Current Biology
Dispatches

Paleoanthropology: How Old Is the Oldest Human?

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http://dx.doi.org/10.1016/j.cub.2015.04.009

A 2.8 Ma old mandible unearthed in Ethiopia fills the gap between ape-like australopithecines and representatives of the genus *Homo*. It pushes the origin of large-brained hominins further back in time and highlights the complexity of the human evolutionary tree.

In 1960, just after finishing school, Jonathan Leakey joined his parents, Louis and Mary, at Olduvai Gorge (Tanzania) to give them a hand on their excavation. A year earlier, the Leakeys had discovered a spectacular hominin skull (*Zinjanthropus boisei*) in a locality called FLK of Olduvai's Bed I. Nowadays, this fossil is assigned to a specialized form of australopithecine, the sister group of the genus *Homo* documented in South and East Africa, as well as in Chad. However, in the months following its discovery "*Zinj*" — as it was nicknamed — was seen as a direct ancestor of later humans.
A major sea change occurred when, on the eve of his 20th birthday, Jonathan discovered the fragments of a new specimen in a dig he had opened a few hundred meters north of the FLK site. "Johnny's child", to be numbered OH7, was represented by a mandible, two parietal bones and a series of hand and wrist bones. Compared to those of *Zinj,* its cranial capacity was significantly larger, with an estimate by Philip Tobias close to 674 cc [1], and its cheek teeth were reduced relatively to its anterior dentition. Although yielded by the same 1.8 million year old deposits, OH7 looked indeed much more human-like than *Zinj* and was soon acknowledged as the genuine and only maker of the crude stone artifacts yielded by Bed I. Its description led to the recognition of a new species of hominins, *Homo habilis* [1], contemporaneous with some australopithecines and arguably ancestral to later forms such as *H. erectus* and *H. sapiens*. However, establishing this new species required a complete redefinition of the genus *Homo*, particularly regarding brain size.
This *ad hoc* revision launched one of the most intense controversies in the history of paleoanthropology and still is not unanimously accepted [2].
A new discovery in the Ethiopian site of Ledi-Geraru re-opens this Pandora's box [3].

In the decades following OH7's discovery, a variety of fossils unearthed at Olduvai, as well as from other sites in Kenya, Ethiopia, Malawi and South Africa, have documented the earliest forms of the genus *Homo*. Their large diversity has fueled persistent debates regarding the meaning of this variability (individual variation, temporal trends, sexual dimorphism, multiple taxa). Among other problems, the possible occurrence of at least three different species of early *Homo* (*H. habilis*, *H. rudolfensis* and *H. erectus*) [4] at the time of OH7 implied an older evolutionary history that was not documented. Furthermore, the proposed candidates to the direct ancestry of these early *Homo* were far from convincing. *Australopithecus garhi*, a 2.5 Ma old fossil from the Bouri area in Ethiopia, was one of them. Its limb proportions were more human-like than other australopithecines, but its dentition was very australopithecine-like, with large molars and small incisors. More recently, *A. sediba* from South Africa was also put forward as a possible ancestor of *Homo* [5]. Its features are ambiguous and at 1.98 Ma before present it actually post-dates many early *Homo*.

The new specimen from Ledi-Geraru is a partial mandible named LD 350-1 (Figure 1). It is dated to 2.80–2.75 Ma and is therefore much older than the earliest *Homo* known to date, a 2.33 Ma old maxilla labeled A.L. 666-1 [6]. Both specimens come from the Afar region, best known for the rich series of australopithecines it has yielded. Among them stands the famous "Lucy", a partial skeleton of *A. afarensis*. *A. afarensis* and its immediate forerunner, *A. anamensis*, represent a primitive australopithecine lineage that evolved in East Africa between 4.2 and 3 Ma. Not only does LD 350-1 fill the chronological gap but also the morphological gap between *A. afarensis* and the later *Homo.*
Although LD 350-1 still retains primitive features, it shares several mandibular and dental traits with *Homo*. Noticeably, it is missing the wear pattern observed in *afarensis* between a still slightly salient upper canine and the first inferior premolar. LD 350-1 molar crowns also don't display the transversal expansion observed in australopithecines. These dental differences suggest that the split between the two groups of hominins might initially relate to distinct diet adaptations.

The divergence between so-called "robust" forms of later australopithecines such as *Zinj* and the *Homo* lineage is generally seen as the adoption of alternative adaptive responses to the growing aridity of their habitats. Some hominins had to cope with tougher vegetal foods requiring an oversized masticatory system. Others evolved omnivorous diets including increasingly more meat. For the latter, brain expansion and tool-making was therefore facilitated and eventually became a core aspect of their adaptive strategy. Africa experienced a major environmental shift between 3 and 2.6 Ma ago that might well have triggered these diverging evolutionary trajectories [7]. Indeed the geological and faunal contexts of LD 350-1 suggest a more open and drier landscape than those where A. *afarensis* previously lived [8]. Whereas robust forms of australopithecines are already known in East Africa since at least 2.7 Ma ago, the

Figure 1. The LD 350-1 mandible in hands of its discover, Chalachew Seyou.
The Ledi-Geraru area provides an invaluable material documenting a critical period of hominin evolution for which the East African fossil record is still very scarce. (Photo credit: Brian Villmoare.)

initial divergence of *Homo* had remained invisible until the Ledi-Geraru discovery.

However, the scenario of a straightforward split of *A. afarensis*' descendants into two lineages might well be overly simplified and many questions remain unanswered. As with other mammalian groups of this time period [9,10], environmental changes have resulted in the multiplication of hominin taxa. On the side of australopithecines, as well as on the *Homo* side, a variety of adaptive trials seem to have been attempted and the picture is far from simple. Homoplasy — the independent development of similar adaptation — is perceptible almost everywhere. Tool use might not have been the monopoly of early *Homo* [11,12] and *Australopithecus* hands adapted to powerful precision grip [13]. Although the issue remains debated, it has been suggested that brain size also increased along the East African robust australopithecines lineage [14]. The South African *A. sediba* displays a number of convergent adaptations with early *Homo* in particular in its locomotion. Finally, *H. rudolfensis* shares some facial features with the robust australopithecines. On the side of two main evolutionary avenues and in response to similar selective pressures, smaller adaptive lanes were explored in a variety of ways and the case of *H. habilis* itself exemplifies this phylogenetic complexity.

The week the discovery of Ledi-Geraru was published, another article [15] appeared proposing a virtual reconstruction of OH7, the type specimen of *H. habilis* found by the Leakeys. Using advanced computer-assisted techniques, Spoor and colleagues have corrected the strong distortion of the mandible and provided a more precise estimate of the cranial capacity. Among other conclusions, this study confirms the morphological distinction between *H. habilis* and *H. rudolfensis.* Surprisingly, OH7 exhibits a quite primitive dental arcade, with long and parallel post-canine rows. This feature is reminiscent of *A. afarensis* and contrasts with the human-like parabolic shape of the older A.L. 666-1 specimen. This pattern implies that *H. habilis* finds its roots further back in time. Although, with a larger volume than initially thought — probably between 729 and 824 ml — OH7 now compares with the early forms of *H. erectus* [16]; it can no longer be seen as a good candidate for the ancestry of later humans.

Ultimately, the lingering question "What should we call *Homo*?" will surface again [2]. We do not yet know the brain size of the species to which LD 350-1 belongs. Even if these hominins cladistically relate to the genus *Homo*, their phenotype might have still been very australopithecine-like. The border between non-human and human is not the sharp Adamic emergence that has long been favored, but is rather a long and fuzzy transition [17]. Africa still has many paleontological secrets to yield. However, human anatomical and likely behavioral features clearly developed in a deep past and among several taxa. And in the end, one of them — *H. erectus* — replaced all of the others and expanded out of Africa, a scenario prefiguring that of modern human expansion almost 2 Ma later.

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Behavioral Genetics: Of Mice, Men, and Internal Bliss

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A mutation in the FAAH gene that enhances endocannabinoid signaling has been difficult to decipher, as it exists only in humans. A new study reports a knock-in mouse expressing an identical mutation, bridging an important translational gap.

"As little as five years ago," William Devane recalled, "most articles concerning the molecular pharmacology of cannabinoid drugs began with the standard refrain 'the cellular bases of cannabinoid actions are unknown'" [1]. The year was 1994, and Devane declared a "New dawn of cannabinoid pharmacology" [1]. Twenty years later, and many chemical footsteps ahead, cannabinoid research remains closer to bench than bedside. In the sociopolitical climate of 2015, translational research is held back by fierce debates over medicinal cannabis legalization. Clinical studies face two translational roadblocks: the first is to harness basic scientific knowledge into production of new drugs, devices and treatments; the second is to bring these promising products to market, and make sure they actually reach those who need them [2]. Translational research of the cannabinoid systems, it seems, has passed the second hurdle before overcoming the first.

Since California's Compassionate Use Act of 1996, over 23 U.S. states and the District of Columbia have legalized cannabis for medical use. Yet, the neural bases of cannabinoid actions in the human brain are largely unknown (Figure 1). Understanding the human cannabinoid system depends heavily on animal research. Animal models are the platform for fine-grained molecular and cellular analysis that is beyond the reach of human brain science. Still, many basic findings in animals never lead to clinical trials. A critical requirement for successful translation is that the phenomenon of interest would have similar phenotypic expression across species. Satisfying this criterion has been especially challenging in the case of the fatty acid amide hydrolase (FAAH) gene of the endocannabinoid system. A single-nucleotide polymorphism in this gene correlates with anxiety in humans [3]. But a major obstacle for animal models seeking to characterize this polymorphism is that the FAAH variant exists only in the human brain. A new study by Dincheva *et al.* [4] has found a way around it. The study reports the development of a knock-in mouse expressing an identical single-nucleotide mutation of the human FAAH gene.

In 1988, while in graduate school, William Devane proved the existence of the cannabinoid receptor in the rat brain [5]. By then, the active ingredient in marijuana that triggers this receptor, tetrahydrocannabinol (THC), had been long known – Rapahel Mechoulam successfully isolated THC from the cannabis plant in 1964 [6]. The missing piece in the puzzle was the identity of the brain chemical, or endogenous ligand, that naturally binds the cannabinoid receptor. Devane joined Mechoulam's lab as a postdoc, to search for the internal equivalent of the exogenous THC. A few years later, Devane found the endogenous ligand [7] and named it 'anandamide', from the Sanskrit word *ananda*, meaning 'bliss'.

A blissful function of the endocannabinoid system is its ability to relieve pain and anxiety [8]. Perhaps for that reason alone, several states have already approved treating post-traumatic stress disorder (PTSD) with marijuana and synthetic cannabinoids, despite the lack of clinical trials substantiating the medicinal efficacy of cannabis in PTSD [9]. Studies in animals, though, do compellingly show that endocannabinoid manipulations influence threat learning [10,11]. At the forefront of PTSD treatment is prolonged exposure therapy [12]. An animal model that captures this therapy's cognitive and behavioral core is extinction of threat learning [13]. To mimic a traumatic event in the laboratory, the animal undergoes threat conditioning by associating a neutral stimulus with a negative outcome; extinction training follows, where the animal repeatedly encounters

