

OLLI 497: Ancient DNA

Session 6: November 2nd

Summary and Observations

Chapter 6: The Collision That Formed India

To begin with, I need to point a few strange things about this chapter. One is that no ancient DNA from India is involved in the analysis (mainly because there is no ancient Indian DNA). Only DNA from present-day Indians is analyzed. Second, all the ancient DNA comes from West Eurasians, including ancient Near Eastern farmers, and East Asians. Present-day Little Andaman Islanders DNA is used as a proxy for ancient Indian DNA. Third, the last section substantially alters the preceding story. But let us begin...

The Fall of the Indus Civilization

Reich begins with a brief account of the story told in the *Rig Veda*, the oldest text of Hinduism. He asks if the account of the invasion of the “Aryans” was real. Archaeologists attempted to answer this question. In the 1920s and 1930s, “... excavations uncovered the remains of an ancient civilization, walled cities at Harappa, Mohenjo-daro, and elsewhere in the Punjab and Sind that dated from forty-five hundred to thirty-eight hundred years ago. These cities and smaller towns and villages dotted the valley of the river Indus in present-day Pakistan and parts of India, and some of them sheltered tens of thousands of people. Were they perhaps the fortresses... of the *Rig Veda*?”

He goes on to describe the cities and civilization uncovered. He notes that “... the people of the Indus Valley Civilization engaged in prolific trade and commerce, as reflected in the stone weights and measures they left behind, and their trading partners, who lived as far away as Afghanistan, Arabia, Mesopotamia, and even Africa.”

Much of this civilization remained “enigmatic”: “The greatest mystery is its decline. Around thirty-eight hundred years ago, the settlements of the Indus dwindled, with population centers shifting east toward the Ganges plain. Around this time, the *Rig Veda* was composed in Old Sanskrit, a language that is ancestral to the great majority of languages spoken in northern India today and that had diverged in the millennium before the *Rig Veda* was composed from the languages spoken in Iran. Indo-Iranian languages are in turn cousins of almost all of the languages spoken in Europe and with them make up the great Indo-European language family. The religion of the *Rig Veda*, with its pantheon of deities governing nature and regulating society, had **unmistakable similarities** to the mythology of other parts of Indo-European Eurasia, including Iran, Greece, and Scandinavia, providing further evidence of cultural links across vast expanses of Eurasia.”

“Some have speculated that the collapse of the Indus Valley Civilization was caused by the arrival in the region of **migrants from the north and west** speaking Indo-European languages, the so-called Indo-Aryans. In the *Rig Veda*, the invaders had horses and chariots. We know from archaeology that the Indus Valley Civilization was a pre-horse society. There is no clear evidence of horses at their sites, nor are there remains of spoke-wheeled vehicles, although there are clay figurines of wheeled carts pulled by cattle. Horses and spoke-wheeled chariots were the weapons of mass destruction of Bronze Age Eurasia. Did the Indo-Aryans use their military technology to put an end to the old Indus Valley Civilization?”

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Reich notes that pursuing research in this area was, and still is, problematic. “Since the original excavations at Harappa, the “**Aryan invasion theory**” has been seized on by nationalists in both Europe and India, which makes the idea difficult to discuss in an objective way.... The Nazis’ interest in migrations and the spread of Indo-European languages has made it difficult for serious scholars in Europe to discuss the possibility of migrations spreading Indo-European languages. In India, the possibility that the Indus Valley Civilization fell at the hands of migrating Indo-European speakers coming from the north is also fraught, as it suggests that important elements of South Asian culture might have been influenced from the outside.”

He goes on to note that archaeologists have not discovered evidence of a sudden destruction of the civilization, nor evidence of a mass migration. He compares the decline of the Indus Valley Civilization to the collapse of the Roman Empire, noting similarities. But: “It is possible that in the apparent depopulation of the Indus Valley, too, we might be limited by the difficulty archaeologists have in detecting sudden change. The patterns evident from archaeology may be obscuring more sudden triggering events.”

Reich then asks: “What can genetics add? It cannot tell us what happened at the end of the Indus Valley Civilization, but it can tell us if there was a collision of peoples with very different ancestries. Although mixture is not by itself proof of migration, the **genetic evidence of mixture** proves that dramatic demographic change and thus opportunity for cultural exchange occurred close to the time of the fall of Harappa.”

A Land of Collisions

Reich terms India as the “Land of Collisions.” The most obvious one is the Himalayas, but he also means collisions of cultures and civilizations. For example, “... farming was not invented in India. [But] Indian farming today is born of the collision of the two great agricultural systems of Eurasia. The Near Eastern winter rainfall crops, wheat and barley, reached the Indus Valley sometime after nine thousand years ago according to archaeological evidence... Chinese monsoon summer rainfall crops of rice and millet also reached peninsular India around five thousand years ago. India may have been the first place where the Near Eastern and the Chinese crop systems collided.”

“Language is another blend. The Indo-European languages of the north of India are related to the languages of Iran and Europe. The Dravidian languages, spoken mostly by southern Indians, are not closely related to languages outside South Asia. There are also Sino-Tibetan languages spoken by groups living in the mountains fringing the north of India, and small pockets of tribal groups in the east and center that speak Austroasiatic languages related to Cambodian and Vietnamese, and that are thought to descend from the languages spoken by the peoples who first brought rice farming to South Asia and parts of Southeast Asia.”

“The people of India are also diverse in appearance, providing visual testimony to mixture. A stroll down a street in any Indian city makes it clear how diverse Indians are. Skin shades range from dark to pale. Some people have facial features like Europeans, others closer to Chinese.”

In addition, the genetics of Indians yields contradictory results: “Researchers studying mitochondrial DNA, always passed down from mothers, found that the vast majority of mitochondrial DNA in Indians was **unique to the subcontinent**, and they estimated that the Indian mitochondrial DNA types only shared common ancestry with ones predominant outside South Asia many tens of thousands of years ago. This suggested that on the maternal line, Indian ancestors had been largely isolated within the subcontinent for a long time, without

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mixing with neighboring populations to the west, east, or north. In contrast, a good fraction of Y chromosomes in India, passed from father to son, showed closer relatedness to West Eurasians—Europeans, central Asians, and Near Easterners—suggesting mixture.”

The Isolated People of Little Andaman Island

Reich begins this section with a description of how he learned about the Andaman Islands in the Bay of Bengal, and how he obtained access to a rich trove of Indian DNA. He also describes his interaction with Lalji Singh and Kumarasamy Thangaraj of the Centre for Cellular and Molecular Biology (CCMB) in Hyderabad, India. No need to summarize this here.

He next goes on to describe the analysis his lab did on the DNA samples from the CCMB, and their use of principal component analysis to get a picture of the relationships among the samples of DNA. “Using this method to display Indian genetic data on a two-dimensional graph, we found that the samples spread out along a line. At the far extreme of the line were West Eurasian individuals—Europeans, central Asians, and Near Easterners—which we had included in the analysis for the sake of comparison. We called the non–West Eurasian part of the line the “**Indian Cline**”: a gradient of variation among Indian groups that pointed on the plot like an arrow directly at West Eurasians.”

“A gradient in a principal component analysis plot can be caused by several quite different histories, but such a striking pattern led us to guess that many Indian groups today might be **mixtures**, in different proportions, of a West Eurasian–related ancestral population and another very different population. Seeing that the southernmost groups in India—which also spoke Dravidian languages—tended to be farthest away from West Eurasians in the plot, we explored a model in which Indians today are formed from **a mixture of two ancestral populations**, and we evaluated the consistency of this model with the data.”

But which ancestral populations? “We first tested the hypothesis that Europeans and Indians descend from a common ancestral population that split at an earlier time from the ancestors of East Asians such as Han Chinese. We identified DNA letters where European and Indian genomes differed, and then measured how often Chinese samples had the genetic types seen in Europeans or Indians. We found that Chinese clearly share more DNA letters with Indians than they do with Europeans. That **ruled out** the possibility that Europeans and Indians descended from a common homogeneous ancestral population since their separation from the ancestors of Chinese.”

“We then tested the alternative hypothesis that Chinese and Indians descend from a common ancestral population since their separation from the ancestors of Europeans. However, this scenario **did not hold up either**: European groups are more closely related to all Indians than to all Chinese.”

“We found that the frequencies of the genetic mutations seen in all Indians are, on average, **intermediate** between those in Europeans and East Asians. The only way that this pattern could arise was through **mixture of ancient populations**—one related to Europeans, central Asians, and Near Easterners, and another related distantly to East Asians.”

“We initially called the first population “West Eurasians,” as a way of referring to the large set of populations in Europe, the Near East, and central Asia, among which there are only modest differences in the frequencies of genetic mutations from one group to another. These differences are typically about ten times smaller than the differences between Europeans and

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the people of East Asia. It was striking to find that one of the two populations contributing to the ancestry of Indians today grouped with West Eurasians. This looked to us like the easternmost edge of the ancient distribution of West Eurasian ancestry, where it had mixed with other very different people. We could see that the other population was more closely related to present-day East Asians such as Chinese, but was also clearly tens of thousands of years separated from them. So it represented an **early-diverging lineage** that contributed to people living today in South Asia but not much to people living anywhere else.”

“Having identified the mixture, we searched for present-day Indian populations that might have escaped it. All the populations on the mainland had some West Eurasian–related ancestry. However, the people of Little Andaman Island had none. The Andamanese were consistent with being isolated descendants of an **ancient East Asian–related population** that contributed to South Asians. The indigenous people of Little Andaman Island, despite a census size of fewer than one hundred, turned out to be key to understanding the population history of India.”

The Mixing of East and West

A disaster nearly occurred when Reich briefed his Indian colleagues about the results of the analysis, showing one of the ancestral populations as “West Eurasian.” “They did not want to be part of a study that suggested a major West Eurasian incursion into India without being absolutely certain as to **how the whole-genome data could be reconciled with their mitochondrial DNA findings**. They also implied that the suggestion of a migration from West Eurasia would be politically explosive. They did not explicitly say this, but it had obvious overtones of the idea that migration from outside India had a transformative effect on the subcontinent.”

Reich describes the solution. At a meeting the next morning, they “... came up with new names for ancient Indian groups. We wrote that the people of India today are the outcome of mixtures between two highly differentiated populations, “Ancestral North Indians” (ANI) and “Ancestral South Indians” (ASI), who before their mixture were as different from each other as Europeans and East Asians are today. The ANI are related to Europeans, central Asians, Near Easterners, and people of the Caucasus, but we made no claim about the location of their homeland or any migrations. The ASI descend from a population not related to any present-day populations outside India. We showed that the **ANI and ASI had mixed dramatically in India**. The result is that everyone in mainland India today is a mix, albeit in different proportions, of ancestry related to West Eurasians, and ancestry more closely related to diverse East Asian and South Asian populations. No group in India can claim genetic purity.”

Ancestry, Power and Sexual Dominance

Reich now gives us a glimpse into the findings that came out of his analysis, starting with “... the fraction of West Eurasian–related ancestry in each Indian group.”

“In this initial study and in subsequent studies with larger numbers of Indian groups, we found that West Eurasian–related mixture in India ranges from as low as 20 percent to as high as 80 percent. This continuum of West Eurasian–related ancestry in India is the reason for the Indian Cline—the gradient we had seen on our principal components plots. No group is unaffected by mixing, neither the highest nor the lowest caste, including the non-Hindu tribal populations living outside the caste system.”

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“The mixture proportions provided clues about past events. For one thing, the genetic data hinted at the languages spoken by the ancient ANI and ASI. Groups in India that speak Indo-European languages typically have more ANI ancestry than those speaking Dravidian languages, who have more ASI ancestry. This suggested to us that the ANI probably spread Indo-European languages, while the ASI spread Dravidian languages.”

“The genetic data also hinted at the social status of the ancient ANI (higher social status on average) and ASI (lower social status on average). Groups of traditionally higher social status in the Indian caste system typically have a higher proportion of ANI ancestry than those of traditionally lower social status, even within the same state of India where everyone speaks the same language. For example, Brahmins, the priestly caste, tend to have more ANI ancestry than the groups they live among, even those speaking the same language. Although there are groups in India that are exceptions to these patterns, including well-documented cases where whole groups have shifted social status, the findings are statistically clear, and suggest that the ANI-ASI mixture in ancient India occurred in the context of social stratification.”

“The genetic data from Indians today also reveal something about the history of differences in social power between men and women. Around 20 to 40 percent of Indian men and around 30 to 50 percent of eastern European men have a Y-chromosome type that, based on the density of mutations separating people who carry it, descends in the last sixty-eight hundred to forty-eight hundred years from **the same male ancestor**. In contrast, the mitochondrial DNA, passed down along the female line, is almost entirely restricted to India, suggesting that it may have nearly all come from the ASI, even in the north. The only possible explanation for this is major migration between West Eurasia and India in the Bronze Age or afterward. Males with this Y chromosome type were extraordinarily successful at leaving offspring while female immigrants made far less of a genetic contribution.”

Finally, he is able to resolve the “... discrepancy between the Y-chromosome and mitochondrial DNA patterns.... a possible explanation is that most of the ANI genetic input into India came from males.... the common thread is that males from populations with more power tend to pair with females from populations with less. It is amazing that genetic data can reveal such profound information about the social nature of past events.”

Population Mixture at the Twilight of the Harappa

Reich moves on to determining when the population mixture occurred. “One possibility we considered is that the mixtures we had detected were due to great human migrations at the end of the last ice age, after around fourteen thousand years ago, as improving climates changed deserts into habitable land and contributed to other environmental change that drove people hither and yon across the landscape of Eurasia.”

“A second possibility is that the mixtures reflected movements of farmers of Near Eastern origin into South Asia, a migration that could be a possible explanation for the spread of Near Eastern farming into the Indus Valley after nine thousand years ago.”

“A third possibility is that the mixtures occurred in the last four thousand years associated with the dispersal of Indo-European languages that are spoken today in India as well as in Europe. This possibility hints at events described in the *Rig Veda*. However, even if mixture occurred after four thousand years ago, it is entirely possible that it took place between already-resident

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populations, one of which had migrated to the area from West Eurasia some centuries or even millennia earlier but had not yet interbred with the ASI.”

Reich reminds us that the admixture of ANI and ASI chromosomes would still be subject to shortening and breaking up through the process of recombination during meiosis. Measuring the size of stretches of ANI and ASI DNA in chromosomes, his team arrived at a date. “We found that all Indian groups we analyzed had ANI-ASI mixture dates between four thousand and two thousand years ago, with Indo-European-speaking groups having more recent mixture dates on average than Dravidian-speaking groups.”

The last part of this dating result needs some explanation. He finds a solution in the hypothesis that there were waves of migration and mixture in northern India, followed by subsequent movement of admixed peoples into other parts of India. “A hard look at the genetic data confirms the theory of multiple waves of ANI-related mixture into the north. Interspersed among the short stretches of ANI-derived DNA we find in northern Indians, we also find quite long stretches of ANI-derived DNA, which must reflect recent mixtures with people of little or no ASI ancestry.”

“Remarkably, the patterns we observed were consistent with the hypothesis that all of the mixture of ANI and ASI ancestry that occurred in the history of some present-day Indian groups happened within the last four thousand years. This meant that the population structure of India before around four thousand years ago was profoundly different from what it is today. Before then, there were unmixed populations, but afterward, there was **convulsive mixture** in India, which affected nearly every group.”

“So between four thousand and three thousand years ago—just as the Indus Civilization collapsed and the **Rig Veda** was composed—there was a profound mixture of populations that had previously been segregated. Today in India, people speaking different languages and coming from different social statuses have different proportions of ANI ancestry. Today, ANI ancestry in India derives more from males than from females. This pattern is exactly what one would expect from an Indo-European-speaking people taking the reins of political and social power after four thousand years ago and mixing with the local peoples in a stratified society, with males from the groups in power having more success in finding mates than those from the disenfranchised groups.”

The Antiquity of Caste

Reich next asks: “How is it that the genetic marks of these ancient events have not been blurred beyond recognition after thousands of years of history?”

He points to an obvious culprit: “One of the most distinctive features of traditional Indian society is caste—the system of social stratification that determines whom one can marry and what privileges and roles one has in society.... Caste was outlawed in 1947 with the birth of democratic India, but it still shapes whom people choose to socialize with and marry today.”

“A sociological definition of a caste is a group that **interacts economically** with people outside it (through specialized economic roles), but **segregates itself socially** through endogamy (which prevents people from marrying outsiders).”

“Caste in India is organized at two levels, *varna* and *jati*.” Reich spends the next several paragraphs describing these levels in the Indian cast system. You should read it, but I won’t

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summarize it here. He ends up noting: “These ancient tribal groups have preserved their distinctiveness through the caste system and endogamy rules”

“The theory of the caste system is undeniably old, as it is described in the ancient *Law Code of Manu*, a Hindu text composed some hundreds of years after the *Rig Veda*.... However, revisionist historians, led by the anthropologist Nicholas Dirks, have argued that in fact strong endogamy was not practiced in ancient India, but instead is largely an innovation of British colonialism. Dirks and colleagues showed how, as a way of effectively ruling India, British policy beginning in the eighteenth century was to strengthen the caste system, carving out a natural place within Indian society for British colonialists as a new caste group. To achieve this, the British strengthened the institution of caste in parts of India where it was not very important, and worked to harmonize caste rules across different regions. Given these efforts, Dirks suggested that strong endogamy restrictions as manifested in today’s castes might not be as old in practice as they seem.”

Reich begins his counter-argument: “To understand the extent to which the *jatis* corresponded to real genetic patterns, we examined the degree of differentiation of each *jati* from which we had data with all others based on differences in mutation frequencies. We found that the degree of differentiation was at least three times greater than that among European groups separated by similar geographic distances. This could not be explained by differences in ANI ancestry among groups, or differences in the region within India from which the population came, or differences in social status. Even comparing pairs of groups matched according to these criteria, we found that the degree of genetic differentiation among Indian groups was many times larger than that in Europe.”

“These findings led us to surmise that many Indian groups today might be the products of **population bottlenecks**. These occur when relatively small numbers of individuals have many offspring and their descendants too have many offspring and remain **genetically isolated** from the people who surround them due to social or geographic barriers.”

“We looked for the telltale signs of population bottlenecks in India and found them: identical long stretches of sequence between pairs of individuals within the same group. The only possible explanation for such segments is that the two individuals descend from an ancestor in the last few thousand years who carried that DNA segment. What’s more, the average size of the shared DNA segments reveals how long ago in the past that shared ancestor lived, as the shared segments break up at a regular rate in each generation through the process of recombination.”

“The genetic data told a clear story. Around a third of Indian groups experienced population bottlenecks as strong or stronger than the ones that occurred among Finns or Ashkenazi Jews. We later confirmed this finding in an even larger dataset that we collected working with Thangaraj: genetic data from more than 250 *jati* groups spread throughout India.”

“Many of the population bottlenecks in India were also exceedingly old. One of the most striking we discovered was in the Vysya of the southern Indian state of Andhra Pradesh, a middle caste group of approximately five million people whose population bottleneck we could date (from the size of segments shared between individuals of the same population) to between three thousand and two thousand years ago.”

“The observation of such a strong population bottleneck among the ancestors of the Vysya was shocking. It meant that after the population bottleneck, the ancestors of the Vysya had maintained strict endogamy, allowing essentially **no genetic mixing** into their group for thousands of years. Even an average rate of influx into the Vysya of as little as 1 percent per

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generation would have erased the genetic signal of a population bottleneck. The ancestors of the Vysya did not live in geographic isolation. Instead, they lived cheek by jowl with other groups in a densely populated part of India. Despite proximity to other groups, the endogamy rules and group identity in the Vysya have been so strong that they maintained strict social isolation from their neighbors, and transmitted that culture of social isolation to each and every subsequent generation.”

“Rather than an invention of colonialism as Dirks suggested, long-term endogamy as embodied in India today in the institution of caste has been overwhelmingly important for **millennia.**”

“What the data were showing us was that the genetic distinctions among *jati* groups within India were in many cases real, thanks to the long-standing history of endogamy in the subcontinent. People tend to think of India, with its more than 1.3 billion people, as having a tremendously large population, and indeed many Indians as well as foreigners see it this way. But genetically, this is an incorrect way to view the situation. The Han Chinese are truly a large population. They have been mixing freely for thousands of years. In contrast, there are few if any Indian groups that are demographically very large, and the degree of genetic differentiation among Indian *jati* groups living side by side in the same village is typically two to three times higher than the genetic differentiation between northern and southern Europeans. The truth is that India is composed of **a large number of small populations.**”

Indian Genetics, History, and Health

Having established that a significant portion of the Indian population has experienced a population bottleneck, Reich points to the opportunity this presents for finding the genes for rare recessive diseases. But first, he notes that population bottlenecks can have serious health consequences when both parents contribute mutations to their offspring. They can lead to **“founders’ diseases.”** “Because of... population bottlenecks, rare disease-causing mutations that happened to have been carried in the founder individuals have dramatically increased in frequency. Rare mutations that are innocuous when a person inherits a copy from only one of their parents—they act recessively...—can be lethal when a person inherits copies from both parents. However, once these mutations increase in frequency due to a population bottleneck, there is an appreciable chance that individuals in the population will inherit the same mutation from both of their parents.” He gives as an example Tay-Sachs disease among Ashkenazi Jews.

“India, of course, has far more people who belong to groups that experienced strong bottlenecks, as the country’s population is huge, and as around one-third of Indian *jati* groups descend from bottlenecks as strong or stronger than those that occurred in Ashkenazi Jews or Finns. Searches for the genes responsible for disorders in these Indian groups therefore have the potential to identify risk factors for thousands of diseases.” He gives as an example the Vysya, who have a rare recessive mutation which results in prolonged muscle paralysis in response to muscle relaxants.

“... the history of India presents an important opportunity for biological discovery, as finding genes for rare recessive diseases is cheap with modern genetic technology. All it takes is access to a small number of people in a *jati* group with the disease, whose genomes can then be sequenced.”

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A Tale of Two Subcontinents: The Parallel History of India and Europe

An added complexity to (a total rewrite of?) the story of the mixing of populations in India arose in 2016 with the publication of "... the first genome-wide ancient DNA from some of the world's earliest farmers, people who lived between eleven thousand and eight thousand years ago in present-day Israel, Jordan, Anatolia, and Iran. When we studied how these early farmers of the Near East were related to people living today, we found that present-day Europeans have strong genetic affinity to early farmers from Anatolia, consistent with a migration of Anatolian farmers into Europe after nine thousand years ago. Present-day people from India have a strong affinity to ancient Iranian farmers, suggesting that the expansion of Near Eastern farming eastward to the Indus Valley after nine thousand years ago had as important an impact on the population of India. But our studies also revealed that present-day people in India have strong genetic affinities to ancient steppe pastoralists. How could the genetic evidence of an impact of an Iranian farming expansion on the population of India be reconciled with the evidence of steppe expansions?" A similar situation occurred in Europe.

With this new ancient DNA data on early farmers in hand, Reich's team then did a further analysis of their data from India. They found that almost every population group in India today has ancestry from "... Little Andaman Islanders, ancient Iranian farmers, and ancient steppe peoples."

The applied mathematician Nick Patterson, working in Reich's lab, then worked his magic to rewrite the story of ancestral India: "When Patterson inferred what would have been expected for a population of entirely ANI ancestry—one with no Andamanese-related ancestry—he determined that they would be a mixed population of Iranian farmer-related ancestry and steppe pastoralist-related ancestry. But when he inferred what would have been expected for a population of entirely ASI ancestry—one with no Yamnaya-related ancestry—he found that they too must have had substantial Iranian farmer-related ancestry (the rest being Little Andamanese-related)."

"This was a great surprise. Our finding that both the ANI and ASI had large amounts of Iranian-related ancestry meant that we had been wrong in our original presumption that one of the two major ancestral populations of the Indian Cline had no West Eurasian ancestry. Instead, people descended from Iranian farmers made a major impact on India twice, admixing both into the ANI and the ASI."

"Patterson proposed a major revision to our working model for deep Indian history. The ANI were a mixture of about 50 percent steppe ancestry related distantly to the Yamnaya, and 50 percent Iranian farmer-related ancestry from the groups the steppe people encountered as they expanded south. The ASI were also mixed, a fusion of a population descended from earlier farmers expanding out of Iran (around 25 percent of their ancestry), and previously established local hunter-gatherers of South Asia (around 75 percent of their ancestry). So the ASI were not likely to have been the previously established hunter-gatherer population of India, and instead may have been the people responsible for spreading Near Eastern agriculture across South Asia. Based on the high correlation of ASI ancestry to Dravidian languages, it seems likely that the formation of the ASI was the process that spread Dravidian languages as well."

"These results reveal a remarkably parallel tale of the prehistories of two similarly sized subcontinents of Eurasia—Europe and India. In both regions, farmers migrating from the core region of the Near East after nine thousand years ago—in Europe from Anatolia, and in India from Iran—brought a transformative new technology, and interbred with the previously

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established hunter-gatherer populations to form new mixed groups between nine thousand and four thousand years ago. Both subcontinents were then also affected by a second later major migration with an origin in the steppe, in which Yamnaya pastoralists speaking an Indo-European language mixed with the previously established farming population they encountered along the way, in Europe forming the peoples associated with the Corded Ware culture, and in India eventually forming the ANI. These populations of mixed steppe and farmer ancestry then mixed with the previously established farmers of their respective regions, forming the gradients of mixture we see in both subcontinents today.”

“The Yamnaya—who the genetic data show were closely related to the source of the steppe ancestry in both India and Europe—are obvious candidates for spreading Indo-European languages to both these subcontinents of Eurasia. Remarkably, Patterson’s analysis of population history in India provided an additional line of evidence for this. His model of the Indian Cline was based on the idea of a simple mixture of two ancestral populations, the ANI and ASI. But when he looked harder and tested each of the Indian Cline groups in turn for whether it fit this model, he found that there were six groups that did not fit in the sense of having a higher ratio of steppe-related to Iranian farmer-related ancestry than was expected from this model. All six of these groups are in the Brahmin varna—with a traditional role in society as priests and custodians of the ancient texts written in the Indo-European Sanskrit language—despite the fact that Brahmins made up only about 10 percent of the groups Patterson tested. A natural explanation for this was that the ANI were not a homogeneous population when they mixed with the ASI, but instead contained socially distinct subgroups with characteristic ratios of steppe to Iranian-related ancestry. The people who were custodians of Indo-European language and culture were the ones with relatively more steppe ancestry, and because of the extraordinary strength of the caste system in preserving ancestry and social roles over generations, the ancient substructure in the ANI is evident in some of today’s Brahmins even after thousands of years. This finding provides yet another line of evidence for the steppe hypothesis, showing that not just Indo-European languages, but also Indo-European culture as reflected in the religion preserved over thousands of years by Brahmin priests, was likely spread by peoples whose ancestors originated in the steppe.”

“The picture of population movements in India is still far less crisp than our picture of Europe because of the lack of ancient DNA from South Asia. An outstanding mystery is the ancestry of the peoples of the Indus Valley Civilization, who were spread across the Indus Valley and parts of northern India between forty-five hundred to thirty-eight hundred years ago, and were at the crossroads of all these great ancient movements of people.” Reich describes three potential scenarios for these peoples, but concludes: “These scenarios have very different implications, but with ancient DNA, this and other great mysteries of the Indian past will soon be resolved.”