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Gene: X

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Cebú, Thailand and Taiwanese aboriginal populations according to Y-STR loci

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ARTICLE INFO

Keywords:

Cebú
Thailand
Y-STR
Taiwanese aboriginal populations

ABSTRACT

Here we report for the first time the Y27-STR Yfiler plus profiles of the insular population of Cebú in the central region of the Philippine Archipelago and the general continental population of Thailand, two strategic locations of interest in connection with the Austronesian expansion. Traditionally, the peopling of Taiwan has been envisioned as a single wave of agriculturists migrating from mainland Southeast Asia. Yet, more recent data support a scenario in which a number of migrations from the continent populated the island. Genetic affinity parameters from this study indicate that certain Formosan tribes are genetically closer to geographical distant populations in the Solomon Island than to other nearby Taiwanese tribes. Furthermore, Taiwanese aboriginal populations in this study partition into three clusters, one associated with populations from the Philippines and Thailand, a second one segregating with populations of the Solomon Islands and a third grouping made up exclusively of Taiwanese aboriginal tribes. The populations within each of these three clusters exhibit different degrees of differentiation among them suggesting unique population histories. All together, these differential genetic affinities of specific Taiwanese tribes to groups from different geographical regions and to each other are compatible with multiple origins of the Austronesian expansion from Formosa as well as from mainland Southeast Asia.

1. Introduction

Contrary to prevailing notions, anatomically modern humans (AMHs) first arrived to the island of Formosa as early as the Late Paleolithic (Olsen and Miller-Antonio, 1992). Although often overlooked in the literature, the original peopling of Taiwan may date back to a period between 50,000–10,000 ya (Sung, 1981) as part of the Out of Africa dispersal. The settlement of Formosa is often reported in the literature to have occurred more recently exclusively during the Holocene approximately six thousand years ago (kya) as a consequence of the Agricultural Revolution in South East Asia as mainland farmers were depleted of agricultural land and migrated to the island (Trejaut et al., 2005). One of the implications of a much earlier colonization of

the island during the Late Paleolithic is a potentially richer more diversified genetic history that combine with subsequent migrations may have contributed to contemporary insular gene pools.

It is likely that this initial Paleolithic settlement by AMHs occurred when the Taiwan Strait was a dry-land expanse. Currently, not exceeding 100 m deep, the Strait of Taiwan is a shallow 130 km body of water that separates the island from the province of Fujian in the southeast coast of mainland China (Rolett et al., 2011). During glaciation, the Strait of Taiwan has been periodically transformed into a dry land bridge (Severinghaus and Brook, 1999). The last time this dry passageway was available for terrestrial crossing was at the end of the last glaciation, 15,000 to 11,300 ya when the East China Sea was about 140 m below the current levels (Emery et al., 1971). Subsequently,

Abbreviations: STR, short tandem repeat; AMH, anatomically modern human; kya, thousand years ago; MSEA, Mainland South East Asia; SEA, South East Asia; ISEA, Island South East Asia; MDS, multidimensional scaling; AMOVA, Analyses of Molecular Variance

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<https://doi.org/10.1016/j.gene.2018.100001>

Received 21 November 2018; Accepted 24 November 2018

Available online 06 December 2018

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during the last postglacial period, from 11,000 to 7000 ya, sea levels increased rapidly to its present state. Prior to the last dry glacial epoch, a period of marine transgression, between 38,000 and 18,000 ya flooded the Taiwan Strait preventing land crossings (Huang and Chen, 1988).

The Baxiandong and Cailiaoxi Late Paleolithic sites provide evidence that AMHs were on the island of Formosa during the Late Paleolithic. The AMH remains (nickname Zuozhen Man) including seven cranial fragments, a number of molars and lithic artifacts found in the caves and rock shelters of Cailiaoxi, in the southwestern plains of Taiwan, have been directly dated as early as 20,000 to 30,000 ya with the occupation possibly extending to as recent as 7000–6000 ya (Lian, 1981; Tsang et al., 2011). The tools found in these Paleolithic assemblages belong to the Changbinian tradition and some were found overlain by Middle or Late Neolithic deposits (Hung and Carson, 2014). Also, the presence of Upper Paleolithic-like tool inventories in Taiwanese Neolithic communities suggest that these different communities likely met, co-existed and were involved in technology transfer (Zhang, 2000). Furthermore, genetic data in the form of Y-STR variation distribution suggest a Late Paleolithic incursion of AMHs into Formosa about 17,000 ya or even earlier (Trejaut et al., 2014).

The current aboriginal populations of Taiwan are a heterogeneous group of tribes that differ genetically, culturally and linguistically from each other (Zeng et al., 2014). Even though all aboriginal groups speak Austronesian languages, each vernacular exhibits considerable phonological and lexical diversity to the point of being mutually unintelligible. Although it is generally assumed that a single human dispersal from South East Asia introduced an Austronesian proto-language that then evolved *in situ* to all 9–12 contemporary aboriginal Taiwanese tongues, all native languages represent distinct parallel branches that cannot be nested (Ross, 2012). Furthermore, recent archeological evidence supports the contention that several independent migrations from various regions of the coast of Mainland South East Asia (MSEA) populated Taiwan (Hung and Carson, 2014). Thus, it is likely that the contemporary Taiwanese populations do not derive from a single source population in MSEA. Specifically, these data suggest that the Taiwanese tribes derive from a number of continental groups such as the Shandong (foxtail millet-cultivating Longshan culture or Black Pottery culture) of the Late Neolithic that populated southern Formosa, coastal Fujians (fishing-based Dapenkeng culture) that settled the northern most tip of the island approximately 6000 and 5000 ya and coastal Guangdong's (Yuanshan culture) that settled northern Taiwan. Thus, a single-migration model from the mainland is not supported by archeological and linguistic evidence and the most parsimonious explanation for the data is that AMHs arrived to the island from various sources and regions in MSEA, likely at different time periods starting in the Late Paleolithic.

Notwithstanding the crucial role that South East Asia and Taiwan played in the Austronesian expansion, limited studies have evaluated the various dispersion theories into and out of Taiwan. Yet, in recent years a number of studies have reported on the genetics of South East Asian (SEA) populations setting the stage for comparative studies (Delfin et al., 2011; Su et al., 2000; Friedlaender et al., 2008; Cai et al., 2011; Kim et al., 2011; Abbott et al., 2006; Tumonggor et al., 2013). Genetically, all Taiwanese populations have been reported to be internally highly homogeneous but extremely diverse among themselves. Remarkably, the genetic heterogeneity among Taiwanese tribes surpasses the diversity observed among worldwide populations (Zeng et al., 2014). This diversity may stem from genetic drift resulting from founding effect events and/or isolation subsequent to the settlement of limited number of dispersing groups from the mainland and/or migration of various genetically unique groups into the island. Subsequent to the seminal work of Melton and colleagues in 1998 (Melton et al., 1998), which implicated Taiwan as the source of the Austronesian expansion, a number of reports argued for an initial Austronesian genesis in MSEA, some underscoring Taiwan as a stepping-stone in the dispersal

into the Pacific (Trejaut et al., 2014; Tabbada et al., 2010; Loo et al., 2011) while others pointing to a direct exodus from MSEA to Oceania bypassing the island altogether (Delfin et al., 2011; Tumonggor et al., 2013; Karafet et al., 2010; Hwa et al., 2010; Wu et al., 2013; Li et al., 2008) or both, and still others suggesting northward dispersals from ISEA to Taiwan (Soares et al., 2008). Altogether, these studies suggest a number of complex scenarios for the Austronesian expansion that likely included bidirectional migrations.

In the current study, we report for the first time on the Y27-STR Yfiler plus profiles of two key South East Asian populations from Thailand and the Cebú province of the Philippines, and compared them to Taiwanese aboriginal tribes. Thailand provides data on the current Y chromosome constitution of a Coastal South East Asian (CSEA) location while Cebú examines the Y-STR composition of a key island South East Asian (ISEA) group. These two populations were selected because they provide strategic point of references to address specific hypotheses regarding the in and out of Taiwan dispersals. With this in mind, we explore the genetic partitioning of Taiwanese aboriginal populations with an eye on any differential association with SEA groups. Based on the available archeological, genetic and linguistic data, we theorized that the aboriginal tribes of Formosa would demonstrate differential genetic affinities to each other and SEA populations suggesting a complex dispersal and settlement history throughout ISEA and Oceania.

2. Materials and methods

2.1. Sample collection and DNA extraction

Buccal swabs were collected from a total of 209 unrelated male individuals from Thailand (n = 140) and the island of Cebú (n = 69) in the Philippines. Genealogical information was gathered for a minimum of two generations to confirm the descent of potential donors. Individuals were questioned to verify lack of familial links to other donors. Only unrelated individuals were sampled. Buccal swabs were processed utilizing the Genra Buccal Cell Kit (Puregene, Genra Systems, Minneapolis, MN) according to the manufacturers' specifications. Samples were stored as stock solutions in 10 mM Tris–EDTA at –80 °C. All samples were procured from donors voluntarily with informed consent.

2.2. Loci examined and reference populations

Allelic frequencies for a total of 27 loci (DYS19, DYS385 a/b, DYS387S1 a/b, DYS389 I/II, DYS390, DYS391, DYS392, DYS393, DYS437, DYS438, DYS439, DYS448, DYS449, DYS456, DYS458, DYS460, DYS481, DYS518, DYS533, DYS570, DYS576, DYS627, DYS635 (Y GATA C4), and Y GATA H4) were accessed using the Yfiler plus multiplex PCR system (Applied Biosystems, Foster City CA). The geographical locations, abbreviations used to define each population throughout the article, number of individuals and references reporting on the populations are all provided in Supplementary Table 1.

2.3. DNA amplification and genotyping

DNA samples were examined for Y-chromosome variations with a panel of 27 Y-STR loci provided by the Y27-STR Yfiler plus system (Applied Biosystems, Foster City, CA).

Amplification reactions were performed in an ABI PRISM1 GeneAmp1 9700 Silver block Thermal Cycler (Life Technologies) using the 9600 emulation mode for 30 cycles. All analyses used the internal lane standard and the allelic ladder mix provided by the Y27-STR Yfiler plus system. PCR products were separated and detected on an ABI PRISM1 3130xl Genetic Analyzer (Life Technologies) following manufacturer's instructions, using the LIZ-120 internal size standard as a basis for comparison. Fragment sizes were assigned using the software GeneMapper v3.1 (Applied Biosystems, Foster City, CA) and alleles

were designated by comparison to an allelic ladder supplied by the manufacturer (Applied Biosystems).

2.4. Accession numbers

The 27-loci haplotypes for all the individuals of the two populations reported for the first time in this publication have been successfully submitted and are now included in the YHRD database under the following accession numbers: Thailand YA004250 and Cebú (Philippines) YA004255.

2.5. Data analysis

Allelic frequencies were calculated with the PowerMarker V3.25 program (Liu and Muse, 2005). Population genetics parameters for the populations from Thailand and Cebú were estimated using the software package Arlequin V3.5 (Excoffier et al., 2007). DYS385 was excluded from the haplotype diversity calculations because is not possible to discriminate between the DYS385a and DYS385b loci with the Y STR kit. In addition, the size of the DYS389I allele was subtracted from the DYS389II for all analyses. Discrimination capacity was calculated by dividing the number of different haplotypes by the total number of individuals in the population. The fraction of unique haplotypes was determined as the percent proportion of unique haplotypes. Inter-population pair-wise genetic distances (Rst values) were calculated based on the loci using the Arlequin software V3.5 (Excoffier et al., 2007). The pair-wise population comparisons were performed at a significance level of 0.05 with 10,000 permutations (Kayser et al., 2003) and P-values were adjusted with the sequential Bonferroni correction. Samples carrying microvariants were excluded from the Rst calculations. Nei's genetic distances were employed to generate a multidimensional scaling (MDS) plot using the Statistical Package for the Social Sciences (SPSS) v 14.0 software (SPSS, 2001). Arlequin V3.5 was employed to perform Analyses of Molecular Variance (AMOVA) (Excoffier et al., 2007) to explore the potential statistical significance of the population clusters observed in the MDS plot. Significance was assessed at $\alpha = 0.05$ using 1023 permutations.

3. Results

3.1. Frequencies of haplotypes, alleles and parameters of population genetics interest

Supplementary Tables 2 and 3 provide the 27-loci haplotypes of 140 males from the general population of Thailand and 69 males from the province of Cebú, respectively. The allelic frequencies for the 27 Y-STR loci analyzed in the Thailand and Cebuano populations are illustrated in Supplementary Tables 4 and 5, respectively. The most frequent haplotypes are presented in Supplementary Table 6.

3.2. Forensic and population genetic parameters

Table 1 provides the values of population genetics parameters for the two genotyped populations. Using the 27 loci included in the Y27-STR Yfiler plus system, the Thailand and Cebú populations exhibit high levels of genetic diversity, with haplotype diversity values of 0.9999 and 1 as well as fraction of unique haplotypes of 0.9857 and 0.9710, respectively. Discrimination capacity values of 0.9929 and 0.9855 were estimated for Thailand and Cebú, respectively. In general the increment of 10 additional loci in the Yfiler plus system as compared to the 17-loci Yfiler multiplex improves the resolution of discrimination for both populations, especially for the Cebú population, which possesses fewer individuals. For example, the discrimination capacity in the Cebú population increases from 0.9275 to 0.9855 when the Y27-STR Yfiler plus system is employed (Table 1). All microvariants were confirmed by repeating the amplification process.

Table 1
Population genetics parameters of the Cebú and Thailand populations.

Haplotypes	CEB	THA
Sample size	69	140
27 Y-STR		
Number of haplotypes	68	139
Unique haplotypes	67	138
Fraction of unique haplotypes	0.9710	0.9857
Discrimination capacity	0.9855	0.9929
Haplotype diversity (HD)	1	0.9999
(HD) \pm SD	\pm 0.0025	\pm 0.0009
17 Y-STR		
Number of haplotypes	64	139
Unique haplotypes	61	138
Fraction of unique haplotypes	0.8841	0.9857
Discrimination capacity	0.9275	0.9929
Haplotype diversity (HD)	0.9966	0.9999
(HD) \pm SD	\pm 0.0037	\pm 0.0009

3.3. Phylogenetic analyses

The phylogenetic affinities of Thailand and Cebú were investigated in relation to CSEA and ISEA populations using a battery of analyses including Rst pair wise comparisons, MDS partitioning and AMOVA. In our approach, we focused on the differential genetic relationships of Taiwanese aboriginal populations among themselves and in relation with other East Asian populations (Supplementary Table 1). A review of the Rst values (Supplementary Table 7) demonstrate that most of the Taiwanese aboriginal populations (e.g., Ami) are genetically closer to ISEA groups such as Cebú (Rst = 0.0853, P = 0.0000) and CSEA populations like Thailand (Rst = 0.1177, P = 0.0000) than to a number of Formosan tribes, for instance Bunun (Rst = 0.6979, P = 0.0000). Furthermore, Taiwanese tribes such as Yunlin exhibit closer Rst distances to Near Oceania populations such as Vella (Rst = 0.2569, P = 0.0000) from the Solomon Islands than to other Taiwanese tribes for instance the Ami (Rst = 0.3626, P = 0.0000).

The MDS plot based on Rst Euclidian distances also illustrates differential segregation of the Taiwanese populations into three clusters (Fig. 1). One aggregation in the upper left quadrant includes the Bunun, Saisiyat and Yunlin tribes of central Taiwan. A second tight grouping brings together a number of major aboriginal tribes including the Ami, Paiwan, Puyuma and Rukai as well as the Yami from the small Orchid Island off the south east coast of Taiwan. The tribes congregated in this close cluster reside in the southern portion of Formosa. In close association with these tribes are a number of ISEA and MSEA populations that include Cebú and Thailand, respectively. In order to better visualize the relationships among the populations in this compact grouping an expanded view of the area is provided in Fig. 2. The third cluster seen in the lower right quadrant is made up of an aggregate of Formosan tribes including the Atayal, Tsou and Taroko (Truku) of the mountainous central portion of the island. To further test the statistical significance of the partitioning delineate by the three clusters, an AMOVA test was performed (Table 2). The AMOVA confirmed the visual differential segregation of the three groupings of Taiwanese populations at a P-value < 0.00001 (Table 2). The percent variations among groups (clusters), among populations within clusters and within populations were estimated at 12.61%, 13.98% and 73.41%, respectively.

4. Discussion

Although traditionally the peopling of Taiwan has been envisioned as a single wave of agriculturists migrating from MSEA in search of cultivable land, early (Ferrell, 1969; Chang, 1969) and more recent reports (Jiao, 2013; Li, 2013) have suggested otherwise, multiple dispersals. Ferrell (1969) indicated three unique aboriginal cultural

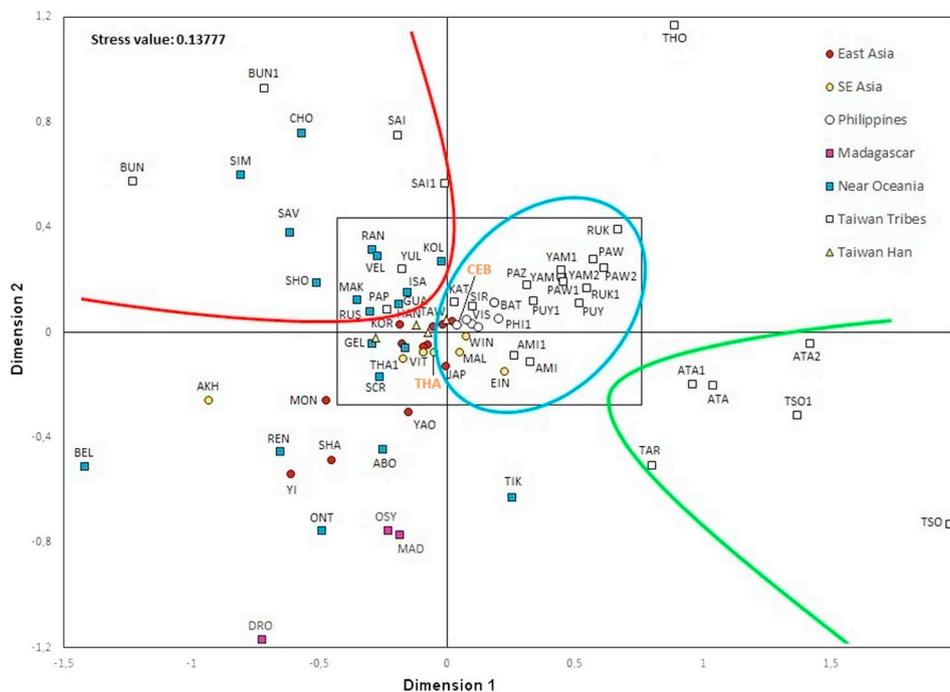


Fig. 1. MDS plot.

complexes in Taiwan based on archeological and linguistic diversity. This number corresponds to the number of clusters in the MDS plot (Fig. 1). Overall our results are compatible with the notion that the island of Taiwan was populated by AMHs by multiple dispersals. The high degree of genetic diversity observed in the paternal lineages is congruent with unique waves of mainland migrants that arrived to the island likely at different times from various locations in MSEA. Considering the ancient and ample time line of settlements of Formosa possibly dating back to the Late Paleolithic some 50,000–25,000 ya to the Holocene about 6000 ya, it is not unexpected that the contemporary populations of the island exhibit a considerable degree of genetic

heterogeneity. In other words, this variability would be anticipated if the various migrant groups represented diverse cultures from the mainland that once on the island continued separate evolutionary paths. Nevertheless, it is still possible that a number of evolutionary forces such as geographical isolation and genetic drift may have led to the partitioning of a single wave of migrants into non-interbreeding populations with distinct characteristics once on the island. Yet, the data presented here is more parsimonious with multiple dispersals from the mainland.

As an earlier report indicated (Zeng et al., 2014), Taiwanese aboriginal populations exhibit extensive genetic heterogeneity. Our

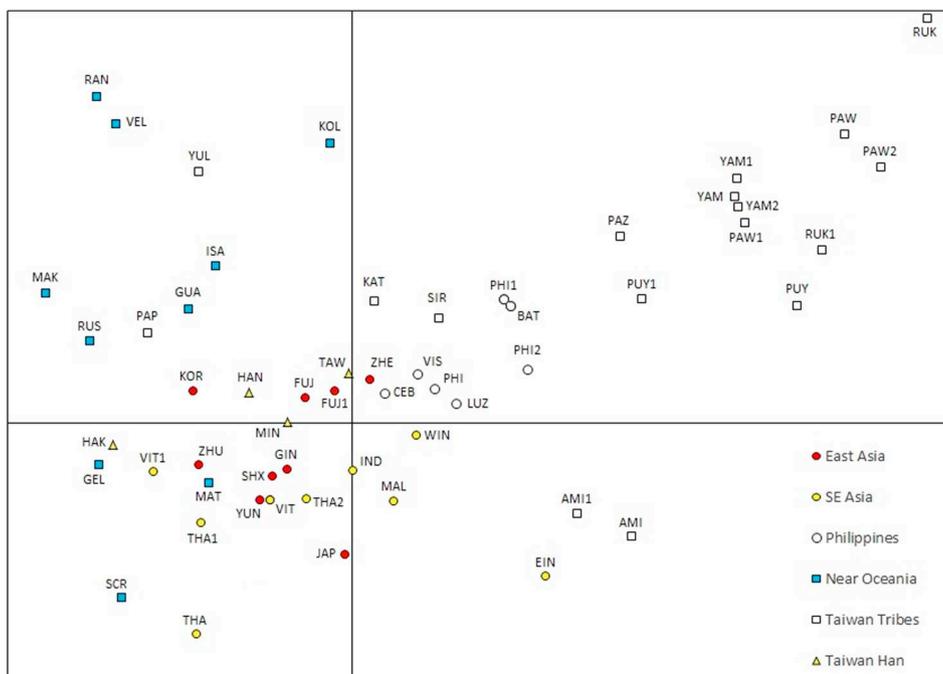


Fig. 2. Expanded center of MDS plot in Fig. 1.

Table 2
Analysis of Molecular Variance (AMOVA) among Taiwanese aboriginal populations using Y-STRs.

Classification criterion	Total variation (%)	Fixation indices		
		Φ_{ST}	Φ_{SC}	Φ_{CT}
Clusters (3 groups)				
Among groups	12.61			0.13*
Among populations within groups	13.98		0.16*	
Within populations	73.41	0.27*		

Partitioning (3 groups): Cluster 1 - BUN, BUN1, PAP, SAI, SAI1, YUL; Cluster 2 - AMI, AMI1, KAT, PAW, PAW1, PAW2, PAZ, PUY, PUY1, RUK, RUK1, SIR, YAM, YAM1, YAM2; Cluster 3 - ATA, ATA1, ATA2, TAR, TSO, TSO1.

* P-value < 0.00001.

current results corroborate this high inter-specific diversity. The estimated genetic R_{st} distances among Formosan tribes reported here demonstrate that these contiguous neighboring groups from a single island are greater than the genetic distances of some Taiwanese tribes to geographical distant populations such as the Solomon Islands. The close genetic affinities of specific Taiwanese tribes to groups from different regions in Oceania (e.g., Solomon Islands), ISEA (e.g., Cebú in the central region of the Philippines) and MSEA (e.g., Thailand) may be the result of multiple origins of the Austronesian expansion from Formosa as well as from MSEA, as previously suggested (Trejaut et al., 2004; Li et al., 2008; Mirabal et al., 2013). Since most Taiwanese tribes segregate closely with populations from the Philippines (e.g., Cebú) and Thailand, the fact that other tribes such as Bunun, Saisiat and Yunlin exhibit greater genetic affinities with groups from the Solomon Islands in Near Oceania may suggest that different aboriginal Taiwanese populations contributed separately to different migration branches of the Austronesian expansion. It is also possible that the paternal gene pools of the Philippines and the Solomon Islands derive from different sources at different times.

The observed differential partitioning of aboriginal Taiwanese as well as SEA and Oceanic populations into three distinct clusters (Fig. 1) also corroborates genetic diversity among the aborigines and is compatible with multiple origins and migration waves into and out of Taiwan. Our AMOVA results indicate strong statistical significance for the partitioning of the tribes into the three clusters. The compact aggregation of populations at the center of the MDS plot represent Taiwanese tribes that reside in the southern region of the island and includes the Yami, a population culturally and linguistically linked to the Batan Islands from the northern most region of the Philippines. The cultural and linguistic affinity of the Yami of Orchid Island to the Philippine Archipelago is corroborated by the presence of the Cebú population within this cluster. Unlike the other Formosan tribes, the Yami shares the same branch within the Austronesian languages, the Malayo-Polynesian subgroup, with the Polynesian island nations of the Pacific Ocean. In addition to Cebú, five other Philippine populations from various provinces from throughout the archipelago group tightly within this aboriginal Taiwanese cluster. These include Visayas, Luzon, Batan and two general collections from the Philippines. The genetic closeness of the Taiwanese aboriginal populations in this cluster to the groups from the Philippine Archipelago is greater than to a number of MSEA and ISEA populations such as Thailand, Vietnam and Eastern Indonesia (Figs. 1 and 2). These relationships are compatible with paternal gene flow between certain southern aboriginal Taiwanese groups and the Philippine Archipelago as a whole. The lesser genetic affinities between the Taiwanese tribes in this cluster to Thailand, Vietnam and Eastern Indonesia may represent a dilution of an Austronesian genetic signal from Formosa as the dispersion wave(s) dispersed southeasterly into an autochthonous background of inhabitants.

The Bunun, Saisiyat and Yunlin tribes of central Taiwan characterize a more diffuse group of native populations. All the non-

Taiwanese aboriginal populations in this cluster reside in the Solomon Islands of Near Oceania. This data is compatible with an independent dispersal out of Taiwan towards Melanesia. The absence of many Taiwanese tribes from this conglomerate may suggest that the Austronesian expansion was not a single homogeneous dispersal but occurred at different times. Noteworthy from the MDS plot and the R_{st} values are the greater genetic distances among the Bunun, Saisiyat, and Yunlin tribes in this cluster compare to the aboriginal populations in the closely packed central cluster. This suggests greater genetic differentiation of these central mountainous tribes. To account for this greater differentiation of the Bunun, Saisiyat and Yunlin tribes, it is possible that the Bunun, Saisiyat and Yunlin groups represent an earlier arrival of MSEA groups to Taiwan that then migrated inland and became isolated in the less accessible regions of the island.

Similarly, a second diffused group of Formosan tribes including the Atayal, Tsou and Taroko (Truku) of the mountainous central region partitions away from the tight conglomerate in the center of the plot. This loose cluster argues for a different group of Taiwanese tribes, unique from the Bunun-Saisiyat-Yunlin assembly, that experienced higher degree of differentiation compared to the populations in the center cluster. Likewise, the grouping made up of Atayal, Tsou and Taroko (Truku) may represent a unique ancient dispersal into Taiwan that ended up being displaced into the central mountainous area of the island.

5. Conclusion

Altogether the genetic data presented here and in previous reports paint a picture of a series of protracted and complex processes that lead to the peopling of Taiwan and Oceania. The data does not contradict the Out of Taiwan hypothesis but underscore scenarios of multiple dispersals into and out of the island contributing to the settlements of the Philippine and Solomon Archipelagos, separately. Although the notion of a single Neolithic farming dispersal into Taiwan is usually invoked to explain the peopling of the island, the diversity of the archeological and linguistic evidence indicates at least three cultural complexes (Ferrell, 1969). The fact that all Taiwanese tribes speak distinct Austronesian languages may result from continuous flow of pre-Austronesian languages from the mainland and linguistic changes within the island.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gene.2018.100001>.

Declaration of interest statement

We have no personal interest, direct or indirect, in any matter that relates to this manuscript.

References

- Abbott, W.G., Winship, I.M., Gane, E.J., Finau, S.A., Munn, S.R., Tukuitonga, C.E., 2006. Genetic diversity and linkage disequilibrium in the Polynesian population of Niue Island. *Hum. Biol.* 78, 131–145.
- Cai, X., Qin, Z., Wen, B., Xu, S., Wang, Y., Lu, Y., et al., 2011. Human migration through bottlenecks from Southeast Asia into East Asia during Last Glacial Maximum revealed by Y chromosomes. *PLoS One* 6, e24282.
- Chang, K.C., 1969. Fangpitou, Tapenkeng and Taiwan Prehistory. Yale Univ. Press, New Heaven.
- Delfin, F., Salvador, J.M., Calacal, G.C., Perdigon, H.B., Tabbada, K.A., Villamor, L.P., et al., 2011. The Y-chromosome landscape of the Philippines: extensive heterogeneity and varying genetic affinities of Negrito and non-Negrito groups. *Eur. J. Hum. Genet.* 19, 224–230.
- Emery, K.O., Niino, H., Sullivan, B., 1971. Post-pleistocene east China sea levels. In: Turekian, K.K. (Ed.), *The Late Cenozoic Glacial Ages*. Yale Univ. Press, New Heaven.
- Excoffier, L., Laval, G., Schneider, S., 2007. Arlequin (version 3.0): an integrated software package for population genetics data analysis. *Evol. Bioinformatics Online* 1, 47–50.
- Ferrell, R., 1969. *Taiwan Aboriginal Groups: Problems in Cultural and Linguistic Classification*. Monogram series no. 17. Institute of Ethnology, Academia Sinica, Taipei.
- Friedlaender, J.S., Friedlaender, F.R., Reed, F.A., Kidd, K.K., Kidd, J.R., Chambers, G.K., et al., 2008. The genetic structure of Pacific islanders. *PLoS Genet.* 4, e19.
- Huang, Y., Chen, J., 1988. Sea level changes along the coast of the South China Sea since

- late Pleistocene. In: Whyte, P., Aigner, J.S., Jablonski, N.G., Taylor, G., Walker, D., Wang, P.X., So, C.K. (Eds.), *The Palaeo Environment of East Asia From the Mid-Tertiary*, Centre of Asian Studies. University of Hong Kong, Hong Kong.
- Hung, H., Carson, M.T., 2014. Foragers, fishers and farmers: origins of the Taiwanese Neolithic. *Antiquity* 88, 1115–1131.
- Hwa, H.L., Tseng, L.H., Ko, T.M., Chang, Y.Y., Yin, H.Y., Su, Y.N., et al., 2010. Seventeen Y-chromosomal short tandem repeat haplotypes in seven groups of population living in Taiwan. *Int. J. Legal Med.* 124, 295–300.
- Jiao, T.L., 2013. First farmers and their coastal adaptation in prehistoric Taiwan. In: Underhill, A.P. (Ed.), *A Companion to Chinese Archaeology*. Blackwell, London.
- Karafet, T.M., Hallmark, B., Cox, M.P., Sudoyo, H., Downey, S., Lansing, J.S., Hammer, M.F., 2010. Major east-west division underlies Y chromosome stratification across Indonesia. *Mol. Biol. Evol.* 27, 1833–1844.
- Kayser, M., Brauer, S., Schädlich, H., Prinz, M., Batzer, M.A., Zimmerman, P.A., 2003. Y chromosome STR haplotypes and the genetic structure of U.S. populations of African, European, and Hispanic ancestry. *Genome Res.* 13, 624–634.
- Kim, S.H., Kim, K.C., Shin, D.J., Jin, H.J., Kwak, K.D., Han, M.S., et al., 2011. High frequencies of Y-chromosome haplogroup O2b-SRY465 lineages in Korea: a genetic perspective on the peopling of Korea. *Investig. Genet.* 2, 10.
- Li, K.T., 2013. The Neolithic archaeology of Southeast China. In: Underhill, A.P. (Ed.), *A Companion to Chinese Archaeology*. London; Blackwell.
- Li, H., Wen, B., Chen, S.J., Su, B., Pramoongjago, P., Liu, Y., et al., 2008. Paternal genetic affinity between Western Austronesians and Daic populations. *BMC Evol. Biol.* 8, 146.
- Lian, Z., 1981. Excavation of Pinan site. *Sci. Mon.* 12, 40–45.
- Liu, K., Muse, S.V., 2005. PowerMarker: an integrated analysis environment for genetic marker analysis. *Bioinformatics* 21, 2128–2129.
- Loo, J.H., Trejaut, J.A., Yen, J.C., Chen, Z.S., Lee, C.L., Lin, M., 2011. Genetic affinities between the Yami tribe people of Orchid Island and the Philippine islanders of the Batanes archipelago. *BMC Genet.* 12, 21.
- Melton, T., Clifford, S., Martinson, J., Batzer, M., Stoneking, M., 1998. Genetic evidence for the proto-Austronesian homeland in Asia: mtDNA and nuclear DNA variation in Taiwanese aboriginal tribes. *Am. J. Hum. Genet.* 63, 1807–1823.
- Mirabal, S., Cadenas, A.M., Garcia-Bertrand, R., Herrera, R.J., 2013. Ascertaining the role of Taiwan as a source for the Austronesian expansion. *Am. J. Phys. Anthropol.* 150, 551–564.
- Olsen, J.W., Miller-Antonio, S., 1992. The Palaeolithic in Southern China, *Asian Perspectives* 31, 129–160.
- Rolett, B.V., Zheng, Z., Yue, Y., 2011. Holocene sea-level change and the emergence of Neolithic seafaring in the Fuzhou Basin (Fujian, China). *Quat. Sci. Rev.* 30, 788–797.
- Ross, M., 2012. In defense of nuclear Austronesian (and against Tsouic). *Language and Linguistics* 13, 1253–1330.
- Severinghaus, J.P., Brook, E.J., 1999. Abrupt climate change at the end of the last glacial period inferred from trapped air in polar ice. *Science* 286, 930–934.
- Soares, P., Trejaut, J.A., Loo, J.H., Hill, C., Mormina, M., Lee, C.L., et al., 2008. Climate change and postglacial human dispersals in southeast Asia. *Mol. Biol. Evol.* 25, 1209–1218.
- Su, B., Jin, L., Underhill, P., Martinson, J., Saha, N., McGarvey, S.T., et al., 2000. Polynesian origins: insights from the Y chromosome. *P. Natl. Acad. Sci. USA* 97, 8225–8228.
- Sung, W., 1981. On Pleistocene people and culture of Taiwan. In: *Essays of International Conference of Sinology, Historical Archaeology Section*.
- Tabbada, K.A., Trejaut, J., Loo, J.H., Chen, Y.M., Lin, M., Mirazon-Lah, M., et al., 2010. Philippine mitochondrial DNA diversity: a populated viaduct between Taiwan and Indonesia? *Mol. Biol.* 27, 21–31.
- Trejaut, J.A., Kivisild, T., Loo, J.H., Lee, C.L., He, C.L., Hsu, C.J., Li, Z.Y., Lin, M., 2005. Traces of archaic mitochondrial lineages in Austronesian-speaking Formosan populations. *PLoS Biol.* 3, e247.
- Trejaut, J.A., Poloni, E.S., Yen, J., Lai, Y., Loo, J., Lee, C., He, C., Lin, M., 2014. Taiwan Y-chromosomal DNA variation and its relationship with Island Southeast Asia. *BMC Genet.* 15, 77.
- Trejaut, J.A., Tsai, Z.-U., Lee, H.-L., Chen, Z.-X., Lin, M., 2004. Cytokine gene polymorphisms in Taiwan. *Tissue Antigens* 64, 492–499.
- Tsang, C.H., Chen, W.S., KT, L.I., Zeng, Y.X., 2011. Report of the Baxiandong Cave Sites, Changbin, Taidong County (The Second Year). Academia Sinica, Taipei.
- Tumonggor, M.K., Karafet, T.M., Hallmark, B., Lansing, J.S., Sudoyo, H., Hammer, M.F., Cox, M.P., 2013. The Indonesian archipelago: an ancient genetic highway linking Asia and the Pacific. *J. Hum. Genet.* 58, 165–173.
- Wu, F.C., Chen, M.Y., Chao, C.H., Pu, C.E., 2013. Study on the genetic polymorphisms of Y chromosomal DNA short tandem repeat loci applied to analyzing the relative affinities among ethnic groups in Taiwan. *Forensic Sci. Int. Genet.* 4, e69–e70 Suppl. Ser.
- Zeng, Z., Rowold, D.J., Garcia-Bertrand, R., Calderon, S., Regueiro, M., Li, L., Zhong, M., Herrera, R.J., 2014. Taiwanese aborigines: genetic heterogeneity and paternal contribution to Oceania. *Gene* 542, 240–247.
- Zhang, S.H., 2000. The Epipaleolithic in China. *J. East Asian Archaeol.* 2, 51–66.