# Hominin Paleoecology and Environmental Archaeology

Isabelle C. Winder[1], Isabelle S. Heyerdahl-King[2] and Nick P. Winder[3]
[1]Department of Archaeology, University of York, York, UK
[2]Department of Archaeology, University of Sheffield, Sheffield, UK
[3]International Centre for Cultural and Historical Studies, University of Newcastle, Newcastle, UK

## Introduction

Reconstructing the lives of our closest fossil relatives is relevant to our understanding of the history of the human lineage, our biology, and our relationship with the environment. Further back in time, evidence of material culture dwindles until, at around 2.6 million years ago, there ceases to be any surviving record. Prior to this, researchers must work with the same record of fossils, sediments, and rocks as any paleontologist. For the period before 2.6 million years ago, an ecological perspective – as opposed to the archaeological one usually employed for *Homo sapiens* – is therefore necessary. But the value of the paleoecological approach is not limited to species which predate material culture. The insights to be gained from studies of trophic relationships, ecological structures, and hominin interactions with the physical environment ensure that this perspective remains important to the study of human evolution up to and including *Homo sapiens*.

## Definition

Paleoecology is the study of ancient ecology. Environmental archaeology, in its broadest definition, is also concerned with the ecology of the past, specifically with an ecological approach to past human populations. The two fields are thus very similar, with the key difference lying in their scale and subjects. Hominin paleoecologists largely study fossil specimens of extinct species, and their study spans the entirety of paleontological history. Environmental archaeology is more circumscribed, focusing on a single species typically represented by subfossil and archaeological evidence. There are exceptions to this, as in the case of the paleoecological study of subfossil specimens like *Homo floresiensis* (Flores, Indonesia) or specimens of our own species. Both fields draw upon methods from biology and geology, but paleoecology, by virtue of the nature of its source evidence, has a somewhat stronger relationship with the geological sciences, particularly the study of taphonomy (Hardt et al. 2007).

"Hominin" denotes all those species more closely related to modern humans than to their closest living relatives *Pan paniscus* and *Pan troglodytes* (Wood & Lonergan 2008). Panins and hominins shared a common ancestor some 5–6 million years ago. For much of their history, two or more hominin species have coexisted, resulting in a complex and unstable taxonomy. While different authors champion different demarcations between species and even genera, this article recognizes the genera *Sahelanthropus*, *Orrorin*, and *Ardipithecus* as stem hominins and *Australopithecus*, *Paranthropus*, and *Homo* as later, more certain forms.

## Key Issues/Current Debates

Given the diversity of paleoecological research, which can include everything from isotope studies of ocean sediments through to microscopic studies of fossil teeth and computer modeling of paleoclimates, it is difficult to produce a general classification of the field. There is much ongoing debate and many questions remain unanswered, focusing at all scales from the individual site or specimen through to intercontinental studies of evolutionary ecology and dispersal of lineages and at every intermediate scale. There are four major topics in the literature, specifically:

1. Diet: what hominins ate, how they obtained their food, and the implications for anatomy, behavior, and energetics
2. Ecological interactions and intrinsic ecology: the relationships between hominin taxa and

between hominins and other organisms, life history, and adaptations

3. Environment: the environmental tolerances and preferences of the hominins
4. System dynamics, agency, and cooperation

These topics are interlinked by the complex relationships between paleoecological evidence and its interpretation. A paleoecological dataset can typically be used for more than one purpose, and specific research questions can be approached in several ways through different analyses. For example, Bobe et al. (2002) used data on faunal samples from strata in the Omo Valley in Ethiopia between 4 and 1.9 million years old to reconstruct changes in the abundance of different taxa. Skeletal element counts were used to evaluate the role of taphonomic processes in producing these patterns. The resulting environmental reconstructions were then checked against evidence from marine dust records and found in part to reflect climatic changes at the time (Bobe et al. 2002). This sort of multi-proxy approach is becoming ever more common as it provides the opportunity to validate and enhance reconstructions based on a single line of evidence and to identify or reduce the impact of taphonomic bias. Research may also draw on computer modeling, studies of modern analogue environments and ecosystems, and comparative data on primates and other taxa. These comparisons may be with homologous taxa (those closely related to hominins) or analogous ones which perform similar ecological roles. The use of diverse methods has had a key impact on paleoecology. It raises second-order questions of data quality, the choice and accuracy of specific methods, and the role of theories and assumptions which are almost as important as first-order concerns about diet, environment, and ecology.

## Hominin Diets

The earliest proposals of hominin diet were heavily influenced by contemporary anthropological emphases on the "humanness" of fossil specimens and the importance of hunting and meat eating in setting humans (and hence hominins) apart from our closest relatives. Despite significant new methodological advances, such as the advent of tooth microwear studies, isotopic analyses of dental enamel and bones, and enamel microstructure analyses, scientists remain uncertain about hominin diets. Between 4.4 and 2.3 million years ago, the early hominins (*Australopithecus anamensis*, *Au. afarensis*, and *Au. africanus*, with initial signs also in *Ardipithecus ramidus*) developed a characteristic pattern of small incisors, large flat molars, thick tooth enamel, and robust mandibles which would have enabled them to eat both hard and soft, though not tough, foods (Teaford & Ungar 2000). This would have permitted a flexible diet consisting of a range of foods from savannah and forest. *Paranthropus robustus*, in contrast, may have been capable of processing more tough plant foods as well (Teaford & Ungar 2000). Later species likely made more use of higher-quality resources, perhaps including terrestrial and aquatic animal foods, honey, or tubers (Braun et al. 2010).

As more specimens of each species have been subjected to analysis, the significance attributed to intraspecies dietary variation has increased. The flexible adaptations of *Australopithecus*, and the mosaic patterns of dietary evolution in this taxon, suggest that they could have eaten a wide range of foods (Teaford & Ungar 2000), and indeed evidence for this is found in isotopic analyses of *Au. africanus* and *P. robustus* which are both more extreme generalists even than modern baboons (Codron et al. 2008). Emphasis has shifted from a focus on absolute dietary differences between taxa to one which recognizes the potential role of "fallback foods" – those which are important in times of scarcity, but which may not typically form a central part of the diet – in anatomy and ecological adaptation. Current debate centers on questions of dietary variability, niche breadth, niche overlap, and flexibility at the individual and species level. Concomitant considerations include "adequate" sample sizes, theoretical frameworks for adaptive evolution which might explain the complex relationship between food consumption and craniofacial anatomy, and analytical robusticity.

## Ecological Interactions and Intrinsic Ecology

Questions of diet are closely linked to those of ecological interaction, including predation, competition, commensalism, and parasitism. Characterizing the communities at hominin sites is one priority and involves analyzing environmental context and taphonomy in an attempt to move from the paleocommunity (the species represented in a fossil assemblage) to an understanding of the living community. Studies of modern analogue communities and interpretations of an organisms' ecological niche based on that of their living relatives can be used to check or confirm these reconstructions (Potts 1998). In many cases, there is a focus on comparisons between sites or strata, as in the study by Bobe et al. (2002) of change in the dominance of suids, bovids, and cercopithecids through time in the Omo Valley. Another example is Lewis and Werdelin (2007)'s work on the ecological structure of the carnivore guild at various east African sites. These studies may help in placing hominins within a particular ecological group and in the identification of broader patterns in faunal evolution and ecology. Two examples are the "turnover pulses" characteristic of African mammal lineages which may correlate with hominin adaptive radiations or ecological shifts (Potts 1998) or changes in vegetation distributions and structures which might cause ecological divergence of hominins and panins (Hardt et al. 2007).

Closely linked to the question of the ecological position of hominins with respect to animals and plants are those of niche separation and coexistence among hominins themselves. Multiple hominin species have existed in parallel, often in the same regions and similar habitats, for all but the last few tens of thousands of years, with perhaps as many as six in certain periods (Wood & Lonergan 2008). Their classification into species and genera implies some sort of evolutionary and hence ecological separation from one another. Identifying precisely what this might imply, especially when all aspects of hominin ecology are showing increasing evidence of intra- and interspecies variability, is difficult and is an area which focuses on the synthesis of external factors (environment and community ecology) with intrinsic ecological ones relating to life history and behavior (Senut 2007). Aspects of life history, such as lifespan, fertility, and reproductive rates may determine the long-term strategies available to hominins. They can be reconstructed for fossil species using "life history-related variables" like body mass, dental, and osteological development patterns and brain growth schedules (Robson & Wood 2008), through the application of general rules based on primate and mammal studies.

The first specimen to show a developmental pattern similar to that of extant *Homo sapiens* appears late in our history. Smith et al. (2007) identify a juvenile from Jebel Irhoud, North Africa, as this individual – but the relatively small sample size of immature hominins throws into context the issue of paleoecologists' reliance on individual specimens which may not always be representative of their populations. This humanlike pattern is not something which appears steadily from an apelike precursor. Robson and Wood (2008) note that early attempts to describe hominin life histories tend to focus on characterizing the shift from "apelike" (usually characterized by members of *Pan*) to "humanlike," but that in more recent research, it has become increasingly apparent, once again, that hominin life history variables not only change at different rates and periods but also show unique, distinctive configurations that differ from all living species. *Paranthropus*, in particular, has a pattern of dental development which sets it apart from both living African apes and humans (Robson & Wood 2008). Understanding these patterns, and how they fit with hominins' ecological strategies and niches, is thus less a question of characterizing evolution as it is of developing a more detailed understanding of each species' unique ecology. Questions of theoretical perspectives and their validity, and of how and why scientists approach hominin ecology (historically as intermediate between us and the nonhuman apes, or more recently as distinctive in their own right) are therefore central.

## Hominin Environments

The interactions between hominins and the physical environment are also very important. The identity and role of specific environments which drove "hominization" or the acquisition of key human/hominin ecological and anatomical characters are of particular interest. There are two major groups of hypotheses as to the nature of the key environment. The first group focuses on simple shifts, either in the nature of the environment, for example, aridification and the expansion of grassland, or in the preferences and tolerances of hominins. The second group focuses on changes in environmental variability or evolutionary turnover, like the turnover pulse hypothesis or the variability selection model (Potts 1998). A new suggestion, focusing on spatial (as opposed to temporal) variability and the role of physical landscape rather than climate or vegetation in driving hominin evolution, has also recently been proposed (King & Bailey 2006), highlighting the role of spatial mosaics in environments and of rough topography in providing resource-rich refugia and tactical advantages over predators.

These environmental hypotheses are usually based on theories of the way(s) specific contexts might influence hominin precursors living in them, but they are closely tied to paleoenvironmental evidence from fauna, flora, geology, isotopes, and sediments for validation. Such studies are responsible for recent proposals which highlight the role of forests in generating hominin traits, as studies of the stem hominins *Ardipithecus*, *Orrorin*, and *Sahelanthropus* have suggested that forests and lakesides, rather than open plains, were typical of their localities (Senut 2007). Later species have been found in a variety of contexts, and questions today center not just on the nature of habitats but on the role of taphonomic bias and preservational factors in generating observed patterns in distributions and habitat associations (King & Bailey 2006). Fossils are often found in lake and river sediments, because these are the places where deposition is common and preservation most likely. A range of paleoenvironmental methods, modern analogue studies, and modeling techniques are therefore used to contextualize specific sites. This enables researchers to fill the gaps left in the fossil record by taphonomic bias, transport of remains, and uncertain dating (Potts 1998). Later studies often focus on the role of coasts and other environments as dispersal routes for *H. erectus* and *H. sapiens* and the interactions of *Homo* spp. with the environments and ecosystems they encountered.

## System Dynamics, Agency, and Cooperation

Much of the seminal literature on hominin paleoecology actually predates the word "ecology" and is closely linked to broader paradigms in biology and archaeology. Alfred Russel Wallace's paper on the origin of human races mounts a powerful challenge to the coevolutionary model presented in Darwin's *Origin* (Wallace 1864). Wallace argues that advanced cognitive skills effectively enabled humans to evade the universal effects of natural selection. In his later writings, notably *What is Life*, Wallace argues that this intellectual and technological liberation cannot be explained in purely scientific terms and infers the existence of a universal intelligence comparable to Henri Bergson's *élan vital*. Wallace's idea undermines all those chapters in Darwin's *Origin* that deal with cooperation and creative synergy. Wallace seems to have believed that only humans, with their superior intelligence and technology, could set natural selection in abeyance and influence the course of evolution.

Charles Darwin's *Descent of Man* presents a naturalistic model, which the older Wallace and Bergson rejected. Darwin believed higher cognitive function may actually have reduced the relative fitness of some individuals but would have persisted if it increased the fitness of the community in which the individual is embedded. Similar arguments are made in *Origin*, where Darwin discusses the coevolution of humans and their domesticated commensals and of plants and their pollinators. An insect that can only feed from rare, long-throated flowers, for example, may not enjoy the same reproductive success as a generalist but can persist as long as the community of plants and insects maintains the fitness of all. This difference of emphasis between Darwin and Wallace prefigures the twentieth-century tension between neo-Darwinists (who favor Wallace's model) and coevolutionary ecologists, who allow for the possibility that selection pressures can be mitigated by interspecies cooperation. This anticipation is all the more remarkable when one observes that Thomas Henry Huxley argued for a stick-slip model of evolution, which anticipated Hugo de Vries' later work on "mutationism" and later twentieth-century theories about "punctuated equilibria."

Although some of the key concepts of later twentieth-century systems ecology were well documented in the 1860s and 1870s and discussed almost continually since, the ideas did not become scientifically respectable until the 1960s and 1970s, when an innovation cascade fueled by postwar perestroika and the development of new computer methods led to a partial rehabilitation of Darwinian complexity. The first scholarly biological papers to explicitly use the word "coevolution" date from the 1960s; research on behavioral ecology and ethology that had been the preserve of natural historians and amateurs now came into the scientific mainstream, and models of stick-slip evolutionary dynamics and continental drift were rehabilitated. Although some textbook and popular literature presents this as a cascade of scientific discoveries, the primary sources are more consistent with an institutional veto that pushed complex dynamics beyond the pale, as it were.

In archaeology, this innovation cascade produced a number of confusing hybrids that tried to meld classic and complex approaches. It is helpful here to distinguish large-P from small-p processual archaeology. Large-P processualism had been a hybrid of classic and complex systems approaches that strove to link new developments in anthropological archaeology to classic science, particularly to Karl Hempel's concept of the scientific law. Small-p processualism or "new archaeology," on the other hand, was a more pragmatic attempt to integrate systems ecology, new scientific methods, and anthropological archaeology. Thus, by the time Lewis Binford (1981) published his research on taphonomy and hominin ecology, he had publicly repudiated his earlier processual polemics, rejecting the quest for universality in favor of what he called "middle-range theory." By studying animal modifications of bones, Binford learned to distinguish the shearing and crushing actions that can be effected using jaws alone from modifications that could only have been effected by hominins. By analyzing faunal data in the light of this understanding, he felt able to reject the "man the hunter" hypothesis and suggested that early hominins were scavengers. The essential feature of Binford's later (small-p) processual research was a separate effort of research on process and transformation designed to provide an inferential platform. Middle-range theory identifies inferential links between the mundane and frankly uninteresting phenomena we can observe and unobservable phenomena that interest us.

As the processual vs. post-processual debates intensified in the later 1980s and 1990s, a number of new archaeologists became interested in more dynamic models of paleoecology. Where post-processual debates often degenerated into a paradigmatic argument about agency, scale, and the relative merits of environmental determinism and agency, the dynamic approach looked for some common ground. All socio-natural systems are "dynamic" in the sense that they change, but the studies referred to here involve co-dynamic situations, where cultural and natural systems create and recreate each other. This approach invites us to consider a stick-slip dynamic in which one set of causal structures can become unstable and a new, qualitatively different type of co-dynamic interaction can emerge.

The (co-)dynamic or coevolutionary approach is rare in archaeology as a whole, but two examples can be found in Pleistocene hominin paleoecology. Bailey's (1997) Epirus Project included a study of predator-prey interaction based on a hypothesis of constant disequilibrium. The result was an individual-based "toy-world" model of plant, herbivore, and predator interaction that suggested resilience could be lost if this open-ended game of hide and seek was constrained, for example, by obstacles to dispersal. By relating these middle-range insights to climate and sea-level changes, the project was able to predict the distribution of hunting sites through space and time, including some in regions that currently lie offshore.

A second example of co-dynamic paleoecology in Pleistocene ecology is provided by Mithen's (1993) work on mammoth populations. Mithen developed a simple model of mammoth reproductive behavior and used it to show that a relatively small human cull (less than 3 %) could reduce the resilience of a healthy population, rendering it susceptible to relatively minor fluctuations in predation pressure and natural disasters. Again, the focus is on resilience and co-dynamic interaction between populations. Our final example uses a more ethnographic approach to systems analysis. Like Binford, Ezra Zubrow (2005) is concerned with developing methodological protocols for interpreting patterns in space and time. Where Binford's analyses were, at a first level of approximation, a-spatial, Zubrow is interested in GIS and exploring a form of auto-ethnography. Pleistocene hominins did not use the abstract, analytic skills we deploy, but those abstract methods are based on a similar cognitive foundation. By exploring the concepts of patchiness and crowding and the ways people perceive spatial pattern, Zubrow hopes to gain new insights into paleoanthropology and the dynamic ecologies of culture.

## Conclusions

Our understanding of hominin paleoecology is variable and rapidly changing. Certain topics – for instance, diet in *Paranthropus* species, the interactions of species at major sites like the Omo and Olduvai, and the environments that may have driven hominization – have been intensively studied, while others are less well known. Both direct questions about ecology and more abstract problems of taphonomy, data quality and use, and methodological validation remain under active investigation. Progress is driven by a combination of methodological advances and refinements, new fossil discoveries, novel approaches to existing questions, and synthetic "meta-analyses" that integrate data from several sources and projects. Hominin paleoecology is a highly relevant and wide-reaching field with much to contribute to our understanding of the human past.

## Cross-References

- ▶ Australopithecines
- ▶ Fossil Records of Early African *Homo*
- ▶ Hominids, Earliest African
- ▶ *Homo erectus*
- ▶ *Homo ergaster*
- ▶ *Homo habilis*
- ▶ *Homo heidelbergensis*
- ▶ *Homo neanderthalensis*
- ▶ *Homo sapiens*
- ▶ Human Evolution: Theory and Progress
- ▶ Olduvai Gorge Archaeological Site
- ▶ *Paranthropus*
- ▶ Taphonomy in Human Evolution

## References

Bailey, G.N. 1997. *Klithi: palaeolithic settlement and Quaternary landscapes in northwest Greece*. Cambridge: McDonald Institute Monographs.

Binford, L.R. 1981. *Bones: ancient men and modern myths*. London: Academic Press.

Bobe, R., A.K. Behrensmeyer & R.E. Chapman. 2002. Faunal change, environmental variability and late Pliocene hominin evolution. *Journal of Human Evolution* 42: 475-97.

Braun, D.R., J.W.K. Harris, N.E. Levin, J.T. McCoy, A.I. R. Herries, M.K. Bamford, L.C. Bishop, B.G. Richmond & M. Kibunjia. 2010. Early hominin diet included diverse terrestrial and aquatic animals 1.95 Ma in East Turkana, Kenya. *Proceedings of the National Academy of Sciences* 107: 10002-7.

Codron, D., J.A. Lee-Thorp, M. Sponheimer, D. de Ruiter & J. Codron. 2008. What insights can baboon feeding ecology provide for early hominin niche differentiation? *International Journal of Primatology* 29: 757-72.

Hardt, T., B. Hardt & P. Menke. 2007. Paleoecology: an adequate window on the past? in W. Henke & I. Tattersall (ed.) *The handbook of paleoanthropology*: 503-44. Heidelberg: Springer-Verlag.

King, G. & G. Bailey. 2006. Tectonics and human evolution. *Antiquity* 80: 1-22.

Lewis, M.E. & L. Werdelin. 2007. Patterns of change in the Plio-Pleistocene carnivorans of eastern Africa: Implications for hominin evolution, in R. Bobe, Z. Alemseged & A.K. Behrensmeyer (ed.) *Hominin environments in the East African Pliocene*: 77-105. Dordrecht: Springer.

Mithen, S. 1993. Simulating mammoth hunting and extinction: implications for the late Pleistocene of the Central Russian Plain. *Archeological Papers of the American Anthropological Association* 4: 163–78.

Potts, R. 1998. Environmental hypotheses of hominin evolution. *Yearbook of Physical Anthropology* 41: 93-136.

Robson, S.L. & B. Wood. 2008. Hominin life history: reconstruction and evolution. *Journal of Anatomy* 212: 394-425.

Senut, B. 2007. The earliest putative hominids, in W. Henke & I. Tattersall (ed.) *The handbook of paleoanthropology*: 1519-38. Heidelberg: Springer-Verlag.

Smith, T.M., P. Tafforeau, D.J. Reid, R. Grun, S. Eggins, M. Boutakiout & J.-J. Hublin. 2007. Earliest evidence of modern human life history in North African early *Homo sapiens*. *Proceedings of the National Academy of Sciences* 104: 6128-33.

Teaford, M.F. & P.S. Ungar. 2000. Diet and the evolution of the earliest human ancestors. *Proceedings of the National Academy of Sciences* 97: 13506-11.

Wallace, A.R. 1864. The origin of human races and the antiquity of man deduced from the theory of "natural selection". *Journal of the Anthropological Society of London* 2: clviii-clxxxvii.

Wood, B. & N. Lonergan. 2008. The hominin fossil record: taxa, grades and clades. *Journal of Anatomy* 212: 354-376.

Zubrow, E.B.W. 2005. Prehistoric space: an archaeological perspective. *Journal of World Anthropology* 2: 1-42.

## Further Reading

Gell-Mann, M. 1994. *The Quark and the Jaguar: adventures in the simple and the complex*. London: Little, Brown and Company.

---

# *Homo erectus*

Emily R. Middleton[1] and Susan C. Antón[2]
[1]Department of Anthropology, New York University, New York, NY, USA
[2]Department of Anthropology, New York University and New York Consortium for Evolutionary Primatology, New York, NY, USA

## Introduction

*Homo erectus* is a geographically widespread and temporally long-lasting fossil hominin species known from Africa and Asia between c. 1.9 Ma and 500 ka (but perhaps to <100 ka). The taxon subsumes a large amount of skeletal variation, and one of the central debates concerns whether this variation should be partitioned into multiple species. *Homo erectus* was the first hominin to disperse out of Africa as well as the first to take important steps toward modern human form, development, and behavior. *Homo erectus* has traditionally held a canonical position in hominin evolution, chronologically succeeding *Homo habilis* and preceding *Homo sapiens*. However, this simple time-successive progression has been complicated by additional fossil discoveries in Africa that confirm the presence of multiple species of non-erectus early *Homo* (Leakey et al. 2012) as well as the temporal and geographic overlap of *Homo erectus* and *Homo habilis* (Spoor et al. 2007). Nonetheless, *H. erectus* remains the presumptive common ancestor for *H. sapiens*.

## Definition

### Species History and Distribution

The *Homo erectus* nomen dates to the 1940s, but fossils attributed to this species have been known since the nineteenth century. Spurred by the prevailing hypothesis that human ancestors would be found in Southeast Asia, Eugène Dubois sought and found fossils in Java in the 1890s that were recognizably nonhuman but possessed brain sizes well above those of modern apes. He assigned the material to a new species, *Pithecanthropus erectus* (upright ape-man; Dubois 1894). Subsequent discoveries at the site of Zhoukoudian in China were dubbed *Sinanthropus pekinensis* (Black 1927). Both genera, along with others named in Indonesia and South Africa, were eventually subsumed into *Homo* based on their similarities to each other and relationship to modern humans. The original species name was retained to create *Homo erectus* (Mayr 1944). Discoveries at Olduvai Gorge in the 1960s (e.g., OH 9) expanded the known range of *Homo erectus* into East Africa. The species is known from East, South, and possibly North Africa and West, East, and Southeast Asia.

*Homo erectus* is defined by its distinctive cranial morphology, including a long, low vault and the presence of cranial suprastructures such as sagittal keeling, an angular torus, a bar-like or