Ancient genetic landscape of archaeological human remains from Panama, South America and Oceania described through STR genotype frequencies and mitochondrial DNA sequences

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Abstract

The settlements of the Americas and Oceania are particularly fascinating topics. On the one side is the settlements of Australia and New Guinea (30,000 – 50,000 years ago) were the scenarios of one of the earliest migration events carried out by modern humans after left Africa, while Polynesia around 3,000 years ago was the stage of the last major colonization event. Regarding America, despite broad agreement that the Americas were initially populated via Bering, during the Upper Pleistocene 14,600 years ago, it is still a topic controversial, mysterious, shifting, and continuously conflictive as the Ice Age archaeology of the Americas, since, the dates and routes of the peopling of the Americas remain unresolved. Thus, ancient DNA studies on archaeological human remains from Oceania and America are useful to explore the genetic history of these human groups. Given that Near Oceania colonization was the endpoint of one of the earliest Out-of-Africa migrations about 50,000 years ago, and the islands of East Polynesia were the last region of the world to be colonized by humans approximately 1,000 years ago. Whilst, in America, one of the most contentious issues is whether the settlement occurred by means of a single migration or migration streams of migrations from Siberia. Because the gene flow is an important mechanism that contributes to genetic diversity among populations, the presence or absence of certain haplogroups changes the distribution of genetic diversity within populations. Thus, to understand the population dynamics of Oceanians and American peoples before European contact, it was necessary to describe the grade of nuclear and mitochondrial DNA genetic variation. One hundred twenty-five paleo-anthropological remains were analysed via genotyping of six short tandem repeats (STR) markers (nuclear DNA). Moreover, the genetic variation, inferences of demographic histories and clustering trends of these samples were evaluated through the hypervariable segment I (HVSI) of mitochondrial DNA (mtDNA). 35% of the archaeological remains analysed were genotyped successfully. Mitochondrial genetic diversity observed in Oceanian, South American and Panamanian samples reflected the genetic drift effects on these individuals through the founder effect, which happened during Upper Pleistocene when the modern humans reached these regions for the first time. The inferences of historical demographic patterns suggest that ancient individuals from Oceania went through population expansion about 37,972 years ago, which is consistent with the initial colonization of Melanesia. Whilst, ancient individuals from South America and Panama went through population expansions about 14,150 and 9,468 years ago, respectively, correspond to the initial settlement of America during the Upper Pleistocene.

The clustering patterns showed that ancient individuals from Bismark Archipelago and Papua New Guinea, and the ancient individuals from New Zealand and Samoa exhibited greater affinity with each other. The cluster branch of America exhibited genetic affinities between ancient Panamanian and South American samples, probably resulted from a migratory event, along the Pacific North Coast, from North America to South America that took place between the Middle and the Upper Holocene.

1 Introduction

The settlements of the Americas and Oceania are particularly fascinating topics. Despite broad agreement that the Americas were initially populated via Beringia, during the Upper Pleistocene 14,600 years ago; however, when and how the peopling of the Americas occurred remains unresolved (Reich et al., 2012; Moreno-Mayar et al., 2018). Whilst, the settlements of Australia and New Guinea (30,000 – 50,000 years ago) were the scenarios of one of the earliest migration events carried out by modern humans (Matisoo-Smith, 2015). Besides, Oceania was also the stage of the last major colonization event, the settlement of Polynesia around 3,000 years ago (Matisoo-Smith and Robins, 2004).

Nonetheless, it is important to considerate the migratory events that allowed anatomically modern humans (AMHs) to reach the regions of the Americas and Oceania during the Upper Pleistocene about 11,700– 125,000 years ago (Walker et al., 2009; Waters et al., 2015; Timmermann and Friedrich, 2016; Coccioni et al., 2018; Mutterlose et al., 2021), since this gives a better understanding of the evolutionary history and genetic structure of these populations. Moreover, other points to bear in mind are the environmental conditions and demographics pressures whose fluctuations have given rise the shaping of global population distributions (Boivin et al., 2013; Larrasoaña et al., 2013; Williams et al., 2015; Timmermann and Friedrich, 2016).

On the basis of geological, stratigraphic and paleoclimatic records, during the upper Pleistocene, the climate system of the Earth went through variations both at the gradual and abrupt level (Boivin et al., 2013; Timmermann and Friedrich, 2016). The causes of these weather fluctuations were various, such as changes in orbital parameters, variations in solar radiation, continental drift or periods of intense volcanism (Petit et al., 1999). Undoubtedly, these changes in the climate system of the Earth became the drivers of early human migrations (Timmermann and Friedrich, 2016).

1.1 Brief overview of early human migrations out of Africa

Before addressing the arrival of the first anatomically modern humans (*Homo sapiens*) to Oceania and America, it is necessary to mention the main migratory routes that these human groups followed to leave Africa and reach the Middle East, Oceania and finally America, besides to know the main causes that drove them to leave Africa during Chibanian stage (Middle Pleistocene), about 129,000 – 774,000 years ago, it includes the transition in palaeoanthropology from the Lower to the Middle Palaeolithic over 300,000 year ago (López et al., 2015; Posth et al., 2016; Clarkson et al., 2017; Coccioni et al., 2018; Mutterlose et al., 2021).

At the end of the Chibanian stage, approximately 129,000 years ago, Africa was a savannah with wetlands, gallery forest and permanent freshwater sources (Larrasoaña et al., 2013; Tierney et al., 2017). These environmental conditions were known as "Green Sahara" (GS) enabled human dispersion to continue through the continent (D'Atanasio et al., 2018). Nevertheless, around 70,000 years ago, the climate in the horn of Africa changed from a wet phase to drier conditions than the current ones (Tierney et al., 2017). Probably, this sharp change in the weather caused the migration of the first AMH out of the continent during Tartarian age (Timmermann and Friedrich, 2016; Tierney et al., 2017; Mutterlose et al., 2021).

Although, it is widely accepted by consensus that Africa is the birthplace of the anatomically modern humans, also there is a strong debate on the dispersal patterns and the main routes followed by AMHs to leave Africa (Tierney et al., 2017; Vizzari et al., 2020). This heated debate is focused on two dispersion models, one of them is a single dispersal almost simultaneously over Asia and Europe, and the other one is the AMHs dispersion by two main waves, first through the Arab Peninsula into southern Asia and Australo-Melanesia, and later through a northern route crossing the Levant (Eastern Mediterranean region of Western Asia) (López et al., 2015; Posth et al., 2016; Bergström et al., 2021).

According to the palaeoanthropological records of most out of Africa fossils, and the dating of the divergence between Eurasians and African populations based on mitochondrial DNA and whole genome data point to a major dispersal event around 65,000 years ago (Posth et al., 2016; Chen et al., 2019; Beyer et al., 2020; Bergström et al., 2021). However, archaeological findings in Saudi Arabia dated at least 85,000 years ago (Groucutt et al., 2018; Vizzari et al., 2020; Beyer et al., 2020), in Levant (present day Israel) at least about 90,000 – 194,000 years ago (Hershkovitz et al., 2018; Callaway, 2018; Beyer et al., 2020; Vizzari et al., 2020; Currat et al., 2021), and in Greece dated from around 210,000 years ago (Harvati et al., 2019; Beyer et al., 2020), which point to previous migrations out of Africa, which might have reached as far as China (Liu et al., 2006; Liu et al., 2015; Beyer et al., 2020).

Notwithstanding, it is important to bear in mind that the first migrations and expansions out of Africa were carried out by archaic humans about 2,000,000 years ago (López et al., 2015; Tassi et al., 2015; Harvati et al., 2019; Bons et al., 2019; Vizzari et al., 2020; Bergström et al., 2021; Hublin, 2021). On the island of Java, Indonesia, there are fossil records of *Homo erectus* dating back 1,800,000 years ago (Malaspinas et al., 2016; Wolf and Akey, 2018; Harvati et al., 2019; Vizzari et al., 2020; Bergström et al., 2021). In Europe, archaic human remains such as the *Homo antecessor* with an age of 900,000 years ago were found in the Iberian Peninsula (Spain) (Hopkin, 2008; López et al., 2015; Bermúdez-de-Castro et al., 2017; Duval et al., 2018; Vizzari et al., 2020; Garnier and Lafontaine, 2021). Whilst, Germany has fossil records of ancient humans such as *Homo heidelbergensis* (presumable ancestor of *Homo neandethalensis*, *Homo denisova*, and *Homo sapiens*) with an approximate age of 500,000 years ago (Wayman, 2012; Posth et al., 2016; Bermúdez-de-Castro et al., 2017; Akkuratov et al., 2018; Walker et al., 2018; Duval et al., 2018; Castro et al., 2021; García-Martínez et al., 2021; Callaway, 2021; Bergström et al., 2021).

Genomic evidence has suggested probably previous migration waves, might have left a small genetic contribution around 1% in modern inhabitants of Papua New Guinea (Akkuratov et al., 2018; Beyer et al., 2020; Bergström et al., 2021; Callaway, 2021; Choin et al., 2021). Whilst the genomes of modern non-Africans usually harbour about 2% Neanderthal ancestry (Tassi et al., 2015; Akkuratov et al., 2018; Chen et al., 2019; Beyer et al., 2020). Although, early migratory events of populations of archaic humans (genus Homo) out of Africa and throughout Eurasia, also collectively known as Out of Africa I, took place about 2,100,000 – 200,000 years ago (Hershkovitz et al., 2018; Herries et al., 2020; Baab, 2021; Scardia et al., 2021).

However, these archaic human populations were replaced by populations of AMHs (Homo sapiens) through events of effective global expansion from Africa to Eurasia (out of Africa II) about 65,000 years ago (Tassi et al., 2015; Clarkson et al., 2017; Hershkovitz et al., 2018; Bons et al., 2019; Harvati et al., 2019; Vizzari et al., 2020; Bergström et al., 2021). Nonetheless, some modern populations of Homo sapiens keep genetic traces of archaic humans embedded in their genome (Pääbo, 2015; Reich, 2018; Hashemi, 2020; Keyser et al., 2021). Genomic evidence suggests that through interbreeding with AMHs, both Neanderthal and Denisova contributed to the modern human genetic pool (Qin and Stoneking, 2015; Vernot et al., 2016; Reich, 2018; Bergström et al., 2021).

The amount of Neanderthal DNA in Europeans is about 1.7%, in Asian 1.8% and in Africans about 0.3% (Vernot et al., 2016; Price, 2020; Wu, 2020; Callaway, 2021). Otherwise, the Denisovan introgression occurred within the Pacific region instead of on the Asian mainland (Qin and Stoneking, 2015; Vernot et al., 2016; Reich, 2018; Choin et al., 2021). The Melanesian genome about 1.9 – 3.4% derives from Denisova genome (Teixeira et al., 2021). Papuans have less Denisovan ancestry about 1%, while, Asians and Native Americans have 0.2% of Denisovan ancestry (Vernot et al., 2016; Zubova et al., 2017; Reich,

2018; Teixeira et al., 2021). However, such low percentages could indicate infrequent interbreeding between modern and archaic humans, or else it is also possible that interbreeding was more common with a different population of modern humans that did not contribute to the current genetic pool (Browning et al., 2018; Reich, 2018; Wolf and Akey, 2018; Callaway, 2021).

Han Chinese, Japanese, and Dai genomes showed that modern East Asians have Denisovan DNA similar to that found in Papuan genome and Denisovan DNA closer to Denisovan genome from Denisova Cave (Browning et al., 2018; Chen et al., 2019; Choin et al., 2021). This could indicate two separate introgression events involving two different Denisova populations (Chen et al., 2019; Hashemi, 2020; Choin et al., 2021). This succession of migratory, expansion and introgressions events between archaic humans and anatomically modern humans show that both the genetic, evolutive and demographic history of the Homo sapiens are more complex and fascinating it than it seems (Currat et al., 2021; Scardia et al., 2021; Teixeira et al., 2021).

1.2 Peopling of Oceania by Anatomically Modern Humans

About 100,000 years ago, during the Upper Pleistocene (Tarantian age), Australia, Tasmania and New Guinea formed a single continent, called Sahul. At the time, the sea level was as much as 120 meters lower than is today (Bergström et al., 2009; Timmermann and Friedrich, 2016; Bergström, 2017; Beyer et al., 2020; Bradshaw et al., 2021; Purnomo et al., 2021). On the other hand, many of the islands of Indonesia were joined to the South East Asian mainland in another ancient continent, called Sunda (Malaspinas et al., 2016; Bradshaw et al., 2021). Likely, this continental configuration enabled the settlement and dispersion of the anatomically modern *Homo sapiens* through and within the Oceania continent.

By around 65,000 years ago, a group of anatomically modern humans (150 – 1,000 individuals) (Zhivotovsky et al., 2003; Haber et al., 2019) came out of Africa through the Arabian Peninsula at Bab-el Mandeb (the Gate of Tears), reached the Middle East, Southeast Asia (Sundaland) and Oceania (Sahul) (Fig. 1) (Kivisild et al., 2004; Henn et al., 2012; Clarkson et al., 2017; Haber et al., 2019; Bradshaw et al., 2021). This dispersal stage of anatomically modern humans is often known as the Southern Dispersal scenario or coastal migration hypothesis (Posth et al., 2016; Lipson et al., 2018; Haber et al., 2019), since this route describes the initial peopling of West Asia, India, Southeast Asia, New Guinea, Australia, Near Oceania, and coastal East Asia (Posth et al., 2016; Lipson et al., 2018; Haber et al., 2019; Bradshaw et al., 2021).

The initial colonisation of Oceania by humans happened around 55,000 – 65,000 years ago (Clarkson et al., 2017; Bedford et al., 2018; Lipson et al., 2018; Matsumura et al., 2018; Posth et al., 2018; Llamas et al., 2020; Prasetyo et al., 2021) when a group of people (1,300 – 1,550 individuals) crossed the boundary from Sunda into Sahul and reached New Guinea (Fig. 1) (Bradshaw et al., 2019; Llamas et al., 2020; Bradshaw et al., 2021), followed by colonization of the Bismark Archipelago by 33,000 years ago and the Solomon Islands

about 29,000 years ago (Fig. 1) (Matisoo-Smith, 2015; Veth et al., 2017; Bird et al., 2019; Bradshaw et al., 2021; Pugach et al., 2021). Whilst, the final peopling of the Pacific regions, which included the Southeast of Melanesia, Solomon Islands archipelago, the extremes of the Polynesian triangle and Micronesia, begun around 3,000 – 3,500 years ago and finished by 800 – 1,000 years ago (Fig. 2) (Petchey et al., 2014; Crabtree et al., 2021; Duggan and Stoneking, 2021; Pugach et al., 2021).

Peoples from Island Southeast Asians west of the Wallace line admixed with the ancestors of the Austro-Asiatic speaker, which came from a previous expansion that took place about 10,000 years ago to eastern mainland Asia (Llamas et al., 2020; Prasetyo et al., 2021; Sun et al., 2021). Later, a large-scale dispersal (Austronesian expansion or also called the Out of Taiwan model) associated with the Lapita culture spread the Austronesian languages and agriculture into Island Southeast Asia and Polynesian islands about 3,000 – 5,000 years ago, further expanding as far as Hawaii and Easter Island (Llamas et al., 2020; Prasetyo et al., 2021).

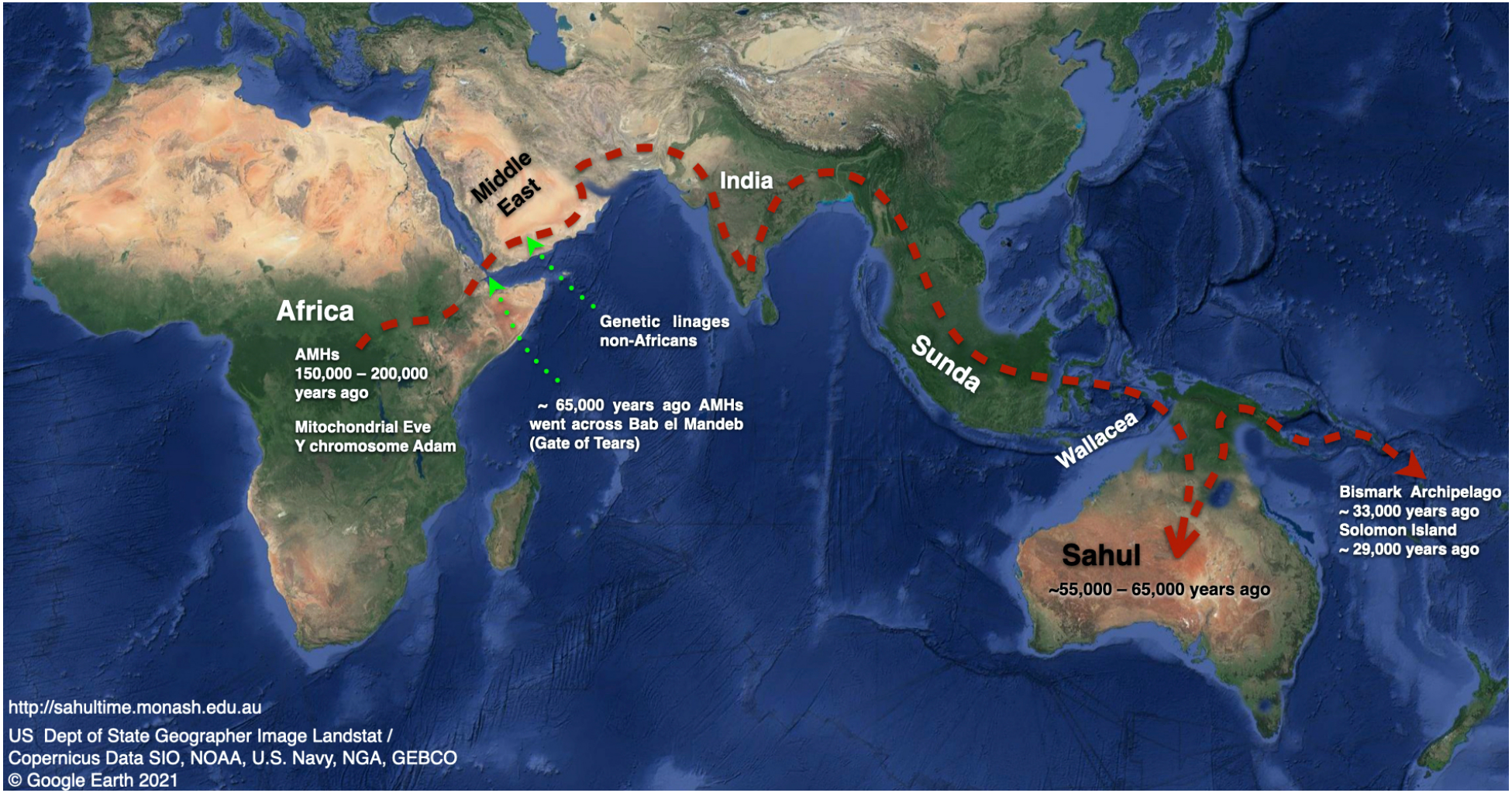

Figure 1. Southern Dispersal. The most recent anatomically modern humans migration wave out of Africa. The AMHs crossed the Red Sea strait at Bab el Mandeb until reaching Near East, Sunda and Sahul. (Matisoo-Smith, 2015; Posth et al., 2016; Veth et al., 2017; Lipson et al., 2018; Bradshaw et al., 2019; Llamas et al., 2020; Bradshaw et al., 2021; Purnomo et al., 2021).

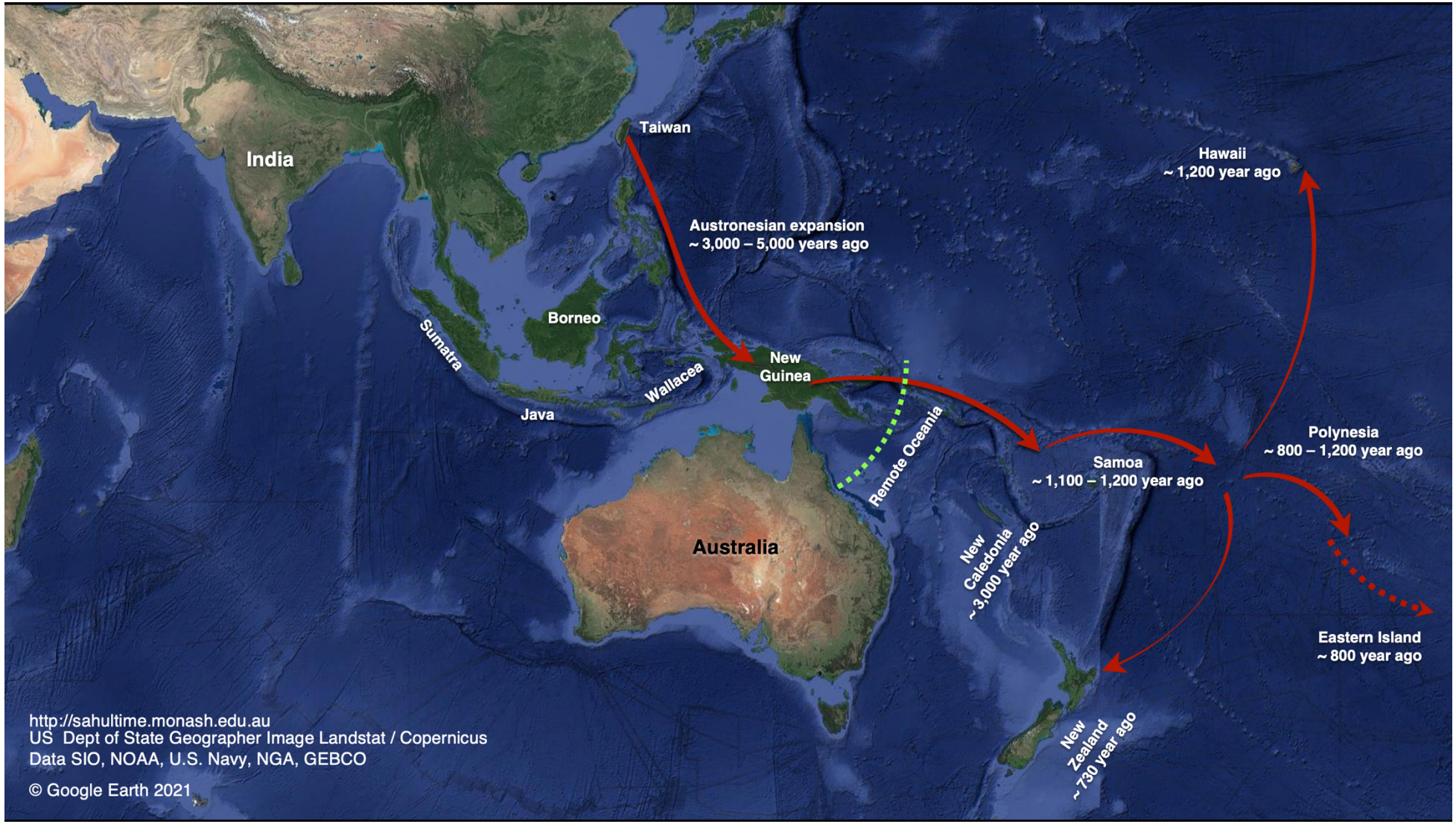

Figure 2. Peopling of Remote Oceania. Final colonisation of the greater Pacific region by anatomically modern humans and Austronesian expansion (Matisoo-Smith, 2015; Posth et al., 2016; Veth et al., 2017; Lipson et al., 2018; Bradshaw et al., 2019; Llamas et al., 2020; Bradshaw et al., 2021; Purnomo et al., 2021).

Colonization of Oceania from the linguistic point of view

Besides archaeological, anthropological and genetic evidence about peopling of Oceania introduced earlier the linguistic information is also used to understand the dispersion and colonization patterns of the humans through greater Pacific region (Kennedy, 2006; Bedford et al., 2018; Prasetyo et al., 2021). Proto-Oceanic is the probable common ancestor of all languages spoken in the Bismarck Archipelago, east of Papua New Guinea about 4,200 years ago (Pawley and Green, 1984; Ross, 1988; Duhamel, 2018; Janda et al., 2020; Janic and Witzlack-Makarevich, 2021). This language is derived from the Austronesian linguistic family, and by default, it is related to Proto-Austronesian language (Pawley and Green, 1984; Ross, 1988; Janda et al., 2020; Prasetyo et al., 2021). Austronesian languages family has around 1,200 languages spread from Taiwan to New Zealand and Madagascar to Easter Island (Gray et al., 2009; Bedford et al., 2018; Lipson et al., 2018; Posth et al., 2018; Prasetyo et al., 2021).

According to linguistic studies, the Austronesian languages evolved in Taiwan around 5,000 – 4,000 years ago from a proto-language introduced from the south Chinese mainland by dispersing rice farmers about 6,000 – 5,000 years ago (Oppenheimer and Richards, 2001; Klamer, 2019; Cho, 2020; Crevels and Muysken, 2020). The Austronesian-speaking agriculturalists subsequently spread throughout the Philippines and into Indonesia (Oppenheimer and Richards, 2001; Kennedy, 2006; Bedford et al., 2018; Lipson et al., 2018; Posth et al., 2018; Padilla-Iglesias et al., 2020; Prasetyo et al., 2021). Later, they moved on through the coastal parts of Melanesia, leaving intact the horticulturist populations of New Guinea, and finally spread out into the Polynesian islands (Oppenheimer and Richards, 2001; Duhamel, 2018; Matsumura et al., 2018; Klamer, 2019; Samper Carro et al., 2019; Fuentes et al., 2021). As the Austronesians spread along New Guinea and into the Solomons, they developed the Lapita cultural complex which extended through the whole Pacific region (Gray et al., 2009; Llamas et al., 2020; Prasetyo et al., 2021; Sun et al., 2021).

Proto-Polynesian is a daughter language of the Proto-Austronesian, and it is the ancestor of all modern Polynesian languages (Pawley and Green, 1984; Crevels and Muysken, 2020; Blench, 2021). The linguistic evidence suggests that the origins of the peoples who spoke Proto-Polynesian were near Tonga, Samoa, and nearby islands (Gray et al., 2009; Crevels and Muysken, 2020; Blench, 2021 Moyse-Faurie, 2021; Middleton, 2021). Lexicostatistical tests have allowed establishing the interrelationships of Fijian and Polynesian languages from three reconstructed stages of Proto-Polynesian languages (Proto-Central Pacific (PCP), Proto-Nuclear Polynesian (PPN) and Proto-Eastern Polynesian (PEP) (Hockett, 1976; Crevels and Muysken, 2020; Grice and Kügler, 2021).

Glottochronological data report that around 1,200 – 1,000 years ago the Proto-Central Pacific language split into two branches, one of them gave the origin of modern Fijian and Bauan languages, and the other one gave the origin of the Proto-Polynesian language (Hockett, 1976; Janda et al., 2020; Schütz, 2020; Davis, 2021; Moyse-Faurie, 2021; Pukui et al., 2021). The modern languages of Tonga, Niue, Samoa and eastern islands of Pacific, and the Proto-Eastern Polynesian language diverged from the Proto-Polynesian language around ~500 years ago (Hockett, 1976; Crevels and Muysken, 2020; Schütz, 2020; Pukui et al., 2021). The most recent modern languages of the Polynesia eastern region (Rarotongan, Tuamotuan, Maori, Thaitian, Marquesan and Hawaiian) diverged from Proto-Eastern Polynesian language about ~300 years ago (Hockett, 1976; Crevels and Muysken, 2020; Schütz, 2020; Pukui et al., 2021).

Consequently, most the today peoples from Near Oceania speak a Papuan (Bedford et al., 2018; Posth et al., 2018) (geographical grouping of western Pacific languages, without proven linguistic family so far) (Ross, 2005; Duhamel, 2018; Benjamin, 2021), while Remote Oceania peoples almost exclusively speak Oceanic languages of the Austronesian family (Bedford et al., 2018; Posth et al., 2018). Finally, the most of the data provided by the archaeology, linguistics, anthropology, and genetic fields about the arrival of the first

anatomically modern humans to Oceania and their expansion through Pacific region are congruent between them allowing to a better understanding about the cultural and biological patterns followed by these ancient peoples, since encompass the topic of the colonization of Oceania from different but complementary point of views (Oppenheimer and Richards, 2001; Bedford et al., 2018; Lipson et al., 2018; Posth et al., 2018; Llamas et al., 2020; Crevels and Muysken, 2020; Basu and Majumder, 2021; Prasetyo et al., 2021).

Genetic history of Oceanian peoples from uniparental Markers

Over decades, the population geneticists have shown a remarkable interest in describing the genetic history of Oceanian peoples. The early studies on this field encompassed the analysis of globin gene variants, then the researches were focused on the analysis of mitochondrial DNA hypervariable region (HVS I, II, and III), Y chromosome markers, Single Nucleotide Polymorphisms (SNPs), and currently, the genomic information obtained via Next Generation Sequencing (NGS) deepen on genetic origins of these human groups (Matisoo-Smith, 2015; Duggan and Stoneking, 2021; Purnomo et al., 2021). Below are some of the most relevant researches that have marked evident progress on this issue.

Hill et al. (1987), provided the first conclusive biological evidence of Oceanic origins for Polynesians by discovering high rates of globin gene mutations in Polynesians, which could only have been inherited from populations in Near Oceania (Matisoo-Smith, 2015). Subsequently, Melton et al. (1995), presented evidence that linked the Polynesian origins with Islands Southeast Asia, through a nine base pairs deletion (Polynesian motif) in the intergenic region of mitochondrial DNA between the COIl and $tRNA^{Lys}$ (Melton et al., 1995; Redd et al., 1995; Matisoo-Smith, 2015). These results were consistent with linguistic evidence of Taiwanese origin for the proto-Polynesian expansion, which spread throughout Oceania by way of Indonesia (Melton et al., 1995; Matisoo-Smith, 2015; Blench, 2021; Duggan and Stoneking, 2021).

Inasmuch as, the entry of the first anatomically modern humans into Oceania has stayed registered in the mitochondrial DNA and Y chromosome haplotypes of the Aboriginal Australian and Papuan populations as a recognizable genetic signature (Matisoo-Smith, 2015; Crabtree et al., 2021). When analysing the mitochondrial DNA (mtDNA) control region, were observed the genetic lineages M, O, P, and S found mostly in Australia (Redd and Stoneking, 1999; van Holst Pellekaan, 2013; Matisoo-Smith, 2015; Pedro et al., 2020; Purnomo et al., 2021), while mtDNA lineages P, Q, M27, M28 and M29 found mostly in New Guinea and Near Oceania (Merriwether et al., 2005; Matisoo-Smith, 2015; Pedro et al., 2020; Purnomo et al., 2021), this proves that modern humans crossed the Wallace line to colonize Southeast Asia and Sahul, and later New Guinea (Llamas et al., 2020); which in turn suggests that Aboriginal Australians have more genetic affinities with peoples from Southern India than with Papua New Guinean populations (Redd and Stoneking, 1999; van Holst Pellekaan, 2013; Matisoo-Smith, 2015; Pedro et al., 2020).

However, the Y-chromosome lineages K, M, S, and C are generally restricted to Oceanic populations and are generally believed to have originated in Near Oceania during the Pleistocene period of human occupation (Scheinfeldt et al., 2006; Matisoo-Smith, 2015; Duggan and Stoneking, 2021). Nevertheless, Pacific populations also carry Y chromosomes belonging to the O branch, which is widespread in Asia and likely these were brought into the Pacific during the Holocene, presumably as part of the Austronesian expansion (Kayser, 2010; Matisoo-Smith, 2015; Bird et al., 2019; Duggan and Stoneking, 2021). Thus, both the mtDNA and Y-chromosome haplotypes, as well as archaeological and linguistic evidence, suggest more than one migratory event in the peopling of Oceania, which makes more complex the history of the modern human settlements in this region as well as its population interactions (Redd and Stoneking, 1999; Matisoo-Smith, 2015; Bedford et al., 2018; Lipson et al., 2018; Posth et al., 2018; Bird et al., 2019; Llamas et al., 2020; Bradshaw et al., 2021; Duggan and Stoneking, 2021).

Nagle et al. (2016), when typifying Single Nucleotide Polymorphisms (SNPs) on the Y-chromosome of a group of Aboriginal Australian males, revealed that 56% of their Y-chromosomes could have Eurasian origins (Nagle et al., 2016; Duggan and Stoneking, 2021). In Australia, the haplogroup C of Y chromosome is the most frequent, as this lineage represents 44.4% of indigenous male chromosomes in this region, the haplogroup C has a coalescence time of about 5,665 years ago with male chromosomes of southern India and Sri Lanka (Redd et al., 2002; Oven et al., 2014; Crevels and Muysken, 2020; Basu and Majumder, 2021). Jinam et al. (2017), reached similar results when analysing Aboriginal Australians, New Guineans, island Southeast Asians, and Indians via genome-wide (GWAS) genotyping, since this study revealed that 11% of Australian ancestry came from Southern India, with divergence times estimated about 36,000 years ago (Pugach et al., 2013; Jinam et al., 2017; Posth et al., 2018; Bird et al., 2019; Bradshaw et al., 2019; Bradshaw et al., 2021).

Pedro et al. (2020), analysed whole mitochondrial genomes of individuals from Island South East Asia, Oceania and Australia. The results revealed that 7.4% of samples were affiliated to non-indigenous Northern Sahul haplogroups (B4a1a1 and E1a). These haplogroups are only detected in the coastal region of New Guinea and the Bismarck Archipelago (Friedlaender et al., 2007; Duggan et al., 2014; Pedro et al., 2020). The vast majority of the mtDNA genomes, 92%, were affiliated with the main indigenous Northern Sahul haplogroups: M27 (1.3%), M28 (<1%), M29 (<1%), Q (47%), and P (43%) (Pedro et al., 2020). Haplogroups M27, M28, and M29 are almost exclusively found in Near Oceania and given that they are most diverse and frequent here could have originated in this region (Ricaut et al., 2010; Lipson et al., 2018; Pedro et al., 2020; Purnomo et al., 2021).

Archaeological and genetic data broadly converge regarding the dates of the first settlement of Sahul (50,000–55,000 years ago) (O'Connell et al., 2018; Pedro et al., 2020; Bradshaw et al., 2021). Coalescence ages estimated for mitochondrial haplogroups M29'Q is 55,000 years ago (95% CI 42,000 – 67,000 years ago), while for linage M27 is about 51,000

years ago (95% CI 40,000 – 62,000 years ago) (Pedro et al., 2020). The age estimated for M28 is 32,000 years ago (95% CI 22,000 – 42,000 years ago) (Pedro et al., 2020), this date is quite close to the beginning of the Last Glacial Maximum (LGM) (28,000 years ago) (O'Connell et al., 2018; Pedro et al., 2020; Cadd et al., 2021). The diversification of the main lineages took place around a transition period between LGM (18,000 – 28,000 years ago) and the postglacial warming period (10,000 – 18,000 years ago) (Hope, 2014; Golson et al., 2017; Pedro et al., 2020). All derived lineages (M27a, M27b, M28a, M28b, M29) and arising from the expansion periods are clustered geographically (Bedford et al., 2018; Pedro et al., 2020; Duggan and Stoneking, 2021).

Haplogroups P3a, P3b2, P4b, P5, P6, P7, P8, new P13a are distributed across Southern Sahul, while, the lineages P1, P2, P3b1, P4a, new P13b1 are found in Northern Sahul and haplogroups P9 and P10 are in the Aeta and Agta indigenous groups from the Philippines, suggesting that the P haplogroup may have evolved in Sunda or Wallacea (Gomes et al., 2015; Arenas et al., 2020; Pedro et al., 2020). Both Northern and Southern Sahul P haplogroups have coalescence ages close to the early settlement period around 45,000 – 50,000 years ago (95% CI 32,000 – 62,000 years ago) (Pedro et al., 2020). This lineage diversified earlier in Southern Sahul than in Northern Sahul, nonetheless, Northern Sahul hosts specifics haplogroups from lineage P, which are both more frequent and diverse in highland New Guinea, supporting their possible emergence/diversification in this region, suggesting that populations of Northern and Southern Sahul shared an ancestral population that harboured high P diversity (Gomes et al., 2015; Arenas et al., 2020; Ono et al., 2020; Pedro et al., 2020).

On the other hand, the Q mitochondrial lineage diverged from M29'Q around 55,000 years ago (95% CI 42,000 – 67,000 years ago) after an isolation period of almost 15,000 years (Pedro et al., 2020). During the initial settlement of Northern Sahul (high-land and coastal New Guinea and Near Oceania) and the LGM about 18,000 – 28,000 years ago, the Q

mitochondrial variant diversified into three Subhaplogroups (Q1, Q2, and Q3) around 38,000 years ago (95% CI 28,000 – 52,000 years ago) (Brandão et al., 2016; Duggan and Stoneking, 2021). Both haplogroup Q and its Subhaplogroups have their greatest frequency and diversity in high-land and coastal New Guinea and Near Oceania, suggesting probable origins within this region (Brandão et al., 2016; Pedro et al., 2020; Duggan and Stoneking, 2021).

Haplogroup Q1 is found most often in Near Oceania and Highland and coastal New Guinea, this mitochondrial lineage diversified at the end of Last Glacial Maximum around 19,000 years ago (95% CI 15,000 – 22,000 years ago) (Pedro et al., 2020). Whilst, haplogroup Q2 in Near Oceania, particularly the Bismarck Archipelago and Q3 in highland New Guinea diversified early in the Last Glacial Maximum period about 30,000 years ago (95% CI 20,000 – 40,000 years ago) and 28,000 years ago (95% CI 20,000 – 36,000 years ago) respectively (Pedro et al., 2020). Subhaplogroups Q1b, Q1c and Q1e are found in Near Oceania, Sunda and Wallacea islands (Taiwan, Philippines, and Madagascar) have the linage Q1d, while, mitochondrial variant Q1a is in northern Australia and subclades Q1b, Q1e, and Q1f are in Remote Oceania (Solomon Islands, Vanuatu, Fiji, Samoa, and the Cook Islands) (Pedro et al., 2020). The Q1 lineages present in Australia belonged to individuals with Torres Strait Islander ancestries, which are known for their close links with New Guinea (Nagle et al., 2017; Pedro et al., 2020; Choin et al., 2021).

However, the Q2b lineage (western Indigenous Australian) branches deeply within the Q clade and may reflect earlier connections between Northern and Southern Sahul populations (Hudjashov et al., 2007; Nagle et al., 2017; Pedro et al., 2020; Crabtree et al., 2021). Subclades Q3a, and Q3b are in coastal New Guinea, Near Oceania and Timor, all associated with coalescence ages around 18,000 – 28,000 years ago (Pedro et al., 2020). The Q3 subclades shared between Timor and coastal New Guinea could reflect a possible ancient connection between the island zone around Timor and continental Northern Sahul (Gomes et al., 2015; Clarkson et al., 2017; Pedro et al., 2020; Duggan and Stoneking, 2021).

Polynesia, one of the last regions of the world to be populated by Anatomically Modern Humans (Matisoo-Smith and Robins, 2004; Matisoo-Smith, 2015; Thompson, 2019; Thomas, 2021). Even though, the peoples of this Pacific Ocean region are considered by linguistic, archaeological and human genetic ancestry as a subset of Austronesian peoples who migrated by sea, the history, and origins of Polynesia inhabitants are still a topic of debate (Matisoo-Smith, 2015; Thompson, 2019; Thomas, 2021). The Polynesian peoples are associated with Lapita Cultural Complex (LCC) (Bedford et al., 2018; Posth et al., 2018; Lipson et al., 2018; Bedford and Spriggs, 2019; Thomas, 2021). Lapita pottery has been found in Near Oceania as well as Remote Oceania, as far west as the Bismarck Archipelago, as far east as Samoa, and as far south as New Caledonia (Bedford and Spriggs, 2019; Prasetyo et al., 2021). Circa 3,000 – 5,000 years ago, a human migratory movement associated with Lapita culture spread the Austronesian languages and agriculture into Island Southeast Asia and Polynesia, this culture spread to Hawaii and Easter Island (Thompson, 2019; Llamas et al., 2020; Matsuda, 2021).

Although, the appearance of people associated with the Lapita culture in the South Pacific 3,000 years ago marked the beginning of the last major human dispersal to unpopulated lands, the relationship of these pioneers to the long-established Papuans of the New Guinea region is unclear (Skoglund et al., 2016; Bedford and Spriggs, 2019). According to linguistic evidence, the Polynesian peoples originated in Asia, while, the archaeological evidence suggested that the Polynesian peoples originated in Melanesia (Kayser, 2010; Hudjashov et al., 2018; Thompson, 2019; Schütz, 2020; Pukui et al., 2021). Kayser et al. (2000), described the three models of the spread of modern humans across the Pacific to Polynesia. The first one of them, supported by most current human genetic data, linguistic data, and archaeological data, known as the “Express Train” model, proposes a recent expansion about 1,000 – 3,000 years ago out of Taiwan via the Philippines and eastern Indonesia and from the north-west of New Guinea on to Island Melanesia around 1,400 years

ago, reaching western Polynesian islands by roughly 900 years ago (Kayser et al., 2000; Lesniewski, 2009; Thompson, 2019; Duggan and Stoneking, 2021). The second, known as the "Entangled Bank" model emphasizes the long history of Austronesian speakers' cultural and genetic interactions with indigenous Island South-East Asians and Melanesians along the way to becoming the first Polynesians (Kayser et al., 2000; Thompson, 2019; Duggan and Stoneking, 2021). Finally, the third model, supported by the Y-chromosome data, which show that haplotypes of Polynesian Y chromosomes can be traced back to Melanesia, known as the “Slow Boat” model, similar to the Express Train model but with a long hiatus in Melanesia, this model assumes that the genetics of the modern-day Polynesian people are a direct reflection of the prehistoric migrants into Polynesia (Kayser et al., 2000; Lesniewski, 2009; Thompson, 2019; Duggan and Stoneking, 2021).

Kayser et al. (2006), when analysing the Non-recombining Region of the Y chromosome (NRY-DNA) and mitochondrial DNA markers from Polynesian, Melanesian, Southeast and East Asian, and Australian populations, identified a dual genetic heritage of Polynesians, which containing both Melanesian and Asian genetic components. Overall, in Polynesia, the proportion of Melanesian haplogroups was eleven-fold higher for Y chromosomes (65.8%) than for mtDNAs (6%), and of Asian haplogroups was more than threefold higher for mtDNAs (93.8%) than for Y chromosomes (28.3%), suggesting a dual genetic origin of Polynesians in agreement with the ‘‘Slow Boat’’ model (Kayser et al., 2000; Delfin et al., 2012; Thompson, 2019). These results suggest a pronounced admixture bias in Polynesians toward more Melanesian men than women, maybe because of matrilocal residence in the ancestral Polynesian society (Kayser et al., 2000; Delfin et al., 2012; Thompson, 2019).

The male haplogroups C, K and O are predominant Y-chromosome haplogroups present in indigenous populations in the Pacific (Gosling et al., 2021), while M353 and O-M122 lineages are restricted to Polynesia (Kayser et al., 2000). O-M122 lineage is associated

with a triplication event involving the DYS385 microsatellite (Kayser et al., 2006). The shortest allele of this triplication event involves the DYS385A copy with a length of twelve repeats, the DYS385B copy with thirteen repeats of length, and the DYS385C copy, generated from DYS385B allele, with sixteen repeats of length (Kayser et al., 2006). The association pattern O-M122/DYS385 suggests a simple origin of DYS385 triplication in Polynesia, although the Y-STR haplotype diversity associated with DYS385tri/O-M122 was highest in Tuvalu, around 76%, suggesting that Tuvalu is the likely place of origin (Kayser et al., 2006). The age of this lineage is estimated at 3,700 years ago, providing evidence for a Polynesian founder effect and for a recent from west-to- east expansion within Polynesia (Kayser et al., 2006).

Gosling et al. (2021), when analysing the Y-chromosome diversity in Tokelau archipelago, located approximately 500 km north of Samoa, detected six haplogroups among the Tokelauan men (C1b2a-M38 = 1.6%, C1b2a-M208 = 1.6%, K-M9 = 6.4%, K-P79 = 53.2%, O2-M122 = 27.4%, and R-M207 = 9.7%). The lineages C1b2a-M38/C1b2a-M208 and K-M9/K-P79 have genetic origins in Near Oceania, while the variant O2-M122 has its origins in East Asia, and R-M207 variant is an European derived (Kayser, 2010; Gosling et al., 2021). In Y-STR locus DYS390 is observed alleles of short fragment length (19–21 repeats) in Cook Islands, mainland and Papua New Guinea, eastern Indonesia and Australia, whereas other populations had exclusively alleles of 21–27 repeats in length (Kayser et al., 2000).

Nonetheless, all Cook Islanders with alleles 19–21 has a deletion of the 390.3 segment, and all the length variation is in the combined 390.2–390.4 segment, excepting Australians who instead had a deletion in 390.1 (Forster et al., 1998; Kayser et al., 2000). The DYS390.3 deletion is associated with a C→T (Y-SNP) mutation at position 711 of the RPS4Y gene (Bergen et al., 1999; Kayser et al., 2000). The DYS390.3del/ RPS4Y711T haplotype has a frequency of 82% in the Cook Islands, 26% in coastal Papua New Guinea,

10–15% in the Moluccas and Nusa Tenggara Islands of eastern Indonesia, 9–12% in island Papua New Guinea (New Britain, Trobriand Islands), however, this haplotype is not present in Southeast Asian, East Asian or Australian populations, suggesting a Melanesian origin for some Polynesian genes (Kayser et al., 2000; Kayser, 2010).

On the other hand, Polynesian mitochondrial lineages belong pre-dominantly to haplogroup B and in particular sub-haplogroup B4, which does not appear to have been introduced to the Pacific during this first phase of population migrations, but arrived in the region much later, sometime in the mid-Holocene (4,000 – 8,000 years ago) (Matisoo-Smith, 2017; Bedford et al., 2018; Gosling and Matisoo-Smith, 2018; Lipson et al., 2018; Posth et al., 2018; Gosling et al., 2021). Five Polynesian mtDNA haplogroups have an Asian origin: B4, B4a, B4b1, B4a1a1a1 (Polynesian motif), and M7c1c, which means that 93.8% of Polynesian mitochondria have Asian origin, of which 77.6% belong to a single haplogroup (B4a1a1a1) (Kayser et al., 2006; Razafindrazaka et al., 2010; Matisoo-Smith, 2017; Gosling et al., 2021). Besides, four Polynesian mtDNA lineages have a Melanesian origin: P1, Q1, Q2, and M28, which means that 6 % of Polynesian mitochondria have Melanesian origin (Kayser, 2010; Matisoo-Smith, 2017; Horsburgh and McCoy, 2017; Gosling and Matisoo-Smith, 2018; Thompson, 2019; Gosling et al., 2021).

Gosling et al. (2021), when analysing archaeological human remains from Atafu, the northernmost Tokelau atoll, and Korase island in Micronesia, found that the ancient inhabitants of Atafu possessed relatively little mitochondrial diversity, since the individuals analysed belonged to either haplogroup B4a1a1, B4a1a1a, or B4b1a2i. The B4b1a2i haplotypes were not found among the modern Inhabitants of Tokelau, although this haplogroup is shared with ancient individuals from Kosrae (Gosling et al., 2021). B4b1a2i haplogroup is relatively rare in the Pacific; however, it appears to be relatively common in Micronesia; hence, this could be an important lineage for understanding Micronesian settlement (Gosling et al., 2021).

Haplogroup B4a1a1ab occurs at a frequency among modern inhabitants from of Atafu = 14.2%, Fakaofo = 7.5%, and Nukunonu = 8.7%, but is not common in the wider Pacific region, and it was also not detected among any of the ancient Atafu individuals (Gosling et al., 2021). This haplogroup occurs at a frequency among Samoans = 1.7%, Tongans = 1.0%, and Ontong Java in the Solomon Islands = 12.5% (Gosling et al., 2021). B4a1a1x is another rare lineage in the Pacific that is shared by some inhabitants of Atafu and Nukunonu, this lineage has thus far only been reported in Tuvalu with a frequency of 3.8%, and on the Micronesian atolls of Majuro and Kapingamarangi (Pierson et al., 2006; Gosling et al., 2021). Haplogroup Q1f1 was detected in a single individual among the modern inhabitants of Nukunonu, this lineage is derived from haplogroup Q, which has its origins in New Guinea (Friedlaender et al., 2005; Gosling et al., 2021). This particular haplogroup has been detected among Cook Island Māori, Society Islanders, Samoans, and the inhabitants of Tikopia, again, a Polynesian Outlier, Q1f1 lineage is observed among modern individuals from Kiribati, suggesting connections with other Pacific populations (Duggan et al., 2014; Hudjashov et al., 2018; Gosling et al., 2021).

Ancient DNA from Vanuatu and Tonga dating to about 2,600 – 2,900 years ago, has revealed that the ‘‘First Remote Oceanians’’ associated with the Lapita archaeological culture were directly descended from the population that spread Austronesian languages from Taiwan to the Philippines, western Melanesia, and eventually Remote Oceania right about 5,000 years ago (Lipson et al., 2018). Thus, ancestors of the First Remote Oceanians must have passed by the Papuan-ancestry populations they encountered in New Guinea, the Bismarck Archipelago, and the Solomon Islands with a minimal admixture (Skoglund et al., 2016; Lipson et al., 2018; Posth et al., 2018; Lipson et al., 2020). However, present-day populations in Near and Remote Oceania harbor >25% Papuan ancestry, implying that additional eastward migration must have occurred (Lipson et al., 2018; Posth et al., 2018; Lipson et al., 2020). People with almost entirely Papuan ancestry arrived in Vanuatu by roughly 2,300 years ago, People of

almost entirely by around 2300 BP, most likely reflecting migrations a few hundred years earlier at the end of the Lapita period (Lipson et al., 2018). The Papuan ancestry in Vanuatu derives from the Bismarck Archipelago, however, the Papuan ancestry in Polynesia and the most remote Pacific islands derives from different sources, suggesting a third stream of migration from Near to Remote Oceania (Lipson et al., 2018; Posth et al., 2018; Lipson et al., 2020).

1.3 Peopling of the Americas

The last colonisation and expansion event of anatomically modern *Homo sapiens* took place during the Upper Pleistocene around 20,000 – 23,000 years ago, when the humans (~250 individuals) (Fagundes et al., 2018) crossed Bering and entered by first time to American continent (Skoglund et al., 2015; Moreno-Mayar et al., 2018; Suarez and Ardelean, 2019; Gruhn, 2020; Hoffecker et al., 2021). Nonetheless, despite of this consensus, the peopling of the Americas has been the subject of extensive genetic, archaeological, anthropological, and linguistic research and controversy, since some details about the colonisation, history and population dynamics of this event remain unresolved (Moreno-Mayar et al., 2018; Gruhn, 2020; Hoffecker et al., 2021). One of the most contentious issue is whether the settlement occurred by means of a single migration or migration streams of migrations from Siberia (Perego et al., 2009; Reich et al., 2012; Reich, 2018; Suarez and Ardelean, 2019; Gruhn, 2020; Hoffecker et al., 2021).

According to archaeological evidence, groups of hunters that lived in northeast Siberia around 28,000 years ago could have entered to Beringia, because of they were adapted to cross the landmass, that is now submerged, between Eurasia and Alaska (Pitulko et al., 2004; Goebel et al., 2008; Meltzer, 2009; Skoglund and Reich, 2016; Gruhn, 2020; Hoffecker et al., 2021). Nonetheless, about 26,000 – 33,000 years ago during the Last Glacial Maximum (LGM), this region was marked by harsh Climates and glacial barriers, since at its eastern end the Cordilleran and Laurentide ice sheets merged with at the continental divide, forming an area of ice that contained one and a half times as much water as the Antarctic ice sheet does today (Evans et al., 2014; Heintzman et al., 2016; Hoffecker et al., 2016; Moreno-Mayar et al., 2018; Gruhn, 2020).

Likely, the extreme weather conditions led to the isolation of populations for extended periods and sometimes complicated the dispersal across the region (Moreno-Mayar et al.,

2018; Becerra-Valdivia and Higham, 2020). However, when deglaciation commenced in the Northern Hemisphere around ~20,000 years ago, caused an abrupt rise in sea level (Evans et al., 2014). The retreated of ice from Pacific coast ~16,000 years ago could have given the possibilities of a coastal migrations (Evans et al., 2014; Timmermann and Friedrich, 2016; Puzachenko et al., 2021). Decline of the West Antarctica ice sheet occurred about 14,000 – 15,000 years ago, what provoked another abrupt rise in the sea level ~ 14,500 years ago, also a habitable corridor opened through the centre of the continent between the two ice sheets (Petit et al., 1999; Evans et al., 2014; Colella et al., 2021; Puzachenko et al., 2021).

Migration routes of expansion

Historically, according to archaeological, paleontological, anthropological, and geological records, there are two main possible routes that humans could have used to expand inside the American continent. One of them is the interior route or Ice-Free Corridor (IFC) and the other one is North Pacific Coast (NPC) (Evans et al., 2014; Braje et al., 2020; Colella et al., 2021). Nonetheless, before addressing this topic, it is important to considerate three main criteria to establish a route as viable: 1. Presence of substantial barriers (massive glaciers or proglacial lakes blocking mountain valley passes or coastal margins) that would have impeded human migration (Pedersen et al., 2016; Potter et al., 2016; McLaren et al., 2020); 2. Biological productivity to support human populations (Erlandson et al., 2015; Potter et al., 2016; Dobson et al., 2021); and 3. Availability of knowledge and technology to either extract resources from surrounding environment and moving freely without substantial risk inside high-latitude marginal environments, open water boating, and sea mammal hunting (Erlandson et al., 2015; Potter et al., 2016; Hoffecker et al., 2021).

Interior route or Ice-Free Corridor

Geomorphological data indicate that when the Laurentide Ice Sheet (LIS) and Cordilleran Ice Sheet (CIS) retreated, the corridor opened zipper- like from north to south, and the lakes in the northern dammed by LIS were draining (Dyke, 2004; Kennedy et al., 2010; Potter et al., 2016; Dobson et al., 2021). Radiocarbon dating establishes the date of this event about 14,800 – 16,545 years ago (Dyke, 2004; Kenady et al., 2011; da Silva Coelho et al., 2021). On the other hands, Stroeven et al. (2014), suggested that the retreated of the ice happened by 18,500 – 19,300 years ago. Whilst, a reconstruction of IFC landscape revealed that approximately 15,000 years ago the corridor had between 150 – 300 km wide from north to south, while the breadth for this route about 14,000 years ago was 300 – 600 km (Munyikwa et al., 2017; Colella et al., 2021).

Considering the radiocarbon dating, the northern IFC was viable with plant and animal resources supported the human migration by ~13,650 – 15,000 years ago (Pedersen et al., 2016). Therefore, the first humans reached Bering 18,000 – 20,000 years ago (Moreno-Mayar et al., 2018; Suarez and Ardelean, 2019; Hoffecker et al., 2021) and expanded through America about 15,000 years ago could have been adapted to deal with rigours the IFC offered (Potter et al., 2018; Suarez and Ardelean, 2019; Marshall et al., 2021; Puzachenko et al., 2021).

North Pacific Coast Route

The viability of the coastal route is partially dependent on the state of deglaciation and minimization of ice barriers. According to radiocarbon dating, the glacial recession of southwestern and south-central Alaskan coastlines occurred during upper Pleistocene, at the end of Tarantian age approximately 17,000 – 19,000 years ago (Goebel and Potter, 2016; Potter et al., 2018; Braje et al., 2020; da Silva Coelho et al., 2021; McLaren et al., 2020; O'Shea, 2021). Nonetheless, the presence of ice sea and recurrent volcanism are important

factors to consider the viability of coastal habitat (Potter et al., 2018; Suarez and Ardelean, 2019; Braje et al., 2020;).

In addition, utilizing the NPC as an option to expand inside America, the people should have had the necessary technology and knowledge to hunt specifics types of sea mammals and face the hazards of navigating in that type of extreme marine environment (Tamm et al., 2007; Kitchen et al., 2008; Potter et al., 2016; Suarez and Ardelean, 2019; Dobson et al., 2021). Archaeological data about upper Pleistocene human occupation, marine mammal hunting and watercraft technology along the coastal route is scarce, since there no known sites with human settlements along the southern coastal or near coastal stretches of Eastern Beringia before 9,000 years (Davis et al., 2016; Suarez and Ardelean, 2019; Braje et al., 2020; Dobson et al., 2021).

The direct archaeological evidence relating to America human expansion through NPC is affected by sea-level rise owing to deglaciation (Davis et al., 2016; McLaren et al., 2020; O'Shea, 2021). As the ice receded, the glacial refuge located in the uplifted parts along the coast flooded rapidly, the large mountains of ice collapsed owing of action of snowbreak and the volcanic eruptions that occurred 13,100 – 14,600 years ago (Kennedy et al., 2010; Goebel and Potter, 2016; Pedersen et al., 2016; Potter et al., 2018; Dobson et al., 2021).

Therefore, although the marine ecosystem along the North Pacific Coastal Route was likely productive at the end of the Pleistocene, to utilize this road to carry out the expansion inside the continent supposed dealing many of obstacles own ice age. During the coastal deglaciation period about 14,700 – 17,000 years ago, hunter-gatherers moving along the coast would have encountered marine mammals but would have been contending with sea ice and broken glaciers, which surely hindered the migration of humans towards inside and through America by those times (Stroeven et al., 2014; Davis et al., 2016; Potter et al., 2016; Suarez and Ardelean, 2019; Braje et al., 2020)

In summary, the issue about what's migration routes the humans used to reach the inner of the continent continue being a controversial topic (Shugar et al., 2014; Potter et al., 2018; McLaren et al., 2020; O'Shea, 2021). In concordance with, available archaeological and geomorphological evidence, a Pacific coast migration from the Bering Strait to South America could have been possible thousands of years before Clovis culture, but also the expansion of Native Americans populations might have occurred through Ice-Free Corridor to inner continent around 15,000 years ago, according to paleoecological and genetics studies (Potter et al., 2018; Suarez and Ardelean, 2019; da Silva Coelho et al., 2021). Given that above, likely both routes may have been used at different times by one or more populations that moved from north to south (Goebel et al., 2008; Potter et al., 2016; Suarez and Ardelean, 2019; Braje et al., 2020; McLaren et al., 2020; Dobson et al., 2021; O'Shea, 2021).

Notwithstanding, parallel to the mainstream about peopling America through Bering, there is an alternative hypothesis concerning the origins of first Native Americans, whose approach is the possible incursions of persons with Australo-Melanesian and Polynesian origins in South America (Clarke et al., 2011; Reich, 2018; Ioannidis et al., 2020; Silva et al., 2021). This proposal is based on archaeological, cultural, linguistic and anthropological evidence, which is complemented, at present, with DNA work, so that the combined information of aforementioned fields suggests connections between Oceania and Americas before pre-Columbian contact (Storey et al., 2007; Tyler-Smith, 2014; Raghavan et al., 2015; Skoglund et al., 2015; Nielsen et al., 2017; Reich, 2018; Wallin, 2020; Silva et al., 2021).

Different models have been proposed to elucidate the origins of the founding populations of America, along with the number of migratory waves and routes used by these first settlers (Ioannidis et al., 2020; Silva et al., 2021). Notwithstanding, despite those settlements along the Pacific coast and on land have been evidenced in genetic and archaeological studies, the number of migratory waves and the origin of immigrants are still

controversial topics (Silva et al., 2021). A signal of genetic affinity between present-day and ancient natives from South America and present-day indigenous groups of South Asia, Australia, and Melanesia has been previously reported (Raghavan et al., 2015; Skoglund et al., 2015; Moreno-Mayar et al., 2018; Posth et al., 2018; Ioannidis et al., 2020; Wallin, 2020; Silva et al., 2021). The controversial Australasian population genetic component (Ypikuéra population" or "Y population component) was identified exclusively in the present-day Amazonian populations, suggesting at least two different founding waves leading to the formation of the people of this region (Skoglund et al., 2015; Reich, 2018).

Silva et al. (2021), suggest that the first modern humans migratory wave to South America was composed of direct descendants of the Beringian standstill population, and a second wave was formed by an admixed population of Beringian and southeast Asian ancestors that reached Beringia more recently, both populations would have settled and admixed in the Amazon region. Rapa Nui has been considered a likely locus for contact, since, it is the closest inhabited Polynesian island to the Americas with the most elaborate megalithic culture, the reason some researchers focused on this place to carry out genetic studies to investigate the possibility of prehistoric contacts between Polynesian and Native American populations (Ioannidis et al., 2020). As a consequence, these studies reached opposing conclusions about pre-European contact between Polynesian individuals on Rapa Nui and Native American individuals (Moreno-Mayar et al., 2014; Fehren-Schmitz et al., 2017; Ioannidis et al., 2020; Silva et al., 2021).

After the Chilean annexation of Rapa Nui in 1888, the only recorded events potentially connecting Pacific islanders with Native American ancestry are the Peruvian slave raids of ad 1862–1863 (Maude, 1981; Ioannidis et al., 2020). During this year, thousands of Pacific islanders were kidnapped and taken to Peru as forced labourers, including 1,407 Rapanui individuals (Maude, 1981). Ioannidis et al. (2020), analysed the genome-wide

variation in individuals from islands across Polynesia for signs of Native American admixture, the results suggested that a single contact event occurred in eastern Polynesia, before the settlement of Rapa Nui, between Polynesian individuals and a Native American group most closely related to the indigenous inhabitants of present-day Colombia.

Furthermore, a new line of evidence indicates that the first American clades split in East Asia, not in Beringia, which makes the gene flow of the Y ancestry from the ancestral East Asian groups even likelier (Silva et al., 2021). In this sense, the Y population would be part of the first colonizing groups of the American continent (Ioannidis et al., 2020; Silva et al., 2021). Thus, the Australasian population contribution was introduced in South America through the Pacific coastal route before the formation of the Amazonian branch, likely in the ancient coastal Pacific/Amazonian population (Silva et al., 2021). This Australasian−Native American connection persists as one of the most intriguing and poorly understood events in human history (Reich, 2018; Ioannidis et al., 2020; Wallin, 2020; Silva et al., 2021).

Native American languages

Thousands of Amerindian languages were spoken in the continent, before the arrival of Europeans in the New World (Campbell, 2000). However, nowadays the Spanish, English and Portuguese languages are politically dominant in the Americas (Campbell, 2000; Boas, 2010). In 1987 Joseph Greenberg suggested the Amerindian hypothesis to classify all indigenous languages of the Americas (Greenberg, 1987). According to the linguistic method (mass comparison) used by Greenberg (1987), indigenous languages of the Americas can be classified into three phylogenetic units or macrofamilies (Eskimo-Aleutian, Na-Dene and Native American languages) (Greenberg, 1987).

The Eskimo-Aleut languages diverged from common ancestor at least 4,000 years ago, while the Eskimo language family split into the Yupik and Inuit branches around 1,000 years ago (Jacobson, 1987). Both Chukotko-Kamchatkan and Eskimo-Aleut language families have circumpolar ancestry belonging to Paleo-Siberian languages (Baker et al., 2017). On the other

hands, the Na-Dene is a linguistic family from northwestern North America, correlated with Amerindian and Circumpolar languages (Baker et al., 2017). The Na-Dene includes the Athabaskan, Eyak and Tlingit languages (Sicoli and Holton, 2014), whose divergence time was approximately 5,000 years ago (Greenberg et al., 1986).

Amerindian languages consist of dozens of distinct language families, which diverged more than 11,000 years ago (Greenberg et al., 1986). The indigenous languages of the Americas are divided into three main groups according to the geographical area (Greenberg and Ruhlen, 2007). The first group encompass the North–Central Amerind languages as the Almosan–Keresiouan, Penutian–Hokan, Mayan, Mixe–Zoque, Totonac, Tanoan,Uto-Aztekan and Oto-Manguean (Greenberg and Ruhlen, 2007). The second group encompass the Southern Amerind languages as the Andean, Chibchan and Paezan. Whilst, the third group include the Equatorial and Tucanoan laguages (Greenberg and Ruhlen, 2007).

In summary, the linguistic diversity in the American continent is immense and complicated resulting from its colonization complex history and human expansions (Reich, 2018). The linguistic information provides clarity and possible resolutions on cultural heterogeneity in the ancestry data, while the genetic ancestry data yield insight into a deeper past (Baker et al., 2017). Both approaches enable to describe the evolutionary history of the human populations within the cultural and biological contexts, since both language and genes are inherited "vertically" (from parents to children) and change "horizontally" depending on the contact between populations (Creanza et al., 2015).

Genetic history of America peoples

At present, the origin of Native American populations is one of the most fascinating, intriguing, challenging and debated topics in the study of ancient human migrations, which puzzles academics from many different fields (Dillehay, 2009; Gnecchi-Ruscone et al., 2019; Suarez and Ardelean, 2019; Hoffecker et al., 2021). On the one hand, the exact timing, route and process of the initial peopling of the Americas remain uncertain, while on the other hand, extensive European and African admixture coupled with loss of Amerindian lineages makes the reconstruction of pre-Columbian history of Native Americans based on present-day genomes extremely challenging (Dillehay, 2009; Llamas et al., 2016; Gnecchi-Ruscone et al., 2019; Suarez and Ardelean, 2019; Hoffecker et al., 2021).

Genetic Analyses have revealed that the ancient Beringian populations and other Native Americans descended from a single founding population that initially split from East Asians around 36,000 years ago (Nielsen et al., 2017). The gene flow from ancient north Eurasians to proto-Native Americans peoples took place approximately 20,000 – 25,000 years ago (Llamas et al., 2016; Nielsen et al., 2017; Ardelean et al., 2020; Willerslev and Meltzer, 2021). Whilst, the branching off ancient Beringians occurred around 18,000 – 22,000 years ago, what it is consistent with the Beringia standstill model (Tamm et al., 2007; Mulligan et al., 2008; Nielsen et al., 2017). On the other hands, the Native American groups divergence happened around 14,600 – 17,000 years ago (Nielsen et al., 2017).

Y-chromosome studies indicate Y-haplogroups Q-M19, Q-M3, Q-M242, and C-RPS4Y711 are restricted to the Americas and Asia (Melton, 2008; Battaglia et al., 2013; Gómez et al., 2021; Willerslev and Meltzer, 2021). The haplogroup Q-M19 was found only in populations from northwestern South America (Ticuna and Wayuu) (Bortolini et al., 2003; Huang et al., 2018; Pinotti et al., 2019; Sharma et al., 2021). The parental haplogroup Q-M3 is found in a mean frequency of 77% in the most Amerindian populations, albeit it is in a low

frequency in South Amerindian (9%) and in the Chipewyan (6%) from Canada, but was not found in Mongolia (Bortolini et al., 2003; Huang et al., 2018; Pinotti et al., 2019; Sharma et al., 2021).

The mean frequency of haplogroup Q-M242 in Mongolia is pretty low (4%) compared with haplogroup C-RPS4Y711, whose frequency in this population reached 56%, while in South and North America (Chipewayan) the mean frequency was 6% (Bortolini et al., 2003; Schurr and Sherry, 2004; Huang et al., 2018; Gómez et al., 2021). America and Asia lack of lineages P-M45, K-M9, Y, DE-YAP and E-M2. However, P-M45 is found in low frequency in South America around 4% and Mogolia 6%, but is the most common in Europe (52%) and the Chipewayan (63%) (Bortolini et al., 2003; Dillehay, 2009; Huang et al., 2018; Barbieri et al., 2019; Pinotti et al., 2019; Sun et al., 2019).

According to microsatellite polymorphisms on Y-chromosome, the male lineages have a differentiated ancestry for populations from North and South America, since the data for this genome indicate the occurrence of two major male migrations from Southern / Central Siberia to the Americas, the second migration was restricted to North America, besides the male lineages in the Americas have a share ancestry in Central Asia (Bortolini et al., 2003; Reich et al., 2012; Huang et al., 2018; Gómez et al., 2021).

The Y lineage specific to South America (Q-M19) indicates an isolated during the initial colonization of the region, which suggests an early onset of tribalization of Native Americans, suggesting different patterns of evolution owing to local differentiations due to demographic events, likely triggered by the introduction of agriculture and associated with the flourishing of the great empires in the region (Bortolini et al., 2003; Dillehay, 2009; Huang et al., 2018; Barbieri et al., 2019; Pinotti et al., 2019; Sun et al., 2019; Gómez et al., 2021; Sharma et al., 2021).

Mitochondrial DNA (mtDNA) studies based on modern DNA indicate that Native American populations have four major founding haplogroups (A2, B2, C1, and D1) and five potential haplotypes (C4c, D2a, D3, D4c, and X2a) that could be considered as founder lineages (Schurr and Sherry, 2004; Melton, 2008; Noguera-Santamaría et al., 2015; Hoffecker et al., 2021). These haplogroups account for between 95-100% of mtDNA polymorphisms found in Amerindian populations (Achilli et al., 2008; Melton, 2008; Noguera-Santamaría et al., 2015). The haplogroup X2a is restricted to North American populations and has never been identified in any ancient or living Central or South American groups (Melton, 2008).

The haplogroup A2 is divided into 13 subclades (A2c, A2d, A2d1, A2d2, A2e, A2f, A2g, A2h, A2i, A2j, A2j1, A2k, and A2k1), what become it in the most diverse haplogroup of Native American populations (Achilli et al., 2008; Noguera-Santamaría et al., 2015; Hoffecker et al., 2021). A2 is present in all American continent but also been detected in Siberian populations (Tamm et al., 2007; Moreno-Mayar et al., 2018; Hoffecker et al., 2021). The haplogroup A2 is divided into 13 subclades (A2c, A2d, A2d1, A2d2, A2e, A2f, A2g, A2h, A2i, A2j, A2j1, A2k, and A2k1), what become it in the most diverse haplogroup of Native American populations. A2 is present in all American continent but also been detected in Siberian populations (Achilli et al., 2008; Hoffecker et al., 2021).

On the other hands, the haplogroup B2 encompass at least four subhaplogroups (B2a-B2d). B2a is found throughout North America and is common among the Pima, Ojibwa, and Navajo (Tamm et al., 2007; Melton, 2008; Moreno-Mayar et al., 2018). Whilst, B2d is most frequent in lower Central and northern South American populations and it has been detected in both Wayuú from Colombia and Ngöbé from Panama (Achilli et al., 2008). Another haplogroup that is well represented in America is the C1, which is divided into three subclades (C1b, C1c, and C1d), haplogroup C4c is only known in a single population (Ijka)

from Colombia (Tamm et al., 2007; Melton, 2008; Noguera-Santamaría et al., 2015; Barbieri et al., 2019; Delgado et al., 2021).

Haplogroup D2 consists of two sister subclades (D2a, D2b) with D2b being found only in Siberia and D2a only in the Arctic and subarctic populations (Tamm et al., 2007; Melton, 2008; Barbieri et al., 2019; Delgado et al., 2021). Haplogroup X2a has only been found in North American populations but has yet to be detected in South American populations (Melton, 2008). The absence of these haplogroups in southern Amerindian populations and the concomitant detection in arctic and subarctic peoples support partially the hypothesis about that the genetic ancestry of the Na-Dene, Eskimos, and Aleuts from Beringian or Alaskan is different from the genetic sources that give rise to the first Amerindians (Perego et al., 2009; Suarez and Ardelean, 2019; Willerslev and Meltzer, 2021).

de Saint Pierre et al. (2012), identified two novel mtDNA monophyletic clades, preliminarily designated B2l and C1b13 with D1g sub-haplogroup have locally high frequencies and are restricted to populations from the extreme south of South America. The estimated ages of D1g and B2l, about 15,000 years ago, what agrees with the dating of the earliest archaeological sites in South America (Monte Verde, Chile, 14,500 years ago) (de Saint Pierre et al., 2012). D4h3a5 sub-haplogroup is restricted to Fuegian-Patagonian populations, suggesting the extant native populations inhabiting South Chile and Argentina are a group which had a common origin (de Saint Pierre et al., 2012). Therefore, Patagonia would have been settled at least about 15 years ago by migrants that followed the Pacific coast route (de Saint Pierre et al., 2012; Gómez-Carballa et al., 2018).

Once arriving to Monte Verde area, the migrants could not be advanced further along the Pacific coast owed to the extension of the glaciers, which covered most of the coast of Patagonia (de Saint Pierre et al., 2012; Gómez-Carballa et al., 2018; Roca-Rada et al., 2021). Then, the migrants crossed the Andes and continued their southern advance on the eastern

side; hence, the early colonization process was not just an expansion from north to south, but also included movements across the Andes (de Saint Pierre et al., 2012; Gómez-Carballa et al., 2018; Roca-Rada et al., 2021; Willerslev and Meltzer, 2021).

Haplogroup B2l arose early from the B2 haplogroups, likely this lineage brought by the early colonizers in the Pleistocene-Holocene limit evolved independently of the B2 lineages highly represented in northern Chile and Argentina (de Saint Pierre et al., 2012; Posth et al., 2018; Nakatsuka et al., 2020). Lineage C1b13 is found in Yámana (Argentina and Chile), Kawésqar (Chile), Pehuenche (Argentina and Chile), Tehuelche (Argentina, and Chile), Mapuche (Argentina, and Chile) and Huilliche (Chile) peoples (de Saint Pierre et al., 2012). Lineages D1g (Early Holocene) and D1j (Middle Holocene) are local clades of Southern Cone of South America (SCSA), whose ages agree with the dating of the earliest archaeological sites in South America, indicating that Paleo-Indians might have reached that region from Beringia in less than 2000 years (de Saint Pierre et al., 2012; Roca-Rada et al., 2021).

Reich et al. (2012) used high-resolution genetic data to address the issue of the pattern of dispersals within the Americas. They assembled data from fifty-two Native Americans and seventeen Siberian groups genotyped at 364,470 single nucleotide polymorphisms (SNPs). The data revealed that the Native Americans descend from at least three streams of Asian gene flow. Most descend entirely from a single ancestral population that they called ‘First American’ (Reich et al., 2012). Speakers of Eskimo–Aleut languages from the Arctic came from the second stream of Asian gene flow, and the Na-Dene-speaking Chipewyan from Canada inherit roughly came from a third stream (Reich et al., 2012).

The data of Reich et al. (2012), also showed that the initial peopling followed a southward expansion facilitated by the coast, with sequential population splits and little gene flow after divergence, especially in South America. However, there is a major exception is in

Chibchan speakers on both sides of the Panama isthmus who have ancestry from both North and South America (Reich et al., 2012; Achilli et al., 2013; Capodiferro et al., 2021). During the Holocene, migrations from Asia introduced the Saqqaq/Dorset Paleoeskimo population to the North American Arctic ~4,500 years ago whose ancestry is connected with ancestry found in Athabaskan-speakers today (Skoglund and Reich, 2016; Suarez and Ardelean, 2019).

This was then followed by a major new population turnover in the high Arctic involving Thule-related peoples who are the ancestors of present-day Inuit (Skoglund and Reich, 2016; Davis et al., 2016; Suarez and Ardelean, 2019; Puzachenko et al., 2021).

Currently, ancient DNA and mitogenomes studies provide detailed evidence about the initial migrations from Northeast Asia source population with differential relatedness to present-day Australasian populations, followed by a divergence into northern and southern Native American lineages (de Saint Pierre et al., 2012; Skoglund and Reich, 2016; Reich, 2018). Genome-wide studies have revealed that some Amazonian Native Americas descended partly from a Native American founding population that carried ancestry more closely related to indigenous Australians, New Guineans and Andaman Islanders than to any present-day Eurasian or Native Americans (de Saint Pierre et al., 2012; Raghavan et al., 2015; Skoglund et al., 2015; Nielsen et al., 2017).

Nakatsuka et al. (2020), analysed genome data of Andean archaeological human remains dating around 500 – 9,000 years ago, and observed that individuals from South Peru Highlands shared more alleles with individuals from North Peru Highlands than with individuals from Lauricocha, Peru North Highlands (5,800 years ago). Also, there was an important allele swapping between North Peru Highlands and North Peru Coast than with Lauricocha, Peru North Highlands (5,800 years ago) and Central Peru Coast (Fehren-Schmitz et al., 2014; Nakatsuka et al., 2020). About more than 2,000 years ago, there was a gene flow that connected the Titicaca Basin to the South Peru Highlands and North Chile,

matching cultural exchange in this region at that time (Santoro et al., 2017; Suarez and Ardelean, 2019; Olson et al., 2020; Nakatsuka et al., 2020).

The differential kinship among North American, Southern Peru and North Chile started about 4, 200 years ago and was fully integrated around 2,000 years ago (Posth et al., 2018; Nakatsuka et al., 2020). The bidirectional gene flow between the North and South Highlands, and between the Highlands and Coast, generated genetic heterogeneity in Tiwanaku, Titicaca Basin and Cusco about 500 – 2,000 years ago (Nakatsuka et al., 2020). Thus, genetic heterogeneity gave way to Cosmopolitanism (people of diverse ancestries living side-by-side) in the heartlands of the Tiwanaku and Inca polities (Nakatsuka et al., 2020).

Delgado et al. (2021), studied the genetic variation on archaeological human remains belonging to late Pleistocene (12,164 years ago) and the final of late Holocene (2,751 years ago), from Sabana de Bogotá, Colombia, this region played an important role in the initial human expansion into South America. The results showed some individuals from Holocene exhibited a back mutation at position 16111 and an insertion at position 64, describing the haplogroup as A2+(64)+@16111 (Cardoso et al., 2008; Pérez Sepúlveda, 2016; Delgado et al., 2021). Mitochondrial lineages observed in these Pre-Hispanic individuals fell within the Native Amerindians branches A2, B2, C1b, D1 and D4h3a, suggesting genetic maternal filiation and continuity in northern South America (Fehren-Schmitz et al., 2015; Llamas et al., 2016; Posth et al., 2018; Noguera-Santamaría et al., 2020; Delgado et al., 2021).

Capodiferro et al. (2021), analysed pre- Hispanic individuals from Panama dated around 630 – 1,430 years ago and Amerindian groups presently living in Panama. The results revealed, the Isthmus shows an excess of share allele with modern and ancient Indigenous populations from Central and South America compared with Ancestral Beringia (USR-1, Upward Sun River, Alaska 11,500 years ago) (Potter et al., 2014; Moreno-Mayar et al., 2018)

and Northern Native American (ASO, Ancient Southwestern Ontario, 4,200 years ago) (Posth et al., 2018; Scheib et al., 2018; Waters, 2019). Thus, pre-Hispanic demographic events currently contributed to the extensive genetic structure seen in the area, which is also characterized by a distinctive Isthmo-Colombian Indigenous component (Capodiferro et al., 2021). This component drives these populations on a specific variability axis and derives from the local admixture of different ancestries of northern North American origin(s) (Capodiferro et al., 2021).

However, the Isthmus seems more closely related to Spirit Cave (Nevada, 10,900 years ago) (Gross, 2018) than to Anzick-1 (Montana, 12,800 years ago) (Rasmussen et al., 2014) in comparison with Ancestral Beringian (Capodiferro et al., 2021). Two ancestries were differentially associated with Pleistocene Indigenous groups that also moved into South America, leaving heterogenous genetic traces (Capodiferro et al., 2021). An additional Pleistocene ancestry was brought by a still unsampled population of the Isthmus (UPopI) that remained restricted to the Isthmian area, expanded locally during the early Holocene, and left genomic traces up to the present day (Capodiferro et al., 2021).

Usually, The Pacific coast populations (Los Rieles, Chile, 10,900 years ago) (Jackson et al., 2012; Capodiferro et al., 2021) exhibit greater affinity to Spirit Cave, while the ancient genomes from the Atlantic side show the same pattern as Anzick-1 when considering individuals older than 7, 000 years ago (Lagoa Santa, Brazil, 10,400 years ago) (Neves et al., 2013; Capodiferro et al., 2021). Probably, the ancient populations from America had distinctive genetic signals that persisted about 7,000 years ago, when they were likely erased by a major population turn- over in South America (Moreno-Mayar et al., 2018; Posth et al., 2018; Capodiferro et al., 2021), facilitated by a widespread population decline resulting from mid- Holocene climate changes (Riris and Arroyo-Kalin, 2019; Capodiferro et al., 2021).

1.4 Molecular genetic overview

There are between 25,000 to 20,000 exons in the human genome (International Human Genome Sequencing Consortium, 2004). The human genome has only 1,5% of protein exons and 98,5% correspond to Introns or non-coding DNA such as repeat elements, pseudogenes, gene fragments, introns or UTR (Untranslated Region) sequences, among others (Melton, 2008; Alberts et al., 2015). The current biological function of these genomic regions is unknown and genetic polymorphisms in this region are considered selectively neutral (Melton, 2008). Therefore, the absence of natural selection as an evolutionary explanation for genetic variation in human noncoding regions allows only for two potential evolutionary outcomes, genetic drift or gene flow (Melton, 2008).

The mutation in noncoding regions do not exceed a frequency of 1% within a population (Melton, 2008; Crawford, 2018). Molecular polymorphisms are useful for understanding population structure and dynamics in the human genome including single nucleotide polymorphisms (SNPs); insertion/deletions (indels); microsatellites (STRs), minisatellites (VNTRs), retroelements (Alus, LI, endogenous retroviruses) (Rubicz, 2007). Repetitive DNA sequences comprise approximately 50% of the human genome (Treangen and Salzberg, 2011). About 8% of the human genome consists of tandem DNA arrays or tandem repeats, low complexity repeats sequences that have multiple (Duitama et al., 2014). The tandem sequences may be of variable lengths, from two nucleotides to tens of nucleotides (Duitama et al., 2014). These sequences are highly variable, even among closely related individuals, and so are used for genealogical DNA testing and forensic DNA analysis (Pierce, 2013).

Short Tandem Repeats (STRs) markers

Microsatellites (STR _short tandem repeats) are DNA sequences in which a fragment (whose size ranges from two to six base pairs) is repeated consecutively, the variation in the number of repeats creates different alleles (Butler, 2005; Richard et al., 2008; Shrivastava et al., 2020). The Combined DNA Index System (CODIS) is the United States national DNA database created and maintained by the Federal Bureau of Investigation (FBI) (https://www.fbi.gov, 2019). Until December 31, 2016, CODIS included the following thirteen loci: CSF1PO, FGA, THO1, TPOX, VWA, D3S1358, D5S818, D7S820, D8S1179, D13S317, D16S539, D18S51 and D21S11 (https://www.fbi.gov, 2019). However, from January 1, 2017, the CODIS Core Loci added the following seven loci: D1S1656, D2S441, D2S1338, D10S1248, D12S391, D19S433 and D22S1045 (https://www.fbi.gov, 2019). The loci used in CODIS have been chosen because they are in regions of non-coding DNA (https://www.fbi.gov, 2019) and, therefore, these genetic sections should not be able additional information about the person such as their hair or eye colour, or their race (ethnic group) (Augenstein, 2017).

Because STRs markers generate genetic profiles, they are used in a wide variety of applications, such as cancer diagnosis, forensic and medical fingerprinting, kinship analysis, genetic linkage analysis, sex identification, population genetics, and plant breeding (Pierce, 2013; Duitama et al., 2014; Shrivastava et al., 2020). In the same way, with the advent of the ancient DNA (aDNA) revolution, the microsatellites have turned out to be very useful to study the population genetic dynamics, authenticate results and reconstructing kinship among the occupants of a necropolis, providing a detailed portrait of the community considered (Oh et al., 2012; Seidenberg et al., 2012; Deguilloux et al., 2014; Nores et al., 2020; Shrivastava et al., 2020; Alterauge et al., 2021).

Hawass et al., (2010), analysed royal mummies belonging to the 18th dynasty of the New Kingdom (~ 1550-1070 BC) from Ancient Egypt, via sixteen Y-chromosomal short tandem repeats (DYS456, DYS389I, DYS390, DYS389II, DYS458, DYS19, DYS385, DYS393, DYS391, DYS439, DYS635, DYS392, Y-GATA-H4, DYS437, DYS438, DYS448) and eight polymorphic microsatellites of the nuclear genome (D13S317, D7S820, D2S1338, D21S11, D16S539, D18S51, CSF1PO, FGA). The genetic fingerprinting obtained from these mummies allowed the rebuilding of the family tree of Tutankhamun, identifying the Akhenaten (KV55) and KV35YL as the parents of Tutankhamun (KV62) (Hawass et al., 2010). The results also suggested that Amenhotep III (KV35) and Tiye (KV35EL) mummies were the Tutankhamun's grandparents, while Yuya (KV46) and Thuya (KV46) mummies were his great-grandparents (Hawass et al., 2010).

Pilav et al. (2017), evaluated the allele frequencies from fifteen STR loci (Penta E, D18S51, D21S11, TH01, D3S1358, FGA, TPOX, D8S1179, vWA, Penta D, CSF1PO, D16S539, D7S820, D13S317 and D5S818) in the populations of Bosnia and Herzegovina. The study revealed that, when comparing the aforementioned populations, with neighbouring populations, there were significant differences in allele frequencies between Bosnian and Herzegovinian, and the Turkish, Croatian, Austrian, and Italian populations (Pilav et al., 2017). The genetic distance analysis showed that the Bosnian and Herzegovinian populations had closer genetic relationships with the Serbian, Slovenian and Hungarian populations than with Turkish populations (Pilav et al., 2017).

Whilst, Russo et al. (2018), determined the genetic structure of the South-Central Andes area populations from individuals dated 900 – 1,4300 years ago, via analysis of fifteen STR loci (D2S1338, D3S1358, vWA, FGA, D5S818, D7S820, D8S1179, D13S317, D16S539, D18S51, D19S433, D21S11, TH01, CSFPO, and TPOX). The results revealed structuring signals into Lauricocha, North West Argentina and Inca, Peru populations (Russo et al., 2018). Genetic distances showed a strong differentiation between Peruvian Inca

individuals and individuals from Quebrada de Humahuaca and Lauricocha (Russo et al., 2018). In South America, genetic structuration occurs from west to east between the Andean and lowland regions (Rothhammer et al., 2017; Russo et al., 2018). Therefore, genetic differentiation of the populations of the South-central Andes Area preceded European contact, suggesting divergence among temporally different populations might be reflecting socio-political changes that occurred in the pre-Hispanic Andean societies (Russo et al., 2018).

STR markers in ancient DNA studies are frequently used to ascertain the migration patterns of human population by crossing comparison of population genetic signals between DNA of ancestral remains from a specific place and people living there today (Zar and Aslamkhan, 2020; Zhou et al., 2021). Also, STRs markers are most useful to identify an unknown person from his/her skeletal material by matching his/her DNA to a known relative, allowing to establish a genetic link between dead and living individual and solving in this way some historical mysteries (Zar and Aslamkhan, 2020). An example of this type of studies is kinship evaluation of human remains deposited in the Merovingian necropolis sarcophagi, Jau Dignac et Loirac, France, 7th–8th century AD, by ancient DNA analysis (Deguilloux et al., 2014) or Lichtenstein cave, Germany (10th–9th century BC), where the researches wanted to clarify whether the cave was used as a sacrificial site or as a burial place (Seidenberg, 2017). The ancient DNA analysis resulted in the kinship reconstruction (genealogy) of a Bronze Age family clan, indicated that, the cave has been used as a burial place (Seidenberg, 2017).

Alterauge et al. (2021), performed a genetic studied of three noble families from the seventeenth to nineteenth centuries AD entombed in burial crypts at the cloister church of Riesa, Germany by STR and mtDNA analysis. Ancient DNA extracts were amplified through using of the AmpFLSTRTM™, NGM SElect™ and NGM Detect™ commercial kits (Alterauge et al., 2021). The results revealed family relationships of first to third-degree within the cohort (Alterauge et al., 2021). Biostatistics and lineage markers linked four

unknown individuals to the von Felgenhauer family (Alterauge et al., 2021). In addition, the pedigrees of the families Hanisch/von Odeleben and von Welck were reconstructed (Alterauge et al., 2021).

Finally, Muinde et al. (2021), evaluated the geographical and linguistic structure in Kenyan peoples from twenty-one autosomal STRs, analysed via GlobalFiler^{TM} multiplex. The genetic material belonged to indigenous Kenyans from eight former provinces, forty-three of its forty-seven counties, three main linguistic families, and all twenty-nine ethnic groups (Muinde et al., 2021). This study revealed significant genetic differentiation among the three Nilotic languages sub-families, with Western Nilotes (the Luo ethnic group) showed greater genetic similarity to the Bantu than the Southern and Eastern Nilotes which themselves showed closer affinity to the Cushitic speakers (Muinde et al., 2021). The genetic information obtained in this research concurred with linguistic and social studies, suggesting that both the distribution of languages and the distribution of the genetic diversity of ethnic groups analysed to tend to correspond to each other (Muinde et al., 2021).

Mitochondrial DNA (mtDNA)

Mitochondrion genome is a double-strand circular DNA, consisting of ~16,569 bp (Fernández Domínguez, 2005; Floros et al., 2018; Mingroni-Netto, 2021). It contains a coding region with thirty-seven exons, distributed in twenty-two transference ribonucleic acids (tRNA), thirteen structural genes, coding for the enzymatic complexes of oxidative phosphorylation system and two ribosomal RNA (rRNA) (Pakendorf and Stoneking, 2005; Floros et al., 2018; Stewart and Chinnery, 2021). Furthermore, it contains a non- coding region known as the control region, which includes a section of 1,200 bp known as the D loop, and it is located between genes that coding for proline tRNA and phenylalanine tRNA (Pakendorf and Stoneking, 2005; Burr et al., 2018; Mingroni-Netto, 2021).

Control region stands out for its high mutation rate, approximately ten times higher than in the coding regions, this corresponds to $0.075\text{-}0.167\times10^{-6}$ substitutions/site/ year, and for its high intrapopulation variability (Stoneking et al., 1992; Hasegawa et al., 1993; Pakendorf and Stoneking, 2005; Marquis et al., 2017; Floros et al., 2018; Kopinski et al., 2019; Mingroni-Netto, 2021). This variability is centralized in three regions or hypervariable segments: HVSI in position 16024-16365, HVSII in position 73-340 and HVSIII in position 440-560 (Fernández 2000; Mingroni-Netto, 2021). Moreover, the mitochondrion genome is also presented polyplasmy (Fernández 2000). Polyplasmy refers to the high number of mtDNA copies that exist in each mitochondrion and consequently, in the cell (Fernández Domínguez, 2005; Kopinski et al., 2019; Stewart, 2021).

A mitochondrion can have approximately 10,000 – 1,000 copies of mtDNA, these multiple copies are not necessarily all identical (Shitara et al., 1998; Fernández Domínguez, 2005; Pakendorf and Stoneking, 2005; Marquis et al., 2017; Burr et al., 2018; Nissanka and Moraes, 2020; Rebolledo-Jaramillo et al., 2021).

Different mtDNA molecule in an individual is known as heteroplasmy. Usually, the populations have a heteroplasmy of around 14% (Pakendorf and Stoneking, 2005; Wei et al., 2019; Mingroni-Netto, 2021). However, at the individual level, the homogeneity of mtDNA molecules suggests during the early stages of oogenesis the number of mitochondrial is reduced owing to a severe bottleneck (Fernández Domínguez, 2005; Pakendorf and Stoneking, 2005; Kopinski et al., 2019; Atilano et al., 2021).

Mitochondrion DNA lacks recombination since it is transmitted by the maternal line (Campbell et al., 2006; Melton, 2008; Marquis et al., 2017; Floros et al., 2018; Kopinski et al., 2019; Wei and Chinnery, 2020). The sperm mitochondria are marked by ubiquitination and selectively destroyed in the oocyte thus, paternal mtDNA is not present in the fertilization product (Shitara et al., 1998; Eker et al., 2019; Sayed et al., 2021). This mode of uniparental inheritance allows researchers to trace the relationship between lineages over time, highlighting the maternal ancestry of a population, without being confused with the effects of nuclear DNA recombination on biparental inheritance (Henze and Martin, 2003; Wei et al., 2019; Mingroni-Netto, 2021). In summary, Polyplasmy, maternal inheritance and high mutation rate make mtDNA especially useful in the reconstruction of the recent past of human populations (Gilbert et al., 2008; Crawford, 2018).

Early human mtDNA genetic history studies used high-resolution restriction fragment length polymorphism (RFLP) analyses and focused on the entire mtDNA genome (Barrantes, 1993; Schurr, 2004; Crawford, 2018). These were used to identify mitochondrial lineages or haplogroups, to characterize and study the evolutionary history of different populations around the world (Schurr and Sherry, 2004; Melton, 2008). Therefore, any observed variation in mtDNA can be attributed to mutation and the timing of the event can be estimated using the mutation rates (Melton, 2008).

The advances in molecular method and analysis techniques, such as polymerase chain reaction (PCR), automatic sequencing and next-generation sequencing (NGS), have allowed a better characterization of polymorphisms in the human genome (Schurr and Sherry, 2004; Melton, 2008; Matisoo-Smith and Ramirez, 2010; Nowakowska, 2017; Gates et al., 2021; Soni et al., 2021). Whilst, Bayesian and multivariate statistical methods have generated phylogenetic trees with higher resolution (Melton, 2008; Yang and Zhu, 2018; Pett and Heath, 2020; Yon et al., 2021). This has allowed studying at microevolutive level the population dynamics and understood how the evolutive forces shaping the genetic structure of the populations (Stoneking et al., 1992; Rubicz, 2007; Relethford, 2012; Geer, 2020; Okazaki et al., 2021).

Nowadays, the ancient mtDNA studies have enabled to trace early human migrations at the genetic level, to infer demographic events that took place in pre-LGM (Last Glacial Maximum) and post-LGM era in Europe (Fu et al., 2016; Posth et al., 2016; Ehler et al., 2019). Moreover, mtDNA was used in several kinship studies as a molecular marker which excludes direct maternal kinship between ancient individuals (Haak et al., 2008; Lee et al., 2014; Juras et al., 2017; Mathieson et al., 2018; Ehler et al., 2019). Consequently, the ancient mtDNA offers the opportunity to trace demographic changes that shaped past and modern populations mtDNA variation (Ehler et al., 2019).

1.5 Justification and Goals

Ancient DNA researches offer a valuable opportunity to expand the current knowledge about the genetic structure and demographic histories of Oceania, Central and South America via DNA fingerprinting and mtDNA sequences. Additionally, social, medical and forensic sciences could use this sort of data as feedback to improve their background about the ancestry and ethnic admixture of the population aforementioned, which would enable to perform comparative studies between modern and ancient human populations to evaluate the level of genetic erosion on these populations via determination of deleterious gene variants that could provoke genetic diseases. Besides, the presence and effect of these genetic variants could be traced in the current populations, which would allow establishing the genetic charge or susceptibility to a disease in a given population.

The goals of this dissertation are structured as follows: a general objective which consists of to describe the ancient genetic landscape of Oceania, South America and Panama populations via archaeological human remains analysis, and four specifics aims which consist of 1) to describe the grade of genetic variation mitochondrial DNA of the Oceanian, Panamanian and South American samples; 2) to determine the genetic profile of archaeological human remains using STR genotyping; 3) to identify and assess the presence of genetic variants considered as uncommon or rare in the current populations; and 4) to infer the ancient phylogenetic relationships among populations under study.

2 Materials and Methods

2.1 Sample selection and bone material description

One hundred twenty-five paleo-anthropological remains were analysed. According to their geographical origins, these individuals belonged to the continental regions of Oceania and America. The Oceania samples came from the subregions of Melanesia and Polynesia, also there were individuals whose specific subregion within Oceania was unknown. Whilst, the America samples came from Panama and South America (Peru, Chile, Venezuela, Bolivia and Brazil) subregions. Consequently, this study encompassed three population groups, which belong to ten different countries within two continental regions (Table 1).

Samples and Populations

According to the archaeological and anthropological records of the Historical Anthropology and Human Ecology Institute of the Georg-August University of Göttingen, Germany, the samples from Oceania and South America date to pre-European contact period, between 500 – 800 years ago. While the Panamanian samples provided by the archaeology laboratories of Smithsonian Tropical Research Institute also fall into the pre-European period, and their dated ages with C^{14} range between 590 – 1150 years ago. It is important to bear in mind that the age ranges of Oceania and South America are based on the archaeological records from ethnohistorical Institute of Hamburg University.

The Panamanian samples were included in this work, since this region is considered as a land bridge or biological corridor between North and South America. Therefore, these samples could be considered as a link between the peoples of both hemispheres of the American continent. The first anatomically modern humans reached the Isthmus of Panama (southeast of Central America between the Pacific and Atlantic oceans) around ~11,000 years ago (Cooke, 2005). After this migration wave, the human groups that lived in this continental area established contact, developed agriculture about ~ 7,000 – 9,000 years ago and established rudimentary societies around ~4,500 – 7,000 years ago (Cooke, 2005; Cooke et al., 2013).

Thus, the archaeological and anthropological evidence provided by Cooke, 2005 about the arrival of the first humans to what is now the Isthmus of Panama is supported by genetic information provided by the work of Posth et al., 2018 about the deep history of the population of Central and South America.According to Posth et al., 2018 research the Clovis-associated Anzick-1 genome at ~12,800 shares distinctive ancestry with the oldest Chilean, Brazilian, and Belizean individuals, this supports the theory of a population expansion that spread from North America towards Central and South America (Posth et al., 2018) which is consistent with the evidence of the human presence in Panama about 11,000 years ago (Cooke, 2005).

Table 1. Geographical distribution of populations and number of individuals (N) (Appendix 6.1 – 6.3).

Zone / Country	Subregion	Region / Continent	N
New Zealand	Polynesia	Remote Oceania	1
Samoa	Polynesia	Remote Oceania	1
Bismark Archipelago	Melanesia	Near Oceania	22
Unknown	Without assign	Oceania	10
Venezuela	South America	America	2
Bolivia	South America	America	2
Brazil	South America	America	3
Chile	South America	America	5
Peru	South America	America	18
Panama	Central America	America	61

2.2 Selection of skeletal material

Petrous bone and the cementum layer of unbroken teeth roots are skeletal tissues better known to best preserve endogenous DNA (Hansen et al., 2017). Moreover, given their location in the skull, these skeletal elements provide good protection for DNA in many environments, since both the compact structure of these skeletal materials and the chemical composition of their extracellular matrix, which is primarily made up of an inorganic salt called hydroxyapatite ($Ca_5(PO_4)_3(OH)$), they provide a high density to both petrous bone and dental cementum, allowing high resistance against chemical, physical and biogenic decomposition (Kendall et al., 2018), and under certain circumstances they seem to be less susceptible to contamination with modern DNA (Adler et al., 2011; Pinhasi et al., 2015). In 2007, Rohland and Hofreiter managed to extract DNA starting from teeth and bones from samples of cave bears and mammoths belonging to the Pleistocene epoch (Rohland and Hofreiter, 2007).

Fehren-Schmitz et al. (2010) extracted DNA from pre-Columbian archaeological human remains from the southern coast of Peru, where the population dynamics of these individuals was studied through the analysis of their mtDNA (Fehren-Schmitz et al., 2010). Similarly, Seidenberg et al. (2012) recovered ancient DNA from German paleoanthropological samples belong to Bronze Age, and early nineteenth century, as well as from archaeological human remains from the Peruvian highlands dated approximately 800 years ago. The aDNA of these samples was used to develop a miniSTR heptaplex system to evaluate the genetic fingerprint of samples with very low DNA concentration (Seidenberg et al., 2012).

Pinhasi et al. (2015) got an optimal ancient DNA yields from the inner ear part of the human petrous bone when analysed paleoantropological samples from Central Europe, Central Asia, Southeast Asia, the Levant, Anatolia, and North Africa. The age of these specimens ranged between 10,000–1,800 years ago (Holocene) (Pinhasi et al., 2015). The high efficiency in preserving endogenous DNA from bioarchaeological samples has shown that both petrous bone and dental roots are the best substrates to extract aDNA from ancient samples (Hansen et

al., 2017). Therefore, owing to above, petrous bone and teeth are the best choices to recover DNA from paleoanthropological samples belong to tropical environments and pre-European contact times in Oceania and America.

Petrous part of the temporal bone is wedged between sphenoid and occipital in the cranial base, is inclined up and anteromedially; it has a base, apex, three surfaces and margins. The acoustic labyrinth is within it (Williams et al., 1989). The petrous bone is among the most basal elements of the skull and forms part of the endocranium (Fig. 3) (Williams et al., 1989). The otic capsule, of particular interest to this study, develops from the cartilaginous differentiation of the mesenchyma encompassing the inner ear (Pinhasi et al., 2015).

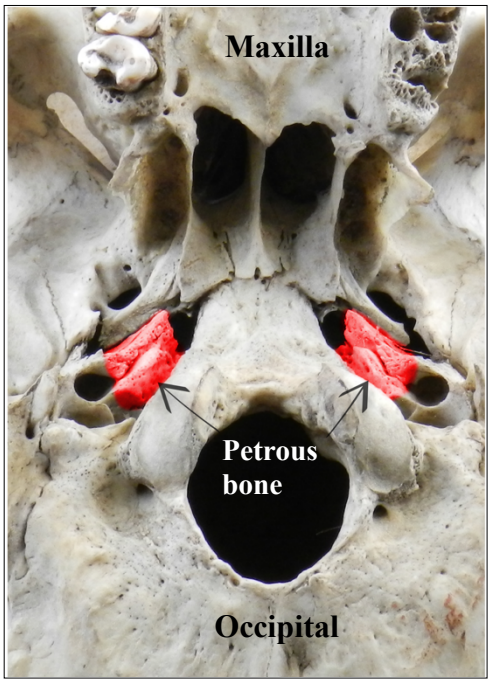

Figure 3. Red parts indicate the petrous bone of archaeological specimen from Oceania.

The teeth are a hard anatomical organ embedded in the alveolar processes of the maxillary bones and jaw through a special type of joint called gomphosis (Williams et al., 1989). The parts of the tooth are: the enamel, dentin, cementum, and pulp (Fig. 4) (Williams et al., 1989; Nanci, 2017).

Enamel is the hardest and most highly mineralized substance of the body, ninety-six per cent consists of calcium phosphate crystalline (hydroxyapatite), and four per cent is water and organic material (Nanci, 2017).

Dentin is porous, yellowish, made up of seventy per cent of inorganic materials, twenty per cent organic materials and ten per cent water (Nanci, 2017).

Cementum is a substance covering the root of a tooth, it is compound by approximately forty-five per cent of inorganic material (mainly hydroxyapatite), thirty- three per cent organic material (mainly collagen) and twenty-two per cent water (Williams et al., 1989; Nanci, 2017).

Dental pulp is the central part of the tooth filled with soft connective tissue, along the border between the dentin and the pulp are odontoblasts, which initiate the formation of dentin (Williams et al., 1989; Nanci, 2017).

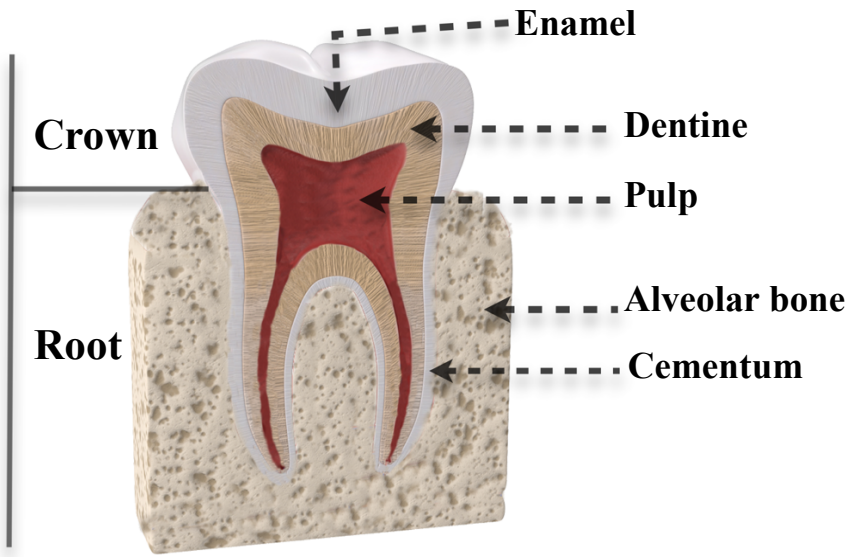

Figure 4. Schematic representation of tooth parts and its regions.
Picture credits: https://www.turbosquid.com/3d-models/human-tooth-anatomy-model-1230174

2.3 Sample preparation for DNA extraction

To make sure of working with samples (as far as teeth concerning) whose contact with environmental materials and modern DNA (from archaeologists, anthropologists, technicians, students, and others) would have been minimal, only those teeth that were attached to the dental alveolus (tooth sockets) of the maxilla or mandible were selected for DNA extraction.

Cleaning and prevention of contamination

Before to start with the sampling process in the preparation room, all surfaces and instruments (tweezers and spatulas) were cleaned with Alconox®, 6 % sodium hypochlorite (NaClO), double distilled water (ddH_2O), and 70% ethanol (Fehren-Schmitz et al., 2010; Seidenberg et al., 2012; Flux et al., 2017). Glassware, tweezers and spatulas were sterilized through washes with hot water, Alconox® and NaClO, then they were rinsed, first with hot water and after with ddH_2O and 70% ethanol. Before handling each skull, the hands covered with latex gloves without powder were washed with warm water and Alconox®, and then they were rinsed with water and 70% ethanol. Instruments and work areas were cleaned and sterilized after working each sample.

Extraction of teeth and petrous bone

To soften the bone tissue covered the tooth, ddH_2O was added around dental alveoli. Later, the tooth was extracted with tweezers, exerting little pressure and gently pulling. The extraction should be clean that is, the dental root should be intact. Afterwards, the dental crown was separated from the root using a dental saw was used (Fig. 5). Subsequently, the root was cleaned immersing it per 15 min in a glass beaker with 6% NaClO, and it was rinsed up immersing it immediately, after the previous step, per 15 min in a glass beaker with ddH_2O. This process was performed to avoid contamination with modern DNA or environmental dirt (dust, soil particles among others). The samples were placed on foil inside an oven at 37°C overnight.

For the petrous bone, the process was simpler, the part petrous of temporal bone was separated from the skull (Fig. 5) using the instrument aforementioned to disjoin the crown of the dental root. The cleaning and drying process was identical to the tooth. Later, the root and petrous bone were ground up until getting bone powder. Mill conditions were 24 Hz/s per 15 – 20 seconds. Afterwards ground up process, the bone powder was placed in a 15 mL sterile Falcon® tube and stored at -20°C until DNA extraction.

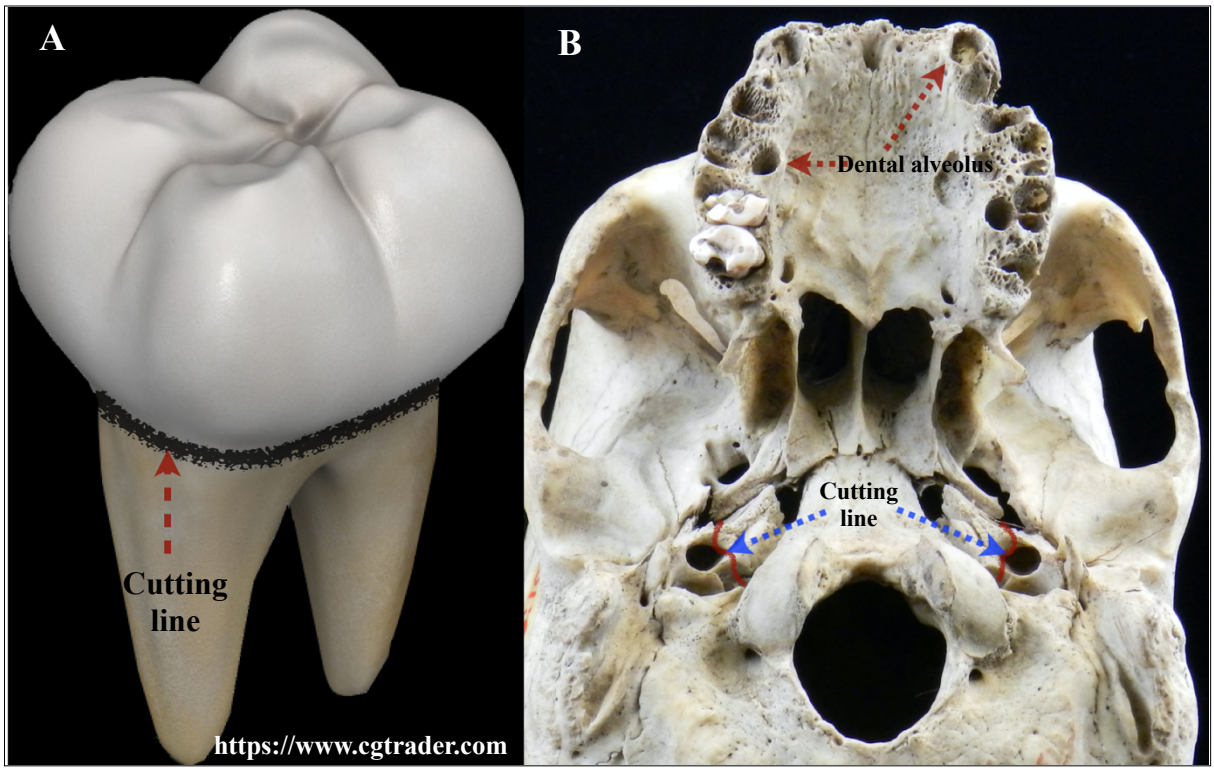

Figure 5. Cutting lines to obtain tooth root and petrous bone. A. Molar with the mark off area to disjoin the crown from the root. B. Skull from palaeoanthropological sample from Oceania.

2.4 Contamination prevention measurements

Paleogenetics or archaeogenetics is a relatively new field, compared with traditional genetic research. The most important fact about this kind of research is the high risk of contamination of bioarchaeological material under study with modern DNA. Thus, failed researches owing to shortage of endogenous DNA, unlikely or null results and contamination are the most common nemesis of the paleogeneticists when working with this type of samples. These concerns increase when referring to samples from the tropical humid and oceanic climates since these environmental conditions do not benefit the preservation of the samples and much less of the DNA (Herrmann and Hummel, 1994; Llamas et al., 2017).

Therefore, to avoid contamination and getting valid results is important to follow authenticity criteria and biosecurity protocols (Llamas et al., 2017). Given that archaeological human remains used in this work belonged to anthropological collections, was impossible to know whether the exhumation methods used by archaeologists or anthropologists during the fieldwork were suitable for ancient DNA studies. Accordingly, a rigorous sample decontamination protocol was followed as well as the preparation of blanks and positive control for each stage of DNA extraction and PCR amplification.

To control the contaminating DNA in the laboratory, all samples were processed in a dedicated ancient DNA laboratory. The risk of contamination with modern DNA was controlled through genotyping and mitochondrial DNA sequencing of all personnel that had contact with the samples (researchers and technicians). Finally, the exposure to contaminating DNA was controlled and limited in the laboratory since during the handling of samples, latex and nitrile gloves, chemistry protection goggles, laboratory suit, mask and cap were used (Llamas et al., 2017).

Sample preparation was carried out following the Korlević et al. (2015) protocol, whose principle is the chemical destruction of contaminating DNA and removing of environment material via treating the sample with bleach and double-distilled water. Although this method

could affect the endogenous DNA, it is the most suitable cleaning option for small or delicate samples as hair, dental calculus, teeth and small bones fragments (Korlević et al., 2015; Llamas et al., 2017). All samples used in this study were cleaned with 6% NaClO per 15 min and rinsed double-distilled water per 15 min, then they placed inside an oven at 37°C overnight.

For each sample were carried out two separate DNA extractions. Extraction controls consisted of blanks and positive controls for each batch of extraction. The blanks or negative controls were used as monitors for DNA contamination during the extraction process (Llamas et al., 2017), while the positive controls were used as extraction process success monitors. Regarding PCR amplification, for each DNA extraction, two separated PCR reactions were performed with their respective negative and positive controls. In this point, each sample had two independent DNA extracts and eight PCR amplification, four for genotyping, and four for mitochondrial DNA HVSI sequence.

Experimental replications were performed to control the inconsistencies of the results (Llamas et al., 2017) if any. The genotyping of samples validated the authenticity of ancient DNA, genetic fingerprinting was done via six Combined DNA Index System (CODIS) STRs markers and amelogenin gene (Seidenberg et al., 2012). Whilst, the authenticity of mitochondrial DNA sequences was verified through phylogenetic and population genetic analyses (Fehren-Schmitz et al., 2010; Llamas et al., 2017).

2.5 DNA extraction processes

Prior to address the DNA extraction process, it is important to consider the climatic conditions of the regions where samples came from. Both for Oceania and Panama and South America, the climatic conditions are tropical, which made difficultly but not impossible the DNA extraction with the conventional or standard methods. It is because of that in the present work, the traditional protocols to extract DNA were tested and adapted until getting two successful methods for tropical samples.

The protocol used on Oceania samples was developed in the paleogenetics and forensic genetics laboratories of Historical Anthropology and Human Ecology Department of the Johann Friedrich Blumenbach Institute for Zoology and Anthropology, at Georg-August University of Göttingen by Hummel, 2003 and Flux et al., 2017. While for the Central and South American samples was used a protocol especially developed, in this work, for tropical "picky" samples. This methodology is based on Hummel, 2003, Rohland and Hofreiter, 2007 and Flux et al., 2017 ancient DNA extraction methods.

Protocol for Oceanian sample materials

This DNA extraction procedure consisted of three incubation rounds. During the first round, it was added 3.9 mL of EDTA (Ethylenediaminetetraacetic acid) Titriplex®III, Merck 0.5 M pH 8.0 and 100µL of proteinase K (PK) Merck 600 U/mL pH 7.5 to 200 mg of bone powder, and it was incubated at 37°C per 18 hrs with rotation at 350 rounds per hour (rph) (Hummel, 2003). To avoid leaks or drips of bone powder solution during this process, the 15 mL Falcon® tube was sealed with Parafilm® M, American National Clan™

In the second incubation round, 50µL of proteinase K was added to the bone powder solution and it was incubated at 56°C per 2hrs at 350 rph. Finally, in the third incubation round, 50µL Sodium dodecyl sulfate (SDS) Sigma-Aldrich® 10mg/mL was added to the bone powder solution, and it was incubated at 65°C per 5 min with rotation at 350 rph, and at the end of the

incubation process, the tubes with the lysis product were centrifuged with a short spin (Hummel, 2003; Flux et al., 2017).

Subsequently, two 15 mL Falcon® tubes were used per each sample, since one of them contained 3 mL of Roti®Phenol ($C_6H_6O_6$), and the other one had 4,5 mL of LiChrosolv® chloroform (CH_3Cl), Merck, these tubes were labelled with the sample ID and the name of its respective reagent. The lysis product was added to the phenol tube and mixed it softly by inversion per 6 min at room temperature (RT), and then it was incubated at 56°C per 10 min. Afterwards, the aqueous phase was transferred to chloroform tube and the same processes was repeated with phenol (Flux et al., 2017). The DNA binding was carried out through using the commercial binding buffer from Qiagen® (PB-buffer).

The aqueous phase from the previous step with chloroform was transferred to a 50 mL Falcon® tube, labelled with sample ID, which contained 16 mL of Qiagen® PB-buffer and 100 µL of sodium acetate ($C_2H_3NaO_2$) or (NaOAc) Invitrogen™, 3M pH 5.2. This solution was mixed softly by inversion and centrifuged at 3,300 relative centrifugal force (rcf) per 3 min (Flux et al., 2017). Later, the solution of 50 mL Falcon® tube was transferred to a funnel connected to a MinElute™ spin column, with sample ID, which in turn was connected to vacuum system Qiagen® Qiavac and started the draining process of Qiagen® PB-buffer once this stage was finished, the funnel was disconnected from the column. The remainders of Qiagen® PB-buffer salts, in the silica membrane, were washed adding 700 µL of Qiagen® PE-buffer and incubating at RT per 5 min, and incubating at RT per 5 min, and then, the vacuum system was turned on to remove the Qiagen® PE-buffer, this process was repeated two times more.

To remove the remains of PE-buffer, the MinElute™ column was centrifuged at 1,300 rpm per 1 minute and then it was incubated at RT per 5 min to evaporate the ethanol. DNA elution step was carried out using pre-heated nuclease-free water at 56°C. The MinElute™ column was placed inside a 1.7 mL Eppendorf® tube, previously labelled with sample ID,

extraction date and name initials of the person in charge of the extraction process. it was added 20 µL of Ambion® nuclease free water, Invitrogen into silica membrane, left to incubate at RT per 5 min, this process was repeated two times more. After the final elution, the DNA was stored at -20°C until PCR amplification.

Protocol for Panamanian and South American sample materials

Usually, paleoanthropological samples from tropical regions, especially from Panama and South America stand for a struggling challenge to carry out paleogenetic studies on these areas, which represent a critical point as for the study of the peopling of America and subsequent human migrations through the continent. It is for this reason that working with this type of samples, besides being a challenge; it is also an opportunity to understand the dynamics of populations in these regions prior to European contact.

The improvement or adjustment of some DNA extraction and amplification protocols allows obtaining suitable or at least viable amounts of ancient DNA (aDNA) endogenous. Once obtained this genetic material, it is possible to infer the genetic landscapes and studying the ancient genetic profiles, population dynamics, demographic histories and more of ancient peoples belonging to Central and South America.

Given that, these batches of samples presented more problems than Oceania samples to obtain DNA. It was necessary to develop a suitable protocol for Central and South America samples. The base protocols used to develop the aDNA extraction method for tropical samples were the following: Rohland and Hofreiter, 2007; Fehren-Schmitz et al., 2010; Flux et al., 2017. These protocols are based on organic extraction methods with phenol-chloroform, Sigma-Aldrich® Guanidine thiocyanate (GusSCN), Sigma-Aldrich® Guanidine hydrochloride (GuHCl) and some commercial buffer from Qiagen® Company.

South America

The composition of extraction buffer was the first thing changed since it was necessary to increase the proteinase K activity, whereby two non-ionic detergents were added to the bone digestion reaction. Triton™ X-100, Sigma-Aldrich® and Tween® 20 molecular grade, Sigma-Aldrich®, and ultra-pure water/ nuclease-free or LiChrosolv® HPLC (High Performance Liquid Chromatography) water Merck were used to prepare an additive capable of increasing the effectiveness of proteinase K without affecting the activity of the other chemical components in subsequent steps. The stock solution concentration for this reagent was prepared at 50X (50 times concentrated). While the final concentration into the digestion or lysis reaction should be 1X.

This DNA extraction process began by adding of adding 3.82 mL EDTA, 80 µL additive and 100 µL of proteinase K to 200 mg bone powder then it was incubated at 38°C per 18 hrs with rotation at 350 rph. To avoid leaks or drips of bone powder solution during this process, the 15 mL Falcon® tube was sealed with Parafilm® M, American National Clan™. Subsequently, between 100 µL of proteinase were added to the digestion reaction and it was incubated at 56°C per 2 hrs at 350 rph. Finally, starting from the third incubation round, the stages of extraction with phenol-chloroform, binding and elution of DNA were identical to those used in the Oceania protocol above explained.

Panama

On this occasion, besides to utilise the modified extraction buffer, also a new DNA binding buffer was prepared, its main component was guanidine thiocyanate 5M, whose function was to prevent the RNase and DNase activity by denaturation and also allowing the highest DNA binding to the silica membrane assembled within the MinElute™ column (Esser et al., 2006). This buffer was prepared the same day of its use, albeit it is possible to prepare it a few days before its use and store it in a dark room at RT (20 – 23°C) (Rohland and Hofreiter,

2007). The maximum storage time is three weeks before the GuSCN loses its activity and become unstable for DNA binding use (Rohland and Hofreiter, 2007).

To protonate the DNA or create the cations bridge between silica matrix and DNA, sodium acetate 3M pH 5.2 was used. Dynamics of this chemistry interaction, in a nutshell, is as follows: the GuSCN generates a stable layer of cations around the silica matrix negatively charged (Cockle et al., 1978; Esser et al., 2006). Whilst, the NaOAc increases the ionic strength forming the cation bridge with sodium ions, which join to the phosphate groups of DNA and to the silica matrix, thus improve the elution process of DNA (Esser et al., 2006; Wang et al., 2013). The salts were removed from the silica membrane through several washed with a commercial buffer (PE), in this case, from Qiagen® company, this procedure leaves the DNA free of salts and ready for the elution and storage process.

The DNA extraction process began by adding 3.82 mL EDTA Titriplex®III, Merck, 80 µL additive and 100 µL proteinase K, Merck to 200 mg of bone powder then it was incubated at 38°C per 18 hrs with rotation at 350 rph. To avoid leaks or drips of bone powder solution during this process, the 15 mL Falcon® tube was sealed with Parafilm® M, American National Clan™. Subsequently, 100 µL of proteinase K, Merck were added to the digestion reaction, and it was incubated at 56°C per 2 hrs at 350 rph.

The third incubation round and the stages of extraction with phenol-chloroform were identical to those used in the Oceania protocol above explained. The aqueous phase from the previous step with chloroform was transferred to a 50 mL Falcon® tube labelled with sample ID, which contained between 16 mL of GuSCN buffer 5M and 100 µL of NaOAc Invitrogen™, 3M pH 5.2. This solution was mixed softly by inversion and centrifuged at 3,300 rcf per 3 min.

Later, the solution of 50 mL Falcon® tube was transferred to a funnel connected to a MinElute™ spin column, with sample ID, which in turn was connected to vacuum system Qiavac Qiagen® and started the draining process of GuSCN buffer once this stage was finished, the funnel was disconnected from the column. The remainders of GuSCN buffer salts, in the

silica membrane, were washed adding 700 µL of PE-buffer and incubating at RT per 5 min, and incubating at RT per 5 min, and then, the vacuum system was turned on to remove the PE-buffer, this process was repeated two times more.

To remove the remains of PE-buffer, the MinElute™ column was centrifuged at 1,300 rpm per 1 minute, and then it was incubated at RT per 5 min to evaporate the ethanol. DNA elution step was carried out using pre-heated nuclease-free water at 56°C. The MinElute™ column was placed inside a 1.7 mL Eppendorf® tube, previously labelled with sample ID, extraction date and name initials of the person in charge of the extraction process. It was added 20 µL of nuclease-free water into silica membrane, left to incubate at RT per 5 min, this process was repeated two times more. After the final elution, the DNA was stored at -20°C until PCR amplification.

2.6 PCR amplification

Due to the nature of the samples, explained above, the PCR reactions and conditions were adjusted, in the same way as was done during the DNA extraction process. For Oceanian samples, the PCR reaction and conditions for amplification were performed without major problems. However, Central and South American samples needed two different PCR reaction enhancers, also developed during this work. PCR cycles during the annealing stage of amplification process also were adjusted. In a nutshell, the Polymerase Chain Reaction (PCR) consists of cycles of reaction heating and cooling (Mullis and Faloona, 1987).

Each temperature plateau is used to control a defined stage of the reaction and the incubation times (Douglas and Atchison, 1993). The initial denaturation phase consists of a period at high temperature, during which the secondary structure of the complex double-stranded DNA (dsDNA) is melted to become single-stranded DNA (ssDNA) (Douglas and Atchison, 1993). During the shorter denaturation step that initiates the cycling (10 sec to 1 min at 95°C), the DNA strands of the target sequence separate to form single strands, just as in the initial denaturation stage. The reaction is then cooled to the primer annealing temperature (Douglas and Atchison, 1993).

The annealing step (30 sec to 1 min, at temperatures 45°C – 60°C), is required so that the primers bind to the complementary sequence on each of the DNA single strands (Douglas and Atchison, 1993; Morrison and Gannon, 1994). The final stage is the extension step (20 sec to 1 min at 72°C), which is performed so that the DNA polymerase extends the primer sequences from the 3’ of each primer to the end of the amplicon (Morrison and Gannon, 1994). At the start of the second cycle, two forms of the template are in the reaction; original DNA strands and the newly synthesized DNA strands, consisting of the primer sequence followed by variable lengths of the amplicon extended at the 3’ end (Morrison and Gannon, 1994).

Remaining original DNA strands that were not primed in the first cycle may be captured in the second and result in molecules consisting of primer and extension product (Douglas and Atchison, 1993; Morrison and Gannon, 1994). The molecules from the first cycle that were primed and extended will be the template for primers that are complementary to the newly synthesized material (Douglas and Atchison, 1993). In the third cycle, the newly synthesized target region DNA resulting from the second cycle comprises only the amplicon and therefore becomes the specific template (Morrison and Gannon, 1994; Kainz, 2000). Cycling is repeated continuously, resulting in exponential amplification of the copied sequences (Kainz, 2000). At the end of the reaction, the amplification products are analysed using gel electrophoresis (Kainz, 2000).

aDNA fingerprinting and sequencing of HVSI

The genetic profile of archaeological human remains selected for this study was determinate with a short amplicon autosomal short tandem repeat (miniSTR) heptaplex system, which was developed by Seidenberg et al. (2012), especially for highly degraded DNA since the length of the amplicons do not exceed 200bp, with the exception of some rare alleles in the FGA and D21S11 systems (Seidenberg et al., 2012). This primer set encompasses the Amelogenin fragment that contains the information to determine the biological sex of people and six CODIS STR loci D5S818, D13S317, D18S51, D21S11, FGA, and TH01 (Seidenberg et al., 2012).

The HVSI of mitochondrial DNA was used to infer the genetic history and the possible biological relationships of the populations selected for this study. Fehren-Schmitz et al. (2009) designed a set of four primer pairs for mitochondrial HVSI. These primers were designed also for highly degraded DNA since the length of PCR products do not exceed 180bp, in point of fact the ranged size of these fragments is between 157 – 180bp (Fehren-Schmitz et al., 2010). These primers were designed also for highly degraded DNA since the lengths of PCR products

do not exceed 180bp, in point of fact, the ranged size of these fragments is between 157 – 180bp (Fehren-Schmitz et al., 2010).

The pairs of primers mt_H_15995 and mt_L_16256 were used in a singleplex reaction to obtain a fragment of ~261bp (Fehren-Schmitz et al., 2010). Later, It was prepared another single PCR reaction with the pairs of primers mt_H_16194 and mt_L_16429 to get a fragment of ~236bp (Fehren-Schmitz et al., 2010). Subsequently, the PCR products of heptaplex and mitochondrial HVSI were analysed in an agarose gel electrophoresis, and then in an ABI 3500 Genetic Analyzer of Applied Biosystem company.

Oceanian samples genetic profiles

Heptaplex STR amplification was carried out following the indications in Seidenberg et al. (2012). The total volume of the PCR reaction was 25 µL and its components were 12.5 µL Qiagen® Multiplex Plus Master Mix kit, 2.85 µL heptaplex primer set, 4.65 µL ultrapure water nucleases-free and 5 µL DNA extract. PCR amplification took place in an Eppendorf® Mastercycler gradient under the following conditions: initialization at 95°C per 5 min, 45 cycles of 1 minute at 94°C denaturation, 2.5 min at 59°C annealing/elongation and final elongation at 60°C per 45 min, and a final soak for 10 min at 10°C step (Seidenberg et al., 2012). The number of cycles was the only thing that was changed from the original protocol of Seidenberg et al. (2012) since they suggest to use 40 cycles, however, the Oceania samples needed five cycles more to have a successful PCR amplification.

PCR success and product quantity were checked by gel electrophoresis. To prepare a 2.5% agarose gel (Seidenberg et al., 2012), 40mL of Tris-Borate-EDTA (TBE) buffer was added to 1 gr of Roti®Agarose, Roth low melting point, the solution was heated until melting the agarose, after 1.5 µL of ethidium bromide. Afterwards, 8 µL of PCR product was mixed with 2 µL of loading dye. To check the amplicon size 4 µL of DNA ladder (New England Biolabs inc.) was used. The gel was run under the following conditions: 110 volts, 69 milliamperes per ~45 min. Finally, a photographic registration system was used to make evident and store the PCR

amplification results. Afterwards, the alleles were determined via capillary electrophoresis on ABI 3500 Genetic Analyzer (Applied Biosystems).

The chemistry reaction for determining the alleles in the genetic analyzer contained 12 µL of Hi-Di™ Formamide,Applied Biosystems™, 0.25 µL of GS ROX 500 and between 1 – 2 µL of PRC product. Denaturation cycle was performed in a Mastercycler gradient (Eppendorf®) at 95 C per 5 min followed by a cooling step at 4°C per ~2 min. The instrument was set to run under the fragment analysis protocol 36 POP 7 D with run module fragment analysis 36 POP 7, dye set D and base calling FLA_ROX 500_PA protocol for heptaplex assay (Seidenberg et al., 2012). For alleles evaluation, the GeneMapper software (Applied Biosystems™) version 4.1 was used.

Analysis of HVSI of mitochondrial DNA of Oceanian samples

To generate a DNA fragment of ~430bp was necessary to carry out two singleplex sets of amplification with two pairs of primers. Singleplex amplifications were performed in a total reaction volume of 25 µL containing 12.50 µL AmpliTaq Gold™ 360 Master Mix (Applied Biosystems™), 0.5 µL mt_H_15995 primer, 0.5µL mt_L_16256 primer, 6.50 µL ultrapure water nucleases-free and 5 µL DNA extract. In the second singleplex amplification used the same reagents and quantities that in the previous reaction, it was only changed the pair of the oligonucleotides, in this case, the pair of primers mt_H_16194 and mt_L_16429 were used.

PCR amplification took place in a Mastercycler gradient (Eppendorf®) under the following conditions: initialization at 95°C per 10 min, 45 cycles of 1 min at 95°C denaturation, 1 minute at 55°C annealing/elongation and final elongation at 72°C per 1.5 min, and a final soak for 10 min at 10°C step. PCR success and product quantity were checked by gel electrophoresis. The agarose gel preparation, registration of results and run conditions were the same as those used in the previous section, here the amount of PCR product used was 5 µL instead of 8 µL used in the previous section.

The amplicons generated in previous amplification processes were purified via ExoSAP-IT™ Express PCR Product Cleanup Reagent (Anffymetrix®). Cleaning up process consisted of mixing 5 µL of the post-PCR reaction with 2 µL of ExoSAP-IT™ Express reagent, then incubate at 37°C per 4 min to degrade excess of primers and nucleotides and an incubation step at 80°C per 1 minute to inactivate ExoSAP-IT™ Express reagent and final step of cooling at 4°C. The samples were stored at -20 until cycle sequencing reaction.

Cycle sequencing reactions were prepared using the forward primers (mt_H_15995 and mt_H_16194) and sometimes reverse primers (mt_L_16256 and mt_L_16429). The total volume of the PCR reaction was 20 µL and its components were 4 µL Bigdye buffer, 2 µL ABI Prism® BigDye®, 0.30 µL mt_H_15995 or mt_H_16194 primer, 11.70 µL ultrapure water nucleases-free and 1 – 2 µL PCR product purified or cleaned. This PCR amplification was carried out in a Mastercycler gradient (Eppendorf®) under the following conditions: initialization at 95°C per 10 min, 25 cycles of 10 seconds at 96°C denaturation, 5 seconds at 50°C annealing/elongation and final elongation at 60°C per 4 min, and cooling step at 10°C per 5 min.

Afterwards, clean-up of sequencing reaction was performed via NucleoSEQ kit (Macherey-Nagel GmbH & Co. KG). The general procedure to clean up the sequencing reaction consisted of spinning down the column with dried gel resin at 2,700 rpm per 30 seconds. Later, the gel resin was hydrated with 600 µL of HPLC water, the vortex mixer was used to eliminate the bubbles, and then the gel resin was incubated at RT between 30 min – 2 h. The water excess was removed off the gel resin through centrifugation at 2,700 rpm per 2 min., after the column was transferred to a collect tube (2 mL Eppendorf® tube) labelled with sample ID. Finally, the sample (20 µL of sequencing reaction) was loaded placing it to the centre of gel resin, and it was centrifuged at 2,700 rpm per 6 min.

Subsequently, the full content of the collection tube (~20µL) was transferred to a sequencing plate, where after a short spin at 3,500 rpm per 30 seconds, the analysis of DNA fragments was carried out capillary electrophoresis on ABI 3500 Genetic Analyzer (Applied Biosystems). The instrument was set to run under the fragment analysis protocol RapidSEq 36 POP 7 E with run module fragment analysis Seq POP 7, BDT v 1.1, and base calling BDT v1.1 PA Protocol POP 7 for mtDNA assay (internal protocol of Historical Anthropology and Human Ecology Institute at the Georg-August University of Göttingen). For sequences evaluation MEGA X 10.1 (Kumar et al., 2018) and Chromaseq 1.5 (Maddison and Maddison, 2018) computer programs were used.

Panama and South America genetic profiles

As in the previous sample batch here, the heptaplex STR primer set (Seidenberg et al., 2012) was also used to try to obtain the genetic fingerprint from Central and South America samples. Nonetheless, the PCR reaction and amplification conditions were slightly changed. The total volume of the PCR reaction was 25 µL (without water) and its components were 12.5µL Qiagen® Multiplex Plus Master Mix kit, 2.85µL heptaplex primer set, 9.65µL DNA extract. PCR amplification took place in a Mastercycler gradient (Eppendorf®) under the following conditions: initialization at 95°C per 5 min, 45 cycles of 1 minute at 94°C denaturation, 2.5 min at 59°C annealing/elongation and final elongation at 60°C per 45 min, and a final soak for 10 min at 10°C step (Seidenberg et al., 2012). PCR success and product quantity were checked by gel electrophoresis using the same protocol as in Oceania samples. The alleles determination was performed via capillary electrophoresis on ABI 3500 Genetic Analyzer (Applied Biosystems™) The procedure was exactly the same as that used to determine the genetic profiles of the samples from Oceania.

Analysis of HVSI of mitochondrial DNA of Panamanian and South American samples

To generate a DNA fragment of ~430bp was necessary to carry out two singleplex sets of amplification with two pairs of primers. However, the singleplex reactions were modified, since Central, and South American samples needed a PCR reaction enhancer to have a successful amplification. Prior to describing the details of the PCR reaction and amplification for these sample batches, it is necessary to explain the features and benefits of reagents selected to prepare the two PCR reaction enhancer solutions. Two Non-ionic detergents (Triton™ X-100, Sigma-Aldrich® and Tween® 20 molecular grade, Sigma-Aldrich®) and a derived protein from blood (serum) albumin of bovines (BSA), New England Biolabs inc., were the core components to prepare the PCR additives.

The main works of Triton™ X-100 and Tween® 20 in the PCR reactions are: Stabilise Taq polymerase, suppress the formation of secondary structures, and battle SDS contamination, which is a common carryover from the DNA extraction and can greatly inhibit Taq polymerase (Arnheim, 1990; Saunders et al., 1999), the final concentration of both detergents into the PCR reaction should be 5X. Whilst, the BSA main functions in the PCR reactions are: Prevent the reaction components from sticking to the tube walls, combat the humic acids carryover from the DNA extraction and battle PCR inhibitors such as melanin or phenolic compounds (Majorek et al., 2012), the final concentration of BSA into the PCR reaction should be 1X. Triton™ X-100 at 10%, Tween® 20 at 2% and BSA (New England Biolabs inc.) at 25mg/mL provoke the inhibition of PCR reaction by reducing Taq polymerase activity (Saunders et al., 1999).

PCR amplification was performed in a total volume of 25 µL containing 12.50 µL AmpliTaq Gold™ 360 Master Mix (Applied Biosystems™), 0.5 µL mt_H_15995 primer, 0.5 µL mt_L_16256 primer, 2.33µL ultrapure water nucleases-free, 4.17µL additive 5X (final concentration 1X) and 5 µL DNA extract. In the second singleplex amplification used the same reagents and quantities that in the previous reaction, it was only changed the pair of the

oligonucleotides, in this case, the pair of primers mt_H_16194 and mt_L_16429 were used. It is important to consider that South American samples batch; the components of PCR additive were only the two non-ionic detergents, while the PCR enhancer for Central American samples has three components, the two non-ionic detergents plus BSA.

PCR amplification took place in a Mastercycler gradient (Eppendorf®) under the following conditions: initialization at 95°C per 10 min, 45 cycles of 1 min at 95°C denaturation, 1 minute at 55°C annealing/elongation and final elongation at 72°C per 1.5 min, and a final soak for 10 min at 10°C step. PCR success and product quantity were checked by gel electrophoresis. The agarose gel preparation, registration of results and run conditions were the same as those used in the previous section (2.6.2 subsection Mitochondrial DNA_HVSI). The amplicons generated in previous amplification processes were purified via ExoSAP-IT™ Express PCR Product Cleanup Reagent (Anffymetrix®) following the same procedure used in the analysis of HVSI of mitochondrial DNA of Oceanian samples. Cycle sequencing reactions, clean-up of the sequencing reaction, analysis of DNA fragments and sequence evaluations for these sample batches were carried out following the same chemical processes and instrument protocols used with the Oceanian samples.

2.7 Population genetics Analyses

Nuclear DNA

The evaluation of the allele frequencies for six STRs loci (D13S317, D21S11, D18S51, TH01, D5S818 and FGA) was performed by contrasting the gene information obtained from archaeological human remains dating to the pre-European contact period (data obtained in this work), to samples of the derived populations after European contact from Oceania and America (data obtained from online databases) and samples of the ancestral populations (Africa, Asia and Europe) of America and Oceania.

The data set corresponding to Oceania contained individuals with self-declared ethnicity as New Zealanders from eastern Polynesia and New Zealanders from western Polynesia (Table 2). While the data set corresponding to America contained individuals self-defined as Hispanics or Mestizos (Argentina and Chile) (table 2). The genetic information of these six STRs loci for nine modern human populations belonging to five geographic regions (Africa, Asia, Europe, Oceania and Hispanic America) was downloaded from ALLST*R Autosomal Database for Short Tandem Repeats (http://allstr.de).

Table 2. Modern human populations used in this study and their respective sample size (N).

Continent	Zone / Country	N	Reference
Africa	General*	342	Hill et al., 2013
Asia	General*	97	Hill et al., 2013
Oceania	New Zealand_Western Polynesia	10998	Bright et al., 2010
	New Zealand_Eastern Polynesia	41504	Bright et al., 2010
Europe	Caucasians *	361	Hill et al., 2013
	Spain	658	Paredes et al., 2003
America	Hispanic America	236	Hill et al., 2013
	Argentina	562	Marino et al., 2006
	Chile	732	Vergara et al., 2012

*U.S. population samples. The individuals were selected considering their self-declared ethnic ancestry.

Statistical tools

Genetic landscapes were evaluated through R version 4.0.3 software (R Core Team, 2020) via Ridgeline plots. These charts allow visualizing the changes in distributions over time or space of several numeric variables (Chang, 2018; Wilke, 2021). The partially overlapping lines create the impression of a mountain range landscape (Wickham, 2010; Chang, 2018; Wilke, 2019; R Core Team, 2020). These graphics use a statistical technique called kernel smoother, estimating a real-valued function as the weighted average of neighbouring observed data (Wickham, 2010; Chang, 2018; Wilke, 2019; R Core Team, 2020). The weight is defined by the kernel, such that closer points are given higher weights (Wickham, 2010; Chang, 2018; Wilke, 2019). The estimated function is smooth, and the level of smoothness is set by a single parameter (Chang, 2018; Wilke, 2021). Thus, the genetic landscapes were visualized using the packages ggplot2 (Wickham, 2010) and ggridges (R Core Team, 2020).

The genetic structure in this work was evaluated with Arlequin 3.5.2.2 software, which is an integrated software for population genetics data analysis (Excoffier and Lischer, 2010). This software analyses the data both intra-population and inter-population level. In the first level, the statistical information is extracted independently of each population, whereas in the second level, samples are compared to each other (Excoffier and Lischer, 2010). Arlequin calculation settings were the following: Polymorphism control five per cent, it is mean whether a sample has more than five percent of missing data it will be excluded from the analysis.

Ten thousand permutations were used to execute both Analysis of Molecular Variance (AMOVA) and population comparisons (F-statistics). The estimative F-statistics including Fst (population sub-structure) the average genetic differentiation or subdivision (population-specific) and genetic variation (intra-population), Fis (inbreeding coefficient), and Fit (total inbreeding coefficient) (Hedrick, 2011). Tests were executed under one million steps of Markov chain and one hundred thousand dememorization steps. Both comparison and differentiation of the populations were analysed at five percent of the significance level.

Genetic affinities were evaluated via the informatics program Structure 2.3.4, which was used to infer the possible phylogenetic relationships among ancient samples from Oceania and samples from ten modern population belonging to five continental regions (Table 2). Structure analyses differences in the distribution of genetic variants (genotype data from unlinked markers) among populations with a systematic Bayesian clustering approach. This analysis also applying the Markov Chain Monte Carlo (MCMC) estimation to place samples into groups whose members share similar patterns of variation (Pritchard et al., 2000; Porras-Hurtado et al., 2013).

Occasionally, the starting configuration of the software generates some iterations that could lead spurious results owing to smaller sample sizes in each population (Pritchard et al., 2000; Oldt and Kanthaswamy, 2020). To minimize this effect before collecting data, the burn-in length was adjusted to ten thousand runs for each simulation. Whilst, to get accurate estimates, MCMC repetitions after burn-in were adjusted to one hundred thousand runs for each simulation. Considering the general history of the ancestry of the genetic groups analysed in this study, the model for the allele frequencies that best fitted to these data set was the correlated allele frequencies model, since assume that frequencies in the different populations are likely to be similar probably owed to migration or share ancestry (Pritchart et al, 2000).

Mitochondrial DNA

The main application of the genetic material of the mitochondria in population studies is to evaluate the possible genetic interrelationships of historically linked human groups, as well as to infer the maternal evolutionary history of populations. Therefore, the interpretation of the mitochondrial DNA sequences requires a frame of reference, which is given by the definition of the haplogroups of the individuals under study and the phylogenetic analysis based on the comparison of the sequences of the D-loop_HVSI (control region) of mtDNA.

Alignment of DNA sequences

Edition of the sequences was carried out via DNA Baser Sequence Assembler 5.15 software (Heracle BioSoft, 2018). Whilst, the alignments were done through MEGA X software (Kumar et al., 2018), the ClustalW algorithm, which in turn uses progressive methods based on sequence weighting, position-specific gap penalties and weight matrix choice to improve the sensitivity of multiple sequences alignments (Thompson et al., 1994). The number of polymorphic sites and the number of substitution events (transition /transversion), in the set of ancient samples sequences from Oceania, South America and Panama, were evaluated through DnaSP 6 (Rozas et al., 2017) and MEGA X software. Both the polymorphic sites and the number of transition and transversion events are affected by entropy levels inside a set of aligned sequences (Hall, 2001). Additionally, these parameters provide insight into the process of molecular evolution since they reflect the genetic variation by position in the sequences analysed (Strandberg and Salter, 2004).

In information theory, entropy, also called information entropy or Shannon entropy, measures the uncertainty of an information source (Gray, 2011; Dehghanzadeh et al., 2020). The basic concept of entropy in information theory has a lot to do with the uncertainty that exists in any experiment or random signal (Torkashvand et al., 2021). It is also "noise" or "disorder" that a system contains or releases (Gray, 2011; Dehghanzadeh et al., 2020; Chanda et al., 2020; Torkashvand et al., 2021). The information is defined in bits, which represent the

amount of information that a signal carries to encode the message (Chanda et al., 2020; Torkashvand et al., 2021). R version 4.0.3 software was used to visualize the entropy in each set of sequences through ggseqlogo package (Wagih, 2017).

Haplogroups definition

Definition of the haplogroups was performed via Haplogrep mtDNA haplogroup classification tool (Kloss-Brandstätter et al., 2011; Weissensteiner et al., 2016). To avoid biases in the definition of the haplogroups of the individuals analysed, those sequences with ambiguities were discarded. After the assignment of the haplogroups, the sequences whose haplogroups lacked coherence, with respect to the general set of analysed individuals, were discarded from further analyses.

Genetic diversity

Genetic diversity was quantified through the evaluation of diversity indexes, such as segregating sites (the number of variable positions or polymorphisms in a sample of DNA sequences), average number of nucleotide differences and haplotype diversity. The probability that two random sequences are different is known as nucleotide diversity, this can be expressed on a per site (π) or on per sequence basis (κ) (Rozas, 2009; Hedrick, 2011; Fusté, 2012; Fuchs Castillo, 2019). Whilst, haplotype diversity (H) is the probability that two random sequences are different, this is also known as gene/allele diversity or expected heterozygosity (Rozas, 2009; Hedrick, 2011; Fusté, 2012; Fuchs Castillo, 2019). Both the statistics based on site by site, and those based on haplotypes were evaluated using the DnaSP 6 software (Rozas et al., 2017).

The proportion of nucleotide sites that differ in the populations is estimated by

$$\pi = \frac{\kappa}{m} \quad \text{Nucleotide diversity} \tag{1}$$

$$\kappa = \frac{2}{n(n-1)} \sum_{i<j} d_{ij} \tag{2}$$

Mean number of nucleotide differences

$$\kappa = \sum_{i=1}^{m} h_i \tag{3}$$

$$h = \frac{n}{n-1} \sum_{j=1}^{4} \chi_{ij}^2 \quad \text{Heterogeneity/heterozygosity in at site i} \tag{4}$$

Where **m** is the total number of nucleotide positions; **κ** is the mean number of nucleotide differences; **n** is the number of sequences; $\mathbf{d_{ij}}$ is the number of nucleotide differences between sequences i and j; $\mathbf{h_i}$ is the heterogeneity at site i; $\boldsymbol{\chi_{ij}}$ is the relative frequency of nucleotide **variant j** at site 1 (Rozas, 2009).

Haplotype diversity or expected heterogeneity/heterozygosity in a set of sequences is defined as

$$H = \frac{n}{n-1}\left(1 - \sum_{i=1}^{h} P_i^2\right) \tag{5}$$

where **n** is the number of sequences; **h** is the number of haplotypes and $\mathbf{P_i}$ is the relative frequency of haplotype i (Rozas, 2009).

Neutrality test

The aim of the neutrality test is to distinguish between a DNA evolving randomly (neutrally) and one evolving under a non-random process, including directional or balancing selection, demographic expansion, or contraction (Templeton, 2006). A randomly evolving DNA sequences contain mutations with no effect on the fitness and survival of an organism (Hamilton, 2009; Hedrick, 2011; Fuchs Castillo, 2019). In the populations, these mutations fluctuate randomly through genetic drift. Tajima's D (Tajima 1989) and Fu's Fs (Fu 1997) are standard neutrality tests, their function is to identify sequences which do not fit the neutral theory equilibrium between mutation and genetic drift (Hamilton, 2009; Hedrick, 2011; Fuchs Castillo, 2019). Tajima's D uses mutation frequency information and is based on an infinite

sites model without recombination (Tajima 1989). Therefore, this statistic is more appropriate for short DNA sequences (Melton, 2008). Fu's Fs is also based on the infinite-site model without recombination but utilizes information from the haplotypes distribution. Fs is a more sensitive indicator of population expansion than Tajimas D (Melton, 2008). MEGA X, DnaSP 6 software were used to carry out the neutrality tests via Tajima'D and Fu's Fs parameters.

Tajima's D is calculated as the difference between estimators of nucleotide diversity ($\theta\pi$) and the polymorphic site (θ_S). Thus, the mathematical details of this test, according to Tajima, 1989, are following:

$$D - \frac{d}{\sqrt{\hat{V}(d)}} = \frac{\hat{\kappa} - \frac{S}{a_1}}{\sqrt{e_1 S + e_2 S(S-1)}} \tag{6}$$

$$\hat{\kappa} = \theta_\pi = \frac{2}{n(n-1)} \sum_{i<j} d_{ij} \tag{7}$$

$$\frac{S}{a_1} = \theta_S = \frac{S}{\sum_{k=1}^{n-1} \frac{1}{\kappa}} \tag{8}$$

$$\sqrt{e_1 S + e_2 S(S-1)} = \sqrt{var(\theta_\pi - \theta_S)} \tag{9}$$

$$D = \frac{\theta_\pi - \theta_S}{\sqrt{var(\theta_\pi - \theta_S)}} \tag{10}$$

$D \approx 0$ suggests drift-mutation equilibrium.
$D > 0$ Suggests recent population bottleneck or some form of balancing selection.
$D < 0$ Suggests population expansion or purifying selection.

Fu's Fs Mathematical definition (Fu, 1997).

$$F_S = ln\left(\frac{\hat{S}}{1-\hat{S}}\right) \tag{11}$$

$\hat{S}$ is the probability of having fewer alleles in a sample.

$$\hat{S} = p(\kappa_0 \leq \kappa | \theta = \theta_\pi) = \sum_{\kappa \geq \kappa_0} \frac{|S_\kappa| \theta_\pi}{S_n \hat{\theta}_\pi} \tag{12}$$

F_S is positive suggests recent population bottleneck.
F_S is negative suggests population expansion.

Mismatch distribution and population growth

Distribution of pairwise differences (mismatch distribution) can summarize the genetic diversity of a population (Jobling et al., 2013). However, the most important approach of this parameter is the inference of the demographic history of the population through changes in the effective population size such as expansion, contraction, or bottlenecks (Templeton, 2006; Hedrick, 2011; Jobling et al., 2013). Nonetheless, the DNA sequences must comply with the assumptions of neutrality, which it involves being in mutation/genetic drift equilibrium (Jobling et al., 2013). Raggedness index of Harpening is used to determine if the populations are consistent with the sudden population expansion model, which is based on the infinite allele model proposed by Kimura in 1971 (Rozas et al., 2017). The demographic history and expansion times of ancient samples from Oceania, South America and Panama were inferred through the pairwise differences and population size changes via DnaSP 6 software.

Inference of phylogenetic relationships

Hypervariable region I from mitochondria DNA was used to infer the possible phylogenetic relationships between the archaeological human remains from Oceania, South America and Panama. Additionally, the genetic clustering trends of seven modern populations belonging to two continental regions (Table 10) were evaluated, in order to determine whether the individuals from modern populations exhibited patterns of genetic clustering similar to the ancient samples of populations aforementioned. Before performing the construction of the phylogenetic trees, Iqtree 1.6.12-MacOSX program (Nguyen et al., 2015) was used to determine the most suitable evolutive model for the data set under study. Once selected the substitution model along the branches of the tree, a phylogenetic reconstruction was carried out via Maximum Likelihood algorithm (one thousand replications). Bayesian inference of phylogeny was carried out using one million of Markov chain Monte Carlo (MCMC) generations, this analysis was performed through MrBayes 3.2 software (Altekar et al., 2004) and Beast2 computer package (Bouckaert et al., 2019). Finally, Network 10.2.0.0 software

(Forster and Forster, 2020) and PopART (Population Analysis with Reticulate Trees) software (Leigh and Bryant, 2015) were used to construct and visualize evolutionary relationships via phylogenetic networks (Whitfield, 2011) through median-joining network algorithm and infer the coalescence time of mitochondrial lineages. The phylogenetic networks differ from phylogenetic trees by the explicit modelling of richly linked networks, by means of the addition of hybrid nodes instead of only tree nodes (Fagny and Austerlitz, 2021).

3 Result

3.1 PCR amplification

Samples from Oceania were the most successful regarding nuclear and mitochondrial DNA amplification with a success rate closer to one hundred percent for both genomes. Sadly, nuclear DNA amplification of Panamanian samples failed, inasmuch as they got only almost two percent of success (Fig. 6). Whilst, South American samples got moderated results for nuclear DNA amplification, they got just over thirty percent of success (Fig. 6); unfortunately, the number of individuals from the South America sample batch with successful PCRs was not enough to include them in the population genetic analyses, however, the genetic information obtained from them was useful to complement the information of their anthropological records.

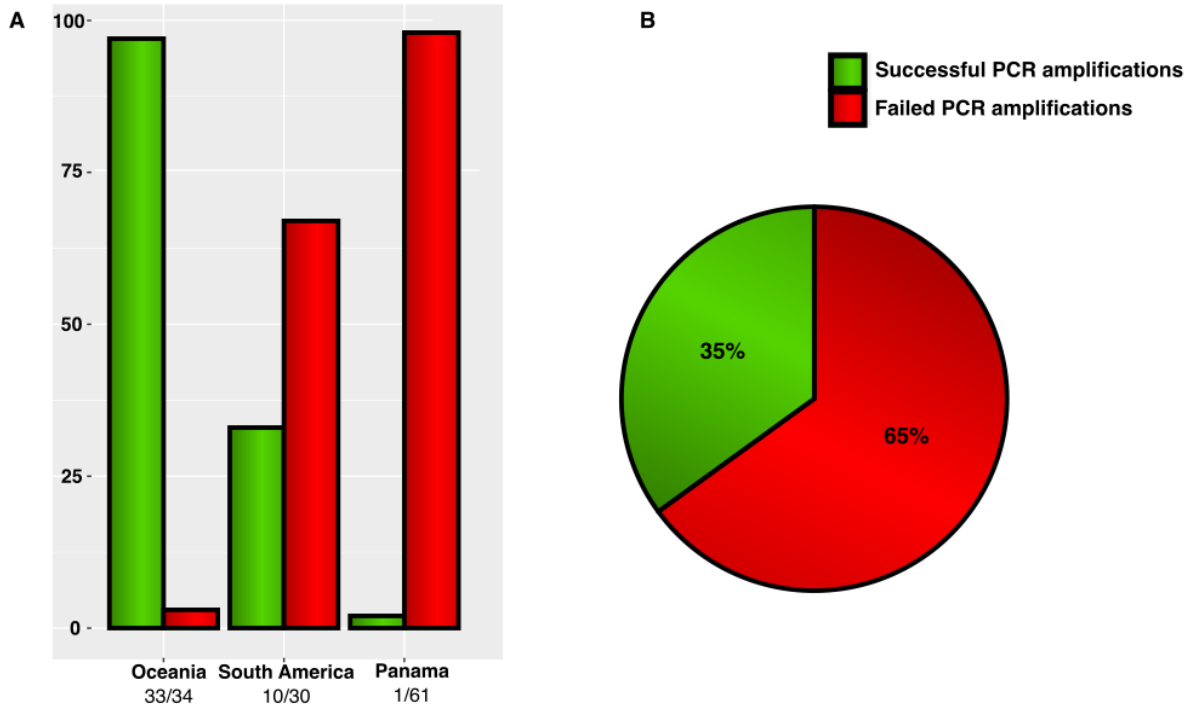

Figure 6. Success rate of nuclear DNA PCR amplification. Values on the ordinate axis show percentages of success or failure. **A**. Success rate by population. The abscissa axis shows individuals with success in PCR, starting from the total number of samples for each population. **B**. General success rate, considering the total number of samples for each population.

Fortunately, mitochondrial DNA amplification was very successful, since both Panamanian and South American samples reached success rates closer to one hundred percent, such as Oceania samples (Fig. 7). In general terms, the rate of success of nuclear DNA amplification could be considered between moderate to low, because only thirty-five percent of samples had successful PCRs. On the other hand, the general rate of success of mitochondrial DNA could be considered highly successful, since almost one hundred percent of the samples had successful PCRs for this genome.

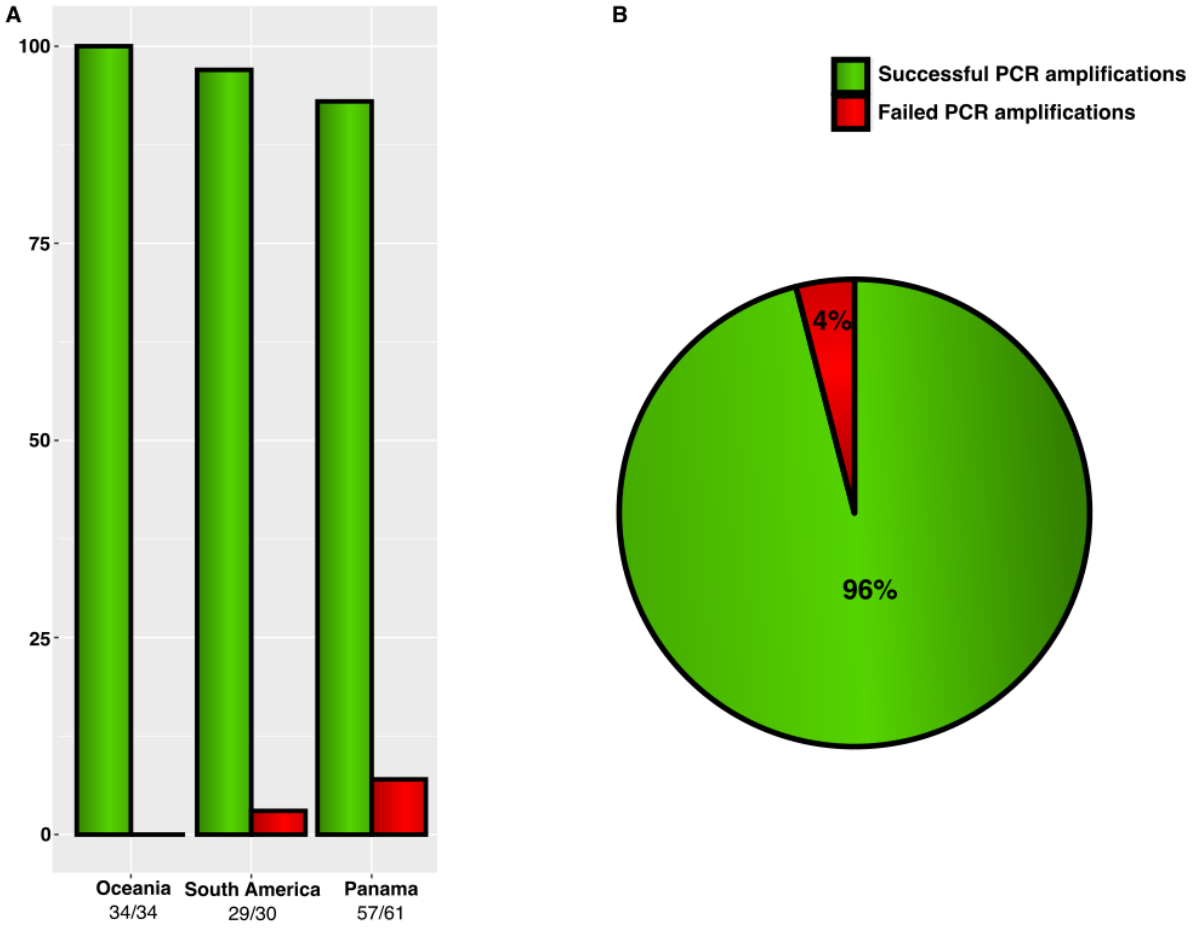

Figure 7 Success rate of mitochondrial DNA(HVSI) PCR amplification. Values on the ordinate axis show percentages of success or failure. **A**. Success rate by population. The abscissa axis shows individuals with success in PCR, starting from the total number of samples for each population. **B**. General success rate, considering the total number of samples for each population.

Biological sex was determined via the Amelogenin gene and then contrasted with morphological sex estimates. The aim of this comparison was to evaluate the congruence rate between anthropological and molecular biology methods to determine the biological sex of archaeological human remains. Oceania samples got a perfect congruence (100%) between biological and morphological sex (Fig. 8). Nonetheless, South American samples got a low match (20%) between biological and morphological sex. The samples from Panama were not in this analysis because of they did not get enough positive results for nuclear DNA after their PCR amplification. Generally, the correspondence rate between biological and morphological sex, for this work, could considerate moderately high (81%).

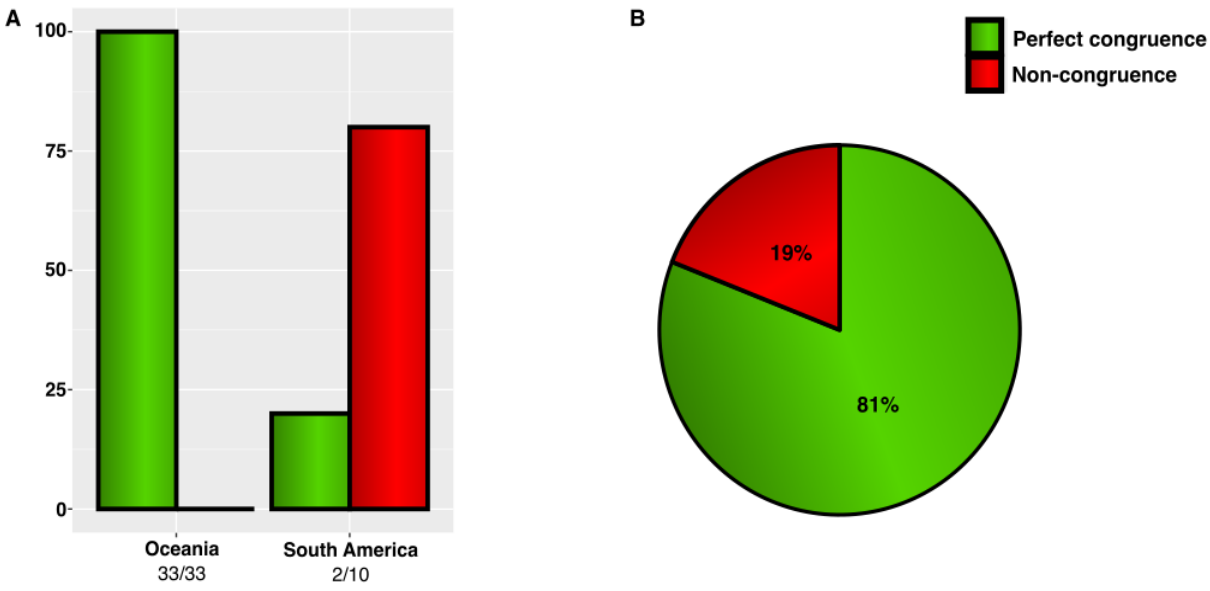

Figure 8. Congruence rate between biological and morphological sex. Values on the ordinate axis show percentages of success or failure. **A**. Success rate by population. The abscissa axis shows individuals with a perfect congruence between biological and morphological sex, starting from the numbers of successful PCRs amplification. **B**. General congruence rate, considering the total number of samples for each population.

3.2 Nuclear DNA

Behaviour of the allele frequencies and genetic landscapes

Patterns of allele frequency distributions of six STRs loci (D13S317, D21S11, D18S51, TH01, D5S818 and FGA) were evaluated on ancient samples from Oceania (baseline contrast population), and on nine modern populations (Table 1). These analyses showed that most of the modern populations had private alleles (Table3), and even some of them shared uncommon alleles at different loci (Table 4). Furthermore, when evaluating the pattern of allele frequency density distributions in modern individuals from Spain (Paredes et al., 2003), Argentina (Marino et al., 2006), New Zealand_Western Polynesia (Bright et al., 2010), New Zealand_Eastern Polynesia (Bright et al., 2010), and modern populations of Hispanics from the US (Hill et al., 2013) and modern European /Caucasian individuals from the US (Hill et al., 2013), it was observed that the behaviours of the allele frequency distribution for the six STR loci between modern Caucasians and Spaniards were very similar to each other, the same happened between modern Argentineans, Chileans, and Hispanics from US, and between modern New Zealanders from Western Polynesia and New Zealanders from Eastern Polynesia. Therefore, to avoid population redundancy, about the pattern of allele frequency density distributions, when contrasting the genetic landscapes between individuals from modern populations and ancient individuals from Oceania, five modern populations were selected (Africans, Asians, New Zealanders from Western Polynesia, Caucasians from the US and Argentineans) to perform these comparative populations (Fig. 9 - 11).

Ancient Oceanians did not exhibit rare or shared alleles with other modern populations which they were compared to. The allele frequency density distributions of these individuals also did not resemble any of the five modern populations shown in figures 9 to 11. This is likely resulting from the temporal distance between the modern populations and the ancient samples from Oceania. Furthermore, it is important to consider the genetic history and population

dynamics of the ancient Oceanians, which could be influenced by migratory events and ancestral miscegenation, as well as by the cultural and social aspects of the temporal space where to these individuals belonged. These factors could have affected the segregation patterns of some genetic markers in these individuals, which probably produced the distribution pattern of allelic densities that are observed in figure 9A.

According to genealogical arguments, alleles are related through a common ancestor (Hedrick, 2014; Cutter, 2019). Thus, the coalescent with symmetric stepwise mutation model is able to explain the formation of private alleles in a given population (Szpiech and Rosenberg, 2011; Hahn, 2018; Hartl, 2020). This model assumes that if a microsatellite allele has a point mutation that causes it to change in state by disrupting stretches of repeats, this mutation only can occur by only one step at a time either to add or remove repeat units, independent of the size of the allele (Saetre and Ravinet, 2019; Hartl, 2020; Talarico et al., 2021). In human populations, the number of derived alleles decrease with increasing distance from Africa, providing support for migration models out of Africa (Botigué et al., 2013; Talarico et al., 2021). This pattern is evidenced in figure 9B and Table 3, since of the ten populations analysed, six showed private alleles. Modern Africans exhibited twelve private alleles distributed in three STR loci, showing a greater allelic diversity compared to the rest of the modern populations analysed. The private alleles of the modern population of Africa (Fig. 9B), Asia (Fig. 9C), New Zealand _Western Polynesia (Fig 10B), Argentina (Fig. 11B) and modern Caucasians from the US (Fig. 11C), tend to be found in the tails rather than in the interior of allele size distribution, this allele behaviour usually is in the function of the genetic structure of the population; thus, the more the populations differ from each other, the probability of private allele occurrence in them increases (Szpiech and Rosenberg, 2011; Kinney et al., 2021).

Table 3. Private allele by population

Population	Locus	Allele	Frequency
Modern Africans	D21S11	29.3	0.002
		37	0.002
		38	0.002
		39	0.002
	D18S51	13.2	0.004
		15.2	0.002
		21.2	0.002
	FGA	16.2	0.002
		17.2	0.002
		25.2	0.002
		30.2	0.002
		31.2	0.002
Modern Asians	D21S11	28.2	0.005
		30.3	0.010
	D18S51	28	0.005
	FGA	43.2	0.005
Modern New Zealanders from Western Polynesia	D18S51	26	0.002
	D5S818	17	0.002
	FGA	20.2	0.002
Modern Argentineans	D13S317	7	0.002
	D21S11	36.2	0.002
	TH01	4	0.002
	D5S818	16	0.002
Modern Spaniards	D5S818	12.1	0.002
	FGA	26.2	0.004
Modern European Caucasians	D18S51	16.2	0.002
Modern Hispanics from US	D21S11	26.2	0.002

The allele frequency density distribution in the ancient Oceanic (Fig. 9A) presented a bimodal topology in the loci TH01, FGA, D5S818 and D13S317, which generated a double-ridge morphology, while D18S51 locus exhibited a subtle pattern double-ridge owing to quasi bimodality; however, D21S11 locus exhibited a unimodal topology with a single ridge morphology. The modern African genetic landscape (Fig. 9B) exhibited unimodal topological patterns with single-ridge morphology at the FGA, D5S818 and D13S317 loci. The D18S51 and D21S11 loci exhibited a multimodal pattern giving rise to a ridge line, while the TH01 locus exhibited a double-ridge morphology resulting from a bimodal topological pattern. Modern Asians (Fig. 9C) have an opposite pattern of allele frequency density distribution to ancient Oceanians, since the TH01 and D13S317 loci are the only ones that present a bimodal density distribution in their genetic landscape, although the D21S11 locus exhibited a subtle double-ridge pattern because of a quasi-bimodality, while the FGA, D5S818 and D18S51 loci presented a single-ridge morphology owing to its unimodal topology.

The genetic landscape of modern New Zealanders from Western Polynesia (Fig. 10B) exhibits a diverse topology and morphology in terms of allele frequency density distributions. The TH01 locus presents a density pattern of three modes, two to the left of the density distribution and one to the right, generating a plateau-like morphology on the left side resulting from the proximity of the two ridges, while on the right side shows a single ridge. The FGA locus has the highest density points distributed in three modes, being the highest one found in the centre of the allele distribution. The topology and morphology of the D5S818 locus corresponds to a trimodal pattern where the allele frequencies density distribution found on the right side is slightly higher than those found on the left side, generating a plateau-like

morphology with a subtle lift to the left side. The highest densities of the D21S11 locus are found towards the centre of the distribution, generating two subtle ridges, being the one on the left side slightly more prominent than the right side. Both the topology and the morphology of the D18S51 locus genetic landscape obey to bimodal density patterns, which generate two well-defined ridges towards the centre of the allele frequency distribution. Finally, the D13S317 locus presents a trimodal density topology, where the allele density distribution on the left side exhibits a subtle ridge, while the allele frequency density distributions on the right side are higher and generate a plateau-like morphology with a slight lift towards the right end, which represent the highest allele density point in this genetic marker.

TH01 and D13S317 loci of modern Caucasians (Fig. 10C) exhibit a shape and distribution similar to those observed in modern New Zealanders from Western Polynesia, although to the left side of the allele frequency density distribution of these loci the morphology and topology varied adopting a specular or chiral behaviour about that observed in modern New Zealanders from eastern Polynesia. D5S818 locus exhibit a bimodal topology where to the highest values of the allele frequencies density are located towards the centre of the distribution and also these values are quite close to each other, generating a subtle double ridge morphology. FGA locus in modern Caucasians exhibits a jagged ridge morphology resulting from a multimodal topology with the highest density of allele frequencies towards the centre of the distribution, the same is observed at the D21S11 locus; where to the point of higher density is slightly higher than in the anterior locus. Finally, D18S51 locus presents a multimodal topology with allele frequency density distribution values very close to each other, generating a morphology similar to a jagged plateau.

The modern Argentinians (Fig. 11B) genetic landscape shows that locus TH01 exhibits a double-ridge morphology, where to the left side ridge exhibit a wide bandwidth, regarding the right-side ridge, resulting from an allele frequency density topology multimodal where the differences between allele frequencies that sculpting the left side ridge is minimal. FGA locus

shows a faint multimodal topology resulting from the value closeness of the allele frequency multimodal distributions, generating a subtle double ridge morphology. D5S818 locus exhibit a single ridge pattern because of the highest allele frequency density values are located towards distribution centre. The locus D21S11 also shows a single ridge pattern with wider bandwidth regards to locus D5S818. The genetic landscape of D18S51 locus exhibits a trimodal topology with a triple ridge morphology. D13S317 locus shows a double-ridge morphology with wide bandwidth for both, nonetheless, although the ridges are not very pronounced, they are well-defined, because of the highest density points are grouped in two set, one of them are located towards decreasing number of repeats, while the another one is located towards increasing number of repeats.

Populations evaluated previously showed that morphology and topology of their genetic landscapes do not keep similarities to each other, since each one in their respective temporal space has their own genetic history and population dynamics which have sculpted their genetic landscapes. Some modern populations, such as those of America have at least three genetic components in the genome of their inhabitants; this biological inheritance was acquired around 500 years ago during the European period of colonization and exploration through miscegenation. Genetic (ethnic) admixture and replacement that occurred in some countries half a millennium ago, altered the allelic frequencies of the populations, generating the genetic landscapes that were observed in the New Zealanders (Fig. 10B) from Western Polynesia and Argentineans (Fig. 11B). Modern Asian, African and European populations have also undergone changes in their allele frequencies as well as certain admixture processes, which have shaped the genetic landscapes earlier observed. In summary, both the morphology and topology of genetic landscapes undergo changes over time owed to interbreeding processes, migration events, genetic drift and mating patterns.

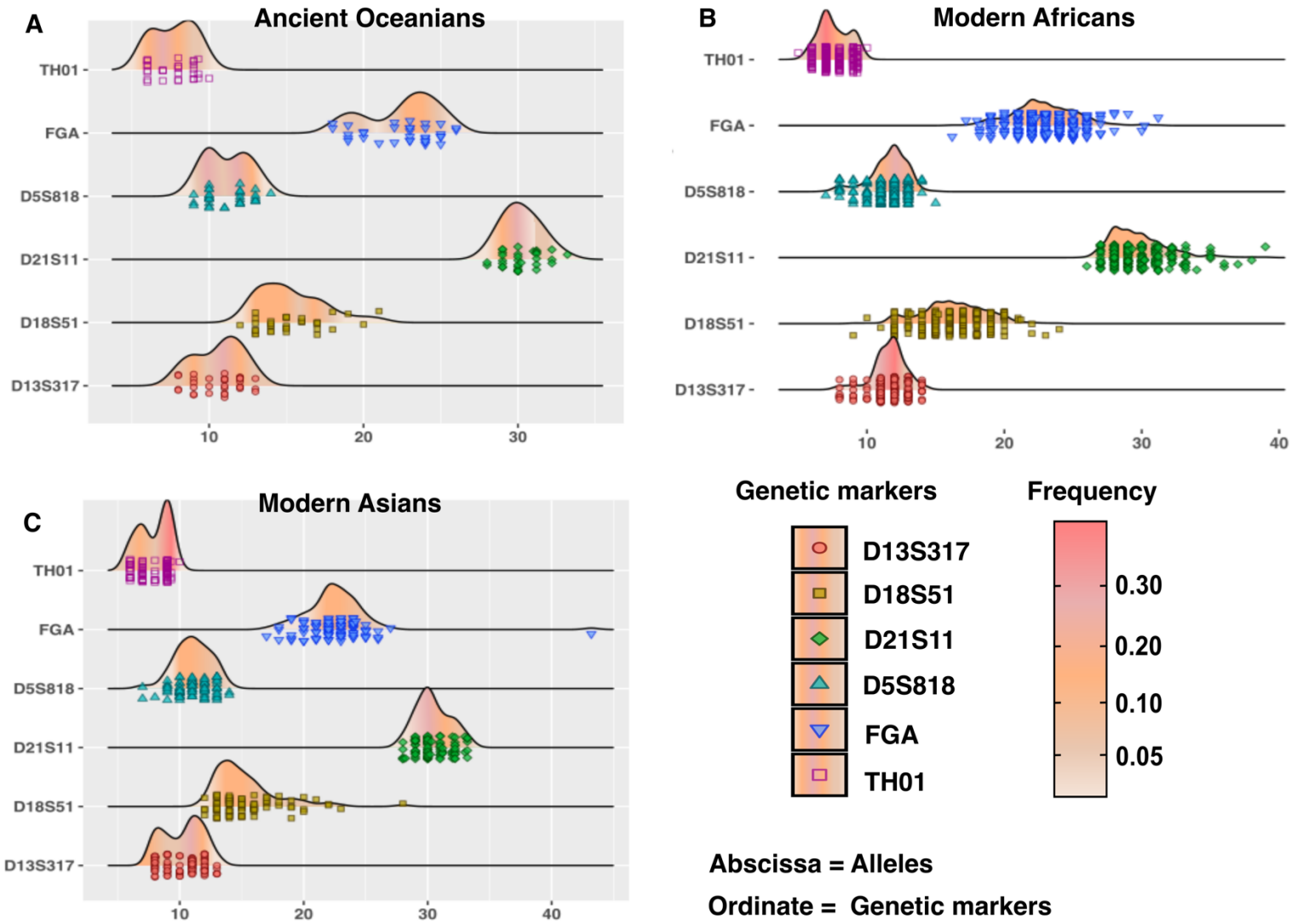

Figure 9. Genetic landscapes based on allele frequency density and distribution. The colour geometric forms onto the graphics describe the allele frequencies behaviour for each STR marker. Whilst, the genetic landscapes were described through the changes in the density distribution of alleles between ancient Oceanians, modern Africans, and modern Asians.

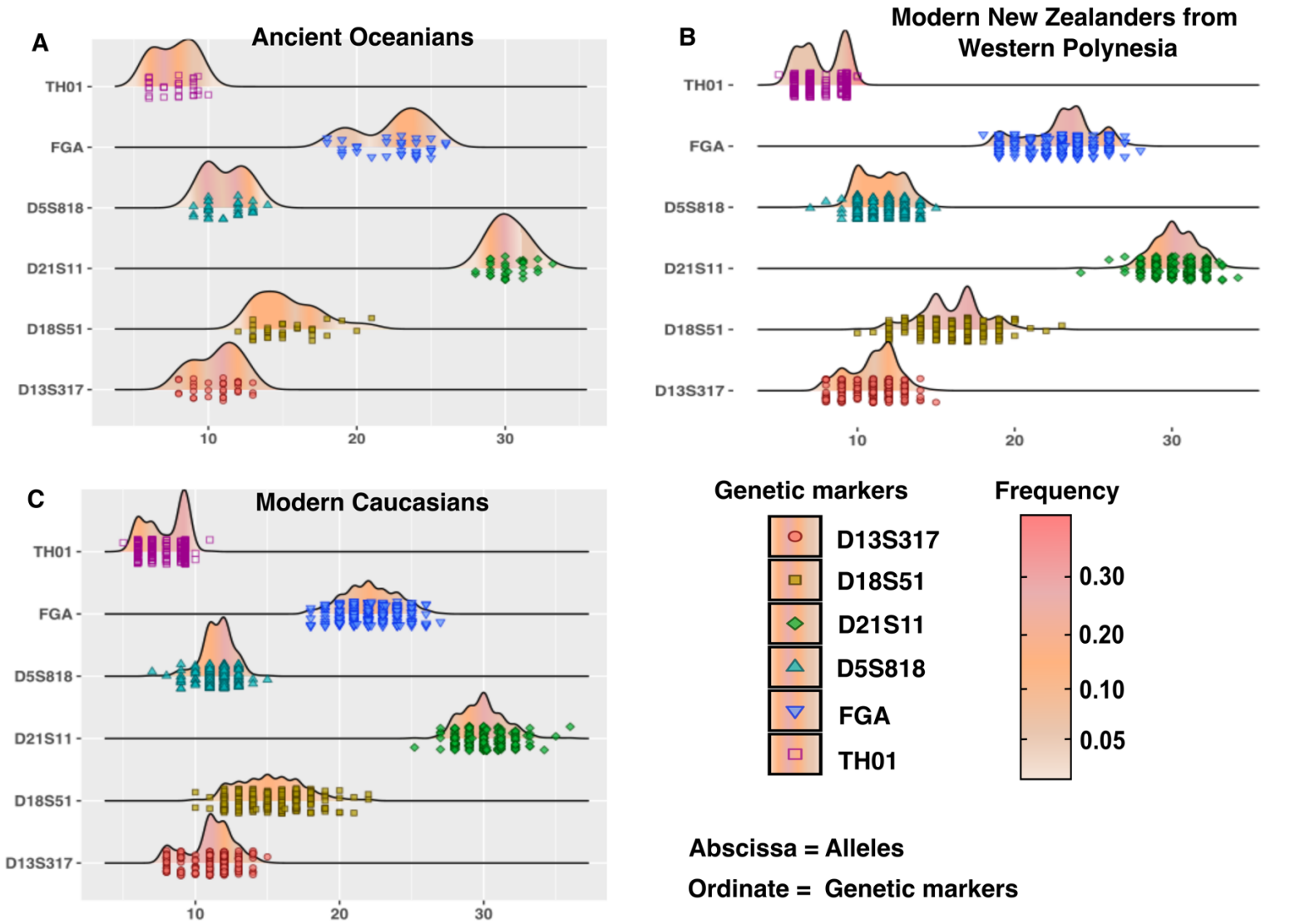

Figure 10. Genetic landscapes based on allele frequency density and distribution. The colour geometric forms onto the graphics describe the allele frequencies behaviour for each STR marker. Whilst, the genetic landscapes were described through the changes in the density distribution of alleles between ancient Oceanians, modern New Zealanders from Western Polynesia (similar to New Zealanders from Eastern Polynesia), and modern Caucasians.

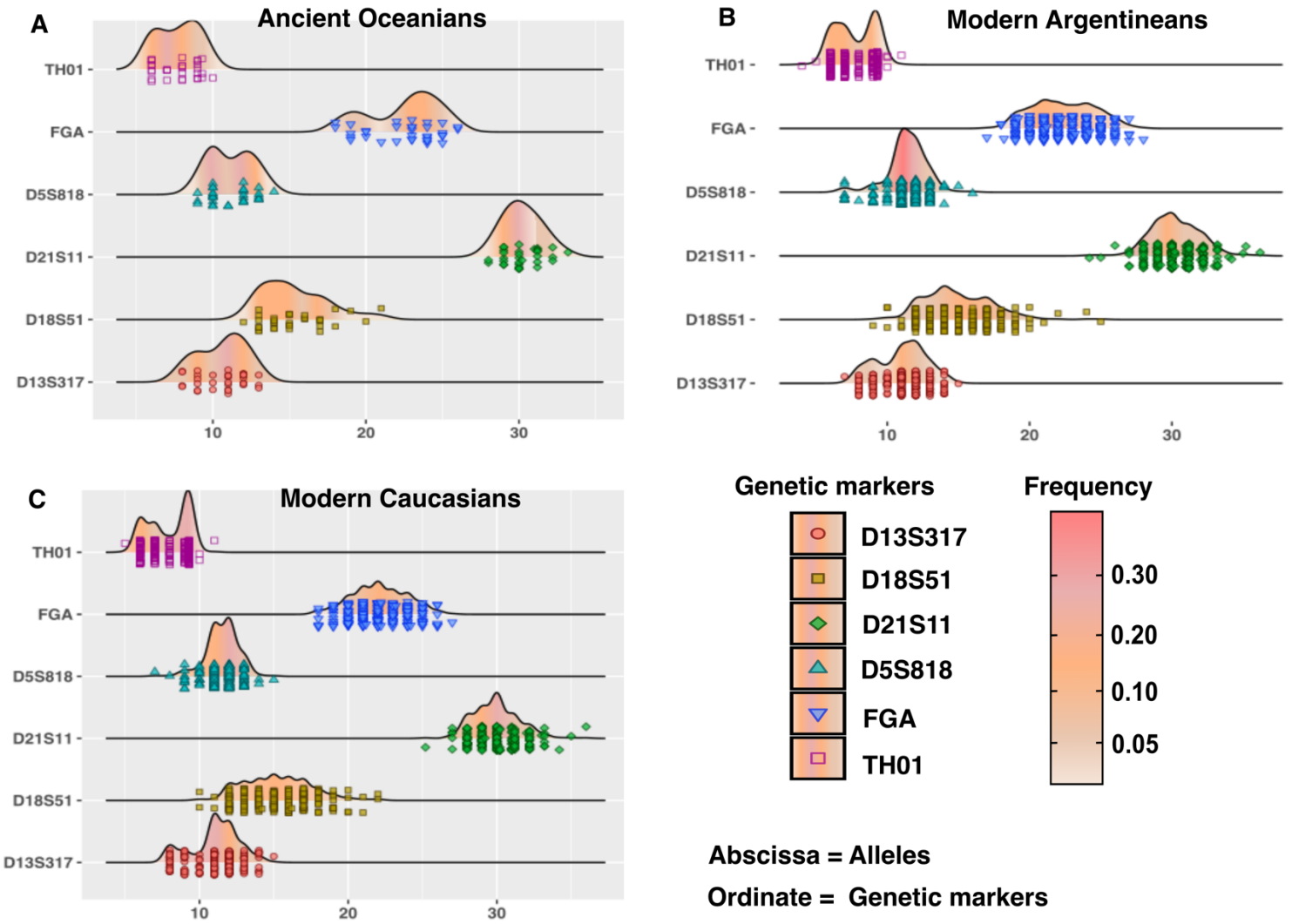

Figure 11. Genetic landscapes based on allele frequency density and distribution. The colour geometric forms onto the graphics describe the allele frequencies behaviour for each STR marker. Whilst, the genetic landscapes were described through the changes in the density distribution of alleles between ancient Oceanians, modern Argentineans (similar to modern Chileans and US Hispanics), and modern Caucasians (similar to modern Spaniards).

Shared uncommon or rare alleles are good gene flow indicators among different panmictic populations (Hedrick, 2014; Cutter, 2019; Hartl, 2020), besides the allele frequency, it is possible to infer the origin population of a given allele, based on source-sink model (Hahn, 2018; Saetre and Ravinet, 2019; Talarico et al., 2021). Shared alleles could be identical by descendant (IBD) or identical by state (IBS). IBD alleles are the same DNA inherited molecule several times through generations, this kind of alleles has high inbreeding rate, since they tend to inherit through consanguineous cross-breeding (Hedrick, 2014; Cutter, 2019; Hartl, 2020). Whilst, IBS alleles are different DNA molecules come from two different groups or populations, but they have the same genetic structure. IBS alleles are also IBD because of have been inherited from a common ancestor (Hedrick, 2014; Cutter, 2019; Hartl, 2020). The difference between IBS and IBD lie in that, IBD alleles come from a direct consanguineous cross-breeding between two individuals genetically related, while IBS alleles share a common ancestor dating back several generations (Hahn, 2018; Saetre and Ravinet, 2019; Talarico et al., 2021).

Four of the six genetic markers analysed had shared alleles (Table 4). The alleles 25 and 35.2 from D21S11 locus were shared by modern Argentineans and Spaniards. The frequencies of 25 and 35.2 alleles were two times higher in modern Spaniards than in modern Argentineans; thus, it can be assumed that de origin of these alleles in the modern Argentinean population is Spaniard. D18S51 locus exhibited two shared alleles (9 and 14.2). The 9-repeat allele is shared between modern Argentineans and Africans, and the allele in the Argentinean population has a clear African origin since its allele frequency is 3 times higher in Africans than Argentineans. The allele 14.2 was shared by modern Hispanics from the US and Caucasians from the US,

here the origin of this allele is unclear since the higher frequency is exhibited by modern Hispanics from the US, suggesting that the source population of 14.2 allele might be an Amerindian population and the presence of this allele in Caucasians from US could have given by genetic admixture.

Allele 5 from TH01 genetic marker was shared by modern Argentineans, Caucasians from the US, Africans, and New Zealanders from Eastern Polynesia, the source of this allele is evidently African since the allele 5 frequency is two times higher in modern Africans than Argentineans, and four times lower in modern Caucasian from the US and Zealanders from Eastern Polynesia regarding Africans. Finally, FGA locus had the 17 allele shared between modern Argentineans, Hispanic from the US, Spaniards and Asians. The origin population for 17 allele is evidently Asian, since its allele frequency five times higher in Asians than modern Hispanics from the US and six times lower in modern Argentineans and Spaniards regarding Asians.

Table 4. Shared uncommon alleles by locus

Locus	Allele	Frequency	Population
D21S11	25	0.0009	Modern Argentineans
		0.0018	Modern Spaniards
	35.2	0.0009	Modern Argentineans
		0.0018	Modern Spaniards
D18S51	9	0.0009	Modern Argentineans
		0.0029	Modern Africans
	14.2	0.0021	Modern Hispanic_US
		0.0014	Modern Caucasians _US
TH01	5	0.0022	Modern Argentineans
		0.0014	Modern Caucasians_US
		0.0044	Modern Africans_US
		0.0010	Modern New Zealanders_ Eastern Polynesia
FGA	17	0.0018	Modern Argentineans
		0.0021	Modern Hispanic _US
		0.0018	Modern Spaniards
		0.0103	Modern Asians_US

Genetic structure and diversity

Heterozygosity is the first step to quantifying the genetic diversity of the populations. The relative frequency of observed heterozygotes (Ho) can be affected by endogamy and population structure (Fuchs Castillo, 2019; Hartl, 2020; Láruson and Reed, 2021; Lohmueller and Nielsen, 2021). For this reason, it is important to determine the relative frequency of heterozygotes expected (He) under Hardy-Weinberg equilibrium (Fuchs Castillo, 2019; Hartl, 2020; Láruson and Reed, 2021; Lohmueller and Nielsen, 2021). Thus, the expected heterozygosity is the statistic commonly used to report the genetic diversity of the populations (Fuchs Castillo, 2019; Hartl, 2020; Láruson and Reed, 2021; Lohmueller and Nielsen, 2021). Thereby, the expected heterozygosity can be used to infer how often different alleles will be added in a population to form heterozygous (Nei, 1973; Harris and DeGiorgio, 2017; Fuchs Castillo, 2019; Hartl, 2020; Láruson and Reed, 2021; Lohmueller and Nielsen, 2021).

At the global level, populations displayed heterozygosity values among seventy-nine and eighty percent (Table 5). These results suggest that the populations show high diversity and that at genetic systems each locus has elevated probabilities to increase heterozygous in the populations. On the other hand, the population sub-structure coefficient (Fst), global level, exhibited a low value (0.018), indicating that there is no distinguishable genetic structure within populations. The inbreeding level of individuals within the population groups was low since the Inbreeding coefficient, Fis= 0.005. Nevertheless, the total inbreeding coefficient indicates that within-population groups there is a panmixia (random mating) level between low and moderated, Fit = 0.023.

Analysis of molecular variance (AMOVA) showed that the vast majority of genetic variation is found within individuals (almost 98%), and not between them. Nonetheless, there is a small genetic differentiation between population groups (1.02%). However, when contrasting the Fst of each population (Fig. 12), it is possible to notice that there are subtle differences between the population groups, providing some insight into the degree to which

populations were historically connected (Holsinger and Weir, 2009). When comparing ancient samples from Oceania with individuals from modern populations, it could see that between ancient Oceanians and modern Africans, there was more genetic variation than with modern individuals from Eastern Polynesia, Spain, Argentina, Chile. These genetic variations and similarities between ancient and modern populations might be attributed to the genetic admixture that took place about 500 years ago between the old (Europe) and new world (America and Pacific region). European colonization and exploration period in America and Oceania brought with it a progressive erase of ancient genetic structures and gene pool replaced of indigenous populations, this population replacement was mediated by miscegenation processes either voluntary or forced.

Modern individuals from Western Polynesia, Asia y European Caucasians exhibited a moderated genetic differentiation regarding ancient individuals from Oceania, which might be explained with the aforementioned. Basically, when comparing the ancient Oceanians with modern populations what is observed is the population dynamics between two different temporalities, whose apparent divergences and convergences regarding their Fst values could be biased due to the different population dynamics that they have been through the modern population in the last 500 years.

Table 5. Expected and observed heterozygosity.

Population	Ho	He
Ancient Oceanians	1.000	0.808
Modern Argentineans	0.820	0.819
Modern Chileans	0.826	0.817
Modern Hispanic Americans	0.838	0.818
Modern European Caucasians	0.804	0.798
Modern Spaniards	0.812	0.807
Modern Africans	0.802	0.794
Modern Asians	0.802	0.795
New Zealanders Western Polynesia	0.786	0.786
New Zealanders Eastern Polynesia	0.802	0.800

Table 6. AMOVA results for ten population based on six STR loci.

Source of variation	Sum of squares	Variance components	Percentage variation
Among groups	869610.943	181.268	1.020
Among populations within groups	328648.706	136.757	0.770
Among individuals within populations	35366895.921	83.130	0.470
Within individuals	35207512.500	17446.736	97.750

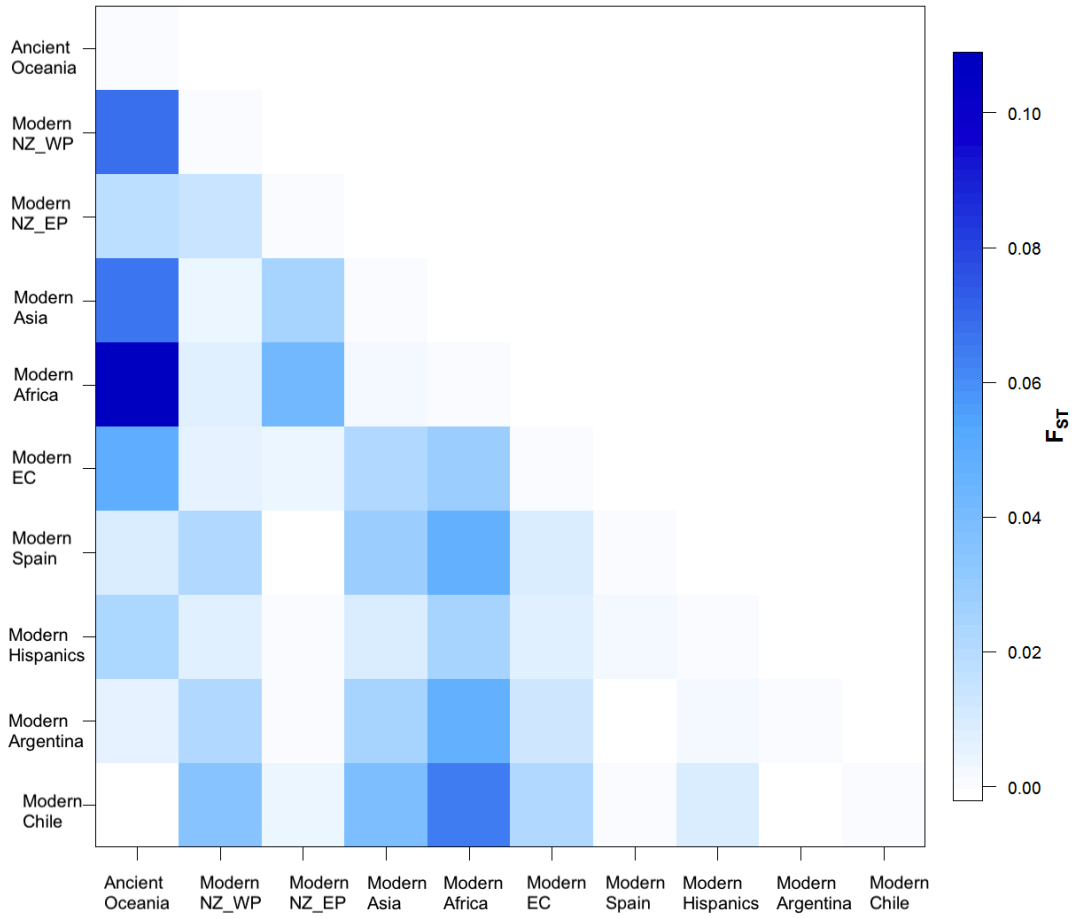

Figure 12. Genetic differentiation. Fst values show the degree of genetic differentiation between populations. NZ_EP: New Zealanders from Eastern Polynesia, NZ_EP: New Zealanders from Western Polynesia, EC: European Caucasians from USA.

3.3 Mitochondrial DNA

Genetic variation of archaeological human remains at the sequences level

The evaluation of the HVSI_mtDNA sequence alignments of ancient samples revealed that skeletal remains from Oceania exhibited around one hundred substitution events, whose transition (TS): transversion (TV) ratio (based on Maximum Likelihood Estimate of Substitution Matrix (MLESM)) (Table 7 - 9) was around 5.6:1. While South American and Panamanian samples batches also had one hundred events with TS: TV ratios= 7.6:1 for South America and 7.9:1 for Panama. On the other hand, the levels of entropy are a way of visualizing or predict the distribution of genetic variability by position (Strandberg and Salter, 2004), since the entropy is conceived as a measure of disorder or the peculiarity of certain combinations into a set of sequences. DNA can maximally carry two bits of information, and protein sequences about 4.3 bits, since, DNA consists of four bases A, T, G, and C, so there are four possibilities; so, the maximum amount of information $\log2(4) \approx 2$ bits (Dehghanzadeh et al., 2020). In proteins, there are 20 different amino acids; so, the maximum amount of information one amino acid can carry is $\log2(20) \approx 4.3$ bits (Dehghanzadeh et al., 2020). Thus, the number of segregating or polymorphic sites of the populations aforementioned can be visualized through their entropy levels via sequence logo (Fig. 13 -15). The positions in an aligned sequence set with the lowest amount of bits are those that provide the most information about the level of polymorphism in a population (Torkashvand et al., 2021)

Table 7. Oceania TS and TV events

	A	T	C	G
A	-	1.58	2.63	**10.65**
T	2.41	-	**29.81**	0.97
C	2.41	**17.89**	-	0.97
G	**26.45**	1.58	2.63	-

Table 8. South America TS and TV events

	A	T	C	G
A	-	1.14	1.93	**7.09**
T	1.77	-	**40.16**	0.7
C	1.77	**23.72**	-	0.7
G	**17.93**	1.14	1.93	-

Table 9. Panama TS and TV events

	A	T	C	G
A	-	1.39	2.19	**8,02**
T	2.1	-	**35.65**	0.81
C	2.1	**22.6**	-	0.81
G	**20.76**	1.39	2.19	-

Tables 7 - 9. Maximum Likelihood Estimate of Substitution Matrix. These matrices show the probability of substitution from one base to another. Transition events (TS) are shown in bold and those of transversions events (TV) are shown with normal typography.

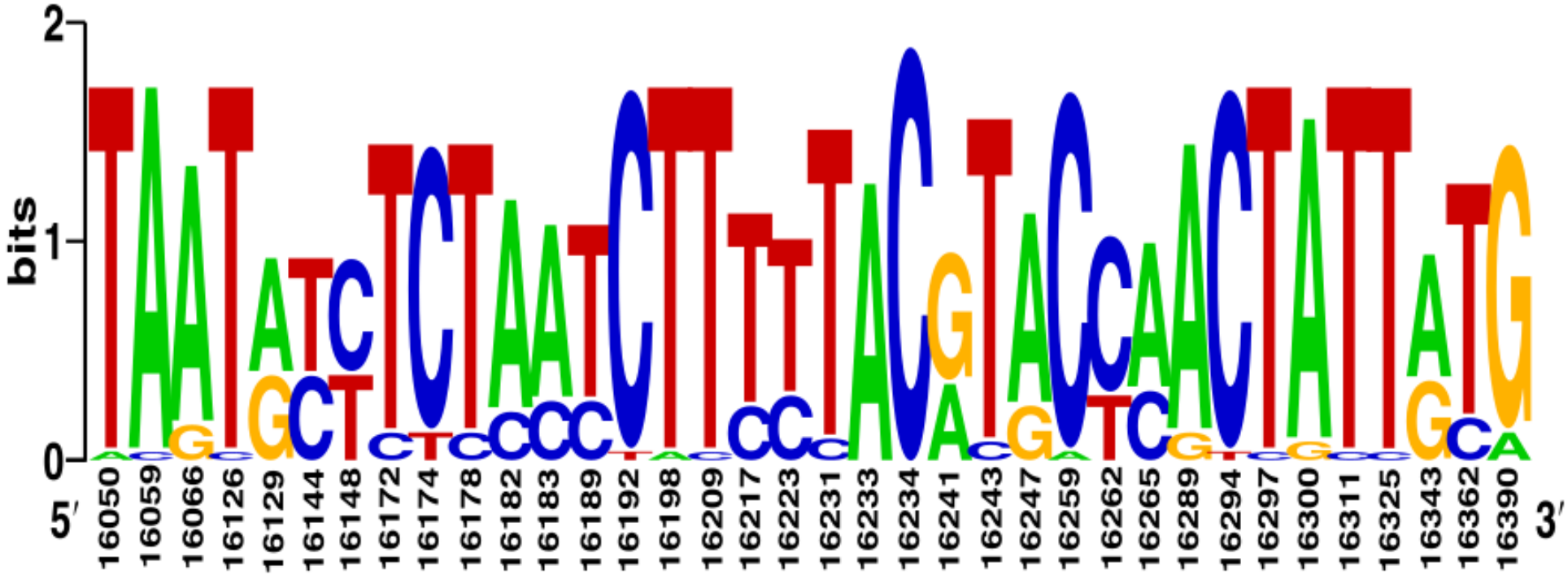

Figure13. Sequence logo of ancient Oceanians. This chart shows the entropy levels and hence the informativeness about all polymorphic sites found in this batch of aligned sequences. Position with less than 2 bits provides more information about the polymorphism for instance if it is frequent or uncommon such as positions 16129, 16172 or 16182.

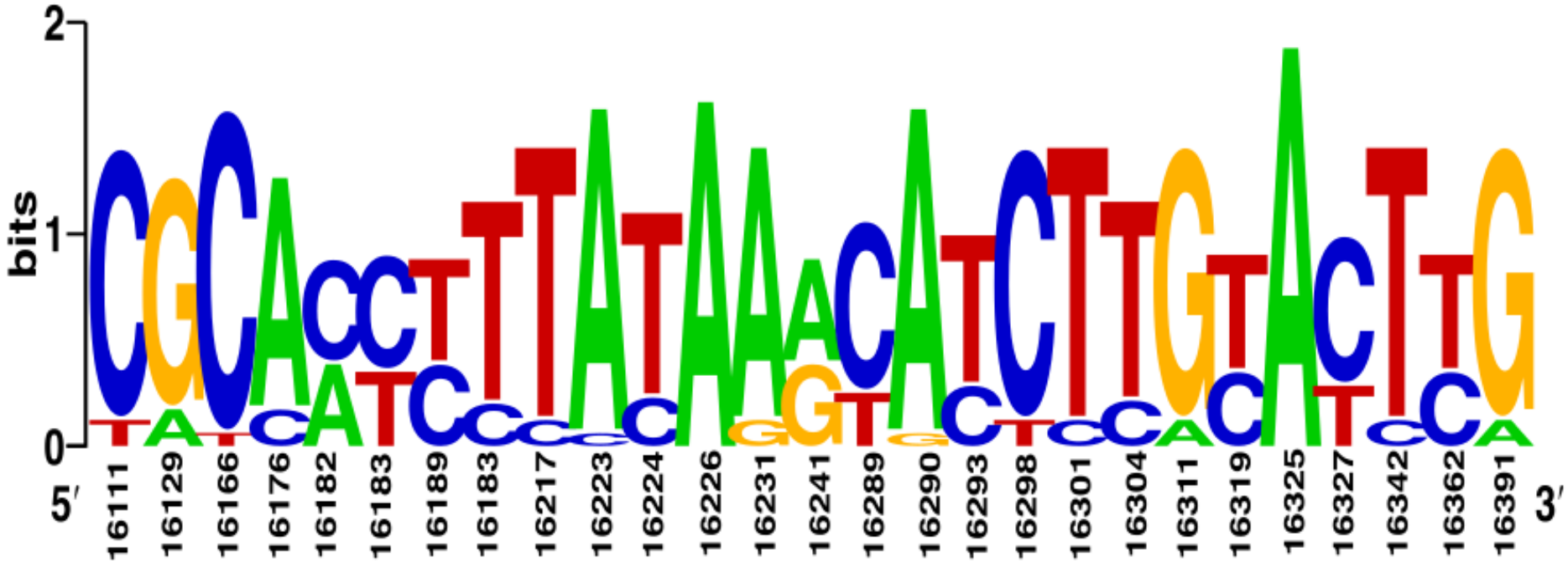

Figure 14. Sequence logo of ancient South Americans. This chart shows the entropy levels and hence the informativeness about all polymorphic sites found in this batch of aligned sequences. Position with less than 2 bits provides more information about the polymorphism for instance if it is frequent or uncommon such as positions 16129, 16176 or 16183.

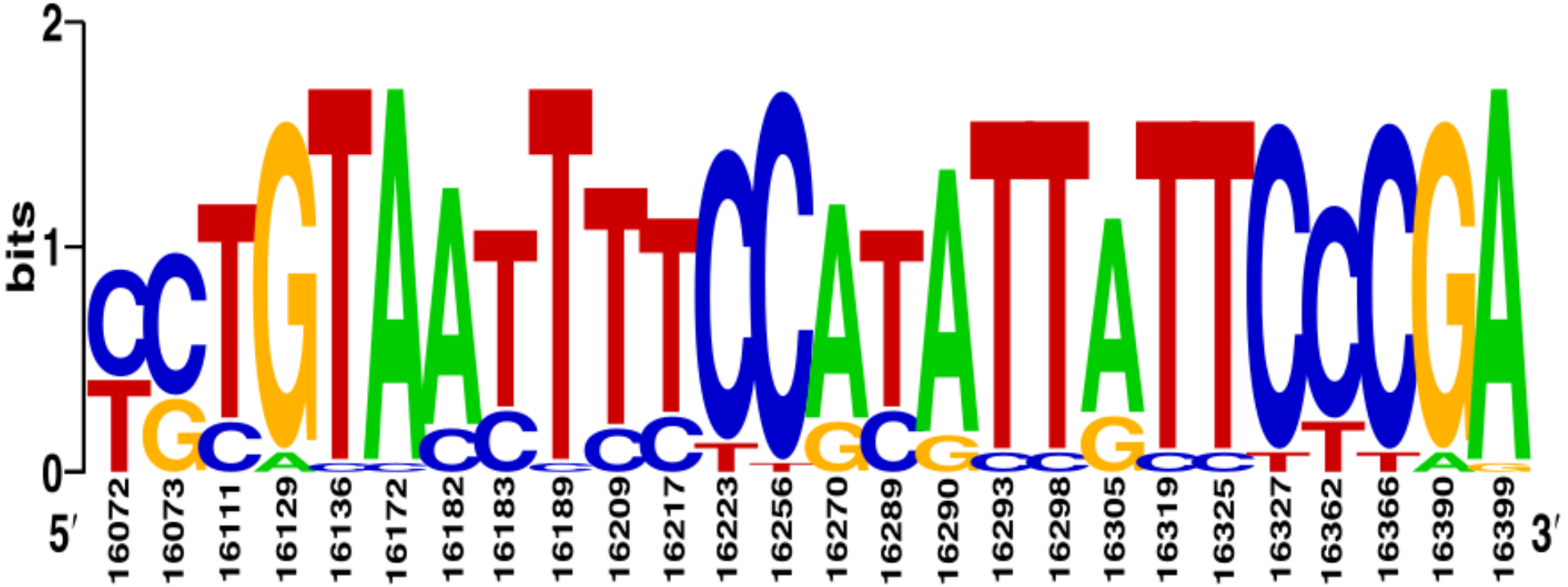

Figure 15. Sequence logo of ancient Panamanians. This chart shows the entropy levels and hence the informativeness about all polymorphic sites found in this batch of aligned sequences. Position with less than 2 bits provides more information about the polymorphism for instance if it is frequent or uncommon such as positions 16072, 16111or 16293.

Genetic diversity

Genetic variation of the ancient samples set from Oceania, South America and Panama were estimated through the number of segregating or polymorphic sites, nucleotide and haplotype diversity. The θ parameter is a diversity estimator, which can be interpreted as the probability of mutation between the sites of a set of aligned sequences (Fuchs Castillo, 2019; Hartl, 2020). The genetic diversity among the different sequence sets was estimated, considering the average number of nucleotide differences per site among DNA sequences.

Thus, ancient samples from Oceania, South America and Panama exhibited a low proportion of segregating sites (8.22%, 6.10% and 6.36%). The nucleotide diversity fluctuated between 0.024 and 0.018, while haplotype diversity oscillated between 0.132 and 0.032 (Table 10), indicating a low genetic diversity, and suggesting that the evaluated mitochondrial region in the populations previously mentioned, exhibit vestiges of the founder effect and/or genetic bottlenecks by which their respective ancestral populations went through during the initial settlement of these regions.

Table 10. Genetic diversity of HVS-I mtDNA of archaeological human remains from Oceania, South America and Panama.

Sample set	S	% Segrating sites	θs	θπ	θh
Oceania	31	8.22	0.026 ± 0.016	0.024 ± 0.013	0.132 ± 0.039
South America	23	6.10	0.018 ± 0.010	0.029 ± 0.016	0.106 ± 0.034
Panama	24	6.36	0.021 ± 0.011	0.018 ± 0.011	0.032 ± 0.019

S= number of polymorphic (segregating) sites; θs = probability of segregating sites; θπ = nucleotide diversity; θh = haplotype diversity; ± = standard deviation.; Confidence Interval (CI) = 95%; significance level (α) = 5%.

Ten mtDNA lineages were detected in ancient Oceanian samples (Fig. 16). 70.59% of identified mitochondrial lineages belonged to Oceanian mtDNA haplogroups. Whilst, 17.65% of these mitochondrial lineages belonged to Asian Haplogroups. The remaining 11.76% were mtDNA variants, whose polymorphisms did not correspond to Oceanian or Asian lineages or the sequences showed many ambiguities; thus, these individuals were excluded from the analyses since they could generate distortions in the results.

East and Southeast Asian haplogroups

The haplogroup B4c1a1 had a frequency of 2.94% in ancient Oceanians. The coalescence age of this lineage is at 8,300 years (95% CI 5,100 – 11,450 years), usually this mitochondrial variant is found in Japan (Tokyo and Aichi) (Mikami et al., 2013; Yao et al., 2021; Jinam et al., 2021). Haplogroup E1a2 exhibited a frequency of 5.88% in ancient Oceanians. This mtDNA variant appears to have arisen in Island Southeast Asia 9,400 years ago (95% CI 6,550 – 12,250 years ago) (Issiki et al., 2018). Haplogroup E1a2 has been linked to the Austronesian expansion model from Taiwan to Oceania via the Philippines (Issiki et al., 2018). Usually, this lineage is found in Taiwan, Malay Archipelago, and Papua New Guinea (Issiki et al., 2018; Duggan and Stoneking, 2021). The 2.94% of ancient Oceanias were affiliated to haplogroup D4h1. This mitochondrial variant is present in China (Chunxiang et al., 2020). Haplogroup D arose in East Asia 47,500 years ago (95% CI 35,000 – 60,000 years ago), in the Upper Pleistocene, before the Last Glacial Maximum and the settlement of the Americas (Chunxiang et al., 2020; Thompson, 2019; Duggan and Stoneking, 2021; Hoffecker et al., 2021).

Haplogroup M7b1a1i exhibited a frequency of 2.94% in ancient Oceanians. This lineage is found in Taiwan, Philippines, Malaysia, and also in Borneo, Indonesia (Jiao, 2021). The mitochondrial variant M65a was also found in 2.94% of ancient Oceanians. Haplogroup M65a is found in India, Pakistan, Gorno-Badakhshan, Tajikistan, Ladakh, Myanmar, and China (Peng et al., 2018). Haplogroup M arose about 60,000 years ago (95% CI 55,000 – 65,000 years ago)

in South Asia, Southwest Asia, Southeast Asia or East Africa (O'Connell et al., 2018; Vai et al., 2019; Jiao, 2021). This lineage is associated with modern human expansions out of Africa, since, all non-African mtDNA haplogroups are descendants of either haplogroup M or N (O'Connell et al., 2018; Vai et al., 2019).

Oceanian haplogroups

The 38.24% of ancient Oceanias were affiliated to haplogroup Q1. This mitochondrial variant is present in Australia belonged to individuals with Torres Strait Islander ancestries, which are known for their close links with New Guinea, and are associated with the Q1 lineage expansion during the postglacial warming period at 10,000 – 18,000 years ago (Nagle et al., 2017; Pedro et al., 2020; Choin et al., 2021). However, the 8.82% of individuals showed the haplogroup Q2, while Q2a3b had a frequency of 2.94% in this set of samples. This Q2 lineage is found mainly in the Bismarck Archipelago, Melanesia, it is linked with the demographic expansions following the initial settlement of New Britain around 35,000 years ago, and its diversification (restricted to Near Oceania) began in the post-Last Glacial Maximum period and continued into the Holocene; although a few Q2 lineages have been observed in Remote Oceania with coalescence ages in the Upper Holocene (Pedro et al., 2020).

B4a1a1 lineage had a frequency of 17.65% in ancient Oceanians. This haplogroup is associated with coalescence age around 7,000 years ago (95% CI 6,600 – 7,500 years ago), it is commonly observed in Vanuatu, Papua New Guinea and Tokelau atoll populations (Gosling et al., 2021), it is considered as the immediate precursor of Polynesian motif (B4a1a1a1), and is associated with Austronesian expansion (Soares et al., 2011; Fehren-Schmitz et al., 2017; Davis, 2021; Duggan and Stoneking, 2021). The 2.94% ancient Oceanians were affiliated to haplogroup B4a1a1a11b. This mitochondrial variant is found in the Solomon Islands (Bellona) and Cook Islands (Davis, 2021).

Pan-American haplogroups

Seven mtDNA lineages were detected between ancient South American and Panamanian samples (Fig. 17 – 18). Haplogroup A2 represent 58.97% of the mtDNAs in ancient samples from Panama, while 8.33% of ancient South Americans exhibited a A2 lineage. Mitochondrial variant A2 is the most common in Amerind ethnic groups of North and Central America, it is also found in South American Amerind groups but in low frequencies (Moreno-Mayar et al., 2018; Posth et al., 2018; Llamas et al., 2020; Suarez and Ardelean, 2019; Hoffecker et al., 2021). The coalescence age of this lineage is at 10,600 years (95% CI 9,600 – 11,700 years) (Barrantes, 1993; Meltzer, 2009; Suarez and Ardelean, 2019; Delgado et al., 2021). Haplogroup A might be descended from a population that has emerged from a bottleneck approximately 20,000 years ago, in East Asia (Moreno-Mayar et al., 2018; Posth et al., 2018; Llamas et al., 2020; Hoffecker et al., 2021). 20.83% of South American samples exhibited the B2 lineage, while 10.26% of ancient Panamanian showed this mitochondrial variant. Coalescence time of haplogroup B2 is about 16,500 years (95% CI 13,800 – 19,200 years) (Tamm et al., 2007; Achilli et al., 2008; Hoffecker et al., 2021). The B2 lineage, like A2 mtDNA variant, is a Pan-American lineage, B2 mitochondrial variant is widespread in North, Central and South America, and it has a high frequency in the South American Andean region and Aridoamerica region (the Southwestern United States and Northern Mexico) (Morales-Arce et al., 2017; Barbieri et al., 2019; García et al., 2021).

Haplogroup B2a had a frequency of 2.56% in ancient Panamanian samples, however, this lineage in this sample set lacked its distinctive polymorphism (16483 A) (Kemp et al., 2010; Perego et al., 2012; Morales-Arce et al., 2017). When assigning haplogroups to Panamanian samples in HaploGrep version 2; B2a showed a not reliable assignment probability; thus, this individual was excluded from analyses. The B2a lineage has not been found in Mesoamerican or Central American groups (Kemp et al., 2010; Perego et al., 2012; Morales-Arce et al., 2017).

This haplogroup might have originated around 12,100 years ago in North America, and today it is present at high frequency in Southern Athapaskan groups (Apache: 14.8%; Navajo: 15.1%) (Achilli et al., 2013; Morales-Arce et al., 2017). A total 12.50% of the ancient South Americans were affiliated to haplogroup B2i1. The coalescence time of the B2i lineage is around 19,300 years (95% CI 12,200 – 26,600 years) (de Saint Pierre et al., 2012; Gómez-Carballa et al., 2018). This mitochondrial variant is found in the Kayapo tribe in the Brazilian Amazonian (de Saint Pierre et al., 2012; Gómez-Carballa et al., 2018; Suarez and Ardelean, 2019).

Haplogroup C1 represent 25.00% of the mtDNAs in ancient samples from South America. C1 lineage is commonly found in native populations from South America (Brazil, Bolivia, Chile, and Paraguay) (Simão et al., 2019), and tend to be absent in the Isthmo-Colombian area (Morales-Arce et al., 2017; Hoffecker et al., 2021). The Coalescence age of C1 mitochondrial variant is around 17,000 years (95% CI 12,700 – 22,300 years) (Perego et al., 2009; Simão et al., 2019). Two individuals from ancient Panamanian samples were affiliated to C1 lineage, nonetheless, this haplogroup showed a critical assignment probability, when assigning haplogroups to Panamanian samples in Haplogrep HaploGrep version 2. Besides, the fragment from HVR-II that confirms this haplogroup with a deletion in 290–291 (Kemp et al., 2010; Perego et al., 2012; Morales-Arce et al., 2017) was amplified in this work; therefore, the authenticity of this result cannot be confirmed, thus, these individuals were excluded from analyses.

Haplogroup D1a1 represent 8.33% of the mtDNAs in ancient samples from South American samples. This lineage is frequently found in Surui and Gavião tribe from Brazil (de Saint Pierre et al., 2012; Simão et al., 2019). The coalescence time of haplogroup D1 is about 16,300 years (95% CI 13,900 – 18,700 years) (Perego et al., 2009; Gómez-Carballa et al., 2018; Simão et al., 2019). The D4h3 lineage had a frequency of 8.33% in ancient South Americans. This haplogroup is found in native populations from Peru, Chile, Argentina, and North America

(Mexico and USA), its coalescence age is around 14,300 years (95% CI 11,400 – 17,200 years) (Perego et al., 2009; de Saint Pierre et al., 2012; Simão et al., 2019). D4h3a lineage is detected at low frequencies in modern and ancient population samples of both North and South America, with an overall higher frequency and peaks along the Pacific coast and the western side of the Andes, supporting the hypothesis that the Pacific coast was the major entry and diffusion route of this haplogroup for the early Paleo-Indians (Perego et al., 2009; de Saint Pierre et al., 2012; Gómez-Carballa et al., 2018; Simão et al., 2019; Suarez and Ardelean, 2019; Hoffecker et al., 2021). Finally, 16.667% of ancient South American samples (Fig. 17) and 30.77% of ancient Panamanian samples (Fig. 18) were mtDNA variants, whose polymorphisms did not correspond to the Pan-American or the Isthmo-Colombian area haplogroups or the sequences showed many ambiguities; thus, these individuals were excluded from the analyses since they could generate distortions in the results.

SampleID	Range	Haplogroup	Input_Sample	General Distribution
121_10	16040-16420;	M7b1a1i	16126C 16129A 16192T 16223T 16297C	**East Asia**: Taiwan (Amis). **Southeast Asia** Philippines and Malaysia.
440_10	16040-16420;	M65a	16223T 16289G 16311C	**East Asia** China **Central Asia** Tajikistan. **South Asia** Pakistan (Balochi, Sindhi). **Southeast Asia** India, Myanmar and Ladakh.
10_14	16040-16420;	Q1	16129A 16144C 16148T 16241G	**Near Oceania** **Melanesia** Papua New Guinea, Bougainville and Vanuatu. **East Indonesia** Smaller islands in the Sunda and in the Moluccas. **Remote Oceania** **Polynesia** Samoa and Cook Islands.
10_19	16040-16420;	Q1	16129A 16144C 16148T 16172C 16241G 16265T 16311C 16343G	
27_22	16040-16420;	Q1	16129A 16144C 16148T 16241G 16265C 16311C 16343G 16362C	
29_19	16040-16420;	Q1	16129A 16144C 16148T 16178C 16223T 16241G 16265C 16311C 16343G	
79_10	16040-16420;	Q1	16129A 16144C 16148T 16223T 16241G 16265C 16311C 16343G	
80_10	16040-16420;	Q1	16129A 16144C 16148T 16223T 16241G 16311C 16343G	
116_10	16040-16420;	Q1	16129A 16144C 16148T 16223T 16241G 16311C 16343G	
117_10	16040-16420;	Q1	16129A 16144C 16148T 16223T 16241G 16243C 16265C 16311C 16343G	
120_10	16040-16420;	Q1	16129A 16144C 16148T 16223T 16241G 16243C 16265C 16311C 16343G	
260_10	16040-16420;	Q1	16129A 16144C 16148T 16172C 16174T 16223T 16241G 16259A 16265C 16300G 16311C 16343G	
268_10	16040-16420;	Q1	16129A 16144C 16148T 16172C 16174T 16223T 16241G 16265C 16300G 16311C 16343G	
284_10	16040-16420;	Q1	16059C 16129A 16144C 16148T 16223T 16241G 16265C 16311C 16343G	
443_10	16040-16420;	Q1	16129A 16144C 16148T 16241G 16265C 16311C 16343G 16362C	
15_10	16040-16420;	Q2	16066G 16178C 16223T 16241G 16325C	**Oceania** Australia **Near Oceania** **Melanesia** Fiji. **Papua New Guinea:** New Britain and New Ireland. **Remote Oceania** **Polynesia** Futuna.
162_10	16040-16420;	Q2	16066G 16129A 16209C 16223T 16241G	
20_10	16040-16420;	Q2	16066G 16129A 16178C 16223T 16241G 16325C	
25_22	16040-16420;	Q2a3b	16066G 16129A 16223T 16241G 16261T	**Near Oceania** **Melanesia**: Solomon Islands
438_10	16040-16420;	E1a2	16223T 16261T 16362C 16390A	**East Asia**: Taiwan. **Near OceaniaMelanesia**: Malay Archipelago, Papua New Guinea.
439_10	16040-16420;	E1a2	16223T 16261T 16362C 16390A	
22_22	16040-16420;	D4h1	16174T 16223T 16362C 16390A	**East Asia**: China
16_10	16040-16420;	B4a1a1	16182C 16183C 16189C 16217C 16231C 16247G 16261T	**Near Oceania** **Melanesia** Vanuatu and Papua New Guinea
17_10	16040-16420;	B4a1a1	16182C 16183C 16189C 16217C 16247G 16261T 16304C	
19_10	16040-16420;	B4a1a1	16183C 16189C 16217C 16247G 16261T	
21_19	16040-16420;	B4a1a1	16182C 16183C 16189C 16217C 16241G 16247G 16261T	
259_10	16040-16420;	B4a1a1	16182C 16183C 16189C 16217C 16247G 16261T 16294T	
26_19	16040-16420;	B4a1a1	16182C 16183C 16247G 16261T	
19_19	16040-16420;	B4c1a1	16183C 16189C 16198A 16217C 16231C 16289G 16311C	**East Asia** **Northwest Pacific Ocean** **Japan**: Tokyo and Aichi
28_19	16040-16420;	B4a1a1a11b	16182C 16183C 16189C 16217C 16247G 16289G	**Near Oceania** **Melanesia:** Solomon Islands (Bellona) **Remote Oceania** **Polynesia**: Cook Islands
14_10	16040-16420;	B4	16183C 16189Y 16192Y 16217Y 16289G	Far East, Siberia, America and Oceania
470_10	16040-16420;	L2a1i	16189C 16192T 16261Y 16294Y 16311Y 16362Y 16390R	**West Africa**: Burkina Faso, Sierra Leone, G. Bissau, Yoruba. **America** **USA:** Afro-Americans.
23_22	16040-16420;	U5b1c2	16111A 16174T 16192T 16266T 16270T 16293G 16357C	**Europe**: Ireland or UK, Italy, Spain, Poland and Croatia
24_22	16040-16420;	H42a	16183C 16294T 16311C	Europe

Figure 16. Ancient Oceanians haplogroups. Colours in this chart represent geographic areas or Amerindian groups where these mitochondrial variants are most commonly found. Reddish colour indicates the samples with haplogroups that do not belong to Oceania and therefore were excluded from the analyses.

SamppleId	Range	Haplogroup	Polymorphisms										General Distribution
12_2016	16040-16420	A2	16111T	16217C	16223T	16290T	16319A	16362C					**North America** **Native Papulations** **Canada** Peoples with Dogrib language (Tłįchǫ Yatı). **USA** Pennsilvania, California. **Mexico:** Zapotec. **South America** **Native Populations** **Colombia**: Arsario. **Ecuador:** Cayapa or Chachi. **Brazil**: Poturujara, Kayapo, Katuena. **Northerm Brazil and Guyana**: Waiwai. **Brazil** **Northwest Mato Gross and South Rondônia:** Zoró. **Northern Brazil** **Pará**: Surui; **Amapá**: Waiapi. **Paraguay**: Aché. **Guaraní** (Uruguay, Paraguay, Argentina, Brazil, Bolivia). **Peru**: Aymara and Atacameño.
10_2016	16040-16420	A2	16111T	16223T	16290T	16319A	16362C						
110_1880	16040-16420	B2	16182C	16183C	16189C	16217C	16231C						**North America** **Native Papulations** **Yaqui** or Hiaki or Yoeme Mexico and Southwester USA. **South America** **Native Populations** **Quechua**: Peru, Ecuador, Bolivia, Argentina, Chile, Colombia. **Guaraní:** Uruguay, Paraguay, Argentina, Brazil, Bolivia. **Colombia**: Coreguaje.
12_15	16040-16420	B2	16183C	16189C	16217C	16231C	16289G						
15_15	16040-16420	B2	16183C	16189C	16217C	16231C	16289G						
15_24	16040-16420	B2	16183C	16189C	16217C	16231C	16289G						
4_30	16040-16420	B2	16129A	16182C	16183C	16189C	16217C	16289G	16290T				
7_14	16040-16420	B2i1	16176T	16183C	16189C	16217C	16293G	16311C					**South America** **Brazil** Kayapo.
23_20	16040-16420	B2i1	16183C	16189C	16217C	16311C							
9_6	16040-16420	B2i1	16183C	16189C	16217C	16290T	16311C	16362C					
22_20	16040-16420	C1	16129A	16223T	16298C	16304C	16325C	16327T	16391A				**South America** **Native populations:** **Brazil:** Wai-Wai, Zoró, Arara, Poturujara. **Bolivia:** Quechua, Aymara, Tiwanaku. **Chile** Mapuche Huilliche Kawesqar. **North America** **Ancient DNA** USA Nevada Wizard's Beach America
30_19	16040-16420	C1	16223T	16289G	16298C	16325C	16327T						
6_29	16040-16420	C1	16182C	16183C	16189C	16223T	16289G	16298C	16325C	16327T			
8_6	16040-16420	C1	16183C	16189C	16223T	16289G	16298C	16325C	16327T				
B2443	16040-16420	C1	16223T	16289G	16298C	16325C	16327T						
11_15	16040-16420	C1	16183C	16189C	16223T	16289G	16298C	16325C	16327T				
7_6	16040-16420	D1a1	16189C	16223T	16325C	16362C							**South America** Brazil Surui and Gavião
B3694	16040-16420	D1a1	16223T	16290T	16325C	16362C							
44_2016	16040-16420	D4h3a	16129A	16223T	16224C	16241G	16301T	16304C	16311C	16342C	16362C	16391A	**South America** **Native Populations** **Peru:** Aymara. **Chile** Mapuche Huilliche Kawésqar or kawashkar. **Argentina:** Tehuelche. **Yaghan** also called Yagán Yahgan Yámana Yamana or Tequenica (Argentina, Chile). **North America**: Mexico and USA.
17_15	16040-16420	D4h3a	16223T	16224C	16241G	16301T	16342C	16362C					
18_15	16040-16420	B2	16189Y	16217C	16224C	16289R	16290Y	16316R					**South America** Native Populations.
1_31	16040-16420	C1b8	16223T	16290T	16298C	16319R	16325C	16327T	16362C				**North America:** Mexico and USA.
13_15	16040-16420	D4o	16162R	16209Y	16223T	16289R	16290T	16362C					**Eurasia** **Russia** Siberia Buryats. **Teleuts** areTurkic people living in Kemerovo Oblast, Russia. **Uyghurs**: China, Kazakhstan, Turkey, Uzbekistan, Kyrgyzstan.
35_87_05	16040-16420	H2a2a1g	16166G	16182C	16183C	16189C	16231C						**Europe**

Figure 17. Ancient South Americans haplogroups. Colours in this chart represent geographic areas or Amerindian groups where these mitochondrial variants are most commonly found. Reddish colour indicates the samples with haplogroups that do not belong to South America and therefore were excluded from the analyses.

SampleID	Range	Haplogroup	Input_Sample	General Distribution
5052	16040-16420 ;	A2	16111T 16183C 16223T 16289G 16290T 16319A 16362C	
113	16040-16420 ;	A2	16072T 16073G 16111T 16223T 16289G 16290T 16319A 16362C	
114	16040-16420 ;	A2	16111T 16223T 16290T 16319A 16362C	**North America**
139	16040-16420 ;	A2	16072T 16073G 16111T 16129A 16223T 16256T 16290T 16319A 16362C	**Native Papulations**
125	16040-16420 ;	A2	16111T 16189C 16223T 16319A 16362C	**Canada**
140	16040-16420 ;	A2	16072T 16073G 16111T 16223T 16290T 16319A 16324C 16362C	Peoples with Dogrib language (Tłı̨chǫ Yatı).
126	16040-16420 ;	A2	16111T 16223T 16290T 16319A 16362C	**USA**: Pennsilvania, California.
127	16040-16420 ;	A2	16111T 16223T 16290T 16319A	**Mexico**: Zapotec
128	16040-16420 ;	A2	16111T 16129A 16290T 16319A 16362C	**South America**
55	16040-16420 ;	A2	16072T 16073G 16111T 16223T 16290T 16319A 16362C	**Native Populations:**
573	16040-16420 ;	A2	16111T 16189C 16223T 16256T 16270T 16289G 16290T 16304C 16319A 16362C	**Colombia:** Arsario.
58	16040-16420 ;	A2	16111T 16223T 16290T 16304C 16319A 16362C	**Ecuador**: Cayapa or Chachi
69	16040-16420 ;	A2	16111T 16223T 16290T 16319A 16362C	**Brazil:** Poturujara, Kayapo, Katuena,
70	16040-16420 ;	A2	16072T 16073G 16111T 16223T 16290T 16319A 16362C 16366T 16390A	**Northerm Brazil and Guyana**: Waiwai.
71	16040-16420 ;	A2	16072T 16073G 16111T 16223T 16290T 16319A 16362C	**Brazil**
61	16040-16420 ;	A2	16072T 16111T 16223T 16290T 16319A 16362C	**Northwest Mato Gross and South Rondônia**
65	16040-16420 ;	A2	16072T 16073G 16111T 16223T 16290T 16319A 16362C	Zoró. **Northern Brazil**
66	16040-16420 ;	A2	16072T 16073G 16111T 16223T 16290T 16319A 16362C	**Pará**: Surui; **Amapá**: Waiapi.
129	16040-16420 ;	A2	16111T 16290T 16319A 16362C	**Paraguay**: Aché.
2948	16040-16420 ;	A2	16072T 16111T 16223T 16289G 16290T 16319A 16362C	**Guaraní** (Uruguay, Paraguay, Argentina, Brazil, Bolivia).
123	16040-16420 ;	A2	16111T 16172C 16223T 16290T 16319A 16362C 16399G	**Peru**: Aymara and Atacameño.
118	16040-16420 ;	A2	16111T 16223T 16290T 16319A 16362C	
119	16040-16420 ;	A2	16111T 16189C 16223T 16290T 16319A 16324C 16362C 16366T 16390A	
115	16040-16420 ;	B2	16072T 16183C 16189C 16217C 16293G	**North America**
				Native Papulations:
				Yaqui or Hiaki or Yoeme (Mexico and Southwester USA.
				South America
5015	16040-16420 ;	B2	16073G 16183C 16189C 16217C 16289G	**Native Populations**
5127	16040-16420 ;	B2	16183C 16189C 16217C 16289G	**Quechua** (Peru, Ecuador, Bolivia, Argentina, Chile, Colombia).
				Guaraní (Uruguay, Paraguay, Argentina, Brazil, Bolivia)
124	16040-16420 ;	B2	16189C 16217C 16293G	**Colombia**
				Coreguaje.
138	16040-16420 ;	B2a	16111T 16182C 16183C 16189C	**North America**
				Papulations
				Northwestern Canada
				Tsimshian
				Mexico
				Chihuahua.
109	16040-16420 ;	C1	16209C 16223T 16290T 16298C 16325C 16327T	**North America**
				Ancient DNA
				USA
				Nevada
				Wizard's Beach America
				South America
				Native populations
				Brazil (Wai-Wai, Zoró, Arara, Poturujara).
				Bolivia (Quechua, Aymara, Tiwanaku).
110	16040-16420 ;	C1	16072T 16073G 16223T 16293G 16298C 16325C 16327T	**Chile** (Mapuche, Huilliche, Kaweşqar).
112	16040-16420 ;	B2i1	16183C 16189Y 16217C 16293R 16311C	
				South America
142	16040-16420 ;	B2i1	16183C 16189C 16217C 16311Y	Kayapo (Brazil).
415	16040-16420 ;	M8	16183C 16189Y 16223T 16298C	**East Siberia**
				Evenk, Yukaghir, Yakut, Tuvan.
				East Asia
				Pacific Ocean
135	16040-16420 ;	D4b2a2a	16189Y 16223T 16362Y	Japan
				Central Asia
				Kyrgyzstan
CA:3_BT	16050-16420 ;	H1af	16337T 16357C	**Europe**
117	16040-16420 ;	H15a1a1	16189C 16366T	**South Asia**
				India
68	16040-16420 ;	H15a1a1	16072T 16073G 16173T 16189C 16324C 16366T 16390A	**North India**
72	16040-16420 ;	H15a1a1	16189C 16324C 16366T 16390A	Chaturvedi Brahmin.
120	16040-16420 ;	U5b2a1	16189C 16192T 16293G	**Europe**

Figure 18. Ancient Panamanians haplogroups. Colours in this chart represent geographic areas or Amerindian groups where these mitochondrial variants are most commonly found. Reddish colour indicates the samples with haplogroups that do not belong to Central America or Isthmo-Columbian area and therefore were excluded from the analyses.

Additionally, an AMOVA was carried out to evaluate the genetic variation among population groups (Table 11). This analysis revealed that most of the genetic variation is found Within populations (76.40%) and not among them. The variation among groups is 21.69%, while the variation among populations within groups is only 1.91%. The population genetic differentiation resulting from the genetic structure was evaluated by calculation of fixation index (Fst). This statistic measures the deficit of genetic variation that occurs in the populations owing to the loss of diversity because of genetic drift (Fuchs Castillo, 2019; Hartl, 2020). The global Fst = 0.571 indicates that at the mitochondrial level there is a high grade of genetic differentiation between ancient populations of Oceania, South America and Panama. When contrasting pairs of populations, it was evident that Oceania exhibited a high grade of genetic differentiation regarding South America (Fst = 0.359) and Panama (Fst = 0.476), while South America and Panama showing a moderate genetic differentiation (Fst = 0.235). This genetic variation distribution could be related to founder effect, since the founder populations bring only a subset of the genetic variation from their ancestral population. As the founders become more geographically separated, the probability that two individuals from different founder populations will mate becomes smaller (Cutter, 2019; Hartl, 2020). The assortative mating reduces the gene flow between geographical groups and to increase the genetic distance between groups (Cutter, 2019; Hartl, 2020). Thus, the genetic drift increased fluctuations in neutral polymorphisms in founder populations, thereby new polymorphisms that arose in one group were less likely to be transmitted to other groups because of gene flow was restricted. In other words, the greatest genetic variability is found within the source population; however, when the main population subdivided into small (founder) populations with a part of the genetic diversity of the original population, the genetic variation among groups is less compared with total genetic variation of source population. However, the genetic differentiation increases among population depending on their ancestries, geographic and genetic distance.

Table 11. AMOVA results: ancient population samples from Oceania, South America and Panama based on HVSI_mtDNA sequences.

Source of variation	Sum of squares	Variance components	Percentage variation
Among groups	82.78	1.31	21.69
Among populations within groups	11.02	0.11	1.91
Within populations	345.49	4.61	76.40

Measures of neutrality

In order to determine if HVSI_mtDNA sequences were statistically significant under the neutral equilibrium model, two neutrality tests were performed: Tajima's D and Fu's Fs. The neutral evolution model is based on the standard Wright-Fisher evolutionary model and makes the following five assumptions: 1) a constant population size of N individuals; 2) random mating; 3) no overlapping generation; 4) no recombination; and 5) infinite sites, constant rate neutral mutation process whereby an offspring differs from its parent allele by a Poisson-distributed number of mutations with mean μ (Simonsen et al., 1995). When the neutrality assumptions are broken, Tajima's D is considered significant when the probability value is less than 0.05, while Fu's Fs is significant if its p-value is less than 0.02, this is due to the critical point of statistical significance, which is below the second percentile of its empirical distribution (Fu, 1997, Excoffier and Lischer, 2010).

If there have been no changes in population size and the population is in drift-mutation equilibrium the Tajima's D and Fu's Fs statistics should be $D \approx 0$ and $Fs \approx 0$, and the estimative θ for Tajima's D should be equivalents: $\theta\pi \simeq \theta s$ (Fuchs Castillo, 2019). On the other hand, if $\theta\pi < \theta s$ then D will be negative ($D < 0$) suggesting a recent population expansion, while if $\theta\pi > \theta s$ then D will be positive ($D > 0$) suggesting a recent population bottleneck (Tajima, 1989; Hedrick, 2011; Fuchs Castillo, 2019). Fu's Fs is a more sensitive indicator of population expansion than Tajimas D, therefore if $Fs < 0$ then there is evidence of a recent population expansion, in contrast, if $Fs > 0$ then there is evidence of a recent population bottleneck (Fu, 1997; Hedrick, 2011; Fuchs Castillo, 2019).

The results of the neutrality tests performed on the population sample sets from Oceania, South America and Panama suggest that HVSI_mtDNA of these human groups is under the neutral evolution model (Table 12). Regarding population size changes, Tajima's D and Fu's Fs suggests that the populations of Oceania, South America and Panama went through a population expansion. Nonetheless, Fs estimative should be complemented with the

Harpending raggedness index and mismatch distribution of the sequences, since these parameters give more robustness to the inferences about population size changes and demographic history of the populations. Thus, if the populations are expanding, the population size grows. This implies that the mutations that appear have little probability of being lost (because N is high, the drift has little force); however, they occur in low frequency. For this reason, a gene in a population with population expansion will also have negatives D and Fs; this will happen even if the gene is neutral (Fuchs Castillo, 2019; Cutter, 2019; Hartl, 2020).

Table 12. Measures of neutrality. Tajima's D and Fu's Fs

Sample set	D	p-value	Fs	p-value
Oceania	-0.605	0.403	-3.325	0.622
South America	-0.511	0.345	-3.824	0.667
Panama	-0.590	0.330	-2.941	0.504

Mismatch distribution and population growth

Population size changes in the ancient samples set from Oceania, South America and Panama were inferred through assessing genetic differences between pairs of individuals in each sample set. The mismatch distribution summarizes the information about patterns of nucleotide site differences between pairs of subjects through the construction of histograms or scatter plots, these graphics display the relative frequencies of pairs that differ by zero sites, by one site, by two sites etc (Rogers and Harpending, 1992). Usually, the mismatch distribution is ragged and erratic (multimodal) in samples drawn from populations at demographic equilibrium but is expected to be smooth and with a single peak (unimodal) in populations that have undergone a recent demographic expansion (Rogers and Harpending, 1992; Dadi et al., 2012; Grant, 2015). Thus, the signature of ancient population expansion is apparent even in the low- resolution mtDNA (Rogers and Harpending, 1992).

To distinguish between population expansion and bottleneck in the mismatch distribution graphics, it should be considered that the bottlenecks generate a wave with an extremely steep leading face (Rogers and Harpending, 1992). Besides, the bottleneck model generates elevated upper tail probabilities and the pairs of individuals differ by more than twenty-five sites, with probability 32% (frequency 0.32) (Rogers and Harpending, 1992). Whilst, the model of sudden expansion makes this probability only 2% (frequency 0.02) (Rogers and Harpending, 1992). Consequently, bottlenecks should often generate ragged empirical distribution with many peaks at large values, while sudden expansion should generate many peaks but at small values (Rogers and Harpending, 1992).

Harpending raggedness index (r) is a statistic parameter, which quantifying the smoothness of the mismatch distribution and allows distinguishing between expanded and stationary populations with good confidence (Harpending, 1994). Raggedness values above the critical cutoff point of 0.03 ($r > 0.03$) are characteristic of demographically stationary populations (Harpending, 1994). Whilst Raggedness values below the critical cutoff point of

0.03 ($r < 0.03$) are characteristic of populations went through a demographic expansion (Harpending, 1994). The unit of mutational time in the past tau (τ) is used to infer the expansion or coalescence time (Harpending, 1994; Hedrick, 2011). Thus, the conventional unit of time is $\tau=2\mu t$, where t is time in generations and μ is the mutation rate (Harpending, 1994). The expansion times were estimated through the mitochondrial mutation rate 1.91×10^{-8} (95% CI $1.72 – 2.10\times10^{-8}$) mutations/site /year (Cabrera, 2021), and a generational time of 26 years (Macaulay et al., 2019). The mutation rate was calculated considering the time dependency effect on the evolution rate with increasing acceleration in recent times, and the transient polymorphisms, which slow down the evolutionary rate (Cabrera, 2021). To correct the uncertainties in the calculation of evolutionary rates, the most divergent lineages within the haplogroups were used (Cabrera, 2021).

Tajima's D, and Fu's Fs statistic of archaeological human remains from Oceania, South America and Panama suggest that these populations went through a demographic expansion. This was ratified by the Harpending raggedness index, for which the populations aforementioned exhibited values less than 0.03, the pairwise differences of the analysed individuals were less than twenty-five sites and the peaks generated in their pairwise mismatch distributions exhibited values less than 0.32 (Fig. 19-21). Regarding the estimates of expansion times, these suggest that ancient Oceanians went through a demographic expansion about 37,972 years ago (95% CI 34,537 – 42,167 years ago), reflecting the initial settlement of Melanesia during the Upper Pleistocene, and hence the population divergence between Oceanian and Southeast Asian peoples, which took place 36,000 years ago (Pugach et al., 2013; Jinam et al., 2017; Posth et al., 2018; Bird et al., 2019; Bradshaw et al., 2019; Bradshaw et al., 2021).

Ancient South American peoples went through a demographic expansion about 14,150 years ago (95% CI 15, 713 – 12,870 years ago), reflecting the expansion of the first anatomically modern humans through America 15,000 years ago (Potter et al., 2018; Suarez

and Ardelean, 2019; Marshall et al., 2021; Puzachenko et al., 2021). This date could also reflect the Native American groups divergence 14,700 - 17,000 years ago (Nielsen et al., 2017). Ancient Panamanian peoples went through a demographic expansion 9,468 years ago (95% CI 8,611 – 10,513 years ago), reflecting the expansion of hunter-gatherers from North America to Central and South America during the postglacial period in the Holocene 10,000 – 11,700 years ago (Cooke et al., 2013; Posth et al., 2018; Antczak, 2019; Suarez and Ardelean, 2019; Gruhn, 2020; Ranere and Cooke, 2021). The time of expansion of the ancient Panamanians also encompasses the temporal range of the Proto-Chibcha group divergence 7,000 – 10,000 years ago (Barrantes, 1993; Ruiz-Narváez et al., 2005; Núñez-Castillo, 2012; Suarez and Ardelean, 2019; Ranere and Cooke, 2021).

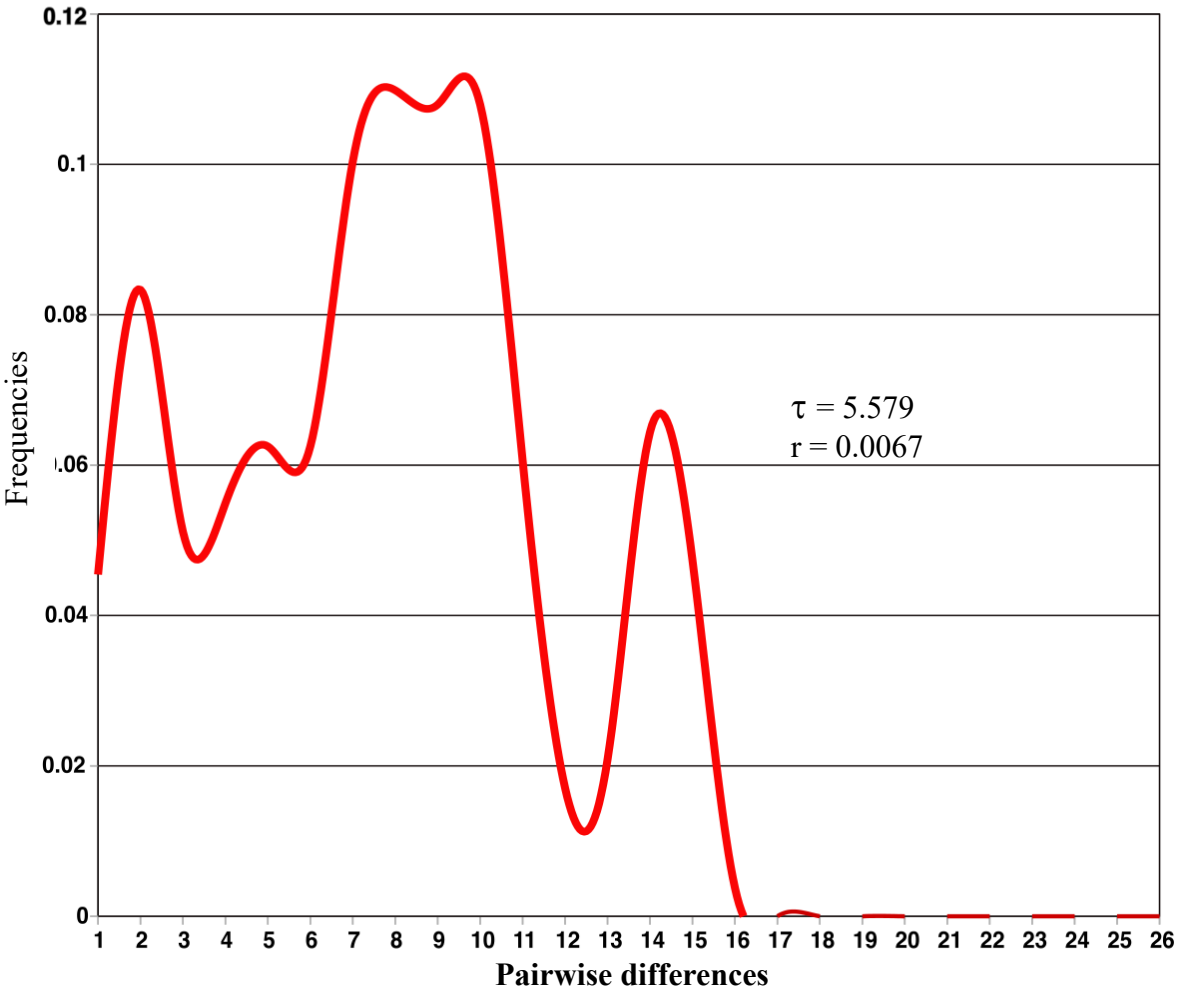

Figure 19. Ancient Oceanians mismatch distribution. The maximum frequency exhibited in these pairwise differences is 0.12, indicating population expansion, which in turn is supported by a raggedness index lower than 0.03. There are 5.579 mutational units, suggesting that the population expansion occurred about 1,460 generations ago (95% CI 1,328 – 1,622 generations ago), or what is the same 37,972 years ago (95% CI 34,537 – 42,167 years ago).

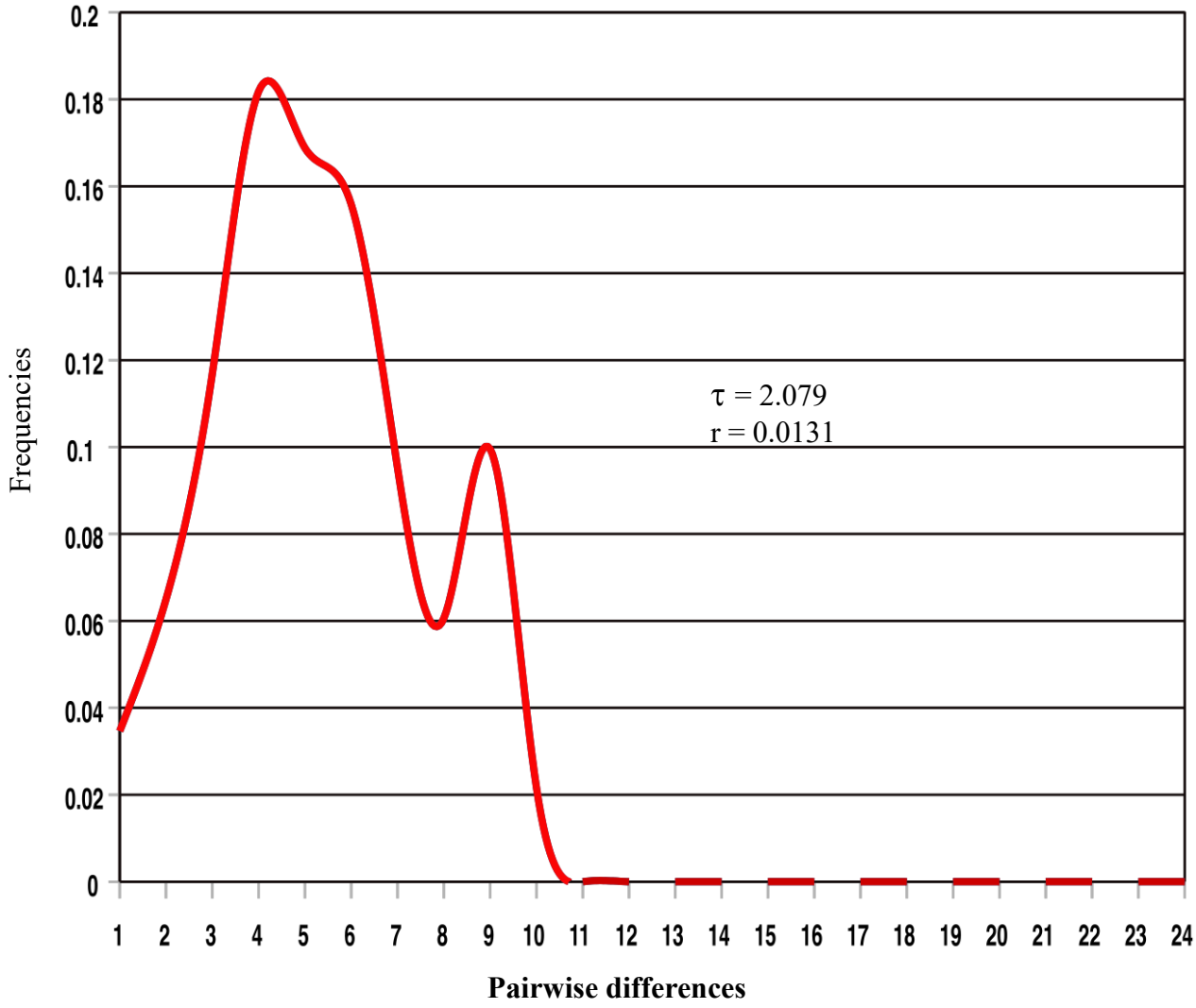

Figure 20. Ancient South American mismatch distribution. The maximum frequency exhibited in these pairwise differences is ~ 0.18, indicating population expansion, which in turn is supported by a raggedness index lower than 0.03. There are 2.079 mutational units, suggesting that the population expansion occurred about 544 generations ago (95% CI 495 – 604 generations ago), or what is the same 14,150 years ago (95% CI 15, 713 – 12,870 years ago).

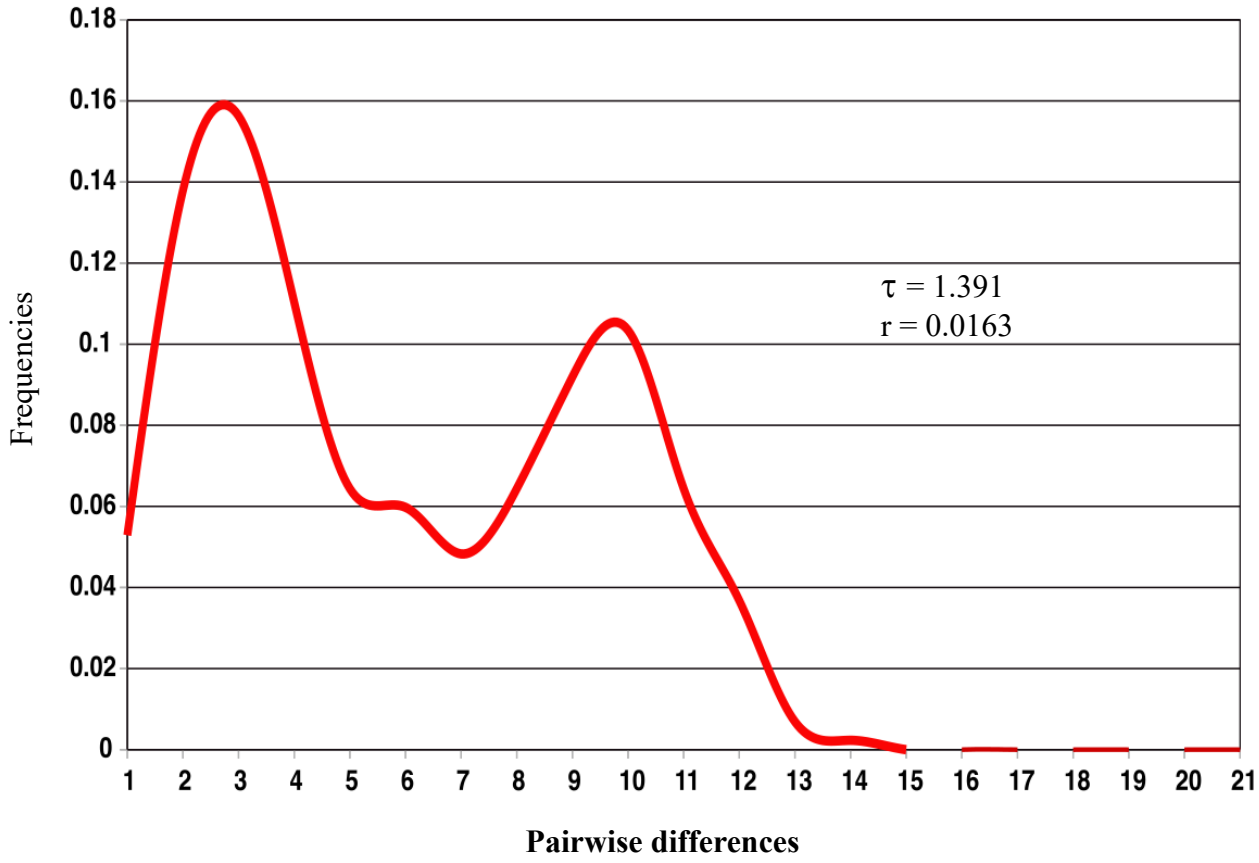

Figure 21. Ancient Panamanians mismatch distribution. The maximum frequency exhibited in these pairwise differences is 0.16, indicating population expansion, which in turn is supported by a raggedness index lower than 0.03. There are 1.391 mutational units, suggesting that the population expansion occurred about 364 generations ago (95% CI 331 – 404 generations ago), or what is the same 9,468 years ago (95% CI 8,611 – 10,513 years ago).

Median-Joining Networks

Haplotype networks are used in the analysis of population genetic data to visualize analysing and visualizing the relationships among DNA sequences within a population or species, as well as to make inferences about biogeography and the history of populations (Huson, 2010; Whitfield, 2011; Fagny and Austerlitz, 2021; Garcia et al., 2021). Coalescence time for the defined haplogroups in ancient Oceanians, South Americans and Panamanians was estimated via rho (ρ); according to the standard parameters of the Network 10.2.0.0 software (Forster and Forster, 2020). The rho statistic is commonly used to infer chronological dates for molecular lineages, especially from mitochondrial DNA sequences obtained in anthropological contexts (Macaulay et al., 2019). Thus, when divided rho by a given mutation rate (μ), the ρ (rho) statistic provides a simple estimator of the age of a clade within a phylogenetic network by averaging the number of mutations from each sample in the clade to its root (Macaulay et al., 2019; Cabrera, 2020; Sun et al., 2021)

Ancient Oceanians

Coalescence age estimate for haplogroup Q1 was at ~ 17,200 years (95% CI 14,523 – 19,877 years). This lineage is found most frequently on the islands of Sunda and Wallacea, and it is associated with Australian individuals with Torres Strait Islanders ancestry, which are known for their close ties to New Guinea (Pedro et al., 2020). Haplogroup Q2 has a coalescence age estimate at ~ 30,270 years (95% CI 26,870 – 33,670 years). This lineage is linked to demographic expansions following the initial settlement of New Britain around 35,000 years ago and it is found in Near Oceania, particularly the Bismarck Archipelago (Pedro et al., 2020). Diversification of this haplogroup began in the post-Last Glacial Maximum period and continue into the Holocene, but was largely restricted to Near Oceania, however a few lineages have been observed in Remote Oceania with coalescence ages in the late Holocene (Pedro et al., 2020; Choin et al., 2021). Haplogroup Q2a3b has a coalescence age estimate at ~ 17,700 years (95% CI 9,357 – 26,043 years), this lineage is found in the Solomon Islands (Duggan et

al., 2014; Duggan and Stoneking, 2021). 50% of archaeological human remains from ancient Oceania were affiliated to Q lineage (Q1, Q2, and Q2a3b) (Fig. 22), which is found in high frequencies in the Region of Melanesia (Pedro et al., 2020), supporting the Melanesian origin of these individuals, according to the geographical assignment of the samples given by the Ethnohistorical Institute of the University of Hamburg, where these individuals were assigned to the Bismarck archipelago area, northeast of the island of New Guinea (Melanesia, Near Oceania).

The coalescence age estimate for haplogroup E1a2 was at ~ 10,000 years (95% CI 7,500 – 12,500 years). This lineage is linked to the Austronesian expansion from Taiwan to Oceania via the Philippines around 6,000 – 10,000 years ago (Matisoo-Smith, 2015; Issiki et al., 2018), which took place during the postglacial period in Holocene (~ 10,000 – 18,000 years ago) (Matisoo-Smith, 2015; Issiki et al., 2018; Pedro et al., 2020). Haplogroup D4h1 has a coalescence age estimate at ~ 17,200 years (95% CI 12,900 – 21,500 years). This mitochondrial variant is present in East Asia (Chunxiang et al., 2020). The M7b1a1i lineage has a coalescence age estimate at ~ 16,700 years (95% CI 13,000 – 20,400 years). This lineage is found in Taiwan, Philippines, Malaysia, and also in Borneo, Indonesia (Jiao, 2021). The coalescence age estimate for haplogroup M65a was at ~ 18,000 years (95% CI 11,300 – 24,700 years). M65a lineage is found in Central South and Southeast Asia (Peng et al., 2018). B4c1a1 has a coalescence age estimate at ~ 9,600 years (95% CI 4,000 – 15,100 years), usually, this mitochondrial variant is found in Japan (Tokyo and Aichi) (Mikami et al., 2013; Yao et al., 2021; Jinam et al., 2021). 17.65% of archaeological human remains from ancient Oceania were affiliated to Southeast Asia lineages (B4c1a1, E1a2, D4h1, M7b1a1i and M65a) (Fig, 22), suggesting a possible ancestral link to Holocene expansion from South Asia to Near Oceania, and Remote Oceania (Austronesian expansion).

Haplogroup B4a1a1 has a coalescence age estimate at ~ 4,500 years (95% CI 1,400 – 7,600 years). This lineage is found in Near and Remote Oceania (Soares et al., 2011; Fehren-Schmitz et al., 2017; Davis, 2021; Duggan and Stoneking, 2021; Gosling et al., 2021). The coalescence age estimate for haplogroup B4a1a1a11b was at ~ 3,500 years (95% CI 1,025 – 5,975 years), is also found both in Near and Remote Oceania (Davis, 2021; Gosling et al., 2021). 20.59% of ancient Oceanians were affiliated to Near and Remote Oceanian haplogroups (Fig.22), suggesting a possible ancestral link to the last colonization event, the settlement of Polynesia around 3,000 years ago, during the Holocene (10,000 – 11,700 years ago).

Ancient South Americans and Panamanians

Coalescence age estimate for haplogroup A2 was at ~ 9,300 years (95% CI 8,300 – 10,200 years). Mitochondrial variant A2 is the most common in Amerind ethnic groups of North and Central America, it is also found in South American Amerind groups but in low frequencies (Moreno-Mayar et al., 2018; Posth et al., 2018; Llamas et al., 2020; Suarez and Ardelean, 2019; Hoffecker et al., 2021). The haplogroup B2 has a coalescence age estimate at ~ 15,000 years (95% CI 12,300 – 17,700 years). Haplogroup B2i1 has a coalescence age estimate at ~ 18,500 years (95% CI 13,300 – 23,700 years), and it is found in a Brazilian Amazonian tribe (Kayapo) (de Saint Pierre et al., 2012; Gómez-Carballa et al., 2018; Suarez and Ardelean, 2019). The coalescence age estimate for the C1 mitochondrial variant was at ~ 17,300 years (95% CI 13,000 – 21,600 years). 9.52% of archaeological human remains from South America were affiliated to haplogroup C1 (Fig. 23). This lineage is commonly found in native populations from South America (Brazil, Bolivia, Chile, and Paraguay) (Simão et al., 2019).

The haplogroup D1a1 has a coalescence age estimate at ~ 4,500 years (95% CI 1,150 – 7,850 years) (Fig. 23), and it is found in Surui and Gavião tribe from Brazil (de Saint Pierre et al., 2012; Simão et al., 2019). Haplogroup D4h3a has a coalescence age estimate at ~ 13,500 years (95% CI 10,900 – 16,100 years), and it is found in native populations from Peru, Chile,

Argentina, and North America (Mexico and USA) (Perego et al., 2009; de Saint Pierre et al., 2012; Simão et al., 2019). Thus, B2, B2i1, C1, and D4h3a lineages might be linked to the divergence of Native American groups 14,700 - 17,000 years ago (Nielsen et al., 2017; Llamas et al., 2020), and to the expansion of the first anatomically modern humans through America 15,000 years ago (Potter et al., 2018; Suarez and Ardelean, 2019; Marshall et al., 2021; Puzachenko et al., 2021). Whilst, A2 and D1a1 lineages might be linked to hunter-gatherers dispersion that took place during the Early Archaic age of America in the Paleoindian period about 8,900 – 11,500 years ago (Cooke et al., 2013; Posth et al., 2018; Antczak, 2019; Suarez and Ardelean, 2019; Gruhn, 2020; Ranere and Cooke, 2021).

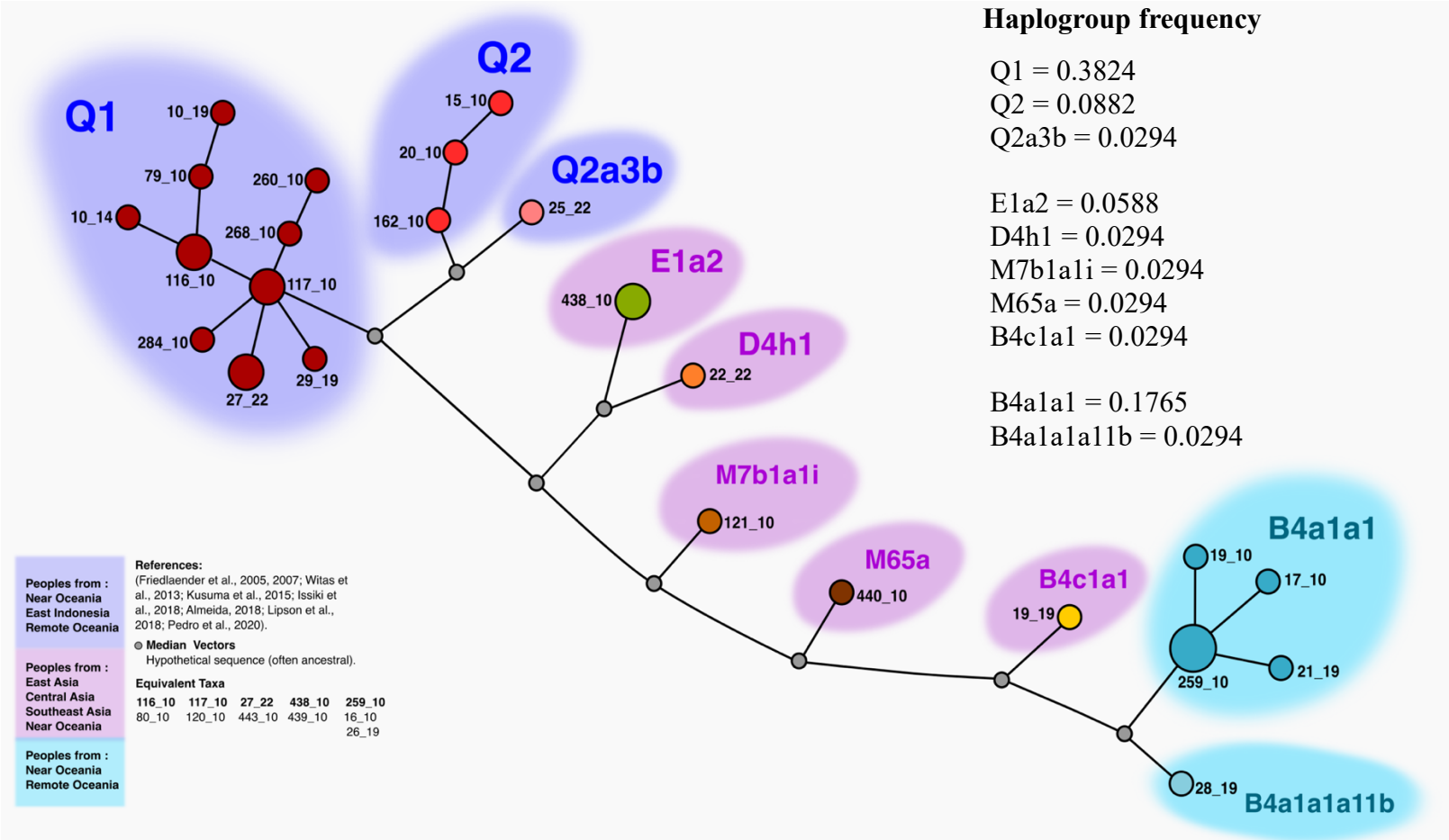

Figure 22. Ancient Oceanians phylogenetic network. The most common mtDNA variants among the archaeological human remains from Oceania were the Near Oceania haplogroups (50%), followed by Near and Remote Oceania (20.59%), and Southeast Asia (17.65%) haplogroups. 11.76% were mtDNA variants, whose polymorphisms did not correspond to Oceanian or Asian lineages or the sequences showed many ambiguities; thus, these individuals were excluded from the analyses since they could generate distortions in the phylogenetic network.

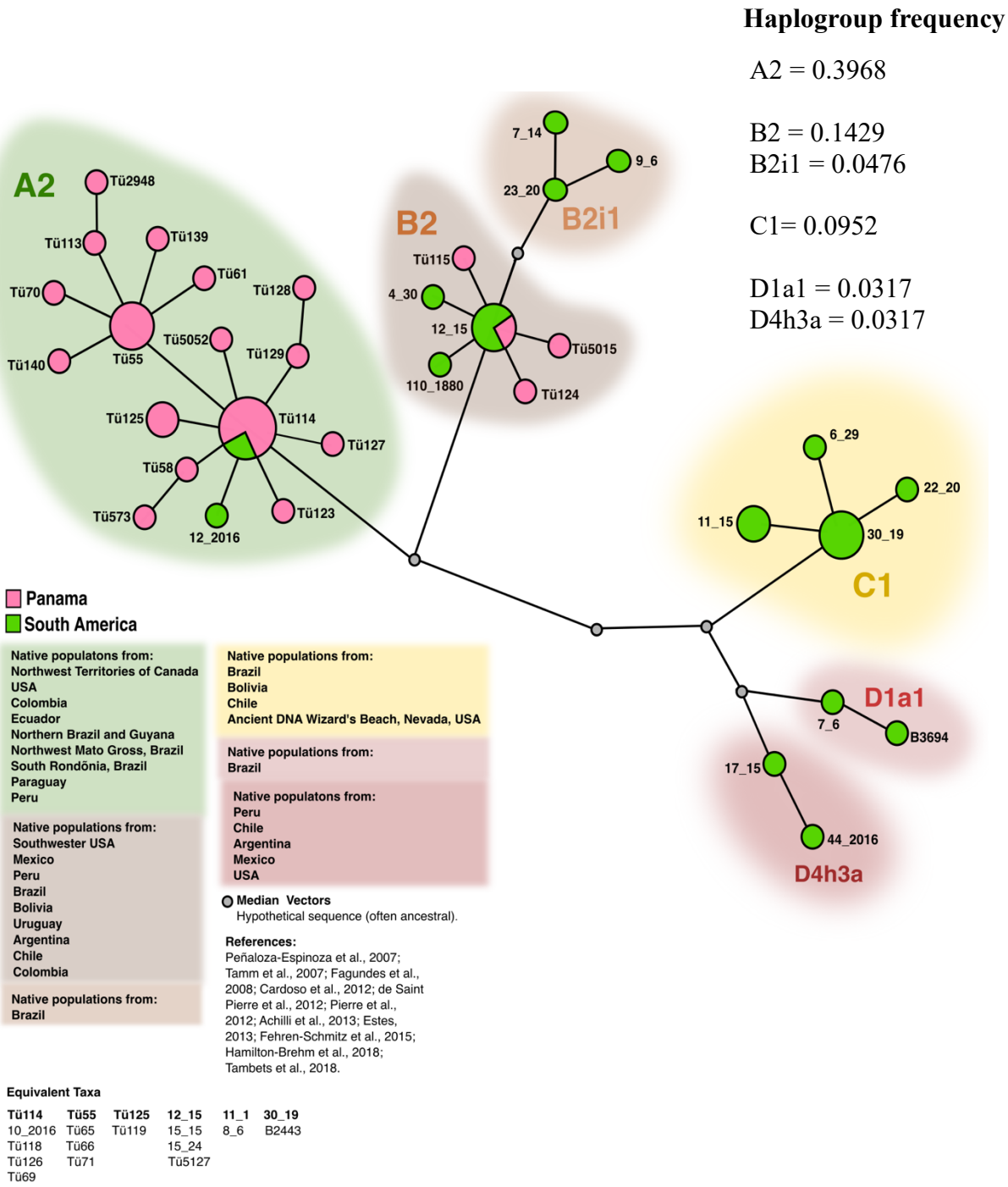

Figure 23. Ancient South American and Panamanian phylogenetic network. The most common mtDNA variants among the archaeological human remains in this set of samples were the Pan-American lineages A2 (39.68%), followed by haplogroups B2 (14.29%), B2i1 (4.76%), C1 (9.52%), D1a1 (3.17%), and D4h3a (3.17%). 25.40% were mtDNA variants, whose polymorphisms did not correspond to Pan-American lineages or the sequences showed many ambiguities; thus, these individuals were excluded from the analyses since they could generate distortions in the phylogenetic network.

Clustering trends

According to the Bayesian Information Criterion, the evolutionary model TPM2u+F+G4 (Kimura's two-parameter model with unequal base frequencies (Kimura, 1980; Nguyen et al., 2015) + Empirical state frequency observed from the data + four Gamma categories (Yang, 1994; Nguyen et al., 2015)) was the best fit model to infer the possible phylogenetic relationships between ancient and modern samples from Oceania, South America and Panama. On the other hand, to give polarity (direction) to the phylogeny, the HVSI_mtDNA of the *Homo sapiens neanderthalensis* (Mezmaiskaya 1) (Briggs et al., 2009) and *Homo sapiens ssp. Denisova* (Denisova 2) (Krause et al., 2010) were used as outgroups.

Anatomically modern *Homo sapiens* and *Homo neanderthalensis* diverged approximately 465,700 years ago (321,200 – 618,000 years ago, 95% HPD (highest posterior density), calibration method= strict clock) and 487,500 years ago (95% HPD= 219,700 – 778,800 years ago; calibration method= relaxed clock) (Krause et al., 2010). Whilst the divergence between Denisova hominin, Neanderthals and modern humans occurred about 1,040,900 years ago (95% HPD= 779,300 – 1,313,500 years ago; calibration method= strict clock) and 1,129,100 years ago (95% HPD= 585,100 – 1,763,800 years ago; calibration method= relaxed clock) (Krause et al., 2010).

The ancient samples from Oceania, South America and Panama exhibited a clear pattern of clustering. Phylogenetic inferences showing both Oceanian and American individuals are clustered in two different branches (Fig. 24). The American branch, showing that individuals from Peru and Brazil exhibited more genetic affinities with Panamanian samples than with Venezuela and Chile. This is not surprising since Panama is located in the lower part of the Central American isthmus, and historically this place has been considered as a biological bridge between the northern and southern parts of the continent. The Oceanian branch, showing that the individuals from Near Oceania (Bismark Archipelago and Papua New Guinea) had greater

genetic affinity between them. Similarly, the clusters of Remote Oceania (New Zealand and Samoa) showing greater affinity between them. However, the cluster of the individuals who did not have a defined subregion (Oceania_xx and Melanesia_xx) seem to have a certain genetic affinity with the individuals from Remote Oceania. Probably, at some point in the demographic history of these populations, they may have had biological contact, which could have generated the genetic affinities between these human groups.

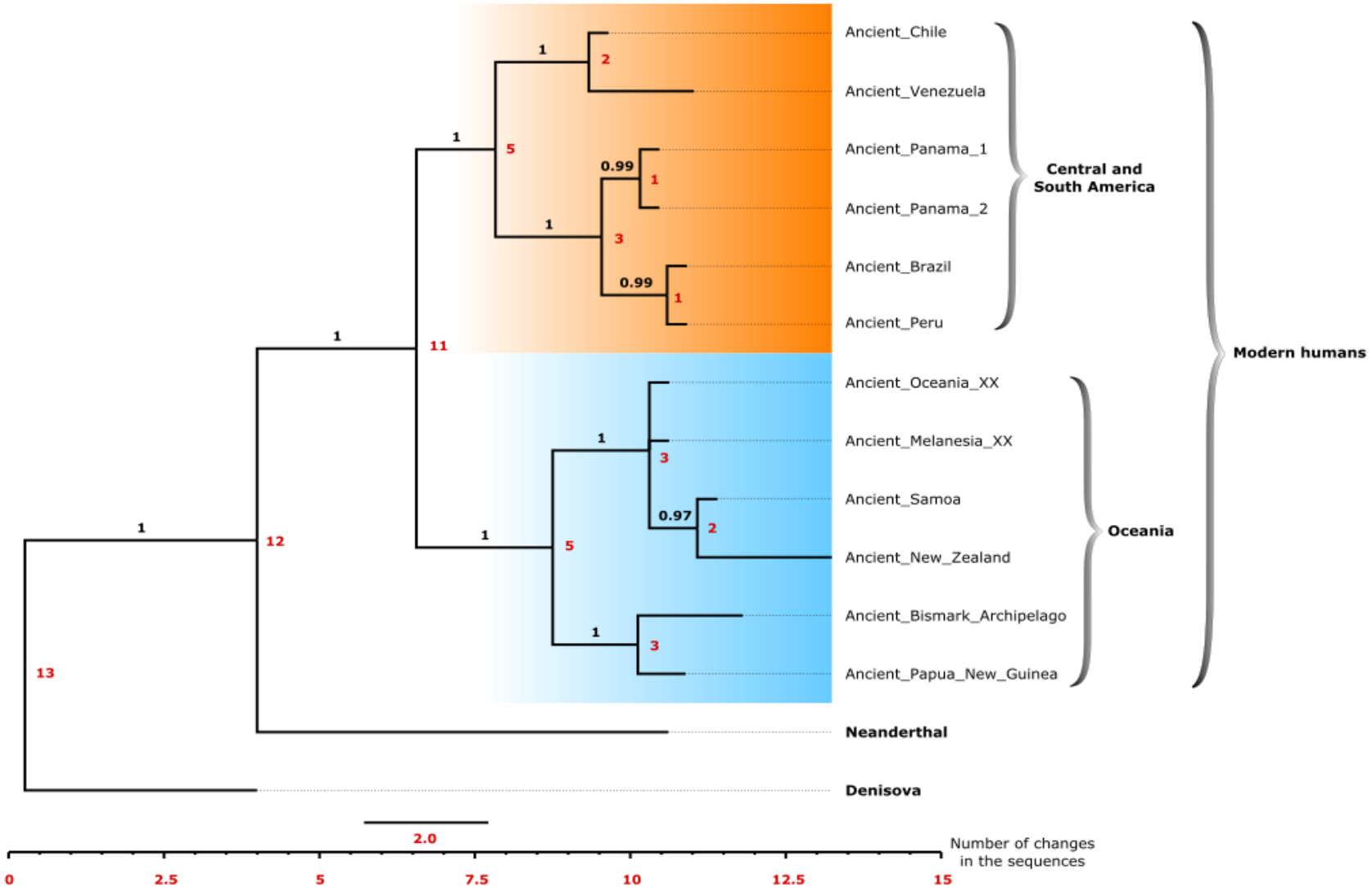

Figure 24. Clustering trends of HVSI_mt DNA. Ancient individuals from Oceania, South America and Panama. The phylogeny was estimated with a Bayesian approach under the TPM2u+F+G4 model.
XX= Unknown Subregion.

4 Discussion

4.1 Recovery of ancient DNA from tropical samples and pre-European burial rites

Usually, genetic analyses performed on bioarchaeological samples tend to be a bit more complicated than those carried out on contemporary samples. Due to post-mortem hydrolytic and oxidative processes, DNA preserved in archaeological specimen highly fragmented and only found in low quantity (Seidenberg et al., 2012; Llamas et al., 2017; Rohland et al., 2018; Feuerborn et al., 2020; Ferrari et al., 2021). These characteristics of aDNA are even more abundant in samples coming from tropical region, since the environmental conditions in these places promote the quick degradation of biological material hindering, even more, the recovery of the useful genetic material for genetic studies. However, STR typing can be carried out successfully on highly fragmented DNA because of the short length of the tandemly repeated structure (Hummel, 2003; Masuyama et al., 2017; Božič et al., 2021). On the other hand, the "easiest" genetic material to recover from bioarchaeological samples is the mtDNA, since it degrades twice as slow as nuclear DNA (Allentoft et al., 2012; Grass et al., 2015; Rohland et al., 2018; Chierto et al., 2021) and it has a high number of copies per cell (Pakendorf and Stoneking, 2005; Eduardoff et al., 2017; Gojobori, 2021), what allows recovering a greater number of mtDNA molecules for genetic analysis.

The success of PCR amplification for nuclear DNA and mitochondrial DNA from ancient samples from Oceania could be related not only to suitable extraction and amplification protocols, but also the preservation state of the biological material resulting from former burial rituals carried out by the human groups that inhabited the great Pacific region during the Holocene. During this period, the corpses were buried in graves not very deep, once the soft parts of the body decomposed, and only the bone material remains, the skulls were unearthed and hung in the houses to be taken care and venerated as a protection element for the family or his / her descendants (Codrington, 1891; Strauss, 2016; Wasef et al.,

2020; Adams et al., 2021; Enari and Lemusuifeauaali'i, 2021). Sometimes, the corpses were placed into sealed wooden structures, which were hung up in the house of their sons or in the public canoe-house (Codrington, 189; Strauss, 2016; Wasef et al., 2020; Adams et al., 2021). After some years, the corpses were removed from wooden structures, then the skulls and jawbones were separated from their bodies, and finally, the rest of the skeletons were buried in a common cemetery or in the family burying-place, depending on of the social status (Codrington, 1891; Strauss, 2016; Wasef et al., 2020; Adams et al., 2021).

Therefore, considering that the environmental conditions of Oceania are not the best to preserve the genetic material of bioarchaeological samples since this region has a humid tropical climate that promotes the fast degradation of organic material. The funerary practices performed by ancient peoples of Oceania might have helped to preserve part of the genetic material of these samples since the postmortem rituals aforementioned could have avoided that humic acids affected the preservation of the genetic material in the skulls and jawbones. When these bone remains were separated from the rest of the body and placed inside the houses as a sacred element of protection and veneration of the ancestors, possibly the DNA degradation process elapsed slower favouring recovery of this genetic material.

Regarding South America and Panama individuals, the recovery of feasible genetic material for DNA analysis was quite complicated because of samples conditions. This situation led to the modification of the standard protocol used in the host laboratory for extracting and amplifying ancient DNA. However, the PCR amplification of nuclear DNA of these samples was not as successful as Oceania samples. Notwithstanding, the PCR amplification of mtDNA was as successful as Oceania samples. Probably, the differential success of PCR amplification of nuclear DNA between ancient samples from Oceania and America lies in the way the ancient societies from South America and Panama handled the corpses during their burial rites.

It is an undeniable fact that environmental conditions affect the state of DNA preservation (Grass et al., 2015; Bálint et al., 2018; Matange et al., 2021). However, apparently, the way the corpses were handled during the burial rites in ancient societies also plays a relevant role regarding the state of genetic material preservation, as earlier discussed with Oceania samples. The ancient societies of South America mummified the bodies of their deceased relatives (Eeckhout and Owens, 2015; Gill-Frerking, 2017; Lombardi and Arriaza, 2020; Montt et al., 2021). This process could be natural or artificial, in both cases, the corpses were wrapped with mats of plants fibres or animal skins (Camelid) (Arriaza et al.,1994; Trancho, 2012; Eeckhout and Owens, 2015; Gill-Frerking, 2017; Lombardi and Arriaza, 2020; Montt et al., 2021).

Natural mummification occurred when the corpses were buried in arid places (high salinity and dryness conditions), such as the Atacama, Paracas deserts or their surroundings or when the bodies were buried in places with low temperatures, such as the Andean Mountain range (Llullaillaco, Aconcagua, Ampato, or Chuscha) (Arriaza et al.,1994; Trancho, 2012; Eeckhout and Owens, 2015; Gill-Frerking, 2017; Lombardi and Arriaza, 2020; Montt et al., 2021). While the artificial mummification involved an intentional alteration of the corpses, which usually included the removal of organs and filling the body cavities with organic and inorganic substances to preserve the body (Arriaza et al.,1994; Trancho, 2012; Eeckhout and Owens, 2015; Gill-Frerking, 2017; Lombardi and Arriaza, 2020; Montt et al., 2021). Undoubtedly, the mummification processes helped preserve the bone material and part of the skin of the bioarchaeological samples. Nonetheless, this process wreaked havoc on the genetic material of these individuals, since the effects of natural organic decomposition and the environmental conditions degraded the DNA of these individuals greatly, which made it difficult for the recovery of feasible DNA to perform genetic analyses with nuclear STR markers or mitochondrial DNA.

The burial practices of some Panamanian ancient societies (Gran Cocle) involved the preparation of deep graves with straight walls that penetrated the bed rock or funerary holes lined with stones and the construction of funerary urns with clay (Cooke et al.,1998; Martín-Seijo et al., 2021; Ranere and Cooke, 2021). Usually, the corpses were placed inside the graves and after some years, the bone material was placed inside a funerary urn or stacked in "packages" and then they were placed in the same grave again (Cooke et al.,1998; Cooke et al.,1998; Martín-Seijo et al., 2021; Ranere and Cooke, 2021). However, these burial structures (graves) could be used several times to bury other family or clan members (Cooke et al.,1998; Cooke et al.,1998; Martín-Seijo et al., 2021; Ranere and Cooke, 2021). Finally, although the bodies were underground within a burial structure, simultaneously they were exposed to water seepage from the surface, which increased the moisture levels in the grave, and along with the high temperature of the region favoured the activity of the decomposing organisms, such as fungi and bacteria. Probably, these conditions allowed the rates of organic decomposition to increase, which also provoked the quick degradation of the biological material and thus great damage to the genetic material of these individuals. This made it impossible to obtain information from the nuclear DNA of these samples, although it was possible to obtain genetic information for population analysis via mtDNA.

4.2 DNA typing of the past, genetic landscapes, diversity and structure

The lack of private alleles in ancient samples from Oceania, absence of sharing alleles between ancient Oceanians and modern Africans, Asians, New Zealanders from Western Polynesia, Caucasians from the US and Argentineans, and the lack of topological and morphological affinities among the genetic landscapes of ancient Oceanians and the five modern populations aforementioned is likely resulting from the effects of the population dynamics considering the temporal and spatial distances among ancient samples from Oceania and the individuals of modern populations. Thus, the horizon of biological events associated with the singularities observed in the behaviour of the density distributions of allelic frequencies, mainly involves migratory movements driven by social and / or environmental pressures, and ancestral miscegenation, which could be influenced by the systems of social mating and postmarital coexistence (uxorilocality and virilocality) (Bentley et al., 2021).

Undoubtedly, the evolutionary forces that generate diversity in populations or subpopulations are mutation, the origin of all diversities, and gene flow that promote the gene exchange or the transference of alleles among populations (Fuchs Castillo, 2019; Hartl, 2020; Láruson and Reed, 2021; Lohmueller and Nielsen, 2021). Whilst, genetic drift and natural selection are the evolutionary forces that sculpt and define both genetic landscapes and structure of populations (Fuchs Castillo, 2019; Hartl, 2020; Láruson and Reed, 2021; Lohmueller and Nielsen, 2021). The mutations will generate alleles and depending on their initial frequencies, they will be fixed or eliminated by genetic drift (Fuchs Castillo, 2019; Hartl, 2020; Lohmueller and Nielsen, 2021). Whilst, the natural selection will promote the presence of some alleles into populations through differential survival of genotypes (Fuchs Castillo, 2019; Hartl, 2020; Lohmueller and Nielsen, 2021).

Observed differences in the allele frequency density distribution patterns between the ancient Oceanians and modern Africans, Asians, New Zealanders from Western Polynesia, Caucasians from the US and Argentineans reflect both differential fixed of genotypes by natural selection because of the alteration of the segregation patterns on the genetic markers evaluated and the random changes that occurred at the allele frequencies owing to genetic drift, which is accelerated by bottlenecks or founder effect. Ancestral gene flow and genetic admixtures promoted by panmictic mating and social mating systems have influenced the genetic history and population dynamics of the ancient Oceanians. The gene pool in some modern populations (America and Oceania) was drastically altered via gene flow, Genetic/ethnic admixture and replacement half a millennium ago, during the European period of colonization and exploration. The allele frequencies of Modern Asian, African and European populations have also been affected by certain admixture processes and gene flow. In summary, the interbreeding processes, migration events, genetic drift and mating patterns (panmictic mating and social mating systems), evolutionary processes that underlie population dynamics and genetic history of the human peoples, sculpting and modelling the genetic landscapes of the different human populations over the generations.

Ancient Oceanians might be exhibiting those alleles that have already been fixed in the population several generations ago, which today are recognized as common alleles within the STRs loci analysed. Considering the ancestral population dynamics and the genetic history of the ancient individuals of Oceania, it might infer that the first anatomically modern humans who reached Sahul via Sunda and Wallacea had a genetic heritage whose structure would have been influenced by the gene pool of populations from the Middle East, India, and Southeast Asia and modified by genetic drift effects on the founder populations. Probably, ancient individuals from Oceania carried alleles identically by state (IBS), given the size of the founder population (150 - 1,000 individuals) (Zhivotovsky et al., 2003; Haber et al., 2019) could have become identical alleles by descendant (IBD) during some generation, because of

a high inbreeding rate resulting from consanguineous cross-breeding. The genetic drift fixed or eliminated alleles according to their initial frequencies, this genetically homogenized the ancestral peoples of Oceania via the reduction in genetic diversity within populations and increased the genetic variance between populations, differentiating the ancestors of ancient Oceanians from their parental populations. Regarding the populations with a high miscegenation proportion in their gene pool (modern individuals from America and Oceania), their IBS alleles come from the Indigenous, European and African populations, providing a triple genetic heritage in these individuals.

The most modern populations exhibited private or rare alleles at least in one of the genetic markers analysed. These allelic singularities in the modern populations could have their origins within the Aboriginal or indigenous populations, since the genetic information of the modern human groups used in this work comes from derivate populations (mestizos) from European, African and indigenous populations, as mentioned earlier. It is not a peculiar or strange event that human groups that have shared ancestry also share some alleles, which could be uncommon or even non-existent in other populations. This is resulting from most of the modern human populations exhibit a certain miscegenation degree with either nearby human groups or at an intercontinental level. Despite modern populations exhibited rare alleles (allele frequency ≤ 0.005), HWE expectations were not affected, since the amount of these allelic singularities within the evaluated genetic systems were not enough to disturb the genetic equilibrium configuration of these populations.

Genetic diversity is quantified through evaluation of genotypes to determine the frequency of heterozygotes (Fuchs Castillo, 2019; Hartl, 2020; Láruson and Reed, 2021; Lohmueller and Nielsen, 2021). Given that relative frequency of observed heterozygotes (Ho) can be affected by endogamy and population structure, then, the relative frequency of heterozygotes expected (He) under Hardy-Weinberg equilibrium should be determined to obtain a better estimative of populations genetic diversity, which would allow inferring how

often different alleles will be added in a population to form heterozygous (Nei, 1973; Harris and DeGiorgio, 2017; Fuchs Castillo, 2019; Hartl, 2020; Láruson and Reed, 2021; Lohmueller and Nielsen, 2021). Although the main effect of the genetic drift is the reduction of genetic diversity within populations, heterozygosity was not affected in the ancient samples of Oceania, since the expected heterozygosity in this sample set exhibited lofty values, He = ~80%, similar to the expected heterozygosity values in modern populations. Hardy-Weinberg expectations (HWE) were also unaffected by the genetic drift effects; since all populations meet the Hardy-Weinberg proportions. Probably, the alleles with high frequency were fixed by genetic drift, while the alleles whose low frequencies altered the Hardy-Weinberg expectations were eliminated also by genetic drift, a couple of generations ago, thus restoring the genetic equilibrium of the population.

At the global level, the population sub-structure coefficient Fst, exhibited a low value, indicating that there are no allele frequencies variations among subpopulations, so there is no Wahlund effect (heterozygous deficit). Therefore, if there is no Wahlund effect, then there is no spatial gene structure or more correctly, genetic diversity is not spatially or geographically structured between subpopulations. The inbreeding coefficients both at individuals within the population groups and the total within-population groups exhibited values between low and moderated, indicating that populations are panmictic. Thus, the patterns of genetic diversity, density and distribution of the alleles frequencies in the genetic systems evaluated shaped the nuclear DNA genetic structure as well as the genetic landscapes of these populations through the action of evolutionary forces. Nevertheless, the genetic landscape morphology and topography of ancient samples from Oceania could be considered as a picture or radiography of the genetic structure of these individuals before the European contact (~ 500 years ago).

4.3 Mitochondrial DNA diversity

According to the genetic information obtained from six STR markers, both ancient individuals from Oceania and individuals from modern populations got high values of heterozygosity, and thus high levels of genetic diversity. However, for mtDNA, heterozygosity is equivalent to nucleotide diversity and segregating sites (Hedrick, 2011; Fuchs Castillo, 2019; Hartl, 2020; Láruson and Reed, 2021; Lohmueller and Nielsen, 2021). Thus, both the values of nucleotide diversity (π or $\theta\pi$) and segregating sites (S or θs) can be considered as expected heterozygosis, since they are a very precise way to estimate genetic variation on DNA sequences because of both are based on the number of differences by position according to the length of nucleotide sequences in the alignment (Hedrick, 2011; Fuchs Castillo, 2019; Hartl, 2020; Láruson and Reed, 2021; Lohmueller and Nielsen, 2021). The uncertainty levels generated by the information entropy (Shannon entropy) in a set of aligned sequences allow visualizing the distribution of genetic variability by position through the detection of informative polymorphic sites, giving an idea of the positions that exhibit greater genetic variability (Torkashvand et al., 2021).

Between 41.94% and 50% of polymorphic sites of ancient individuals from Oceania, South America and Panama exhibited less than one bit of contained information by position, providing unambiguous information about the real informatively level and genetic variation on these segregating sites. The most common observed mutations in these set of sequences were transitions, both pyrimidine and purine type. The occurrence of this kind of substitution in the populations mentioned above ranged between 76.92% and 90%. The frequency of this type of substitutions is not random, because evolutionarily the transitions are more favoured than transversions owed to the transitions cause less entropy in the DNA, and therefore, they

are less recognized as errors and therefore, decreasing the probability to be corrected, and being neutral mutations (in this case), they do not affect the fitness of individuals.

Regarding haplotype diversity, ancient individuals from Oceania exhibited a greater quantity of mitochondrial variants with origins between East, South Central, and Southeast Asia, and Near and Remote Oceania, evidencing the flow of mtDNA molecules with mutations regionally defined in ancient samples from Oceania, as well as, the evolution of some mitochondrial variants that became in mtDNA lineages typical of Remote Oceania. The presence of the matrilineal Asian genetic heritage in these samples is linked to the initial settlement of Oceania during the Upper Pleistocene 55,000 – 65,000 years ago (Clarkson et al., 2017; Bedford et al., 2018; Lipson et al., 2018; Matsumura et al., 2018; Posth et al., 2018; Llamas et al., 2020; Prasetyo et al., 2021), as well as the Austro-Asiatic (10,000 years ago) (Llamas et al., 2020; Prasetyo et al., 2021; Sun et al., 2021) and Austronesian (3,000 – 5,000 years ago) (Llamas et al., 2020; Prasetyo et al., 2021) expansion that took place during Holocene. The South American and Panamanian samples showed Pan-American haplogroups, where ancient individuals from South America exhibited higher haplotype diversity than ancient Panamanians.

Ancient South American individuals have mitochondrial lineages linked to both the early settlement of America through the Pacific coastline or the continental interior route via Ice-Free Corridor during the Upper Pleistocene about 14,700 – 17,000 years ago (Perego et al., 2009; de Saint Pierre et al., 2012; Stroeven et al., 2014; Gómez-Carballa et al., 2018; Davis et al., 2016; Potter et al., 2016; Simão et al., 2019; Suarez and Ardelean, 2019; Hoffecker et al., 2021), and mtDNA lineages linked to the hunter-gatherers dispersion that took place during the Holocene about 8,900 – 11,500 years ago (Cooke et al., 2013; Posth et al., 2018; Antczak, 2019; Suarez and Ardelean, 2019; Gruhn, 2020; Ranere and Cooke, 2021).

Whilst, the ancient individuals from Panama have mitochondrial lineages mainly linked to the dispersion event mentioned above. This exposes the molecular evolution, at mitochondrial lineages level, of the human groups of America, since they split from the mother populations of Northeast Siberia and Bering, as well as the migratory events that provoke the peopling of the continent.

When the settlement of Oceania and America had occurred, the effective number of individuals involved in these events ranged from approximately 150 – 1,000 people to Oceania (Zhivotovsky et al., 2003; Haber et al., 2019) and 250 to America (Fagundes et al., 2018) respectively. Thus, the first modern humans who arrived in these regions represented only a small portion of the total genetic diversity that was found in the mother populations of these individuals. This made the effect of genetic drift more evident in populations derived from the founder groups of Oceania and America. Therefore, the low genetic diversity observed (at mtDNA level) in the sequence sets of the ancient samples from Oceania, South America and Panama (Table 10) could be reflecting the vestiges of the founder effect that occurred when these individuals arrived at these regions about 14,600 years ago.

When evaluating the sources of genetic variation both in the nuclear DNA and mitochondrial DNA, it was possible to notice that the main variation sources for both nDNA and mtDNA were found within the individuals and not among the populations. Regardless of the mode of inheritance of these genomes, both indicate that the migrants bear a fraction of allele combinations and a few mitochondrial lineages. Over time, these genetic variants will accumulate mutations in the founder populations that differentiate them from the mother populations. The high global Fst indicate that at the mitochondrial level, the genetic variation is spatially or geographically structured among these populations. Whilst, Fst value between ancient samples from Panama and South America suggested a moderate genetic

differentiation, indicating that the genetic variation between these human groups is moderately structured around the geographical regions. Given that the Fst reflects the ancestral genetic conditions of populations; the genetic structure of these populations could be resulting from the human expansions that occurred on the continent during the Upper Pleistocene.

4.4 Inferring historical demographic patterns and clustering trends

Tajima's D, Fu's Fs, Harpending raggedness index and the mismatch distribution of the sequences suggest that the populations of Oceania, South America and Panama went through a demographic expansion. Geologically, the temporal range of these expansions is between the Upper Pleistocene (129,000 – 11,700 years ago) and the Holocene (11,700 years ago – present); while from the climatological point of view they are located within the Last Glacial Period (LGP) or Wisconsin / Würm glaciation (11,000 – 75,000 years ago). During the last ice age (Wisconsin / Würm glaciation), the concentration of ice on the continents lowered the level of the oceans by about 120 meters (Clayton and Attig, 1987; Fagan, 2019; Steeves, 2021). This descent caused that in several points of the planet terrestrial connections were created, like for example Australia with Tasmania and New Guinea; The Philippines and Indonesia; Japan and Korea; and Asia and America (Harff et al., 2016; Kawai and Rogers, 2021).

The ancient samples from Oceania suggest by roughly 37,972 years ago (95% CI 34,537 – 42,167 years ago) individuals from this region underwent a population expansion. This expansion corresponds with the temporal range of the Upper Paleolithic (12,000 – 50,000 years ago). In accordance with the literature, during this period the initial settlement of Melanesia took place as well as the divergence between Oceanian and Southeast Asian peoples, which occurred ~36,000 years ago (Pugach et al., 2013; Jinam et al., 2017; Posth et al., 2018; Bird et al., 2019; Bradshaw et al., 2019; Bradshaw et al., 2021). Mitochondrial lineages Q1, Q2 and Q2a3b whose coalescence ages estimate at ~ 17,200 – 30,270 years are linked particularly to the migratory event that gave rise to the initial peopling of the Bismarck Archipelago through the New Britain Island colonization about 35,000 years ago (Pedro et al., 2020), and the settlement of Solomon Island about 29,000 years ago (Matisoo-Smith, 2015; Veth et al., 2017; Bird et al., 2019; Bradshaw et al., 2021; Pugach et al., 2021).

The East and Southeast Asian haplogroups, D4h1, M7b1a1i and M65a whose coalescence ages estimate at ~ 17,000 – 18,000 years, besides being linked to the peopling of some Oceania regions, during de Upper Palaeolithic, also support Asian ancestry of some human groups from Oceania. Whilst, the mtDNA variants B4c1a1 and E1a2, also from East and Southeast Asia, and whose coalescence ages estimate at ~ 9,600 – 10,000 years, are linked to the human expansion known as the Austronesian expansion happened around 6,000 – 10,000 years ago (Matisoo-Smith, 2015; Issiki et al., 2018), and that took place in Remote Oceania, during the Early Holocene, after the last glacial period.

While the peopling of Melanesia occurred, nineteen thousand years after the first Anatomically Modern humans crossed the boundary of Sunda into Sahul, somewhere in East Asia around 36,000 years ago, a group of individuals splits off their mother population to give rise to the founder population of Beringia human groups and some Native America peoples (Moreno-Mayar et al., 2018). North or South America first? From here, the debate on the peopling of America begins, which is characterized by the passion shown by scientists, the variety of theories, and sub-theories, the contradictory results, the number of studies, and counter studies and striking headlines in the newspapers (Suarez and Ardelean, 2019). The antiquity of humans in America is subject to great scientific controversy. The latest date is the one held by proponents of the late settlement theory and is related to the Clovis culture, which undoubtedly established a human presence 13,500 years ago (Sonneborn, 2006; Fagan, 2019; Ardelean et al., 2020; Steeves, 2021). Proponents of this theory argue that the date of entry to the continent could not be earlier than 14,000 years, because it was at that time that the free corridor opened following the Mackenzie River through present-day Canadian territory (Pauketat and Sassaman, 2020; Young et al., 2020). This hypothesis has been definitively disproved by the dating of Monte Verde, Chile, 14,800 years old (Suarez and Ardelean, 2019; Gruhn, 2020; Becerra-Valdivia and Higham, 2020; Pauketat and Sassaman, 2020; Dillehay et al., 2021), and later with the dating of a human footprint (called the Pilauco Footprint (Chile),

discovered at the Pilauco Bajo paleontological site, which has antiquity dated 15,600 years old (Gruhn, 2020; Pauketat and Sassaman, 2020; Roca-Rada et al., 2021; Steeves, 2021).

The ancient samples from South America suggest by roughly 14,150 years ago (95% CI 15, 713 – 12,870 years ago) individuals from this region underwent a population expansion. This expansion corresponds to the temporal range of the American Paleo-Indian period (8,000 – 20,000 years ago). This date could be reflecting a possible but challenging hunter and gatherer migration along the North Pacific Coastline 14,700 – 17,000 years ago, as well as the divergence of Native American groups (Stroeven et al., 2014; Davis et al., 2016; Potter et al., 2016; Timmermann and Friedrich, 2016; Nielsen et al., 2017; Suarez and Ardelean, 2019; Llamas et al., 2020; Braje et al., 2020; Puzachenko et al., 202; Steeves, 2021). Nonetheless, although the marine ecosystem along the Pacific Coastal Route was productive enough to support human migrations, the human groups that would have used this road to migrate across the continent would have been struggling with sea ice and broke glaciers, which surely hampered the migration of humans inland and across the Americas by those times (Stroeven et al., 2014; Davis et al., 2016; Potter et al., 2016; Nielsen et al., 2017; Suarez and Ardelean, 2019; Llamas et al., 2020; Braje et al., 2020; Steeves, 2021).

The ancient samples from Panama suggest by roughly 9,468 years ago (95% CI 8,611 – 10,513 years ago) individuals from this place underwent a population expansion. This expansion corresponds to the temporal range of the Early Holocene (8,200 – 11,700 years ago), which coincides with the Early Archaic period of America. These temporary estimates of population expansion match archaeological evidence of the presence of human groups in the isthmus of Panama 7,000 – 13,000 years ago (Cooke et al., 2013; Ranere and Cooke, 2021; Capodiferro et al., 2021), as well as Proto-Chibchan groups divergence, and the microphylum Lenmichi fragmentation 7,000 – 10,000 years ago (Barrantes, 1993; Ruiz-Narváez et al., 2005; Constenla Umaña, 2008; Boas, 2010; Núñez-Castillo, 2012; Langebaek, 2019; Chavarría, 2021). Mitochondrial lineages B2, B2i1, C1 and D4h3a whose coalescence

ages estimate at ~ 13,300 – 18,5000 years might be linked to the gen flow that happened between eastern Siberia (Asia) and western Alaska (America) by rough 15,000 – 25,000 years ago (Fagan, 2019; Llamas et al., 2020; Steeves, 2021), towards the end of Wisconsin / Würm glaciation (Ice Age), during the Upper Pleistocene, when glaciers that covered the northern half of the continent began to gradually melt, exposing new land for occupation. The temporal estimates of these lineages might also be linking them to the divergence of Native American groups 15,000 - 17,000 years ago (Nielsen et al., 2017; Llamas et al., 2020). Likewise, these mitochondria variants might be reflecting the initial peopling of South America during the Upper Paleolithic, around 14, 500 – 15,600 years ago (de Saint Pierre et al., 2012; Suarez and Ardelean, 2019; Gruhn, 2020; Becerra-Valdivia and Higham, 2020; Pauketat and Sassaman, 2020; Dillehay et al., 2021; Roca-Rada et al., 2021). Whilst, A2 and D1a1 lineages whose coalescence ages estimate at ~ 4,500 – 9,3000 years might be linked to the hunter-gatherers gene flow that took place about 8,900 – 11,500 years ago, when climate stabilized leading to a rise in population and lithic technology advances (Sonneborn, 2006; Fagan, 2019; Pauketat and Sassaman, 2020), during the Middle Holocene, which corresponds to the Early Archaic period of America (Cooke et al., 2013; Posth et al., 2018; Antczak, 2019; Suarez and Ardelean, 2019; Gruhn, 2020; Ranere and Cooke, 2021).

Thus, the human groups that dispersed into the continent were groups of hunters and gatherers who crossed Beringia, during the Paleoindian Period, looking for food, subsequently becoming the first American residents. Once settled on the continent, these human groups developed the first stone tools and the bases of the ethnic and linguistic diversity of pre-Hispanic America. During the Holocene, anatomically modern humans went from being a group of nomadic people, whose lifestyle was based on hunting and gathering to clans with a more sedentary lifestyle where agriculture became the main source of food. This laid the foundations for the development of the great civilizations and empires that existed on the continent before European contact.

The phylogenetic tree exhibited a clear clustering trend, where Panamanian and South American individuals grouped together in a clade, while Oceania individuals are grouped in another clade, the Oceanian branch, showing that the individuals from Near Oceania showed greater genetic affinity between them. Also, the Remote Oceania clusters exhibited greater affinity with each other. However, the cluster of individuals without a defined subregion seemed to have a genetic affinity with the individuals from Remote Oceania, so that the tagged individuals as Oceania_xx and Melanesia_xx could have mitochondrial links associated with Polynesian ancestry or these samples could have been mislabelled, which is not a situation with a low probability of occurrence, considering that during the second war at the end of July 1943 a bombing was carried out on the German city of Hamburg (Operation Gomorrah) by the Royal British Air Force and United States Army Air Forces (Lowe, 2007). This attack affected the Ethnohistorical Institute of the University of Hamburg, where the samples used in this study were stored. Unfortunately, the fire that broke out from the bombing destroyed part or all the archaeological and anthropological information of some samples. After World War II, some anthropologists tried to geographically order and relocate the specimens of the anthropological collection of this institute. During this work, some samples lacked essential information to relocate them geographically, so they were labelled only inferring the continental region they probably belonged to.

The American branch, showing that individuals from Brazil and Peru exhibited more genetic affinities with Panamanian samples than with Venezuela and Chile. This clustering pattern is similar to that found by Ruiz-Narváez et al. (2005) when analysed the genetic distances generated from Y-Chromosome microsatellites in Chibchan groups from Lower Central America (LCA) and South American tribes from the Andean and Amazonian regions. The phylogenetic inference generated by Ruiz-Narváez et al. (2005) showed that the Chibchan groups exhibited more genetic affinities with tribes Cayapa from Ecuador, Gaviao from Brazilean Amazonian, and Tayacaja, and Arequipa from the Peruvian Andean region.

The phylogenetic relationships observed between the tribes Chibchan, and South American could be explained by Wang et al. (2007), when examined genetic diversity, and population structure in the American landmass using 678 autosomal microsatellite markers genotyped in 422 individuals representing 24 Native American populations sampled from North, Central, and South America. This study showed that the dispersal of the human populations happened from North America to South America, and the genetic similarities between South and Central American populations were likely resulting from a recent gene flow along the Pacific North Coast (Wang et al., 2007), which probably took place between the Middle and the Upper Holocene about 4,200 – 8,200 years ago (Fagan, 2019; Suarez and Ardelean, 2019; Pauketat and Sassaman, 2020; Steeves, 2021). By roughly 4,200 years ago, there was a population expansion from the California Channel Island to the southern Peruvian Andes, generating an ancestry shared between North and South (Posth et al., 2018). The human groups that peopled Oceania and America went through demographic expansions and population splits so that, the groups derived from these population dynamics were more susceptible to the genetic drift effects since having a low number of individuals, generated small differences that became part of the typical genetic pool of these human groups, giving rose to the modern indigenous populations of Oceania and America.

5 Conclusions

1. The genetic landscapes of the ancient individuals from Oceania did not keep similarities to the modern Africans, Asians, New Zealanders from Western Polynesia, European from the US and Argentineans genetic landscapes, since the gene pool of populations is the product of their own genetic history and population dynamics which has sculpted and determined their genetic landscapes and structure. The genetic landscapes of these populations reflected the change of allele frequencies through time and space, as well as the effect of the miscegenation process on the genomes, in terms of diversity, of Oceania and America, which went through a forced genetic admixture process half a millennium ago.
2. The probability of segregating sites (θs), nucleotide diversity (θπ), and the probability of haplogroup (θh) or haplotype diversity indicated that hypervariable region I of the mitochondrial genome of the ancient samples from Oceania, South America and Panama had low levels of genetic diversity, probably resulting from the founder effect that occurred when the modern humans arrived at these regions by the first time during the Upper Pleistocene. Mitochondrial lineages found in these samples set were linked to the geographic regions under which the samples had been classified, indicating, in this case, that the genetic and anthropological information matches each other.
3. Phylogenetic inferences showed clear clustering patterns, where the individuals from Bismark Archipelago and Papua New Guinea exhibited closer genetic affinities between them. Likewise, the individuals from New Zealand and Samoa exhibited greater affinity with each other. Moreover, the phylogenetic analyses were useful to clarify a bit the geographical origin of some samples, such as the samples tagged as Oceania_xx and Melanesia_xx, which had genetic affinities with Polynesia. The

American branch exhibited genetic affinities between Panamanian and South American (Brazil and Peru) samples, probably resulting from a migratory event, along the Pacific North Coast, from North America to South America that took place between the Middle and the Upper Holocene.

4. The expansion time of ancient individuals from Oceania 37,972 years ago (95% CI 34,537 – 42,167 years ago) is consistent with the initial colonization period of the Bismark archipelago and the Solomon Islands. Likewise, the expansion time of ancient individuals from South America 14,150 years ago (95% CI 15, 713 – 12,870 years ago) correspond to the initial settlement of South America during the Upper Pleistocene. Whilst, the expansion time of ancient individuals from Panama 9,468 years ago (95% CI 8,611 – 10,513 years ago) is consistent with the migratory event that happened during the Early Holocene and that gave rise to the initial peopling of the Isthmus-Columbian area.

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7 Appendix

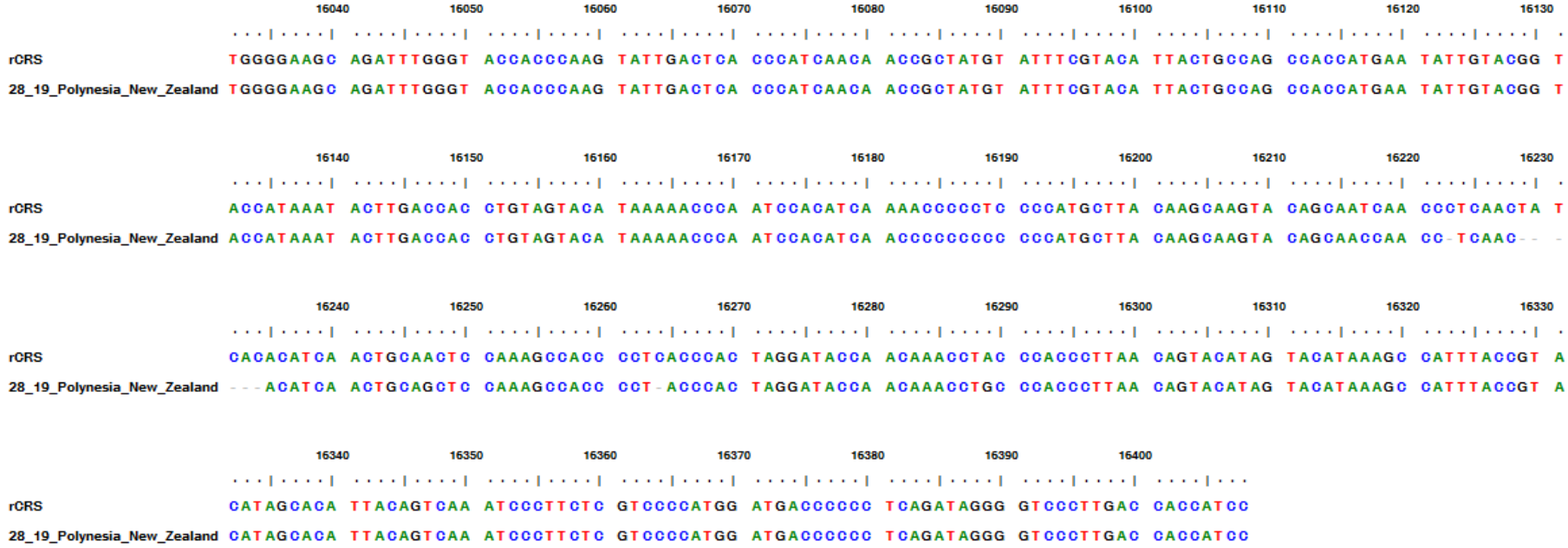
7.1 Data sheets on individuals from Oceania

Sample ID: 28:19
Morphological sex: ♂
Region: Oceania
Subregion: Polynesia
Country: New Zealand

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
X/Y	12/13	28/30	15/17	6/9.3	10/13	19/24

Haplogroup: B4a1a1a11b

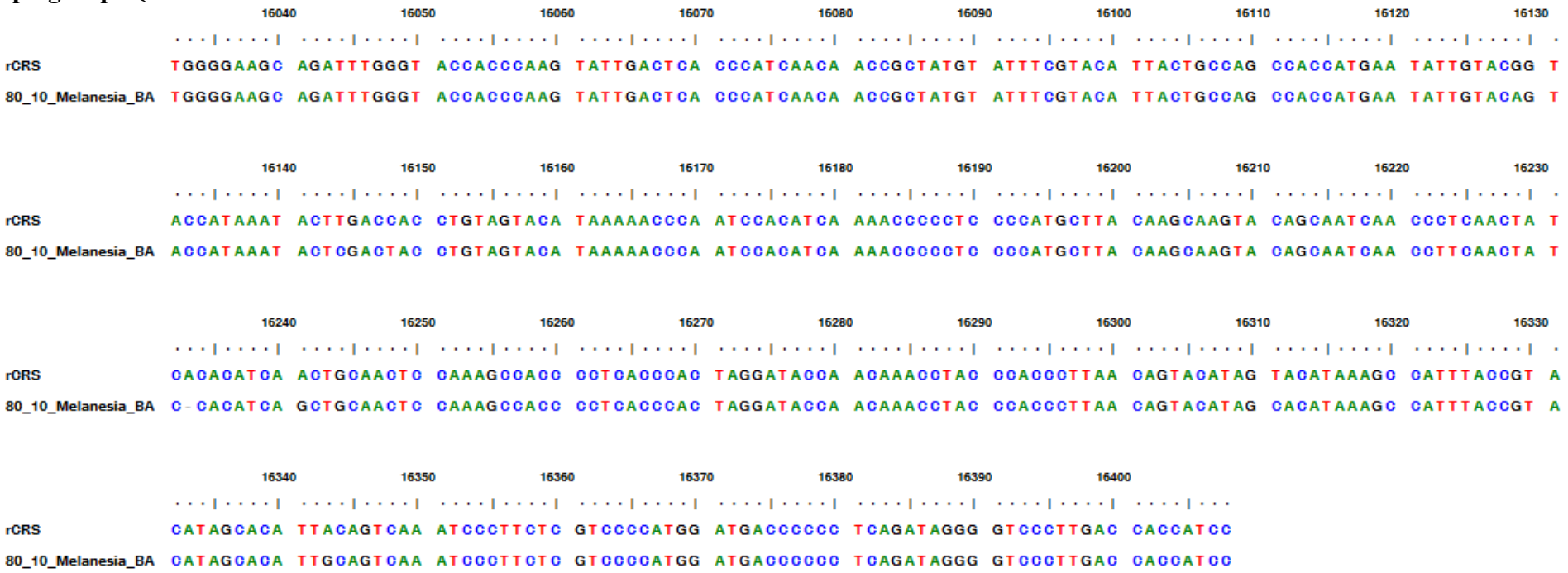


Sample ID: 80:10
Morphological sex: ♂
Region: Oceania
Subregion: Bismark Archipelago, Melanesia
Country: Admiralty Islands

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
X/Y	8/10	29/30	14/16	6/9	10/12/20	24/25

Haplogroup: Q1

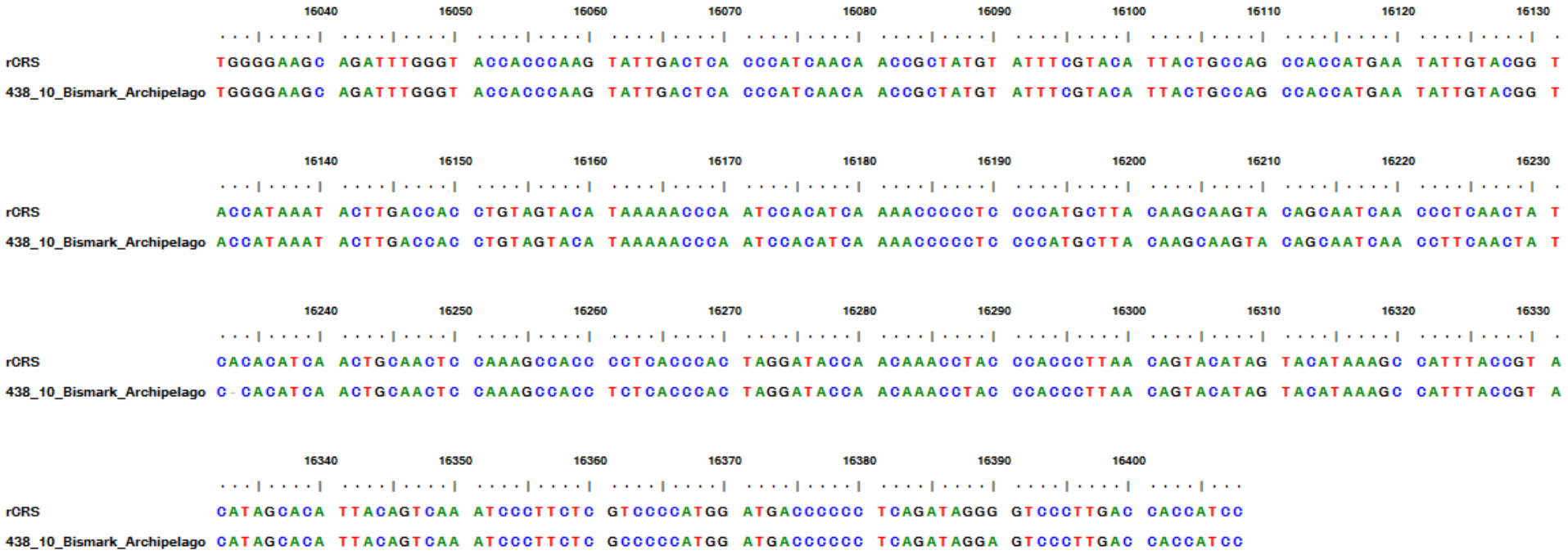


Sample ID: 438:10
Morphological sex: ♀
Region: Oceania
Subregion: Bismark Archipelago, Melanesia
Country: Admiralty Islands

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
X/X	11/12	29/30	-/13	8/9	-/10	-/20

Haplogroup: E1a2

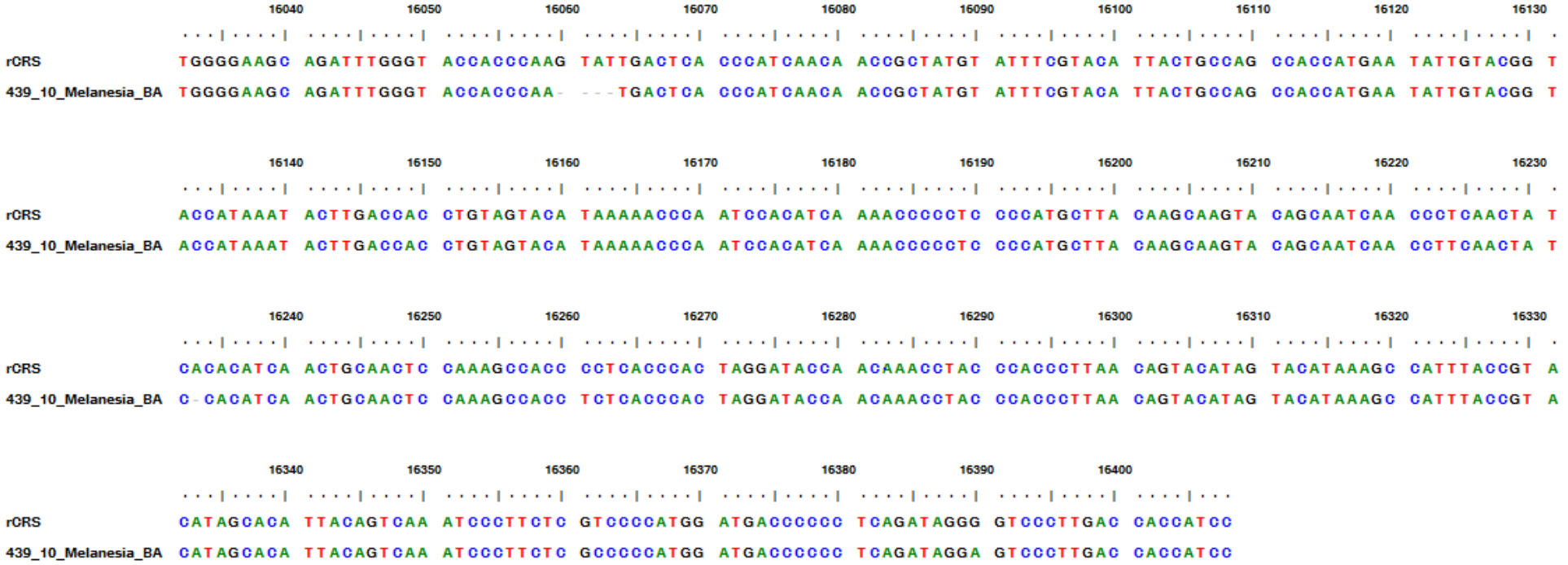


Sample ID: 439:10
Morphological sex: ♀
Region: Oceania
Subregion: Bismark Archipelago, Melanesia
Country: Admiralty Islands

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
X/X	11/12	28/30	-/13	-/9	-/13	-/20

Haplogroup: E1a2

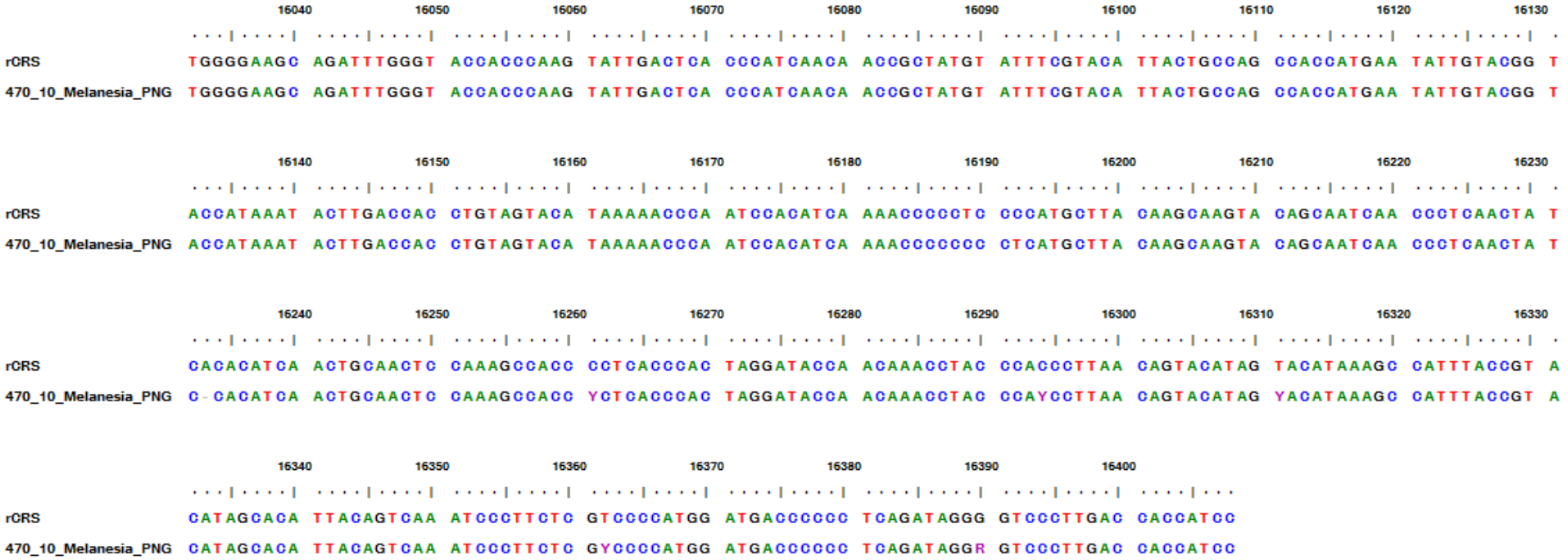


Sample ID: 470:10
Morphological sex: ♂
Region: Oceania
Subregion: Bismark Archipelago, Papua New Guinea, Melanesia
Country: New Pomerania

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
X/Y	9/11	-/-	-/18	6/9	-/10	23/25

Haplogroup: L2a1i

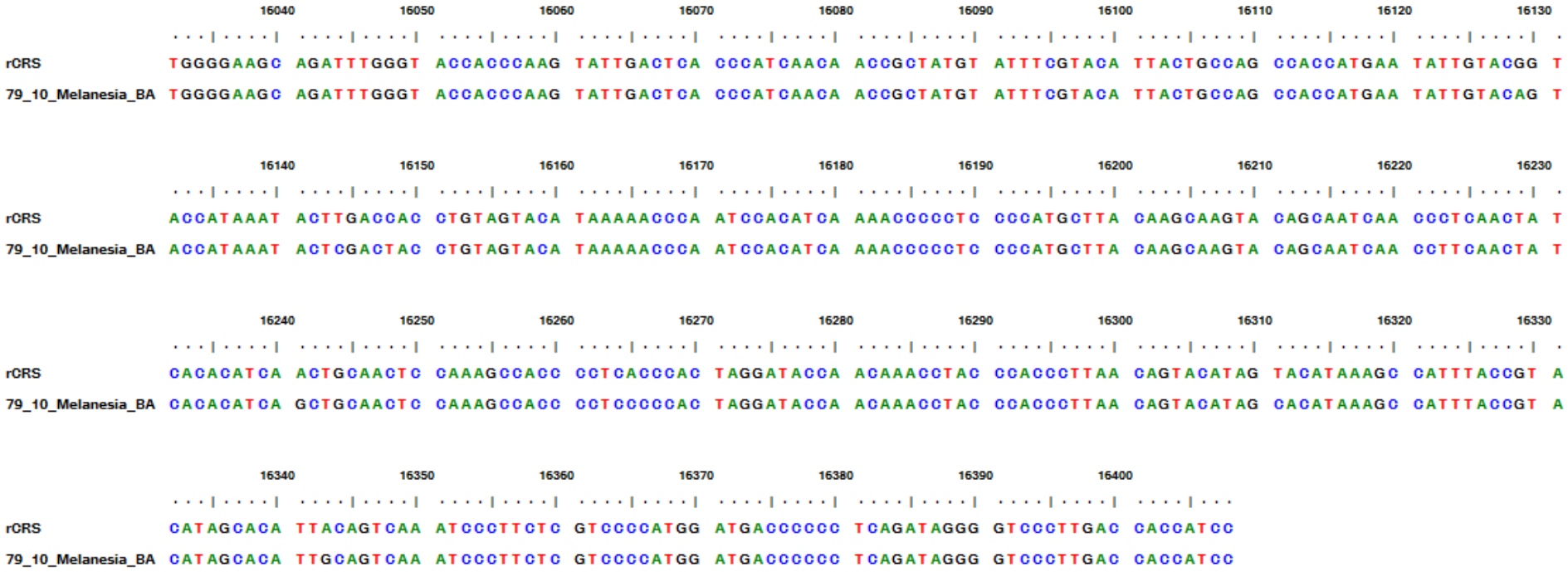


Sample ID: 79:10
Morphological sex: ♂
Region: Oceania
Subregion: Bismark Archipelago, Melanesia
Country: Admiralty Islands

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
X/Y	11/12	31.2/32.2	14/15	7/9	10/13	22/25

Haplogroup: Q1

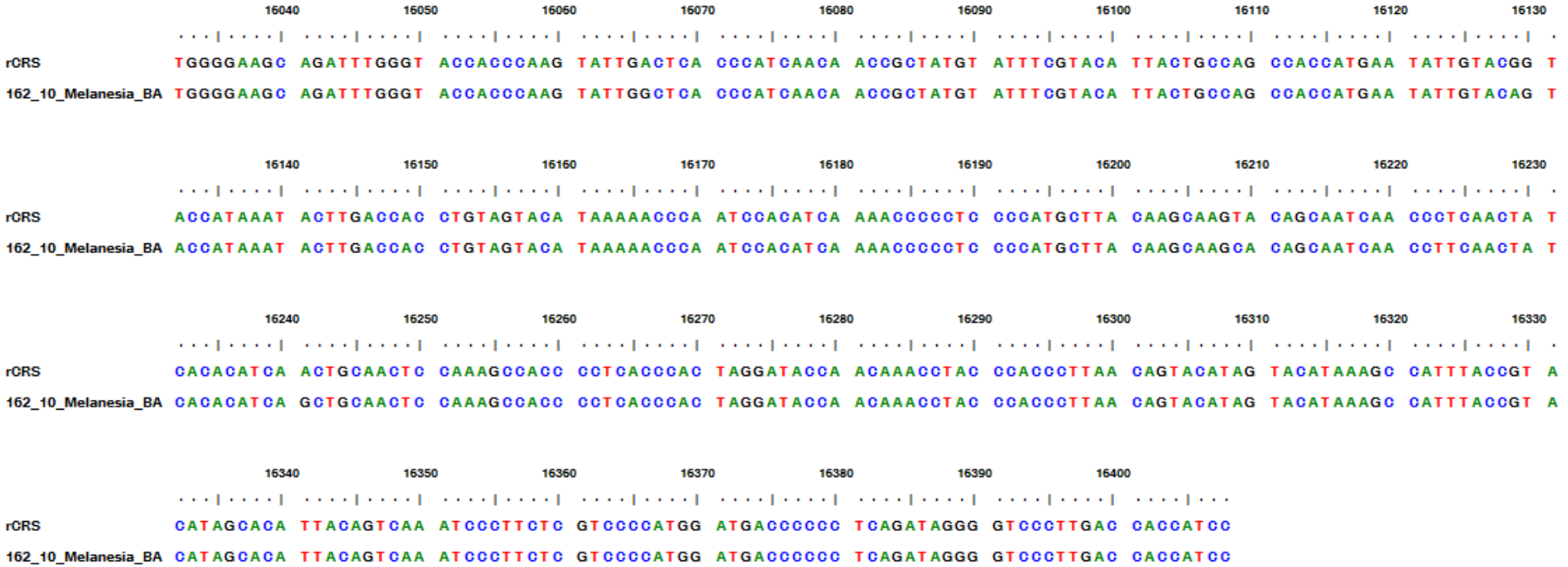


Sample ID: 162:10
Morphological sex: ♀
Region: Oceania
Subregion: Bismark Archipelago, Melanesia
Country: Admiralty Islands

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
X/X	-/11	29/30	15/17	7/8	12/13	24/25

Haplogroup: Q2

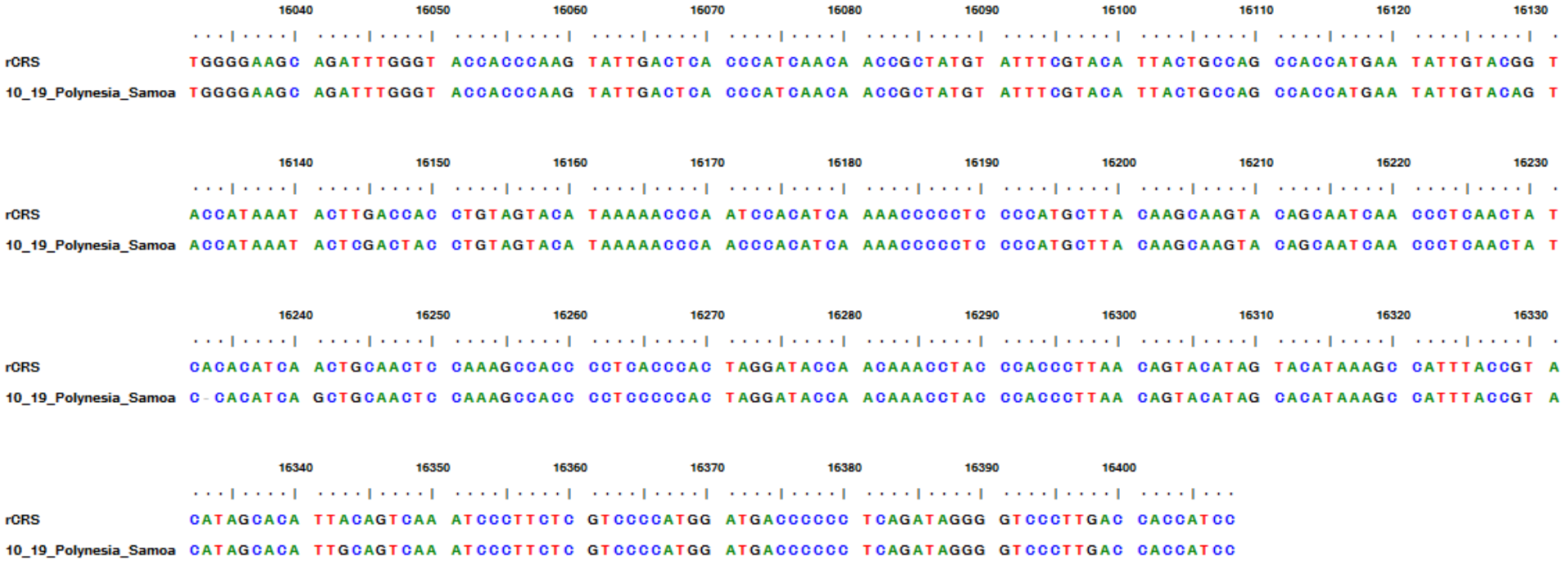


Sample ID: 10:19
Morphological sex: ♂
Region: Oceania
Subregion: Polynesia
Country: Samoa

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
X/Y	11/13	31.2/32.2	15/17	-/8	10/12	22/23

Haplogroup: Q1

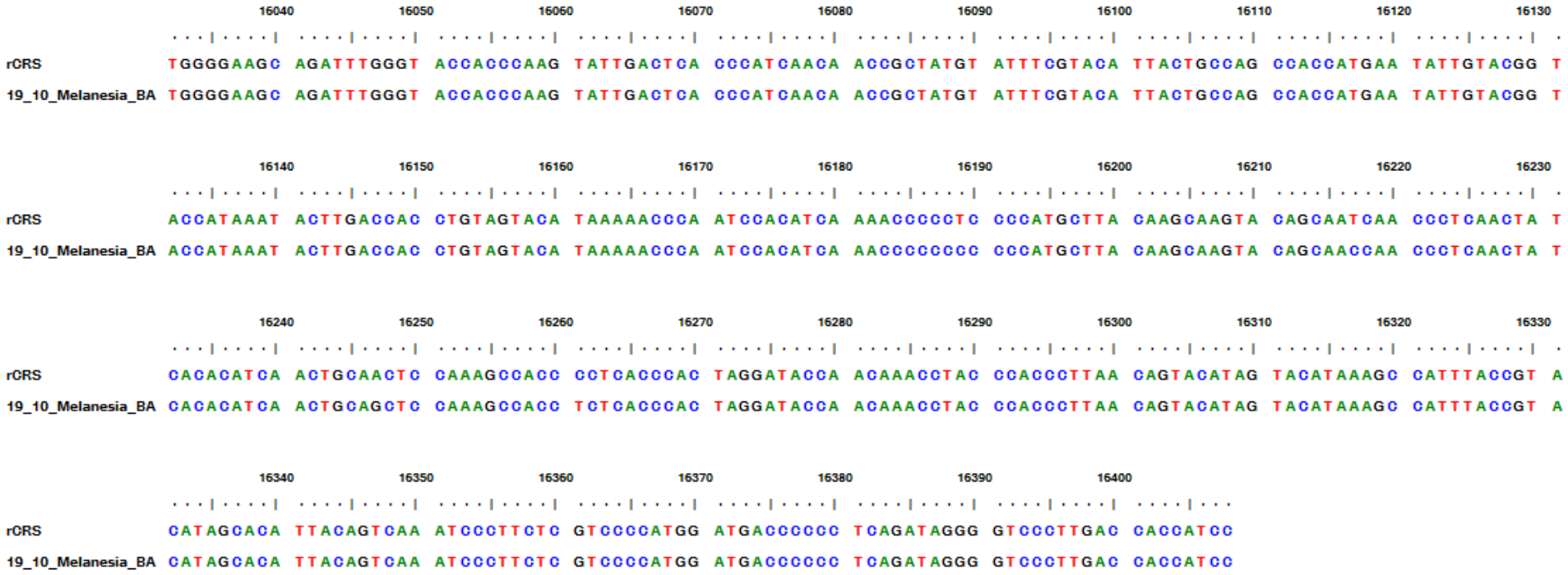


Sample ID: 19:10
Morphological sex: ♀
Region: Oceania
Subregion: Bismark Archipelago, Melanesia
Country: Mussau Island, St. Mathias Islands

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
X/X	8/9	28/31.2	15/20	7/8	-/10	18/21

Haplogroup: B4a1a1

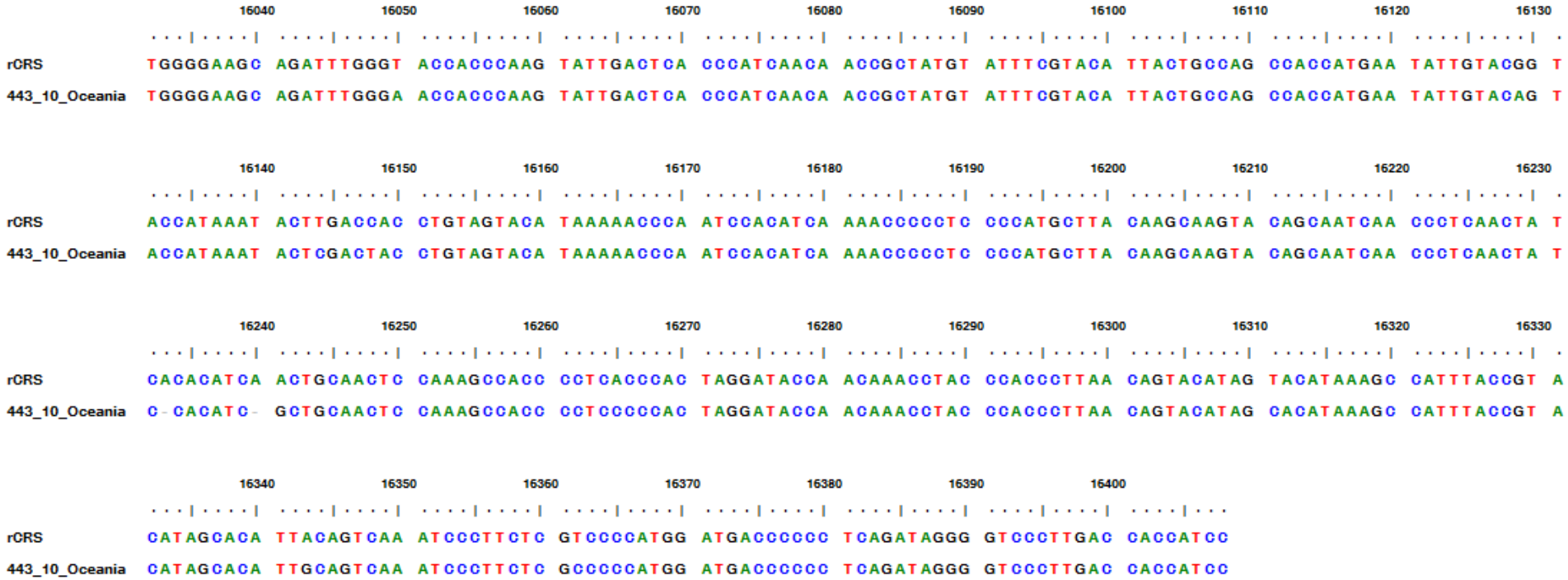


Sample ID: 443:10
Morphological sex: ♀
Region: Oceania
Subregion: Unknown
Country: Unknown

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
X/X	8/13	30.2/31.2	12/13	7/9.3	10/12	23/26

Haplogroup: Q1

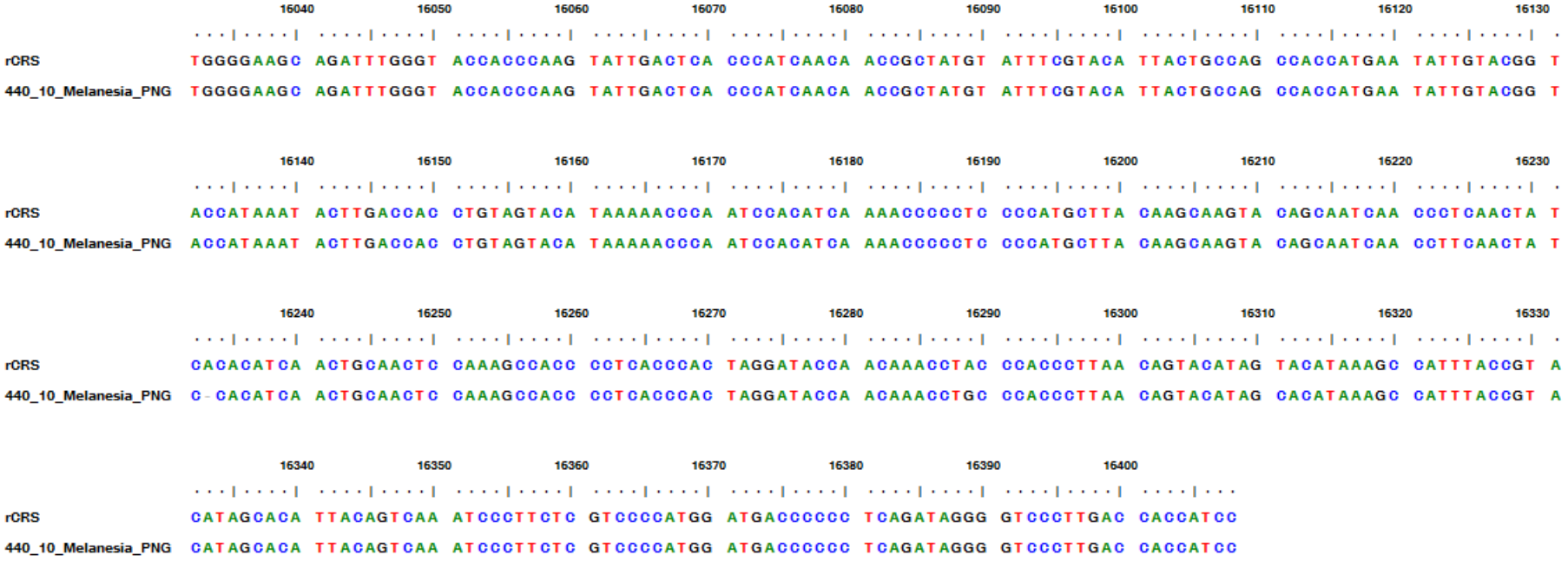


Sample ID: 440:10
Morphological sex: ♂
Region: Oceania
Subregion: Bismark Archipelago, Papua New Guinea, Melanesia
Country: New Pomerania

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
X/Y	8/9	-/-	-/-	9.3/10	10/11	23/26

Haplogroup: M65a

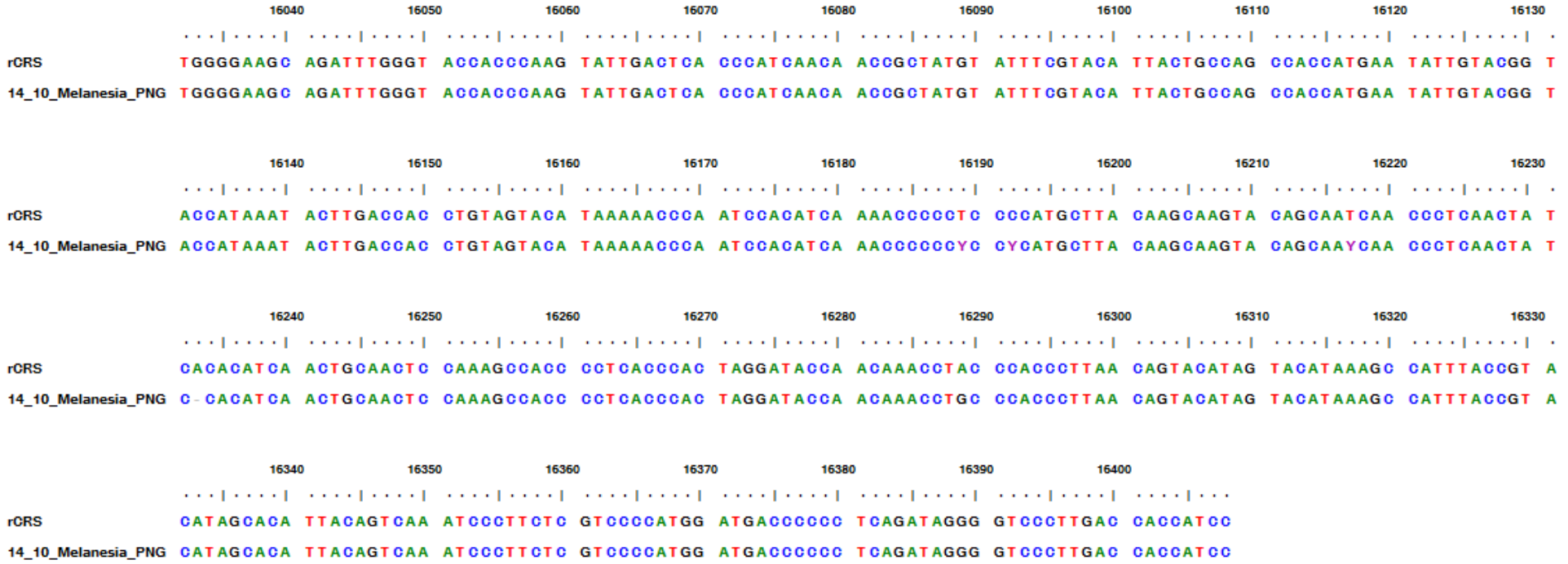


Sample ID: 14:10
Morphological sex: ♂
Region: Oceania
Subregion: Bismark Archipelago, Melanesia
Country: Mussau Island, St. Mathias Islands

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
X/Y	9/13	29/31.2	15/16	6/9	11/12	24/25

Haplogroup: B4

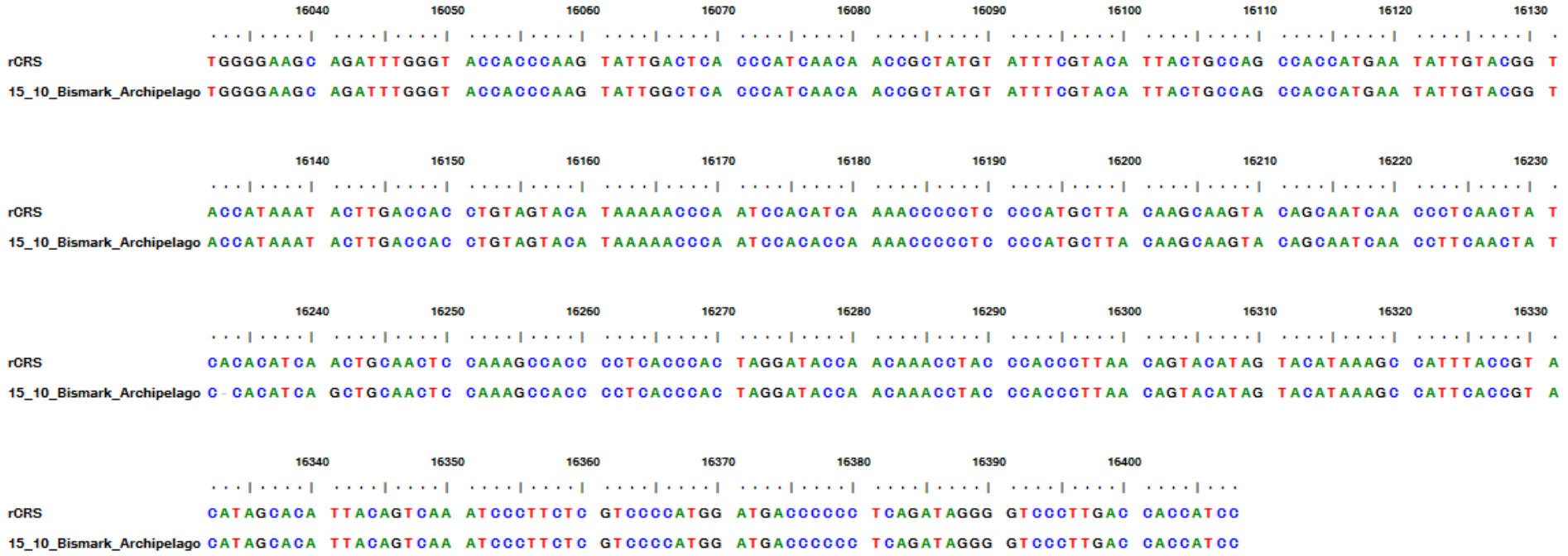


Sample ID: 15:10
Morphological sex: ♂
Region: Oceania
Subregion: Bismarck Archipelago, Melanesia
Country: Mussau Island, St. Mathias Islands

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
X/Y	8/11	31.2/32.2	13/19	8/9.3	10/12	19/24

Haplogroup: Q2

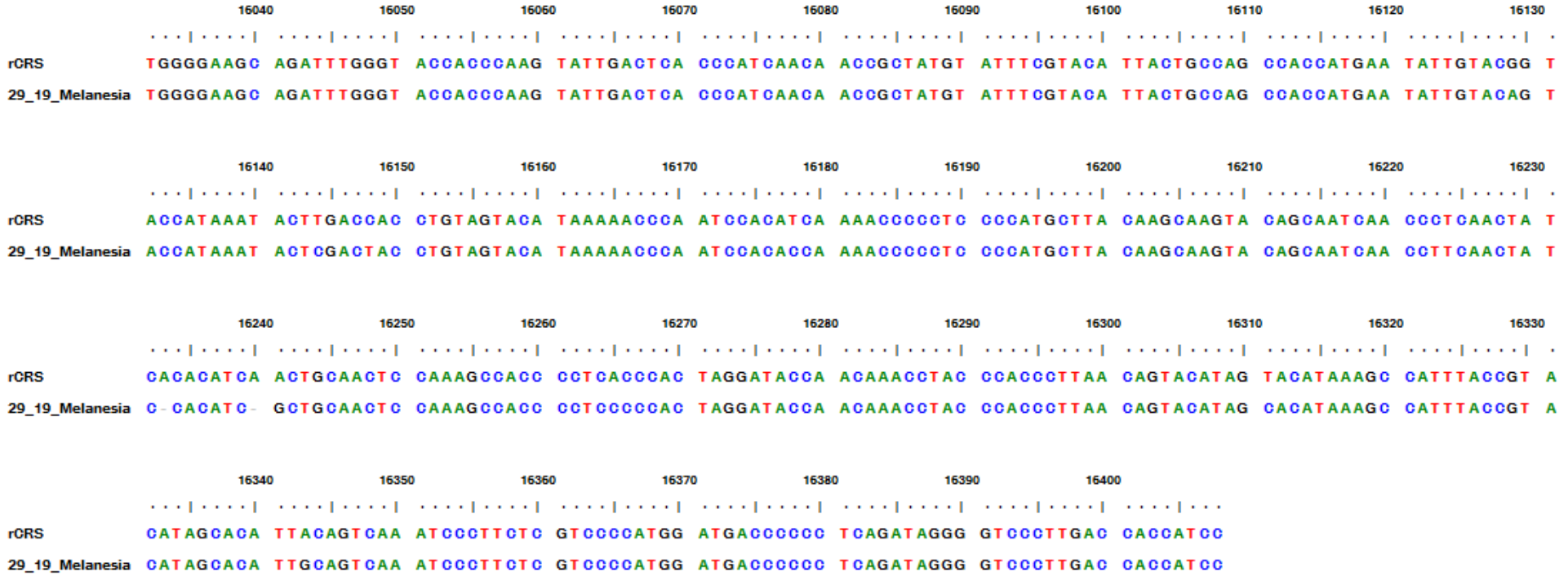


Sample ID: 29:19
Morphological sex: ♂
Region: Oceania
Subregion: Melanesia
Country: Malakula

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
X/Y	8/12	31.2/32.2	14/18	6/9	9/10	19/20

Haplogroup: Q1

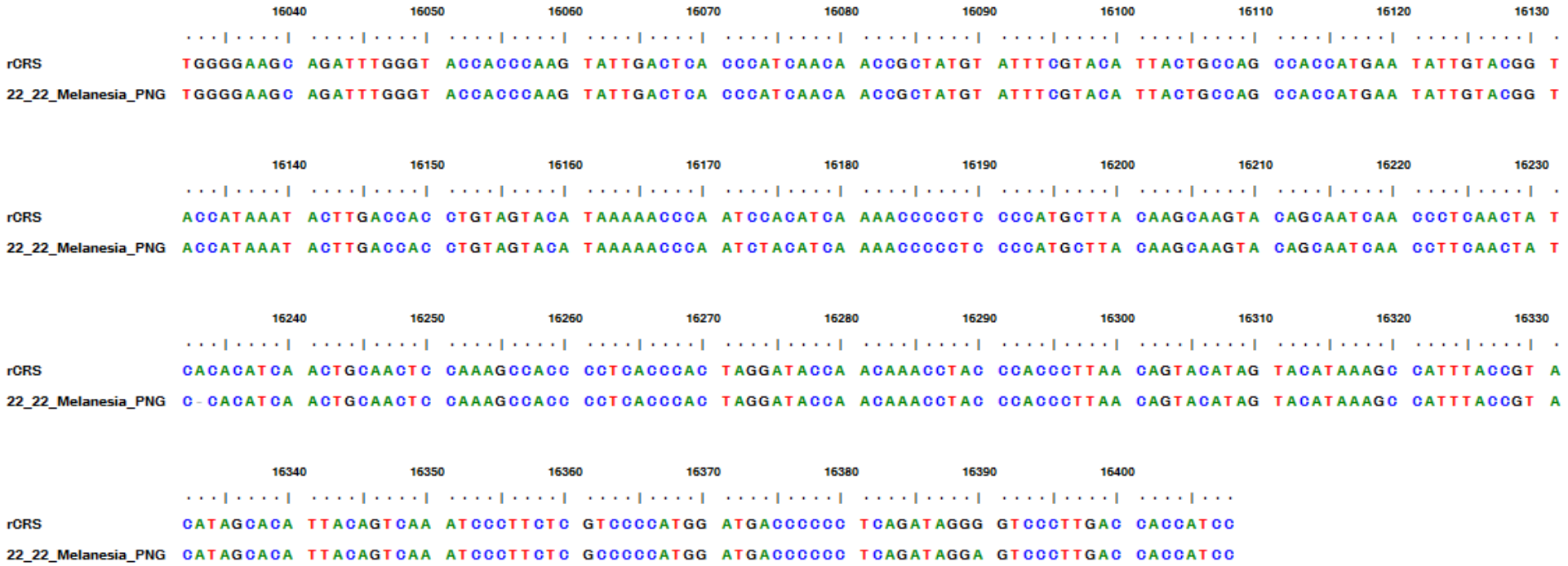


Sample ID: 22:22
Morphological sex: ♀
Region: Oceania
Subregion: Bismark Archipelago, Papua New Guinea, Melanesia
Country: New Pomerania

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
X/X	-/8	30/31.2	13/14	-/6	12/14	24/25

Haplogroup: D4h1

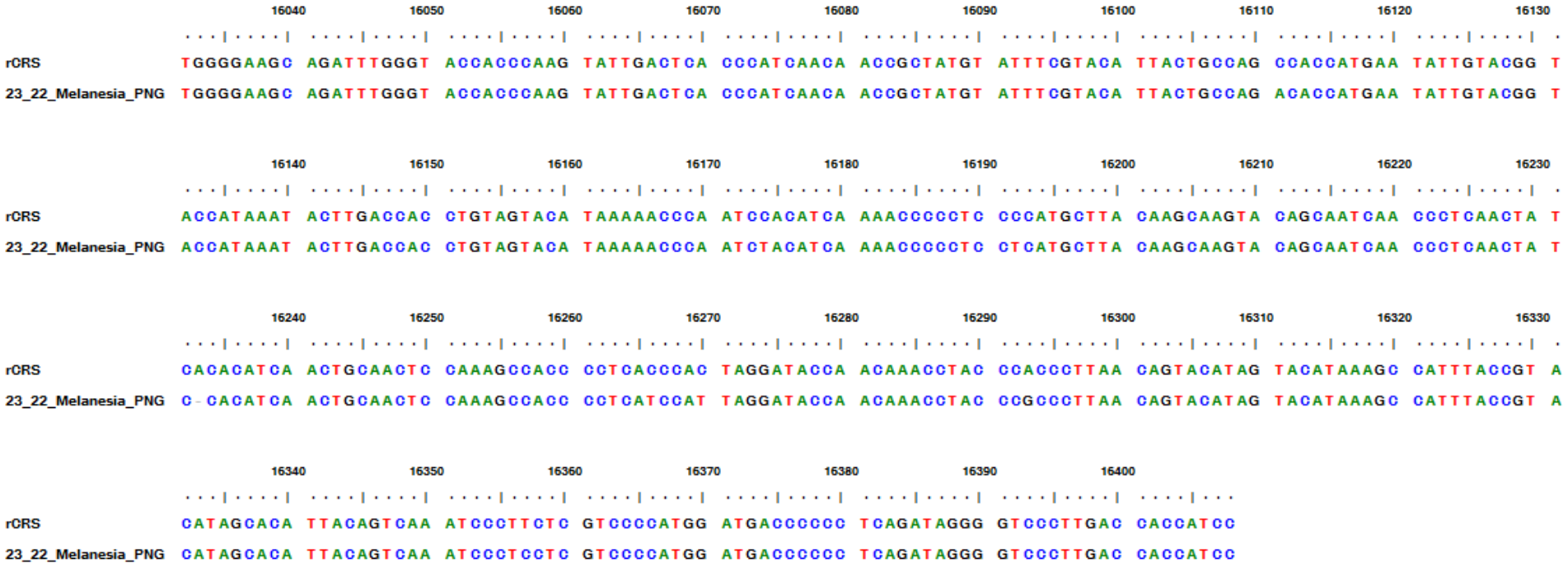


Sample ID: 23:22
Morphological sex: ♀
Region: Oceania
Subregion: Bismark Archipelago, Papua New Guinea, Melanesia
Country: New Pomerania

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	9/12	-/-	-/-	-/-	-/12	-/-

Haplogroup: U5b1c2

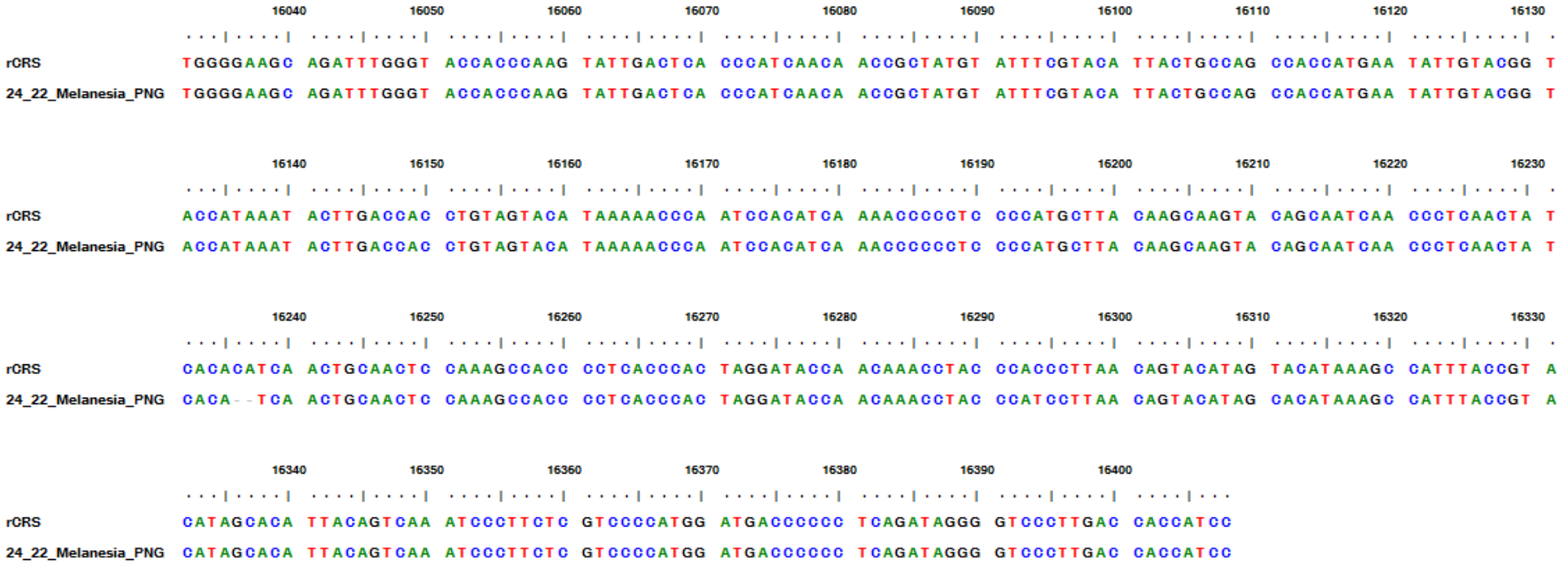


Sample ID: 24:22
Morphological sex: ♂
Region: Oceania
Subregion: Bismark Archipelago, Papua New Guinea, Melanesia
Country: New Pomerania

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
X/Y	11/13	31.2/32.2	13/18	6/8	-/10	20/23

Haplogroup: H42a

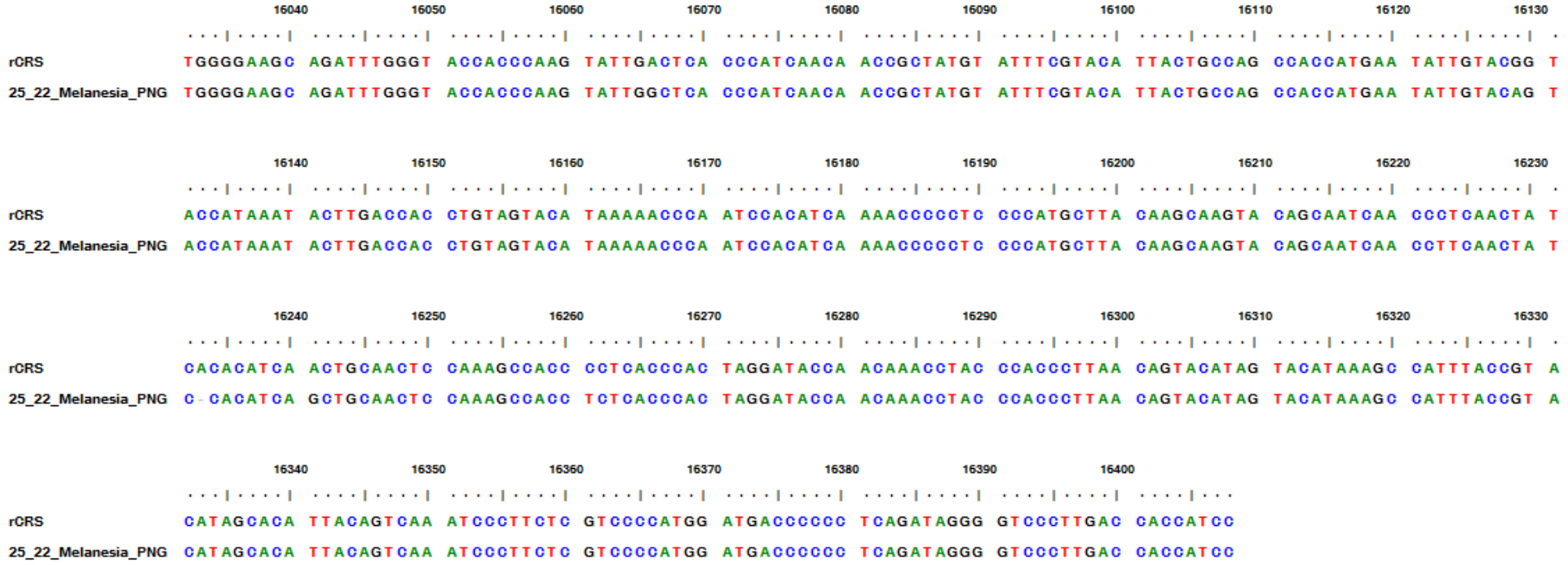


Sample ID: 25:22
Morphological sex: ♂
Region: Oceania
Subregion: Bismark Archipelago, Papua New Guinea, Melanesia
Country: New Pomerania

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
X/Y	10/12	29/30	14/16	6/8	9/10	24/25

Haplogroup: Q2a3b

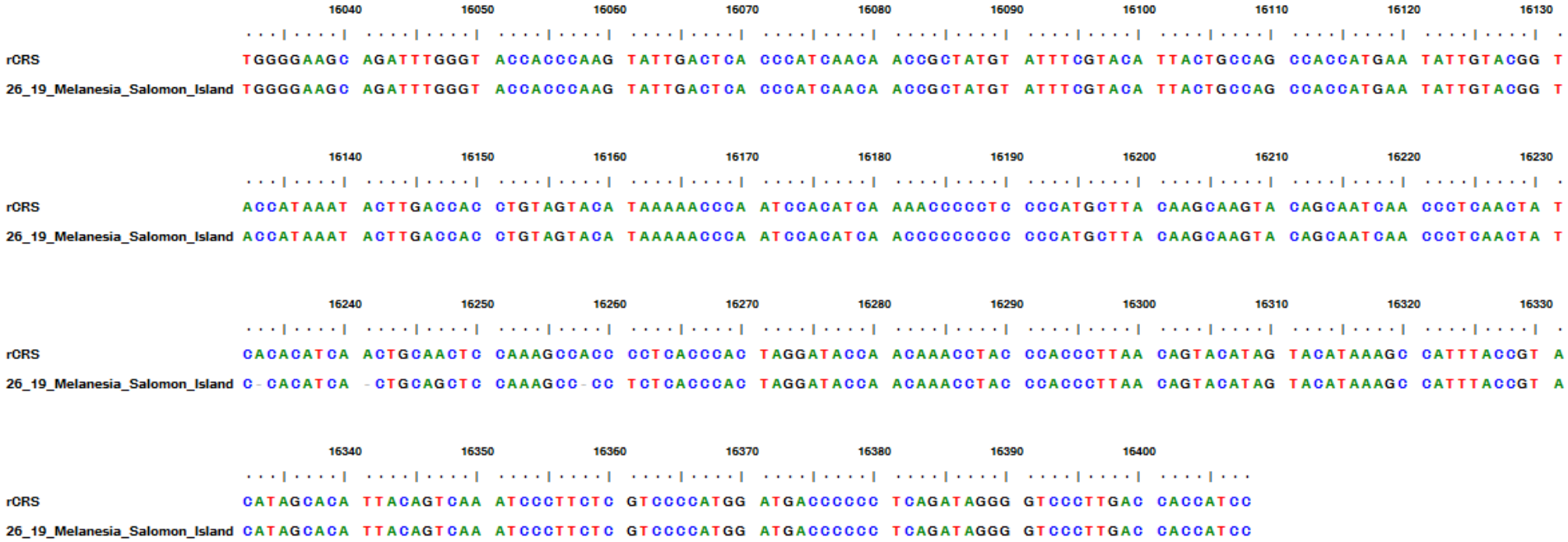


Sample ID: 26:19
Morphological sex: ♀
Region: Oceania
Subregion: Melanesia
Country: Salomon Island

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
X/X	10/11	-/-	-/16	-/8	9/10	24/25

Haplogroup: B4a1a1

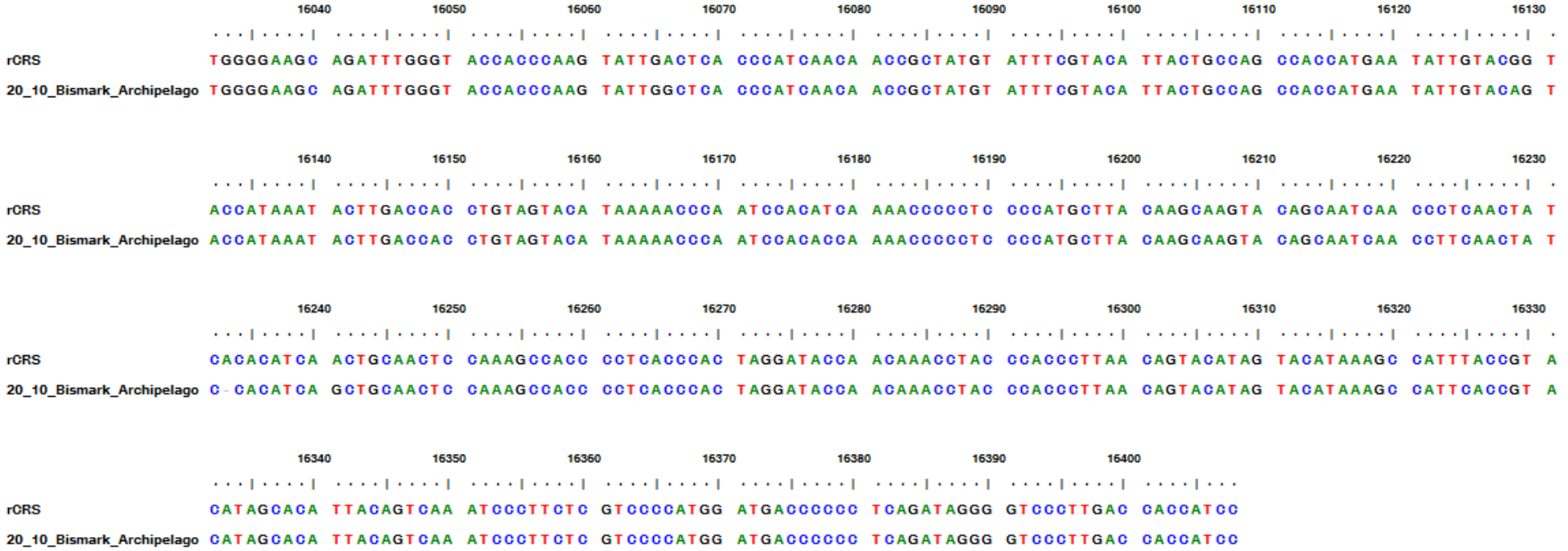


Sample ID: 20:10
Morphological sex: ♂
Region: Oceania
Subregion: Bismarck Archipelago, Melanesia
Country: Mussau Island, St. Mathias Islands

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
X/Y	-/9	-/-	-/14	7/9	-/14	18/19

Haplogroup: Q2

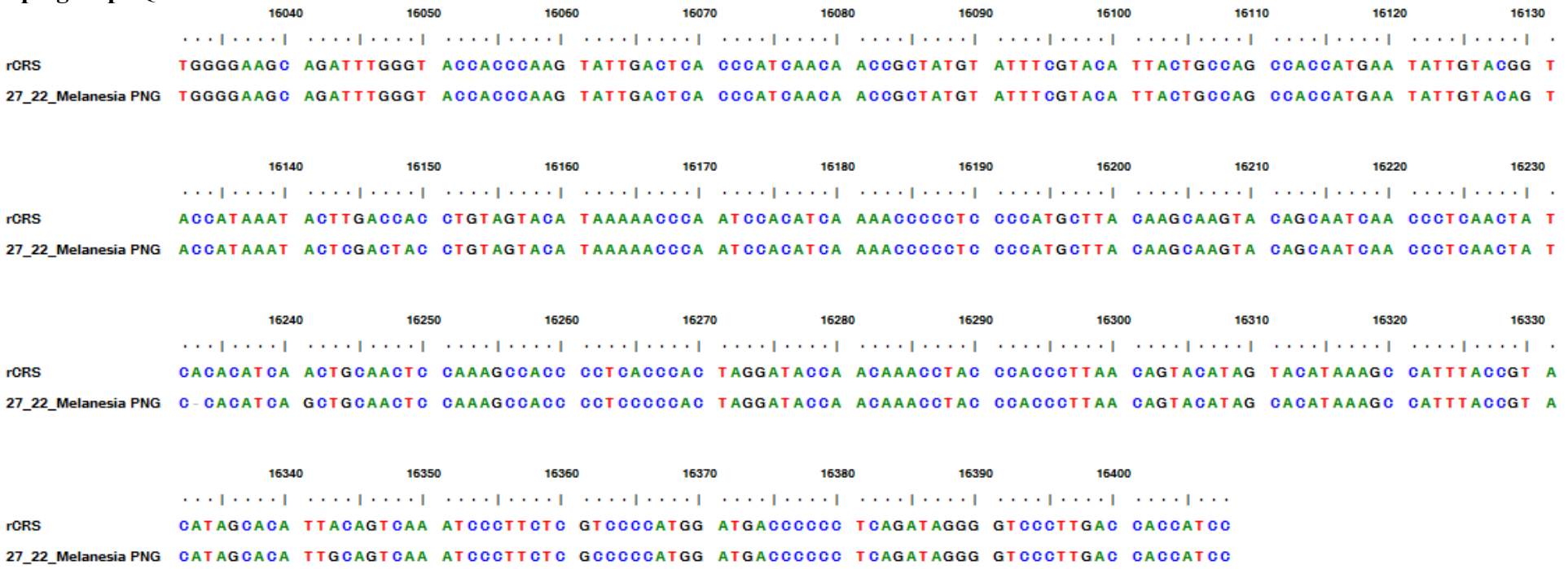


Sample ID: 27:22
Morphological sex: ♂
Region: Oceania
Subregion: Bismark Archipelago, Papua New Guinea, Melanesia
Country: New Pomerania

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
X/Y	-/9	29/30	16/17	9/10	9/10	23/26

Haplogroup: Q1

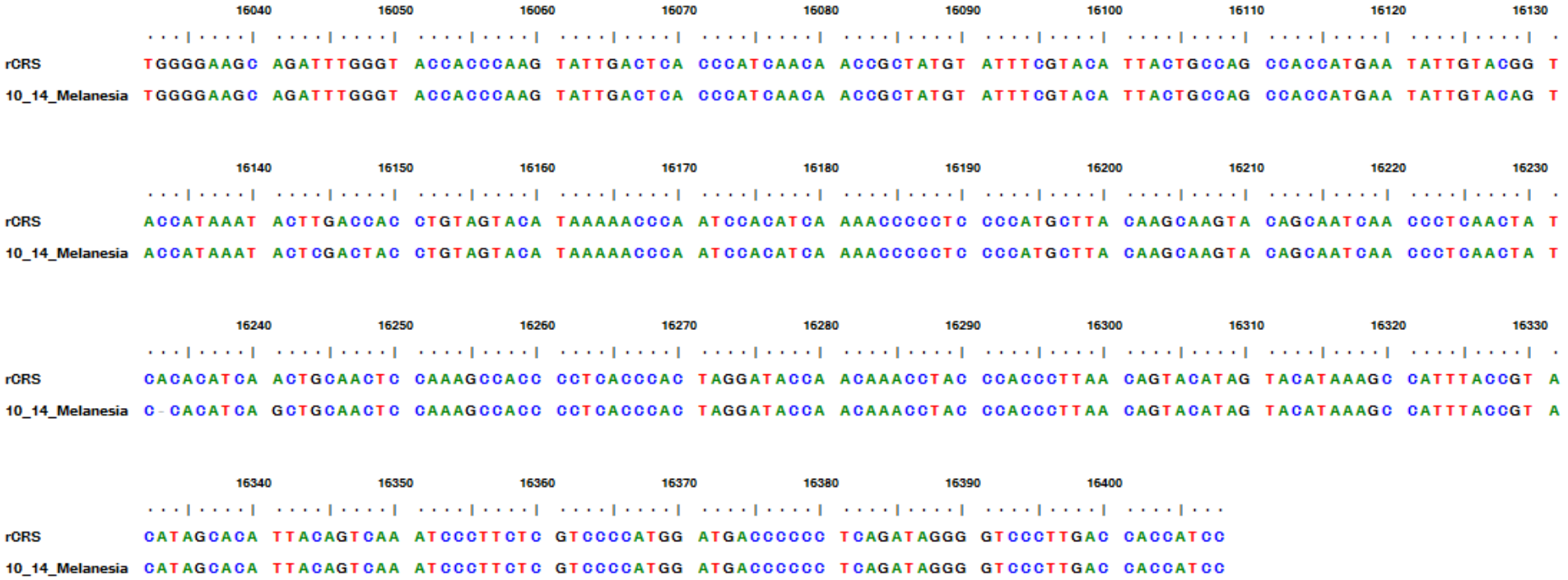


Sample ID: 10:14
Morphological sex: ♂
Region: Oceania
Subregion: Melanesia
Country: Makula

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
X/Y	11/12	29/30	13/21	8/10	10/12	19/26

Haplogroup: Q1

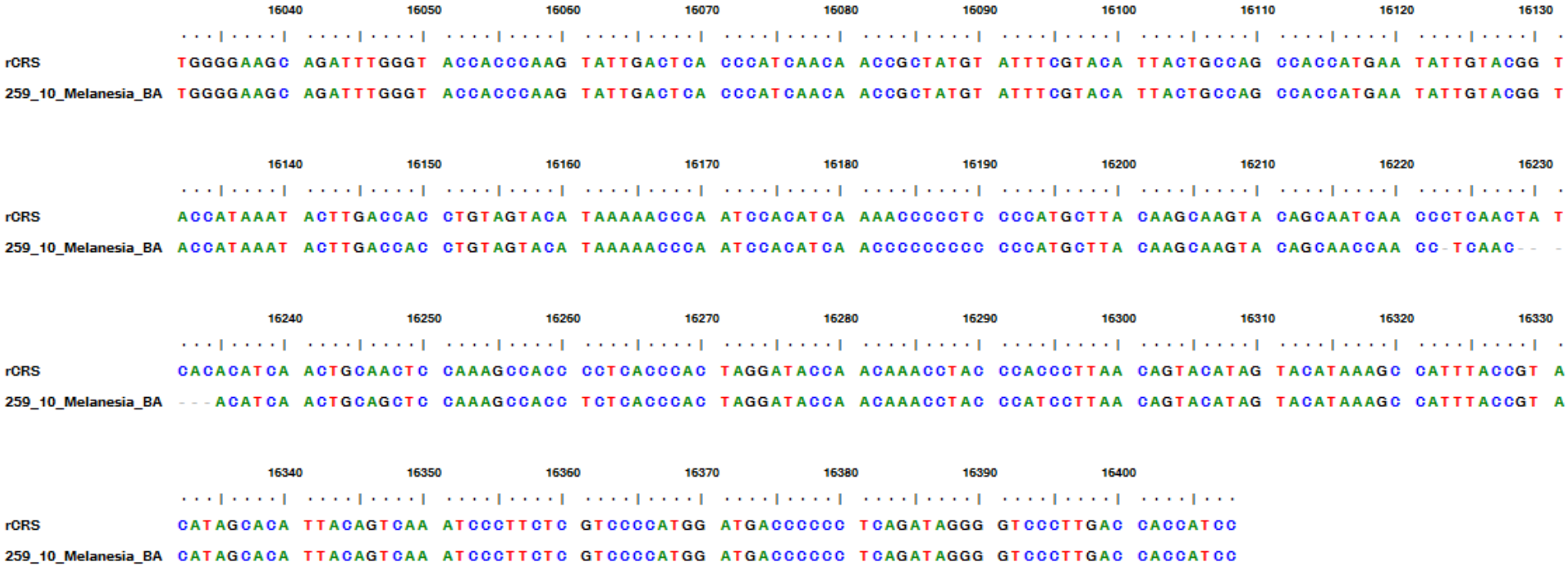


Sample ID: 259:10
Morphological sex: ♀
Region: Oceania
Subregion: Bismarck Archipelago, Melanesia
Country: Admiralty Islands

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
X/X	8/12	30/32.2	15/17	6/9	10/13	22/23

Haplogroup: B4a1a1

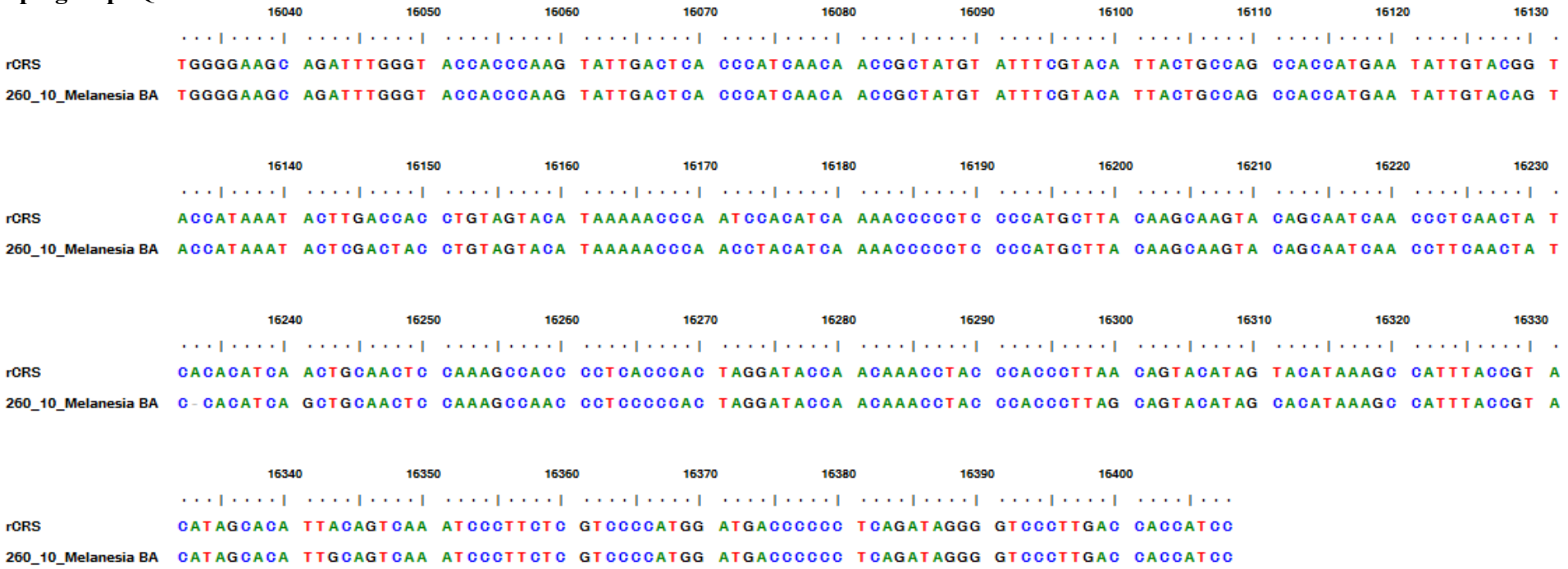


Sample ID: 260:10
Morphological sex: ♂
Region: Oceania
Subregion: Bismarck Archipelago, Melanesia
Country: Admiralty Island

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
X/Y	11/12	29/31.2	14/17	6/9	10/12	22/25

Haplogroup: Q1

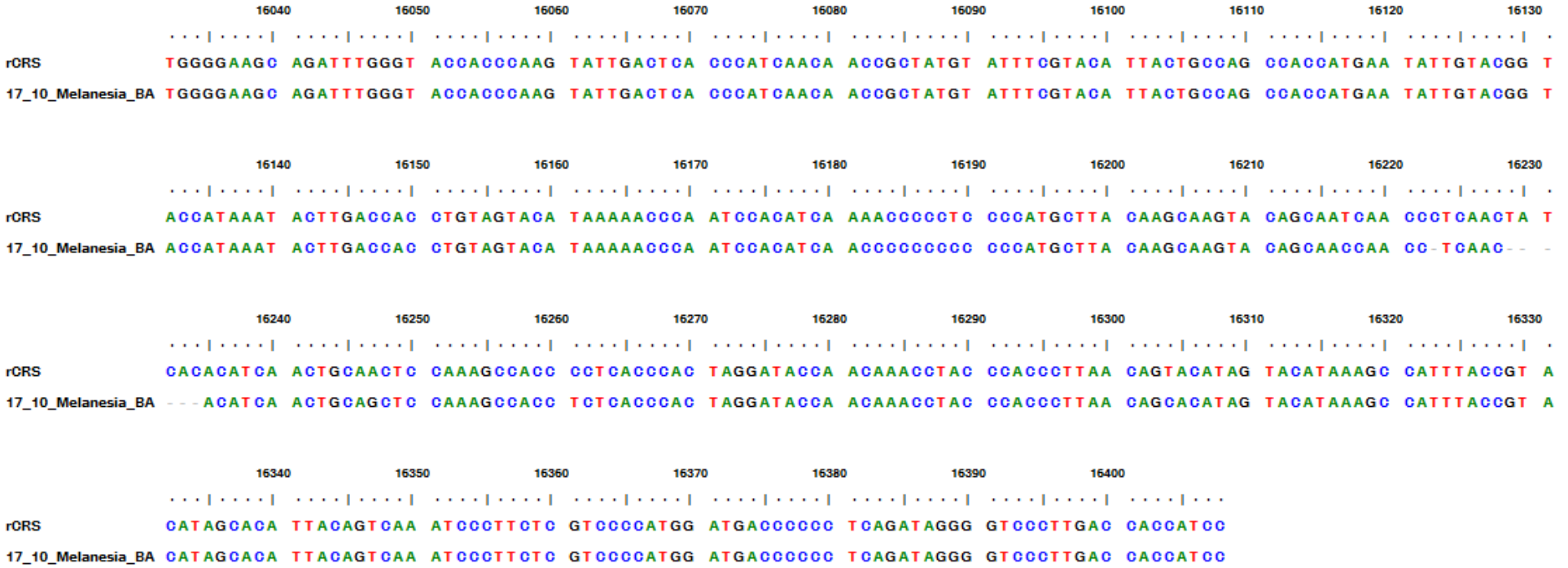


Sample ID: 17:10
Morphological sex: ♂
Region: Oceania
Subregion: Bismark Archipelago, Melanesia
Country: Mussau Island, St. Mathias Islands

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
X/Y	9/11	31.2/32.2	15/20	6/7	12/13	18/19

Haplogroup: B4a1a1

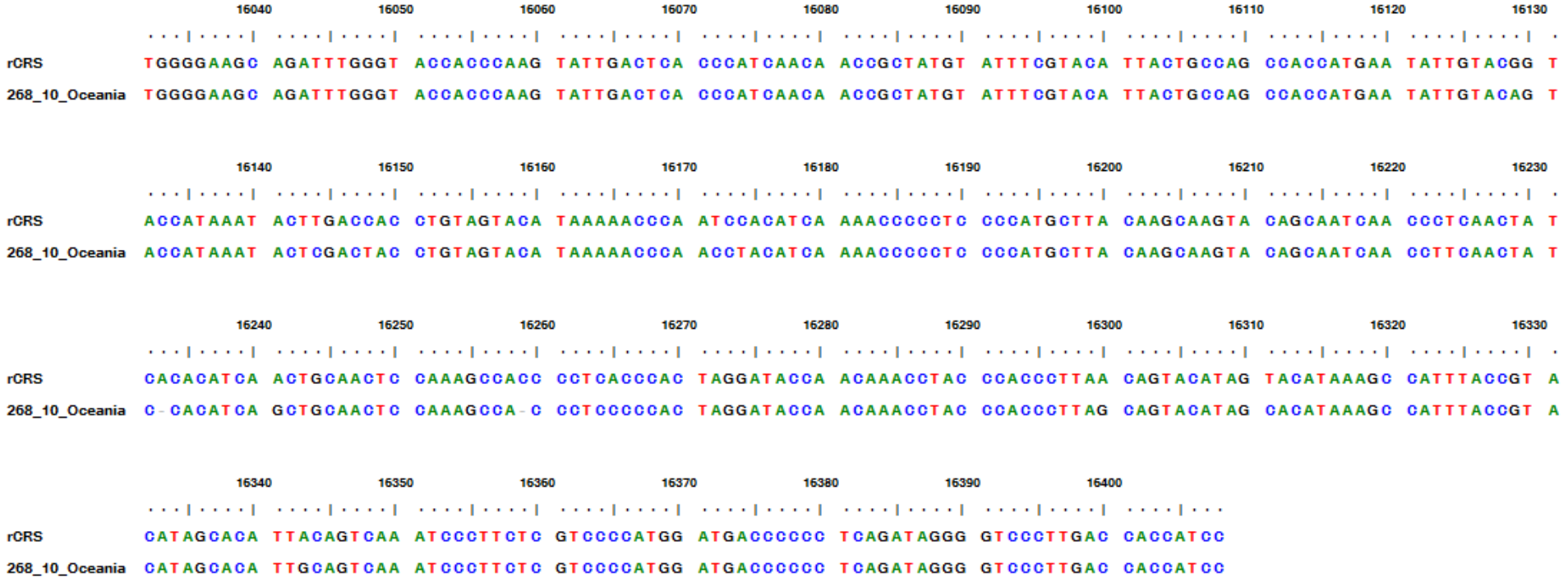


Sample ID: 268:10
Morphological sex: ♀
Region: Oceania
Subregion: Unknown
Country: Unknown

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
X/X	9/11	30/31.2	13/17	8/9	10/11	19/24

Haplogroup: Q1

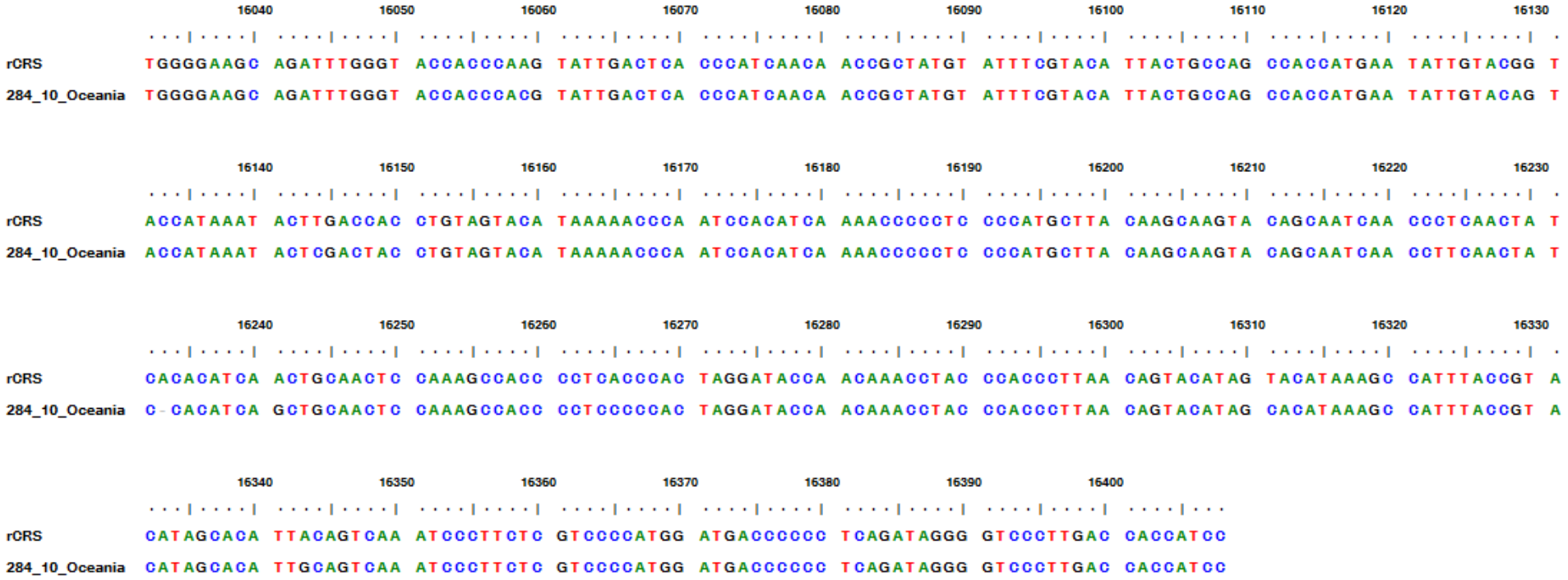


Sample ID: 284:10
Morphological sex: ♂
Region: Oceania
Subregion: Unknown
Country: Unknown

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
X/Y	11/12	29/33.2	-/18	6/9	9/12	23/24

Haplogroup: Q1

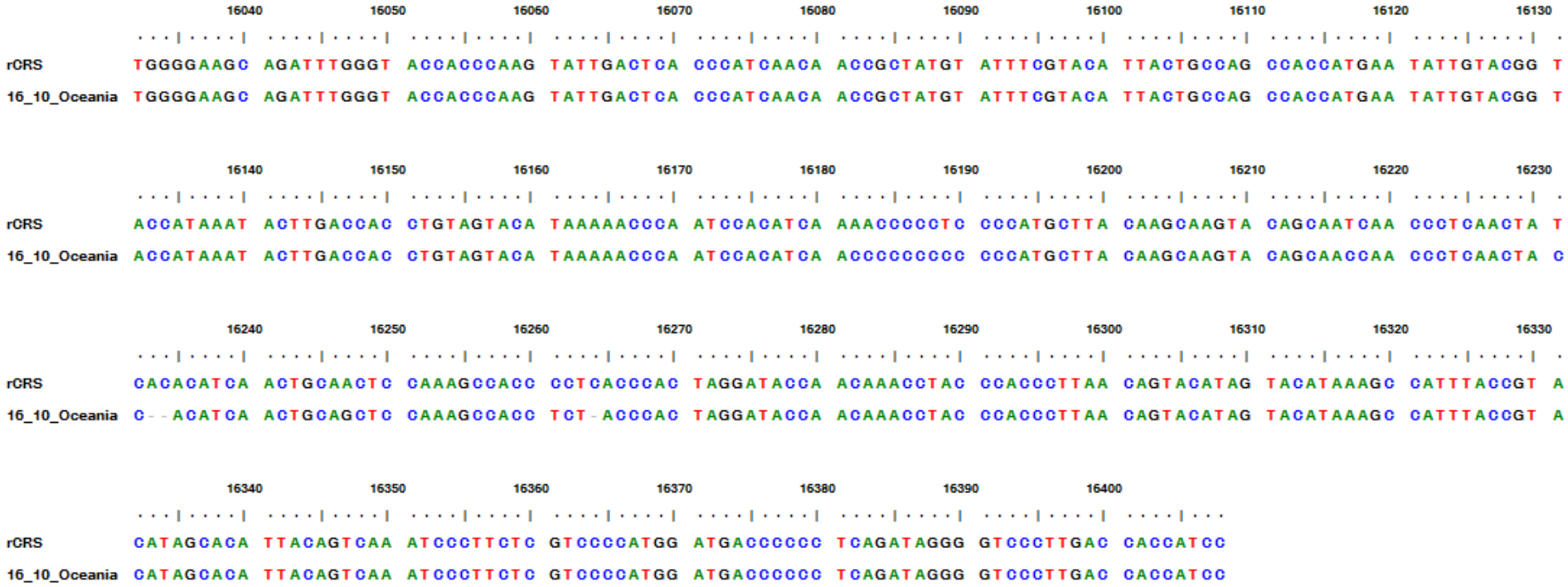


Sample ID: 16:10
Morphological sex: ♂
Region: Oceania
Subregion: Unknown
Country: Unknown

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
X/Y	12/13	30/31	14/20	6/8	10/13	19/21

Haplogroup: B4a1a1

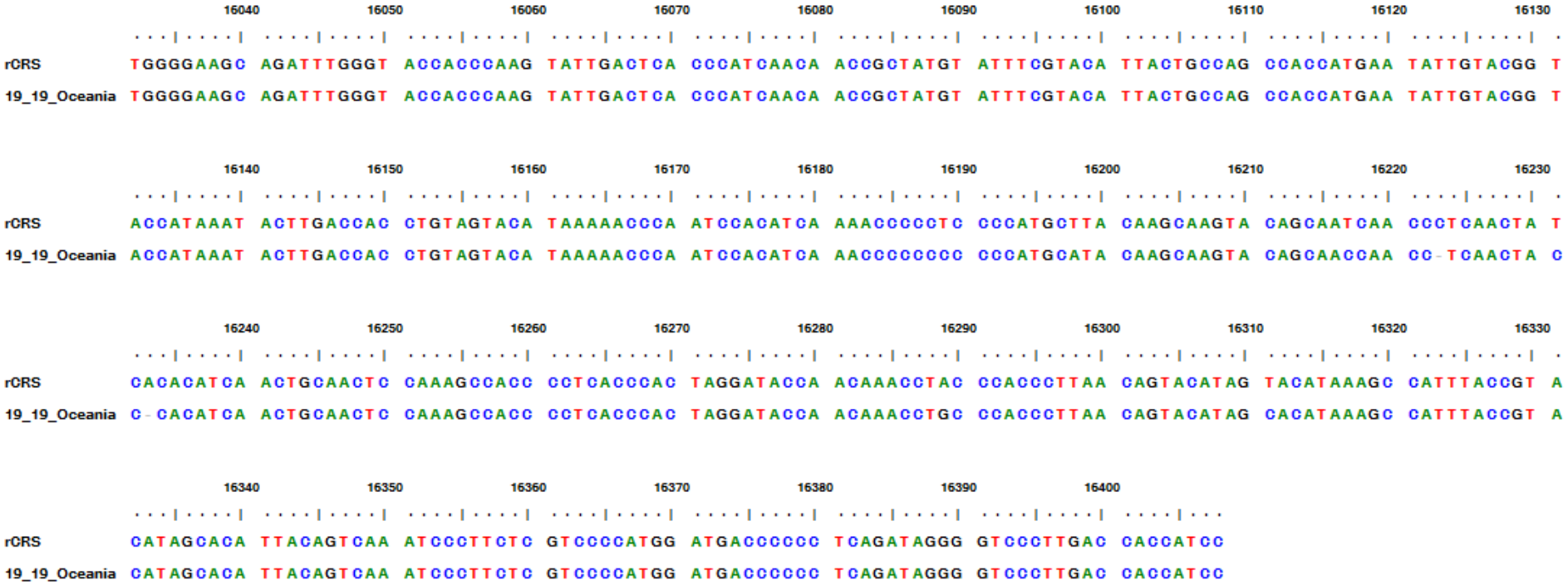


Sample ID: 19:19
Morphological sex: ♀
Region: Oceania
Subregion: Unknown
Country: Unknown

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
X/X	10/11	-/29	14/17	7/9.3	-/10	23/24

Haplogroup: B4c1a1

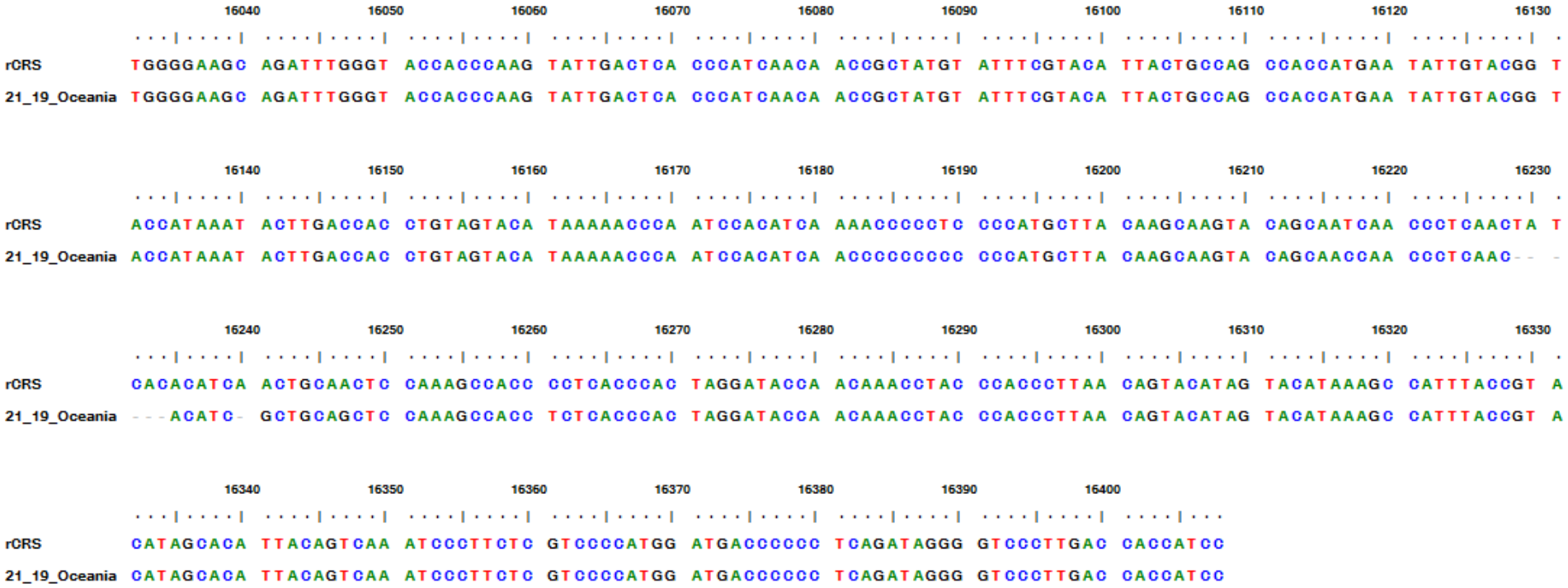


Sample ID: 21:19
Morphological sex: ♂
Region: Oceania
Subregion: Unknown
Country: Unknown

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
X/Y	11/12	30.2/31.2	14/15	6/7	10/12	23/24

Haplogroup: B4a1a1

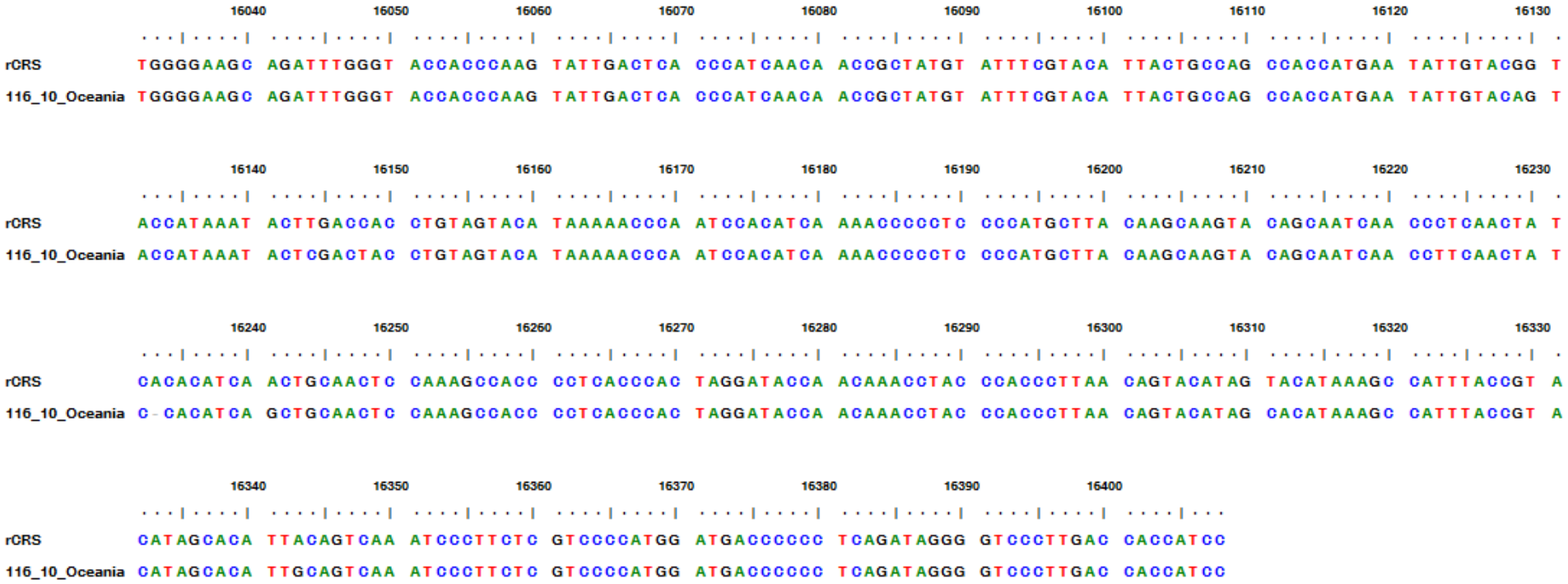


Sample ID: 116:10
Morphological sex: ♀
Region: Oceania
Subregion: Unknown
Country: Unknown

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
X/X	11/12	-/31	14/15	7/8	10/13	22/23

Haplogroup: Q1

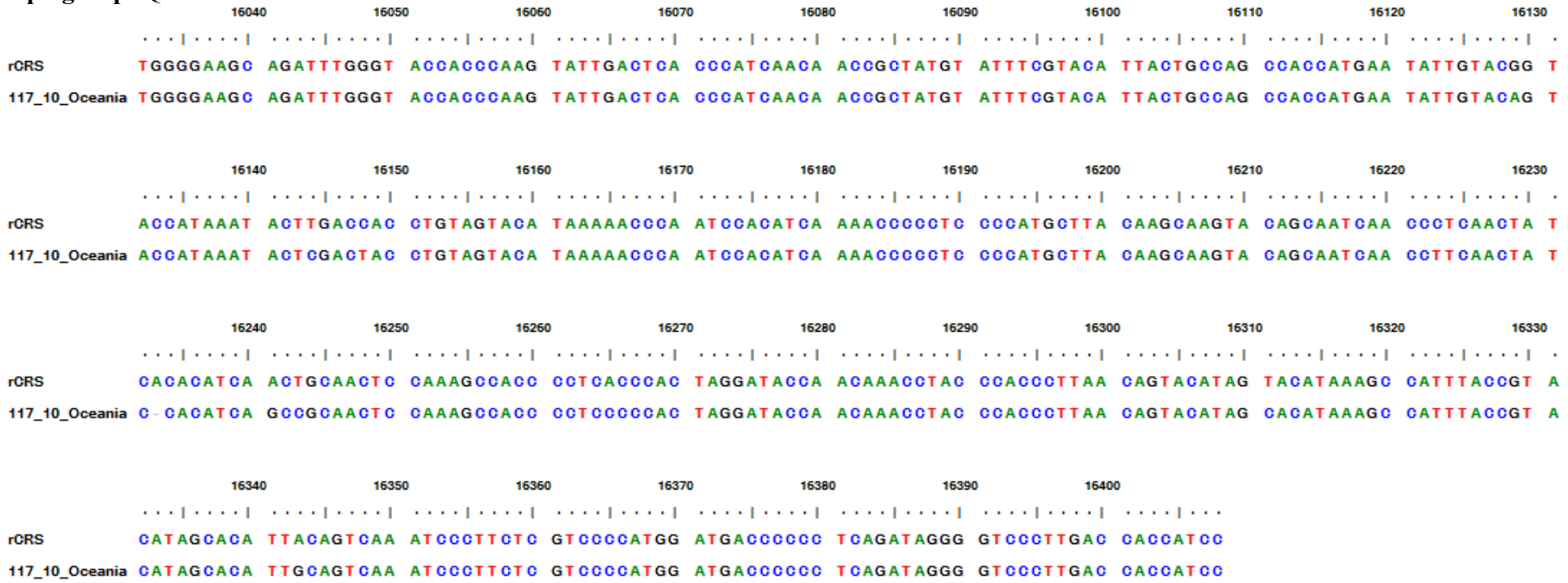


Sample ID: 117:10
Morphological sex: ♂
Region: Oceania
Subregion: Unknown
Country: Unknown

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
X/Y	-/10	29/30	13/17	6/8	-/11	23/24

Haplogroup: Q1

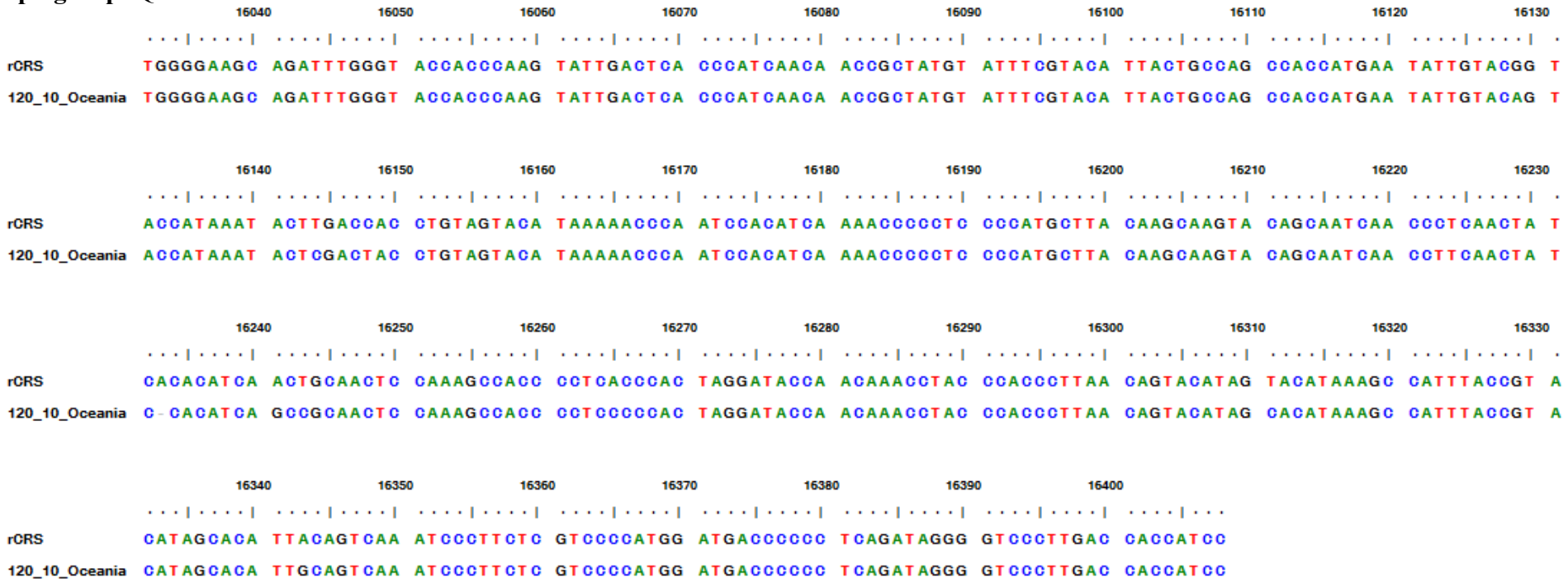


Sample ID: 120:10
Morphological sex: ♀
Region: Oceania
Subregion: Unknown
Country: Unknown

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
X/X	9/12	29/30	13/15	8/9.3	12/13	23/25

Haplogroup: Q1

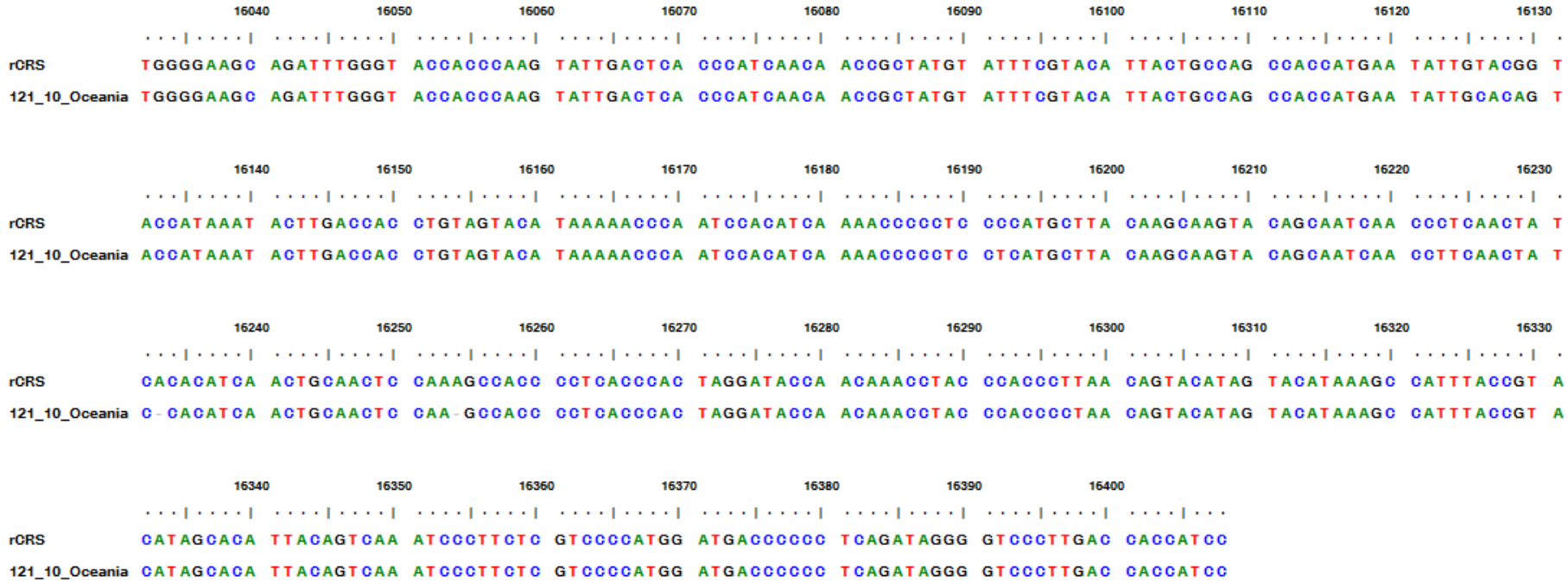


Sample ID: 121:10
Morphological sex: ♀
Region: Oceania
Subregion: Unknown
Country: Unknown

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
X/X	10/13	29/30	13/19	8/9	-/12	20/24

Haplogroup: M7b1a1i



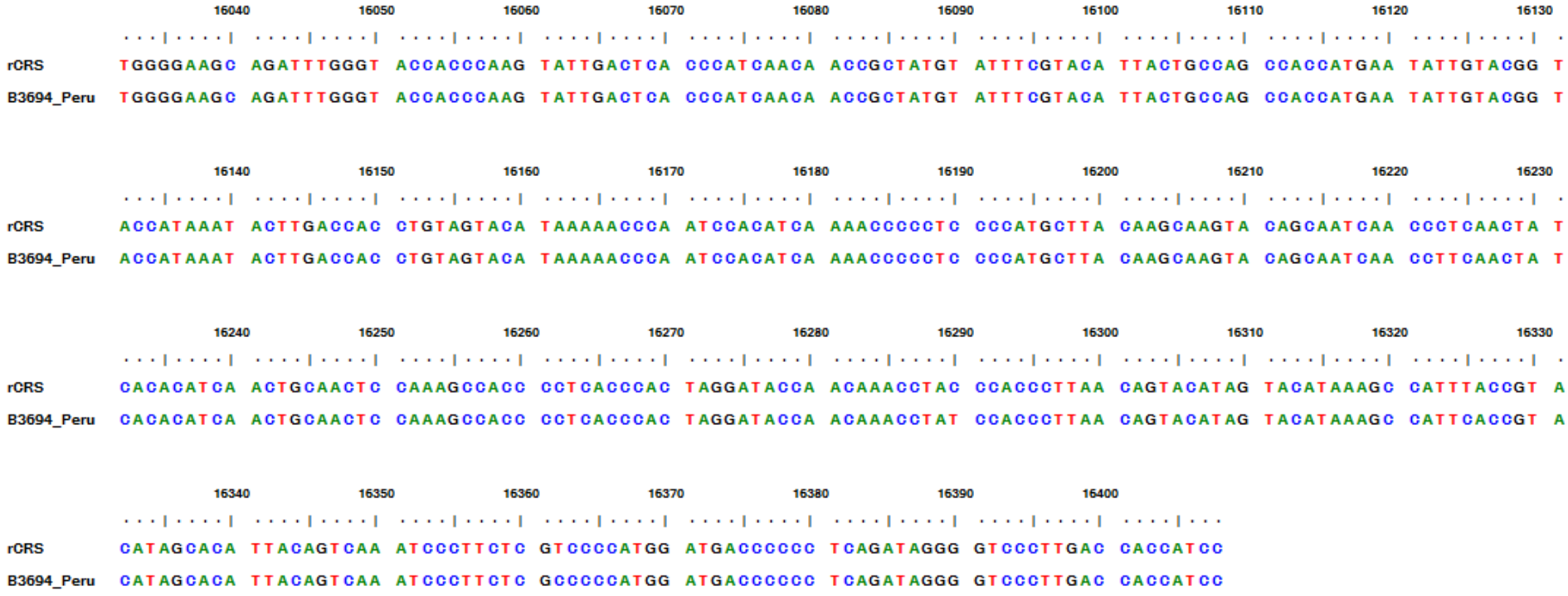
7.2 Data sheets on individuals from South America

Sample ID: B3694
Morphological sex: ♂
Region: America
Subregion: South America
Country: Peru

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
X/X	-/10	-/31.2	-/-	-/7	-/-	19/26

Haplogroup: D1a1

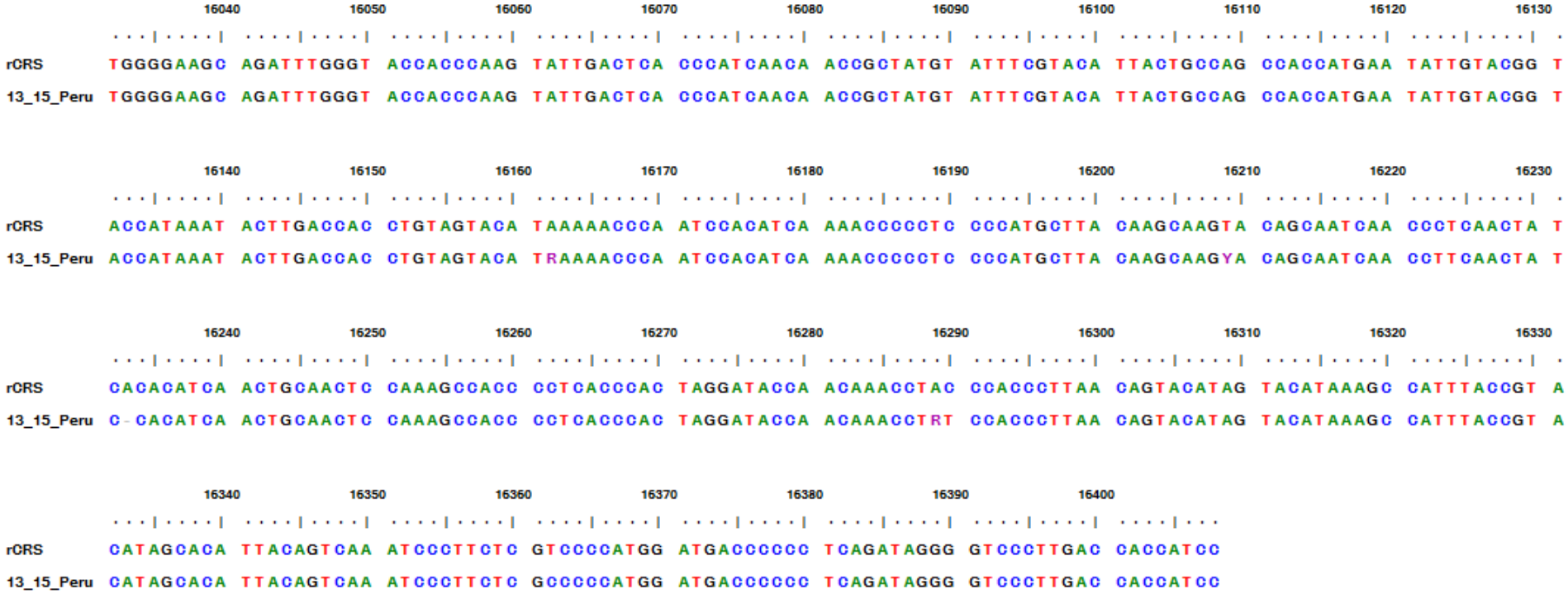


Sample ID: 13:15
Morphological sex: ♂
Region: America
Subregion: South America
Country: Peru

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: D4o

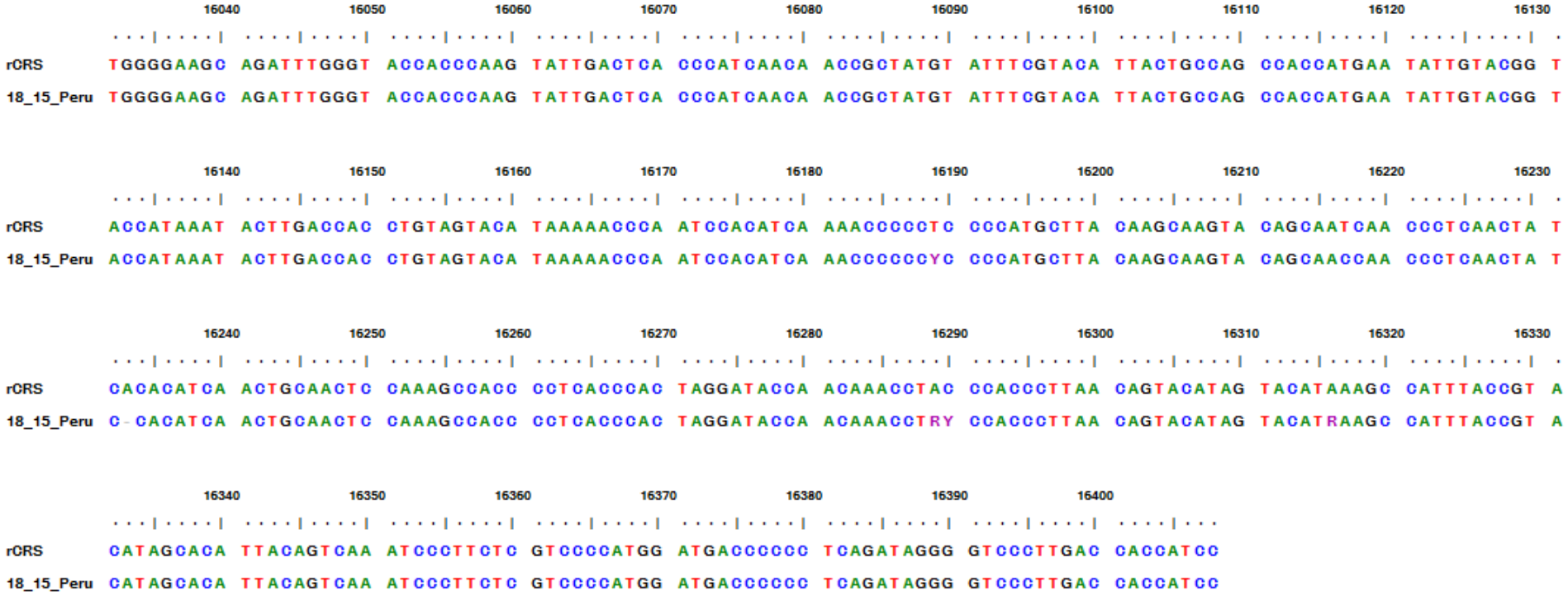


Sample ID: 18:15
Morphological sex: ♂
Region: America
Subregion: South America
Country: Peru

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: B2



Sample ID: 1:31
Morphological sex: ♂
Region: America
Subregion: South America
Country: Peru

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
X/Y	12/13	30/31	16/17	-/6	-/11	24/25

Haplogroup: C1b8

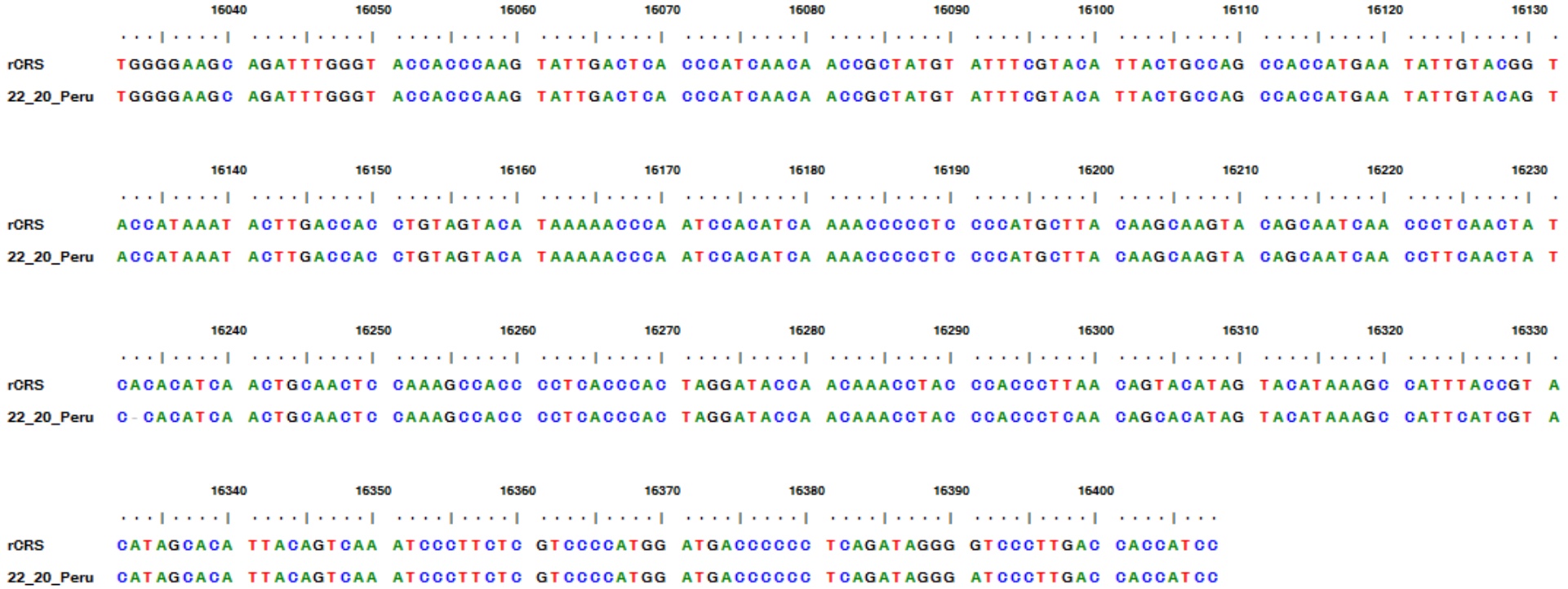
```
                16040     16050     16060     16070     16080     16090     16100     16110     16120     16130
                ...|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| .
rCRS            TGGGGAAGC AGATTTGGGT ACCACCCAAG TATTGACTCA CCCATCAACA ACCGCTATGT ATTTCGTACA TTACTGCCAG CCACCATGAA TATTGTACGG T
1_31_Peru       TGGGGAAGC AGATTTGGGT ACCACCCAAG TATTGACTCA CCCATCAACA ACCGCTATGT ATTTCGTACA TTACTGCCAG CCACCATGAA TATTGTACGG T

                16140     16150     16160     16170     16180     16190     16200     16210     16220     16230
                ...|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| .
rCRS            ACCATAAAT ACTTGACCAC CTGTAGTACA TAAAAACCCA ATCCACATCA AAACCCCCTC CCCATGCTTA CAAGCAAGTA CAGCAATCAA CCCTCAACTA T
1_31_Peru       ACCATAAAT ACTTGACCAC CTGTAGTACA TAAAAACCCA ATCCACATCA AAACCCCCTC CCCATGCTTA CAAGCAAGTA CAGCAATCAA CCTTCAACTA T

                16240     16250     16260     16270     16280     16290     16300     16310     16320     16330
                ...|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| .
rCRS            CACACATCA ACTGCAACTC CAAAGCCACC CCTCACCCAC TAGGATACCA ACAAACCTAC CCACCCTTAA CAGTACATAG TACATAAAGC CATTTACCGT A
1_31_Peru       C-CACATCA ACTGCAACTC CAAAGCCACC CCTCACCCAC TAGGATACCA ACAAACCTAT CCACCCTCAA CAGTACATAG TACATAAARC CATTCATCGT A

                16340     16350     16360     16370     16380     16390     16400
                ...|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|...
rCRS            CATAGCACA TTACAGTCAA ATCCCTTCTC GTCCCCATGG ATGACCCCCC TCAGATAGGG GTCCCTTGAC CACCATCC
1_31_Peru       CATAGCACA TTACAGTCAA ATCCCTTCTC GCCCCCATGG ATGACCCCCC TCAGATAGGG GTCCCTTGAC CACCATCC
```

Sample ID: 22:20
Morphological sex: ♂
Region: America
Subregion: South America
Country: Peru

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
X/Y	-/9	30/31.2	-/15	-/6	-/11	19/21

Haplogroup: C1

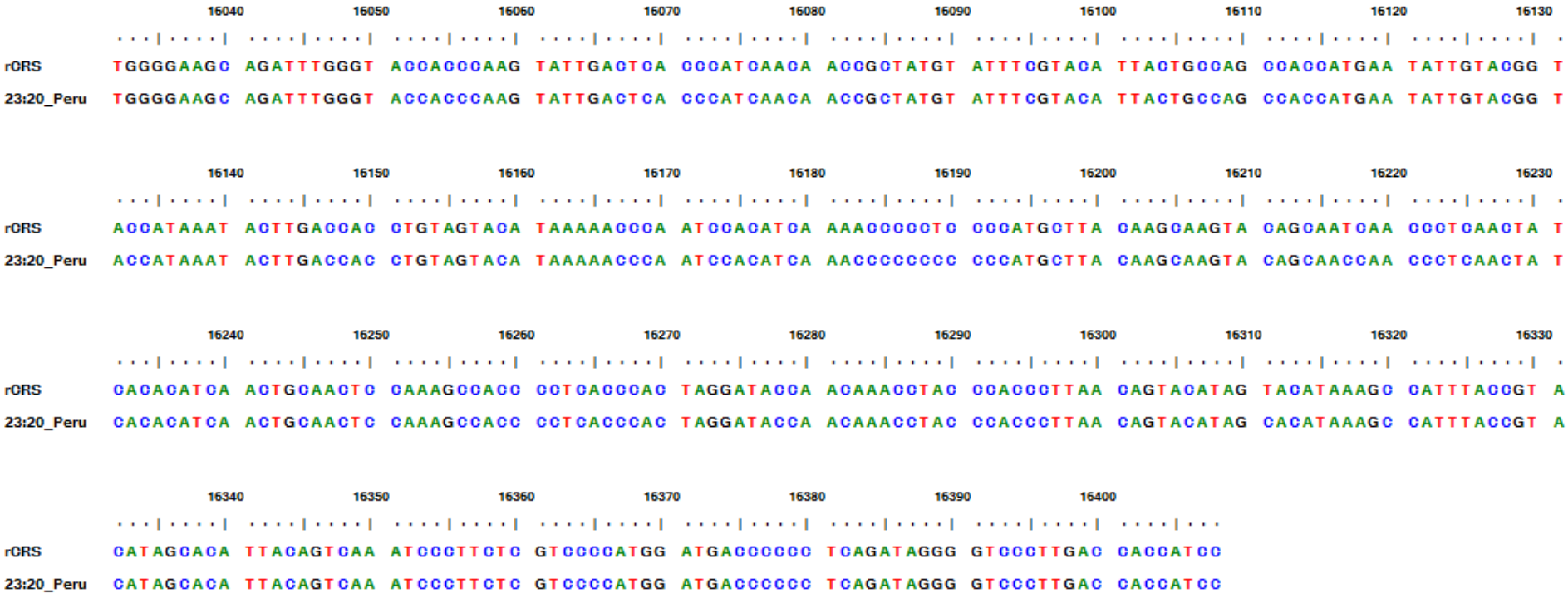


Sample ID: 23:20
Morphological sex: ♀
Region: America
Subregion: South America
Country: Peru

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
X/Y	-/12	-/-	14/17	-/7	9/11	20/24

Haplogroup: B2i1

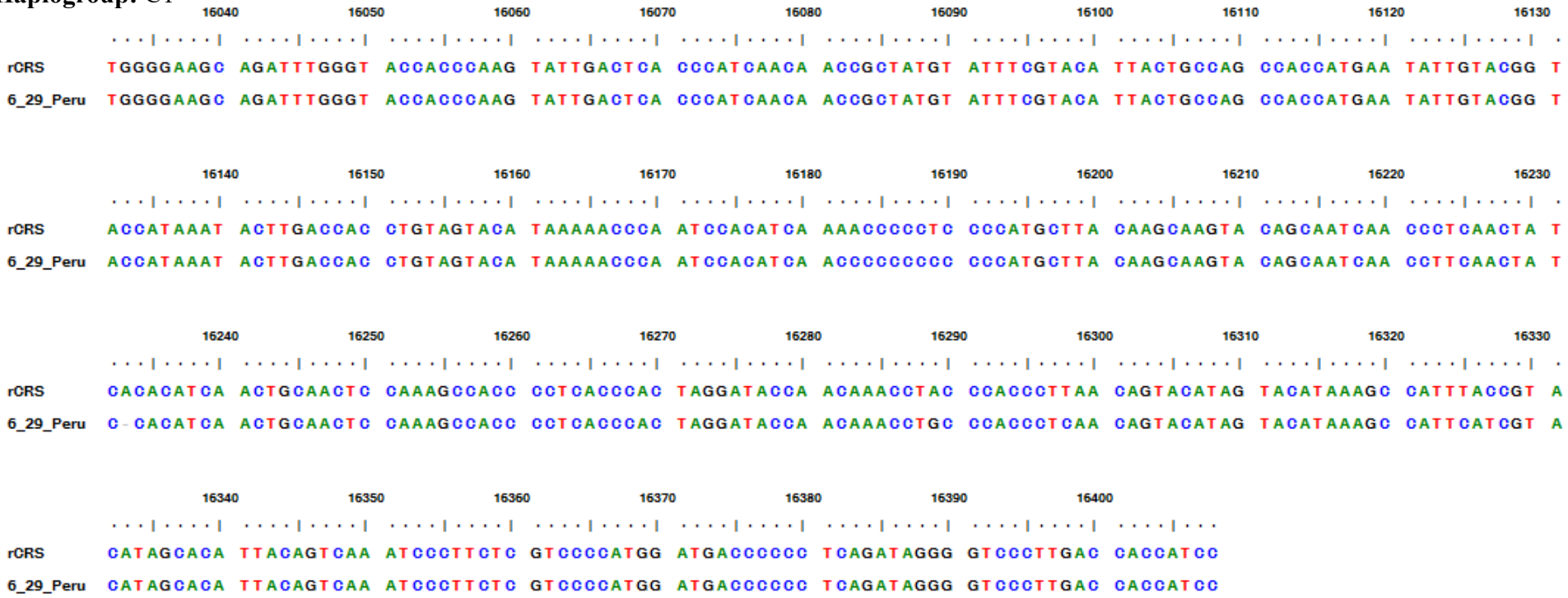


Sample ID: 6:29
Morphological sex: ♀
Region: America
Subregion: South America
Country: Peru

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: C1

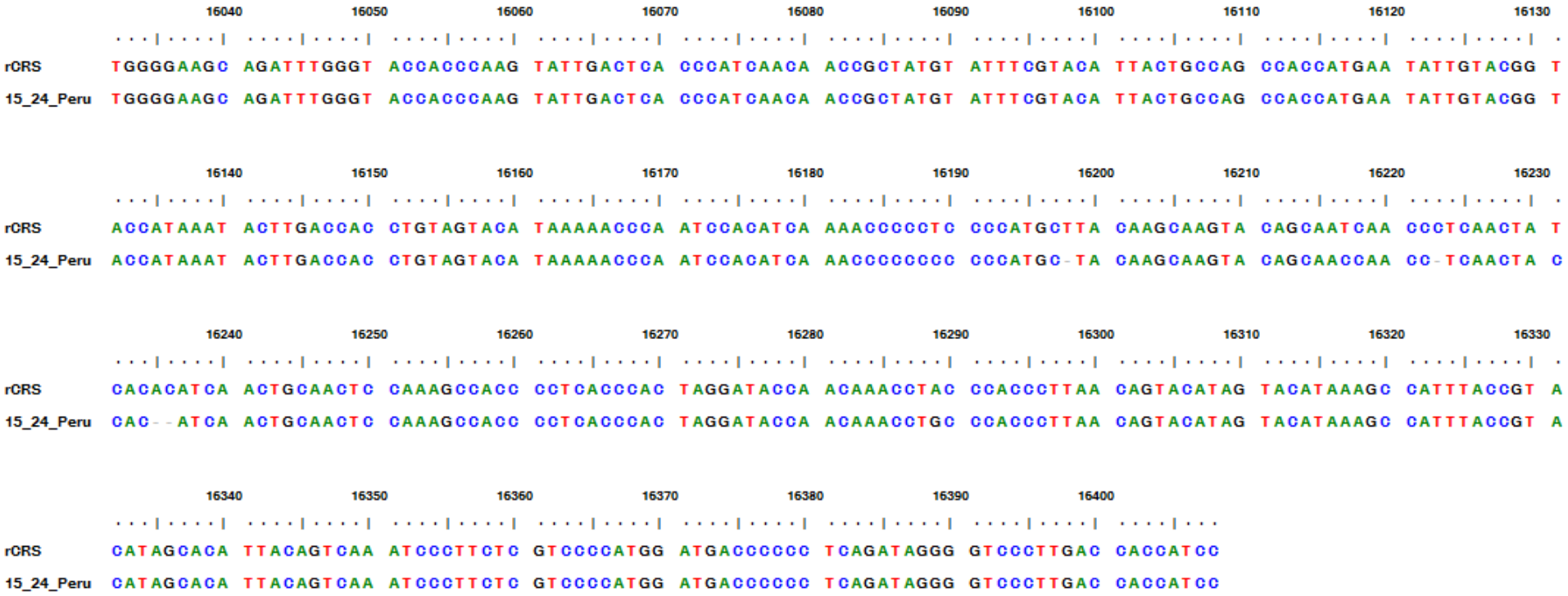


Sample ID: 15:24
Morphological sex: ♀
Region: America
Subregion: South America
Country: Peru

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: B2

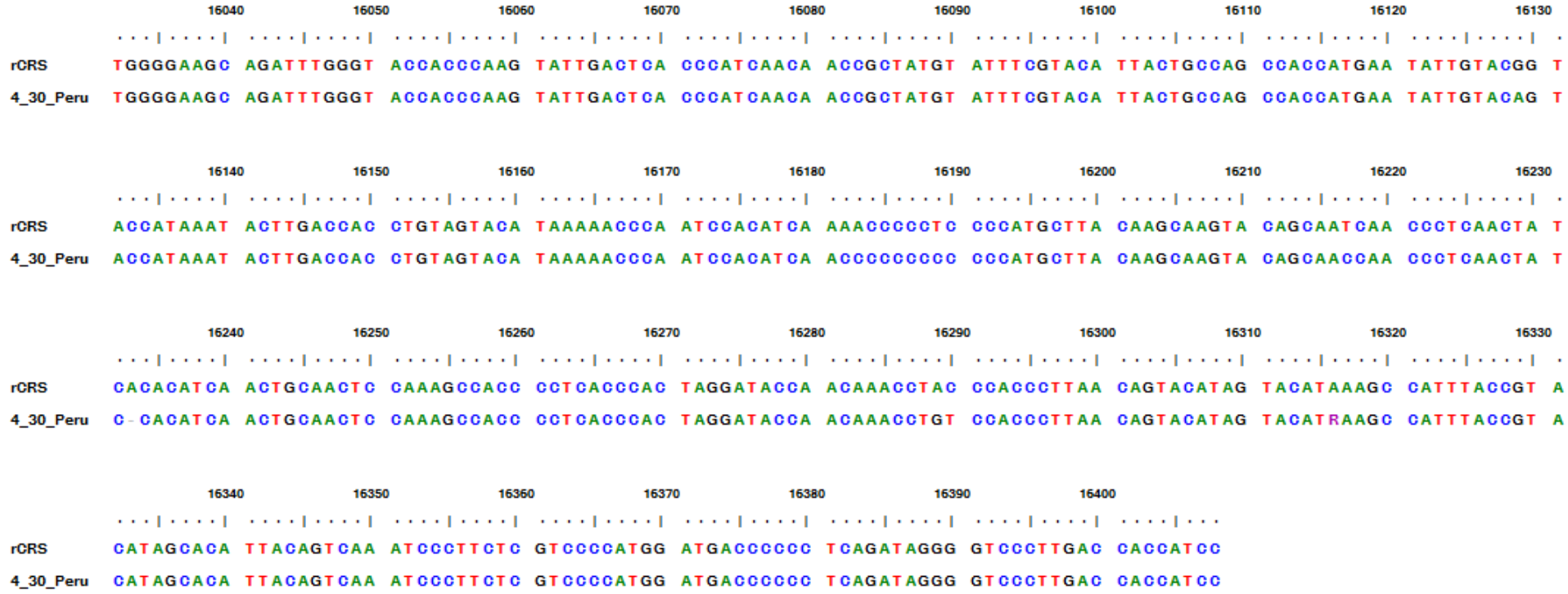


Sample ID: 4:30
Morphological sex: ♂
Region: America
Subregion: South America
Country: Peru

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
X/Y	9/12	-/-	15/17	-/7	-/-	-/-

Haplogroup: B2

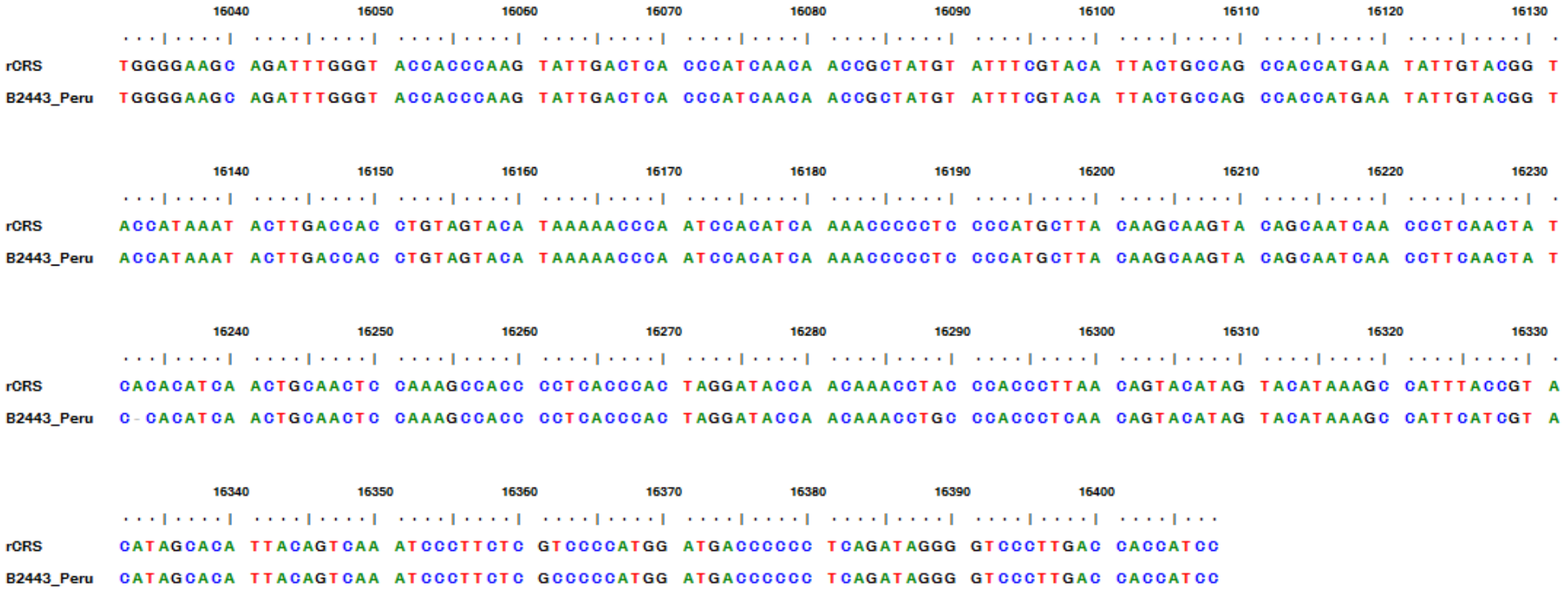


Sample ID: B2443
Morphological sex: ♂
Region: America
Subregion: South America
Country: Peru

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: C1

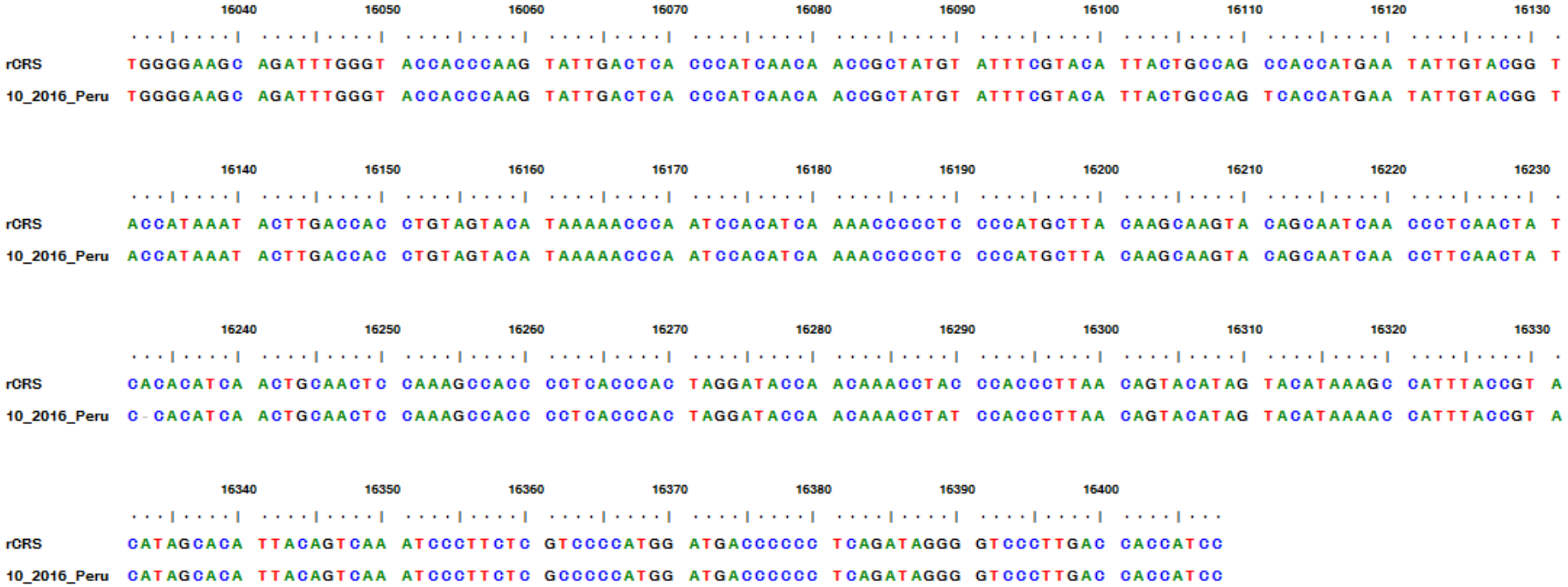


Sample ID: 10:2016
Morphological sex: ♀
Region: America
Subregion: South America
Country: Peru

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: A2

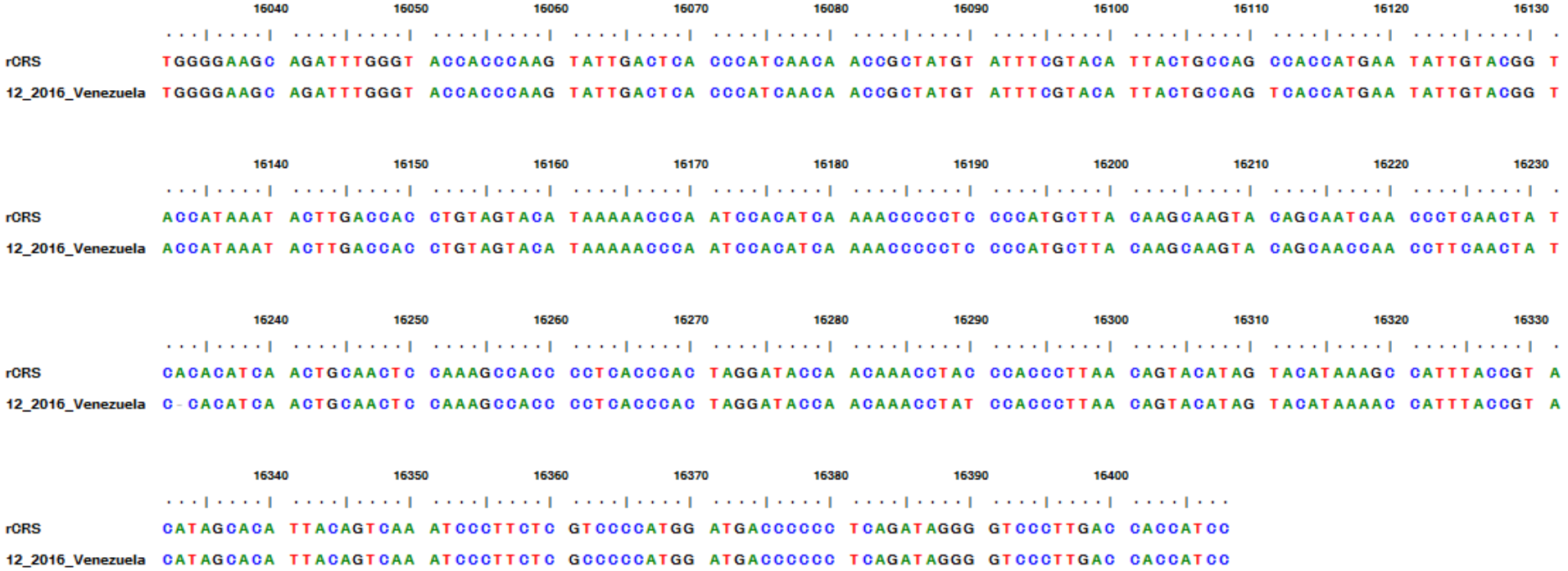


Sample ID: 12:2016
Morphological sex: ♀
Region: America
Subregion: South America
Country: Venezuela

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
X/X	9/14	30/33.2	15/19	-/7	-/-	20/23

Haplogroup: A2

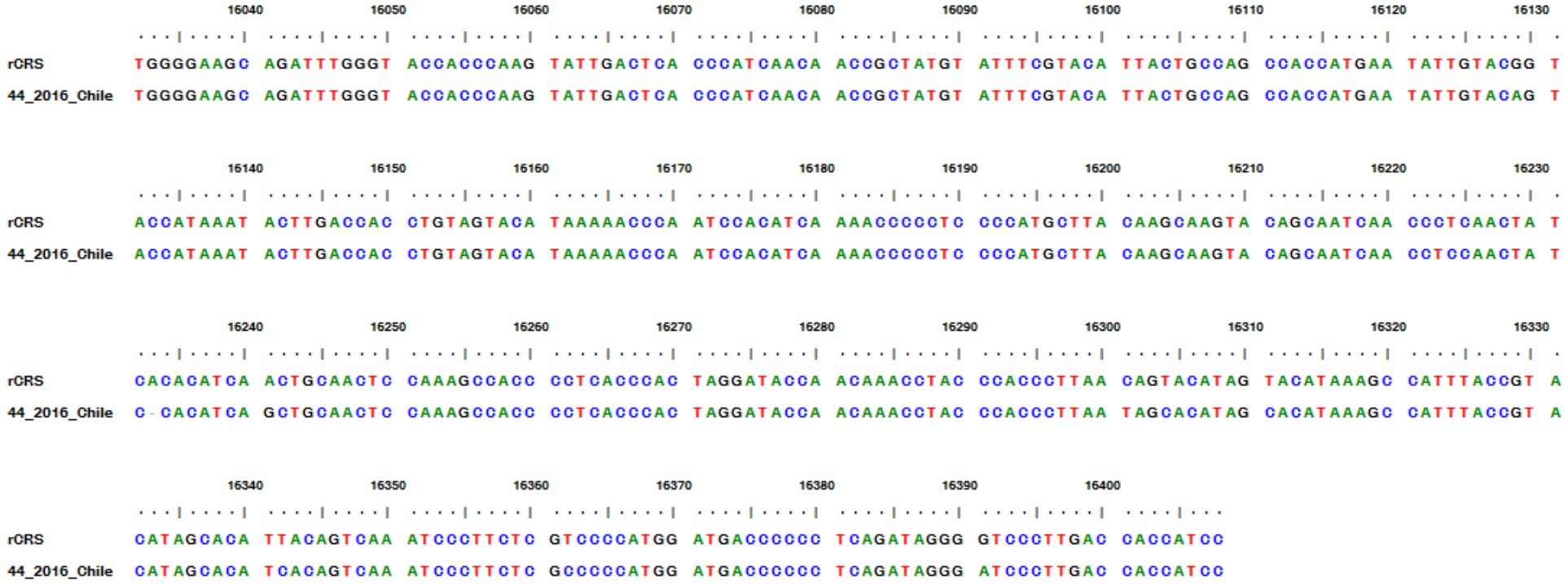


Sample ID: 44:2016
Morphological sex: ♂
Region: America
Subregion: South America
Country: Chile

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
X/Y	-/13	-/-	-/13	6/7	-/-	25/26

Haplogroup: D4h3a



Sample ID: 45:2016
Morphological sex: ♂
Region: America
Subregion: South America
Country: Chile

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/7	-/-	-/-

Haplogroup: No Sequence

Sample ID: 45:19
Morphological sex: ♀
Region: America
Subregion: South America
Country: Venezuela

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

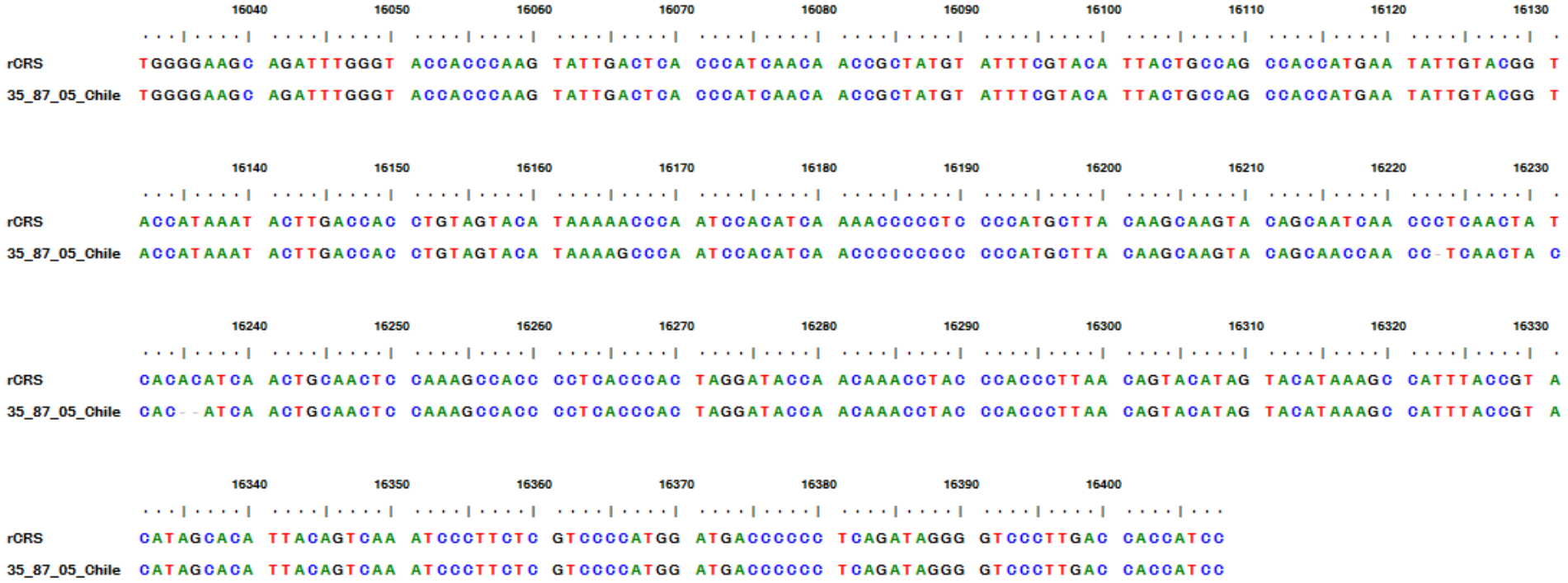
Haplogroup: No Sequence

Sample ID: 35:87:05
Morphological sex: ♀
Region: America
Subregion: South America
Country: Chile

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
X/X	13/14	31.2/32.2	12/17	-/7	-/7	24/26

Haplogroup: H2a2a1g

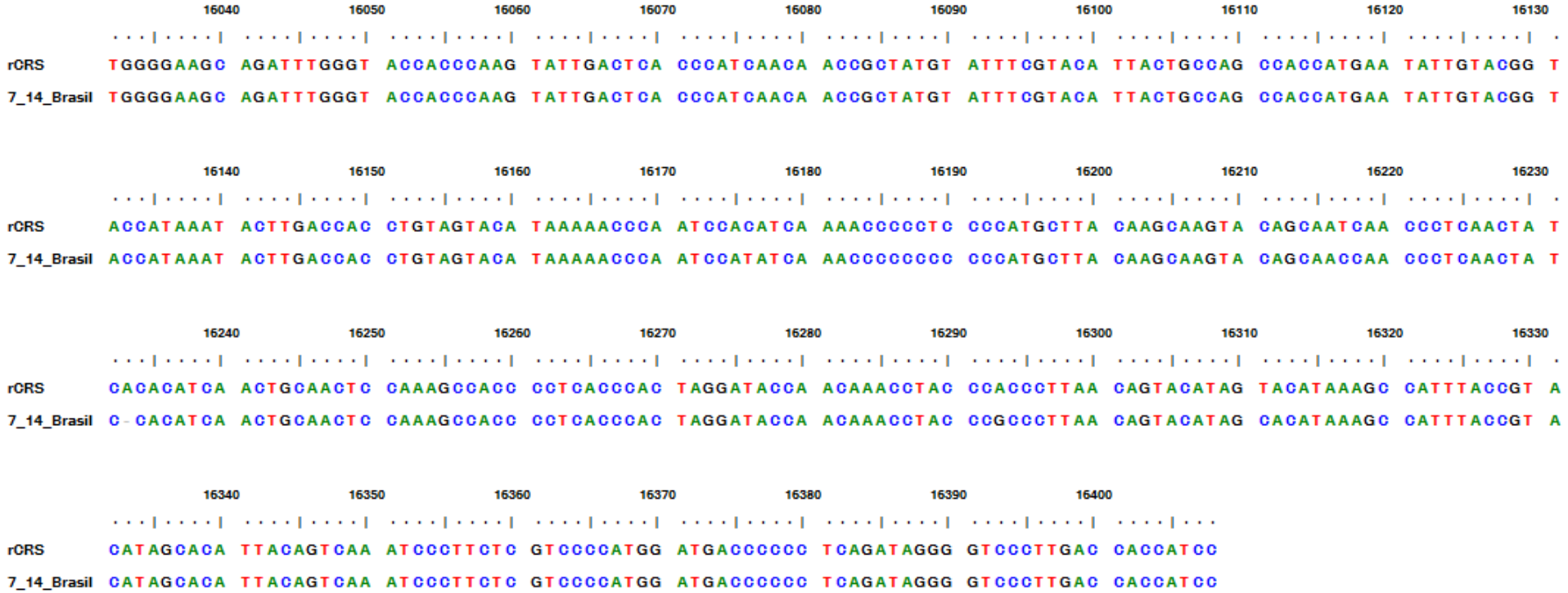


Sample ID: 7:14
Morphological sex: ♂
Region: America
Subregion: South America
Country: Brasil

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: B2i1

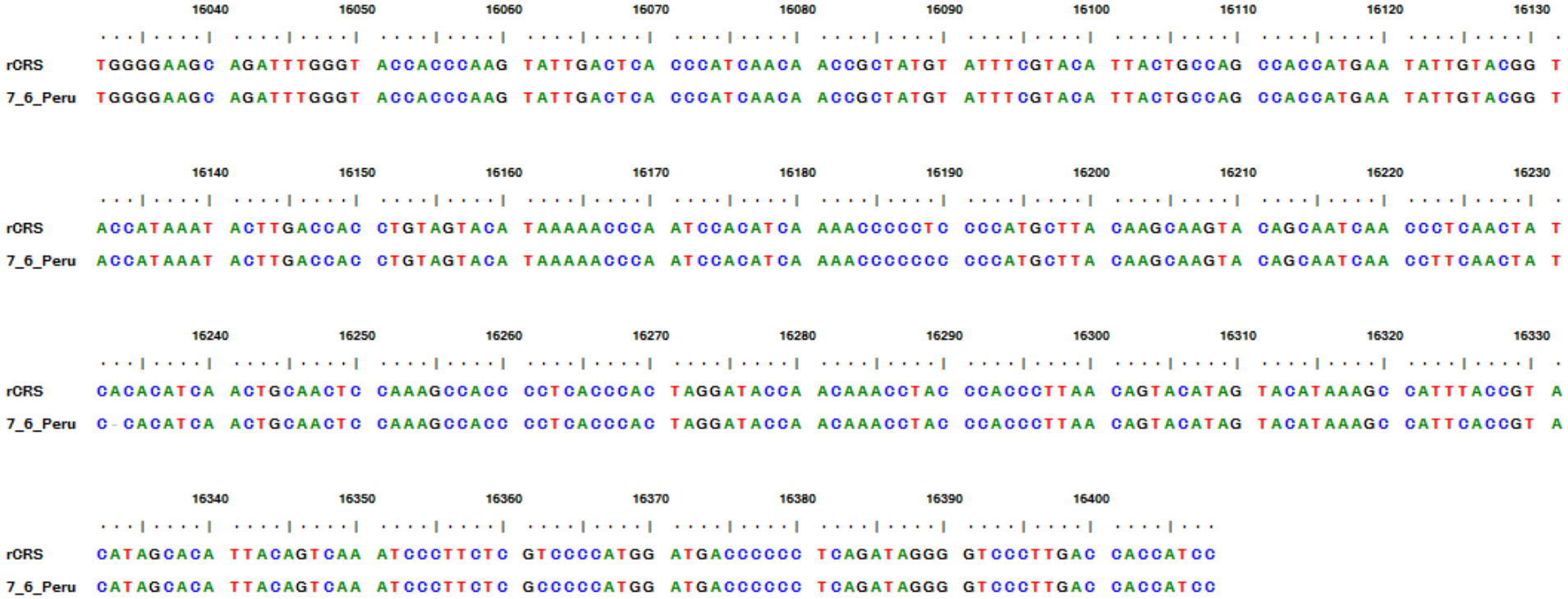


Sample ID: 7:6
Morphological sex: ♂
Region: America
Subregion: South America,
Country: Peru

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
X/Y	9/11	29/30	10/17	7/9	-/10	-/19

Haplogroup: D1a1



Sample ID: 8:6
Morphological sex: ♀
Region: America
Subregion: South America
Country: Peru

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
X/X	-/9	-/-	-/-	-/7	-/-	-/-

Haplogroup: C1

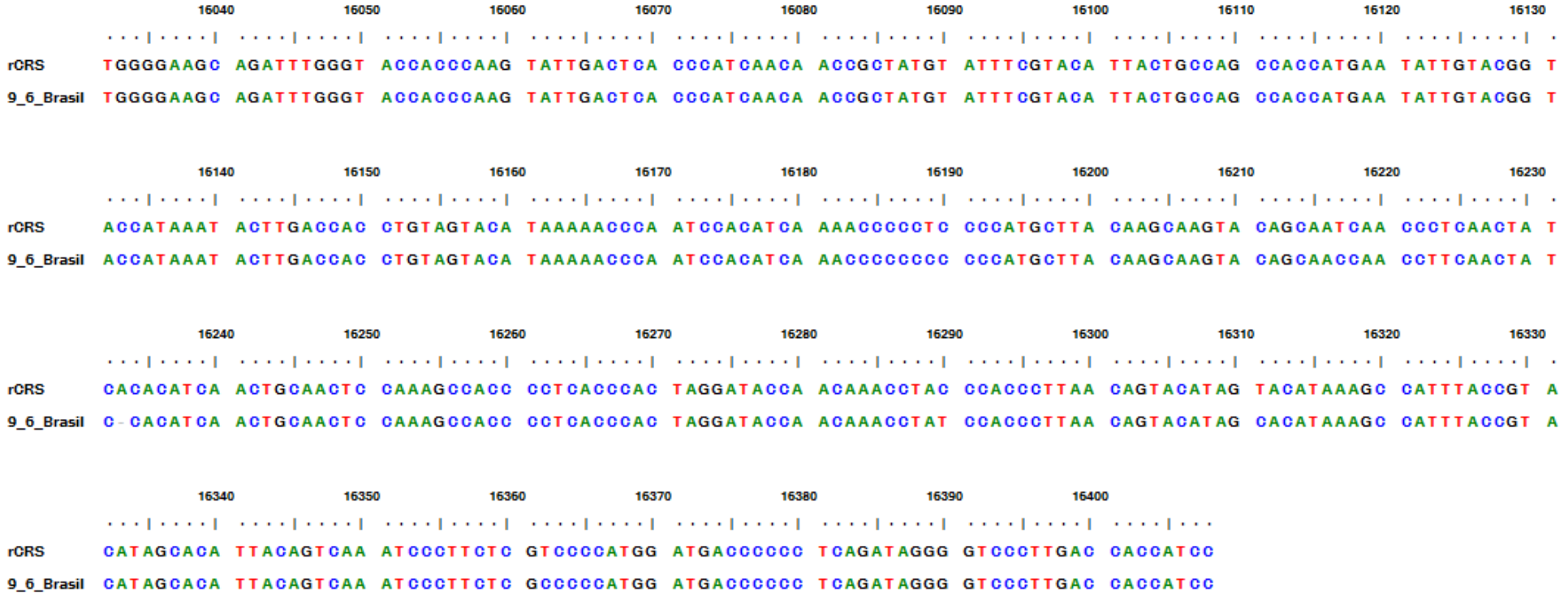
```
                16040     16050     16060     16070     16080     16090     16100     16110     16120     16130
                ...|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| .
rCRS            TGGGGAAGC AGATTTGGGT ACCACCCAAG TATTGACTCA CCCATCAACA ACCGCTATGT ATTTCGTACA TTACTGCCAG CCACCATGAA TATTGTACGG T
8_6_Peru        TGGGGAAGC AGATTTGGGT ACCACCCAAG TATTGACTCA CCCATCAACA ACCGCTATGT ATTTCGTACA TTACTGCCAG CCACCATGAA TATTGTACGG T

                16140     16150     16160     16170     16180     16190     16200     16210     16220     16230
                ...|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| .
rCRS            ACCATAAAT ACTTGACCAC CTGTAGTACA TAAAAACCCA ATCCACATCA AAACCCCCTC CCCATGCTTA CAAGCAAGTA CAGCAATCAA CCCTCAACTA T
8_6_Peru        ACCATAAAT ACTTGACCAC CTGTAGTACA TAAAAACCCA ATCCACATCA AACCCCCCCC CCCATGCTTA CAAGCAAGTA CAGCAATCAA CCTTCAAC- - -

                16240     16250     16260     16270     16280     16290     16300     16310     16320     16330
                ...|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| .
rCRS            CACACATCA ACTGCAACTC CAAAGCCACC CCTCACCCAC TAGGATACCA ACAAACCTAC CCACCCTTAA CAGTACATAG TACATAAAGC CATTTACCGT A
8_6_Peru        - - -ACATCA ACTGCAACTC CAAAGCCACC CCTCACCCAC TAGGATACCA ACAAACCTGC CCACCCTCAA CAGTACATAG TACATAAAGC CATTCATCGT A

                16340     16350     16360     16370     16380     16390     16400
                ...|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|...
rCRS            CATAGCACA TTACAGTCAA ATCCCTTCTC GTCCCCATGG ATGACCCCCC TCAGATAGGG GTCCCTTGAC CACCATCC
8_6_Peru        CATAGCACA TTACAGTCAA ATCCCTTCTC GTCCCCATGG ATGACCCCCC TCAGATAGGG GTCCCTTGAC CACCATCC
```

Sample ID: 9:6
Morphological sex: ♀
Region: America
Subregion: South America
Country: Brasil

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
X/X	12/14	-/32.2	14/15	-/7	-/10	25/26

Haplogroup: B2i1



Sample ID: 14:15
Morphological sex: ♀
Region: America
Subregion: South America
Country: Brasil

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: No Sequence

Sample ID: 16:15
Morphological sex: ♂
Region: America
Subregion: South America
Country: Peru

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: No Sequence

Sample ID: 120:05
Morphological sex: ♀
Region: America
Subregion: South America
Country: Chile

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: No Sequence

Sample ID: 10**:**15
Morphological sex: ♀
Region: America
Subregion: South America
Country: Bolivia

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

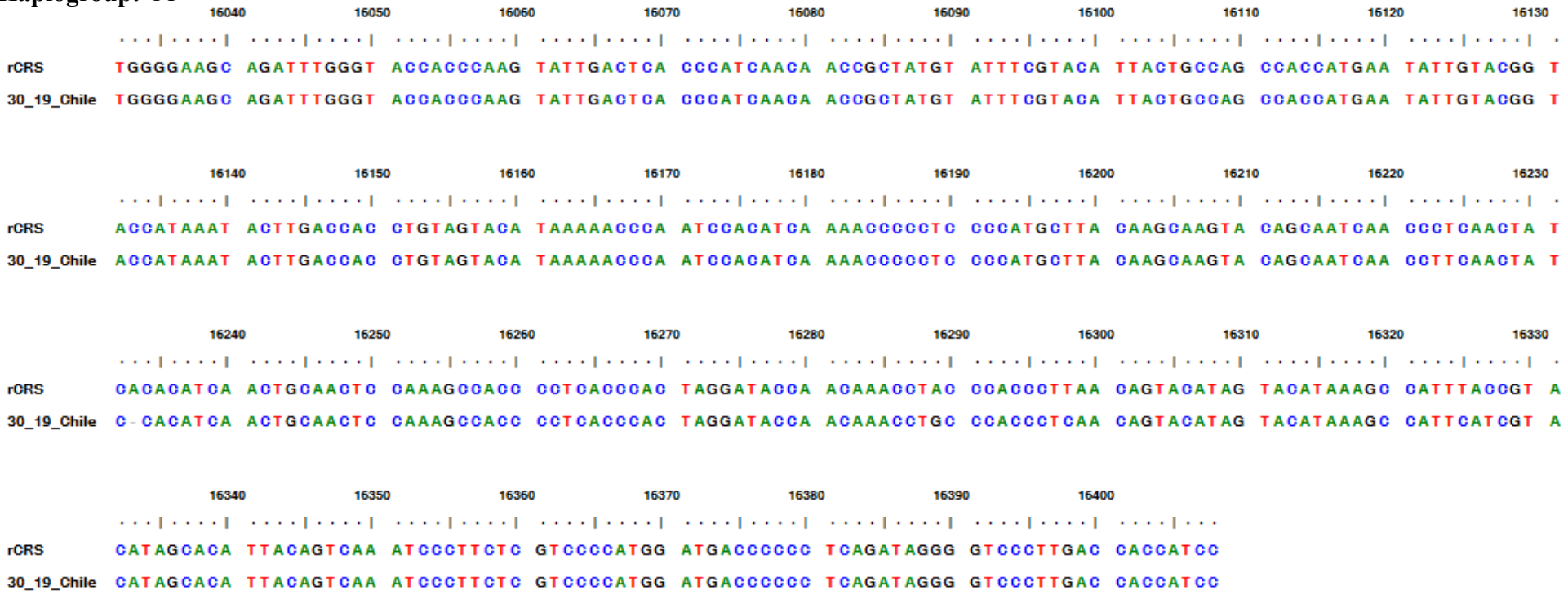
Haplogroup: No Sequence

Sample ID: 30:19
Morphological sex: ♀
Region: America
Subregion: South America
Country: Chile

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
X/X	-/9	-/32.2	16/19	-/9.3	-/11	19/25

Haplogroup: C1

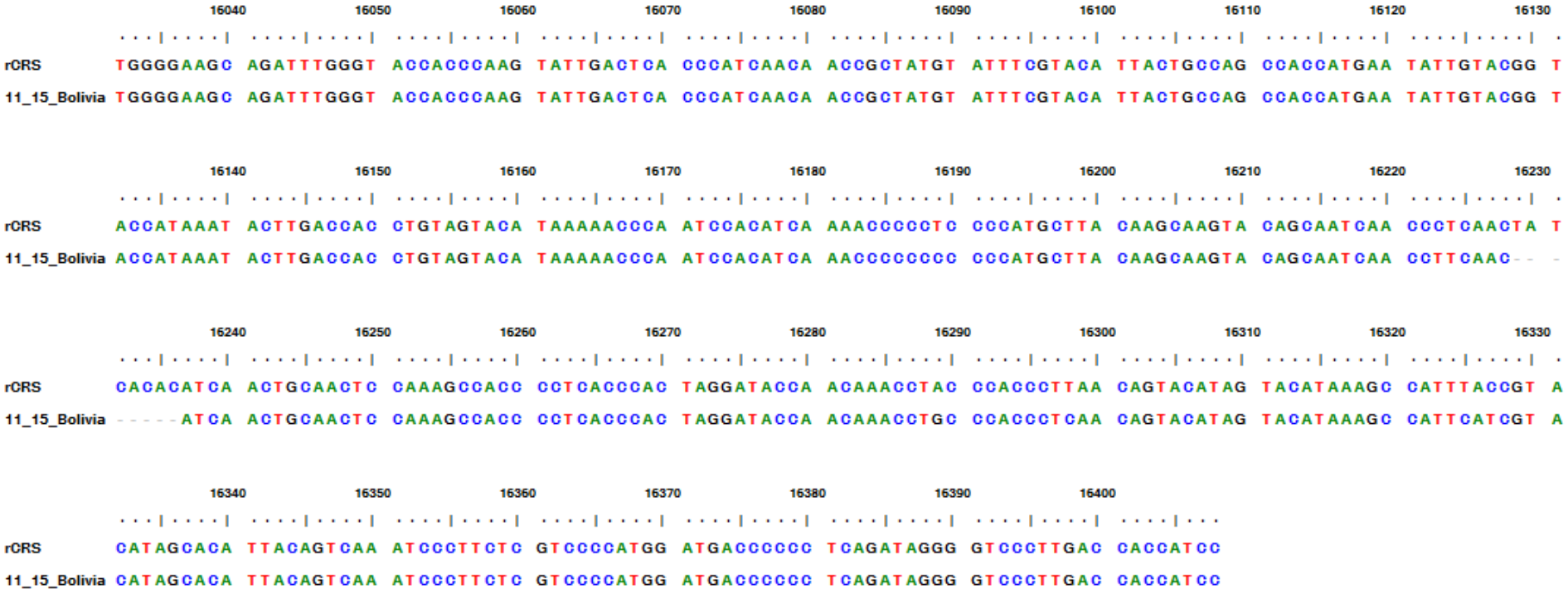


Sample ID: 11:15
Morphological sex: ♀
Region: America
Subregion: South America
Country: Bolivia

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: C1

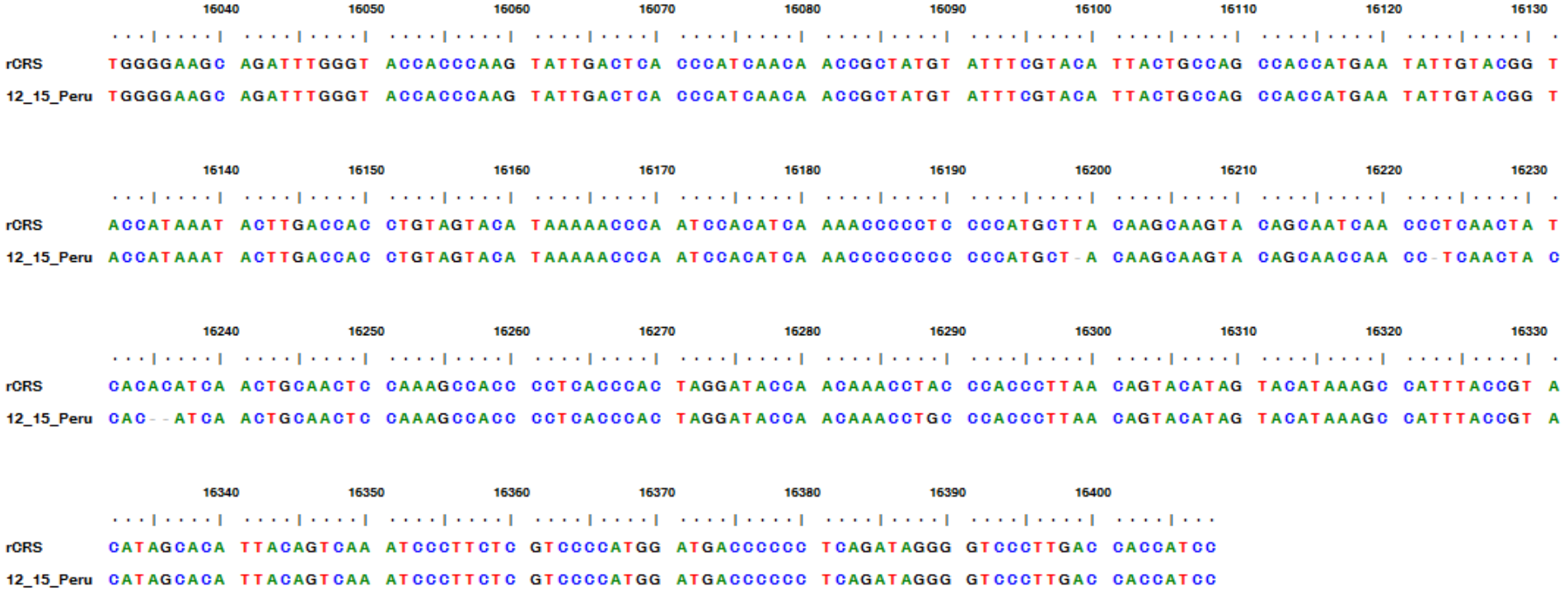


Sample ID: 12:15
Morphological sex: ♂
Region: America
Subregion: South America
Country: Peru

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: B2

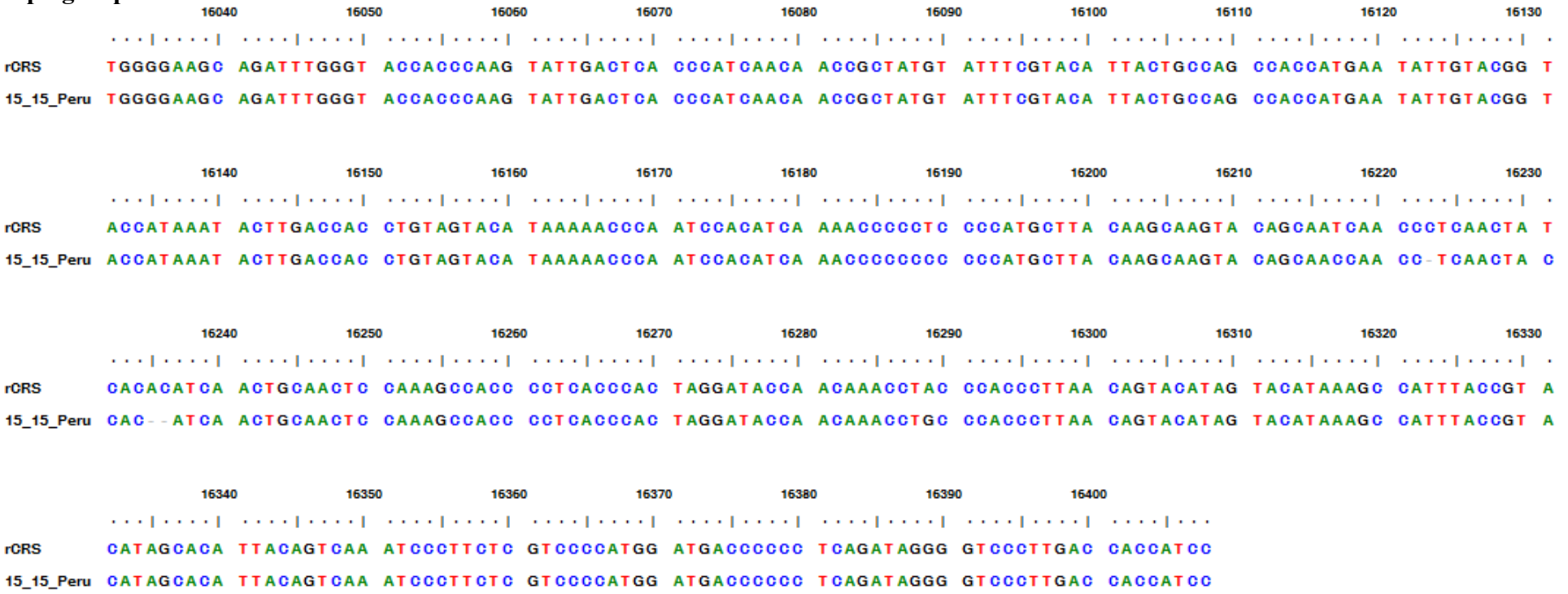


Sample ID: 15:15
Morphological sex: ♂
Region: America
Subregion: South America
Country: Peru

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: B2

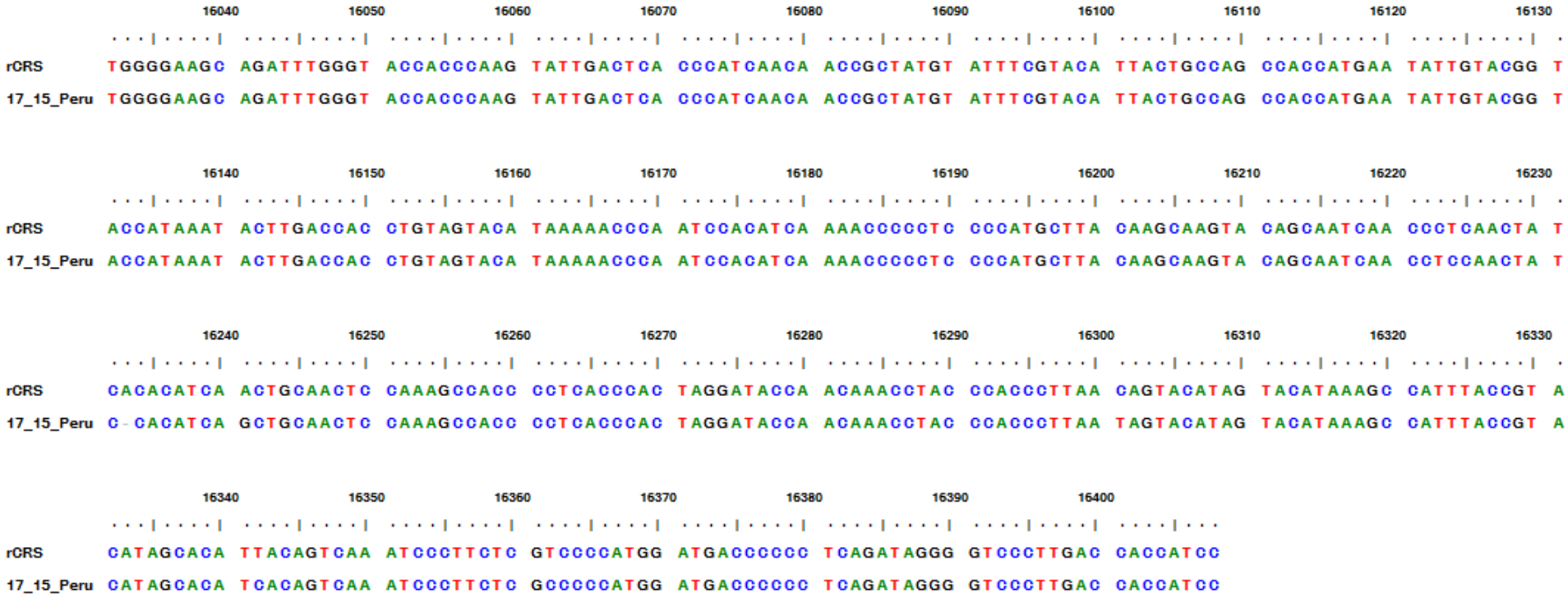


Sample ID: 17:15
Morphological sex: ♂
Region: America
Subregion: South America
Country: Peru

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: D4h3a

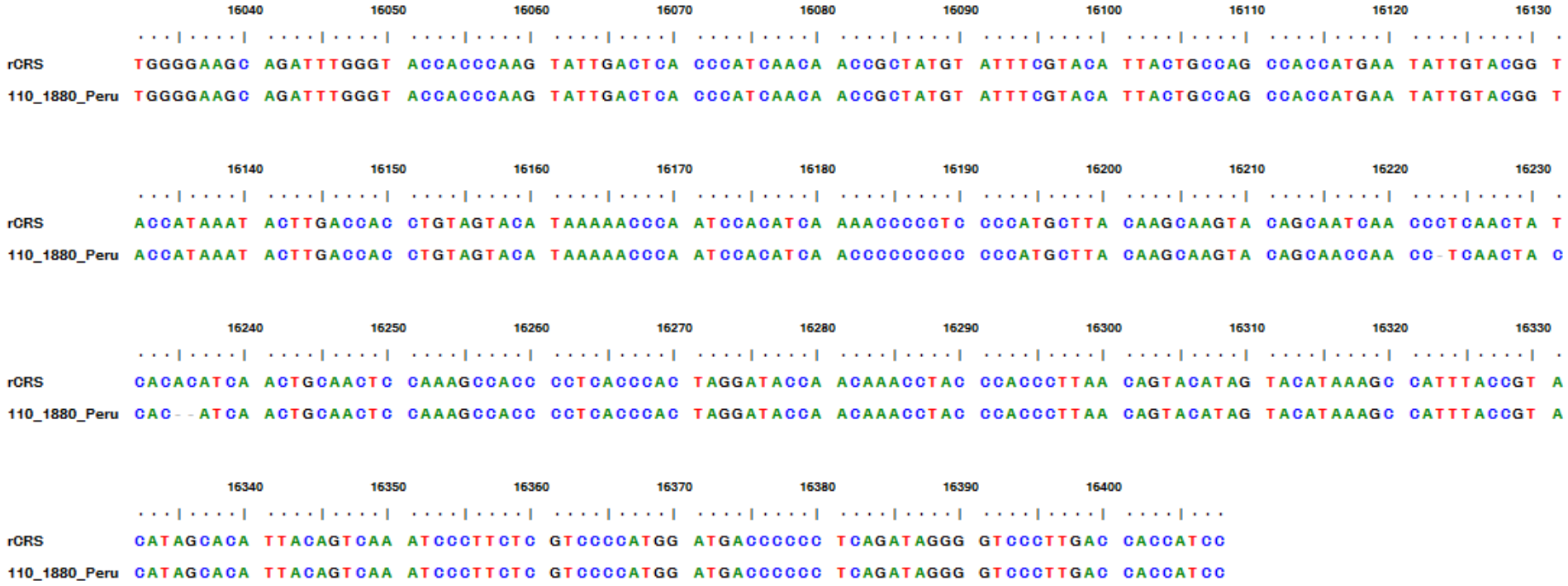


Sample ID: 110:1880
Morphological sex: ♂
Region: America
Subregion: South America
Country: Peru

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
X/Y	10/14	30.2/31.2	13/15	6/7	-/11	24/26

Haplogroup: B2



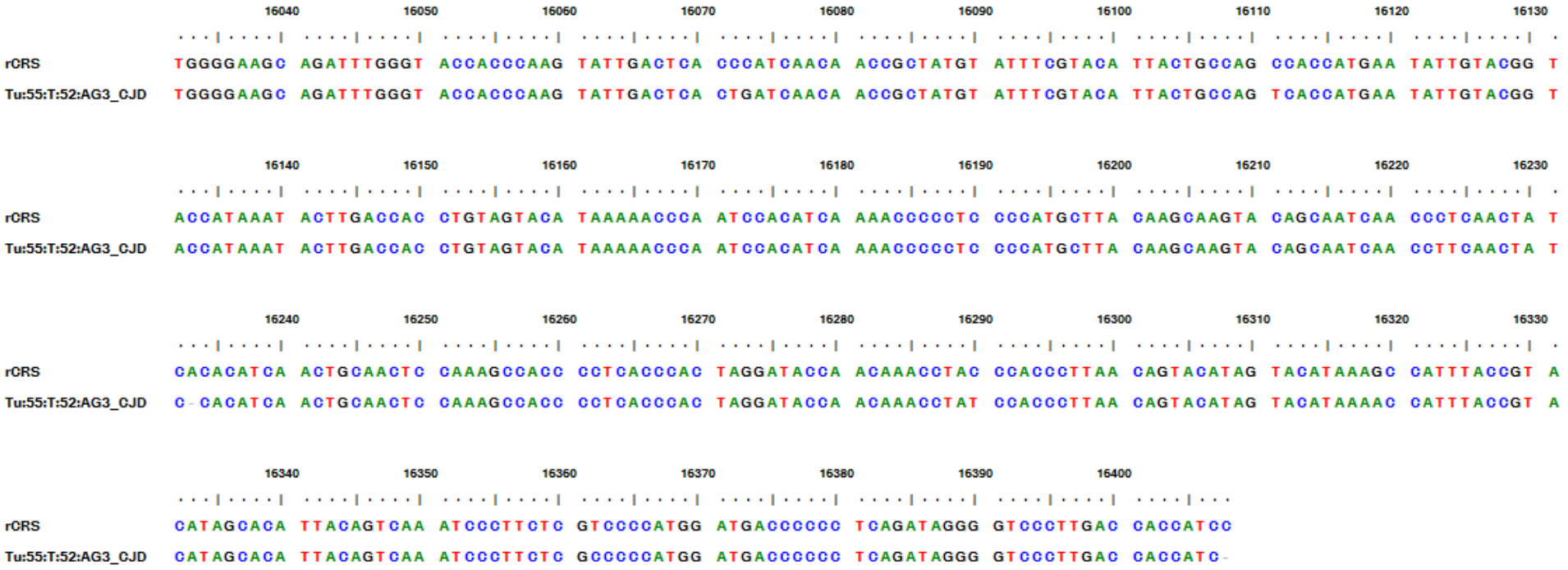
7.3 Data sheets on individuals from Panama

Sample ID: Tü:55: T:52 AG3 w. trench burial
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: A2



Sample ID: Tü:56: T:45 AG3 A-4
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: No Sequence

Sample ID: Tü:57: T:47 AG3 B-7
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

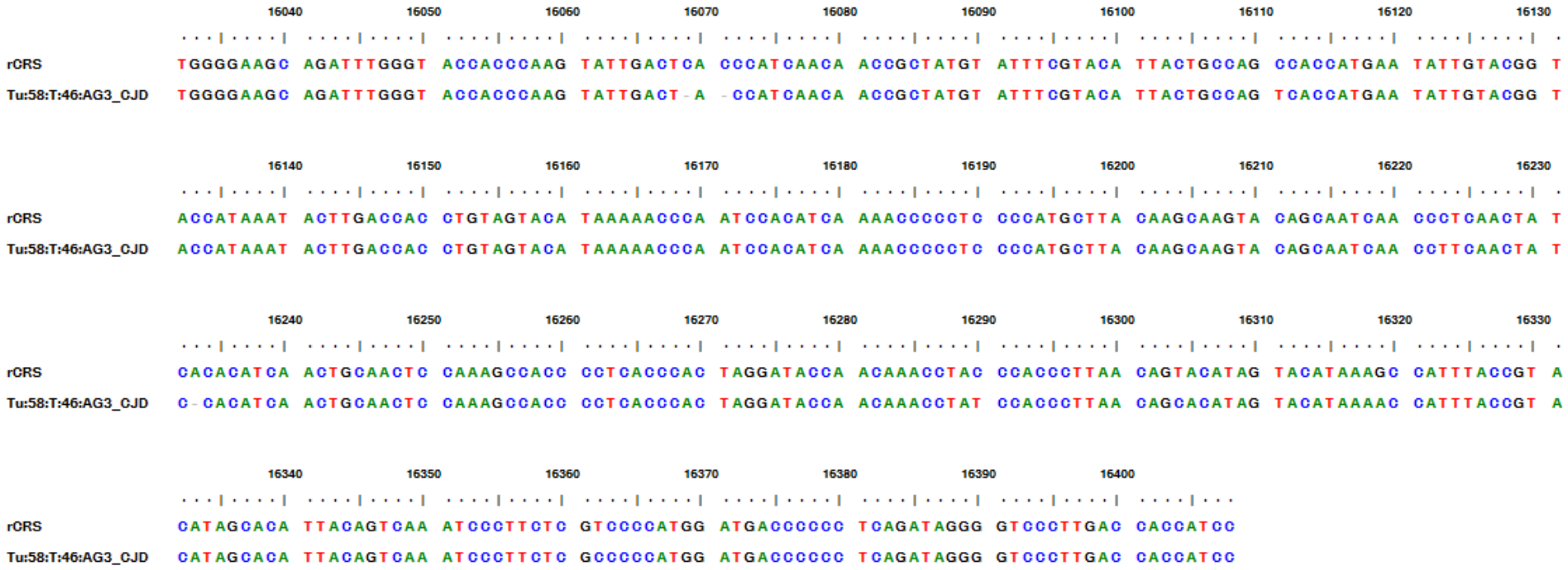
Haplogroup: No Sequence

Sample ID: Tü:58: T:46 AG3 B-3
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: A2



Sample ID: Tü:59: T:44 AG3 A-2
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: No Sequence

Sample ID: Tü:60: T:51 AG3 B-20
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

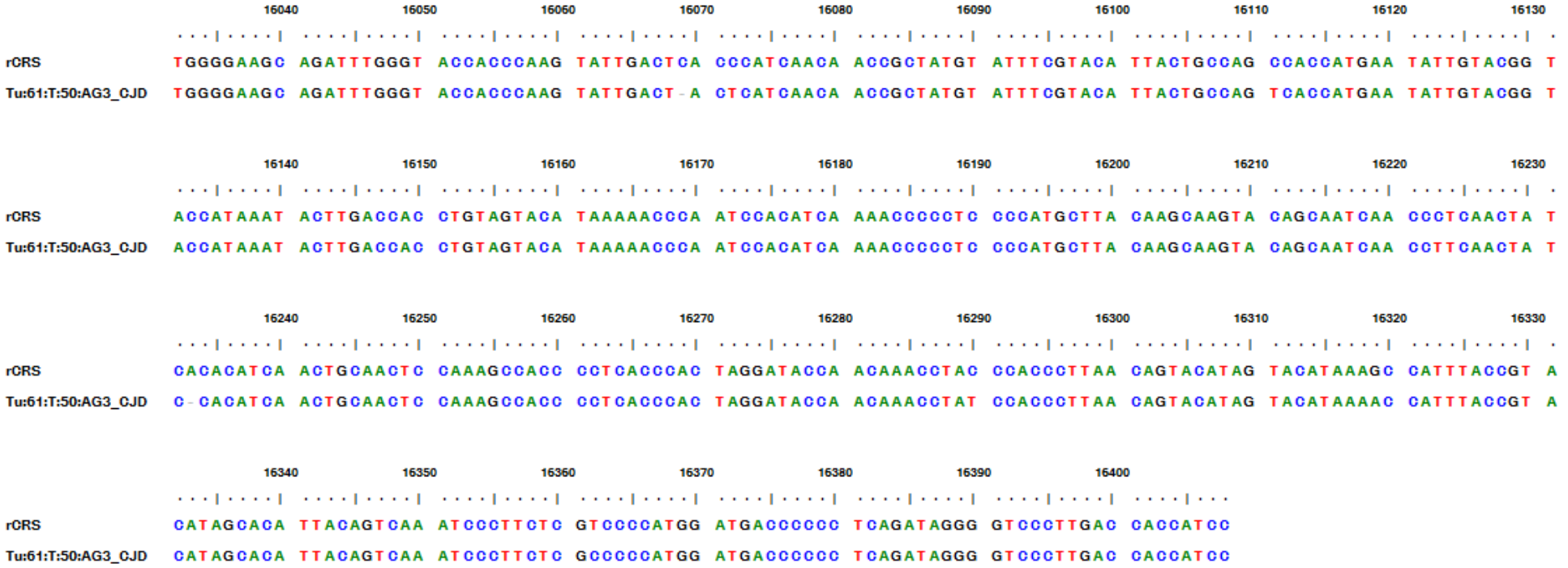
Haplogroup: No Sequence

Sample ID: Tü:61: T:50 AG3 B-16
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: A2



Sample ID: Tü:62: T:49 AG3 B-13
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: No Sequence

Sample ID: Tü:63: T:43 AG3 A-1
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: No Sequence

Sample ID: Tü:64: T:48 AG3 B-8
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

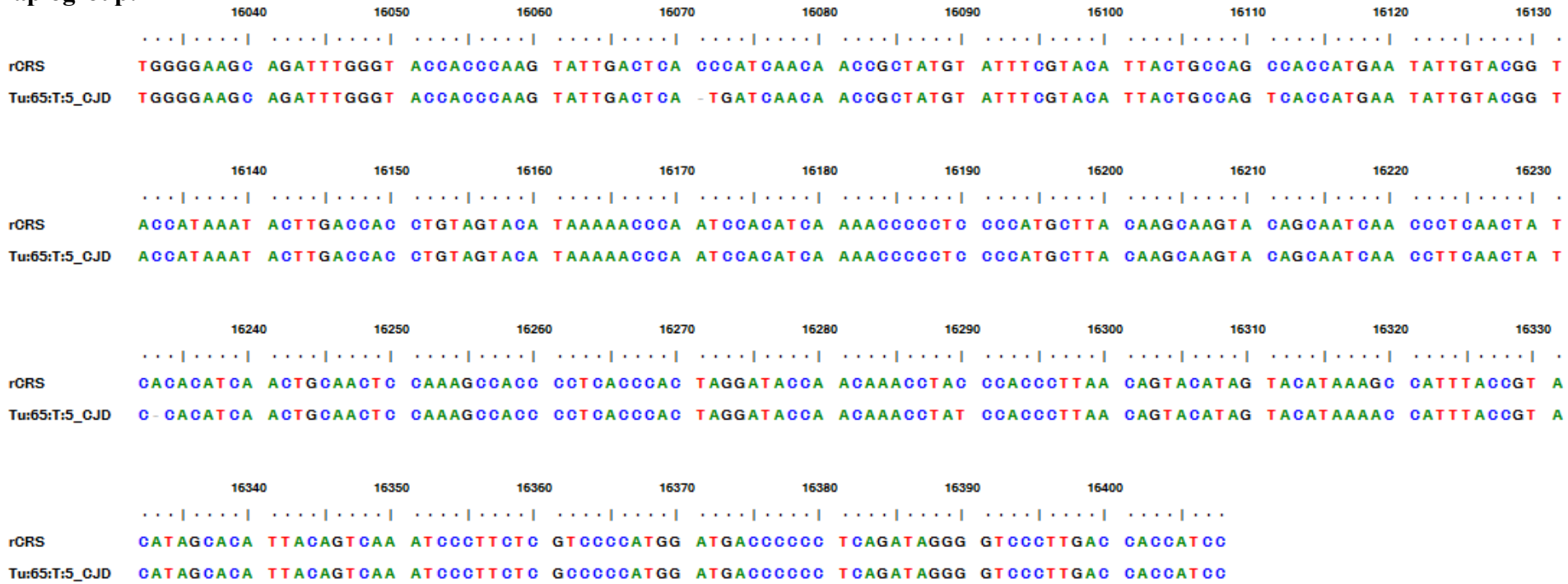
Haplogroup: No Sequence

Sample ID: Tü:65: T:5 CJD Op.3, T.87 Ind. 33
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: A2



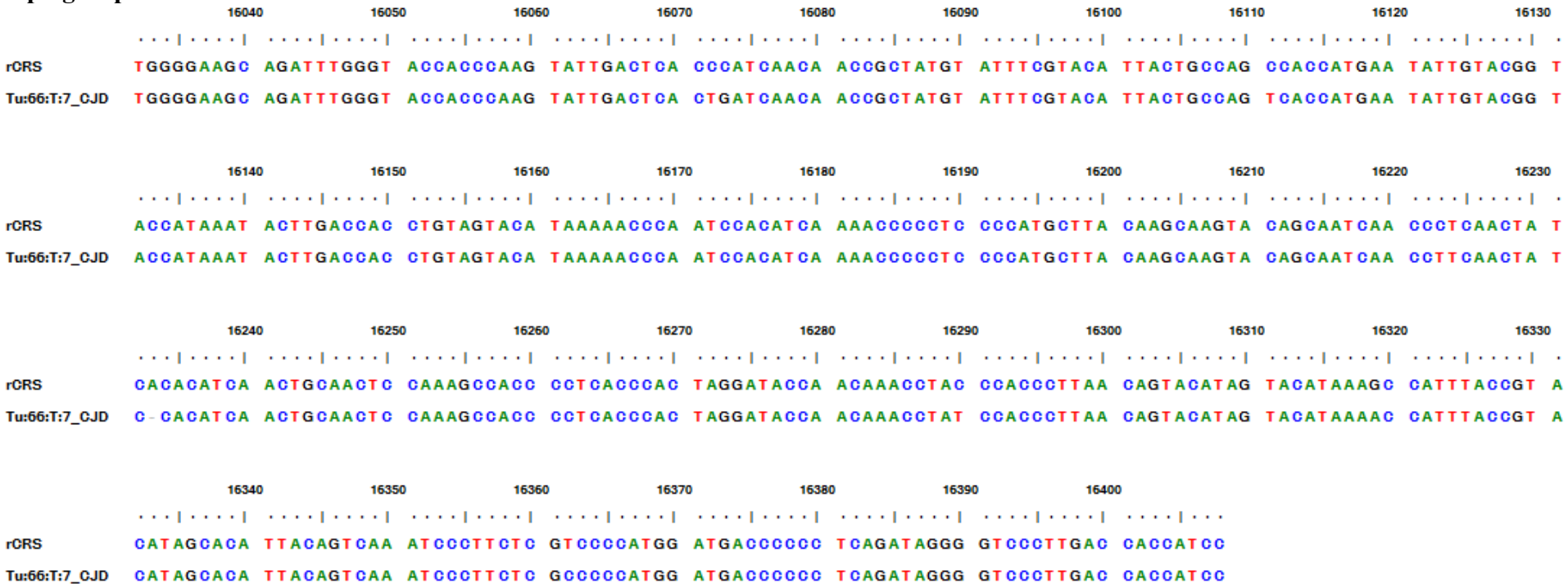
Sample ID: Tü:66: T:7 CJD U.3 T.115 Ind.44

Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/7	-/-	-/-

Haplogroup: A2



Sample ID: Tü:67: T:3 CJD U.3-Sub. U.8 T.82 Ind.15
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

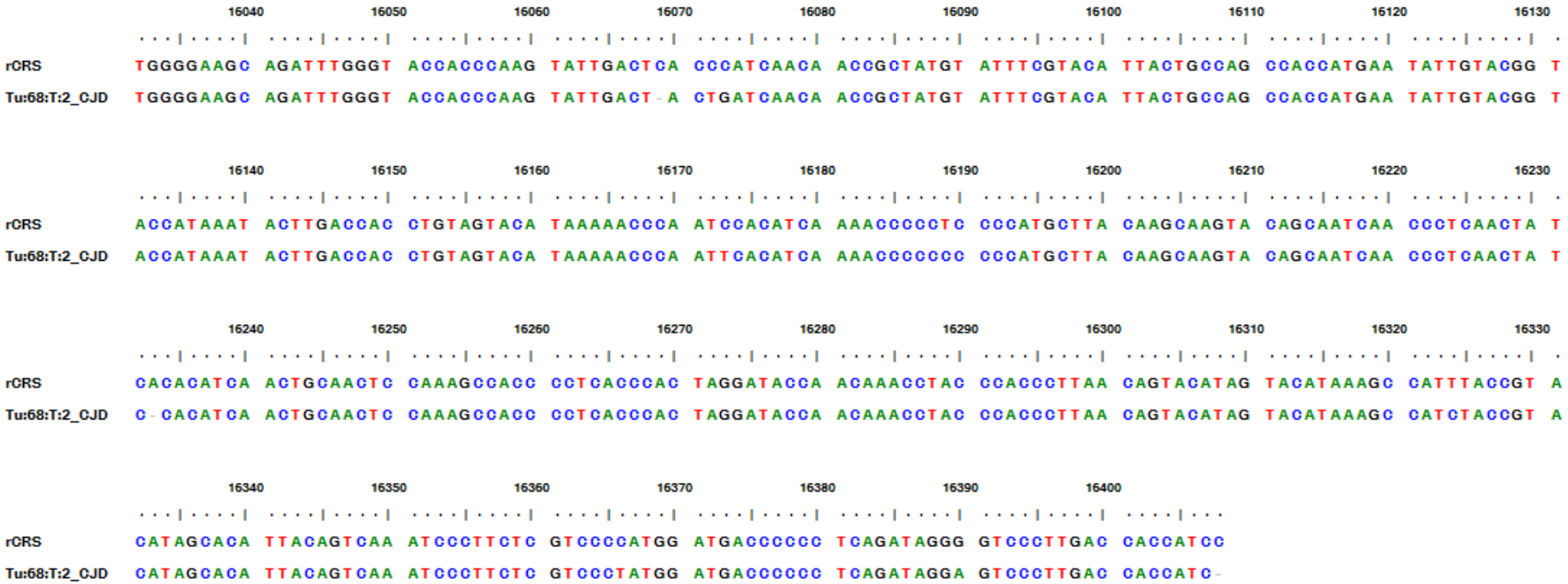
Haplogroup: No Sequence

Sample ID: Tü:68: T.2 CJD U.3-Sub. 9 T.74 Ind.20 H-1
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: H15a1a1

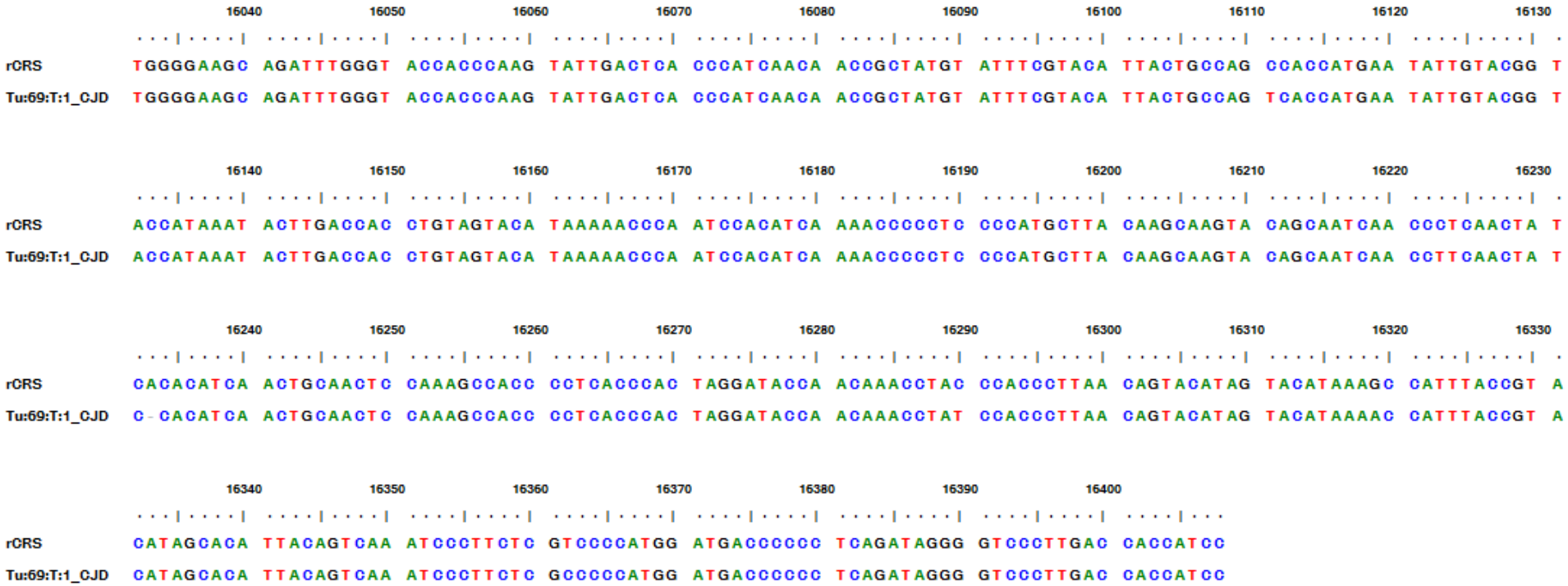


Sample ID: Tü:69: T:1 CJD Op.3 T.73 I.17
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: A2

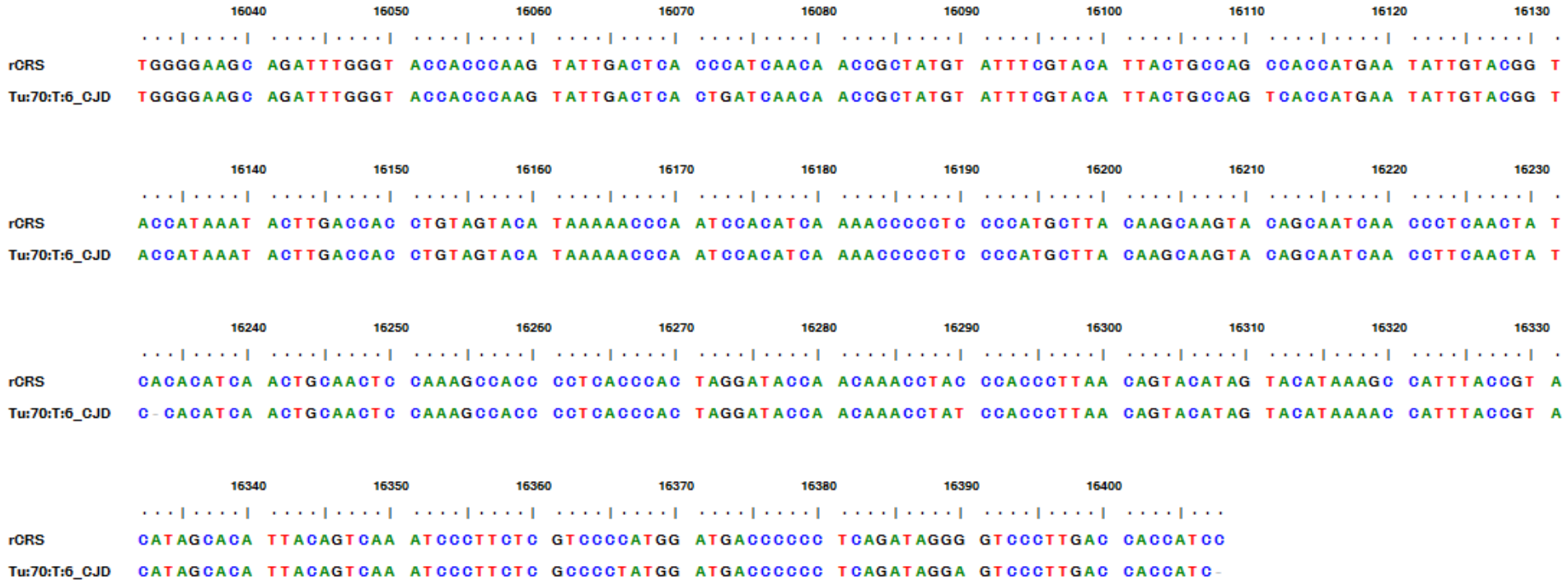


Sample ID: Tü:70: T:6 CJD Op.3 T.90 I.34
Morphological sex: Ø
Region: America
Subregion: Central America,
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: A2

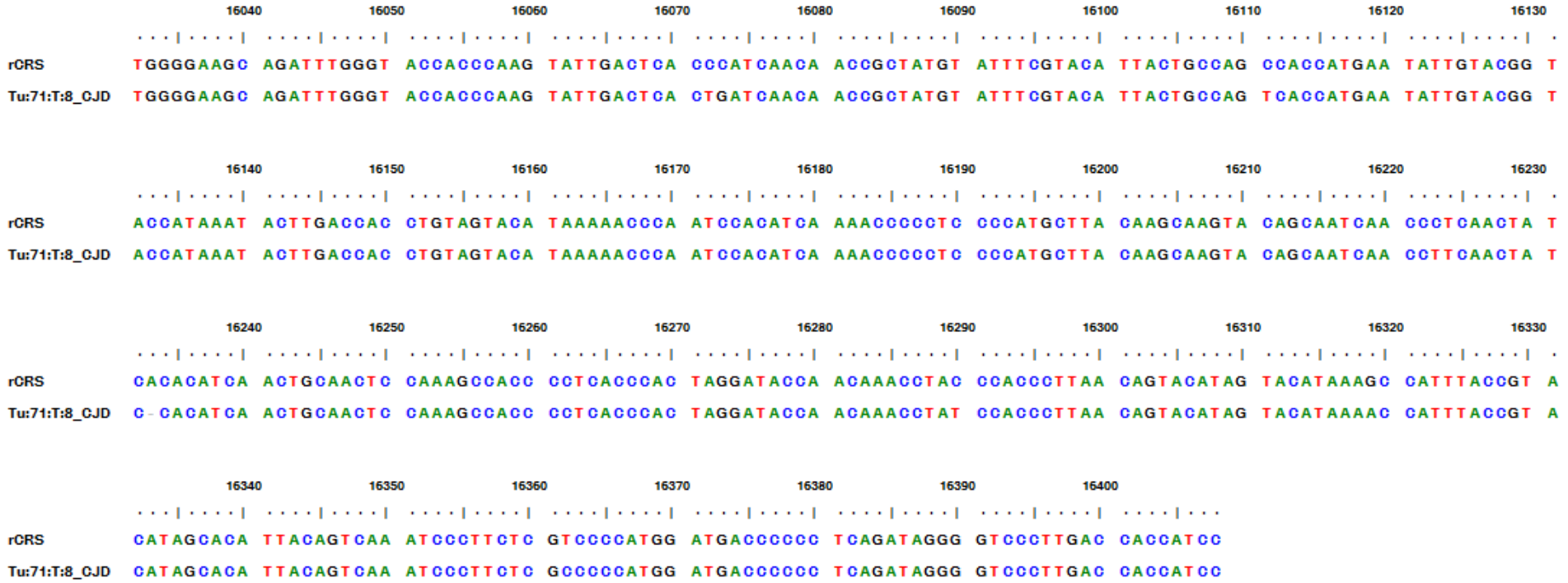


Sample ID: Tü:71: T:8 CJD Op.3 T.115 I.39
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: A2

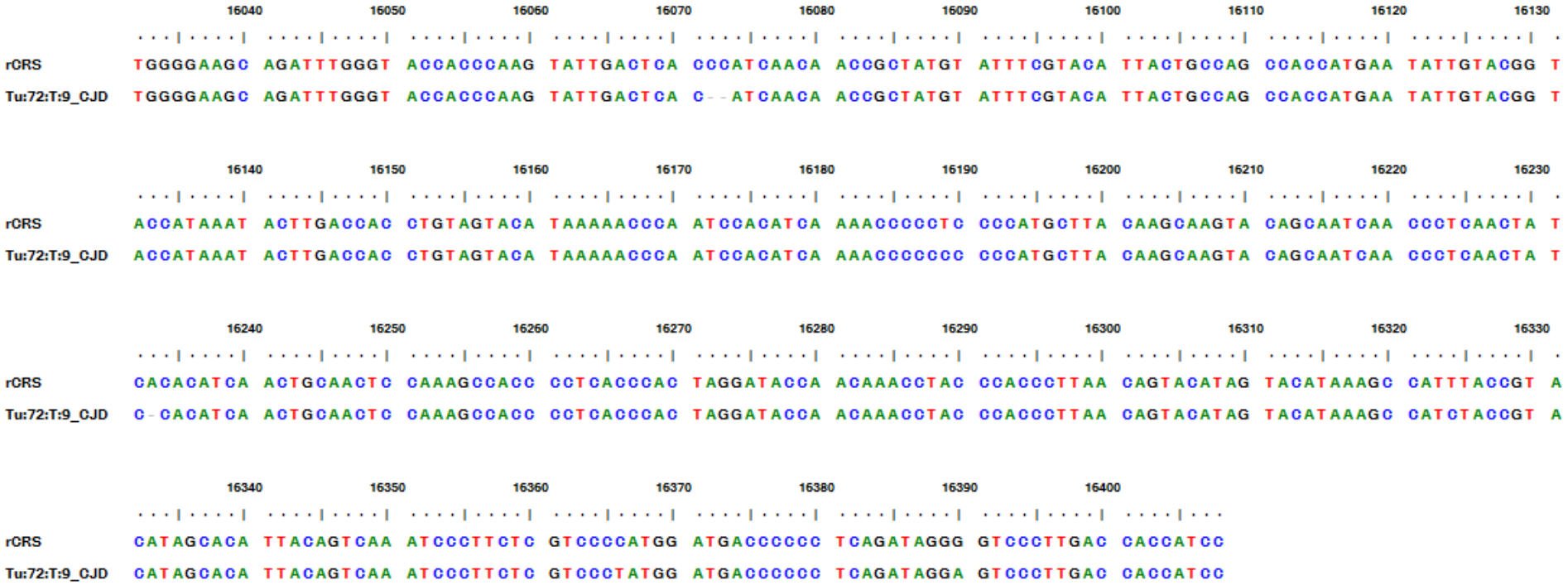


Sample ID: Tü:72: T:9 CJD Op.31-95 E1-I1 tr-1 stratum 1 packet Z
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: H15a1a1



Sample ID: Tü:73: T:10 CJD Op.3 R1.I.1
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: No Sequence

Sample ID: Tü:74: T:4 CJD U.3, T.87 second level Ind.31 CH
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

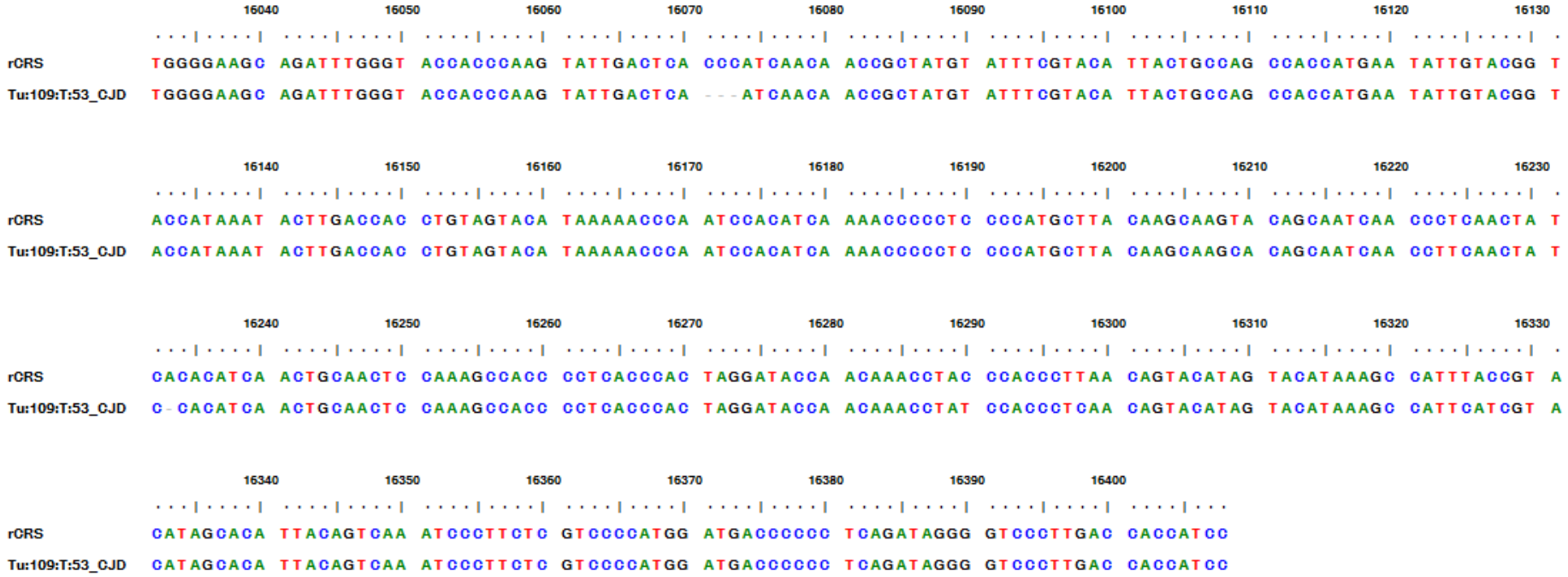
Haplogroup: No Sequence

Sample ID: Tü:109: T:53 CO-40 Ind.6A
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: C1



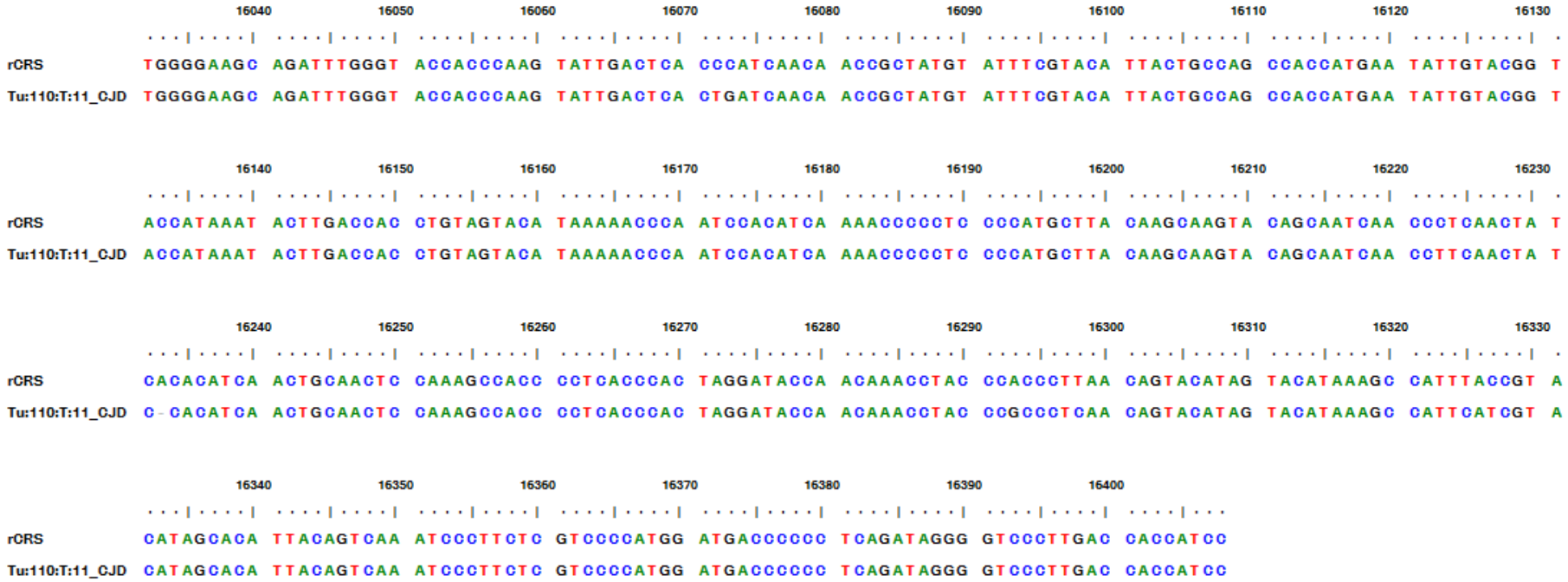
Sample ID: Tü:110: T:11 CJD Op.3 T.2 Pkt.2 Skull A
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama

Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: C1



Sample ID: Tü:111: T:12 CJD Op.3 T.2 Pkt.2 Skull D
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

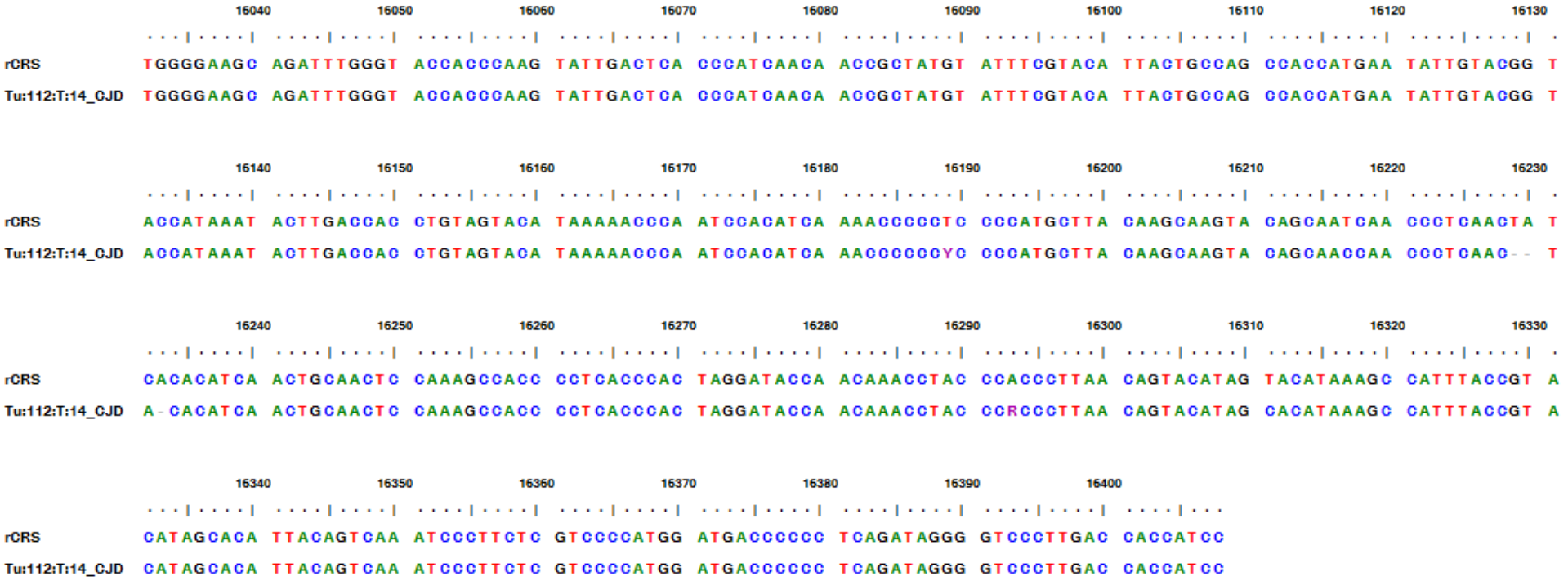
Haplogroup: No Sequence

Sample ID: Tü:112: T:14 CJD Op.3 T.2 Pkt.2 Skull F
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: B2i1

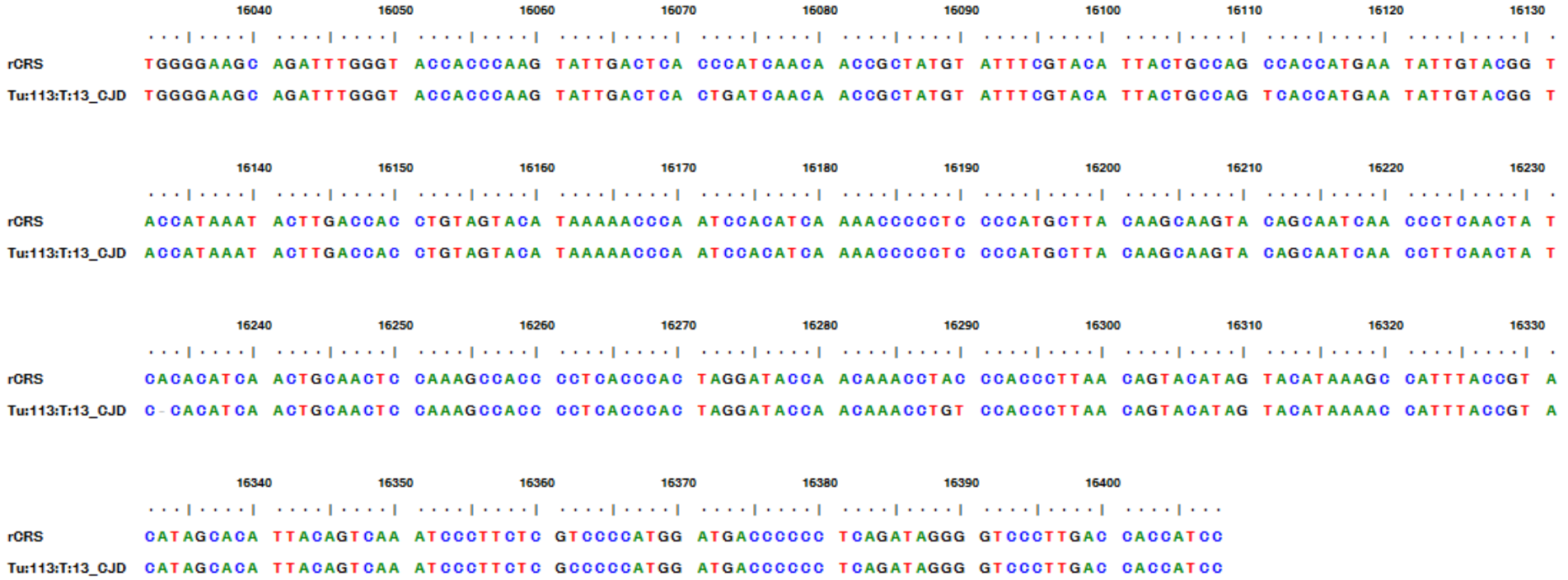


Sample ID: Tü:113: T:13 CJD Op.3 T.2 Pkt.2 Skull E
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: A2

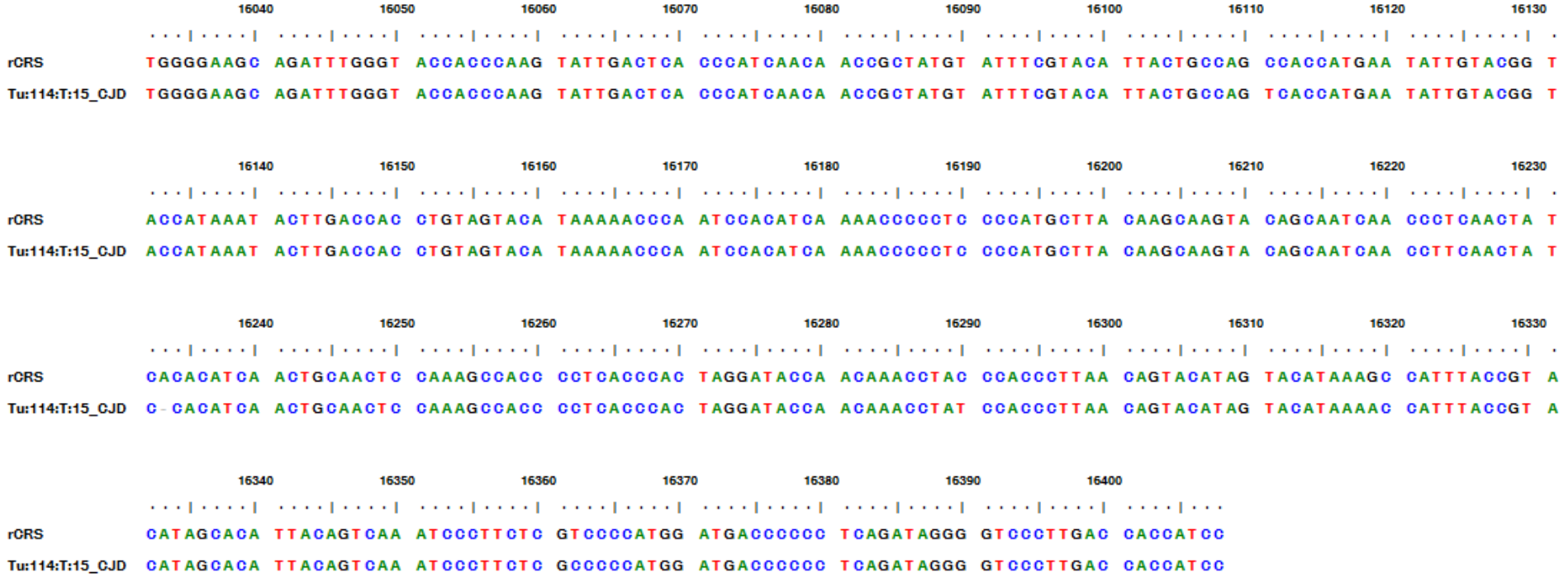


Sample ID: Tü:114: T:15 CJD Op.3 T.2 Pkt.2 Skull G
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: A2

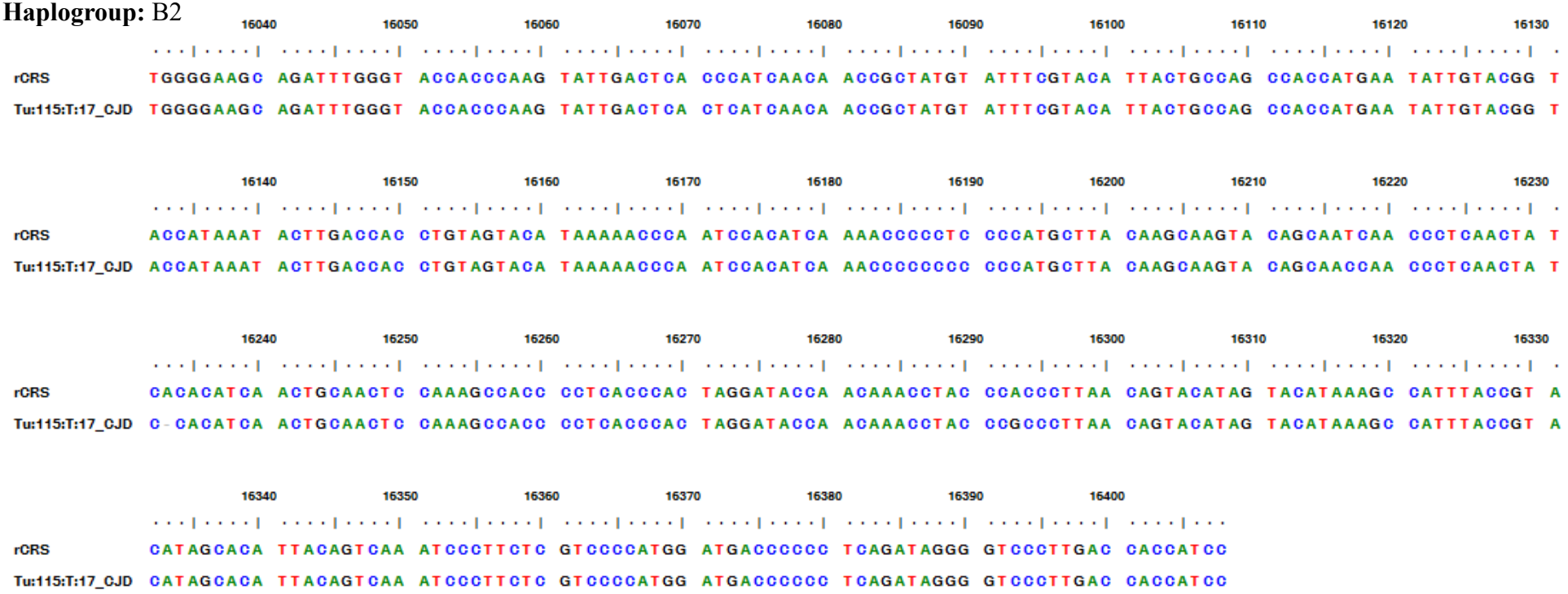


Sample ID: Tü:115: T:17 CJD Op.3 T.2 Pkt.2 Skull H.24
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: B2



Sample ID: Tü:116: T:18 CJD Op.3 T.2 Pkt.2 Skull H.82
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

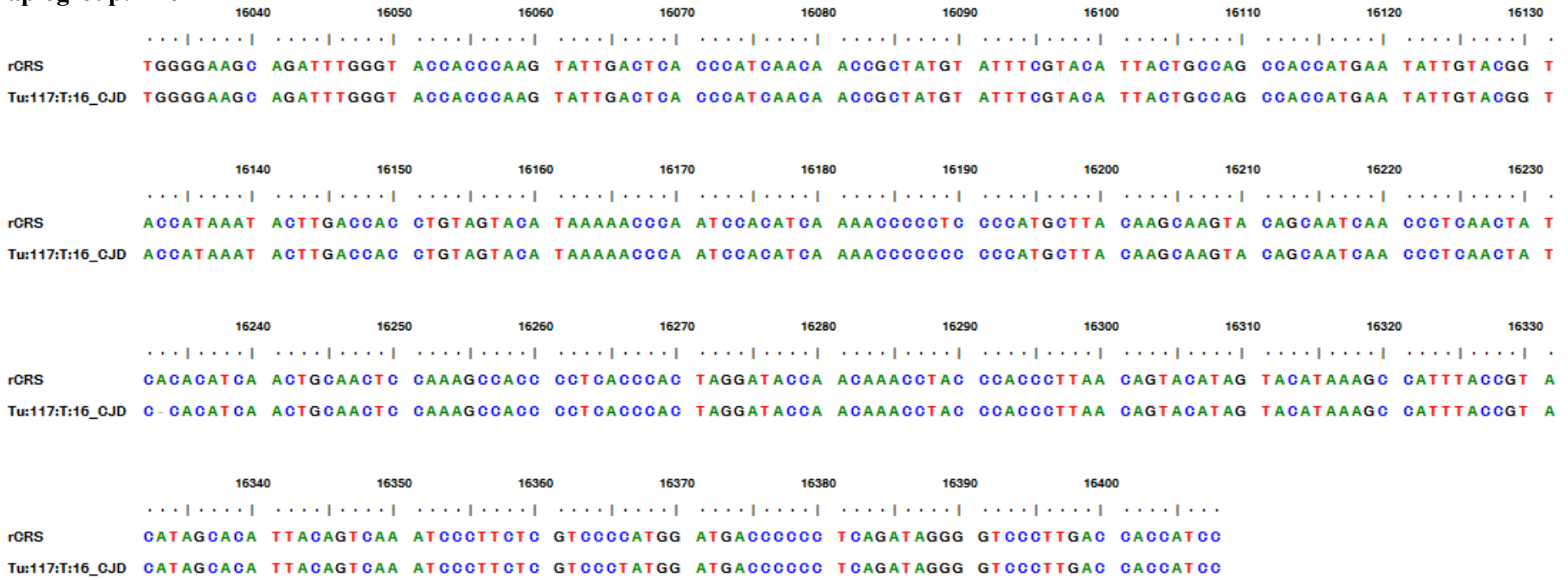
Haplogroup: No Sequence

Sample ID: Tü:117: T:16 CJD Op.3 T.2 Pkt.2 Skull H
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: H15a1a1

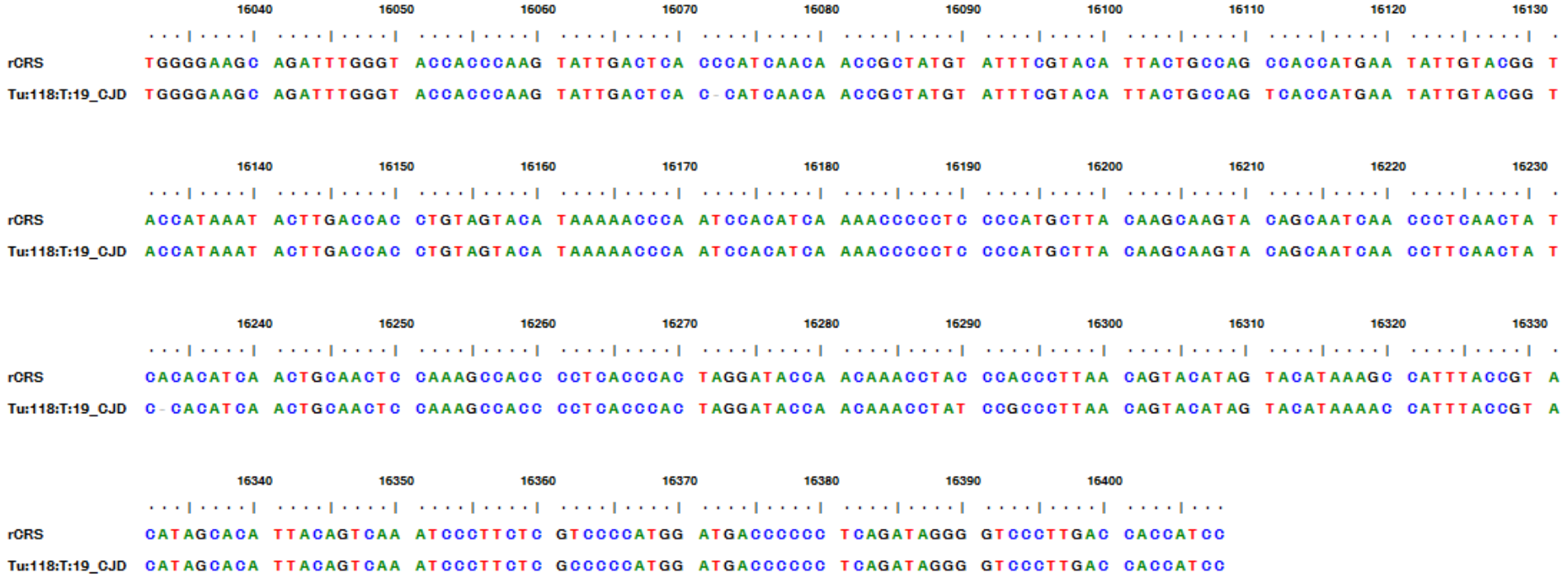


Sample ID: Tü:118: T:19 CJD Op.3 T.2 Pkt.2 Skull I
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: A2

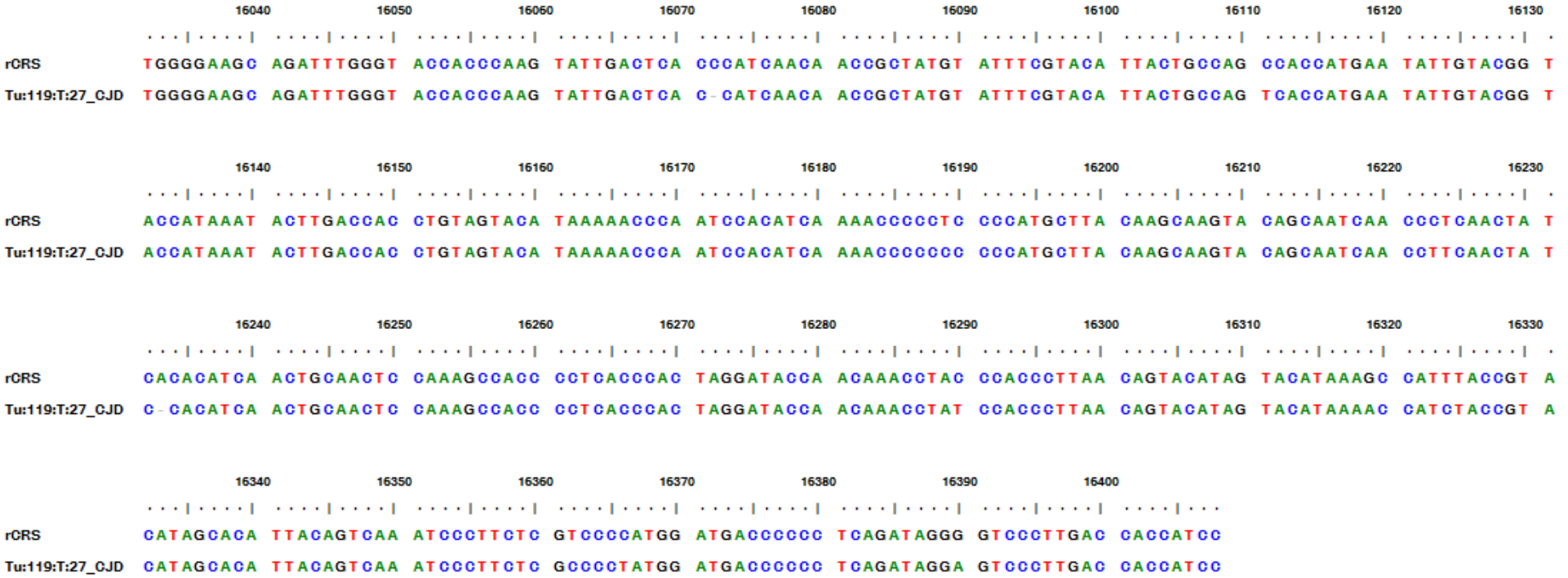


Sample ID: Tü:119: T:27 CJD Op.3 T.2 U.3 Pkt.10
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: A2

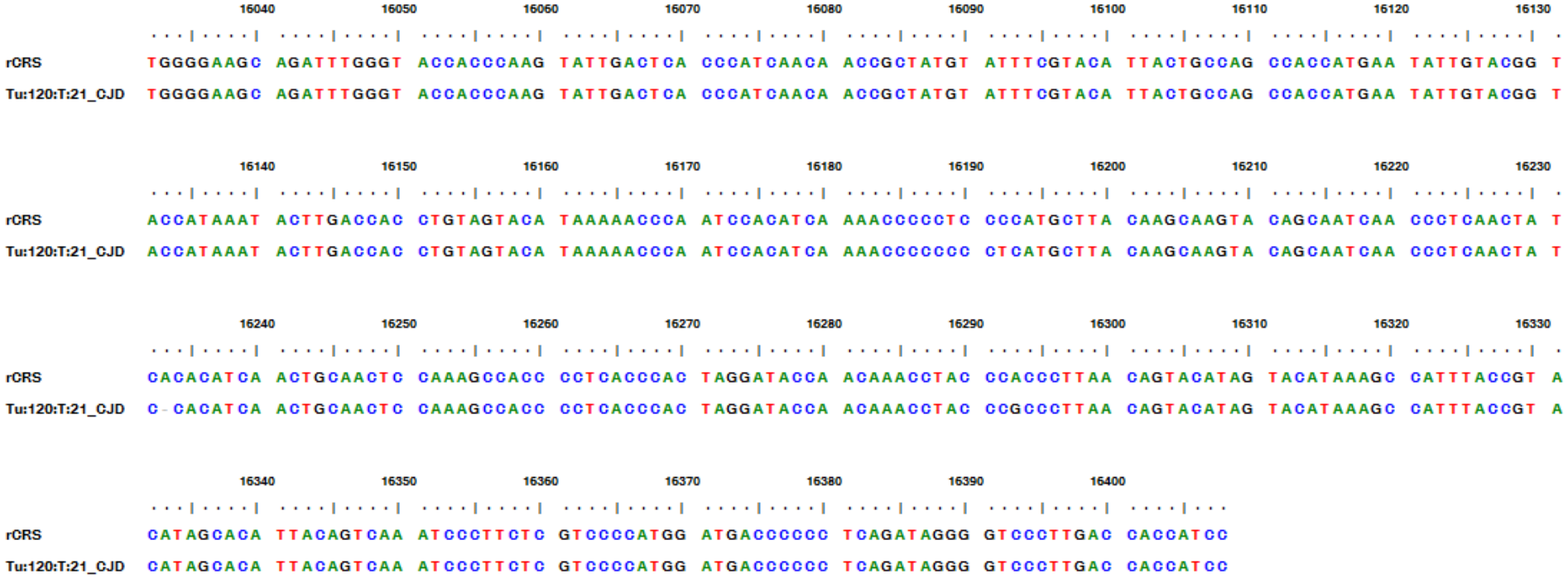


Sample ID: Tü:120: T:21 CJD Op.3 T.2 Pkt.4 Skull H.156
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: U5b2a1



Sample ID: Tü:121: T:23 CJD Op.3 T.2 Pkt. 8
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: No Sequence

Sample ID: Tü:122: T:29 CJD Op.3 T.2 Pkt. 13
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

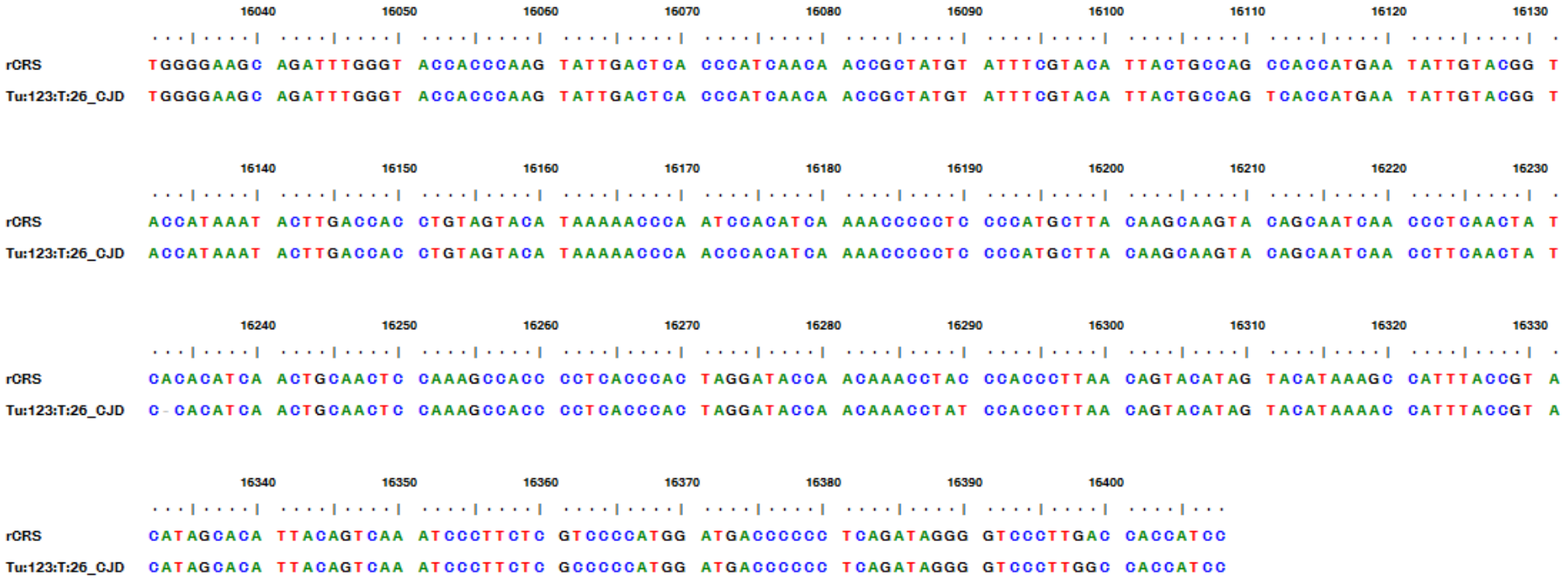
Haplogroup: No Sequence

Sample ID: Tü:123: T:26 CJD Op.3 T.2 U.3 Pkt.1
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: A2

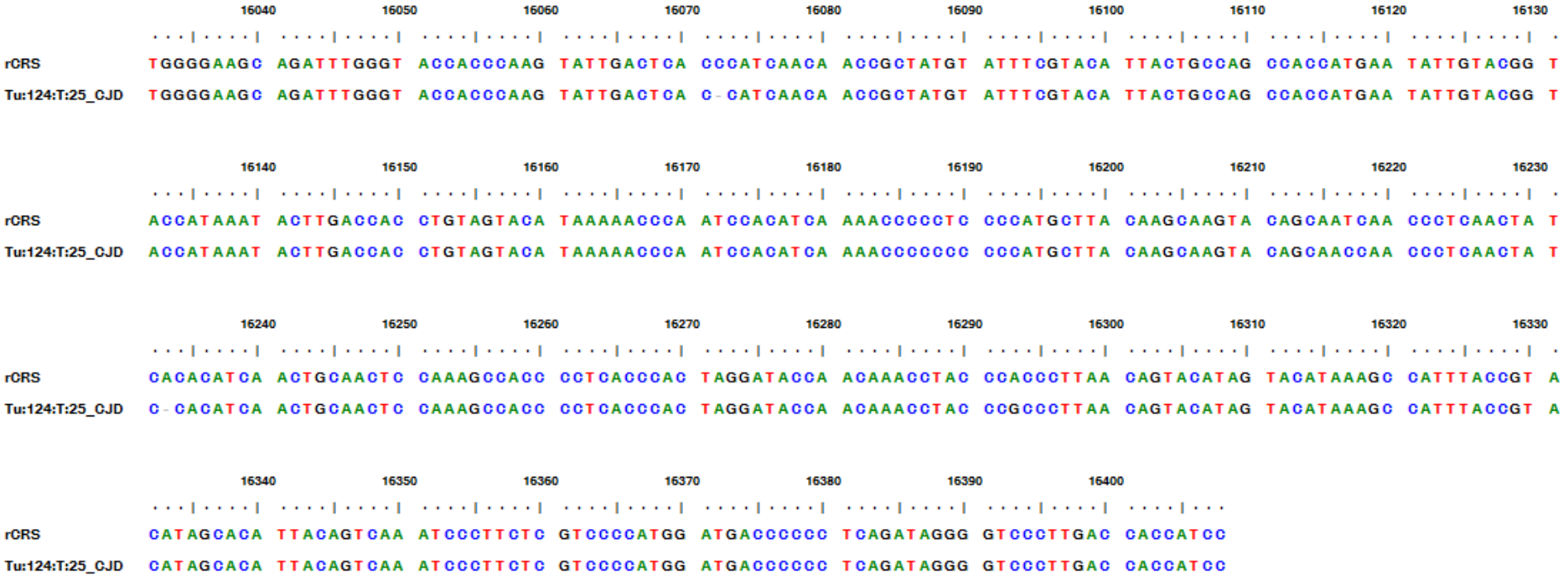


Sample ID: Tü:124: T:25 CJD Op.3 T.2 Pkt. 9
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: B2

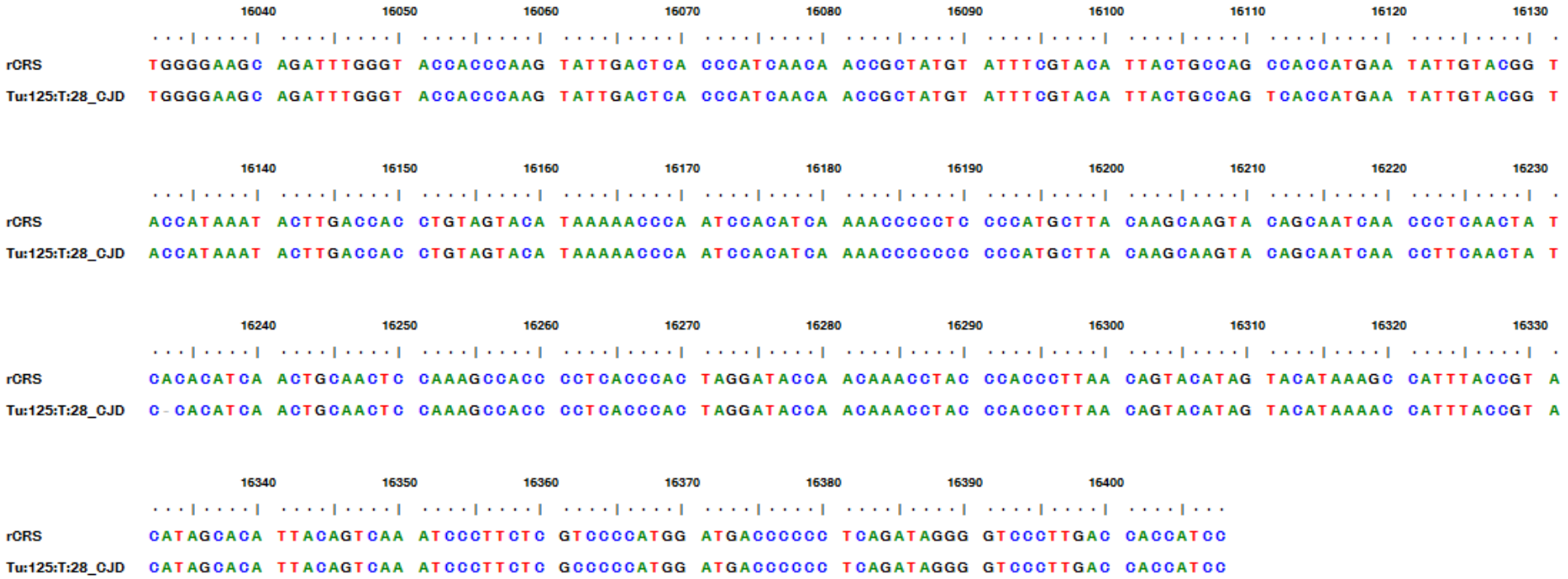


Sample ID: Tü:125: T:28 CJD Op. 3 T.2 U. 3 Pkt.11-12 H281
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: A2

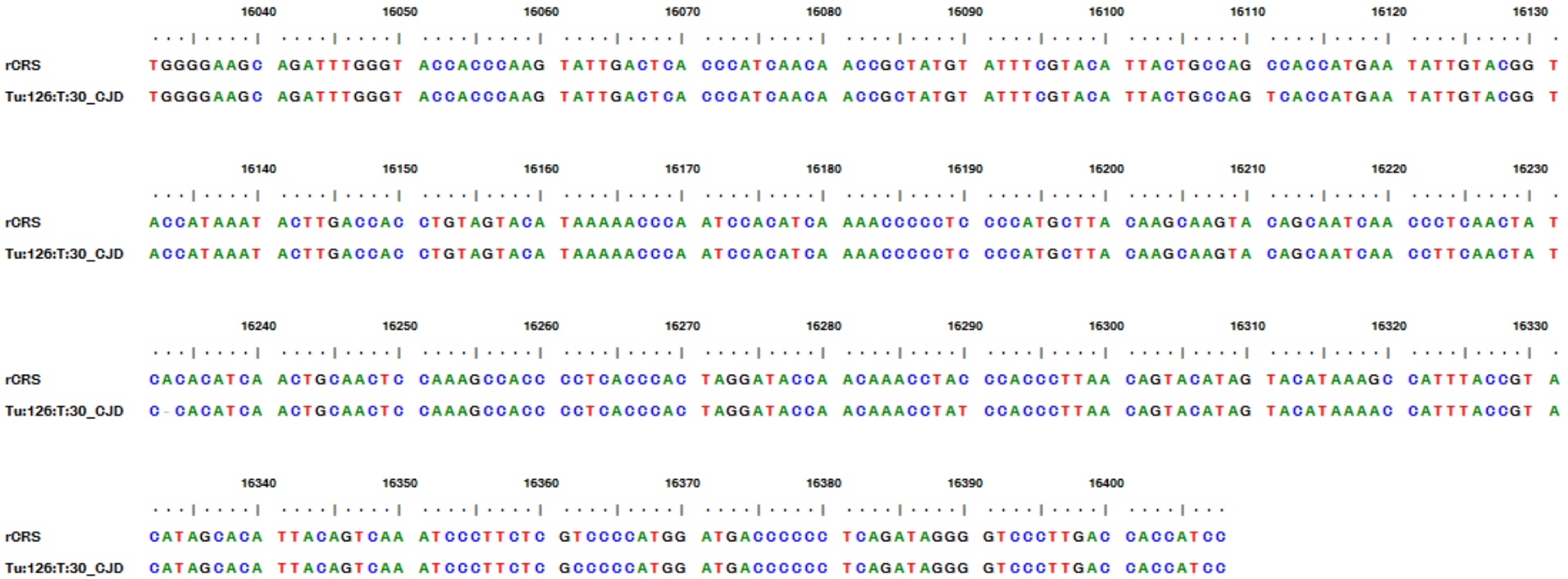


Sample ID: Tü:126: T:30 CJD Op.3 T.2 U.3 Pkt.5 H.120
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: A2

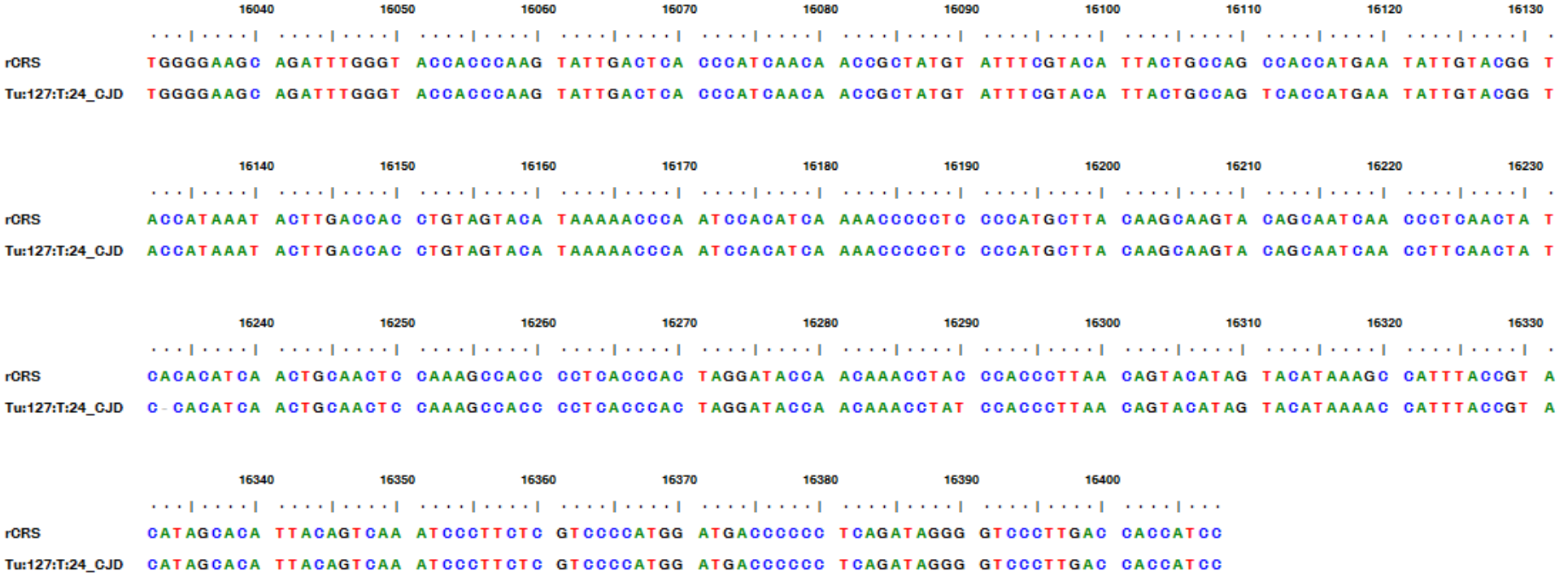


Sample ID: Tü:127: T:24 CJD Op.3 T.2 Pkt.8 Skull H.62
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
X/X	8/12	30/33.2	-/14	6/8	11/12/20	21/23

Haplogroup: A2

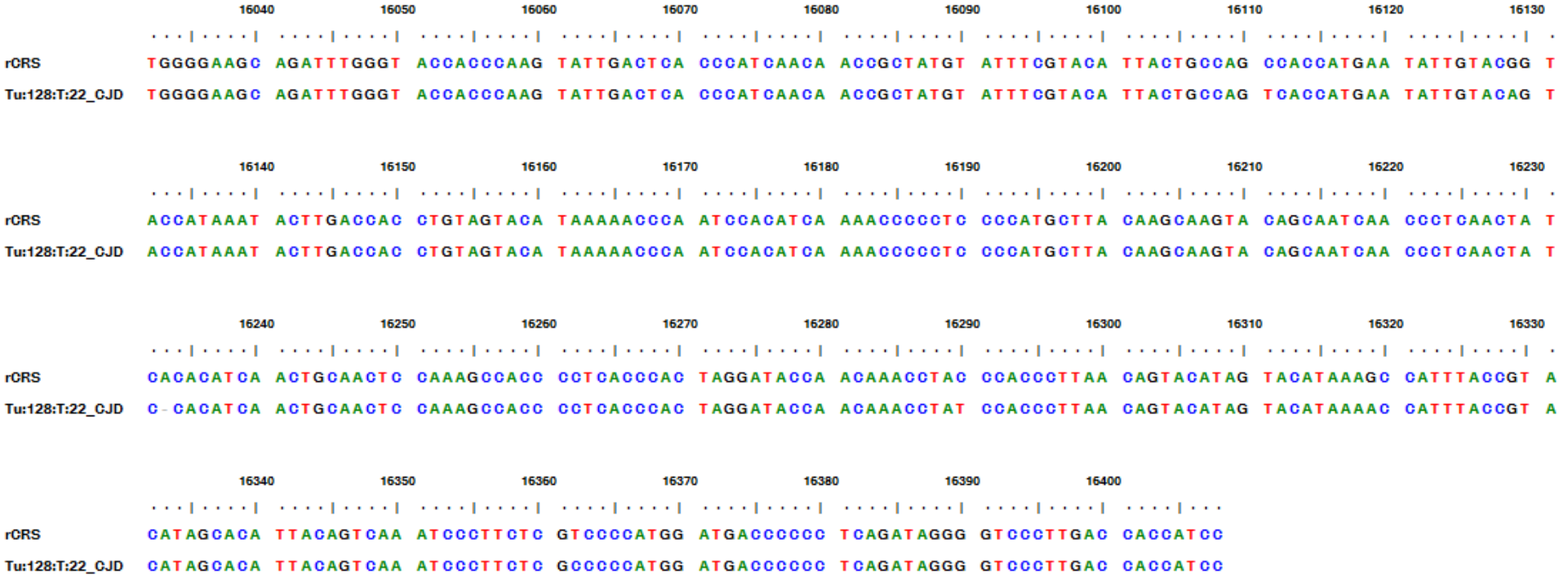


Sample ID: Tü:128: T:22 CJD Op.3 T.2 Pkt.6
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: A2

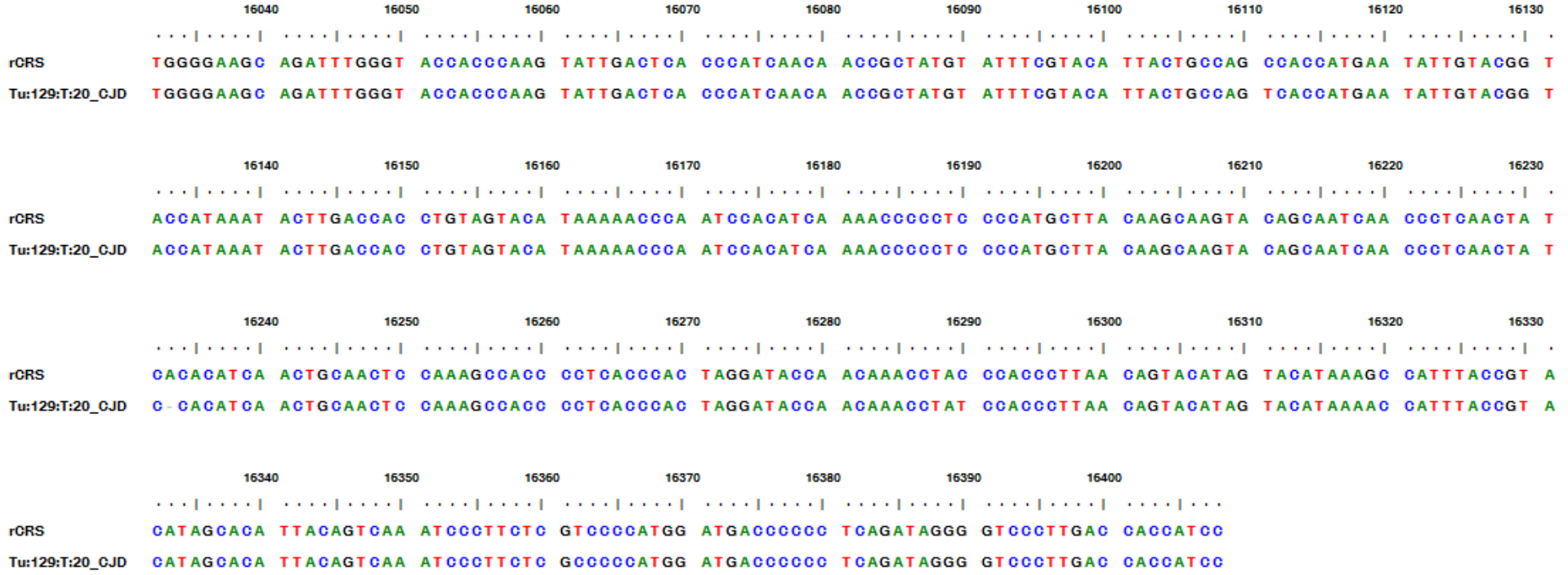


Sample ID: Tü:129: T:20 CJD Op.3 T.2 U. 3 Pkt.4
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: A2



Sample ID: Tü:130: T:31 CJD Op.3 T.16 Skull 11- 3570
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: No Sequence

Sample ID: Tü:131: T :41 CJD Op.3 T.16 Skull 13- 3431
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: No Sequence

Sample ID: Tü:132: T:40 CJD Op.3 T.16 No-No 2Y10
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: No Sequence

Sample ID: Tü:133: T:33 CJD Op.3 T.16 Skull 3- 3621
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: No Sequence

Sample ID: Tü:134: T:32 CJD Op.3 T.16 Skull 14- 3570/3698
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

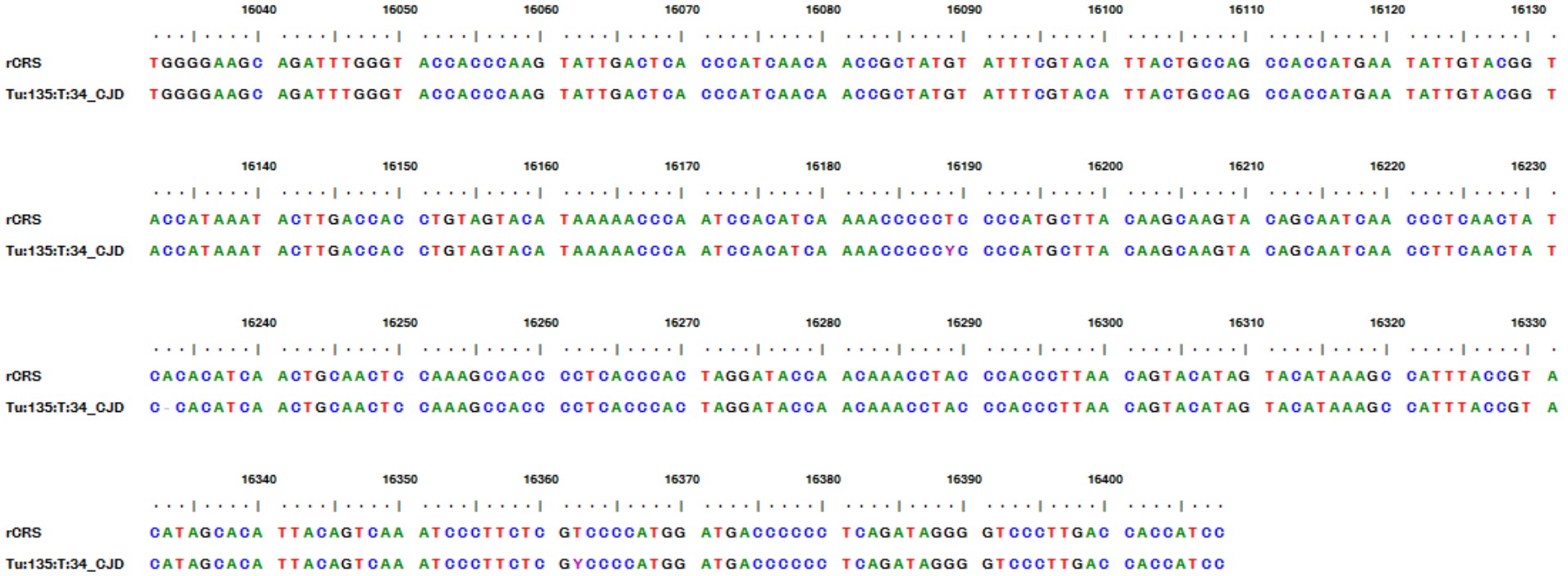
Haplogroup: No Sequence

Sample ID: Tü:135: T:34 CJD Op.3 T.16 Skull 17- 3794
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: D4b2a2a



Sample ID: Tü:136: T:39 CJD Op.3 T.16 Skull 1- 3170
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: No Sequence

Sample ID: Tü:137: T:37 CJD Op.3 T.16 H.191- 3456
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

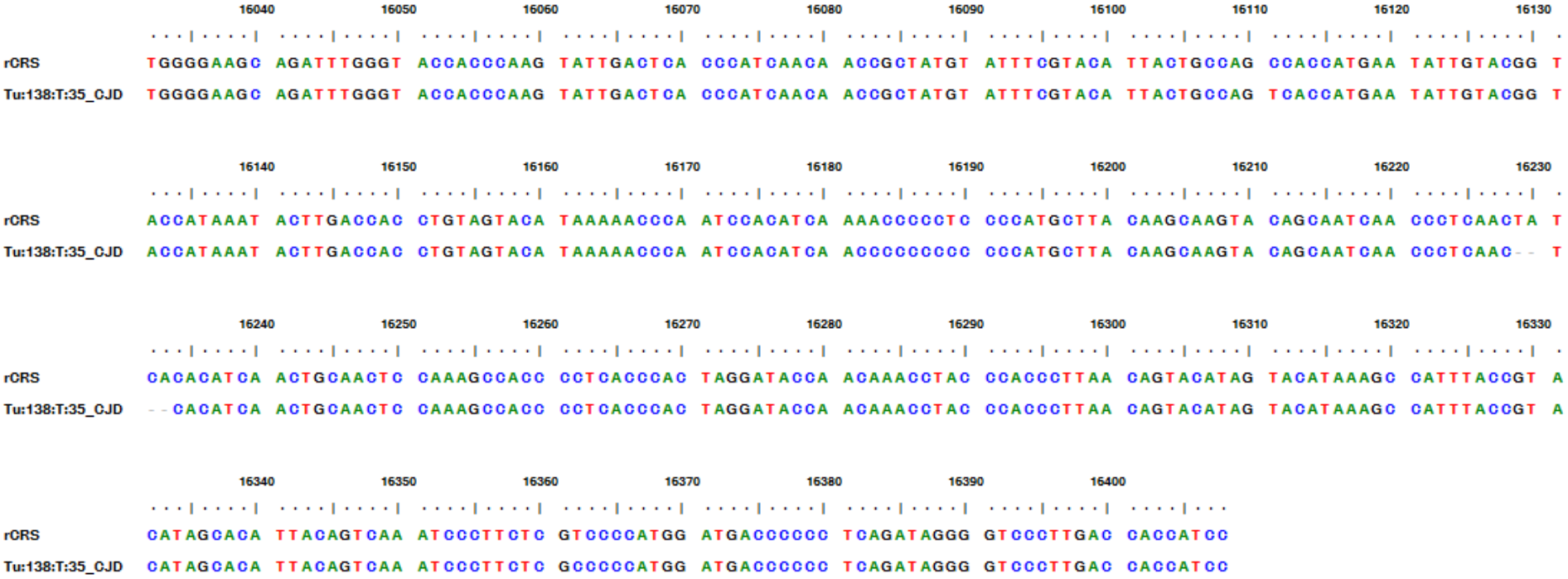
Haplogroup: No Sequence

Sample ID: Tü:138: T:35 CJD Op.3 T.16 Skull 7- 3781
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: B2a

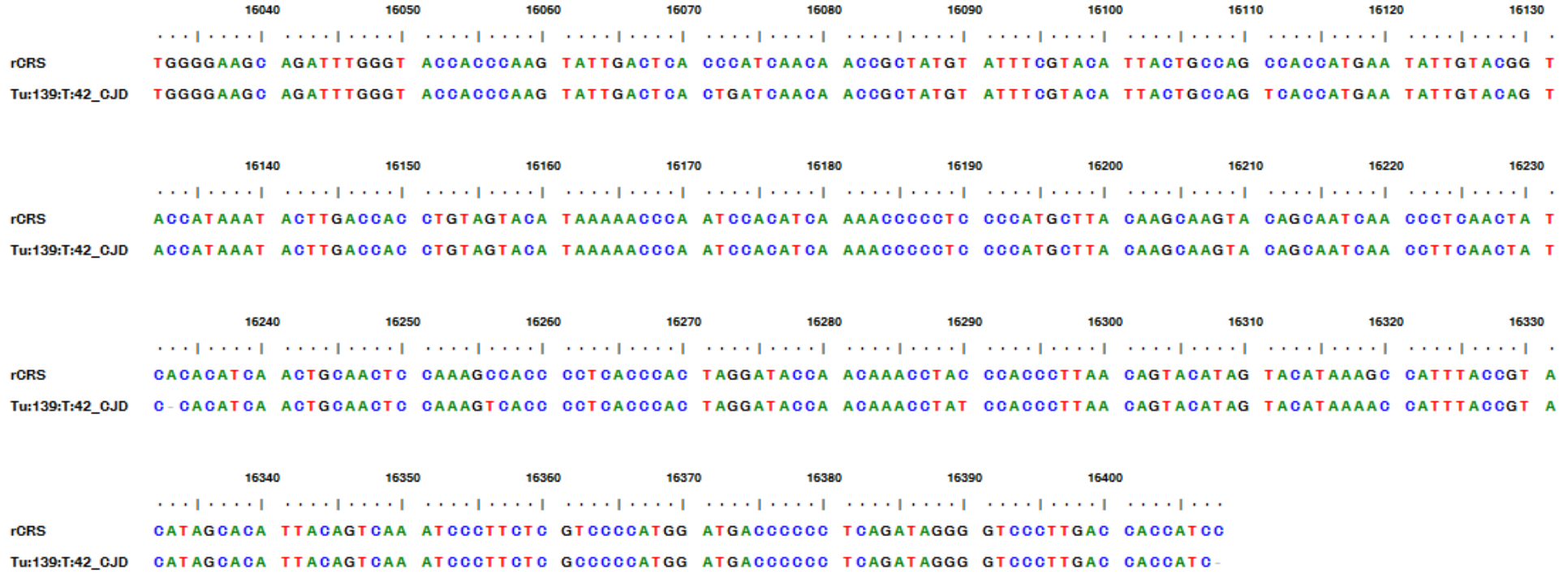


Sample ID: Tü:139: T:42 CJD Op.3 T.16 Skull 20- 3141
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: A2

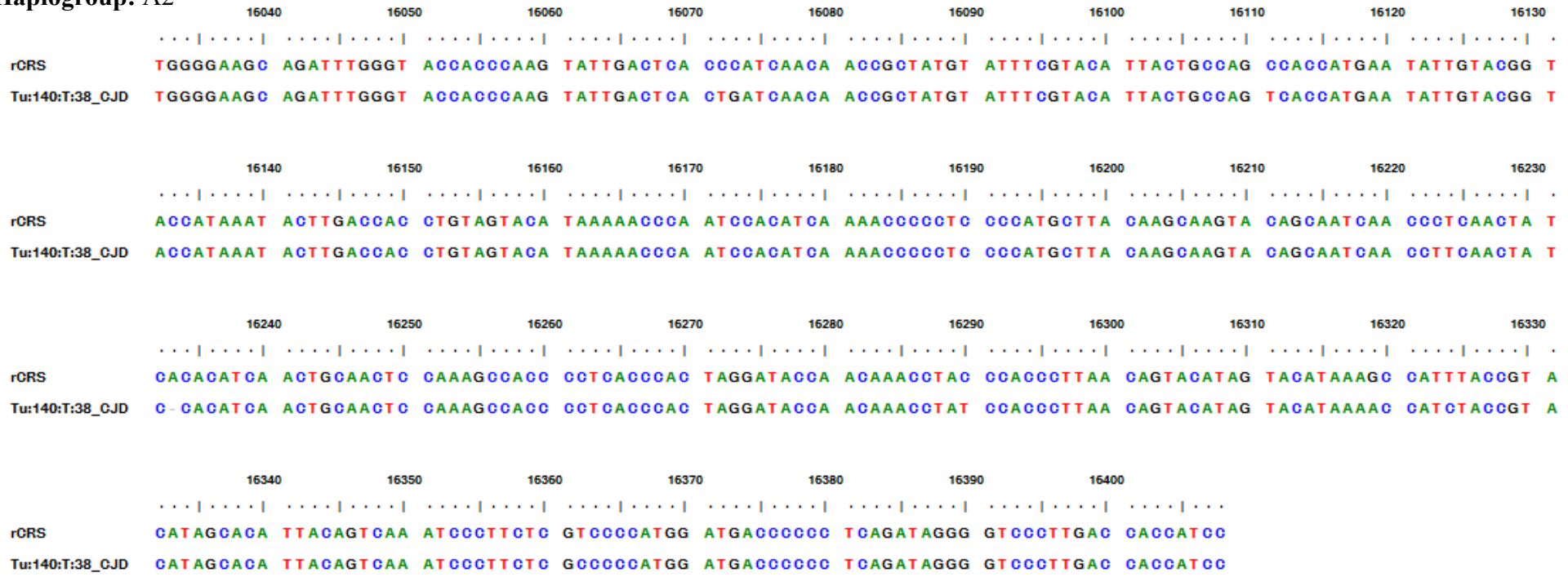


Sample ID: Tü:140: T:38 CJD Op.3 T.16 Skull 16- 3629
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: A2



Sample ID: Tü:141: T:36 CJD Op.3 T.16 Skull 10- 3505
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

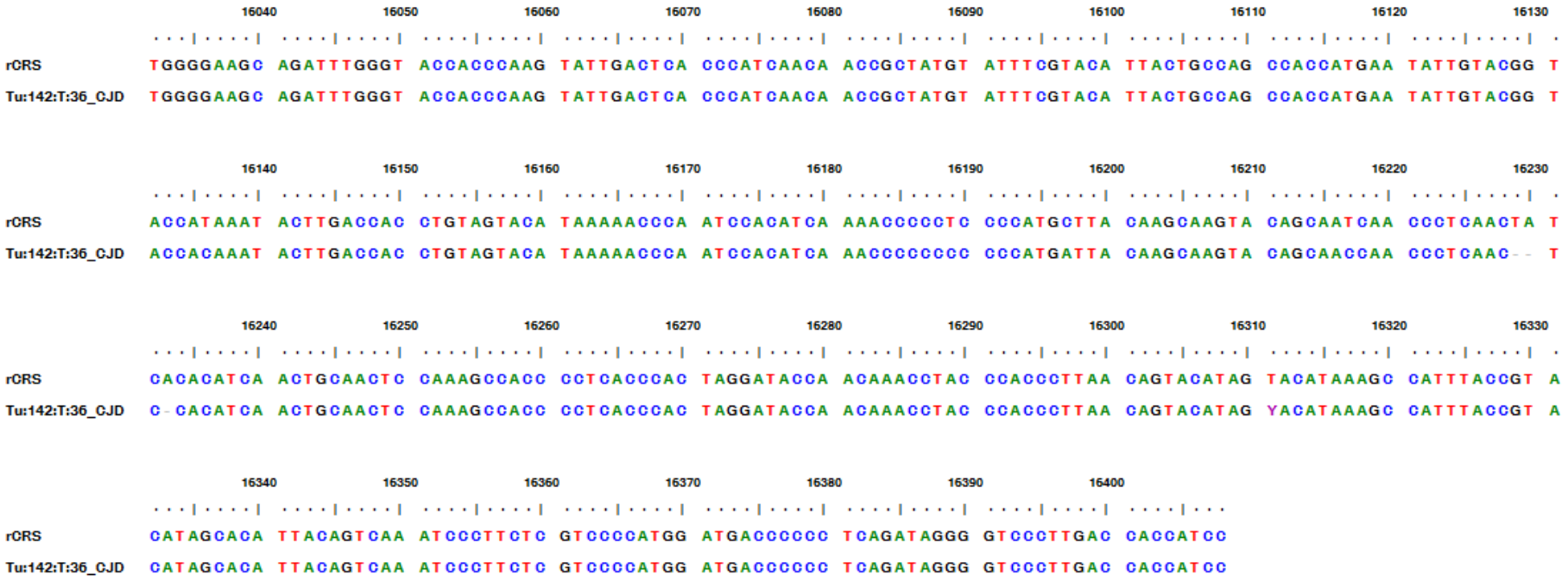
Haplogroup: No Sequence

Sample ID: Tü:142: T:54 PG-PDB L-20 K17 N16
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: B2i1



Sample ID: Tü:143: T:55 PG-PDB L-20 J17 N22
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

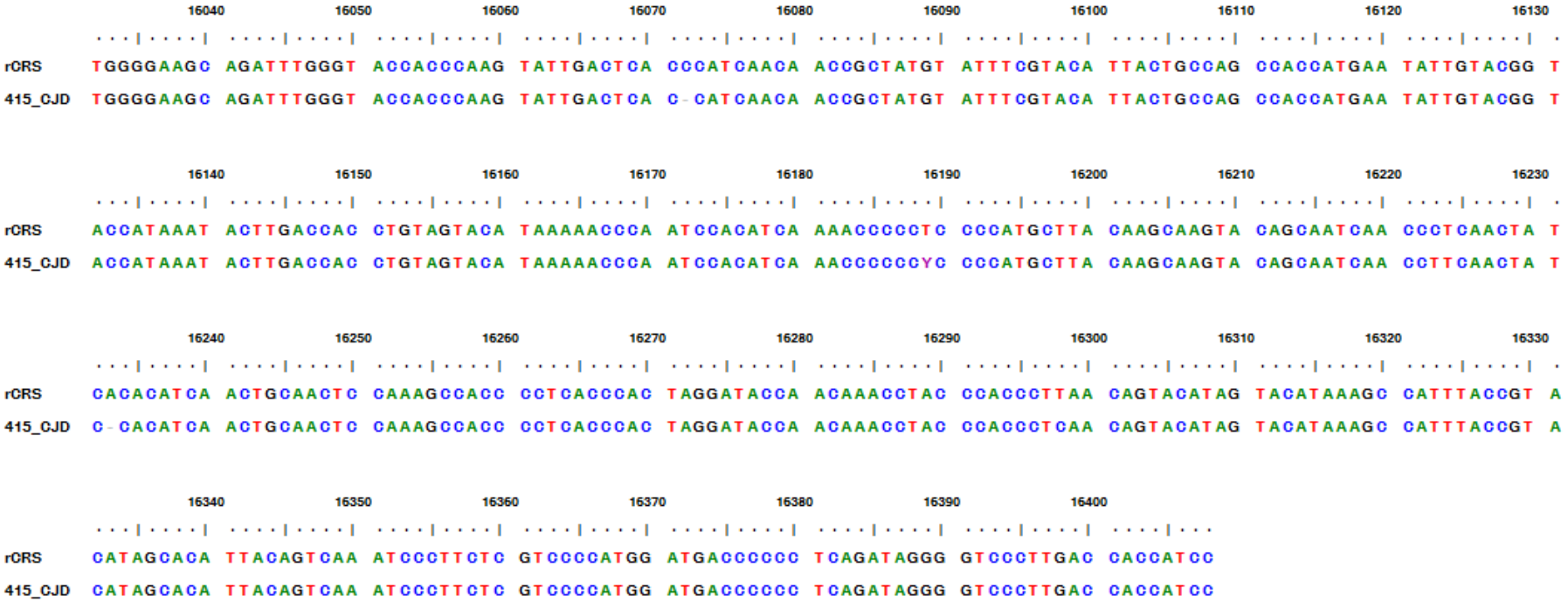
Haplogroup: No Sequence

Sample ID: 415: T:3 CJD Op. 7 R 15 Ind. 415
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: M8

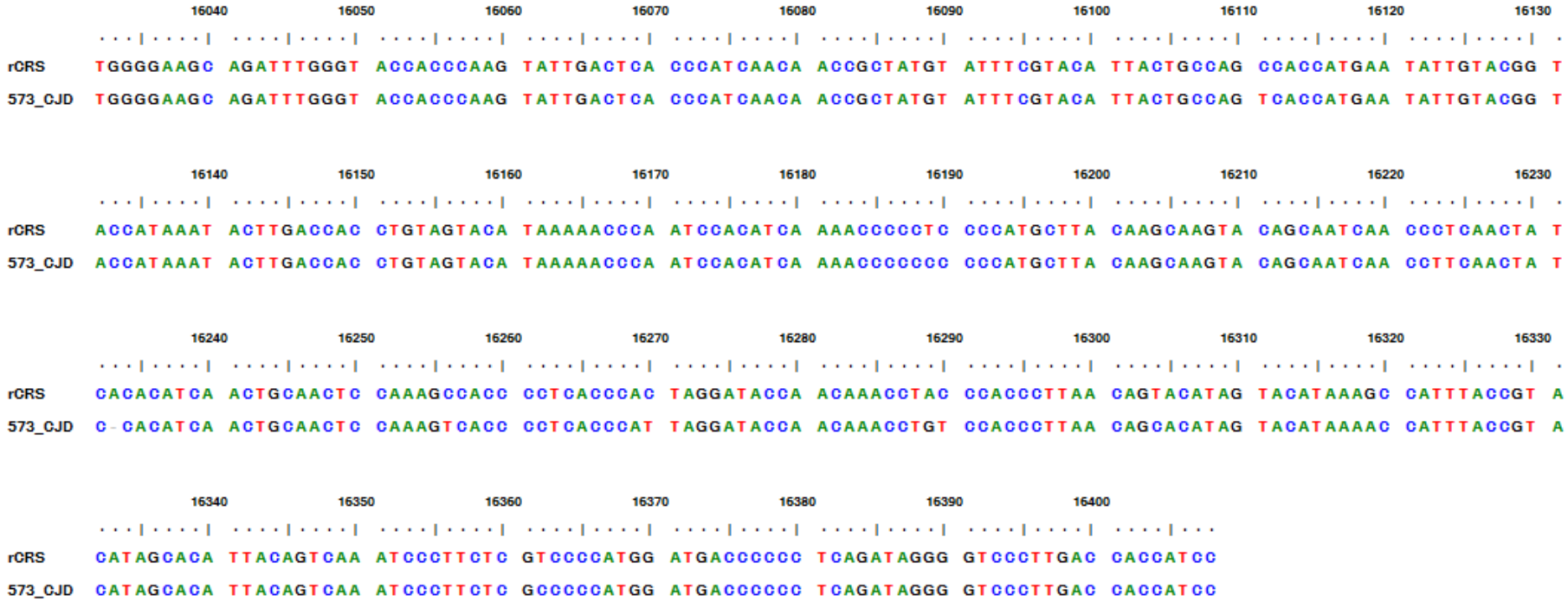


Sample ID: 573 CJD Op. 31-95 P.H.13 Bag # 573
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: A2

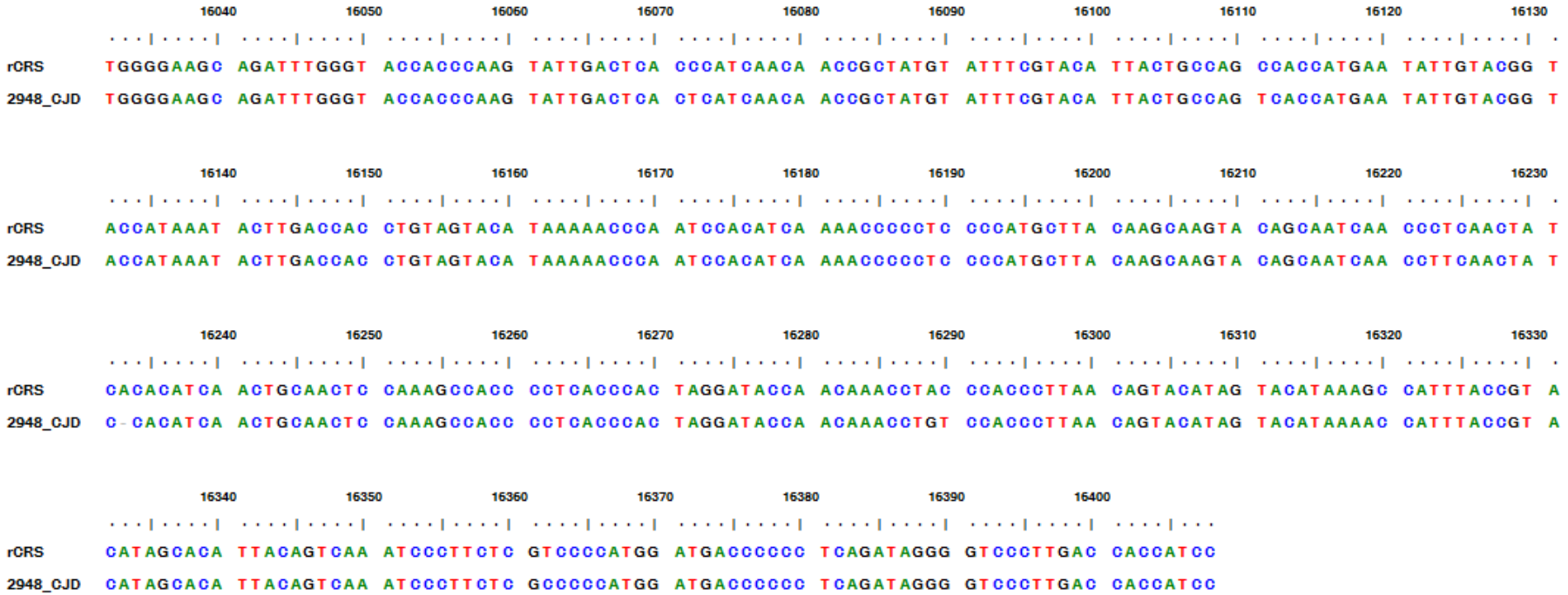


Sample ID: 2948: CJD Op. 3 P.H. 88 2948
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: A2

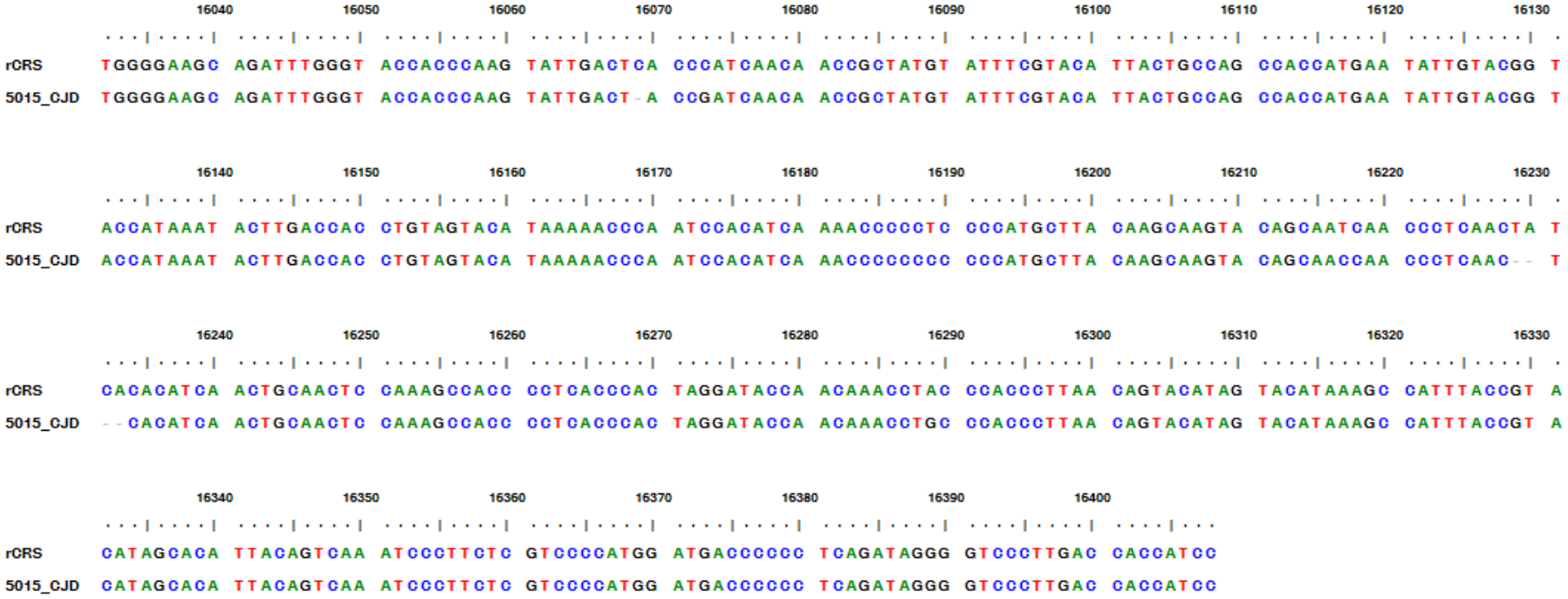


Sample ID: 5015: CJD Op. 3
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: B2

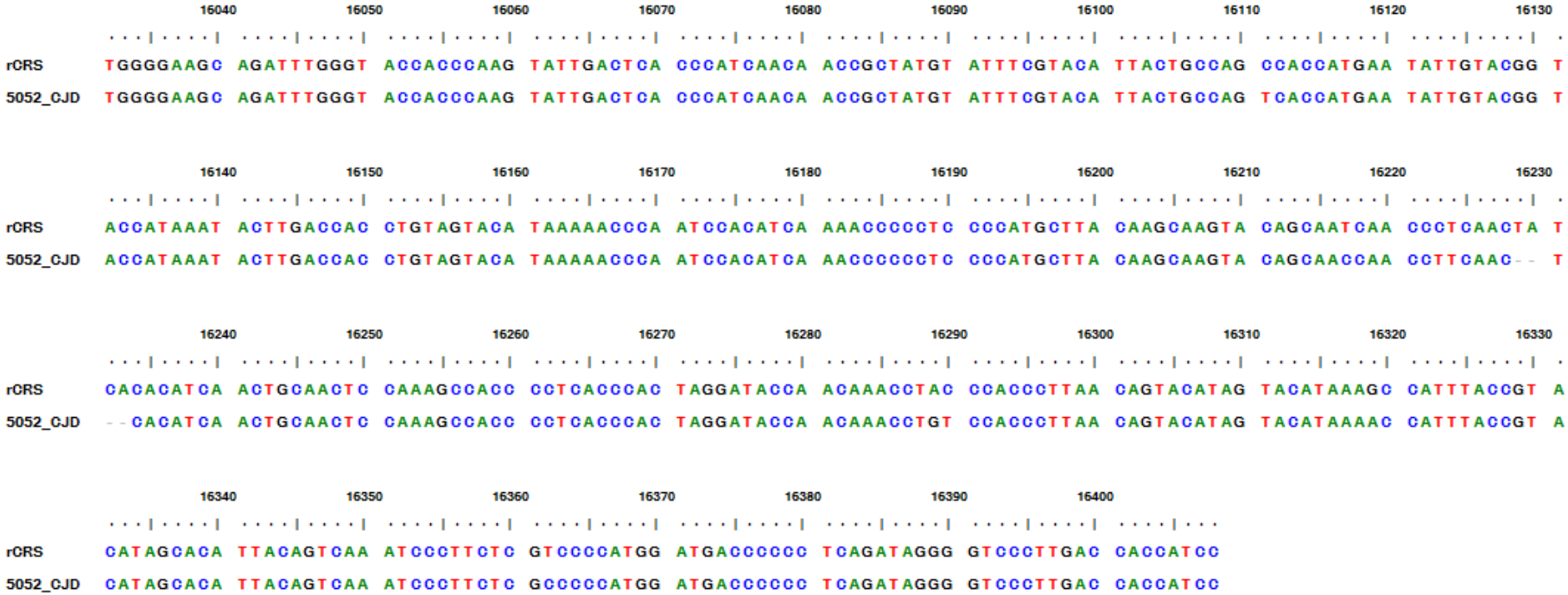


Sample ID: 5052: CJD Op.3 P.H. 95 5052
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: A2

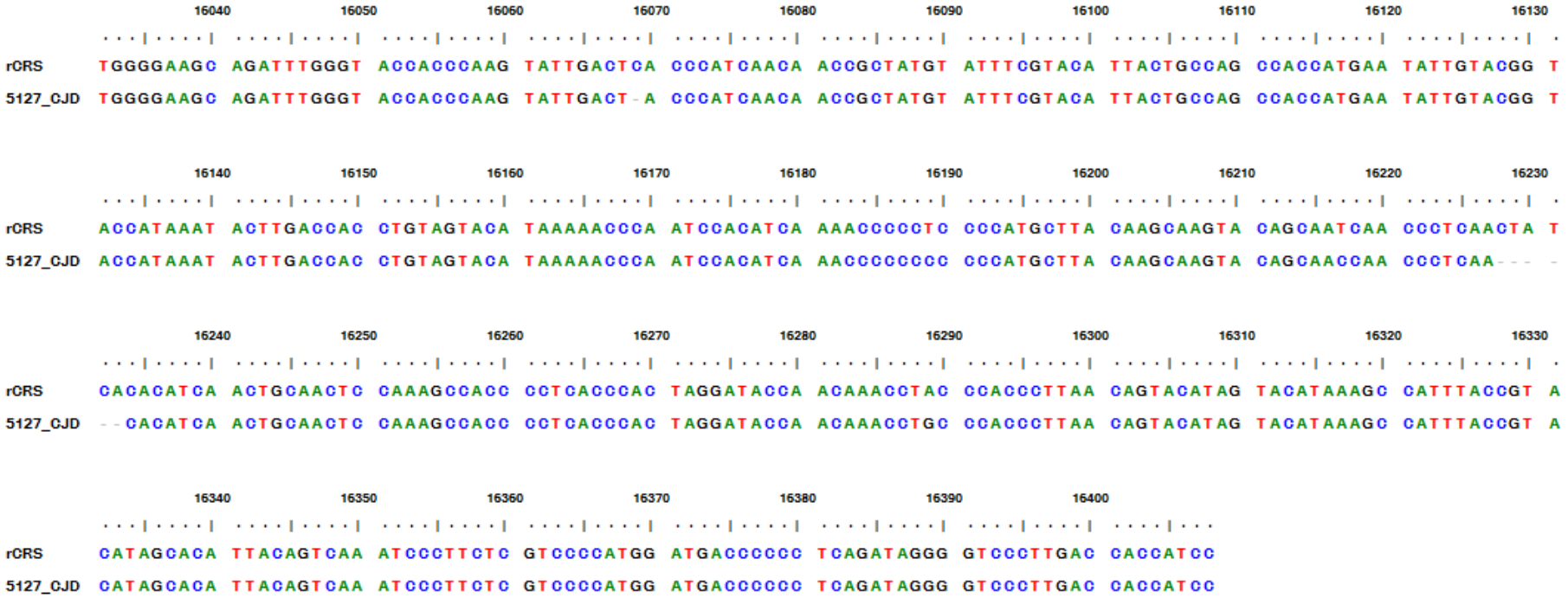


Sample ID: 5127: CJD Op. 3 P.H. 94 5127
Morphological sex: Ø
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: B2

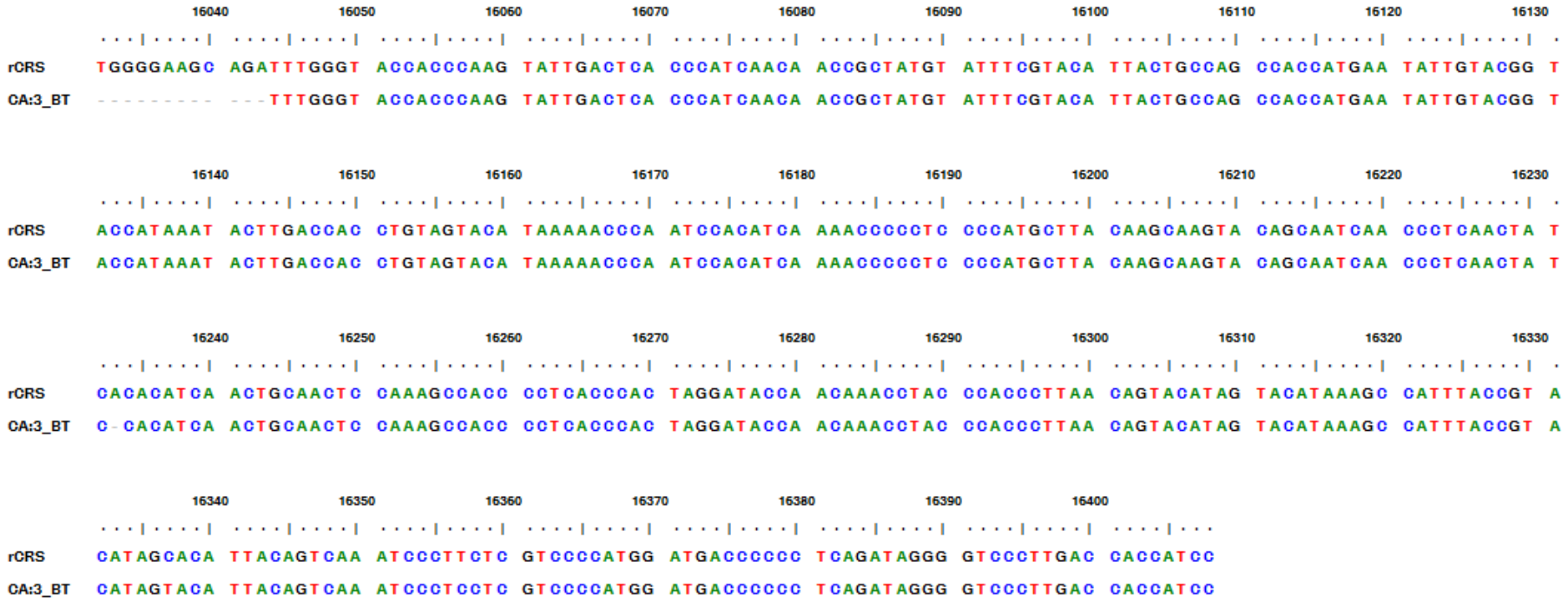


Sample ID: CA:3_BT CA-3 burial 6H
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: H1af

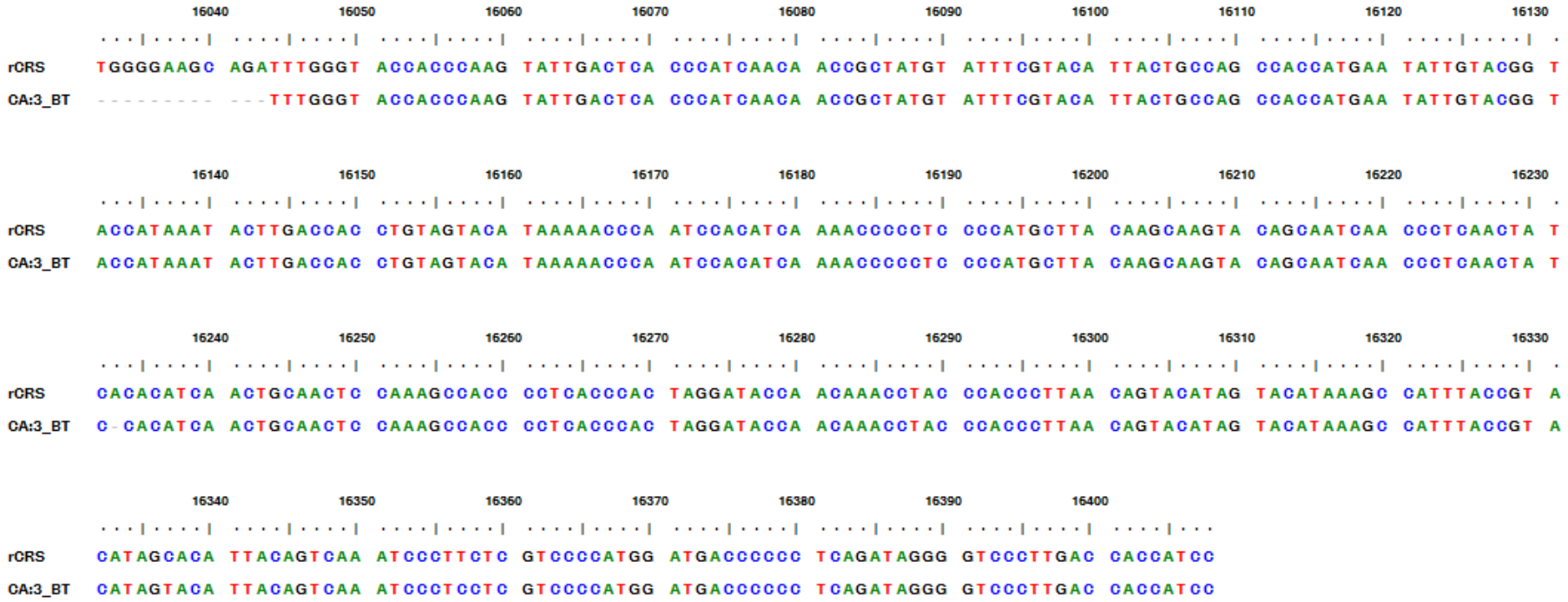


Sample ID: CA:3_BT CA-3 burial 6H
Region: America
Subregion: Central America
Country: Panama
Archaeological site: Cerro Juan Díaz

Genetic profile: Heptaplex

Amelogenin	D13S317	D21S11	D18S51	TH01	D5S818	FGA
-/-	-/-	-/-	-/-	-/-	-/-	-/-

Haplogroup: H1af



CURRICULUM VITAE

Mélida Inés Núñez

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Education	Master degree in Biology with emphasis on Genetic and Molecular Biology. University of Costa Rica, San José, Costa Rica. 2012. Seminar Workshop on Bioinformatics and Computational Biology. Earth University, Costa Rica. 2010. Diplomaed of Human Genetic. Medicine Faculty at University of Panama. 2006. Bachelor in Biology oriented in Microbiology and Parasitology. University of Panama. 2005.
Scholarships	German Academic Exchange Service (DAAD) Scholarship (2016- 2020). German Academic Exchange Service (DAAD) Scholarship (2008- 2011).
Professional Experience	**Smithsonian Tropical Research Institute (STRI), Molecular Biology and Evolution section** Barcoding technician. April 2014- 2015 **Genetic Specialized Center (CEGEN), Autonomous University of Chiriquí-Panama** Technician Analyst. March 2012-2013 **Smithsonian Tropical Research Institute (STRI), Molecular Biology and Evolution section** Intern in the project Barcoding of Birds and amphibians. Oct.2007-Dic.2007. Volunteer in the Molecular Biology and Evolution Laboratories. February 2006-2007. **Institute of DNA and the Human Genome** Research Assistant. March 2002-2004

Teaching (Seminar)

Summer Semester 2018. Genetics of populations. University of Göttingen, Germany

Supervision of lab work in master degree

Identification of Animal Species from Skeletal Remains of the Bronze Age Lichtenstein Cave by Madlin Michehl. University of Göttingen, Germany. 2018.

Research on Degraded DNA of 3,000-Year-Old Skeletal Remains of Horses of the Bronze Age Lichtenstein Cave by Lisa Hirsch. University of Göttingen, Germany. 2017-2018.

Academic activities

Personal Collaboration in the experimental design and statistical analysis in the following theses:

Germination: The Initial Stages in the Trichoderma virens - Plant Interaction by Fernando Sasso. Technion - Israel Institute of Technology, Israel. 2019.

Genetic characterization of introduced nile tilapia (*Oreochormis niloticus*) in Panama by Angelica Allard-Guerra. University of Panama. 2017.

Taxonomic re-assessment *of Idotea ochotensis* Brandt, 1851 (Crustacea, Isopoda, *Idoteidae*) species complex by Lovely Alvear. University of Hokkaido, Japan. 2016.

Muscle regeneration after myonecrosis induced by *Bothrops asper* venom: assessment of microvascular damage and apoptosis of myogenic cells by Rosario Hernández. University of Costa Rica. 2011.

M.I.N.C

15.10.2021