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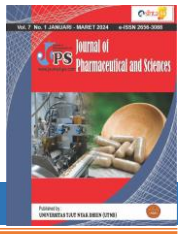

Tracing the Development, Current Status, and Future Prospects of DNA Testing in Human and Non-Human Forensic Applications: A Narrative Review

Menelusuri Perkembangan, Kondisi Terkini, dan Prospek Masa Depan Pengujian DNA dalam Aplikasi Forensik Manusia dan Non-Manusia: Tinjauan Naratif

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Abstract

DNA typing has become a cornerstone of modern forensic science, profoundly influencing criminal investigations, forensic human identification, and non-human forensic applications. Since its introduction in the mid-1980s, forensic DNA analysis has evolved from restriction fragment length polymorphism-based methods to polymerase chain reaction-based short tandem repeat profiling, and more recently to sequence-based approaches enabled by massively parallel sequencing, resulting in substantial improvements in analytical sensitivity, robustness, and discriminatory power. This narrative review aims to trace the historical development, examine the current state, and explore future directions of DNA typing in both human and non-human forensic contexts, with particular emphasis on empirical case studies from Asia. A narrative review methodology was employed through a comprehensive analysis of peer-reviewed literature published between 2015 and 2026, sourced from major scientific databases including Google Scholar, PubMed, and ScienceDirect, with studies selected based on forensic relevance, methodological rigor, and regional significance. The review highlights the extensive application of DNA typing in routine criminal casework, disaster victim identification, missing persons investigations, wildlife forensic genetics, food fraud detection, and biosecurity, and documents emerging technologies such as portable DNA systems and CRISPR-based detection. Despite these advances, significant challenges remain related to data interpretation, validation requirements, contamination control, ethical and legal governance, and uneven forensic capacity across regions. Overall, this review underscores the continuing evolution of forensic DNA typing and emphasizes the importance of standardized protocols, interdisciplinary collaboration, and region-specific validation to ensure the reliable and responsible application of DNA evidence in modern forensic science.

Keywords: *Forensic DNA typing, Short Tandem Repeats (STRs), Massively Parallel Sequencing (MPS), Wildlife forensic genetics, Disaster victim identification*

Abstrak

Pengujian DNA telah menjadi landasan utama ilmu forensik modern, secara signifikan mempengaruhi penyelidikan kriminal, identifikasi forensik manusia, dan aplikasi forensik non-manusia. Sejak diperkenalkan pada pertengahan 1980-an, analisis DNA forensik telah berkembang dari metode berbasis polimorfisme panjang fragmen restriksi (RFLP) menjadi profilasi pengulangan tandem pendek (STR) berbasis reaksi rantai polimerase (PCR), dan lebih baru lagi ke pendekatan berbasis urutan yang didukung oleh sekuensing paralel massal, yang menghasilkan peningkatan signifikan dalam sensitivitas analitis, ketahanan, dan daya diskriminasi. Ulasan naratif ini bertujuan untuk melacak perkembangan historis, mengkaji kondisi terkini, dan menjelajahi arah masa depan pengujian DNA dalam konteks forensik manusia dan non-manusia, dengan penekanan khusus pada studi kasus empiris dari Asia. Metodologi tinjauan naratif diterapkan melalui analisis komprehensif literatur yang telah direview oleh rekan sejawat yang diterbitkan antara tahun 2015 dan 2026, yang bersumber dari basis data ilmiah utama termasuk Google Scholar, PubMed, dan ScienceDirect, dengan

studi yang dipilih berdasarkan relevansi forensik, ketelitian metodologis, dan signifikansi regional. Tinjauan ini menyoroti penerapan luas pengujian DNA dalam kasus kriminal rutin, identifikasi korban bencana, penyelidikan orang hilang, kejahatan satwa liar, deteksi penipuan makanan, dan keamanan biologis, sambil juga mendokumentasikan teknologi baru seperti sistem DNA portabel dan deteksi berbasis CRISPR. Meskipun ada kemajuan ini, tantangan signifikan tetap ada terkait interpretasi data, persyaratan validasi, pengendalian kontaminasi, tata kelola etika dan hukum, serta kapasitas forensik yang tidak merata di berbagai wilayah. Secara keseluruhan, tinjauan ini menyoroti evolusi berkelanjutan dari pengujian DNA forensik dan menekankan pentingnya protokol standar, kolaborasi interdisipliner, dan validasi spesifik wilayah untuk memastikan penerapan yang andal dan bertanggung jawab dari bukti DNA dalam ilmu forensik modern.

Kata Kunci: *Pengujian DNA forensik, Short Tandem Repeats (STRs), Massively Parallel Sequencing (MPS), Genetika forensik satwa liar, Identifikasi korban bencana.*

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Introduction

DNA typing has become one of the most influential scientific tools in modern forensic science, fundamentally transforming the way biological evidence is generated, interpreted, and applied within criminal justice systems and beyond [1,2]. Since its introduction in the mid 1980s, forensic DNA analysis has evolved from early fragment-length-based methods into a highly sophisticated, technology-driven discipline capable of producing reliable genetic information from minute, degraded, or complex biological samples. [3,4]. This evolution has significantly expanded the scope of forensic investigations, enabling applications that range from routine criminal casework to forensic human identification and non-human forensic analysis.

The importance of DNA typing lies not only in its high discriminatory power but also in its adaptability across diverse forensic contexts. [1,2]. In human forensic applications, DNA analysis is routinely employed to establish associations between individuals, biological evidence, and crime scenes, often providing decisive information in cases involving mixed samples, low template DNA, or complex kinship relationships [5,6]. In parallel, non-human forensic DNA analysis has gained increasing prominence as a critical tool for addressing wildlife forensic genetic, food fraud, and biosecurity threats [7,8]. These expanding applications highlight the growing relevance of forensic DNA typing beyond traditional criminal investigations.

Today, DNA typing plays a critical role not only in active criminal investigations but also in wrongful conviction appeals, missing persons identification, disaster victim identification, and transnational crime investigations [1,2]. Its progressive evolution from restriction fragment length polymorphism analysis to polymerase chain reaction based short tandem repeat profiling, and more recently to advanced platforms such as next generation sequencing, reflects its central importance in contemporary forensic science [3,4]. Emerging approaches, including CRISPR-based DNA detection, further illustrate the expanding technological landscape of forensic genetics [9,10]. With increasing integration into national DNA databases and global forensic information networks, DNA typing continues to exert a profound influence on the administration of justice worldwide.

Advances in molecular biology and sequencing technologies have been central to the continued development of forensic DNA analysis. The transition from restriction fragment length polymorphism analysis to polymerase chain reaction based short tandem repeat typing represented a major milestone in

improving sensitivity, robustness, and standardization [1]. More recently, massively parallel sequencing has introduced sequence-level resolution into forensic genetics, enabling the simultaneous analysis of multiple marker systems and revealing previously undetectable genetic variation [3,11]. While these technological innovations have greatly enhanced analytical capability, they have also introduced new challenges related to data interpretation, validation requirements, contamination control, and ethical and legal governance [2,4].

Despite the global expansion of forensic DNA technologies, their implementation and impact remain uneven across regions [2]. Asia, in particular, represents a complex and heterogeneous forensic landscape shaped by differences in infrastructure, legal frameworks, population genetics, and biodiversity [12]. Several Asian countries have developed advanced forensic DNA laboratories and national databases, while others continue to face resource constraints and challenges with standardization. At the same time, Asia's exceptional biodiversity poses unique difficulties for non-human forensic DNA typing, particularly in species identification and population assignment, underscoring the need for region-specific validation and collaborative approaches [7,8].

Against this background, this narrative review aims to trace the historical development, examine the current state, and explore future directions of DNA typing in both human and non-human forensic applications. By integrating technological evolution, methodological advances, empirical case studies with an emphasis on Asia, and emerging ethical, legal, and social considerations, this review seeks to provide a comprehensive and forward-looking synthesis of forensic DNA typing and its evolving role in modern forensic science.

Research Method

For this review article, a narrative review methodology was employed to synthesize and critically evaluate the scholarly literature on the development, current applications, and prospects of DNA typing in human and non-human forensic science. Relevant evidence was collected from reputable scientific databases, including Google Scholar, PubMed, and ScienceDirect, which are widely recognized for indexing peer-reviewed forensic, genetic, and biomedical research. The literature selection emphasized empirical studies, validation research, and applied forensic investigations to ensure the review reflected practical, evidence-based developments in forensic DNA analysis.

The literature search was conducted in English using predefined keywords, including "forensic DNA typing," "short tandem repeat analysis," "mitochondrial DNA forensics," "massively parallel sequencing in forensics," "wildlife forensic genetics," and "non-human forensic DNA analysis." The initial searches yielded a large number of records across the selected databases. Inclusion criteria comprised articles published between 2015 and 2026, studies focusing on methodological developments or applied use of DNA typing in forensic contexts, and publications from internationally recognized scientific journals. For sections addressing historical development, earlier landmark studies were included where necessary to provide essential background context. Exclusion criteria included articles published outside the defined timeframe without historical relevance, studies lacking a clear forensic application, opinion pieces without empirical support, and publications not available in full text.

After removing duplicate records and preliminary screening based on titles and abstracts, a subset of articles was selected for full-text assessment. The final selection prioritized studies that provided robust methodological detail, validation data, or applied casework insights relevant to both human and non-human forensic applications. Data extracted from the selected studies were synthesized narratively to identify key technological trends, methodological challenges, regional perspectives with an emphasis on Asia, and emerging directions in forensic DNA typing. This narrative synthesis approach enabled an integrative, contextually grounded assessment of the field, rather than a quantitative meta-analysis, which was not feasible given the methodological heterogeneity of the included studies.

Discusion

Historical Evolution of DNA Typing

The history of DNA typing in forensic science began with a groundbreaking discovery in 1985 by British geneticist Sir Alec Jeffreys, who identified specific regions in the human genome that contained tandemly

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repeated sequences of DNA, known as Variable Number Tandem Repeats (VNTRs) [13,14]. These sequences varied greatly between individuals, and Jeffreys developed a method to detect these differences, laying the foundation for what he called "DNA fingerprinting" [13,14]. The potential of this technique was quickly realized when, in 1986, it was applied for the first time in a forensic investigation involving the sexual assault and murder of two young girls, Lynda Mann and Dawn Ashworth, in Narborough, Leicestershire, England. Although an initial suspect confessed to the crime, DNA testing excluded him, making this the first instance in which DNA was used not to convict, but to exonerate an individual [14].

A large-scale DNA screening programme involving thousands of local men was conducted to identify the perpetrator [14]. Subsequent DNA analysis revealed that the DNA profile of Colin Pitchfork matched semen samples recovered from both crime scenes, leading to his arrest and conviction. This landmark case demonstrated the evidentiary power of DNA profiling in forensic investigations and underscored its potential to enhance objectivity and fairness within the criminal justice system. The investigation employed multi-locus RFLP DNA fingerprinting, as originally described by Jeffreys in 1985 [14].

Despite its revolutionary impact, early DNA analysis using Restriction Fragment Length Polymorphism (RFLP) had several limitations. RFLP required large amounts of high-quality, non-degraded DNA, typically around 10–25 nanograms, to generate reliable results. While highly discriminative, the method was labor-intensive, time-consuming, and poorly suited for forensic casework involving degraded, old, or trace samples. RFLP was most applicable to fresh, abundant biological samples such as blood or semen, but lacked the flexibility required in routine forensic contexts [15]. These constraints drove the development of faster, more sensitive, and robust techniques.

The next breakthrough came with the invention of the Polymerase Chain Reaction (PCR) in 1983 by Kary Mullis, who was inspired during a drive through the mountains of Northern California. Although the conceptual framework for primer-based DNA amplification had been outlined by Khorana and colleagues as early as 1971 [16], it was Mullis's work that transformed it into a practical and revolutionary tool. PCR enabled the amplification of specific DNA regions from minute samples and even from degraded samples, thereby overcoming the limitations of RFLP. It became a foundational technology in forensic DNA analysis, earning Mullis the Nobel Prize in Chemistry in 1993. Cetus Corporation's commercial development of PCR and its eventual acquisition by Roche Molecular Systems marked the beginning of widespread practical use of DNA amplification in biological sciences.

Building on the PCR revolution, forensic science soon adopted Short Tandem Repeat (STR) typing in the mid-to-late 1990s. STRs are highly polymorphic DNA regions composed of 2–7 base pair repeating units, commonly located in non-coding regions of the genome. These sequences vary in the number of repeat units between individuals, making them ideal for forensic identification [17]. STR analysis, performed using multiplex PCR and capillary electrophoresis, enabled the simultaneous analysis of multiple loci with high precision, sensitivity, and discrimination. STRs became the new standard in forensic DNA typing due to their stability, reproducibility, and compatibility with degraded or mixed DNA samples. The loci selected for forensic use, especially tetranucleotide repeats, were chosen for their low mutation rates and ease of separation, making them ideal for database comparison and courtroom presentation [18]

Early forensic DNA typing relied predominantly on fragment length–based analysis rather than direct sequencing [11]. Although DNA sequencing technologies had been established decades earlier, their initial role in forensic science was limited due to technical and operational constraints [19]. Classical Sanger sequencing, while highly accurate and capable of producing relatively long reads, was characterized by low throughput, high per-sample cost, and lengthy processing times. These limitations rendered it impractical for routine forensic casework, which requires rapid, robust, and highly standardized analytical workflows [20]. Consequently, early forensic genetics favored PCR-based fragment analysis using capillary electrophoresis, particularly for Short Tandem Repeat (STR) profiling, rather than sequence-based approaches [1].

A fundamental conceptual distinction between fragment–length–based typing and sequence-based analysis lies in the type of genetic information obtained. Conventional STR profiling measures allele size based on the length of amplified repeat regions, implicitly assuming that alleles of identical length share identical sequence composition [11]. However, subsequent empirical studies demonstrated that STR alleles of the same length may differ at the sequence level due to variation in internal repeat structure or flanking region polymorphisms. This hidden sequence diversity, undetectable by capillary electrophoresis, represents an intrinsic limitation of length-based STR analysis and constrains its discriminatory power in certain forensic contexts, particularly when dealing with complex mixtures or closely related individuals [21].

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Advances in high-throughput sequencing technologies during the mid-2000s fundamentally altered the feasibility of DNA sequencing for applied forensic use [19]. The emergence of massively parallel sequencing (MPS), also known as next-generation sequencing (NGS), enabled the simultaneous sequencing of millions of DNA fragments in a single run, dramatically increasing throughput while reducing the cost per base. This period also saw the development of early single-molecule sequencing platforms that demonstrated amplification-free sequencing concepts, although their limited efficiency and throughput constrained direct forensic applicability**.** Unlike traditional sequencing methods, MPS platforms combine clonal amplification of DNA fragments with parallelized sequencing-by-synthesis or sequencing-by-ligation chemistries [22]

Empirical validation studies conducted between 2015 and 2020 demonstrated that MPS-based approaches could successfully generate sequence-level data for forensic markers, including autosomal STRs, Y-STRs, single-nucleotide polymorphisms (SNPs), and mitochondrial DNA [19]. Importantly, these studies showed that sequence-based STR typing not only preserved compatibility with existing length-based allele nomenclature but also revealed additional allelic variation, thereby increasing discriminatory capacity without altering established forensic interpretation frameworks [21]. Such performance has been reported across a range of short-read MPS platforms, predominantly based on sequencing-by-synthesis chemistries implemented through flow-cell and nanoball-based architectures. These findings marked a pivotal transition in forensic genetics from fragment length–based profiling toward sequence-informed DNA typing [11].

Parallel to short-read MPS platforms, third-generation sequencing technologies based on single-molecule, real-time sequencing principles emerged during the 2010s. Long-read sequencing platforms, such as nanopore-based and single-molecule real-time systems, enable sequencing of DNA molecules exceeding several kilobases without prior amplification. While these technologies present clear theoretical advantages for resolving complex genomic regions and structural variants, empirical forensic studies have highlighted persistent challenges related to per-base error rates, data consistency, and validation requirements [23]. As a result, long-read sequencing remains largely exploratory within forensic science and has not yet achieved routine operational adoption [4].

To provide a structured comparison of major DNA sequencing technologies and their technical characteristics, Table 2 summarizes the chronological development, sequencing principles, amplification strategies, read lengths, and key advantages and limitations of platforms that have influenced modern forensic genomics.

Table 2. The Development of DNA Sequencing Technology Based on Chronological Order and Technical Characteristics

Technology	Generation	Sequencing Types	Technology Principles	Types of Amplification	Read Length (bp)	Advantages	Disadvantages	References
Sanger Sequencing	First Generation	Chain termination sequencing	DNA polymerase incorporates 2′,3′-dideoxynucleotide triphosphates (ddNTPs) lacking a 3′-OH group, causing termination of DNA strand elongation at specific bases; resulting fragments are separated by denaturing polyacrylamide gel	None (no PCR amplification)	~15–300 bp (occasionally up to ~300 bp from priming site)	High sequencing accuracy; clearer band patterns compared to the plus/minus method; relatively simple enzymatic approach	Low throughput; labor-intensive and manual gel-based process; use of radioactive labeling; limited read length and difficulty with homopolymer regions	[24]

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			electrophoresis and visualized by autoradiography					
Maxam-Gilbert Sequencing	First Generation	Chemical cleavage sequencing	End-labeled DNA is subjected to base-specific chemical modification followed by cleavage of the DNA backbone; fragment sizes are determined by denaturing polyacrylamide gel electrophoresis	None	Not explicitly specified	Does not require DNA polymerase or primers; applicable to double-stranded DNA	Uses hazardous chemicals; labor-intensive; technically demanding; low throughput	[25]
454 Pyrosequencing	Second Generation	Sequencing by synthesis (SBS)	Detection of light from pyrophosphate release during nucleotide incorporation	Emulsion PCR	400–700 bp	Long reads, fairly fast, suitable for metagenomics	Errors in homopolymers, high costs, and the platform was discontinued	[22,26,27]
Ion Torrent	Second Generation	Sequencing by synthesis (SBS)	Incorporation of natural nucleotides by DNA polymerase releases hydrogen ions, producing a pH change that is detected by ion-sensitive field-effect transistor (ISFET) sensors on a CMOS semiconductor chip	Emulsion PCR (clonal amplification on beads)	~100 bp routinely; reads >200 bp reported	Non-optical detection; massively parallel; reduced instrument complexity and cost	Homopolymer-associated errors; signal interpretation affected by phasing and buffering effects	[28]
Illumina/Solexa	Second Generation	Sequencing by synthesis (SBS)	Cyclic reversible termination sequencing in which fluorescently labelled, reversible	Bridge amplification (solid-phase PCR on flow cell)	~25–100 bp (early systems)	Massively parallel sequencing; high accuracy; uniform signal	Short read length; phasing and dephasing errors	[29]

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			terminator nucleotides are incorporated one base at a time and imaged after each cycle			across clusters		
PacBio (SMRT)	Third Generation	Single-molecule real-time sequencing	Sequencing-by-synthesis, based on real-time imaging of fluorescently tagged nucleotides as a DNA polymerase along individual DNA template molecules, incorporates them	Without PCR	Average ~3,000 bp; reads up to ~20,000 bp or longer	Very long read lengths; no amplification bias; direct detection of DNA base modifications (e.g., methylation); highly accurate consensus sequences with sufficient coverage	Higher raw single-read error rate (~11–14%) compared to short-read platforms	[30]
Nanopore (Oxford Nanopore)	Fourth Generation	Nanopore-based single-molecule sequencing	Single DNA molecules translocate through a biological or solid-state nanopore under an applied voltage, and characteristic disruptions in ionic current are used to identify nucleotide sequences	Without PCR	Ultra-long reads (~10^4–10^6 bp reported)	Label-free detection; ultra-long read length; minimal sample preparation; no amplification required	High error rate (early systems); fast DNA translocation complicates single-base resolution	[31]

Collectively, the chronological evolution of DNA sequencing technologies reflects a gradual yet transformative shift in forensic genetics from fragment-length–based profiling to sequence-informed DNA analysis. While advances in massively parallel and long-read sequencing have expanded the analytical resolution and potential applications of forensic DNA typing, their successful integration into routine casework has depended not only on technological capability but also on the development of robust interpretative frameworks, quality assurance measures, and legal acceptance. Consequently, the impact of these technological innovations cannot be fully understood without considering the parallel evolution of standards, validation practices, and judicial recognition of DNA evidence [4].

As scientific progress advanced, legal systems began to formally recognize and standardize the use of DNA evidence [32]. The landmark U.S. case *People v. Wesley* in 1988 marked the first time DNA evidence was admitted in court [33]. This was followed by the FBI's establishment of the Combined DNA Index System (CODIS) in 1998, which allowed law enforcement agencies to compare DNA profiles across jurisdictions and solve cold cases [34]. During the late 1990s, quality assurance standards for forensic DNA laboratories were

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formally issued in the United States, with guidelines developed by TWGDAM/SWGDAM and Quality Assurance Standards promulgated by the FBI, encompassing validation, personnel qualifications, and casework review requirements [35]

Current State of DNA Typing

In addition to autosomal STRs, several complementary genetic markers are routinely used to enhance forensic DNA analysis, particularly under challenging sample conditions. These include Y-chromosomal STRs (Y-STRs), single nucleotide polymorphisms (SNPs), and mitochondrial DNA (mtDNA), each offering distinct advantages in specific forensic contexts [11].

Mitochondrial DNA analysis, characterized by maternal inheritance and a high copy number per cell, remains especially valuable for the examination of severely degraded biological material, such as hair shafts, skeletal remains, and historical samples where nuclear DNA may be insufficient or absent. Recent forensic studies have demonstrated that advances in sequencing and interpretation strategies have further enhanced the reliability and resolution of mtDNA typing in such contexts [3].

Y-chromosomal STRs (Y-STRs) are widely applied for the identification of male genetic profiles in mixed DNA samples, particularly in sexual assault investigations where female DNA is present in substantial excess. Contemporary empirical studies have confirmed the effectiveness of Y-STR analysis in isolating male contributors from complex mixtures, while also acknowledging its inherent limitations related to paternal lineage sharing [36].

The application of DNA typing in human forensic analysis represents one of the most mature and impactful uses of molecular genetics within contemporary forensic science. Ongoing advances in analytical sensitivity, marker selection, and interpretation strategies have enabled DNA evidence to address increasingly complex investigative scenarios, ranging from routine criminal casework to forensic human identification efforts involving missing persons and mass fatality incidents [2].

In criminal investigations, forensic DNA analysis is routinely employed to establish associations between individuals, biological evidence, and crime scenes. One of the most persistent analytical challenges in this context involves mixed DNA samples containing genetic material from multiple contributors, which commonly arise in violent crimes such as sexual assault and homicide. While autosomal STR profiling remains the primary method for mixture interpretation, its effectiveness may be limited when male DNA is present in low proportions relative to female DNA. In such cases, Y-chromosomal STR analysis provides a valuable complementary approach by selectively targeting male-specific genetic markers. Empirical forensic studies have consistently demonstrated that Y-STR typing enhances the detection and interpretation of male contributors in complex mixtures, particularly in sexual assault investigations where female DNA is present in substantial excess. However, these studies also emphasize the inherent limitation of Y-STR analysis related to shared paternal lineages, underscoring the importance of interpreting Y-STR results in conjunction with autosomal STR data rather than as standalone evidence [5].

Another significant challenge in criminal casework involves the analysis of low-template DNA, which is frequently encountered in trace evidence such as touch DNA samples [5]. Although improvements in PCR sensitivity have expanded the applicability of STR typing to low-level DNA samples, such analyses remain susceptible to stochastic effects, including allelic drop-out, drop-in, and peak imbalance. Empirical studies published since 2015 have highlighted the need for rigorous laboratory practices, replication strategies, and enhanced interpretation frameworks to mitigate these effects and ensure reliable evidentiary conclusions. The increasing adoption of probabilistic genotyping approaches has further strengthened the interpretation of low-template DNA by explicitly modeling uncertainty and providing a more robust statistical basis for evaluating evidential weight in criminal proceedings [37]

Beyond direct individual identification, DNA typing is also central to complex kinship analysis in criminal investigations, particularly in cases involving missing suspects, indirect familial relationships, or deficient pedigrees. While autosomal STRs remain the cornerstone of kinship inference, supplementary genetic markers such as X-chromosomal STRs and SNP panels have demonstrated added value in resolving challenging relationship scenarios. Contemporary forensic studies have shown that the strategic integration of these markers can improve likelihood ratio estimates in cases involving half-siblings, avuncular relationships, or missing parental references, thereby enhancing the robustness of kinship-based conclusions when conventional approaches are insufficient [38].

Recent international casework has further demonstrated the practical value of X-chromosomal STR (X-STR) markers in resolving complex kinship scenarios [6]. In a study conducted in Colombia, Quiceno Cerinza

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et al. (2024) reported the application of X-STR analysis, combined with specialized statistical software (FamLinkX), to address deficiencies in cases where conventional autosomal STR markers provided limited discriminatory power. The cases involved complex pedigree structures, including half-sibling and indirect paternal relationship testing, where the absence of key reference individuals reduced the evidentiary strength of autosomal analysis alone [38].

By incorporating X-STR haplotype evaluation and likelihood ratio calculations consistent with international interpretative guidelines [6], the investigators were able to substantially strengthen kinship hypotheses in scenarios where autosomal STR results were inconclusive [38]. The study highlighted the importance of considering the unique inheritance pattern of the X chromosome, particularly in cases involving female individuals and paternal lineage assessment [6]. These findings reinforce the growing recognition that X-STR markers serve as a powerful supplementary tool in forensic genetics, especially in deficiency testing and complex pedigree reconstruction [6,38].

In addition to criminal investigations, DNA typing plays a vital role in forensic human identification, particularly in identifying missing persons and unidentified human remains. These cases frequently involve degraded biological material, limited reference samples, and complex family structures, requiring flexible, resilient analytical strategies. In such contexts, mitochondrial DNA analysis remains a key tool due to its high copy number per cell and maternal mode of inheritance, which increase the likelihood of successful DNA recovery from severely degraded samples such as skeletal remains or environmentally exposed biological material. Empirical studies conducted since 2015 have demonstrated that advances in sequencing technologies and interpretation methods have enhanced the resolution and reliability of mtDNA analysis, supporting its continued relevance in missing persons investigations and historical casework [3].

Kinship-based DNA identification is frequently used when direct reference samples from missing individuals are unavailable, requiring comparisons with biological relatives. Recent forensic research has emphasized the importance of combining multiple marker systems, including autosomal STRs, lineage-specific markers, and SNP-based approaches, to strengthen kinship inferences in complex or deficient pedigree scenarios. Such integrative strategies have been shown to improve the statistical robustness of identification outcomes, particularly in cases involving distant or incomplete familial relationships [6]

DNA analysis also constitutes a central component of Disaster Victim Identification (DVI) operations following mass fatality incidents. In these contexts, DNA evidence is integrated with other identification modalities, including fingerprints, dental records, and anthropological assessments, to establish victim identities systematically and reliably. Empirical studies have demonstrated that autosomal STR and mitochondrial DNA typing remain indispensable tools in DVI workflows, particularly when remains are fragmented, commingled, or severely degraded. The successful application of DNA typing in mass disaster contexts underscores its critical role in forensic human identification response efforts and highlights the importance of coordinated, multidisciplinary identification strategies [39]

Beyond human identification, DNA typing has become an essential tool in non-human forensic investigations, supporting the enforcement of laws related to wildlife conservation, agriculture, and biosecurity [8]. In wildlife forensic investigations, genetic analysis is routinely applied for both species identification and individualization, particularly in cases involving illegal trade, poaching, and trafficking of protected species. DNA-based species identification enables the determination of the taxonomic origin of seized biological materials, including meat, ivory, skins, and processed derivatives, which are often morphologically indistinguishable. Empirical studies published since 2015 have demonstrated the reliability of DNA barcoding and targeted genetic markers across diverse taxa, while individualization using microsatellites, STRs, or SNPs has strengthened evidentiary links between seized specimens, specific animals, and geographic populations. However, forensic wildlife investigations frequently face challenges in biodiversity-rich regions, where high species diversity, hybridization, and limited reference databases can complicate interpretation and reduce discriminatory power, underscoring the need for comprehensive and regionally representative genetic reference datasets [7].

In agricultural and biosecurity contexts, non-human forensic DNA analysis is widely used to detect food fraud, monitor invasive species, and trace plant and animal pathogens [40]. Genetic testing provides objective evidence of species substitution and mislabeling in food products, even when samples are highly processed and unsuitable for traditional morphological identification. Since 2015, applied studies have shown that DNA-based approaches can reliably identify fraudulent practices and support regulatory enforcement and consumer protection. In addition, molecular genetic tools play a critical role in the early detection of invasive species and in reconstructing transmission pathways during disease outbreaks affecting agriculture,

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aquaculture, and wildlife. By enabling high-resolution source attribution and tracking of pathogenic strains, DNA analysis supports forensic investigations into biosecurity breaches and highlights the importance of coordinated, multidisciplinary responses to environmental and agricultural threats [40,41]

Methodological Advancements and Challenges

Next-generation sequencing (NGS), also referred to as massively parallel sequencing (MPS), represents one of the most significant methodological advancements in forensic DNA analysis over the past decade [19]. Unlike conventional capillary electrophoresis–based approaches, which rely on fragment length information, MPS technologies enable the simultaneous sequencing of millions of DNA fragments, providing sequence-level resolution across multiple genetic marker systems within a single analytical workflow [19]. This capacity has fundamentally expanded the scope of forensic DNA typing by allowing the parallel analysis of autosomal STRs, Y-STRs, single nucleotide polymorphisms (SNPs), and mitochondrial DNA, thereby increasing both the depth and breadth of genetic information obtainable from forensic samples [3].

Since 2015, numerous empirical validations and applied casework studies have demonstrated that MPS-based forensic assays achieve high analytical sensitivity, reproducibility, and concordance with established length-based STR profiles [21], while simultaneously revealing additional sequence variation that enhances discriminatory power. Sequence-based STR typing has been shown to uncover isoalleles that are indistinguishable using capillary electrophoresis [21], offering improved resolution in complex mixtures and kinship analyses without disrupting existing allele nomenclature or interpretative frameworks [11]. These studies underscore MPS's ability to complement rather than replace conventional forensic DNA methodologies, facilitating a gradual, compatible transition toward sequence-informed forensic genetics.

Beyond STR analysis, MPS has enabled the routine incorporation of SNP panels and full mitochondrial genome sequencing into forensic workflows, particularly in cases involving degraded samples, complex kinship scenarios, or ancestry inference. Empirical research has shown that SNP-based approaches benefit from the short amplicon lengths and low mutation rates inherent to these markers, making them well-suited for challenging forensic samples. Similarly, MPS-based mitochondrial DNA analysis has provided increased haplotype resolution and improved detection of heteroplasmy, thereby enhancing the reliability of mtDNA evidence in missing persons investigations and disaster victim identification contexts [3]

Despite its demonstrated advantages, adopting MPS in routine forensic practice poses several methodological and operational challenges. These include increased complexity in laboratory workflows, the need for specialized bioinformatics pipelines, and the requirement for extensive validation and standardization before courtroom implementation. Moreover, interpreting sequence-based data requires updated guidelines and training to ensure consistency and transparency across laboratories. As a result, while MPS has become an established tool in research, validation, and specialized forensic applications, its integration into routine casework continues to evolve in parallel with the development of quality assurance frameworks and interpretative standards [4].

The increasing adoption of massively parallel sequencing (MPS) has significant implications for the future development of X-chromosomal short tandem repeat (X-STR) analysis in forensic genetics [3,4]. While conventional capillary electrophoresis (CE)-based X-STR typing relies on fragment length determination, MPS enables sequence-level characterization of repeat regions and flanking sequences, thereby revealing additional genetic variation beyond size-based allele designation [19,21].

One of the most important advantages of MPS in STR analysis is the detection of isoalleles, defined as alleles with identical fragment lengths but distinct internal sequence structures [21]. In CE-based systems, such isoalleles are indistinguishable and therefore treated as identical genotypes. However, sequence-based STR studies have demonstrated that previously hidden sequence variation increases allelic diversity and enhances discriminatory power compared to length-based analysis alone [19,21]. Although many validation studies have focused primarily on autosomal STR markers, the same conceptual framework applies to X-STR loci, suggesting that sequence-informed X-STR typing may improve statistical power in complex kinship testing scenarios.

The added resolution provided by MPS may be particularly valuable in deficiency cases, half-sibling testing, and complex pedigree reconstruction, where conventional autosomal STR analysis may provide limited discriminatory strength [6,38]. Given the unique inheritance pattern of the X chromosome, accurate haplotype inference is critical for likelihood-ratio calculations in kinship evaluation [6]. Sequence-based characterization of X-STR loci has the potential to refine haplotype definition within linked marker clusters, thereby strengthening statistical interpretation in accordance with international forensic guidelines [6].

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Miniaturization and the development of portable DNA typing technologies have driven a significant shift in forensic genetics toward rapid, decentralized analysis. Advances in microfluidics, lab-on-a-chip platforms, and integrated amplification–detection systems have enabled downsizing conventional forensic DNA workflows, enabling extraction, PCR amplification, and STR profiling to be performed within compact, automated devices. Since 2015, empirical validation studies have demonstrated that rapid DNA systems can generate STR profiles from reference-quality samples within substantially reduced timeframes and with high concordance to conventional capillary electrophoresis–based methods. These capabilities have supported the controlled adoption of rapid DNA technologies in law enforcement and border security settings, where timely genetic identification can enhance investigative efficiency and operational decision-making [42].

In parallel, portable sequencing technologies have expanded the scope of field-deployable genetic analysis beyond STR profiling. Handheld and benchtop sequencing platforms, particularly those based on nanopore technology, have been evaluated for rapid species identification, pathogen detection, and preliminary human identification in remote or resource-limited environments [43]. Applied studies published since 2016 have demonstrated the feasibility of generating usable genetic data under field conditions, although challenges related to per-base error rates, data interpretation, and standardization remain. Consequently, portable sequencing platforms are currently viewed as complementary tools for screening and investigative intelligence rather than substitutes for fully validated laboratory-based forensic workflows, highlighting the need for continued technological refinement and rigorous validation before routine forensic implementation [44]

Despite substantial technological advances in forensic DNA analysis, challenges related to sample quality and quantity continue to affect the reliability of genetic evidence. Forensic biological samples are frequently degraded, limited in amount, or exposed to adverse environmental conditions such as heat, humidity, ultraviolet radiation, and microbial activity. These factors can result in DNA fragmentation, chemical damage, and the presence of inhibitory substances that compromise amplification efficiency and data quality[45]. Even with improvements in PCR sensitivity and sequencing technologies, low-template and degraded samples remain particularly susceptible to stochastic effects, including allelic drop-out, peak imbalance, and incomplete profiles, necessitating careful laboratory handling and conservative interpretation [11].

Contamination and DNA transfer represent additional critical challenges, particularly as analytical sensitivity has increased to levels capable of detecting minute quantities of genetic material [45]. Empirical research has shown that DNA may be transferred through secondary or tertiary contact and can persist on surfaces or objects without direct involvement in a criminal act [45]. Such findings complicate the interpretation of DNA evidence, especially in cases relying on trace DNA, where the presence of a genetic profile does not necessarily reflect the manner or timing of deposition [46]. These risks underscore the importance of rigorous contamination control measures, including controlled laboratory environments, strict workflow separation, reagent monitoring, and comprehensive staff training, to preserve the integrity and evidentiary value of forensic DNA results [46].

A further challenge lies in interpreting and implementing increasingly complex DNA data, particularly with the adoption of probabilistic genotyping, massively parallel sequencing, and portable DNA technologies. While these approaches have enhanced the ability to analyze mixtures and low-level samples, they rely on sophisticated statistical models, population databases, and computational algorithms that must be carefully validated and transparently applied. Differences in analytical software, parameter settings, and interpretative assumptions can influence evidential weight estimates [45,46], raising concerns about consistency and reproducibility across laboratories. Moreover, the integration of new technologies into routine forensic practice introduces operational challenges related to cost, bioinformatics infrastructure, data management, and legal admissibility, highlighting the need for harmonized standards, ongoing training, and interdisciplinary collaboration to ensure that technological innovation translates into robust and defensible forensic practice [45].

The expanding capabilities of forensic DNA analysis raise important ethical and legal considerations regarding privacy, consent, and the scope of genetic information used in criminal justice systems. As forensic technologies evolve from simple identity testing toward sequence-based approaches capable of revealing ancestry, kinship, and other biologically informative markers, concerns have intensified regarding the potential misuse or unintended disclosure of sensitive genetic data. The collection, storage, and long-term retention of DNA profiles, particularly in national and international databases, pose challenges in balancing public safety interests with individual rights. These issues are further complicated by practices such as familial

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searching and investigative genetic genealogy, which may implicate individuals who have not themselves provided DNA samples, thereby extending forensic scrutiny beyond traditional consent boundaries.

In addition to privacy concerns, the legal and social implications of advanced DNA technologies center on issues of transparency, equity, and admissibility. The increasing complexity of probabilistic genotyping, massively parallel sequencing, and algorithm-driven interpretation frameworks places greater demands on judicial understanding and expert testimony, raising questions about explainability and the risk of overreliance on technologically sophisticated evidence. Disparities in database composition and forensic infrastructure across regions may also contribute to unequal investigative outcomes, reinforcing the need for standardized validation, oversight, and training. Addressing these ethical, legal, and social challenges requires not only technological safeguards but also clear regulatory frameworks, interdisciplinary dialogue, and ongoing public engagement to ensure that forensic DNA analysis remains scientifically robust, legally defensible, and socially responsible.

DNA Typing in Asia: Current Status and Challenges

The forensic science infrastructure across Asia is characterized by substantial diversity, reflecting wide variations in economic development, legal systems, population size, and technological capacity among countries in the region [47]. Several Asian nations, particularly those with well-established criminal justice systems, have developed centralized forensic laboratories equipped with advanced DNA typing technologies, national DNA databases, and standardized quality management systems. Empirical studies and regional assessments published since 2015 indicate that countries such as China, Japan, South Korea, and Singapore have invested heavily in forensic genomics, adopting STR profiling, mitochondrial DNA analysis, and increasingly, massively parallel sequencing within accredited laboratory environments [47]. These infrastructures support large-scale criminal investigations, disaster victim identification, and missing persons programs, often aligned with international standards such as ISO/IEC 17025 and guidelines issued by global forensic science bodies [48].

In contrast, other parts of Asia continue to face structural and operational challenges that limit the consistent application of advanced forensic DNA technologies [49]. Variability in laboratory accreditation, workforce training, funding stability, and access to modern instrumentation has resulted in uneven forensic capacity across the region. Studies focusing on forensic service delivery in Asia have highlighted constraints, including backlogs, limited reference databases, and disparities in legal frameworks governing DNA collection, retention, and use. Additionally, differences in population genetics and the underrepresentation of regional genetic data in global reference datasets pose challenges for the interpretation and statistical evaluation of DNA evidence [49]. Together, these factors underscore the need for regional capacity building, harmonization of standards, and increased cross-border collaboration to ensure that forensic DNA analysis in Asia is both scientifically robust and legally defensible in an increasingly interconnected criminal justice landscape.

The implementation of X-STR analysis in forensic practice should be aligned with internationally recognized interpretative standards, particularly the guidelines issued by the DNA Commission of the International Society for Forensic Genetics (ISFG) [6]. These guidelines provide detailed recommendations on marker selection, haplotype treatment, linkage considerations, mutation rate evaluation, and likelihood ratio calculation in kinship analysis. Importantly, the ISFG emphasizes the need to account for linkage groups on the X chromosome and to use appropriate statistical models when analyzing related individuals, especially in cases of deficiency.

While these guidelines establish a robust scientific framework, their direct implementation in Asia may encounter several practical challenges. First, many Asian populations exhibit complex population substructure and admixture patterns, which require comprehensive and region-specific allele frequency databases to ensure accurate likelihood ratio estimation [2]. Second, disparities in laboratory accreditation, bioinformatic capacity, and access to validated statistical software may limit the uniform application of advanced haplotype-based interpretation models [4]. Third, the limited availability of large-scale, publicly accessible X-STR population datasets from Southeast Asian populations may constrain statistical confidence in cross-border or transnational casework [47,50].

Empirical case studies across Asia demonstrate the extensive application of DNA typing in criminal investigations, disaster victim identification, and missing persons cases, highlighting both technological capability and operational scale [39]. In China, large-scale forensic DNA databases based on autosomal STR profiling have been instrumental in solving violent crimes and cold cases, with empirical studies reporting the

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successful linkage of crime scene evidence to suspects through database searches involving millions of profiles [12]. Similarly, applied forensic research from Japan and South Korea has documented the routine use of STR and mitochondrial DNA analysis in criminal casework and in investigations of unidentified human remains, particularly in cases involving degraded samples or limited reference material [39]. These studies illustrate how standardized DNA typing workflows, supported by centralized laboratory infrastructures, have enabled reliable and reproducible forensic outcomes in high-throughput investigative environments

Beyond routine criminal investigations, empirical case studies from Asia have underscored the critical role of DNA typing in mass disaster and forensic human identification contexts. Following major natural disasters and transportation accidents in the region, forensic teams in countries such as Japan and China have employed integrated DNA-based identification strategies combining autosomal STRs and mitochondrial DNA to identify fragmented and commingled remains [39]. Published case analyses have shown that DNA evidence was often decisive when traditional identification methods, such as fingerprints or dental records, were unavailable or inconclusive [39]. In parallel, recent empirical studies from Asia forensic laboratories have reported the validation and pilot application of massively parallel sequencing for challenging forensic cases, including complex kinship analysis and low-quality samples, demonstrating the gradual transition toward sequence-based forensic genetics within Asian casework [50]. Collectively, these case studies highlight both the maturity and the ongoing evolution of DNA typing practices across Asia, emphasizing the importance of empirical validation, standardized protocols, and regional collaboration in addressing diverse forensic challenges.

In addition to its well-established role in human forensic identification, DNA typing has increasingly been applied to non-human forensic investigations, reflecting the expanding scope of forensic genetics beyond the human context. Asia is one of the most biodiverse regions in the world, encompassing a wide range of terrestrial and aquatic ecosystems that support an extraordinary diversity of animal and plant species. While this biodiversity presents significant conservation value, it also poses substantial challenges for non-human forensic DNA typing, particularly in wildlife forensic investigations [7]. High species richness, the presence of closely related taxa, and frequent hybridization events can complicate genetic species identification and reduce discriminatory power when reference datasets are incomplete or poorly representative [7,8]. Empirical forensic studies have shown that conventional DNA barcoding markers may lack sufficient resolution to distinguish among closely related or recently diverged species common in biodiversity-rich regions, increasing the risk of misidentification in legal contexts [8]. These challenges highlight the need for carefully selected genetic markers and robust analytical frameworks tailored to complex taxonomic landscapes [7]

The implications of biodiversity extend beyond species identification to population assignment and individualization, which are increasingly important for linking seized biological materials to specific geographic origins or poaching hotspots. In regions with high intraspecific genetic variation, limited population genetic data can undermine the statistical confidence of assignment tests and complicate the interpretation of forensic evidence [7]. Empirical research conducted since 2015 has demonstrated that multi-locus approaches, including the integration of STRs, SNP panels, and genome-wide markers, can improve resolution and reliability in biodiversity-rich settings, particularly when supported by regionally curated reference databases [8]. However, the development and maintenance of such databases require sustained investment, cross-border collaboration, and standardized data-sharing practices [7]. Consequently, biodiversity in Asia simultaneously enhances the forensic utility of DNA typing while underscoring its methodological and interpretative challenges, reinforcing the need for region-specific validation and cooperative forensic frameworks in non-human forensic genetics.

Conclusions and Future Directions

This narrative review has traced the historical development, current applications, and emerging technological directions of DNA typing in both human and non-human forensic contexts. From early fragment length–based approaches to contemporary sequence-informed methodologies enabled by massively parallel sequencing, forensic DNA analysis has evolved into a highly sophisticated and versatile scientific discipline. Advances in analytical sensitivity, marker selection, probabilistic interpretation, and sequencing technologies have substantially improved the ability to resolve complex mixtures, degraded samples, and intricate kinship scenarios.

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Despite these advancements, the integration of advanced marker systems such as X-chromosomal STRs (X-STRs) and sequence-based platforms into routine forensic practice remains uneven, particularly across regions with heterogeneous infrastructure and population diversity. In Asia, where genetic diversity, population substructure, and demographic complexity may influence allele frequency estimation and likelihood ratio calculations, region-specific validation and database development are especially critical. Without adequate population reference data and harmonized interpretative frameworks, the full evidentiary potential of X-STR analysis cannot be realized.

To strengthen the scientific robustness and practical implementation of X-STR analysis in the region, several strategic directions should be considered. First, developing collaborative regional initiatives to generate comprehensive, representative X-STR population databases would enhance statistical reliability and promote standardization. Second, targeted validation studies evaluating both capillary electrophoresis–based and sequence-based X-STR panels within Asian populations are necessary to ensure reproducibility and courtroom defensibility. Third, as massively parallel sequencing becomes more integrated into forensic workflows, standardized nomenclature systems and bioinformatic interpretation pipelines specific to X-STR loci must be established in alignment with international guidelines. Finally, strengthening professional training in X-chromosome inheritance patterns, haplotype interpretation, and likelihood ratio calculation will be essential to support accurate and consistent application in complex kinship investigations.

Looking forward, the convergence of X-STR analysis, massively parallel sequencing, and probabilistic interpretative frameworks represents a promising frontier in forensic genetics. However, technological advancement alone is insufficient. Sustainable progress requires coordinated scientific validation, regional collaboration, standardized interpretation practices, and responsible governance. Through these integrated efforts, forensic DNA analysis can continue to evolve as a scientifically rigorous, ethically grounded, and globally responsive tool for human identification and justice.

Conflict of Interest

All authors declare that there is no conflict of interest in this review article.

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Supplementary Materials

No supplementary material is included in this article.

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