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Mitochondrial DNA Diversity of the Nangan Islanders Living in the Mazu Archipelago of the Taiwan Strait

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Abstract

This study investigates the genetic relationship of the Mazu peoples on the east coast of China in the Taiwan Strait. Using partial and complete mitochondrial DNA (mtDNA) sequences, we compare Mazu with surrounding East Asia populations. Mazu shows no exclusive affinities with either Southeast or Northeast Asia. High genetic diversity and a very high number of exclusive haplogroups of various Asian origins suggest that Mazu resulted from a process of continuous resettlement that started when it first became an archipelago at the end of the last glacial maximum and that continued till the last century. As a result, genetic drift did not contribute to an exclusive Mazu profile. The structure of haplogroups that show signatures of the Neolithic era (N9a10a), or influx from Island Southeast Asia (F1a4a) suggest recent gene flows and Mazu relationship with it's pre-Neolithic era (presence of pre-E1a or R9/pre-F from Liangdao man) was not seen.

Keywords: Mazu Population, Mitochondrial DNA Inheritance, Haplotype sharing with Taiwan and surrounding East Asia populations.

Abbreviations: MSEA- Mainland Southeast Asia, TWIP- Taiwan Indigenous People, ISEA- Island Southeast Asia, MMD- Mismatch Distribution.

Introduction

NanGan island, in the Taiwan Strait of the China Sea, is part of a 36 island and islets archipelago. The main islands are not all inhabited and comprise Hsijiu, Tungjiu, Nangan, Beigan, Gaudeng, Dachiu, Hsiaochiu, Liangdau, Shiyin, and Tungyin. Along with Penghu and Kinmen islands further south in the Taiwan Strait, the Mazu archipelago is a separate customs territory of Taiwan and is administrated by the Lienchiang County of Taiwan, (also termed Lianjiang, and often referred to Mazu County) (https://www.cia.gov/library/publications/the-world-factbook).

Following the establishment of garrisons on some islands, the population rapidly numbered to 17000 [1]. Like urban people in Taiwan, most natives of Mazu believe they share their origin with Northern Fujian and Fuzhou peoples who migrated to Taiwan in the last 400 years. The finding of large shell mounds with radio-carbon dating ranging from 8000 to 4000 years BP showed that a hunter-gatherer culture, with coastal foraging lifestyle, inhabited Mazu Islands [2]. More recently, a study combining ancient DNA (aDNA) from two 8000 years BP human skeletons in Liang island (nearby island to Nangan; (**Figure 1**) and complete mtDNA genome sequences representing modern Taiwan indigenous and non-indigenous peoples showed these skeletons belonged to mitochondrial haplogroups E1 and R9/F and proposed they were ancestors of the Formosan indigenous peoples, predating Taiwan Neolithic era of demographic expansion 6,000 BP, and likely had been speakers of proto-Austronesian [3].

During the Yuan Dynasty at the beginning of the XIIIe century, fishermen from nearby Fujian and Zhejiang on the east coast of China used the islands for shelter while few eventually settled there permanently. But starting In the XVII century and during the entire length of the Qing Dynasty, the east coast of China became a very frequented maritime highway. Because of these successive events, fishermen, traders, sea nomads, and pirates may have successively contributed to displacing the first or former residents [2].

Present-day Mazu peoples use a Sinitic sub dialect spoken in the nearby Chinese city of Fuzhou. A minority of individuals with a sea-dwelling mode of living use different dialects thought to be related to Mainland Southeast Asia (MSEA) populations [4]. However, Mandarin Chinese has now become the official language. Because of its administrative relationship with Taiwan, and its pre-Neolithic heritage, the genetic diversity of the Mazu people is important to an understanding its genetic relationship with Taiwan Han (TwH), Taiwan Indigenous People (TWIP), Northeast Asia (NEA), East and Southeast Asia (EA and SEA), Mainland Southeast Asia (MSEA) and Island Southeast Asia (ISEA) [5-7]. In this study, Mitochondrial DNA (mtDNA) is used to characterize the genetic diversity and characterize the relationship of the Mazu peoples with Asian populations of distinct languages and cultures.

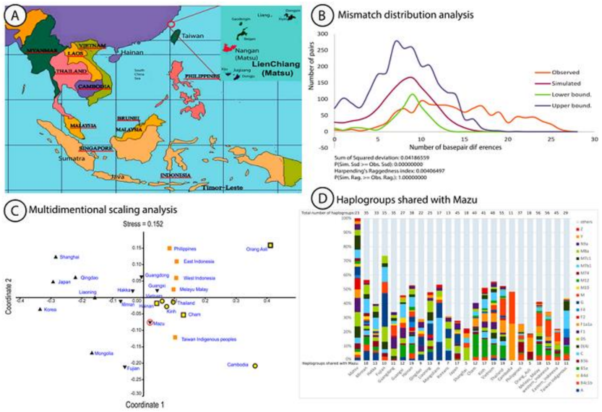

Figure 1: A) Map of Southeast Asia and the Mazu archipelago. B) Pairwise Mismatch Distribution (MMD) plots. The observed distribution (red) indicates the demographic history of Mazu with evidence of a demographic equilibrium. C) Multidimensional Scaling analysis (MDS) using FST statistic (Stress: 0.152). Yellow: Mainland Southeast Asia; Black: China; Orange: Island Southeast Asia. Squares: Austronesian Speakers; Triangles Sinitic (Upper triangles: North Asia; Inverted triangle South China); Circles: Austro-Asiatic; D) Proportions of Mazu maternal genetic material shared with other Asian populations. Identical colors correspond to identical haplogroups. Light blue represent all haplogroups not seen in Mazu.

Material and Method

A subset of 50 mouth swabs of unrelated Mazu individuals from Nangan island (Mazu) was analyzed by sequencing for mitochondrial DNA diversity using coding region (Nucleotide Positions (nps) 8000 to 9000 and nps 9800 to 10873), and the control region of the Hyper-Variable Segment II (HVSII) nps 16030 to 16410. This totaled to 2453 loci of which 116 were polymorphic. Ambiguous haplogroups assignments using the HaploGrep version 2 software were confirmed using further determination of pertinent SNPs of the coding region [7,8]. For the distribution analyses, the genetic data for current populations from North and South Asia, Southeast Asia and Mainland Southeast Asia were retrieved from published reports. Statistical analyses and pairwise genetic distances of Rst between different populations were carried out using the Arlequin software 3.1 and visualized using the MDS tool available in the PAST software [9,10]. the Network software [11].

Results and Discussion

Out of 38 exclusive mtDNA haplotypes observed among the 50 Mazu individuals, 29 haplogroups were seen only once. At a lower assignment level eight basal phylogenetic haplogroups lineages (D4, D5, F1, F2, G and M7) had a frequency greater than 5% and represented 64% of the total diversity. Among them, sub-types of D4, D5, F2 and G prevail in modern populations of NEA, while Sub-types of F1 (F1a1', F1a1a, F1a1c, F1a4a and F1c1a1) and M7 (M7c1', M7c1b2b and M7c1c2) are rarely seen in Northeast Asia and prevailed in SEA and MSEA where they likely originated [12,13]. M8a2'3, M10a1+16129, M12a1a1, M74. Other haplogroup that are common in MSEA were M8a2'3, M10a1+16129, M12a1a1, M74. B4d1 seen only once was unique in Mazu. Although Northeast Asian (Japan 77.8% and Liaoning 51.9%) and Taiwan Han (Minnan 55.6% and Hakka (51.9%) are the highest contributor of haplogroups to Mazu.

The specific relationship of Mazu with Taiwan was minimal. Using our raw data level of haplogroups assignment only haplogroups, B4c1b2a and F1a4a', showed similar patterns of distribution in insular East Asia, with low prevalence among Taiwan Han but common among Formosan indigenous people and the Philippines. Except for the low occurrence of F1c1a1 and N9a1'3 among Taiwan Han and Taiwan Pingpu none of the other Mazu haplogroups showed prevalence in Taiwan.

The heterogeneous profile described above was supported by a high haplogroups diversity (h) (h=0.988; SE 0.003) and a nucleotide diversity (average over loci) of 0.005763 +/- 0.002916. Interestingly the tests of neutrality of Tajima's D and Fu's Fs (Schneider et al., 2000) [9] showed negative values (D=-1.700; p=0.019 and Fs=-24.32 p<0.0001 respectively), suggesting population expansion. However, the high haplogroup diversity, the high number of single haplogroups presume a relatively high number of unique nucleotide variations, are indicative of an ethnically heterogeneous population, and are the result of numerous and separate gene flow from various regions of East Asia that likely started in the Neolithic era until the present days [14,15].

In support to this observation, the mismatch distribution analysis (Figure 1B) showed a flat and wide uni-modal observed curve (in red in Figure 1B) between 5 and 25 base-pair differences (bp) and a bp mean of 14.5. In contrast with Tajima's D and Fu's Fs tests, we here reject the hypothesis of sudden expansion, this is shown by a significant Sum of Squared Deviation (SSD) test (SSD=0.042. p<0.0001), and a low value of Harpending's raggedness (r=0.0041, p=0.95) (Figure 1 B) indicating a robust analysis and are the result of mixtures of groups of many Asian origins rather than sudden population expansion [16].

Multidimensional Scaling analysis using FST statistic, a measure of population substructure comparisons (Figure 1C), was used to test the matrilineal spatial genetic distribution between Mazu and other Asian populations (Figure 1C). The distribution plot (stress: 0.152) differentiated clearly NEA and SEA Chinese groups (Black) from ISEA groups (Orange) and MSEA (Yellow). These ethnic clusters also associated well with the distribution of Sinitic, Austronesian, and Austroasiatic languages (triangles, squares, and circles respectively). Low FST values were seen between Mazu and Hainan, or Mazu and Vietnam, however, both FST values were significant (FST 0.02, p< 0.0001, and FST 0.007, p=0.72 respectively) suggesting distant relationships. Interestingly, all FST values between Mazu and other populations of NEA, SEA, MSEA, ISEA, Taiwan Han and Taiwan Indigenous people showed significant FST values (p< 0.001) (data not shown) or relationship of the past. These observations support the very high level of genetic differentiation described above, and the likely probability that Mazu was never settled for a long time by the same group.

To this date, no archaeological traces indicating the passage of anatomically modern humans in Mazu during the Pleistocene (40,000 to pre-Holocene) [3]. The first incursion modern human in the Mazu archipelago is dated in early Holocene on Liang island (herein referred to as Mazu) most likely already an Island by 8,000 YBP. Marking this period, ancient human mtDNA remains have revealed haplogroups R9/pre-F and a precursor of E1a, both of southeast China origin [3].

These haplogroups have no descendant ramifications, but sister descendants seen among Austronesian speakers of Taiwan and the ISEA. To clarify the genetic relationships of modern Mazu with a pre-Neolithic past, we collected mtDNA genome data from 50 unrelated Mazu individuals. When compared with other populations of East Asia, the haplogroups profile showed population differentiation to an extent not expected in present-day East Asians Islanders, and revealed a complex population history.

The mid-Neolithic period to the start of the first millennium of our era went through the start of food globalization and the spread of northern East Asians toward southern East Asia which affected the genetic ancestry of southern China [4].

Similarly, movements of coastal groups such as migrants, traders, Pirates, and sea nomads from MSEA to North Asia and back suggests that gene flow also played an important role in the prehistorically genetic makeup of coastal East Asia and Mazu. These population movements continue throughout this era, up to the last century, with Mazu archipelago becoming a temporary refuge to local fishermen. The introduction of more recent settlers and the establishment of garrison from Taiwan in the last century after Mazu became administrated by Taiwan resulted in a major increase of the Mazu population.

The present-day genetic variation is characterized by a very high polymorphism, with numerous mtDNA lineages (from MSEA, NEA, SEA, and Taiwan Han). None of these phylogenetic lineages are deeply related by descent, indicating a shallow to no evolutionary time and recent series of temporary settlements of Mazu.

In general, all these people signed their passage into the genetic structure of Mazu with a slightly more marked Northeast Asian than Southeast Asian/MSEA influence, with little gene flow from the Taiwan Indigenous people. Finally, No traces of descent of R9/pre-F and pre-E1a from the original pre-Neolithic settlers were found in the extant population.

Summary

In summary, the maternal inter-population comparisons reveal that the Mazu people have a similar affinity with northern Asian populations (Chinese, Japan, Korea) and the Southern Asian Population (SEA and MSEA; 48%). Affinities with Austronesian speaking groups were rare. Bar-chart of haplogroups sharing suggested important multi-regional gene flows and along with the MDS, analysis supported a pattern of admixture reflecting the complex settlement process of Coastal East China. All traces of descent of R9/pre-F and pre-E1a from the original pre-Neolithic settlers were diluted in the extant population.

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Competing Interests

No benefits in any form have been received or will be received from a commercial party related directly or indirectly to the subject of this article. The authors have declared that no competing interests exist.

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