) general paleoenvironmental context and associated fauna from a limited area and stratigraphic thickness.
- *Collecting area, stratigraphic member or sub-member* more time and space typically represented in the combined fossil evidence from these entities, e.g., 10^4-10^5 years.

Table 4.1 Pliocene sites in Africa with fossils assigned to the genus *Australopithecus*, including some for which these records are not certain based on fragmentary remains, or are likely but not yet published

Collecting area	Sites	Country	Habitat interpretation	Lower age	Upper age	Taxon	References
Northern Awash Basin	Hadar	Ethiopia	Bushland, open woodland, wooded grassland	3.4	2.9	<i>A. afarensis</i>	Campisano (2007), Campisano and Feibel (2008), Reed (2008)
Northern Awash Basin	Dikika	Ethiopia	Woodland, open grasslands	3.8	3.4	<i>A. afarensis</i>	Alemseged et al. (2006), Wynn et al. (2006)
Northern Awash Basin	Ledi-Geraru	Ethiopia	Bushland, open woodland, wooded grassland	3.4	2.95	<i>A. afarensis</i>	Geraads et al. (2012)
Northern Awash Basin	Woranso-Mille	Ethiopia	Mix of riparian forest, open woodland, grassland	3.8	3.57	<i>A. anamensis</i> , <i>A. afarensis</i>	Haile-Selassie et al. (2010a, b)
Middle Awash Basin	Asa Issie	Ethiopia	Closed to grassy woodland	4.2	4.1	<i>A. anamensis</i>	White et al. (2006)
Middle Awash Basin	Aramis	Ethiopia	Grassy woodland savanna	4.2	4.1	<i>A. anamensis</i>	White et al. (2006)
Middle Awash Basin	Maka	Ethiopia	Woodland-bushland	3.78	3.42	<i>A. afarensis</i>	White et al. (1993)
Middle Awash Basin	Bouri	Ethiopia	Lake margin with grasslands	2.52	2.1?	<i>A. garhi</i>	Asfaw et al. (1999)
Middle Awash Basin	Belohdelie	Ethiopia	No information	3.7?	3.7?	<i>A. afarensis</i>	Asfaw (1987)
Southern Awash Basin	Galili	Ethiopia	Woodland to bushland	4.5	3.5	<i>A. anamensis</i> , <i>A. afarensis</i>	Kullmer et al. (2008)
Turkana Basin	Fejej	S. Ethiopia	No information	4.2?	4.06	<i>A. afarensis</i> ?	Kappelman et al. (1996)
Turkana Basin	East Turkana	Kenya	Riparian forest, wet grassland, woodland	4.3	2.7	<i>A. afarensis</i>	Kimbel (1988), Brown et al. (2013)
Turkana Basin	East Turkana – Allia Bay	Kenya	Mosaic of closed woodland and open grasslands	4.1	3.8	<i>A. anamensis</i>	Macho et al. (2003), Schoeninger et al. (2003)
Turkana Basin	West Turkana	Kenya	Woodland and forest- edge; riparian woodland	4.3	2.5	<i>A. afarensis</i> , <i>Kenyanthropus platyops</i> , <i>Australopithecus</i> sp.	Brown et al. (2013), Leakey et al. (2001)
Turkana Basin	Lothagam	Kenya	Mix of riparian forest, open woodlands, grassland	6.5	5.5	<i>A. afarensis</i> ?	Hill et al. (1992), McDougall and Feibel (1999)
Turkana Basin	Lothagam	Kenya	Open, seasonally dry	3.5	3.5	<i>A. afarensis</i>	Leakey and Walker (2003)

(continued)

Table 4.1 (continued)

Collecting area	Sites	Country	Habitat interpretation	Lower age	Upper age	Taxon	References
Turkana Basin	Kanapoi	Kenya	Mix of wooded and open grassland	4.17	4.07	<i>A. anamensis</i>	Harris et al. (2003)
Turkana Basin	Omo (Shungura, Usno)	Ethiopia	Riparian forest and woodland	3.44	2.44	<i>A. afarensis?</i> <i>A. garhi?</i>	Brown et al. (2013), Suwa et al. (1996), White (2002)
Laetoli	Laetoli Fm.	Tanzania	Mosaic of woodland, shrub-land, bushland, grassland	3.8	3.5	<i>A. afarensis</i>	Harris et al. (1987), Su and Harrison (2008), Kovarovic and Andrews (2007)
Bahr el Ghazal		Chad	Open grassland and lake margin	3.5	3	<i>A. bahrelghazali</i>	Brunet et al. (1996)
Cave	Sterkfontein	South Africa	Open woodland, riparian forest, bushland	2.8	2.2	<i>A. africanus</i> , <i>A. sp?</i>	Clarke (2013), Herries et al. (2013)
Cave	Makapansgat	South Africa	Mosaic of riparian woodland, bushland, edaphic grassland	3.5	?	<i>A. africanus</i>	Dart (1952), Reed (1997), Herries et al. (2013)
Cave	Taung	South Africa	Dense woodland	3	2.0?	<i>A. africanus</i>	Dart (1925), Berger and Clarke (1995)
Cave	Gladysvale	South Africa	Closed/open vegetation	2.5	1.9	<i>A. africanus</i>	Berger and Tobias (1994)
Cave	Malapa	South Africa	No information	2.1	~1.9	<i>A. sediba</i>	Berger et al. (2010), Dirks et al. (2010)

- *Basin* a tectonic depression that has accumulated a thick sequence of sedimentary deposits, representing 10^5 – 10^6 years and providing information on environmental and paleontological change through time for one sub-region.
 - *Region* tectonic and latitudinal context, comparisons of different hominin-bearing (and non-hominin-bearing) habitats through time or across space.
 - *Continent* range of environments, latitudes, habitats, first and last appearances of hominin species.
 - *Global* climate variation over space and trends and/or cycles through time.
1. Small samples of fragmentary remains for any given hominin taxon may not represent the average or modal characteristics of that taxon.
 2. Even in large samples, selective preservation of hominin population sub-samples, such as robust individuals and/or body parts, could skew the range of body sizes and anatomical features that are available for collection and study relative to the once-living populations.
 3. Available samples of depositional and paleogeographic contexts where fossil remains of this large-sized primate occur are likely only partially representative of the range of habitats and geographic areas where it actually lived.
 4. Available assemblages of associated fossil mammals and hominins represent different degrees of time-averaging and spatial sampling from the original ecosystems. This blurs the meaning of “paleocommunity” and may bias comparisons of diversity and other ecological properties in faunas from different areas, depositional settings, and time periods (including comparisons to modern faunas).
 5. Ecological indicator species may be unevenly preserved in the fossil record or are difficult to interpret in terms of their ecological requirements, either due to lack of modern analogues or to missing body parts.

Paleoenvironments, Taphonomic Biases and Research Strategies

The paleontological record is imperfect, and taphonomy often has to provide “reality checks” on assumptions about the biological fidelity of this record and what we can and cannot know about the past. For australopiths, these limitations may result from the following potential sources of bias:

Table 4.2 Types of evidence relating the paleoecology of *Australopithecus*, at increasing spatial and temporal scales, with examples of autecological and synecological data that can be inferred from this evidence

Evidence	Temporal scale	Spatial scale	Examples	Autecology of hominins	Synecology of hominins
Trackways	Seconds, minutes	10^0 – 10^1 m	Laetoli footprint layers	Presence in specific habitat, on a specific substrate, behavioral information	Contemporaneous fauna, within hours to days
Single individual with associated skeletal parts	Lifetime of the individual	Habitat of the individual	Sterkfontein “Little Foot”, Hadar “Lucy”, Dikika “Salem”	Taxonomic, ecomorphic, isotopic information on body size, diet, locomotion, etc.; burial environment	Taphonomic evidence of scavengers, trauma in life (e.g., damage to teeth)
Multiple associated individuals of a single taxon	Combined life span of individuals in the group	Habitat of group	Hadar “First Family”, South African Malapa site(?)	Sexual dimorphism, demography, body size, diet, locomotion, burial environment and circumstances	Taphonomic evidence of scavengers, trauma in life (e.g., damage to teeth)
Single or multiple hominin specimens from a locality, collecting area, or well-defined stratigraphic interval	10^3 – 10^5 years	Habitat area sampled by organic remains, e.g., 10^2 – 10^5 km ²	South African cave sites, East Turkana, West Turkana, Lothagam, Kanapoi, Hadar, Bouri, Chad, Laetoli, etc.	Habitat based on ecomorphology of associated fauna and/or co-occurrence with specific ecological indicator taxa	Community structure and ecological preferences inferred from co-occurring vertebrate taxa
Combined sample from a geological formation and region	10^5 – 10^6 years	Area covered by fossiliferous deposits and their source areas, e.g., 10^4 – 10^6 km ²	Hadar, Middle Awash, Omo, East and West Turkana, Lothagam, Kanapoi, Sterkfontein, Makapansgat	Persistence, abundance, disappearance of individual hominin taxa through a stratigraphic interval	Through-time patterns of mammalian taxonomic richness, major group dominance, evenness, relationships to environmental parameters, evidence for immigration events
Basin with a thick, partially continuous stratigraphic record	10^5 – 10^6 years	Basin-scale	Turkana Basin, Awash Basin (Afar Depression)	Depositional context, taphonomy, and ecomorphology of hominin specimens within a single basin through time	Variation in time and space of faunas and paleocommunities, correlation with shifting physical environments
Region with multiple localities and sequences	10^5 – 10^6 years	Sub-continental scale	East Africa, South African Cave Sites	Variation in depositional context, taphonomy, and ecomorphology of hominins among regions	Variation in mammalian diversity and community structure in different tectonic settings, latitudes, climatic zones

We can address the problems above with taphonomic and paleoenvironmental data in a variety of ways. Obviously, more data collecting and the opening up of new areas will help with points (1) and (3), though there will never be enough fossils to resolve many finer-scale questions about regional variation and hominin occupation of areas lacking a paleontological record (i.e., most of the African continent). Understanding the limitations of the samples that we have, however, is a big step toward learning how effectively to tackle the

questions that can be answered with the data in hand. There are ways to calibrate the degree of bias in the preservation of different body parts, body sizes, and taxa in order to address Point (2) above. An “isotaphonomic” approach that compares samples from specific, well-documented paleoenvironmental contexts such as fluvial channel lags or lake margin paleosols can help to control for ecological and taphonomic variables that differ across environments (Points (3) and (4)). The use of “taphonomic control” taxa, i.e., species with body

Alternative Scenarios for Fossil Assemblage Formation at Kanapoi

Australopithecus anamensis

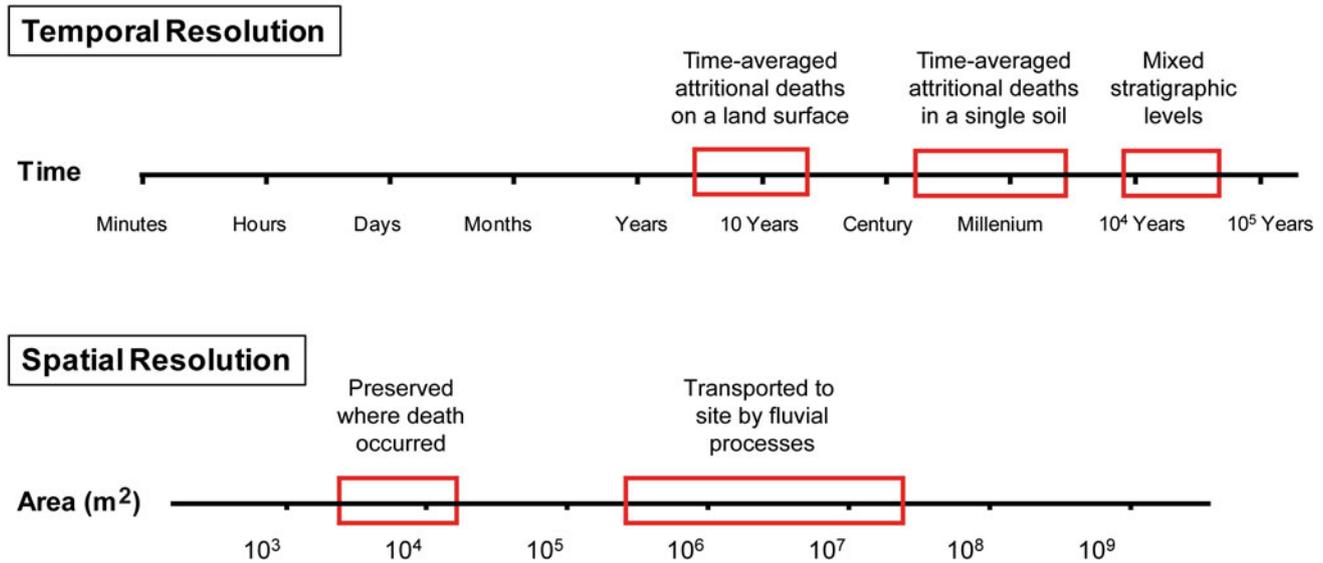


Fig. 4.3 Scale bar showing the different amounts of time-averaging implied by the paleosol context of each of the two levels at the Kanapoi *Australopithecus anamensis* site (left gray box) and the

combined sample of hominins and associated faunal remains from both levels (right gray box)

size and morphology similar to hominins, such as baboons, can help to identify variations in abundance of species that are more likely to be biologically meaningful rather than taphonomically altered (Point (5)).

The “taphonomic control” approach was used to compare similar-age portions (Sidi Hakoma (SHT) and Tulu Bor tuffs) of the Hadar and East Turkana sequences (Behrensmeyer et al. 2004). *Australopithecus* is common at Hadar and rare at East Turkana, but is this the effect of a smaller fossil sample at East Turkana or a bias against primate preservation in this area? In both areas, the extinct baboon *Theropithecus* and *Australopithecus* co-occur through the 3.4–2.8 Ma time interval. Similar controlled survey fossil samples from these two areas indicate that, relative to the number of specimens of *Theropithecus* and other large monkeys recorded in the Hadar Formation and the Tulu Bor Member of the Koobi Fora Formation, there should be 2.5 hominin specimens in the East Turkana sample *if* hominins were as common relative to baboons as they are at Hadar (Behrensmeyer et al. 2004). However, only one hominin (a tooth fragment) was found in the Tulu Bor Member. This suggests (but does not prove) that *Australopithecus* was less common in the East Turkana region around 3.4 Ma than at Hadar. More tests of this kind could improve understanding

of taphonomic versus ecological causes of hominin fossil abundance.

Two Examples of Site-Based Studies of *Australopithecus* Habitats

The types of evidence that feed into habitat reconstructions, as well as the limitations on inferences imposed by the fossil record, are illustrated in the following two examples of well-studied *Australopithecus* sites in East Africa.

Kanapoi

The Kanapoi locality in the southwestern Turkana Basin, Kenya, provides evidence for the paleoecology of *Australopithecus anamensis*, primarily from fossils preserved in fluvial sands and paleosols deposited within a time interval between 4.17 and 4.07 Ma (Harris et al. 2003). These deposits lie above and below a lacustrine interval, and the fauna is a time-averaged sample from two similar alluvial

land surfaces (paleosols) that may have been formed tens of thousands of years apart (Fig. 4.3). Ecodiversity analysis of the faunas indicates that the two levels are only slightly different in terms of the percentage of terrestrial (ground-dwelling) mammals and the percentage of fresh grass grazers, i.e., mammals eating more water-dependent/seasonal wetlands grasses (Harris et al. 2003: Figs. 32 and 33; Behrensmeyer et al. 2007). The combined fauna is used to characterize the paleoecology of Kanapoi at the time of *A. anamensis* and is interpreted as a closed woodland habitat based on comparisons with analogue environments using ecological structure analysis (Reed 1997). Other lines of evidence suggest the existence of open habitats as well, based on stable isotopic signals in tooth enamel, possible non-arboreal monkeys, and micromammals, and characteristics of the paleosols (Wynn 2000; Manthi 2006). Whether these different habitat types were associated with each other across space, representing a persistent mosaic environment, or changed through the interval of time-averaging cannot be resolved with these analyses.

The amount of time represented by the Kanapoi faunal samples is clearly long by modern ecological standards and could include numerous habitat shifts across the areas of fossil accumulation. Also, the characteristics of the soils are superimposed on parent sediment that could represent ecological circumstances different from those during the period of pedogenesis. The Kanapoi *A. anamensis* remains (Leakey et al. 1995) could have been buried (1) during the initial sedimentary event(s), (2) during the early stages of pedogenesis affecting this parent material, or (3) later in the hundreds to thousands of years represented in the two fossiliferous units (Behrensmeyer et al. 2007).

Was *A. anamensis* associated with closed woodland, more open areas, or a mix of these habitat types? This is an important question from the standpoint of hominin evolution because it would indicate either habitat flexibility or specificity at ~4.2 Ma. In the case of shifting habitats through time, *A. anamensis* and other species could be closely tied to one habitat versus another, but still occur as mixed-habitat fossil assemblages. In the case of a mosaic of both closed and open habitats, species would have more opportunities, and perhaps also more selective pressure, to adapt to a variety of contemporaneous resources and substrates.

The Kanapoi hominins and associated fauna provide one of the most age-constrained and carefully documented examples of paleoecological evidence available at present, but it is still not possible to discriminate between alternative habitat models because of the amount of ecological time represented by the combined faunal sample. Mixed-habitat faunas do not necessarily mean mixed-habitat adaptations for the species on the faunal list. To improve temporal resolution, we need better ways of assessing the relative probabilities of these alternatives, such as more precise

documentation of the depositional and taphonomic history of the fossil remains in each of the source paleosols, or stable isotope data from hominin and associated mammals' tooth enamel (Levin et al. 2011).

Hadar A.L. 333: Environmental Context of the "First Family" Locality

This example shows how the combination of detailed geological analysis and information from associated faunas contribute to reconstructing the context of an important accumulation of at least 15 *Australopithecus afarensis* individuals (W. Kimbel, personal communication). The A.L. 333 locality in the Denen Dora Member of the Hadar Formation is dated at ~3.2 Ma and has produced over 260 surface and excavated specimens of *A. afarensis* (Behrensmeyer et al. 2003; Behrensmeyer 2008; Harmon et al. 2003). Most of the hominin fossils were collected along with other faunal remains from an area of approximately 40 m × 80 m (3200 m²) on steep slopes up to the stratigraphic level of 19 excavated specimens. It has long been assumed that the surface hominin fossils were derived from the same sedimentary unit as the in situ remains, and that this unit was part of a distinct, carbonate-rich paleosol (Aronson and Taieb 1981). Further study has shown that the in situ hominin fossils were buried prior to the formation of overlying paleosols (Behrensmeyer 2008).

Preserved bedding structures in the fine-grained, hominin-producing strata provide evidence that the abandoned channel swale continued to aggrade before sustained pedogenesis. The reconstructed paleodrainage of the DD-2 sandstone is oriented south to north with a trunk channel ~40 m wide and 3–5 m deep connecting a tributary system south of A.L. 333 to a distributary system to the north, which likely ended on the deltaic plain associated with the basin's depositional center. The burial of the hominin remains in the upper part of the channel involved fine-grained deposition indicating low-energy, seasonal flood events, and there is no sedimentological evidence for a high-energy, catastrophic flood that caused the demise of the hominins (Behrensmeyer 2008).

Although there is no direct record of vegetation at the A.L. 333 site, other than CaCO₃ root casts associated with pedogenesis, palynological research in the lower Denen Dora Member (DD-1 sub-member) suggests that the regional habitat prior to DD-2 and A.L.333 was predominantly a dry grassland (Bonnefille et al. 2004). Researchers (Aronson and Taieb 1981; Bobe and Eck 2001; Reed 2008) note that fossils of the genus *Kobus* (waterbuck) and other reduncines, which indicate moist substrates with "fresh grass" forage (Reed 1997), are common in the Denen Dora

Alternative Scenarios of Fossil Assemblage Formation for Hadar A.L.333

Australopithecus afarensis

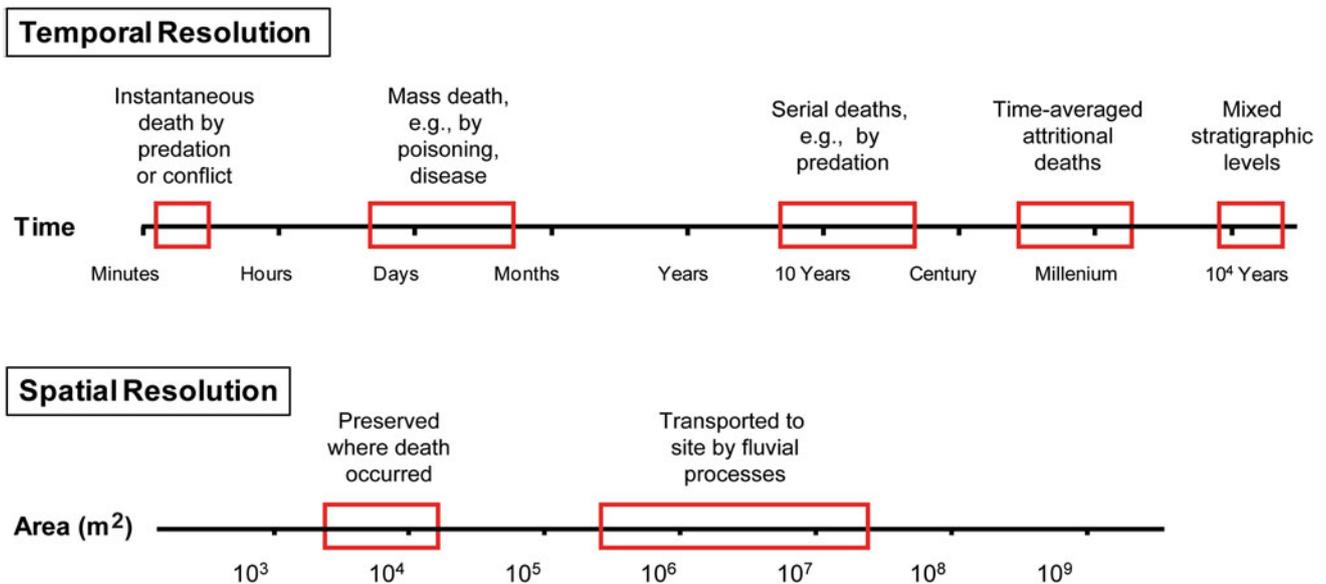


Fig. 4.4 Scale bar showing the different amounts of time-averaging that would be implied by alternative scenarios for the taphonomic origin of the A.L.333 *A. afarensis* assemblage. The biological and

behavioral meaning of this as a population sample depends on which scenario is supported by paleoenvironmental context and taphonomic evidence

Member. Recent geo-faunal analysis by Campisano (2007; Campisano and Feibel 2008) indicates paleogeographic differences in the DD-2 sub-member, with edaphic grasslands and marshy conditions to the east and more closed, bush or woodland habitats to the west in the vicinity of A.L. 333. This agrees with stable isotope analysis of pedogenic carbonates at the excavation site indicating 30–34 % C_4 grassland (Hailemichael 2000), which is a relatively low proportion of grass compared with Hailemichael's other samples from the Denen Dora Member.

The in situ hominin remains at A.L. 333 can be related to a death—and possibly life—association of multiple hominin individuals with an abandoned channel swale that crossed an alluvial plain several kilometers from a paleolake to the north or northeast. The combined evidence indicates that both wooded and open grassland habitats were present in the DD-2 sub-member (Reed 2008), with a gradient from more closed in the west to more open edaphic grasslands to the east (Campisano 2007; Campisano and Feibel 2008). Hominins and other animals may have moved along linear depressions left by abandoned channels when they ventured across open savanna environments or used such areas for foraging and shelter. Therefore, as in the Kanapoi example, it is difficult to specify either open grassland or more bush

to woodland as a “preferred” habitat for the A.L. 333 *A. afarensis*; the conservative interpretation is that they were associated with a mix of these types of vegetation.

Paleoenvironmental context provides only part of the history of the A.L. 333 hominin assemblage, and ongoing research is investigating alternative scenarios for the accumulation of the hominins based on taphonomic evidence from the fossils themselves, their spatial patterns of preservation, and co-occurring organisms (Behrensmeyer et al. 2003; Harmon et al. 2003). These scenarios cover a range of temporal scales and processes of death and burial (Fig. 4.4) and additional taphonomic analysis likely will shed new light on the paleoecology of this unusual fossil hominin accumulation.

Using Faunas to Infer Hominin Habitats

Today African habitats range from rain forests to deserts. The amount of rainfall, temperature, sunlight, evapo-transpiration, soil type, landscape physiography, and weather patterns/seasonality are the abiotic factors that cause differentiation in habitats. Floras and faunas are sensitive

indicators of these environmental conditions, even on a relatively small spatial scale. Thus, ecological analysis of fossils provides a window into past habitats, which in turn can be used to reconstruct climatic conditions (Archibold 1995; Andrews 2006). In the tropical belt, the seasonal pattern and the amount of rainfall are the most important determining factors of the vegetation physiognomy (Hawkins et al. 2003). Habitats of various types often occur together in a particular spatial region because of changes in soil types, subterranean water, etc. For example, it is possible to have forests along rivers adjacent to near desert-like habitats, a condition that occurs where the present-day Awash River flows through the Afar hominin fossil beds in Ethiopia. These habitats are either called ecotonal or mosaic. Often mosaic habitats are indicated by ecological analysis of fossil assemblages; if this is due to time averaging of shifting habitats then the reconstruction of a contemporary mosaic of habitats could be incorrect. On the other hand, varying faunal compositions from time-synchronous collections over a broad spatial area, would lend support to the interpretation of a mosaic habitat structure. Occasionally, it is possible to reconstruct the habitat associated with hominin remains in a small spatial region and arrive at an interpretation for a non-mosaic (homogeneous) habitat at this scale (e.g., White et al. 2009).

Patterns of species occurrence at particular sites and their persistence and turnover through stratigraphic successions, combined with ecomorphic features of these species, provide evidence for ecological characteristics of hominin species and even for different populations of the same species (e.g., *A. afarensis* at Laetoli and Hadar; Su and Harrison 2008). Regional patterns can be combined in studies of larger-scale biogeographic and ecological patterns across the African continent. When compared with independently documented habitat shifts, species turnover patterns at individual sites may provide information on the eurytopic (“adaptable”) and stenotopic (“specialized”) nature of lineages, including hominins. One might expect that eurytopic species would occur consistently through time, despite habitat shifts, and across the landscape in a variety of habitats. In contrast, stenotopic species may only be recovered if particular habitats are sampled and may be consistently fewer in fossil assemblages, perhaps suggesting movement in and out of regions through time in response to habitat fluctuations. Over time stenotopic lineages may exhibit higher extinction and diversification rates (Vrba 1980; Badgley et al. 2008).

Because of collection practices, time-averaging, and spatial restrictions, it is probable that most fauna-based habitat reconstructions of Pliocene hominin localities represent a temporal (time-averaged) scale of 10^4 – 10^5 years, as illustrated in the Kanapoi example above, a relatively coarse level of resolution that may incorporate numerous

shorter-term ecological shifts. On the other hand, reconstructions based on paleosols and pollen from specific sites may signal habitats of small area or short duration that may or may not be associated with the place and time where the sampled vertebrate fauna or hominins actually lived.

Paleoecological Evidence and Current Interpretations of *Australopithecus* Sites

The following section reviews various *Australopithecus* taxa (Table 4.1) and the information that is known about the paleoecological context of each locality.

Sites with Hominins of Uncertain Taxonomic Assignment

- *Lothagam Hill, Kenya*. There is abundant fauna from Lothagam, but hominins are very rare throughout the 7.0–3.5 Ma time span. Only two teeth are known from ~6.5–5.5 Ma in the upper Nawata Formation and one poorly preserved mandible from the overlying Apak Member of the Nachukui Formation (Leakey and Walker 2003). The bovid fauna of the upper Nawata is dominated by aepycerotins, alcelaphins, and reduncins, indicating a mix of gallery forest, open woodlands and grasslands. Fewer alcelaphins and more tragelaphins in the Apak Member as well as an increase in colobines provide evidence for a more closed habitat at ~5.0 Ma (Leakey and Harris 2003), although $\delta^{13}\text{C}$ analysis of Apak Member bovid tooth enamel indicates a significant component of C_4 vegetation (Cerling et al. 2003). The loss of *Etheria* (oyster) reefs in the Apak Member indicates a change to an ephemeral flow regime. Carbon isotope analysis of pedogenic carbonates and tooth enamel through the Lothagam succession indicates “a mosaic ecosystem with stands of pure C_3 vegetation interspersed with mixed C_3/C_4 floras” but no pure C_4 grasslands (Cerling et al. 2003). Given the number and excellent preservation of other mammalian fossils, the scarcity of hominins throughout the Nawata Formation indicates this group was rare to absent in Lothagam’s late Miocene paleocommunity (Leakey and Harris 2003).
- *Omo (Shungura Formation), Ethiopia*. There are thousands of faunal specimens from this locality, largely consisting of isolated teeth, including some attributed to *Australopithecus* (Suwa et al. 1996) or more recently to *Australopithecus garhi* (White et al. 2002). Through the 1.2 Myr of likely *Australopithecus* occupation of this environment, the fossils

derive from fluvial depositional settings associated with the paleo-Omo River. The habitats associated with the hominins include riparian forest and woodland habitats from 3.2 to 2.0 Ma; alcelaphins and antilopins are a notably small component of the fauna during this time, indicating that open grassland habitats were limited in extent in the paleo-Omo River Valley (Bobe and Eck 2001; Bobe et al. 2002; Alemseged et al. 2007).

- *West Turkana, Kenya.* A number of hominin remains are identified as *A. afarensis* (Leakey et al. 2001), and at least 42 catalogued, but unpublished, specimens are assigned to *Australopithecus* (E. Mbua, personal communication). The fossils are mostly teeth from above the 3.4 Ma Tulu Bor Tuff, in the Lomekwi Member of the Nachukui Formation. *Kenyanthropus platyops* also occurs in the Lomekwi and underlying Kataboi Member, indicating the presence of two contemporaneous hominin genera. Based on the bovid fauna, the habitat of the lower through upper Lomekwi members has been interpreted as a mosaic dominated by woodland and forest-edge vegetation (Harris et al. 1988; Leakey et al. 2001). This is supported by abundant *Theropithecus brumpti*, a species regarded as indicating more closed habitats than *T. darti*, which is common in the contemporaneous Hadar Formation in Ethiopia (Leakey et al. 2001).

A. bahrelghazali

- *Bahr el Ghazal, Chad.* This site is dated between 3.0 and 3.5 Ma and is the only central African site from which any *Australopithecus* species has been recovered. The fauna associated with this hominin lacks tragelaphins and aepycerotins but has abundant alcelaphins, reduncins, and antilopins, indicating open grassland and lake margin habitats (Geraads et al. 2001).

A. anamensis

- *Allia Bay, Kenya.* Hominin remains consisting mostly of isolated teeth are preserved in a fluvial channel lag context associated with the base of the Moiti Member at ~4.0 Ma. Based on analysis of stress lines in the enamel of fossil herbivore teeth from this channel deposit, Macho et al. (2003) suggest that the habitat of *A. anamensis* was quite seasonal and similar to Masai Mara in Kenya today. Schoeninger et al. (2003), using carbon and oxygen stable isotope analysis of tooth enamel, infer a mosaic habitat of closed woodland and grasslands with higher rainfall than the region receives today.

- *Kanapoi, Kenya.* A total of 59 specimens of *A. anamensis* have been reported from this locality. The abundant associated fauna is derived from floodplain paleosols and distributary sands that span an estimated total time period of about 100 kyr (see earlier discussion about Kanapoi time-averaging and habitat reconstruction) (Harris et al. 2003). Faunal eco-diversity analyses of these two levels are similar and indicate either wooded habitat or a mosaic with wooded and more open areas, while stable isotopes, the possible non-arboreal monkeys, and micromammals indicate presence of open grasslands. Wynn (2000) suggests, based on the characteristics of the paleosols where hominin remains were recovered in situ, that *A. anamensis* at least occasionally was associated with open conditions within a spatially variable ecosystem, typified by a mosaic of habitats, ranging “from forb-dominated edaphic grassland to gallery woodland, providing a larger view of the mixed ecosystem in which *A. anamensis* lived.”
- *Aramis and Asa Issie, Ethiopia.* White et al. (2006) recovered *A. anamensis* from two localities near Aramis in the Middle Awash. The Asa Issie fauna has high percentages of colobine monkeys and tragelaphine bovids as well as forest-adapted avifauna and micromammals leading these authors to interpret the habitat as closed to grassy woodlands. The Aramis *A. anamensis* locality lacks other fauna but stable carbon analysis of pedogenic carbonate provide an average of ~25–35 % C₄, interpreted as indicating a “humid, grassy, woodland savannah environment.” (White et al. 2006: 885).
- *Woranso-Mille, Ethiopia.* Haile-Selassie et al. (2010b) report a sample of 26 hominin remains of *Australopithecus*, recovered from the northernmost locality in the Afar thus far and dated to ~3.57–3.8 Ma. These fossils consist of isolated teeth and partial mandibles and maxillae that exhibit features of both *A. anamensis* and *A. afarensis*, thus a possible transitional form. The fauna from four collection sites indicates a mix of riverine forest, open woodland and grassland habitats, based on relatively abundant *Theropithecus oswaldi* aff. *darti* and tragelaphin, aepycerotin, and bovin bovids, which Haile-Selassie et al. (2010a) note is more similar to the older Kanapoi fauna than that of age-contemporaneous Laetoli (see below).
- *Galili, Ethiopia.* This site has produced *Australopithecus* teeth and a femur (Kullmer et al. 2008; Viola et al. 2008) identified as most similar to *A. anamensis*. The fauna suggest a comparable date with Kanapoi, and the Kataboi Member of the Nachukui Formation, although there are some similar fauna with the younger lower Hadar Formation. Galili proboscideans are primarily grazers, but browsing rhino (*Diceros*) and giraffe also are present, and bovids are dominated by tragelaphins followed by bovins

and reduncins. The habitat is reconstructed as primarily woodland to bushland, although open grassland is indicated by the grazing proboscideans and equids (Kullmer et al. 2008).

- *Fejej, Ethiopia*. Although originally described as *A. afarensis*, Van Couvering (2000) suggests that these specimens may be *A. anamensis*, but only based on their age (Kappelman et al. 1996).

A. anamensis summary. Faunal and other paleoecological evidence from seven different areas indicate a range of habitats from closed woodland (Assa Issie) to open grassland (Kanapoi). Wynn's (2000) assessment that this hominin "thrived in varied ecosystems" seems appropriate based on current evidence. As discussed in Haile-Selassie et al. (2010a), the mammalian species recovered in the Woranso-Mille are different from those at Kanapoi, Allia Bay, and other deposits of the approximately the same age. Whether this is due to differences in environment or reflects a larger-scale biogeographic phenomenon requires further study.

A. *afarensis*

- *Lothagam, Kenya*. Four isolated teeth found in the fluviually deposited Kaiyumung Member of the Nachakui Formation, dated at ~3.5 Ma, have been attributed by Leakey and Walker (2003) to *Australopithecus* cf. *A. afarensis*. The dominant bovid tribes of this member, aepycerotins, alcelaphins, and bovins, indicate relatively open and seasonally dry conditions (Harris et al. 2003). This interpretation is supported by a decrease in Colobinae and an increase in *Theropithecus* relative to the underlying Apak Member.
- *Laetoli, Tanzania*. *Australopithecus* fossils are relatively rare in the Laetoli deposits in Tanzania. According to Su and Harrison (2008), the Laetoli environment during *Australopithecus*' times was a mosaic of woodland, shrubland, and grassland with ephemeral streams and/or ponds. In contrast, Kovarovic and Andrews (2007) reconstruct it towards the wooded end of the savanna spectrum, i.e., a mosaic of dense woodland and bushland. In either case, there are no aquatic animals, and thus no evidence of permanent water, which may have contributed to low numbers of *A. afarensis* on the landscape as well as in the fossil assemblages.
- *Woranso-Mille, Ethiopia*. Haile-Selassie et al. (2010a) describe a partial skeleton of *A. afarensis* from the Korsi Dora vertebrate locality that has an estimated age of ~3.58 Ma. Additional fragmentary hominin remains are assigned to *A. afarensis* but also bear traits of *A. anamensis*. Over 1500 vertebrate specimens from this paleontological study area (Haile-Selassie et al. 2010b) indicate a mix of riverine forest, open woodland and grassland habitats (see discussion under *A. anamensis*).
- *Dikika, Ethiopia*. This locality has sediments of the Basal and lower Sidi Hakoma members of the Hadar Formation. Wynn et al. (2006) suggest that the fossils of *A. afarensis* are associated with a delta and a wooded environment, although certain species indicating open grasslands were also present. This site may have cut marked bones, which are controversial but if confirmed would show that this species incorporated meat or animal products into its diet (McPherron et al. 2010; for alternative viewpoint see Dominguez-Rodrigo et al. 2010).
- *Hadar, Ethiopia*. *A. afarensis* occurs in three successive members of the Hadar Formation, persisting through ~500 kyr in spite of shifts in the fauna and vegetation (Bonnefille et al. 2004; Campisano 2007).
 - Sidi Hakoma Member. The Sidi Hakoma deposits range in time from ~3.42–3.26 Ma (Campisano 2007). The deposits in the lowermost part of the unit indicate higher annual rainfall and less seasonal environments than found in any other Hadar sub-member (Reed 2008). The rest of the Sidi Hakoma Member fluctuates between bushland and open woodland with a riverine component until the top of the member when there is a transgression of paleolake Hadar into the collection areas.
 - Denen Dora Member. The entire Denen Dora Member encompasses only about 56 kyr (Campisano 2007). There is a major increase in the abundance of reduncine bovids in the middle part of this time period, indicating extensive wetland and floodplain habitat. After this episode, there is faunal evidence for open wooded grassland (Campisano et al. 2004; Behrensmeyer 2008; Reed 2008) (see earlier discussion of the A.L. 333 locality).
 - Kada Hadar Member. There are two collection units that encompass ~3.2–2.94 Ma separated by the Bouroukie Tuff 1 (BKT-1) at ~3.12 Ma (Campisano 2007). The separation is important as the habitats shift from open woodland with some edaphic grassland to more arid and scrub woodland habitats. The KH-2 fauna also has high proportions of antilopin and alcelaphin bovids, which indicate more arid environments (Vrba 1975), especially when contrasted with other Hadar Formation sub-members (Reed 2008).
- *Ledi-Geraru, Ethiopia*. Two *A. afarensis* molars were recovered from the Denen Dora Member of the Hadar Formation (Wood 2011). They were recovered with reduncin bovids indicating a lakeshore environment, as well as antilopins and alcelaphins that indicate more shrubland and grassland habitats (Reed et al., in preparation).

- *Maka and Belohdelie, Ethiopia*. White et al. (1993) conclude from faunal evidence that there was woodland-bushland at the time of deposition of the Maka material, which is similar to the faunal interpretation for the Denen Dora Member of the Hadar Formation. *A. afarensis* has also been assigned to the frontal from Belohdelie, but no information is available for the ecological context of the find (Asfaw 1987).
 - *East Turkana (Koobi Fora), Kenya*. The older deposits (Tulu Bor and Lokochot members) have a moderately large faunal collection but *Australopithecus* is rare. The Tulu Bor Member of the Koobi Fora Formation is contemporaneous with the entire Hadar Formation in time (3.4–2.7 Ma) but has yielded only a few *A. afarensis* specimens (Kimbel 1988; Campisano et al. 2004). Feibel et al. (1991) described the depositional environment during Tulu Bor times as fluvial with floodplain lakes. Harris (1991) suggested that the habitat at this time included gallery forests amid floodplains, wet grasslands and woodlands. Controlled paleontological surveys of the Lokochot and Tulu Bor members at East Turkana support the comparative scarcity of *Australopithecus* fossils at East Turkana (Behrensmeyer et al. 2004), suggesting that the pattern is ecological or paleobiogeographic rather than taphonomic.
 - *West Turkana, Kenya*. As mentioned previously, at least 42 catalogued but unpublished specimens are assigned to *Australopithecus*, and at least some of these are assigned to *A. afarensis*. These derive from above the Tulu Bor Tuff and other fauna indicates gallery forest and woodland (Leakey et al. 2001).
 - *Fejej, Ethiopia*. Hominin specimens from this site were the oldest assigned to *A. afarensis* at 4.0–4.2 Ma (Kappelman et al. 1996), although some are now regarded as *A. anamensis* (Delson et al. 2000), but this is based solely on the age of the remains. There is no available information on the associated fauna or paleoenvironment.
- A. afarensis* summary. White et al. (1993) suggested broad habitat tolerance for *A. afarensis*, and the geological and faunal evidence from ~12 different localities from northern Ethiopia to Tanzania supports this earlier assessment; the fossil remains of this species are associated with habitats ranging from relatively open grassland to woodland, shrubland and riparian forest. There is no evidence that *A. afarensis* preferred any particular habitat, although low relative abundance at Laetoli and scarcity at East Turkana suggests some limits on its ecological flexibility. Given that this species was widespread and ecologically eurytopic (Reed 2008), then what caused its disappearance or extinction at ~2.7 Ma? This question could possibly further examined if: (1) the parameters of the reconstructed habitats could be refined in terms of abiotic factors (e.g., seasonal extremes in temperature and moisture), (2) patterns

indicating competition or niche-partitioning could be reconstructed for other eurytopic mammalian species coexisting with *A. afarensis* (e.g., via stable isotope analysis) and (3) morphological changes within the lineage (Lockwood et al. 2000) could be associated with responses to habitat change.

Australopithecus* or *Paranthropus aethiopicus

- *Omo (Shungura Formation), Ethiopia*. Suwa et al. (1996) assign 19 isolated hominin teeth from a total sample of 48 to this species between 3.0 and 2.0 Ma. These occur from members C–F, i.e., between 2.9 and 2.3 Ma; later relatively robust teeth are assigned to *Australopithecus (Paranthropus) boisei*. This species co-occurs with a “non-robust” hominin, represented by teeth that could belong to *A. afarensis*, *A. africanus*, or early *Homo*. The environment was predominantly riparian forest and woodland based on associated faunas, which lack a strong open grassland-adapted component until after 2.0 Ma (Bobe and Eck 2001; Bobe et al. 2002; Alemseged et al. 2003; see earlier section).

A. africanus

- *Makapansgat, Member 3, South Africa*. This deposit contains an extremely large number of mammalian specimens (greater than 30,000), of which 24 are *A. africanus*. The deposit was accumulated in the cave by fossil hyaenid and porcupine species (Maguire et al. 1980). Mammalian community structure suggests that this region was a habitat mosaic that contained riparian woodland, bushland, and edaphic grassland (Reed 1998). Other habitat reconstructions range from woodland (Vrba 1980) to forest (Cadman and Rayner 1989).
- *Makapansgat, Member 4, South Africa*. *A. africanus* is represented by only three out of a total of 257 mammalian specimens. Cercopithecine monkeys make up 80 % of the collection; and the likely accumulators were birds of prey and leopards (Reed 1996). Member 4 fossil deposits suggests a more wooded habitat than Member 3, but this could be a function of sample size and predation bias rather than an actual change of habitat at the site. As Members 3 and 4 are roughly contemporaneous, both assemblages probably represent a similar woodland–bushland habitat mosaic.
- *Sterkfontein, Member 2, South Africa*. The skeleton of Stw 573 has been attributed, thus far, to *Australopithecus* sp. but is still embedded in rock, preventing thorough

taxonomic analysis (Clarke 1999). Dating for the locality ranges from 2.8 to 2.6 Ma (Pickering and Kramers 2010). The fauna recovered with Stw 573 thus far is mostly cercopithecoids and carnivores with very few ungulates (Pickering et al. 2004). These researchers suggest an open woodland habitat in a valley setting surrounded by rolling hills covered with rocks and shrubs. A riverine forest is also proposed based on the presence of numerous monkeys and a leopard. The fauna, other than the hyaenid *Chasmaporthetes*, is also present at Sterkfontein Member 4 and other younger localities in South Africa. Thus, if the deposit overlaps in time with Sterkfontein Member 4 (see below), there may be two *Australopithecus* species present at roughly the same time. It is worth noting that Pickering et al. (2004) state that most of the fauna recovered are “climbers” and this may have implications for Stw 573 as well.

- *Sterkfontein, Member 4, South Africa*. This member has been dated to between 2.2 and 2.6 Ma (Herries et al. 2013). The faunal community suggests a habitat of open woodland, with bushland and thicket areas (Reed 1997). Other habitat reconstructions of this member at Sterkfontein have indicated medium density woodland (Vrba 1975) and an ecotone between dry sandy highveld grassland and Kalahari thornveld (Avery 2001). Bamford (1999) notes the presence of lianas, which indicate fairly dense riverine forest.
- *Taung and Gladysvale, South Africa*. The single specimen of *A. africanus* from Taung was likely incorporated into a meal of a bird of prey. The eagles suggested as the predator range in their hunting regions from forests through deserts (Berger and Clarke 1995). The other fauna associated with this deposit suggests a habitat that is fairly dense woodland (e.g., *Tragelaphus*, *Cephalophus*, *Panthera*, cercopithecoids). The hominin teeth recovered from Gladysvale are associated with other fauna recovered from the ex situ material that indicate deposition during a period of relatively wet climate and closed vegetation (Berger and Tobias 1994; Plug and Keyser 1994).

A. africanus summary. Although there is some evidence for closed forest habitats (e.g., fossil wood, lianas), the associated fauna recovered with this species indicates a mosaic of habitats ranging from forest to open grassland. Certainly the higher latitude of these deposits means important climatic differences compared with those nearer to the equator, especially with respect to seasonal temperature fluctuations. Also, the irregular upland terrain of the South African limestone plateau contrasts with the lower, more even topography of the aggrading rift basins in East Africa

A. sediba

This species, recently discovered at the site of Malapa in South Africa, is represented by relatively complete remains of a number of juvenile and adult specimens from a cave fill dated to ~1.9 Ma. Thus far, no other fauna has been published from the locality, but remains of other species are present, and information on the paleoecology will no doubt be forth-coming (Berger et al. 2010; de Ruiter et al. 2013; Dirks et al. 2010).

Kenyanthropus platyops

This taxon was recovered from the Nachukui Formation on the west side of Lake Turkana (Leakey et al. 2001). According to these researchers, fauna recovered near the specimens suggest a habitat that is more wet and closed than habitats at Hadar. We include this taxon because, though not placed in the genus *Australopithecus*, it is from the same time interval as early *Australopithecus* in East Africa.

A. garhi

- *Bouri, Ethiopia*. This species has been recovered from the Hata Member of the Bouri Formation, and is a late East African (2.5–2.1? Ma) representative of the genus (Asfaw et al. 1999). The fauna associated with *A. garhi* indicates the presence of a shallow lake surrounded by grasslands (de Heinzelin et al. 1999). Cut marked bones were found in the same strata as *A. garhi*, and meat-eating behavior is attributed to this species (de Heinzelin et al. 1999). White (2002) has suggested that some of the teeth from the Omo Shungura Formation are *A. garhi* and as such would be found in the more closed woodland habitats of the region (Bobe and Eck 2001; Bobe et al. 2002; Alemseged et al. 2003).

Discussion: Australopithecus Paleoecology

Returning to the questions that were posed at the beginning of this paper, what can we say about the paleoecology of australopiths in light of current taphonomic, paleontological, and geological information from the many known occurrences of *Australopithecus* in the African fossil record?

1. *What was the range of habitats associated with Australopithecus, and is it possible to discern each species' preferred habitat?* Even the earliest records for the genus include evidence for diverse habitats, from forests and woodlands to more open vegetation, suggesting eurytopic ecological adaptations from the beginning. This evidence is time-averaged over ecologically long time intervals, thus limiting what we can infer about habitat preferences within the available vegetation mosaics. We also do not yet know whether any of the species in this genus preferred one of these habitat types or a mix of open and closed habitats. However, Campisano (2007) has shown that across similar time intervals at Hadar, *A. afarensis* is more abundant in drier regions. The documented existence of *Australopithecus* from Chad to Ethiopia to South Africa indicates continent-scale distribution, considerable seasonal temperature tolerance, and adaptability to different topographic settings.
2. *What were the most important limiting ecological variables (e.g., food, water, shelter, competition with other species, predator avoidance, intra-species interactions) for the australopiths?* There is a possibility that the genus was limited by climatic conditions and associated vegetation types that disappeared at Hadar during the 2.8–2.35 Ma interval of increased aridity, when it went locally extinct. Relative scarcity of *A. afarensis* fossils at Laetoli suggests dependence on water sources and vegetation associated with water. Otherwise, understanding of these variables remains unknown.
3. *How did habitats vary among australopith species and across different regions?* There is evidence from regional faunal differences for some degree of either habitat variability or biogeographic isolation among the different species. Contrary to the hypothesis that hominin evolution is linked with retreating forests and expanding grasslands, the habitats of the earliest species, *A. anamensis* have been reconstructed as rather open, followed by a mosaic of open and closed habitats for *A. afarensis*. *A. bahrelghazali* appears to have existed in the most open grassland habitat, which is interesting considering its location in a lake basin in central Africa. *A. africanus* appears also to have been associated with mosaic habitats, although the habitats contributing to the mosaic change through time in southern Africa. There is as yet no overlap in species between South and East Africa during the temporal range of *Australopithecus*, evidence that this hominin genus was one of the most widely distributed members of the Pliocene mammalian fauna of Africa. Differences in its patterns of occurrence among basins within East Africa and, indeed, among localities on the west and east side of Lake Turkana, also suggest that *Australopithecus* was a eurytopic genus. These observations and supporting data provide a foundation for developing and testing hypotheses regarding responses to climate change experienced on local and regional scales. New research to obtain high resolution drill core records of environmental change from Plio-Pleistocene paleolakes along the East African Rift can also be applied to these hypotheses.
4. *Was there more than one Australopithecus species sharing an ecosystem at any given place and time?* This appears possible given the evidence from West Turkana, Omo, Galili, Woranso-Mille, and Sterkfontein (Table 4.1), but at present there is hard evidence for only one species at any one stratigraphic level and site. Time-averaging of hominin remains from different time periods may create the appearance of co-occurrence in a paleocommunity. Further fieldwork and taxonomic research are needed on deposits that may include different hominins.
5. *Was Australopithecus a maker and user of stone tools?* There are tantalizing occurrences of purported cutmarks on bones at two *Australopithecus* sites, Dikika and Bouri, but these finds are contested. More in situ evidence is needed, including the artifacts themselves, to provide a definitive answer to this question.
6. *Was there change in habitat use through time? Did niche breadth increase or decrease within individual lineages as Australopithecus evolved?* We do not know the answers yet, but higher resolution paleoecological research, additional hominin sites, and stable isotope studies of hominin enamel through sequences such as the Hadar Formation could provide new information bearing on these questions.
7. *How might global or continental-scale climate change between 4.5 and 2.0 Ma have affected the paleoecology of Australopithecus?* Some degree of climate forcing is probable, but understanding this will take careful study of regional variability in paleoclimates in southern versus eastern versus central Africa and comparisons with deep sea and continental lake records of global and continental-scale climate change. These data, in turn, can be used in paleoclimatic models of more localized regions to arrive at better models of climatic change through the Pliocene.

Habitats

The localities where the different species of *Australopithecus* have been documented provide evidence for varying amounts of closed woodland to forest as well as open grassland and shrubland habitats. This evidence is based primarily on associated fauna and stable isotopes, with

some input from the paleobotanical record. The genus *Australopithecus* can be characterized as eurytopic because its species are found in deposits that have faunal and isotopic evidence for a wide range of habitats. It is not clear, however, whether individual species were eurytopic or stenotopic with respect to the inferred spectrum of vegetation types because hominin sample sizes are generally too small to show statistically significant associations with particular ecological indicator taxa (e.g., Bobe et al. 2002). The one exception where there is enough hominin fossil material at one locality to begin to examine this questions is *A. afarensis* at Hadar, which persists for ~500 kyr through changing environmental conditions, indicating eurytopicity with respect to these conditions (Bonnefille et al. 2004; Reed 2008). That the microwear of *A. afarensis* indicates little variability in diet (Grine et al. 2006a, b), however, may indicate that although the species inhabited different environments, it ate something similar in all of them (see below).

Given limited samples of hominins and known biases introduced by taphonomic processes, pinning down an association of a particular hominin species with a “preferred” habitat may be possible using quantitative analysis associations with ecological indicator taxa. Progress in this approach will require more data points consisting of carefully controlled associations of hominins and faunal or other proxies to allow higher temporal and spatial resolution of the consistency of these associations. Growth in understanding ecological indicator species associated, or not associated, with hominins will also help this approach. Autecological investigations including expanded stable isotope analysis of hominin tooth enamel using minimally destructive laser-ablation technology could also provide direct evidence of dietary preferences and variability. Microwear and anatomical traits indicating adaptation for climbing, walking, etc., could also support higher resolution inferences about preferred habitats.

Diet and Food Procurement

There has been recent research that sheds light on the diet of some *Australopithecus* species but also brings up further questions. It has long been known that *A. africanus* microwear indicates a variable diet, but not as variable as *Paranthropus robustus* recovered from the same geographic region. In contrast, *A. anamensis* and *A. afarensis* appear to have been more limited in their selection of foods due to the low variation in the fine scratches that appear on their teeth through time (Grine et al. 2006a, b). Stable isotopes of *Australopithecus* taxa are discussed in Sponheimer (2013) and Grine et al. (2012), but indicate both C₃ and C₄ plants

were consumed. Finally, evidence suggests that some of these hominins may have been consuming meat or marrow (de Heinzelin et al. 1999; McPherron et al. 2010). Thus, while there is interesting autecological evidence provided for many of these taxa, there are still many questions as to how they were utilizing their habitats.

Conclusion and Future Research

We know much more about the paleobiology of *Australopithecus* than we did 30 years ago, and in spite of taphonomic and time-averaging caveats, the large number of documented sites now provides convincing evidence that the genus had an impressive breadth of tolerance for varied habitats and climates. Better-coordinated research in faunal analysis, habitat reconstruction, spatial distribution, and taphonomic biases of the hominin fossil record at local, regional, continental, and global scales, as well as additional new sites, should greatly expand this knowledge in the coming decades.

Used in conjunction with species turnover patterns and evidence for abiotic environmental change, the evidence provided in this paper can serve as a baseline for continuing research on the ecological context of hominin evolution. Further advances in habitat reconstruction for *Australopithecus* will depend on careful attention to the scale of the evidence (temporal and spatial) versus the scale of the desired reconstruction. Particular caution is needed to avoid interpreting ecological features of a time-averaged faunal list as a “snapshot” (single time-plane) sample of the habitat of *Australopithecus* or any other hominin.

In a succession of fossiliferous strata, we usually are dealing with varying proportions of different habitats (e.g., closed vs. open, or wetter vs. drier habitats) rather than the extremes of one or the other. How these habitat “mosaics” are recorded in the fossil record depends on the spatial scale of the sample as well as the amount of time represented. Shifts of an ecotone across a depositional area through time can also result in a similar mixed habitat signal (Behrens-meyer et al. 2007). There is no simple solution to the problem of time-averaged ecological signals, but in some fossil-bearing sequences there are ways to calibrate the scale of habitat patches and evaluate the adaptations of individual species. These include:

1. Higher resolution sampling and morphological analysis of faunas associated with *Australopithecus*-bearing strata, including intra- and inter-basin comparisons of mammalian species associated most commonly with *Australopithecus*. What are the morphological and abundance similarities and differences among species that co-occur, or do not co-occur, with *Australopithecus*?

To the same end, analyses of tooth wear patterns and stable isotopes in the same species across space and/or through time at individual localities will give us information regarding diets that may be consistently different in particular basins.

2. Coordinated lateral sampling of faunas and paleoenvironmental variables in Pliocene sequences where *Australopithecus* is common versus uncommon or absent (e.g., Hadar vs. Turkana Basin, Omo Shungura vs. Tugen Hills vs. Lothagam).

While pursuing increased resolution and refinement of taphonomic and ecological evidence, it also will be important to adjust the spatial and/or temporal scale of paleoecological interpretations to take account of the inevitable limitations of the record. Much remains to be learned about resolving ecological information in the fossil record of *Australopithecus*, or any other intriguing extinct mammalian genus.

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