

## Quantum Criticality from Within

The traditional description of classical phase transitions may be insufficient to describe some of the subtleties now being observed experimentally in systems exhibiting quantum phase transitions. In contrast to the traditional methods that describe the "order parameter" of the bulk phases, and then home in on the quantum critical point (QCP), **Senthil et al.** (p. 1490; see the Perspective by **Laughlin**) approach the problem from within. They look at the theoretical description of the QCP itself and how it evolves as the parameters are varied. By using theoretical tools involving deconfined excitations and "fractional" particles, they describe the phases of a square-lattice antiferromagnet.

## Stress and Drink

Corticotropin-releasing factor (CRF) is strongly linked to the behavioral changes associated with stress and alterations in the hypothalamic-pituitary-adrenal stress axis. Stress-induced drinking of alcohol and relapse behavior have a significant genetic component. The basic mechanisms underlying the interaction between stress, brain CRF, and alcohol are not fully understood. **Nie et al.** (p. 1512) found that CRF receptor knockout mice lacked the enhancing effect of CRF and ethanol on GABAergic neurotransmission in the central amygdala, a brain region prominently involved in alcohol dependence and reinforcement. CRF1 antagonists blocked both CRF and ethanol effects in wild-type animals, suggesting a direct role for CRF receptor-mediated processes in the acute effects of ethanol.

## Magnetic Metamaterials

The magnetic response of materials found in nature generally tend to be limited to the lower frequency gigahertz bands of the electromagnetic spectrum. **Yen et al.** (p. 1494) have fabricated artificial materials, or metamaterials, that consist of arrays of split-ring resonators with tunable magnetic responses in the higher frequency terahertz range. The components themselves have no permanent magnetic moments. The ability to tune the magnetic response simply by varying the dimensions of the individual components opens the possibility to extend the effect into the optical regime.

## Wnts in Development

During embryogenesis, cells may acquire new identities concomitantly with their migration to new locations. Morphogenetic changes are often induced by extracellular ligands and their receptors. What signaling pathways coordinate changes in gene expression with dynamic changes in cell adhesion and migration? **Nelson and Nusse** (p. 1483) review evidence of possi-

ble interrelationships between Wnt and other growth factor signaling and cadherin-mediated cell adhesion.

## Pathogens Caught in Neutrophil NET

Neutrophils are cells of the immune system that exude a fibrous matrix when activated by a range of bacterial pathogens. **Brinkmann et al.** (p. 1532; see the cover and the Perspective by **Lee and Grinstein**) have found that the matrix consists of DNA, which provides a skeleton for a network of enzymes, including elastase, cathepsin G, myeloperoxidase, lactoferrin, and gelatinase. These neutrophil extracellular traps (NETs) appear to be a type of innate immune response that ensnares pathogens and disarms their virulence factors.

## The Genetics of Mosquito Biting

Throughout the world, mosquitoes of the ubiquitous *Culex pipiens* species complex are important vectors for several infections, and currently are most notorious for transmission of West Nile Virus. This complex constitutes a bewildering variety of mosquito types showing different behavioral traits that,

until now, could not be distinguished genetically. **Fonseca et al.** (p. 1535; see the news story by **Couzin**) investigated the genetics of these mosquitoes in relation to biting preferences and hence their capacity to transmit zoonotic viruses. All New World *C. pipiens* populations tested showed evidence of hybridization with the human-feeding *Culex quinquefasciatus*, which confers biting characteristics likely to permit West Nile Virus transmission.

## Reconstructing European Climate

Reconstructions of climate for the past 1000 years provide insufficient regional and seasonal detail to allow an accurate picture of climate variability. **Luterbacher et al.** (p. 1499) present a high-resolution reconstruction of temperature patterns for European land areas back to 1500 A.D. in a multiproxy approach that includes early instrumental data series and proxy records. The authors determine monthly or seasonal mean tempera-

## Taking a Bite Out of Early Hominid Genera

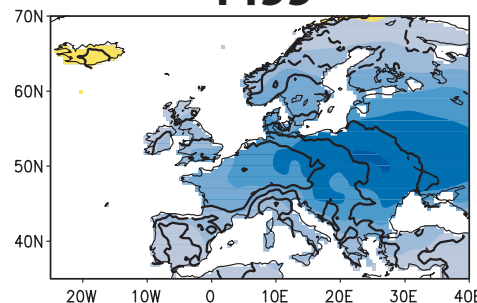
The last common ancestor of chimps and humans is thought to have lived about 6 million years ago; several recent fossil finds (ascribed to three genera) are starting to resolve the early evolution of hominids immediately after this split. **Haile-Selassie et al.** (p. 1503; see the Perspective by **Begun**) describe six new early hominid teeth, including a diagnostic canine, from deposits in Ethiopia that date to 5.2 to 5.8 million years ago. Clear differences in wear are evident versus comparable teeth of apes and ape ancestors. Comparison to other, admittedly sparse material from the few other early hominids implies that available hominid finds may represent less than three genera.

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cathepsin G, and other proteases secreted by leukocytes have been postulated to be important not only for microbial killing, but also for cell migration and tissue remodeling. But uncontrolled activity by these degradative enzymes poses the risk of diffuse tissue damage. Endogenous soluble inhibitors may constrain the range of action of elastase and the cathepsins (4). Meanwhile, NETs may contribute to focusing the activity of proteases by precluding their diffusion. Although not addressed in the paper, it is also possible that NETs sequester cytokines in the local environment of the neutrophil, preventing untoward dissemination of the inflammatory response and thus minimizing damage to surrounding host tissues (5).

The proposed antimicrobial role of NETs seems to be at odds with the use of DNase in mucolytic therapy for treating patients with cystic fibrosis. The hallmark of this common inherited lung disease is tenacious and purulent sputum, whose components include a complex of DNA and elastase (6), reminiscent of NETs. The abundance of proteases immobilized by extracellular DNA in the sputum would appear to be ide-

ally suited to limiting the chronic respiratory infections suffered by cystic fibrosis patients. Hence, degradation of DNA in the sputum by inhaled DNase (which destroys NETs) would be expected to aggravate the disease, not only by impairing these bactericidal tools, but also by releasing elastase and other mediators that could exacerbate the inflammatory condition (7). Paradoxically, therapy with inhaled DNase reduces the symptoms of cystic fibrosis and improves pulmonary function (8). It is possible that excessive NET formation may be counterproductive, preventing proper mechanical clearance of the airways, which is driven by ciliary motion. The cilia themselves may get tangled in the NETs.

The discovery of NETs raises a number of other questions. Do all activated neutrophils make NETs, and if not, what determines which ones do? At what stage of the activation cascade are the NETs "woven"? These questions are important because the notion of activated neutrophils laying down a dense web of extracellular fibers is difficult to reconcile with their need to migrate by chemotaxis toward sites of infection. Indeed,

NETs could conceivably act as a barrier to the recruitment of more white blood cells and thereby impede the clearance of chronic infections, as is the case with the formation of abscesses. Along the same lines, it is not apparent how NETs might be dismantled when the infection has been cleared.

The observations of Brinkmann *et al.* suggest the crucial nature of extracellular killing of bacteria by neutrophils. Whether this antimicrobial action is the result of an active, targeted process by live neutrophils or an altruistic post mortem contribution to the well-being of the organism remains to be defined. Complex though these NETs may be, they should yield to further unraveling during future studies.

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#### ANTHROPOLOGY

## The Earliest Hominins—Is Less More?

David R. Begun

**F**ossil and molecular evidence are converging on a consensus that the human lineage diverged from that of the chimpanzee between ~6 and 8 million years ago (Ma). Recent fossil discoveries in Africa are consistent with this conclusion and are beginning to paint a picture of the pattern of speciation that led to the origin of our lineage. On page 1503 of this issue, Haile-Selassie *et al.* (1) announce a new late Miocene African hominid (2) species, the third in the past 3 years (1, 3, 4). *Ardipithecus kadabba* is a nearly 6-million-year-old hominin (2) that Haile-Selassie and colleagues elevate to the species level from *Ardipithecus ramidus kadabba*. The new discovery renews discussion of the number of taxa that lived shortly after the human lineage diverged from that of chimpanzees, and may shed light on the very nature of the first humans (2). Although Haile-Selassie and co-workers argue that all known African hominids

between ~7 and 4.4 Ma may belong to one genus and see little taxonomic diversity near hominin origins, they may in fact have evidence of more diversity than previously recognized (see the figure).

The new evidence, discovered in the Middle Awash region of Ethiopia, is a handful of teeth including premolars and canines that are indeed distinct from *A. ramidus* (1, 5, 6). But the relationship of this older and smaller sample of specimens to *A. ramidus* is uncertain. *A. ramidus* from the Middle Awash study area (locality of Aramis) has been dated at 4.4 Ma, whereas the morphologically distinctive *A. kadabba* sample from Asa Koma and several other localities also in the Middle Awash study area is older, 5.6 to 5.8 Ma (one specimen, an enigmatic foot phalanx, is dated to 5.2 Ma) (7, 8). On the basis of their interpretation of a gradual transformation from ape-like to humanlike canine/premolar morphology, and the expectation of high levels of diversity within genera or even species, Haile-Selassie *et al.* argue that *A. kadabba* represents an early phase in the development of human anterior teeth. They suggest

that *A. kadabba* represents a transition between chimpanzees (with large, dagger-like canines) and *A. ramidus*, *Australopithecus*, and *Homo* (with unimpressive canines that wear down from the tips). Two other late Miocene hominins, *Orrorin tugenensis* and *Sahelanthropus tchadensis*, show predictable variability in this evolving lineage. This is a plausible scenario. However, *Ardipithecus*, *Orrorin*, and *Sahelanthropus* offer evidence of striking diversity. *Orrorin* has modern-looking thickly enameled molars and robust jaws but has postcranial morphology that is distinct from that of Pliocene hominins (the epoch following the Miocene when clearly bipedal humans are found) (3, 9). *Sahelanthropus* is also quite distinct from Pliocene hominins in craniofacial and dental morphology (4, 10). Do these samples represent stages in early hominin evolution or discrete lineages? In other words, how many taxa are represented by these fossil samples?

Could all of these fossils belong to the same genus, or even the same species? This is implied by Haile-Selassie *et al.* but seems unlikely to me. Comparisons among these taxa are difficult because they preserve little in common. Nonetheless, we know that *Orrorin* has mandibular and molar morphology similar to that of australopithecines, but female canines resembling those of apes (3, 11). *Sahelanthropus* has a unique combination of superficially modern-looking facial and periorbital morphology, primitive-looking teeth and braincase,

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and a probably homologous hominin suite of features of the basicranium (4, 10). *A. kadabba* is distinctive in having canines that appear to partly hone or sharpen against the lower first premolar (P3 by paleontological convention), not as much as in apes but more than in humans. In crown cross section and shape, however, the canines are more hominin-like than the more chimpanzee-like *Orrorin* canines. But *Orrorin* has australopithecine-like thickly enameled teeth, usually associated with a diet requiring powerful chewing forces, whereas *Sahelanthropus*, *A. ramidus*, and *A. kadabba* have intermediate-thickness enamel (less thick than in other hominins, but much thicker than in African apes) (5). Miocene hominids range from thinly enameled chimpanzee-like molars, as in *Dryopithecus*, to *Australopithecus*-like thickly enameled molars, as in *Sivapithecus* and *Ouranopithecus*, and it is unclear which among these or the intermediate condition in *Ardipithecus* and *Sahelanthropus* represents the ancestral condition for hominins. Differences in enamel thickness often distinguish taxa at the genus level and usually reflect dietary adaptation rather than phylogeny.

*Orrorin* is said to share hominin synapomorphies (newly evolved, shared characteristics indicating a recent common ancestry) of the lower limb related to bipedalism (3, 9), but this is far from established. The most important features suggesting bipedalism either are found in nonbipeds (the groove for the obturator externus muscle) or appear different enough from the morphology of known bipeds to call the functional homology of these features into question (the linea aspera, which is unusually laterally displaced in *Orrorin*, or the asymmetric femoral neck cortical bone, which is less asymmetric than in known bipeds) (12). *A. kadabba* also lacks synapomorphies of *A. ramidus* and *Australopithecus* in canine, premolar, and last molar morphology, which suggests that the Asa Koma and other older samples belong to another genus (note that *A. ramidus* was originally named *Australopithecus ramidus* because of an understandable hesitation to name a new human genus, and was later elevated to a new genus when no *Australopithecus*-*Homo* synapomorphies were discovered).

It is tempting to see evidence of anagenesis (unilinear evolution) in the late Miocene hominin record in part because continuity is suggested by claims for some evidence of bipedalism in all known taxa. The evidence from *Orrorin* is ambiguous (see above), whereas that from *Sahelanthropus* is indirect, based only on the position of the foramen magnum. The

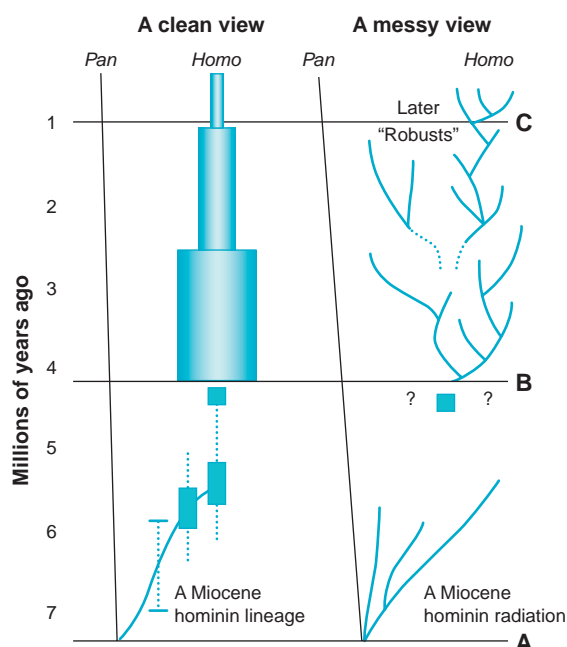
region is severely distorted in the only cranial specimen of *Sahelanthropus*, and even the describers recognize the uncertainty (4). *A. kadabba* is interpreted as a biped on the basis of a single toe bone, a foot proximal phalanx, with a dorsally oriented proximal joint surface, as in more recent hominins (6). However, the same joint configuration occurs in the definitely nonbipedal late Miocene hominid *Sivapithecus* (13), and the length and curvature of this bone closely resembles those of a chimpanzee or bonobo. In addition, the specimen is 400,000 to 600,000 years younger than the rest of the *A. kadabba* sample, 800,000 years older than *A. ramidus*, and from a locality that is geographically much closer to Aramis than to Asa Koma. It may or may not be from a biped, and if it is, which biped?

Another issue is the canine/premolar complex. Tall crowned interlocking ca-

nines are usually associated with agonistic (aggressive) displays typical of primate societies characterized by strong male competition (14). A shorter canine crown in humans is interpreted as an indication of greater levels of male coalitionary behavior, or at least reduced competitiveness. Chimpanzee males are intermediate between humans and most other great ape males in canine crown height and competition levels, and bonobos are intermediate between chimpanzees and humans. But the remarkable reduction of canine crown height in humans is thought to signal a dramatic increase in the degree of male cooperation, cited as a hallmark of human origins [e.g. (15)]. The diversity of canine/premolar morphology described by Haile-Selassie *et al.*, from chimpanzee-like to humanlike, represents a striking and unlikely degree for a single genus, especially

in an anatomical complex strongly correlated to an aspect of socioecology that is considered to be a primary distinction between apes and humans.

Both clade (synapomorphies) and grade (diet, locomotion, and socioecology) criteria suggest more rather than fewer taxa among the earliest possible hominins. Why the different interpretations? Evidence is scarce and fragmentary, and uncertainty predominates. Interpretations rely especially heavily on past experience to make sense of incomplete evidence. Haile-Selassie and colleagues interpret diversity in fossil hominids in terms of variability and gradual evolutionary change in an evolving lineage. Others see cladistic diversity as opposed to ancestor-descendant relations (see the figure). Ancestor-descendant relations must exist, but adaptive radiation and cladogenesis also must exist, or organic diversity would be the same today as it was at the beginning of biological evolution. Rather than a single lineage, the late Miocene hominin fossil record may sample an adaptive radiation, from a source either in Eurasia or yet undiscovered in Africa (16), the first of several radiations during the course of human evolution (see the figure). Regardless, the level of uncertainty in the available direct evidence at this time renders irreconcilable differences



**What you see is what you get.** Two perspectives on hominin evolution driven by different models of the origin and evolution of diversity in the fossil record. (Left) A "clean" view of hominin evolution depicts an evolving lineage of Miocene taxa with progressively less apelike canines and a primitive form of bipedalism (A). Miocene *A. kadabba* is ancestral to *A. ramidus*, which is broadly ancestral to a somewhat larger diversity of younger Pliocene hominins (*Au. anamensis*, *Au. afarensis*, *Au. africanus*) (B) that is increasingly winnowed to one genus, *Homo* (C). (Right) A "messy" view depicts a series of adaptive radiations, migrations, and adaptive innovations. A new kind of hominid radiates into a number of taxa with new adaptations (facultative bipedalism, megadontia, canine reduction, or some combination of all three) (A). One of these radiates into the impressive diversity of Plio-Pleistocene hominins (B). This second radiation yields two terminal clades, one hypermegadont (robust australopithecines) and the other hypercerebral (*Homo*) (C). The degree of "messiness" in chimpanzee (*Pan*) evolution is unknown. Most recent accounts of human evolution are either "messy" or "clean."



## PERSPECTIVES

of opinion inevitable. The solution is in the mantra of all paleontologists: We need more fossils!

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## ASTRONOMY

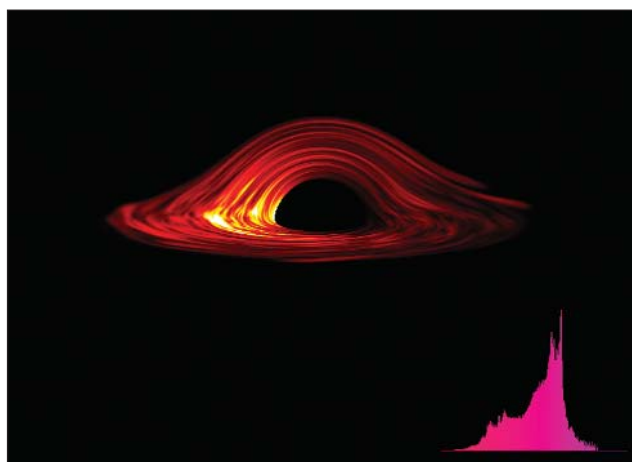
# Watching Black Holes Spin

Stéphane Corbel

By definition, black holes cannot be observed directly. Their effects on nearby light and matter, however, have been seen so often that we are forced to conclude that black holes really do exist. To some extent, we can even understand how they are created. When a massive star dies, it leaves behind a “compact object.” If the mass of the residual compact object is more than about three times the mass of the Sun (the so-called Oppenheimer-Volkov limit), then nothing can hold back gravity and the residual core of the death star becomes a black hole (1).

These strange beasts can be found in x-ray binaries in which the black hole (with a typical mass of  $10 M_{\odot}$ , where  $M_{\odot}$  is the mass of the Sun) is accreting material from a companion star (similar to the Sun, for example) via an accretion disk. Black holes can also be very massive (from  $10^6$  to  $10^9 M_{\odot}$ ) and are found at the center of galaxies (2). Another population of intermediate-mass black holes (tens to thousands of solar masses) may also exist in the so-called ultraluminous x-ray sources (ULXs) (3). For stellar-mass black holes in an x-ray binary, the mass can be measured accurately with spectroscopic optical and/or near-infrared observations of the companion star (4). Similarly, the mass of the black hole Sgr A\* at the center of our own Galaxy has been estimated as  $3.6 \times 10^6 M_{\odot}$  by looking at the motion of stars very close to the black hole (5). Alternative methods (2) also exist for measuring black hole mass in active galactic nuclei (AGN).

In addition to their mass, black holes are also characterized by their spin. The existence of radio pulsars demonstrates that stellar remnants are spinning rapidly when



**Signs of spin.** Predicted appearance of a turbulent accretion disk around a Schwarzschild black hole as viewed by a distant observer at an inclination angle of  $80^\circ$  (that is, the disk is almost edge-on). The plot in the lower right shows the profile of iron line emission from the disk, assuming that the line is excited locally by the predicted disk emission. (See also the animation at [http://jilawwww.colorado.edu/~pja/black\\_hole.html](http://jilawwww.colorado.edu/~pja/black_hole.html))

formed, so it seems likely that all stellar-mass black holes are spinning, at least initially. The rotation (6) of black holes is quantified by the dimensionless spin parameter  $a^* = Jc/GM^2$ , where  $J$  and  $M$  are the angular momentum and mass of the black hole, respectively,  $c$  is the velocity of light, and  $G$  is the gravitational constant. Gas flowing toward the black hole slowly reaches the inner part of the accretion disk up to the innermost stable circular orbit (ISCO). The crucial difference between a spinning black hole (called a Kerr black hole) and one that is not spinning (a Schwarzschild black hole) is that rotation allows the ISCO to move inward in case of corotation (7). This allows the accretion disk to reach closer into the black hole, which in turn permits higher orbital frequencies and higher orbital velocities in the disk. In recent years, there have been growing indications that black

holes may indeed be spinning. These mainly come from two new observational constraints that shed light on the accretion flow close to the black hole.

In the immediate vicinity of black holes, millisecond variations of x-ray emission are expected. This has been observed in the form of high-frequency quasiperiodic oscillations (QPOs) in the x-ray power density spectra of stellar-mass black holes (8, 9). Usually, these QPOs are detected when the soft x-ray emission is very high, which is when the accretion disk is very close to the black hole. How close is a matter of debate, as it is directly relevant to the spin of the black hole. However, the frequencies of these QPOs correspond to an orbital radius that cannot be smaller than the ISCO (7). The ISCO of a Schwarzschild (non-rotating) black hole corresponds to a maximum orbital

frequency of  $220[M/(10 M_{\odot})]^{-1}$  Hz (where  $M$  is the black hole mass). To date, the Rossi X-ray Timing Explorer (RXTE), with its unprecedented time resolution and collecting area, has detected high-frequency QPOs above this frequency in several black hole candidates (8, 9). Such findings could indicate significant spinning of the black hole if these oscillations are related to the orbital frequency of accreting gas at the ISCO. However, the identification of the physical mechanism behind these oscillations is ambiguous. Indeed, these QPOs could also be related to diskoseismic oscillations in which the disk acts as a resonant cavity under influence of general relativity effects (10) or to relativistic dragging of the black hole inertial frame (11). In any case, both of these models also imply significant spinning of the black hole.

Recently, near-infrared flares (possibly associated with emission of nonthermal

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The 20th century (1901 to 2000) was the warmest since 1500. There was a strong warming trend of  $+0.08^{\circ}\text{C} \pm 0.03^{\circ}\text{C}$  per decade within the 20th century. The last 30 years (1974 to 2003,  $\Delta T = +0.43^{\circ}\text{C}$ ) were  $\sim 0.45^{\circ}\text{C}$  higher than the second warmest 30-year periods (1722 to 1751 and 1750 to 1779) of the reconstructions. When we consider the uncertainties of earlier periods, the late 20th- and early 21st-century European warmth at multidecadal (30-year) scale is very likely unprecedented for more than the past 500 years. The nine warmest European years on record have occurred since 1989. The year 1989 ( $\Delta T = +1.3^{\circ}\text{C}$ ) and the decade 1994 to 2003 ( $\Delta T = +0.84^{\circ}\text{C}$ ) were very likely the warmest for more than half a millennium.

Our >500-year continental-scale surface temperatures provide evidence of current European climate change. Comparing recent temperature changes with those of the past and taking into account reconstruction uncertainties, we show that the late 20th- and early 21st-century warmth very likely exceeds that of any time during at least the past 500 years. The high-resolution reconstruction also sheds light on the spatial structure of regional temperature anomalies and extremes back in time. Furthermore, our temperature estimates provide a key test of the General Circulation Model's continental and seasonal response to different forcings (22, 43).

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# Late Miocene Teeth from Middle Awash, Ethiopia, and Early Hominid Dental Evolution

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Late Miocene fossil hominid teeth recovered from Ethiopia's Middle Awash are assigned to *Ardipithecus kadabba*. Their primitive morphology and wear pattern demonstrate that *A. kadabba* is distinct from *Ardipithecus ramidus*. These fossils suggest that the last common ancestor of apes and humans had a functionally honing canine–third premolar complex. Comparison with teeth of *Sahelanthropus* and *Orrorin*, the two other named late Miocene hominid genera, implies that these putative taxa are very similar to *A. kadabba*. It is therefore premature to posit extensive late Miocene hominid diversity on the basis of currently available samples.

The phylogenetic status of the earliest hominid genera *Sahelanthropus*, *Orrorin*, and *Ardipithecus* (1–6) and the definition of the family Hominidae (7–10) are in de-

bate. By what derived characters should the hominid (1, 11) clade be recognized? Bipedality might be an arbiter of hominid status, but "bipedality" involves a large and complex set of anatomical traits and is not a dichotomous character. Femora attributed to *Orrorin tugenensis* at  $\sim 5.8$  million years ago (Ma) constitute the earliest postcranial evidence for early hominid bipedality (2, 12). However, the *O. tugenensis* femora are different from those of later hominids such as *Australopithecus afarensis* (13). Indeed, some question

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whether *Au. afarensis* was habitually bipedal (14–17), despite evidence indicating that some form of bipedality appears to have arisen before 5 Ma (1, 2).

Early hominids have also been identified through dental characters. For example, a functional canine–third premolar (C/P3) honing complex is present in fossil and modern apes but absent in all hominids. Among late Miocene hominids, derived features of the lower canines of *Sahelanthropus tchadensis* and *A. ramidus kadabba* have contributed to the recognition of these two taxa as early hominids. However, only one partial upper canine of *S. tchadensis* and a complete crown of *O. tugenensis* are known. Here, we describe teeth from the late Miocene of the Middle Awash, Ethiopia.

In 2001, hominid fossils from the Middle Awash that were dated 5.2 to 5.8 Ma

(18) were assigned to *A. r. kadabba* (1). Continued work in November 2002 produced additional remains. An upper canine and a lower third premolar are among six new teeth (19) recovered from Asa Koma Locality 3 (ASK-VP-3), with an estimated age of 5.6 to 5.8 Ma (18). The new fossils illuminate hominid dental evolution near the divergence of apes and humans, and they require revision of the taxonomic status of *A. r. kadabba*.

The following is a description of *A. kadabba* sp. nov., elevated here from the subspecies *A. r. kadabba* (1): Order Primates Linnaeus, 1758; Suborder Anthropoidea Mivart, 1864; Genus *Ardipithecus* White, Suwa, and Asfaw, 1995; Species *Ardipithecus kadabba* sp. nov.

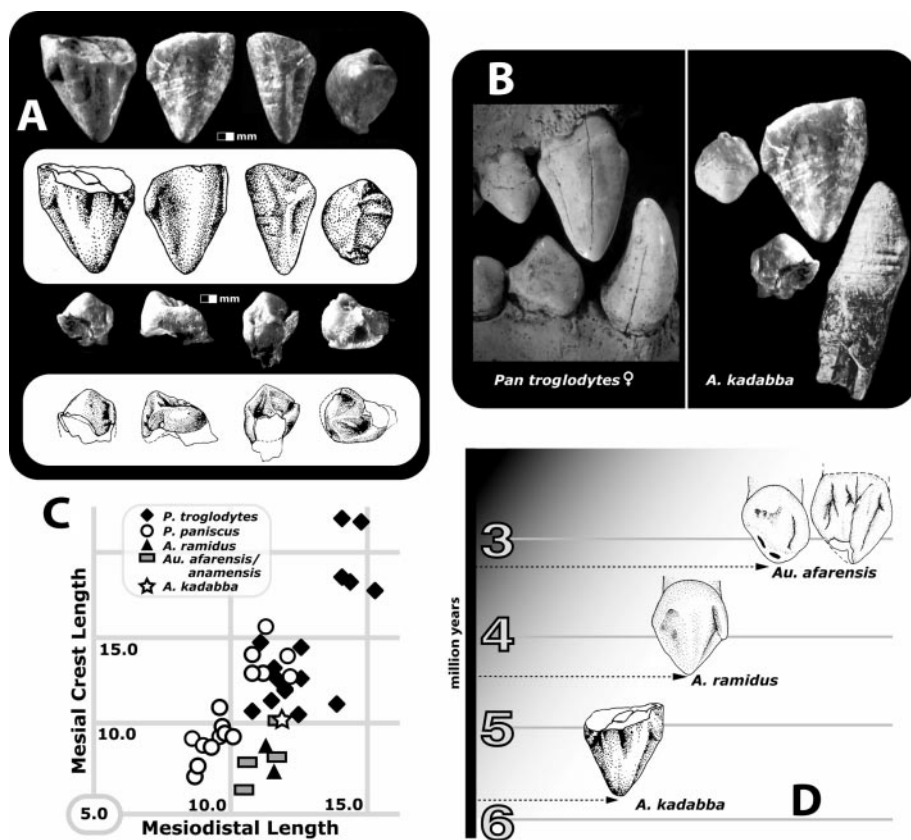
**Holotype, localities, and horizons.** Same as described for *A. r. kadabba* (1).

**Referred material.** The holotype and paratype of *A. r. kadabba* listed in (1), and ASK-VP-3/400 (right upper canine); ASK-VP-3/401 (right upper first molar); ASK-VP-3/402 (left upper first molar); ASK-VP-3/403 (left lower P3); ASK-VP-3/404 (lingual half of left upper P4); ASK-VP-3/405 (right upper P4 fragment).

**Diagnosis.** *A. kadabba* differs from fossil and extant apes by features enumerated in (1) and by the presence of a clearly defined anterior fovea of the lower P3, demarcated by a foldlike buccal segment of the mesial marginal ridge. It differs from extant apes and *O. tugenensis* by its more circular upper canine crown outline in occlusal view. In addition to the features distinguishing *A. r. ramidus* from *A. r. kadabba* (1), *A. kadabba* also differs from *A. ramidus* by the morphology of the upper canine (more basal termination of the mesial and distal apical crests) and morphology of the lower P3 (more asymmetrical crown outline and relatively smaller anterior fovea).

Specimen ASK-VP-3/400 is a right upper canine lacking root and some crown base (Fig. 1; the preserved buccolingual and crown height dimensions of the canine are >10.1 mm and >15.5 mm, respectively). The mesial crest runs from mesial crown shoulder to crown tip, losing sharpness toward the apex. This mesial crest bears a long vertical facet from occlusal contact with the lower canine, extending from the apex and approximating the mesial crown shoulder. The crown tip shows no apical wear except minimal surface polishing. A similar configuration is often seen in chimpanzees at an early wear stage. In later hominids such as *Au. afarensis*, this mesial occlusal facet is not as steep and may be associated with relatively extensive apical wear. The mesial lingual groove is deep toward the base and shallow toward the apex. The rest of the lingual crown face is relatively flat and lacks the apparently stronger hollowing seen in the lone upper canine of *O. tugenensis* (BAR 1425'00) and in chimpanzee homologs (where a lingual cingulum usually contributes to this effect). The mesial shoulder of ASK-VP-3/400 is relatively more basally placed than in *A. ramidus*. This leads to a primitive, tall, pointed crown outline in lateral view.

Relative to basal diameters, the Asa Koma upper canine crown is taller than in *O. tugenensis*, but the latter's canine has an even more basal mesial shoulder than that of ASK-VP-3/400. *Au. afarensis*, *Au. anamensis*, and *A. ramidus* upper canines have relatively lower crowns than those of female *Pan troglodytes*. The new *A. kadabba* upper canine lies at the margin of the fe-



**Fig. 1.** (A) Lingual, labial, mesial, and occlusal views of ASK-VP-3/400 (top two rows), and buccal, distal, lingual, and occlusal views of ASK-VP-3/403 (bottom two rows). Scale bars, 1.0 mm (each segment). (B) Lateral views of a female common chimpanzee and *A. kadabba* upper and lower canines and premolars (upper canine ASK-VP-3/400, lower canine STD-VP-2/61, upper premolar ASK-VP-3/160 reversed, lower premolar ASK-VP-3/403 reversed). (C) Bivariate plot of upper canine mesiodistal length and mesial crest length (in millimeters; see text for discussion). The *Pan troglodytes* sample includes five males and 11 females; the *P. paniscus* sample includes six males and 10 females. The *Au. afarensis/anamensis* sample consists of L.H.-3, L.H.-6, A.L.333x-3, and KNM-KP 35839; the *A. ramidus* sample consists of ARA-VP-6/1 and ARA-VP-1/300. Mesiodistal length was taken either across the mesial and distal shoulders, or, in modern apes, at the crown bases adjacent to the shoulders when the latter yielded slightly larger dimensions. (D) Trajectory of evolutionary change in the early hominid canine, lingual view. Bottom canine is *A. kadabba* (ASK-VP-3/400 reversed) from Asa Koma; middle canine is *A. ramidus* (ARA-VP-6/1) from Aramis; top two canines are *Au. afarensis* from Hadar (A.L.400-1b reversed) and Laetoli (L.H.-3). Arrows indicate temporal placement of the fossils. [Illustrations by Luba Gudž]



male *P. troglodytes* distribution (Fig. 1). The *O. tugenensis* upper canine is relatively more elongate mesiodistally, as are the homologs of female chimpanzees.

ASK-VP-3/403 is a left lower P3 lacking the mesiobuccal crown base and distolingual enamel. The roots are missing except for a portion immediately below the lingual cusp. The crown is asymmetric in occlusal outline, more so than in any known hominid P3. A small facet occupies the mesiobuccal crown face close to the protoconid apex, caused by contact with the lingual surface of an interlocking upper canine. The transverse crest descends from the tip of the protoconid to the metaconid, which is hardly expressed as a distinct entity. It forms a high divide between the larger posterior fovea and the smaller, more restricted anterior fovea. In its occlusal crown outline, the premolar is narrow lingually and broad buccally. The distobuccal face has a vertical enamel ridge delineated by a small groove anterior to it. The anterior fovea is constricted and positioned at the mesiobuccal angle of the occlusal surface, apparently defined only by the buccal segment of the mesial marginal ridge. The mesial protoconid crest is longer than the distal. The protoconid and metaconid are basally defined by a strong constriction of the mesial crown contour. Comparison with *A. ramidus* shows that ASK-VP-3/403 is more asymmetric and therefore more similar to Miocene and extant apes. This corresponds with the Asa Koma upper canine and the previously described morphology of upper third premolars and lower canines of *A. kadabba* (1).

Functional honing is the phenomenon by which all extant and Miocene apes sharpen the distal edge of the upper canine against the mesiobuccally extensive buccal crown surface of the lower P3. The distolingual surface of the upper canine crown is often extensively scalloped by honing wear. Even in the case of female ape canines that are not well sharpened, a distal wear strip extends and faces distolingually because of its occlusal relationship with the lower P3. Of all the African and Eurasian Miocene apes, *Ouranopithecus* has been recognized as having a C/P3 complex that approximates the hominid condition (20). We interpret *Ouranopithecus* as nonhominid because its upper canine is sharpened by wear and because its masticatory specializations are divergent from African hominids predating *Australopithecus*. In contrast, the Pliocene hominids *Au. afarensis*, *Au. anamensis*, and *A. ramidus* usually show vertically elongate wear facets on the distal crest of the lower canine and on both mesial and distal crests of the upper canine. The latter facet is positioned on the distal

crest itself and does not carve into the upper canine lingual crown face. In some cases, occlusal overlap does create a slight lingual bevel on the upper canine and a narrow facet along the mesial crest of the occluding P3 (*Au. afarensis* specimens such as A.L.128-23 and L.H.-5, for example). No known *A. ramidus* (5, 6), *Au. afarensis* (21, 22), or *Au. anamensis* (23, 24) lower P3 exhibits any sign of a mesiobuccally oriented facet on its buccal crown face. The primitive morphology of the Asa Koma C/P3 complex closely approaches the extant and fossil ape conditions, and thereby helps identify *A. kadabba* as a species distinct from *A. ramidus*. The single *Orrorin* upper canine is apparently not worn enough to assess a possible honing condition (2). The few known C/P3 elements of *S. tchadensis* are described as showing no sign of functional honing (3), despite its apparent antiquity (25).

Late Miocene hominid fossils from Chad, Ethiopia, and Kenya have been ascribed to three different genera and interpreted as evidence of phylogenetic diversity (26) despite close anatomical resemblances in comparable parts. The small constellation of derived characters of the *A. kadabba* and *S. tchadensis* dentitions (1, 3) and the *O. tugenensis* femora (12) is shared exclusively with later hominids. Collectively, these fossils provide important outgroup comparisons to geologically younger *A. ramidus* and *Au. anamensis*, confirming these later taxa as cladistically hominid on the basis of their increasingly derived C/P3 complex. The distinctly primitive characters in the *A. kadabba* dentition—such as the projecting, interlocking upper and lower canines, and the asymmetric lower P3 with buccal wear facet—imply that its last common ancestor with chimpanzees and bonobos retained a functioning C/P3 complex. But wear on the upper and lower canines of *Sahelanthropus* (3) and the lower canine of *A. kadabba* from Alayla (1) suggest a lack of consistently expressed functional honing in these earliest hominids. Now that dental remains of the earliest hominids and their descendants are available, a trajectory of canine morphological change from the late Miocene hominids to Pliocene *A. ramidus*, *Au. anamensis*, and *Au. afarensis* can be envisioned (Fig. 1).

Metric and morphological variation within available small samples of late Miocene teeth attributed to *A. kadabba*, *O. tugenensis*, and *S. tchadensis* is no greater in degree than that seen within extant ape genera. Despite claims of molar enamel thickness differences among these late Miocene fossils (2), we question the interpretation that these taxa represent three separate genera or even lineages. Given

the limited data currently available, it is possible that all of these remains represent specific or subspecific variation within a single genus.

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