pathways in sperm (*2, 4*) are based on analogies with the odorant signaling cascade of olfactory neurons. Binding of ligands to neuronal ORs dissociates nearby heterotrimeric G proteins, activating adenylyl cyclase and increasing the cyclic AMP messenger, which then directly binds to and opens cyclic nucleotide–gated cation channels at the cell surface. The Na^+ and Ca^{2+} ions that enter through these channels produce the depolarizing electrical signal that is communicated to higher centers in the brain. Consistent with the proposal of analogous mechanisms in sperm, Spehr *et al.* observe that the Ca^{2+} ion signals induced by bourgeonal are blocked either by an inhibitor of conventional adenylyl cyclases or by removal of external Ca^{2+}. Additional work will be required to reconcile these results with evidence that the predominant, unconventional adenylyl cylcase of sperm does not couple to G proteins (*7, 8*) and that the known cyclic nucleotide–gated channel of sperm strongly prefers cyclic GMP rather than cyclic AMP (*9*).

Studies of sperm model systems indicate that increased Ca^{2+} is the signal for the flagellum to beat asymmetrically and thus for the swimming path to turn. Paradoxically, turning is desirable (*10*) and observable (*5*) for invertebrate sperm when they move away from the source of the attractant that signals Ca^{2+} to rise. For sea urchin sperm, a proposed solution to this paradox is sketched in considerable (*10*) but not completely defined (*11*) detail. A complete description of hOR17-4 action must also explain how Ca^{2+} signals modulate flagellar function and direct swimming toward the source of attractant. Spehr *et al.* (*1*) find robust Ca^{2+} signals in nearly half of all the sperm examined without special precautions in their preparation or treatment. Thus, study of the responses of single sperm in defined gradients of bourgeonal should be feasible and informative.

Study of marine invertebrates has also taught us that the molecules mediating interactions between the gametes are under intense evolutionary pressure (*12*). A past comparison of the extent of divergence for rodent OR orthologs found that testicular ORs are more conserved than nasal ORs (*13*). If hOR17-4 is crucial for sperm chemotaxis, then sequence comparisons among its orthologs may show even stronger conservation.

Identification of a bona fide G protein–coupled receptor in mature sperm, together with a potent agonist and an effective reversible antagonist, constitutes a landmark event. New insights into Ca^{2+} and cyclic AMP signaling in sperm are sure to follow. The additional finding of Spehr *et al*. that an identified odorant alters sperm swimming behavior should also stimulate much future work. Some may interpret the Spehr *et al*. work as indicating that the human egg produces an attractant that is a ligand for hOR17-4 expressed by sperm, and may even conclude that attraction between the sexes extends to the level of the gametes themselves. A more guarded view is that this work provides the tools to examine the question of mammalian sperm chemotaxis in meaningful new ways. Soon we may have definitive evidence of whether the successful sperm is the one that stops to smell the roses.

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PALEOANTHROPOLOGY

Early Hominids—Diversity or Distortion?

Tim White

Ernst Mayr once described hominid taxonomy as a "bewildering diversity of names" (*1*). George Gaylord Simpson later lamented "the chaos of anthropological nomenclature" (*2*). These founding fathers of modern taxonomy brought paleoanthropological and zoological systematics into conformity—but only temporarily.

Many of today's paleoanthropologists herald each new fossil as evidence of ancient hominid biodiversity, following Gould's prediction of a "bushy" hominid tree (*3*). Completing the circle, the resulting taxonomic inflation is widely proclaimed as evidence of "a many-branched bush of diversity" [(*4*), p. 33]. But whether judged from fossil evidence or zoological considerations, the metaphor of an early hominid bush seems seriously misplaced.

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For example, last summer's announcement of the "Toumai" hominid cranium from Chad (*5*) was enthusiastically greeted as "the tip of an iceberg of taxonomic diversity during hominid evolution 5–7 million years ago" (*6*). The same author even predicted a Late Miocene "African ape equivalent of the Burgess Shale" (*6*). How could a single fossil from a previously unknown period warrant such claims?

Paleoanthropology has readily adopted "diversity" systematics over the last 10 years, partly because of new fossils. But as Wilford astutely noted (*7*), the embrace of ethnic diversity among contemporary academics may be creating a peculiar form of politically correct paleoanthropology. Hominid phylogenies now regularly recognize up to 20 species. New hominid fossils are routinely given new species names such as *Ardipithecus ramidus*, *Australopithecus anamensis*, *Australopithecus garhi*, and *Homo antecessor*. At the same time, long-abandoned names such as *H. heidelbergensis* and *H. rhodesiensis* have recently been resurrected. Textbook authors and publishers eagerly adopt these taxa. But does the resultant nomenclature accurately reflect early hominid species diversity?

To evaluate the biological importance of such taxonomic claims, we must consider normal variation within biological species. Humans (and presumably their ancestors and close relatives) vary considerably in their skeletal and dental anatomy. Such variation is well documented and stems from ontogenetic, sexual, geographic, and idiosyncratic (individual) sources. Populations and species lineages also change through time, introducing an additional dimension of variation.

As an example of how biological variation is currently assessed in fossil hominids, consider the African middle Pliocene (between 3.5 and 4.0 million years ago). Until recently, a substantial collection of fossils from eastern Africa dated to between 4.1 and 3.0 million years ago was thought to sample an evolving species lineage (*Australopithecus anamensis* to *Australopithecus afarensis*). The fossils showed substantial size and shape variation, but this variation readily conforms to that in modern analog species such as the African apes.

Then, in 2001, a new Kenyan cranium, KNM-WT 40000, was interpreted by its

discoverers to represent a second middle Pliocene hominid lineage. Named *Kenyanthropus platyops* ("flat-faced man from Kenya") by Leakey and colleagues, this fossil was heralded as evidence of an early diet-driven adaptive radiation (*8*).

There are two questions to be asked in considering whether the fossil constitutes evidence of early hominid species diversity. First, are the described morphological differences from the *A. anamensis* to *A. afarensis* lineage real, or are they merely artifacts of postmortem fossilization processes? Second, does the putatively new morphology lie outside the expected range of phenotypic variation of this lineage? Fortunately, the history of vertebrate paleontology provides a largely unappreciated but critically important perspective on the first question. Modern primate skeletal collections help to address the second.

In the early 1900s, thousands of fossils from the western badlands flooded America's museums. Among them were the oreodonts—medium-sized pig relatives from 33.7 to 23.8 million years ago. Paleontologists named a multitude of oreodont species and inferred an adaptive radiation from the "diversity" they created. In retrospect, "oreodont taxonomy and concepts of phylogeny became chaotic" until subsequent analysis trimmed the oreodont tree to realistic proportions [(*9*), p. 498].

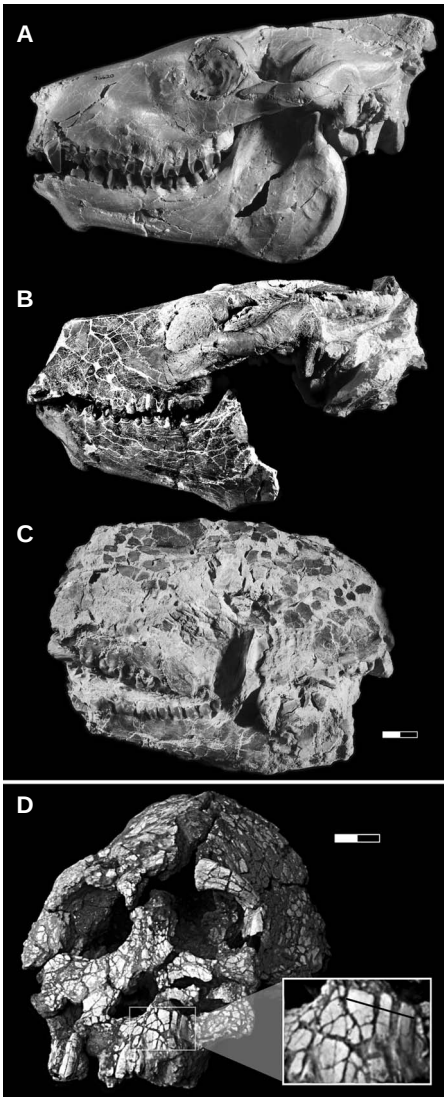
The early systematic exuberance of oreodont paleontologists is a textbook example of postmortem deformation driving the creation of invalid fossil taxa. Distorted oreodont crania were selected as type specimens for *Platychoerus platycephalus* (flat-headed flat pig) and *Stenopsochoerus* (narrow pig) (*10*). But the fossils had been flattened and narrowed by geological deformation, not natural selection. Typological systematics had combined with postmortem distortion to create a diversity that proved chimeric (*9*).

Early hominid crania are usually rare and isolated, in contrast to abundant oreodonts. The KNM-WT 40000 specimen is the only known cranium of *Kenyanthropus*. Its describers claim it to be distinguished by a supposedly diagnostic combination of craniofacial characters (*8*). However, these characters have virtually all been influenced to varying degrees by expanding matrix distortion (EMD) (see the first figure).

The most insidious aspect of EMD is its ability to radically alter morphology in a nonlinear manner. Because matrix expansion does not enlarge all dimensions equally, it often causes highly complex distortion such as that seen in *Kenyanthropus*. The published photographs of KNM-WT 40000 (*5*) show that this fossil suffered EMD stage 4 distortion, with its original surface anatomy splintered into individual bone particles of mostly subcentimeter size (panel D, first figure).

There are about 1100 separate bone pieces in the anterior projection of the *Kenyanthropus* face alone, each isolated by varying thicknesses of matrix fill (*11*). Even the single preserved tooth crown is distorted (*12*). Comparable high-stage EMD is rare in other medium-sized vertebrate crania, even in collections where EMD is relatively common (*13*). In the hominid fossil record, only the Pleistocene Yunxian crania are so severely distorted (*14*). Unfortunately, it is apparently not yet possible to reliably correct for EMD of this magnitude by computerized tomography or other imaging techniques (*8*).

Because the only known cranium of *Kenyanthropus* suffers such a high level of distortion, additional fossil evidence from 3.5 million years ago in the Turkana basin is required to establish whether it represents a valid taxon or is simply an early Kenyan variant of *A. afarensis*. Given the



Distortion. (**A** to **C**) Oreodonts from the John Day Formation, Oregon, illustrate the effects and progression of a particular form of postmortem distortion formalized here as EMD. Small bone fragments are separated by matrix-filled cracks of varying dimensions and geometry. This series typifies different stages of EMD, from slight [(A), stage 1] to severe [(C), stage 5]. Scale bar, 2 cm. (**D**) The cranium of *Kenyanthropus platyops* (EMD stage 4). The anterior facial surface contains about 1100 matrix-separated pieces of bone. A conservative estimate is that the overall specimen comprises about 4000 such individual bone particles.



Variation. Craniofacial variation in a modest (n = 30) sample of bonobos (an extant African ape). The two female specimens occupy opposite positions in the observed ranges of variation but are not outliers of the sample. This variation is normal in a single sex of an extant species; even more variation is present in other extant ape species.

CREDIT: (LEFT) PANEL D: PHOTO, FRED SPOOR/COPYRIGHT NATIONAL MUSEUMS OF KENYA; (RIGHT) PHOTOS, GEN SUWA

extensive deformation of this specimen and the known cranial variation in early hominid species and among modern apes and humans (see the second figure), proclamations that it signals Pliocene hominid diversity seem premature at best.

Is there really a great diversity of hominid lineages waiting to be found and recognized in Africa? Was this diversity like that in extant *Anopheles* mosquitoes (about 500 species), Old World fruit bats (173 species), cercopithecid monkeys (94 species), or even African soft-furred rats (8 species)? Or did just a few demographically expansive and cosmopolitan hominid species expand their ranges and invade new habitats during the Pliocene (5.3 to 1.8 million years ago)?

As Mayr and Simpson appreciated, species recognition is at the core of the paleontological enterprise and is an essential component in building an accurate understanding of evolution. As the hominid fossil record expands, we should not forget their cautions about typological thinking. Confusing true biological species diversity with analytical mistakes (*15, 16*), preservational artifacts, diachronic evolution, or normal biological variation grossly distorts our understanding of human evolution. Past hominid diversity should be established by the canons of modern biology, not by a populist zeal for diversity.

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12. Leakey *et al.* (*8*) reported mesiodistal and buccolingual measurements of 11.4 mm by 12.4 mm for the right upper second molar of KNM-ER 40000 but did not comment on how that measurement was derived. Even accepting the published estimates for the single distorted crown available, it is extremely unlikely that this tooth's size was significantly different from a small *A. anamensis* to *A. afarensis* sample.
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ATMOSPHERIC SCIENCE

Pinatubo, Diffuse Light, and the Carbon Cycle

Graham D. Farquhar and Michael L. Roderick

In studies of the global carbon cycle, light has traditionally been characterized in terms of its intensity. However, as Gu *et al.* demonstrate on page 2035 of this issue (*1*), its geometry can also be important, with potentially global effects.

Visual artists know that subtle differences between light and shade are primarily a result of the geometry of the light source in relation to the subject (see the figure). The same principles also apply in photography: As we age we may prefer to be photographed in a "softer" light from a more diffuse source, which reduces shadows and hence hides wrinkles.

Outdoors, the reduction in shadows is readily observed on cloudy days, but can also happen for other reasons. After volcanic eruptions like that of Mount Pinatubo in 1991, there is a sudden increase in the proportion of diffuse sunlight and hence a reduction in shade. The atmospheric CO_2 concentration usually decreases after volcanic eruptions (*2*); isotopic data suggest that the CO_2 anomaly observed after the Pinatubo eruption was a terrestrial response (*3*). Gu *et al.* (*1*) report how the net exchange of CO_2 by a hardwood forest changed as a result. They show that the increased diffuse light observed under cloudless conditions immediately after the Pinatubo eruption resulted in a sink for CO_2 because of an increase in gross photosynthesis.

The idea that whole-canopy photosynthesis is sensitive to the geometry of light is not new (*4*). It arises because leaf photosynthesis has a saturating response to light intensity. Hence, photosynthesis is typically greater if two leaves receive moderate light than if one receives bright light while the other is in deep shade. On a bright, sunny day, light is concentrated in a beam and the sky is relatively dark elsewhere, resulting in a lot of deep shade within the canopy. In contrast, on a cloudy day, more of the sky is bright—it is a more diffuse source—and hence leaves lower in the canopy are more likely to "see" some relatively bright sky than they would on a sunny day.

Canopy-scale gas exchange measurements have confirmed that such effects are important (*5*). But although the importance of diffuse light has long been recognized in the agricultural community (*6*), its effects have yet to be incorporated in large-scale terrestrial primary production models. Hence, when Pinatubo erupted, the resulting dramatic slowdown in the rise of atmospheric CO_2 concentrations was widely attributed to the effects of temperature on plant and soil respiration (*2, 7*). However,



View of Vetheuil (1880), Claude Monet. Claude Monet wrote that "The subject of my painting is not light and shade, but the painting placed in light and shade."

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