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DNA Barcoding and Its Applications: A Review

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Authors' contributions

This work was carried out in collaboration among all authors. Author CMAC coordinated, and supervised the work. Authors RTM, KCAA, CJCC, JMA and GAGS conducted the literature review and wrote the original draft of the manuscript. All authors reviewed and edited the draft and have read and agreed to the submission of the manuscript.

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Review Article

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ABSTRACT

The use of DNA sequences has revolutionized biological classification, specifically through the utilization of the DNA barcode technique, which involves amplifying a standardized DNA fragment for the identification of plant and animal species. The methods and techniques involved in DNA barcoding are introduced and visualized in the paper. As incorporated in various applications in diverse fields, a comprehensive discussion on DNA barcoding is presented, highlighting its

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relevance and use in species identification and discovery. Furthermore, we explore its different roles, ranging from biodiversity assessment and conservation to food safety, forensic science, biosecurity, and public health. We also introduce the current limitations of the technique and its potential use in future applications of genetics-based discoveries.

Keywords: Applications; barcode; eukaryotic identification; cytochrome c oxidase subunit I.

1. INTRODUCTION

A universal language in the form of DNA sequences revolutionized the world of biological classification. From visual examinations, morphological characteristics, and extensive taxonomic knowledge transformed into a snippet of a genetic code can easily unravel the mysteries of biodiversity. Such a revolutionary technique was proposed by Herbert in 2003, a standardized genetic marker for the wide identification of biological specimens – the DNA barcoding, where its principle lies on amplifying a 648-base pair region from the mitochondrial cytochrome c oxidase subunit I [1]. Consequently, numerous projects rose to promote the use of this molecular method including (1) the Barcode of Life project, which focused on the identification of eukaryotes, (2) the Consortium for the Barcode of Life (CBOL), which was established in 2004 for developing a standard protocol along with an extensive DNA barcode library, and (3) a recent international collective effort to initiate a DNA barcode library for all eukaryotic species from the International Barcode of Life project (iBOL) [1]. The acquisition of large-scale genetic data allowed researchers to transcend from traditional methods to a promising technique for rapid and accurate eukaryotic identification**.**

DNA barcoding aims to utilize genetic information from standardized short sequences of DNA, and the gene region must fulfill the three criteria: (1) possess genetic variability and divergence on a species level; (2) contain conserved flanking regions for creating universal PCR primers in a taxonomic application; and (3) own relatively short sequence length advantageous to current DNA extraction and amplification techniques. Such requirements will enable the development of accurate species-level barcodes for identification, where a comprehensive online digital repository of DNA barcodes will serve as a reference database for matching unidentified samples from various environments [2].

In this review paper, the advanced research and application of DNA barcoding in various fields are discussed. It focuses on species identification and discovery, as well as the resolution of taxonomic ambiguities. It also highlights the role of DNA barcodes in biodiversity assessment and conservation as well as the identification of endangered species. Furthermore, this review discusses DNA barcoding as an important tool in food safety, forensic science, biosecurity and public health.

2. DNA BARCODING: OVERVIEW ON METHODS AND TECHNIQUES

As the name suggests, DNA barcoding, similar to supermarket barcodes that undergo scanning at the counter to display product information, resembles that concept as a biodiversity, biological, and taxonomical research tool. According to Lebonah et al.,[3] identifying or assigning a "barcode" to an organism in a manner that makes it distinct from other species uses sequenced data from PCR amplicons produced at specific regions via DNA barcoding. Moreover, varying species morphology, ecology, and behavior constitute the criteria that determine DNA sequences [4]. Therefore, the recognition of species subsequently becomes possible using their genetic markers in a method by Kress & Erickson [5]. This includes: (1) building the barcode library of known species and (2) matching or assigning the barcode of the unknown sequence of the unknown sample against the barcode library for identification. To ensure a high level of specificity, DNA barcoding ensues by using the DNA sequence's short fragment functioning to code for the mitochondrial cytochrome c oxidase subunit I gene also called the cox1 or CO1 gene. Furthermore, establishing a library of DNA barcodes relies on the sequences compared to a taxonomically known sample to determine taxonomical identification [6]. On the other hand, two chloroplast gene fragments from the RuBisCo large subunit (rbcl) and maturase K (*matK*) genes are widely used in plants [7]. To understand the workflow of DNA barcoding, a visual example is shown below:

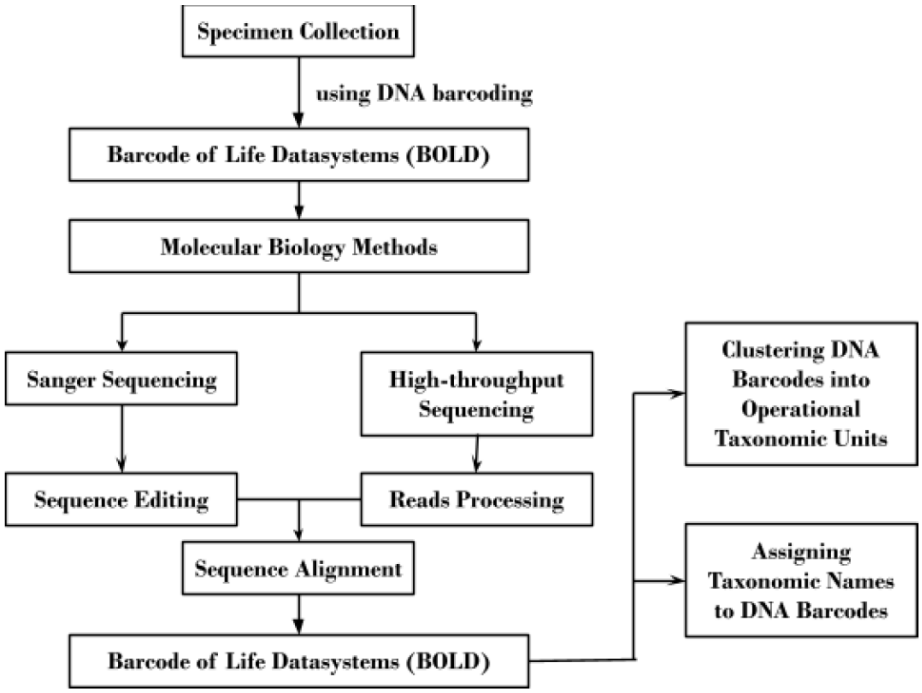

Fig. 1. The DNA barcoding workflow based on Wilson et al. [6]

3. APPLICATIONS OF DNA BARCODING

The characteristic of DNA being unalterable, detectable, and species-specific in every cell makes it a highly effective basis for finding solutions to issues in almost, if not all, every field of research. As such, the use of DNA barcodes in studies has had profound advantages in various fields, including ecology, food science, forensic science, and medical science, as it primarily involves the analysis of specific regions of an organism's DNA for identification. Its applications—to be further discussed below—continue to drive advancements in such fields, thus proving to be invaluable in offering new insights and possible solutions to ever-increasing challenges brought about by the present technological society.

3.1 Species Identification and Discovery

The identification of organisms is a fundamental element in assessing biodiversity and establishing our core understanding of the biological world. There are an estimated 8.7 million eukaryotic species on Earth, and a report says that 86% of land species and 91% of marine species have yet to be discovered and described [8]. These figures will increase even more if we try to account for the prokaryotic species. This only shows that species identification is a hard and slow process because it requires an accurate method, skilled taxonomists, and substantial funds. Traditionally, taxonomy was based on morphological characterization, which is time-consuming, requires skilled taxonomists, and may give false identification due to overlapping characters, phenotypic plasticity, and the occurrence of cryptic species [9-10]. Because of these issues, new methods have been introduced to support a morphology-based taxonomy. Over the past decade, several molecular tools have emerged for taxonomists to identify species, one of which is DNA barcoding. DNA barcoding is an effective method for identifying species at any stage of development, as well as when phenotypic plasticity and cryptic creatures are a concern [11]. DNA barcoding differs from other molecular tools primarily in the use of standard markers that differ between kingdoms.

Hebert et al. [12] proposed the mitochondrial gene cytochrome c oxidase subunit 1 (COI) as a universal marker or 'DNA barcode' for the global bioidentification for animals. Different sections or fragments of this gene are used to 'barcode' animal phyla, including invertebrates, birds, fish, and mammals. Mitochondrial genes are generally haploid, lack introns, and contain limited recombination [13]. COI is prioritized over other mitochondrial genes due to its ability to generate

sequence data within a fair amount of time in a cost-effective way [14]. Furthermore, mitochondrial COI is preferred over nuclear genes as universal animal barcode because it is more informative in differentiating or distinguishing closely related species [15]. This owes to the ability of the mitochondrial DNA to mutate and evolve at a high rate compared to the nuclear DNA [16].

To date, the COI gene has been utilized as a barcoding gene in several animals. DNA barcoding was largely successful in identifying immature specimens, [17-18] extinct species, [19-20] and individual species in different stages of their life cycles [21-23]. Potential cryptic species were also identified by using this technique. For instance, an underestimated genus *Triplophysa* from the Qinghai-Tibet Plateau has been studied by Wang et al. [24] Based on the combination of morphological methods and DNA barcoding of 1,630 specimens, it was found out that there were 24 native species, two of which were cryptic species, namely *T. robusta* and *T. minxianensis*. While it was established that COI is a standard marker for DNA barcoding of animals, other researchers have tried other genes to test the appropriateness of COI as a marker. For instance, in a primate study by Jackson & Niman, [25] they evaluated the efficiency of 12 mitochondrial protein-coding genes (cytochrome c oxidase subunits I, II, and III; cytochrome *b;* NADH dehydrogenase subunits 1, 2, 3, 4, 4L, and 5; and ATPase subunits 6 and 8) using Great Apes as a model. The results revealed that NADH dehydrogenase 5 (ND5) and cytochrome c oxidase subunit II (COII) produce the most pronounced barcoding gaps within the genus and family level than between species compared to COI. Because of this, it was recommended that these two genes (ND5 and COII) be used as appropriate markers in primate species delineation.

Although the COI gene is regarded as a universal barcode in animals, its effectiveness in fungi and plants is unreliable. In fungi, the internal transcribed spacer (ITS) region has been recognized as a standard barcode marker because it is more effective than the COI gene at distinguishing closely related taxa [26]. In plants, there are various prospects for DNA barcoding. The Consortium for the Barcode of Life (CBOL) Plant Working Group in 2009 proposed the chloroplast genes maturase K (matK) and ribulose bisphosphate carboxylase (rbcL) as fundamental barcodes, and intergenic sequence trnH-psbA and nuclear gene ITS as the supplementary barcodes of plants [27].

3.2 Biodiversity Assessment and Conservation

DNA barcoding plays a crucial role in the assessment and conservation of biodiversity, offering a powerful tool to scientists and researchers. The purpose of DNA barcoding lies in its ability to provide accurate species identification, overcome limitations of traditional taxonomy, and enhance our understanding of ecosystems [12].

DNA barcoding aids in assessing and monitoring biodiversity by gaining useful information about the diversity and abundance of life by documenting and analyzing the DNA of numerous species within an ecosystem. Several studies have demonstrated the effectiveness of DNA barcoding in biodiversity assessment. For instance, Hebert et al. [27] conducted research on bird species and found that DNA barcoding successfully differentiated closely related species with high accuracy. Similarly, Hajibabaei et al. [28] focused on terrestrial arthropods and demonstrated that DNA barcoding rapidly and accurately identified species, even in complex ecosystems. This data proves essential to understanding ecosystem health, tracking changes in species composition over time, and recognizing invasive species [28].

Furthermore, DNA barcoding contributes to conservation efforts by making it easier to identify endangered or threatened species. Numerous studies have shown that DNA barcoding is useful for conservation. Drescher et al. [29], for example, used DNA barcoding to detect illegally traded shark fins in the Hong Kong market, resulting in focused conservation activities. DNA barcoding aids in the discovery and prevention of illegal wildlife trade by allowing species to be identified even when they are processed or fragmented. Moreover, by examining DNA samples from populations, DNA barcoding aids in the monitoring and protection of endangered species. By accurately identifying these species through DNA barcoding, conservationists can prioritize their protection, implement targeted conservation measures, and enforce legislation to prevent their illegal trade [12].

3.3 Food Safety and Authentication

Several articles have reviewed the application of DNA barcoding to food safety, traceability, and

piracy in freshly commercialized and processed products [30-32]. The increase of general public interest in food origins and its nutrient value spur the demand for modern technologies that test food integrity. DNA barcoding is one such method that is used for the identification and authentication of raw or manufactured food materials from either single or mixed species products, where common methods of characterization often fail. This helps in the detection of adulterated food products, making it crucial in ensuring high quality standards in the global food industry and market.

Applications of DNA barcoding to the traceability of seafood, meat, and plant ingredients are particularly well-studied [31]. Essentially, it is an extension of the current technology used for taxonomic and phylogenetic research, as previously discussed. Direct sequencing of targeted DNA amplicons allows for species identification even in highly modified food products; thus, a more in-depth and "true" analysis of the product's composition is made possible. For example, DNA barcoding has been used in assessing meat and poultry species in food products, authenticating commercial seafood products, and tracing minor crops and plant products [33-35]. Such applications show how DNA barcoding can become a standard routine test for food quality control and traceability.

3.4 Forensic Science and Crime Investigations

The use of DNA barcoding in the field of forensic science has been of great help in providing valuable insights into criminal investigations. Cases that involve the need for species identification of animals and plants and the analysis of trace biological materials are greatly impacted by the advent of this molecular method. Particularly, the application of DNA barcoding in the illegal wildlife trade and in the analysis of crime scenes has helped provide accurate and reliable information to help further their respective investigations.

3.5 On Illegal Wildlife Trade

The origins of the illegal wildlife trade are often hard to detect due to their vast network. Moreover, proper identification of wildlife parts and products may require DNA-based methods due to them being naturally degraded or modified in ways that make it hard for traditional techniques to be applied [36]. As such, DNA barcoding becomes an invaluable tool in determining whether a plant or animal product or part is protected or is legally traded through species identification. Analysis of the sequences of mtDNA that are conserved among species makes accurate identification of such species possible. Moreover, the geographical origin of a sample can also be identified through analyzing within-species variability in the mtDNA sequences, thus, providing information as to the possible main source of the products and parts for further investigation [37].

3.6 On Crime Scene Analysis

A well-known method for acquiring evidence from crime scenes is through DNA profiling. Although not as specific in a way that it creates a unique genetic profile of an individual from specific regions of an individual's genome, DNA barcoding, compared to DNA profiling, can be applied to gathering evidence from environmental DNA (eDNA) through metabarcoding. Metabarcoding follows the same principle as barcoding but involves the analysis of multiple species in a mixed sample. An example is exhibited in a case discussed by Liu et al., [38] wherein a suspect was identified through metabarcoding plant DNA from eDNA collected from the crime scene. Dried mud removed from the pants of one of the suspects was found to match the mud from where the crime occurred; thus, solving the case. Although prevalent challenges currently block the continued application of this method in criminal investigations such as the lack of an "ideal" barcode for plant species, it still shows high potential for extensive applications [38].

DNA barcoding is also applied in the fields of forensic entomology and palynology, which respectively refer to the study of insects and pollen in criminal investigations [39-40]. However, having a comprehensive DNA barcode reference database is especially crucial in obtaining accurate and reliable results when conducting species determination tests in such fields. With that, research efforts are ongoing for the establishment of barcode libraries for this purpose [40-43].

3.7 Biosecurity and Public Health

DNA barcoding has had several important applications in the fields of biosecurity and public health in recent years. The use of this molecular

method in the taxonomic determination of pathogenic organisms is crucial in differentiating morphologically similar species that cause different diseases and in understanding how it interacts with the human body. Specifically, identification of parasitic species that act as vectors to a certain disease can be done through DNA barcoding [7].

Numerous studies have also used DNA barcoding to investigate the integrity of medicines and their pharmaceutical ingredients. The application of DNA barcoding in the pharmaceutical field includes the identification of specific animal or plant species used as ingredients in various medicines. It specifically allows for the detection of unlabeled and threatened plant or animal species used in various types of medicines, including raw materials and processed products [44]. This proves to be especially helpful with the persistence of various threats to biological diversity, which has caused a rise in the emergence of unlisted substances added to products either intentionally or by accident. Authentication of plant species used in traditional medicines in Asia is significantly well-studied [45-49]. For example, a DNA barcoding system for common herbal plants, such as black pepper, ginger, and guava, along with 109 other species in the tropics, was established using the *rbcl* and *trnH-psbA* genes for primary and secondary differentiation [48]. Another study that involves the use of barcoding to address this issue is applied in the DNAINK project, which aims to detect the deterioration of medicinal products over time and monitor its authenticity [50].

4. PRESENT LIMITATIONS AND FUTURE PROSPECTS

DNA barcoding has had significant success in animal differentiation due to a 648-base pair in the cox1 gene, a short gene. Comparatively, plant identification requires a recommended plant DNA barcode of 1 and 2 genomic regions by the ITS (internal transcribed spacer) [51]. However, according to the same set of authors, the use of chloroplast regions does not pose an accurate measure of plant identification due to their background as maternally inherited hybrids. In discerning target species from closely related species, a minimum of 3% difference between species is a suitable barcode for identification at the species level [52]. The former, being the basis, also considers that taxonomic groups may contain genetic differences. Amid the challenges to DNA barcoding related to genomic loci in identifying plants, DNA analysis in closely related species does not conclude beyond the grasp of feasibility.

Standardization is a property that makes DNA barcodes fundamentally new but with much controversy as it proposes one or more reference genes for phylogenetic analyses effective in the microbial community but has stirred debates due to its "one size fits all" notion [53]. A clear barcode gap and monophyletic species in plants would make a barcode system effective. In addition, the CO1 gene used in animals is deemed ineffective in discriminating against hybrid species [54]. From these two, the limitations of using a DNA barcode seem to diminish its potential. Challenges reek in the use of genetic information, but DNA barcodes continue to offer a positive outlook in the form of prospects.

In immense consideration of the applications of DNA barcoding, the prospects are remarkable, especially in a critical era of possible mass extinction of species, where this multifaceted tool equips biodiversity conservation advocates with an identifier of species at greater risk of ceasing existence. The initially stated discussion on methodology also stresses how DNA barcoding uses a library of DNA barcodes to help identify new species, thus introducing a reference for comparison of extant species in attempts to name discoveries. Outside of biodiversity, DNA barcoding holds a cascade of benefits for criminal investigations, particularly in forensic matters. For instance, illegal activities have negatively consumed wildlife to capitalize on the wildlife trade. In crime scene investigations, further accompanied with better leads, DNA barcoding enables product sourcing of either plant or animal, consequently determining the nature of acquisition—which might be unauthorized or illegal, otherwise approved for trade. In biosecurity and public health, DNA barcoding is a protective barrier against the permeation of falsified animal- or plant-based medicines that might compromise pharmacological credibility and amplify health risks among consumers. In unmonitored circulation at accessible prices, the dangers of these medications will impact healthcare quality and might result in fatal cases among consumers seeking alternatives. With DNA barcoding, the future of the fields mentioned above heavily leans toward becoming promising as it expands in applications and delivers more strong points as a tool concentrated on genetics.

5. CONCLUSION

The birth of DNA barcoding, a revolutionary technique in species identification and classification, opened doors to applying molecular diagnoses to various fields focusing on species identification and discovery, biodiversity assessment and conservation, food safety and authenticity, forensic science and crime investigations, and biosecurity and public health. Through the use of specific genetic markers, such as the mitochondrial cytochrome c oxidase subunit I (COI) gene in animals and chloroplast gene fragments in plants, a reference database or barcode library is founded where barcodes of unknown samples are matched.

In the field of species identification and discovery, DNA barcoding boosted the accurate identification of organisms, overcoming limitations posed by traditional morphology-based taxonomy. DNA barcodes were particularly successful in addressing the challenges of phenotypic plasticity as well as untangling cryptic species. DNA barcoding has been widely used in animals, plants, and fungi. The mitochondrial COI is highly favored over nuclear genes for its ability to generate sequence data quickly and cost-effectively. While COI has been successfully used in barcoding animals, other genes have been tested, like ND5 and COII, that show promise as markers for primate species delineation. In fungi, the ITS region is the preferred barcode marker, while for plants, various genes proposed as barcodes include matK, rbcL, trnH-psbA, and ITS.

For biodiversity assessment and conservation, DNA barcoding contributed to documenting and analyzing DNA from various species within an ecosystem. With accurate differentiation of closely related species, DNA barcoding has provided valuable information regarding species diversity, abundance, changes in species composition over time, and the existence of invasive species in complex ecosystems. In addition, DNA barcodes aid in the identification of endangered species and the detection of illegal wildlife trade, pushing strong conservation efforts and law enforcement.

Another application of DNA barcoding encompasses food safety and authentication, involving the technique's usage in recognizing the significance of food quality by detecting product adulteration and tracing food origins, ensuring high-quality standards in the global food industry. Similarly, in forensic science and crime investigations, the tracing of biological materials by species identification of animals and plants is done through DNA barcoding to combat illegal wildlife trade, identify suspects via environmental DNA analysis, and provide evidence in criminal investigations. Whereas in the context of biosecurity and public health, DNA barcoding is used for the taxonomic determination of pathogenic organisms and the identification of parasitic vectors. Moreover, the molecular technique contributes to the integrity of medicines by detecting unlabeled and threatened plant or animal species that were used as ingredients. Additionally, DNA barcoding has been extensively applied for the authentication of plant species used for traditional medicines, particularly in Asia.

Considering the extensive application of DNA barcoding, there are hindrances that are nonetheless feasible to solve. The current progress of DNA barcode technology holds bright prospects, including the establishment of comprehensive barcode libraries, the development of new markers for specific taxonomic groups, and the integration of DNA barcoding with other technologies for the enhancement of biodiversity research and conservation. More significantly, it opens new horizons for the protection and conservation of species at risk of extinction at the hands of illegal trading systems, and misuse and falsification in medicinal healthcare.

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COMPETING INTERESTS

Authors have declared that no competing interests exist.

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