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Genomic investigation of a non-travel *Plasmodium falciparum* case linked to imported malaria in China's post-elimination era

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Abstract

Background Although China has achieved malaria elimination, the risk of reintroduction persists due to imported *Plasmodium falciparum* cases. Occasional infections without a clear travel history present challenge to routine epidemiological investigation and underscore the need for advanced tracing tools.

Methods Whole-genome sequencing (WGS), principal component analysis (PCA), and identity-by-descent (IBD) analysis were applied to investigate a *P. falciparum* case reported in Chongqing, China, in 2019. The patient had no overseas travel history but was treated at the same hospital with a confirmed imported case from the Democratic Republic of the Congo (DRC).

Results Genomic analysis placed the unidentified case within the West and Central African parasite cluster. IBD analysis showed a high degree of relatedness (IBD = 0.9) between this case and the DRC-imported case, suggesting a potential transmission link. These findings indicate the likely Central African origin of the infection and raise concerns about local transmission risk even in a post-elimination setting.

Discussion This case highlights the limitations of traditional epidemiology in detecting cryptic transmission routes. Genomic epidemiology enables finer-scale resolution of parasite origin and relatedness, providing critical evidence in elimination-phase malaria control.

Conclusions Genomic tools such as WGS, PCA, and IBD analysis can enhance national malaria surveillance systems by identifying infection sources and clarifying transmission routes. Their integration supports elimination-stage strategies and helps prevent malaria reintroduction in formerly endemic regions.

Keywords *Plasmodium falciparum*, Genome, Local transmission, Genomic tools

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Background

Malaria is a potentially fatal disease caused by *Plasmodium* parasites transmitted by *Anopheles* mosquitoes [1]. With the highest global burden in terms of morbidity and mortality among parasitic diseases, malaria remains a major public health challenge [2]. Recent efforts by countries and international organizations have significantly advanced malaria control and elimination, narrowing its global scope. China has made remarkable progress in eliminating malaria through its National Malaria Elimination Programme (NMEP), launched in 2010 to interrupt local transmission. By 2017, China reported zero local malaria cases for the first time, marking a major milestone. After a 3-year validation period, China received malaria elimination certification from the World Health Organization (WHO) in 2021 [3]. However, the risk of re-establishing transmission remains due to the increasing number of imported cases, largely from Chinese labourers returning from malaria-endemic regions and foreign travellers. This highlights the need for robust surveillance and response systems to prevent malaria reintroduction and sustain elimination.

Malaria imported from Africa constitutes the majority of cases in China. For example, 2488 malaria cases were reported in 2023, with 2487 imported and 2016 of which were from 42 African countries, accounting for 81.1% of total cases [4]. According to the WHO 2024 World Malaria Report, 263 million cases were reported globally, with 94% in Africa, and an estimated 608,000 deaths in 2023 [5]. In non-endemic areas, most cases are imported, though occasional reports of cases without travel history necessitate investigation for alternative transmission routes [6], such as airport malaria [7], transfusion-transmitted malaria [8–10], or local vector bites (introduced malaria). In such cases, existing surveillance mechanisms may benefit from more refined tools to trace the geographic origin and potential transmission chain, especially when traditional epidemiological data are limited.

In this context, a unique *Plasmodium falciparum* malaria case reported in 2019 in Chongqing, a metropolis in southwest China, was investigated. The patient with no travel history to malaria-endemic areas raising concerns about the origin and potential transmission route of the infection. To enhance the investigational power of the current surveillance framework, we introduced whole-genome sequencing (WGS) alongside analytical methods, such as Identity by Descent (IBD), Principal Component Analysis (PCA), and phylogenetic reconstruction to trace the likely geographic source of this case. The analysis identified a strong genetic link to African isolates, suggesting that the infection was related to a previously confirmed imported case. This study demonstrates how incorporating genomic methods into malaria surveillance systems can strengthen case-tracing accuracy and support post-elimination control efforts.

Methods

Surveillance framework: China's "1–3-7" strategy

To prevent re-establishment of malaria following elimination, China has implemented the "1–3-7" surveillance and response strategy [11]. This approach requires case reporting within 1 day, case verification and classification within 3 days, and response actions (e.g., treatment, spraying, education) within 7 days [11, 12]. Figure 1 illustrates the operational flow of this strategy for different *Plasmodium* species and transmission seasons [13].

Case presentation

On April 22, 2019, the District Centers for Disease Control (CDC) in Chongqing reported a *P. falciparum* malaria case. The patient, a 38-year-old woman residing in Yubei District, a part of Chongqing municipality, exhibited fever, chills, and headache following a cervical cyst excision. Bone marrow smears confirmed *P. falciparum* infection, later validated by microscopic examination and PCR assay. The epidemiological investigation revealed no history of blood transfusion or prior malaria infection. Coordination with local police and customs confirmed no overseas travel. The case was investigated under China's "1–3-7" pipeline [14]. No indigenous malaria transmission had been reported in Yubei for decades. Five imported malaria cases were reported in 2019, one of which, from the Democratic Republic of the Congo (DRC), had been hospitalized in the same hospital but in a different ward. Vector surveillance with mosquito traps failed to capture any *Anopheles* mosquitoes, and no breaches in hospital protocols were found.

Sampling of *P. falciparum* parasites and whole-genome sequencing

Among the five imported *P. falciparum* cases reported in Chongqing in 2019, two samples met the sequencing quality criteria and were included in the study. One of these, referred to as Chongqing02 in our analysis, was hospitalized at the same time and in the same facility as the Yubei case of unknown origin. Because of this unique overlap, particular attention was given to this sample as a potential source of secondary transmission. The other sequenced sample from 2019, Sample-D-Pf6-1, was also confirmed to be imported from the Democratic Republic of the Congo (DRC). Additionally, a retrospective investigation was conducted for all malaria cases reported in Chongqing over the past 5 years. All available case samples were subsequently sequenced, including samples imported from countries such as Angola (AO), Republic of the Congo (ROC), South Sudan (SD), Tanzania (TZ),

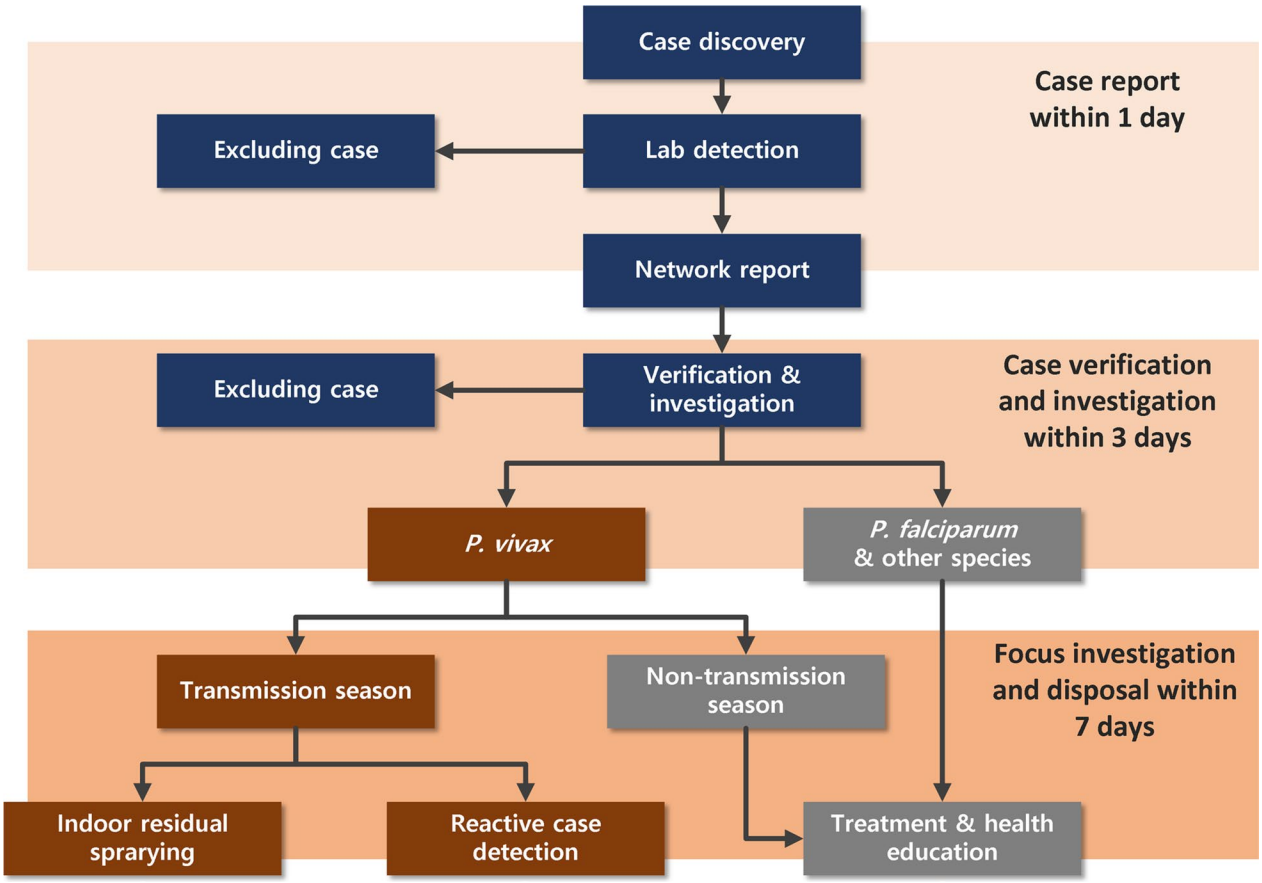

Fig. 1 Workflow of China's "1-3-7" malaria surveillance and response strategy. The system ensures rapid case reporting, verification, and focused intervention, helping to prevent onward transmission of imported cases

Central African Republic (CF), Uganda (UG) and Zambia (ZM). To assess the robustness of the IBD analysis, a pair of samples from the same DRC patient—collected before and after treatment—was included. All cases included in this study were Chinese nationals who had acquired *P. falciparum* infections during travel abroad and were diagnosed upon return to China.

Samples were selected based on high parasite density (200,000–300,000 parasites/μl) to ensure sequencing integrity. A total of 25 samples were analysed, including 21 cases reported in Chongqing (3 from 2019 and 18 from 2015 to 2018), 2 IBD control samples from another province, and 2 previously published samples from the China–Myanmar border (CMB) [15] used for regional validation. All samples met quality control standards and were included in the final analysis (Table S1). Direct whole-genome sequencing was performed as previously described [16, 17]. Briefly, DNA was extracted from each frozen whole blood sample using DNeasy Blood & Tissue Kit (Qiagen, UK) and sheared into 350 bp fragments to construct genome libraries (Covaris Inc., Woburn, MA). All libraries were sequenced on Illumina X-10 and generated paired-end reads. All reads were filtered by removing low-quality sequences using Trimmomatic [18] and mapped to the *P. falciparum* 3D7 genome using BWA [19]. Bam file modification was undertaken using Picard 2.6, and the genotyping was performed using a base quality score recalibration pipeline based on GATK4 workflows [20]. Variable proportions of reads from all isolates were mapped to the 3D7 reference genome and aligned onto 95% of the reference genome at 14–59-fold coverage. The annotated *P. falciparum* 3D7 reference genome sequence was downloaded from the PlasmoDB.org [21]. Thirty samples from each of 13 countries were selected using the Pf3k Project database (Table S2). The samples were chosen randomly from the dataset available through MalariaGEN's publicly available VCF files. SNP data were extracted from these samples to establish a reference database for comparison with our study isolates [22, 23].

Population structure and genetic analysis

PCA was performed using the ade4 R package to visualize the genetic structure of the Chongqing sample in comparison to global *P. falciparum* samples. Additionally, a Neighbour-Joining (NJ) tree was constructed to trace the phylogenetic relationships and determine the origin of the Chongqing sample. To explore potential kinship and transmission links, IBD analysis was performed across the genomes of all imported *P. falciparum* samples detected in Chongqing city that year. Pairwise IBD was measured using hmmIBD with default parameters, calculating the fraction of IBD for each position across accessible regions of the chromosomes [24, 25].

Results

PCA of Chongqing and reference populations

This study presents, for the first time, *P. falciparum* genomic data from African countries including Angola, DRC, ROC, South Sudan, Zambia, Uganda, and Tanzania, generated from imported cases in China. 23 blood samples from Chinese nationals who had traveled to Africa and were diagnosed with *P. falciparum* malaria upon returning to Chongqing or another province. Of these, 3 were reported in 2019 and 18 were previously archived cases from 2015 to 2018; the remaining 2 were reference samples from a DRC case used for IBD validation. In addition, 2 previously published CMB samples were included for comparison. PCA was applied to explore the population structure of the imported samples in the context of publicly available genomes from 13 African countries and the CMB.The F1F2 and F2F3 plots revealed that *P. falciparum* samples clustered according to their geographic origin, forming two distinct groups: one comprising Asian samples and another consisting of African samples. Notably, the two Chongqing samples consistently clustered within the African group, indicating a clear African origin. This was particularly relevant because the two samples — namely, the unknown Chongqing case and a related case from the same hospital—were initially considered to be genetically linked. The CMB samples clustered appropriately within the Asian group (Fig. 2), confirming the reliability of the analytical approach.

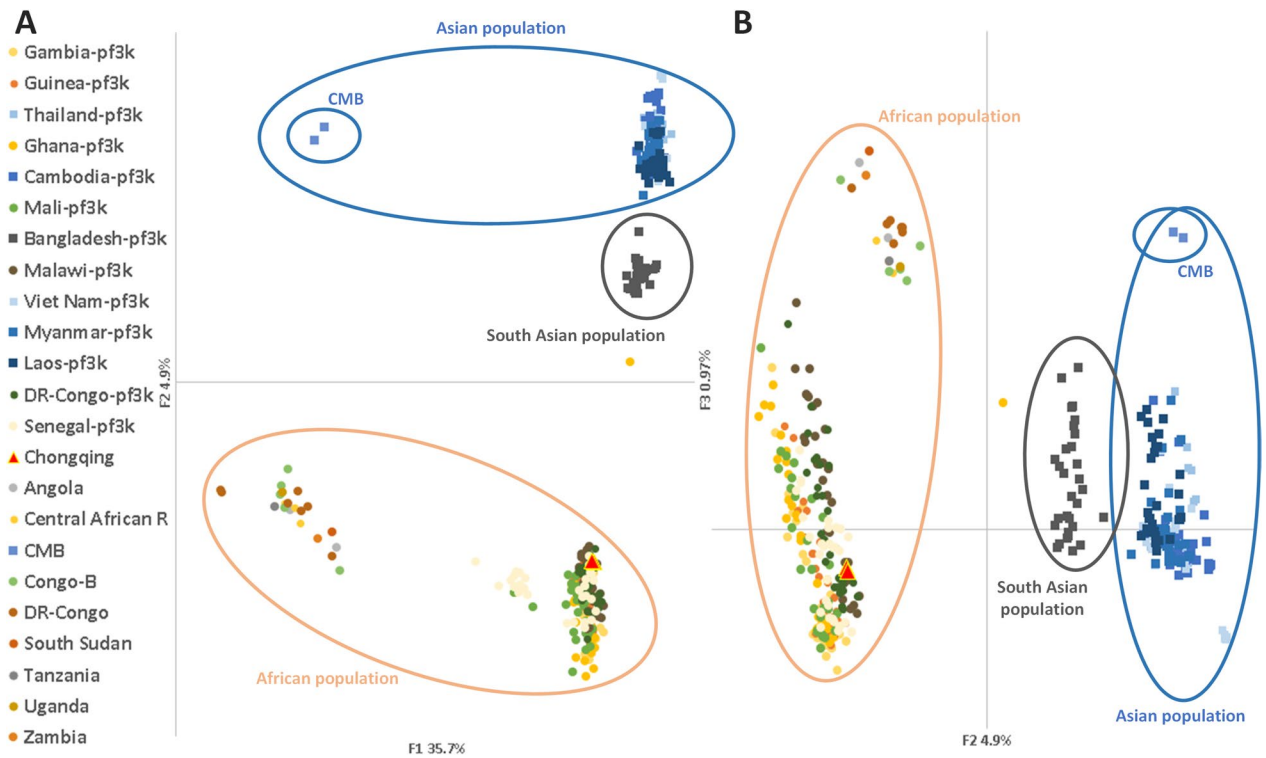

Fig. 2 Principal component analysis (PCA) of *P. falciparum* samples from this study and reference datasets. **A** PCA based on the first two components (F1 and F2), which explain 35.7% and 4.9% of the total variance, respectively. **B** PCA based on the second and third components (F2 and F3), which explain 4.9% and 0.97% of the variance. Each point represents a single sample: circles indicate African-origin samples, and squares indicate Asian-origin samples. Colours denote different countries. The sample marked with a red triangle represents the Chongqing case of unknown origin. Despite differences in SNP density and sequencing platforms between this study and Pf3K data, PCA demonstrates that African and Asian *P. falciparum* populations are clearly separated along F2, and finer-scale geographic substructure can be resolved with F3

Phylogenetic analysis and geographical origin of Chongqing case

A neighbor-joining (NJ) tree was constructed using reference samples from Africa and Asia. The tree revealed clear genetic clustering by geographic origin. Notably, the two Chongqing samples clustered with African isolates, particularly those from ROC, Angola, DRC, South Sudan, and Tanzania, suggesting an African origin, likely from the DRC. In contrast, Asian and Southeast Asian samples, including those from Thailand, Myanmar, and Vietnam, formed distinct clusters, highlighting the genetic divergence between African and Asian populations. The CMB samples also formed a separate cluster, reinforcing their unique genetic profile. This clustering pattern (Fig. 3) validates the reliability of our genetic analyses in determining the Chongqing samples' geographic origin.

IBD analysis of Chongqing samples

The IBD analysis included 23 samples from imported *P. falciparum* cases in Chongqing, including the unknown Chongqing case and another case from the same hospital, with a particular focus on cases from countries surrounding the DRC. As a control, 2 of these samples are pre-treatment and post-treatment sample from the same patient to assess the accuracy of the IBD analysis [26].

The results revealed two pairs of samples with IBD values greater than 0.5. The control pair of pre- and post-treatment samples showed an expected IBD value close to 0.8, confirming the reliability of the method. More notably, a second pair, consisting of the unknown Chongqing sample and a sample from another patient hospitalized in the same facility with a travel history to the DRC, exhibited an IBD value of 0.9, suggesting a high degree of relatedness. This finding supports the hypothesis that the two cases are genetically linked, indicating a shared transmission origin. In contrast, the remaining pairs had IBD values below 0.3, showing no significant kinship or transmission links. These results confirm the absence of secondary local transmission, further validating that the Chongqing case was imported rather than locally acquired (Fig. 4).

To validate the methods and ensure robustness, two rounds of method verification were conducted. First, during the traceback process, samples from the CMB were introduced and correctly clustered within the Asian group in both PCA and NJ-tree analyses. Second, during the follow-up investigation, a control pair from the same patient before and after treatment was included, showing an expected IBD value of 0.718. Additionally, all other sample pairs had IBD values less than 0.5, supporting the accuracy of the analytical approach. The overall IBD values being less than 0.3 provided evidence against local secondary transmission, which was consistent with the observed findings.

Discussion

China has reached a significant public health milestone by eliminating malaria, reducing the number of cases from 30 million to zero indigenous cases. However, while this achievement is remarkable, it does not equate to eradication. Every year, a large number of Chinese citizens travel to Africa, Southeast Asia, and other regions with high malaria prevalence for work, business, and tourism, increasing the risk of acquiring malaria abroad [27], This presents ongoing risks and challenges in preventing the reintroduction of malaria and maintaining China's elimination status [28].

Among the regions contributing to the global malaria burden, sub-Saharan Africa, and particularly the DRC, stands out as a critical hotspot. The DRC and its neighbouring countries bear a disproportionately high malaria burden, with poverty playing a central role in sustaining transmission (Table S3). Limited access to healthcare, inadequate public health infrastructure, and insufficient funding for vector control programs are compounded by widespread socio-economic challenges. For instance, many families in these regions live below the international poverty line, making preventive measures, such as bed nets or timely treatment, inaccessible. Frequent travel between China and malaria-endemic regions for work, particularly by migrant labourers from impoverished communities, introduces a persistent risk of importing cases into malaria-free areas like China. Understanding the socio-economic and epidemiological contexts of these source countries is essential to tailoring prevention strategies and mitigating the reintroduction of malaria.

In this context, determining the origin of cases like the one described in this study is crucial to sustaining China's malaria elimination status. However, the current malaria surveillance system in China does not yet fully leverage technological advances such as genomic analysis to address these challenges. This study conducted a genomic investigation of a malaria case with an unknown source in Chongqing, China, in 2019. The analysis provided valuable insights into the origin and potential transmission pathways of imported malaria cases, demonstrating the utility of genomic tools in tracing the sources and understanding the dynamics of malaria transmission. This is especially important even in regions like China that have successfully eliminated the disease, as it supports efforts to prevent the re-establishment of local transmission.

In 2019, five *P. falciparum* malaria cases were reported in Chongqing, China, all classified as imported except one case from Yubei District with

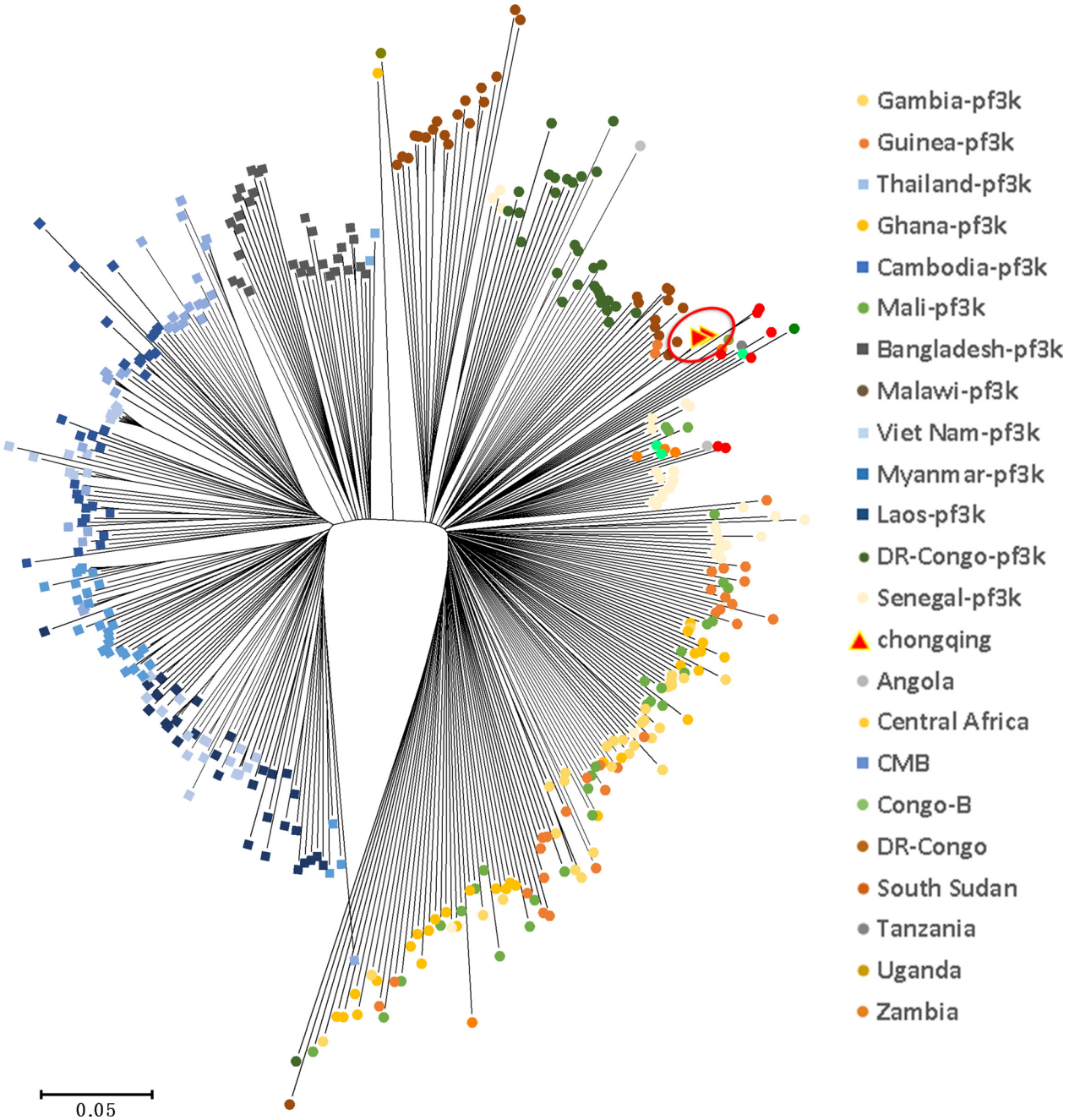

Fig. 3 Phylogenetic tree of *P. falciparum* samples from this study and reference datasets. Neighbour-Joining tree was constructed using genome-wide SNPs from imported samples and publicly available reference samples from the Pf3K project. Branch length corresponds to genetic distance (scale bar = 0.05 substitutions/site). Colors indicate country of origin, and shapes represent regional grouping (Circles: African samples, Squares: Asian samples). The sample of unknown origin from Chongqing is highlighted with a red triangle. Sample labelling follows the same symbol and colour conventions as Fig. 2 for consistency and ease of comparison

no documented travel history. This case was initially recorded as a potential local transmission event, raising public health concern in a country that had already achieved malaria elimination. Accurate source tracing was therefore critical to distinguish between imported and indigenous transmission and to assess whether secondary spread had occurred.

The PCA and NJ tree analyses placed the unknown Chongqing case within the African cluster, closely aligned with isolates from the DRC, while CMB samples

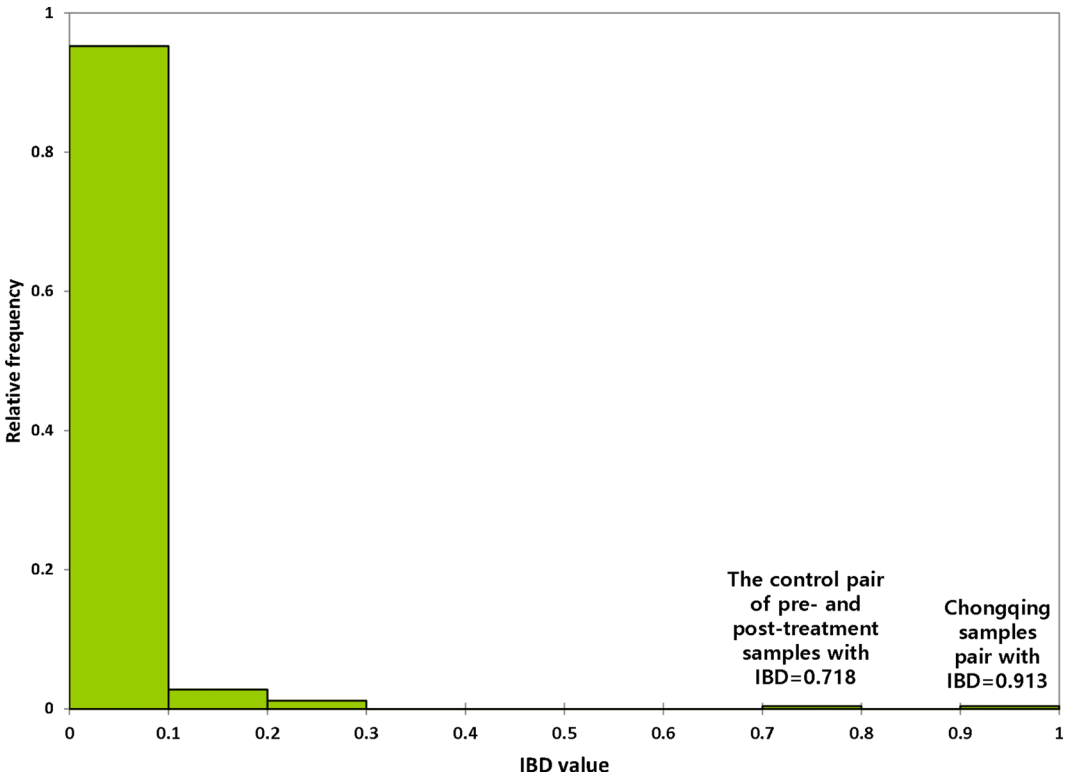

Fig. 4 Distribution of pairwise identity-by-descent (IBD) values among *P. falciparum* isolates. Most sample pairs exhibit low IBD values (< 0.1), indicating unrelated infections. The control pair of pre- and post-treatment samples from the same DRC case had an IBD of 0.718. In contrast, the Chongqing case of unknown origin and the DRC-imported case from the same hospital showed an exceptionally high IBD of 0.913, suggesting a strong genetic relationship. The x-axis represents pairwise IBD values; the y-axis shows their relative frequency

clustered with the Asian group, validating geographic separation [29, 30]. This placement strongly suggests that the unknown case was of African origin, likely from the DRC. To further investigate, an IBD analysis was performed, revealing high genetic relatedness (IBD = 0.9) between the unknown case and a confirmed imported case from the DRC who was hospitalized in the same facility [31, 32]. Although direct transmission cannot be confirmed due to the time gap and lack of epidemiological linkage, the genetic evidence supports the hypothesis of a shared infection source. Notably, all other IBD values were low, and no further clustering was observed, indicating that the introduction was isolated and did not result in local spread—critical for sustaining China's malaria-free status.

These findings demonstrate that WGS can serve as a valuable complement to traditional surveillance, especially within the framework of China's "1–3-7" strategy. Tools such as PCA and IBD analysis provide enhanced resolution for tracing transmission patterns and confirming the imported nature of ambiguous cases. In this instance, WGS provided conclusive evidence to resolve a case that could not be confidently classified through standard epidemiological investigation alone [33]. As countries move into the post-elimination phase, incorporating WGS into surveillance systems will be essential to prevent misclassification and ensure early detection of potential reintroduction.

Going forward, the integration of genomic data with epidemiological methods will be essential for a more comprehensive understanding of malaria transmission. Continuous refinement of genomic tools will further strengthen the 1–3-7 strategy, helping sustain malaria-free status and contributing to global malaria eradication efforts.

Conclusion

This study demonstrates that integrating genomic tools—such as WGS, PCA, IBD, and phylogenetic reconstruction—can effectively trace the source and relatedness of imported *P. falciparum* malaria cases. The findings support the value of applying such tools alongside traditional surveillance strategies, particularly in post-elimination settings like China. As global efforts to eliminate malaria continue, incorporating genomic epidemiology into

routine case investigations will be essential for maintaining malaria-free status and preventing reintroduction.

Abbreviations

DRC	Democratic Republic of Congo
ROC	Republic of the Congo
AO	Angola
SD	South Sudan
CF	Central African Republic
TZ	Tanzania
WGS	Whole-genome sequencing
CDC	The District Centers for Disease Control
SNP	Single nucleotide polymorphism
ML	Maximum-likelihood
PCA	Principal-components analysis
IBD	Identity by descent
CMB	China-Myanmar border
PCR	Polymerase chain reaction assay

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s12936-025-05476-6.

Supplementary material 1. Sequencing and mapping summary statistics for the unknown Chongqing strain and imported cases.

Supplementary material 2. The countries and the mean coverage of samples used as references.

Supplementary material 3. Economic and Malaria Burden Indicators of Major Source Countries for Imported Malaria Cases.

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Author contributions
HMS and DJ analyzed the data and wrote the first draft; SZ, FL, JRX, YT, MPY, JX and SPY collected the samples and performed the field investigations; JHC, SZ, FL and HMS reviewed the manuscript for critical intellectual content; JHC, FL and HMS designed the experiments, guided the English writing, and revised the first draft. All authors read and approved the final manuscript.

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Data availability
All data supporting these findings is contained within the manuscript and supplementary tables. All Illumina raw sequencing reads have been submitted to the NCBI Short Read Archive (BioProject no. PRJNA1181645).

Declarations

Ethics approval and consent to participate
The study was conducted based on the principles expressed in the Declaration of Helsinki. Per the study protocol, the potential risks and benefits were explicitly explained to the participants, from whom blood was collected after receiving written informed consent according to the institutional ethical guidelines and approval by the ethics committee at Chongqing Center for Disease Control and Prevention.

Consent for publication
Not applicable.

Competing interests
The authors declare no competing interests.

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