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Review

The genetic history of Peninsular Malaysia



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ABSTRACT

This article explores the genetic history of the various sub-populations currently living in Peninsular Malaysia. This region has received multiple waves of migrants like the Orang Asli in prehistoric times and the Chinese, Indians, Europeans and Arabs during historic times. There are three highly distinct lineages that make up the Orang Asli; Semang, Senoi and Proto-Malays. The Semang, who have 'Negrito' characteristics, represent the first human settlers in Peninsular Malaysia arriving from about 50,000 ya. The Senoi later migrated from Indochina and are a mix between an Asian Neolithic population and the Semang. These Asian genomes probably came in before Austroasiatic languages arrived between 5000 and 4000 years ago. Semang and Senoi both now speak Austro-Asiatic languages indicative of cultural diffusion from Senoi to Semang. In contrast, the Proto-Malays who came last to the southern part of this region speak Austronesian language and are Austronesians with some Negrito admixture. It is from this group that the contemporary Malays emerged.

Here we provide an overview of the best available genetic evidences (single nucleotide polymorphisms, mitochondrial DNA, Y-chromosome, blood groups, human platelet antigen, human leukocyte antigen, human neutrophil antigen and killer-cell immunoglobulin-like receptor) supporting the complex genetic history of Peninsular Malaysia. Large scale sampling and high throughput genetic screening programmes such as those using genome-wide single nucleotide polymorphism analyses have provided insights into various ancestral and admixture genetic fractions in this region. Given the now extensive admixture present in the contemporary descendants of ancient sub-populations in Peninsular Malaysia, improved reconstruction of human migration history in this region will require new evidence from ancient DNA in well-preserved skeletons. All other aspects of the highly diverse and complex genetic makeup in Peninsular Malaysia should be considered carefully for genetic mapping of disease loci and policy formation by health authorities.

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Abbreviations: ISEA, Island Southeast Asia; HLA, human leucocyte antigen; mtDNA, mitochondrial DNA; SNP, single nucleotide polymorphism; NGS, next generation sequencer; ya, years ago.

1. Introduction

Peninsular Malaysia lies along a major trading route between East and West. It has long been a crossroad between widely differing peoples, languages and cultures (Diamond, 2014). It is not surprising, therefore, that the history of its population has been one of complex blending of

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disparate elements. What is perhaps surprising is that to date there have been few complete accounts of this story. Some are now beginning to emerge e.g. from Deng et al. (2014, 2015), Hatin et al. (2014) and Aghakhanian et al. (2015) and these include testing of anthropological hypotheses using high resolution genetic data.

Today the Malays form the majority of the population (54.6%) together with Chinese (24.6%) and Indians (7.3%) – see Population and Housing Census of Malaysia (2010). The Malays have a formal political definition (Article 160(2), Constitution of Malaysia) as a:

'Malaysian citizen born to a Malaysian citizen who professes the religion of Islam, habitually speaks the Malay language, conforms to Malay custom and is domiciled in Malaysia'.

However practical this definition might be, it does not take full account of their anthropological status as an ethnic group of the Austronesian peoples who speak a Malayo-Polynesian language (Bellwood, 1993, 2007). Neither does it take account of the various constituent Malay subethnic groups or their genetic ancestry and their place alongside the indigenous Orang Asli (Nagata, 1974; Fernando, 2002). In turn, the Orang Asli themselves consist of at least three genetically distinct lineages (Semang, Senoi and Proto-Malays) of people (Fix, 2008; JAKOA – see Table 1 for their subgroups, geographical locations and languages). Presently they make up only approximately 0.5% of national population of Peninsular Malaysia. Some might say it would be better to classify these three populations linguistically, Aslian versus Malayo-Chamic; the Senoi plus the Semang and the Proto-Malays plus the Malays respectively. However, this would be to neglect the deep time origin of the Semang and their presumed lost Proto-Papuan language. Nonetheless, the significance of the Orang Asli should not be understated. The Malays who make up the majority of population living Peninsular Malaysia are thought to be admixed descendants of Proto-Malays by intermarriage with other late arrival ethnicities, including Chinese and Indians (Simon, 2012).

2. Waves of prehistoric migration build the layer cake

It is now appropriate to construct a historic account of the settlement of the region as these successive waves of people arrived. Not only did they follow one another in time, but also they came from quite different directions. The Semang are the smallest Orang Asli group and are believed to be the very first settlers (~74–40 kya) in Peninsular Malaysia (Zuraina,

Table 1Orang Asli groups and sub-groups in Peninsular Malaysia.

Groups ^a	Sub-groups ^a	Locations ^a	Language ^b
	Kensiu	Baling, Kedah	Austro-Asiatic
	Kintak	Gerik, Hulu Perak	Austro-Asiatic
C	Lanoh	Perak	Austro-Asiatic
Semang	Jahai	Remote areas of Perak and Kelantan	Austro-Asiatic
	Mendriq	Gua Musang, Kelantan	Austro-Asiatic
	Bateq	Pahang, Kelantan and Terengganu	Austro-Asiatic
	Che Wong	Raub and Temerloh, Pahang	Austro-Asiatic
	Mah Meri	Coastal areas of Selangor, Putrajaya, and Negeri Sembilan	Austro-Asiatic
Senoi	Jahut	Temerloh and Jerantut, Pahang	Austro-Asiatic
	Semoq Beri	Pahang and Terengganu	Austro-Asiatic
	Semai	Pahang, Perak and Selangor	Austro-Asiatic
	Temiar	Perak, Kelantan, and Pahang	Austro-Asiatic
	Kuala	Batu Pahat and Pontian, Johor	Austronesian
	Kanaq	Kota Tinggi, Johor	Austronesian
Proto-Malay	Seletar	Coastal regions of Johor	Austronesian
F10t0-Walay	Jakun	Southern parts of Peninsular Malaysia	Austronesian
	Semelai	Pahang, Negeri Sembilan and Johor	Austro-Asiatic
	Temuan	Negeri Sembilan, Selangor and Johor	Austronesian

^a Jabatan Kemajuan Orang Asli (JKOA; http://www.jakoa.gov.my, accessed 5th May 2015).

1990; Barker et al., 2002; Barker, 2005; Hill et al., 2006; Bellwood, 2007; Oppenheimer, 2012; Baer, 2014). Today these people remain as small bodied survivors in the forests of central Malaya. They are associated with the first of 'Out of Africa' dispersal wave by Anatomically Modern Humans. Other branches of this lineage stretch even further to Australia and Papua New Guinea (i.e. Papuans) (Bellwood, 2007). In Malaysia, these phenotypically dark-skinned, frizzy haired Semang speak Aslian (a branch of Mon-Khmer), which is believed to have first been introduced to them by the Senoi (Austroasiatic speaking peoples who entered Malaya from the north, perhaps around 4000 years ago if we link their arrival with the arrival of Neolithic cultures from southern Thailand) leading eventually to linguistic replacement; see Blust, 2013 and Peter Bellwood, personal communication). The Senoi are physically taller and lighter than Semang and migrated south from mainland of Southeast Asia to Peninsular Malaysia (Hill et al., 2006). They were thought to have arrived as late as 4000 ya, but see Jinam et al. (2012) for genetic evidence suggesting the possibility of an even earlier arrival from around 10,000 ya. A date this early is totally impossible for the Aslian languages themselves. The Austroasiatic language family has an agricultural proto-language with terms for rice, first attested in the general region around 4000 years ago. People living 10,000 years were Hoabinhians, hunter-gatherers, with Australo-Papuan craniofacial features (Peter Bellwood, personal communication). Neolithic material culture including cord-marked pottery and rice cultivation has been described for several archaeological sites linked the Senoi way of life in Southern China, Vietnam and Thailand (Bellwood, 2005). These linguistic and archaeological reconstructions match well with those early studies on mtDNA and Y-chromosome markers (Ballinger et al., 1992; Melton et al., 1995, 1998; Kayser et al., 2000; Su et al., 2000; Macaulay et al., 2005; Trejaut et al., 2005; Hill et al., 2006; Ricaut et al., 2006).

The Austronesians make up the final wave of the major human migration into the Island South East Asia (ISEA) region extended to include Peninsular Malaysia. The original story that developed from genetic studies generally pointed to either Taiwan or ISEA as the homeland of the Austronesians. These apparently competing accounts depended to some extent on which populations were being studied and what genes were tested (Chambers, 2006; Chambers and Edinur, 2015). Sometimes completely different pictures emerged because different genetic loci were used. For instance, data generated from a maternal marker (i.e. mitochondrial DNA) seemed to contradict those from paternal Y-chromosome DNA polymorphisms. The matrilineal mtDNA data suggested a Taiwanese ancestry for Austronesians in accord with 'Out of Taiwan' hypothesis (Hill et al., 2006; Melton et al., 1995). On the other hand, Y-chromosome patrilines indicated ISEA as the distal source of the great Austronesian Diaspora (Underhill et al., 2001). The controversy has been clarified by Tabbada et al. (2010) and Ko et al. (2014). These authors showed clear evidence for a southward dispersal of Austronesian mtDNA haplotype lineages, consistent with the 'Out of Taiwan' migration pattern leading into ISEA and across the Melanesia (Near Oceania) and Polynesia (Remote Oceania). Movement of the Austronesian-speaking populations is coupled with genderbiased introgression of paternal markers from indigenous Semang and Papuan populations, respectively. This is a particularly important process and arises because the Austronesian populations practise matrilocal marriages which greatly contribute towards the gender-biased gene flow (Jordan et al., 2009; Hage and Marck, 2003).

It must be admitted that genetic evidence has its own limitations particularly when it arises from sex-limited genepools. Pre-historic reconstruction using these markers is much more affected by founder events and genetic drift than autosomal genes. It is fortunate, then, that several large scale, high resolution studies of autosomal loci have recently been reported; see the HUGO Pan-Asian SNP Consortium (2009), Deng et al. (2014, 2015), Hatin et al. (2011, 2014), Jinam et al. (2012), Lipson et al. (2014). These new works have provided a reliable genetic framework upon which to test historic reconstructions like the one advanced here. We will return to these later.

^b Ethnologue languages of the World (http://www.ethnologue.com, accessed 5th May 2015).

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