



Climate and Human Evolution

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these genes arose not by whole genome duplications, as is the case for many human paralogs, but through an accumulative process by which the *Daphnia* genome gained more genes by tandem duplication and lost fewer genes than other lineages.

Gene duplication is an important evolutionary force (11, 12). The conventional view of the fate of duplicated genes is that genetic redundancy reduces constraints on their evolution, allowing for the accumulation of mutations. If these genes escape silencing, they may evolve altered functions. As a consequence, three variables—time since duplication, sequence divergence, and the degree of functional change—should correlate positively with each other, a pattern present in the *Daphnia* genome. In addition, Colbourne *et al.* support an entirely different model for the evolution of novel functions in duplicated genes. In this model, benefits arise from novel gene-gene interactions. The expression pattern of the duplicated gene changes as the result of interactions with a different interacting gene at, or soon after, the time of its duplication. Novel combinations of interacting genes may be expressed in a different tissue, phase of development, or under different environmental conditions. Novel expression patterns may arise by integrating the copied gene into a new genomic location or dissociating the gene from its previous regulatory framework. To support this claim, the authors provide evidence that paralogs, with no or little sequence differences, have in many cases diverged in their expression patterns.

But where is the link to the environment? A strength of the *Daphnia* system, as the present study beautifully demonstrates, is the way it allows investigators to conduct gene expression experiments under diverse ecological conditions. Using expressed sequence tag libraries and genome-wide tiling microarray experiments, the authors demonstrate that genes responsive to specific ecological conditions are overrepresented in duplicated genes, in genes without known homologs, and in genomic regions without gene models (intergenic regions). Thus, *D. pulex* is equipped with a large array of genes with environment-specific functions, allowing these critters to call into play an extraordinary degree of phenotypic plasticity. The same seems to be true for *D. magna*, whose draft genome has been used in some of the comparative work conducted by Colbourne *et al.*

The *Daphnia* model is currently being used in such fields as ecotoxicology, population genetics, the evolution of sex, phenotypic plasticity, ecophysiology (including global change biology), and *Daphnia*-par-

asite interactions. The publication of the *D. pulex* genome will allow this list to expand to embrace the emerging field of environmental genomics. Scientists in this field have already begun exploring how organisms adapt genetically to environmental stressors like heavy metals, rising temperatures, emerging diseases, and bioreactive organic compounds. By focusing on how organisms like *Daphnia* have evolved to cope with such stressors, this new approach goes well beyond questions of what these stressors are, and boldly takes on uncovering the kinds of solutions that evolution can bring about (13, 14). The signatures of these evolutionary answers, of course, are archived in the genomes of populations with different histories and ecologies. As global and local environmental change dominates world news today, understanding links between genes and environments becomes more and more vital. With the *D. pulex* genome, environmental health has found its genomic model.

ANTHROPOLOGY

Climate and Human Evolution

Peter B. deMenocal

Climate change and its effects on African ecosystems may have played a key role in human evolution.

Did climate change shape human evolution? This question has old, deep roots (1, 2), but in recent decades, the fossil record of hominin evolution and behavior has improved, although it remains incomplete, and great progress has been made in the quality and number of African paleoclimate records from land and ocean sediments (3). A recent National Research Council (NRC) report (4) examines emerging faunal and paleoclimate evidence underlying the hypothesis that past climate changes may have influenced our evolution.

The basic premise is that large-scale shifts in climate alter the ecological structure and resource availability of a given setting, which leads to selection pressures (3, 5). Indeed, some of the larger climate shifts in Earth history were accompanied by unusually high rates of faunal turnover—bursts of biotic extinction, speciation, and innovation (6–8). For example, a large turnover event occurred near 34 million years ago (Ma) when Earth cooled abruptly and large glaciers first expanded upon Antarc-

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tica (8, 9). Many of the taxa that appeared after 34 Ma were better adapted to the new environments that emerged, which included cooler polar regions, greater seasonality, and arid grasslands.

Notable hominin extinction, speciation, and behavioral events appear to be associated with changes in African climate in the past 5 million years. First appearance and extinction events, as well as key behavioral milestones, cluster between 2.9 and 2.6 Ma and again between 1.9 and 1.6 Ma (see the figure, panel A). In the earlier group, these events include the extinction of *Australopithecus afarensis* (“Lucy”) near 2.9 Ma; the emergence of the robust australopiths (*Paranthropus* spp.), with large jaws and grinding teeth, near 2.7 Ma; and the emergence of the larger-brained *Homo* lineage sometime after 2.6 Ma, near the time when the first evidence for Oldowan stone tool manufacture, use, and transport appears (10).

Important evolutionary developments between 1.9 and 1.6 Ma (4) included the first appearance of *Homo erectus*—the first hominin species to resemble modern humans, with large brains, similar dentition, and a lithe frame—near 1.9 Ma. By 1.6 Ma, the

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more developed and refined Acheulean stone tool industry appears, including bifacial hand axes. This period also includes the first hominin exodus out of Africa and into Europe and South Asia.

For any given time period, the number and diversity of hominin fossils is low relative to most other taxa. Paleontologists have turned to another mammalian group that shared the African landscape with our ancestors, the bovids, for evidence of climate influences. These even-toed ungulates, such as antelopes, represent roughly one-third of African fossils [hominin fossils constitute <1% (11)]. An all-Africa analysis of bovid evolution spanning the past 6 million years revealed several turnover events where rates of speciation and extinction were well above background levels (5). The two largest of these events occurred near 2.8 Ma and 1.8 Ma (5), and the nature of the faunal changes implicates aridification and grassland expansion as a likely cause; for example, many new grazing bovid species appeared with specialized dentition (hypsodont molars) for processing the abrasive, grassy diet (12).

African climate changes during the past 5 million years bear the signatures of two separate processes (13). Orbital precession forcing (with a period of ~20,000 years) acted as a “monsoonal pacemaker” that switched between wet and dry conditions. A long-term

trend toward increasing drier and more variable conditions is superimposed on these wet-dry cycles, commencing after ~3 Ma and peaking near 1.8 to 1.6 Ma.

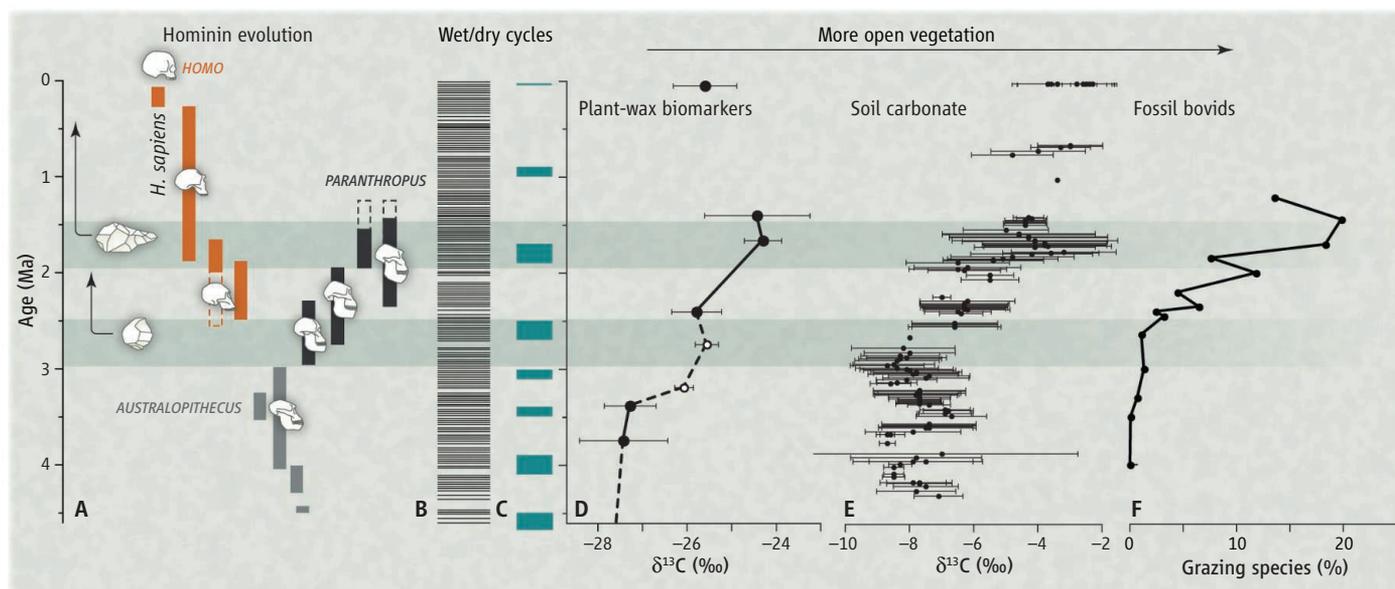
The African wet-dry cycles are impressive: From 15,000 to 5000 years ago, the modern Saharan Desert was nearly completely vegetated, with large, permanent lakes and abundant fauna (14). Precessional increases in summer radiation invigorated the monsoon, delivering more rainfall deeper into Africa, and enhanced Nile river runoff flooded into the eastern Mediterranean Sea. The resulting freshwater stratification created anoxic conditions and led to deposition of organic-rich sediments (sapropels) on the seafloor. Stratigraphic sections representing many millions of years contain hundreds of these sapropel layers (15), and these layers are commonly bundled into 100,000- and 412,000-year packages associated with the modulation of orbital precession monsoon cycles with the eccentricity of Earth’s orbit (see the figure, panel B). Many East African rift valley lakes in Ethiopia, Kenya, and Tanzania were high during a few, but not all, of these high-eccentricity intervals (see the figure, panel C) (16, 17).

The long-term drying trend is documented by increases in African wind-borne dust after 2.8 Ma, with peak values near 1.8 to 1.6 Ma off East Africa (13). Carbon isotopic

analyses of plant wax biomarker compounds from a drill site in the Gulf of Aden (18) (see the figure, panel D) and analyses of soil carbonate nodules near hominin fossil localities (19, 20) (see the figure, panel E) indicate that East African savannah grasslands expanded at these times. Increased numbers of grazing bovid species parallel the grassland expansion (see the figure, panel F) (12).

Hypotheses linking African climate and faunal change are constrained by these new observations. Faunal lineages typically persisted throughout dozens of wet-dry climate cycles, so it is unlikely that the orbital-scale variability alone was a selection agent. Similarly, early hypotheses emphasizing only the unidirectional development of open vegetation do not capture the now-evident complexity of African climate variability. An emerging view is that African fauna, including our forebears, may have been shaped by changes in climate variability itself. These views posit that increasing climate variability led to climate and ecological shifts that were progressively larger in amplitude (3, 21, 22).

The evolutionary signatures of these climate changes are recorded by the appearance of new traits, such as the increase in larger, more hypsodont grassland bovid species, after 3 Ma and especially after 1.8 Ma (5, 11, 12). For hominins, these environmental transition periods were coincident with fun-



A snapshot of African evolutionary and paleoclimate changes. (A) Summary diagram of human evolution spanning the past 4.6 million years [no phylogenetic relations are indicated; compiled from (4, 10)]. First appearances and approximate durations of Mode 1 (Oldowan) and Mode 2 (Acheulean) stone tools are indicated (11). (B) Occurrences of Mediterranean sapropel deposits compiled from marine and land sediment sequences (15). (C) Compilation of sedimentary evidence indicating deep lake conditions recorded in several East African paleolake basins (16, 17). (D) Carbon isotopic analyses of plant-wax biomarker compounds

measured at Site 231 in the Gulf of Aden, currently the most proximal ocean drilling site to hominin fossil localities (18). The shift to higher values after 3 Ma indicates a greater proportions of C4 vegetation, or savannah grasslands. (E) Carbon isotopic values of soil carbonate nodules compiled from several studies (19, 20), also indicating grassland expansion after ~3 Ma, peaking between 1.8 and 1.6 Ma. (F) Relative abundance of African mammals indicative of seasonally arid grasslands in the lower Omo Valley (Ethiopia), showing an initial increase in grassland-adapted mammals after 2.5 Ma with peak values after 1.8 Ma (12).

damental speciation, extinction, and morphological and behavioral milestones that ultimately produced those traits that define us as human and distinguish us from other primates (4, 5, 21). On the basis of an analysis of coexisting East African hominin and bovid fossil assemblages, Reed (23) concluded that “*Homo* species appear the first to be adapted to open, arid environments.”

One strategy articulated in the NRC report (4) is to investigate the key evolutionary milestone events as natural history experiments. The grand challenge will be to develop coordinated sets of observations to test proposed links between African climate and faunal change. The foremost task will be to improve the fossil and paleoclimate records, especially for those intervals where

available evidence is most suggestive of climatic forcing of adaptive evolutionary change.

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PSYCHOLOGY

Happy People Live Longer

Bruno S. Frey

There is a longstanding idea that happiness causes people to live longer, healthier lives. However, convincing evidence that subjective well-being (the more scholarly term for happiness) contributes to longevity and health has not been available. Recently, however, social psychologists Diener and Chan (1) showed that many kinds of studies, using different methods, conclude that happiness has a positive causal effect on longevity and physiological health.

Previous studies had offered widely different and competing findings. Some found no causation or reverse causation, in particular that healthy people are happier (which is undisputed) (2). Others suggested that unidentified, unobserved factors influence both happiness and longevity and health. Diener and Chan's survey presents solid evidence for the benefits of happiness. For example, a meta-analysis (3) based on 24 studies estimated that happy people live 14% longer than persons who report that they are unhappy. In a survey of people living in industrial countries, happier people enjoy an increased longevity of between 7.5 and 10 years (4). Happier people are also less likely to commit suicide, and they are less often the victims of accidents.

How can researchers measure the influ-

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Happy? Satisfaction is linked to healthier, longer lives.

ence of happiness on physical health and longevity? One important method is the longitudinal study, in which investigators follow individuals over many years, to identify whether the happier ones live longer. The “nun study” (5) has become particularly famous. Nuns are well suited for a longevity study because they live under very similar conditions. Before young women entered a monastery, researchers asked them about their subjective happiness level. Those who perceived themselves to be happier died at a median age of 93.5 years. In contrast, those who considered themselves to be less happy died at a median age of 86.6 years.

Researchers can also examine how external, or exogenous, factors that induce changes in happiness are related to specific physiological processes known to affect health and longevity. Emotions can be manipulated in laboratory experiments, for instance, by showing subjects a joyful or a sad film. Investigators can then measure how particular physiological factors, such as blood pressure, change. The effect on happiness of naturally occurring events, such as tempests, inundations, and earthquakes, also can be analyzed. Researchers also study how personal shocks, such as losing a companion, affect health. For example, one study (6) finds that the mortality of