

system Simon *et al.* report that Xist RNA accumulates first on gene-rich regions followed by gene-poor regions. When Xist RNA is depleted, the gene-poor regions lose Xist RNA association first, suggesting that these regions have lower affinity for Xist RNA. In the inducible system, Engreitz *et al.* provide additional resolution of gene-dense regions. Comparison of the one hour and three hour time points revealed that Xist RNA accumulates first at silent gene-dense regions and then progresses to active gene-dense regions. Together these studies suggest that Xist RNA coating is a multi-step process that depends on 3D chromosomal organization, gene density, and gene activity.

To determine whether any steps in Xist RNA spread are important for silencing, Engreitz *et al.* employed a male ESC line that inducibly expresses a mutant *Xist* defective in silencing due to deletion of a conserved element, the A-repeat (Δ AXist) [9]. Δ AXist RNA accumulated at 3D contacts and silent gene-dense regions but failed to efficiently accumulate over active gene-dense regions. Thus, Xist RNA interacts with active chromatin in a different manner than inactive chromatin. In earlier cytological studies Δ AXist RNA did not co-localize with active genes, though it still coated the X [10]. Together the high resolution and cytological studies highlight that silent and active regions of the X are sequestered in 3D space.

What is the relationship between nucleation at 3D contact points and the spread to encompass the entire X?

The findings that Xist RNA preferentially associates with gene-dense regions, and that within these gene-dense regions it accumulates first on silent and then on active genes, indicate that underlying chromatin features associated with gene density and activity may affect Xist RNA affinity. These characteristics suggest two broad classes of models that may explain Xist RNA spread (Figure 1). One possibility is that while the *Xic* spends the most time at 3D contact sites, it samples the entire X over time, and that affinity of Xist RNA for chromatin features at each region determines how much Xist RNA accumulates at each region. Alternatively, it may be that once Xist RNA has moved from the *Xic* to a distal site it makes an alteration at the distal site to increase the affinity for and promote local *cis*-spread of Xist RNA.

Together, Engreitz *et al.* and Simon *et al.* offer a new view of how Xist RNA coats the X. This lncRNA exploits the 3D contacts between the *Xic* and other regions of the X to access distal sites. This mode of spread contrasts with fly and worm dosage compensation complexes, in which defined sequence elements recruit the complexes to their sites of action. These new insights into Xist RNA spread will likely inform our understanding of how other lncRNAs can act at a distance.

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Paleoanthropology: *Homo erectus* and the Limits of a Paleontological Species

The bushy nature of the human evolutionary tree in the past 3 million years is widely accepted. Yet, a spectacular new fossil of early *Homo* has prompted some paleoanthropologists to prune our family tree.

Jean-Jacques Hublin

The last time I had seen this face, it was still covered with ash. One day in

the summer of 2005, on a short visit to the site of Dmanisi in Georgia, I was able to witness the unearthing of the best-preserved skull of early

Homo found so far. Only a few years later, now cleaned, it graced the cover of a recent issue of *Science* magazine. In their article, its discoverer David Lordkipanidze and colleagues [1] describe the spectacular fossil (D 4500) and compare it to its conspecifics from the same site as well as earlier African forms. This has led them to lump three early *Homo* taxa into a single species, *Homo erectus*.

To date, the oldest fossil assigned to the genus *Homo* is a maxilla found in Hadar (Ethiopia). It derives from a stone

tool bearing horizon dated to 2.33 million years ago [2] and was tentatively determined as *Homo* 'aff. *habilis*', a small-brained hominin documented in East and South Africa until 1.44 million years ago [3] (Figure 1). Another group of African hominins that displays distinctive facial and dental features was called *Homo rudolfensis*. *H. rudolfensis* is well represented around 2.06–1.78 million years ago [4] but might date back to as early as 2.4–2.5 million years ago [5]. *H. erectus* is believed to be a quite distinct species. Although exhibiting a broad size variation, it generally has a larger brain than the two previous forms and displays a suite of characteristic cranial features, including extremely protruding bony brow-ridges and a strong thickening across the occipital bone (Figure 1). Importantly, *H. erectus* is the first hominin that occupied substantial portions of Eurasia. Its latest representatives lived in the Far East at least as recently as ca. 300,000 years ago.

H. erectus is usually thought to have originated in Africa before 1.89 million years ago, therefore overlapping with *Homo habilis* both temporally and geographically. However, lately some have questioned this African origin and have suggested that a more primitive form of *Homo* initiated the colonization of Eurasia. *H. erectus* could therefore not have migrated 'out-of' but 'in-to' Africa [6]. With some human artifacts dated at 1.85 million years ago, the Georgian site of Dmanisi has played a central role in this debate. It is, however, best known for its around 1.77 million year-old fossil hominins, a truly impressive collection because of its preservation and the number of specimens found on a limited surface. The scientists working at the site have already unearthed five skulls, four mandibles and numerous post-cranial elements of the same individuals.

Since the first discoveries, discussions have surrounded the nature of this population, which does not really match the usual picture of *H. erectus*. In several aspects it is more primitive and 'habilis-like'. For example, the endocranial volume of D4500 is only 546 ml, at the lower range of *H. habilis* (509–687 ml), while the endocranial volumes of *H. erectus* range between 691 and

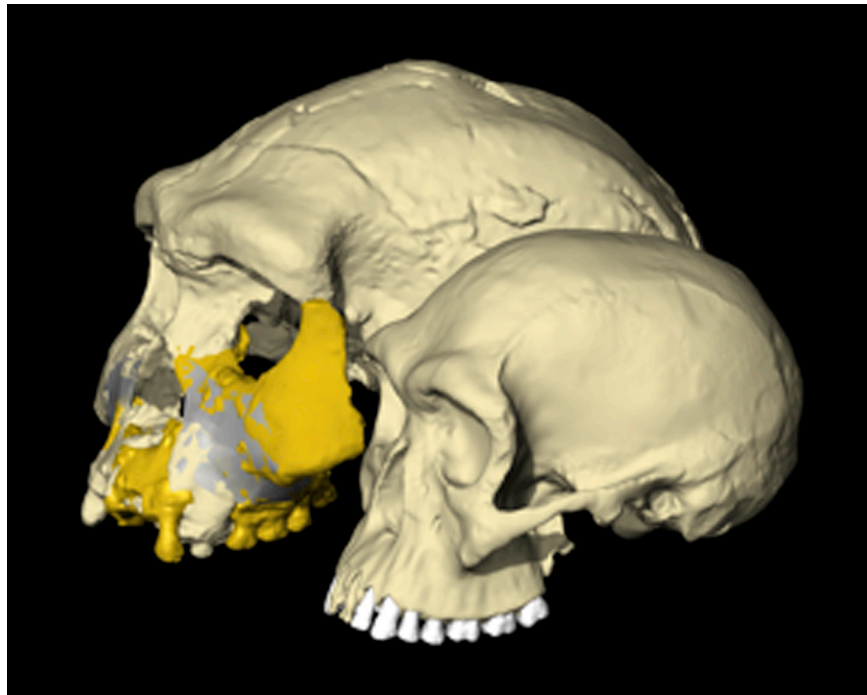


Figure 1. Early *Homo* head to head.

Reconstructions of the best preserved skulls of Javan *Homo erectus* (Sangiran 17) [14] ca. 1–1.3 million years old and East African *Homo habilis* from Koobi Fora, Kenya (KNM-ER 1813) [15], ca. 1.9 million years old. Besides size, the two specimens display differences in the face and braincase shapes, notably the presence of bone buttresses over the orbits or on the occipital. On anatomical, ecological and phylogenetic grounds some have proposed to exclude *H. habilis* from the genus *Homo* to call it '*Australopithecus habilis*' [16].

1251 ml. In 2000, a very large mandible (D2600) found in the site was even assigned to a new species, *Homo georgicus*, distinct from *H. erectus* [7]. We know now that this mandible and the skull D4500 both belong to the same individual — a large male who exhibited a primitive face, a large-boned masticatory system and a small brain.

Lumpers and Splitters

Instead of following the trend of species splitting that is prevalent in paleoanthropology, the new study swings the pendulum in the opposite direction. At Dmanisi, the human remains were accumulated in dens of carnivores such as giant cheetahs, Eurasian jaguars and saber-toothed cats. Whether large cats preyed on humans or humans scavenged on the kills of these predators is still unclear. After some time the dens collapsed and because of the very rapid accumulation of fossils — geologically speaking — the authors have no doubt they are dealing with individuals from a single species. They argue that the shape variability among the Dmanisi skulls is

comparable to that observed among recent modern humans, bonobos and chimpanzees. Furthermore, Lordkipanidze *et al.* [1] suggest that the morphology seen in Dmanisi skulls and crania encompasses not only that seen in *H. erectus*, but also that seen in *H. habilis*, and *H. rudolfensis*.

The provocative proposal to lump all these fossils within one polymorphic species — *H. erectus* — that would have lived for ca. 2 million years in Africa and Eurasia has revived a long-lasting debate in hominin taxonomy — that between 'lumpers' and 'splitters'. Researchers in favor of merging species, the 'lumpers', are rejoicing, and several blogs have already resuscitated the 'single species hypothesis' [8]. This model, launched at Michigan University in the 1960s, argued that hominins occupied such a peculiar ecological niche, in which culture plays a central role, that no more than a single hominin species could have existed at any given time in the past. One decade after it was formulated, the demonstration of a temporal overlap

between late australopithecines and early *Homo* in East Africa and between Neandertals and modern humans in southwestern Asia triggered the decline of this oversimplified concept.

In the camp of the ‘splitters’, many express skepticism about the methodology used by Lordkipanidze *et al.* [1] to assess cranial variability. To do this the team used geometric morphometrics, a powerful multivariate statistical technique that analyzes the spatial distribution of anatomical landmarks to quantify shape similarities. In this case, the chosen measurements primarily capture the overall skull shape, in particular the relative size of the face and the braincase. As a result, a number of anatomical details, such as the dental features that distinguish *H. habilis* and *H. rudolfensis*, are not addressed. Notably, closely related species of apes, such as common chimpanzees and bonobos, are not completely separated by this analysis, while other subtler geometric morphometric studies are able to discriminate even sub-species of apes [9,10]. The substantial variation in the Dmanisi sample mostly results from Lordkipanidze *et al.*'s [1] decision to include one specific skull (D3444) in the analysis. This elderly individual with a rounded cranial vault is totally edentulous and its facial morphology was strongly remodeled by bone resorption after tooth loss. Finally, another problem relates to the large proportion in the fossil record of non-adult individuals who did not yet fully develop some aspects of their cranio-facial robustness. When all this is taken into account the claim that there is complete overlap between the morphology of *H. erectus* and other African early *Homo* taxa becomes questionable.

Fossil Taxonomy

In biology, species are primarily defined based on whether their members can have fertile offspring. Unfortunately, reproductive incompatibility between contemporaneous fossil species or between ancestors and descendants along the same lineage cannot be tested. Most sister species of mammals that have separated in a similar time-frame, since the beginning of the Pleistocene 2.59 million years ago, can still interbreed [11], even if they rarely do outside of zoos. Most likely, all

Pleistocene hominins would have therefore been able to interbreed to some extent, but the fact remains that the amount of gene flow between hominin lineages such as Neandertals and modern humans only amounts to a few percent [12]. This kind of hybridization may indeed have occurred only under quite peculiar geographic or demographic circumstances. Merging most of the Pleistocene hominins within a single messy ‘species’ as proposed by the most extreme ‘lumpers’ would not help much to elucidate human evolutionary history. The challenge faced by paleoanthropologists is then to follow through time and space phenotypically distinct populations even before they eventually become fully separated species. From ‘recognition species’ to ‘genetic species’, the many concepts of species that have been proposed in biology actually match the succession of gradual stages these populations go through in what has been called a ‘gray zone’ [13]. Not surprisingly, paleontological species tend to combine ancestors and descendants in the same evolutionary lineage.

From a taxonomical point a view, some have bypassed the difficulty by favoring the use of vernacular terms, such as ‘early modern humans’ or ‘Neanderthals’ over that of binomial Linnaean Latin terms. Specifically regarding recent humans, this also resolves some philosophical issues that do not apply when one only deals with Pleistocene mice or bears. However, these vernacular terms are usually very loosely defined. In many instances, vague wording such as ‘archaic’ or ‘modern’ to designate groups of late Pleistocene humans has become almost completely meaningless. The use of infra-specific Linnaean denominations is not the answer, either. The choice between species and sub-species in paleontology is often purely rhetorical. A caricature example is provided by Lordkipanidze *et al.* [1] themselves, when they finally assign the Dmanisi hominins to “*Homo erectus ergaster georgicus*” [1]. The exceptional discoveries of Dmanisi remind us once more how crucial intra-population variability is when dealing with the fossil record. It will, however, clearly not put an end to the debate on the limits of *H. erectus*. Nature did not make it easy for those

who want to classify species still in their making.

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