

Article

Entanglements
of Time,
Temperature,
Technology, and
Place in Ancient
DNA Research:
The Case of the
Denisovan Hominin

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Abstract

The study of ancient DNA (aDNA) has gained increasing attention in science and society as a tool for tracing hominin evolution. While aDNA research overlaps with the history of population genetics, it embodies a specific configuration of technology, temporality, temperature, and place that, this article suggests, cannot be fully unpacked with existing science and technology studies approaches to population genetics. This article explores this configuration through the 2010 discovery of the Denisovan hominin based on aDNA retrieved from a finger bone and tooth in Siberia. The analysis explores how the Denisovan was enacted as a technoscientific object through the cool and even temperatures of Denisova Cave,

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assumptions about the connection between individual and population, the status of populations as evolutionary entities, and underlying colonialist and imperialist imaginaries of Siberia and Melanesia. The analysis sheds light on how aDNA research is changing the parameters within which evolutionary history is imagined and conceptualized. Through the case study, it also outlines some ways in which the specific technoscientific and cultural entanglements of aDNA can be critically explored.

Keywords

ancient DNA, hominin evolution, Denisovan, ontology, population genetics

Introduction

During the past decade in particular, the study of ancient DNA (aDNA) has emerged as a thriving field that promises to fill in gaps in existing knowledge of evolutionary history. Thanks to advances in sequencing technologies, increasingly old and small fragments of prehistoric material have been subject to genetic analysis. The promises of analyzing ancient hominin DNA have enthralled across culture. This cultural resonance is visible, for example, in the excited coverage of aDNA discoveries in major newspapers and on news websites (e.g., Devlin 2018; Purcell 2018; Raff 2018). It is also reflected in how direct-to-consumer genetic ancestry tests are offering analyses of the customer's shared percentage of Neanderthal or Denisovan DNA (e.g., Genographic Project, 23andMe, EthnoGene). These developments show how aDNA is becoming a means through which stories of roots and belonging are told on communal as well as personal levels. How aDNA research will develop and how it is invoked and negotiated in culture are thus issues of growing social and political significance.

aDNA research overlaps with the field of population genetics, which has sought to trace similarities and differences among populations and thereby reconstruct patterns of evolutionary history. However, while population genetics has relied primarily on contemporary samples and deduced evolutionary pasts from modern DNA, aDNA research builds on genetic material retrieved from old remains. This makes aDNA research more than an extension of population genetics: aDNA research produces evolutionary trajectories connecting modern and ancient samples, invoking a different set of temporalities and material conditions than population genetic analyses of modern populations.

Science and technology studies (STS) scholars have provided insightful critiques of the role of underlying assumptions of ethnicity, race, population, and gender in population genetic projects, providing a helpful starting point for STS analyses of aDNA research (e.g., Koenig, Lee, and Richardson 2008; Nash 2015; M'charek 2005; Reardon 2005; TallBear 2013; Wailoo, Nelson, and Lee 2012; Whitmarsh and Jones 2010). However, these approaches are not designed to capture the specificities of aDNA. This article starts from the observation that aDNA studies involve unique configurations of technologies, materialities, temporalities, and imaginaries that need to be analyzed in order to fully understand how aDNA research is shaping ideas of roots and relatedness. This article traces the challenges that aDNA research poses for STS, outlining some ways of unpacking its material and temporal underpinnings.

The article explores aDNA through the 2010 discovery of the Denisovan hominin. In 2008, researchers conducting a routine archeological study in Denisova Cave in the Altai Mountains in Siberia found a prehistoric finger bone (a distal manual phalanx) (Reich et al. 2010). The region was known to have been inhabited by both Neanderthals and anatomically modern humans. In 2010, the bone was subjected to mitochondrial (mtDNA) genetic analysis, which suggested that it belonged to a previously unknown hominin group (Krause et al. 2010). This result was confirmed by nuclear DNA analysis later in the year (Reich et al. 2010). An unidentified hominin tooth discovered earlier in Denisova Cave and anatomically different from both Neanderthals and modern humans became also genetically connected to this newly discovered hominin population, now named Denisovan. Based on the genetic analyses, researchers concluded that Denisovans coexisted with anatomically modern humans and Neanderthals. In the absence of substantial archeological and paleoanthropological evidence, the scientists tended to "refrain from any formal Linnaean taxonomic designations that would indicate species or subspecies status for either Neanderthals or Denisovans" (Reich et al. 2010, 1059). Nevertheless, the Denisovan emerged as an evolutionary entity with its own "distinct population history" and characteristic genetic markers (Reich et al. 2010, 1059).

Probably the most astonishing aspect of the discovery was the scarcity of evidence: the new hominin was reconstructed from nearly 50,000-year-old biological material consisting only of a finger bone from the little finger of a juvenile female and a molar from an adult male. This biotechnological marvel was echoed in media responses at the time. For example, *The New York Times* opened its report of the mtDNA analysis in March 2010 with the following words: "A previously unknown kind of human group vanished

from the world so completely that it has left behind the merest wisp of evidence that it ever existed—a single bone from the little finger of a child" (Wade 2010). Here, the scarcity of evidence emphasizes technoscientific progress: aDNA analysis did not require a wealth of bones like, for example, paleoanthropology. Another article in *The New York Times* on the nuclear genetic analysis in December highlighted scientific achievement by describing the geneticists at Max Planck Institute for Evolutionary Anthropology—chief architects of the Denisovan mtDNA study as well as many other aDNA studies—as "rescuing fragments of ancient DNA from fossils and stitching them together" (Zimmer 2010). Again, aDNA research is depicted as amazingly technologically advanced and yet wonderfully simple. These assumptions of straightforward access to a genetic past are highly prominent in current cultural discourses on aDNA, such as the news stories cited in the opening paragraph of this article (Devlin 2018; Purcell 2018; Raff 2018).

My focus is on the initial genetic construction of the Denisovan hominin in 2010, as it illustrates the epistemic, material, and cultural dynamics through which aDNA research operates. While a number of genetic studies have been published since (e.g., Reich et al. 2011; Meyer et al. 2012; Sawyer et al. 2015; Slon et al. 2017), and additional teeth and a bone from Denisova Cave have been analyzed (Slon et al. 2018), the technoscientific apparatus traced in this article remains largely in place. In what follows, I show that contrary to popular representations of aDNA, the Denisovan hominin was not discovered but made through technoscientific practices and material circumstances involving developments in sequences technologies, the even temperatures of Denisova Cave, and theories of "molecular clock." It was made through assumptions about connections between individuals and populations and the status of populations as evolutionary entities. The Denisovan was also made through place—Siberia and Melanesia—and the complex imperialist and colonialist histories those place names carry. My analysis investigates these entangled practices and imaginaries in the making of the Denisovan, showing key ways in which aDNA research differs from population genetic studies of modern samples as a lens into evolutionary history.

The first section outlines the theoretical starting points of this article, especially the ontology of technoscientific phenomena as situated and enacted. The following analytical sections interrogate the making of the Denisovan hominin through configurations of time, temperature, technology, and place. The first of the sections places the Denisovan within the history of aDNA research, exploring the technoscientific apparatuses that

enabled its making. The second section focuses on temporality and temperature, especially the idea of the cave as a natural refrigerator for samples, and the theorization of DNA as a temporally invested object. The third section looks into the performative role of the assumption that individual samples represent populations as well as the assumption that populations are ontologically separate evolutionary entities. The fourth section turns to place, especially the role of Siberia and Melanesia in imagining the Denisovan. I conclude by elaborating on the implications of aDNA research for STS.

Analytical Approach

My analysis builds on STS engagements with the *ontology* of technoscientific phenomena. The significance of ontology for STS has been debated extensively in the past decade in particular (see, e.g., Woolgar and Lezaun 2013a). A central strain within STS approaches to ontology has focused on ontology as a process of construction: objects emerge from the technologies, methods, material circumstances, and cultural imaginaries through which they are conceptualized, analyzed, and lived. This means that the ontology of things is "accomplished" rather than discovered (Woolgar and Lezaun 2013b, 333).

A central characteristic of accomplished objects is that they are ontologically multiple. Annemarie Mol's (2002) groundbreaking book *The Body Multiple* demonstrates how the vascular disease atherosclerosis *is* different in the outpatient clinic, the operating theater, or the pathology lab. Yet, these different atheroscleroses share points of juncture that hold the phenomenon "atherosclerosis" together—at least most of the time (see also Law and Singleton 2005). The Denisovan is a different kind of object than atherosclerosis in that it is a theorization built initially around two fragments of biological material. Ontological multiplicity is present in *tensions* between the technological practices and imaginaries that enabled the production of the Denisovan hominin in the first place.

My analysis focuses on technological practices, methodological choices, and theoretical models involved in the making of the Denisovan. In this, I draw on Amade M'charek's (2005) work on how differences are enacted in the population genetic lab. M'charek shows that concepts such as race and gender, or similarity and distance, exist only in situated scientific practices that rely on a host of other factors such as circulation of samples or sequences through transnational networks between labs. M'charek (2014) also shows the temporal layering of scientific objects such as cell lines or

reference sequences. My exploration of the making of the Denisovan seeks to capture this type of technological detail. That is, the Denisovan is not a product of a general turn toward aDNA in the past decade but of specific technologies and material conditions. Such focus also helps elucidate how the apparatuses of aDNA research depart from those of population genetics based on large contemporary data sets.

The Denisovan case touches on a specific ontological question in the history of evolutionary theory: the ontological status of species. Evolution is a curious process in that it can be detected only in retrospect. Evolutionary events seldom look like events when they happen, taking often generations to emerge; evolution can be traced only when we know what it gave rise to. Furthermore, evolution is premised on the presence of variation within populations, as selection cannot happen without difference to select from. Darwin recognized this clearly. In the Origin of Species, he notes that "the only distinction between species and well-marked varieties is, that the latter are known, or believed, to be connected at the present day by intermediate gradations, whereas species were formerly thus connected" and that we should give up "the vain search for the undiscovered and undiscoverable essence of the term species" (Darwin [1859] 1985, 455). From this viewpoint, the constructed nature of the Denisovan becomes clearly visible. If the boundary between species, subspecies, and variation is blurry, and there is no precise moment when a species emerges from genetic variation, then the question of Denisovan's species status is likely to be ontologically irresolvable.

Despite Darwin's words of caution, the history of paleoanthropology and study of human evolution are full of attempts to identify "missing links" between modern humans and apes. The fossilized remains of Neanderthals (Goulden 2009; Sommer 2006), Java Man (Swisher, Curtis, and Lewin 2002), and Peking Man (Leibold 2006; Sautman 2001), as well as the infamous Piltdown Man hoax (Goulden 2009), have all been mobilized to construct hominin evolutionary histories as temporally organized series of species and subspecies. The ultimate goal of these histories has often been to understand the evolutionary status of modern humans. The case of the Denisovan is part of this scientific history. However, it also epitomizes the increasing significance placed on genetics in the study of hominin evolution.

Technoscientific Histories and Performative Practices

The most important history that enabled the making of the Denisovan was the development of aDNA sequencing techniques. First successful studies

of aDNA were conducted in the mid-1980s with relatively recent specimens from museums and focusing on short sections of mtDNA; mtDNA was chosen because it was easier to retrieve and analyze than nuclear DNA (Anastasiou and Mitchell 2013; Ermini et al. 2015). The development of the field was hampered by the problem of contamination by modern DNA (left by archeologists, museum workers, geneticists themselves) as well as by the degradation of DNA due to material conditions (humidity, temperature, type of soil) (Anastasiou and Mitchell 2013; Ermini et al. 2015). Many of the crucial problems were solved by 2005, after which aDNA research has expanded guickly. The focus of research has also moved from mtDNA, which can trace only direct maternal lineages and gives little additional information, to nuclear DNA, which focuses on genome-wide inheritance as well as physical characteristics such as eye color or metabolism (Anastasiou and Mitchell 2013; Ermini et al. 2015). Since 2010, there has been a rapid increase in nuclear studies of aDNA, thanks to the increasing financial and technological feasibility of genome-wide sequencing. Furthermore, DNA that was earlier thought to be of insufficient quality for analysis has generated significant ancient sequences (e.g., Rasmussen et al. 2015; Brace et al. 2019). These studies differ from most population genetic projects in that their starting point is individual aDNA sequences rather than a large database of samples.

These technological developments underlie the 2010 construction of the Denisovan hominin from a finger bone and molar, an endeavor that would have appeared impossible a decade earlier. The two key papers on the Denisovan hominin—the mitochondrial analysis published in *Nature* in April (Krause et al. 2010) and the nuclear analysis published in the same journal in December (Reich et al. 2010)—show the remarkable speed with which the nuclear analysis of the Denisovan phalanx followed the mtDNA analysis. They also demonstrate that the Denisovan was enacted as an evolutionary actor: the two types of genetic material (mtDNA and nuclear DNA) produced strikingly different evolutionary histories. The mitochondrial paper suggested that Denisovans shared mitochondrial ancestry with both Neanderthals and anatomically modern humans about one million years ago, thus being an outgroup to both Neanderthals and modern humans who shared a mitochondrial ancestor some 500,000 years ago (Krause et al. 2010). The nuclear analysis in turn posited the Denisovans as a sister group to Neanderthals, arguing that while "the divergence of the Denisova mtDNA to present-day human mtDNAs is about twice as deep as that of Neanderthal mtDNA, the average divergence of the Denisova nuclear genome from present-day humans is similar to that of Neanderthals" (Reich

et al. 2010, 1055). In this respect, the two papers illustrate a central characteristic of population genetic knowledge production: different types of genetic material engender different patterns of ancestry (M'charek 2005; Nash 2015; Oikkonen 2015, 2018). Which genetic markers and molecular loci are chosen for analysis also matters, as patterns of relatedness are produced by comparing markers (Hamilton 2012; M'charek 2005, 2014; Sommer 2016; Oikkonen 2018). This is particularly important in aDNA research, as the qualities of a single aDNA sequence often represent a whole population.

STS scholarship on population genetics has shown that ancestry is *relational*, that is, it is produced through comparison to other samples (Bolnick 2008; Fujimura et al. 2010; Hinterberger 2012; M'charek 2005; Oikkonen 2018). This is also the case with aDNA research. Krause et al. (2010, 895) write: "We aligned the Denisova hominin mtDNA sequence to 54 present-day modern human mtDNAs, a Late Pleistocene mtDNA recently determined from an early modern human from Kostenki, Russia, six complete Neanderthal mtDNAs, one bonobo (Pan paniscus) mtDNA and one chimpanzee (*Pan troglodytes*) mtDNA." Likewise, Reich et al. (2010) report that, apart from comparing the Denisovan nuclear genome to Neanderthal and chimpanzee samples, they also

analysed the relationship of the Denisova genome to the genomes of five present-day humans that we previously sequenced to about fivefold coverage (a Yoruba and a San genome from Africa, a French genome from Europe, a Han genome from China and a Papuan genome from Melanesia), as well as seven present-day humans that we sequenced to 1-2-fold coverage for this study (a Mbuti genome from Africa, a Sardinian genome from Europe, a Mongolian genome from Central Asia, a Cambodian genome from South-East Asia, an additional Papuan genome from Melanesia, a Bougainville islander genome from Melanesia, and a Karitiana genome from South America). (p. 1057)

The two quotes highlight the productive role of comparison in population genetics, suggesting that the Denisovan sample, even after genomewide analysis, cannot alone reveal ancestries. Yet, the Denisovan case differs from population-level studies of modern samples in that the point of comparison for Denisovan DNA is a relatively small set of geographically diverse modern samples.

The performative power of individualized comparison becomes visible in Reich and colleagues' (2010) analysis of the Denisovan nuclear genome.

The authors identify a previously unknown pattern of relatedness between the Denisovan genome and three present-day Melanesian genomes (see the quote above). They conclude that this suggests that Denisovans "have at least at some point been present in an area where they interacted with the ancestors of Melanesians" (Reich et al. 2010, 1059). Crucially, the connection between Denisovans and Melanesians is based only on one ancient and three modern samples. These four situated samples enact relatedness as taking shape through previously unimagined paths of migration and reproduction in prehistoric Asia and the Pacific region. Such reliance on individual modern sequences is intriguing in the age of big data and population-level biobanks, both phenomena widely discussed in STS analyses of population genetics (e.g., Koenig, Lee, and Richardson 2008; Whitmarsh and Jones 2010). It highlights the importance of paying attention to the situatedness of individual samples in aDNA research, as individual samples dispersed across time and space become nodes where evolutionary relatedness is anchored.

Entangled Temporalities and Temperatures

aDNA research departs from population genetic analyses of modern DNA also in its unique configuration of temperature and temporality. The discovery of the Denisovan relies on the constant cool temperatures that enabled the preservation of DNA in the phalanx and molar. The Denisovan is not the first prehistoric figure that draws on naturally cryopreserved aDNA. For example, "Ötzi the Iceman" discovered in the Alps in 1991 was preserved in permafrost for 5,000 years. Turnbull's (2017) analysis of the case shows how "Ötzi" is enacted through technologies and approaches including paleontology, microbiology, blood analysis, pollen analysis, DNA analysis, analysis of stomach contents, and forensic analysis of wounds. The Denisovan hominin provides an interesting point of comparison because it differs from Ötzi in key ways. Unlike the Denisovan, Ötzi's remains are almost complete including blood cells and half-digested meals, and genetic analysis played only one part in the analysis. Furthermore, the interest around Ötzi has centered on him as a unique individual belonging to a population whose existence was already known, whereas the Denisovan case concerns a whole population in a much more distant past whose very existence was unknown until the discovery of the phalanx.

The Denisovan differs from Ötzi also in the degree of cold: the Denisovan finger bone and molar were preserved in temperatures around zero degrees Celcius. Reich at al. (2010) remark that "the Denisova phalanx is

one of few bones found in temperate conditions that are as well preserved as many permafrost remains" with "the fraction of endogenous relative to microbial DNA" being 70% (as opposed to the typical figure of below 1% in Neanderthal remains) (p. 1059). They further note that "[i]t is not clear why this is" as "the fraction of endogenous DNA in the tooth is 0.17%" (Reich et al. 2010, 1059). This emphasis on the *quality* of DNA highlights the central role of the techniques of *amplification* in genetic analysis: a little of good-quality material may be enough, thanks to the possibility of amplification. The exceptional preservation of the phalanx in temperate conditions is also interesting from the perspective of cryopreservation, as it shows how the "degrees" or "registers" of cold (Radin and Kowal 2017, 5) may not have a direct or predictable effect on the temporalities of biological material, such as the speed of the decay of DNA molecules. The connection between temporality and temperature appears to evade a simple model of causality.

The role of temporalities in aDNA research is complex also on other levels. First, DNA itself is a temporally invested object. While DNA is often framed as what makes us unique, it is also what we share, and the differences between people are ultimately relatively few. In the 1980s, geneticists seeking to trace human evolutionary history analyzed mtDNA with the help of the concept of *molecular clock*. The idea of molecular clock arose in the 1960s from the theory of *molecular evolution*, which proposed that neutral molecular changes could be used to evaluate evolutionary histories (Kumar 2005). By counting mutations at particular molecular sites, the evolutionary relationships between entities (individuals, populations, species) could be traced. In this framework, mutations measured the passage of time from moments in the past when mitochondrial lineages diverged. The same model was applied to Y-chromosome lineages in the mid-1990s (see Oikkonen 2015). This premise still underlies Krause et al.'s study of Denisovan mtDNA.

Second, aDNA carries specific temporal investments. While population geneticists have traditionally theorized evolutionary patterns through the accumulation of mtDNA and nuclear mutations, aDNA appears to render past genetic variation concrete and material instead of merely statistically deduced. In particular, aDNA shows genetic variation, such as genetic sequences from now extinct species or subspecies, that cannot be accessed through modern samples. As a result, aDNA analyses produce evolutionary trajectories between the present and the past that depart from trajectories imagined though modern samples. Such trajectories appear as both more precise and more complicated than trajectories deduced from modern

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genetic variation. This is likely one reason why evolutionary reconstructions using aDNA resonate so strongly in culture.

These temporal configurations come together in the naturally occurring cryopreservation of the phalanx and molar in Denisova Cave. In her study of extinction narratives, Stephanie Turner shows how DNA of extinct species preserved in cold has become a source of imagining the continuation of life forms that no longer exist. In this framework, "species like woolly mammoths and Neanderthals are not lost after all, but continue to exist as the genetic codes residing in their remains" with the result that "[b]oth conceptually and informatically (that is, in terms of the posthumous existence of the genetic code in a computer database), extinction is becoming less and less absolute" (Turner 2007, 58-59). Although the Denisovan case does not involve the potential cloning of an extinct species (at this stage at least), it is about "latent life" (Radin 2013) residing in the genetic code retrieved from the phalanx and sequenced through high-throughput technologies. Denisovan DNA, cryopreserved in the coolness of the cave, becomes the materialization of life itself in the databases of hominin samples. While cryopreservation was able to halt the effects of time for thousands of years, there is less need for continuing cryopreservation when the mtDNA and nuclear sequences have been given a digital form. Yet, the digital existence of the Denisovan hominin relies on cryopreservation, without which digital life would not exist.

Jay Clayton (2002) has used the term *genome time* to describe how the idea of DNA as digital information makes DNA appear as timeless, as (metaphorically) frozen in time, and yet reversible. The Denisovan case shows that both these characteristics—timelessness and temporal flexibility—are products of complex technoscientific work in aDNA research. The ontological status of the digitized Denisovan DNA sequences as *pure*, *indestructible life* is achieved through sequencing technologies and software as well as cryopreservation by nature. Crucially, digital information alone does not mean anything in aDNA studies, as meaning is produced through temporally invested comparisons to modern, ancient, and interspecies samples, and statistical models of evolutionary distance and assumptions of evolutionary time. In this configuration, cryopreservation operates indeed as "temporal prosthesis" (Radin and Kowal 2017, 12) that enables ontologies that would be otherwise unachievable.

These multiple configurations of time and temperature complicate the role of aDNA as a lens to the evolutionary past. While the Denisovan mitochondrial and nuclear sequences constitute metaphorically frozen latent life (with theoretical potentiality of rewriting), they are also products

of the logic of molecular clock that seeks to standardize and measure the ticking of evolutionary time. The reconstructed sequences are also means of producing patterns of difference and sameness between people, populations, and species in the present moment. These multiple temporalities are not without inherent tensions: they render aDNA paradoxically pastoriented, future-oriented, and atemporal (digital, frozen). Yet, these temporal tensions and ambiguities tend to disappear from the view amid cultural narratives that insist that genetics engenders epistemically privileged, objective knowledge (Turner 2007; Wald 2000). For this reason, it is pivotal that STS analyses recognize the entangled configurations of temperature and time that underpin the preconditions of aDNA research and its future discoveries.

On Populations and Individuals

Like population genetic projects in general, the making of the Denisovan hominin from aDNA relies on establishing connections between individuals and populations on the one hand and between populations on the other. STS scholars have shown that the concept of population is blurry and lacks a fixed meaning, yet it plays a constitutive role in the making of genetic roots (Bolnick 2008; Fujimura et al. 2010; Hinterberger 2012). Population genetic studies build on the assumption that an individual sample can be connected to a population and, indeed, made to represent a population (M'charek 2005). However, Linking samples and populations is not easy; the process of assigning individuals to populations before the study often relies on naturalized assumptions of racialized belonging and genetic homogeneity of geographically located populations (Hinterberger 2012; Kohli-Laven 2012; Reardon 2008). An important question haunts such attempts: how can we know that a person is a typical representative of a population? Importantly, this question cannot be addressed through physical appearance, as a person's genetic ancestry is typically invisible to the eye.

The challenge of linking individuals to populations applies to the Denisovan phalanx and molar. In the absence of other samples, these two individuals—a juvenile female and an adult male—were made to stand for the Denisovan hominin. However, we do not know whether they represent typical Denisovan genetic inheritance or whether they are located somewhere in the margins of the population. While this challenge underlies population genetics in general, it is particularly acute in aDNA research due to the scarcity of samples and absence of other kinds of evidence. Furthermore, focusing on populations erases the complex and entangled

histories of migration and interaction that these two gendered and situated individuals are part of on *personal and interpersonal* levels. Focusing on individuals as representatives of populations erases the possibility that kinship and belonging are communally located, temporally layered, and full of inherent tensions. This same observation also applies to the samples chosen by Krause et al. and Reich et al. as representative of typical present-day genetic make-up in particular geographic regions. While the studies utilize previous collections of geographically diverse DNA samples, we simply do not know the genetic and cultural histories that materialize in these specific temporally, spatially, and culturally situated individual sequences. Should the scientists get the sampled individual's ancestries partly wrong, the Denisovan hominin—constructed through comparisons between samples—would be enacted slightly differently. While this might not have major statistical consequences, it has ontological implications as it points to the enacted nature of the Denisovan.

The Denisovan also draws on the assumption that populations are ontologically distinct entities that migrate and reproduce. That is, populations are entities that *preexist* selection and genetic drift. Yet, as the quote from Darwin suggested, populations or species are never stable but rather changing formations with porous and overlapping borders. Populations are constantly shaped by heterogeneous and situated evolutionary processes. Assuming ontological separation of species blurs the working of entangled, multisited, and unsynchronized evolutionary processes. For example, interbreeding emerges as activity between three ontologically distinct entities—Denisovans, Neanderthals, and modern humans—in both scientific and popular discourses of the Denisovan. References to "gene flow" in scientific articles do not resolve this issue, as the three hominin populations are posited as ontologically prior to the reproductive acts they engage in. Again, the question is particularly central to aDNA research because there is so little evidence beyond the few sequenced ancient samples.

In the media, the ontological separation of species is even more distinct, as gene flow is framed as "interbreeding," "mating," or "sex" between species. For example, a BBC article published after the 2010 nuclear DNA analysis was titled "Ancient Humans, Dubbed 'Denisovans,' Interbred with Us," with lots of symbolic weight placed on the distinction between *them* and *us* (Ghosh 2010). This framing has prevailed in the media coverage of more recent research on the Denisovan, as when the *Los Angeles Times* writes in 2018 after the fourth Denisovan sample was analyzed: "Humans weren't just making babies with Neanderthals back in the day. A new study that compares the genomes of different groups of modern humans has found

that our ancestors interbred with another close relative, the Denisovans, more than once" (Khan 2018). While suggestions of interbreeding may sound refreshing and even transgressive, they operate on the assumption of ontologically distinct populations who mate and subsequently share genes.

The assumption of populations as ontologically distinct entities has significant implications as it makes some research questions appear as meaningful and natural: is the studied population a species, subspecies or a group? To what extent did these populations contribute to each other's genetic makeup (i.e., what is the extent of gene flow between the populations)? At the same time, other kinds of questions and framings appear less likely. What would happen, for example, if we looked at geographically complex patterns of migration and co-existence between temporally, spatially, and culturally situated local communities rather than hominin populations? What if the ontology focusing on populations as entities was replaced with one that centers on situated and evolving webs of interaction involving individuals and communities? While this would depart from the technoscientific framework of population genetics and could not be carried out through a few samples of aDNA, it does offer an imaginative viewpoint that opens up new ways of thinking about hominin evolution beyond the level of population or species. For STS scholarship, asking these (and other related) questions would make visible the naturalized nature of the theoretical premises on which narratives of hominin evolution are told in science, media, and culture at large.

On Place and Space and Their Histories

Finally, the affective cultural investments around aDNA research differ from other types of population genetic research. aDNA is entangled with cultural imaginaries of prehistoric and mythic geographies, which need to be unpacked in order to understand how aDNA operates as part of larger cultural dynamics around science. The Denisovan hominin was enacted in relation to two places: Siberia and Melanesia. Both places are associated, respectively, with distinctly colonial imaginaries of harsh life and exotic authenticity. While these imaginaries did not explicitly organize the scientific articles, they made the announcement of the Siberian home of the Denisovan and the mysterious hominin's travels in Melanesia resonate with longstanding cultural fantasies. Such fantasies rendered the discovery of the Denisovan an appealing narrative involving adventurous life, lost species, interspecies encounters, evolutionary struggle for life, and eventual success

of modern humans. These imaginaries of space thus played a role in the making of the Denisovan as a culturally recognizable evolutionary entity.

To begin with, Siberia embodies two significant histories. One concerns the rich prehistory of this vast region that reaches along the Arctic Sea from the borders of Europe to Mongolia. Siberia is known for its fossils, many of them preserved in permafrost for millennia. Perhaps the best known of the now extinct species is the woolly mammoth (Turner 2007). The nearly mythic animal lived especially in northern Siberia above the Arctic Circle until about 10,000 years ago. Its massive size and simultaneous existence with prehistoric hominins has made it a symbol of the fantasized masculine bravery of prehistoric hominin hunters. Its imagined physiological majesty suggested danger as well as ultimate human triumph and survival.

The other history is an explicitly political one: Siberia is widely associated with political exile and imprisonment. Geographically in Asia, Siberia was annexed by Russia in the seventeenth century and has since been seen as embodying the shadowy margins of Europe. As part of the Russian Empire and subsequently the Soviet Union, Siberia operated as a place where leaders sent their political opponents to penal labor camps or exile (e.g., Khlevniuk 2004). Being "sent to Siberia" often meant in practice death from extended starvation, disease, and hard labor in dangerous conditions. Many indigenous peoples of Siberia were also displaced or suffered from the consequences of settler colonialist exploitation of natural resources (e.g., Sablin and Savelyeva 2011). This history has rendered Siberia symbolic of harsh life, endurance, danger, and struggle for survival. Because of its political history, it is also associated with secrecy: what happens in Siberia stays outside official public knowledge. Significantly, these imaginaries of isolation and hardship resonate with the discourses of Siberia as a desolate prehistoric site where early humans fought for their lives while hunting mammoths. Together, these two imaginaries imply that any hominin who lived in Siberia must have been strong in both body and mind.

Melanesia, where the Denisovan DNA is most clearly present, is embedded in a different type of colonial past. Its neighboring archipelago, Indonesia, in particular was a place where nineteenth-century and early twentieth-century paleoanthropologists searched for fossils that would prove a "missing link" between modern humans and apes. The region turned out to be rich in hominin fossils. For example, beginning in the 1890s, Java became a source of several *Homo erectus* discoveries, giving rise to "Java Man" (Swisher, Curtis, and Lewin 2002). In 2004, more than a century later, scientists discovered in Java small-sized hominin fossils,

named *Homo floresiensis*. Discoveries like these have rendered South East Asia and Melanesia an imagined world of lost hominins. These spatial imaginaries are echoed in the recent media coverage of *Homo luzonensis*, an ancient hominin discovered in the Philippines: a news story on the BBC website suggests that "human evolution in the region may have been a highly complicated affair, with three or more human species in the region at around the time our ancestors arrive" (Rincon 2019). Furthermore, the history of Western anthropology includes a number of studies of the indigenous cultures of Melanesia.

Read in this context, the reports of interbreeding between Denisovans and ancestors of present-day Melanesians paralleled the nineteenth-century paleoanthropological search for a missing link on the islands of South East Asia and Melanesia—this time carried out through the tools of genetics. This parallelism subtly implied that the genetic connection between Denisovans and Melanesians might indeed provide answers to some of paleoanthropology's oldest questions. Interestingly, Reich et al.'s genetic analysis tentatively suggested that the Denisovan genome may carry genetic traces of an even older hominin group, rooting Melanesia, by association, firmly in the imaginaries of hominin origins. At the same time, the idea of searching for the genetic secrets of hominin evolution in the Pacific Islands reinforced old colonial imaginaries of Melanesia as fundamentally foreign and exotic: a place that holds the secrets of human evolution yet cannot ever be fully known.

These imaginaries of space linger in current discourses around the Denisovan. For example, a 2015 article in the National Geographic focusing on Denisova Cave echoes narratives of masculine bravery and struggle for survival. The text accounts how the Denisovan molar was initially mistaken for a tooth of a cave bear, and how scientists had to rule out DNA contamination by "ancient hyenas, which seem to have long prowled the cave" (Greshko 2015). The cave as a site of hominin struggle for survival is also reflected in how the text quotes the director of the Max Planck Institute for Evolutionary Anthropology, Svante Pääbo's words: "It's an amazing place...because it's actually the only place in the world where we know that three different groups of humans with very different histories all lived." At the same time, a 2016 article on the CNN news site appears mesmerized by Melanesia and Pacific Islanders (Strickland 2016). While the piece opens by exploring human genetic inheritance in general—"the traits we have in common with early humans, Neanderthals and Denisovans, and how our histories crossed paths" (Strickland 2016; my emphasis)—the article quickly moves to positing Pacific Islanders as an evolutionary

enigma and a key to the secrets of early hominin evolution. This colonial rhetoric of past-oriented indigeneity is reinforced visually by an immediately culturally recognizable image of Papua New Guineans on a wooden dinghy in a sunset.

These examples show how aDNA becomes smoothly embedded within cultural imaginaries of space as it travels from high-throughput sequencing apparatuses to science journalism and public discourse. Crucially, the two regions in relation to which the Denisovan was constructed are mythic places in the Euro-American imperialist and colonialist imagination, an imagination that continues to organize discourses around science (TallBear 2013). These mythic resonances confirmed the idea that the Denisovan constituted a highly significant scientific discovery. They also gave epistemic authority to the very idea that aDNA provides a privileged and unmediated gateway to human evolutionary roots.

Conclusion

This article has explored the implications of the rise of aDNA research for STS scholarship. I have argued that while STS literature on population genetics provides a useful starting point, aDNA embodies material and cultural specificities that differ from other types of population genetic research. I have used the case of the Denisovan hominin to illustrate the complex technoscientific work through which a previously unknown prehistoric hominin is enacted from two aDNA samples. The analysis has demonstrated that the Denisovan relies on complex configurations of temporality, temperature, technology, and spatial imaginaries, which are, in many instances, unique to aDNA. I have highlighted the performative nature of the techniques and assumptions through which the Denisovan was established as an evolutionary actor. For example, the coolness of the cave (or in other cases of aDNA, permafrost) emerges as halting processes of material degradation and thus the working of evolutionary time and thereby paradoxically securing the procession of evolutionary time as a digitizable and measurable force. The relationship between individual and population also gains increased salience in aDNA, as researchers work with small numbers of geographically and temporally situated samples instead of a large database. Furthermore, cultural ideas of place—desolate and harsh Siberia and mysterious and impenetrable Melanesia—also co-constituted the Denisovan in ways that resonated, respectively, with narratives of brave and unique ancestry and colonialist imaginaries of spatialized difference.

The Denisovan case shows that aDNA projects are seldom straightforward discoveries but rather complex technoscientific endeavors that mobilize a range of historically shaped technologies, naturalized practices, material conditions, and cultural imaginaries. Developing STS tools to engage critically with the specificities of aDNA research is pivotal because the techniques and practices on which ancient hominins like Denisovans rely are often erased in public accounts, as the various media examples in the article demonstrate. For example, the ways in which cryopreservation by nature, or cultural imaginaries of space, have become naturalized around aDNA research, call for careful analysis. As the cultural appeal of aDNA research is likely to grow, it is crucial that science communication and public engagement around aDNA discoveries make these situated complexities clearly visible. While the Denisovan hominin is based on valid science, it is not epistemically or politically innocent. Rather, the Denisovan is the result of particular ways of looking at and manipulating temporality, materiality, temperature, and technology. Crucially, these ways of looking are likely to be reflected in other aDNA discoveries. Understanding how the Denisovan was enacted in 2010 may thus help us analyze the likely appearance of new aDNA samples from other remains and locations in the future.

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Note

Mitochondria are organelles located in the cytoplasm of the cell outside the
nucleus. They have their own distinct genome inherited maternally. Nuclear
DNA refers to what is commonly understood as "the genome," that is, genes
located in the chromosomes in the cell nucleus. With the exception of the
Y-chromosome, nuclear genes are inherited from both parents.

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