

Issues in human evolution

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New discoveries, new methods, and new theories continue to boost understanding of human evolution. Genetics has shown that contrary to what anatomy alone has long suggested, people and chimpanzees are more closely related to each other than either is to any of the other great apes. This finding has forced a change in long-standing taxonomic practice, and specialists now commonly place all of the great apes, including people, in the family Hominidae, previously reserved for people. People, living and extinct, are then separated from the other apes at the tribal level as Hominini, anglicized to hominini (1). This PNAS Special Feature showcases some recent discoveries and ideas on what makes the hominin mind unique, on the environmental backdrop to hominin evolution, on whether early hominin evolution should be characterized as a ladder or a bush, on what ancient DNA tells us about the demographic history of living humans and their closest fossil relatives—above all the Neanderthals—on the extent to which the Neanderthals differed behaviorally from modern humans, and finally on how prehistoric modern humans, following their expansion from Africa 50–40 ka, impacted other species.

In the opening article, MacLean (2) argues that hominins share many features of cognition with other species, particularly the great apes, but that hominin cognition nonetheless remains unique. Thus, like humans, the other great apes can grasp the intentions and desires of others, but only humans routinely use the information for communal or cooperative purposes, beginning around age one. Common chimpanzee males hunt cooperatively, but the spoils go almost entirely to the successful captor, with little or none of the communal sharing that occurs when humans hunt in groups. This uniquely human tendency to collaborate for the good of the social unit largely explains the difference between human culture and what has been called chimpanzee culture. The question remains of how to identify uniquely human collaboration in the fossil or archaeological records and then to trace its evolution. The collaboration was certainly present 50 ka, when archaeological residues often fully anticipate the material culture of historically observed hunter-gatherers, and

it seems likely that it appeared long before, but specialists hotly debate exactly when.

Uno, Polissar, Jackson, and deMenocal (3) present new observations on vegetational change in eastern Africa over the past 24 Ma, and conclude that the C4 grasses that currently dominate east African grasslands and savannas (wooded grasslands) first appeared regionally about 10 Ma and expanded linearly thereafter. This conclusion stems from stable isotope analysis of terrestrial plant wax biomarkers in marine cores from the floors of the Somali Basin and the Red Sea. River discharge from the east African coast provided the wax-bearing sediments, which thus reflect broad regional as opposed to strictly local conditions. The authors' view may appear to contradict an earlier one that C4 grasses expanded in eastern Africa only after 8–5 Ma, but the previous one was based mostly on a much less continuous record of stable isotopes in mammalian dental enamel and soil carbonates, and the records behind the two views may be fruitfully combined. The appearance of C4 grasses roughly 10 Ma could then explain a roughly contemporaneous dietary shift to some C4 grazing in proboscideans (broadly understood as elephants) and equids, whereas the burgeoning of C4 grasses after 8–5 Ma ago could explain the roughly simultaneous appearance of the hominins and an evolutionary burst in grazing antelopes. Taken together, the stable-isotope and faunal records support the "savanna hypothesis" (4–6) (my conclusion), according to which bipedalism and other uniquely human specializations were adaptive responses to progressive savanna expansion and woodland shrinkage across eastern and southern Africa after 8 Ma.

Haile-Selassie, Melillo, and Su (7) review hominin fossils dated between roughly 4 and 3 Ma and conclude that they represent at least three contemporaneous species. The fossils come mostly from sites in or near the Great Rift Valley between northern Tanzania and north-central Ethiopia. Like other specialists, Haile-Selassie et al. believe that most of the specimens represent *Australopithecus afarensis*, epitomized by the famous partial skeleton of "Lucy" and other fossils from Hadar, Ethiopia. However, the authors think that

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three dentitions their team recovered in the Woranso-Mille survey area about 35 km north of Hadar represent a new species, which they have named *Australopithecus deyiremeda*. The dentitions date from between 3.5 and 3.3 Ma, firmly within the known time range of *Au. afarensis*, which also occurs at Woranso-Mille. The jaw and dental differences from *Au. afarensis* are relatively subtle, and the recognition of a new species can be contested. However, a partial foot skeleton, dated to about 3.4 Ma from another site at Woranso-Mille, displays an opposable big toe and other features that distinguish it from the foot of *Au. afarensis*, in which the big toe lay alongside the others, as it does in all known later hominins. If the hominin status of the foot is accepted, it demonstrates more clearly than jaws or teeth that a second hominin species existed alongside *Au. afarensis* between 4 and 3 Ma. Bahr el Ghazal, Chad, and West Turkana, Kenya, have provided additional fossils that some specialists assign to yet further species. The presence of multiple hominin species between 4 and 3 Ma requires that we identify the natural selective forces that triggered their separation and the behavioral and ecological differences that then allowed them to coexist, even overlap geographically.

Roebroeks and Soressi (8) summarize archaeological evidence for the behavior of the European Neanderthals and their African contemporaries between 120 and 50–40 ka. The Africans were anatomically near-modern, meaning that they shared some but not all of the derived anatomical traits observed in fully modern people after 50–40 ka. Fossils and genetics imply that a subpopulation of near-modern Africans gave rise to the fully modern humans who replaced other nonmodern Africans beginning about 50–40 ka and who dispersed from Africa to replace the Neanderthals and other nonmodern Eurasians at about the same time. Many authorities assume that if Africans were near-modern in their anatomy between 120 and 40 ka, they must also have been near-modern in their behavior, and the point seems to be confirmed by the sporadic discovery of putative art objects and ornaments in their sites. These objects are thought to anticipate the much less equivocal and more elaborate art objects and ornaments that occur in artifact assemblages left by the earliest fully modern people after 50 ka. Roebroeks and Soressi note, however, that Neanderthal sites have sporadically produced equally compelling “symbolic” artifacts and other supposed markers of precocious, fully modern behavior. It follows that if all we had were the archaeology, we could argue about whether modern humans originated in Africa or Europe. A more important inference (mine) is that the shift to fully modern behavior in Africa probably occurred abruptly around 50 ka rather than gradually between 120 and 50 ka, and that it prompted the out-of-Africa expansion.

Slatkin and Racimo (9) survey the rapidly growing ancient DNA evidence for hominin population history, including indications that the Neanderthals and another archaic Eurasian group known as the Denisovans exchanged genes with each other and with modern humans. The Denisovans are so far known almost entirely from their DNA, extracted from four morphologically uninformative fossils found in Denisova Cave, south-central Siberia. Genetics implies that the ancestors of the Denisovans diverged from those of the Neanderthals after the ancestors of the Neanderthals had diverged from those of modern humans, and archaeology suggests the Denisovans disappeared about the same time as did the Neanderthals, around 50–40 ka. The Neanderthals, the Denisovans, and living Eurasians share autosomal genes that they do not share with living Africans and also presumably with the subpopulation of fully modern Africans who colonized Eurasia

50–40 ka. The most economic explanation is that the shared genes originated from the Neanderthals and Denisovans. The Neanderthal genomic contribution to living Eurasians is now estimated at 1–4%, depending on the place. The contribution is greatest in east Asians, which was unexpected, because fossils indicate that the people who occupied eastern Asia in the Neanderthal time range, between roughly 200 and 40 ka, were on a separate evolutionary track (10). DNA assay may one day show that they were Denisovans, but this would raise the question of why Denisovan DNA is absent or rare in living east Asians; it is common, comprising 4–6% of the genome, only in Australian aborigines and their Melanesian neighbors. This result was also unexpected, because the aborigines came from southeast Asia 50–45 ka (11), and modern southeast Asians have little or no Denisovan DNA. Another surprising finding outlined by Slatkin and Racimo (9) is that Native American genomes contain a small amount of Australo-Melanesian DNA and that the amount is greater in Native South Americans than in North Americans. Finally, it seems odd that Neanderthal/modern human interbreeding left traces only in the autosomes. No Neanderthal (female-inherited) mitochondrial DNA has been found in living humans or in early modern Europeans, and the (male-inherited) Neanderthal Y-chromosome also appears to be extinct (12). It's possible to imagine how genetic drift or natural selection could have removed Neanderthal mitochondrial DNA and the Y-chromosome from modern humans, and similarly, to accommodate after the fact the discrepancies between population admixture implied by DNA and expectations from geography and the fossil record. Still, paleoanthropologists may be unsettled by the recurrence of unexpected results.

In the final paper, Boivin et al. (13) document the substantial impact that people have had on other species since the modern human expansion from Africa 50–40 ka. An oft-cited example is the extinction of large vertebrates at or near the end of the Last Glaciation, 14–12 ka, especially in the Americas, where people had only recently arrived. North America lost 35 (>70%) of its large mammal genera about this time, and South America lost even more. The earliest Americans have often been blamed, although the issue is contentious because the extinctions coincided broadly with glacial-to-interglacial climate change, and some of the lost genera may actually have disappeared before people arrived. The European cave bear (*Ursus spelaeus*) provides a less-ambiguous example of early modern human impact on a charismatic large mammal. Cave bear bones are often as common as stone artifacts in caves that the Neanderthals occupied before 40 ka, and both bones and the oldest known European wall-paintings show that the cave bear survived the modern African invasion at 50–40 ka. However, the cave bear then became increasingly rare in Europe, and there is no secure occurrence postdating 25 ka. The explanation is probably that cave bears needed to hibernate in caves and the growth of European early modern populations terminated the previous time-sharing arrangement (14, 15). The widespread advent of agriculture, beginning roughly 12 ka, provides especially abundant and secure evidence for human impact on other species, as people moved domesticated plants and animals from their places of origin and inadvertently or purposefully altered regional environments to accommodate them. Local extinctions of indigenous species became common, and the pace accelerated after 6–5 ka, when cities and states appeared in some places. As Boivin et al. (13) trace prehistoric human impact on other species, they demonstrate that a destructive process we are so concerned about today has deep roots.

