

The Evolution of Hominin Diets: Integrating Approaches to the Study of Paleolithic Subsistence

Jean-Jacques Hublin and Michael P. Richards (eds.)

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The Evolution of Hominin Diets is comprised of 20 papers that were initially presented as part of a symposium held at the Max Planck Institute for Evolutionary Anthropology in 2006. The papers reflect a wide variety of approaches to studying hominin diet, ranging from traditional faunal analyses to lithic and fossil perspectives on the origins of projectile technology. In the brief preface to the volume, the editors express the hope that the book will serve two purposes—first, to provide an up-to-date account of research on human dietary evolution; and second, to provide an introduction to aspects of research on the topic that are being undertaken in fields that may not be the reader's own. With a few minor exceptions, the volume succeeds at both of these goals, and as such, it will serve as a useful resource to anyone interested in human evolution more broadly.

The book opens with a number of chapters that utilize data from studies of living populations in order to draw inferences about ancient hominin diet. Hohmann (Chapter 1) provides a broad but concise overview on the diets of non-human primates—as someone not familiar with this literature, I found his review both useful and accessible. Given what we know about non-human primate diets, Hohmann suggests that certain behaviors such as food sharing, hunting, meat eating, and provisioning were likely already in place by the time *Pan* and *Homo* split.

Snodgrass and colleagues (Chapter 2) explore the energetics of encephalization, using data from modern species and hominid fossils in order to test several hypotheses that address the relationships between dietary quality, brain size, and body mass/composition. The paper is well done and should be considered required reading for anyone interested in the topic; among their most interesting results was the finding that non-human primates actually have similar sized guts relative to other mammals, which seems to be at odds with the expectations of the Expensive Tissue Hypothesis (Aiello and Wheeler 1995).

Lucas et al. (Chapter 3) investigate the relationship between dietary change and the reduction in tooth size evidenced during the Paleolithic. Because foods that have been cooked or otherwise processed often require less chewing, Lucas and colleagues propose that in order to avoid overwhelming the gut, the rate of oral processing must be slowed—and a reduction in tooth size is a primary way to accomplish this. While the authors admit that this is not the only possible pathway by which a “food avalanche” to the gut could be avoided, they are right to point out that a con-

sideration of digestive processes and the role of the mouth in digestion can provide important insights on the impacts of dietary change on human evolution.

Lindeberg (Chapter 4) reviews what we know about human nutritional requirements (in terms of vitamins/minerals, protein, fats, etc.) in order to try to reconstruct what foods may have been part of the ancestral hominin diet, concluding that humans are well adapted to a wide variety of meat and plant foods. It seemed to me that this paper might have benefited from a broader comparative perspective—for example, Lindeberg addressed the fact that many modern populations require iodine-enriched foods in order to meet the recommended daily intake. This raises questions about how early hominins obtained sufficient iodine—perhaps data on primate nutrition would be informative?

An additional three chapters focus on reconstructing the diets of a variety of early hominin species. Alemseged and Bobe (Chapter 13) utilize paleoenvironmental data in order to take on the claim that *Paranthropus* was more specialized in its habitat preference (and thus its diet) than was *Homo*. Using data from the Shungara Formation in Ethiopia, they propose that both species relied upon similarly diverse habitats, but may have exploited different fallback foods, with *Homo* relying on animal resources from wooded environments and *Paranthropus* relying upon the hard foods found in more open habitats. It will be interesting to see if this pattern holds in other regions in which both species have been identified.

Sponheimer and Dufour (Chapter 18) review a variety of arguments relating to the timing and significance of increased dietary breadth, focusing in particular on the contribution of biogeochemical data to these debates. Of particular note is their summary of the carbon isotope data for early hominin diets; based on the $\delta^{13}\text{C}$ values, Sponheimer and Dufour argue that *Paranthropus*, early *Homo*, and *Australopithecus* all obtained a significant portion of their diets from C_4 (savanna) resources. This was found to be in striking contrast to chimpanzees, as isotopic data from savanna-dwelling chimpanzees show no evidence for the consumption of C_4 foods. The authors thus suggest that early hominins had in fact broadened their diet in such a way that they could survive in habitats too open and xeric for chimpanzees.

Interestingly, the conclusions drawn by Sponheimer and Dufour contrast with those of Schoeninger (Chapter 17), who analyzed carbon isotope data from a range of C_3 -feeding species (primarily primates) which occupy habitats

with varying degrees of canopy cover. Her results indicated an unexpectedly wide range of $\delta^{13}\text{C}$ values among species with no C_4 consumption, with primates occupying open canopy and/or dry, deciduous forests showing much less negative values than are generally associated with C_3 -exclusive diets. Given her results, she argued that only *Australopithecus africanus* fell clearly outside of the range of values for C_3 -exclusive diets, implying that C_4 foods were not necessarily a significant part of the diet of *Paranthropus* or early *Homo*. Despite potential disagreement on the fraction of C_4 foods in the diet, Schoeninger points out that the data do indicate that these species were exploiting more open habitats than most chimpanzees, which has important implications for social and subsistence behaviors.

One of the things I found a bit surprising about the volume was the nearly complete absence of papers that address the subsistence behavior of *H. erectus* and its contemporaries. The only contribution which addresses this topic in any detail is that of Villa and Lenoir (Chapter 5), who also provide one of the few truly integrative studies in the volume, tackling both the faunal and lithic records from the European Lower and Middle Paleolithic in order to review our current state of knowledge on hunting practices during this period. Given the rich faunal record from Africa, and the integral role that this dataset has played in debates about the animal procurement strategies of early and large-bodied *Homo*, this absence seems particularly marked. That being said, the chapter by Villa and Lenoir is incredibly valuable, as the authors present faunal data from a wide variety of sources that were originally published in several different languages and thus may have been unfamiliar to many readers.

A majority of the contributions (11 of 20) deal with a variety of aspects relating to Middle and Upper Paleolithic subsistence. Here again there is a very strong Eurasian (particularly European) focus. The first paper in this group was by Hofferker (Chapter 6), who addresses the evidence for Neanderthal and modern human diet in Eastern Europe. As is the case elsewhere in Europe, the available evidence suggests that Neanderthals were primarily exploiting large mammals. Given the harsh conditions on the Eastern European Plain, Hofferker proposes that exploitation of megafauna such as mammoth and rhinoceros may have been key to the survival of Neanderthals in this region, although he admits that compelling evidence for the exploitation of these species is thus far lacking. In contrast, the faunal data suggest that modern human occupation of the region (particularly of the central Plain) was supported by expanded dietary breadth, which likely depended on the development of novel technologies.

Gaudzinski-Windheuser and Niven (Chapter 7) focus on the evidence for Middle and Upper Paleolithic subsistence in Northwestern Europe. Once again, the compilation and detailed presentation of data from several sites makes this contribution incredibly useful. The authors were able to identify clear differences in subsistence tactics between the MP and the *later* UP, both in terms of the exploitation of small game and in terms of reindeer carcass utilization—

Gaudzinski-Windheuser and Niven propose that these differences are at least partially attributable to changes in settlement dynamics. However, what I found more interesting was the surprising degree of similarity between the MP and *early* UP—for both aspects of subsistence considered by the authors—and yet, the potential significance of these similarities was not addressed.

Utilizing evidence from the Southern Caucasus, particularly from the site of Ortvale Klde, Adler and Bar-Oz (Chapter 9) also found few differences in the hunting practices of the late Middle and early Upper Paleolithic occupants of the region, leading them to suggest that “Neanderthals and modern humans were sympatric to the point of exclusion (127).” While the data presented here has largely been published and discussed elsewhere (e.g., Adler et al., 2006), the current summary is not without merit. The data tables are particularly useful; while an error by the publisher resulted in these being left out of the publication, an erratum containing the tables has now been made available.

In the only contribution that focused on the Middle and Later Stone Age of sub-Saharan Africa, Steele and Klein (Chapter 8) modified the criteria that Stiner and colleagues have used to compare Middle and Upper Paleolithic subsistence in the Mediterranean region (e.g., Stiner and Munro 2002) for application to the South African record. The available data indicate significant differences in subsistence behavior between the MSA and LSA. In considering the implication of these results, the authors argue that because resource intensification is not evidenced until the LSA—and because they believe that this intensification required the development of LSA technology—“modern human behavior more likely arose at the beginning of the LSA and not during the MSA (123)”. This struck me as a bit of a leap, as I am uncertain as to why a relative lack of resource intensification must equate with non-modern behavior during the MSA—it seems there are several other lines of evidence that would more directly speak to the cognitive abilities of MSA populations (e.g., Henshilwood and Marean 2003).

Bocherens (Chapter 19) and Richards (Chapter 20) present back-to-back chapters on the isotopic evidence for the dietary habits of Neanderthals vs. those of Upper Paleolithic humans. Both employ carbon and nitrogen isotope values; of the two, Bocherens’ comes off as stronger because he provides more background detail on methodology and potential caveats, making the paper more accessible to non-specialists. Consistent with previously published results, Bocherens concludes that Neanderthals obtained much of their dietary protein from large, open-dwelling herbivores; Richards found that while animal protein remained an important component of Upper Paleolithic diets, aquatic foods were more commonly consumed.

Rounding out the consideration of Neanderthal and modern human subsistence are contributions that address the division of labor (Stiner and Kuhn), plant use (Jones), hunting technology (Shea), skeletal morphology (Churchill and Rhodes), and energetics (Macdonald et al.). The chapters by Stiner and Kuhn (Chapter 11) and Shea (Chapter 14) cover much of the same ground as their heavily cited pa-

pers on the same topics (Kuhn and Stiner 2006; Shea 2006); this may be a reflection of the fact that the symposium on which the volume is based was held the same year that these influential papers were published. Regardless, both contributions are well suited to the current volume, which sought not only to present new data but also to provide summaries of recent research.

Jones' (Chapter 12) discussion of plant use in the Paleolithic is largely theoretical in orientation, but raises some very interesting points for those interested in cognitive evolution. Evidence for behaviors that involve long processing sequences, such as multi-component, multi-stage artifact production, has often been cited as an indicator of advanced cognitive abilities. Jones provides a convincing argument that plant use may be more informative about cognitive evolution than we have previously considered; for example, many plant foods require long (and sometimes complex) processing sequences in order to be made edible. Given the growing interest in exploring evidence for complex cognition outside of the symbolic realm (e.g., Wadley et al. 2009), this contribution feels particularly timely.

Churchill and Rhodes (Chapter 15) look to two aspects of upper limb morphology—glenoid fossa shape and ulnar supinator crest morphology—that may be informative about the origins of habitual throwing behaviors (and thus the origins of projectile hunting weaponry). Although admitting that their results were somewhat equivocal, they argue that, as a whole, osteological data are consistent with the hypothesis that projectile technology originated in Africa during the later MSA and moved into Europe with the earliest modern humans in that region.

Rather than viewing the differences between Neanderthals and anatomically modern humans as being driven primarily by cognitive differences, Macdonald and colleagues (Chapter 16) focus on the potential consequences of the higher energy requirements of the Neanderthals. Their brief example addresses the ways in which these requirements would have impacted Neanderthals' mobility strategies and use of space, and does serve to illustrate the potential utility of an energetics approach to thinking more broadly about the differences between Neanderthals and modern humans.

Finally, I would be remiss if I did not mention the sole contribution that addresses the changes in human diet witnessed at the end of the Paleolithic—Munro (Chapter 10) provides a well-written summary of the current state of knowledge on subsistence intensification during the Levantine Epipaleolithic, addressing the implications of this

data to our understanding of the transition to agriculture.

While the absence of any contributions that focused on the African evidence for the origins of meat consumption and early hunting behavior means that the current volume does not quite stand as "one-stop-shopping" for those interested in the evolution of human diets, the volume does admirably well at providing both a summary of current research in the field while also presenting some new perspectives. My only real complaint is that given that the purpose of the symposium (and the subsequent volume) was to promote integrative approaches to the study of hominin diets, it would have been nice had more individual contributions actually employed multidisciplinary perspectives. Regardless, the volume will be a valuable addition to the libraries of those interested in dietary evolution, and would also serve as a useful jumping-off point for graduate-level seminars on the topic.

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