

Haplogroup J-Z640-Genetic Insight into the Levantine Bronze Age

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Abstract

This article aims at researching the evolution of J-Z640 using an interdisciplinary approach in order to clarify the leading historical and anthropological events that shaped this particular branch of the human Y chromosome. We compiled a STR (short tandem repeat) and SNP (single nucleotide polymorphism) dataset of 145 known or predicted J-Z640 samples among the customers of Family Tree DNA and Full Genomes Corporation, as well as publicly available samples. Amongst these, we analyzed the results of 41 samples that had undergone Next-Generation Sequencing (NGS) and 32 samples that had undergone SNP testing using Sanger Sequencing. From this data, we constructed a J-Z640 phylogenetic tree that was dated using the method. Our data revealed that Haplogroup J-Z640 is a Y chromosome lineage found most notably, in several minority groups within the Near East such as the Samaritans, Druze, Armenians and Jews. J-Z640 originated during the Bronze Age, most likely in the Levant. During the Bronze Age the haplogroup rapidly expanded with multiple ancient branches surviving to the present, evidencing population growth. Further population expansion, and contraction, was also observed in later periods. Based on its geographic dispersal and age of the haplogroup and its subclades, the founder population most likely belonged to Canaanites found in the Levant. Following the collapse of the late Bronze age system, from the Iron Age onwards there followed a period of "differentiation by culture", with many of the ancient branches surviving to the present separated along ethno-religious lines.

Keywords: J-Z640; Levant; Population genetics; Bronze Age; Ethnogenesis

Introduction

The last decade has seen a boom in population genetics studies, in particular of Y-chromosomal studies. Many of these research works were targeted towards general population analysis [1,2-6] based on geographical location or group self-identification and, in general, involved mainly analyses of a small number of STRs and SNPs identified through conventional Sanger sequencing.

Increased interest in genetic genealogy and self-testing within the general population has allowed researchers access to a larger and more in-depth datasets. Genetic genealogy results are increasingly being used as a scientific resource [2,7-12]. Furthermore, the development of Next-Generation Sequencing (NGS) technologies focused on the Y chromosome such as Family Tree DNA's "Big Y", FullGenomes Corporation's "Y-Elite", Whole-Genomic Sequencing (WGS) like FullGenomes Corporation's "Genome Guide" and such as undertaken in the 1000 Genomes Project [13,14] have allowed for collaborative research between professionals and citizens [15-17]. In light of all of these developments, there still has been a lack of interdisciplinary approaches combining historical and anthropological analysis of Y-Chromosomal phylogeny [18].

J-Z640, an un-researched subclade of J-M267, is the focus of our study. J-Z640 was first identified in 2011 from 1000 Genomes Project samples by Bonnie Schrack, according to the International Society of Genetic Genealogy yBrowse tool. Like its ancestral haplogroup SNP J-P58, the evolution of J-Z640 has not been researched and is poorly understood. Here we conduct an interdisciplinary analysis of the available data in order to better understand the phylogeny and chronological development of J-Z640 and attempt to place the genetic results within a historical and anthropological context.

Materials and Methods

Based on STR and SNP data, we compiled a dataset of 145 samples

belonging to or predicted to belong to J-Z640 using the databases of FamilyTreeDNA and FullGenomes Corporation as well as published academic samples. A sample was identified as belonging to J-Z640 in the event that it had previously tested positive for the Z640 SNP and/or the defining SNPs of one of its reported subclades. A sample was predicted to belong to J-Z640 based on the proximity of the STR results of the sample to confirmed J-Z640 samples. Out of 145 samples within our dataset NGS testing was carried out on 41 samples (in addition to 8 academic samples previously published) and targeted SNP testing using Sanger Sequencing was carried out on an additional 46 samples. In conducting further NGS testing priority was given to samples which showed the most genetic variability within the dataset. Informed consent was obtained from all participants. Supplementary Table 1 summarizes the number of samples obtained for J-Z640 and its subclades. Part of the dataset included academic samples identified in a review of genome variation databases and the academic literature. Through the review, we identified additional samples belonging to the relevant haplogroups for analysis from the Personal Genome Project, the 1000 Genomes project, Sardinian population study [19,20] and Gulf Arab population testing [21] described in Supplementary Table 2. These academic samples (8 in total) were merged with the samples obtained from commercial databases as described above.

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Genealogies from the Portuguese New Christian, were accessed at the Amsterdam and Rotterdam Municipal Archives (Netherlands), the Arquivo Nacional da Torre do Tombo in Lisbon (Portugal), the Archivo Historico Nacional in Madrid (Spain). For descendants of the de Caliz

Significant occupation of the interior Arabian Peninsula takes place only after the domestication of the camel around the year 1,000 BCE [26,27]. Until the domestication of the camel, most of the Arabian Peninsula could not support significant human populations or long-distance trade routes across them. Within North and Central Arabia there is evidence of significant human habitation only during the Iron Age [28].





Figure 3: Heat map for J-Z640 samples identified.

Additionally, recent research into ancient DNA in the southern Levant has indicated, through PCA analysis, that the Bronze Age population of the southern Levant shows a significant proportion of genetic material found in ancient DNA samples from the Caucasus, specifically, from the region of historic Armenia. There are also multiple examples within the ancient samples of what appear to be migrations from the Caucasus into the Southern Levant (Liran Carmel and Shai Carmi, personal communication). Strengthening the argument for a Levantine origin and corresponding with the ancient DNA results are the existence of a number of samples from Turkey and Armenia, as well as two Sanger-Sequenced J-Z640 Azeris, found within separate

There is a clear distinction within J-Z640 between the branches populated predominantly by modern Arab populations and the branches populated predominantly by other modern Levantine populations. In the event that the haplogroup had expanded from the

subclades of J-Z640 with early branching off dates (Late Bronze Age-Early Iron Age) from the other Z640 samples.

A Mesopotamian origin for the haplogroup seems unlikely due to the sparsity of Iraqi samples in J-Z640. The Iraqi samples that have been documented within the haplogroup either belong to individuals with recent origins from the Arabian Peninsula or to individuals, as stated above, who cluster within a Levantine branch.

The only other significant population represented with multiple lineages within the dataset was of individuals of Iberian origins. An origin in the Iberian Peninsula was also discounted seeing as all of the Iberian lineages tested with NGS closely matched Jewish lineages, with the majority of the branching dating to around the 7th-9th century CE. The most plausible explanation was that the lineages reached Iberia with Jewish migrants, either through internal migration in the Roman Empire or later with the Arab Conquest of the Peninsula, and were not indigenous to the region (although later branches most likely first appeared in Iberia). There are some additional Arab-Iberian clusters within J-Z640 predicted currently by STR analysis, which also seem to have reached Iberia with Arab migrations; however, because they have not undergone NGS, they cannot be included within the dating and future NGS testing and analysis will shed light on these predicted clusters.

The early expansion of J-Z2293

The ancient branches of the J-Z2293 haplogroup all date with high probability to the period of the late Bronze Age. These branches are all estimated with a high probability to predate the collapse of the late Bronze age system between 1200-1177 BCE. The multitude of different ancient branches appearing within a similar timeframe within J-Z640 provides evidence of population growth taking place in the Eastern Mediterranean region.

The late Bronze Age period was remarkable for its globalism and cosmopolitanism as well as marked by the development of territorial states governing several cities and their hinterlands. Egypt, Assyria and Babylonia attained a size and cohesion never known before in their histories. It seems likely that in this period a combination of relative prosperity through extensive trade and diplomatic relations combined with constant low level warfare, the movement of armies and the displacement of the rural populations due to the excessive demands of the urban elites led to the wide dispersal of populations as well as steady population growth. Lawrence et al. [29] points out that the complex relationships sustaining urban growth during this later period resulted in an increase in system fragility and ultimately impacted on the sustainability of cities in the long term. The site occupational data and population estimates demonstrate that the Late Bronze Age was a period of substantial settlement and even urban settlement in Canaan, and that the population had continued to increase and expand from the Middle Bronze Age. This trend of expansion, however, is only logical as populations increase and settlements expand or are newly created over time [30].

During the relevant historical period, the main populations present in the Levant were the Egyptians in the South, the Canaanites in the Syro-Palestinian region, the Hittites in Anatolia, the Mittani in eastern Anatolia and northern Syria, the Assyrians from Mesopotamia, and the various peoples of the Aegean. J-Z640 haplogroup has not been identified to date in contemporary populations in Egypt, Greece, and Western Anatolia/Asia Minor. It is also rare in Iraq. There are multiple lineages coming from Central-Southern Anatolia and from the Southern Levant. We propose that the founder population that J-Z640 and its ancient branches belong to best fits the Canaanites. The

only Anatolian samples, 1 Turkish and 2 Armenian, each representing different branches, come from Central-Southern Anatolia. In the case of the Armenians, Yardumian [31] notes that the ethnogenesis of Armenians is a subject not yet thoroughly understood. However, classical and epigraphic sources place a people with this name in southeastern Anatolia about 500 BCE. Furthermore, Yardumian [31] argues that affinities shared between Bronze Age pottery types in the Caucasus and eastern Anatolia, as well as between eastern Anatolia and the Levant (the Khirbet Kerak ware of Jordan and Palestine, and Kura-Araxes wares of Georgia and Armenia being the most conspicuous example), are indicative of cultural, if not population, continuity between these regions. Herrera et al. [32] studying the Y-STR variance and haplotype distributions of Armenians concluded that most of the observed paternal lineages in the Armenian Plateau were likely introduced into Armenia from the Levant. The existence of J-Z640 within these samples, could represent trade and or movement between the Canaanite city-states and the more dominant economic and military powers to their north. We would expect to see additional Anatolian samples that cluster within the haplogroup, were the Hittites or the Mitanni the founding population.

Conversely, J-Z640 is found within populations that currently inhabit or have historical ethnogenesis in the region comprising all of the territory of the Canaanite city-states and their hinterland. Furthermore, the different typology of population expansion, could point to different settlement patterns of the Canaanite peoples in the area, along the nomadic versus pastoralist divide.

Differentiation by culture

The lack of branching events following the collapse of the late Bronze Age ties in with the reorganization seen during the Iron Age, in which new polities established themselves including the Neo-Hittites in Southeastern Anatolia, north Syria, and points further east; the Phoenicians, Philistines and Israelites in what had once been Canaan [33] as well as the Arabs in the Arabian peninsula. Haber et al. [34] has previously concluded that contemporary genetic stratifications in the Levant are driven by the religious affiliations of the populations within the region. Similarly, the vast majority of the populations currently represented in our study are separated along ethno-religious lines, and most of them, including the Jews, the Samaritans, the Arabs, and the Armenians, trace their ethnogenesis to the Iron Age.

J-Z640 and the Arab lineages

The Arab branches within J-Z640 represent ancient basal branches dating to the middle and late Bronze Age, which sit in near to other branches that are populated by Levantine minority groups. These branches can be categorized according to self-reported tribal affiliation or lack thereof. The most populated Arab branch (and the oldest identified branch of J-Z640) J-BY74 as well as both a basal branch of J-Z2293 and a subclade of the J-Z2293, J-ZS1380, include multiple individuals who self-report their ancestry as belonging to tribal groups which form part of the al 'Azd tribes. Considering the origins of the 'Azd tribes, Ulrich [35] based on several ESA inscriptions from the 3rd Century CE, identifies two 'Azd tribal "kingdoms" which existed in southwestern Arabia north of Yemen during the third and fourth centuries AD. Ulrich [35] believes that these tribes formed the southern Arabian identity grouping that evolved into al-'Azd. The genetic results of the two Arab Azd branches cannot confirm or disprove the connection with the earlier Azd tribal kingdoms; however, while insufficient NGS testing has been carried out on these branches, considering the TMRCAs of BY74 and J-ZS1380, the STR data, and the large number of individuals belonging to these branches who identify

themselves as al-'Azd, this is a good indication of the longevity of the association of both branches (and their subclades) with these tribes. The Arab branches of J-Z640 could also potentially shed light on the ethnogenesis of the post Islamic Arab identity. Based on the distribution and use Eph'al [36] has noted that the term "Arabs" was originally a northern concept applied exclusively to nomadic tribes present in the cup of the Fertile Crescent and northern Arabia. The earliest reliable reference is given in an inscription dated 853 BCE of the Assyrian king Shalmaneser III in which he mentions the 10,000 camels of Gindibu' of Arabia amongst a coalition of small kingdoms. Other information on nomads in the border regions of Syro-Palestine in the Ninth and the first half of the Eighth Centuries BCE comes from the Book of Chronicles. Webb [37], has interpreted "the literary tradition of 'Arab' cognates in Mesopotamian and Hellenistic writing as the legacy of an externally imposed label". Likewise, he also posits that the term Arab in the Jewish literary tradition is a catch-all term for either a different way of life outside the boundaries of ancient Israel or peoples living on periphery of the Israelite polities. This, he believes, explains why the term is used far less frequently following 106 CE and practically disappears for around 300 years following the 3rd century CE.

Webb [37] argues that the ethnogenesis of the modern Arab peoples is intertwined with the rise of Islam, which constructed "to create a sense of ethnic kin-interrelation to maintain their communal cohesion" with the adoption of a new religion. This ties in with many other Levantine and Middle Eastern populations, in which the ethnogenesis can tie together ethnic and religion to form an ethnoreligious identity such as exemplified by the Jewish, the Samaritan, the Druze, the Armenians, and several Christian identities such as Syriac, Assyrian, Maronite, and Coptic.

Considering the geographic distribution of J-Z640 and its presence amongst Levantine populations as well as the longevity and isolation of the Arabian branches during the early Iron Age, these lineages seem good candidates for having formed part of the nomadic tribes present in the border regions of Syro-Palestine referred to by the Assyrians and Israelites as Arabs. The domestication of camels enabled a new type of nomadism. Instead of sheep and goat pastoralism that utilized areas in between permanent settlements, camel nomads could traverse long stretches of the desert. It is possible that as these nomadic tribes expanded into the territories of the sedentary populations of Central and Southern Arabia, culminating in the conquest of the settled land by the desert, so the term "Arabs" was preserved in the collective memory of these tribes and reimagined with the advent of Islam, reflecting the prominence of the al 'Azd both pre- and post-Islam in the Arabian Peninsula.

Expansions of J-Z640 from the Eastern Mediterranean to Europe

Other than the Iberian, which cluster exclusively with Sephardi and Ashkenazi Jewish samples, several other J-Z640 branches have been identified to date amongst European populations. Zalloua, et al. [38] has previously noted that "expansions from the Eastern Mediterranean could include the initial peopling by modern humans during the Paleolithic era, the subsequent Neolithic-era transition originating in the Fertile Crescent ~8000 BCE, and later events, such as the Greek expansion or the Jewish Diaspora." However, in essence, it was only around 1,200 BCE that technological innovations enabled people from the Levantine coastal harbors to traverse the entire Mediterranean, the most significant of these being the first-millennium Phoenicians BCE [39].

The most intriguing of these branches is a branch currently only

associated with one Sardinian J-Z642 sample from Cagliari identified by Francalacci et al. [19]. The Sardinian branch, J-ZS8025, branches off from J-FGC30543 approximately 3,300 ybp. While the poor quality of the sequencing meant excluding it from the dating of this branch, it was positive for these above SNPs, allowing us to differentiate this as a new branch. In the period 750-650 BCE a series of Phoenician settlements were established along the South and Southwest coasts of Sardinia. These Phoenician settlements included Cagliari where the Francalacci et al. [19] sample is from. One possible explanation of the presence of J-Z642 in Sardinia is that this is a genetic remnant of the Phoenician colonies, which once existed on Sardinia. However, the rarity of the haplogroup amongst the Sardinian population (the haplogroup was only found amongst 2 related individuals out of 1557 males) left open the possibility that J-Z642 had reached Sardinia at a later date.

Jews and Iberians-The golden age of al-Andalus

The Jewish and Iberian lineages within J-Z2285 and J-FGC30542 cluster together. Significant to both subclades, the Jewish lineages identified to date are exclusively Sephardic with two out of three families documented Portuguese New Christian (Jews who were forcibly converted to Catholicism) lineages, one from Amsterdam and the other from Aleppo and Livorno, and the third, carrying a known Portuguese name, also from Aleppo.

In J-Z2285, the SNP representing the Jewish and Iberian branch is J-Z2272. This branch is estimated to share a common ancestor 1,200 ybp (with a 95% error range of 1,900-700), which is very similar to the age of J-FGC5206 discussed below. This branch further splits into two sub-branches: the first, currently defined by SNPs J-Z2289 and J-Z27745, which three 1000 Genomes Project samples (two from Peru, one from Puerto Rico) belong to as well as the Portuguese New Christian lineage from Aleppo and Livorno; and the second, a basal branch shared by several Hispanics, including a family that reports Jewish origins.

The Jewish and Iberian branch of J-FGC30542 presents a different story. This branch, J-FGC30544 (J-ZS5769) is downstream of J-FGC30542 by several levels and is estimated to share a common ancestor between 3,400- 1750 ybp. When the Iberian branch and the Sephardic branch arrived in Iberia is currently unknown. Unlike J-Z2272, which clearly shows a high likelihood of formation in the Iberian Peninsula, this likely represents a parallel migration from the Levant to the Iberian Peninsula. The Iberian branch has several samples belonging to families who trace genealogically to the region of Galicia in Spain as well as two more samples from the 1000 Genomes Project collected from Medellín, Colombia.

The Sephardic branch defined by SNP J-FGC30546, shares a common ancestor between 1150-300 ybp with a 95% probability.

The development of J-FGC5230 within the same period as J-Z2293 and J-BY74 thus provides another piece of evidence pointing to a population boom during the late Bronze Age in the Levant. Based on the population distribution, the age of the subclades, and the correlation also seen with the Sephardic-Iberian clusters in J-Z2293, it is very likely that J-FGC5206 originated in the Iberian Peninsula.

While it is impossible to ascertain when this lineage arrived in Iberia, the emergence of the three branches of J-FGC5206 occurs with the highest probability during a period in which the Jewish population on the Iberian peninsula underwent a population boom [40]. The Jewish population between 800-900 CE was estimated at 25,000 and by the 11th century, it had more than doubled. By the 12th century, the Jewish population of southern Spain surpassed that of the Jews of in all the other European countries combined. This period is regarded as

the Golden Age of al-Andalus. The genetic evidence we have both in J-FGC5206 and J-Z2285 also suggests a period of population expansion during this same period.

In this work we recreated in detail the phylogenetic tree for J-Z640 and a rigorous historical and anthropological analysis of the haplogroup was carried out. The results provided insights into the Bronze Age in the Levant, identified possible population expansions in the late Bronze Age and the Golden Age of al-Andalus, and shed light on the ethnogenesis of several Levantine populations. Further sample analysis as well as the availability of ancient J-Z640 DNA samples will surely refine the global interdisciplinary analysis we started here. Past interdisciplinary approaches [4,18,41] for genetic studies have provided successful models in undertaking the personal and fraught nature of working with peoples' own genetic footprints. By applying a critical, but inclusive approach, this study can provide a model for understanding population movements, ethnogenesis, and, ultimately, the mutability of identity both historically and today.

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Conflict of Interest

The analysis of the raw data in this study was conducted by Full Genomes Corp., in which Leon Kull is on the board of directors and Gregory Magoon consults for, and YFull in which Vadim Urasin is one of the founders of. The other authors claim no competing financial interests associated with this paper.

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