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Multiple Domestication Centers of the Indian Pig Population

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Abstract

The domestication of animals is a major milestone in human history and has been studied in various fields. Pig domestication, in particular, has been widely studied, and it is believed that India is one of at least six domestication centers. However, there is a lack of systematic studies using high-resolution genetic markers, including complete mitogenomes, to investigate the domestication and genetic roots of pigs in India. In the present study, we investigated the origin and evolution of Indian pigs using mitochondrial genetic data to complement archaeological data sets. The phylogenetic status of Indian pig breeds was determined by analyzing all available mitochondrial data, incorporating a global data set of 239 mitogenomes. The Bayesian and maximum likelihood tree analyses unveiled at least eight haplogroups diverging from three main branches, two of which are geographically restricted to India. We propose that the North Indian domestic haplogroup might represent an independent in situ domestication event in North India, probably dating before ∼5,000 YBP. An additional North East Indian domestic haplogroup is nested within a widespread Asian clade that also includes Indian mitogenomes from the Andaman and Nicobar Islands that diverged more recently from distinct East and Southeast Asian roots. In conclusion, we propose that North Indian farmers could have been responsible for the independent domestication of local wild boars giving rise to the current domestic lineage identified in North India. At least one additional domestic lineage arrived in India more recently and remained mainly localized in the northeast. Domestic mitogenomes from the Indian islands show a notable connection with pig populations from Vietnam, and their arrival might be related to Austroasiatic-speaking human populations. Overall, this study provides valuable insights into the complex dynamics of pig domestication in India.

Key words: domestication, pig, Indian subcontinent, boar, migration.

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Significance

The study of past human populations and their demography in South Asia can be challenging in the absence of ancient DNA data. However, the study of animal domestication can be helpful in understanding past human migration and their colonization. Utilizing the power of mitochondrial DNA data ($N = 239$), coupled with archaeological data, we explored aspects of pig domestication in India. In our study, we detected at least three different domestic pig lineages, one of which from North India seems to be an independent domestication at least before ~5,000 YBP, rather than brought from the Near East, as was thought, and supports the hypothesis of the existence of farmers in North India in parallel with the Indus Valley civilization. The second lineage (Andaman and Nicobar Island) must have been brought by people from Southeast Asia (after 3,000 BCE), which corroborates with the Austroasiatic people migration. Pigs from Northeast India (third lineage) show diverse patterns of their origin but are heavily influenced by wild boar/pigs from China. Thus, our study provides valuable insights into the local origin and importation of different lineages of pigs in India and their correlation with human populations.

Introduction

Domestication studies have been pivotal to many interdisciplinary studies to answer various questions related to domestication from fields like geoarchaeology, zooarchaeology, archaeobotany, archaeology, and genetics (Dobney and Larson 2006; Jensen 2014; Larson et al. 2005, 2014). The domestication of plants and animals was one of the most significant cultural and evolutionary transitions for the human species during the Neolithic period (Larson et al. 2014). The adoption of such practices has revolutionized the transition from hunter-gatherers to stock-raised and sedentary lifestyles. These led to a massive expansion of human populations and demographic increase outward from the center of domestication and agricultural origins (Larson et al. 2014).

Wild boars (*Sus scrofa*) originated in Southeast Asia (SEA) around 4 to 4.5 million years ago (Mya) and have colonized nearly all of Europe and mainland Asia over the past 1 million years (Groenen 2016; Larson et al. 2010, 2014). Utilizing the molecular clock hypothesis, with fossil calibration priors, it has been estimated that European and Asian wild boar populations diverged well before domestication, around 1.5 to 2 Mya (Frantz et al. 2013, 2015). Even within Asia, wild boar populations appeared to be well diverged; the estimated divergence time in North China, South China, and India ranges from around 1.5 to 0.5 Mya (Frantz et al. 2013, 2015; Choi et al. 2020). Due to its wide distribution, *S. scrofa* was the only species among the Suidae family that was domesticated. The domestication of pigs (hereafter referred to as domesticated pigs) occurred independently at two different locations, in eastern Anatolia and China, ~9/10 thousand years ago (KYA) (Giuffra et al. 2000; Groenen 2016). Following this initial domestication, pigs accompanied early farmers as they spread from East Anatolia to Europe and throughout China, respectively (Cai et al. 2019; Larson et al. 2007, 2014; Tanaka et al. 2008; Larson et al. 2010). The domestication of pigs has been extensively studied with different approaches in archaeology (Jing and Flad 2002; Flad et al. 2007; Barton et al. 2009) and genetics (Ai et al. 2021; Chen et al. 2018; Choi et al. 2020; Larson et al. 2005, 2007, 2010; Wu, Jiang, et al. 2007). These diverse studies have concluded that there were multiple domestication centers (East Asia, Tibetan Plateau, SEA, India, and Anatolia) like in the case of other domesticated animals (Luikart et al. 2001; Troy et al. 2001; Vilà et al. 2001; Liu et al. 2006). However, previous studies were based on low-resolution sequences (D-loop region of mitochondrial DNA [mtDNA]) (Choi et al. 2020; De et al. 2021; Fang and Andersson 2006; Kusza et al. 2014; Larson et al. 2005; Ramírez et al. 2009; Scandura et al. 2008; Sharma et al. 2023; Veličković et al. 2015, 2016; Vilaça et al. 2014). Such low-resolution studies have caused confusion regarding which lineage is basal between India and Island of SEA (ISEA) (Cho et al. 2009; Ashrafzadeh et al. 2018). Moreover, recent studies using complete mitochondrial (Chen et al. 2018; Ni et al. 2018; Khederzadeh et al. 2019) and genomic data (Ai et al. 2015, 2021; Ma et al. 2019) have revealed many interesting insights, but no studies have focused specifically on the domestication in India.

The Indian wild boar (*S. scrofa cristatus*) seems to be highly diverse and unique (Gupta et al. 2013). Previous studies (Choi et al. 2020) detected two clades within India, one of which (clade B) was very close to the most basal branch of phylogeny (ISEA), whereas the other (clade C1) formed a sister branch with European and East Asian wild boar. It was recognized that there was a possibility of independent (cryptic) domestication in India from native wild boars (Larson et al. 2005, 2010). It was also suggested that the pigs might have been introduced from Eastern Asia or Near Eastern sources and are massively mixing with the indigenous wild population. Few complete sequences of pigs and wild boar from India have been sequenced and studied so far, mainly limited to mitochondrial assembly (Singh et al. 2017; De et al. 2019; Kumar et al. 2019; Das et al. 2024), except for a study on the pig lineage from Andaman and Nicobar Islands (De et al. 2021).

Table 1 Haplotype diversity (HD), nucleotide diversity per site (Pi), and average number of nucleotide differences (k) among Eurasian domestic pigs

Population	HD ± SD	Pi	K
All population (239)	0.998 ± 0.001 (204)	0.00463	75.7012
Europe (11)	0.982 ± 0.046	0.00090	14.764
East China (27)	0.986 ± 0.014	0.00106	17.521
East Asia (4)	0.833 ± 0.222	0.00398	65.500
South West China (25)	1 ± 0.011	0.00110	18.047
South Central China (82)	0.993 ± 0.003	0.00084	13.897
Indian_North East (14)	0.989 ± 0.031	0.00389	63.978
Tibet (6)	1.00 ± 0.096	0.00084	13.800
North Indian domestic pigs (4)	1.00 ± 0.177	0.00530	87.000

Here, we undertook a detailed study on the pig domestication in India, using available modern mtDNA data and adding three novel complete mitochondrial sequences ($N = 239$). These data were complemented by archaeological data (rock art depictions and excavated bone remains). We discussed the phylogeography of species with a focus on domestication in India. Specifically, we examined the origin of Indian pig lineages, their relationship to the global population (including the wild population), and possible human association with archaeological data to support domestication.

Results

Mitogenome Variability

Mitogenome variability was checked among all populations (with sample size > 3), including wild boar and domestic samples. The haplotype diversity was 0.9983 ($H = 204$), where multiple haplotypes were shared in close geographic proximity. However, we did not find any haplotype sharing between wild boar and domestic samples. There were 1520 polymorphic sites with 879 parsimony information. Although genomic diversity was variable among all groups (Table 1), Southwest China, Tibet, Indian domestic pigs, and South-Central China were highly diverse in haplotype diversity. In contrast, pigs from East China and Northeastern India were the most diverse with high levels of polymorphisms.

Reconstruction of the Phylogeography of Domestic Pigs and Wild Boar

Maximum likelihood (Fig. 1) and Bayesian inference (Fig. 2) phylogenies were built using 239 complete mitogenomes. Both topologies are largely consistent with each other and with the median-joining network shown in Fig. 3, despite its known limitations (Kong et al. 2016). All phylogenies were constructed with *Sus verrucosus* as an outgroup. Our results corroborate previous studies (Larson et al. 2005; Zhang, Liu, et al. 2022) with a clear distinction between the European and Asian clades. It is worth mentioning that wild boar and domestic pigs are mostly intermingled within the tree. This is particularly evident for the major branches, including both Asian and Indian pigs, without any clear microgeographic distribution pattern. Starting from the root, the wild boar from Malaysia (SEA) represents a basal lineage. Pigs from India show a peculiar pattern. After the initial split of North (peninsular) Indian wild boars, a distinct domestic clade encompasses mostly pigs from North India and two mitogenomes from North East India, one from the Doom breed of Assam, MZ846190.1 nondescript breed, ON804887.1. Most of the other breeds from North East India form a distinct clade embedded in the major widespread Asian branch. Mitogenomes from Andaman and Nicobar Islands also fall into this clade but in different positions, highlighting distinct mitochondrial connections. The Andaman mtDNA is closer to Chinese samples, whereas the Nicobar mitogenome shares the most recent common ancestor with Vietnamese pigs (Figs. 1 and 2).

Taking into account that wild boar and domestic pig of India form separate clades (Fig. 2), in addition to original data ($N = 239$), we incorporated 110 D-loop sequences from Indian pigs and wild boar (Larson et al. 2005; Sharma et al. 2023), to double-check the possibility that domestic pigs and wild boars from India share the same haplotype. The parsimony network tree obtained strongly supports the hypothesis that North Indian pigs might have been domesticated from local wild boars (supplementary fig. S1, Supplementary Material online).

Our survey of the rock art and faunal remains of wild boar and pig suggests their predominance in North India, where they are depicted in various contexts, e.g. hunting, deification, and domestication from the Mesolithic to the historical period (supplementary tables S3A and S3B, Supplementary Material online). The rock art pattern also suggests they were hunted and/or domesticated not only for food (Suryanarayan et al. 2021) but also for religious (deification) purposes. Our field survey to the tribal areas of North and Central India has revealed an age-old system where pigs have been regularly sacrificed in front of village deities (*Gram Devta Deeh*).

Haplogroup Classification

Taking into account the phylogenetic outcomes, the pig mtDNA haplotypes were classified into haplogroups using a nomenclature system similar to the human one (Y Chromosome Consortium 2002; van Oven 2015), but consistently as possible with the recent one proposed for pigs by Zhang, Liu, et al. (2022). It is worth mentioning that any defined haplogroup should encompass at least three mitogenomes with a minimum of two haplotypes (i.e. differing by at least one homoplasmic mutation) and should

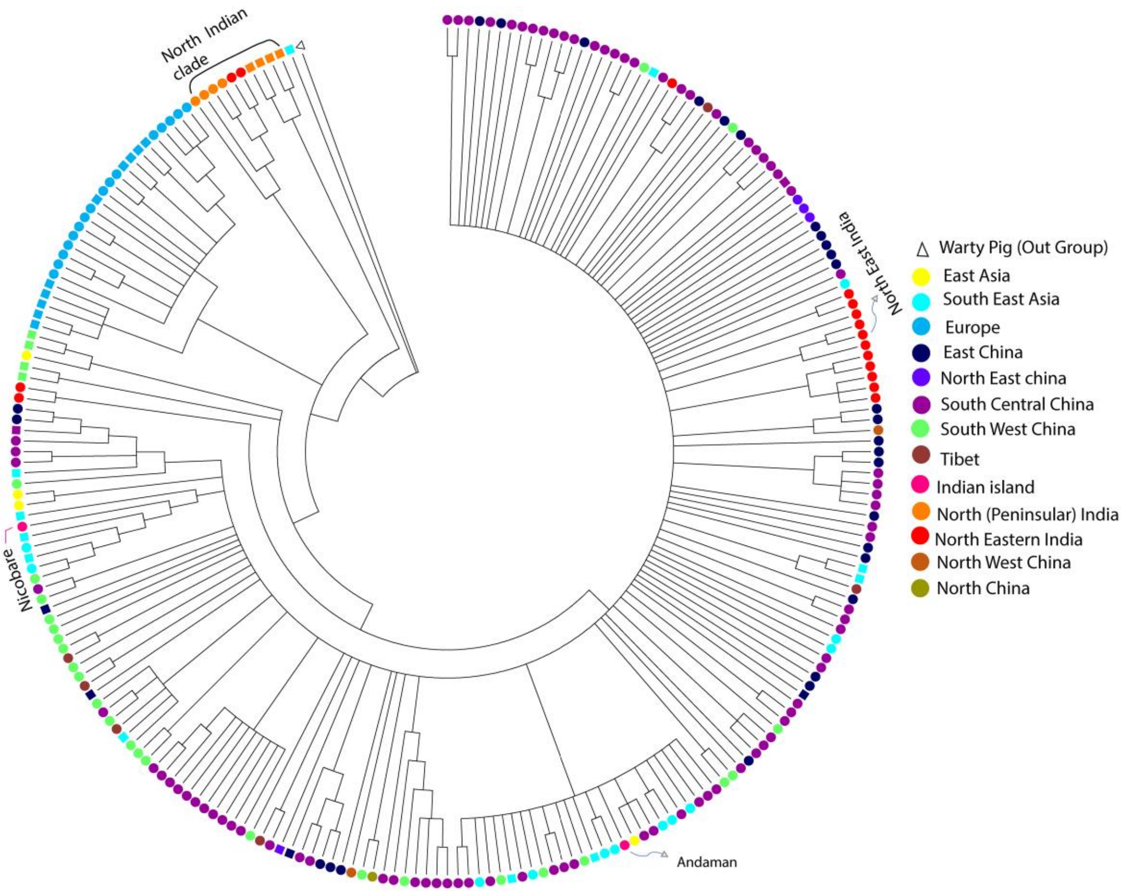

Fig. 1. Maximum likelihood tree representing three different lineages (North Indian Clade, North East India, Andaman, and Nicobar) in India. The circle and square shapes represent domesticated and wild samples, respectively, whereas different index colors within the circle and square represent different groups.

be defined by at least one mutation in the coding region, as in Olivieri et al. (2017). A total of eight major haplogroups were identified, each with a characteristic mutational motif and Bayesian age estimates (supplementary fig. S2, Supplementary Material online). The nomenclature for the major haplogroups takes into account its geographic distribution. However, as we moved toward the tips, we did not observe such clear patterns, but rather signs of founder effects and star-like expansions (supplementary fig. S2 and S3, Supplementary Material online).

The haplogroups In1_W with Indian wild boars and In2_D with North Indian domesticated breeds are geographically restricted to India. As previously mentioned, North East Indian breeds fall into the Asian widespread haplogroup AS4_W/D, which also includes pigs from the Andaman and Nicobar Islands, but with different relationships, the first with Chinese breeds, the former with Vietnamese pigs. Interestingly, haplogroup AS1_W is restricted to Southwestern China and Taiwan, while AS2_W and AS3_W are mostly limited to Southwest China and East China, respectively (Figs. 1 to 3). As expected, Haplogroup Eu1_W and Eu2_D/W are completely restricted to Europe.

Discussion

The spatial and temporal distribution and comigration of humans and animals have been key questions that require a detailed investigation. Multiple domestication events have been detected in nearly all major domesticated species (Achilli et al. 2012; Larson et al. 2014). Although the domestication of pigs has been widely studied, the genetic variation of pigs in India has not been extensively explored. There is a consensus that wild boar originated in the ISEA and that domestication occurred primarily in the Near East, East Asia, and Tibet (Larson et al. 2005, 2010; Yang et al. 2011; Cai et al. 2019). A local domestication in India has already been proposed but has not been thoroughly investigated. Here, we collected a data set with 239 complete mitogenomes to understand better the origin, evolution, and timing of domestication in India and its relationship to the global wild boar and pig populations.

The basal position of the Malaysian wild boar in our phylogeny agrees with previous studies supporting its outgroup behavior (Larson et al. 2005; Cho et al. 2009), although some others have suggested that it could be a sister clade

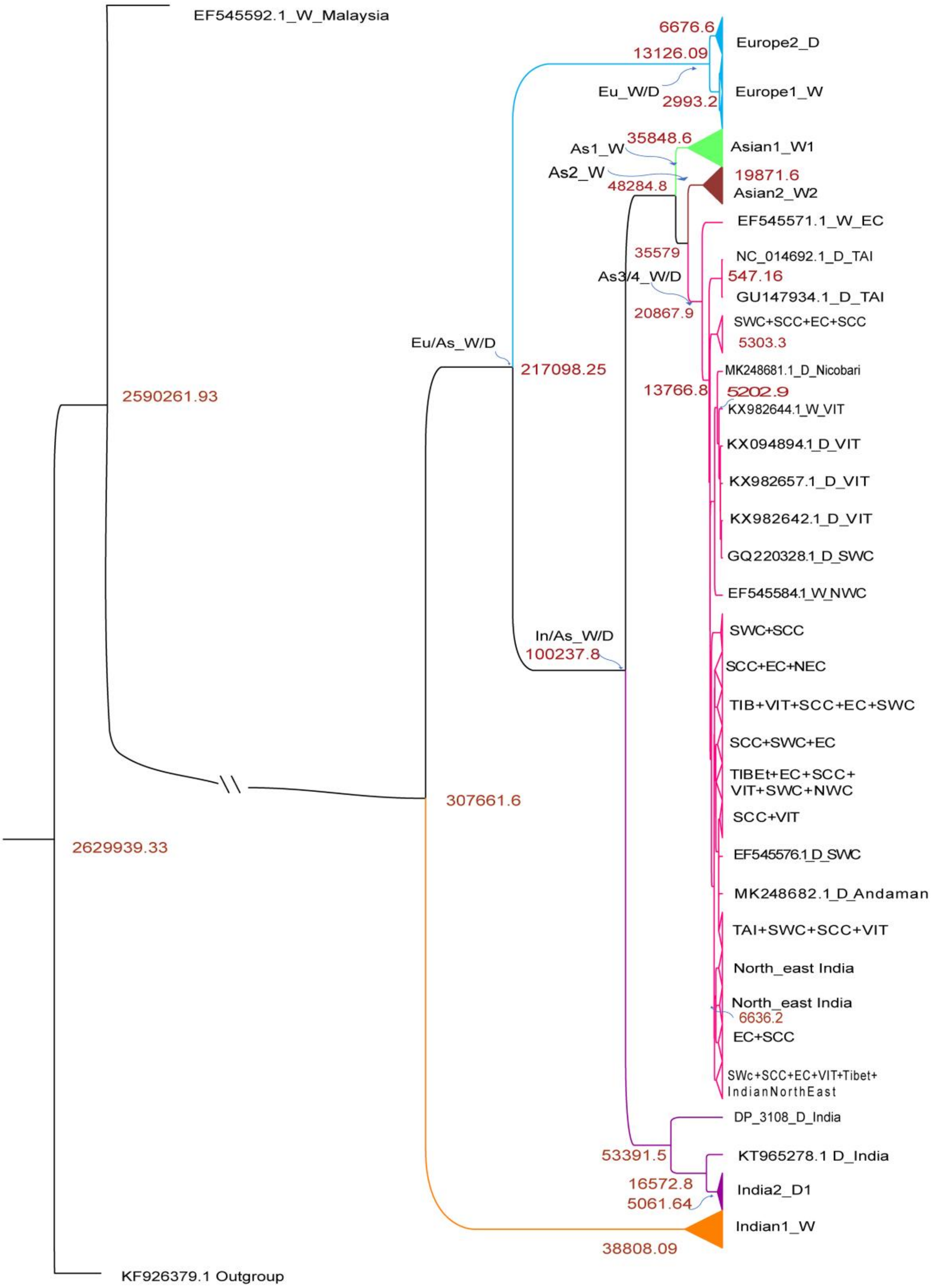

Fig. 2. The Bayesian time tree of Eurasia samples, where each different haplogroup has been colored to make it distinct with an appropriate name, and other samples have been grouped for better visualization.

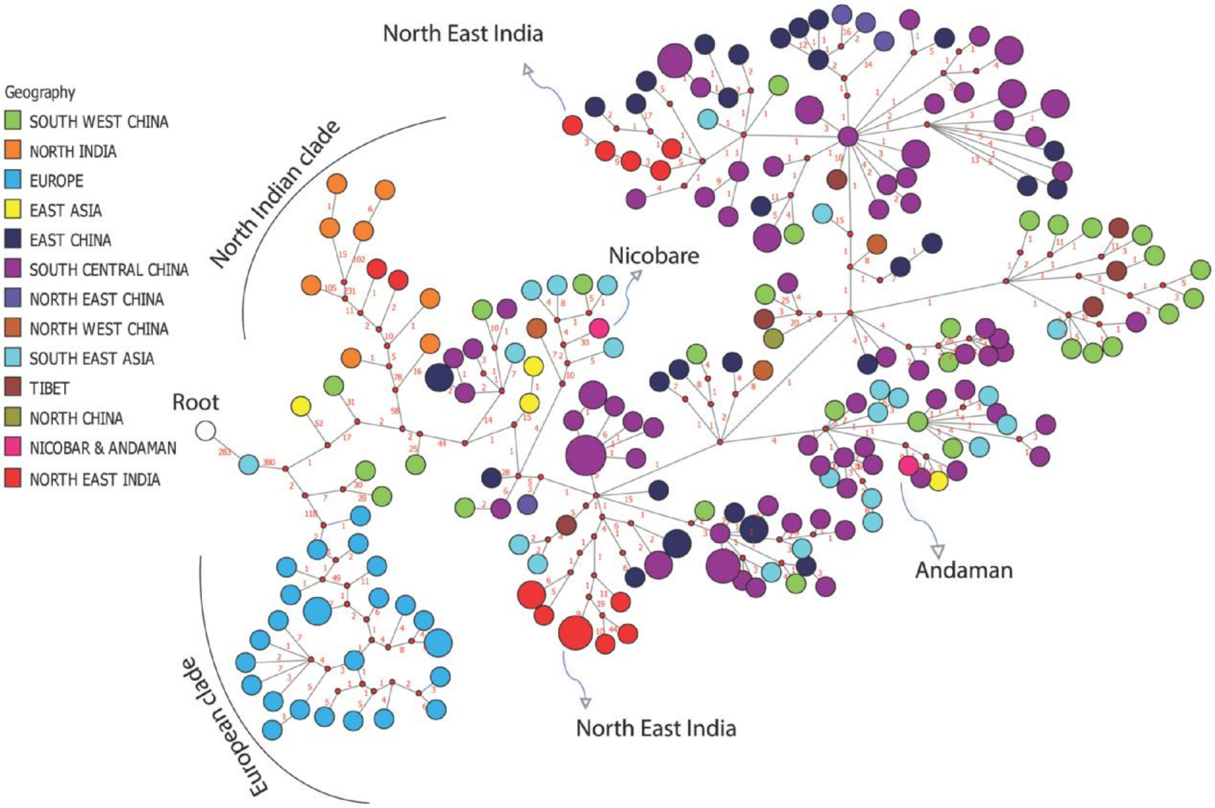

Fig. 3. Medium joining network tree constructed with NETWORK, based on complete mitochondrial sequence, representing three domestic pig lineages (North Indian, Andaman and Nicobar Islands, and North East India) of India.

of the Indian wild boar (Ashrafzadeh et al. 2018). Another controversial issue concerns possible gene flow between European and Asian pigs (Ashrafzadeh et al. 2018; Choi et al. 2020; Kusza et al. 2014; Veličković et al. 2015; Wu, Yao, et al. 2007; Khalilzadeh et al. 2016; Larson et al. 2005). Our phylogenies, built with three different approaches, provide clear evidence for two separate sister clades diverging from a common ancestor of about 217,000 YBP from a mitochondrial perspective.

Domestication in India from Local Wild Boars

Wild boar, after originating in ISEA, diverged off onto the mainland and subsequently spread through the Indian subcontinent. Within India, the wild boar has a wide distribution and is considered an agricultural pest in many parts of India (Desai et al. 2021). An existing study based on a partial control region detected the presence of domestic pigs from central India clustered with the wild boar from the same area (Larson et al. 2005). Therefore, it was hypothesized that India harbors at least one independent center of pig domestication. Our mitogenome analyses revealed that all sequences of wild boar and domestic pigs have unique haplotypes, indicating high diversity and variation likely stimulated by multiple introgressions. India has an ancient lineage of wild boar (In1_W) (De et al. 2021; Kumar et al. 2019). Here, we suggest that the Indian haplogroup In2_D is the result of local domestication. The two pig samples from Assam, which fall in the same clade, add credibility to this domestication event. It is worth mentioning that the high number of mutations differentiating the present-day North Indian wild boars and domestic pigs (supplementary figs. S2 and S3, Supplementary Material online) might suggest a domestication from now-extinct wild boars. A previous study (Larson et al. 2005; De et al. 2021, 2022) has shown that wild boars from North India form a single clade, with animals from west and south and separated from East India. Moreover, several subclades indicate a high level of population structure within the wild boar population of India that could have provided the necessary variation for local domestication events.

There is evidence of early rice domestication by farmers in the Ganga Plain during the Neolithic period (Tewari et al. 2006). The early branching pattern of haplogroup In2_D from the wild lineage (Fig. 2) strongly suggests that the same early farmers might also have been responsible for an indigenous pig domestication event in North India.

In support of this scenario, many remains of domesticated animals have been reported in the Indus Valley Civilization (Thomas and Joglekar 1994), along with pig lipid residues from pottery, more recently (Suryanarayan et al. 2021). In addition, various rock art depictions and pig remains have been found across India from the Mesolithic to the historical period (supplementary tables S3A and S3B, Supplementary Material online). Domestication in the Indian subcontinent has been reported for zebu cattle (*Bos taurus*) and water buffalo, ~8000 and 4500 YBP (Fuller et al. 2011; Larson et al. 2014), which also supports the existence of early farming communities in the Indian subcontinent.

Taken together, the paleo-artistic and mtDNA data are consistent with a possible local domestication event in North India that likely occurred before 5,000 YBP.

Nicobar Islands and Austroasiatic Migration

The Andaman and Nicobar Islands, a Union Territory of India, are part of the ISEA. The Andaman and Nicobar Islands archipelago is located in the Bay of Bengal and the Andaman Sea and is known for its high endemism of faunal species (De et al. 2021, 2022). Andaman has its own native wild boar (*S. s. andamanensis*), which is genetically more similar to the wild boar of North East India, but phenotypically and genetically distinct from mainland wild boar (De et al. 2022). However, despite the proximity of the islands, Andaman and Nicobar pigs show very distinct relationships and occupy different clades in phylogenetic trees, sharing more recent common ancestries with Southeast Asian and East Asia lineages (Figs. 1 to 3). This link can be related to human dispersal, as genetic studies suggest an earlier arrival of Nicobarese populations to the Indian subcontinent (De et al. 2021; Thangaraj et al. 2005, 2006), which in turn might have brought pigs to the Islands. The human genetic data are consistent with the migration of pigs from SEA to the Nicobar Islands in the last 5,000 years (Mishra et al. 2024). Similarly, our Bayesian analysis indicates a split of the Nicobarese pigs from the Vietnam ones around 5,000 YBP (Fig. 2), which is corresponding to the dispersal of the Nicobarese human population to the Island (Mishra et al. 2024).

Complexity on the Identity of Indian Eastern Pigs

Among the registered breeds in India, the majority are from the northeastern part of India. These breeds are unique; they form several separate clades in maximum likelihood trees (Fig. 1) and Bayesian trees (Fig. 2), but they are far from North Indian pigs, which indicates that they might be domesticated from different sources of wild boar. Moreover, they are genetically closer to Southeast and East Asian breeds. Therefore, there is an influence of the Chinese wild boar population, which can be explained by the maximum likelihood tree and the Bayesian tree (Figs. 1 and 2). This suggests a diverse spread of local North East Indian lineage and comigration of East Asian-related pig lineages with humans into the North East Indian region (Tamang et al. 2018). However, few sporadic mitogenomes from North East India clustered with the East Asia clade (Fig. 1), which might be due to the recent influence of East Asian breeds. Overall, Northeast Indian breeds form a single clade, which might reflect their uniqueness, but to meet demand, a large number of commercial (hybrid) breeds are being used specifically in the Northeast part of India, which may endanger unique local genetic pools. Furthermore, the haplogroup As4_W/D contains pigs from almost all regions (including eastern Indian and the Indian islands), showing the clear homogenization with local wild boar and pigs in recent times and the massive human influence.

Conclusion

Our detailed study provides comprehensive insights into the genetic roots of indigenous pig breeds in India, shedding light on their domestication history and phylogeographic distribution. By integrating genetic and archaeological data, we have traced the complex dynamics of pig domestication in the Indian subcontinent. Genetic analyses of complete mitochondrial sequences revealed at least three distinct lineages of pigs in India, with one lineage indicating an independent in situ domestication event in northern India around 5,000 YBP. These findings challenge previous hypotheses and highlight the significance of local domestication by early North Indian farmers. In addition, our study highlights the genetic connections between Indian pig populations and those from other regions, such as the Andaman and Nicobar Islands, which show notable affinities with Southeast Asian populations, particularly Vietnam, possibly related to linguistic and genetic affinities of the Nicobarese.

Constraints of Research and Future Recommendations

Although there are limitations in the sample size from India, this can be considered as the first systematic study to discuss domestication in India and to underline the uniqueness of wild boar and domestication event(s) from India. The present study provides new insights into the genetic diversity of Indian boars and pigs and their relationship to the global population. The first domesticated pigs in Europe were brought from the Near East by early farmers around 7,500 YBP, but a Near Eastern signature was completely lost in Europe and they acquired the mtDNA haplotype found in local European wild boar (Frantz et al. 2015, 2019; Larson et al. 2007; Ottoni et al. 2013), which suggests the postdomestication gene flow. Therefore, to understand pre- and postdomestication gene flows, a large number of samples from modern as well as ancient DNA need to be undertaken.

Materials and Methods

Sample Collection and Data Retrieval

Complete mitochondrial sequences were retrieved from the National Center for Biotechnology Information (NCBI). We assembled and analyzed 369 modern mitochondrial genomes. These complete mitogenomes covered almost all major regions of the world. We sequenced three novel samples from North India. The DNA was extracted from tissue, and the method was described by Gupta et al. (2013). Three samples belong to Uttarakhand (DP_2776-UK), Uttar Pradesh (DP-1-UP), and Chhattisgarh (DP-3108-CH) states of India. After quality control, we selected 239 mitochondrial genomes for statistical analysis.

DNA Extraction, PCR Amplification, and Sequencing

Genomic DNA (gDNA) was extracted from the collected samples using the DNeasy Blood & Tissue Kit (Qiagen, Hilden, Germany). Polymerase chain reactions (PCRs) were conducted in 10 µl volumes containing ~80 to 100 ng of extracted gDNA, 5 µl of QIAGEN Multiplex PCR Buffer Mix, and 5 pmol of each primer. PCR amplification utilized 23 overlapping fragments of complete mtDNA (supplementary table S1, Supplementary Material online). The PCR cycling conditions included an initial denaturation step at 95 °C for 15 min, followed by 35 cycles of denaturation at 95 °C for 40 s, annealing at 56 to 58 °C for 40 s, extension at 72 °C for 1 min, and a final extension step at 72 °C for 15 min. The reaction efficiency and reliability were monitored using controls. The amplification of PCR products was visualized by electrophoresis on a 2% agarose gel under UV light after staining with ethidium bromide dye. The amplified PCR products were treated with Exonuclease-I and Shrimp alkaline phosphatase (USB, Cleveland, OH, USA) at 37 and 80 °C, respectively, for 15 min each to remove any residual primer. The purified amplicons were then sequenced bidirectionally using BigDye Terminator 3.1 on an automated Genetic Analyzer 3500XL (Applied Biosystems, Carlsbad, CA, USA).

Data Analysis

Phylogeographic Analysis

All 239 sequences were aligned with the wild boar reference sequence (Accession no: EF545567.1) by Muscle in MegaX (Kumar et al. 2018). After the alignment, the data were double-checked manually for errors. The tandem repeat between nucleotide positions 700 to 919 (220 BP) in the D loop was not included in downstream analyses. The number of repeats was variable within samples, indicating a high degree of heteroplasmy. Also, it has been previously shown that repeats are not helpful for phylogenetic reconstruction (Ghivizzani et al. 1993; Yu et al. 2013). Javan warty pig (*S. verrucosus*) was used as an outgroup for phylogeny construction. Based on the geographical origin of each sequence, data were classified into geography groups (supplementary table S2, Supplementary Material online). This geographical stratification was solely for study purposes.

Bayesian Analysis and Time-Divergent Analysis

BEAST v2.7.7 (Bouckaert et al. 2014) was used to generate Bayesian trees. After several attempts, the best-fitting model (highest posterior probability and likelihood) was obtained using only complete mitogenomes to retain mitogenome sequences with <5% of missing data. The model (TrN + I + G) and substitution rate (1.2612×10^{-7} for the complete mitogenome) were used in agreement with Zhang, Yang, et al. (2022). Internal node age estimates previously based on high-quality whole-genome sequencing data (Zhang, Liu, et al. 2022) were also used as priors: *Sus* speciation time at 1.36 Mya; divergence time between European and Asian wild pigs at 219 KYA; and split between European wild and domesticated pigs at 13 KYA. The MCMC chain was run for 50 million, storing data every 10 K runs and discarding the first 10% of runs as burn-in. The log value was checked using Tracer v1.7.1, where all effective sample size (ESS) values > 200 were retained. The final Bayesian tree was computed with TreeAnnotator (burn-in of 10% and posterior probability bound of 0.95) and visualized with FigTree V.1.4.4 (Rambaut et al. 2018).

Haplogroup Classification and Genetic Variability

We have used a systematic approach and implemented the classification of clades into haplogroups, similar to humans (Y Chromosome Consortium 2002; van Oven 2015). To classify all sequences into haplogroups, we used a designated reference (EF545567.1). This reference was used previously to classify the haplogroups, with limited samples, mostly from one clade (Wu, Yao, et al. 2007). Also, Indian samples were lacking in that analysis. Hence, in the present study, 239 full mitochondrial sequences of both domestic pigs and wild boar were classified. PAUP v5.0 (Phylogenetic Analysis Using PAUP*) was used for haplogroup classification, which generates the parsimony tree as well as a diagnostic mutation on each branch. Haplogroups were classified by observing branches, nodes, and specific mutation motifs. Besides this, basic indices of genetic variability among each group, like haplotype diversity, nucleotide diversity, and polymorphism, were calculated using DNASP 6 (Rozas et al. 2017) and Arlequin ver 3.5.2.2 (Excoffier et al. 2007).

Supplementary Material

Supplementary material is available at *Genome Biology and Evolution* online.

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Author Contributions

G.C., A.A., S.K.G., and S.D. conceived and designed this study. A.K. and S.K.G. collected samples and performed molecular experimental works. S.D., N.R.M., P.P.S., R.K.P., R.K.M., and A.K. performed computational analyses. S.K.T. provided and wrote the archaeological aspects of pig and boar. G.C., S.D., P.P.S., R.K.P., A.K., S.K.G., A.K., A.C., S.K.T., N.R.M., and A.A. wrote the manuscript. All authors approved the final version of the manuscript.

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Conflict of interest

The authors declare no conflict of interest.

Data Availability

The three new sequences have been submitted to the NCBI with accession numbers: PV057163 (DP_2776_UK), PV057164 (DP_3108_CH), and PV057165 (DP_Uttar_pradesh).

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