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Commentary

On Peopling of India: Ancient DNA perspectives *By* K Thangaraj and Niraj Rai

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In recent years, studies on ancient DNA (aDNA) of humans have become of monumental importance in investigating human migrations, identifying fine population structures and human adaptation. The Indian subcontinent is a rich potpourri of genetic and socio-cultural diversity shaped by the mingling of its autochthonous people who came to India from Africa during the Late Pleistocene, with immigrants arriving though diverse routes (Quintana-Murci *et al.* 1999; Bamshad *et al.* 2001; Basu *et al.* 2003; Macaulay *et al.* 2005; Mellars 2006; Sengupta *et al.* 2006). However, as the authors Thangaraj and Rai aptly pointed out, till date aDNA studies have been largely restricted to Western Eurasia, comprising Europe, Central Asia and Mediterranean regions (Lazaridis *et al.* 2016; Esposito *et al.* 2018). The existing results from ancient genomics studies have been devoid of information pertaining to South Asia; consequently, the overall picture of origin and migration of South Asians across the Indian subcontinent have remained unclear. However, ancient DNA analysis on 4500-year-old skeletal remains excavated from a Harappan civilization site at Rakhigarhi, in Haryana, may soon change this scenario and provide a valuable glimpse into the prehistory of India.

Thangaraj and Rai, in this review, have provided an exhaustive account of various archeological sites across India. Further, they have meticulously reviewed how ancient DNA-based investigations have impacted evolutionary biological studies over the years and appropriately pinpointed the major issues in obtaining good-quality ancient biological materials from the India subcontinent. The Indian subcontinent, owing to its tropical geographical location, is prone to unpredictable climatic fluctuations, engendering overall conditions that are not amenable for DNA preservation over long periods of time. However, as indicated by the authors, recent advancements in laboratory techniques have been able to surmount this problem. Their description of the discovery and subsequent analyses of Neanderthal and Denisovan genomes is not only informative but also highlights the importance of ancient DNA studies in dissecting the complex relationships among ancient and modern humans, and other extinct hominins.

I note here that the main focus of the article is to shed light on the 'peopling of India'. While the authors here extensively described the aDNA studies initiated and completed in India, the section on 'ancient DNA and South Asian ancestry' could have provided more insight into how recent ancient DNA studies have helped in understanding the origin and migration of South Asians. A recent aDNA study based on 362 ancient genomes, mentioned by the authors, sheds light on complex origin of South Asians (Narasimhan *et al*. 2018). It suggested that a South Asian hunter-gatherer lineage with close genetic proximity to the present-day Andamanese people (AASI) admixed with Iranian agriculturists approximately in the 3rd millennium BCE and were referred to as the 'Indus Periphery' gene pool; it was suggested that this gene pool was the major source of the subsequent peopling of the Indian subcontinent. The Ancestral North Indian (ANI) and Ancestral South Indian (ASI) gene pools likely arose around 2nd millennium BCE during the decline of Indus Valley Civilization (IVC), which spurred numerous waves of human migrations spanning across the Indian subcontinent. The southward migration of Middle to Late Bronze Age people from Steppe (Steppe MLBA) into the Indian subcontinent is hypothesized to have occurred around this time. It was envisioned that the Indus-Periphery-related groups admixed with the Steppe MLBA immigrants to form the ANI, while other Indus Periphery people migrated further south and eastward within peninsular India to mingle with AASI and formed the ASI (Narasimhan *et al*. 2018). Thus, the ASI ancestry appears to be mostly derived from AASI. While the obvious limitation to the above-mentioned aDNA study was unavailability of ancient South Asian genomes, the investigators here endeavored to overcome this problem by implementing three samples from Turan, referred to as the 'Indus Periphery' samples owing to their geographic proximity to the IVC region and genomic proximity to Swat Protohistoric

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Graves in Swat Valley, Pakistan (SPGT). Further, this aDNA study precisely indicated the Steppe MLBA and not the Steppe EMBA genomes to be the plausible source of Steppe ancestry among South Asians genomes (Early Mid Bronze Age). This has been corroborated by previous Y-chromosome-based analyses (Underhill *et al.* 2015; Silva *et al.* 2017) and a recent study determining West Eurasian Ancestry among Pakistani Hazara population (Das and Upadhyai 2019).

Thangaraj and Rai appropriately mentioned that Indian populations are prone to population-specific recessive diseases due to founder effects likely resulting from the millennia-old practice of endogamy. However, given that the impact of endogamy is not limited only to susceptibility towards ancestry-specific diseases, a more elaborate discussion on the same was warranted. Notably, endogamy plays a crucial role in preserving and maintaining genomic integrity of the Indian communities, which may be crucial for investigating their genomic affinity with various ancient and modern-day populations. For example, a recent study has shown the genomic affinity of Ror people from northwest India with the ancient individuals from Swat Valley (Pathak *et al*. 2018). It surmised this genomic similarity to be a result of genetic continuity since the Bronze Age migrations from the Steppe people rather than a recent admixture. The genomic integrity of Rors has been preserved since then likely due to the practice of endogamy in the community.

The review by Thangaraj and Rai concludes on a promising note. The tropical environs of the Indian subcontinent inherently obstruct aDNA studies due to the problems in securing well-preserved biological materials that can potentially yield good-quality DNA. However, given that it has become increasingly possible to obtain endogenous aDNA from petrous bones found in hot tropical conditions, it is expected that relevant information will soon become available from South Asian aDNA analysis, which is anticipated to provide invaluable direct insights to our own prehistory. Finally, as Thangaraj and Rai reflected, meaningful aDNA analyses demand large-scale interdisciplinary collaborations bringing together population geneticists, anthropologists, archeologists and even linguists. As is evident, the time to rediscover India's glorious evolutionary heritage is here; the current review collates fundamental principles, existing literature, findings and future scopes in this context which will hopefully excite and enthuse researchers across the spectrum to engage in studies shattering boundaries between the fields of science and humanities.

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