Integrated advances and emerging strategies for the control of avian coccidiosis: A comprehensive review

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Abstract

Avian coccidiosis, caused by protozoan parasites of the genus *Eimeria*, remains one of the most economically important diseases in poultry, particularly chickens, with profound impacts on global food security. The disease leads to reduced growth performance, poor feed conversion, increased mortality, and substantial treatment costs. While clinical outbreaks are easily identified, subclinical infections—responsible for nearly 70% of the total economic losses—often remain undetected, causing chronic productivity decline. This review provides an integrated perspective on the epidemiology, economic burden, host–parasite interactions, diagnostic advances, and control measures against avian coccidiosis. Seven classical *Eimeria* species (*E. tenella*, *E. acervulina*, *E. maxima*, *E. necatrix*, *E. brunetti*, *E. mitis*, and *E. praecox*) along with three cryptic Operational Taxonomic Units (OTUs) exhibit species-specific pathogenicity and intestinal tropism. Globally, the disease has a pooled prevalence of ~44%, with higher incidence in warm and humid regions, and causes annual losses exceeding £10 billion. Although anticoccidial drugs remain the cornerstone of control, resistance is widespread, highlighting the urgent need for sustainable alternatives. Promising strategies include phytogenic compounds, probiotics, and a new generation of vaccines—ranging from live attenuated and subunit formulations to vector-based platforms—though challenges in cost, production, and efficacy remain. Molecular diagnostics (PCR, qPCR, NGS) are increasingly valuable for species-level identification and epidemiological monitoring. Ultimately, an integrated control strategy that combines advanced diagnostics, effective vaccination, and novel therapeutics is essential for mitigating the burden of coccidiosis and ensuring sustainable poultry production. This review also identifies critical knowledge gaps and research priorities needed to develop innovative solutions for long-term control.

Keywords*:* Coccidiosis, *Eimeria* spp., Poultry, Control

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Introduction

Poultry term refers to a diverse group of domesticated bird species, including chickens, turkeys, ducks, geese, guinea fowls, and ostriches, which are primarily raised for the production of meat and eggs for human consumption. Among these, chickens are the most widely reared and economically significant species, owing to their adaptability to a broad range of environmental conditions across the globe. As a major source of high-quality animal protein, poultry plays a critical role in enhancing human nutrition and food security. In developing countries, poultry production represents a vital component of both agricultural systems and rural livelihoods, serving as an accessible and sustainable means of income generation and poverty reduction, particularly for landless and resource-poor households (Chauhan, 1996; Guèye , 1998).

Poultry production, particularly in rural areas such as those in Iran, faces numerous challenges that significantly constrain its growth and productivity. Among the most critical of these are diseases, malnutrition, predation, inadequate housing, and poor management practices. Infectious diseases such as Newcastle disease, salmonellosis, chronic respiratory disease, and nutritional deficiencies contribute to high mortality rates, with losses ranging from 20–50%, and in severe outbreaks, reaching as high as 80%. These health constraints not only impair bird welfare and performance but also result in substantial economic losses, particularly in low-input production systems. The situation is further exacerbated in intensive farming systems, where overcrowding and stress elevate disease prevalence and severity. In this context, the persistence of disease represents a major bottleneck to improving poultry productivity and threatens both local food security and the broader stability of the global food supply chain (Ahmad *et al*., 2022; Aganovic *et al*., 2021; Williams, 1998; Waldenstedt, 2004; Sørensen *et al.*, 2006).

Among the various diseases affecting poultry, coccidiosis stands out as a particularly insidious challenge due to its widespread prevalence, economic impact, and subclinical complexity. Caused by protozoan parasites of the genus *Eimeria*, coccidiosis leads to intestinal damage, poor feed efficiency, and impaired growth, especially in young birds. Although clinical cases can result in significant mortality, the true burden of the disease lies in its subclinical form, which often goes undiagnosed yet substantially reduces productivity. Estimates suggest that nearly 70% of the economic impact of coccidiosis is attributable to its subclinical effects undermining weight gain and feed conversion rates (Conway and McKenzie, 2007; Morris and Gasser, 2006; Hoerr, 2010; Haug *et al*., 2008; Etuk *et al*., 2004). Despite its global presence, diagnosis, management and control of subclinical coccidiosis remain insufficiently understood or implemented. This data gap underscores the need for a comprehensive investigation of poultry coccidiosis.

Therefore, the present review aims to synthesize current knowledge on its epidemiology, economic implications, diagnostic challenges, and control strategies, highlighting its role as a key limiting factor in sustainable poultry production. This study is conducted specifically on chickens as a representative and economically significant sector of the broader poultry industry.

Etiology

As mentioned, coccidiosis is caused by intracellular protozoan parasites of the genus *Eimeria*, within the phylum Apicomplexa and class Coccidia. These parasites infect specific regions of the intestinal tract in chickens, leading to variable clinical outcomes ranging from mild subclinical infections (coccidiasis) to severe clinical disease with high mortality. Pathogenesis is largely driven by the destruction of epithelial cells during the asexual (schizogony) and sexual reproductive stages of the parasite's life cycle. The damage caused includes intestinal hemorrhage, inflammation, impaired digestion, and malabsorption, all of which contribute to reduced growth performance and feed efficiency (Foreyt, 2013; Clark and Blake, 2012; Williams, 2002; Haug *et al*., 2008; Khazandi, 2006; Madlala *et al*., 2021).

Seven species of *Eimeria* are classically recognized in chickens, each with distinct biological, pathological, and morphological traits. In addition, three cryptic Operational Taxonomic Units (OTUs)—*E. lata*, *E. nagambie*, and *E. zaria*—have recently been identified and proposed as new species based on molecular and phenotypic evidence. These cryptic species are increasingly associated with persistent, subclinical infections and reduced farm profitability in developing poultry industries, particularly in Africa and Asia (Jenkins *et al*., 2025; Blake *et al*., 2021; Mathis *et al.,* 2024; Tirfie and Lulie, 2024; Clark *et al*., 2016; Jatau *et al*., 2016; Nabian *et al*., 2018). The table below provides a structured overview of these species, including their oocyst morphology, primary site of infection and pathogenicity (Table 1).

Life cycle

As mentioned, coccidiosis in chickens is caused by ingestion of sporulated oocysts, which represent the infective stage of *Eimeria* spp. (Fig.1). The transmission occurs via the fecal-oral route, primarily through contaminated feed, water, or litter. Upon ingestion, the oocysts pass through the upper gastrointestinal tract and are exposed to digestive enzymes and mechanical forces within the gizzard. This leads to excystation, where each oocyst releases sporozoites (the motile invasive form) (Nabian *et al*., 2018; McMullin, 2020).

Once released, the sporozoites invade intestinal epithelial cells, initiating the asexual reproduction phase (schizogony or merogony). During this stage, the parasites undergo two to four rounds of replication, depending on the species, producing large numbers of merozoites. These merozoites burst the host cells and infect new epithelial cells, amplifying tissue damage (Kaufmann, J., 2013). Following asexual replication, the life cycle transitions into the sexual phase (gametogony).

Table 1: Oocyst morphology, primary site of infection and pathogenicity of *Eimera* species which infect chickens.

Eimeria Species	Oocyst Size (µm)	Site of Infection	Severity	Asexual Generations	Signs
Eimeria tenella	19.5 × 16.5	Caeca	High	2	Causes bloody diarrhea; highly pathogenic
Eimeria acervulina	18.0 × 14.0	Upper intestine	Mild to moderate	3	Most prevalent; causes white plaque lesions
Eimeria maxima	30.5 × 20.7	Mid intestine	Moderate	2	Largest oocyst; major cause of reduced weight gain
Eimeria necatrix	20.0 × 17.0	Mid intestine	High	4	Severe hemorrhagic enteritis; resembles *E. tenella*
Eimeria brunetti	26.0 × 18.0	Lower intestine	Moderate	2	Less common; inflammation of the rectum and cloaca
Eimeria mitis	15.6 × 14.2	Lower intestine	Mild	2	Least pathogenic; often subclinical
Eimeria praecox	18.0 × 15.0	Upper intestine	Mild	2	Rarely causes disease; very mild
Eimeria lata (OTU-X)	30.8 × 23.8	Intestinal tract	Subclinical	Unknown	Emerging; widespread in Africa and Asia
Eimeria nagambie (OTU-Y)	26.7 × 22.8	Intestinal tract	Subclinical	Unknown	Detected in Nigeria; part of cryptic *Eimeria* group
Eimeria zaria (OTU-Z)	17.7 × 15.2	Intestinal tract	Subclinical	Unknown	Associated with productivity losses in Sub-Saharan Africa

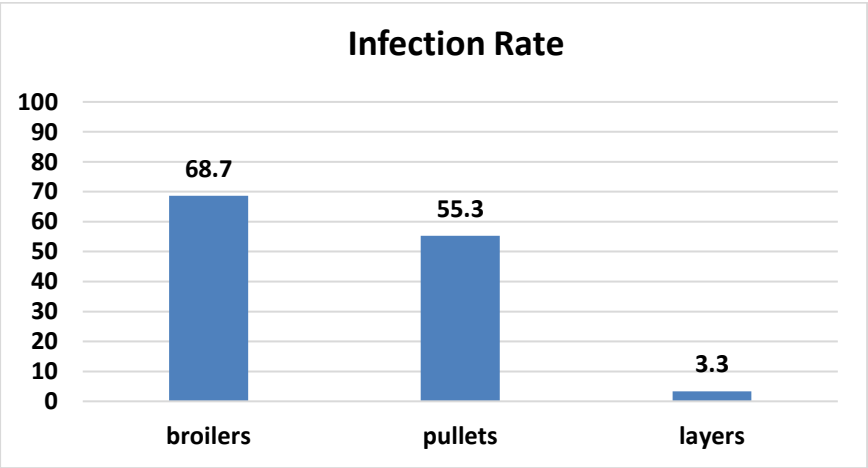

Figure 1: Chicken *Eimeria* spp. infection rates align with reports from Iran, Nigeria and India.

Merozoites differentiate into male (microgametes) and female (macrogametes) gametocytes. Fertilization occurs in the intestinal lining, forming a zygote that develops into an oocyst, which is excreted in the feces (McMullin, 2020; Kaufmann, 2013).

Outside the host, in the presence of favorable environmental conditions (oxygen, warmth, and moisture), the oocyst undergoes sporulation, completing the cycle. This typically occurs within 1–2 days. A single ingested oocyst can result in the production of hundreds of thousands to millions of new oocysts, contributing to rapid environmental contamination and re-infection (Fanatico, 2006; Trees *et al*., 2001).

Epidemiology of chicken coccidiosis

Coccidiosis is frequently encountered in intensively managed poultry operations, particularly where suboptimal hygiene and biosecurity measures prevail. Environmental conditions are central to the transmission dynamics of the disease, as the sporulation and subsequent infectivity of *Eimeria* oocysts depend heavily on temperature, moisture, and oxygen availability. Damp litter with a moisture content above 30% and ambient temperatures ranging from 25 to 30 °C provide ideal conditions for oocyst sporulation within 24 to 48 hours. In contrast, sporulation is delayed or inhibited entirely under dry conditions at 10 °C, while high temperatures between 45–50 °C can accelerate sporulation to less than a day. However, oocysts are heat-labile and can be destroyed by exposure to 56 °C for one hour. Outbreaks often follow the sudden ingestion of large quantities of sporulated oocysts by immunologically naïve birds, particularly those between 3 and 8 weeks of age, reflecting the interplay between environmental contamination and host susceptibility (Etuk *et al*., 2004; Trees *et al*., 2001; Musa *et al*., 2010; De Gussem, 2007; Abebe and Gugsa, 2018; Sun *et al*., 2009; Lee *et al*., 2010; Khan *et al*., 2002; Al-Natour *et al*., 2002).

Host susceptibility and disease progression

Chickens of all ages are susceptible to *Eimeria* infections, but clinical disease is more frequently observed in young birds, particularly within the first 3–18 weeks of life. Following ingestion, clinical signs of intestinal coccidiosis may appear as early as 3 days post-infection, with typical incubation periods of 5 days for intestinal and 5–6 days for cecal forms. Infected birds may show varying severity of disease depending on the infecting *Eimeria* species and oocyst load. Co-infection with multiple *Eimeria* species is common and can lead to compounded pathological effects (Abebe and Gugsa, 2018; Poulsen *et al*., 2000; Singh *et al*., 2012).

Species-specific localization in the intestine

Each *Eimeria* species exhibits a predilection for specific regions of the gastrointestinal tract in chickens. For

instance, *Eimeria acervulina* primarily invades the duodenum, while *E. maxima* and *E. mitis* target the midsection of the small intestine. In contrast, more pathogenic species such as *E. tenella*, *E. necatrix*, and *E. brunetti* colonize the caeca, rectum, and distal segments of the small intestine, where they induce more severe lesions. The resulting tissue damage varies in intensity depending on the species involved, influencing the overall clinical outcome and mortality rate (Etuk *et al*., 2004).

Risk factors and environmental influences

Multiple risk factors contribute to the occurrence and severity of coccidiosis outbreaks. These include poor litter management, such as moisture content exceeding 30%, leaking water lines, and failure to remove contaminated litter. The absence of an all-in-all-out system, improper use or suboptimal inclusion of anticoccidials in feed, concurrent infections, dietary changes, and other environmental or management-related stressors also predispose flocks to outbreaks. Furthermore, immune suppression and the overuse of coccidiostats can promote resistance and increase susceptibility. The persistence of sporulated oocysts in the environment, combined with favorable climatic conditions and intensive rearing practices, sustains endemicity and facilitates disease transmission. In rural or backyard poultry systems, mixed parasitic infections (including mites, lice, helminths, and *Eimeria* spp.) are commonly reported, complicating disease control and further influencing the epidemiology of avian coccidiosis (Poulsen *et al*., 2000; Singh *et al*., 2012; Chanie *et al*., 2009; Singla *et al*., 2007; Pattison *et al*., 2007).

Prevalence of coccidiosis in poultry production systems

The prevalence of *Eimeria* infections in poultry has been extensively documented across diverse production systems and geographic regions. Various studies have reported *Eimeria* infections in commercial and backyard flocks worldwide, with regional variations influenced by climatic conditions, breed susceptibility, and management practices. In South Africa, Malatji et al. reported a prevalence of 29.46% among local chickens in Limpopo and KwaZulu-Natal. Similarly, Muazu et al. observed a 52.9% prevalence across all 36 Nigerian states and the federal capital. Reports from Asia and the Middle East have indicated an even higher infection rate, with prevalence estimates exceeding 50% in countries such as India, Pakistan, Jordan, and Iran. Mortality rates associated with *Eimeria* infections vary significantly, reaching 92% in Romania, 88.4% in Argentina, 78% in Jordan, 71.9% in Pakistan, and 70.9% in Ethiopia, illustrating the potential for severe losses in affected flocks (Sultana *et al.,* 2023; Györke *et al*., 2016; Gharekhani *et al*., 2014; Mohammed and Sunday, 2015; Malatji *et al*., 2016; Muazu *et al*., 2008; Karaer *et al*., 2012; Sharma *et al*., 2013; Oljira *et al.,* 2012; Ali *et al*., 2004).

Climatic and seasonal influence on prevalence

Environmental factors, especially climate and seasonal variations, are strongly associated with the epidemiology of coccidiosis. Warm, humid conditions characteristic of the rainy season create an ideal environment for oocyst sporulation and survival. Multiple studies report peak infection rates during or shortly after rainy periods in tropical and subtropical regions. For instance, Eimeria infections in Egypt peak during the winter months (December to February), which coincide with the rainy season, while in Ethiopia and the Kashmir Valley, incidence rises after the October rains and between September to November, respectively. This seasonal trend supports the association between moisture levels and oocyst development, particularly under open-house or backyard systems, where litter moisture can rise above 60%, facilitating sporulation. Under optimal conditions (25–30°C and 75% humidity), sporulated oocysts may remain viable in the environment for over 600 days (Abebe and Gugsa, 2018; , Oljira *et al*., 2012; Gari *et al*., 2008; Lawal *et al*., 2016; Attree *et al*., 2021; Ahmed *et al*., 2018).

Breed and production system-specific prevalence

Variation in the prevalence of coccidiosis is closely associated with poultry breed and production systems. Exotic breeds generally exhibit higher susceptibility compared to indigenous or scavenging village chickens, likely due to differences in genetic resistance and increased exposure to infective oocyst loads in confined housing environments. Lawal et al. reported the absence of infection in village chickens maintained under scavenging systems, in contrast to significantly higher infection rates in exotic breeds. Among commercial poultry, broilers showed the highest infection prevalence (68.7%), followed by pullets (55.3%) and layers (3.3%), a trend that may be attributed to differences in stocking density, housing systems, and overall management intensity (Table 2). These findings are consistent with previous reports from Nigeria, Iran, and India. While prevalence values may vary across countries due to differences in husbandry practices, environmental conditions, and biosecurity levels, the reported figures provide a representative estimate that is expected to be broadly reflective of global trends under comparable rearing systems (Lawal *et al*., 2016; Nematollahi *et al*., 2009; Nnadi and George, 2010; Jatau *et al.,* 2012; Naphade, 2013; Bachaya *et al*., 2012; Dakpogan *et al*., 2013; Adhikari *et al*., 2008; Iqbal and Begum, 2010).

Global prevalence patterns

Synthesizing the available data reveals a global pooled prevalence of 44.3%, with *Eimeria tenella* being the most frequently isolated species (38.7%), and the most pathogenic, often causing hemorrhagic lesions and high mortality. The consistently high prevalence across studies highlights the endemic nature of coccidiosis in both intensive and extensive poultry systems.

Table 2: Molecular diagnostic techniques for *Eimeria* species in poultry.

Technique	Principle	Advantages	Limitations	Applications in *Eimeria* Diagnosis
PCR (ITS-1 & ITS-2)	Amplifies species-specific ITS regions of rDNA using designed primers	High specificity; differentiates all 7 chicken *Eimeria* spp.; small DNA quantity needed	Requires thermocycler; lab-based	Routine species identification; molecular epidemiology
RAPD	Uses short, arbitrary primers to amplify random genomic segments	Simple; no prior sequence information needed	Low reproducibility; less specific	Initial genetic fingerprinting; development of SCAR markers
SCAR markers	Uses longer, specific primers derived from RAPD fragments	High specificity and reproducibility	Requires prior RAPD data	Confirmatory species identification; multiplex PCR assays
qPCR	Amplifies and quantifies target DNA in real-time using fluorescent dyes/probes	Quantitative; sensitive; fast	Requires specialized equipment; higher cost	Quantifying parasite load; monitoring infection dynamics
Multiplex PCR	Simultaneous amplification of multiple target sequences in one reaction	Detects several species at once; cost- and time-efficient	Primer design complexity; potential cross-reactivity	Simultaneous detection of all chicken *Eimeria* spp.
LAMP	Isothermal DNA amplification with loop primers	Rapid (<1 hr); no thermocycler needed; field-applicable	Primer design is complex; limited multiplexing	Point-of-care detection; field surveillance
NGS	Massively parallel sequencing of whole genomes or targeted regions	Detects cryptic/novel species; high-resolution phylogeny	High cost; requires bioinformatics	Discovery of variants (*E. lata*, *E. nagambie*, *E. zaria*); genomic epidemiology

Although commercial operations often implement prophylactic anticoccidial regimens, the persistence of the parasite reflects challenges in achieving full control.

Interestingly, contrary to expectation, several studies reported higher coccidiosis prevalence in backyard flocks (e.g., 25% in Nepal and 36% in Bangladesh), potentially due to environmental exposure, lack of medication, and poor biosecurity. However, lower prevalence in commercial layers and broilers in the same regions may reflect the benefits of routine prophylaxis through medicated feed and water. These findings underscore the complex interplay of

environmental, genetic, and managemental factors shaping the epidemiology of *Eimeria* infections in poultry globally (Badri *et al*., 2024; Fossum *et al*., 2009; Macdonald *et al*., 2017; Martynova-Van Kley *et al*., 2012; Zhou *et al.,* 2020; Alwan *et al*., 2025; Györke *et al*., 2013; Fornace *et al.,* 2013).

Economic impact of coccidiosis

Coccidiosis imposes a substantial financial burden on the global poultry industry, with recent estimates placing total annual losses at approximately £10.36 billion—a significant increase from earlier global projections exceeding $2 billion. In the United States alone, losses have been estimated at $450 million per year, with an additional $100 million allocated to preventive and therapeutic measures. These rising figures reflect not only inflation and global poultry expansion but also the growing economic vulnerability of high-performance broiler lines to enteric diseases (Blake *et al*., 2021; Györke *et al*., 2016; Blake and Tomley, 2014; Kadykalo *et al*., 2018; Blake *et al*., 2021; Bera *et al*., 2010; Kinung'hi *et al*., 2004; Maikai *et al*., 2007; Owai and Gloria, 2010).

Cost structures encompass reduced weight gain, impaired feed conversion, mortality, and expenses related to anticoccidial drug use and vaccination programs. Resistance to anticoccidial compounds has compounded these challenges, leading to diminished efficacy and higher input costs. Region-specific studies reinforce these trends: per-bird economic losses in Ethiopia ranged between 0.53 and 0.55 Birr; in Romania, the average flock-level cost reached €3,162.40 in 2010. In Algeria, the 2022 cost of coccidiosis was £86.66 million, with a per-bird cost of £0.30; nearly twice the global average estimated in 2016 (Kadykalo *et al*., 2018; Kinung'hi *et al*., 2004; Blake *et al*., 2020; Dierick *et al*., 2019; Peek and Landman, 2011; Rushton *et al*., 2018; Williams, 1999).

In Indonesia's Central Java region, broiler production systems suffered over 3 trillion rupiah in direct economic losses, including 2.5 trillion in production impacts and 500 billion in disease control efforts. Despite widespread use of coccidiostats, biosecurity measures, and vaccination, prevalence rates remain high; especially in broilers fed with commercial diets; pointing to limitations in current control strategies. The persistence of high infection levels, alongside growing concerns over drug resistance, highlights the need for reassessment of intervention approaches (Pawestri *et al*., 2020).

Immune responses of chickens against *Eimeria* infection

Innate immunity

The innate immune system forms the first line of defense against *Eimeria* in chickens, comprising physical barriers, soluble immune molecules, and cellular components such as macrophages, dendritic cells, and natural killer cells. Infection induces structural changes in the intestinal epithelium, triggering recruitment and activation of immune

cells that detect pathogen-associated molecular patterns (PAMPs) through pattern recognition receptors (PRRs). PRRs including TLR1LA, TLR4, TLR5, TLR7, and TLR21, along with cytokines such as IFN-α, IFN-β, IFN-γ, IL-1β, IL-12, and IL-22, are upregulated following exposure to *E. tenella* sporozoites or in infected tissues, indicating TLR-mediated recognition pathways. Although the role of profilin recognition by PRRs in *Eimeria* remains unclear, evidence supports the involvement of macrophages, dendritic cells, and intraepithelial lymphocytes in initiating immune responses. However, the precise mechanisms by which innate immunity presents *Eimeria* antigens to elicit adaptive responses remain insufficiently understood (Wang *et al*., 2022; Ivanova *et al*., 2019; Sumners *et al*., 2011; Zhou *et al*., 2013).

Adaptive immunity

Adaptive immunity is critical for long-term protection against *Eimeria*, relying on antigen-specific T and B lymphocyte activation. $CD4^+$ helper T cells and $CD8^+$ cytotoxic T cells mediate cellular responses, while B cells produce antibodies targeting *Eimeria* antigens, potentially contributing to cross-presentation and enhanced protection. Although the exact role of humoral immunity is unresolved, antigen-specific memory is a hallmark of protection, forming the basis for vaccination strategies. In immunized chickens, sporozoites are often located within or near memory γδ and αβ $CD8^+$ T cells, with αβ T cells playing a central role in recall responses. Tissue-resident memory cells, localized in the gut, rapidly proliferate upon reinfection, restricting parasite development at early schizont stages. Experimental transfer of small numbers of $CD8^+$ T_{RM} cells provides protection comparable to larger quantities of gut-associated $CD8^+$ T cells, underscoring their potency. These findings have significant implications for the design of live oocyst-based vaccines. Additionally, T stem cell memory (T_{SCM}) cells (known for their longevity and self-renewal) represent a promising but underexplored avenue in *Eimeria* vaccine development (Lee *et al*., 2009; Qin *et al*., 2016; Kamenjarin *et al.,* 2023; Milner *et al*., 2020; Shi *et al*., 2023; Pogonka *et al*., 2010; Ferreira *et al*., 2020).

Diagnosis and control strategies for avian coccidiosis

Diagnostic approaches

Accurate identification of *Eimeria* species is essential for the effective diagnosis and control of coccidiosis, particularly in commercial poultry production where economic losses can be substantial. Traditionally, diagnosis has relied on a combination of clinical signs, gross pathological findings at necropsy, and microscopic evaluation of oocysts. Classical methods include macroscopic observation of lesion location and severity, along with microscopic assessment of oocyst size and shape, and, in some cases, examination of other developmental stages. Clinical signs in affected birds typically include ruffled feathers,

depression or drowsiness, reduced feed and water intake, and watery, whitish, or bloody feces. These signs often progress to dehydration, impaired weight gain, and, if untreated, mortality. Histopathologically, *Eimeria* spp. invade the intestinal mucosa, where meronts, gamonts (the developmental stage that produces gametes), and oocysts cause marked epithelial alterations, including cell distortion, rupture, separation from adjacent cells, and sloughing, accompanied by inflammation. Such mucosal damage also reduces brush border enzyme activity, leading to malabsorption and further compromising growth performance. In cases where greater diagnostic precision is required (Ali *et al*., 2004; Carvalho *et al*., 2011; McDougald *et al*., 2017; Barrios *et al*., 2017; Hauck *et al*., 2019; Hinsu *et al*., 2018; Yun *et al*., 2000; Greenacre and Morishita, 2021; Adams *et al*., 1996).

Gross lesion scoring is a common method for assessing the severity of infection. Lesions are scored on a standardized scale from 0 to 4, depending on the Eimeria species involved. This scoring system is often complemented by quantitative oocyst counts using the McMaster technique or droppings analysis. More recently, the Mini-FLOTAC method has emerged as a rapid and efficient tool for processing large sample volumes both in laboratory and field settings, based on flotation principles (Johnson and Reid, 1970; Price, 2012; Bortoluzzi *et al*., 2018).

Molecular diagnostic techniques provide enhanced specificity and sensitivity for *Eimeria* species identification. Among these, PCR targeting the internal transcribed spacer regions (ITS-1 and ITS-2) of ribosomal DNA is widely employed. The ITS sequences—non-coding regions located between structural rRNA genes—exhibit high interspecific variability, enabling differentiation among all seven recognized *Eimeria* species in chickens (*E. acervulina, E. brunetti, E. maxima, E. mitis, E. necatrix, E. praecox,* and *E. tenella*). Random Amplified Polymorphic DNA (RAPD) uses short, arbitrary primers to generate species-specific DNA fingerprints, which have been adapted to produce Sequence Characterized Amplified Region (SCAR) markers—longer, specific primers that reliably amplify defined target sequences for species confirmation. Quantitative PCR (qPCR) incorporates fluorescent dyes or probes to quantify parasite DNA in real time, while multiplex PCR combines multiple primer sets in a single reaction to simultaneously detect several *Eimeria* species. Loop-Mediated Isothermal Amplification (LAMP) is a rapid, field-friendly method that amplifies DNA at a constant temperature using specially designed primers, eliminating the need for thermocyclers. With the advent of Next-Generation Sequencing (NGS), whole-genome and targeted sequencing approaches allow the detection of cryptic, emerging, or region-specific variants (such as *E. lata, E. nagambie,* and *E. zaria*) and support broader epidemiological and phylogenetic studies (Fornace *et al.,* 2013; Haug *et al*.,

2007; Vrba *et al*., 2010; Barkway *et al*., 2011; Moraes *et al*., 2015; Hamidinejat *et al*., 2010; You, 2014; Shirley and Bumstead, 1994; Fernandez *et al.,* 2004). In Table 2, different molecular diagnostic techniques are summarized and compared.

Anticoccidial drugs

The control of coccidiosis in poultry has historically relied on the prophylactic use of anticoccidial drugs, a practice initiated in 1948 with the introduction of sulfaquinoxaline. Since then, numerous compounds have been developed and incorporated into poultry health management programs. Anticoccidials are broadly classified into two main categories: synthetic compounds and ionophores**.**

Synthetic compounds comprise chemically diverse agents such as quinolones, pyridones, alkaloids, thiamine analogues, and triazine derivatives. Their modes of action target critical parasite metabolic processes, including inhibition of mitochondrial respiration, disruption of the folic acid pathway, and competitive inhibition of thiamine uptake. Although the development of novel synthetic agents has been limited in recent years, ethanamizuril (a new triazine derivative) has been approved for use in China, demonstrating ongoing innovation in this field (Kadykalo *et al*., 2018, Chapman and Rathinam, 2022; Fu *et al*., 2021).

Ionophores, or polyether antibiotics, are fermentation products of microorganisms such as *Streptomyces* spp. and *Actinomadura* spp. They are classified into monovalent ionophores (e.g., salinomycin, monensin, narasin), monovalent glycosidic ionophores (e.g., maduramicin, semduramycin), and divalent ionophores (e.g., lasalocid). Ionophores are valued for their broad activity against *Eimeria* spp., effectiveness against both asexual and sexual stages, and relatively slow development of resistance. By partially inhibiting parasite development (through disruption of ion transport (Na^+, K^+) in sporozoites and early trophozoites) ionophores allow the host to develop protective immunity while controlling clinical disease (Peek and Landman, 2011; Chapman and Rathinam, 2022; Noack *et al*., 2019; Antoszczak *et al*., 2019).

Anticoccidial drug resistance

The extensive and sustained administration of anticoccidial agents in poultry production has precipitated a pervasive rise in drug resistance among *Eimeria* species. While *Eimeria tenella* remains the principal focus of resistance studies, increasing evidence highlights the emergence of resistant strains in *Eimeria acervulina* as well as other species frequently encountered in mixed infections under natural conditions. To investigate and obtain resistant *Eimeria* isolates, researchers have employed several methodologies. One approach involves the direct recovery of drug-resistant parasites from field samples, reflecting naturally evolved resistance. Another strategy utilizes stepwise exposure to incrementally higher drug

dosages to select for resistant phenotypes under controlled laboratory conditions. More recently, innovative protocols have been developed that replicate the natural selection process by subjecting drug-sensitive *Eimeria* strains to medicated hosts, enabling the expedited generation of resistant populations within a reduced timespan (Sun *et al*., 2023).

The initial body of research predominantly emphasized epidemiological characterization of resistance patterns. Subsequently, focus shifted toward deciphering the molecular and biochemical underpinnings of resistance. Early investigations revealed that certain anticoccidial compounds, including decoquinate and clopidol, target mitochondrial electron transport in unsporulated oocysts, implicating mitochondrial pathways in drug action and resistance. With the advent of advanced molecular technologies, proteomic analyses have facilitated the identification of protein biomarkers that correlate strongly with resistant phenotypes, offering valuable tools for resistance detection and mechanistic study. Moreover, transcriptomic profiling via RNA sequencing has allowed for a comprehensive comparison of gene expression between drug-susceptible and drug-resistant strains, uncovering critical genetic alterations associated with resistance. Collectively, these multidisciplinary studies indicate that resistance arises through multiple mechanisms, chiefly involving modifications of drug target sites, diminished intracellular drug accumulation—potentially due to altered transport or sequestration—and disruption of drug activation or metabolic inactivation processes within the parasite. This enhanced understanding at the molecular level is instrumental in guiding the development of novel anticoccidial interventions designed to circumvent existing resistance challenges (Chapman 1997; Thabet *et al*., 2017; Xie *et al*., 2020).

Natural alternatives for coccidiosis control

Amid rising concerns over drug resistance and food safety, attention has shifted toward natural and sustainable alternatives for the control of avian coccidiosis. These include phytogenic compounds, prebiotics, probiotics, and essential oils, which primarily exert their effects through immunomodulation and modulation of the gut microbiota. Some of these compounds are discussed in following literature.

Probiotics, prebiotics, and phytochemicals

Probiotics, key modulators of intestinal microbiota and immune function, have demonstrated significant potential in controlling avian coccidiosis. Studies highlight strains such as *Lactobacillus plantarum*, *L. salivarius*, and *L. johnsonii*, along with *Saccharomyces cerevisiae*, which enhance antioxidant defenses and strengthen gut barrier integrity, thereby increasing resistance to *Eimeria* infections. Prebiotics, which promote the growth of beneficial

microbes, synergize with probiotics to amplify these protective effects, notably reducing disease severity in *E. tenella*-infected birds. Additionally, phytochemicals such as saponins and tannins contribute anti-inflammatory and antiparasitic activities by inhibiting parasite invasion and supporting epithelial repair. The combined application of probiotics, prebiotics, and phytochemicals represents a promising integrated approach to enhance poultry resilience against coccidiosis (Mohsin *et al*., 2022; Awais *et al*., 2019; Zhang *et al*., 2019; Burt *et al*., 2013; Santos *et al*., 2022)

Garlic (Allium sativum L.)

Garlic is rich in bioactive sulfur compounds, including allicin and diallyl sulfides, with known antioxidant and immunomodulatory properties. These compounds disrupt cellular membranes and energy metabolism of pathogens, leading to decreased oocyst sporulation and parasite viability. Garlic extract has demonstrated in vivo and in vitro efficacy against Eimeria species through reduced oocyst shedding and enhanced immune response (Kim *et al*., 2013; Ahmad *et al*., 2023).

Artemisia annua

Artemisia annua and its active compound, artemisinin, have shown promising anticoccidial properties. Supplementation in poultry diets significantly reduces oocyst counts and intestinal lesion scores. Although some reduction in body weight gain has been noted, feed conversion efficiency and overall health indicators often improve. A. annua also positively influences gut microbiota and offers a multi-targeted approach to disease control (Lang *et al*., 2019; Coroian *et al*., 2022; de Almeida *et al*., 2012; Fatemi *et al*., 2017).

Bidens pilosa (*B. pilosa*)

Inclusion of B. pilosa in poultry feed at concentrations of 0.025% or higher has been shown to reduce oocyst shedding, enhance growth performance, lower feed conversion ratios, and increase anticoccidial index. Its efficacy lies in reducing pathogen burden and supporting beneficial gut flora (Chang *et al*., 2016).

Oregano essential oil

Oregano oil, particularly due to its high content of carvacrol and thymol (70–80%), has demonstrated notable anticoccidial effects. Supplementation improves gut absorption, enhances antioxidative defenses, and reduces lesion severity without impairing growth. In both vaccinated and unvaccinated birds, oregano oil reduced infection severity and oocyst output, indicating its potential as both a preventive and therapeutic agent (Abdelli *et al*., 2021; Tsinas *et al*., 2011; Mohiti-Asli and Ghanaatparast-Rashti, 2015).

Anticoccidial vaccines

With increasing drug resistance in *Eimeria* and concerns over residues in animal products, anticoccidial vaccines have become essential tools for coccidiosis control. Current commercial

options include virulent strain-based, attenuated, transmission-blocking subunit vaccines, and newer genetic or vector-based approaches (Attree *et al*., 2021; Soutter *et al*., 2020).

Virulent strain-based vaccines

These contain defined mixtures of wild-type *Eimeria* strains (e.g., Immucox®, Coccivac®) and provide strong protection, but improper use can cause clinical coccidiosis, necrotic enteritis, and mortality (Soutter *et al*., 2020; Zaheer *et al*., 2022).

Attenuated vaccines

Precociously selected or embryo-adapted *Eimeria* strains retain immunogenicity with reduced pathogenicity (e.g., Paracox®, Neca™, SCOCVAC®, Livacox®). Limitations include lower fecundity, higher production costs, and risks of unstable attenuation or reversion (Liu *et al*., 2023; Chapman, 2014).

Transmission-blocking subunit vaccine

CoxAbic® contains affinity-purified *E. maxima* gametocyte antigens, used to immunize hens and confer maternal antibody protection to chicks. Production is costly, time-consuming, and labor-intensive due to reliance on native antigen purification (Sharman *et al*., 2010; Chen *et al*., 2021).

Precocious line-based gene knockout vaccines

CRISPR/Cas9 enables targeted deletion of virulence or developmental genes in precocious lines, enhancing vaccine safety. Progress depends on identifying key developmental regulators in *Eimeria* (Tang *et al*., 2020; Cheng *et al*., 2021; Clark *et al.,* 2008).

Vector-vaccines

Live vectors (e.g., probiotics, yeast, attenuated *Salmonella*, fowl pox virus, adenovirus, transgenic *Eimeria*) can deliver *Eimeria* antigens via natural infection routes, enhancing protective immunity. Strategies include incorporating molecular adjuvants (IL-2, Fc, profilin) or expressing antigens from multiple *Eimeria* species in a single strain (Xu *et al*., 2022; Baron *et al*., 2018; Konjufca *et al*., 2008; Li *et al*., 2015; Pastor-Fernández *et al*., 2018; Tang *et al*., 2018).

Other vaccines

Structural vaccinology and nanoparticle-based platforms offer precision antigen delivery, stability, and enhanced immune responses. Dendritic cell-targeting vaccines aim to efficiently present antigens to T cells, potentially improving protection (Impagliazzo *et al*., 2015; Zhou *et al*., 2018; Yassine *et al*., 2015; McLellan *et al*., 2013).

Conclusion

Coccidiosis remains one of the most persistent and economically damaging diseases in poultry production, its impact intensified by the emergence of drug resistance and the limitations of current vaccines. Historically reliant on chemical control, the industry now faces mounting pressures related to food safety, sustainability, and animal

welfare, prompting a shift toward integrated and innovative solutions. Advances in molecular biology, immunology, and microbiome science—ranging from CRISPR/Cas genome editing and multiomics profiling to precision immunology—are revolutionizing our understanding of *Eimeria* biology and enabling the design of highly specific, durable, and safe control tools. The future landscape includes multi-antigen, molecularly optimized vaccines, structural vaccinology-guided formulations, and genetically attenuated strains capable of inducing long-lasting protection. In the authors' perspective, the path forward lies in uniting these molecular innovations with phytogenic compounds, probiotics, and other natural interventions, tailored to local epidemiology and production systems. Such a cross-disciplinary, field-validated approach holds the greatest promise for transitioning from reactive management to proactive, precision control, ultimately reshaping the global strategy for sustainable coccidiosis prevention.

Conflicts of interests

The authors declare no competing interests.

Authors' contributions

Mohamadreza Roudaki and Morteza Nikad were involved in the idea, design, data collection, and paper preparation. Morteza Nikad contributed to the study's supervision, as well as the manuscript's drafting. All authors were approved the final version of the article.

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