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Yu Dong
Shandong University

Chunxiang Li
Jilin University

Fengshi Luan
Shandong University

Zhenguang Li
Shandong Provincial Institute of Cultural Relics and Archaeology

Hongjie Li
Jilin University

See next page for additional authors

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Authors

Yu Dong, Chunxiang Li, Fengshi Luan, Zhenguang Li, Hongjie Li, Yinqiu Cui, Hui Zhou, and Ripan S. Malhi

Low Mitochondrial DNA Diversity in an Ancient Population from China: Insight into Social Organization at the Fujia Site

Yu Dong^{1,2*}, Chunxiang Li³, Fengshi Luan¹, Zhenguang Li⁴, Hongjie Li³, Yinqiu Cui^{2,3}, Hui Zhou³, Ripan S Malhi^{2,5}

¹Department of Archaeology, Shandong University, Jinan, Shandong 250100, China

²Department of Anthropology, University of Illinois at Urbana-Champaign, Urbana, IL 61801, USA

³College of Life Science, Jilin University, Changchun, Jilin 130012, China

⁴Shandong Provincial Institute of Cultural Relics and Archaeology, Jinan, Shandong 250012, China

⁵Institute for Genomic Biology, University of Illinois at Urbana-Champaign, Urbana, IL 61801, USA

*Correspondence to Yu Dong, School of History and Culture, Shandong University, Jinan, Shandong Prov. 250100, P. R. China. E-mail: yudong@sdu.edu.cn.

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Abstract

To gain insight into the social organization of a population associated with the Dawenkou period, ancient DNA analysis of 18 individuals from human remains from Fujia site,

Shandong Province, China was completed. Directly radiocarbon dated to 4800–4500 cal BP, the Fujia site is assumed to be associated with a transitional phase from matrilineal clans to patrilineal monogamous families. Our results reveal a low mitochondrial DNA diversity from the site and population. Combined with Y-chromosome data, the pattern observed at the Fujia site is most consistent with a matrilineal community. The patterns also suggest that the bond of marriage were de-emphasized compared to the bonds of descent at Fujia.

Introduction

Reconstructing aspects of social organization, including kinship system, post-marital residence patterns, labor division, wealth and status, is of great interest to archaeologists (Costin and Hagstrum 1995; Kolb and Snead 1997; Allen et al. 2008; Peterson and Shelach 2012). Kinship in humans is more than biological relatedness: it is also socially constructed, and kinship systems vary widely among cultures (Carsten 2000). Gamble (2008) argues that the extended and socially constructed kinship system distinguishes us from other primates, and facilitated the early modern human global diaspora. While one can learn a lot about the social organization of ancient Chinese societies with the help of ancient literature and early writings on oracle bones and bronze wares (e.g. von Falkenhausen 2006), little is known about prehistoric kinship systems because they are difficult to reconstruct with archaeological evidence (Jiao 2001). In this article, we analyze mitochondrial DNA (mtDNA) and Y-chromosomal DNA diversity in a late Neolithic community in Shandong Province, China in order to reconstruct the social organization at this community. Considering the paucity of empirical data on social organization in Neolithic China, we focus our discussion and analysis on how DNA from uniparental systems can be used to infer kinship systems in ancient populations.

Several approaches were used in an attempt to investigate prehistoric kinship practices. Ember (1973) and Divale (1977) used cross-cultural ethnographic analysis to propose that based on the living floor area of the average house, one could predict post-marital residence patterns, with matrilocal societies having a larger living floor area than patrilocal ones. Zhang (1985) analyzed the burial arrangements of the Yuanjunmiao

cemetery, Yangshao Culture (7000–5000 BP) and noted that juvenile females had more elaborate burials than males. From this he argued that the community was organized in matrilineal clans and was probably also matriarchal. Gao and Lee (1993) performed craniometric measurements of human remains at the Shijia site, Yangshao Culture, and found individuals are more closely related within one multiple burial than among different burials, hence they argue that individuals found in the same multiple burial are brothers and sisters. Because female burials were underrepresented in this site, the authors rejected the possibility of a matrilocal and matriarchal community (Chen 1990; Keightley 1999). Stojanowski and Schillaci (2006) provided an extensive review on how biodistance analysis based on morphology could provide insights on kinship and post-marital residence.

Inference of kinship and social organization can also be obtained from isotopic and ancient DNA analysis. Bentley et al. (2005) compared the strontium isotopic ratios of males and females from a prehistoric site in Thailand and argued that the community was likely matrilocal because females had more restricted isotopic variance than males, suggesting more restricted geographic origins of females. Haak et al. (2008) combined strontium isotope and ancient DNA analysis and demonstrated that a Late Stone Age society in Germany was exogamous and patrilocal.

Many Chinese archaeologists assume that early Chinese Neolithic societies were organized in matrilineal, matrilocal clans, and gradually evolved to patrilineal patrilocal monogamous families, with patrilineal clans as a transitional stage. This model of the evolution of social organization reflects the influence of Engels (1884) in China. The

terms matrilineal, matrilocal, and matriarchal are used relatively synonymous among Chinese archaeologists, and the assumption is that a matrilineal society is always a matrilocal and matriarchal one, and vice versa (e.g., Wang 1982; Zhang 1985; Zhang 2000; Zhang 2003). However, matrilineal and matrilocal do not always go hand in hand (Schneider and Gough 1961), and matriarchal societies are extremely rare (Schneider and Gough 1961; Murdock 1967; Hua 2001).

During the first well recorded dynasty in China--Shang, both the royal family and ordinary people traced their descent through paternal lines, and their cemeteries were organized accordingly (Chang 2005; Lu and Yan 2005). It is hypothesized that Dawenkou was the critical period during which the society began to change from matrilineal/ matrilocal to patrilineal/patrilocal; and the social organization was already patrilineal/ patrilocal during late Dawenkou (5000–4600 BP), if not earlier (He 1994; Luan 1997). However, this hypothesis has been challenged (Pearson 1988; Shelach 2004), and has not been thoroughly tested. In this study we will test this hypothesis with ancient DNA analysis of a Dawenkou cemetery, the Fujia site, Shandong Province. Due to the nature of DNA analysis, we will focus our discussion on kinship and residence pattern (i.e., matrilineal, patrilineal, matrilocal, patrilocal) and leave the debate of whether this society was matriarchal or patriarchal to other studies.

DNA analysis has successfully been used to infer the social organization of ancient communities (Keyser-Tracqui et al. 2003; Haak et al. 2008; Baca et al. 2012). Mitochondrial DNA (mtDNA) analysis can be used to determine the maternal relationships among individuals, the non-recombining region of the Y-chromosome

(NRY) traces paternal relationships and population history, and microsatellite analyses of autosomal nuclear DNA are regularly used in kinship identification in the forensic sciences (Butler 2012). Different DNA patterns observed in uniparental systems (mtDNA and Y chromosome) can be used to infer sex-biased gene flow through time. For example matrilineal societies should have relatively lower mtDNA diversity and higher Y-chromosomal diversity. Conversely, among patrilineal communities, the expectation is a relatively higher mtDNA diversity and lower Y-chromosome diversity. This hypothesis has been well tested in modern matrilineal and patrilineal communities (Oota et al. 2001; Kumar et al. 2006; Gunnarsdóttir et al. 2011). In addition, there are cases where married couples do not live together but live with family members of their own lineage (Gough 1959, 1965; Hua 2001). In such cases, one would expect to find individuals to be maternally closely related in a matrilineal community or paternally closely related in a patrilineal community. As DNA analyses have only been completed on a limited number of prehistoric populations in China (ADLJU 2001; Gao et al. 2007; Li et al. 2007; Zhang et al. 2010; Cui, Li, et al. 2013; Fu et al. 2013), how or whether ancient communities changed in kinship organization and post-marital residence in different regions within China remains largely untested.

Dawenkou Culture

The late Neolithic Dawenkou Culture (6300–4600 BP, Figure 1, SPICRA 2005) in Shandong, northern Anhui and Jiangsu Province, had a diversified agricultural food production system, elaborate burial practices, and signs of incipient social stratification.

The Dawenkou Culture is defined by its unique ceramic vessel style, including the hollow-foot tripod pitcher (*gui*) and stem cup with perforations (*loukong bei*). Millet agriculture was established during the preceding Beixin Culture era (ca. 7300–6000 BP, SPICRA 2005) in this region, and intensified in Dawenkou and Longshan Culture (ca. 4600–4000 BP) with introduced crops such as rice (Jin 2008). Dawenkou is well known for its extremely elaborate burials indicating differences in wealth, incipient social stratification and changing gender relationships (Pearson 1981; He 1994; Luan 1997; Underhill 2000, 2002). While many graves were small and accompanied by less than ten artifacts, others were large, elaborately constructed tombs filled with finely worked ceramic vessels, jade objects, water deer canines, and pig skulls. Most Dawenkou cemeteries had uniform body orientations within each cemetery. Wu (1990) argued that the burials were oriented to the hypothetical origin place of Dawenkou people, in the Yimeng region, Shandong Province.

Dawenkou houses were built with posts and mud, sometime partly underground, and sometimes above ground. Unfortunately, the residential areas of Dawenkou sites are rarely well preserved or extensively excavated (SPICRA 2005; SPICRA and ZMCB 1996; IA CASS 2001). Therefore the archaeological evidence for social organization or the transition from “matrilineal/matriarchal clans” to “patrilineal/patriarchal families” comes mainly from Dawenkou cemeteries. At the Dawenkou site, Han (1994) found burials located in the “north 1” section of the cemetery were more elaborate than others during phase one, hence he argued that the initial social stratification was among big families, not among individuals, and the social organization was transforming from clans to

families. The appearance of “couple burials”, those with one male adult and one female adult buried together, was also used to argue for the shift of the emphasis to nuclear families (He 1994). However, in most cases, “couple burial” was not the dominant form in the cemetery; it comprises 1% to 5% of burials among different Dawenkou sites. In addition, it is unknown if they were actually married couples, siblings, or had other relationships.

Materials and Methods

Samples

Well-preserved samples of dense long bone shafts were selected from the Fujia site, Guangrao County, Shandong Province (Table 1). Accelerator Mass Spectrometry radiocarbon dating on human bone collagen samples suggests the site was occupied between 4800–4500 cal BP (Dong 2013). This is consistent with the relative chronology, which also indicates late Dawenkou based on pottery styles. Fujia has been excavated several times, and at least 343 burials have been identified (Zheng 1988; Han and Chang 1989; SPICRA and Dongying Museum 2002). Stable isotope analysis of human and pig remains suggest the community was largely millet agriculture based (Dong 2013). Even though a large number of burials have been excavated at Fujia, not all human remains were properly collected and curated. Only individuals that have clear and consistent context information were selected for this study. Of the 160 burials with contextual information, samples of bone of 18 individuals were randomly selected for ancient DNA analysis in this study; we tried to keep a balanced sample of sex groups (9 females, 8

males, one indeterminate, based on skeletal morphological traits), and groups of burials defined on the basis of grave goods, grave type, and body orientation. Information on individual sex, age, burial position, accompanying artifacts, and burial orientation is provided in Table 1. Most burials were primary, with individuals placed in extended supine positions, while four were secondary burials (disarticulated skeletal elements out of anatomical position). The tombs were rectangular simple pits in most cases, while two were constructed in the *ercengtai* (earthen ledge) style indicating higher labor input in tomb construction. Most burials had few grave goods, ranging from zero to five. However a few burials had been disturbed and likely had more grave goods than were found during excavation. There were no observable wealth differences among different individuals in this cemetery. In addition, unlike most Dawenkou cemeteries, these burials were oriented in two major directions, northeast (NE) and southeast (SE). No significant differences in burial treatment can be discerned between the NE oriented and SE oriented groups.

DNA Extraction

DNA extraction, amplification, and sequencing were carried out at the Ancient DNA Laboratory, Research Center for Chinese Frontier Archaeology, Jilin University (Fu et al. 2007; Gao et al. 2007; Xie et al. 2007; Cui et al. 2010; Li et al. 2010, 2011). Bone samples were first abraded using a Strong 90 Micro Motor (Saeshin Precision Co.) with a carbide drill bit to remove outer layers and also the porous inner layers. Bone and tooth samples were then soaked in NaClO solution (~5% effective Cl) for 15 minutes, rinsed

with ethanol, and then put under UV light overnight for surface decontamination. Each tooth or bone was powdered in a 6750 or 6850 SPEX Freezer Mill. Powdered samples were digested in 0.5M EDTA (pH=8) for 24 hrs on a rotator. 100µl of 20mg/mL proteinase K was then added and the digestion solution was placed on a rotator at 50°C overnight. The supernatant from digested samples was condensed using Amicon® Ultra-4 centrifugal filter units (Millipore) to about 100µl. Each sample was then extracted with a QIAquick® PCR Purification Kit (QIAGEN) following the manufacture's protocol, except using a smaller amount of Elution Buffer (60µl). We performed two or more independent extractions per sample.

Amplification and Sequencing

The first hypervariable region (HVSI) of mtDNA was amplified and sequenced in two overlapping fragments using primers listed in Table 2 (Li et al. 2011). To further confirm the mitochondrial haplogroup, each sample was tested by amplified product-length polymorphisms (APLP; Shinoda et al. 2006). In addition, the amelogenin (AMG gene) fragment was amplified for sex confirmation for morphologically assigned male individuals (Stone et al. 1996), and confirmed samples were chosen for further analysis. We screened all male samples with three bi-allelic markers on the Y-chromosome (M89-F, M9-K, and M214-NO) that define major branches (F, K, and NO) on the Eurasian haplogroup tree (Consortium 2002; Karafet et al. 2008). Subsequent analysis was restricted to markers (M231-N, M175-O) on the appropriate sub-branch of the haplogroup tree (Li et al. 2007; Karafet et al. 2008). Polymerase chain reaction (PCR)

amplification was carried out in 12.5µl reactions containing 3µl template, 1 U Taq polymerase (Promega), 1X reaction buffer, 2.5 mM MgCl₂, 0.2 mM dNTPs, 2 mg/ml bovine serum albumin and 2µM of each primer. Amplification products were checked on a 2% agarose gel and purified with QIAquick Gel Extraction Kit (QIAGEN). PCR products were sequenced using the ABI 310 Terminator Sequencing kit (PE Applied Biosystems) and were analyzed on the ABI PRISM 3100 automatic sequencer (PE Applied Biosystems). DNA sequences were analyzed using Sequencher 4.7 (Gene Codes Corporation). A minimum of two amplifications per sample were conducted. If no consensus sequencing results were obtained by two amplifications and sequencing, additional extraction and amplification were carried out. HVSI sequences of Fujia individuals have been submitted to GenBank (Accession number: KC879242-KC879257).

Contamination Precautions

Ancient DNA is typically degraded and fragmented, and sometimes modified, mainly due to hydrolytic and oxidative forces (Kaestle and Horsburgh 2002; Pääbo et al. 2004). Thus, it is critical to take every precaution to avoid and detect contamination from modern DNA and also to tease out the false signals within ancient samples due to postmortem modifications (Cooper and Poinar 2000). In well preserved samples, direct PCR usually yields the same sequences as consensus cloning sequences, so cloning was not performed in this study (Winters et al. 2011). Dedicated preparation rooms for ancient samples were used, located in a building away from any PCR amplification activities. Strict procedures,

multiple independent extractions and amplifications, and inclusion of negative controls were practiced. Moreover, as described in the DNA extraction section, all samples were abraded to remove the possibly contaminated outer layers and also the porous inner layers. Then, bone and tooth samples were soaked in NaClO solution and put under UV light overnight to remove any possible contamination from previous handling. All staff wore sterilized laboratory coats, face masks, hair covers, and gloves (which were frequently changed), and strict cleaning procedures were performed by regular treatment with DNA-OFF™ (Q-Biogene) and UV light (254 nm). Laboratory staff were limited in their movements between the ancient DNA laboratory and post-PCR area, and PCR products were never brought into the Ancient DNA Laboratory. The mtDNA profiles of all people involved in processing the samples were determined and then compared to results obtained from the ancient samples. In addition, only female researchers were involved in the pre-PCR procedures in Y-SNP analysis, reducing possible contamination from modern Y-chromosome DNA. These samples were extracted and amplified at the same time as samples from another archaeological site with different mtDNA haplotypes and no cross-sample contamination was observed. Negative controls turned up positive in three instances and were subsequently sequenced. In all cases, the sequencing results of negative controls did not match the sequences of any lab members or samples. Data from amplifications where the negative control amplified were disregarded and the amplification was repeated and only counted when negative controls did not amplify. Randomly selected samples (DWK171, DWK187, DWK193, and DWK199) were sent to a second ancient DNA laboratory at the University of Illinois at Urbana-Champaign

(UIUC) for independent replication and authentication. At UIUC, DNA was extracted from the skeletal samples as in Cui, Lindo, and colleagues (2013) and HVSI sequence was generated using primers and PCR conditions from Kemp et al. (2007).

Measures of Genetic Diversity

Genetic diversity was measured as haplotype diversity for mitochondrial DNA and haplogroup diversity for Y-chromosome DNA.

Results

Of the 18 burials sampled, 16 yielded reproducible mtDNA sequences (Table 3). All samples confirmed at the University of Illinois revealed the same HVSI sequences as those identified in the original laboratory. All individuals shared the same HVSI sequences and coding region Single Nucleotide Polymorphisms (SNPs), belonging to haplogroup D5 or D6. This sequence differs from those of all researchers present in the laboratories where the samples were analyzed and confirmed even though haplogroup D is common in modern China (Kivisild et al. 2002; Wen et al. 2004). Haplogroup D5/D6 individuals were present in a 2000 year old population (Yixi site, 9%, about 30 miles to the southwest of Fujia, Yao et al. 2003) and are still present in modern Shandong Province: 8% at Tai'an City, 10% at Qingdao City, 6% at Zibo City (Yao et al. 2002, 2003) . Because all 16 samples exhibited the same mitochondrial DNA haplotype, the mtDNA haplotype diversity is 0.

Eight morphological assigned males were further tested using the AMG gene for sex confirmation, seven were confirmed to be male, and one (DWK193) was found to be female. The confirmed males were screened for Y chromosome haplogroups. Three failed to yield reproducible sequences. The remaining four males all belong to macrohaplogroup K. Within macrohaplogroup K, DWK167 and DWK199 are further assigned to haplogroup N, and DWK191 is assigned to haplogroup O. Both haplogroup O and N were present at Dadianzi site (ca. 3600 BP), northeastern China (Li et al. 2011). Haplogroup N has a wide geographic distribution throughout northern Eurasia and is found in modern northern and southern China (Karafet et al. 2001; Derenko et al. 2007; Zhong et al. 2011). On the other hand, haplogroup O is dominant among populations of East Asia and Southeast Asia, especially in the Chinese Han population (the major ethnic group in China), with an average frequency of 52.3% (Ke et al. 2001). Y-SNPs analysis of prehistoric people (6400–3100 BP) along the Yangtze River showed that all individuals belonged to haplogroup O (Li et al. 2007). Of the four samples where Y chromosome data was generated three haplogroups were exhibited, therefore the Y chromosome haplogroup diversity is 0.75.

Discussion and Conclusions

There are numerous variations of social organization in modern and ancient communities (Morgan 1871; Murdock 1967; Haviland 1996). Bilateral, neolocal unilateral, patrilocal matrilineal, and matrilineal societies are difficult to reconstruct by mtDNA and Y-chromosome data. Here we focus our discussion on three kinds of communities based

on kinship and post-marital residence: matrilineal community without married-in males, matrilineal community with married-in males, and patrilineal community with or without married-in females (the reasoning is provided below, Table 4). We make two contrasts: one is how descent was traced, either matrilineal or patrilineal. In a matrilineal community, because descent is traced maternally, we expect all females to be maternally closely related and have similar mtDNA haplotypes (excluding patrilocal ones). Conversely, in a patrilineal community, we expect all males to be paternally closely related and have similar Y-chromosome haplotypes (excluding matrilocal ones). The second contrast we make is whether the husband or wife was incorporated into the affinal group or stayed with their own descent group after marriage. For matrilineal communities, if the husbands were not incorporated into their wives' descent group but stayed with their own matrilineal descent group, we expect males to have diverse paternal origins but shared maternal origins; on the other hand, if the husbands were incorporated into their wives' descent groups, we expect males to not only have diverse paternal origins, but also diverse maternal origins. For patrilineal communities, it is not possible to discern whether women are married into their husbands' descent group or if they continued to live with their own patrilineal descent group with uniparental DNA markers since we cannot trace a females' paternal origins. Hence, patrilineal communities with or without married-in females were lumped together.

Based on our ancient DNA analysis, the Fujia community conforms to the pattern expected for a 'matrilineal community without married-in males'. All male and female individuals tested from Fujia cemetery shared the same maternal lines. This suggests that

maternal ties were considered very important, and it is very likely only maternally closely related individuals were buried together. As the site was excavated as a salvage operation, only the part of the archaeological site that was going to be affected by road construction was excavated. This excavated part of the cemetery may have been used by a single maternal lineage. The number of individuals tested in this study is limited; how well this pattern holds across the entire cemetery would require additional genetic analyses.

An alternative explanation for finding the same maternal line in all 16 individuals is genetic drift. In other words, there could have been a large population bottleneck that reduced mtDNA diversity to only this single matriline. A population bottleneck could be caused by pandemic disease with massive death, dramatic environmental change resulting in massive mortality due to severe famine, large scale wars killing or driving people away, or a founder effect resulting from the expansion of a small colonizing population in a new setting. Yet, no available archaeological or paleoenvironmental evidence suggests the existence of a severe bottleneck during the early Holocene in the region. Another explanation for identifying only a single mtDNA haplotype would be the sampling of an extended maternally related family. However, this seems unlikely, considering that the samples selected for analysis were selected randomly from individuals that were excavated from an area that covers 700 m². In the future, we plan to include autosomal DNA marker analyses to elucidate kinship relations among individuals in more detail and potentially reveal sibling and parent-offspring relations.

In order to assess if the single haplotype of 16 individuals is robust to the presence of low mtDNA diversity in the larger sample we completed a probability test.

Without knowing its substructure and population history, we can only assume the chance of finding 1 individual carrying “haplotype A” (129-189-223-362, 5178A) in a given population of 343 individuals is the same as the chance of finding 2 individuals carrying “haplotype A” and also the same as the chance of finding 3, 4, 5...343 individuals carrying “haplotype A”. If there were x individuals carrying “haplotype A” and we randomly select 16 individuals from the population, the probability of finding 16

individuals carrying haplotype A is $prob(x) = \frac{C_x^{16}}{C_{343}^{16}}$. For example, if there are 343

individuals carrying “haplotype A”, the probability of finding 16 individuals carrying

“haplotype A” is $prob(343) = \frac{C_{343}^{16}}{C_{343}^{16}} = 1$; if there are 16 individuals carrying “haplotype

A”, the probability of finding 16 individuals carrying “haplotype A” is

$$prob(16) = \frac{C_{16}^{16}}{C_{343}^{16}} \approx 8.13 \times 10^{-28}$$

. According to our results, the 16 individuals tested at Fujia all carry “haplotype A”, the probability of having at least x individuals carrying

“haplotype A” in this population is $acc\ Prob(x) = \frac{\sum_{i=x}^{343} prob(i)}{\sum_{i=16}^{343} prob(i)}$. For instance, the

probability of having at least 300 individuals carrying “haplotype A” is

$$\begin{aligned}
acc\ Pr\ ob(300) &= \frac{\sum_{i=300}^{343} prob(i)}{\sum_{i=16}^{343} prob(i)} \\
&= \frac{prob(300) + prob(301) + prob(302) + \dots + prob(343)}{prob(16) + prob(17) + prob(18) + \dots + prob(343)} \approx 0.908 ;
\end{aligned}$$

the probability of 200 individuals not carrying “haplotype A” is

$$\begin{aligned}
1 - acc\ Pr\ ob(200) &= 1 - \frac{\sum_{i=200}^{343} prob(i)}{\sum_{i=16}^{343} prob(i)} = \frac{\sum_{i=16}^{343} prob(i) - \sum_{i=200}^{343} prob(i)}{\sum_{i=16}^{343} prob(i)} = \frac{\sum_{i=16}^{199} prob(i)}{\sum_{i=16}^{343} prob(i)} \\
&= \frac{prob(16) + prob(17) + prob(18) + \dots + prob(199)}{prob(16) + prob(17) + prob(18) + \dots + prob(343)} = 0.00007
\end{aligned}$$

In other words, if we randomly select 16 individuals from this population and all 16 individuals carry “haplotype A”, it is very likely at least 200 individuals in the population carry “haplotype A”; there is a 90% chance that there are more than 300 individuals carrying “haplotype A” in the population.

If samples included in this study are somewhat representative of the whole Fujia population, we will find that the bond of marriage seems to be de-emphasized compared to the bonds of descent at death at Fujia. Whether Fujia was a matrilineal community with married-in males largely depends on whether the husband lived with and made contributions to the wife’s descent group or his own descent group. Unfortunately, we do not have information on their daily lives and we can only judge from what was emphasized in the burial arrangement. If we assume exogamy, the husbands of a matrilineal community would have come from other communities, hence are expected to have diverse paternal and maternal origins. However, only one mtDNA sequence was

found in the samples we analyzed, indicating close maternal relatedness. It is possible that the hypothesized exogamous husbands with different mtDNA signatures were buried in other cemeteries that belonged to other maternal lineages. It seems likely that husbands were not incorporated into their wives' descent groups at the time of burial; the bond of marriage was de-emphasized compared to the bonds of descent. However, there are possibilities that some or all the tested individuals were not married, hence undermining testing post-marital residence pattern.

The de-emphasis of the bond of marriage at Fujia, at least expressed in mortuary ritual, is not unique in Neolithic China. Craniometric analysis at the Shijia site, Yangshao Neolithic Culture (ca. 5000-3000 B.C), also suggest close relatedness of individuals in the same burial (Gao and Lee 1993). It is very likely that only relatives from the same descent group were included in the same burial, and affinal links were de-emphasized in the Shijia community.

Contrary to Briffault and Malinowski (1956)'s claim for the centrality and universality of the 'individual family', it is likely that blood ties (i.e., brothers and sisters) were considered more important than affinal links (i.e., husband and wife) in this Dawenkou community. Individual family classifications were previously thought to be important to aid in provisioning young children and pregnant or breastfeeding mothers. However, recent research suggests that hunt yields by males were usually shared among the community, leaving the hunter and his family the minimum share (O'Connell et al. 2002). In other words, the presence of male hunting, either by brothers or husbands would benefit the group in general, not a nuclear family per se. It is not mandatory to

have nuclear family relationships to ensure the wellbeing of the mother and infant. Ethnographic examples of matrilineal societies also support this hypothesis, such as the Nayar from India (Gough 1959, 1965), the Mosuo people from southwestern China (Hua 2001), and Australian aborigines (Malinowski 1913). In these societies the husbands are not incorporated into their wives' descent groups and they work for their own descent groups instead. It is the responsibility of the brothers to take care of the women and their children. Schneider (1961) actually argued that a strong bond of solidarity between husband and wife is not compatible with the maintenance of a matrilineal descent groups.

Multiple hypotheses have been proposed for the practice of matrilineal or matrilocal organization. Korotayev (2003) argues that low internal warfare frequency and high female contribution to subsistence favor matrilocal residence. Opie and Power (2008) argue that the role of grandmothers as foragers for, and caregivers to, their daughters' children were critical to the emergence of hunter-gatherer social adaptations; hence, the earliest human groups were matrilineal. Matrilineal societies found in ethnographic surveys tend to be horticultural instead of pastoral or mixed agricultural food producing economies (Aberle 1961). Holden and Mace (2003) also suggest that matrilineal descent is often associated with swidden cultivation, because women typically do much of the productive work in the fields. Whether Dawenkou agricultural subsistence was related to the matrilineal organization at Fujia site is unknown. Based on stable carbon isotope analysis, subsistence at Fujia was millet-based agriculture (Dong 2013). Faunal analyses of other Dawenkou sites suggest that the pig and deer were the dominant animal resources (Zhou 2000; Yuan and Chen 2001).

As noted above, evidence for social rank in Dawenkou sites comes largely from cemeteries. Interestingly, we can see significant variations in social stratification within late Dawenkou cemeteries: some communities had clearer signs of initial stratification (e.g., Xixiahou site, SAT IA CASS 1964, 1986; Lingyanghe site, Wang 1987), and others were more egalitarian (e.g., Wucun site, less than two miles away from Fujia, SPICRA and Guangrao Museum 1989). It is also possible that social organization, including kinship and marriage patterns were diverse among Dawenkou communities. Fujia is dated to late Dawenkou, during the end of the assumed transition period from matrilineal clans to patrilineal monogamous families. If this transition did occur, it did not occur simultaneously across all Dawenkou sites. Additional archaeological research on social organization is needed to find out how Dawenkou and later communities were organized, and how the transition occurred. For example strontium isotope analysis could help determine whether individuals were buried in the area where they were born and raised, or if they came from a different region (Bentley et al. 2012; Price et al. 2010; Wright 2012).

Another point worth noting is that despite the different body orientations at Fujia site, individuals oriented towards northeast or southeast all had the same mtDNA haplotype. Therefore, they probably all belong to the same maternal lineage. However, we cannot rule out the possibility that two lineages had split quite recently, and had not yet accumulated any genetic differences. The body orientation did not seem to correlate with sex, grave type, or number of grave goods, but do correlate with oxygen isotope

values (Dong 2013). It is possible that those two groups of people with different orientations at Fujia site had access to two different drinking resources.

In conclusion, contrary to the previous assumption that the social organization was patrilineal/ patrilocal by late Dawenkou (5000–4600 BP), our ancient DNA analysis results suggest that matrilineal links were quite important at Fujia, and the community was very likely a matrilineal one. In addition, it seems husbands were not incorporated in to their wives' descent group but stayed with their own matrilineal descent groups instead. This research further demonstrates ancient DNA analysis as an effective tool in ancient kinship studies, and it is especially useful for prehistoric societies without written record. With a specific focus on China, ancient DNA analysis in the future can shed additional light on how ancient societies were organized and how that organization may have gradually transformed in prehistoric societies.

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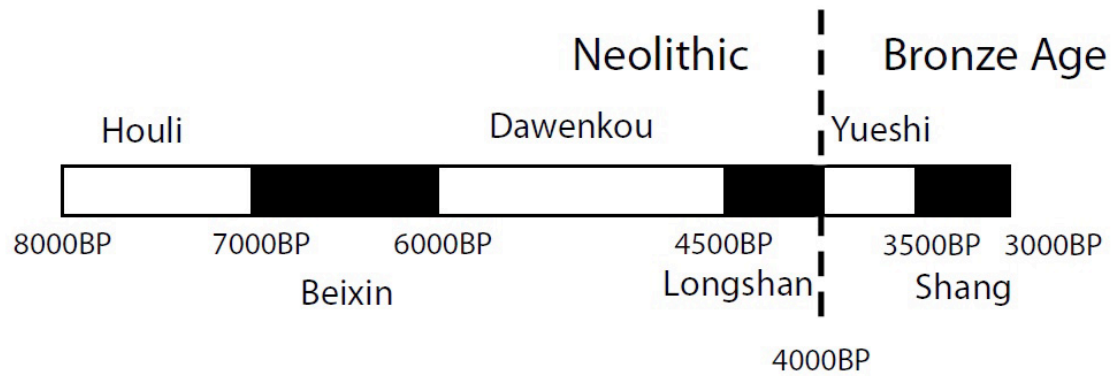


Figure 1. Major prehistoric and early historic cultures in Shandong Province, China and their approximate timeline.

Table 1. Fujia cemetery sampled burials: sex,age group, bone type, skeleton position, grave type, grave goods and orientation.

Lab Number	Burial Number	Morphological Sex Assignment	Age Group	Bone Type	Skeleton Position	Grave Type	Number of Grave Goods	Orient-ation
DWK161	M6	female	adult	tibia	extended supine	simple pit	3	SE
DWK165	M9	male	adult	femur	extended supine	simple pit	1	SE
DWK167	M10	male	adult	humerus	extended supine	<i>ercengtai</i> pit	1	NE
DWK169	M12	female	adult	femur	extended supine	simple pit	1	SE
DWK171	M16	unknown	adolescent	tibia	extended supine	<i>ercengtai</i> pit	3	NE
DWK173	M17	female	adult	femur	extended supine	simple pit	1	SE
DWK177	M24	female	adult	tibia	extended supine	simple pit	1	NE
DWK179	M28	male	adult	humerus	extended supine	simple pit	0	SE
DWK181	M31	female	adult	femur	extended supine	simple pit	0	SE
DWK183	M32	male	adult	tibia	extended supine	simple pit	0	NE
DWK185	M34	female	adult	humerus	extended supine	simple pit	2	NE
DWK187	M101	female	adult	tibia	extended supine	simple pit	1	NE
DWK189	M112	male	adult	femur	secondary	simple pit	5	NE
DWK191	M117	male	adult	tibia	secondary	simple pit	0	
DWK193	M118	male	adult	tibia	unknown	simple pit	0	SE
DWK195	M128	female	adolescent	tibia	secondary	simple pit	2	SE
DWK197	M133	female	adolescent	tibia	extended supine	simple pit	0	SE
DWK199	M140	male	adult	tibia	secondary	simple pit	0	SE

Table 2. Primers used in this study

HVSI fragments	Primers	Length (bp)	
HVSI-AB	L16017 5'-TTCTCTGTTCTTTCATGGGGA	235	
	H16251 5'-GGAGTTGCAGTTGATGTGTGA		
HVSI-CD	L16201 5'-CAAGCAAGTACAGCAATCAAC	209	
	H16409 5'-AGGATGGTGGTCAAGGGA		
Mitochondrial			
haplogroups	APLP Primers	Sites	Length (bp)
D	5178A 5'-TGATCAACGCACCTGAAACAAGA	5178A/C	107 (D)/102
	5178C 5'-GTCGCACCTGAAGCAAGC		
	5178R 5'-CCCATTTGAGCAAAAAGCC		
Y chromosome			
haplogroups	Primers	Sites	Length (bp)
F	M89S 5'-CCACAGAA GGATGCTGCTCA	M89	125
	M89A 5'-CACACTTTGGGTCCAGGATCAC		

K	M9S 5'-GGACCCTGAAATACAGAAC M9A 5'-AAGCGCTACCTTACTTACAT	M9	128
NO	M214S 5'-TATATGTAAGCTTTCTACGGCA M214A 5'-GGGGAAAAAACCATGTACG	M214	109
O	M175S 5'-GGACCCTGAAATACAGAAC M175A 5'-AAGCGCTACCTTACTTACAT	M175	128
N	M231A 5'-TTCTTTGACGATCTTTCCCC M231S 5'-CCTGGAAAATGTGGGCTC	M231	113

Sex Identification	Primers	Length (bp)
AMG gene	XBamel-1 5'-CCTGGGCTCTGTAAAGAATAG XBamel-2 5'-CAGAGCTTAAACTGGGAAGCTG	103 (F)/ 103 and 109 (M)

Table 3. Mitochondrial and Y-chromosome SNPs and haplogroup designation of Fujia samples

Lab Number	Mutations in HVSI (16000+)	mtDNA coding region SNPs	mtDNA haplogroups	Y-CH coding region SNPs	Y-CH haplogroups
DWK161	129-189-223-362	5178A	D5/D6		
DWK165	129-189-223-362	5178A	D5/D6	M89T, M9G, without M175 (5bp del)	K*(XO)
DWK167	129-189-223-362	5178A	D5/D6	M89T, M9G, M214C, M231A	N
DWK169	129-189-223-362	5178A	D5/D6		
DWK171	129-189-223-362	5178A	D5/D6		
DWK173	129-189-223-362	5178A	D5/D6		
DWK177	129-189-223-362	5178A	D5/D6		
DWK179	129-189-223-362	5178A	D5/D6	failed	
DWK181	failed				
DWK183	129-189-223-362	5178A	D5/D6	failed	
DWK185	failed				
DWK187	129-189-223-362	5178A	D5/D6		

DWK189	129-189-223-362	5178A	D5/D6	failed	
DWK191	129-189-223-362	5178A	D5/D6	M89T, M9G, M175 (5bp del)	O
DWK193	129-189-223-362	5178A	D5/D6	molecular identification as female	
DWK195	129-189-223-362	5178A	D5/D6		
DWK197	129-189-223-362	5178A	D5/D6		
DWK199	129-189-223-362	5178A	D5/D6	M89T, M9G, M214C, M231A	N

Table 4. Expected male and female genetic expressions in three kinds of ideal communities.

Ideal Community Label	Females' maternal origin and mtDNA expressions	Males' maternal origin and mtDNA expressions	Males' paternal origin and NRY expressions
matrilineal community without married-in males	similar maternal origins, hence similar mtDNA sequences	similar maternal origins, hence similar mtDNA sequences	diverse paternal origins and diverse Y-chromosome sequences
matrilineal community with married-in males	similar maternal origins, hence similar mtDNA sequences	diverse maternal origins and diverse mtDNA sequences	diverse paternal origins and diverse Y-chromosome sequences
patrilineal community with	diverse maternal origins and diverse	diverse maternal origins and diverse	similar paternal origins and similar

or without married-in females	mtDNA sequences	mtDNA sequences	Y-chromosome sequences
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